The ecology (including physiological aspects) of selected Antarctic marine invertebrates associated with inshore macrophytes

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Richard, M. G. (1977) The ecology (including physiological aspects) of selected Antarctic marine invertebrates associated with inshore macrophytes. Doctoral thesis, Durham University.

THE ECOLOGY (INCLUDING PHYSIOLOGICAL ASPECTS) OF SELECTED ANTARCTIC MARINE INVERTEBRATES ASSOCIATED WITH INSHORE MACROPHYTES.

by M.G. Richardson.

A thesis submitted to the Department of Zoology, University of Durham, as a requirement for the conferal of the Degree of Doctor of Philosophy.

Declaration:

I hereby declare that the work presented in this thesis has been performed by myself and has not been accepted, in whole or part, in any previous application for a higher degree. All quotations have been identified by quotation marks and where data have been drawn from other sources references to authorship are indicated.

M.L. Richardson.

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Chapter 9. The ecology of benthic invertebrates: The brooding antarctic bivalve, Lissarca miliaris.

9.4. Discussion.

ACKNOWLEGEMENTS:

This research was carried out whilst employed by the British Antarctic Survey, (Natural Environment Research Council), Madingley Road, Cambridge, CB3 OET.

I would like to thank the many people who assisted in this work, in particular I am indebted to all the personnel of the Signy Island Station during the years 1971-73, especially Mr. P. Skilling and Ft. Sgt. J. Hyde-Clarke for technical assistance and Mr. J. Hoogesteger, Mr. R. Townly-Malyon and Dr. T.M. Whitaker for the collection of certain samples. Mr. D. Bone (B.A.S.) supplied unpublished data on the respiration of the amphipod *Bovallia gigantea* and Dr. W. Krebs (United States Antarctic Research Programme) collected specimens of *Pontogeneia* spp. from the U.S. Base at Palmer, Antarctic Peninsular. The transmission photomicrographs in Fig. 35 were kindly obtained by Dr. F. Round of the University of Bristol and the other photographs in that Figure were taken by Mr. B. Paddock and Miss P. Simms of the British Museum (Natural History).

Aspects of the work on the feeding of the amphipod *Pontogeneia antarctica* and the composition of the diatom *Navicula glaciei* were carried out jointly with Dr. T.M. Whitaker.

Mr. N. Bonner, Dr. I. Everson and Mr. M.G. White of the British Antarctic Survey and Dr. P. Evans of the Zoology Department, the University of Durham have been sources of help and advice throughout the preparation of this thesis.

Abstract:

Benthic surveys of Borge Bay, Signy Island, South Orkney Islands indicated that the biomass of macrophytes per area, in shallow antarctic waters, was less than in temperate seas. This decrease was mainly attributed to the shading and mechanical attrition of sea ice.

The habitat provided by macroalgae was important as a source of food and shelter to a wide variety of benthic and demersal species.

Feeding relationships within the habitat were complex. Many species relied heavily on phytoplankton or detritus (often phytoplankton 'fall-out') as the main source of food.

The biology of two contrasting invertebrates, commonly associated with the fronds of the brown alga Desmarestia anceps was investigated. The species chosen were the amphipod Pontogeneia antarctica and the bivalve Lissarca miliaris. The mollusc remained in the benthos throughout the year, whilst the crustacean exhibited a major migration to the undersurface of the fast ice during the winter. Despite such obvious ecological differences, some fundamental similarities were apparent in the reproductive biology of these animals. In addition, the growth rates of both species were relatively slow. Studies on metabolism and feeding of P.antarctica indicated that the rate of respiration was higher than expected for the constant low ambient temperature. It is considered that the phenomena of slow growth, increased parentalism and decreased fecundity present in these, and many polar species, can be partly attributed to such elevated metabolism and to the highly fluctuating primary production

of antarctic waters which subsequently affects the overall amounts of energy which can be ingested during the year. Breeding in both animals was synchronised to the period of optimum food supply during early spring or summer.

PREFACE:

The first biological investigations in antarctic waters were confined to the collection of specimens and subsequent taxonomic studies. The early major expeditions, organised by a variety of European countries, did valuable work in describing and classifying the types of organisms present in southern high latitude waters. Taxonomic research is still an important facet of antarctic studies (Thurston, 1972; 1974) though more recently work has been initiated into some of the apparently characteristic ecological and physiological features exhibited by antarctic organisms. The results of such work have been reviewed by Deacon (1964) and Dell (1972).

Aspects of metabolism, breeding biology and ecological adaptation are shared by organisms of the two polar regions and of abyssal areas. These similarities can be directly related to the parallel harsh environmental conditions prevalent in such seas. Despite the recent revival in polar biology, available information on antarctic marine poikilotherms is still scant.

Various features and hypotheses have received considerable attention in antarctic biological studies including the phenomenon of 'metabolic cold adaptation', relative growth rates and aspects of breeding biology. The data from past research have produced a diverse picture, for instance de Broyer (in press) describes the differing strategies of dwarfishness and gigantism in antarctic marine invertebrates. Studies on energy utilisation from many more polar species are required before interrelationships between the allocation of energy to growth, reproduction and metabolism can be assessed.

My study concentrated on aspects of the biology of two common marine antarctic poikilotherms - a benthic/cryopelagic amphipod and a benthic bivalve. The biological strategies adopted by both species are considered, with their differences, to be well adapted to the physically harsh environment of the antarctic shallow sub-littoral.

I have divided the manuscript into two major sections: A, a broad based description of the macroalgal habitat, its fauna and some of their observed feeding relationships and B, more detailed aspects of the biology of the amphipod Pontogeneia antarctica and the bivalve Lissarca miliaris.

Section A:

Chapter 1. The Environment of Borge Bay.

1.1. Introduction:

Marine biological studies carried out from the British Antarctic Survey's research station on Signy Island, South Orkney Islands, have been centred on Borge Bay (lat. 60° 42' S, long. 45° 36' W), an area briefly described, biologically, by Price and Redfearn (1968) and Thurston (1972), and extensively investigated in the course of various ecological and physiological programmes. An historical and introductory description of the island has been presented by Holdgate (1967[a]).

The South Orkney group, composed of four main and many subsidiary islands, lies on the Scotia Arc. This chain of islands and area of relatively shallow seas connects the foot of South America with the northward extension of the Antarctic Peninsula (Fig. 1) and has been shown to be a major 'stepping stone' in the colonisation of the antarctic marine environment (Knox, 1960; Dell, 1972).

Signy Island, triangular in shape, lies to the south of Coronation Island, the main land mass in the South Orkney group (Fig. 2). Signy is relatively small, measuring 8 km. by 5 km. and reaches its highest point at 282 m. The geology of Signy Island has been described by Maling, Matthews and Adie (1967). Regionally metamorphosed sediments, predominantly quartz-mica-schists compose the main structure of the island. Most shores around the island are steeply shelving and constructed either of bedrock, (which can be

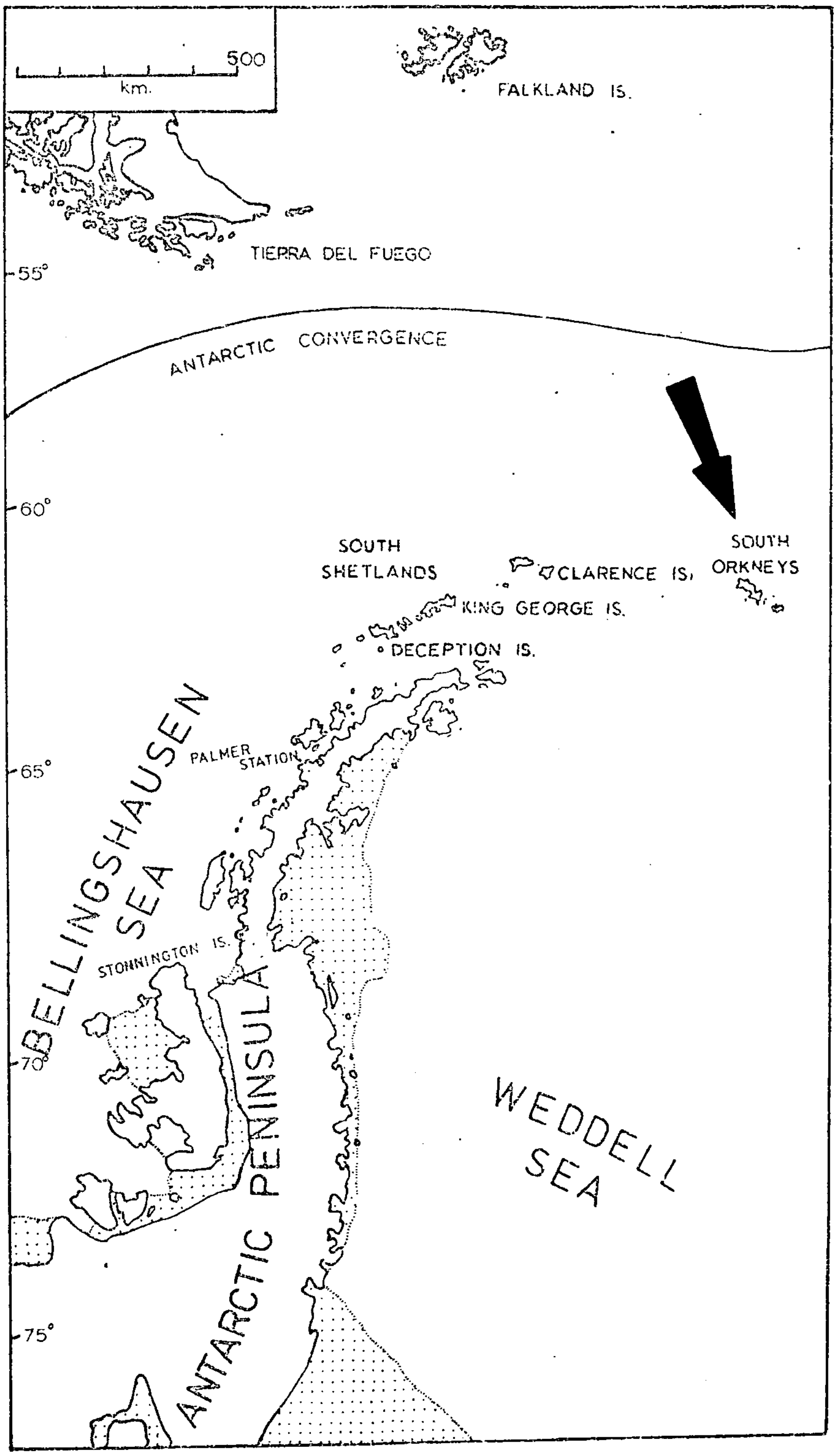

Fig. 1: The Antarctic Peninsula and Scotia Arc.

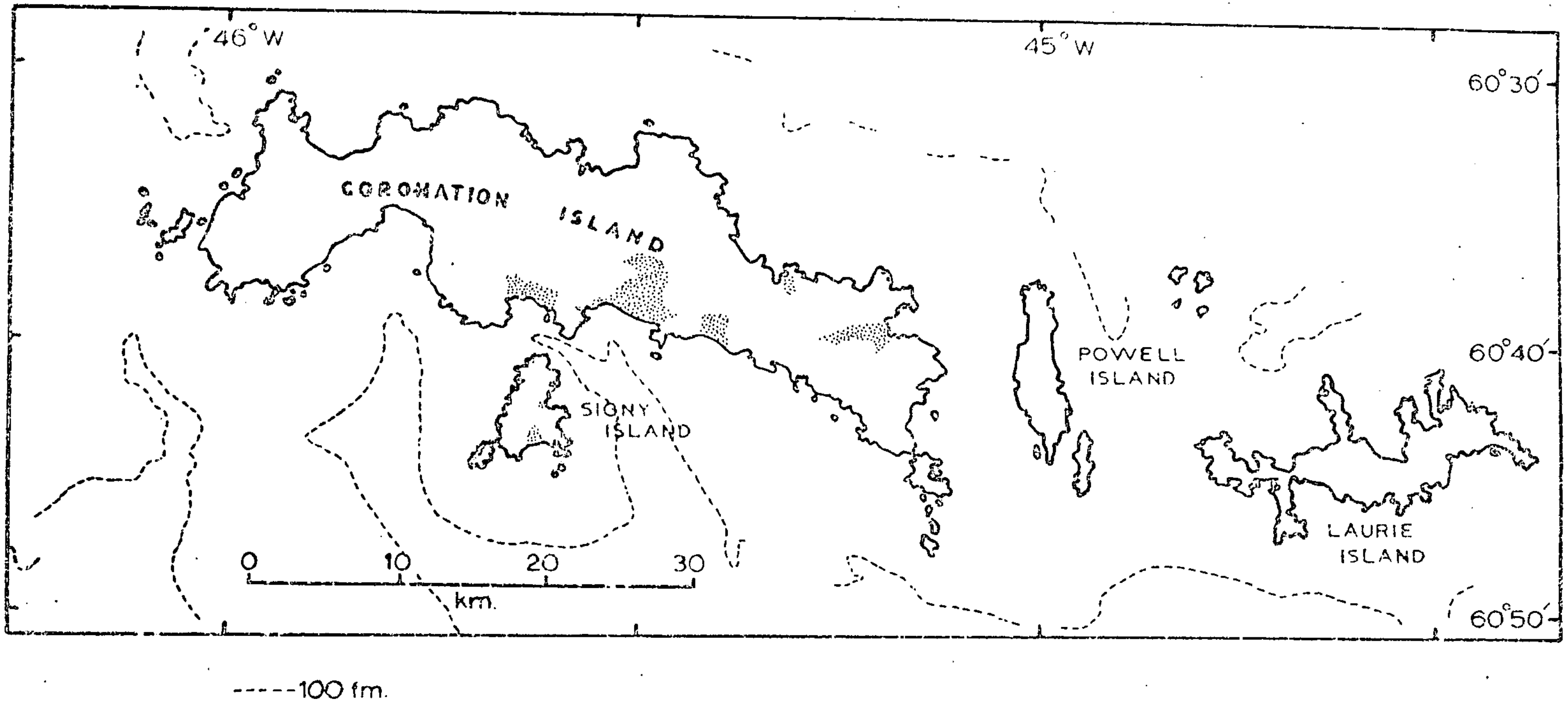

Fig. 2: The South Orkney Islands, indicating the position of the 100 fm. depth contour.

highly fissured or abraded smooth), or composed of a variable boulder beach. Drowned cirques exist in some areas, for instance Paal Harbour.

1.2. Meteorology:

1.2.1. Climate.

Situated on the east of Signy Island, Borge Bay (Fig. 5) is protected from severe surf action or heavy oceanic swells from all but south east gales when wave action in the littoral and shallow sub-littoral may be considerable. Fierce northerly winds, produced by Föhn clouds descending from the central ridge of Coronation Island (rising to a height of 1,200 m.), can also induce rough sea conditions in a short space of time. Such effects are frequent but the limited fetch of less than 8 km. inhibits any water disturbance at depth. The prevailing winds at Signy Island are west to north west, produced by depressions passing west to east along the Scotia Arc and to the south of the South Orkney group. The main central ridges of Snow Hill and Jane Peak give protection to the British Antarctic Survey base and Borge Bay.

The climate of Signy Island is charcteristic of the 'Antarctic Maritime Zone' (Holdgate, 1964). Relative humidity is very low and during the coldest months of the year (July to September), temperatures between -10°C and -12°C are normal with mean lowest temperatures for the winter months as follows:-

	May	June	July	August	September
Temp. (°C)	-21	-25	-29	-26	-21

(figures after Holdgate, 1967[a])

Record minimum temperatures below -40°C were measured during the winter of 1973. The summer months from December to April are characterised by temperatures around or slightly above 0°C. Much of the snow cover at lower altitudes melts off during this period, though approximately 50 percent of the island's surface remains covered by a permanent ice sheet.

1.2.2. The distribution and effects of sea ice.

For a lengthy period of the year the seas around the South Orkneys are considerably influenced by ice. The effects, in the form of icebergs, pack-ice floes, brash, anchor and fast ice, are briefly described by White (1973) whilst its ecological effects are further discussed by this author (in press). Owens and McCann (1970) describe the ice environment of an Arctic beach.

Distribution and duration of sea ice are dependent on a wide variety of interrelated factors including ice movements within adjacent sea areas, wind direction and velocity, (Sanderson, 1975) water currents and both air and sea temperatures. Within the sheltered areas of the coast, including Borge Bay, fast ice is under less physical stress and tends to remain stable for longer periods of the year, whilst pack ice, if driven into shallow waters under adverse conditions of tide and wind, may influence the shallow sub-littoral for extended periods. White (in press) presents an analysis of ice duration at Signy Island indicating the extent of fast ice in Borge Bay during the years 1957-72. Fast ice longevity varied from 70 - 241 days and averaged 148 days ± 49 (S.D.) for the 16 years' observations. These data are reproduced in Appendix I. During 1972 and early 1973,

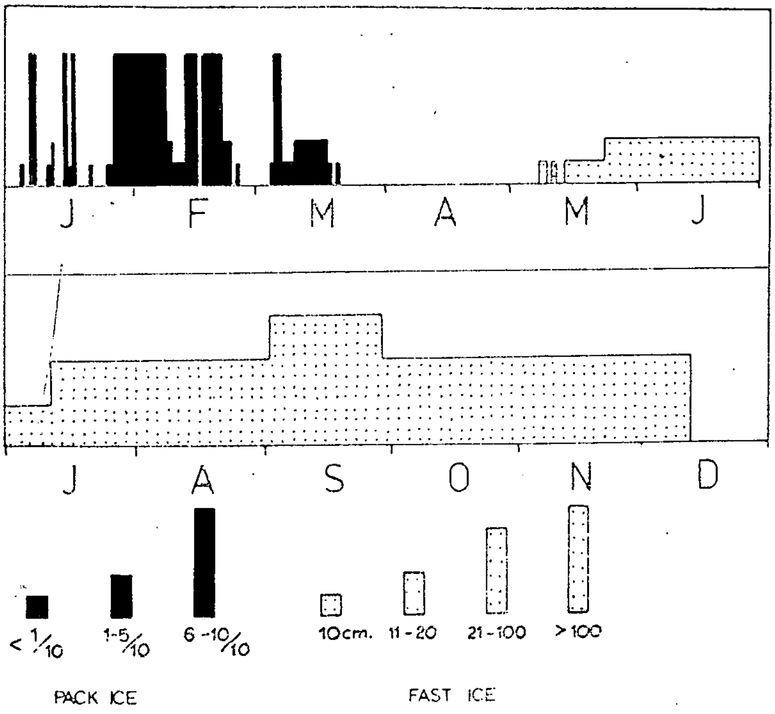

Fig. 3: Sea ice cover, for the year 1972, over the
sector of Borge Bay, Signy Island.

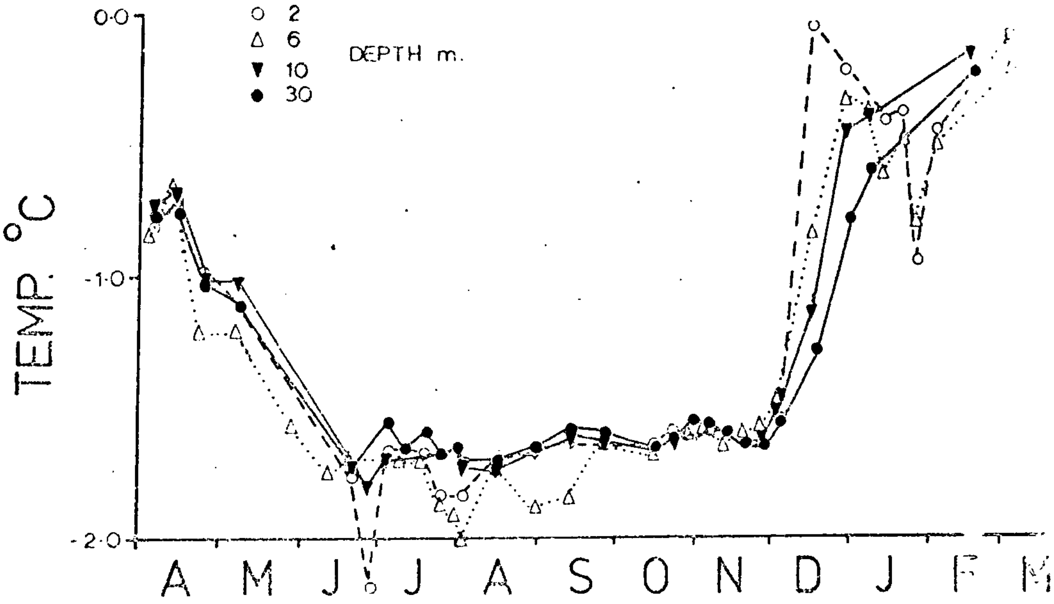

Fig. 4: Temperature profiles at four depth stations, Sig
Island.

ice conditions in the northern sector of Borge Bay (over the study area) were monitored. These observations are shown in Fig. 3. The total ice presence over the Thule transect during 1972 amounted to 271 days (216 days fast ice of varying thickness; 16 days glacier brash ice; 12 days pack ice (1 - 5/10); and 27 days pack ice (6 - 10/10). Sea water temperatures increased during the same period as ice break-out occurred in Borge Bay (Fig. 4).

Medium sized pack ice was observed to have considerable disruptive effects down to 10 m. depth on soft substrates, producing large 'plough' furrows in sands and silt/muds. Ice tracks were normally accompanied by large collections of dead Laternula elliptica and Yoldia eightsii shells, damaged during pack ice disruption.
The characteristic zonation of antarctic inshore benthos has been described by Dayton et al (1970), Gruzov and Pushkin (1970), and Richardson (in press). The mechanical attrition of moving ice reduces fauna to crevice dwelling species perhaps requiring physiological adaptation to survive periods of freezing (White, in press; Rakusa-Suszczewski and McWhinnie, 1976). Further biological effects of ice on the distribution of macroalgae are presented in the following chapter, whilst the more beneficial use of ice as a habitat for crustacea is discussed at length in Chapter 2 (Section B).

1.3. Sea Water Conditions:

The antarctic marine environment is characterised by near constant, low, sea temperatures, high nutrient levels and strong seasonal fluctuations in primary productivity. The latter is influenced by the presence of sea ice. South of the Antarctic Convergence (Fig, 2)

(Deacon, 1964), the sea water temperatures, even at shallow depths, fluctuate relatively little between summer and winter. The maximum temperature recorded during 1972/73 was +0.05°C (March), whilst the minimum (-2.1°C) was recorded during August. Tne temperature charcter--istics at four depths, one station in Factory Cove, Borge Bay at 6 m. and three in Normanna Strait at 2, 10 and 30 m. are shown in Fig. 4 (data from Hoogesteger, 1973). Changes in temperature, though small in scale, tend to occur abruptly and are often closely correlated with alterations in sea ice patterns.

Comprehensive chemical analyses of sea water, from the four stations, are given in Appendix II.

Productivity of high latitude seas is believed to be great during restricted periods of the year (Holdgate, 1967[b]; Horne et al, 1969), though low light levels throughout much of the year considerably reduce overall primary productivity. The depths of sea water to which 10 percent of the incident light penetrated are presented in Appendix III (data after Whitaker, pers. comm.). Phytoplankton blooms occur during, or soon after, sea ice break-out and the appreciable rise in chlorophyll a during December and January (1972/73) is readily apparent in Appendix II.

Chapter 2. The Distribution of Macroalgae in Borge Bay.

2.1. Introduction:

Estimates of the biomass of the epifaunal and infaunal communities of some habitats in Borge Bay have been recently compared (White and Robins, 1972; Hardy, 1972) with those of benthic biomass from other sectors of the Antarctic (Gallardo and Castillo, 1968; 1969; Propp, 1970). Evidence obtained so far points to the diverse faunal nature of antarctic benthos (Knox, 1970; Richardson, in press) and standing crop figures in excess of temperate or tropical benthic systems.

Faunal zonation has previously been described at McMurdo Sound by Dayton et al (1970), at other antarctic localities by Hedgpeth (1969[a]) and Gruzov and Pushkin (1970) and mentioned in passing by most authors on antarctic benthos. Several authors have described algal zonation in antarctic waters (Delépine, 1966; Delépine, Lamb and Zimmermann, 1966; Zaneveld, 1966[a]; Balech et al, 1968) whilst Stephenson and Stephenson (1972) discuss past results in this field. My survey was an attempt to quantify the distribution of macrophytes whose previous zonation patterns had been expressed in purely qualitative terms.

One section of the epibenthos at present under study at the South Orkney Islands is the contribution of the marine macrophytes to the antarctic shallow water sublittoral ecosystem. The dominant macroalga in southern South America and the islands of the sub-Antarctic is the kelp Macrocystis pyrifera. This species is replaced in the

South Orkneys by mixed forests of smaller Phyllogigas grandifolius and members of the genus Desmarestia. Desmarestia ligulata was found intermittently in shallow water (<5m.) whilst Desmarestia menziesii and Desmarestia anceps form the dense beds of plants in deeper water. The brown alga Ascoseira mirabilis is common high in the sublittoral zone and other algae including Iridae, Gigartina, Myriogramme and Phyllophora compose an underflora to the larger plants.

Information obtained from previous research workers at Signy Island has been collated, along with my own observations, and presented in Fig. 5 as a general flora distribution for the Borge Bay area.

2.2. Materials and methods:

From 27 July to 25 August 1971, a survey of plant distribution, substrate types and depth was made on a north to south transect in Borge Bay between the southernmost of the Thule Islands and inner Billie Rocks (Figs. 5 and 6). The study area measured 460 x 100m. (4.22 ha. overall) and was divided into five 20m. wide transects. This locality was chosen as typical of other nearby inshore areas and included depths from the littoral down to 13m. Stable sea ice enabled an accurate survey to be made of the area which was divided into a grid of 20 m^2. sub-units. The survey was restricted to the period when thin sea ice (30 - 50cm.) was easily penetrated by a petrol-powered chain saw. Holes to give access to the sea were cut at the corners and centre of each 20 m^2. The position of each of the 231 holes used in the survey is shown in Fig. 6[a]. Coloured identification markers lowered through each hole produced a simple

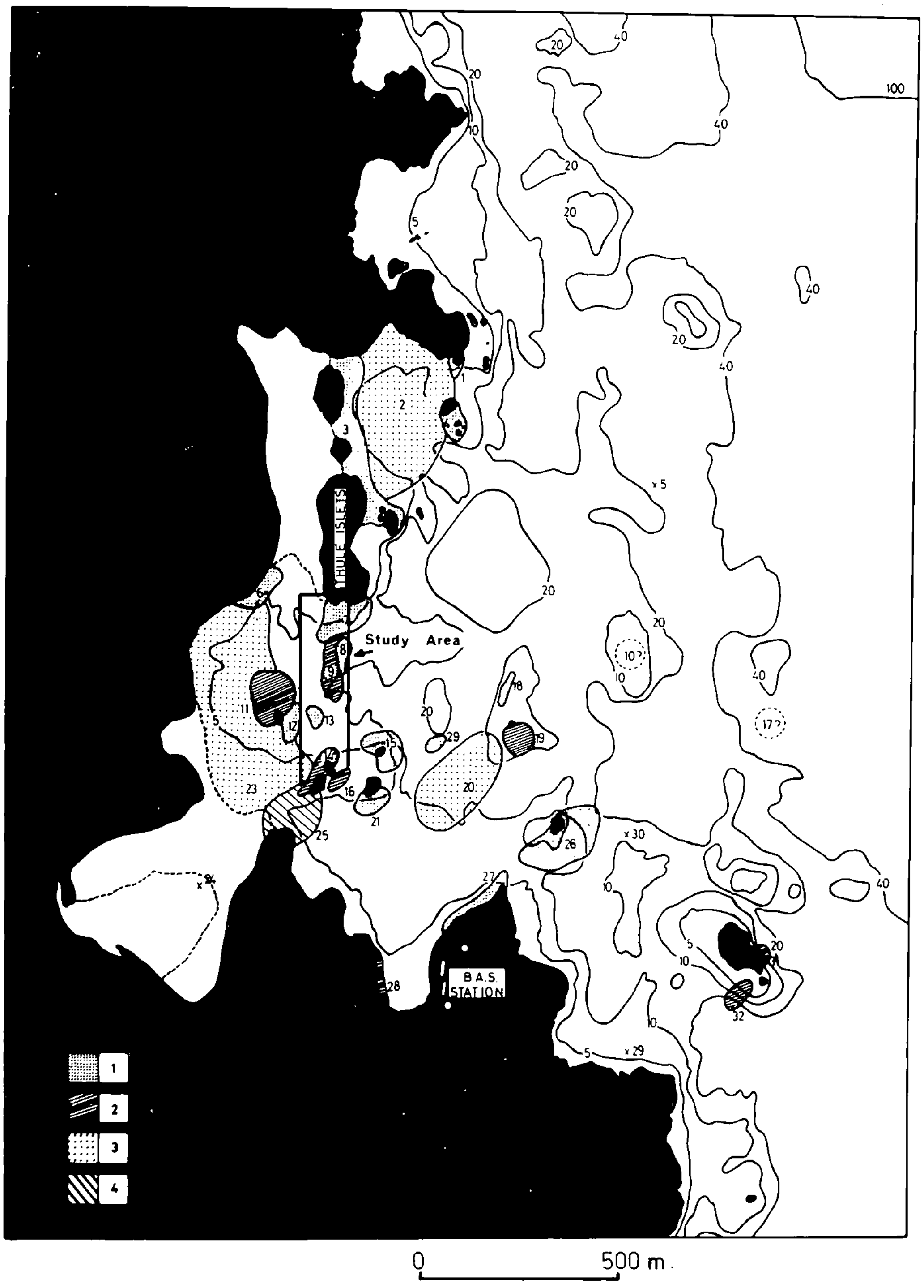

Fig.5: Macroalgae distribution in Borge Bay, Signy Island.

Key.

1. *Desmarestia* spp. beds........... Site Nos. 1,3,4,6,7,8,10,12, 15,18,21,26,27,$30\frac{1}{2}$
2. *Phyllogigas grandifolius* beds... Site Nos. 9,11,14,16,19,28,31, 32.
3. Impoverished areas, supporting diminished sparse flora of *Desmarestia* spp. and *P. grandifolius* Site Nos. 2,20,23,29.
4. Shallow water benthos supporting summer flora of *Adenocystis utricularis* and small Rhodophyceae. Site Nos. 25.
5. Areas with no plants present. Site Nos. 5,24,17.

method for underwater orientation. Two free-swimming divers made the survey by following a north-south line down a series of squares within one transect.

Depth contours (Fig. 6[a]) were determined using a calibrated lead line, all measurements being corrected to the level of mean low water spring tides (M.L.W.S.). Substrate was classified visually into five types (Fig. 6[b]):

(I) Solid Rock, (presumed bedrock).
(II) Variable Boulder pavement.
(III) Pebble - cobble.
(IV) Gravel.
(V) Sand - silt.

Fig. 6[a],[b] and[c]show the area in terms of depth, substrate and plant distribution.

Three transects A,B and C, each 29m. long, were positioned at the northern end of the study area (Fig. 6[a]). The biomass (wet weight) of three different types of macroalgae in 30 one metre squares was determined (Table II). The results in Figs. 7,8 and 9 are presented as percentage cover of plant material related to either depth or substrate. These data were obtained by drawing Fig. 6[a], [b] and [c] to 1:1,000 scale on paper and weighing the respective areas on an analytical balance.

Error was determined to be less than 2.5 percent.

2.3. Results:

2.3.1. Bottom topography.

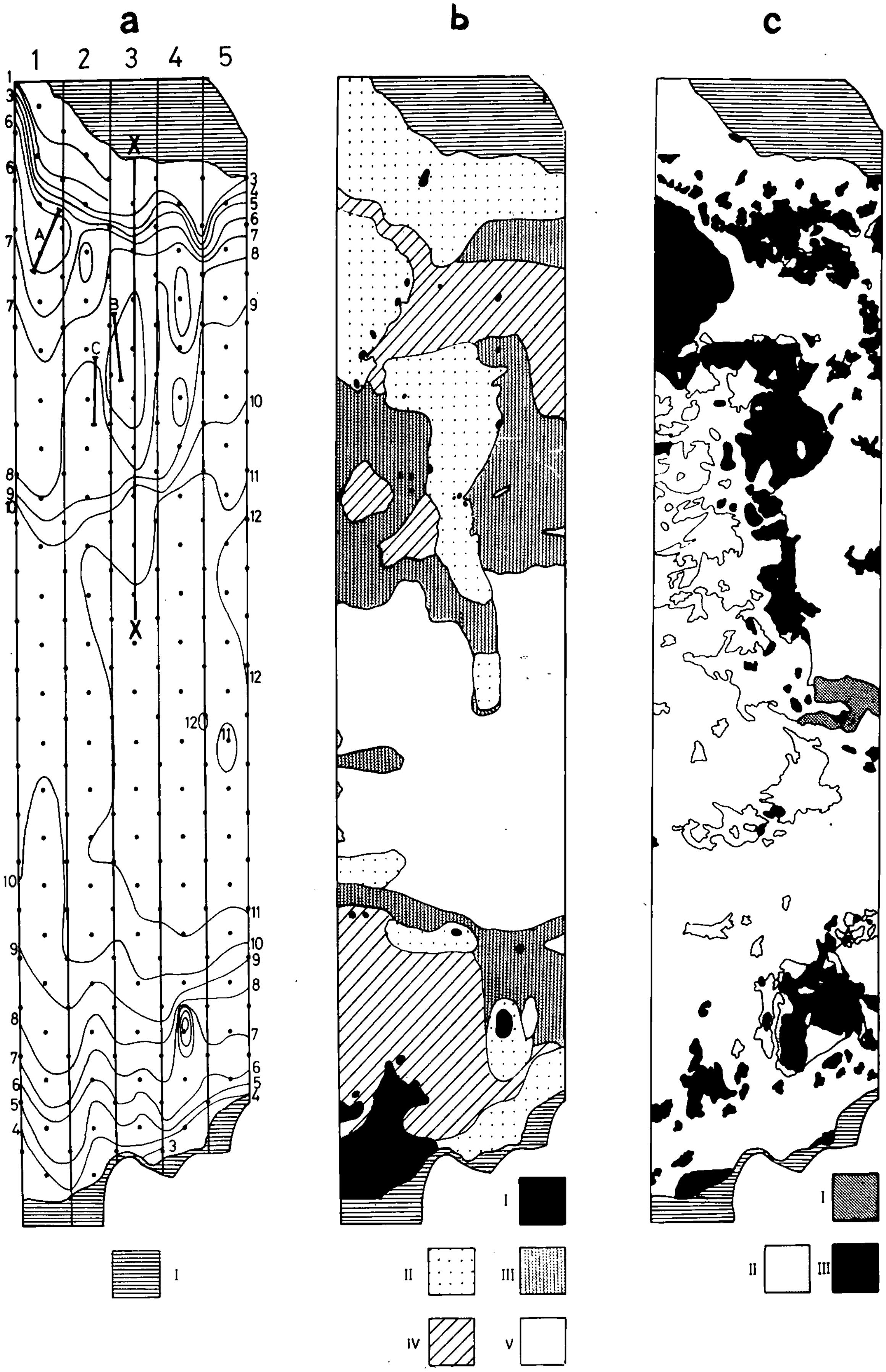

Fig. 6: Thule Islands - Billie Rocks transect survey. (a) Depth profile, showing the grid arrangement of ice holes, the sites of the three transects A, B and C and the transect X - X. The area I is applicable to a, b and c and shows the area with a low ceiling of ice. (b) Substrate analysis, I Rock, II Boulder, III Pebble, IV Gravel, V Sand-silt. (c) Macroalgae distribution, I Decaying macroalgae, II <u>Phyllogigas grandifolius</u>, III <u>Desmarestia</u> spp.

Sediments became finer with increasing depth with the immediate sublittoral boulder rock zone being replaced by smaller graded pebbles and gravels, whilst in deeper water, sand, silt and mud commonly occurred. The submarine topography, within my study area, followed this general pattern. The north and south ends of the transect were similar (Fig. 6[b]). The boulder-rock region nearer the shore occurred on a shelving beach extending to a depth of approximately 6m; at this contour the substrate altered to an irregular band of fine gravel. Large boulders, often 3m. high, were also present. Beyond this gravel layer the substrate became coarse forming a pebble-cobble platform. To the north of the transect the shelving boulder beach was separated from the central ridge of boulder pavement, extending to the 10m. contour, by a narrow gravel-filled gulley. The central bowl of the transect was a flat silt-sand plain at 10 - 12m. depth, where fragments of whale bone, evidence of past whaling activity, were a prominent feature.

Substrates were confined approximately to the following depths:

	Substrate	Depth (m.)
I.	Rock	0 - 5
II.	Boulder (a) - beach	0 - 6
	(b) - pavement	7 - 11
III.	Pebble	7 - 11
IV.	Gravel	6 - 9
V.	Sand - silt	10 - 12

Macroalgae at Signy Island have been recorded from depths of 25 - 30m. (Price and Redfearn, 1968), however the greatest bulk of Desmarestia spp. and P. grandifolius, which together account for a high proportion of the total plant material (Table I) grow above the 13m. depth line. Below this level, diminished light penetration results in smaller specimens of the large algae and a smaller biomass of Rhodophyceae. Only on vertical or overhanging rock faces were viable stands of healthy algae found to be growing below 13m. depth. Such habitats occur infrequently in Borge Bay.

The areas adjacent to the shore line at both Thule Islands and Billie Rocks were not surveyed due to the low ceiling of fast ice. Examination after the spring ice break-out indicated the immediate sublittoral to be totally barren of the larger species of macroalgae, though filamentous diatoms and smaller macrophyte species such as Adenocystis utricularis were found in the littoral during summer.

2.3.2. Bathymetric plant distribution.

Data for the percentage cover of Desmarestia spp. and P. grandifolius are presented as histograms for each of the transects 1 - 5 (Fig. 7) and for the whole area (Fig. 9[a]). Though the maximum values, for percentage cover, and the depths at which these occurred varied the pattern of the histograms is common to all transects. The greatest percentage cover for Desmarestia spp. occurred in shallower water than for P. grandifolius. The modes for Desmarestia spp. vary, between transects, from the 4 - 5m. to the 7 - 8m. depth contour, whilst those for P. grandifolius are confined to depths of 9 - 10m., or in the case of transect 2 to 8 - 12m. A similar bathymetric range of 8 - 15m. was recorded in Arthur Harbour by McCain and Stout (1969).

Species	Boulder		Pebble		Gravel	
	depth (m.)	percentage	depth (m.)	percentage	depth (m.)	percentage
Desmarestia spp.	7-8	75	5-6	56.5	7-8	22.4
Phyllogigas grandifolius	10-11	39	8-9	24.5	10-11	33.5

Table I: The modal peaks (depths) for plant cover on three different substrates, showing the depth range encountered and the percentage cover of plant material.

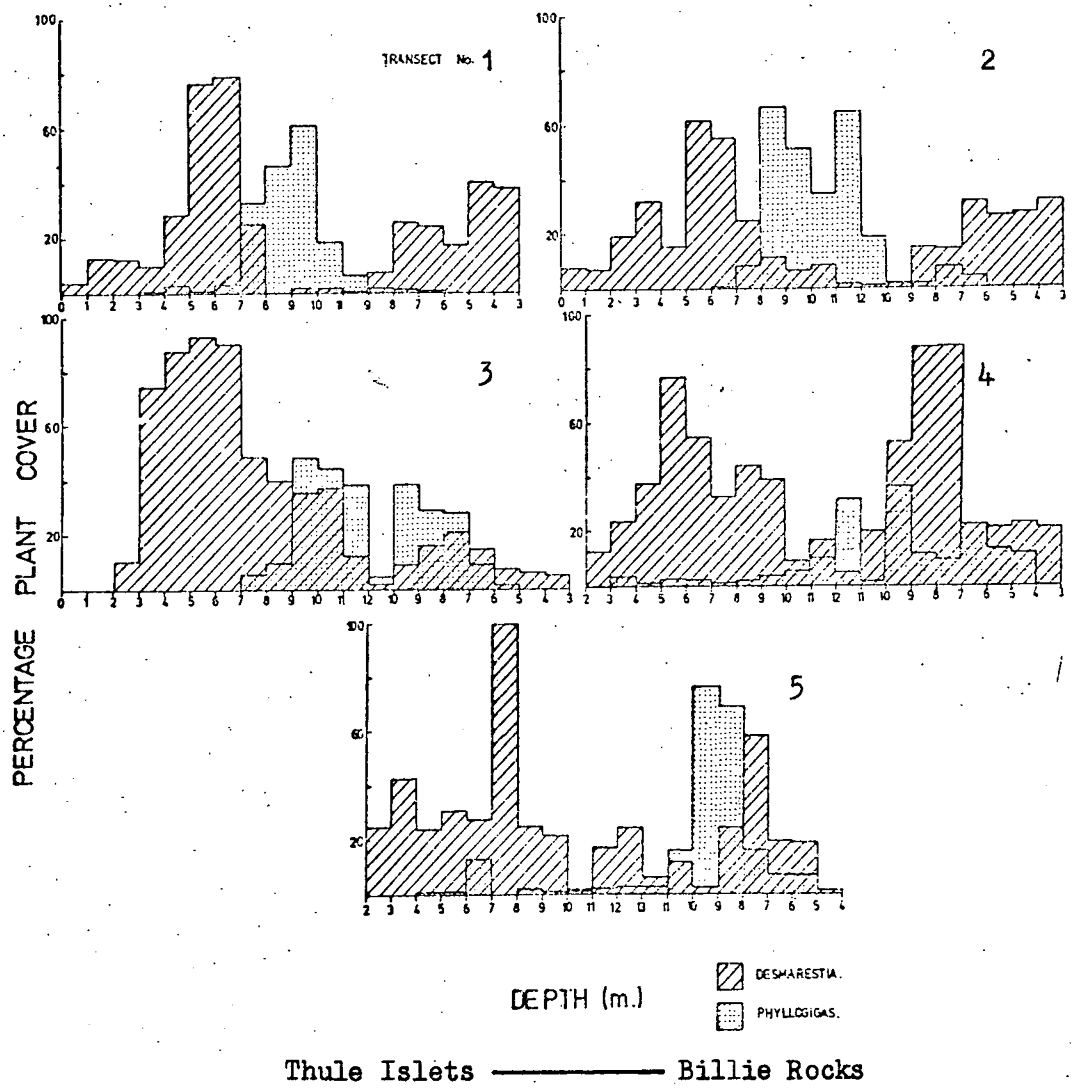

Fig.7: The percentage plant cover with depths for transects 1-5.

▨ *Desmarestia* spp. ⬚ *Phyllogigas grandifolius*

Total plant cover (Fig. 9[a]) increased from the littoral region downwards and reached a peak of 53 percent at 6 - 7m. depth. The percentage cover then decreased with increasing depth to only 27 percent at 12 - 13m. The greatest proportion of plant material within the upper 8m. was composed of various species of Desmarestia. The maximum percentage cover occurred within the 6 - 7m. depth range. There was no rapid decline in the percentage cover of P. grandifolius after the mode indicating a possible greater bathymetric range for this species. Maximum plant cover was present at 8 - 9m. though the percentage cover varied little between 8 - 12m. The high figure of 24 percent cover for P. grandifolius at the 12 - 13m. range is a reflection of the small area sampled within that depth contour ($483m.^2$).

2.3.3. Plant distribution with substrate.

The transitions between adjacent substrate types in Fig. 6[b] were not always as sharply defined as indicated, but often followed a gradation. The contour at which one substrate became dominant was the line at which demarcation was drawn. Results of percentage plant cover with substrate are shown in Fig. 8 for all transects. The mean values are shown in Fig. 9[b]. The highest values for Desmarestia distribution occurred on rock or boulder substrates whereas P. grandifolius occurred chiefly on a pebble bottom except in transect 4 where it was found on sand.

Fig. 9[b] shows that rock, and boulders supported a profuse covering of Desmarestia but less than 10 percent cover of Phyllogigas.

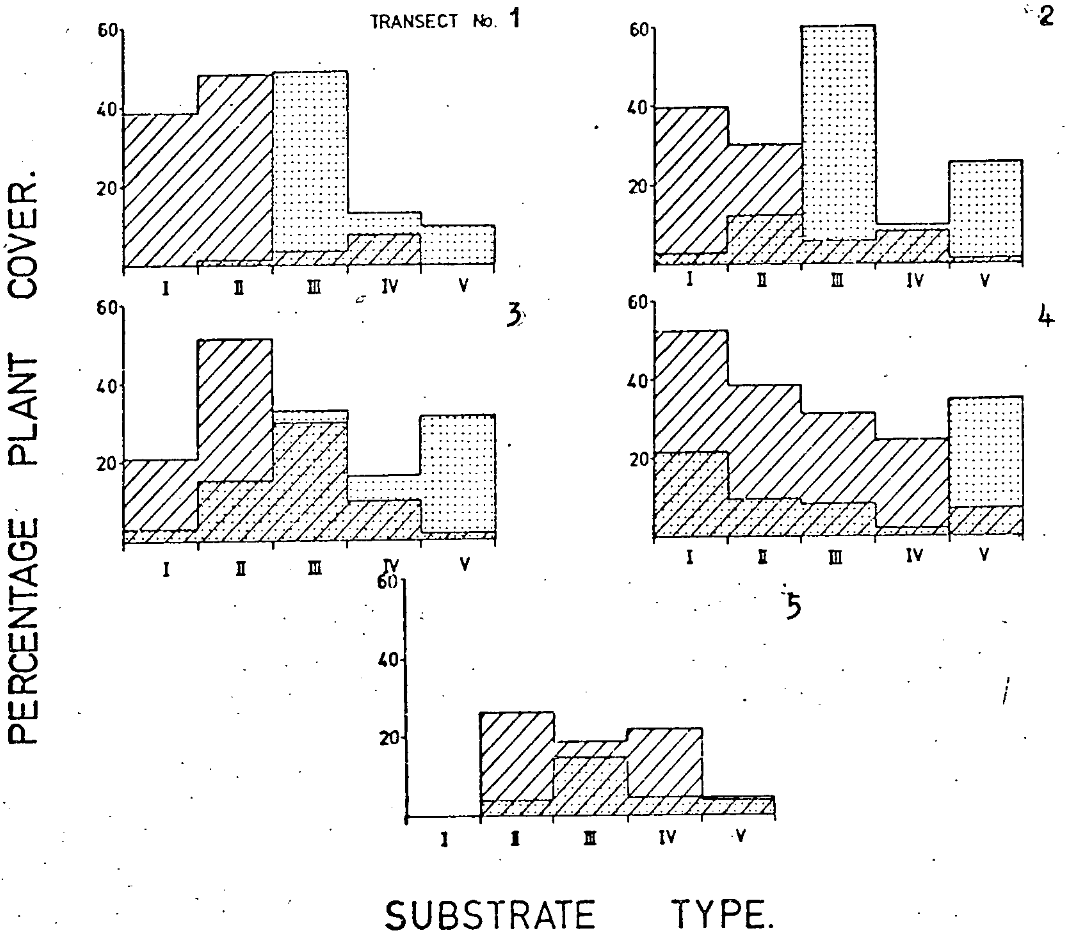

Fig. 8: The percentage cover with substrates I- V (see text) for the five transects.

▨ *Desmarestia spp.*

░ *Phyllogigas grandifolius*

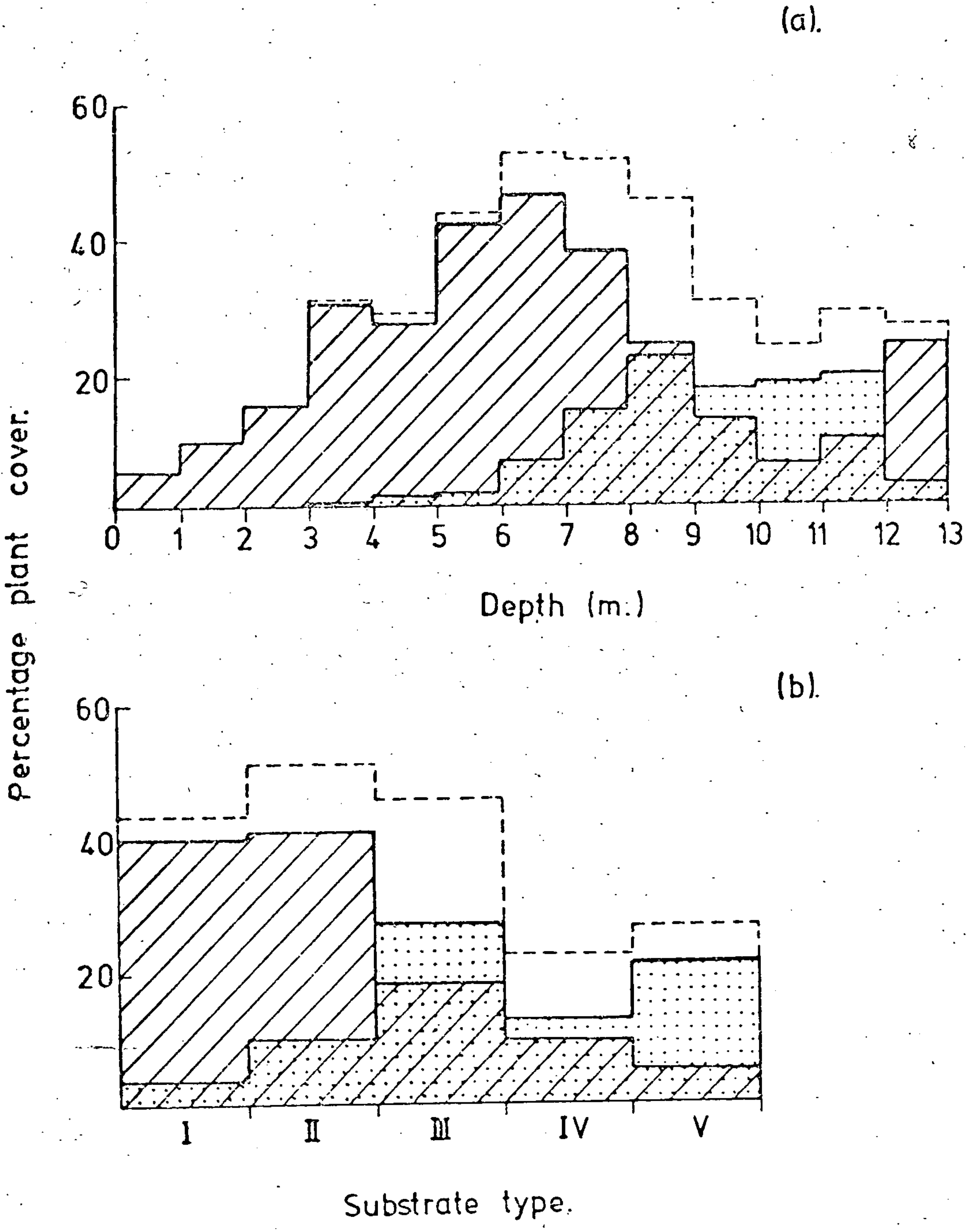

Fig. 9: The mean percentage plant cover for all transects (a) with depths, (b) with substrates.

▨ Desmarestia spp.

░ Phyllogigas grandifoilus.

⬚ Total Plant.

This situation is reversed on the pebble-cobble substrate with P. grandifolius dominant. The status of Desmarestia spp. decreased markedly as the substrate became finer. Sand is always an unsatisfactory substrate for macroalgal colonisation and though plants were present within sand-silt areas, the true substrate was normally a small boulder buried in the sand. In some cases holdfasts were anchored to whale bone.

An area of detached seaweed, mainly D. anceps, occurred in the deepest section of the area and is indicated in Fig. 6[c]. Plants detached from substrates by ice and wave action accumulate in the area of least water movement and slowly decompose over the winter period. Other authors (Price and Redfearn; 1968; Everson, 1970; Lee, 1973; and Ott and Maurer, 1976) have remarked on these decaying plant masses.

2.3.4. The influence of depth and substrate.

The distribution of marine plants is governed by many factors which exert control over their occurrence and biomass. Light and depth, surf and wave action, current, aspect, plant interactions and many physico-chemical parameters contribute to the production of different plant communities. In this study I only investigated data for depth and substrate and both appear to play a major rôle in determining the niche separation of the two dominant algal components. However, as there was some correlation between depth and substrate, it is not clear if both were causative factors in plant distribution.

Fig. 10 shows the percentage cover of *Desmarestia* spp. and *P. grandifolius* for the three substrates, boulder, pebble and gravel plotted against depth. Data for plant cover on rock and sand were statistically inconclusive as insufficient sampling areas were available. Although plants show an association with a particular substrate type, the degree of affinity (percentage cover) with each varied appreciably with depth. The three substrates in Fig. 10 demonstrate the same pattern of weed distribution though at different depths. In all cases the maximum percentage cover of *Desmarestia* spp. was present in water shallower than the maximum for *P. grandifolius*.

The high percentage cover of *Desmarestia* spp. on pebble substrate at 2 - 3m. depth (46.5 percent) and 12 - 13 m. depth (39 percent) may be due to the small number of samples. There was no decrease in the percentage cover, with depth, of *P. grandifolius* on gravel substrates indicating that the peak probably occurred in water deeper than that of the study area. The percentage cover of *Desmarestia* spp. was reduced with decreasing substrate particle size.

2.3.5. Biomass.

The positions of the three transects A, B and C are shown in Fig. 6[a]. Depth range was limited (6 - 8 m.). The results in kg./m^2. (wet weight) for the 30 quadrats examined are presented in Table II. Maximum biomass recorded was 2.05 kg./m^2. with means for total plant material/m^2. for transects A, B and C of 1.14, 0.74 and 1.03 kg./m^2. (wet weight) respectively. The percentage water

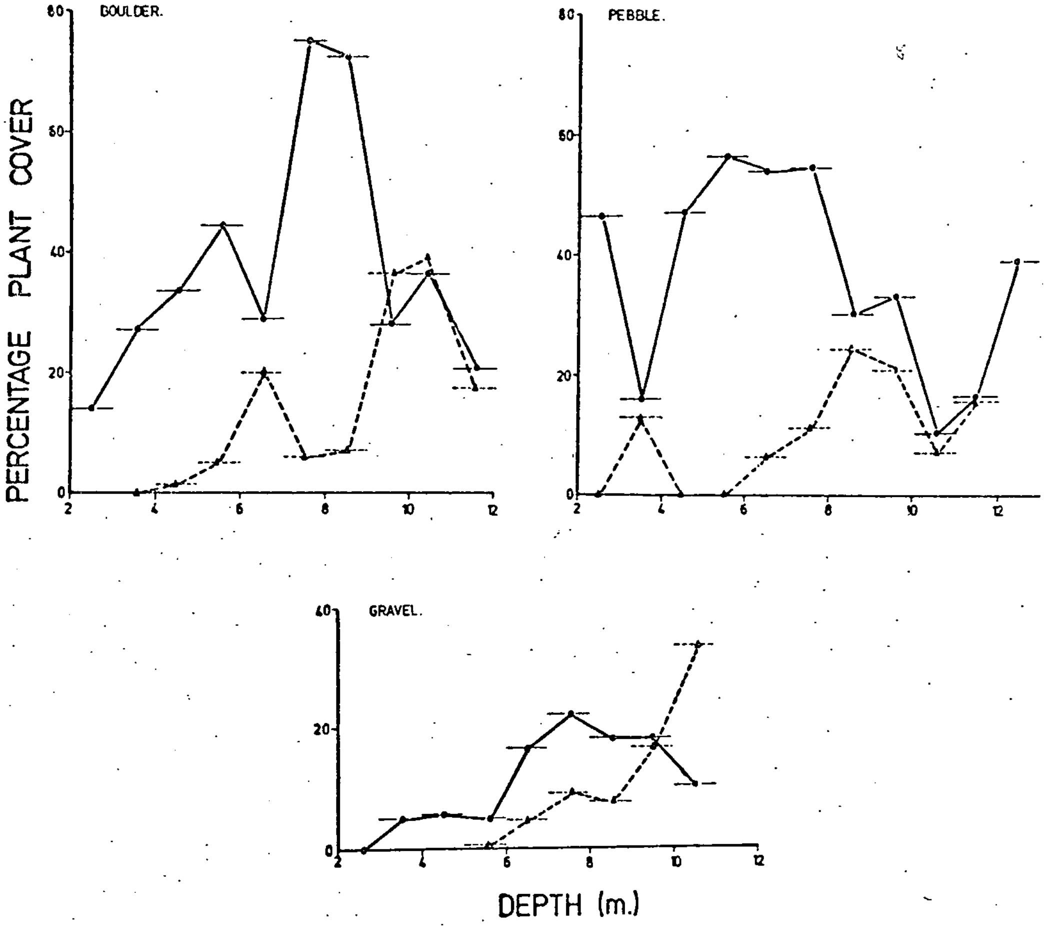

Fig. 10: The mean percentage plant cover for all transects against the depth profile. (—•— 'Open' Histograms)

▲- - -▲ *Desmarestia* spp.

●——● *Phyllogigas grandifolius*

Table II: Macroalgae standing crop (kg./m.^{2} - wet weight) for three transects in Borge Bay, Signy Island.

Jan. 1972.

	Desmarestia spp.			*Phyllogigas grandifolius*			Rhodophyceae			Total Plant		
Transect No.	A	B	C	A	B	C	A	B	C	A	B	C
Range	0.27-1.39	0-1.13	0-1.54	0-0.76	0-1.01	0-1.76	0-0.48	0-0.48	0-0.11	0.71-1.82	0.22-1.60	0-0.20
$\bar{x}$	0.83	0.23	0.61	0.15	0.04	0.04	0.02	0.02	0.01	0.11	0.07	0.10
per cent	72.6	30.0	59.1	13.5	48.9	37.2	13.7	20.9	3.6			
S.D. ±	0.32	0.37	0.69	0.27	0.38	0.60	0.21	0.16	0.05	0.37	0.61	0.52

content of D. anceps fronds and stipes is given in Appendix IV.

Unfortunately my attempts at quantifying the biomass of benthic algae using photographic techniques proved unsuccessful.

2.4. Discussion:

The deeper waters of the Antarctic, where physical parameters remain relatively constant, offer a stable environment fed by the highly productive nutrient enriched plankton. Hence biomass of the benthic fauna from deep water is comparatively increased (Ushakov, 1962; Andriashev, 1968; Belyaev, 1964; Hedgpeth, 1969[b]; Knox, 1970). The shallow water communities are not afforded a similar stability but undergo greater light, salinity and temperature fluctuations and are, in addition, subjected to the mechanical disruptions of increased water movement, ice abrasion and anchor ice (White, in press). The paucity of littoral and immediate sublittoral fauna and flora has been remarked upon by previous authors (Dayton et al, 1970: White and Robins, 1972).

The zonation of antarctic plant benthos can be correlated with many of the same factors found elsewhere in less severe environments, though the reduction in light penetration, with depth, is of prime importance. A variety of features affecting zonation have been described by other authors, for instance John (1971) examined the effect of wave and surf action, light and depth, on macrophyte biomass and concluded that both standing crop and production per unit area declined with an increase in both depth and wave action.

Interspecific competition has been attributed to some of the macro-algal community relationships found in Chilean waters (Dayton et al, 1973; Dayton, 1974) and at Macquarie Island (Kenny and Haysom, 1962). In relation to zonation in polar waters, Lee (1973) suggested that ice was not the greatest physical disruptor in arctic littoral waters but that air temperature and low salinity (due to ice melt) were the main reasons for an impoverished macroalgal flora.

Various zonal arrangements have been recognised by workers investigating southern cold waters (Kenny and Haysom, 1962; Delépine and Hureau, 1963; Arnaud, 1965; Dayton et al, 1973). At Signy Island I was able to recognise four zones between the littoral and the 13 m. depth contour. These are illustrated by a transect taken at points X - X in Fig. 6[a]and Fig. 11 and are as follows:

I. Ice abrasion zone: extending from the littoral down to 2m. This zone bears an impoverished flora, restricted to the fast ice free summer period when growths of filamentous diatoms and A. utricularis are present.

II. Desmarestia, boulder zone: extending from 2 m. to 8 m. The brown alga A. mirabilis is a species also common in this zone.

III. Phyllogigas, pebble-cobble zone: between the 8 - 11 m. depth contours.

IV. Sand and gravel zone: carrying a diminished flora of P. grandifolius, Desmarestia spp. and Rhodophyceae. Most plants present are associated with sub-surface holdfast attachments.

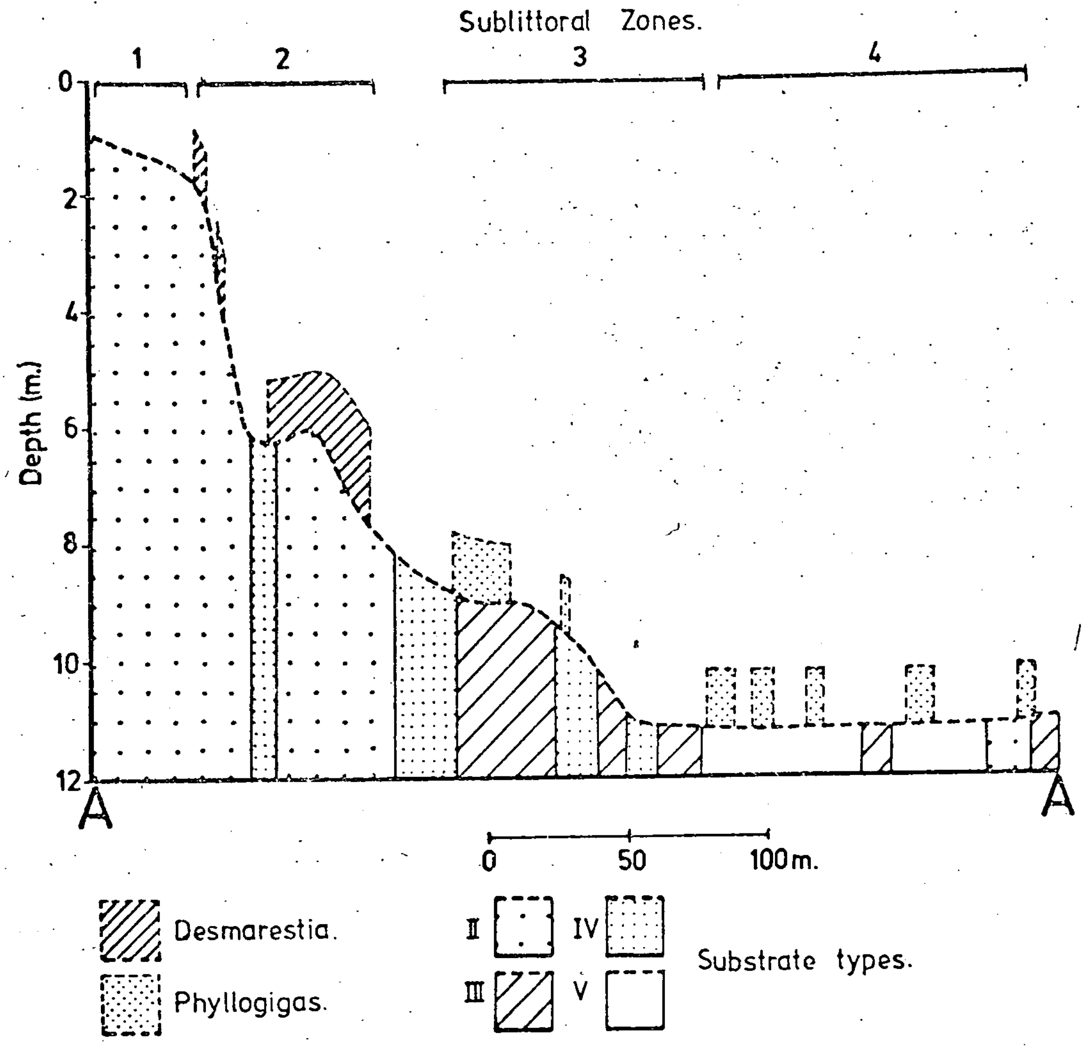

Fig. 11. Schematic transect from southern Thule Islands through the points X - X (Fig. 6 a).

It is readily apparent that Desmarestia spp. exist in shallower water than P. grandifolius. This feature may be a reflection of a greater photosynthetic capability by P. grandifolius which consequently excludes Desmarestia from deeper water. The zonation may demonstrate selection by the different plants to certain substrates or alternatively P. grandifolius may be more susceptible to the ice abrasion effects of the immediate sublittoral.

The greater diversity and high biomass attributed to antarctic faunal benthos is not parallelled by the bottom dwelling plants. Lee (1973) discussed the lack of floral diversity and the small and isolated plant communities present in arctic waters and linked these features to the polar clime and the lack of suitable substrates. My observations indicated that a variable bottom sediment, as found within Borge Bay, can never be fully utilised by macrophytes since much of the sea floor is unsuitable for colonisation. From previous biomass figures for antarctic benthic flora (White and Robins, 1972), and data provided by this study, standing crop per unit area, in shallow antarctic seas, is less than in cold temperate or tropical systems. The maximum biomass recorded was 2.05 kg./m.^{2} (wet weight), with a mean value for all quadrats of 980 g. wet weight/m.^{2} Lüning (1969), working in the turbid waters off Helgoland, recorded biomass for Laminaria of 5.6 to 11.1 kg. wet weight/m.^{2}, and values of a similar order have been obtained from other localities: Norway:- 8 kg./m.^{2} (Grenager, 1953), Scotland:- 6 kg./m.^{2} (Walker, 1954), California:- 14 kg./m.^{2} (Blinks, 1955), Nova Scotia:- average standing crop 3.8 kg./m.^{2}, maximum 16 kg./m.^{2} (Mann, 1972) or earlier estimates (McFarlene, 1952) working on the south west coast determined the mean biomass of Laminaria as 3.8 lbs./yd.^{2} (equiv. 2.1 kg./m.^{2}). Higher order biomass estimates for the sublittoral beds of the angiosperm Zostera in northern arctic waters were 1,150 g. dry weight/m.^{2} (13.6 kg./m.^{2} wet weight) (McRoy, 1970) and these results are parallelled by the californian work of McFarland and Prescott (1959) working on Macrocystis forests.

The paucity of plant biomass at depths just below the littoral zone, on an otherwise suitable substrate, was a direct effect of abrasion and anchor ice formation. This produced the pattern of isolated crevice dwelling plant clumps rather than continuous forest growths. Since less than ten per cent of incident light penetrates 1 m. of sea ice (Appendix III), and this situation is present for a large proportion of the year (White, in press) we might expect a decrease in standing crop, unless the species present are metabolically capable of adequately utilising the short photosynthetic period of ice-free summer. Productivity within algal species is not however uniform for Jónsson (1970), working on the sublittoral at Surtsey, noted that the rate of growth of the genus Desmarestia was more rapid than that of laminarians. Also benthic plants which extend their range to the unfavourable conditions of sub-ice locations are often capable of productivity under climatic extremes (McRoy, 1969), though Kanwisher (1966), working on arctic laminarians, emphasised the drastic effects of ice cover on plant metabolism. Benthic algae of the temperate zones have a single photosynthetic period, the summer. They utilise the assimilation surplus in maximal winter growth (Lüning, 1971). Laminaria does not appear to be a metabolically adapted genus to decreased light but relies on a diminished metabolism as winter progresses coupled with a massive pre-winter food store to avoid 'starvation'. Little work has been attempted on antarctic macrophyte productivity though Zaneveld (1966[b]) observed photosynthetic production in antarctic macroalgae subjected to a régime of 9 - 10 months per year under sea ice.

In conclusion the comparative decrease in standing crop and the pattern of plant zonation in antarctic waters are at least a function of light, ice and substrate and may, in part, be due to decreased productivity.

Chapter 3 The Fauna Associated with *Desmarestia anceps*:

3.1. Introduction:

The habitats provided by the fronds of sublittoral macroalgae have received little attention from antarctic biologists in the past, probably due to the difficulties of quantitatively sampling the macrobenthos. Some of these problems were outlined in a paper by Gerking (1957). This chapter describes some of the fauna associated with *Desmarestia anceps*. Unfortunately in this study I was only able to collect plants not exceeding 5 kg. (dry weight) and normally plants sampled were in the range of 1 - 2 kg. There was thus selectivity in the sampling since larger plants were inaccessible to the collecting gear.

I observed that amphipod species belonging to the families Calliopiidae and Eusiridae were particularly common in the macroalgal habitat. Four species accounted for more than 75 percent of the amphipod biomass and one - *Pontogeneia antarctica* - was chosen for investigation into aspects of the biology of an antarctic crustacean. Similarly the Mollusca, composed of 29 species of gastropods and 4 species of Pelecypods (which accounted for 34 percent by weight and 47 percent by number of the molluscs) were a dominant group. Comparative aspects of the biology of the most important mollusc, *Lissarca miliaris*, are presented in Chapter 9 (Section B). This bivalve accounted for over 98 percent of the Pelecypoda by both weight and number.

3.2. Materials and Methods:

Whole plants of the sublittoral brown alga *D. anceps* were collected at monthly intervals during 1972/73 by SCUBA diving in depths of 5 - 9m. Single plants were regarded as individual sample units. Normally six whole plants were collected each month from the three sampling areas in northern Borge Bay shown in Fig. 6[a]. Additional samples at three distinct depths (2, 5 and 12 m.) were taken twice per year. Samples from the 2m. depth were normally taken, from protected or overhanging rock faces, with a large hand net of mesh size 0.3mm. This was supported by a cylindrical metal frame of length 1.5 m. and a diameter of 0.8 m. This apparatus, shown in Fig. 12, was restricted to a size and weight which could be comfortably handled by two divers under the sea ice with the assistance of one surface attendant. During sampling the mouth of the net remained closed until the last moment so that active free swimming amphipods such as some lysianassids and Pontogeniella spp. were not taken. Holdfasts were severed intact. Then by means of a sharp steel pin and attached drawcord, passing to the rear of the net and back to the operator, the whole plant could be carefully drawn into the collecting bag with the minimum of disturbance. I fould it difficult to quantitatively test the efficiency of this sampling method though observations indicated that amphipods were loathe to leave plant cover. If deliberately disturbed they rapidly regained shelter. The only species which were noted, on occasions, to 'escape' were the slower swimming Acanthonotozomatidae (Paraphimedia integricaudata) and Paramphithoidae (Epimeria monodon).

In the laboratory plants were divided into holdfasts and fronds. Most of the fauna associated with the fronds were extracted by immersing and strongly agitating small sections of plant in a

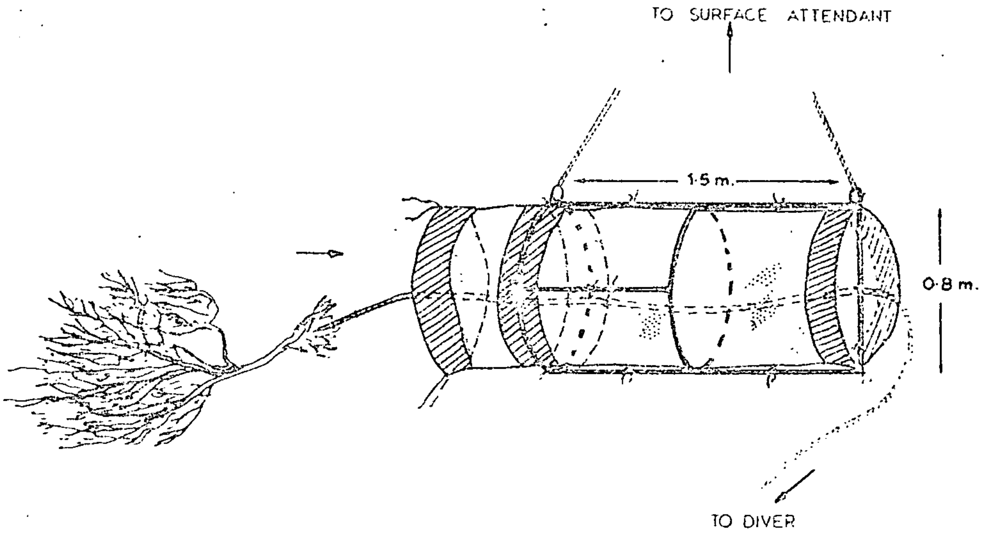

Fig. 12: Sampling frame and net used for collecting <u>Desmarestia anceps</u>.

dilute solution of formaldehyde in seawater (0.25 percent). Any remaining animals were extracted by hand under a x12 stereo dissecting microscope.

The wet weight of holdfasts and fronds were recorded and the fronds dried at 100°C to constant weight. (Data are given in Appendix IV). Animals were collected on a 0.25 mm. sieve and preserved in 5 percent neutralised formol saline for later identification and analysis. Ultimately animals were counted, selected species measured, dried at 80°C and stored under vacuum until weighed. The effects of formaldehyde fixative on dry weight are presented in a paper by Howmiller (1972) and note should be taken of the use of preserved material in this study.

3.3. Results:

3.3.1.The composition of species on *Desmarestia anceps.*

D. anceps with its dense branching fronds and large surface area provides a suitable habitat for a wide range of organisms. My study concentrated on the crustacean Amphipoda and the Mollusca, though observations were made on other organisms present. I ignored the micro-habitat provided by macroalgal holdfasts.

Certain species of demersal fish were present within the macroalgae, particularly within *D. anceps*. *Notothenia coriiceps neglecta* and *Trematomus newnesi* seek shelter within weed beds whilst *Harpagifer bispinis* and *Notothenia gibberifrons* occur on the gravel patches between *Desmarestia* spp. plants. A list of invertebrates recored from *D. anceps* is given in Appendix V.

The Isopoda, especially the Serolidae, though an important invertebrate group of the antarctic soft sediment benthos (Hardy, 1972) are not numerous in the macroalgal association. However the following isopod species were recorded: *Cymodocella tubicauda*, *Paramunna gaini*, *Plakarthrium punctatissimum* (very common on *Phyllogigas grandifolius*), *Gnathia* spp. *antarctica* (?), *Munna antarctica*, *Glyptonotus antarcticus* (small individuals) and *Antarcturus signiensis*. The occurrence of the last two was very sporadic whilst the weight of the remainder per plant was small. When large individuals of *Antarcturus* and *Glyptonotus* occurred their presence was recorded but they were not included in subsequent biomass analysis, for such infrequent 'giants' confuse meaningful interpretation of the data. Specimens of the tanaid *Nototanias antarctica* (?) were also present. The Pycnogonidae were usually represented by the species *Nymphon australe* though occasional individuals of the large *Decalopoda antarctica* were also recorded from the fronds.

One of the most important components of the macroalgal fauna and one which unfortunately received no further attention in my study was the small harpacticoid copepods. Their numerical abundance, and probably their productivity, was considerable. The importance of the copepods and small ostracods as a food resource within the habitat was considerable.

Worms were present in the fronds though it is probable that some of the species recorded originated from either the holdfast interstices or the epiphytes associated with the holdfast region. The large nemertine *Lineus corrugatus* was invariably present within the holdfasts and smaller individuals were found higher up in the fronds. Other species present included *Tetrastemma validum*, *Tetrastemma* longistriatum, Tetrastemma spp. and a species of Amphiporous. T. validum was the most frequently recorded nemertine. The last two species were found only rarely. Eight polychaetes and one oligochaete were isolated from the samples of D. anceps (Appendix V).

Echinoid faecal pellets were common in the washings from samples. Species of echinoderm recorded included Odontaster validus, Cryposterea turqueti and Sterechinus neumayeri.

3.3.2. The Mollusca associated with macroalgae.

Ten samples of D. anceps were examined. Plant weights (wet) ranged from 3.52 kg to 0.14 kg ($\bar{x}$ = 1.25 kg) with a mean frond water content of 82.0 percent.

The numbers and weights of all Mollusca present on D. anceps fronds are given in Table III and the composition in terms of abundance and weight of the four major groups (Pelecypoda, Gastropoda (excluding Nacella concinna), Polyplacophora and Nacella concinna) in Table IV. The data on the antarctic limpet has been categorised separately due to its large weight and sporadic distribution (Walker, 1972). Most of the limpets present on D. anceps fronds were small to medium sized individuals less than 1.0 cm long. The species composition of the molluscan fauna comprised 29 Gastropoda, 4 Pelecypoda and 2 Polyplacophora. The chitons were of rare occurrence, whereas the pelecypods, although represented by few species (two Philobrya spp., Mysella charcoti and Lissarca miliaris), shared a major rôle with the gastropods in the weed habitat. All four bivalves attach themselves to a suitable substrate by byssal threads produced just after post -

Date	SAMPLE		TOTAL MOLLUSCA		GASTROPODA (excluding Nacella concinna)				PELECYPODA					Lissarca miliaris		
	Plant Weight (wet)	(dry wp)	W/kg.wp	N/kg.wp	W	N	W/kg.wp	N/kg.wp	W	N	W/kg.wp	N/kg.wp	W	N	W/kg.wp	N/kg.wp
13.1.72	2,140	389.5	54.38	28,606	13.05	5,455	33.50	14,005	4.59	5,677	11.79	14,575	4.49	5,616	11.53	14,418
19.2.72	3,517	640.1	11.36	7,334	5.00	3,975	7.81	6,210	1.81	835	2.83	1,304	1.76	1,343	2.75	2,098
9.5.72	1,772	322.5	29.22	10,546	5.69	2,113	17.64	6,552	2.95	1,268	9.15	3,932	3.03	1,264	9.40	3,919
9.6.72	945	172.0	27.33	8,808	2.22	594	12.91	3,453	2.48	921	14.42	5,355	2.46	917	14.30	5,331
10.7.72	1,496	272.3	40.34	10,716	6.06	1,043	22.25	3,830	4.79	1,872	17.59	6,875	4.77	1,860	17.52	6,831
16.8.72	450	81.9	89.01	43,894	4.88	2,358	59.58	28,791	2.42	1,237	29.43	15,103	2.39	1,224	29.18	14,945
11.9.72	560	101.9	182.38	61,796	10.00	3,234	98.14	31,737	7.07	3,033	69.38	29,764	7.02	3,019	68.89	29,627
9.10.72	139	25.3	305.53	165,810	1.85	783	73.12	30,949	5.88	3,412	232.41	134,861	5.88	3,384	232.41	133,755
10.11.72	260	98.4	29.80	12,978	2.29	883	23.24	8,974	0.65	381	6.61	3,872	0.64	381	6.46	3,872

TableIII: Numerical and weight composition of the Molluscan fauna associated with Desmarestia anceps fronds, where wp = plant weight (dry), N = abundance and W = weight (g.).

	Sample Weight										
Percentage Weight	13.1.72	19.2.72	9.5.72	9.6.72	10.7.72	16.8.72	11.9.72	9.10.72	10.11.72	$\bar{x}$	S.D. ±
POLYPLACOPHORA	-	-	-	-	-	-	0.2	-	-	-	-
PELECYPODA	21.7	24.9	32.3	52.7	43.6	33.1	38.0	76.1	22.0	38.2	17.5
GASTROPODA	61.6	68.8	60.3	47.3	55.1	66.9	53.8	23.9	77.0	57.2	15.3
<u>N. concinna</u>	16.7	6.0	8.3	-	1.3	-	8.0	-	-	4.5	5.8
Total W (g.)	21.18	7.27	9.42	4.71	10.99	7.30	18.59	7.73	2.93		
Percentage Number											
POLYPLACOPHORA	-	-	-	-	-	-	0.1	-	-	-	-
PELECYPODA	51.0	16.8	37.3	60.8	64.1	34.4	48.2	81.1	29.8	47.1	19.8
GASTROPODA	49.0	82.7	62.1	39.2	35.7	65.6	51.4	18.7	69.2	52.6	19.6
<u>N. concinna</u>	0.1	0.3	0.6	-	0.1	-	0.4	-	0.2	0.2	0.2
Total N	11,142	4,695	3,401	1,515	2,918	3,595	6,297	4,223	1,277		

Total Weight = 90.12 g.

Total Nos. = 39,063

TableIV: The percentage composition, by weight (W) and number (N) of the major mollusc groups present on the macroalga Desmarestia anceps.

larval release.

The pelecypods accounted for 47 percent numerically and 38 percent by weight (dry) of the total molluscan fauna found on D. anceps. The most important group, both numerically and by weight, of the Mollusca was the Gastropoda which accounted for 57 percent of the total weight and 53 percent numerically. The most conspicuous gastropod Laevilacunaria antarctica represented 20.2 percent by weight and 14.6 percent by number of all Mollusca. The relative importance of all species of mollusc which had a weight or number greater than one percent of the total mollusca fauna is shown in Table V. Certain species, although important by weight, were represented by few individuals (e.g. Margarella antarctica and Nacella concinna); others, whose numbers were appreciable (e.g. Cyclostrema meridionale) which formed 20.2 percent by number of the May sample) contributed little to the total weight of molluscs. Without comparative data on growth and population dynamics an assessment of the relative importance in terms of production of each species is not possible.

Table VI presents the relationships between weight (W) and number (N) of the following groups; total Mollusca, Gastropoda, Pelecypoda and Lissarca miliaris and the weight of D. anceps fronds from which they were collected. Expressing N and W per kg. dry weight of D. anceps (wp), a relationship N or W = bwp^m is found. Alternatively expressed as:

$$\log. N \text{ or } \log. W = m\log.\, wp + \log. b$$

in which the two constants m and b can be determined by the method

Percentage Numbers (N) and Weight (W).

Sample Date:	13.1.72		19.2.72		9.5.72		9.6.72		10.7.72		16.8.72		11.9.72		9.10.72		10.11.72		$\bar{x}$		S.D. ±	
	N	W	N	W	N	W	N	W	N	W	N	W	N	W	N	W	N	W	N	W	N	W
Lissarca miliaris	50.4	21.2	14.6	24.2	37.2	32.1	60.5	52.3	63.7	43.4	34.0	32.8	47.9	37.8	80.7	76.1	29.8	21.7	46.6	38.0	20.0	17.6
Gastropod spp.																						
Eatoniella spp.	11.3	4.3	26.3	5.1	14.9	3.8	20.8	4.0	6.6	1.2	4.8	2.1	15.2	3.4	2.4	-	10.1	2.6	12.5	2.9	7.7	1.6
Rissoa spp. 1	-	1.3	3.7	16.5	10.2	26.5	-	1.4	6.5	12.3	10.8	37.2	3.6	7.3	2.0	15.5	8.0	20.0	5.0	15.3	4.1	11.7
L. antarctica	26.2	22.4	48.6	18.8	8.3	11.1	11.3	32.8	15.4	15.1	7.1	2.0	22.0	11.9	7.6	4.1	35.5	13.5	20.2	14.6	14.4	9.3
Pellilitorina *pellita* (rough spine)	-	-	-	6.7	-	3.7	-	-	-	5.0	-	6.6	-	3.9	-	2.1	-	-	-	3.1	-	2.7
Munditia meridionale	1.7	-	-	-	1.2	-	2.0	-	1.5	-	27.1	2.4	4.1	-	5.5	-	6.2	-	5.5	-	8.4	-
Margarella antarctica	-	27.2	-	18.0	-	8.4	-	8.2	-	16.1	-	9.4	1.0	22.2	-	-	2.4	36.6	-	16.2	-	11.2
Pellitorina setosa (smooth spine)	-	-	-	-	-	2.7	-	-	-	3.2	-	-	-	3.3	-	-	-	1.2	-	1.1	-	1.5
Nacella concinna	-	16.7	-	6.0	-	8.3	-	-	-	1.3	-	-	-	8.0	-	-	-	-	-	4.5	-	5.8
Eatoniella spp.	-	-	-	-	-	-	-	-	2.4	-	4.7	2.8	-	-	-	-	1.4	1.3	-	-	-	-
Subonoba spp.	5.4	3.2	1.4	-	2.2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Prosipho hedleyi (?)	-	1.7	1.2	-	-	1.3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Rissoa spp	1.9	-	-	-	20.5	-	2.8	-	-	-	-	-	-	-	-	-	-	-	2.8	-	6.7	-

Table V : The major mollusc species on the fronds of Desmarestia anceps.

	Equation No.	r	m	log. b	var. y $\pm$	var. m $\pm$	P
<u>Lissarca miliaris</u>	1 Number	-0.7793	-1.0057	6.2224	0.1371	0.0934	0.05
	2 Weight	-0.8327	-1.1102	3.7154	0.1142	0.0778	0.02
Pelecypoda	3 Number	-0.7933	-1.0887	6.3850	0.1464	0.0998	0.02
	4 Weight	-0.8325	-1.1043	3.7072	0.1132	0.0771	0.02
Gastropoda	5 Number	-0.7915	-0.8547	6.2321	0.0913	0.0622	0.05
	6 Weight	-0.7358	-0.6250	2.8395	0.0694	0.0473	0.10 ns.
Total Mollusca	7 Number	-0.7915	-0.8547	6.2321	0.0913	0.0622	0.02
	8 Weight	-0.8119	-0.8453	3.5872	0.0774	0.0527	0.02

where log. N or W/kg. wp = mlog. wp + log.b

ns = non-significant

Table VI : Regression analyses for the log./log. relationships for exponents (N) and weight (W). per kg. (dry weight) of plant (wp) against the original dry plant weight of least squares. Values of m and b, and correlation coefficients r are also presented in Table VI. In all equations excluding 6 (which is not significant at P = 0.05) there is a negative relationship between the number or weight of molluscs/unit plant weight and the original dry weight of the sample, i.e. smaller plants had a far higher population of molluscs/unit weight than larger plants. The October sample (wp = 25.3 g.) gave corrected figures for N and W/kg.wp of 305.5 g. and 165,810 individuals whereas February's sample (wp = 640.1g.) gave corresponding figures of 11.36 and 7,334 individuals. My observations on the structural morphology of young and old *D. anceps* plants indicated that the surface area/weight of plant fronds remains nearly constant with size and did not contribute to the massive density increase of molluscs on smaller plants. Since the relationships with increasing weight hold for all types of mollusc, and their differing requirements, the cause is difficult to define, but may be an increased affinity of the fauna for the smaller, more protected, under-storey plants within the weed bed. I could detect no density change of molluscs per unit plant weight within the limited depth range sampled.

3.3.3. Amphipoda associated with macroalgae.

(a) Species composition.

The Amphipoda are one of the most conspicuous invertebrate groups in antarctic waters and occur in high biomass in both the infaunal and epifaunal habitats (Hardy, 1972; Richardson,1972). Macroalgal communities normally contain species characteristic of (a) the fronds and (b) holdfast habitats (Moore, 1973). The latter

Sample date

Percentage weight	13.1.72	19.2.72	9.5.72	9.6.72	10.7.72	16.8.72	11.9.72	9.10.72	10.11.72	$\bar{x}$	S.D.±
AMPHIPODA	78.4	63.7	24.1	74.6	91.3	85.7	52.9	57.5	26.5	61.6	24.1
ISOPODA	20.1	1.7	5.8	15.7	8.7	6.4	7.1	3.6	12.4	9.1	6.0
PYCNOGONIDA	1.5	34.6	70.1	9.7	-	7.9	39.9	38.9	61.1	29.3	25.9
Total wt. (gm)	6.42	13.4	2.76	2.75	4.17	1.10	4.71	4.53	2.37		

Total wt. = 42.21 gm

Percentage number											
AMPHIPODA	94.1	86.1	46.8	99.0	95.0	96.3	82.4	96.5	91.5	87.5	16.2
ISOPODA	5.8	8.5	5.2	0.9	44.7	3.6	12.7	3.1	7.4	10.2	13.4
PYCNOGONIDA	-	5.4	1.3	0.1	-	0.1	4.8	0.4	1.2	1.5	2.1
Total no.	9,900	2,832	5,923	8,454	11,253	2,531	1,281	1,239	5,124		

Total no. = 48,537

Table VII: The percentage composition by weight and number of the major crustacean groups present on the macroalga Desmarestia anceps.

region, in D. anceps, supports species such as Parajassa georgiana, Jassa falcata and Metaleptamphopus pectinatus (this last species being associated with holdfast epiphytes,[Thurston, 1972]). Larger, more mobile species are present in the fronds where the families Calliopiidae and Eusiridae are most strongly represented. Species include Bovallia gigantea, Pontogeneia antarctica and Djerboa furcipes. Thurston (1972) described 33 species frequenting macroalgae in Borge Bay; however, this impressive publication does not always state the species of algae sampled for crustacea. For instance, I recorded Liouvillea oculata, which occurred in slightly deeper water (20 m.), only on Rhodophyceae and not on brown algae.

A list of 39 species from 16 families, recorded from the fronds of D. anceps, is given in Appendix VI. The importance, by weight and number, of the Amphipoda in relation to other crustacean groups is given in Table VII. The pycnogonids' weight per sample appeared to fluctuate considerably probably due to population aggregations for swarms of Nymphon australe were observed, at a number of localities, particularly during early summer. A similar situation was also noted when Agassiz trawling for pycnogonids over a similar bottom ground. The Amphipoda accounted for 62 percent by weight and 88 percent by number of the total crustacea population. The data presented in Tables VIII, IX and X are unfortunately based solely on individual plant samples and not mean values.

The data in Table VIII indicate the relative importance, by weight, of amphipods from samples taken during 1971 and 1972. Though 39 species have been recored from D. anceps fronds, only 11 form more than one percent of the total amphipod population. Four species, Oradarea bidentata, Pontogeneia antarctica, Prostebbingia gracilis and Bovallia gigantea make up 72.5 percent of the total amphipod population by weight. We have already seen in the previous

	Species No.	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Jan	Feb.	March	$\bar{x}$ >1%	s.d ±
Cheirimedon femoratus	19	0.0020	0.0016	0.02	0.0259	-	-	-	0.0020	0.0240	0.031	0.0019	-		
Lepidepecreum cingulatum	32	-	-	0.02	0.0026	-	0.034	0.025	0.025	-	-	0.002	-		
Tryphosa kergueleni	36	-	-	-	-	-	-	0.002	-	-	-	-	-		
Heterophoxus videns	33	-	-	0.05	-	-	-	-	-	-	-	0.01	0.007		
Gitanopsis squamosa	28	-	0.0051	0.07	0.0103	0.94	-	-	0.03	0.002	0.022	0.041	0.076		
Thaumatelson walkeri	5	0.02	0.04	0.03	0.049	0.69	0.54	0.62	0.04	0.02	-	0.56	-		
Prothaumatelson nasutum	31	-	-	0.04	0.0023	-	0.002	0.16	-	0.04	-	0.002	0.04		
Probolisca ovata	6	0.17	0.42	1.51	0.64	0.43	0.57	1.46	0.57	0.76	-	0.84	0.24		
Pariphimedia integricauda	12	0.91	0.60	0.03	1.06	-	1.41	0.73	0.12	0.54	-	0.04	-		
Gnathiphimedia fuchsi	18	0.01	0.0014	0.04	0.039	0.99	0.06	0.88	0.76	0.02	-	0.81	0.76		
Parhalimedon turqueti	27	-	0.0033	0.53	-	-	-	-	0.04	-	-	-	-		
Epimeria monodon	13	0.08	-	-	-	6.00	3.47	5.38	-	2.01	-	4.08	-	1.75	2.35
Oradarea bidentata	7	10.96	7.41	27.79	20.39	8.14	9.76	7.30	21.68	5.40	18.76	14.61	11.59	13.65	7.01
Oradarea ocellata (?)	21	0.48	1.20	-	0.91	9.38	4.21	8.42	6.46	1.43	-	-	0.34	2.74	3.48
Oradarea edentata	29	-	0.22	0.76	0.47	-	0.36	-	-	0.24	-	0.44	0.06		
Oradarea unidentata (?)	34	-	-	1.03	0.40	-	1.20	0.023	0.23	-	-	0.37	-		
Metaleptamphopus pectinatus	2	2.65	0.72	1.56	2.24	1.42	0.63	0.24	1.47	2.59	3.56	1.73	2.64	1.79	0.93
Atyloella magellanica	3	8.85	15.99	5.57	6.37	7.88	4.63	7.07	7.36	7.74	5.42	4.00	12.17	7.75	3.37
Schraderia gracilis	14	0.03	0.55	0.26	0.052	7.11	0.04	6.38	0.004	0.27	-	0.19	0.41		
Schraderia spp.	15	0.04	0.74	0.30	0.17	-	0.72	0.11	0.03	-	-	0.02	0.02		
Schraderia spp. *barnardi* (?)	26	-	0.0014	0.08	-	0.21	0.26	0.19	0.54	-	-	0.14	-		
Djerboa furcipes	10	1.08	0.77	1.13	3.22	1.41	0.71	1.27	1.22	1.65	2.42	1.71	3.42	1.67	0.90
Paramoera edouardi	16	0.02	0.25	0.82	0.16	-	0.05	-	0.25	0.04	-	-	-		
Paramoera spp. (?)	30	-	0.001	0.02	-	-	-	-	-	-	-	-	-		
Paramoera spp.	11	5.51	10.82	6.87	4.67	6.26	5.12	5.61	11.6	9.12	6.957	5.92	6.43		
Paramoera hurleyi	25	-	-	0.40	0.39	0.81	0.96	1.00	-	0.40	-	-	-		
Pontogeneia antarctica	4	18.4	17.22	29.66	24.54	4.59	7.59	8.99	31.49	27.49	33.62	27.59	22.46	7.07	2.24
Pontogeneia redfearni	9	1.73	0.99	0.73	0.20	-	-	-	2.46	0.69	0.67	0.89	1.04		
Prostebbingia gracilis	8	6.05	4.71	13.37	21.64	33.93	11.944	30.44	4.33	12.67	3.07	9.42	20.19	14.31	10.24
Eurymera monticulosa	22	0.46	0.95	0.46	-	-	0.95	-	0.57	-	0.07	0.76	0.43		
Pontogeniella brevicornis	23	0.22	-	-	-	-	0.002	-	0.27	-	-	0.25	-		
Bovallia gigantea	1	10.34	30.46	6.03	12.32	-	24.64	0.482	5.73	17.54	24.78	21.64	17.29	16.77	12.42
Paraceradocus miersi	24	-	0.0027	-	-	-	4.68	-	0.71	-	-	2.06	-		
Paradexamine fissicauda	17	1.66	5.36	-	0.64	0.94	1.63	0.85	2.04	0.43	0.62	0.79	0.84	1.32	1.40
Haplocheira barbimanus	20d	-	-	-	-	-	-	0.03	-	0.004	-	-	-		
Jassa falcata	20a	0.33	0.39	0.83	0.314	4.93	5.92	4.50	0.24	4.21	-	1.59	-	1.94	2.25
Parajassa georgiana	20b	-	-	-	-	-	0.76	-	-	1.12	-	-	-		
Caprellinoides mayeri	38	-	-	-	-	-	-	-	-	0.02	-	-	-		
Type spp.	35	-	0.18	-	-	0.63	-	4.92	-	-	-	-	-		
Type spp.	37	-	-	-	-	0.43	0.38	0.38	-	-	-	-	-		
Unidentified hatchlings		-	-	-	-	2.83	-	2.54	-	3.64	-	-	-		

Table VIII: The percentage species composition, by weight, of Amphipoda present on *Desmarestia anceps* fronds.

	No.	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	March	$\bar{x}$ >1%	s.d. ±
Cheirimedon Femoratus	19	0.01		0.02	0.76		-	-	0.34	0.07	0.07	0.02	-		
Lepidopecreum cingulatum	32	-		0.01	0.02		0.60	0.68	0.028	-	-	0.03	-		
Tryphosa kergueleni	36	-		-	-		-	1.60	-	-	-	-	-		
Heterophoxus videns	33	-		0.07	-		-	-	-	-	-	0.01	0.02		
Gitanopsis squamosa	28	-		1.52	0.89		-	-	0.04	0.02	3.14	1.36	1.02		
Thaumatelson walkeri	5	1.36		2.63	3.18		0.12	1.10	0.08	0.57	-	2.89	-	1.19	1.27
Prothaumatelson nasutum	31	-		2.76	3.27		0.37	0.68	-	0.71	-	0.72	0.70		
Proboliaca ovata	6	3.21		5.67	8.63		6.92	7.78	1.52	2.62	-	2.36	1.46	4.02	3.00
Pariphimedia integricauda	12	0.56		0.01	0.97		0.17	1.08	1.64	0.20	-	0.02	-		
Gnathiphimedia fuchsi	18	0.01		0.04	2.47		0.25	0.08	1.25	0.01	-	0.20	0.05		
Parhalimedon turqueti	27	-		1.74	-		-	-	0.02	-	-	-	-		
Epimeria monodon	13	0.04	d	-	-	d	0.12	0.17	2.42	0.70	-	1.26	-		
Oradarea bidentata	7	30.26	e	18.42	12.47	e	28 31	2.37	27.27	5.70	24.79	19.31	13.96	18.29	9.62
Oradarea ocellata (?)	21	1.31		-	2.06		0.02	0.42	1.45	0.98	-	-	0.45		
Oradarea edentata	29	-	t	1.32	1.04	t	0.70	-	-	0.15	-	0.51	0.08		
Oradarea unidentata (?)	34	-		3.76	1.72		0.12	0.08	1.36	-	-	0.20	-		
Metaleptamphopus pectinatus	2	8.49	n	8.46	6.76	n	6.32	0.17	22.88	5.49	9.46	14.41	8.49	9.09	6.01
Atyloella magellanica	3	6.37		3.74	3.47		2.15	0.42	0.51	3.27	3.67	1.02	8.65	3.33	2.60
Schraderia gracilis	14	0.05	u	1.10	1.64	u	0.84	1.27	2.96	0.51	-	1.34	0.72	1.04	0.86
Schaderia spp. (?)	15	0.76		0.15	0.83		0.08	0.08	0.04	-	-	0.47	0.03		
Schaderia spp. barnardi (?)	26	-	o	0.02	-	o	0.32	0.08	0.40	-	-	0.76	-		
Djerboa furcipes	10	0.76		0.53	1.02		5.61	0.08	1.55	0.70	3.47	3.45	1.53	1.87	1.75
Paramoera edouardi	16	1.43	c	1.16	2.06	c	0.02	-	0.02	0.04	-	-	-		
Paramoera spp. (?)	30	-		0.04	-		-	-	-	-	-	-	-		
Paramoera spp.	11	12.72		8.48	7.65		2.05	2.83	5.46	9.78	10.51	12.71	8.28	9.95	5.27
Paramoera hurleyi	25	-		1.04	3.42		0.05	0.68	-	0.70	-	-	-		
Pontogeneia antarctica	4	9.05		15.32	12.46		7.05	2.79	5.15	9.17	17.42	6.93	16.39	10.17	5.00
Pontogeneia redfearni	9	1.23		0.56	0.80		-	-	1.52	0.32	2.02	1.24	2.08	1.22	0.64
Prostebbingia gracilis	8	13.32		15.71	10.48		12.29	46.28	10.27	15.49	8.71	13.42	26.81	17.28	11.36
Eurymera monticulosa	22	0.04		0.07	-		0.04	-	0.14	-	0.05	0.04	0.31		
Pontogeniella brevicornis	23	0.20		-	-		0.02	-	0.98	-	-	0.02	-		
Bovallia gigantea	1	4.67	t	2.81	5.31	t	2.98	0.04	8.44	7.98	16.19	7.32	8.93	4.47	4.46
Paraceradocus miersi	24	-		-	-		0.01	-	1.04	-	-	0.70	-		
Paradexamine fissicauda	17	1.47	o	-	1.36	o	0.07	0.08	0.056	0.27	0.50	0.39	0.04		
Haplocheira barbimanus	20d	-		-	-		-	0.08	-	0.02	-	-	-		
Jassa falcata	20a	3.74	n	2.86	5.26	n	14.80	4.74	1.02	8.76	-	6.89	-	4.81	4.54
Parajassa georgiana	20b	-		-	-		2.56	-	-	4.24	-	-	-		
Caprellinoides mayeri	38	-		-	-		-	-	-	0.40	-	-	-		
Type spp.	35	-		-	-		-	2.96	-	-	-	-	-		
Type spp.	37	-		-	-		-	1.02	-	8.76	-	-	-		
Unidentified hatchlings		-		-	-		5.04	0.68	-	-	-	-	-		

TableIX : The percentage species composition, by number, of Amphipoda present on *Desmarestia anceps* fronds.

		1971				1972				1973	
		Feb		Aug		Feb		Aug		Feb	
Depth (m)	Sample	a	b	a	b	a	b	a	b	a	b
2	Frond Wt. (dry)	206		not sampled		251	264	380	297	263	247
	Amphipod Wt. /Frond Wt.	31.0				24.4	40.6	32.4	16.8	55.9	28.0
5	Frond Wt. (dry)	234	276	197	282	273		311	253	252	
	Amphipod Wt. /Frond Wt.	19.5	18.7	9.9	14.7	17.1		8.5	9.8	15.4	
12	Frond Wt. (dry)	not sampled		306		214	240	284		not sampled	
	Amphipod Wt. /Frond Wt.			8.2		5.7	15.7	29.4			

Table X Amphipod weight/plant frond weight at three different depths from Borge Bay. Two samples (a & b) were taken from each station.

section (3.3.2.) that besides weight and number, a measure of productivity is required to gain a realistic impression of the importance of any species to a community. Unfortunately lack of knowledge of population turnover for smaller species holds for the antarctic crustacea as well as the molluscs. The numerical status of amphipod species, as percentages of the total Amphipoda, is given in Table IX. It is apparent that 'giants' (de Broyer, in press) such as Bovallia gigantea are relatively infrequent whilst smaller species such as Probolisca ovata and Paramoera spp. (Type species II) can be extremely plentiful.

The most prominent amphipod species in the shallow antarctic sublittoral appears to vary geographically for Paramoera walkeri was the dominant eusirid recorded by Rakusa-Suszczewski and Klekowski (1973) at Alasheyev Bight. It is also conceivable, though not proved, that the dominant amphipod species in the community alters as food availability changes from one year to another.

Macroalgae samples obtained from sites on the Antarctic Peninsular or Scotia Arc are few but contrast markedly with those collected in Borge Bay. These differences can probably be attributed to differences in exposure. One sample (Back Bay, Stonnington Island Fig. 2), collected in March 1973, was made up totally of Pontogeneia spp.(?) - not subsequently identified due to the loss of the sample from the RRS 'Bransfield'. Two samples of D. anceps were obtained from the South Shetland Islands and their details are outlined below:

Sample I: Elephant Island (Cape Valentine) (18.2.71)

24ft., large boulders, dense D. anceps, gravel substrate, evidence of ice scour, steeply shelving bottom.

Sample II: Livingstone Island (cove east of Cape Shireffe) (19.2.71) 20ft., weed encrusting rock, mud substrate, D. anceps and D. ligulata.

Species	Sample % composition I	II
Probolisca ovata	10	-
Gnathiphimedia fuchsi	-	2
Metaleptamphopus pectinatus	-	5
Pontogeneia antarctica	24	8
Eurymera monticulosa	-	62
Bovallia gigantea		21
Paraceradocus miersi	48	-
Jassidae	19	2
n =	121	161

The Stonnington Island sample was taken from a very sheltered area. The South Shetland samples were from stations with frequent heavy oceanic swells. Despite the small size of the samples, the unusually large number of Paraceradocus miersi (adult specimens) was remarkable since they were rarely recorded from Signy Island.

(b) The relationship of the weight of Amphipoda to macroalgae.

As already demonstrated, the Mollusca showed an inverse relationship of faunal weight per unit plant weight to increasing plant weight and the precise reasons for such relationships can not be fully explained. From the analyses of amphipod weights a totally different picture emerged; amphipod weight per unit weight of plant increased linearly with increasing plant weight, even though there was great variation in the number of crustacean species per plant. Some of these differences can be attributed to variable sea conditions and swell differences with the time of year.

I observed that in shallow water during summer (after ice break-out through to March) amphipods often collected along the diatomaceous algal felt area of the shallow sublittoral and swarms of *Pontogeneia antarctica* were observed, within two metres of the surface, at Gourlay Cove (early spring) and also in Borge Bay throughout the summer.

Plotting amphipod dry weight against plant frond weight (dry) gave the following relationship:

$$y = 0.0117x + 6.84$$

(where y = dry weight amphipods (g.), x = dry weight fronds (g.), $n = 25$ and $r = 0.85$

(c). The correlation of crustacea to depth.

Plants with frond dry weights ranging from 200 - 300 g. were collected from three depths, 2, 5 and 12 m. during the summer (February) and winter (August) during the years 1971 to 1973 inclusive. Associated crustacea were not separated into species, though *P. antarctica* was isolated from the remainder.

Total dry weights of amphipods in relation to plant weight are given in Table X. Samples at 2m. depth could not always be collected during winter due to the low ceiling of ice (Fig. 6 [a]), and all samples taken at this depth were from well protected surfaces.

No significant variation, in number, could be established in the samples collected from the 5 and 12 m. depths, though a significant drop in the biomass of P. antarctica occurred during the winter months. P. antarctica along with other species such as Pontogeniella brevicornis (a species not common in the fronds, Table IX) and Prostebbingia gracilis increased on the algae during the summer. This rise is temporary, with the numbers present varying considerably with the weather, sea conditions and pack ice. As can be seen the increase in amphipod biomass at the 2 m. depth was not mirrored by decreases at the 5 and 12 m. stations. This feature was purely an expression of the fact that macroalgae at shallow depths are less extensive than the denser reservoirs of the plant habitat at 5 and 12 m. (Fig. 6 [a]) and an obvious concentration of the fauna takes place with this shortage of habitat.

3.4. Discussion.

3.4.1. The Mollusca:

(a) Epifaunal Biomass.

I have found it difficult to attribute the negative log. log. linear relationships (Table VI) of mollusc density against plant weight to any specific cause. It is apparent that density could vary throughout the year in addition to altering relative to the size of the 'host' plant. However, density fluctuations in relation to time should have been minimised by the non-synchronised reproductive strategies of the different mollusc species.

My observations indicate that the biomass and abundance of antarctic epifaunal molluscs per area are less than the comparable figures for the infauna where densities and biomass may be considerable. For example, Pelecypoda 636.2 g./m.^{2}; Gastropoda 38.4 g./m.^{2} (Hardy, 1972); Yoldia eightsii 1,545 g./m.^{2} (Rabarts, 1971) and Laternula elliptica up to 2,000 g./m.^{2} (Hardy, 1972). Further data for L. elliptica include 50 individuals/m.^{2} (Everson and White, 1969) whereas Gruzov et al (1967) estimated a maximum of 5kg./m.^{2} with a mean of 200 - 300 g./m.^{2} Similar order biomass values for epifaunal species were not recorded, in this study.

Corresponding figures for the mean and maximum recorded biomass of epiphytic molluscs were 47.9 g./m.^{2} and 25.8 g./m.^{2} or numerically 62,540 individuals/m.^{2} and 20,830/m.^{2} These values were derived from a mean weight of macroalgae of 178 g. wp/m.^{2} (980 g. wet weight) with a maximum of 374 g. wp/m.^{2} (2,050 g. wet weight).

The net dry tissue weight of molluscs per unit area was thus small with a maximum of 7.2 g./m.^{2} ($\bar{x}$ = 3.9 g./m.^{2}).

Derived from: $\frac{\text{dry tissue weight}}{\text{total dry weight}} \times 100 = 14.3\%$

Mills (in press) has drawn comparisons between the arctic and antarctic benthos and concludes that low infaunal biomass in antarctic waters is due to the larger biomass of epifauna. This hypothesis is not clearly demonstrated by the data in that publication, nor apparently are antarctic infaunal biomass values particularly low (Ushakov, 1962).

(b). The size of molluscs.

Nicol (1966) after examining 36 shallow water antarctic species of mollusc stated that the tendency towards reduced size was strongly characteristic of the antarctic pelecypod fauna. Undoubtedly some antarctic bivalves can achieve considerable sizes, for instance, the pectinid *Adamussium colbecki* whilst *Laternula elliptica* can reach wet weights of 300 g. However all these larger species are 'demersal' or infaunal. The maximum length of the four epifaunal pelecypods recorded from the fronds of *D. anceps* was less than one cm. Small size would be advantageous in (a) withstanding the swell and tidal turbulence in the epifaunal habitat and (b) remaining inconspicuous to predators. The sporadic availability of food (Horne et al, 1969; Appendix II) to these filter feeding bivales probably contributes, in part, to their small size.

3.4.2. The Amphipoda:

(a) Epifaunal Biomass.

Amphipod communities on macroalgae have been previously described. Such studies, for instance those of Moore (1973) and Scarratt (1961) concentrated on the semi-sessile crustacea of the holdfast communities. It is evident that there are few amphipods on *Laminaria* fronds presumably due to the degree of poor shelter and available food. Macroalgae providing dense shelter, such as *D. anceps* have a far larger population of mobile amphipods associated with their fronds.

Unlike the Mollusca the total amphipod weight increased with increasing plant weight. This contrasting situation is obviously related to the different requirements of these two major groups. Theoretically an increase in the weight of the plant should disproportionately increase the shelter provided (due to the overlap of fronds). Conversely the amount of light reaching the fronds and aiding the growth of epiphytic diatoms would be reduced, so diminishing, relatively, the available food supply to the amphipod population. These two factors (a) increasing shelter and (b) a possible decreasing food supply (per plant weight) may be controlling the amphipod population per plant as described by the equation in 3.3.2.

(b), The biomass in relation to depth.

The weights of amphipods from the 2m. depth were consistently greater than those from 5 and 12 m. This situation was evident during both winter and summer. In winter, plants at shallow depths receive amphipods (almost totally Pontogeneia antarctica) from the sea ice habitat. During spring and summer a more diverse amphipod population grazed the diatom felts in the immediate sublittoral. White and Robins (1972) commented that sheltered overhang communities have a relatively increased biomass more akin to the deeper water benthos. It is not believed that this feature contributed to the greater biomass of amphipods from the shallowest depth station sampled.

Chapter 4 Trophic Relationships in the Macroalgal Habitat:

4.1. Introduction:

I investigated feeding relationships in the macroalgal habitat to gain some knowledge of the inter-relationships between species. In particular it was important to establish to what extent the amphipods feature as 'key' species in the food web. To date only a limited number of autecological studies on antarctic benthic invertebrates have included descriptions of the feeding preferences of crustacea. The ispods have received some attention from White (1972) (Serolis ovata), and White (1975) and Dearborn (1967) (Glyptonotus antarcticus). The rare S. ovata is an active predator of a variety of small benthic crustacea and the larger G. antarcticus is both a predator and scavenger for Tait (1917) noted that G. antarcticus fed on amphipods, though Dearborn (1967) commented that live amphipods would probably be taken only rarely. Tait's results were presumably influenced by catching G. antarcticus with meat-baited traps. These also attract large numbers of amphipods, particularly the lysianassids.

Observations on the feeding of antarctic amphipods are restricted to the studies of Bone (1972), Rakusa-Suszczewski (1972) and Richardson and Whitaker (in press). Paramoera walkeri apparently consumes ice-associated microalgae whilst Bovallia gigantea eats approximately 70 percent animal matter and 30 percent plant material. The former two papers produced only qualitative descriptions of the types of food eaten. Previously the broadest study on feeding by invertebrates, in the antarctic benthos, was that of Arnaud (1970), but this research was directed solely towards the habit of necrophagous feeding.

In this study I investigated a variety of organisms including all the commoner fish species. Studies on the feeding of fish were carried out from April 1971 to March 1973. Previous antarctic literature (Andriashev, 1965; 1970; Holloway, 1969; Hureau, 1970) had described, in varying detail, the rôle of fish as major predators of the Amphipoda and initial investigations of the stomach contents of fish at Signy Island certainly emphasised this trophic relationship. Further analyses were made to determine which species of fish were exerting the greatest predation pressure against the weed-dwelling amphipods. The results of this investigation have been presented as a qualitative list of the diets of inshore fish. Since amphipods often exhibit strict habitat preferences (Bregazzi, 1972) both their occurrence and the species composition in stomach contents emphasises the presence of different feeding niches between fish and the localities in which they feed.

4.2. Materials and Methods:

Amphipoda were captured and treated in the same fashion as described in Chapter 3 (Section A) and Chapter 6 (Section B).

All fish specimens were obtained on the east coast of Signy Island, largely from Borge Bay. The methods of capture were:-

(I) Agassiz trawl (1 m.).
(II) A large diver-operated cylindrical collecting net.
(III) Collecting by hand whilst diving.
(IV) A plankton trawl net (0.33 dia.).
(V) Hook and line.

Individual species of fish tended to be captured by specific techniques. Trematomus newnesi was taken by trawl nets but could not be easily obtained by divers, whilst the slower benthic dwelling Notothenia gibberifrons and Harpagifer bispinis were easily captured underwater using small hand nets.

Specimens taken in trawl nets were isolated from the main catch as soon as possible to prevent any further predation on the other trawl inhabitants. Specimens were killed immediately on return to the laboratory and fixed in 10 percent neutralised formol saline after first exposing the body cavity. Gut analyses and examinations were conducted very soon after death ensuring that the crustacean component of the stomach contents was readily identifiable. Appendix VII summarises the times and places of capture of all the fish examined.

Copepods present in the stomachs could be divided into two discrete size classes:

(a) small - less than 2.0 mm.
or (b) larger than 2.5 mm.

The smaller species were commonly found amongst D. anceps fronds, the larger were only recovered from pelagic trawling. 100 specimens of the most commonly recorded small species in T. newnesi stomachs were measured using an ocular graticule and had a size range of 0.60 - 1.59 mm. ($\bar{x}$ = 1.21 mm., S.D. ± 0.62).

4.3. Results:

4.3.1. The feeding of benthic amphipods.

Gut analyses on 122 amphipods of 15 species have been carried out. The number of each species examined with a schematic illustration of the food types taken are given in Fig. 13. In addition, single individuals of the following species were investigated: Gitanopsis squamosa, Prostebbingia gracilis and Paraceradocus miersi. The feeding of benthic amphipods (of the species examined) has been categorised as follows:

(I) Selective herbivores: consuming diatom species. Macroalgal cells also constituted an important element of the diet. Species include Djerboa furcipes, Oradarea bidentata, Oradarea spp., Pontogeneia redfearni, Gitanopsis squamosa, Paraceradocus miersi and Metaleptamphopus pectinatus.

(II) Omnivores: A wide selection of food types were taken. The diet was predominantly herbivorous. Animal remains, detritus with mineral particles as well as macro and microalgae were however present in the animals examined. Species include: Probolisca ovata, Gnathiphimedia fuchsii, Prostebbingia gracilis and Paradexamine fissicauda. The latter species is the only amphipod examined which consumed the larger benthic diatoms such as Corethron, Gramatophora and Eucampia. P. fissicauda also grazes substantially on Ectocarpus species.

(III) Omnivore - Predator: Substantial quantities of animal matter were present in the gut contents with smaller amphipod species and copepods forming the principal component of the diet. It was found difficult to determine whether diatom species identified in these predators had been ingested by the animals themselves or by their prey species. Species include: Epimeria monodon, Bovallia gigantea, Atyloella magellanica and Cheirimedon femoratus.

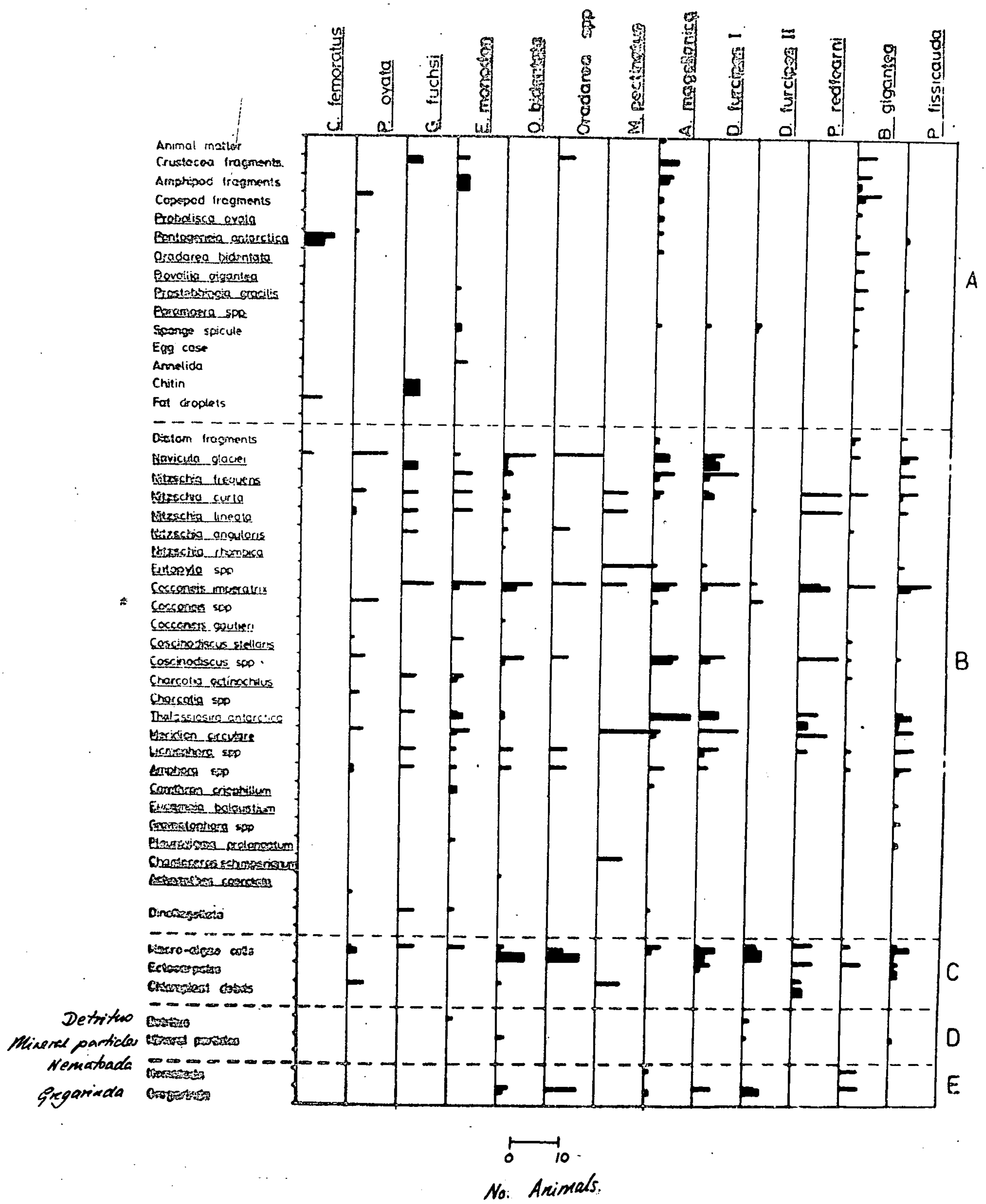

Fig. 13 : The dietary composition of 12 antarctic amphipod species.

The feeding of the amphipod Pontogeneia antarctica has not been presented in the results of this chapter. The diet of this crustacean was studied in greater depth and the results are shown, instead, in Chapter 6 (Section B).

4.3.2. The feeding of molluscs.

Gut analyses on Lissarca miliaris were not conducted, but pelagic or epiphytic diatoms were presumed to be the principal food. Shabica (1974) made histological examinations of Kidderia subquadtratum, a similar sized antarctic byssate bivalve, and in subsequent examinations of his photomicrographs I have identified the common diatom genera Nitzschia, Coscinodiscus and Cocconeis.

4.3.3. The feeding of annelids.

A limited number of gut analyses on the polychaete Neanthes kerguelensis indicated that the worm was feeding exclusively on Desmarestia anceps.

4.3.4. The feeding of fish.

The stomach contents of 225 fish of 7 species have been examined to assess the composition of the diet (Fig. 14). The amphipod fraction of the food has, where possible, been identified to species level and the analyses of the occurrence of amphipods in the stomachs of the four fish species most commonly captured are shown in Table XI.

Species examined:

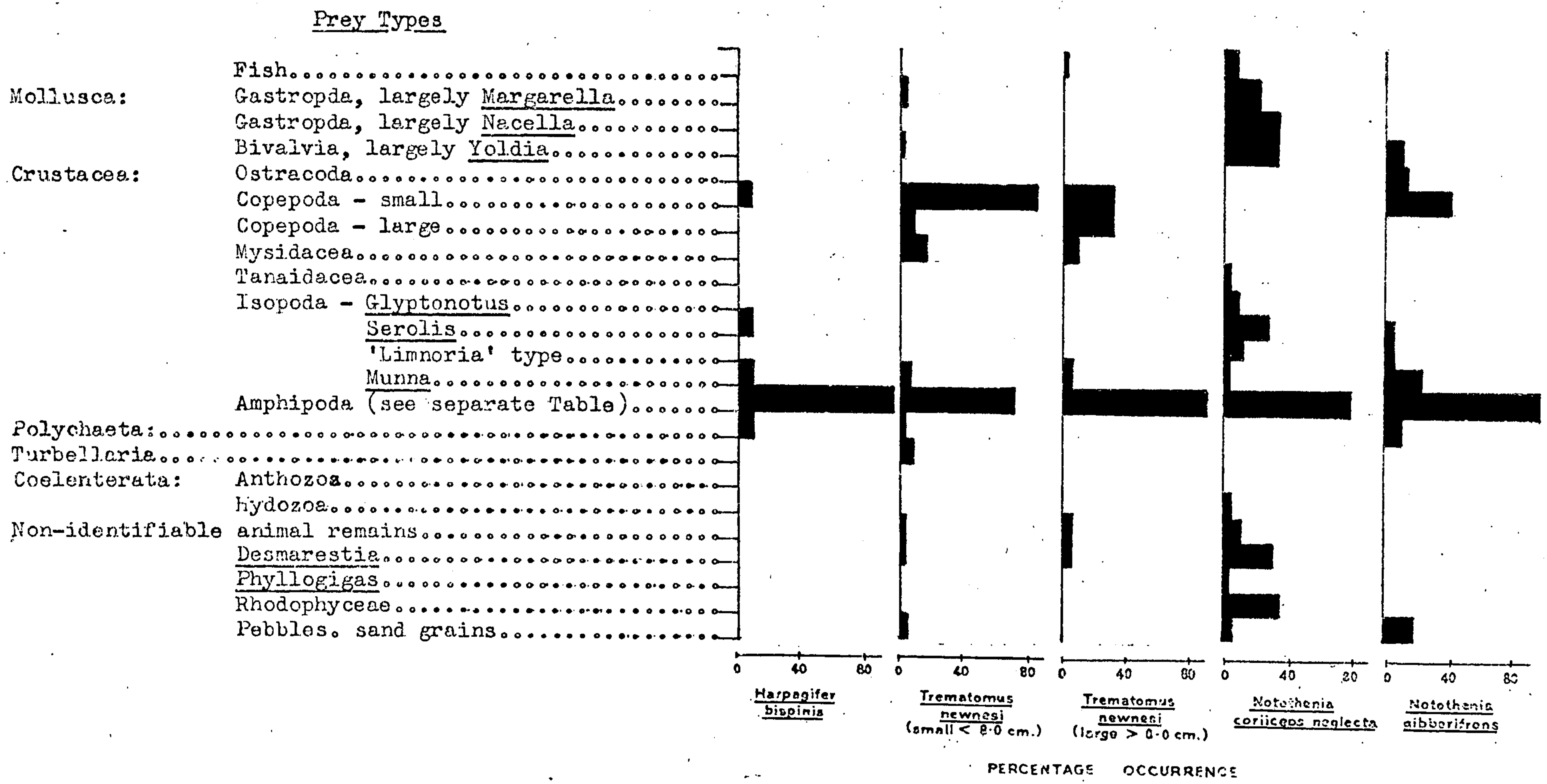

Fig. 14: The percentage composition of prey types in four species of Antarctic fish.

Harpagifer bispinis (42 specimens). Most individuals of this species were obtained from a gravel bottom with associated Rhodophyceae. Standard length ranged from 3.0 - 7.9 cm. ($\bar{x}$ = 4.8 cm., S.D. ± 1.1.). The number of major food types encountered in the diet was the lowest of the four species analysed with Amphipoda occurring in 95 percent of specimens. The only other groups recorded were small copepods, isopods of the genera Serolis and Munna and unidentified polychaetes. 12 amphipod species were recorded from stomach contents of which Pontogeniella brevicornis was the predominant species predated. Thurston (1972) mentions that this amphipod was associated with sandy substrates where algae and boulders were also present. The copepod element of the diet of this species appeared, by comparison, to be small as only one fish contained a small number of this group.

Trematomus newnesi (116 specimens). Individuals of this fish were obtained in various months of the year and Appendix VII outlines the dates of capture. All fish were caught in trawl nets; the four smallest specimens (1.6 - 1.7 cm.) were taken with a plankton net on the 8th March, 1973 whilst the largest individual (15.2 cm.) was caught on the 14th December, 1972 in a benthic trawl collection. The length frequency distribution for T. newnesi was polymodal. The majority (66) were collected during December 1972 and had a trimodal length frequency distribution with size categories estimated using normal probability paper (I) range 5.0 - 6.4 cm., $\bar{x}$ = 5.6 cm., S.D. ± 0.3. (II) range 8.6 - 9.8 cm., $\bar{x}$ = 9.3 cm., S.D. ± 0.4 and (III) 15.2 cm. These three size groups within the sample may be year classes.

To identify the diet of the different sized T. newnesi,

Table XI and Fig. 14 were drawn up after dividing the fish into two size categories; (a) smaller than 8.0 cm. standard length and (b) 8.0 cm. and greater.

A visual estimate of the percentage fullness was made on 65 fishes' stomachs. Fish showed variable amounts of prey in the stomach with 17 percent of the small and 25 percent of the large fish having a more than 90 percent full stomach, whilst 21 percent of the small and 25 percent of the large fish had a 10 percent or less full stomach.

One medium sized fish (8.6 cm.) contained the following:-

Amphipoda	Djerboa furcipes	1
	Oradarea bidentata	2
	Prostebbingia gracilis	23
	Pontogeneia antarctica	1
Copepoda	large	2
	small	3
Macroalgae	D. anceps (fragments)	2

A similar full small specimen (3.4 cm.) had a selection of the following prey types:-

Amphipoda	Probolisca ovata	2
	Paraphimedia integricauda	1
	Paramoera spp. (?)	3
Polychaeta	Specimen (2.6 mm. long)	1
Ostracoda	Specimen (2.2 mm. long)	1
Copepoda	small	20

There are demonstrable differences between the diets of

Table XI : The percentage occurrence of amphipod species in the stomachs contents of four antarctic fish. (Box figures represent a percentage frequency > 19.)

	Harpagifer bispinis	Trematomus newnesi		Notothenia coriiceps neglecta	Notothenia gibberifrons
		small (< 8.0)	large (> 8.0)		
LYSIANASSIDAE					
Cheirimedon femoratus. (Pfeffer.)	4	5	-	$\boxed{60}$	-
Lepidepecreum cingulatum. Barnard.	-	-	-	$\boxed{20}$	-
Tryphosella kergueleni. (Miers.)	-	-	-	$\boxed{50}$	-
PHOXOCEPHALIDAE					
Parharpinia rotundifrons. Barnard.	8	2	-	$\boxed{20}$	-
AMPHILOCHIDAE					
Gitanopsis squamosa. (Thompson.)	-	2	5	-	-
THAUMATELSONIDAE					
Thaumatelson walkeri. Chilton.	-	1	-	-	-
STENOTHOIDAE					
Probolisca ovata. (Stebbing.)	4	6	5	-	$\boxed{35}$
ACANTHONOTOZOMATIDAE					
Pariphimedia integricaudata. Chevreux.	-	4	-	5	-
OEDICEROTIDAE					
Methalimedon nordenskjoldi. Schellenberg.	-	-	-	1	-
Oediceroides lahilli. Chevreux.	-	-	-	-	5
CALLIOPIIDAE					
Oradarea bidentata. Barnard.	-	$\boxed{25}$	$\boxed{45}$	5	15
Oradarea ocellata. Thurston.	-	3	-	-	10
Oradarea unidentata. Thurston.	16	1	-	-	-
Metaleptamphopus pectinatus. Chevreux.	-	2	-	-	-
EUSIRIDAE					
Atyloella magellanica. (Stebbing.)	4	2	-	-	5
Djerboa furcipes. Chevreux.	-	3	$\boxed{20}$	-	-
Schraderia gracilis. Pfeffer.	1	-	5	-	5
Schraderia spp.	-	-	5	-	5
Pontogeneia antarctica. Chevreux.	8	6	15	$\boxed{20}$	5
Prostebbingia gracilis. (Chevreux.)	8	$\boxed{21}$	$\boxed{40}$	-	$\boxed{45}$
Eurymera monticulosa. Pfeffer.	-	-	-	5	-
Pontogeniella brevicornis. (Chevreux.)	$\boxed{73}$	17	5	$\boxed{55}$	$\boxed{40}$
Bovallia gigantea. (Chevreux.)	12	3	15	$\boxed{35}$	-
Paramoera spp. (?).	4	17	15	-	10
GAMMARIDAE					
Paraceradocus miersi. (Pfeffer.)	-	-	-	5	5
DEXAMINIDAE					
Paradexamine fissicauda. Chevreux.	4	8	15	10	-
Gammaridean spp. not identified.	$\boxed{38}$	$\boxed{26}$	15	-	$\boxed{25}$
Hyperidean spp. not identified.	-	2	-	-	-
No. of species in diet.	13	20	13	12	13

small and large fish. Of the major food types shown in Fig. 14 small specimens were found to contain 12 categories, large only 8 (6 categories were common to both fish size groups). Similarly the diversity of amphipod species, as prey, diminishes with increasing size; individuals of large fish, feeding on 13 species as opposed to 21 in small, with 11 species being common to both. The primary food of both size classes is Amphipoda of the Calliopiidae and Eusiridae families.

A greater percentage of large fish feed on O. bidentata, and D. furcipes and whilst the percentage occurrence of the large amphipod Bovallia gigantea appeared roughly the same in both length categories, the individual length of this amphipod in small fishes' stomachs was always less than 1.2 cm. The proportion of small fishes' stomachs containing the smaller copepods (84 percent) was far higher than for any other group. The larger pelagic copepods were not taken so readily, and were found in only 13 percent of the stomachs. However the percentage occurrence of both small and large copepods in the large T. newnesi stomachs was 30 percent. Mysidacea were only found in larger T. newnesi whilst small fish occasionally contained small turbellarians. The majority of food types taken are motile organisms. Benthic detritus and sessile organisms have little importance in the diet.

Notothenia coriiceps neglecta (34 specimens). All individuals were caught by hook and line over a boulder bottom where D. anceps was present. Though the standard lengths of most individuals were not recorded they lay within the 30 - 45 cm. range. The percentage fullness of nearly all guts was very high, over 70 percent. The diversity of food types consumed (Fig. 14) was higher than any other species with appreciable numbers of fish with algae in their stomachs (Rhodophyceae 35 percent, Desmarestia spp. 30 percent). Whether these fish browse plant material deliberately or inadvertently consume portions of plant whilst feeding on animals amongst the algal beds is not clear. Anthozoa and hydroids certainly were actively fed on and N.c. neglecta is large enough to devour some of the bigger individuals of the isopods Glyponotus antarcticus and Serolis polita, and these feature in stomach contents. In contrast to the other species no Copepoda were found in the gut contents. Again differing from other fish - the percentage occurrence of molluscs was high with the limpet Nacella concinna found in 35 percent, the bivalve Yoldia eightsii occurring in 35 percent and gastropods, mainly Margarella antarctica, in 25 percent of the stomachs. Some remains of unidentified fish were apparent in a small number of stomachs. Amphipods were again the predominant food type with 12 species being found. N.c. neglecta was obviously capable of handling larger food types than other species and this becomes apparent in its choice of amphipods, none of the species preyed on were in the small category. B. gigantea featured commonly, as did P. antarctica and Parharpinia rotundifrons. The great bulk of the food is made up of the burrowing lysianassid species, Cheirimedon femoratus, Tryphosella kergueleni and Lepidepecreum cingulatum with P. brevicornis also being readily eaten.

Notothenia gibberifrons (27 specimens). All fish of this species proved to be small, the largest specimen measuring 7.3 cm. ($\bar{x}$ = 5.1

cm., S.D. ± 0.88). The ventral position of the mouth of N. gibberifrons suggests that it is a bottom feeding species and the presence of infaunal representatives of bivalves, ostracods, polychaetes and also pebbles and sand grains reinforces this hypothesis. The fish also takes small numbers of benthic isopods - mainly of the genus Munna. Copepods do not represent a major component of the diet.

The most commonly occurring amphipod constituent of the stomach contents was the species P. brevicornis, P. gracilis, and P. ovata.

Notothenia larseni (4 specimens). The mean length was 5.6 cm. (range 5.0 - 6.4 cm.). Amphipod species represented in the stomach contents were: P.ovata, Gitanopsis squamosa, O. bidentata, P. gracilis, P. brevicornis and Paramoera spp (?). Small copepods were also present in three individuals.

Notothania nudifrons (1 specimen), This single small specimen contained P. antarctica, P. gracilis and over 100 small copepods.

Notothenia rossii (1 specimen). The gut contents consisted solely of unidentified amphipod fragments.

4.4. Discussion:

Correlation between feeding habits and limb morphology is apparent in antarctic amphipods. Herbivores such as Djerboa furcipes and Oradarea bidentata have long slender gnathopods, often heavily setose, with insignificant dactyls. Predator omnivores, for example

Pontogeneia antarctica and *Bovallia gigantea*, are conversely equippped with heavy substantial gnathopods and enlarged dactyls.

Heavy growths of large benthic diatoms (*Biddulphia* spp.) occur as epiphytes on macroalgae and substrates during mid to late summer. Attempts at identifying any invertebrate species which were capable of utilising this considerable primary production were unsuccessful. Though *Paradexamine fissicauda* consumed small quantities of these larger benthic diatoms the herbivorous elememt of the amphipods' diets were primarily obtained from the plankton, either through direct filtration or consumed after the 'fall out' of diatoms. A thick covering of the epibenthos by diatoms (principally *Meridion circulare*, *Thalassiosira antarctica* and *Navicula glaciei*) was visible during early summer. Growths of *Cocconeis imperatrix*, *Navicula glaciei* and *Nitzschia curta* and to a lesser extent *Thalassiosira antarctica* appear able to sustain crustacean populations during the reduced primary production period of winter. One feature common to most species investigated was the high degree of 'opportunistic feeding' which could take place if more normal food supplies were not available. The possession of catholic feeding preferences is advantageous to any species subjected to fluctuating food supplies, as found in the inshore antarctic benthos.

Many species of antarctic fish do not possess swim bladders (Andriashev, 1965) and the indications are that fish feeding in antarctic coastal waters is primarily of a benthic/demersal nature, though workers studying the diets of fish around South Georgia stress the dependence of many species on pelagic feeding areas. A comprehensive survey of the food of 10 fish species occurring at South Georgia has been conducted by the Russians Permitin and Tarverdieva (1972). Many workers have stressed the importance of amphipod crustaceans in the diet of polar fish species (Andriashev, 1970; Holloway, 1969; Bellan-Santini, 1972; Rakusa-Suszczewski, 1972). The diet of the genus *Trematomus* has been investigated by a number of authors: Andriashev (1968; 1970) mentions that the cryopelagic fish *Trematomus borchgrevinki* and *T. newnesi* feed on krill (euphausids) and other Crustacea, whilst the cryophilic adaptation of these species enables young fish to avoid predation by hiding amongst the hollows and cavities within the sea ice. The amphipod *Paramoera walkeri* has been observed (Rakusa-Suszczewski, 1972) being preyed on by these two species of fish at Alasheyev Bight during the antarctic winter. At McMurdo Sound, Wohlschlag (1964) observed that *Trematomus bernachii*, *Trematomus hansoni* and *Trematomus centronotus* along with the amphipod *Orchomenella* spp. were attracted to traps in deeper water. The former two above were studied by Bellan-Santini (1972) who recorded five amphipod species from *T. hansoni* and nine from *T. bernachii*. *Oradarea walkeri* and *C. femoratus* were the commonest prey in *T. hansoni*, *O. walkeri* and *Orchomene nodimanus* in *T. bernachii*. By comparison, *T. newnesi* at the South Orkney Islands preyed on a total of 22 amphipod species. From the preliminary study done by Rakusa-Suszczewski and Piasek (1973) with *T. newnesi* and *T. bernachii* on the protein levels in their pyloric processes and the types of food taken (though identification was limited to very broad food types), it appeared that this genus avoided inter-specific competition by eating different prey. *T. newnesi* has higher pyloric protein levels and feeds on such food sources as copepods, amphipods (*P. walkeri*) hyperiid amphipods and Euphausiidae during winter whilst *Euphausia superba* comprises the total diet of summer feeding *T. newnesi*.

T. bernachii by comparison is a benthic feeder taking a winter diet of polychaetes, amphipods, gastropds, isopods and ostracods and including fish eggs, algae and on occasions euphausids during the summer. My observations at Signy Island parallel those of Andriashev (1965, 1968, 1970)and Horner(1976), indicating the importance of the major food chain:

diatoms ——→ amphipods ——→ fish

I have synthesised all my observations on benthic feeding relationships into Fig. 15 where the major trophic relationships are emphasised.

(Predators of antarctic amphipods also include the large nemertine *Lineus corrugatus*, under laboratory conditions Kellet,(pers. comm.) and bird species particularly the Cape pigeon (*Daption capensis*) which actively feeds on *Pontogeniella* spp.)

The large number of copepods, some mysids and certain types of amphipod indicates that *T. newnesi* is semi-pelagic in its feeding during the whole year with the tendency to feed within the water body increasing with greater body size. Pelagic feeding by this species, at Signy, was not the principal method during the summer, in contrast to the observations of Rakusa-Suszczewski and Piasek(1973) at Alasheyev Bight.

Little work has been attempted on the diet of *Harpagifer bispinis* though this fish is a very common component of the inshore benthos. A paper by Meier (1971) demonstrated a 100 percent frequency of amphipods, and nothing else, in gut contents. No further division

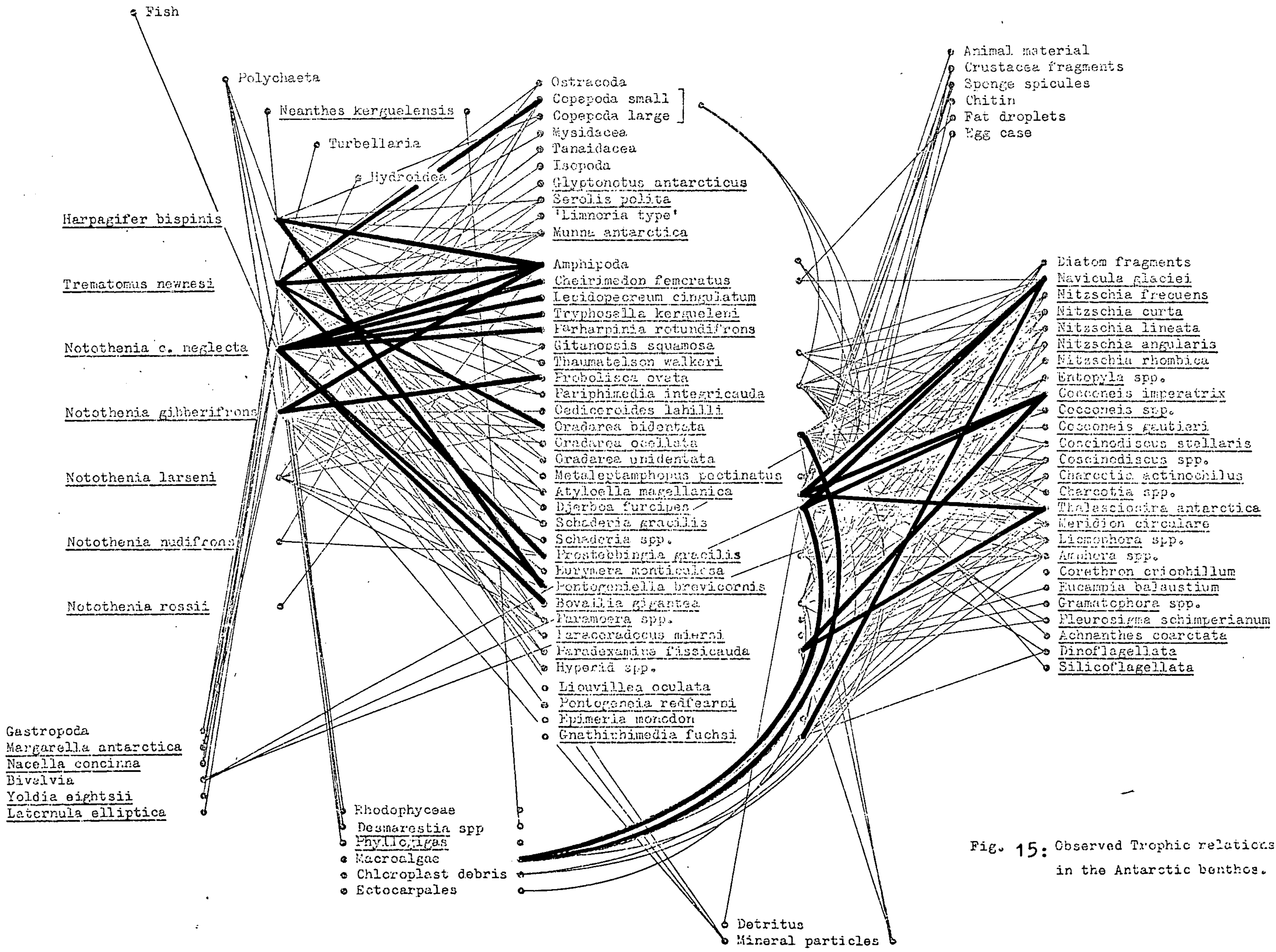

Fig. 15: Observed Trophic relationships in the Antarctic benthos.

of the food was attempted. Certainly my study shows that the diversity of food types in the diet of Harpagifer was low with the infaunal amphipod P. brevicornis constituting the major food.

N. gibberifrons and N.c.neglecta are also exclusively benthic feeders though their different sizes and methods of feeding separates their possible prey species. Bellan-Santini (1972) when looking at N. c. neglecta noted 21 species of amphipod taken as food with O. walkeri, Schraderia gracilis and C. femoratus being most commonly eaten. Most of the fish specimens investigated by Bellan-Santini (1972) were captured by drag net, grab or trap and the latter may well have influenced the percentage occurrence of prey in the fish stomachs. N.c. neglecta is readily attracted to meat-baited traps (Twelves, pers. comm.) along with great numbers of various lysianassids. Bone (1972) mentions B. gigantea being eaten by N.c. neglecta though the percentage of fish containing this large amphipod were far lower (12 percent) than in samples collected by Everson, and subsequently analysed by Bone (1972) (57 percent). Lack of Laternula elliptica, the large bivalves, in the guts is unusual since its biomass is high (Hardy, 1972) and Everson (pers. comm.) noted N. c. neglecta feeding on the fleshy siphons of this mollusc. I have attributed the lack of L. elliptica remains, in the fish investigated, to their probable absence from the fish sampling area. Indications are that the main food of N. c. neglecta at Signy Island is lysianassid amphipods. During the day N. c. neglecta seeks shelter within Desmarestia beds and feeding and increased activity occurs during the evening and darkness when Bregazzi (1973) observed the peak of activity in infaunal amphipods.

The main implications of the results for this small sample of *N. gibberifrons* is that the fish is a benthic feeder obtaining its prey within, or in the near vicinity of algal beds, for no movement away from the weed beds to feed can be implied from stomach analyses of this fish. It must be noted that all *N. gibberifrons* dealt with in this study were small individuals of a fish species that in deeper waters achieves far greater sizes, comparable to *N. c. neglecta*.

Although the sample sizes of the fish species investigated were small, obvious differences in diet and methods of feeding were apparent. *T. newnesi* carried out vertical movements within the water body in the search for food, whilst the indications are that *N. c. neglecta* seeks shelter and food in different benthic habitats. *H. bispinis* and *N. gibberifrons* (of the size range encountered) do not move appreciable distances away from the weed beds. Fish, feeding further from the shore, or in deeper waters, may consume both plankton and benthos but the antarctic fish examined from shallow coastal water at Signy Island relied heavily on benthic amphipods, their main food supply, with pelagic feeding reduced or absent.

Section B:

Chapter 5. The Ecology of Benthic Invertebrates:

(I) The Antarctic Amphipod Pontogeneia antarctica.

5.1. Introduction:

Although the taxonomy of antarctic amphipods has received a considerable amount of interest (Pfeffer, 1888; Chilton, 1912; Chevreux, 1912;1913; Schellenberg, 1931; Barnard, 1932; and Thurston, 1972; 1974) more detailed knowledge of the biology of these crustaceans is based on few studies. For instance, their ecology, (Thurston, 1968; 1970; Bone, 1972; Bregazzi, 1973) or physiology (Armitage, 1962; Klekowski et al., 1973, and Opalinski, 1974).

At the conception of this research a comparison of the total energy budgets of two amphipods with contrasting life styles and diets had been planned. Investigations would have concentrated on the energy expenditure, throughout the life histories, of the carnivore/omnivore Pontogeneia antarctica, Chevreux 1906 and the herbivorous Djerboa furcipes Chevreux 1906. These initial proposals had to be modified because of the difficulties of obtaining adequate numbers of D. furcipes. In addition, nitrogen excretion experiments had to be abandoned after the breakage of all the relevant experimental equipment. As an alternative specific aspects of the biology of two contrasting antarctic invertebrates have been studied and are presented in this second section. The results of this work have identified some similarities in the life strategies of these two species and related such features to the effects of the polar environment. The animals selected were the amphipod Pontogeneia antarctica and the bivalve Lissarca miliaris(Phillipi, 1845). I have already shown that these two species are particularly numerous in the habitat of the D. anceps fronds (Chapter, 3).

P. antarctica (Fig. 16 [a] and [b]) is an important component of the crustacean fauna in water shallower than 20 m. (Tierra del Fuego, 55 m.). Although the amphipod was normally found associated with macroalgae, on a rocky substrate, it exhibited a major migration each year with the winter period spent in association with the sea ice community, the summer within the benthic macroalgae.

Various features of P. antarctica, including distribution and growth, are outlined in this chapter. Subsequent chapters concentrate,in more detail, on (a) feeding , (b) embryology and (c) metabolism, i.e. respiration. These features have been related to those of other antarctic organisms for the topics of embryology and respiration (particularly the phenomenon of metabolic 'cold adaptation') have already received some attention from polar biologists. Studies on feeding were necessary to both quantify ingestion and explain the migratory behaviour of this crustacean.

5.2. Materials and Methods:

5.2.1. Body measurements.

All measurements of amphipods were made using an ocular micrometer at x12 to x50 magnifications. The standard measurement used was the length of the animal from the anterior of the rostrum to the anterior of the telson. Initially the relationships of a

(a)

(b)

Fig. 16 : The amphipod Pontogeneia antarctica (adult females) (a) ovigerous ♀ on sea ice, (b) ♀on D. anceps.

variety of body measurements (mm.) to dry weight were compared. The correlation of total length (as defined above) to weight proved closer than measurements of selected body plates to weight (i.e. length of segment 2 of peraeopod 3 or the length of segment 1 of the anterior uropod). These relationships are outlined in Appendix VIII.

Dry weights were obtained after drying at 80°C. to constant weight.

5.2.2. Field Collection:

Amphipods from the benthos were collected either by the method described in 3.2. or alternatively samples were taken with a 1 m. Agassiz trawl towed behind a boat.

A variety of methods of collecting amphipods under ice were attempted. Disturbance from divers' movements and their expelled air bubbles proved major problems though a 'remote' system working with a surface 'whale' pump also had little success. Consequently samples of ice-associated amphipods were captured either with a small fine meshed (0.2 mm.) hand net or a wide-mouthed (5.5. cm.) syringe.

The diurnal activity of amphipods was followed using both vertical net hauls and underwater funnel traps. These were constructed from 4 lb. 'Kilner' jars fitted with plastic cone shaped mouths. Jars were positioned horizontally in the water column at 0.8 m., 1.8 m. and 2.8 m. depths. The ice hole, for access, above the funnel traps was covered with heavy gauge black plastic sheeting. This prevented amphipods from being unnaturally attracted to the area by increased light penetration. In addition a tent was erected over the ice hole to improve working conditions.

5.2.3. Growth measurements.

To provide data comparable with those from other antarctic Crustacea (Bone, 1972; Bregazzi, 1972; and Thurston, 1968) three methods of assessing growth were attempted.

I. Measurement of monthly random samples of the amphipod population.

II. In addition, experiments were set up using post-hatchling *P. antarctica*. Batches of these amphipods were subjected to three contrasting habitats (and food supplies), (a) the sea water laboratory (b) the ice-foot ledge and (c) the benthic environment at 5 m. depth. Five amphipods, of known length, (ca. 2.0 mm.) were placed in 125 ml. polythene bottles. Each experiment consisted of 50 such bottles (i.e. 750 amphipods in total). Samples (two bottles) were removed from each habitat, at regular intervals, and the crustacea~~s~~ killed, measured and weighed (dry). Details of the foods available in each habitat are given in the following chapter.

III. Experiments to follow the growth and moult intervals of individual animals failed.

5.3. Results.

5.3.1. The winter distribution and activity of P. antarctica.

P. antarctica was observed on the under surfaces of the sea ice shortly sfter its formation during April or May (4.5.71/7.5.72). Amphipods particularly congregated alongside tide cracks, ice holes and at the ice foot. Barnard (1959) emphasised the unsuitability of sea ice as a substrate for crustacea, identifying as one of the reasons the possible increased exposure to predation. My own observations indicate the exact opposite, with utilisation of the sea ice habitat a necessary feature in the existence of some species, including P. antarctica. Certainly both Rakusa-Suszczewski (1972) and Richardson (1975) have recorded the pelagic Trematomus newnesi in the immediate vicinity of the sea ice undersurfaces where these fish were presumably feeding on cryopelagic crustacea, however P. antarctica has adopted a protective behaviour to reduce any such predation pressure. The amphipod remained within 'ice burrows' during daylight and emerged only at night time.

The formation of these 'ice burrows' was not specifically investigated but could have been achieved by a variety of methods, For instance:

(a) 'Black body' conductivity of the amphipod 'melting' its way into the ice.

(b) Differential thawing of the sea ice in the immediate vicinity of the amphipod caused by the regular beating of its pleopods.

(c) Mechanical excavation of ice burrows by amphipods using their peraeopods and mouthparts.

(Showing this close affinity for the ice substrate, P. antarctica could prove to be an ideal subject for further investigations of poikilothermic super-cooling tolerance , a subject briefly investigated by Rakusa-Suszczewski and McWhinnie, 1976).

Fig. 17 schematically illustrates the distribution of amphipods on a cross section of the ice foot. During daylight post-

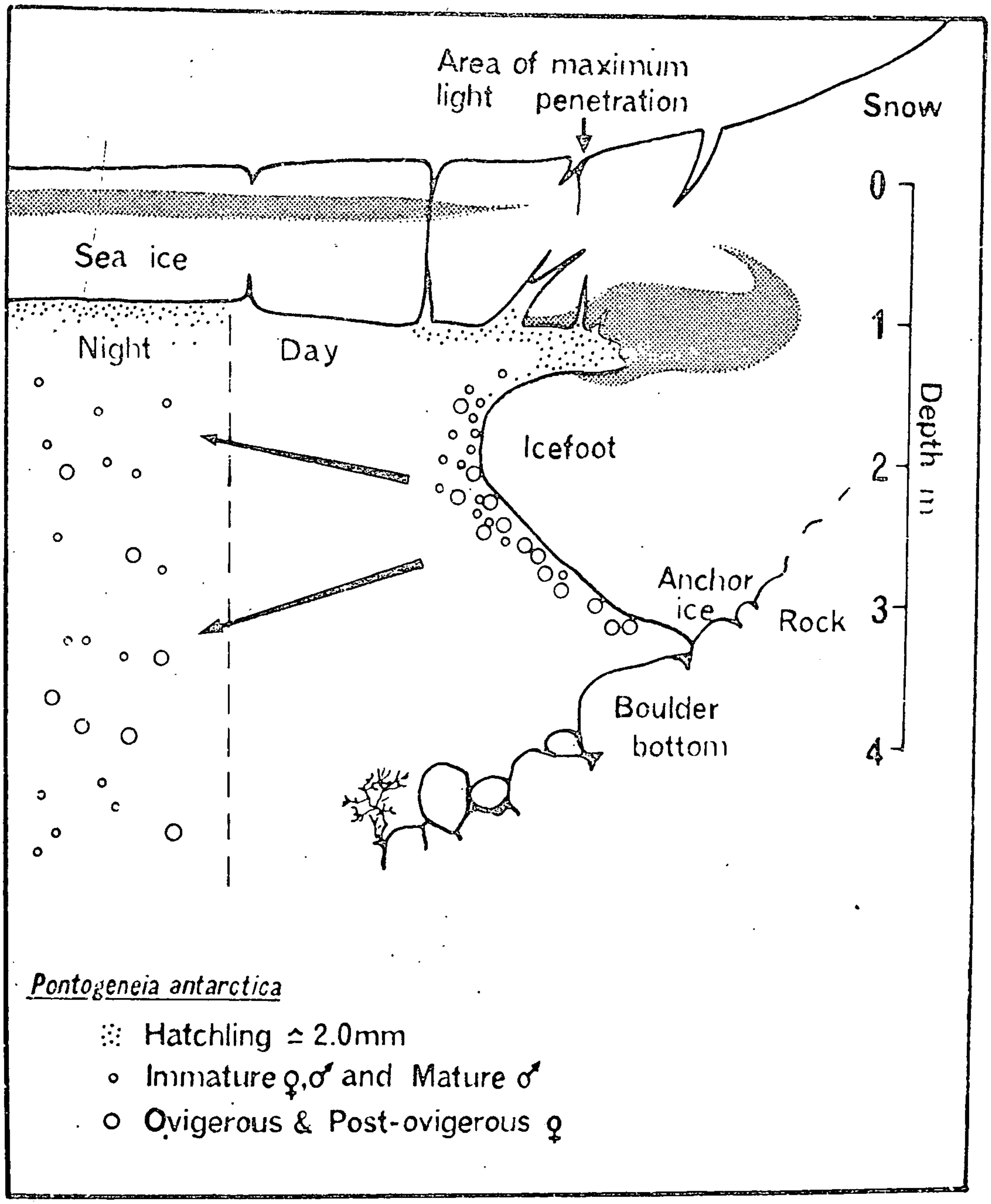

Fig. 17 : Diagrammatic illustration of the ice foot habitat.

hatchlings densely congregated immediately under the ice-foot tide cracks, in the area of maximum light penetration (and diatom concentration). Immature males and females were present lower down the ice wall whilst ovigerous or post-ovigerous females actively sought shelter nearer the base of the ice foot. These responses , which segregatedage classes, were phototropic. Simple experiments, in the laboratory, indicated a postive attraction to light sources, artificial as well as natural, by post-hatchlings. Adult females produced negative responses. The selective advantages of such behaviour include an optimum food supply for the newly released post-hatchlings and a considerable reduction in cannibalism. I have summarised this depth distribution of *P. antarctica*, on the ice foot, in Table XII. These observations on the amphipod distribution were made throughout the winter and the situation I have described altered only immediately prior to the ice break out when substantial quantities of fresh water in-flow reduced the salinity of the top 3 - 4 foot of the water column. This forced the amphipods to deeper water.

The difficulty experienced in sampling the under surfaces of the sea ice has created a lack of quantitative information on the build up, peaking and decline of ice associated amphipods though crude estimates of *P. antarctica* numbers and biomass are given in Table XIII. Nets sweeps in the immediate vicinity of the ice-foot ledge (the area of maximum light penetration, Fig. 17) indicated a mean amphipod density of 12,700 /m.^{3} (S.D. ± 4,000) with a biomass greater than 8 g.(dry weight /m.^{3}). These densities are high but comparable to the 1,000 *Gammarus lacustris lacustris*/m.^{2} reported

Depth (m.)	Numbers	S.D. ±	Dry Wt. (g).	S.D. ±
0.7	7,892	2,406	0.111	0.037
1.0	2,419	1,129	1.759	0.568
3.0	891	870	1.185	0.980

Table XII : The depth distribution (by number and weight) of *P. antarctica* on the Factory Cove ice foot. Samples werer taken down four transects with a collecting syringe at approximately 11.30 hrs, local time.

		% Total			
	Total/m^3	Hatchlings	Immatures	Adults	
$\bar{x}$	12,728	97.24	1.82	1.09	A
S.D. ±	4,016	1.59	1.33	0.74	
$\bar{x}$	8.26	54.46	20.54	24.99	B
S.D. ±	2.78	15.66	15.05	15.69	

Table XIII : The composition (by number and weight) of *P.antarctica* from the ice foot region, Factory Cove:

A, Number,

B, Dry weight (g).

by Anderson and Raasveldt (1974) or 70,000 (of the same species) refered to by these same authors. The post-hatchlings of P. antarctica, which made up 97 percent (S.D. ± 1.6) of net catches, were of a far smaller size than these gammarids and Rakusa-Suszczewski (1972) noted a maximum of 2,136 Paramoera walkeri/m.^{2} at Alasheyev Bight, Antarctica. Grazing rates of the amphipods on the diatom flora of the ice have been calculated from these data.

Amphipod density at the ice-foot was greater than elsewhere on the fast ice under-surfaces, except in the near vicinity of ice holes (produced by Weddell seals or man). The attraction of young amphipods to light was further demonstrated (Table XIV) by transects taken radiating away from an ice hole off Thule Islands (see Fig. 3).

5.3.2. Diurnal activity.

Bregazzi (1973) has already ably documented activity rhythms in two species of infaunal amphipod at Signy Island, but no such rhythms had been established for epifaunal species. Night dives in Borge Bay, during September 1972, indicated that marked behavioural fluctuations were, in fact, prevalent in a variety of animal groups, particularly the Polychaeta and Crustacea. During darkness the water column was dense with actively swimming amphipods and P. antarctica was the major constituent of this nocturnal zooplankton. The spatial distribution of this species in the water column at night is diagrammatically illustrated in Fig. 17. Immature and adult animals were randomly distributed throughout the water (though during one dive, a dense band of amphipods, 1 m. thick. was

Distance from hole (m.)	Transect Number 1 A	 1 B	 2 A	 2 B	 3 A	 3 B	 4 A	 4 B
0 - ½	713	0.10	1,375	0.14	662	0.12	305	0.04
2	356	0.05	153	0.02	51	0.01	458	0.06
4	407	0.06	204	0.02	153	0.02	356	0.05
6	102	0.01	49	0.00	53	0.00	453	0.06
8	108	0.01	154	0.02	155	0.02	255	0.03

Table XIV: The numbers (A) and weights (B) of <u>P. antarctica</u> on the under surface of the sea ice. Four transects were taken, at right angles, from an ice hole. The samples were taken from the Thule Islands area (1.10.72).

Monthly Sample	J	F	M	A	M	J	J	A	S	O	N	D	Total
♀	76	294	251	96	370	-	87	-	154	187	74	104	1,743
♂	112	315	283	84	290	-	59	-	123	137	69	115	1,537
Totals	188	609	534	180	660		146		277	324	143	219	3,280
Ratio ♀/♂	0.68	0.93	0.89	1.14	1.28		1.47		1.25	1.36	1.07	0.90	1.13

χ^2 = 23.01 (significant at $P < 0.05$ [10^{o}F.]).

Table XV: The sex ratio of <u>P. antarctica</u>.

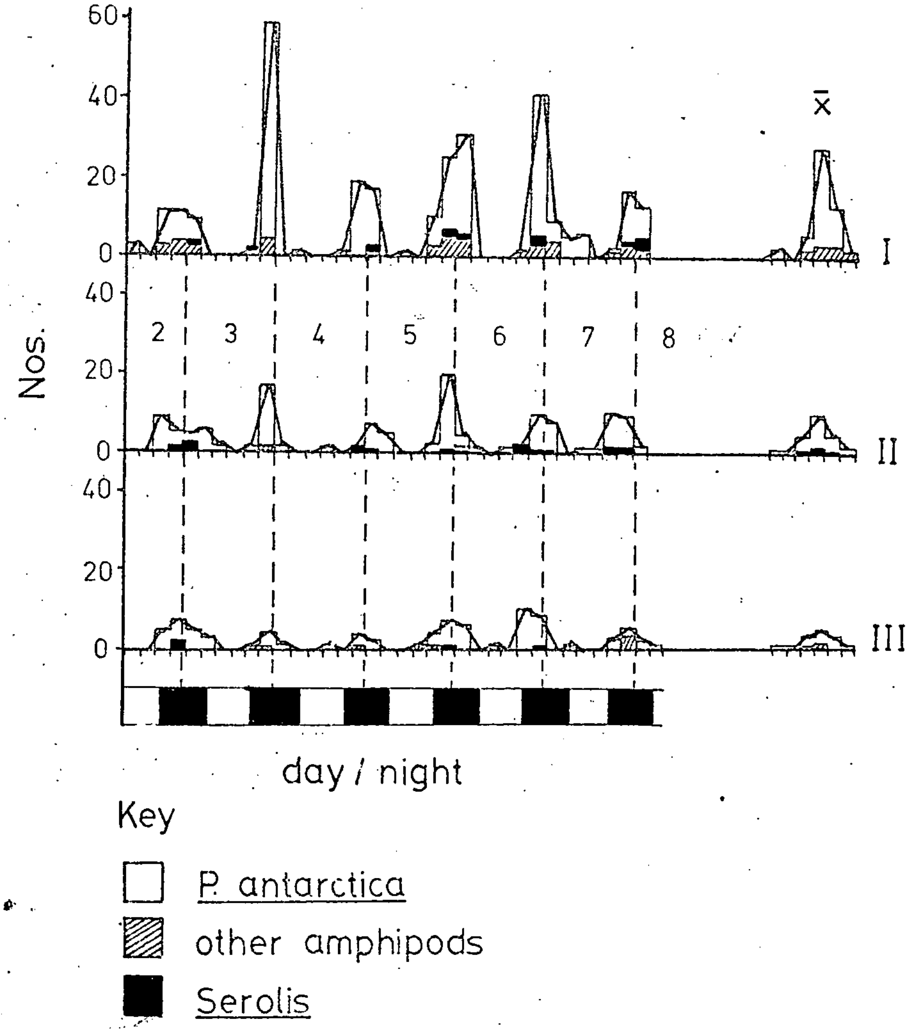

Fig. 18 : The rhythmic activity of various peracarid crustacea~~ns~~, expressed as numbers captured in funnel traps during the period of the 2nd to 8th. Oct. 1972 from three depths: I 0.8m., II 1.8m., III 2.8m.

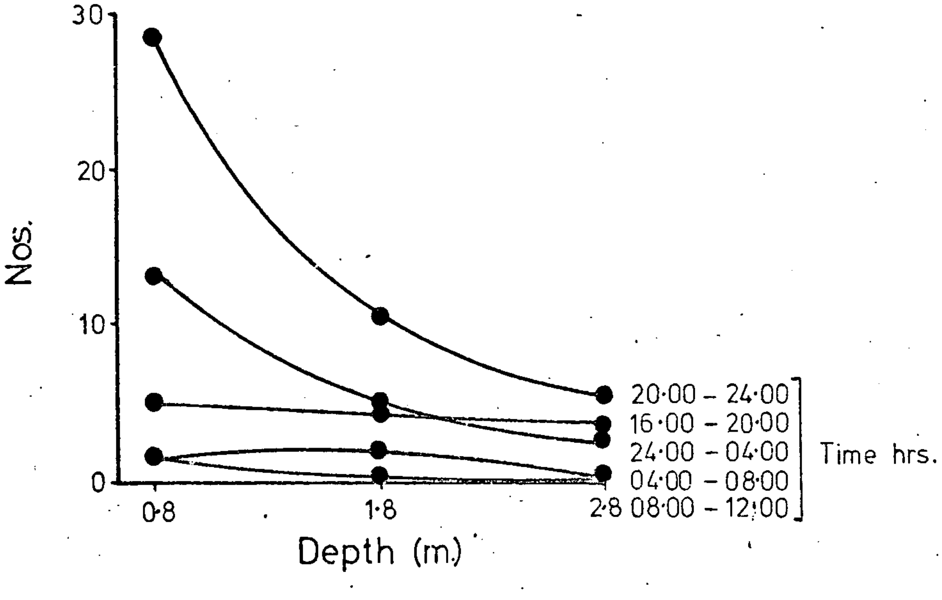

Fig. 19 : The number of P. antarctica captured at different periods of the day from three depth stations.

positioned 2 m. off the substrate at 13 m.) Conversely post-hatchling amphipods migrated laterally from the tide crack to areas immediately underneath the fast ice. The confinement of amphipods, during daylight, to 'ice burrows' suggests that the prime motivation for this nocturnal activity was feeding. The fluctuating presence of P. antarctica in the water column is shown in Figs. 18 and 19, from a station over a five metre depth in Borge Bay. The number of amphipods in the water column decreased with depth (Fig. 19) and the maximum number of amphipods present in the zooplankton was during the period 2000 - 2400 hours (local time). For some unexplained reason these fluctuating rhythms of diurnal activity could not be discerned in physiological responses (8.3.1.).

5.3.3. Reproduction.

The breeding strategies of 19 species of amphipod, from Signy Island, have already been outlined by Thurston (1972) and more detailed information on the two lysianassids Cheirimedon femoratus and Tryphosella kergueleni has been presented by Bregazzi (1973). Unlike most antarctic species P. antarctica has a biannual brooding cycle though the summer production was greatly reduced when compared to the major winter brooding. I noted that the winters' first gravid females were seen during either May or June (4.6.71, 2.5.72 and 7,5.73) and that the release of the winter brood took place from late August onwards, reaching a peak during September or October. The synchronisation of brooding and hatchling release was nowhere near so precise as documented by Bone (1972) and Thurston (1968;1970) for Bovallia gigantea. In common with most amphipod species females were significantly more numerous than males ($P > 0.05$) though the sex ratio varied throughout the year (Table XV).

(a) The fecundity of *P. antarctica*.

The effects of the polar environment are believed to be reflected by the fecundity of species, with typical cold water invertebrates producing large, lipid rich ova but as a consequence fewer eggs per female. I have investigated this phenomenon in some depth in order to relate its significance to the rigorous environment. More detailed measurements of the ova of *P. antarctica* are included in 7.3.1. I have determined the weight of eggs as a proportion of the total gravid female weight and these data are presented in Table XVI. On average, ovigerous females carried almost 20 percent of their own weight as eggs (18.9 %: Stage I) and this value could double for females carrying Stage VI embryos.

I found that the number of eggs produced by *P. antarctica* was proportional to ovigerous female length^3. The species thus conformed to the normal situation reported for other amphipods (Clemens, 1950; Thurston, 1970; Bregazzi, 1972 and Steele and Steele, 1975) though contrary to the fecundity relationships of certain gammarids described by Cheng (1942). This author stated that ' the size of a species bears no relation whatever to the reproductive capacity'! An analysis of 426 ovigerous *P. antarctica* (229 during 1972, 197 during 1973) carrying all stages of egg development indicated that there was no significant statistical difference between the two years' data and because of this Fig. 20 illustrates only the fecundity relationships for 1972. Thurston (1970) derived a relationship for *B. gigantea* between the number of eggs and the length of incubating females but gave no indication as to which egg development stage(s) the data referred. My own figures for *Djerboa furcipes* indicated an overall reduction in the mean number of eggs or embryos carried during brooding: Stage I - 80.4 eggs, Stage II - 110.5, Stage III - 103, Stage IV - 42 and Stage VI - 40 and a similar decrease in the fecundity of *P. antartica* could be detected in the mean values for 1972 and 1973. These indicated overall reductions in the ova carried of 20.2 (1972) and 43.8 percent (1973), (Fig. 20 [b]). I believe these values are greater than should be expected, for the differences between the equations of Fig. 20 [a] were not significant ($P<0.05$). Certainly some mortality would be expected during brooding and ovigerous females were observed carrying infertile eggs. Embryos or eggs may be lost, accidentally or deliberately from the marsupium if the female is grossly disturbed and this phenomenon of discharge from the brood pouch is more likely to occur towards the later stages of development. Bregazzi (1972) noted a sharp decline in the final number of embryos being carried by *Cheirimedon femoratus* and stated that this decline was due both to loss of young from the brood pouch, because of embryo activity and also induced by handling adult females. My samples of ovigerous *P. antarctica*, stored in fixative, showed severe egg loss. Such specimens were not used when assessing fecundity.

(b) The fecundity of antarctic amphipods.

I also investigated the fecundity of another fifteen shallow water amphipods from Signy Island and these data are presented in Figs. 21 and 22. Relationships of the number of eggs to female length

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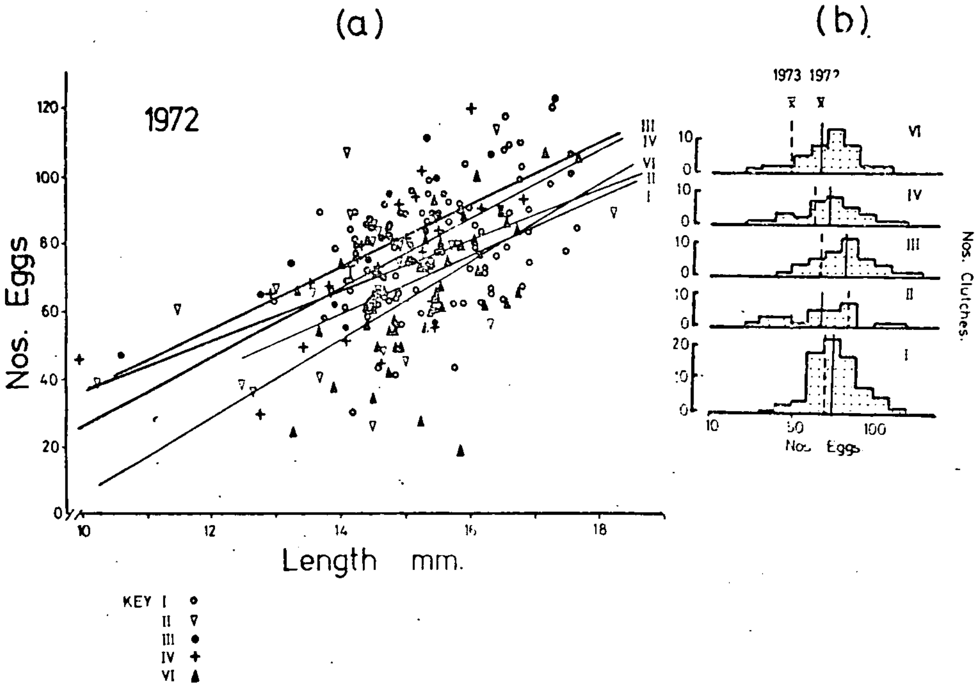


Fig. 20 : The fecundity of P. antarctica (data from 1972).
Regression relationships were:

(a). I. $y = 7.44x - 30.76$ ($r = 0.429$, $n = 76$)
II. $y = 7.76x - 36.46$ ($r = 0.529$, $n = 27$)
III. $y = 9.12x - 54.44$ ($r = 0.695$, $n = 37$)
IV. $y = 10.06x - 74.08$ ($r = 0.706$, $n = 32$)
VI. $y = 11.42x - 108.96$ ($r = 0.560$, $n = 54$)

(b) indicates the values of the number of clutches containing different egg stages with the mean number for the years 1972 and 1973.

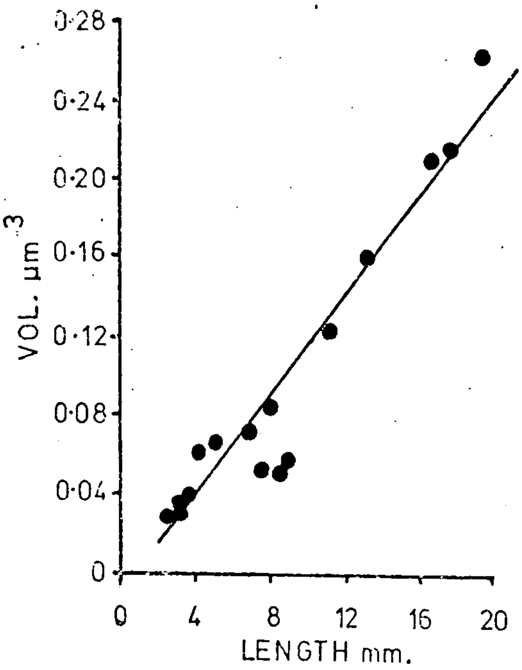


Fig. 21: The relationship of mean individual ova volume (Stage I) to mean parent length. (line drawn by eye).

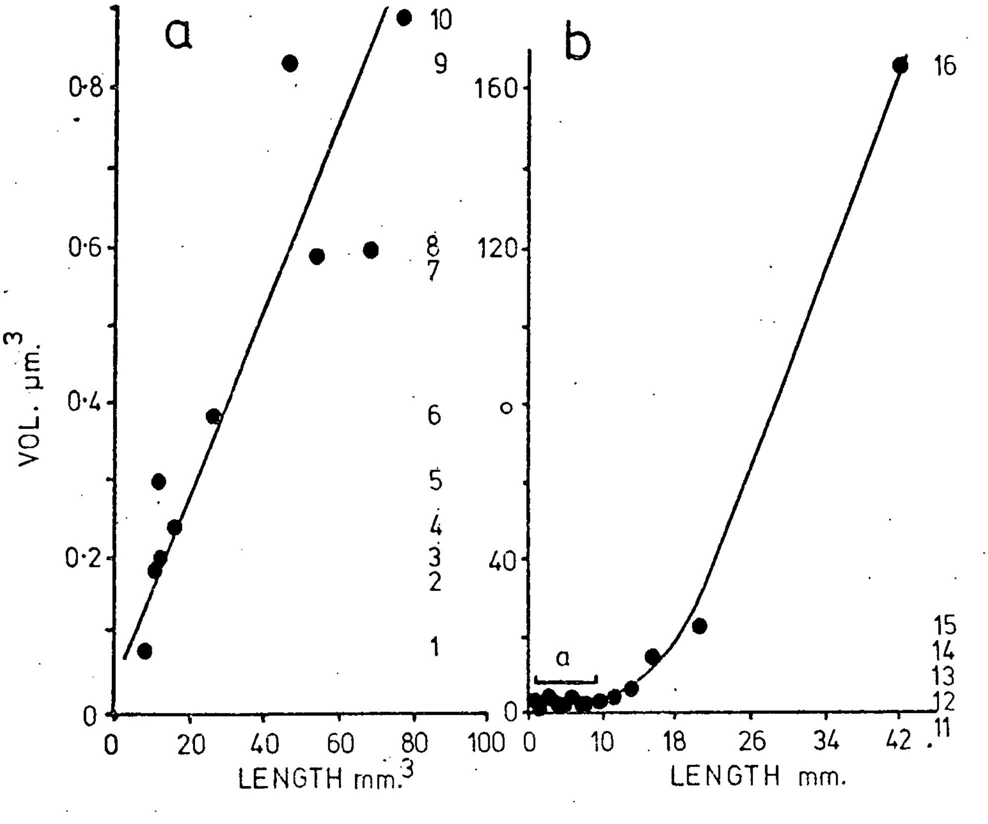


Fig. 22: The relationships of mean total ova volume (Stage I) to mean parent length or length ^{3} (a) for amphipods < 10.0 mm. length, (b) for the total amphipod size range. For amphipods investigated see Appendix VIII.

were given in the papers of Thurston (1972), Bregazzi (1972 and Rakusa-Suszczewski (1972) and of egg volume to female volume by Thurston (1972). My data indicate that the mean volumes of individual amphipod eggs can be directly related to adult size (length) according to the equation:

$$y = 0.013x + 0.095$$

$$(r = 0.96, n = 15)$$

Similarly the egg carrying or producing capacity of species was linearly related to the volume of the females but this relationship only held for species less than 10 mm. in length (Fig. 22 [a]).

When the whole size range of inshore amphipods (i.e. including B. gigantea) was examined (Fig. 22 [b]), the egg carrying capacity exponentially increased so that the total volume of eggs carried by large species was disproportionally large. For instance:-

Metaleptamphopus pectinatus ($\bar{x}$ ♀ length ^{3} = 69.4 mm. ^{3},
total egg volume = 0.84 mm.^{3})

Pontogeneia antarctica ($\bar{x}$ ♀ length ^{3} = 226.5 mm.^{3}
total egg volume = 10.54 mm.^{3})

(i.e. the relative volume of eggs brooded by P. antarctica is over 5 x greater than the smaller M. pectinatus).

(c) Brooding strategy and duration.

The mean length of ovigerous P. antarctica was 13.4 mm. (range 7.48 - 17.69 mm.) and the bi-modal length frequency histogram

(Fig. 23) for *P. antarctica* reinforces the suggestion of Thurston (1972) that this species was one of the few recorded antarctic amphipods brooding twice per year.

The bimodality of Fig. 23 was probably accentuated by the different sampling periods for the three years of observations. It became apparent that the mean size (length) of ovigerous females decreased during winter brooding and this trend is illustrated by the values in Fig. 24. These resulted in a decrease in female length of 26.5% between June and November. Naturally, individual females continued to grow, if only marginally, during their brooding period and this trend in a decrease in length and the double-peaked nature of Fig. 23 were due to the phenomenom of simultaneous brooding by two generations of females. Early in winter (May), ovigerous *P. antarctica* were approximately 20 months old; but as winter progressed some younger females (≏ 12 months old) also began carrying eggs. No precise data are available on the percentage of the female population which undertakes generation 1 brooding, though it is estimated that the majority (ca. 70 percent) of females delay breeding until over a year and a half after their release as post-hatchlings. The influx of generation 1 brooders is portrayed in Fig. 25 where the minimum recorded lengths of females, carrying each egg development stage, all decreased. Some females possibly produced a third brood of young. However, if this event occurred, it did so in a very small proportion of the population. Most second generation ovigerous females examined had considerably reduced their food intake (Fig.33) and showed signs of senescence. In the sea-water laboratory none of a batch of post-ovigerous females (which released their young in

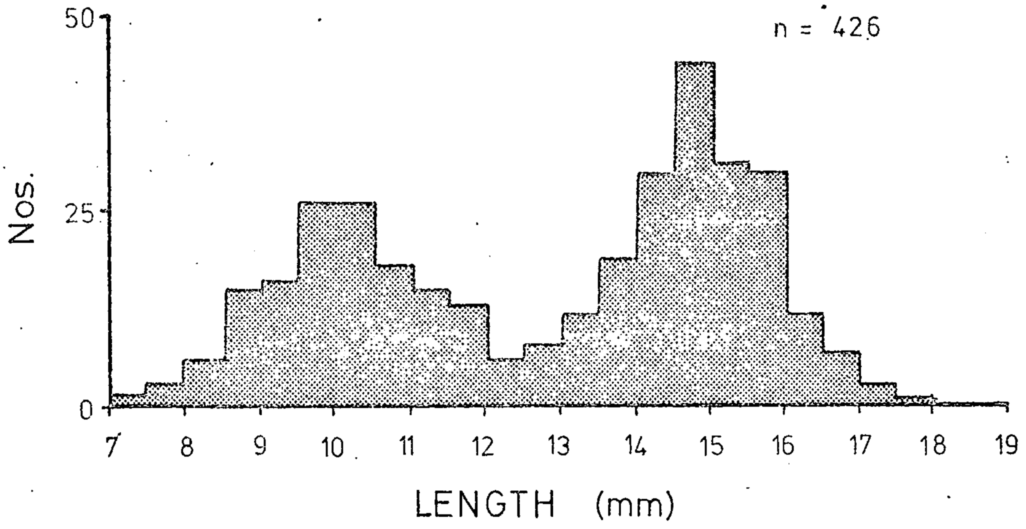


Fig. 23 : The total number of ovigerous P. antarctica of different sizes for all monthly samples (1972, 1973).

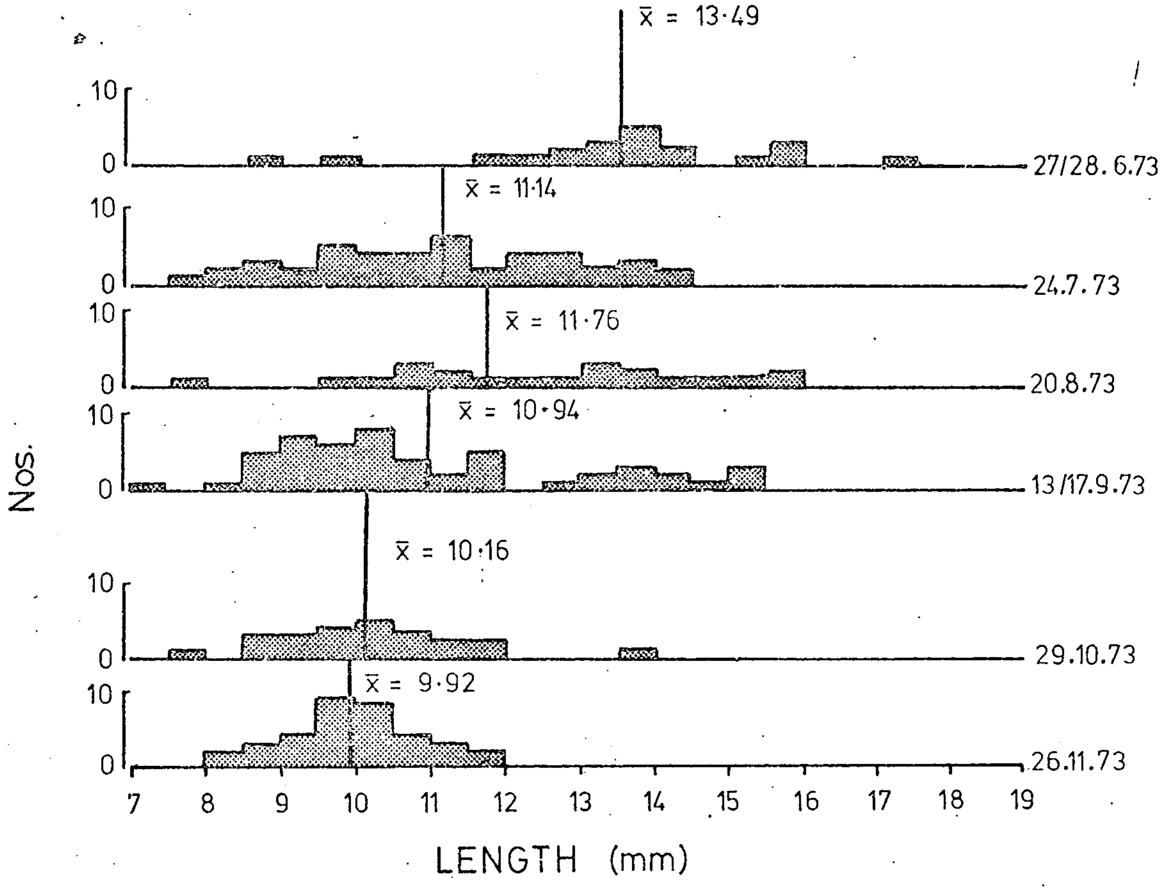


Fig. 24 : The decreasing mean length of ovigerous females during the winter brooding period (1973).

Weight ovig. ♀ (mg.)	Weight ova	No. ova	Ova Stage	% Weight $\frac{ova}{♀}$
24.1	5.28	86	I	17.97
22.8	3.50	98	I	13.30
26.7	6.50	80	II	19.57
18.1	4.90	64	I	21.30
21.7	6.44	92	I	22.88
19.3	5.10	72	IV	20.90
			$\bar{X}$ =	19.32

Table XVI: The relationship of ova dry weight to the dry weight of the brooding parent.

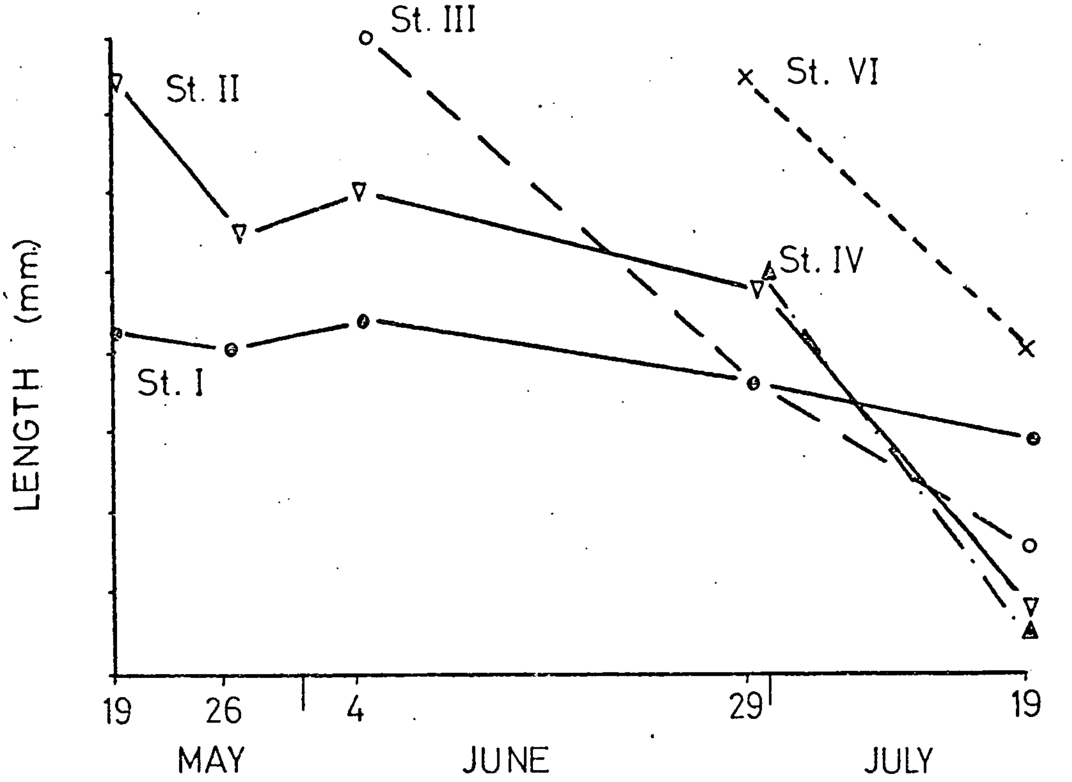


Fig. 25: The decrease in mimimum recorded sizes of ovigerous female P. antarctica carrying different egg development stages. Female lengths decreased from:

Stage I, 13.3 - 12.1 mm.
Stage II, 16.6 - 10.3
Stage III, 17.3 - 10.6
Stage IV, 14.3 - 9.9
Stage V, 16.6 - 13.3

October) survived beyond February of the following year and a sample taken on 23.1.73 indicated that spent females had disappeared, presumably died, from the population. Thurston (1972) mentioned that spent females of P. antarctica were incapable of breeding again immediately and described regressed ovaries and internal tissue degeneration. This statement was presumably supported by examinations solely of generation 2 females, for my dissections of 1st. generation ovigerous females brooding Stage VI embryos indicated fully formed orange-red oöcytes in the ovaries and females of this generation, kept in the sea water laboratory and in the presence of males, exhibited normal second brood release during May. Thurston (1972) deduced biannual brooding in this amphipod from an analysis of 142 ovigerous females (114 of which were collected from one sampling station and on the same date). My data indicates that the brooding of P. antarctica is not of two discrete peaks (one winter and one summer) but rather of a substantial winter breeding period followed by an extension of the winter brooding season (which may vary through until spring and summer) by females a year younger. The bulk of embryo production was from generation 2 females.

The duration of development was extended in this amphipod and this lengthy brooding period can be seen in Table XVII and Fig. 26. These data are derived from 'in field' samples and I have compared these values with those from laboratory rearing experiments in Chapter 7.

5.3.4. The growth rate of P. antarctica.

Growth in antarctic poikilotherms is normally regarded

Egg Development Stage

	I	II	III	IV	V	VI	
4.6.71	1	3					1971
5.6.71	2						
17.5.72	28	2					1972
19.5.72	19	1					
26.5.72	18	2					
29.5.72	1						
4.6.72	14	3	3				
29.6.72	9	3	5	2		1	
18.7.72	4	3	5	5	3		
18.8.72	5	2	6	5		20	
19.8.72	3	1	8	10		16	
21.8.72	7	7	8	9		14	
22.8.72		5	2	5			
24.8.72	7	4	2	4		7	
29.8.72						3	
1.9.72	1					1	
19.10.72	4		4	4		2	
25.10.72	3	4	2	7		6	
21.2.73	6	2		2			1973
27.6.73	6		1				
28.6.73	10	2	1	1			
24.7.73	39	5					
20.8.73	12	5	3	4			
13.9.73	10	9	8	4		1	
17.9.73	9	5	3	2			
(6.10.73)		2	6	3		5	
29.10.73							

Table XVII : The numbers of female P. antarctica carrying ova of different development stages. The bracketed values indicate amphipods from Palmer Station.

Fig. 26 : The same data expressed as histograms for all three years'values.

as slow and I have attempted to follow the rate of growth in this amphipod by the methods described above. The results of a series of measurements on monthly samples of P. antarctica are shown in Fig. 27. From these values, the means of size cohorts have been constructed into a growth curve for the species and this is shown in Fig. 28. I separated the modes of the overlapping size frequency distributions, either by eye (assuming each generation had an approximately bell-shaped distribution), or when this proved difficult by the normal probability paper method (Harding, 1949; Cassie, 1954). The rate of growth was not uniform throughout the lifespan of P. antarctica, though the increased seasonal effect on growth can only be discerned in Fig. 29, for first year animals. Males and females differ in both their longevity and rate of growth for males live approximately two years reaching a length of 12 mm. whilst females can live a further six months and reach a maximum size of just over 20 mm. However, the range of 17.5 - 18.6 mm. is more normal for the larger ovigerous females. Both these phenomena of different adult sizes and longevities have been reported for other amphipod species. For instance, Kanneworff (1965) described the larger females of Ampelisca macrocephala as living for two years, the males only 18 months and most authors on antarctic amphipods have commented on these differences. Since all amphipods brood their young there is presumably a significant advantage to the species in having the increased capacity for egg production and parental brooding that the larger size of the female provides.

No appreciable differences could be determined between the growth rates of post-hatchling P. antarctica from the ice-foot or sea-laboratory experiments. The predominant foods available in these two areas were Cocconeis/Meridion spp. and Nitzschia/Navicula spp. respectively (8.3.3.). The experiment on the ice-foot ledge was unfortunately prematurely curtailed by the sudden in-flow of fresh melt-water from the surrounding land. The resulting substantial salinity decrease in the upper 2 m. of the water column (17.11.72) forced the natural population of amphipods, on the ice-foot to deeper water and the benthos, but killed the experimental amphipods in their containers. The first season's growth curve of post-hatchlings (from the sea water laboratory) is shown in Fig. 29.

Animals maintained in the benthos (where the food supply was Biddulphia spp.) showed a markedly increased mortality, for the experiment was set up on the 26.9.72 and significant deaths were observed by the 3.10.77. These had increased to over 95 percent by the 18.10.77 and were attributed to (a) the lack of a suitable food supply and (b) predation by small nemertines (Tetrastemma spp. ?) which invaded the experimental containers.

(a). Growth factor.

The 'step-wise' growth of arthropods attributed to ecdyses, or body moults has been widely investigated and has lead to the definition of such incremental growth by Dyar's Law (growth factor (K) = 1.25) or Brooke's Law. Przibram (1929) stated that a doubling of body volume. per moult, would produce the Brooke's factor of 1.26,

$$\text{i.e.} \quad \frac{\text{Final size}}{\text{Initial size}} = K(1.26)$$

Values for a variety of temperate arthropods lie within

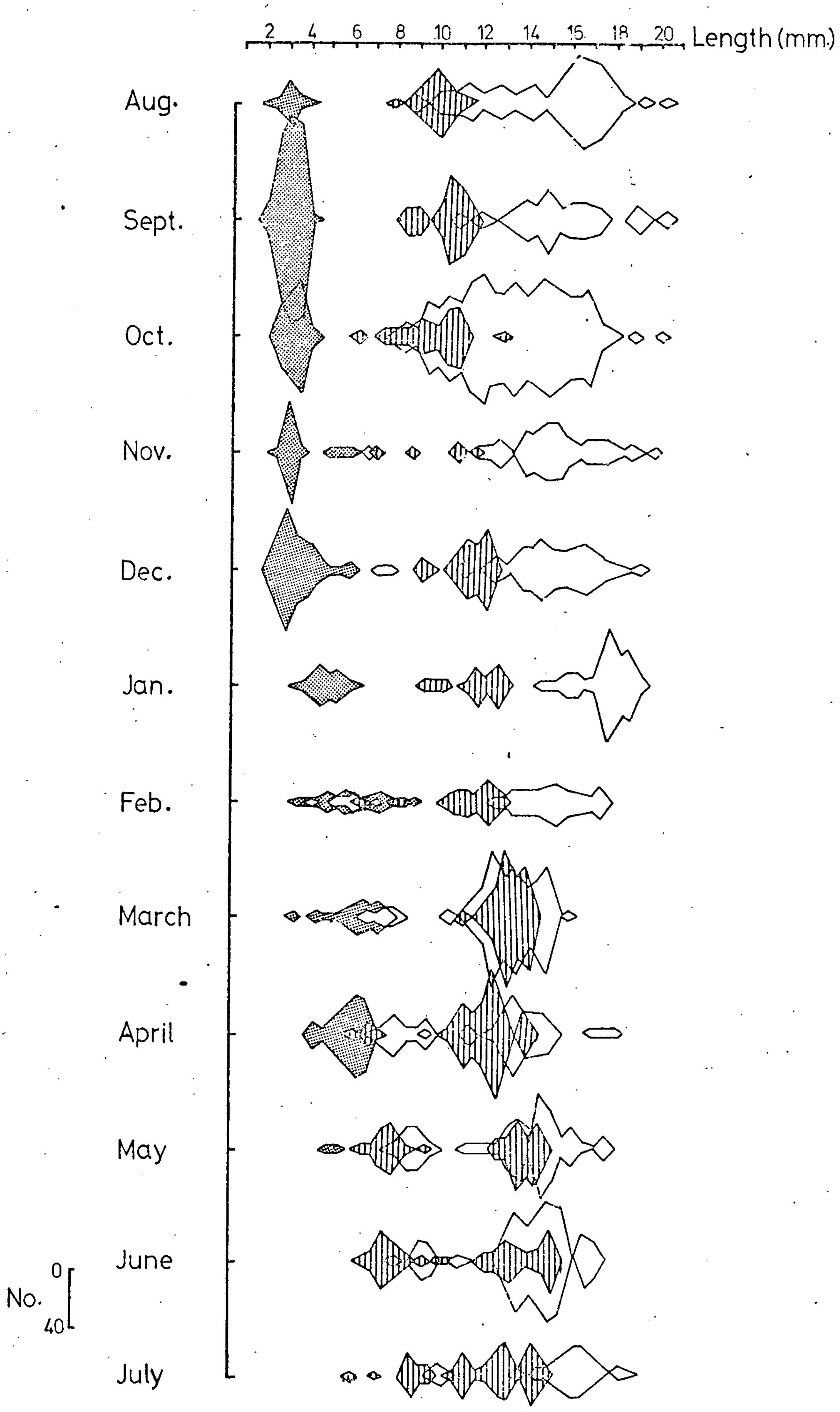


Fig. 27 : Monthly length-frequency diagrams for P. antarctica during 1972. ▨ immatures, ▥ ♂♂, □ ♀♀.

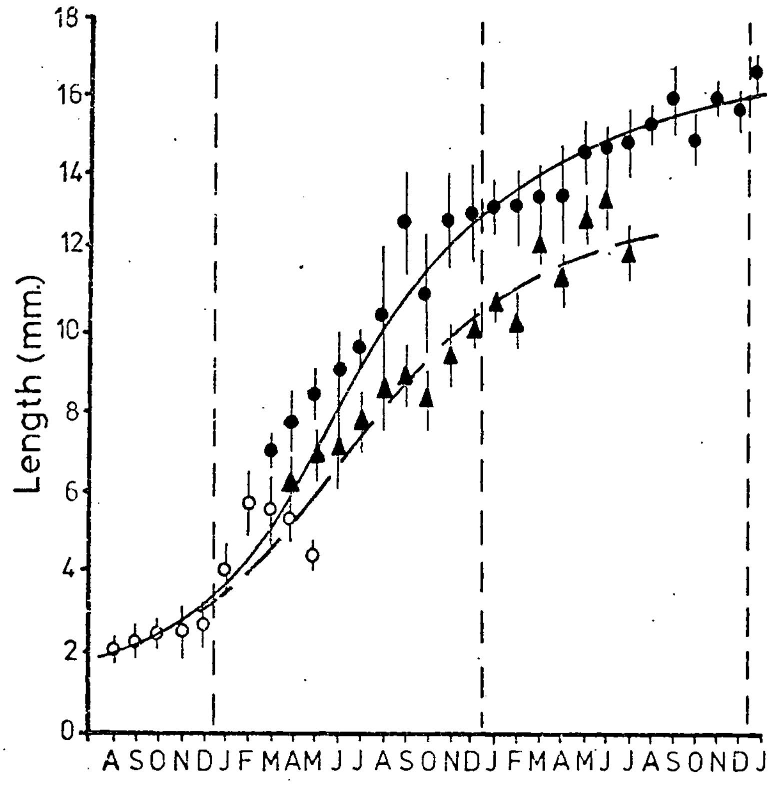


Fig. 28 : The constructed growth curve of the amphipod <u>P. antarctica</u>. ○ immatures, ● ♀♀, ▲ ♂♂. Vertical lines represent one standard deviation either side of the mean.

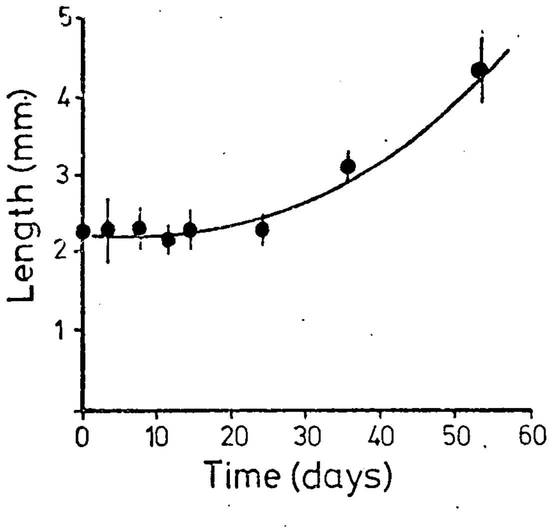


Fig. 29 : The initial growth curve for post-hatchling <u>P. antarctica</u>.

the range of 1.0 - 1.35, e.g. Homocoryphus vicinus K = 1.2 (own unpublished data). K is best evaluated by measuring individual body plates of an animal so that articulated surfaces, which can alter their shape, do not influence the results. In crustacea, a variety of methods for defining K have been employed for Reeve (1969) used total body length of the prawn Palaemon serratus to obtain a mean factor of 1.09 and Sexton (1924) employed a similar method for the amphipod Gammarus chevreuxi (K = 1.25). Head length (Gammarus fasciatus, K = 1.11) or oostegite to total length (Bovallia gigantea, K = 1.20) have also been used by Clemens (1952) and Bone (1972) respectively. It would thus appear from Bone's data that antarctic species have a similar growth factor to that of their temperate counterparts. In determining a value of K for P. antarctica I encountered considerable difficulty in separating moult stages, using the method outlined by Bone but attempted a similar exercise using antennal segment number to length since the number of segments in the antennae of any individual should remain constant throughout each moult stage. Fig. 30 indicates that although differential (allometric) growth of the amphipods' antennae can be distinguished , division into moult stages was not practical (at least for the size of sample investigated). It was however possible, using the same methods, to identify individual moult stages, but only in the immediate post-hatchlings. These gave a mean K value of 1.18.

Although Kurata (1962) had demonstrated that the moult factor did not necessarily remain constant throughout the life history of a crustacean, this feature was not taken into account by Thurston (1968). Similarly with insufficient data I have had to assume constant growth and have estimated that P. antarctica would

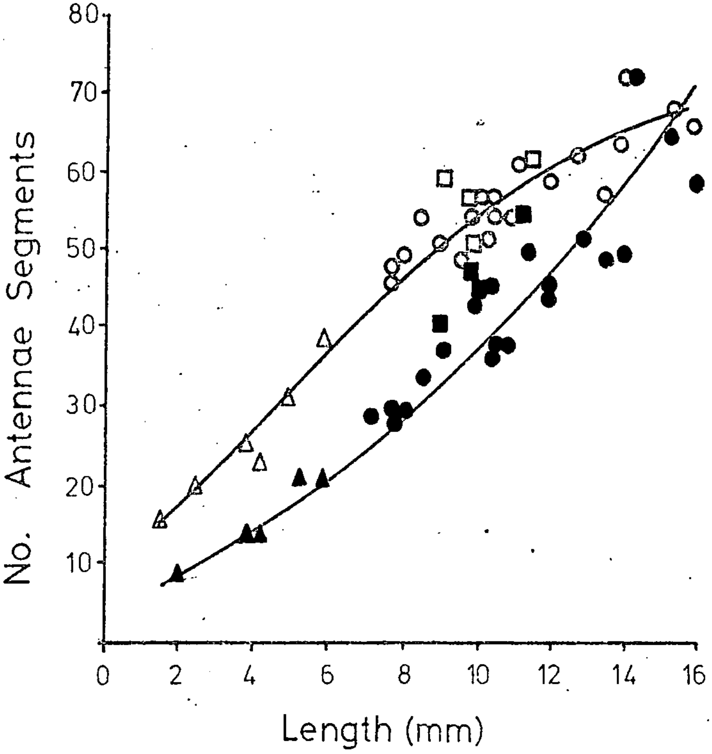


Fig. 30 : The antennae segment number as a function of length for P. antarctica. Black symbols (antenna 1), Open symbols (antenna 2). ▲△ immature, ■□ ♂♂, ●○ ♀♀.

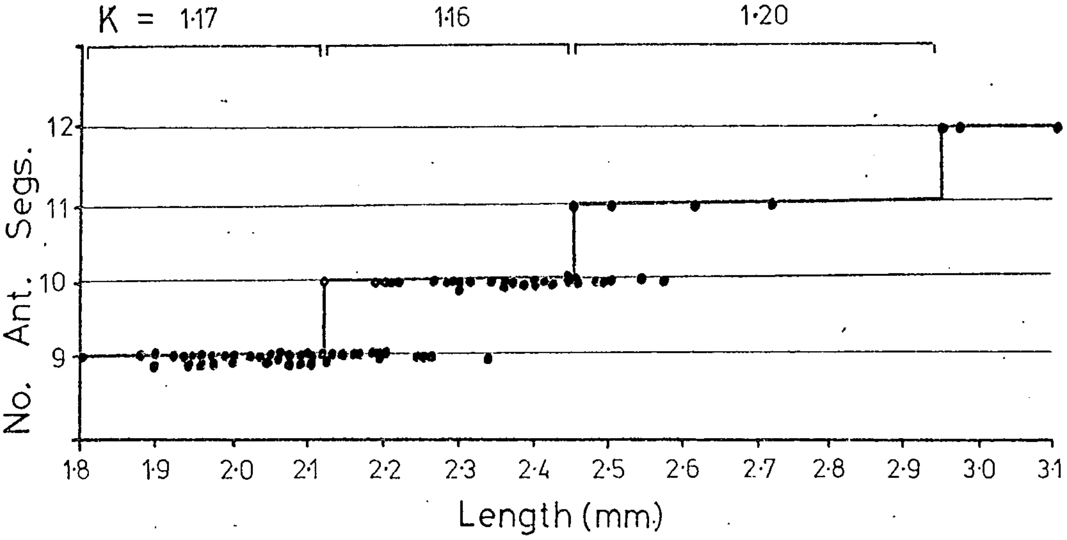


Fig. 31 : The segment numbers of antenna 1 against length for post-hatchling P. antarctica. The mean value of K = 1.18.

moult at least thirteen times to reach a length of 15.9 mm. Sexes would be distinguishable by the sixth moult and sexual maturity would be achieved by the ninth moult in males, the eleventh in females.

5.4. Discussion:

5.4.1. Migration and the cryopelagic existence.

The antarctic amphipod P. antarctica is unusual amongst shallow water benthic Crustacea in migrating during the year to occupy two major ecological niches in the winter and summer. The phenomenon of benthic organisms associated with sea ice can be accidental, i.e. they may become inadvertently frozen in (Medcoff and Thomas, 1974) or a deliberate adaptation, for as Horner (1976) has pointed out organisms closely associated with sea ice have been known to science for more than a century. Thephenomenon has been previously reported for antarctic amphipods (Paramoera walkeri) by Rakusa-Suszczewski (1972). In 1959 Barnard described the cryopelagic habitat of the floating 'Fletcher's Island', in the Arctic;there, the animals associated with ice were basically planktonic and although seven amphipod species were noted from the ice only one, Gammarus wilkitzkii occurred at all frequently. Barnard described the sea ice habitat as 'essentially a pelagic environment covered with a solid unbrella, offering a restricted amount of 'inhospitable' living surface; in a sense, an inverted substratum.' In this author's opinion, sea ice offered few advatages, but many disadvantages to any colonising animal in that (a) animals could not burrow into it, (b) it did not consist of unconsolidated particles which could be moved around, (c) sessile animals could not attach to it, (d) the temperature close to the ice was dangerous to most living organisms, (e) gravity exerted a negative force on any animals clinging to it and lastly (f) that the shape and extent of the ice inter-faces was constantly changing. Because the highly mobile pack-ice is a different situation from the more stable in-shore fast ice, this last feature certainly has some biological significance, but there is little evidence to substantiate these other 'disadvantages'.

The seawater temperature in the immediate vicinity of sea ice at Borge Bay was no colder than elsewhere in the water body (Fig. 4) and Kanwisher (1966) has indicated that even in the temperate zone many littoral species such as littorinids are able to withstand freezing. Presumably animals endemic to the polar seas have a physiology and temperature tolerance evolved to withstand these ambient near freezing conditions. My own observations appear contrary to those of Barnard for the sea ice, receiving more light during winter than the underlying water column, which it shades, acts as a colonising matrix for a variety of microalgae and other unicellular organisms. These in turn attract species of crustacean Amphipoda which rely on this considerable neritic primary production to both feed during winter and in particular to provide the necessary dense food source for their newly released larvae.

At Signy Island, the long porous crystals of the sea ice produced a soft flexible structure, the surface of which was covered with the 'burrows' of P. antarctica.

5.4.2. Reproduction.

A further selective advantage gained by feeding on neritic diatoms during winter appears to be that P. antarctica is able to extend its breeding period, thereby producing more than one brood per generation, and doing so in quick succession. This allows female amphipods to breed a year earlier than they might otherwise and presumably offsets the relatively decreased fecundity of the species.

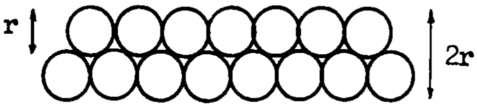
The fecundity of amphipods from Signy Island has already received comment and discussion from Thurston (1972). From his data it is apparent that antarctic species carry, on average, fewer eggs than temperate or tropical amphipods. Polar species, are not especially adapted morphologically (with for instance, elongated oostegites) to carry more eggs than their warmer water counterparts. However why the fecundity of larger antarctic amphipods was relatively increased to such a degree over that of small species could only be theoretically investigated.

Presuming that ova are spherical, the volume of space they occupy in the marsupium ($n\frac{4}{3}\pi r^3$ - where n = number of spheres) is independent of their radii. In addition the proportion of 'waste space' remains constant.

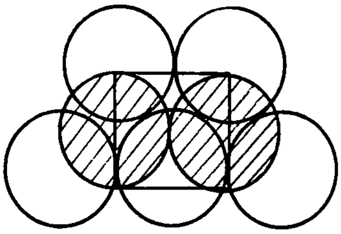
On the assumption that the marsupium was a cuboid with dimensions of x,y and z and packed with spherical eggs, set in rows and columns, orientated parallel to the edges of the cuboid, then the total number of spheres that could be contained within the marsupium would be $\frac{xyz}{8r^3}$ producing a combined volume of:

$$\frac{xyz\pi}{6}$$

This total sphere volume is independent of the size of the spheres within the cuboid and each row of ova in such an arrangement would occupy 2r space.



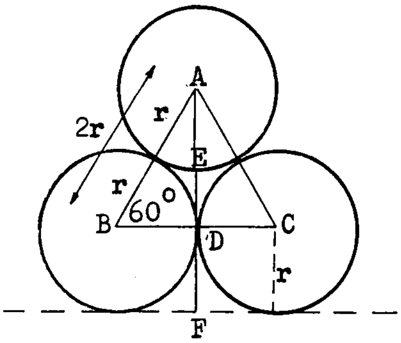
However the optimum packing arrangement would be



when each row occupies $\sqrt{3}r$, producing a total sphere volume of

$$\frac{xyz\pi}{3\sqrt{3}} \quad (\frac{\pi}{3\sqrt{3}} \quad = 0.595)$$

[Proof:]



$AD = 2r \sin 60^\circ$

$= 2r \times \frac{\sqrt{3}}{2} = \sqrt{3}r$

$DE = \sqrt{3}r - r$

$DF = \sqrt{3}r - r + r$

$= \sqrt{3}r$

Thus indicating that only 59.5 percent of the cuboid (marsupium) can be occupied by eggs, the remaining 40 percent (under an optimum packing system) being 'wasted space'.

The_above theory would also hold good for non-spherical egg shapes, providing their volumes and dimensions were constant for the species. It is thus apparent that the relative sizes of the eggs to the parent (or marsupium) are irrelevant to the total egg volume which can be brooded, for as long as the available space is efficiently filled to capacity the percentage of space unoccupied will remain constant. The most obvious explanation of the phenomenon of relatively increased total egg volumes in large amphipods is that the volume of the marsupium is not, in fact, itself related linearly to the volume of the parent crustacean, i.e. marsupial growth is allometric (unfortunately such measurements were not checked). For instance a linear increase of the marsupium by 2.9 in relation to a x2 increase in the length of the brooding female would increase the potential brooding capacity by x24.

Most antarctic poikilotherms, including amphipods, have an extended development period with hatching normally occurring in spring or late winter. Such a situation contrasts with that of temperate amphipods which produce a number of broods during their long reproductive season. This synchrony of brooding, in polar species, is normally considered to be an adaptation, allowing newly released larvae to exploit the spring phytoplankton bloom. Hatching synchrony is not confined solely to obvious planktotrophic species for the predator/scavenger Orchomene plebs also has a synchronised breeding season (Pearse, 1963). This latter fact is however not an indication, as inferred by Thurston (1972) that synchrony is not primarily motivated by the optimum food supply of spring for although the adults of O. plebs are not plant eaters it is probable that their newly released offspring are diatomaceous. Alternatively the release of predatory larvae would be expected to be synchronised with that of their prey species.

5.4.3. Growth.

In common with many polar species the rate of growth of P. antarctica was very slow. The effect of temperature on growth rates has been widely discussed for temperate species (Sexton, 1924; Hynes, 1954) butit was also suggested that the slow rate of growth in antarctic species was mainly due to the constant low temperatures. de Broyer (in press) has analysed mature sizes of a great many antarctic amphipods and concludes that both the phenomenon of dwarfishness and gigantism are common in polar species. Indicating that low temperatures may be one of the ecological features depressing growth rates de Broyer also suggested that limiting food is also of importance. A similar suggestion had been previously put forward by Bregazzi (1972). Whilst temperature may affect growth, the metabolism (respiration) of polar Crustacea is not necessarily depressed. On the contrary, metabolic activity may be elevated above that expected and Dunbar (1968) indicated that such increased metabolism, at low temperatures, could only be possible if other energy consuming processes, for instance growth, were correspondingly reduced. This was on the presumptiom that the energy intake (ingestion) of antarctic and temperate species was approximately the same. In fact, the indication is that although the feeding of P.antarctica is at a comparable rate during summer, the amount of food available during winter is limited.

Chapter 6 The Benthic and Cryopelagic feeding of Pontogeneia antarctica.

6.1. Introduction:

The winter movement by Pontogeneia antarctica, from the benthic macroalgae to the under surfaces of the fast ice, was an important feature of the ecological behaviour of these crustaceans. The main reason for this migration appeared to be associated with the need to acquire a suitable food supply during the winter and early spring periods when primary production in the benthos and water column was greatly reduced.

Amphipods are known to consume a wide variety of food types: bacteria/detritus, (Hyalella azteca, Hargraves, 1971; Gammarus minus, Kostalos and Seymour, 1976); detritus, (Ampelisca macrocephala, Kanneworff, 1965); Crustacea and other invertebrates (Gammarus lacustris, Anderson and Raasveldt, 1974; Gammarus fasciatus, Clemens, 1950; Gammarus spp. Steele and Steele, 1969); fungi (Gammarus pseudolimnaeus, Bärlocher and Kendrick, 1973) and microalgae (Gammarus pulex, Moore, 1975). Moore's statement that insufficient importance had, in past studies, been placed on the rôle of microalgae in amphipods'diets was undoubtedly emphasised by his findings that in G. pulex,a species previously reported as an omnivore/carnivore, 95 percent of the diet consisted of diatoms.

In high latitudes the important link between ice associated diatoms and Crustacea has been acknowledged for some years (Andriashev, 1968; El-Sayed, 1971). However, information on the diets of antarctic amphipods is currently restricted to the brief notes in the papers of Bone (1972) - benthic feeding of Bovallia gigantea - and Rakusa-Suszczewski (1972) - cryopelagic feeding of Paramoera walkeri. The link-up between the migration of amphipods and food availability has been determined from the more detailed feeding studies described in this Chapter. Whether food was a limiting factor to amphipods in either the benthic or cryopelagic habitats was certainly not previously known, and as a means of assessing both the grazing pressure on the sea-ice microflora and the ingestion rate of P. antarctica, some feeding studies, using experimental techniques, were employed.

6.2. Materials and Methods:

6.2.1. Winter feeding.

(a) The ice-foot environment.

A general description of the sea ice and the Borge Bay environment has already been given (1.1. and 1.2.2.). At the point where the fast ice sheet adjoined land, on a shallowly sloping shore, a series of parallel shear cracks were generated by tidal movement. Here the ice inshore of the cracks eventually froze solidly to the beach (Fig. 6[a]). In steeply shelving areas or against cliffs, fewer marginal tide-cracks were produced but a massive ice structure formed under water, completely sheathing the shore down to a maximum of 7 m. This ice bulge (Fig. 17), the ice-foot, had its origins from:

I. The marginal freezing in the splash zone during the period before the fast ice formed.

II. From anchor ice formation (Dayton et al., 1969) accentuated by cold brine draining back from the tide-crack overflow region (Whitaker, in press; Whitaker and Richardson, in press).

III. Creep induced by the accumulated weight of several metres of drifted snow at the fast ice margin. This downward deformation resulted in the creation by July, in 1972 and 1973 (Whitaker, pers. comm.), of a bulge of composite origin, whose top consisted of infiltration ice (snow origin) with a basal section of more solid sea water ice. Fig. 17 shows a typical profile.

(b) Analysis methods.

Ice-associated microalgae and amphipods were obtained by SCUBA diving throughout the austral winter of 1973, between June and November. The microalgae were collected with small fragments of ice from the ice foot at Knife Point, Borge Bay, using 100 ml. plastic bottles. These were pushed into the relatively soft ice substrate. Amphipoda were captured during the same period by towing a net (mesh size 0.3 mm.) along the ice foot. Amphipods from Palmer Station (see Fig. 1) were collected, during winter, from diatom colonisation plates (metal) suspended at a depth of 20 feet. Samples were rapidly transported to the laboratory where ice samples were melted and centrifuged at 2,000 rpm. to concentrate particulate material. Sub-samples were investigated qualitatively under a x 400 magnification, and estimates were made of the relative abundance of microalgal species and any associated material. Amphipods were hand sorted from net catches and killed by placing in warm filtered sea water (+ 10.0°C). Specimens were examined either fresh or fixed and stored in 10 percent sea water neutralised formalin for later analysis. The fresh gut contents of small individuals (approximately 2.0 mm. in length) were examined from squash preparations. Guts from larger animals were dissected out before similar examination under a x 100 and x 400 magnification.

I found that preservation of the material made examination of the smaller animals difficult and consequently all the preserved amphipod material consisted only of large ovigerous or immediately pre- or post-ovigerous females. A measure of feeding activity was obtained by estimations of the amount of material present in the guts of a limited number of animals (180). All amphipods collected from the benthos were obtained by the methods described in 3.2.

(c) Feeding experiments.

The feeding rates of adult and immature P. antarctica ($\bar{x}$ length 11.36 mm., range 6.02 - 18.65 mm.) were determined with a carnivorous diet, using the post-hatchlings of the same species. Batches of 50 ml. plastic bottles containing 30 ml. of water and variable numbers of prey from 10, 30, 60 to 100 and 1 predator amphipod were kept for three days under a constant temperature (+ 0.5°C) and a normal light régime. To prevent the 'prey' from feeding, water in the experimental chambers was 'Millepore' filtered and all amphipods, both prey and predators, starved for three days before experimental runs. The predators were killed, measured and weighed (dry) and any prey remaining counted at the end of each experiment.

Feeding experiments also investigated the grazing of post-hatchling P. antarctica on the diatom Navicula glaciei.

Initial concentrations of Chlorophyll a were measured after 'Millepore' filtration and cold acetone extraction (Strickland and Parsons, 1965). The diatom suspension was stirred and stored in the dark prior to experiments, which were also carried out in the dark. Variable numbers, 25, 50 or 100, of starved amphipods were placed in 35 ml. of known diatom suspensions (Table XXVII) for two days. The numbers of amphipods surviving these experiments and the final chlorophyll concentrations were determined. In addition, a visual analysis of the number of damaged cells in the hind gut of grazing amphipods was conducted.

6.3. Results:

6.3.1. An antarctic food chain.

(a) Observations on the interaction of the amphipod *P. antarctica* with ice-associated microalgae.

Sea ice provides a great variety of sites for microalgal growth. During the winter of 1973 observations were made on the colonisation of the coastal ice foot and on the winter feeding habits of *Pontogeneia antarctica*.

The sympagic microflora started its development in early June with extensive growths of *Phaeocystis antarctica* Karsten. This was replaced, as winter progressed, mainly by diatoms, with *Navicula glaciei* Van Heurck and *Nitzschia curta* (Van Heurck) Hasle the most predominant.

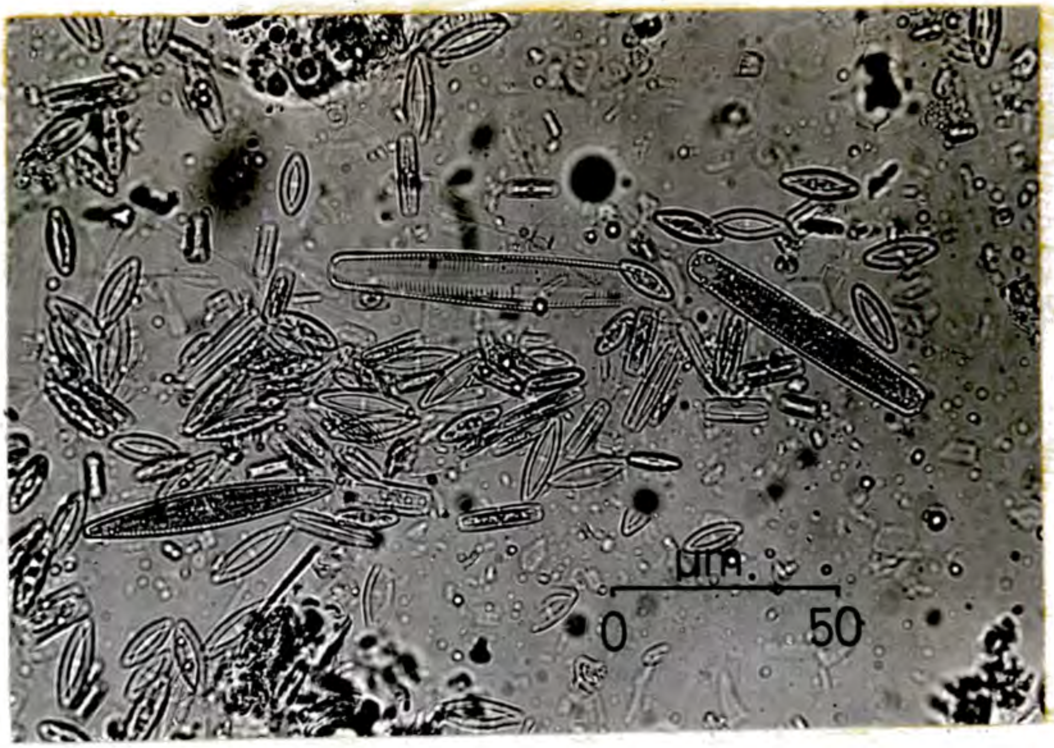
Microalgal growth appears to be possible on any type of submerged marine ice substrate and Whitaker (in press) has tabulated most of these types of habitat present, in winter, at the South

Percentage fullness	Numbers in feeding class Non-ovigerous	Ovigerous	Percentage Non-ovigerous	Percentage Ovigerous
0	0	58	0	38.9
1	2	18	6.5	12.1
2	3	28	9.7	18.8
3	4	24	12.9	16.1
4	6	14	19.3	9.4
5	3	5	9.7	3.3
6	4	2	12.9	1.3
7	5	0	16.1	0
8	2	0	6.5	0
9	2	0	6.5	0
10	0	0	0	0
Total	31	149	100.1	99.9

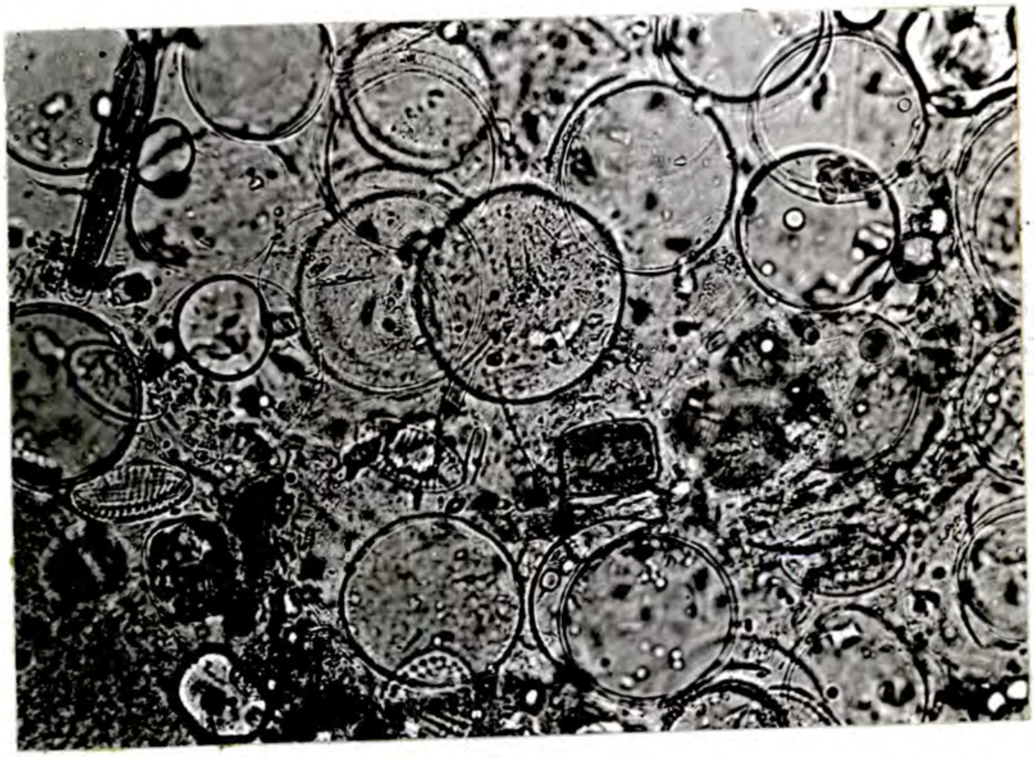
TableXVIII A comparison between the percentage fullness of guts of ovigerous and non-ovigerous female Pontogeneia antarctica of the same size group.

Date 1973	Percentage of material in total fresh samples Algal	Crustacean	Other (Mainly detrital)
13.5	85	5	10
31.5	40	0	60
27.6	75	5	20
24.7	90	0	10
20.8	85	10	5
13.9	95	0	5
5.10	85	10	5
15.10	100	0	0
29.10	100	0	0
26.11	100	0	0
Mean percent	85	3	12

Table XIX : Approximate estmations of relative amounts of food types in guts of Pontogeneia antarctica, on various sampling dates.



(a)



(b)

Fig. 32 : Fore-gut contents of P. antarctica (a) feeding on ice associated microalgae Navicula glaciei and Nitzschia curta and (b) feeding on the pelagic diatom Thalassiosira antarctica.

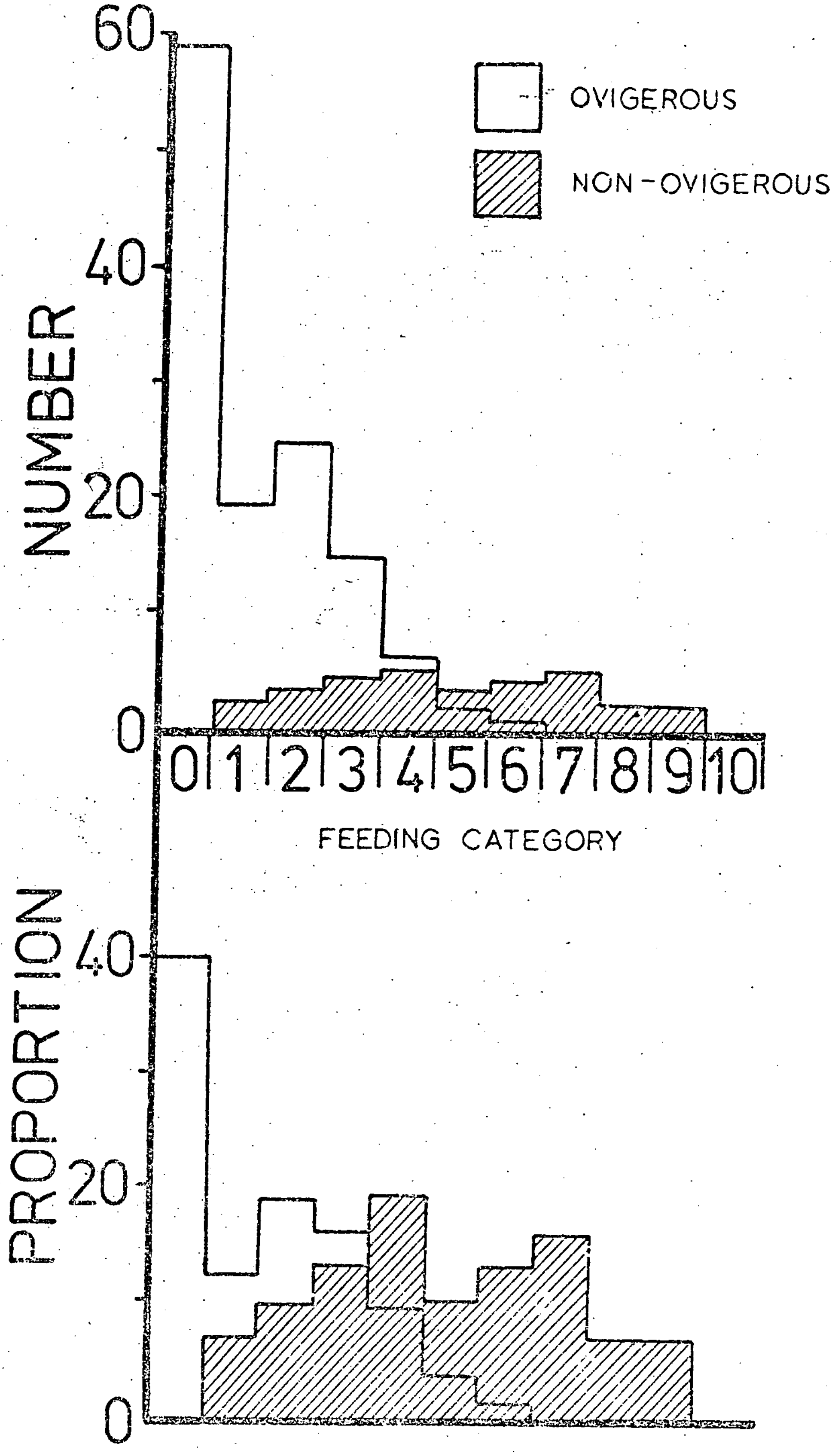


Fig. 33 The feeding activity of ovigerous and non-ovigerous *Pontogeneia antarctica*.

Orkney Islands. Infiltration ice substrates, where snow is soaked by sea water, appear to be peculiarly favourable for extensive microalgal development. Dense concentrations of *Nitzschia closterium* (Ehrenburgh) Wm. Smith have been reported from the infiltration zone of pack ice and *Navicula glaciei* from the tide-crack 'overflow infiltration ice' at Signy Island (Whitaker, in press; Whitaker and Richardson, in press). It is probable that these solid but porous substrates form a pseudo-benthic type of habitat (Horner, 1976). Microalgae comprised the majority of the particulate material on the ice foot although copepods, ciliates, flagellates, motile bacteria and detrital matter were also present. At least 44 species of microalgae were found, of which 35 were diatoms and two species, *Navicula glaciei* and *Nitzschia curta* (Fig. 32[a]) formed over 90 percent of the microalgal material. Species recorded from each sample are outlined in Table XX.

A similar tabulation of the material found in the guts of 303 *P. antarctica* is presented in Table XXI and Table XXII (approximately one third of these animals were examined fresh).

A comparison of feeding activity was made between non-ovigerous females collected on 31.5.73 and ovigerous females collected between 13.5.73 and 29.10.73. The results are shown in Table XVIII and Fig. 33.

(b) Observations on the pelagic feeding of *P. antarctica* at Palmer Station, Antarctic Peninsula.

Analyses on the gut contents of 95 individual amphipods (23 of which were ovigerous) with a mean length of 9.7 mm. (range

CHRYSOPHYTA BACILLARIOPHYCEAE												
Centrales												
Eucampia balaustium Gastr.											+	
Charcotia actinochilus (Ehr.) Hust.	+			+					+	+	+	
Charcotia australis (Karst)												
Thalassiosira tumida (Janisch) Hasle		+		+	+	+	+		+	+	+	+
Thalassiosira spp. (65)			+	+								
Coscinodiscus bouvet Karst								+				
Coscinodiscus oppositus Karst									+	+		
Coscinodiscus oculoides Karst												
Coscinodiscus antarctica Kozlova								+				
Corethron criophillum (Gastr.)						+	+		+	+	+	+
Cocconeis imperatrix A Schm.	+		+		+				+			
Chaetoceros schimperianum Karst	+	++	+		+		++	+	+	+	+	+
Chaetoceros spp.		+					+					
Biddulphia striata Karst							+					
Pennales												
Nitzschia curta (Van Heurck) Hasle	+++	++++	+++	+++	++	++++	++++	+++	+++	+++	++	+
Nitzschia cylindricus (grun.) Hasle												
Nitzschia kerguelensis (O'Meara)			+									
Nitzschia lineata Hasle				+			++	+	+	+		
Nitzschia sublineata Hasle		+			+		+			+		+
Nitzschia rhombica Hasle						+						
Nitzschia closterium (Ehr.) W. Sm.				+					+			
Nitzschia spp. (40)		+++	+	++	+	+	+		+	+	++	+
Nitzschia spp. (42)	+++	++++		+	+	+	+	+	+	+	++	+
Navicula glacieie Van Heurck		++	+++	+	+	+	++		++++	++++	+++	++++
Navicula frequens Van Heurck			+		+		+	+	+	+		
Navicula spp (77)	+											
Amphriprora oestrupii Van Heurck			+	+	+		+	+	+			
Amphriprora spp.	+	+	++	+			+	+	+	+		+
Amphriprora kjelmanii Cl.								+	+	+		
Amphora spp. (18)					+		+	+	+	+		
Amphora spp. (76)	+											
Rhizosolenia inermis Castr.		+					+				+	
Licmophora spp.	+		+									
Gyrosigma attenuatum							+		+			
Grammatophora spp.			+									
Heterochloridales									+			
Chloromeson spp									++	+	+	+
CHOROPHYTA: CHLOROPHYCEA												
Volvocales												
Chlamydomanas spp					+							+
CYANOPHYTA: MYXOPHYCEAE												
Phaeocystis antarctica Karst	++++	++	+									
spp. (74)		++										
spp. (59)			+									
PYRROPHYTA: DINOPHYCEAE												
Spp. (84)									+	+		
Spp. (85)									+	+		
Dictyocha speculum (Ehr.)							+					
Copepoda							+		+			
Ciliata									+			
Flagellata									++			+
Motile Bacteria										+		+
Gregarine spores?									+			

Table XX : The occurrence of Microalgae and other organisms on the ice-foot Factory Cove during the winter of 1973.

+	Present
++	Common
+++	Abundant
++++	Extremely Abundant

	Date (1973)										
MICROALGAE	13.5	31.5	25.6	24.7	20.8	13.9	17.9	5.10	15.10	29.10	26.11
Charcotia actinochilus (Ehr.) Hust			+			+					+
Thalassiosira tumida (Janisch) Hasle		+	+		+			+		+	+
Coscinodiscus oppositus											+
Cocconeis imperatrix A.Schm.	+	+++	++	++	++	++	++	+	++	++	++
Chaetoceros schimperianum Karst								+	++	+	
Nitzschia curta (Van Heurck) Hasle	++	++	+	+	+	+			+	+	
Nitzschia cylindricus (Grun.) Hasle		+			+						+
Nitzschia lineata Hasle	+	+						+		+	
Nitzschia spp.(40)			+	+				+	+	+	++
Nitzschia spp. (42)		+	+		+		+	+	+	+	+
Navicula glaciei Van Heurck	+	+	+	+	+	+	+	++	++	++	++
Navicula frequens Van Heurck					+			+		+	+
Amphora spp. (18)		+	+	+	+	+			+	+	
Licmophora spp.	++	++	+	+						+	+
Amphiprora spp.								+		+	
Nitzschia spp.	+	+		+	+	+	+	+	+		
Coscinodiscus spp.	+++	++	++	+	++	++	++	++	++	++	++
Pennales (not identified)	+	+	+	+	+	+		+	+	+	+
Centrales (not identified)					+	+					
Diatom fragments	++	+	++	+	+	+	++	++	++	++	++
Chloromeson spp.(83)										+	+
Dictyocha speculum (Ehr.)		+	+	+				+	+	+	+
Dinophyceae (not identified)							+				
Macroalgae (not identified)		+	+	+		+	+				
Chloroplast debris	+	++	++	++	++	++	++	++	++	++	++
Detritus	+	+++	++	+++	++	++	++	++		++	++
Mineral particles		+	+	+	+						
Crustacea (not identified)		+	+	+	++	++	++	+		+	+
Isopoda				+							
Amphipoda		+	+	+	+	+	+			+	
Copepoda		+	+	+	+	+	++	+		+	++
Pontogeneia antarctica		+	+	+	++	++	++	+		++	
Oradarea bidentata			+								
Porifera (not identified)		+			+		+				
Spermatophores		+	+	+						+	
Fat droplets	++	+	+	+	+	+		+	++	+	++
Gregarinda	++	++	++	+	+	+	++	+	+	+	+
Nematoda (not identified)										+	
Small ovae (not identified)			+	+	+					+	
Bacteria											+
Empty gut		+		+	+	+	+	+	++	+	++

No. examined:		Total	13.5	31.5	25.6	24.7	20.8	13.9	17.9	5.10	15.10	29.10	26.11
	Fresh	107	11	10	10	10	12	12	0	13	14	10	5
	Preserved	196	1	31	18	45	24	29	18	0	0	23	7
	Total	303	12	41	28	55	36	41	18	13	14	33	12

Table XXI : The dietary composition of Pontogeneia antarctica captured on the ice-foot during the winter of 1973.

% Occurrences in gut

< 20	+
20-60	++
> 60	+++

Date of Sample	June 27	July 24	Aug. 20	Sept. 13	Sept. 17	Oct. 5	Oct. 15	Oct. 29	Nov. 26
Navicula glaciei	▧	▩	▩	▩	▩	▩	▩	▩	▩
Nitzschia spp.(42)	▧	▩	▩	▨	▩	▩	▩	▩	▩
Nitzschia spp.(40)	▧	▩	▨	▨	▨	▩	▩	▩	▩
Nitzschia curta	▩	▩	▩	▩	▨	▨	▩	▩	▩
Chloromeson spp.							▨	▩	▩
Amphora spp.	▧	▧	▧	▧		▨	▩	▩	
Navicularfrequens			▧					▧	▧
Cocconeis imperatrix	▩	▧	▧	▧	▧	▧	▧	▧	▧
Dictyocha speculum	▧	▧				▩	▧	▧	▧
Licmophora spp.	▩	▧						▧	▧
Thalassiosira tum.	▧	▨	▧	▨	▨	▩	▨	▩	▩
Chaetoceros schimp.	▨	▨		▨	▩		▩	▩	
Nitzschia lineata			▨			▩	▨	▩	
Amphriprora spp.	▨	▨	▨			▩	▨	▩	▨
Charcotia actin.	▩		▨				▨	▨	▧
Dinophyceae					▧		▨	▨	▨
Coscinodiscus opposit							▨	▨	▧
Nitzschia sublineata		▨		▨		▨		▨	▨
Corethron criophyllum					▨	▨	▨	▨	▨
Rhizosolenia inermis		▨	▨			▨			
Phaeocystis antarctica	▨	▨							
Gyrosigma attenvatum		▨				▨			
Chlamydomonas spp (89)				▨					▨
Chaetoceros spp. (32)						▨	▨		
Cyanophyceae spp. (74)		▨							
Nitzschia closterium			▨						
Thalassiosira spp (65)			▨						
Nitzschia rhombica					▨				
Bidulphia striata						▨			

Key.

▧	▩	▨
A	B	C

Table. XXII: Winter feeding in Pontogeneia antarctica, A. Species detected in the gut, B, species detected in both the gut and ice-foot and C species only detected in the ice-foot.

5.5 - 19.9 mm.) indicated that three diatom species were the principal food. The benthic diatom *Cocconeis imperatrix* was present in 82 percent of the animals examined and in 37 percent of these formed the major food. The two species, *Navicula glaciei* (45 percent) and *Nitzschia curta* (57 percent) were the other main components of the diet. Diatoms of *Coscinodiscus* spp. were present in 50 percent of the amphipods examined but this plant appeared not to be eaten in any great quantity.

A list of the food of *P. antarctica* from Palmer Station is outlined in Table XXIII. On comparing this synopsis with that of Table XXI, there were some apparent differences. For instance, more species of diatoms, as food, were recorded from Signy Island. This feature may (though this is not substantiated from Borge Bay samples) be some reflection of the effect of preservation on the samples collected from Palmer Station, for, unfortunately, none of these animals could be examined in a fresh state. Again species of *Meridion* were found in a considerable number of amphipods from Palmer Station but not recorded in the ice-associated *P. antarctica* from Borge Bay where *Thalassiosira antarctica* (Fig. 32[b]) was often the exclusive food of any pelagically feeding amphipods. Detritus was also found in a greater number of amphipods from Signy Island. It is not known whether diurnal movements, similar to those reported in *P. antarctica* (5.3.2.) were taking place at Palmer Station or if these indications of benthic feeding, for instance, the presence of sponge spicules and mineral particles in the animals' guts, were due to wave action producing subsequent fall-out onto the metal colonisation plates.

	% Occurrence			
	+	++	+++	Total
Crustacea fragments	6	4	1	11
Amphipod fragments	2	1	-	3
Pontogeneia antarctica	12	2	-	14
Sponge spicules	4	1	-	5
Filamentous diatoms	-	1	-	1
Navicula glaciei	23	17	5	㊺
Nitzschia curta	43	13	1	(57)
Nitzschia lineata	11	-	-	11
Nitzschia angularis	1	-	-	1
Nitzschia kerguelensis	1	1	-	2
Cocconeis imperatrix	45	26	11	(82)
Coscinodiscus spp.	48	2	-	㊿
Coscinodiscus stellaris	1	-	-	1
Thalassiosira antarctica	1	2	-	3
Thalassiosira spp.	5	-	-	5
Meridion circulare	25	2	-	㉗
Licmophora spp.	3	-	-	3
Amphora spp.	12	1	-	13
Green algae	4	1	-	5
Phaeocystis spp.	4	1	-	5
Radiolarians	1	-	-	1
Ciliata	2	-	-	2
Silicoflagellata	3	-	-	3
Chloroplast material	3	6	-	9
Macroalgae cells	5	2	-	7
Ectocarpales	1	-	-	1
Detritus	2	17	-	19
Mineral particles	11	22	3	㊱
Gregarines	28	14	1	㊸

Table **XXIII**: The dietary composition of *Pontogeneia antarctica* from Palmer Station, Antarctica Peninsular, (6 and 20.10.73). ⓝ % frequency > 19.

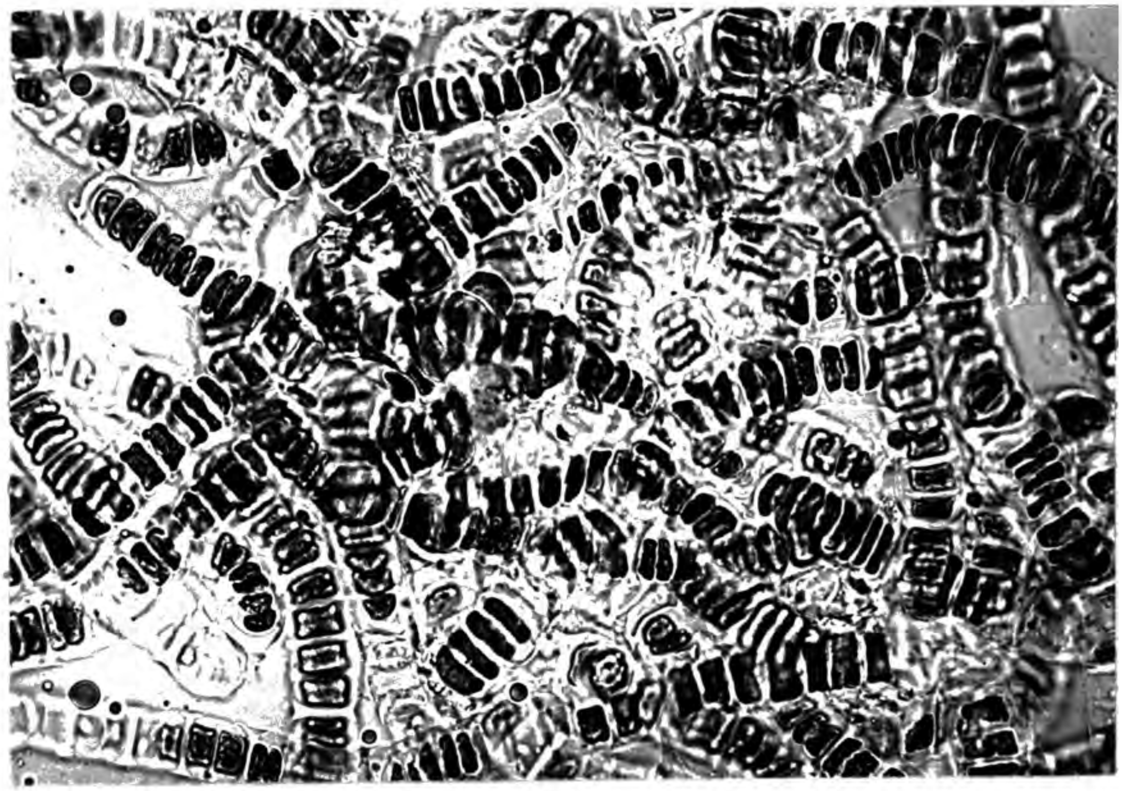
6.3.2. The benthic feeding of P. antarctica and the influence of size.

Since body size has a fundamental effect on the types of food which any organism can effectively consume, I divided the amphipods, for the purpose of analysing their guts, into three size categories: small (2.0 - 4.9 mm.), medium (5.0 - 9.9 mm.) and large (10.0 mm. +). The results, from the analyses on the guts of 145 P. antarctica (from the benthos), are presented in Appendix IX. Benthic diatoms, particularly N. curta, C. imperatrix, Amphora spp. and Meridion circulare provided the major food though some pelagic/ neritic diatoms were also identified in the diet. After falling out from the plankton, species such as Thalassiosira antarctica and Navicula glaciei collected on the epibenthos in substantial quantities and a dense layer of 'fall out' diatoms, forming a detrital blanket over the macroalgae, was noted between the 18th and 20th November 1972. During early December, sea water visibility, 15 cm. off the substrate, was reduced by diatoms to less than 60 cm., though by January this deposited film of pelagic diatoms had been considerably reduced and was replaced by the 18th February 1973 with an active production of Biddulphia striata.

I observed that post-hatchling and immature amphipods often congregated along a lee shore to feed on the localised dense filamentous diatoms growing in the immediate sublittoral (though on exposed shores with more severe wave action amphipods were absent). The typical appearance of a fore gut of an immature P. antarctica, actively feeding on chains of Nitzschia sublineata and Ulothrix/Urospora, is illustrated in Fig. 34(a) and (b).

The variety of the types of food which were ingested increased

(a)



(b)

Fig. 34 : Photomicrographs of fore-gut contents of P. antarctica, from specimens feeding within the littoral zone during summer. (a) Filaments of Nitzschia sublineata with Ulothrix / Urospora. Note the dense chloroplast colouration. (b) Ulothrix / Urospora.

with the size of amphipods. This feature is directly attributed to the inability of smaller amphipods to ingest whole cells of diatom species such as Biddulphia striata, Molleria antarctica and Corethron criophyllum. The frustules of these plants are either substantially thickened (B. striata) or protected by spines (C. criophyllum) thus preventing grazing by smaller crustacea. The variety of diatom species consumed increased from 12 (small amphipods), 15 (medium) to 21 (large). Small amphipods were not, on the whole, carnivorous; conversely, adult P. antarctica were both cannibalistic and consumers of a variety of small crustacea (Appendix IX).

6.3.3. Comparisons of feeding in P. antarctica post-hatchlings.

The methodology, survival and growth rates of young post-hatchling P. antarctica which were subjected to different habitats has already been outlined in 5.3.4. The foods available in the three habitats of A, Factory Cove ice foot; B, the sea water laboratory; and C, the benthos (5 m. depth), contrasted markedly. (a) N. glaciei and N. curta; (b) C. imperatrix; and (c) B. striata were respectively the predominant diatoms which were characteristic of these areas. Appendix X indicates the types and quantities of the food types consumed by post-hatchlings in these three habitats (the data are presented per ten individuals). Amphipods in the benthic environment were feeding on fewer species and their feeding rate was also considerably reduced. The mortality of these animals was severe and I would suggest that the number of individuals obviously consuming detritus was an indication of a chronic food shortage. Amphipods on the ice foot and in the sea water laboratory tanks consumed the common diatoms N. glaciei and *C. imperatrix* in greatest quantities and though *C. imperatrix* was recorded from many amphipods on the ice foot, it never formed an important component of the food.

6.3.4. The major plant foods of *P. antarctica*.

(a) *Navicula glaciei* Van Heurck.

The ice-associated (neritic) diatom *Navicula glaciei* occurs commonly during winter, associated with the 'tide-crack overflow community' described by Whitaker (in press). In this zone of snow, infiltrated by sea water, dense pure natural populations of the diatom stain the snow and ice a deep reddish-brown. Locally the diatom attained concentrations of up to 7.5 mg/l (244 mg.m ^{2}) in the melted infiltration ice substrate. The diatom was also an important component of the microalgal assemblage found in the ice foot at Signy Island (Richardson and Whitaker, in press). During the summer and especially in January and February, the diatom could be found in the benthic community in shallow muddy areas with variable salinity, such as Elephant Flats, Borge Bay.

Further details on the ecology of *N. glaciei* can be found in Whitaker (in press) and Whitaker and Richardson (in press). The results of some analyses (methods not presented here) conducted on this diatom are presented in Appendix XI, but for more complete data on this species the paper of Whitaker and Richardson (in press) should be consulted.

The diatom was identified by Mr. R. Ross of the British Museum (Natural History) and his synopsis of its taxonomy is given in this study. Fig. 35 shows scanning and transmission

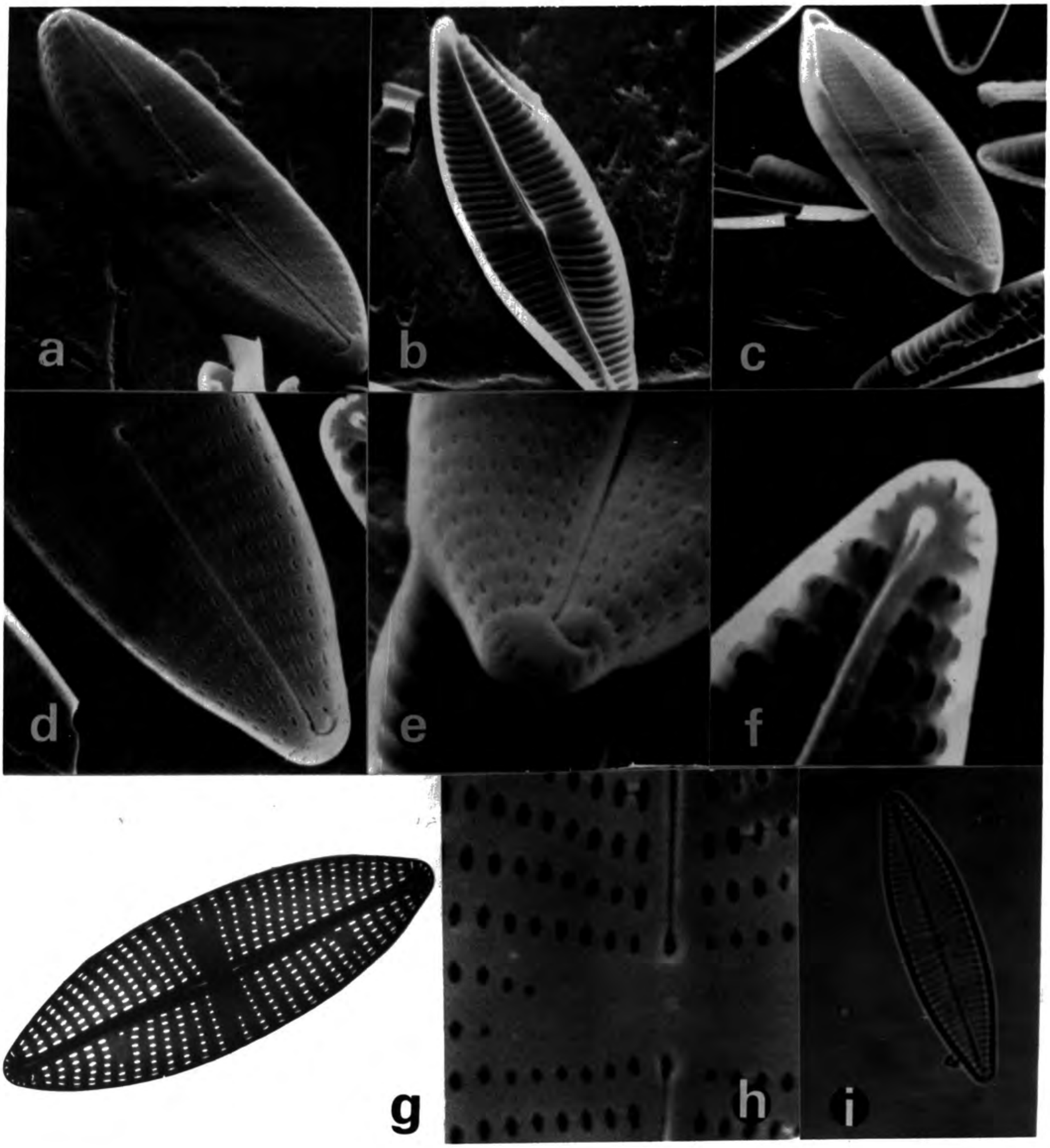


Fig. 35 : Scanning (a - f,h) and Transmission (g,i) electron photomicrographs of the diatom <u>Navicula glaciei</u> Van Heurck.

<table>
<tr><th>Measurements µm</th><th>Mean</th><th>95% Fiducal</th><th>Maximum</th><th>Minimum</th></tr>
<tr><td>Apical axis (Valve length)</td><td>20.0</td><td>0.3</td><td>28.8</td><td>15.6</td></tr>
<tr><td>Transapical axis
Transversal axis (Valve breadth)</td><td>6.0</td><td>1.0</td><td>7.2</td><td>4.8</td></tr>
<tr><td>Pervalvar axis (Principal axis)</td><td>2.5</td><td colspan="3">Not Measurable</td></tr>
<tr><td colspan="2">Mean cell volume</td><td>$208\ \mu m^3$</td><td colspan="2">determined mathematically and graphically</td></tr>
<tr><td colspan="2">Mean cell surface area</td><td>$295\ \mu m^3$</td><td colspan="2">"   "</td></tr>
<tr><td colspan="2">Surface to volume ratio</td><td>1.42</td><td colspan="2"></td></tr>
<tr><td colspan="2">Cell weight</td><td>2.15×10^{-8} µg</td><td colspan="2">determined experimentally</td></tr>
<tr><td colspan="2">Cell density</td><td>1.51</td><td colspan="2">determined mathematically</td></tr>
</table>

Table **XXIV** : The size range of the diatom *Navicula glaciei* Van Heurck.

Table **XXV** : The relationship between Chlorophyll *a*, particulate Carbon and cell numbers of the diatom *Navicula glaciei*.

Chlorophyll *a* (µg/l)	Carbon (µg/l)	Cells (10^9/l)
3490.3	137438	1.80
2223.4	91625	1.21
5362.5	182648	2.27
7488.7	297693	2.23
1702.1	74318	-
222.8	9356	-
1877.0	85288	-
986.3	44121	-
770.5	-	0.29
3107.1	-	1.36
2782.2	-	1.22
2399.0	-	2.21
2823.9	-	0.98

electron photomicrographs of the diatom and Table XXIV the size ranges of the plant.

The relationship between particulate carbon and Chlorophyll a in Table XXV is expressed by the equation:

$$y = 6.95 + 37.1x$$

The relationship between cell numbers and Chlorophyll a is expressed by the equation:

$$y = 0.64 + 0.26x$$

but because of the low number of replicates (9) and the low precision in cell counts, this equation is not significant at 95 percent fiducal limits.

An estimation of the composition of the diatom has been deduced from Appendix XI. For example, crude protein was derived using the multiplication factor of 6.25 x N (Hiller et al., 1948), mean ash and lipid percentages were obtained from experimental data and a value for crude carbohydrate was obtained by composition subtraction. From these estimates, the calorific contributions by each of the major constituents could be calculated using accepted calorific values (Table XXVI), though it was possible to calculate a specific calorific value for lipid using the heat of combustion for the fatty acids present. A value of 9,440 calories per gram was obtained, based on straight chain saturated acids. The value would be fractionally lower if allowance was made for the unsaturated acids present. An estimate of crude carbohydrate can also be obtained by subtracting the calorific contributions of known constituents from the total calorific value. However, this would lead to large discrepancies, with values ranging from 36 - 51

Table XXVI : Calculation of Carbohydrate from compositional data and estimates of calorific contributions by the principal constituents.

Material	Composition percentage	Calorific contribution cals g dry ash-free weight Max.	Min.	Constituent Calorific values cals g Max.	Min.
Ash	33.77	-	-	0	0
Lipid	21.81	2,255	1,862	9,440^{+}	
Crude Protein	25.38	1,434	1,294	5,650	5,100
Crude Carbohydrate	19.04	1,028	781	5,400	4,100
TOTAL	100.00	4,717	3,937		
Discrepancy from Calorimetric determination (5,427 ± 527)		710	1,490		

+ this was a calculated value not a literature recommended value.

percent. These differences could not be wholly accounted for by experimental error. The accuracy of ash (three independent analyses) and lipid (two independent analyses) values could be more closely defined than other parameters. However, the bomb calorimetry and nitrogen analyses are statistically similar in precision. The accuracy of the nitrogen analysis is supported by the observed atomic ratio of P:N:C: of 1:17.3:170 which is similar in magnitude to 1:16:108 given by Redfield et al. (1963) from a variety of data sources. I would have expected an underestimation of calorific values because of the high proportion of ash but my figures closely agree with the values tabulated by Cummins and Wuycheck (1971) who gave values of 3,218 to 4,948 cals/g. wet weight and 5,150 to 5,470 cals/g. ash free dry weight for Bacillariophyceae.

(b) The diatom *Cocconeis imperatrix* A. Schm.

This species occurred commonly in the benthos, predominantly forming the diet of a variety of amphipod species (Fig. 13). The size range of 100 individual diatoms taken from the gut contents of *Pontogeneia* spp. (20.10.73, Palmer Station) are shown in Appendices XII and XIII. The species showed a mean length of 22.6 µm. (range 14.0 µm. - 34.0 µm.) and a mean width of 12.4 µm. (range 6.0 µm. - 20.0 µm.).

6.3.5. The defecation and feeding rates of immature and adult *P. antarctica*.

(a) The effects of capture on feeding and gut voiding.

200 non-ovigerous adult female *P. antarctica* were subjected to either starved or fed conditions during the autumn of 1972. The

100 starved individuals were placed in aerated 'Millepore' filtered sea water which was frequently changed to prevent coprophagy. The second batch of 100 were allowed to graze on a diatom felt consisting predominantly of C. imperatrix. Animals were inspected at 0, 6, 12, 36, 48, 60, 72 and 84 hours after their capture and the results, of the percentage fullness of the hind and fore guts, are shown in Fig. 36, where it can be seen that total gut voiding was not achieved until 84 hours after capture. The animals supplied with an abundant food source showed gut voiding for the initial day after capture. This reaction was presumably due to both the gross disturbance during capture and the transfer of animals to different depth, light and temperature régimes (the experimental sea water laboratory operated at + 0.5°C above ambient sea water). This feature of disturbance was present only during initial capture for no such effects could be determined when animals were transferred, in the laboratory, between containers.

(b) The rate of feeding of adult and immature P. antarctica.

Cannibalism in P. antarctica is evident from Appendix IX and Fig. 42. However, in the field, the different phototropism of post-hatchlings and ovigerous adults of this species is believed to be a mechanism for reducing the adult animals' predation of its own young. Bregazzi (1972) commented on a similar feature in gravid Cheirimedon femoratus (an active predator of young P. antarctica (Fig. 42)), and determined that most ovigerous females of this species had empty guts and furthermore showed a distinct avoidance of any food (C. femoratus was normally readily attracted to any protein substance released into the water).

Young P. antarctica post-hatchlings ($\bar{x}$ length 2.18 mm.,

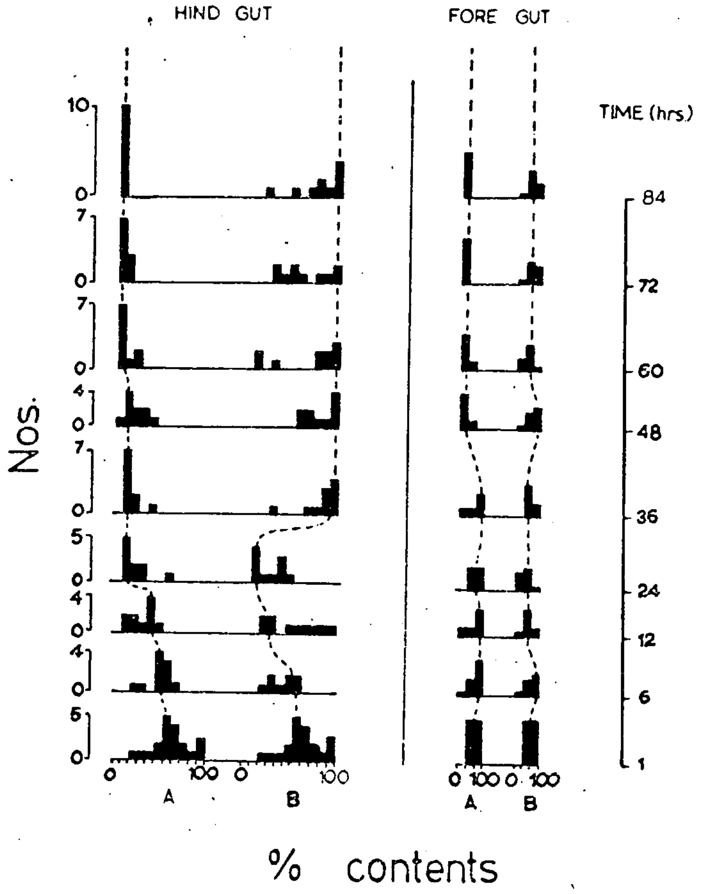


Fig. 36 : The effects of capture and starvation on gut voiding in P.antarctica (A) Starved (B) Fed. Modal values are indicated by the dashed line.

s ± 0.17) were fed to immature and adults of the same species and some results of these investigations are presented in Figs. 37 and 38. Controls consisted of vessels containing the same numbers of 'prey' but no predators (5 controls per 10 experimental vessels). Predation rates varied as a linear function of the size (dry weight) of the predator (Fig. 38), with larger animals eating proportionally less per mg. than smaller individuals. The variation in my data was however considerable (Fig. 38).

The feeding rates of predators increased with greater prey densities, though controls indicated that the mortality of young was also density dependent (young amphipods were observed attacking and killing moulting individuals their own size).

In Fig. 38(a) immatures and (b) adults, the lower and upper lines represent mean control and experimental values of the reductions in prey numbers. The difference (shaded area) is an estimate of the mean number of prey consumed by the predators. This predation rate increased with the prey density of 10 - 60 (0.3 - 2.0 prey/ml.). However, no further increase in predation per time occurred between the densities of 60 - 100 prey amphipods per chamber. The values in Fig. 38 illustrate a three day experimental period. These data are equivalent to the following consumptions (prey/day):

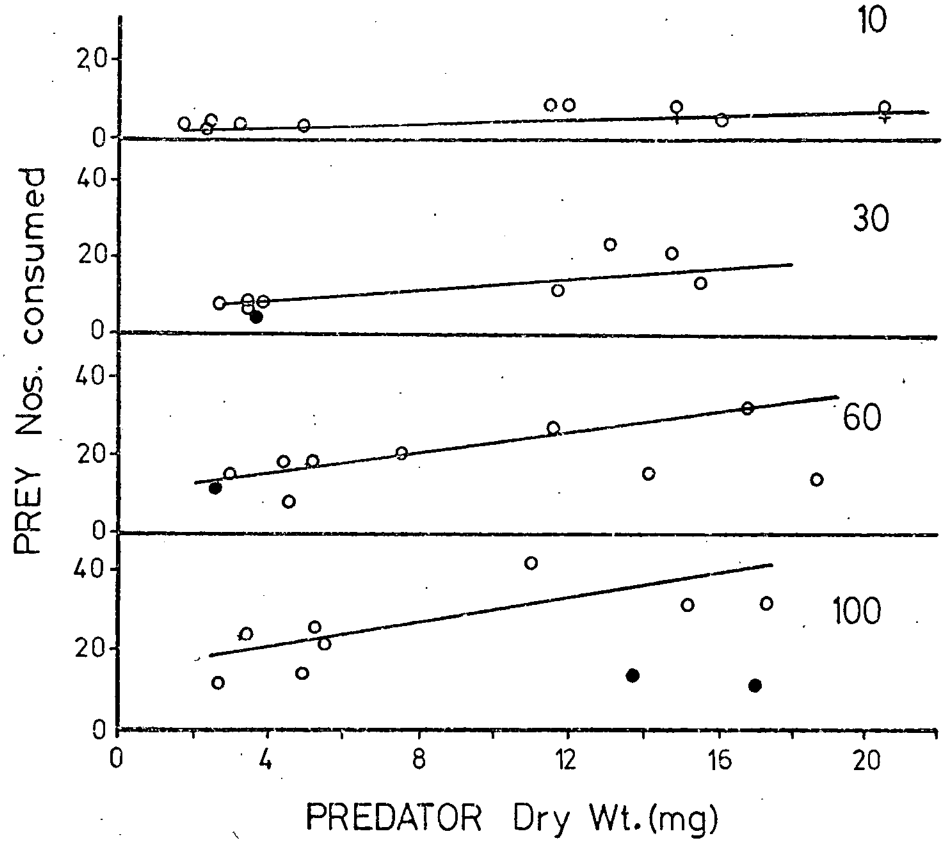


Fig. 37: The cannibalistic predation rate of Pontogeneia antarctica under four prey density regimes.
● males ○ females ♀ ovigerous females.

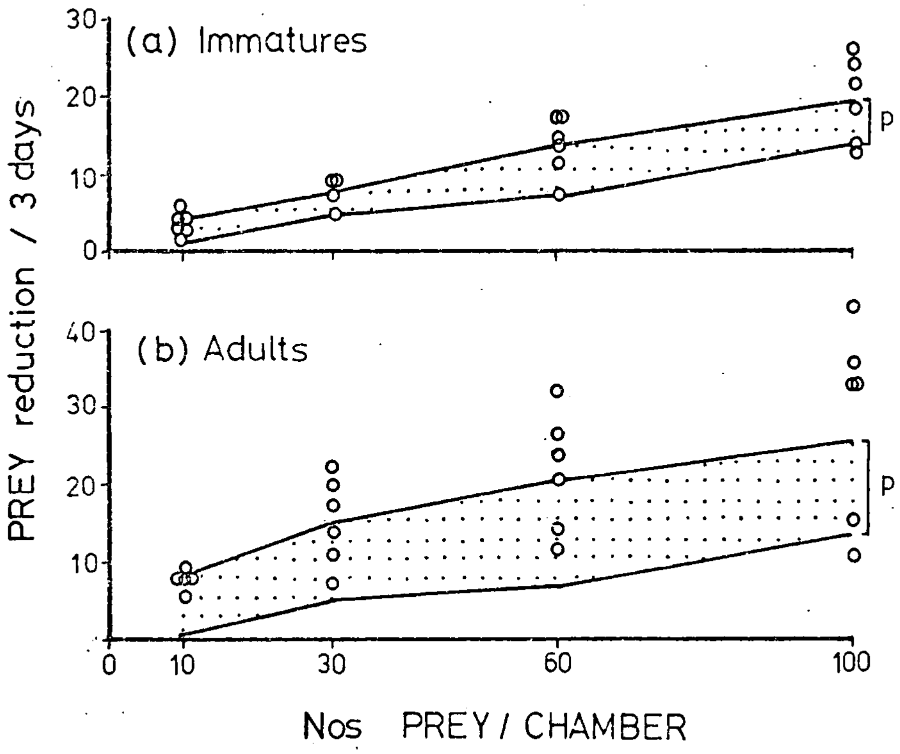


Fig. 38 : The predation loss (p) over three days, after correcting for control values.

	Prey density/ml.			
	0.3	1.0	2.0	3.3
Adult amphipods (>10 mm.) ($\bar{x}$ dry weight = 14.2 mg. s ± 3.1)				
Consumption - rpey/day	2.3	3.3.	4.5.	4.0
-(ug./mg./day)	(158.5)	(226.8)	(309.8)	(275.4)
Immature amphipods (< 10 mm.) ($\bar{x}$ dry weight = 6.3 mg. s ± 2.3)				
Consumption - prey/day	1.5	1.0	2.2	1.8
-(ug./mg./day)	(233.3)	(155.5)	(336.5)	(285.7)

The maximum calorific ingestion rates of adult amphipods were 0.0089kJoules (estimated) or 0.0071kJoules (determined) per day. These values were calculated from the estimated and determined calorific values for Stage VI embryos (8.3.4.). The corresponding values for immature amphipods were 0.0043 and 0.0034. When these values of energy ingestion were corrected to weight specific estimates, figures of 0.00063 or 0.00050kJ./mg. dry weight of adult amphipods per day and 0.00068 or 0.00054kJ./mg. dry weight of immature amphipods per day were calculated.

(c) The feeding rate of post-hatchling *P. antarctica*.

The presence of a virtual monoculture of *Navicula glaciei* on the ice foot in Factory Cove during October and November 1972 enabled some assessment of the grazing pressure of young *P. antarctica* (approximately 2.0 mm. long) to be made. We found that less than one cell in 10^7 was *N. curta*, the commonest 'contaminating' alga (Whitaker and Richardson, in press). Amphipods in known suspensions of non-dividing diatoms reduced Chlorophyll *a* concentrations by the amounts shown in Fig. 39. Values of Chorophyll *a* reduction/day (after correcting for controls) are given in the accompanying Table XXVII. The faecal material of herbivorous crustacea often contains appreciable amounts of plant pigmentation and undamaged plant cells (Shuman and Lorenzen, 1975). This situation has also been reported in amphipods (Hargrave, 1971; Moore, 1975) and is evident in P. antarctica. An examination of the hind guts of 20 individuals, actively feeding on N. glaciei, indicated that on average 17 percent of cells remained undamaged, with the chloroplast material of the cell intact after passage through the gut. Fig. 40(a) and (b) shows the typical appearance of the fore and hind guts of a benthic feeding amphipod.

The acetone extraction and spectrophotometric determinations of Chlorophyll a exclude the Chlorophyll break down products, including the predominant material - phaeophorbide (Shuman and Lorenzen, 1975). These researchers followed the respective decrease of Chlorophyll a and the increase of phaeopigments after the grazing of Coscinodiscus spp. by the marine herbivore Calanus. It has been appreciated in this study that solely using Chlorophyll destruction as a method of determining assimilation can only produce a crude estimation.

It is known that the concentration of food can appreciably affect both the ingestion and assimilation rates and an over abundance of available food produces the phenomenon of 'superfluous feeding' with a subsequent gross reduction in assimilation (Conover, 1966). A decrease in Chlorophyll a destruction per animal with an increasing density of herbivores was evident. Values ranged from 1.22, 0.64 to 0.46 ug. Presumably the higher densities of amphipod reduced their food consumption to a level when ingestion became

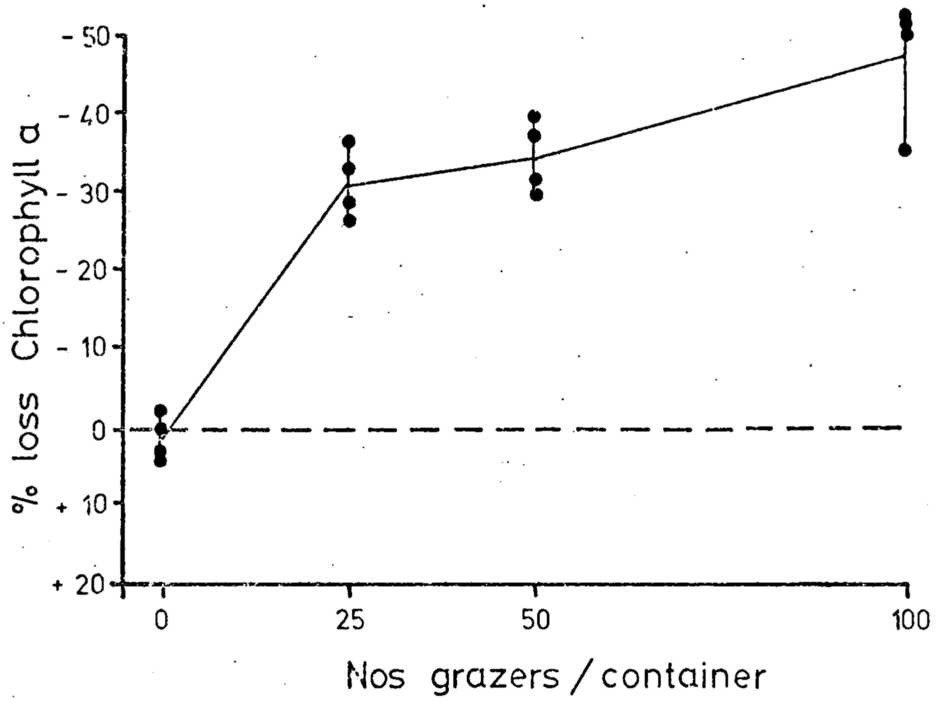
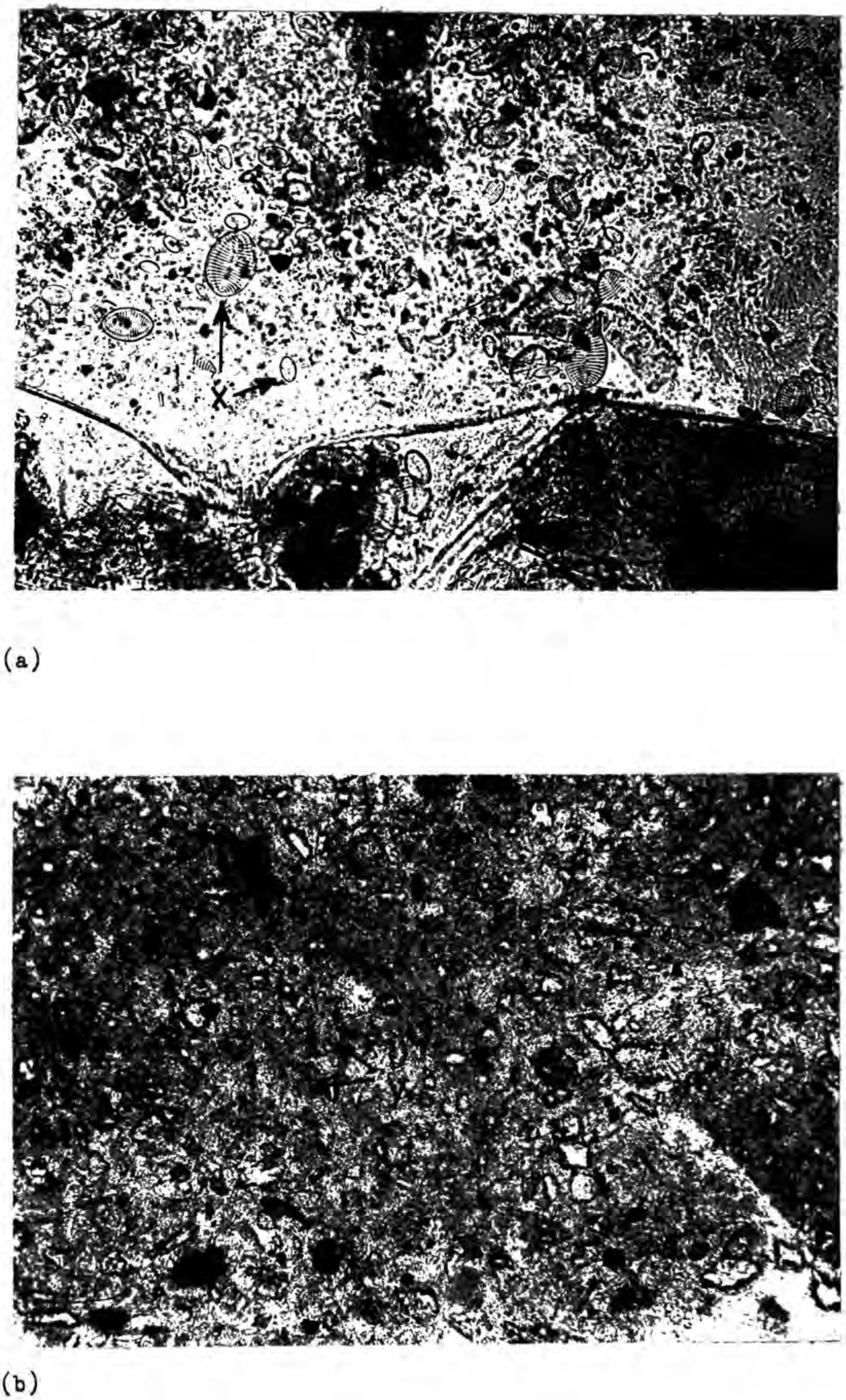


Fig. 39 and Table,XXVII: Chlorophyll a reduction after diatom grazing by *Pontogeneia antarctica* over a two day period.

Grazer No.	(Chlorophyll a levels/L)			$\bar{x}$ Consumption/day (corrected)
	Before	After	Consumption	
25	210.75	133.94	76.81	30.62
	197.42	131.86	65.56	
	182.43	134.64	47.79	
	203.25	144.35	58.90	
50	204.09	123.53	80.56	32.22
	187.43	117.29	70.14	
	179.93	127.70	52.27	
	186.59	127.70	58.89	
100	193.26	92.30	100.96	45.77
	194.92	95.77	99.15	
	193.26	95.77	97.49	
	204.09	121.45	72.64	
Controls	195.76	198.61	+ 2.85	+1.02
	187.43	180.55	- 6.88	
	189.92	191.17	+ 1.25	
	196.59	191.17	- 5.42	



(a)

(b)

Fig. 40 : Photomicrographs of fore (a) and hind (b) gut of P. antarctica feeding on benthic diatoms including Cocconeis imperatrix. Note the macerated appearance of the hind gut contents. (x) C. imperatrix whole cells, (y) C. imperatrix fragments.

progressively 'uneconomic'.

Any errors in the Chlorophyll a method of assessment are towards an underestimation of assimilation rather than the converse. A contrasting method of pre- and post-experimental technique was used to estimate food consumption of the amphipod Hyalella azteca (Hargraves, 1971). In that study, ingestion was determined by comparing the sediment respiration (caused by benthic microflora) on grazed and ungrazed substrates. Inherent in that work were problems of the respiration of the microflora in the crustacean faeces and the nutrient enrichment and mechanical alteration of the sediments by these grazers. Naturally, all these features would require careful calibration. Hyalella consumed 0.12 cals./day (Mathias, 1967)*, an increased ingestion rate compared to the values derived in the previous section for adult P. antarctica. I believe this comparatively elevated consumption can be attributed to (a) an observed decreased food intake by the P. antarctica adults during winter and (b) the presumably relatively increased metabolism of H. azteca due to its smaller size (approximately 700 to 800 μg. dry weight).

Taking the daily consumption rates of P. antarctica post-hatchlings, assimilation equivalents per day are estimated as:

	(min.)	(max.)
Cell numbers	2.08×10^6	5.56×10^6
Particulate Carbon	18.66 μg.	49.92 μg.
Joules (kJ.)	0.688	1.841

Because the mean dry weight of P. antarctica young is approximately 15 percent of that of H. azteca, the calorific ingestion is correspondingly increased with daily particulate Carbon intake (μg.) at a level equivalent to three quarters of the amphipod's

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* quoted by Hargraves (1971)

dry weight.

The few results available (5.3.1.) indicate a mean dry weight of 4.36 g. post-hatchling amphipod/m ^{2} of ice (in the immediate tide crack area). This crustacean biomass would daily consume the Chlorophyll a equivalent of 15.58 mg. The concentration of N. glaciei on the ice foot and its immediately surrounding water reaches maximum levels of 244 mg. Chlorophyll a/m ^{2} and 7.5 mg/1. (7.5g./m ^{3}). Supplies of food do not therefore appear to be a limiting factor during the initial period of post-release growth. It must however be pointed out that densities of amphipods were more normally in the region of 3,000 to 4,000/m ^{2} whilst the mean Chlorophyll a extracts of ice core samples (Whitaker and Richardson, in press) indicated that, presuming (a) the diatom population was self replenishing per day and (b) that other grazers in the habitat were insignificant (which they were), then the sea ice in the tide crack or ice foot region could support 2,200 or 5,900 post-hatchlings/m ^{2} at these determined minimum and maximum feeding levels.

6.3.6. Parasitism.

Intestinal parasites were present in most of the amphipod species investigated. 6 of the 16 species examined possessed nematodes (parasitic and not food prey [Fig. 13]) and it is interesting to note that nematodes were more prevalent in the active predator species B. gigantea and A. magellanica. Although considerable numbers of P. antarctica were examined, few parasitic nematodes were recorded (Table XXI).

Intestinal gregarines were however common in the lumen of the gut of most species (Fig. 13) with parasite species apparently specific to hosts. The degree of infestation was rarely high (+++) and Table XXVII indicates the infestation in P. antarctica. Gregarines were less common in young amphipods and most small individuals (88 percent) were free of the parasites. No amphipods in the 2.0 to 3.0 mm. size range contained any gregarines. The degree of infestation reached 52 percent in medium sized amphipods (5.0 to 9.9 mm.) with 15 percent of specimens indicating a moderate to heavy attack. Bone (1972) noted a 100 percent gregarine infestation in a small sample of B. gigantea whilst trophozoites of the genus Rotundula (?) were identified in the intestinal lumen of Paramoera walkeri (Rakusa-Suszczewski, 1972).

Fig. 41 illustrates bi-associated or single sporadins (gregarine trophozoites do not divide) from the intestinal lumen of P. antarctica. The parasite was not identified but the size range of the cells (80 to 130 µm.) and the apparent lack of an epimerite indicates the genus Cephaloidaphora (family Cephaloidophoridae) rather than Gregarina spp. (family Gregarinidae) which tend to be parasites of land arthropods (orthoptera etc.) (pers. comm. H. Smith) with cells attaining lengths up to 500 µm. (Watson, 1916).

Some of the effects of gregarines on their parasitised hosts have been outlined in the papers of Kamm (née Watson) (1917; 1920-21). Whilst localised damage to the intestinal epithelium, especially in the mid-gut region, may occur, few infestations result in major changes in behaviour, ecology or physiology. Such changes may be induced however by the substantially larger juvenile stages of acanthocephalid worms. The infestation rate of this parasite was comparatively low (<0.5 percent) in mature P. antarctica. The effects of these parasites can be considerable on the host animal and the research of Rumpus (1973) deals

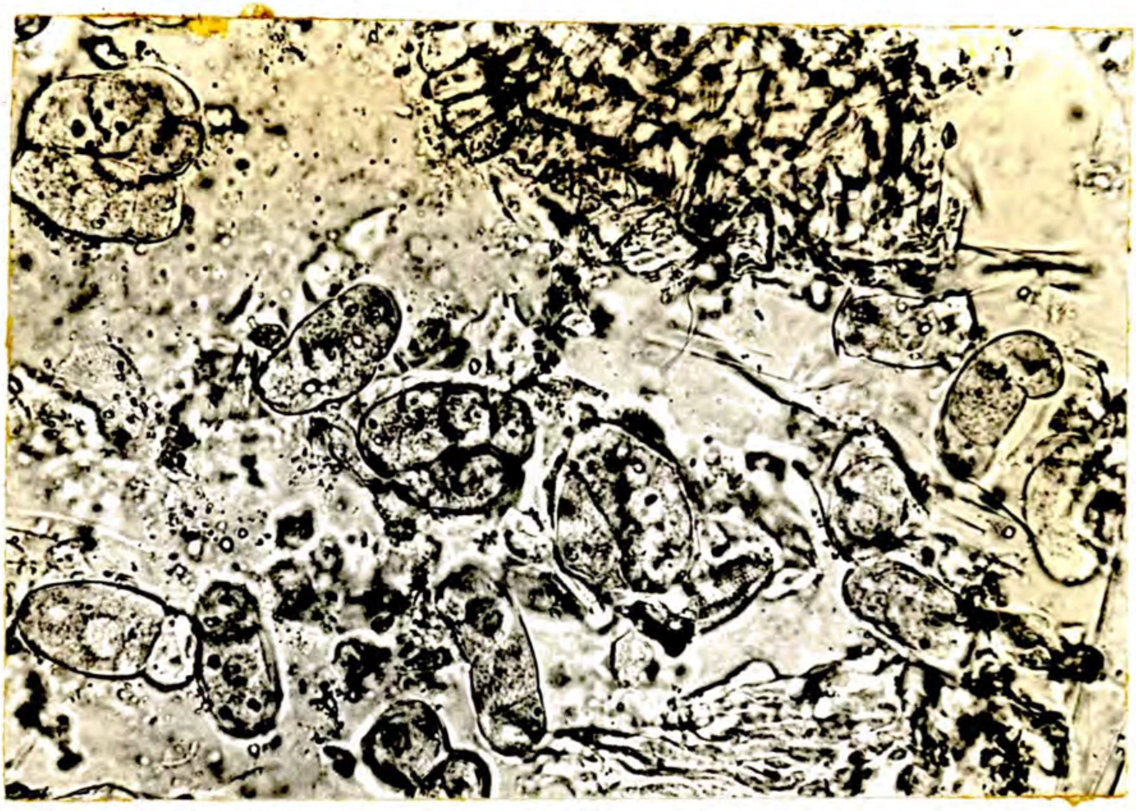


Fig. 41 : Bi-associated or single sporadins of Gregarinda from the intestinal lumen of P. antarctica.

Table XXVIII The Gregarinda infestation rate of P. antarctica.

% Occurrence

Infestation		Amphipod length (mm)		
		2.0-4.9	5.0-9.9	10.0 +
Absent	o	88.4	59.5	66.7
	+	11.0	27.0	27.4
Present	++	0.6	13.5	6.0
	+++	-	1.4	-
	n =	173	74	84

in part with the ecological and physiological implications of acanthocephalid infestation on Gammarus. It may be that some of the variation in respiration rates obtained from P. antarctica was due to the effects of parasites, of one type or another, outlined by Rumpus and Kennedy (1974).

6.4. Discussion:

'Opportunistic feeding', or a degree of non-selectivity of food material, was a major feature of the grazing of P. antarctica. It is known that certain amphipods exhibit a strict selectivity in their diets (Moore, 1975; Gammarus pulex - microalgae; Bärlocher and Kendrick, 1973: Gammarus pseudolimnaeus and Kostalos and Seymour, 1976: Gammarus minus - fungi and leaf detritus). The varied past references to Gammarus feeding (Margalef, 1948: Clemens, 1950 and Deksbakh and Sokolova, 1965) indicate that whilst food preferences can exist (if a choice is available) many amphipod species have adapted an advantageous flexibility in their feeding régimes.

Microalgae, predominantly the diatoms, comprised the natural diet of adult Pontogeneia antarctica, though the results indicate that a wide range of plant and animal material was regularly consumed. These results have all been synthesised into the diagram (Fig. 42). Diatoms were also the major element in the diets of other antarctic amphipods (4.3.1.) and of the benthic grazing echinoid Sterechinus neumayeri (Pearse and Giese, 1966). It is apparent that the degree of selectivity in feeding is governed, in part, by the amphipod's size (Appendix IX) and it is this diminished selectivity and the lack of any suitable benthic foods for the small post-release

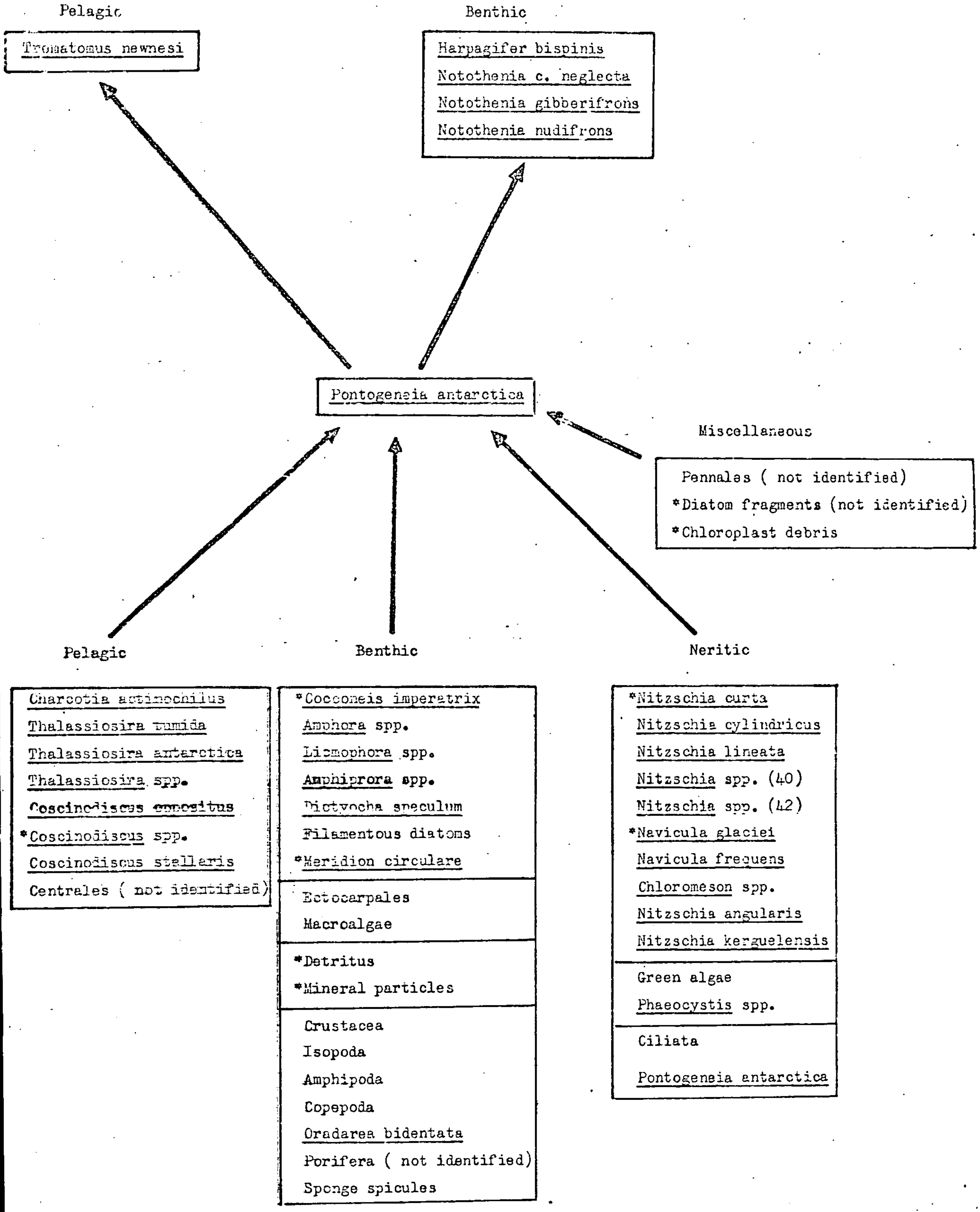


Fig. 42 : The recorded food web of the amphipod Pontogeneia antarctica.

hatchlings, that motivates the distinctive winter migration of this amphipod to the undersurface of the sea ice. Selectivity is also governed by mouthpart morphology, for instance, the adnate diatom *Cocconeis imperatrix* is an important component of the diet of *P. antarctica*, yet Moore (1975) specifically indicated that the similar sized *G. pulex* was incapable of dislodging *Cocconeis* spp from its substrate. Though the winter cryopelagic existence of *P. antarctica* and *Paramoera walkeri* has been documented (Rakusa-Suszczewski, 1972; Richardson and Whitaker, in press), it would be valuable to know how widespread this ice-associated phenomenon is in the polar seas. Barnard (1959) indicated that amphipods were commonly present under the pack ice in the pelagic Arctic. However, whilst dense populations of *P. antarctica* and the diatom *N. glaciei* were observed at Signy Island during the consecutive winters of 1972/73 and 1973/74, both the winters concerned were meteorologically unusual because of their low ambient temperatures and stable, long-lasting sea ice. It is known that diatom populations fluctuate widely from year to year both in their concentrations and species composition, with these oscillations depending on the prevailing sea water conditions (Whitaker, pers. comm.). Horne et al. (1969) reported that during their preliminary study in Borge Bay (1966), the phytoplankton contained a mixture of diatom species: *Corethron criphyllum*, *Fragilariopsis* (*Nitzschia*) spp. and *Thalassiosira antarctica*. By comparison, in the following year, the chain-forming diatom *Biddulphia striata* was virtually the only species present in the water column. It is interesting to speculate, knowing the feeding capabilities of *P. antarctica*, whether populations of this amphipod also fluctuate considerably depending on the availability of species of phytoplankton or neritic diatoms or, alternatively, whether the particularly catholic feeding preferences of P. antarctica would allow the animal to turn exclusively detritivorous. The latter is more probable.

White's hypothesis (1975) of energy expenditure in antarctic poikilotherms was based on the presumption that, whilst metabolism (respiration) was relatively elevated in relation to temperature, the feeding activity of polar species was approximately of the same order as temperate animals. Temperature certainly appears to affect feeding activity in temperate amphipods, for instance, gut voiding of G. pulex varied from 18 to 40 hours with the respective temperatures of 5.0 and 15.0°C, and Moore (1975) noted that survival of the algae (in faeces) was always greater in winter than in summer probably reflecting the effect of low water temperatures on the digestive efficiency of these animals. Of course in this instance the experimental animals existed in a relatively constant, if low, ambient temperature.

Amounts of food consumed are often directly related to the amounts of food available (Breteler, 1975) and this situation is mirrored in my data for P. antarctica. This feature can give rise to the phenomenon outlined by Conover (1966) of 'superfluous feeding'. This type of activity has been observed in P. antarctica when grazing on the littoral filaments of Urospora/Ulothrix (Fig. 34[a], [b]). Chlorophyll a, in passing through the guts of Crustacea, is converted to the green pigments of phaeophytin and phaeophorbide (Yentsch and Menzel, 1963); however, the intact cells of Uraspora/Ulothrix in the faeces of P. antarctica indicated such minimal assimilation.

Feeding experiments conducted on P. antarctica, though crude, pointed to the fact that assimilation was of the same order of magnitude as that of temperate species (Mathias, 1967) though ingestion rates in some temperate amphipod species do appear elevated: for instance, Clemens (1950) observed that G. fasciatus could consume up to 52 Daphnia magna per day!

Despite the subjective nature of the observations it is evident that P. antarctica was a non-selective feeder, consuming detrital, algal or crustacean material within a broad range of particle sizes, according to their availability. This omnivorous feeding combined with protracted hatching release and migration to the sympagic food source present during winter, enhanced the young amphipods' chances of survival in a variable environment. It would appear that contrary to the observations of Barnard (1959), sea ice certainly affords a very attractive habitat for animals capable of survival at low temperatures. It also enables various activities such as growth, reproduction and the release of hatchlings to take place earlier in the year than would otherwise be possible.

Chapter 7 The Embryological Development of Pontogeneia antarctica.

7.1. Introduction:

Despite numerous published statements concerning cold water embryological development, the number of studies which have investigated in any detail the growth of ova of antarctic crustacea (the Amphipoda in particular) are few. Indeed the reproductive biology of southern water amphipods is still little understood. Thurston (1970) described aspects of the reproduction and embryology of the large amphipod Bovallia gigantea emphasising the characteristic extended brooding period. This species received further attention from Bone (1972) though detailed investigations into embryological development were not undertaken. The only other epifaunal species which has been studied is Paramoera walkeri (Rakusa-Suszczewski, 1972).

Detailed embryological descriptions of development in antarctic amphipods are restricted to the studies of Bregazzi (1973) who worked on the two infaunal lysianassids, Cheirimedon femoratus and Tryphosella kergueleni. To date, no study has gone into more detail than the comprehensive descriptions by this author, though similar accounts are available for temperate species, for instance Gammarus duebeni (Steele and Steele, 1969). The results presented here are intended to enlarge on Bregazzi's initial work by following the embryological development of P. antarctica in certain biochemical terms.

7.2. Materials and Methods:

7.2.1. Classification.

Amphipod eggs were divided into arbitrary development stages based principally on the five categorisations adopted by Thurston (1970) for *Bovallia gigantea*. The embryological development of *Pontogeneia antarctica* was however best described by six arbitrary stages. These were as follows:

Stage I: Ovum showing multiple division of the egg but no gross organ differentiation.

Stage II: Initial segmentation of the early embryo apparent.

Stage III: Embryo showing rudimentary limbs, somites and eyes.

Stage IV: Late embryo with limbs complete, articulated antennae fully developed and eyes with colouration.

Stage V: Completely developed embryo still bound within egg membrane.

Stage VI: Embryo hatched from egg membrane but still retained within the marsupium of the ovigerous female.

The stages of ova differentiation outlined by Thurston (1970) were followed by Bone (1972) and Bregazzi (1973). In *P. antarctica*, Stages V and VI are certainly very similar, separated only by hatching. I have inferred that Stage V in previous studies was lumped with Stage IV; though alternatively, certain handling methods of females bearing late embryos may have induced premature hatching. Some previous studies used solely preserved material (Thurston, 1968; 1970). The duration of Stage V is very short (Fig. 45) and consequently this stage is absent from the results of some investigations presented here. This was due to the difficulty of obtaining sufficient ovigerous females bearing this egg stage. (Prior to one respiration experiment, Stage IV embryos were found to develop and hatch within the acclimation period of two days.

Eggs were collected from ovigerous females by the methods described in 8.5.1. Measurements of live ova were made to the nearest 0.02 mm. using a dissecting microscope (x 50) equipped with an eye piece micrometer. Weights were obtained using either a Beckman or Cahn gram, Model G electro microbalance. The descriptions of analytical methods are presented under their relevant sections.

7.3. Results:

7.3.1. The description of development.

Embryological development is summarised by the arbitrary stages illustrated in Fig. 43. The eggs of *P. antarctica* were coloured deep orange and oil droplets were readily apparent within the coloured lipid body. The ova possessed a single egg membrane.

The colour and shape of eggs varied little between individuals of the species, and the size of the eggs (Table XXIX) and stage of development from the same brood were very similar. Less than 5 percent of the clutches examined possessed eggs from more than one development stage. Egg size (volume) was however variable between different sized females though no significant correlation was discerned between ovigerous female size (length^3) and egg volume (mm^3). The data of Table XXIX are derived from measurement only of Stage I eggs whose volumes were calculated from the relationship:

$$V = \frac{1}{6} \pi \, l w^2$$

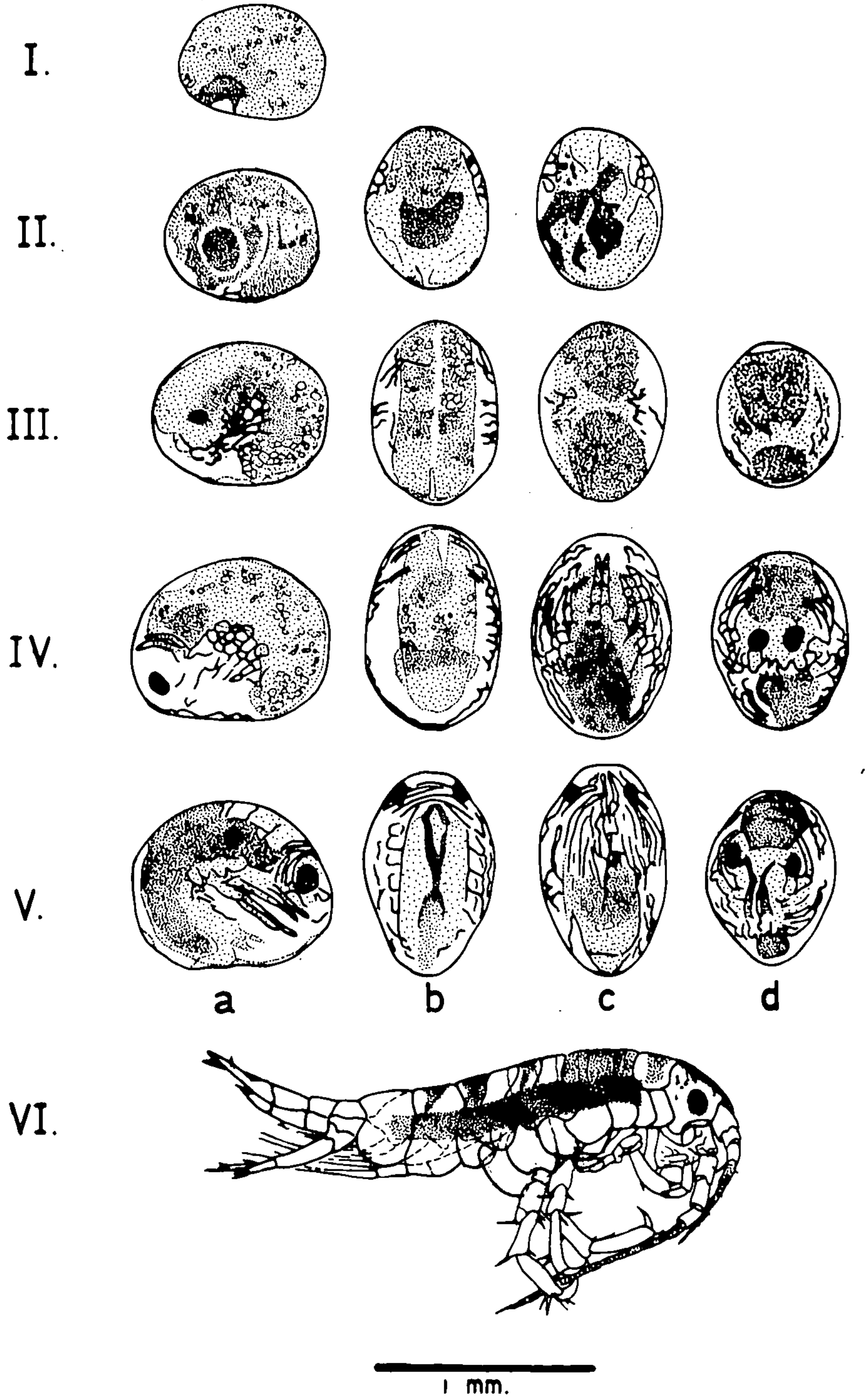


Fig. 43 : Six stages of ova development of <u>P. antarctica</u>.

Illustrations:

a. lateral

b. dorsal

c. ventral

d. anterior

l		w		$1/6\pi l w^2$	
$\bar{x}$ length (mm)	range	$\bar{x}$ width (mm)	range	$\bar{x}$ volume (mm^3)	range
0.73	(0.66 - 0.82)	6.56	(0.54 - 0.62)	0.120	(0.101 - 0.165)
6.73	(0.68 - 0.77)	0.58	(0.56 - 0.60)	0.129	(0.115 - 0.141)
0.73	(0.71 - 0.78)	0.59	(0.57 - 0.61)	0.133	(0.125 - 0.141)
0.73	(0.69 - 0.75)	0.59	(0.57 - 0.62)	0.133	(0.125 - 0.151)
0.74	(0.68 - 0.79)	0.58	(0.56 - 0.64)	0.130	(0.115 - 0.156)
0.74	(0.72 - 0.76)	0.58	(0.56 - 0.60)	0.131	(0.115 - 0.141)

Table XXIX: Size variation within and between clutches of *Pontogeneia antarctica* (Stage I eggs).

where l and w are length and width of eggs respectively (Thurston, 1968).

The individual egg volumes of small ovigerous females tended to be smaller than average (Table XXX) though a few of the larger ovigerous females (> 15.9 mm.) also possessed these smaller eggs. The egg volume between the smallest and largest recorded Stage I ovum varied by the factor 1.63.

The egg volume also increased during development as can be seen in Fig. 43 where all illustrations are drawn to the same scale. The mean length:width ($\frac{l}{w}$) ratio for Stage I eggs was 0.81 (S.D. ± 0.03). This ratio altered as follows:

Stage II - 0.86, Stage III - 0.87, Stage IV and Stage V - 0.86.

Length thus increased at a proportionally lesser rate than width (Kanneworff, 1965). The relative volumes of different egg stages are given in Table XXXI where egg volume $(V) = \frac{1}{6} \pi lwb$ (where b = breadth).

Egg volume increased by 208 percent between Stages I and IV. This value is greater than that reported by Bregazzi (1973) for Cheirimedon femoratus and Tryphosella kergueleni, though Thurston (1968) records a threefold increase in volume in B. gigantea eggs. Increase in egg size is a feature common to amphipod development (Steele and Steele, 1970(a); (b); (c); 1969: Rakusa-Süszczewski, 1972). Many authors have used only embryo length as a measure of this increase, and have taken no account of the various changes in shape throughout development. Immediately prior to embryo release the marsupia of all ovigerous females were greatly distended with the oostegites spread wide. It has already been established

Date	ovigerous ♀ (length^3)	Egg measurements l length (mm)	w width (mm)	$^1/_6 \pi lw^2$ volume (mm^3)	
13.9.73	419	0.66	0.54	0.101	I
13.9.73	553	0.64	0.57	0.107	
26.11.73	605	0.70	0.57	0.119	
13.9.73	623	0.69	0.56	0.113	
26.11.73	677	0.68	0.56	0.112	
28.6.73	1776	0.76	0.61	0.147	II
24.7.7	1816	0.70	0.60	0.134	
28.6.73	2000	0.78	0.61	0.153	
27.6.73	2078	0.73	0.58	0.129	
24.7.73	2122	0.76	0.60	0.142	
27.6.73	2243	0.81	0.62	0.165	
24.7.73	2881	0.75	0.60	0.140	III
28.6.73	3402	0.76	0.60	0.145	
27.6.73	3804	0.75	0.60	0.139	
20.8.73	3922	0.66	0.56	0.110	
20.8.73	3982	0.70	0.57	0.120	

Table XXX Egg sizes of *Pontogeneia antarctica* in relation to the volume (length^3) of ovigerous females, I, small, II medium, III large.

Stage	I	II	III	IV	V
$\bar{x}$ volume	0.130	0.189	0.224	0.330	0.269
S.D. ±	0.0159	0.0305	0.0391	0.0207	-

Table XXXI Mean egg volumes of *Pontogeneia antarctica*;

that mortality of embryos during brooding is measurable and it is believed that the prime factor determining fecundity in amphipods is the volume of Stage VI embryos in relation to marsupial volume.

As development proceeded the amount of orange lipid body within the embryo decreased appreciably until at release the orange fat body was confined to a small quantity within the hind gut.

7.3.2. The duration of development.

The embryological development in antarctic Crustacea is lengthy in all species investigated so far. White (1970) noted that the large isopod *Glyptonotus antarcticus* bred throughout the year with a brooding period of 577 - 626 days. Thurston (1968) estimated a seven months brooding period in *Bovallia gigantea*, a far longer time than previously reported for other amphipods, though Barnard (1959) had recorded an extended brooding time of 5 - 6 months for the large *Gammarus wilkitzkii* which lives in the Arctic. The relict amphipod *Pontoporeia affinis* from the benthic depths shows a similarly long brooding period of 5 - 6 months (Segerstråle, 1967; 1970). Subsequent work has shown that lengthy brooding periods are common in antarctic amphipods, for instance *Cheirimedon femoratus* (115 days), *Tryphosella kergueleni* (97 days) (Bregazzi, 1973) and *Paramoera walkeri* (approximately 4 - 5 months) (Rakusa-Suszczewski, 1972). Thurston (1972) has commented on lengthy brooding periods for a further 14 species. This author has also attempted to categorise the breeding strategies of antarctic Amphipoda. Most species produce a single brood per year, releasing their young during early spring, whereas some species are capable of producing two broods per year. As already described, *Pontogeneia antarctica* followed this latter course. The synchronous release of young appears to be a feature common to many antarctic poikilotherms. Pearse (1963; 1964) noted that early spring release was present in both the asteroid *Odontaster validus* and the amphipod *Orchomenella plebs* and explained this strategy as an adaptation to the time of maximum food availability. Further information has been presented in 9.3.4.(b) for the bivalve *Lissarca miliaris* on larval release and this feature will be discussed later. Certainly, optimum food periods need to be utilised if adequate larval survival is to be maintained. Such synchrony is also more important if brooding is extended and fecundity thereby reduced.

The timing of reproduction of 525 ovigerous females of *Pontogeneia antarctica* are shown in Tables XVII and XXXII. Gravid females appeared during May and young hatchlings became more frequent in the population from mid August onwards. (Aspects of general reproductive biology received preliminary attention in Chapter 5.)

To parallel the results from examinations of ovigerous females, attempts were made to incubate eggs independently of parent females. Early Stage I eggs were collected during 1972 from females and placed in small incubation chambers. These were of two types:

1 - Small 5 ml. 'Jorgensen' glass vials covered with fine (0.1 mm.) mesh and set upright in racks.

2 - Glass crucibles fitted with specially prepared net containers (Fig. 44).

The water supply to the incubating chambers was passed through fine bolting silk to remove possible crustacean predators (including

(a)

Date	I	II	III	IV	V	VI	(n)
14.5.72	60						60
23.5.72	60	2					62
4.6.72	41	25					66
13.6.72	30	24	6				60
19.6.72	5	27	27	1			60
27.6.72	6	12	19				37
15.7.72		2	47	4			53
						Total	398

(b)

21.9.72	50	10					60
29.9.72	50	10					60
13.10.72	40	10		10			60
26.10.72	5	25	10	10			50
						Total	230

TableXXXII Development duration of <u>Pontogeneia antarctica</u> ova from incubation experiments II (see text) (a) and (b) June and September respectively.

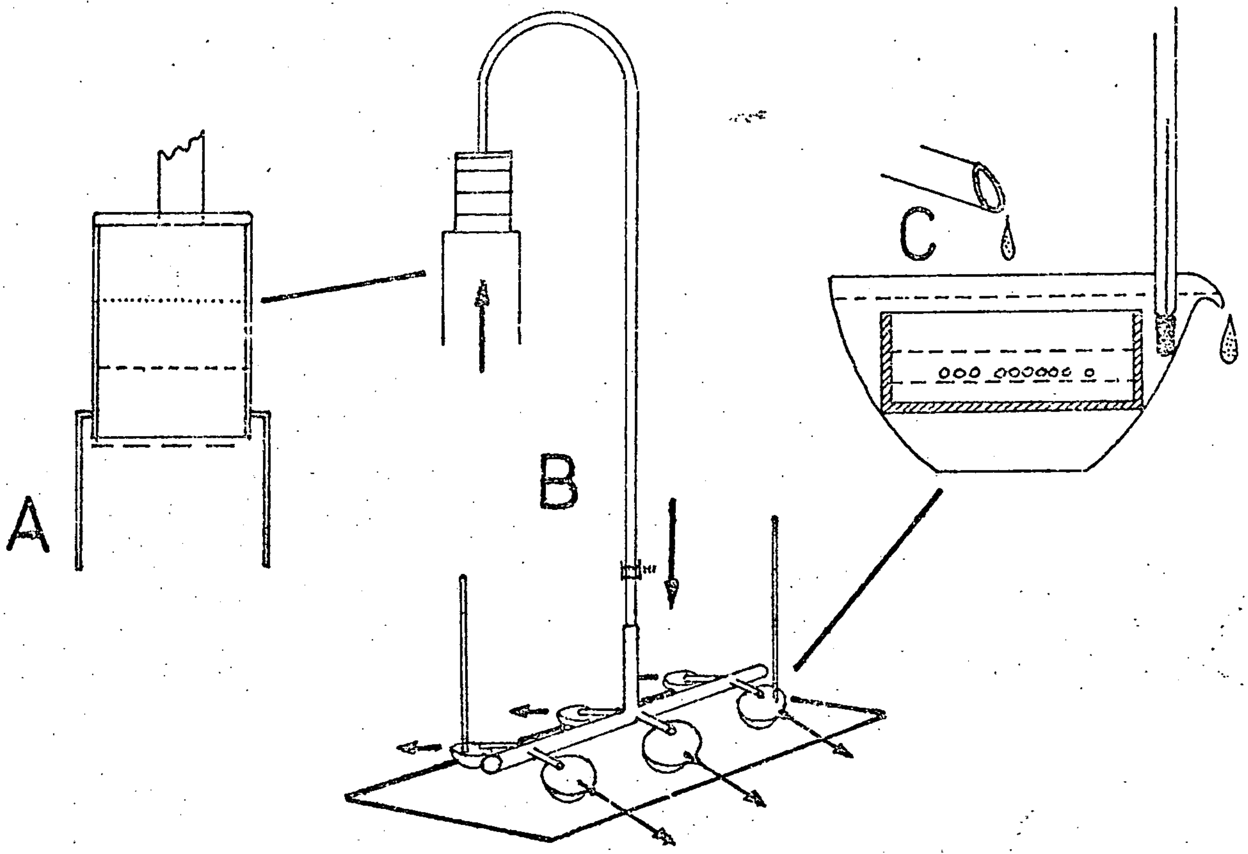


Fig. 44 Incubation apparatus used in embryological studies of *Pontogeneia antarctica* ova.

A. Three phase water filter employing (a) coarse netting 3mm mesh, 38 GGN and 60 GGN netting.

B. Apparatus assembly with six incubation containers and two thermoneters.

C. Individual incubation container using two layers of 60 GGN netting.

copepods) and large 'blanketing' diatom species. The temperature ($\pm$ 0.5°C) of experimental tanks was closely monitored. Experiments were set up as follows:

Experiment I. 30 clutches of Stage I eggs were stripped from ovigerous females on 16.5.72 and broods were placed separately in numbered 'Jorgensen' containers.

Experiment II. Six crucibles, each with 300 Stage I eggs,were set up on 13.5.72 and 16.5.72 and again during September 1972. The containers of experiment I were placed in an aquarium supplied with a flow of running sea water (approximately 0.25°C above ambient). The containers of experiment II received individual drip feeds of filtered sea water (Fig. 44).

The intention was to (a) inspect experiment I at weekly intervals under a x50 dissecting microscope (in the cold) and (b) remove 10 eggs from each crucible container at weekly intervals and inspect for Stage and size.

Experiment I proved to be an almost total failure, most eggs being dead by 4.6.72. Mortality was high even by 26.5.72 (10 days after the experiment was set up) with a mean percentage death rate of 73 percent.

The results of experiment II are shown in Table XXXII(a) and (b) for the June and September series. The data from examinations, both of ovigerous females and incubation studies, have been interpreted in Fig. 45 as a time schedule for the development of <u>P. antarctica</u>. This picture is not wholly conclusive and is regarded here as a tentative estimate. Brooding took an estimated 18 weeks, or a similar incubation time to that reported by Rakusa-Suszczewski (1972) for <u>Paramoera walkeri</u>. The length of time that hatchlings

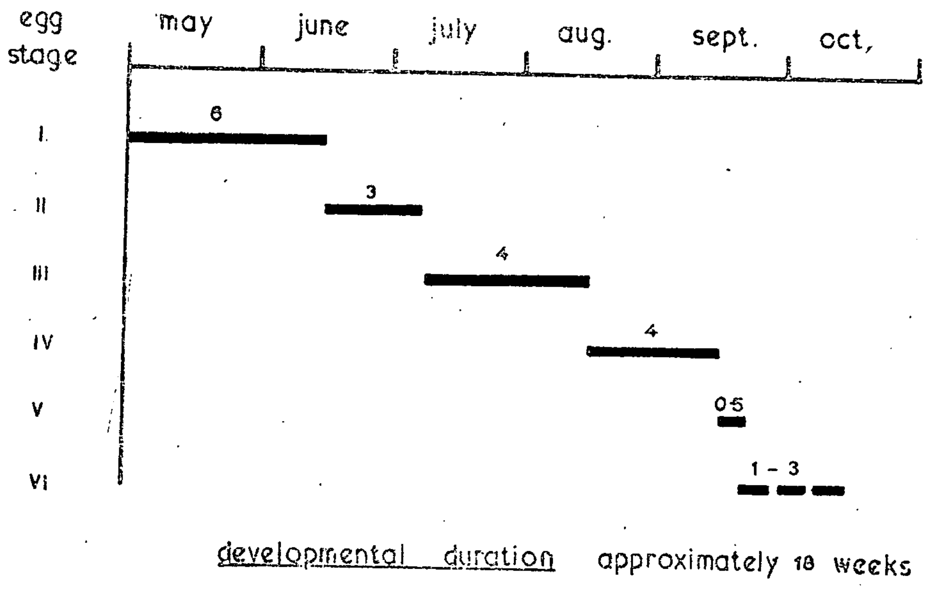


Fig. 45 : Schematic diagram of the duration of embryological development in P. antarctica.

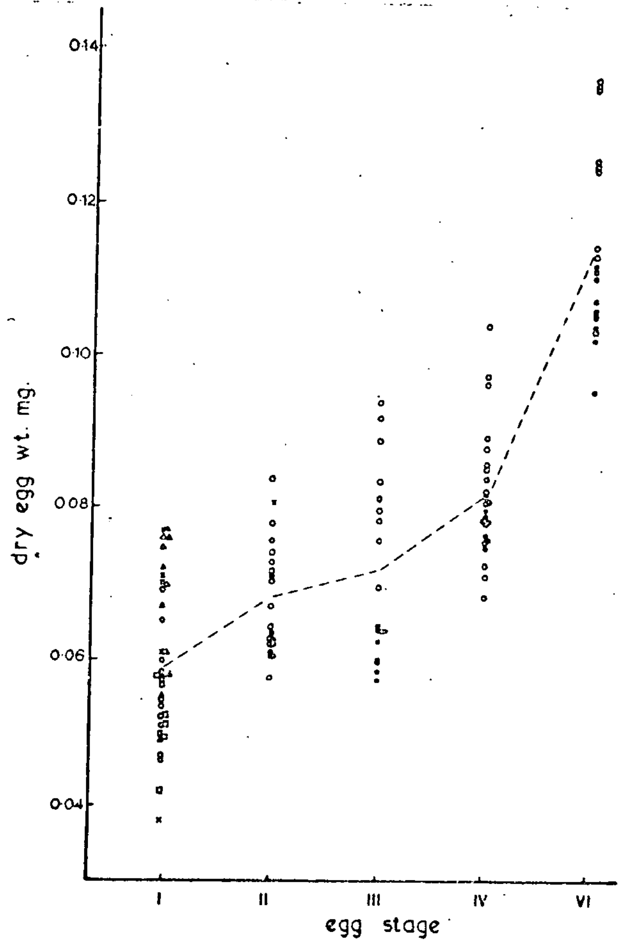


Fig. 46 : Dry weight increase of amphipod ova during development.

were retained within marsupia was never discerned, although Vlasblom (1969) indicated that post hatching retention within the oostegites could be considerable, the young apparently growing and moulting during this period. Because all Stage VI young examined were of similar sizes, this retention period probably does not occur in *P. antarctica*. Certainly no Stage VI embryos were observed feeding whilst in the marsupium.

A feature peculiar to artificial incubation appeared to be that whilst dry weights (W) increased after the trend described in section 7.3.3., the volumes of incubating eggs decreased between 21.9.72 and 13.10.72 (Table XXXIII). Heavy mortality was due to eggs becoming smothered in either small diatom species or attacked by what appeared to be fungal hyphae. A similar feature occurred with incubation experiments using *G. antarcticus* eggs (White, pers. comm.).

7.3.3. Embryological weight changes.

Increased volume changes during development are paralleled by increasing weights between ova stages. Pandian (1970) showed that there was a similar relationship between the uptake of water and inorganic salts throughout development of the lobster *Homarus vulgaris* with the percentage water content altering appreciably from 54.0 percent in egg Stage I to 83.1 percent at Stage V. Water content was shown to be a joint feature of both water uptake and metabolic oxidation processes. The evidence suggests that the absorption of water is a function necessary to development (Zeuthen, 1961), with particular relevance to hatching. Unfortunately no wet weight measurements were made throughout the development of *Pontogeneia antarctica* though a mean percentage water content of

	Egg Stage																
	I					II					III		IV				
Date	l	b	w	V	W	l	b	w	V	W		W	l	b	w	V	W
21.9.72	0.81	0.70	0.71	0.210		0.69	0.62	0.62	0.140								
29.9.72	0.66	0.53	0.53	0.097	0.0638	0.72	0.59	0.59	0.130	0.0618							
13.10.72	0.66	0.52	0.54	0.097	0.0664	0.64	0.54	0.54	0.101	0.0769			0.74	0.61	0.60	0.140	0.0825
26.10.72	not measured				0.0764		(nm)			0.0759	(nm)	0.0838		(nm)			0.0908

Table XXXIII: Mean weight and volume changes for ova under incubation régimes. Where l, b and w = length, breadth and width (mm) rsepectively, V = volume (mm^3), W = weight (mg)

Stage I eggs was recorded as 58.9 percent (S.D. ± 2.2 percent).

The weights of eggs were obtained after drying at 80°C and storing under vacuum. Values were recorded from either individual ova, for instance after Cartesian diver experiments, or alternatively, eggs were batched into lots of five. These results are shown in Fig. 46 and the means with standard errors for egg stages in Table XXXIV. Dry weight increased by 96 percent between Stages I and VI with the largest incremental increase taking place between Stage IV and VI. These data are contrary to those describing the development of the lobster embryo, where a drop of 20.1 percent over the initial egg dry weight of 1.54 mg. (Stage I) was recorded (Pandian, 1970). This loss of weight was attributed by that author to both respiration consumption and the loss of egg membranes. Zeuthen (1961) also recorded egg weight losses in the eggs of the urchin Psammechinus microtuberculatus.

The uptake of inorganic salts is a common feature in crustacean development and Pandian (1970) has quantified this uptake. Salts are continually taken up throughout development though the rate of uptake accelerates towards the later periods of development as the demand for inorganic salts for limb and cuticle formation intensifies. In P. antarctica the dry weight increases cannot be attributed solely to inorganic salt incorporation. Table XXXIV also presents values for ash free weight increases and the corresponding cumulative percentage increase diverges from the comparative percentage increase of dry weights. Percentage ash weight increased from 4.09 percent (Stage I) to 17.88 percent (Stage VI). (Ash weights were obtained from the residues after ignition of samples in a Perkin - Elmer elemental

Egg Stage	$\bar{x}$ dry wt.(mg)	$s/\sqrt{n}$	n	$\bar{x}$ Ash free	% Running increases (dry wt)	% Running increases (Ash free)
I	0.0589	0.00168	37	0.0565		
					16.0	16.5
II	0.0683	0.00763	20	0.0658		
					21.7	20.9
III	0.0717	0.00280	19	0.0683		
					38.9	32.4
IV	0.0818	0.00168	26	0.0748		
V		not measured			95.9	67.8
VI	0.1154	0.00284	19	0.0948		

TableXXXIV: Dry and Ash free weight changes during embryonic development of <u>Pontogeneia antarctica</u>.

analyser. Ignition temperatures were in the region of 900°C). The percentage ash increases are presented in Fig. 48. These values are very similar to those described for the lobster (Pandian, 1970) which varied from 2.7 to 16.7 percent.

7.3.4. Biochemical changes during embryo development.

(I) The results of elemental analysis.

Batched samples of 300 eggs or embryos were isolated from ovigerous females, rapidly freeze-dried at - 40°C and stored at this temperature under nitrogen until subsequently analysed. Sub-samples were further dried in an oven at 60°C for 48 hours and stored under vacuum. Hydrogen, Carbon and Nitrogen values were determined for each egg stage by a Perkin - Elmer elemental analyser (Model 240) connected through an automatic P - E recorder 56. Samples of between 1.84 and 4.45 mg. ($\bar{x}$ = 3.06 mg.) were analysed. The results of these analyses are presented as percentages in Appendices and as weights (µg.) of each element per ovum.

(a) Hydrogen.

Hydrogen formed between 7.8 and 4.5 percent of the total weight of an ovum (8.1 to 5.6 percent of the ash free weight). The percentage levels remained fairly constant throughout development from Stages I to IV, but fell between Stages IV and VI by 2.7 percent (Appendix XIV). The weight of hydrogen per egg increased during embryo growth though the level remained low, never reaching more than 8.0 percent of the total weight. Hydrogen weights per egg increased steadily between Stages I to IV with a decrease to Stage VI (Fig. 49[a]). Lower percentage hydrogen levels for free living crustacea are given as varying from 2.4 to 3.9 for the isopod Sphaeroma (Kerambrum and Szekielda, 1969).

(b) Carbon.

Initially wet oxidation methods (8.7.72) using Stage I ova produced a mean percentage Carbon content of 83.0 (S.D. ± 6.3). This value is an overestimate for subsequent elemental analyses, though determining the major constituent of ova as Carbon, indicated a lower range, varying from 60.1 to 31.8 percent of the total egg weight. The decline in percentage Carbon values was steady over the total development period, Table XXXV, though the weight of Carbon remained relatively constant during the development stages (Fig. 49 [b]).

The only other values of C which can be used for a comparison are the figures reported by Kerambrum and Szekielda (1969). Their percentage values were only half of that determined in this study though their work presented no corresponding increase in the H and N content. Presumably the reason for this can be attributed to the large proportion of the total body weight made up of cuticle, in free-living crustacea. Correspondingly the percentage ash weight would be expected to be elevated.

(c) Nitrogen.

The percentage of N in each egg stage showed an overall increase from Stage I to Stage VI with a peak value present at Stage III. The decline in percentage Nitrogen is partly attributed to the camou~~r~~flaging effects of cuticle formation; that is the percentage

Run 2				Run 4			
Stage	Lipid/sample	% Lipid	$^{s}/\sqrt{n}$	Stage	Lipid/sample	% Lipid	$^{s}/\sqrt{n}$
I	22.9	27.58	0.92	I	22.6	27.19	0.81
II	13.0	41.54	0.53	II	11.6	36.84	0.85
III	17.1	34.52	0.99	III	13.4	27.12	0.07
IV	14.2	30.06	1.24	IV	11.8	24.84	0.50
VI	10.2	17.06	0.28	VI	6.8	11.28	0.89

Table XXXV : The Lipid content of developing amphipod eggs (*Pontogeneia antarctica*) ash weight rising rapidly just prior to Stage VI (Fig. 50 [d]), thus lowering the relative value of Nitrogen. To some extent the nitrogen fluctuations mirror the values for Carbon content.

(d) C : N ratio.

It is considered that the proportion of Carbon to Nitrogen is a measure of the 'physiological condition' of an organism (Boucher et. al., 1976). The initial ration of C : N of 7.6 indicates the relatively substantial amounts of lipid present in early stage eggs. As development proceeds this ratio value characteristically falls, reaching its lowest value at Stage IV. This decline in the C : N ratio describes the channelling of storage Carbon, particularly lipid, to either cell carbohydrate or protein. Within early stage dividing ova protein levels are low but as division proceeds and cellular membranes are laid down so the cell Nitrogen levels increase. This transition is investigated further in the following section.

II Biochemical composition.

(a) Lipid content.

Total lipids were extracted from sub-samples of freeze dried material by the method of Bligh and Dyer (1959) and the percentage of total lipid obtained by colourimetric analysis using the sulphophosphovanillin reaction (Boehringer total lipid kit) based on the research of Watson (1960). The values of percentage lipid content for each stage of egg development are presented in Table XXXV. Previous work (Whitaker and Richardson, in press; Clarke, in press and Barnes and Blackstock, 1973) indicates that

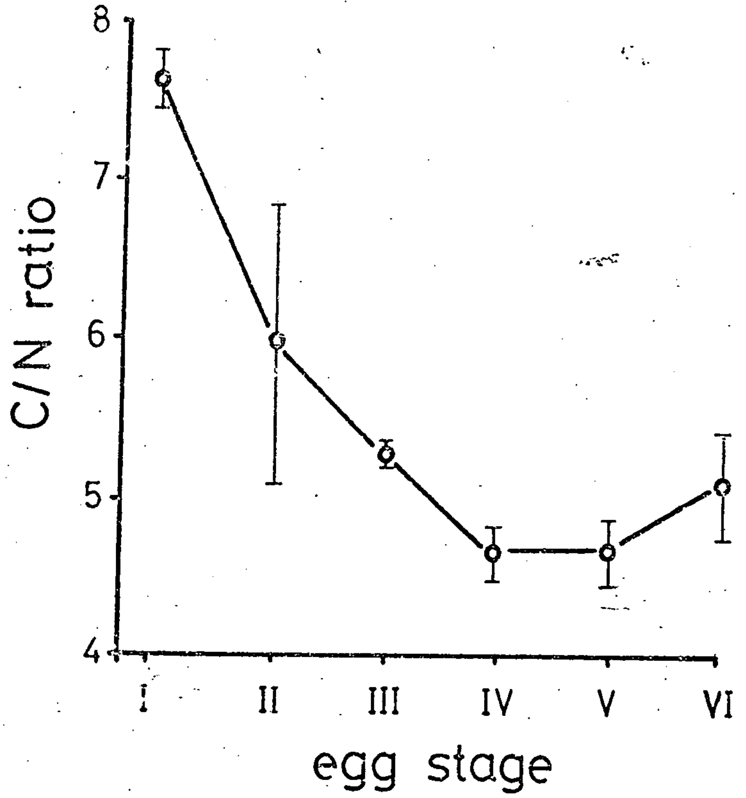


Fig. 47 The mean Carbon:Nitrogen ratios (± one S.D.) for developing Pontogeneia antarctica eggs.

Fig. 48 The mean percentage Ash weight values (± one S.D.) for developing Pontogeneia antarctica eggs.

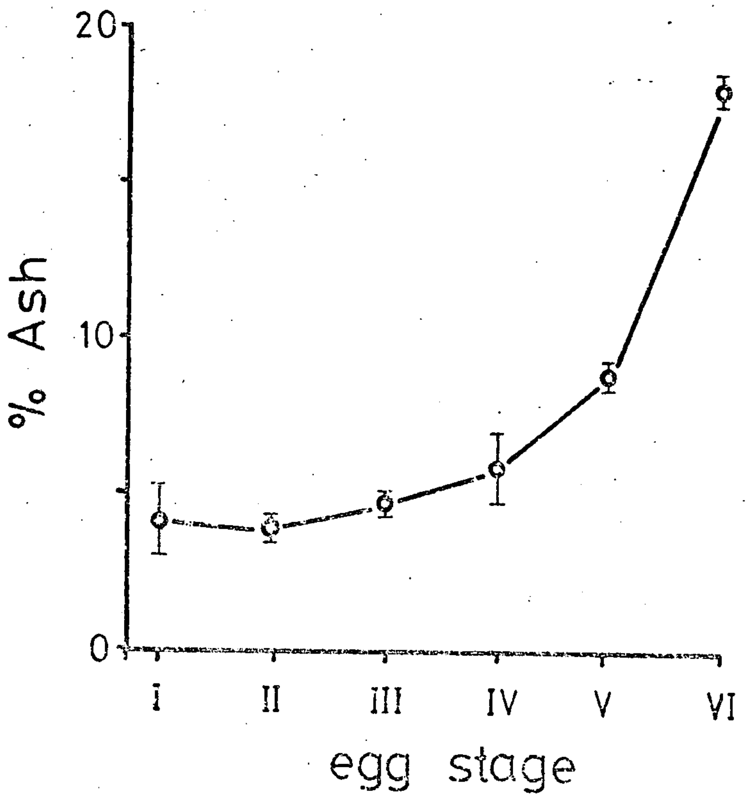


Fig. 49

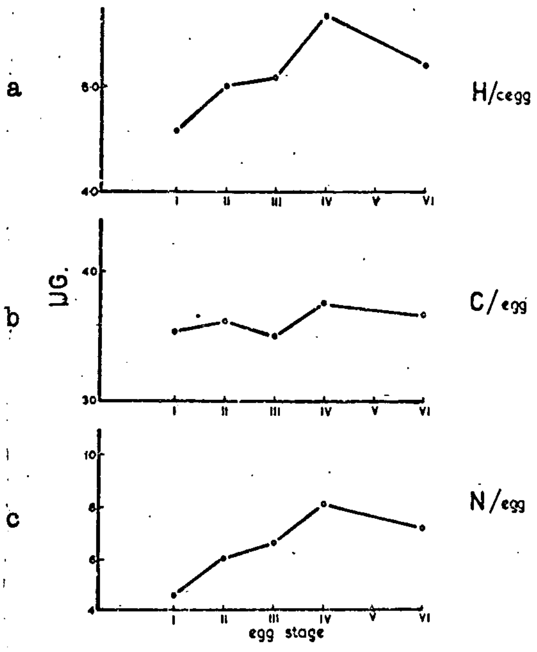


Fig. 50

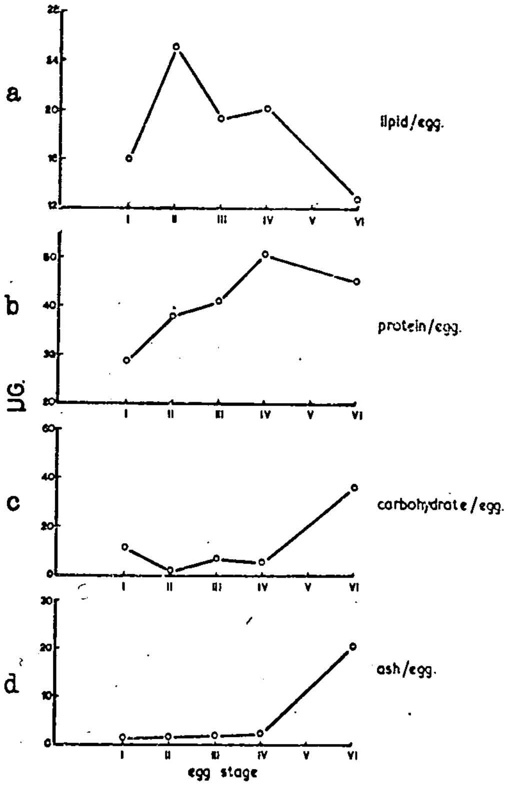


Fig. 49 : (a) Hydrogen, (b) Carbon and (c) Nitrogen levels/egg throughout development.

Fig. 50 : Biochemical constituents/egg for developing amphipod ova: (a) lipid, (b) protein, (c) carbohydrate and (d) ash.

that the Boehringer spectrophotometric method of lipid determination tends to produce an under-estimation of lipid content by 5 to 10 percent when compared to the values obtained by the evaporation and direct weighing procedure.

Although freeze drying techniques may alter fatty acid composition (Hooper and Ackman, 1972), total lipid values should remain unaffected. Morris (1974) demonstrated that the lipid content of preserved rather than frozen samples was apparently lowered. It was apparent that variations existed in experimental runs, due to the differences between standards. The trend from both sets of data was similar with an overall drop in ova lipid during development. Similar results have previously been reported for crustacean eggs by Morris (1974) and Pandian (1970) who indicated an approximate 50 percent drop in lipid level in the eggs of Homarus.

Pontogeneia antarctica exhibited a rise in percentage lipid content in early developing eggs (Stage II) (Fig. 51). Whilst no logical explanation can be presented to fully explain this feature I believe that it is not purely an artefact of collection, preservation or analysis, for a parallel rise in the lipid values of ova is presented in the paper of Clarke (in press) who analysed lipids in the antarctic decapod Chorismus antarcticus. The orange lipid body in pre-hatchling amphipod embryos was very much reduced and the lipid of these Stage VI individuals was recorded at between 11 and 17 percent.

(b) Protein content.

Estimates of the protein levels of developing eggs were

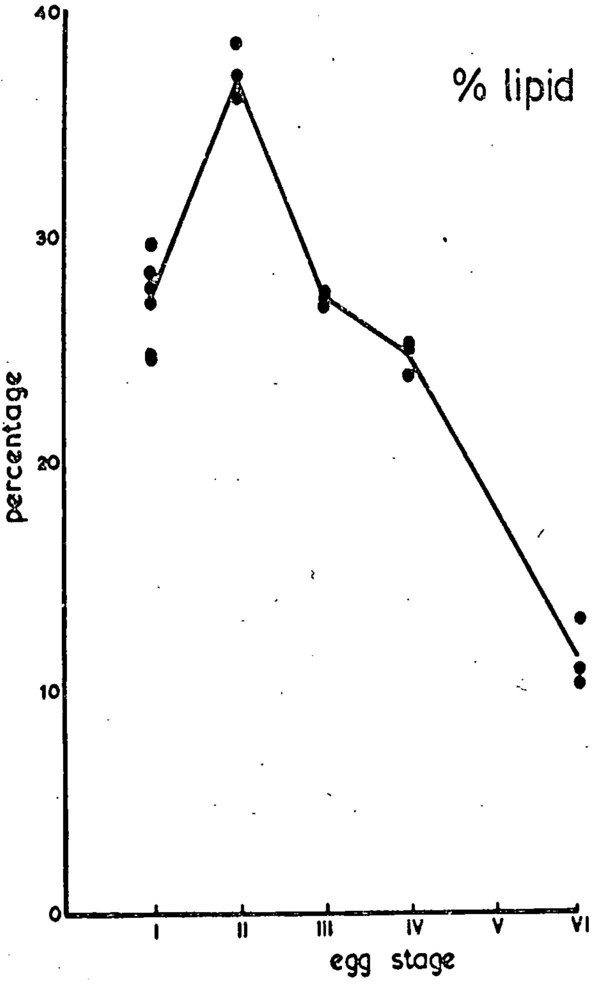


Fig. 51 : The percentage lipid values of developing amphipod eggs (P. antarctica).

made from multiplying total Nitrogen levels by 6.25 (Hiller et al, 1948), these percentage values being shown in Table XXXVI. Naturally protein values per egg follow the trend already shown in Appendix XV for total Nitrogen with protein levels increasing during embryological growth from 29 µg./egg to 45 µg./egg (Fig. 50 [b]). This incraese is a measure of the synthesis of structural protein, and additional membrane material. In addition it might reflect amino acic absorption by the eggs from the surrounding sea water.

(c) Carbohydrate content.

No analyses for carborhydrate content were attempted and the values of carbohydrate in Table XXXVI are regarded as purely tentative, being derived after subtraction of ash, protein and lipid values from the total dry weightof the eggs. These values indicate that carbohydrate levels per egg remained at the low level of 2 - 11 µg./egg until nearing the end of embryological development when they rose to 38 percent. In Crustacea, carbohydrate normally occurs in small quantities (Barnes and Achituv, 1976; Vijverberg and Frank, 1976), and embryological studies elsewhere have shown carbohydrate levels as falling (at least in the initial stages of development)(Hutchens et al., 1941-42). Similarly Zeuthen (1961) demonstrated that either neutral fats or carbohydrates were combusted during the initial days of development in amphipod embryos and Pandian (1970), who also estimated egg carbohydrate levels, noted that they fell from 5.1 to 2.2. percent.

III. Calorific values.

Calorific values from freeze dried eggs were obtained

Egg Stage	Percentage Composition			$\bar{x}$ Ash Free Wt.(ug)
	Lipid	Carbohydrate	Protein	
I	28.6	19.6	51.8	56.0
II	38.5	3.1	58.5	65.0
III	28.8	10.4	60.8	67.4
IV	25.9	7.8	66.2	77.0
VI	13.7	38.4	48.0	93.8

Table XXXVI : Percentage biochemical composition of developing *Pontogeneia antarctica* eggs.

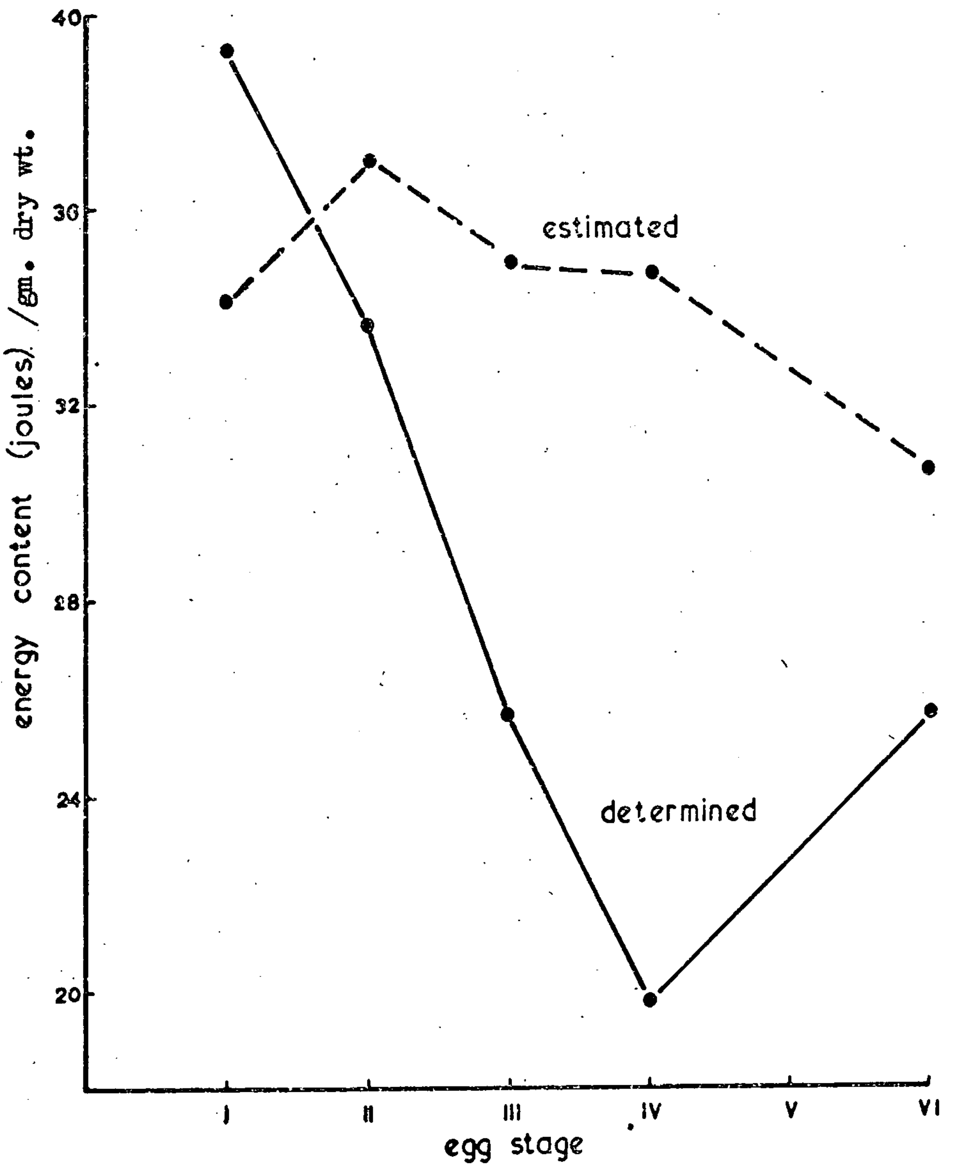


Fig. 52: Determined and estimated calorific values of ova stages.

obtained using a Micro-bomb Calorimeter (Model A.H.9 Newham Electronics, London), connected through a 1 mV. print out recorder. Instrument calibration was established using Benzoic acid pellets (B.D.H. Thermochemical standard batch, No. 790476). Some difficulty was encountered using the apparatus without a constant temperature room, for excessive high ambient temperatures grossly influenced the relative increases of the bomb temperature. Three determinations of egg Stages I,III, IV and V were obtained with five results from Stage VI.

Determined and estimated values (from biochemical compositions) of ova are shown in Fig. 52. The two curves though widely different both show a decrease in energy content throughout development.(The apparent rise in Stage VI eggs, for determined values, is believed to be erroneous). Unfortunately there was insufficient material available to repeat these experiments.

Calorific values are expressed as Joules (J) per ash free weight (1 K. cal. = 4.186kJ.). The estimated calorific value of developing P. antarctica embryos dropped from 31.0kJ. (7,400 cals.), (Stage III) to 24.7kJ. (5,900 cals.), (Stage VI). The calorific values (of ash free weight) for other crustaceans are certainly in the same order of magnitude. Vijverberg and Frank (1976) presented calorific values for a range of Copepoda and Cladocera and further, compared their own data with that of a wide variety of values from other authors. The values for Cyclopoida varied from 5,847 to 6,353 cals./g. organic matter. My determined values for Stage IV embryos fell to a presumably erroneous level of 13.81kJ./g. ash free weight.

7.4. Discussion:

The embryological development of antarctic Amphipoda has been partly described by Bregazzi (1973) who discussed various implications of embryology including the presence, but not function, of the embryonic 'dorsal organ'. The development in Pontogeneia antarctica closely followed that pattern outlined for other antarctic amphipods, for instance: Thurston (1968; 1970), Bone (1972), Bregazzi (1973) and Rakusa-Suszczewski (1972), though a further short Stage V (Fig. 43) has been identified. This stage, which presumably in past studies had been included with Stage IV embryos, was markedly different from its preceding development stage, as shown by the ash weight increases (Table XXXVI).

Both Thurston (1968; 1970) and Bone (1972) have shown the extended development period in the large antarctic amphipod Bovallia gigantea at Signy Island. The duration of development is closely related to temperature in many amphipod species. For example, the embryological development of Gammarus duebeni lasted 14 days at 18°C but 55 days at 5°C (Hynes, 1954) and a similar situation is present in Chaetogammarus marinus with a 9 - 10 day development at 20°C and 42 - 44 days at 5°C. Further details on temperature correlated development are presented by Clemens (1950), Steele and Steele (1969; 1973; 1975), and Vlasblom (1969). Steele and Steele (1975) stated that 'the duration of embryonic development increases directly with the increase in egg size'. Biologically the inversion of this statement would be easier to understand.

The lengthy period of antarctic amphipod development is a physiological response to decreased ambient temperatures with the release period for embryos evolved to coincide with periods of maximum food availability (Chapter 6). The embryo release in Pontogeneia *antarctica*, and many other antarctic amphipods (Thurston, 1972) is related to the increase of daylight during spring and the growth of diatoms, and takes place before the break-out of fast ice in spring. The synchronisation of larval release (in species affected by ice) is not however always related to ice melt or break-out, for Bjerkes (1974) reported that the females of the freshwater *Gammarus lacustris* in Norwegian lakes occurred in a precopula state during the winter and only became ovigerous soon after the disappearance of surface ice.

Ova are normally regarded as self sufficient units containing nutrient stores adequate to complete the development from the initial post-fertilisation egg to a point when hatching can occur. Throughout development, tissue organisation and formation and metabolic losses due to excretion and respiration produce significant changes in the eggs' composition. This change is usually accompanied by an overall weight change. Crustacean embryos, in particular, require substantial quantities of inorganic salts, mainly carbonates, to reinforce their cuticle. Pandian (1970) demonstrated that these salts were absorbed from the surrounding sea water. This author has also shown that substantial amounts of water were taken in by developing *Homarus* embryos. However, despite the absorption of inorganic salts by these decapod larvae, the overall dry weight of ova and embryos decreased. This drop in *Homarus* is steady throughout development. Bregazzi (1973) recorded the dry weights of the eggs of the amphipod *Cheirimedon femoratus* and also of *Tryphosella kergueleni*. These two infaunal lysianassid amphipods showed similar embryological weight changes,with dry weights falling between Stages I and IV but then increasing up to the last stage of development. Overall there was an increase in embryo dry weight. Bregazzi noted that the downward trend in his data for the initial development stages was not statistically significant and the overall increase in dry weight of these lysianassid eggs was not appreciable (approximately 0.8 to 0.85 mg./egg). In contrast P. antarctica showed a steady increase in egg weight with an overall increase of 96 percent (68 percent ash free weight) over Stage I. Some of the weight increase between egg stages was due to an increase in organic material. Though no active feeding was observed in late stage embryos, and is not possible in ova stages still bound within egg membranes, the absorption of dissolved organic matter from the surrounding medium is feasible. This theory, put forward by Conover (1966) has been verified for many crustacean groups, but has not been recorded for crustacean embryos. The use of elemental analysis, per se, to follow embryological changes should be treated with some caution. The complexities of metabolism during development include many synthetic and breakdown processes and the lack of comparative data from other studies, using this analytical technique, makes interpretation of the data more tentative. Kerambrum and Szekielda (1969) used elemental analyses on the isopods Sphaeroma serratum and Sphaeroma hookeri but their studies were directed solely at a comparison of food régimes. Their data however showed high Carbon content though percentage ash values, in adult animals, were also greatly increased.

The decline in egg Carbon levels in P. antarctica is mirrored by a similar drop in egg lipid values. Correspondingly the

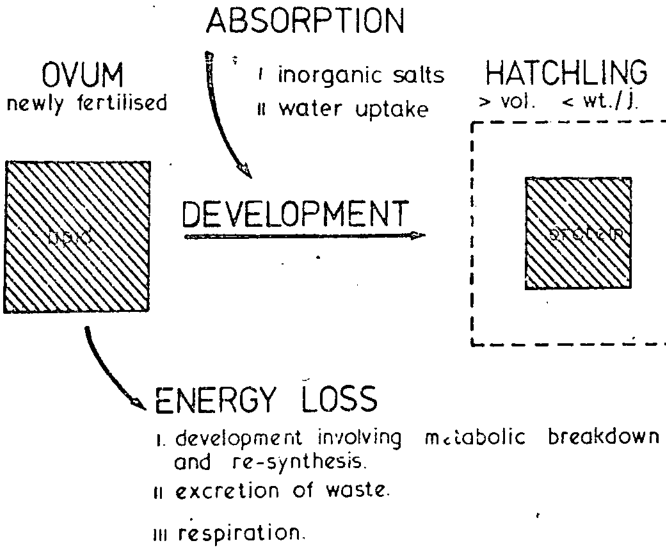


Fig. 53 : Schematic representation of embryological development.

synthesis of structural proteins, membranes and chitin produced a Nitrogen and protein rise. No known studies on the biochemistry of antarctic embryos have been traced, though Rakusa-Suszczewski and Dominas (1974) investigated some biochemical constituents of the antarctic amphipod Paramoera walkeri. Unfortunately these authors did not include the young amphipod stages in their studies. The chitin levels of immature and adult amphipods lay between 5 and 10 percent whilst ash weight varied from 22 to 31 percent.

The calorific value was seen to fall throughout development for both estimated and determined values and the total amount of energy channelled into embryo respiration was 1.05 joules (0.25 cals.). This value was determined from the figures of Table LXV and Fig. 45.

The calorific equivalent of oxygen consumption varies depending on the metabolic substrate however I have presumed that the predominant 'fuel' during development was lipid. The consumption of oxygen during development was as follows:- Stage I 7.70 ul, Stage II 7.22 µl, Stage III 19.42 µl, Stage IV 18.80 µl and Stage VI 20.57 µl and on the assumption that R.Q. values lay between 0.7 and 1.0 calorific equivalents per mole of oxygen these values would yield 495 Joules and 479 Joules respectively.

Chapter 8 The Respiration and Activity of *Pontogeneia antarctica*.

8.1. Introduction:

The paper of Scholander et al (1953) initiated interest in the 'standard metabolism' of poikilothermic organisms at low temperatures. Polar animals appeared to show an appreciably higher rate of standard metabolism (oxygen consumption) than their temperate or tropical counterparts than would be predicted after the rigid application of the thermal coefficient, at equivalent temperatures. This phenomenon of elevated metabolism, which has been demonstrated in both fish and crustacea, is commonly referred to as 'cold adaptation'. It implies that proportionally more of the energy intake is directed towards maintenance, than in temperate species, and consequently that less is available for reproduction and growth. This budget is based on the assumption that the energy required for feeding activities remains similar. By supplying the organism with a degree of environmental independance, such acclimations to low ambient temperatures are considered adaptive.

Despite the original work of Scholander et al, and subsequent research, detailed information on the metabolism of antarctic species is still scarce.

At Borge Bay, although ambient temperatures changed little throughout the year, -1.8°C to + 0.5°C (Fig. 4), I have demonstrated that considerable metabolic shifts, due to small temperature fluctuations, were present. This phenomonon amongst stenothermal species leads to relatively high Q_{10} values, attributed by Bělehrakel

(1930) to initial enzyme 'start-up'.

Few studies have attempted to investigate the metabolic requirements of a species throughout its total size and age range, from ovum to mature animal, though research on the energy requirements of developing embryos (Zeuthen, 1950) indicated the contrasting situations which may be present. Past studies using ovigerous females (often chosen to ease problems of ageing and sexing) may have biased the measurements of metabolic consumption because the weight of such egg or embryo masses to the total weight of the parent may be considerable (5.3.3. [a]). In this study I measured the respiration of amphipods after acclimatising them for two days in order to achieve greater stability in the behavioural and physiological responses of these crustacea.

As a parallel study to these experiments on oxygen consumption, some observations were also made on the metabolism of pleopod beating, under different temperature régimes. For these experiments no acclimation period was incorporated.

8.2. Materials and Methods:

Pontogeneia antarctica were obtained by SCUBA divers using a hand net either along the ice foot or amongst *Desmarestia anceps* at depths not exceeding 13m. Trawling, or other methods of collection were not used since they damaged crustacea. Samples were collected during February to May 1972, inclusive, and in January and February 1973. Sea temperatures varied from -0.5°C to -1.3°C. Suitable amphipods were isolated from the catch and placed in 500ml. flasks;

small specimens were separated from adult females to prevent cannabalism. The water in the flasks was kept at a temperature of ± 0.25°C from the intended experimental temperature. Since previous experimenters have shown the effect of nutritional state on metabolic activity of crustacea (Newell et al, 1974; Aldrich, 1975), only animals starved for a 3 - 5 day period were used,for P. antarctica required at least 3 days of starvation to clear its gut (Fig. 36). Sea water in the holding flasks was changed every 12 hours to prevent coprophagy. Amphipods were transferred to 50 ml. beakers in a constant temperature bath (± 0.1°C) for 12 hours (overnight) before any measurements of oxygen consumption were taken. Uptake was measured at the same period each day, under artificial light, even though initial 24 and 48 hour experiments revealed no significant diurnal rhythm of oxygen consumption (Fig. 56).

Two methods of measuring oxygen consumption were used:

(1). Constant pressure respirometry (Davies, 1966) and

(2). Micro-Winkler techniques (Van Dam,1935) modified by Fox and Wingfield (1938), White (1975).

I found it convenient to use small 2 cm^2. sections of fine mesh netting in both the constant pressure and micro-Winkler respirometry chambers, for given a suitable perching substrate, amphipods became quiescent and ceased their erratic bouts of active swimming. Halcrow and Boyd (1967) demonstrated the degree to which excitement raised the metabolic rate in several crustaceans.

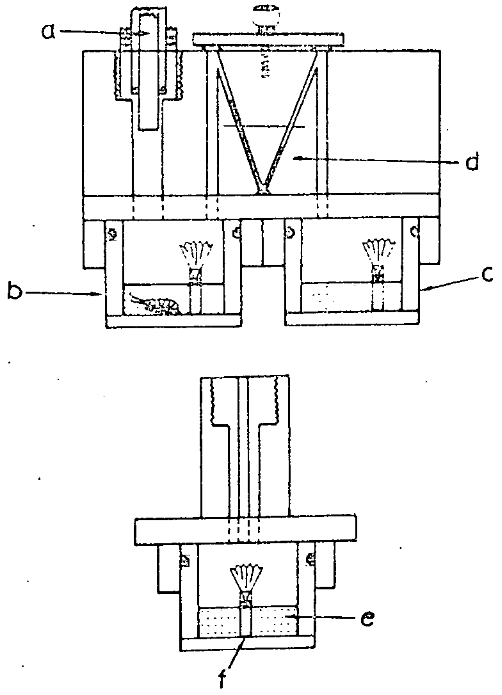
Water in all experiments was obtained from uncontaminated sources, away from the vicinity of the station huts, and'Millepore' filtered, cooled and vigorously aerated to saturation for 12 hours.

8.2.1. Constant Pressure Respirometry.

Small calibrated respirometers were constructed, under the guidance of Dr. P.S. Davies, by the Zoology Department of Glasgow University. Flask sizes were determined from the presumed size range of animals of 0.1 - 0.01 g. (wet weight), producing theoretical O_2 consumption rates of 6.2 µl./hr. (at 0^oC) to 24.6 µl./hr. (at 20^oC) for 0.1 g. amphipods, and 1.0 µl./hr. (at 0^oC) to 4.3 µl./hr. (at 20^oC) for 0.01 g. animals (calculations were based on derivations from Hemmingsen's relationship (1960). Flask construction was a compromise between practical size range for manufacture, experimental handling and sensitivity. Fig. 54 (a) shows the arrangement of the modified Spencer Davies respirometers, which were constructed from 38.1 mm. internal dia. perspex with 4.8 mm. thick walls. Flask heights of 25.4 mm. produced volumes of 16 cc. per flask with a sensitivity of 0.5 mm. of manometer fluid movement (0.63 µl.). For experimental procedures see Davies (1966).

To calculate hourly consumption, a regression of micrometer (mm.) movement against time was derived. To convert these values to µl. of oxygen consumed a multiplication factor of 36.32 (the area of cross section of the micrometer head)was used.

Since valid manometric movement relies on constant and efficient diffusion between gaseous and dissolved oxygen and stirring of the experimental water was only produced by the amphipod's pleopod beat, a compromise between minimum water volume and possible nitrogenous excretion poisoning was required. 5.0 ml. of treated sea water were used per flask and the flasks were chilled to -2.0^oC prior to use. It was found that residual heat in the perspex flasks



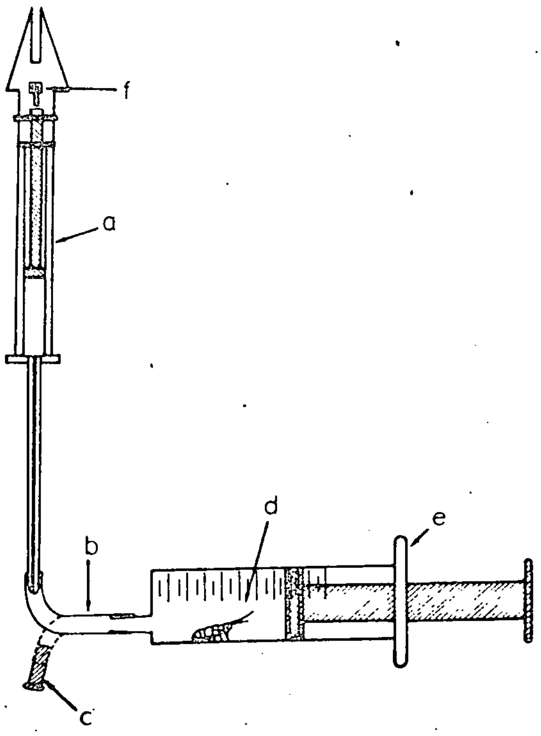


Fig. 54 : Experimental Apparatus:
I. Constant Pressure Respirometer, a. micrometer head, b. experimental flask containing amphipod, c. compensatory flask, d. manometer, e. filtered seawater, f. hydroxide container.
II. Micro-Winkler syringe, a. Agla syringe, b. interconnecting plastic tube, d. experimental amphipod, e. 10 ml. experimental chamber, f. adjusting screw.

could cause subsequent bubble formation and erroneous O_2 consumption results. Therefore an equilibrium period of one hour, or longer, was maintained prior to experimental runs. One serious fault was discovered with the apparatus, for the effect of heat conduction through the micrometer head affected the air space of the left hand chamber. With no compensatory conduction rod in the control chamber, this factor could produce misleading results. It thus proved necessary to ensure that room temperature remained constant ($\pm$ 2.0°C) and that micrometers were handled during readings only with neoprene gloves.

8.2.2. The micro-Winkler Technique.

The experimental procedures were those described by Van Dam (1935) and modified by Fox and Wingfield (1938), Barnes (1959) and White (1975).

10 ml. plastic disposable syringes were used as respiratory chambers with six syringes used in each experiment. Small 2" long sections of flexible nylon tube were fitted to the nozzles of the syringes and stoppered during experimental runs with tapered sections of knitting needle. Using this device part of the contents of the respiratory chamber could be injected into an 'Agla' burette without the simultaneous injection of contaminating air bubbles. The experimental set-up is illustrated in Fig. 54 (b) and followed that described by White (1975). Repeat extractions of water samples (up to a maximum of three) could be taken from any one syringe.

The existing calibrations of the syringes were found to be insufficiently accurate and all experimental syringes were recalibrated from a 10 ml. burette, to include the 'dead space', nozzle and interconnecting tube. Where larger animals were used during final readings, i.e. the volume of sea water in the syringes had already been considerably reduced, due to the extraction of two previous samples, the volume of experimental animals was an important consideration in determining the amount of water available.

The volume of P. antarctica was assessed on the assumption that body sp. gr. = 1.0 (N.B. specific gravity of this amphipod species is slightly greater than this figure). Freshly killed animals were lightly blotted to dryness and weighed in a small glass vial containing a known weight of water. The relationship of volume (measured as wet weight) to length for this amphipod is given by:

$$y = 0.870 + 0.338x$$

(where y = log. length, x = log. volume (n = 31, r = 0.994).
(The three lowest pair points of the scatter diagram (Fig. 55) were not included in the calculation.)

8.3. Results:

A total of 244 determinations of oxygen consumption were made from individual amphipods using the two methods described above. Details of the efficiency of experimental methods, numbers of animals, species and experimental temperatures are presented in Appendix XVI. 189 readings of rates of oxygen consumption in the constant pressure respirometer were made on the amphipod P. antarctica. The experimental temperature range was $-1.5^{\circ}C$ to $+5.0^{\circ}C$ with temperature intervals of $-1.0^{\circ}C$, $0.0^{\circ}C$ and $+2.0^{\circ}C$.

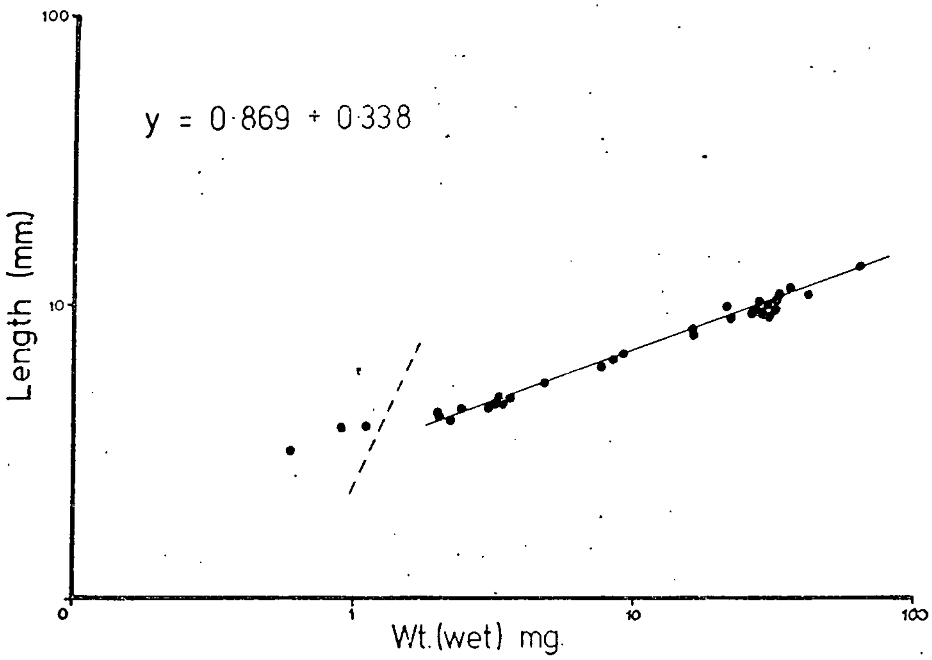


Fig. 55 : The volume of P. antarctica expressed by the relationship of wet weight/length.

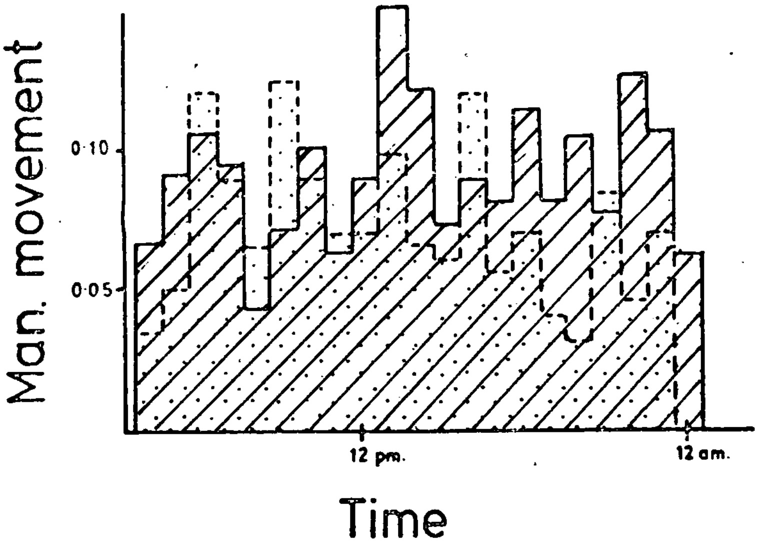


Fig. 56 : The oxygen consumption (as manometer units) for two similar sized Djerboa furcipes, over a twenty four hour period.

Micro-Winkler techniques were used successfully on 44 individuals of this same species (0.0°C and 2.0°C) whilst 11 results were obtained for the larger amphipod Djerboa furcipes using the constant pressure respirometers.

The composition, by age and sex, of amphipods whose metabolism was measured by each experimental technique and temperature is shown in Appendix XVII.

8.3.1. Diurnal metabolic fluctuations.

Field observations (5.3.2.) indicated that marked diurnal rhythms of behaviour and activity occurred in both P. antarctica and D. furcipes and similar rhythms have been noted previously for the infaunal amphipods Cheirimedon femoratus and Tryphosella kergueleni (Bregazzi, 1973). 18 experimental runs , (6 on D. furcipes and 12 on P. antarctica) were conducted over a period of more than 24 hours to investigate possible fluctuations in oxygen consumption. However, perhaps due to the altered light régime and the lack of available swimming space in the experimental flasks, animals exhibited no significant diurnal pattern in their oxygen uptake. Similar results were obtained by McFarland and Pickens (1965). Fig. 56 shows the typical results obtained for two similar sized individuals of D. furcipes expressed as micrometer interval movements per time. A similar pattern emerged for P. antarctica, whose oxygen consumption fluctuated in a random pattern throughout the twenty four hour period with no significantly increased nocturnal O_2 uptake. All subsequent experiments were started at the same time of day (0900 hrs. local time) and run, under artificial light, for a minimum of six hours. A longer period was however needed for small individuals.

8.3.2. Weight related Oxygen uptake.

The rate of metabolism is not normally constant throughout the life cycle of any organism, for energy expenditure varies depending on an animal's size. This phenomenon occurs in both homiotherms and poikilotherms. In the former, the increased surface area to body mass, producing a relatively increased heat loss, is normally the major cause of any elevated oxygen consumption. Invertebrates however also usually show a decreased rate of metabolism as their size (body weight) increases. In determining the O_2 consumption of either the population of a species or following respiration throughout the life span of any individual, determinations must be made for a variety of size categories of the animal.

I found that typical consumption rates for increasing weight were produced by both amphipod species and the results of an experimental run (15.5.72) at 5.0°C, using six chambers over an 11 hour period with different sized P. antarctica are shown in Fig. 57. These values are expressed as micrometer movement per time but converted to µl. O_2 in Table XXXVII. Whilst the oxygen consumption increased as a function of increasing weight (producing the relationship demonstrated in Fig. 58 [a]) increased size and weight also produced a proportionally decreased metabolism. This feature could be shown as a curvi-linear relationship by converting the oxygen consumption to a weight related expenditure. Converting such values to a log. log. format produced the temperature related linear regressions of

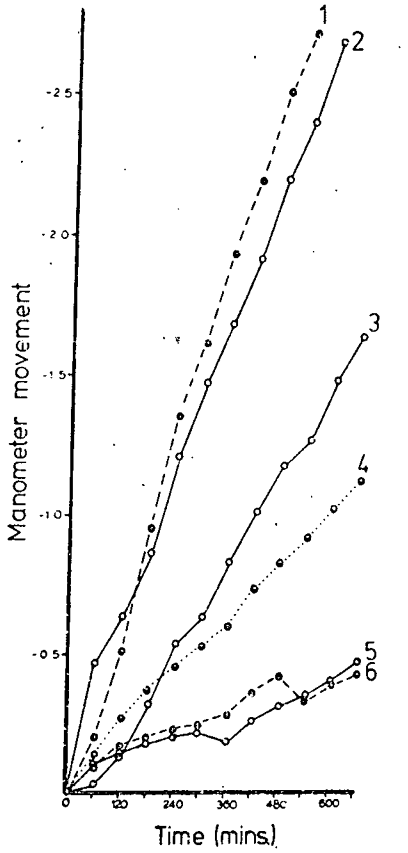


Fig. 57 : The oxygen consumption (as manometer units) for six different sized P. antarctica (Constant Pressure Respirometer, 15.5.72).

Chamber No.	Length (mm)	Dry Wt. (mg)	Sex	Manometer movement/hr	ul/ind/hr.	ul/mg/hr.
1	7.59	4.3	♂	0.280	10.170	2.365
2	14.27	27.4	♀	0.247	8.971	0.327
3	6.44	3.0	♂	0.176	6.392	2.131
4	11.22	13.2	♀	0.107	3.886	0.294
5	7.26	3.8	♂	0.055	1.998	0.526
6	7.34	3.6	♂	0.066	2.397	0.666

Table XXXVII Oxygen consumption results of the experimental run (15.5.72) [Constant Pressure Respirometer] at 5.0°C

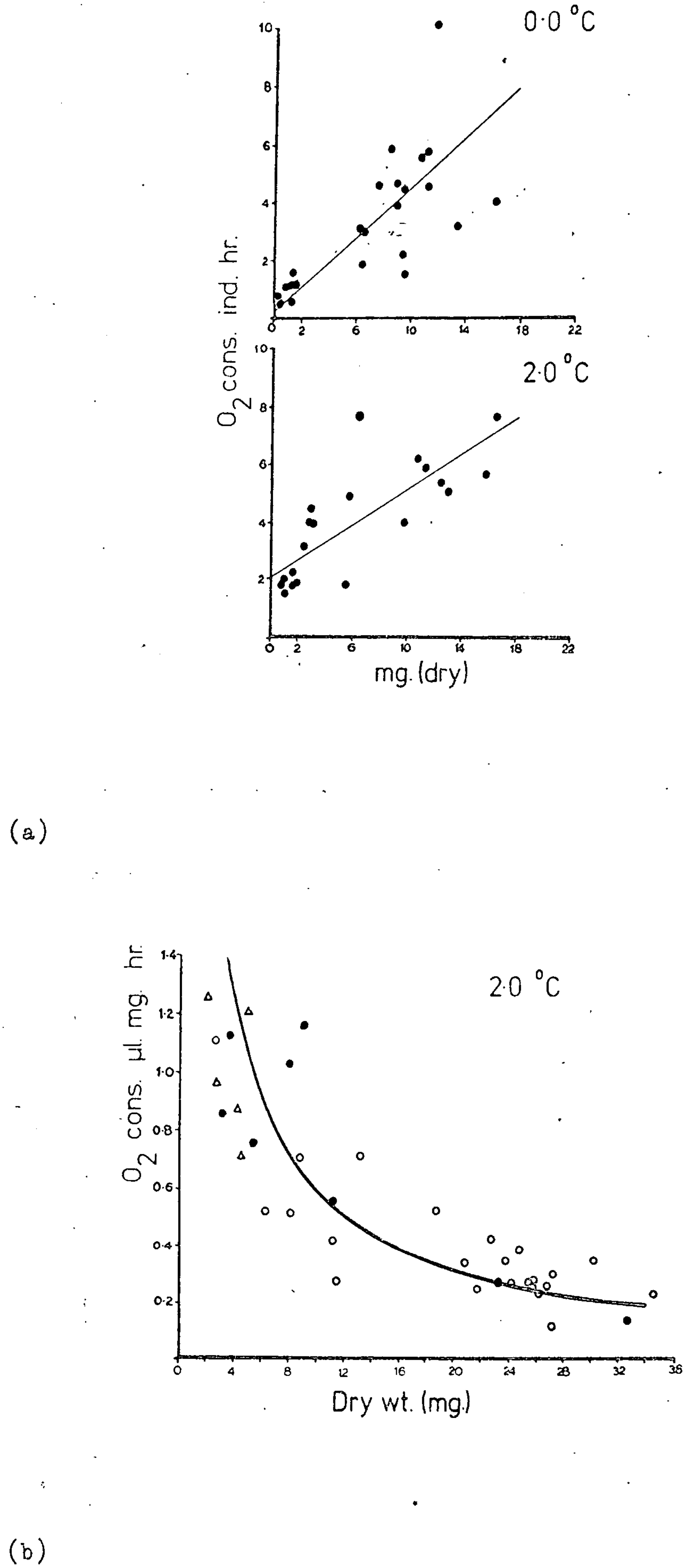


Fig. 58 : (a) The increasing oxygen consumption/weight (at two different temperatures for P. antarctica)

(b) The weight specific oxygen consumption/weight for P. antarctica at 2.0°C. Δ imm., ⊙ ♂, ○ ♀.

Fig. 59 (a) and (b).

The correlations shown by P. antarctica and D. furcipes between a lowered metabolism per unit weight and increasing weight appear to be characteristic of crustacea for Hemmingsen (1960) has discussed at length the various relationships of weight specific O_2 uptake. The increase of non-metabolic structures in older animals, particularly the increasing weight of exoskeleton and metabolic substrates,i.e. lipid, has much to do with this apparent decrease in metabolism.

There was an increasing difference in the weight specific O_2 consumption of larger animals and this feature was dependent on the experimental temperature. From Fig. 64 I have presumed that the maximum weight specific oxygen consumption of P. antarctica lay around the 1.0 mg. (dry weight) range. 30 mg. amphipods, at 2.0°C, used approximately 2x less O_2 than animals 3.5°C lower. In other words larger animals showed a decreasing trend in their metabolism as the experimental temperature increased. Such a trend produced increases in the slopes (t) of the regressions of oxygen consumption in Fig. 59. The slope was abruptly countered at 5.0°C (i.e. greatly reduced) presumably due to aberrant results obtained as the 'heat death' point was approached. The data on these metabolic increases have been outlined in Table XXXVIX, where Q_{10} values are also presented.

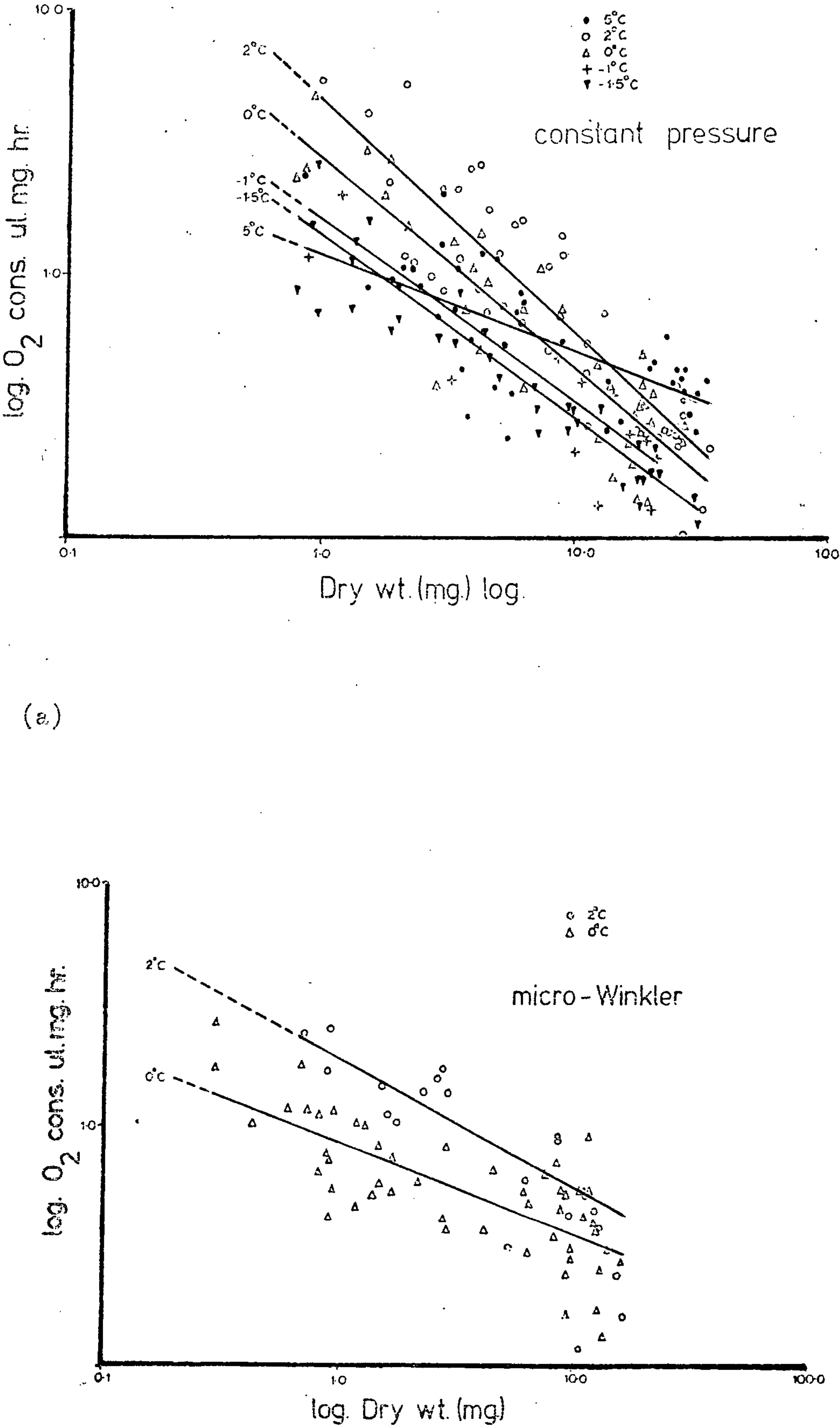
The inference from these data is that temperature tolerances are greatest in young animals. Field observations indicated that adult P. antarctica were rarely found close to the more fluctuating temperatures of the immediate sub-littoral, whilst

% oxygen consumption/mg. (dry weight)/hr.

Temp. °C

Constant Pressure	1.0	10.0	30.0	Weight(mg.)
-1.5	100.0	21.97	10.66	
-1.0	100.0	20.28	9.46	
0.0	100.0	15.46	6.35	
+2.0	100.0	12.81	4.81	
+5.0	100.0	42.46	28.21	
Micro-Winkler				
0.0	100.0	41.59	27.36	
+2.0	100.0	31.42	18.09	

Table XXXVIII: Weight specific oxygen consumption decrease with size in <u>Pontogeneia antarctica</u>.



(a)

(b)

Fig. 59 : log. log. weight specific oxygen consumption of <u>P. antarctica</u>. (a) 5 temperatures - Constant Pressure.
(b) 2 temperatures - Micro-Winkler.

Micro - Winkler

Wt. (mg)			1.0	10.0	30.0
Temp. °C	0.0		0.8482	0.3528	0.2321
		Q_{10}	$\boxed{9.9280}$	$\boxed{7.4985}$	$\boxed{6.5625}$
	+2.0		1.6835	0.5291	0.3046

Constant Pressure

Wt. (mg)			1.0	10.0	30.0
Temp. °C	-1.5		1.3246	0.2910	0.1412
		Q_{10}	$\boxed{24.5140}$	$\boxed{22.644}$	$\boxed{21.7580}$
	-1.0		1.6244	0.3294	0.1536
		Q_{10}	$\boxed{17.1790}$	$\boxed{13.095}$	$\boxed{11.508}$
	0.0		2.7900	0.4314	0.1771
		Q_{10}	$\boxed{8.2070}$	$\boxed{6.7995}$	$\boxed{6.2140}$
	+2.0		4.5794	0.5867	0.2201
		Q_{10}	------	------	$\boxed{5.1195}$
	+5.0		1.1986	0.5089	0.3381

Table XXXIX : Respiration consumption of Pontogeneia antarctica for two experimental procedures and over a range of temperatures. Q_{10} values are indicated as boxed figures.

mortality in the holding tanks prior to laboratory experiments indicated that adult individuals were particularly susceptible to 'heat death'. Experiments on 'ventilation' activity reinforced these observations (Fig. 60). Immature animals appeared capable of withstanding (a) greater temperature and salinity régimes; (b) an overall higher ambient temperature and (c) decreased 0_2 saturation. Post-hatchling amphipods were released at a period of the year when physical and chemical conditions in the sea were altering most rapidly. With less capability of actively avoiding stress conditions, for instance, areas of decreased salinity a 'metabolic elasticity' is an obvious advantage to these immature Crustacea. This feature of amphipods contrasts with the situation in echinoids, in which small individuals of Strongylocentrotus droebachiensis were less tolerant of elevated temperatures than adult animals (Percy, 1972).

The rates of oxygen uptake for the two species I investigated were of a similar order of magnitude to those for temperate amphipods. The consumption varied in P. antarctica from 0.14 µl/mg./hr. at -1.5°C (for adults) to 4.58 µl./mg./hr. at +2.0°C for immature juveniles. The range of uptake at 0.0°C for D. furcipes was 0.11 - 0.65 µl./mg./hr. Figures given by other workers are often difficult to compare directly with these because of variable drying procedures or the frequent use of wet weights. Recalculated figures (assuming a % water content of 60, [derived from my own data] gave the following consumptions [Table XL]).

8.3.3. The level of oxygen uptake by antarctic poikilotherms.

Little information is yet available on the respiratory

Species	O_2 uptake µl/mg(dry)/hr	Temp °C	Cited
Gammarus pulex	0.467-0.767 (immature)	10	Wright and Wright, 1974
" "	0.392-0.608 (adult)		
Gammarus chevreuxi	0.532-0.766	10	Lowenstein, 1934*
Gammarus marinus	0.426-0.567	10	Fox and Simmonds, 1933
Gammarus locusta	0.345		
Gammarus pulex	0.697-0.835		
Gammarus pulex	< 20.0	10	Rumpus, 1973

* dried at 110°C.

Table XL : Weight specific oxygen uptake of temperate amphipods.

metabolism of antarctic poikilotherms, but most groups of animals investigated so far appear to exhibit 'cold adaptation' that is their metabolism is higher than that of a temperate or tropical organism acclimated to the same experimental temperature. Such an increase in metabolism was first described by Krögh (1914) who suggested that ' one would expect animals living at a very low temperature should show a relatively high standard metabolism at that temperature compared with others living normally at a high temperature'.

Elevated metabolisms have since been demonstrated in fish (Ralph and Everson, 1967; Wolschlag, 1957, 1960, 1963 and 1964) and crustacea (Table XLI) *Euphausia superba* (McWhinnie, 1964) and in the amphipods *Paramoera walkeri* (Rakusa-Suszczewski and Klekowski, 1973) and *Orchomenella chilensis* (Armitage, 1962). However, White (1975) demonstrated that the large isopod *Glyptonotus antarcticus* had an oxygen uptake level comparable to, and no higher than, that of isopods from warmer latitudes and the controversy over the existence of elevated metabolism at low temperatures has been further intensified by the paper of Holeton (1974) who demonstrated that oxygen uptake rates in arctic marine fish were on the whole below levels considered to reflect 'cold adaption'. Only one of the species investigated (*Boreogadus saida*) showed increased O_2 uptake. Holeton explained that this feature was more likely to be due to a high level of spontaneous activity than indicative of a specialised metabolic phenomenon.

8.3.4. The effects of temperature on 'standard metabolism'.

The data on oxygen uptake at different temperatures are summarised in Fig. 59 (a) and (b) and Table XLII. The rule of Van't Hoff (1884), which was based on the chemical 'law of mass action', stated that within the temperature limits of the system a rise of 10°C would increase the rate of reaction by a factor of between 2 and 3. This temperature coefficient of Van't Hoff - the Q_{10} - does not normally remain constant throughout the thermal range of an organism. Bělěhrakel (1930) stated that the Q_{10} value decreased with a rise in temperature due to enzyme destruction and this feature has been further demonstrated experimentally by Davies (1966) working on Patella and Ege and Krögh (1914) with goldfish.

Evidence from previous research indicates the wide variation in O_2 uptake, with temperature, that exists. It appears that Q_{10} values at low temperatures are elevated, perhaps due to enzyme induction. For instance, Ege and Krögh (1914) cited a Q_{10} value of 9.8, at 0.0 to -5.0°C, whilst far higher Q_{10}'s (up to 50 for frozen intertidal molluscs [Kanwisher, 1959] and 71.4 for the antarctic amphipod Paramoera walkeri [Klekowski et al, 1973; Rakusa-Suszczewski and Klekowski, 1973]) have been reported. This last value was suspect, due to a mathematical error and recalculations of the data for P. walkeri gave the following Q_{10} values:

Temp. °C.	-1.9 to 0.0	0.0 to 2.0	-1.9 to 2.0
Juveniles	9.48	3.92	6.03
Ovigerous females	6.79	3.63	4.92
$\bar{x}$ for both	8.34	3.81	5.58

Wohlschlag emphasised such elevated metabolism by stating 'It appears that the antarctic species (of fish) have log. hourly

Species	Temp. °C.	O_2 uptake µl./mg./hr.	Cited
COPEPODA			
Rhincalanus gigas	-1.8	0.466	Rakusa-Suszczewski et al, 1976.
ISOPODA			
Glyptonotus antarcticus	-1.8	0.0216	Belman, 1973.
" "	-1.5	0.0217	
" "	+1.5	0.0688	White, 1975.
AMPHIPODA			
Bovallia gigantea	-1.8	0.110	Bone, pers. comm.
" "	+0.2 (summer)	0.150	
" "	+0.2 (winter)	0.164	
" "	+3.2	0.218	
Orchomenella chilensis	-1.8	0.213	Armitage, 1962.
" "	0.0	0.196	
" "	+2.0	0.235	
" "	+4.0	0.207	
" "	+6.0	0.245	
" "	+8.0	0.265	
" "	+10.0	0.385	
" "	+12.0	0.295	
Paramoera walkeri	-1.2	0.150	Rakusa-Suszczewski and Klekowski, 1973.
" "	+12.0	0.774	
Djerboa furcipes	0.0	0.320	this study
Pontogeneia antarctica	-1.5	0.141	
" "	-1.0	0.154	
" "	0.0	0.232 (W)*	
" "	0.0	0.177 (CP)*	
" "	+2.0	0.220	
" "	+5.0	0.338	

*(W) micro-Winkler
*(CP) Constant Pressure Respirometer.

Table XLI : Respiratory rates of Antarctic crustacea. (corrected to µl./mg./hr. - dry weight).

oxygen consumption rates of around 0.03 to a high of 0.12, which may be interpreted to indicate that they have a somewhat greater metabolic response to slight temperature increases than is generally characteristic of more temperate species'.

Q_{10} values for P. antarctica were considerably elevated, but below the maximum figures given by Klekowski et al (1973) for P. walkeri and there was a reduction in Q_{10} values with increasing size (Table XXXVIX). Although this holds for other organisms, in general the temperature coefficient increases with size (Rao and Bullock, 1954).

I believe that the marked increase in the slope of the regression at 5.0°C was an indication of the heavy mortality incurred before, during and after experimental runs at this temperature.

8.4. The activity of Pontogeneia antarctica: Pleopod beats related to increasing temperature:

8.4.1. Materials and Methods.

Experiments on the relationship of pleopod activity to temperature were carried out in November 1972 and January 1973. The experiments were conducted using only the largest specimens (adult females) of P. antarctica,since smaller specimens were more difficult to observe.

The apparatus consisted of six experimental chambers (rectangular glass containers of 20 ml. capacity), each supplied with an accurately calibrated thermometer. Small perches were provided in each chamber to reduce the swimming activity of the animals. The chambers were set in a shallow perspex tray supplied with a circulation of coolant from an adjacent constant temperature bath. At the beginning of each experiment, animals were placed in cooled (-1.8°C) 'Millepore' filtered and aerated water and the system was gradually allowed to warm up over a period of six to seven hours. Three replicate observations were made, at approximately each 0.1 °C rise in temperature, of the time taken for sixty consecutive pleopod beats. The experiment was continued until thermal death occurred of all the individuals. These were then removed from the chambers, measured, dried at 80°C and weighed.

8.4.2. Results:

Experiments were performed on 15 animals and Fig. 60 indicates the relationship of pleopod activity to rising temperature for a group of four individuals (13.1.73). After switching off the constant temperature bath at -1.8°C the rise in temperature in the apparatus was slow, taking three hours before it approached 0°C. The rate of rise of pleopod activity between individuals was similar, and any variation in the behaviour can be attributed to temperature differences between experimental chambers. Pleopod activity rose steadily from around 110 beats/min. (at -1.5°C) to approximately 190 beats/min. at 6.0°C, though a plateau of high activity would sometimes be sustained over an appreciable temperature range. This resulted in a'pre-lethal' peak of activity. However, no animals survived temperatures greater than 8.5°C. Any rise in temperature produced marked activity responses in the animals. This was first seen as increased swimming, often in an erratic pattern. Pleopod

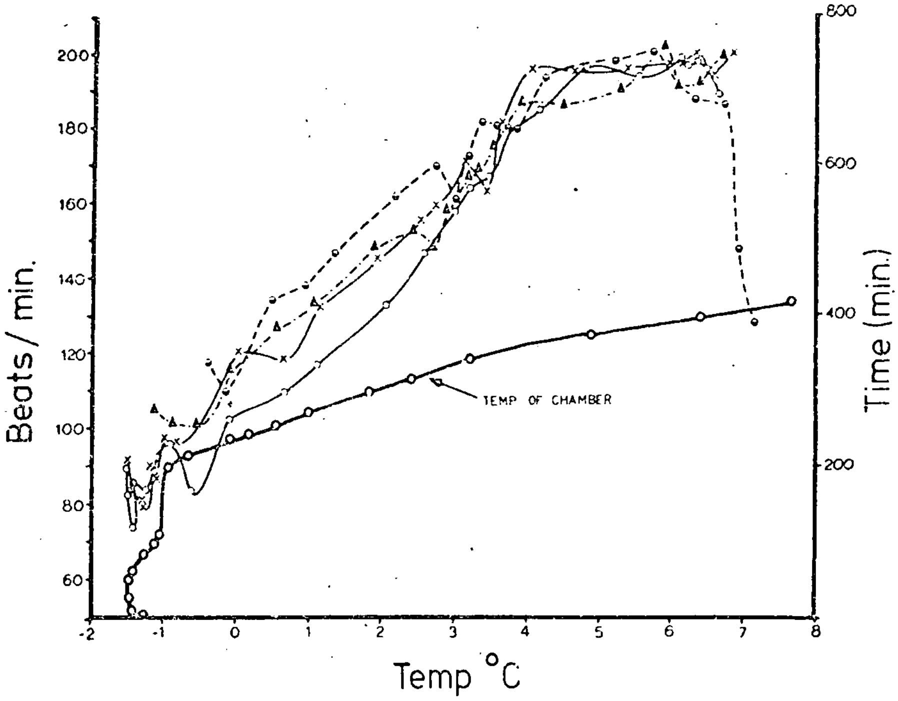


Fig. 60 : The effects of increasing temperature on the pleopod beating of P. antarctica (four specimens)

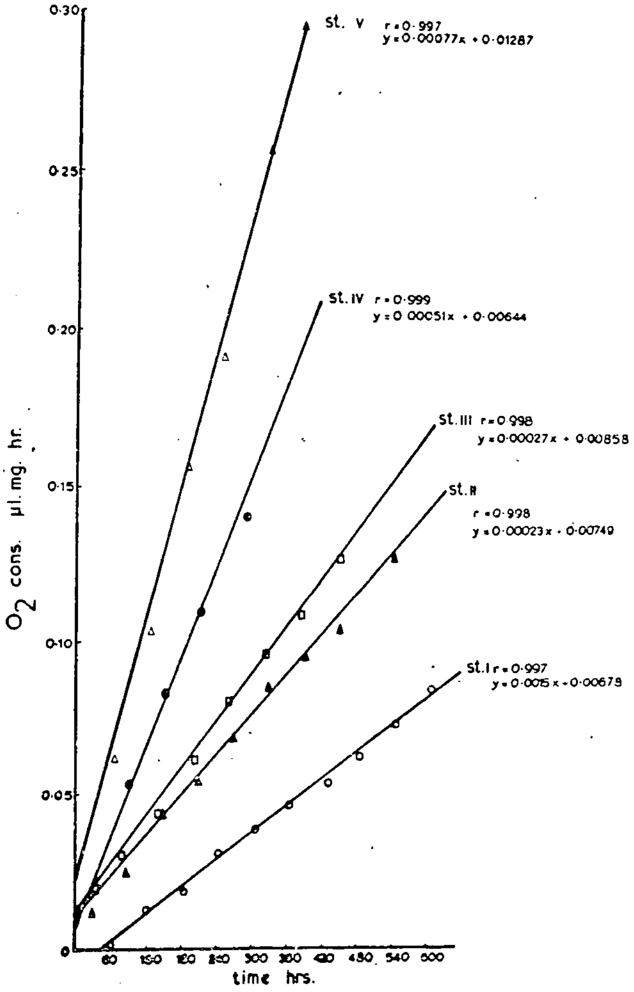


Fig. 61 : The respiration rates of amphipod ova (for results nearest the $\bar{\bar{x}}$ values of each egg stage).

Temp. range °C.	-1.0 to +2.0	-1.0 to +4.0	-1.0 to +6.0
$\bar{x}$ Q_{10}	3.49	3.18	2.69
S.D. ±	0.49	1.00	0.32
n	13	13	10

Table XLII : . Q_{10} values derived from the pleopod activity of <u>P. antarctica.</u>

Table XLIII : . Mean values of pleopod beats/min for each of the experimental animals. Figures for six temperatures are presented.

Date °C	-1	0	2	4	6	8
24.11.72.	-	-	165	195	164	-
25.11.72	-	80	102	120	172	143
13.1.73	105	116	148	187	196	-
	115	115	160	185	194	-
	94	103	132	182	197	-
	97	120	146	196	197	-
14.1.73	87	102	131	183	197	-
	95	118	147	196	197	-
	104	115	150	186	195	-
	110	115	160	187	195	-
23.1.72.	132	150	188	179	-	-
	110	137	169	220	226	140
	123	131	149	150	-	-
	132	150	190	178	-	-
	112	136	166	220	230	-
$\bar{x}$	109	120	154	184	197	142
S.D. ±	14	19	22	24	18	2

beating became irregular, with long pauses between beats and increasing temperature ultimately induced pre-lethal responses with the amphipod collapsing onto its back or side and producing spasmodic pleopodal pulses. Death was defined as the point at which pleopods ceased to beat in any one thirty second period.

Table XLIII gives the pleopod rate as beats/min. for each of the experimental animals, for a variety of temperatures. From these figures, Q_{10} values for the temperature ranges -1.0°C to +2.0°C; 2.0°C to +4.0°C and -1.0°C to +6.0°C could be calculated and these are given in Table XXXXII. The Q_{10} decreased with increasing temperature as the plateau phase of activity was reached (Newell and Northcroft, 1967). The stenothermal range of P. antarctica was similar to that reported for the decapod Chorismus antarcticus (Maxwell, 1976), 7.0°C and for the isopod Glyptonotus antarcticus (White, 1975), who noted that heavy mortality occurred above 6.0°C with 'thermal paralysis' apparent between 8.0 and 10.0°C. Rakusa-Suszczewski (1973) reported from the paper of Somera and DeVries (1967) on the stenothermal fish Trematomus borchgrevinki. This species had a similar lethal temperature at 6.0°C.

8.5. The oxygen consumption of developing amphipod ova.

8.5.1. Materials and Methods:

Ovigerous females of Pontogeneia antarctica were collected during July 1972 from the tide crack area of Borge Bay, and placed in separate containers. Individuals, suitable for egg removal, were isolated in petri dishes supplied with a vigorous flow of oxygen-saturated sea water at ambient sea temperature (-1.8°C). Adult females were killed by de-capitation, the oostegites parted using a soft-haired brush, and eggs or embryos then washed from the marsupium with a fine jet of water. All broods were examined briefly under a x50 microscope to determine the stage of development and any unhealthy opaque ova were discarded. Each clutch was transferred with a small amount of sea water to numbered 250 ml. Erlenmayer flasks. Water used both for storage of eggs and respiration experiments had previously been treated as described for the respiration experiments of free swimming amphipods, that is, filtered, cooled and aerated.

Flasks containing ova were kept in the experimental tank for a three day acclimation period (0.0°C ± 0.01°C) and all measurements on ovarian oxygen consumption were carried out at this one temperature. Further experiments at different temperatures had been planned but had to be curtailed due to the limited availability of equipment.

Determinations of oxygen consumption of individual ova of all development stages were made using a Cartesian diver micro-respirometer (Linderstrøm-Lang, 1943; Holter, 1943). Zeuthen (1950, 1964) gave full details of the use of this equipment which employs reversed stoppered divers. The divers used, in this study, ranged in size from 5.56 - 19.20 µl gas volume and they were calibrated by weighing, at the experimental temperature. The Cartesian apparatus was kept in a cold room maintained at 0°C ± 1.0°C.

Ova were introduced into the divers by the sedimentation method dsecribed by Klekowski (1971). After placing the divers in the respirometer an equilibrium period of one hour was allowed before readings commenced (Zeuthen, 1950). Equilibrium pressure readings were made at hourly intervals and each experimental run lasted at least six and sometimes up to twelve hours. Seven divers were used for each experiment.

After an experiment, ova were removed from the divers and their length and breadth measured (only length measurements were made on Stage VI ova). They were then dried at 80°C and weighed on a Beckman micro-balance. Some eggs were damaged during removal from the divers. Most Stage IV and VI eggs however appeared healthy after release from the divers with active heart beats in the former and vigorous swimming in the latter.

For each individual ovum, a plot was made of the equilibrium pressure against time, a linear regression fitted and the rate of change of the equilibrium pressure calculated. Oxygen consumption was derived from:

$$VO_2 = \frac{EP \times 273 \times Vg}{Po \times T}$$

where: EP = Equilibrium pressure.
273 = Temperature (absolute).
Vg = Diver volume.
Po = Normal pressure (10,000 mm. Broadies manometer fluid).
T = Experimental time.

Measurements were made on 75 individual ova and of these runs 56 were successful i.e. produced a correlation coefficient of the equilibrium pressure against time, greater than 0.98, whilst 87 percent of runs produced values of r in excess of 0.995. Three ova gave a value of r = 1.00. Fourteen of the runs which failed did so in batches, so that the complete seven chambers for two particular experiments yielded erratic results. This indicated that the broods were probably dead before the experiment.

8.5.2. Results:

The increase in weight during the larval development of P. antarctica has been previously described in 7.3.3. Table XLIV gives the mean dry weights (and weight ranges) for each of the stages of egg development used in respiration experiments. The individual measurements of oxygen uptake with time for those ova nearest the mean weight of each development stage are shown in Fig. 61. Regressions were calculated using the method of least squares.

Throughout development oxygen uptake increased with egg stage (Fig, 62), Consumption rose steadily from egg Stages I to IV and then showed a marked increase from Stage IV onwards. Increase in embryonic consumption is to be expected and has been demonstrated with the eggs of other aquatic animals. For instance, Zeuthen (1961) showed that oxygen consumption increased by a factor of 3 in amphibian eggs. The more highly developed eggs of the nematode Haemonchus contortus showed a corresponding increase (Rogers, 1948-49) and Robbie (1946) demonstrated an increase in oxygen consumption by a factor of 4 or 5 soon after fertilisation in sea urchin eggs.

No comparative data are available on developing antarctic

Development Stage	I	II	III	IV	VI
Lean Dry Weight* (mg)	0.0392	0.0416	0.0541	0.0584	0.0884
Oxygen Uptake (µl./ mg./ hr.)	0.195	0.345	0.428	0.479	0.444

Table XLV : The oxygen uptake of developing amphipod ova expressed as µl./ mg./ hr. (lean dry weight) against lean dry weight*

* lean dry weight is defined as dry weight minus the ash and lipid fractions.

Development Stage	I	II	III	IV	VI
$\bar{x}$ weight (dry) mg.	0.0570	0.0702	0.0793	0.0841	0.1248
range	0.0470 - 0.0691	0.0576 - 0.0843	0.0476 - 0.0942	0.0688 - 0.1047	0.1142 - 0.1373
$\bar{x}$ O_2 cons. µl/mg/hr.	0.134	0.204	0.2916	0.3327	0.4905
range	0.084 - 0.273	0.120 - 0.357	0.2161 - 0.3262	0.1949 - 0.4150	0.3921 - 0.9198
n	10	12	10	15	9

Table XLIV :Mean dry weights and mean weight specific oxygen consumption (with ranges) for the developing ova of *P. antarctica*.

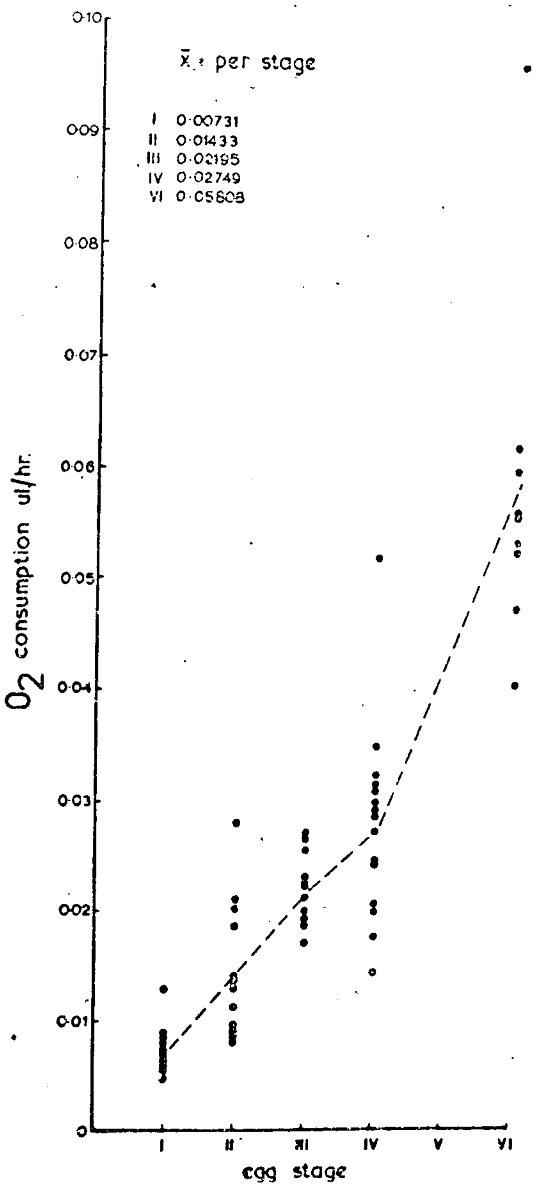


Fig. 62 : The increasing respiration rate with egg stage development.

crustacea though Rakusa-Suszczewski (1973) working on the unfertilised eggs of the antarctic fish Trematomus borchgrevinki and using gross Winkler techniques found a rate of oxygen consumption of 14 µl/hr. for 840 mg. (wet weight of eggs). I have recalculated this figure on the basis of dry weight specific oxygen consumption and obtained a value of 0.084 µl./mg./hr. at -1.0°C or 0.191 µl./mg./hr. at 11.0°C. These figures compare well with the 0.134 µl./mg./hr. consumed by Stage I P. antarctica eggs. It appears that similar consumptions are shown by temperate species for a recalculation of Needham's figures of 1933 (originally based on wet weights) yielded values of 0.71 µl./mg./hr. for Stage I to 2.91 µl./mg./hr. at Stage VII for the embryos of the crab Carcinus maenas. In these calculations it is appreciated that estimates of dry weight from wet weight data are liable to considerable error because of this unknown quantity of water which may be actively taken up by the egg as development proceeds (7.3.3.).

I have expressed the respiration data for P. antarctica ova in Fig. 63 (a) simply as the oxygen consumed in a given time against dry weight. As expected, and in accordance with the results from free-swimming amphipods a linear relationship was derived and oxygen consumption increased approximately six times over the weight range of the ova. It has already been demonstrated that normally the rate of metabolism of an organism decreases with increasing size (weight) (Hemmingsen, 1960) and such a relationship can also be seen in the Cartesian diver data of Jennings (1975) for Tardigrada. However, when I plotted weight specific oxygen consumption, as µl./mg./hr (y) against increasing weight (mg.) (x) the relationship maintained its linearity according to the equation:

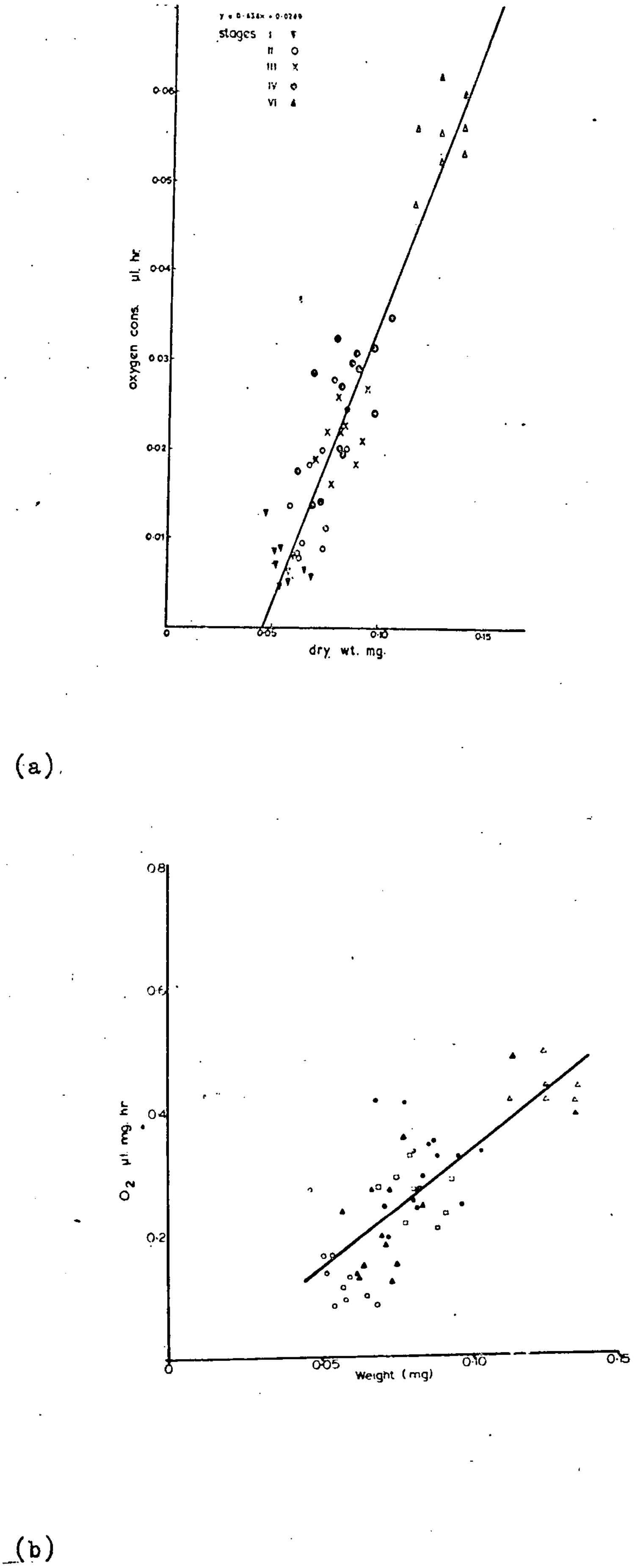


Fig. 63 (a) The oxygen consumption relationship with dry weight for P. antarcica ova.

(b) Weight specific oxygen consumption per weight for P. antarctica ova. $y = 3.70x - 0.0407$.

$$y = 3.70x - 0.041$$

The developing amphipod ova and embryos do not adhere to the general principal of weight related metabolism for contrary to expectation the weight specific consumption continued to rise with an increase in weight.

8.6. Discussion:

There is a lobby amongst physiological researchers to indicate that 'cold adaptation' in some animal groups may be an artefact derived either from misinterpreted data or the use of respirometers not ideally suited to particular requirements. For instance, the results of Rakusa-Suszczewski and Klekowski (1973) using Winkler procedures are higher than those of Klekowski et al (1973) using constant pressure respirometers. Recent papers contradicting the phenomenon of 'cold adaptation' include Holeton (1974); White (1975) and Ralph and Maxwell (a) (in press). Further work on antarctic bivalves (Ralph and Maxwell (b) (in press) indicates that here also "cold adapted metabolism" appeared absent, though investigations are so few on polar Mollusca that no overall cold water physiological strategy for the phylum can as yet be ascertained.

My experiments on Pontogeneia antarctica indicated an elevated metabolism and follow the trend established for Euphausia (McWhinnie, 1964); Orchomenella (Armitage, 1962) and Paramoera (Rakusa-Suszczewski and Klekowski, 1973 and Klekowski et al, 1973). An investigation of growth, respiration and activity should give some indication of the possibility of "metabolic cold adaptation" for it would be difficult for an animal to demonstrate both rapid growth and elevated metabolism without grossly affecting its reproductive strategy. It has already been demonstrated (Chapter 7) that the calorific expenditure of reproduction in this amphipod was appreciable. Growth on the other hand was slow when compared to the growth rates of similar sized temperate amphipods (5.3.4.).

Few metabolic studies of poikilotherms have included parallel investigations of both activity and respiration although Ellenby (1951) demonstrated that the activity of pleopod beating, of Ligia oceanica, was related to temperature. Belman (1975) demonstrated however that unlike most marine isopods the antarctic species, Glyptonotus antarcticus, did not show any change in the rate of ventilation beating as the oxygen concentration decreased, for only at the low levels of 2.0 ml./O_2/l. did the ventilation rate of this isopod drop abruptly. Assuming that Pontogeneia exhibited this same phenomenon then the responses shown in Fig. 60 are solely those of an increasing temperature since the experimental water was kept aerated throughout experiments.

The Q_{10}'s for activity and respiration data differ appreciably and whilst these features can be described, the reason for the discrepancy can not be fully elucidated.

When comparing the weight specific O_2 consumption of pre- and post-hatching amphipods it became apparent that a size range of the amphipod was unfortunately not included. This was due to (a) a lack of suitable experimental animals and (b) the difficulties associated with shifting from one experimental apparatus to another. Post-hatching amphipods were too large and active for Cartesian divers yet too small to obtain reliable results from Constant pressure respirometers or micro-Winkler techniques. I have plotted the results of weight specific O_2 consumption for both ova and the lower size classes of free-swimming amphipods and these are shown in Fig. 64. The highly contrasting respiration rates of developing embryos and post-hatching amphipods can be clearly seen, (N.B. The lines between the two sets of data have been drawn in by eye).

Increasing weight specific O_2 consumption, in P. antarctica appears to be a highly unusual feature,for other studies, on the respiration of crustacean embryos, present the more characteristic decrease for weight related metabolism. For instance, by recalculating Needham's figures (1933) for Carcinus maenas, expenditures of 0.928 $\mu l.O_2/mg./hr.$ for a 355 mg. crab (wet weight) but only 0.183 $\mu l.O_2/mg./hr.$ for a 1,288 mg. crab have been derived. Naturally,it is probable that these values are grossly distorted by the increasing amount of water present in older embryos, actively absorbed as development proceeds. The use of wet weight in physiological experiments is thus suspect. The most ideal method of relating respiration expenditure to body weight would be to express weight in 'metabolic' and'non-metabolic' fractions,for constituents such as exoskeleton and lipid stores (though vital metabolic substrates) do not consume oxygen. I have therefore attempted to relate my data , for amphipod eggs, to a metabolic tissue or 'lean weight', i.e. the total dry weight minus the weight of ash and lipid fractions. However even after the removal of inert structures the situation still indicated an increase (though proportionally less) in weight specific metabolism. The initial increase of activity between

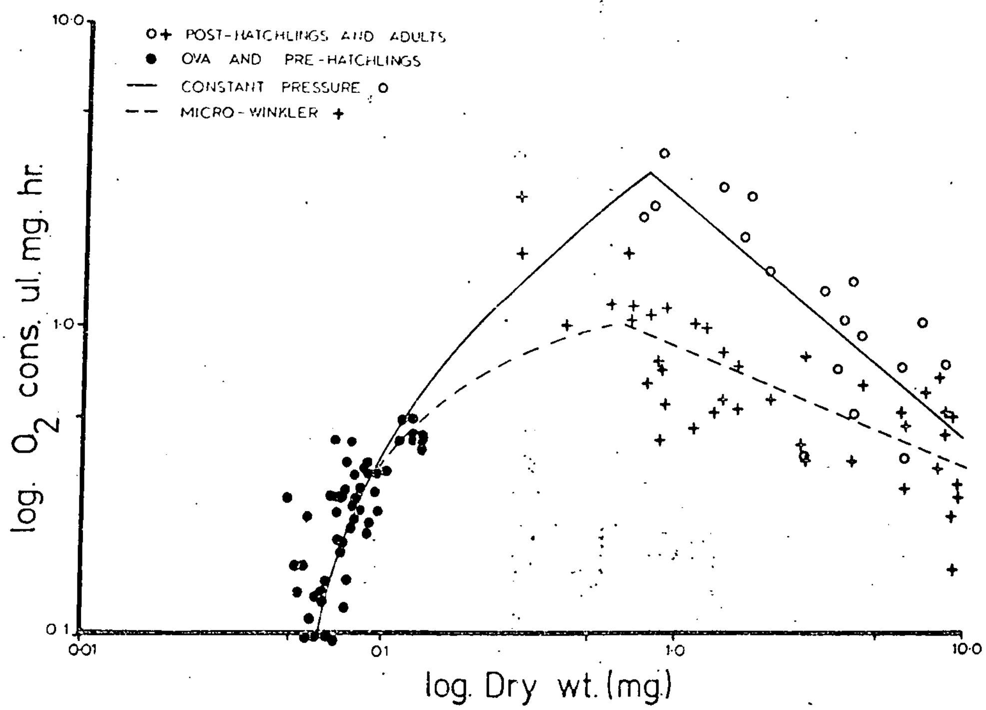


Fig. 64 : The relative oxygen consumption rates (log:log) for both ova and immature/adult P. antarctica using the three methods of: Cartesian Divers,

Constant Pressure Respirometers,

micro-Winkler techniques.

Stages I and II was the most dramatic, due presumably to the relatively low activity of the undifferentiated Stage I egg, for Zeuthen (1950) has correlated the increased consumption with the rate of cell division in the eggs of both the worm _Urechis caupo_ and the urchin _Psammechinus miliaris_. Consumption rates in _P. antarctica_ ova began to decrease at Stage IV with the rate at Stage VI (0.44 µl./mg./hr.) lower than that of Stage IV (0.48 µl./mg./hr.)

Chapter 9. The ecology of Benthic Invertebrates: The brooding antarctic bivalve, Lissarca miliaris.

9.1. Introduction:

Comparative work on the biology of another benthic invertebrate, with an apparently totally different life strategy from that of the amphipod Pontogeneia antarctica, was initiated to identify any fundamental similarities, adapted to the polar environment, which might exist in these two contrasting animals. In particular, aspects of the growth and reproductive biology were studied.

The most appropriate organism appeared to be the sessile bivalve Lissarca miliaris (Philippi, 1845). This species was selected because of its common abundance in the macroalgal habitat (see Chapter 3).

Lissarca miliaris has been described in many antarctic molluscan taxonomic studies, under different specific and generic names (Dell, 1964), whilst Bergmans (1970) has discussed the relationships of the genus Lissarca. The Philobryidae, with the exception of Philobrya setosa, are confined to the Southern Hemisphere and many species are restricted to antarctic and sub-antarctic waters. L. miliaris has been recorded from the Straits of Magellan, Tierra del Fuego, the Falkland Islands, South Georgia and the island groups of the Scotia Arc. The southernmost record is from Deception Island, South Shetland Islands (Soot Ryen, 1951). Ice scour on antarctic shores restricts the species to protected areas and it is absent from the intertidal and immediate sub-littoral zones. The greatest depth at which it has been found is 121m., off Tierra del Fuego (Dell, 1964).

Despite past observations on the numerical and biomass importance of the Mollusca to both the infaunal and epifaunal communities of the antarctic benthos,(Everson and White, 1969; Gruzov et al, 1967; Hardy, 1972 and Rabarts, 1970; 1971), detailed studies on the growth and reproduction of Pelecypoda are restricted to few investigations: Ralph and Everson (1972), (Kidderia bicolor); Rabarts (1970; 1971), (Yoldia eightsii)and Shabica (1974), (Kidderia subquadratum)

9.2. Materials and Methods:

Animals attached to the fronds of D. anceps were collected by the method described in Chapter 3 (3.2.). No plants were, however obtained during March and April and the sample of December 1972 was collected with a 1 m. Agassiz trawl hauled through a bed of D. anceps at 9 m. depth.

Ash weights were obtained after ignition of bulk samples of approximately 50 - 100 mg. dry weight at 500°C for 5 hrs.

9.3. Results:

9.3.1. Biomass.

Lissarca miliaris proved to be the most important single species of mollusc, associated with the fronds of D. anceps, both by weight (W) and number (N), forming mean percentages (of all molluscs) of 38 and 47 respectively (Table V). The October sample contained 76 percent of L. miliaris by weight and 81 percent by number and it accounted for means of 98 percent and 99 percent of the pelecypod population for abundance and biomass.

9.3.2. The biology and growth of Lissarca miliaris.

L. miliaris is a brooding, epifaunal species living attached by byssal threads to macroalgae or other suitable substrates, for instance sponges (Soot Ryen, 1951) and has many of the features common to other antarctic pelecypods (Nicol, 1970; Dell, 1972). The species is small, reaching a maximum recorded length of 5.77 mm., after seven years. Growth is very slow and shows seasonal variation producing characteristic growth rings on the shell.

An unusual feature of L. miliaris, already noted by Dell, (1972) is its colour, a deep purple, colour code 12(D - E)(3 - 6), (Kornerup and Wanscher, 1967) (Fig. 65), for most subantarctic and antarctic species lack shell colour (Nicol, 1970).

It is sometimes difficult to quantify the overall growth of an organism by measuring only a single parameter, for the growth rate of different parts of an animal is not necessarily similar. Various measurements of the shell of L. miliaris were made to test whether growth was uniform (isometric) or non-uniform (allometric). Subsequently I used the maximum antero-posterior length (L.) as the standard measurement and each individual was characterised by this parameter (measured to the nearest 0.08 mm., with an eye piece micrometer). Fig. 67 indicates the relationships of various other parameters to length. The relationship of both log. breadth (B) against log. length and log. height (H.) against log. length were linear although comparisons of the slopes of these regressions to 1.0 using t tests

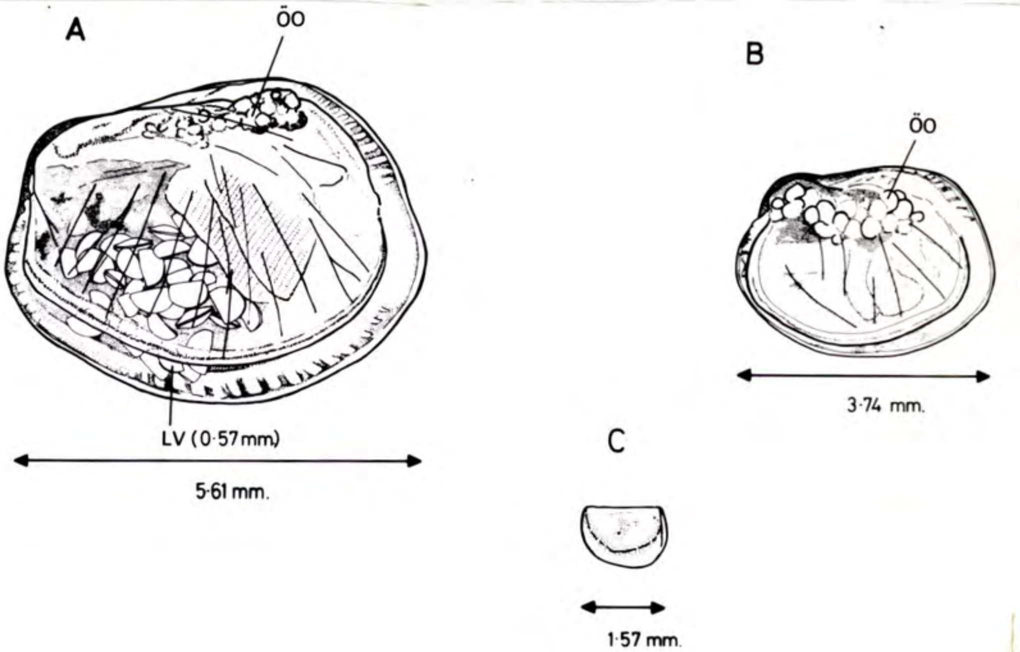


Fig.65 : The brooding bivalve Lissarca miliaris; A, Mature feamale carrying öogonia (öo) and well developed larvae (LV); B, Immature female with öogonia (õo); C, post-release hatchling.

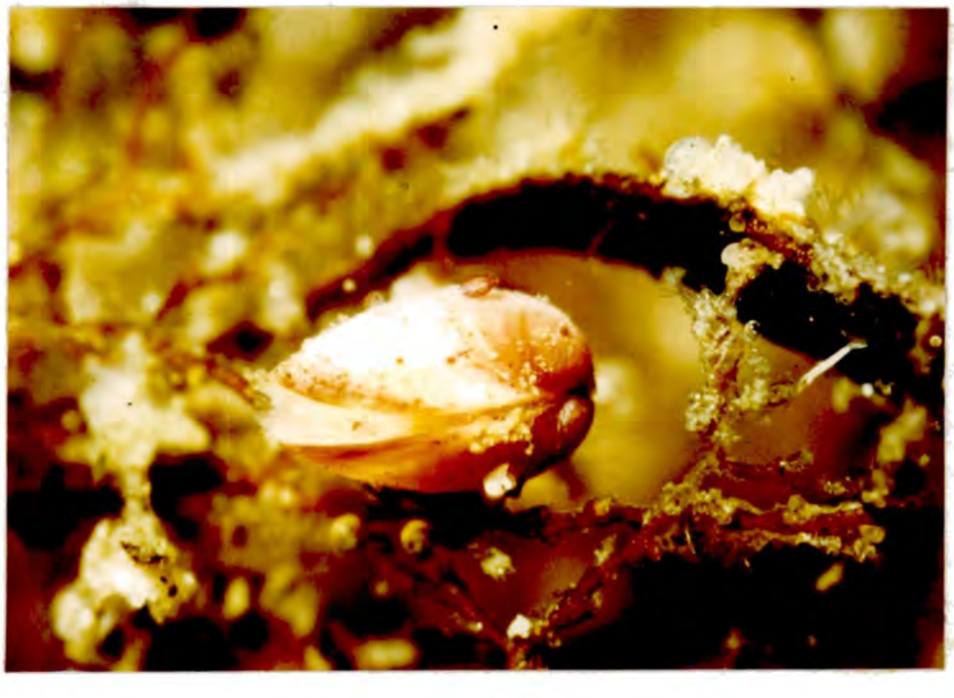


Fig.66 : The bivalve Lissarca miliaris (note the young individual on the upper valve of the adult).

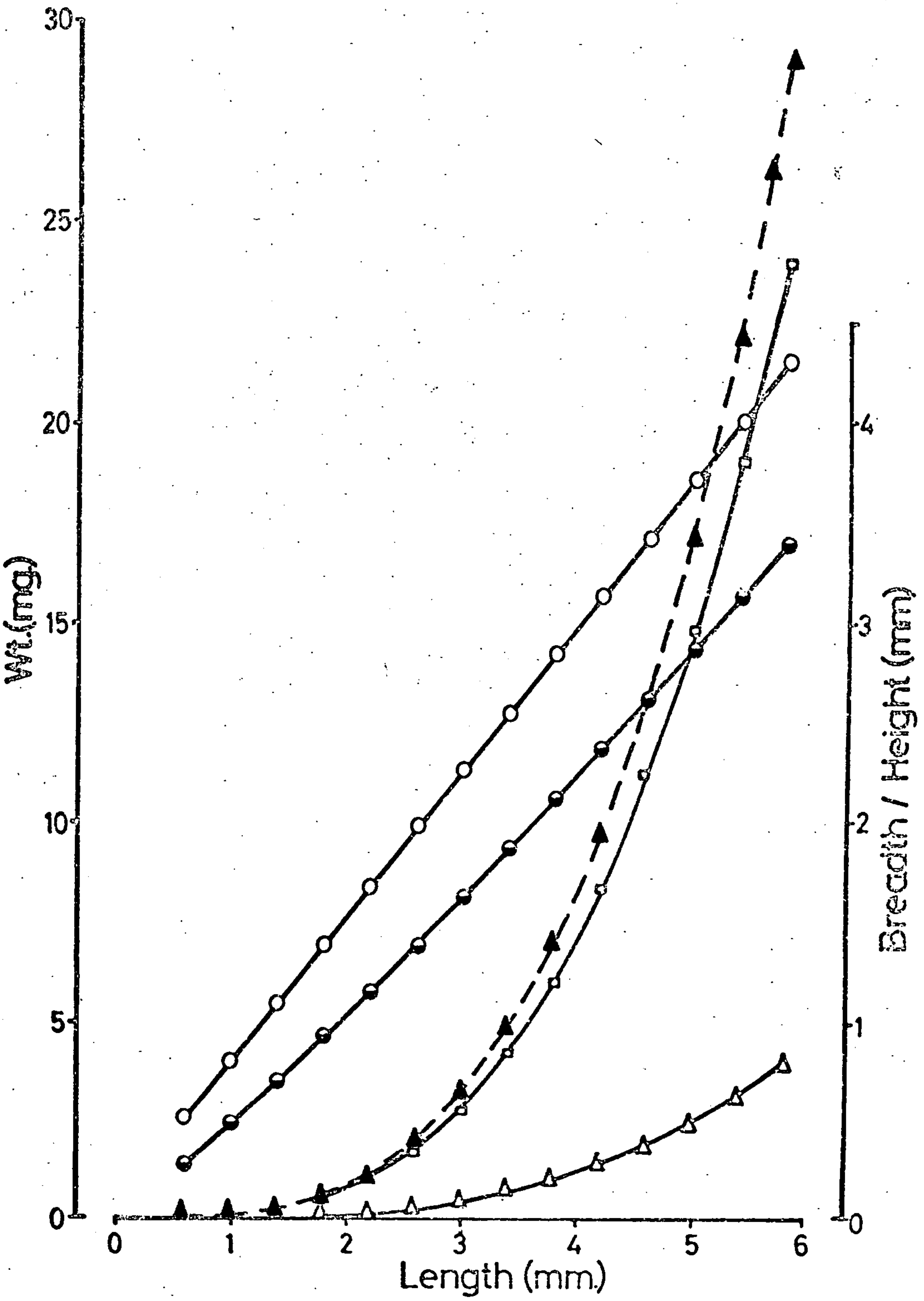


Fig. 67 : Allometric parameters of Lissarca miliaris against length. ○——○ Breadth, ⊖——⊖ Height, ▲- - -▲ Total Weight (dry), □——□ Shell Weight (dry), △——△ Tissue Weight (dry).

indicated that breadth and length were isometric but height and length were allometric ($\underline{t}$ = 1.55 and 6.38 respectively, $P < 0.05$). In other words, the shell valves of older animals progressively deepened with increasing size. The various relationships between measurements of L. miliaris are given in Table XLVI and Appendix XVIII. The regression lines in Table XLVI were fitted by the method of least squares.

Tissue dry weight formed on average 14.3 percent of the total dry weight; similar to figures for other larger pelecypods, for instance Mytilus edulis, 14.0 percent and Mya arenia 11.6 percent (Nixon et al, 1971). The proportion, formed by tissue, in L. miliaris varied slightly with the size of the animal according to the relationship:

$$\text{Tissue weight} = 0.198 \text{ Shell weight} - 0.0121$$

(where r - 0.951, var of y $\pm$ 0.039, var of m $\pm$ 0.0003 and n = 18).

The weight of older animals increased appreciably, not only through deposition of calcium carbonate in the shell, but also through increased tissue weight due to structures absent in immature animals, e.g. reproductive organs .

Ash-free weights of whole animals varied from 25 - 40 percent indicating a shell ash-free weight of 16 - 30 percent. The very high ash-free weights recorded may be due to carbonate sublimation or transformation, however material was not available to repeat these ignition experiments and thus tissue weights and not ash-free weights are referred to later. (Ash weight data for L. miliaris are given in Appendix XIX).

n	y		m	x	b	var. $y^{\pm}$	var. $m^{\pm}$	r
64	log. dry tissue wt.	(mg.)	3.0788	log. length (mm.)	-0.7732	0.0051	0.0370	0.9719
18	log. dry shell wt.	(mg.)	2.8130	log. length (mm.)	-0.8501	0.0025	0.0186	0.9829
96	log. dry total wt.	(mg.)	3.0993	log. length (mm.)	-0.0097	0.0721	0.0358	0.9473
53	log. height	(mm.)	1.1103	log. length (mm.)	-0.4274	0.0006	0.0003	0.9908
53	breadth	(mm.)	0.7324	length (mm.)	+0.0678	0.0102	0.0001	0.9935

Table XLVI: Regression relationships ($y = mx + b$) between various measurements and length, for the bivalve *Lissarca miliaris*.

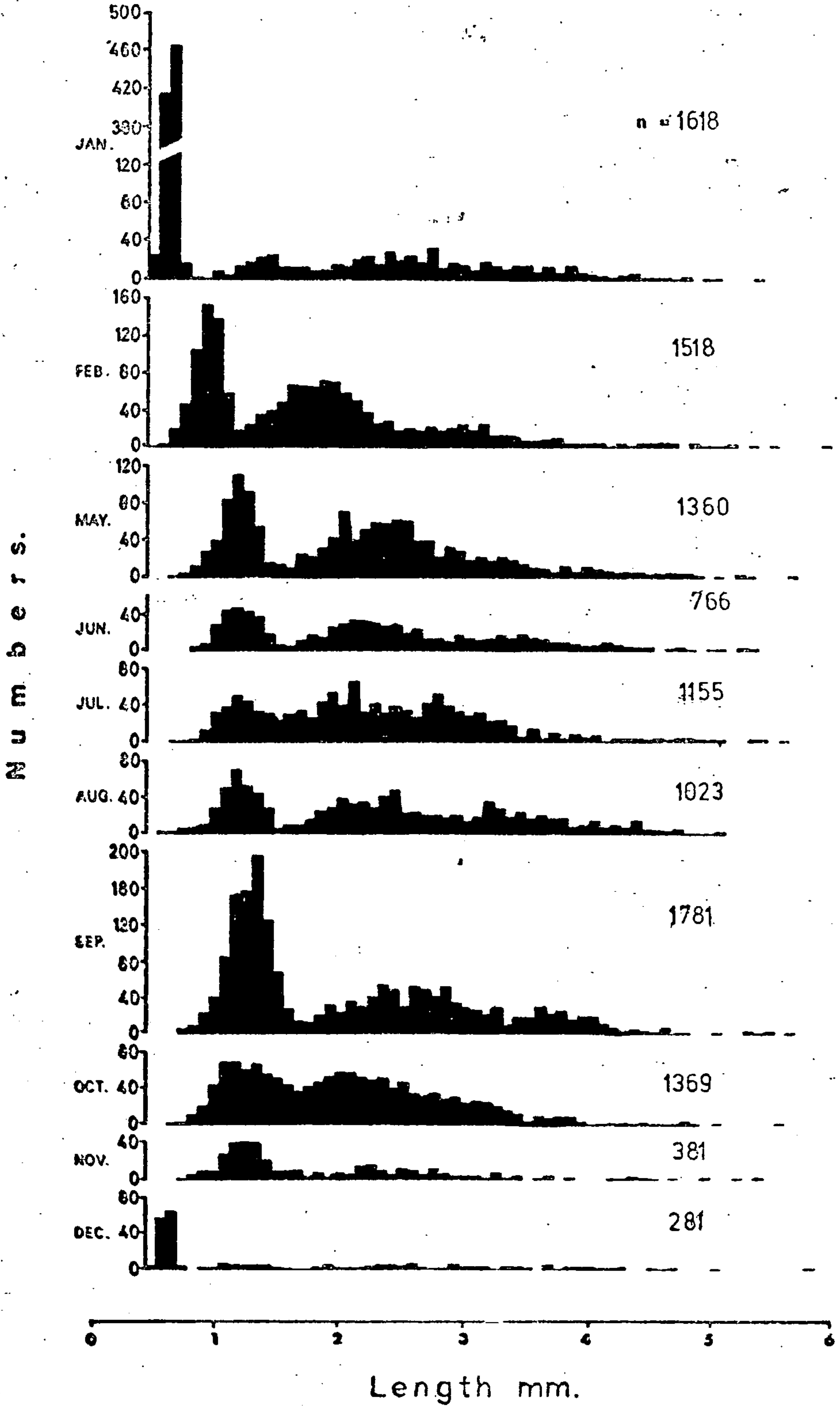


Fig. 68: Monthly population frequency histograms for the bivalve Lissarca miliaris.

9.3.3. Population structure.

The age structure of a population of animals which confines its larval or egg release to short favourable periods of the year can often be determined by examining the various modal classes in length frequency histograms of the species. This is because all individuals recuited into the population in any one breeding season, being of similar sizes, produce discrete cohorts in such histograms. The age composition of the population can however be identified more precisely by examining the ring patterning on the shells of certain molluscs. The composition of the L.miliaris population was examined from the length frequency histograms for the ten monthly sub-samples, Fig. 68. The size of sub-samples varied from n = 281 (December) to n = 1,781 (September) and the totals for monthly samples are shown in Appendix XX. All animals were measured and individuals greater than 2.5 mm in length were examined for reproductive status and sex. The samples for December, January and February demonstrated considerable numerical recruitment, of small sized animals, to the population. My figures indicated that in L. miliaris, despite the presence of a discrete cohort from recruitment, later size classes could be less clearly defined due presumably to variations in sex, reproductive state and growth. The situation was further complicated by mortality which resulted in few individuals present in the older age classes. In most monthly histograms only two or three modes were apparent and age groups could not be resolved using normal probability methods (Harding, 1949; Cassie, 1954).

Many previous workers have however used ring markings, produced by growth retardations in winter, as a means of ageing populations of bivalves. Studies include those on Cerastoderma edule (Walton, 1919; Orton, 1926; Boyden, 1972), Kidderia bicolor (Ralph and Everson, 1972), Macoma balthica and Mya arenia (Burke and Mann, 1974), Mytilus edulis (Seed, 1973), Siliqua patula (Weymouth et al, 1931: Weymouth and McMillin, 1930) and Venerupis pullastra (Quayle, 1951: 1952). The validity of ring markings as indicators of seasonal growth always needs to be checked in each species since cyclical patterning can be induced by a variety of factors. Disturbance (Boyden, 1972) or tides (Evans, 1972) can add extra rings whilst loss of growth patterns due to shell erosion and abrasion can lead to misrepresentation of the age composition of a population. Ideally the incremental patterns observed in the field should be correlated with those of marked animals kept under observation in the same environment. Failing this, some method is required of tracing ring formation from one year to the next. Soot Ryen, (1951) concluded that ring formation in L. miliaris was absent, but this observation may be attributed to preservation peculiarities which can cause shell discolouration thereby obscuring the rings. Two types of ring were present in my samples, with up to seven major rings denoting growths checks in winter and secondary rings, possibly reproductive in origin or induced by disturbance, superimposed. Older animals of breeding age showed a greater frequency of such secondary rings. Coupled with severe pitting and abrasion these increased the difficulty of ring interpretation and the large variances about the means on ring groups in Appendix XX are largely a function of the difficult task of attributing individuals to discrete groups. A more complete picture of the structure of the population can be gained from examining such annual growth rings and Fig. 69 illustrates a typical monthly sample divided up into its respective ring classes. Recruitment can appreciably alter the numerical composition of the population and this feature is demonstrated by a comparison, by ring classes, of the January and August sub-samples (Fig. 70). A rough estimate of the recruitment of small animals to the population can be gained from such a diagram.

Data are presented in Appendix XX for the numbers and means, with standard errors of all ring classes, for each monthly sample. By coupling the means of these ring classes in a direct sequence a 'theoretical' growth curve for L. miliaris could be produced and the configuration of such a relationship was approximately linear.

A more quantitative growth curve for L. miliaris can be derived by applying the Bertalanffy growth equation (von Bertalanffy, 1938) to the means of the ring class lengths in Appendix XX.

The Bertalanffy equation is expressed as:

$$L_t = L_\infty(1 - e^{-K(t - t_o)})$$

where L_∞ is a constant representing the maximum theoretical length of the animal, t = time. L_t = the length at time t and t_o = the theoretical time when the length of the animal is zero.

The constant K describes the growth rate of the animal to its maximum size and can be determined from the slope (e^{-K}) of a Ford-Walford plot (Ford, 1933; Walford, 1946) where L_t is plotted against L_{t+1}. To satisfy the Bertalanffy equation the Ford-Walford

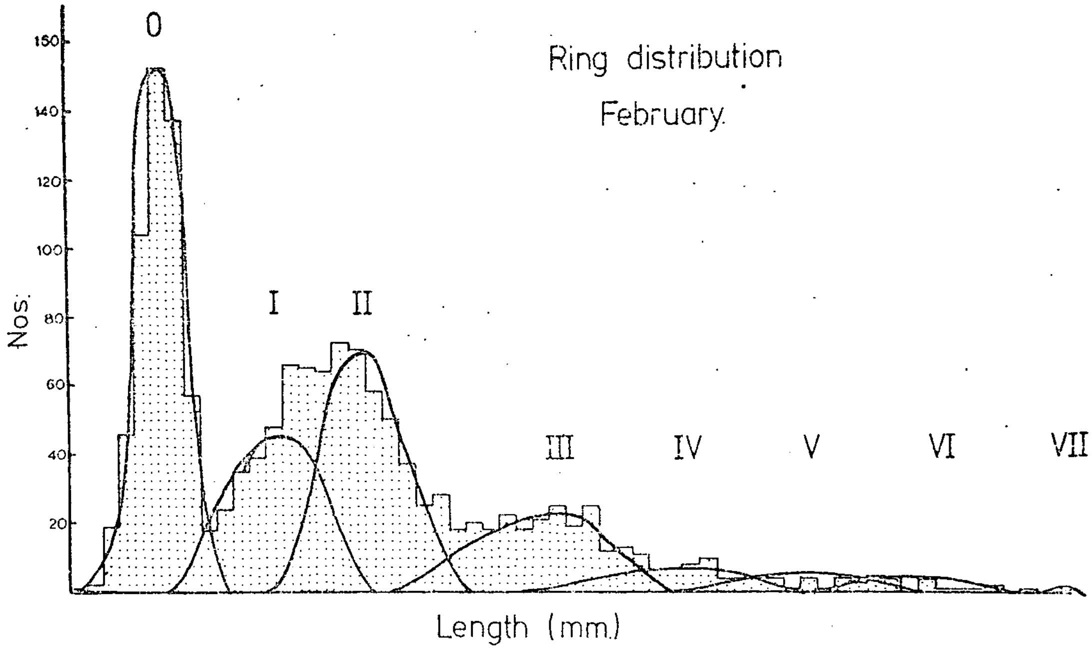


Fig. 69: Length frequency histogram and ring distributions from one monthly sample.

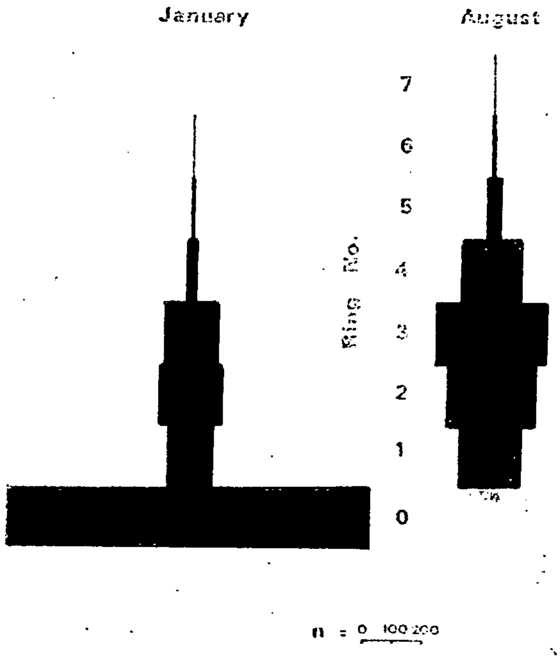


Fig. 70 : Contrasting monthly population compositions for Lissarca miliaris.

plot must be linear and the point on the line where $L_t = L_{t+1}$ is an estimate of the maximum theoretical length of the species (L_∞). The constant t_0 has little biological significance and can be determined by plotting $\log_e(L - Lt)$ against t. The results from the Bertalanffy equation fit the data for L. miliaris and are shown in Fig, 71 and Table XLVII. The percentage incremental length increase, per year (relative growth) showed the typical decrease with age. The rate of growth slowed by a factor of x7 (Fig. 72).

Fig. 73 shows the lengths of animals from the smallest modes of Fig, 68 plotted against time. At the point when primary mode animals (bearing one ring) reach 1 year plus 1 their mean length corresponds to that of animals previously identified as ring 2 class animals. The implication is that animals possessing 1 ring are 3-15 months old, those with 2 rings , 15-27 months etc. The first indication of ring formation takes place just after the onset of winter, when current year juveniles are 3-6 months old. A similar seasonal sigmoidal growth pattern has been shown in the horse clam Tresus capax (Bourne and Smith, 1972).

9.3.4. Reproduction.

Ovoviviparity appears more commonly in species which have to withstand harsh environmental conditions and the occurrence of larval brooding by benthic invertebrates in the Antarctic has been reviewed by Dell, 1972. Brooding avoids the high mortality usually associated with existence as a planktonic larve but is associated with the production of relatively large eggs and consequently a

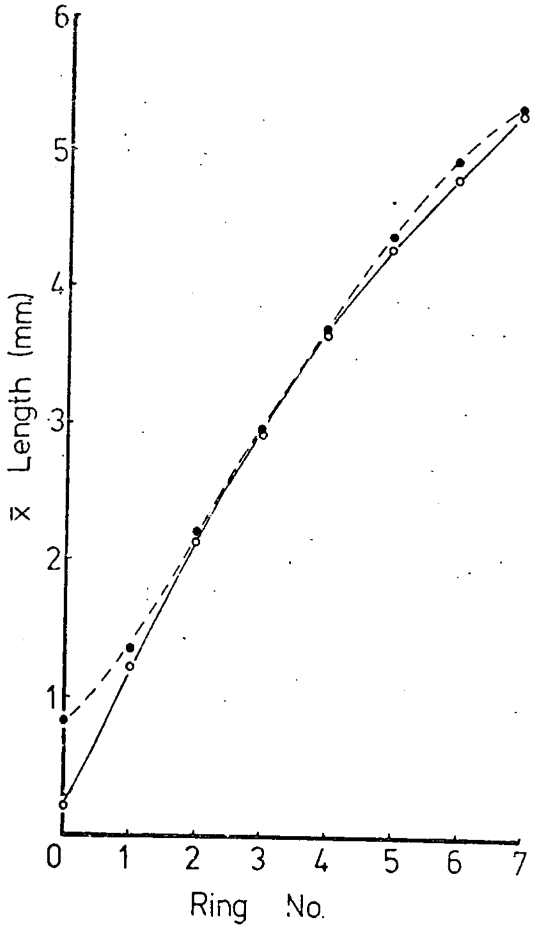


Fig. 71 : Growth curve of *Lissarca miliaris*, from observed data ●------●, and from estimates derived from the Bertalanffy equation ○——○ (K = 0.1304, L_{∞}= 8.61 mm.)

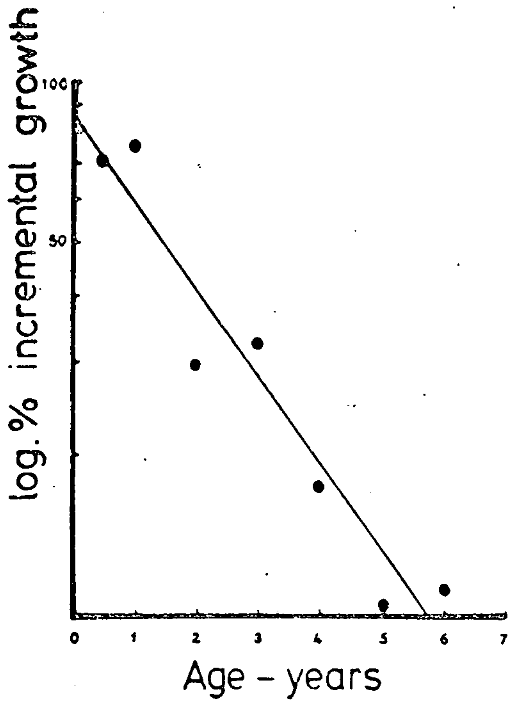


Fig. 72 : Relative growth of *Lissarca miliaris*.

Ring No.	Observed Length (mm)	Calculated Length (mm)
0	0.82	0.20
1	1.38	1.23
2	2.21	2.13
3	2.91	2.92
4	3.67	3.62
5	4.34	4.23
6	4.89	4.76
7	5.27	5.23

Table XLVII: Observed and calculated lengths (using the Bertalanffy equation $L_t = L_\infty(1 - e^{-K(t - t_o)})$ for each ring class of the bivalve Lissarca miliaris. L_∞ = 8.61mm., K = 0.1304, t_o = 0.8212.

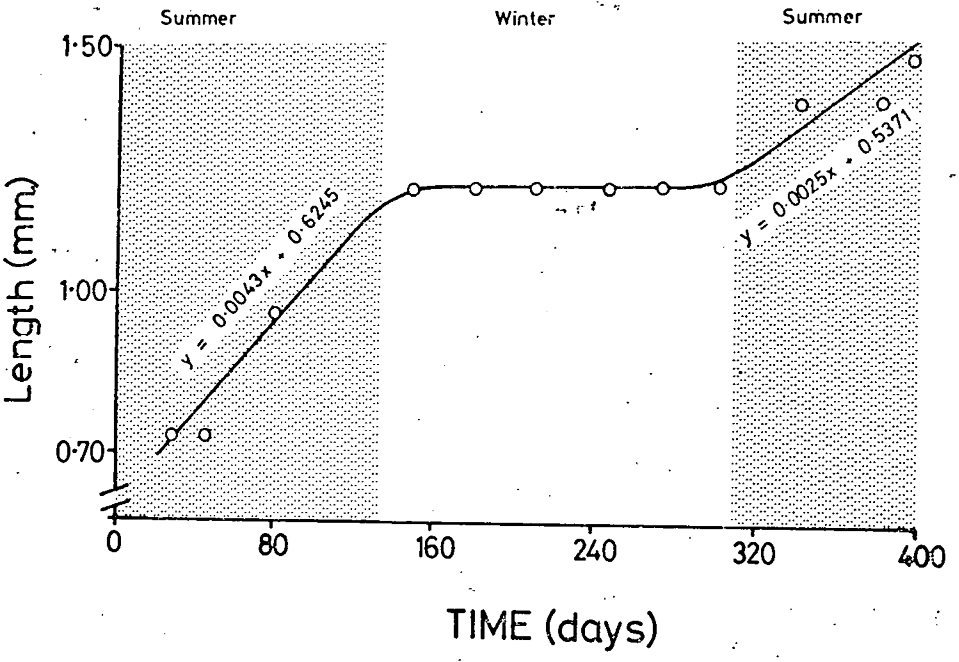


Fig. 73 : Seasonal growth rates of the first year post hatching in Lissarca miliaris. Data obtained from the primary modes of Table XVI.

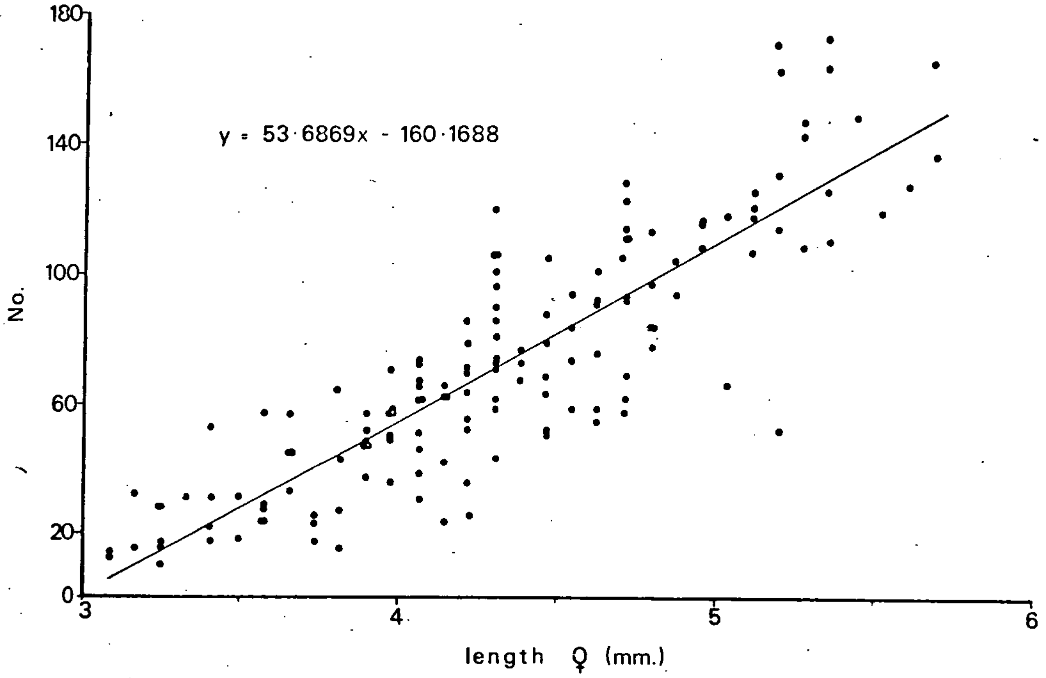


Fig. 74 : Fecundity in Lissarca miliaris. The ralationship between the number of larvae and the length of brooding females. n = 152.

reduced fecundity. In common with other philobryids, L. miliaris exhibits such parental brooding, with the larvae retained within the mantle cavity until they can be released as miniature adults. These retention times can be considerable for Shabica (1974) had recorded a brooding period of a year for the bivalve Kidderia subquadratum.

(a). Fecundity.

The number of larvae that can be produced and carried by any female is related to the development of ovarian tissue and the available internal space of the female and is thus a function of parental age and size. My data indicated that the size of larvae was independent of the length of the parent female.

The relationships of the number of larvae to the length of breeding females were linear. Thus any significant mortality of larvae during the extended brooding period should be identified by comparing, with t tests, any variations between monthly samples in the slopes of the regression lines of fecundity. Such variation proved non-significant with the mean number of larvae per female remaining constant throughout the year (range 54.3 - 70.0 [Table L]) indicating that there was both minimal growth of brooding females during the period of retention and also that the mortality of larvae during brooding was negligible. Accordingly all data was grouped together (Fig. 74) to give a fecundity relationship of:

$$y = 53.69\,x - 160.17$$

where y = the numbers of brooded larvae per female.

x = the length of brooding female (mm.)

($r = 0.864$ and $n = 152$).

(b) Reproductive cycle.

Animals with shells greater than 2.5 mm. long were examined to establish sex ratios and the periodicity of reproduction. L. miliaris is diœious with size ranges of males and females similar. The sex ratio of adult bivalves was significantly weighted towards females (Table XLVIII) with a mean ratio of 1.54 females (± 0.12 st. error) to 1.0 male. Histological investigation of gametogenesis was not conducted, but the onset of öogenesis in female bivalves was readily discernible. Female L. miliaris greater than 3.0mm. long were placed in four arbitrary reproductive classes:

(A). Ovarian tissue undergoing öogenesis, öogonia present in ovaries.

(B). Larvae brooding in mantle cavity.

(C). States A and B both present.

(D). States A and B both absent.

In the majority of examples, categories A and B represent females breeding for the first time whilst older females were identifiable as category C. Females in group D represent spent, infertile or non-breeding individuals and the percentage of bivalves in this group was low, remaining constant throughout the year, never rising above 11.5 percent. The percentage composition of group A

Sample	Jan.	Feb.	May	July	Aug.	Sept.	Nov.	Dec.
♀	66	52	65	45	56	78	20	21
♂	34	37	65	31	36	63	10	12
Totals	100	89	110	76	92	141	30	33
Ratio ♀/♂	1.94	1.41	1.00	1.45	1.56	1.24	2.00	1.75

χ^2 significant (12.72, P 0.05)

Table XLVIII: Sex ratios of *Lissarca miliaris* (for all animals with a length 2.5 mm females declined rapidly from 94.0 percent in January to 8.6 percent in August followed by a steady increase in öogenic females during spring. Conversely the proportion of females brooding larvae in the mantle cavity was very low at the beginning of the year, (1.5 percent), but rapidly rose to a peak of 72.2 percent by May. The maximum level for category C females at 65.5 percent occurred in August. The results for the monthly composition of females, of breeding size, is outlined in Fig. 75 and shown adjacent to the size frequency and breeding status plotted against time for all females (a). The cycle illustrated is however an over-simplification of the field situation, but from interpretation of these two sets of data, Fig. 76 depicting reproductive cycling has been derived.

Overlapping generations of developing young within the parent were apparent and from Fig. 75 a chronology of events can be established. The reproductive cycle for immature L. miliaris is initiated in September when öogenesis begins in the ovaries of individuals over 3.0 mm. long. The percentage of females in this reproductive state increases, until by the beginning of the year most individuals greater than 3.0 mm. are carrying primary öocytes. During February these primary öocytes are released into the anterior section of the mantle cavity. Fertilisation presumably occurs at this time. Brooding within the mantle cavity then commenced and continued until the following December. Meanwhile a second generation of öogonia began development in March, within the ovaries. The complete cycle of egg maturation, through the öogonium, öocyte to the immediate pre-release larva takes 17 to 18 months.

Embryos within the anterior mantle cavity are held in two

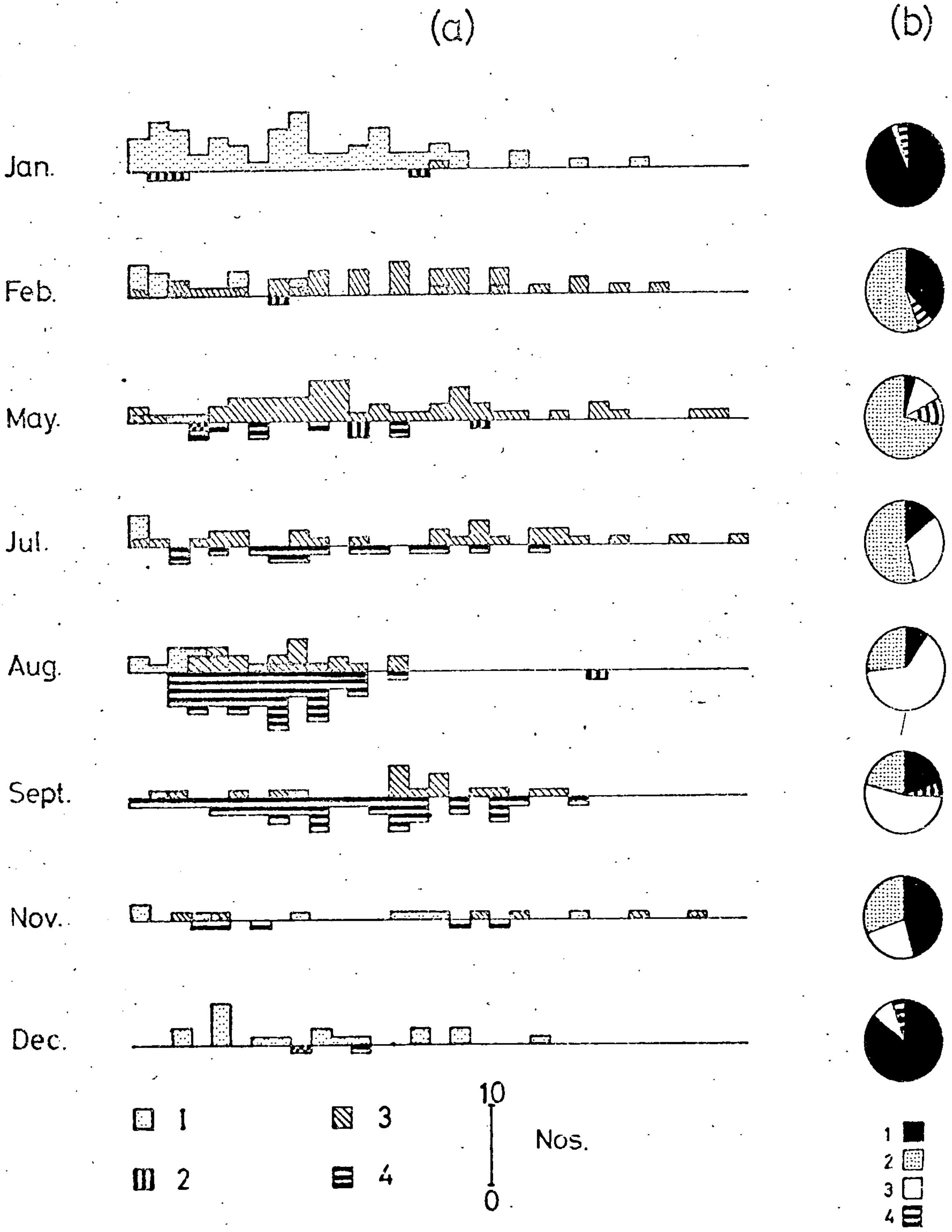


Fig.75 (a) Frequency histograms for size, with time, of the four breeding conditions of *Lissarca miliaris*.

(b) % composition of each breeding condition/brooding population.

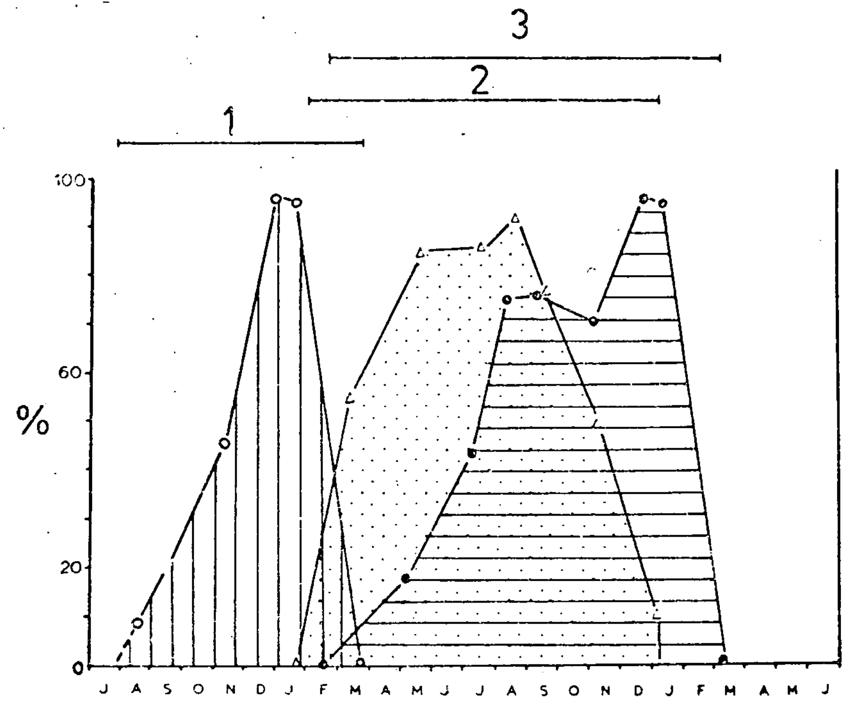


Fig. 76 : Öogenic and brooding cycles of Lissarca miliaris:
1, Öogenesis (generation 1), 2 Brooding, 3 Öogenesis (generation 2).

clusters, one in each of the valves. Each cluster is surrounded by a thin transparent membrane whose function is presumably to prevent premature ejection. Sketches of the appearance of group A and C females plus the typical D - shaped straight-hinged protoconch are shown in Fig. 65.

(c) Larval development.

The öocytes and larvae of L. miliaris are very large compared to those of other bivalves but of comparable size to the brooded larvae of non-polar pelecypods. The growth of larvae within the adult females during the extended retention period was determined by inspecting the broods of up to 20 females per month and measuring and weighing a random sample of ten individual larvae from each brood. Larvae were dried at 60°C and stored under vacuum to obtain weights. Relocation of öocytes into the suprabranchial chamber of the mantle cavity occurred in mid-summer. Males at this time had active gonads and fertilisation probably occurred within the female mantle cavity. Initial embryos were spherical with a diameter of 0.32 mm. (S.D.$\pm$ 0.014) and a mean weight of 7.1 µg. Growth during brooding was very slow and partial-shelled individuals were not apparent until August. Development to the characteristic D - shaped straight-hinged protoconch larvae occurred in the final two months (Dec. and Jan.) of brooding and accounted for the sigmoidal shape of the length/time curve of Fig. 77. The sudden increase in larval length during early austral spring took place during the development of pre- to partial-shelled larvae. In contrast, the

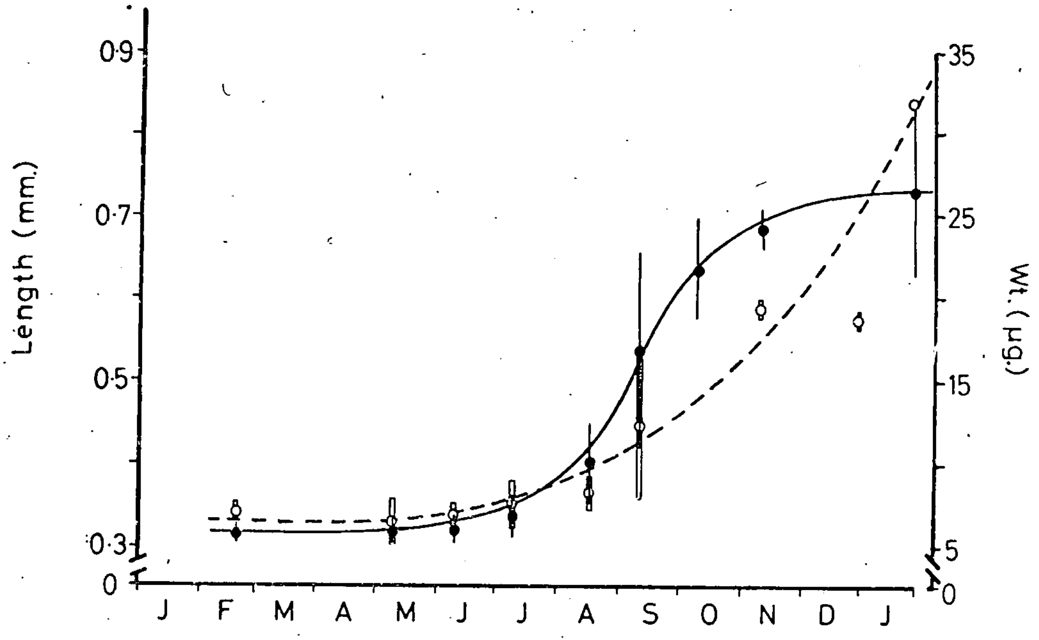


Fig. 77: Length and weight changes during brooded development of larval Lissarca miliaris.

o - - - o weight (µg.)

● —— ● length (mm.)

weight of larvae increased exponentially, and not sigmoidally, until their release during December. The sequence of development during brooding was as follows:

Feb. - July	Aug. - Oct.	Nov. - Dec.	Dec. - Jan.
Pre-shelled	Partial-shelled	Fully-shelled	larval release

9.3.5. Recruitment and Mortality.

Brooded embryos were only found in females of ring classes 4, 5, 6 and 7 with this repeated annual breeding in L. miliaris resulting in the production of three or four generations per female. Though the numbers of larvae produced per individual, in the older age classes, was large, the number of specimens available to reproduce in such ring classes had diminished. Nearly half (45.7 percent [Table XLIX]) of the young produced in each calendar year came from 5 year old females. Four year old females may be still immature, undergoing öogenesis or carrying brooded larvae, and though the numbers of group 4 brooders may be considerable, such bivalves were breeding for the first time and consequently produced few young. Data for the relative numbers of larvae produced for each breeding class, during 1972, are presented in Table XLIX. Some caution needs to be exercised in extrapolating from these figures since annual recruitment, in many bivalve species, is highly variable and depends on a variety of hydrographic features. Whether the 1972 situation, described here, is a general feature of the reproduction of this antarctic species can only receive speculation. Certainly the number of the population

% Production of Larvae

Ring No.	4	5	6	7
Month				
Jan.	-----	-----	-----	-----
Feb.	19.67	43.05	37.28	-----
May	44.64	33.89	14.28	7.18
June	25.04	55.72	19.24	-----
July	9.03	56.38	34.59	-----
Aug.	9.97	46.96	37.78	5.29
Sept.	63.20	19.82	16.98	-----
Oct.	-----	-----	-----	-----
Nov.	20.26	63.77	15.97	-----
Dec.	-----	-----	-----	-----
$\bar{\bar{x}}$	27.40	45.66	25.16	6.24
S.D. ±	19.73	15.05	10.80	1.34

Table XLIX: The relative importance of ring classes to the population production for ten monthly samples (1972) of *Lissarca miliaris*, where the percentage production

$$= \frac{\text{No. larvae per ring class per sample}}{\text{Total larvae per sample}} \times 100$$

brooding at any one time was small and remained low (Table L), never rising above 7.3 percent.

Length frequency histograms (Fig. 68) of the monthly subsamples indicated a large recruitment, of small individuals, during the months of December, January and February. Designating observed recruitment as the ratio of 0 class bivalves to the remainder of the population, observed recruitment:

$$= \frac{\text{0 class animals}}{\text{Total population} - \text{0 class}}$$

This gave the following ratios for these three months:

$$\text{December} \quad \frac{130}{153} = 0.0850$$

$$\text{January} \quad \frac{1012}{606} = 1.670$$

$$\text{February} \quad \frac{516}{1001} = 0.516$$

These data for post-release recruitment appear lower than nearly all the potential production (P_N) figures determined from analyses of brooding females (Table L) where numerically the potential recruitment is expressed as:

$$P_N = \frac{\text{No. of larvae brooded per sample}}{\text{Total sample population} - \text{larvae}}$$

producing a mean ratio of 2.64.

Differences between the observed recruitment and P_N are

Sample date	Sample population number	Percentage brooding	No. larvae	$P/_N$	Percent tissue recruitment	$\bar{x}$ larvae/♀
Feb.	1,518	2.24	2,288	1.51	5.97	67.29
May	1,360	4.41	3,564	2.62	6.67	59.40
June	766	7.31	3,123	4.07	10.10	55.77
July	1,155	3.98	3,111	2.69	6.01	67.63
Aug.	1,023	5.18	3,269	3.20	9.02	61.68
Sept.	1,781	4.83	4,671	2.62	6.92	54.31
Nov.	381	2.89	770	2.02	6.88	70.00
			$\bar{x}$	2.68	7.37	62.30

Table L: Data of the fecundity and potential production of <u>Lissarca miliaris</u>.

$P/_N$ = potential recruitment to the sample population,

$$\text{percent tissue recruitment} = \frac{\text{larval tissue wt./sample } (W_{Lt})}{\text{total sample population tissue weight} - W_{Lt}}$$

are possibly caused by pre- and post-larval mortality, migration of recently released young or sampling inefficiency. Alternatively they may indicate that major fluctuations in breeding success do, in fact, occur in this bivalve, so that the production of 0 class animals in 1973 (i.e. brooded larvae during the period of my observations) may have been far greater than the 1972 production. Migration was presumed to be of a steady state nature with emigration (if present) equal to immigration. Also t tests on the regressions of monthly fecundity have already demonstrated that mortality of embryos during brooding was negligible. The sampling technique used would certainly have collected and extracted representatives of the small animals, if they were attached to macroalgae, and subsequent hand sorting under a 50x dissecting microscope validated the methods. Although the byssus of L. miliaris is secreted shortly after release, ejection of young during storm conditions could result in immediate post-release juveniles being swept away from suitable anchorage into unfavourable habitats. The overall evidence points to the fact that annual recruitment of 0 class animals in the population does not fluctuate wildly. Thus there is no predominance, in the population structure, towards any one particular year class and the data of Fig. 78 (means for all the samples) suggests a steadily declining rate of mortality from year to year. The data suggests that mortality of pre- and post-larvae is the main feature producing the difference between observed and potential recruitment and if this mortality is added to that produced by differences in the population structure between first and second year individuals (Fig. 68, Appendix XX) a net mortality for this small bivalve during its initial year is approximately 60 - 70

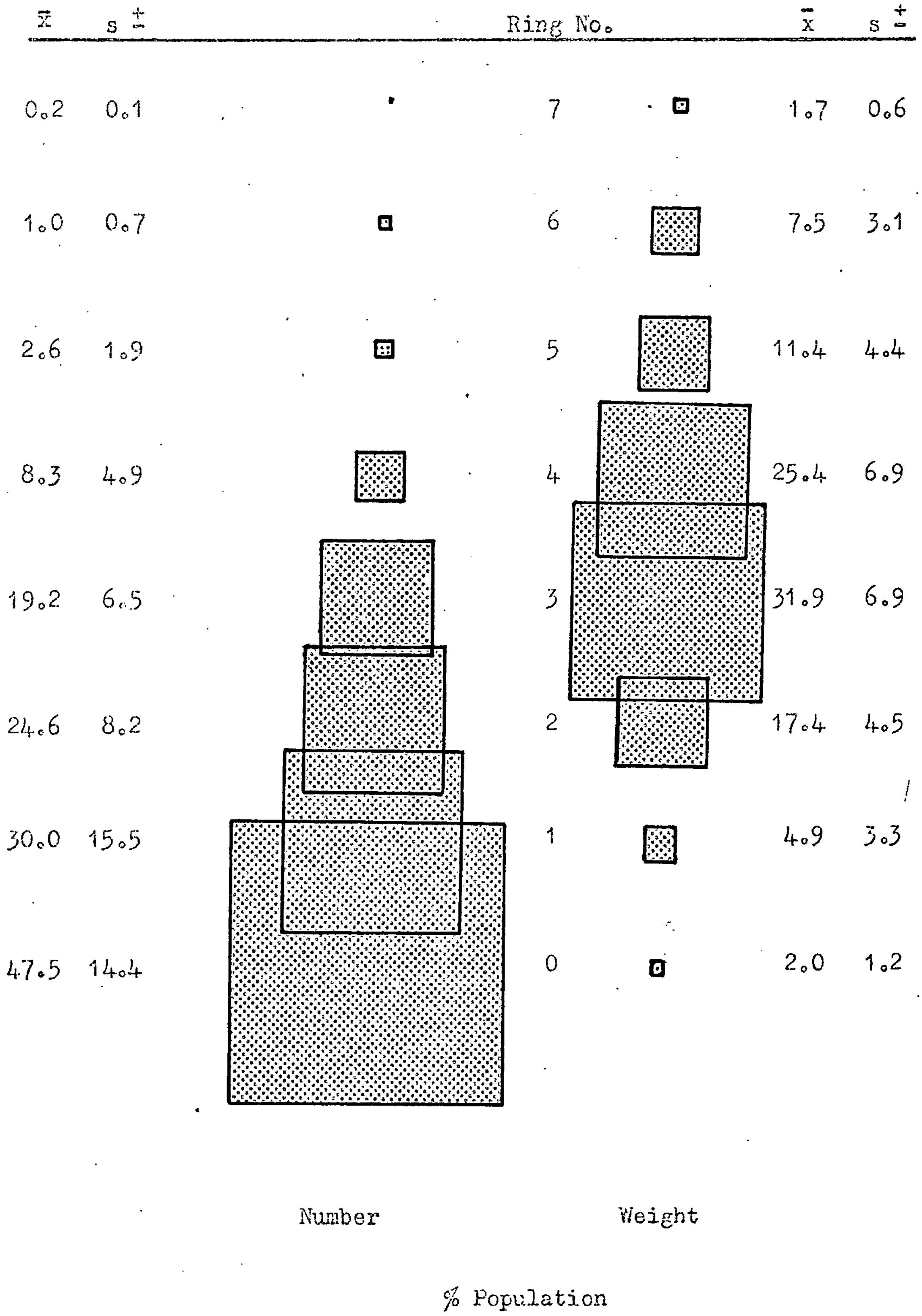


Fig. 78 : Population structure of <u>Lissarca miliaris</u>. Mean percentage values of weight and numerical abundance by ring classes.

percent. However the biomass involved in this loss from the population is of little significance since potential production in terms of dry tissue weight (larvae) over the total dry tissue weight of the population (minus larvae) had only a mean value of 7.4 percent (range 6.0 - 10.1 percent). The relative proportion of first year animals, to the total population can be obtained by summing the 0 and 1 ring classes (Fig. 78) where, despite over a 70 percent numerical dominance of first year individuals in the population, the biomass of this year group contributed only 6.9 percent, by weight. I assumed that the decline in numbers of ascending ring classes (Fig. 78) was a direct measure of population mortality.

9.4. Discussion:

9.4.1. Lissarca dimensions and growth.

Growth of L. miliaris generally followed that of other molluscan species (Seed, 1973). Tissue weight remained a constant function of total weight with the increased weight attributed to calcium deposition in the shell being offset by the development of soft tissues, particularly reproductive. Shell morphology of pelecypods can be considerably altered by location and environmental conditions for Seed (1973), working on mussels from exposed and sheltered shores, demonstrated a marked reduction in growth rate and increased longevity in animals exposed to heavier seas. Weight in L. miliaris increased exponentially in relation to length, producing the double log. relationship of equation I (Table XLVI). Allometry was only apparent, to a small extent, in the inter-umbo distance (H), a condition different to that described by Seed (1973) for Mytilus though comparative figures for Venerupis (Quayle, 1952) showed isometry in all dimensions measured.

Growth studies on molluscs, using winter check rings, are extensive and have been reviewed and discussed by Wilbur and Owen (1964), whilst more specific studies, on Macoma balthica, using individually marked animals, have been followed by Gilbert (1973).

The growth of L. miliaris followed a sigmoid curve (Fig. 71) (or a double sigmoid if larval growth is included in the analysis). Similar patterns have been demonstrated in the Pacific razor clam Siliqua patula (McMillin et al, 1931). These authors described growth using the Gomperz equation (Gomperz, 1825).

$$\log.\ lt = \log.\ L(1 - e^{-K(t-t_1)})$$

where t_1 = time when lt = 1.

Thiesen (1973) working on Mytilus edulis, from Arctic waters, also demonstrated sigmoidal growth with a curve best evaluated using both the Gomperz and Bertalanffy equations. The Gomperz equation was found to fit growth of the animal up to half its maximum length, whilst the Bertalanffy equation gave better fits when the observed lengths related to a size above one third of the maximum length, but proved unsuitable for the smaller individuals in the size range. Thiesen (1973) concluded that 'fit' to the Bertalanffy equation was more realistic for M. edulis.

The estimates derived from the Bertalanffy equation gave a good 'fit' for the observed values of L. miliaris, above the year one class. Since this curve describes all but the initial size group of the animal, further analysis to fit the Gomperz curve was not felt necessary. The value of K (0.1304) derived from the slope e^{-K} of the Ford-Walford plot indicates the slow nature of growth towards maximum size though the L_∞ estimate for the species at 8.61mm. is higher than the observed value of 5.8 mm. length. Relative incremental growth diminished with age by a factor of 7 from 71.6 percent in length for first year animals to 11.2 percent for six year olds. Corresponding values for temperate species indicates faster initial growth; Mytilus edulis, 190 - 300 percent for two to four year olds (Seed, 1973), and Pecten maximus, 200 - 300 percent in two year olds (Gibson, 1956).

Data on the growth rates of southern cold water species are extremely sparse. The small gaimaridan Kidderia bicolor, showed more constant growth with relative incremental increases of 43.6 percent during second year growth, diminishing to 11.0 percent by the fifth (Ralph and Everson, 1972). Similarly, the infaunal pelecypod Yoldia eightsii produced a diminishing relative growth rate from 100 percent for second year animals, 9 percent at 13 years to less than 5 percent at 17 years (Rabarts, 1971).

Comparisons of growth rates for a variety of bivalves are given in Fig. 79, with growth in the antarctic species reduced in both absolute and relative terms. Possible exceptions to this general feature being the relatively large L. elliptica and Adamussium colbecki (Ralph, pers. comm.)

9.4.2. Brooding in bivalves.

Thorson (1936, 1946 and 1950) and Ocklemann (1965) have

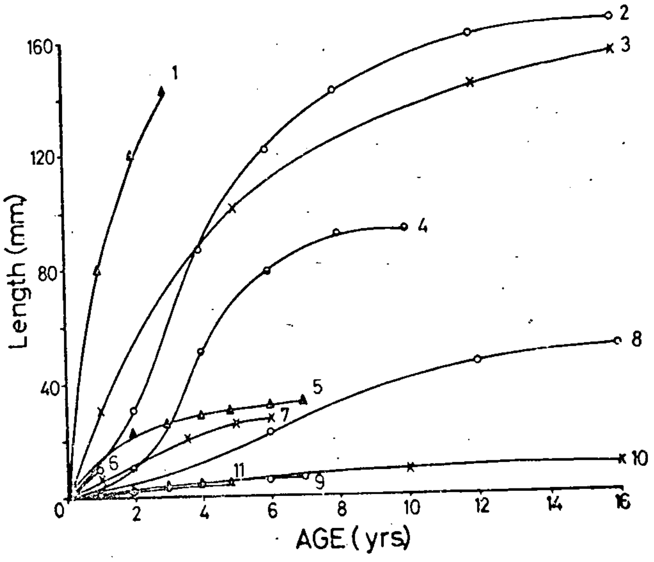


Fig. 79: Size and longevity of pelecypod species within geographic localities: 1, Mytilus californianus, California (Fox and Coe, 1943), 2, Siliqua patula, Pacific (Weymouth and McMillin, 1931), 3, Tresus capax, British Columbia, (Bourne and Smith, 1972), 4, Cardium corbis Pacific (Weymouth and Thompson, 1931), 5, Cerastoderma edule, North Sea (Boyden, 1972), 6 Sphaerium solidulum, Illinois (Foster, 1932), 7, Macoma balthica, Massechusetts (Gilbert, 1972), 8, Mytilus edulis North Sea (Seed, 1973), 9, Lissarca miliaris, Antarctic (this study), 10, Macoma balthica, White Sea (Gilbert, 1973), 11, Kidderia bicolor Subantarctic, South Georgia (Ralph and Everson, 1972).

reviewed relationships between environmental conditions, brooding tendencies and the reproductive variations that increased parentalism involves. Most marine pelecypods shed eggs into the sea, where fertilisation and subsequent development through the typical molluscan planktotrophic trocophore and veliger occurs. The larvae ultimately settle on a suitable substrate and metamorphose. Development in a few specialised groups is initiated from internal fertilisation within the gills or supra-branchial chamber though increased parental protection in bivalves has been observed only in certain groups, for instance the freshwater Sphaeriidae (Sphaerium, Forster, 1932; Zumoff, 1973) and Unionidae (Anodonta, Elliptio and Lampsilis, Wiles, 1975); the marine Erycinidae (Lasaea, Howard, 1963; Mysella, Franz, 1973) and Montacutidae (Montacuta. Oldfield, 1963). In antarctic bivalves (Table LI) the Cyamidae (Kidderia, Ralph and Everson, 1972; Shabica, 1974), Philobryidae (Philobrya, Dell, 1964; Howard, 1953 (P. setosa, a northern hemishere species) and Laternulidae (Laternula, Burne, 1920), brood their young. This last record has never been fully substantiated by more recent workers.

(a). Brooding methods.

Eggs may be retained within the parent body or, in a few examples, Turtonia minuta (Oldfield, 1963) and Nucula delphinodonta (Drew, 1901), enveloped in a protective capsule and deposited external to the parent body. Brooding may be ovoviviparous, releasing young as miniature adults (Lissarca, Lasaea (Oldfield, 1963); Cyclas (Pelseneer, 1935); Kidderia (Ralph and Everson, 1972; Shabica, 1974) and Gaimardia

(Pelseneer, 1903; Maxwell, pers. comm.) or, alternatively larvipary may be present where brooding occurs to only a limited extent and the young embryos are released to follow either a planktotrophic (*Kellia*, Lebour, 1938) or parasitic existence (glochidia) *Anodonta*, *Elliptio* and *Lampsilis*, Wiles, 1975). Oldfield (1955, 1961 and 1963) gave detailed accounts of the embryological development during brooding in certain bivalves.

(b). The ecological implications of brooding.

Thorson (1950) correlated the incidence of brooding to severe environmental conditions and the common occurrence of brooding in antarctic invertebrates (Dell, 1972) and Pelecypoda(Soot Ryen, 1951) adds support to this statement. The lack of pelagic larvae appears to be an adaptation by species subjected to extreme conditions and limited available food. Planktotrophism in antarctic waters could be of selective advantage to young stages if a high degree of synchronisation of larval release to maximum primary productivity could be satisfactorily achieved and maintained through different climatic years.

(c). Fecundity.

The ovoviviparity in *L. miliaris* had been previously remarked on by Soot Ryen (1951) but detailed fecundity relationships for antarctic species have only been established for very few species. Burne (1920) noted 'masses' of eggs within the mantle cavity of *L. elliptica* whilst Dell (1964) records *P. sublaevis* as containing 175 large, developed eggs between the gills and *Philobrya capillata* had 400 eggs attached to its gills. *L. elliptica* apparently possesses a specially enclosed supra-branchial chamber to hold eggs and this feature is also prominent in *Myochama* and *Cochlodesma*. Fecundity is normally dependant on the size of the parent though Ralph and Everson (1972) found no such correlation in *K. bicolor* at South Georgia, and Franz (1973) compiled a linear relationship between log. fecundity and arithmetic length in *Mysella planulata*. The fecundity of *L. miliaris* was, in contrast, directly related to the length of the parent females (Fig. 74) and a similar situation was described by Shabica (1974) for *K. subquadratum*. However, in this latter example the variance about the slope for this relationship was considerably increased and although Shabica discussed the presence of fatality throughout brooding in *Kidderia*, I could detect no such brood mortality.

Fecundity in brooding species is greatly reduced because of the relatively large egg and larvae sizes and the restraint on numbers brooded being the available internal volume of the parent. The increased parentalism offsets the vast mortality incurred by the pelagic existence of many molluscan planktotrophic larvae. In *L. miliaris* the öocyte or embryo size remained constant in relation to either clutch number or parent length, a condition also reported by Wolda (1970) for the snail *Cepaea nemoralis*.

The disparity in sizes of eggs and embryos of molluscs, with different reproductive strategies, has been widely discussed (Thorson, 1936, 1946 and 1950; Ocklemann, 1965; von Oertzen, 1972, and in the Gastropoda, Knox, 1955). Thorson (1952) determined the critical transition egg size,for bivalves brooding their young, at 100 - 120 μm

Species	Cited
Pseudokellya cardiformis	Pelseneer, 1903.
Mysella arthuri	Dell, 1964.
Kidderia bicolor	Soot-Ryen, 1951; Everson and Ralph, 1972.
Kidderia subquadratum	Shabica, 1974.
Gaimardia trapesina trapesina	Pelseneer, 1903; Maxwell (pers. comm.).
Laternula elliptica	Burne, 1920.
Lasaea rubra	Pelseneer, 1903.
Adacnarca nitens	Burne, 1920; Soot-Ryen, 1951; Dell, 1964. Nicol, 1966.
Cyamiocardium crassilabrum	Dell, 1964.
Lissarca miliaris	Soot-Ryen, 1951; Richardson, this study.
Lissarca notorcadensis	Dell, 1964.
Philobrya sublaevis	Soot-Ryen, 1951; Dell, 1964.
Philobrya capillata	Dell, 1964.
Bathyarca sinuata	Pelseneer, 1903...probably a brooding species.

Table LI: The incidence of brooding in antarctic Pelecypoda.

diameter and von Oertzen (1973) reported on fecundity and egg diameters of pelagic planktotrophic species. These are compared below with those of brooding species:

	No. eggs	Diameter (µm.)	Reproductive strategy
Macoma calcarea	14,500	95	PLANKTOTROPHIC
Cyprina islandica	400,000	70	
Cerastoderma lamarcki	20,000	65	
Macoma balthica	3,500	110	
Mysella planulata	1,000	140	larviparous
Lissarca miliaris	60	305	BROODING- OVOVIVIPAROUS
Philobrya sublaevis	175	'large'	
Lasaea rubra	6-22	300	
Turtonia minuta	8-19	170	capsular

The development period in most brooders, from other geographical localities, is far shorter than the lengthy, brooding period from öogonia.,öocytes to pre-release embryos reported for the two antarctic species whose reproductive biology is known. The capsular brooder *T. minuta* (Oldfield, 1955) takes 3 - 4 weeks for young to complete their brooding development. In comparison, the öogenic period of 5 months in *L. miliaris* produces a total brooding time (Fig. 76) only equalled by that of *Kidderia subquadratum* (15 - 19 months).

Franz (1973) speculated on the comments of Sellmer (1967) that brooding amongst bivalves was most prevalent in smaller species, with very small animals perhaps lacking sufficient energy resources to create the vast numbers of planktotrophic larvae required for species survival. Further work on the necessary energy required to produce independent young from ovoviviparous, larviparous and planktotrophic organisms will be needed to clarify this hypothesis.

Assuming that energy expenditure is related to the volume of eggs produced, a figure of decreased reproductive output for brooders (expressed as egg volumes) can be derived as follows:

L. miliaris - Ovoviviparous $6.70 \times 10^{8} \mu m^{3}$ ($\bar{x}$ total egg vol.)
L. planulata - Larviparous $1.44 \times 10^{9} \mu m^{3}$
C. islandica - Planktotrophic $5.39 \times 10^{10} \mu m^{3}$

Conversely, if increased egg volume leads to a proportionally increased lipid content, as suggested by Thorson (1936) then the energy expenditure between these different reproductive categories may in fact be far closer than the above figures indicate. Most brooding species produce more than one clutch, with *Sphaerium* brooding twice per year and this repetition of brooding by individuals at different ages of the population may allow greater stability in populations subjected to a severe environment.

Summary Discussion:

Recent marine research in the Antarctic has deviated away from the qualitative and taxonomic studies of earlier workers to present, detailed quantitative accounts of the ecology of certain benthic organisms, for instance the research of Everson (1970) on the fish Notothenia coriiceps neglecta and of Pearse (1963) and Pearse and Giese (1966) on the echinoids at McMurdo Sound. However, the inter-relationships between the biology of individual marine organisms and their surrounding environment has still received little attention. In particular, the organisation of the major food chains in antarctic waters requires further attention; for the relationships both within and between the benthos and plankton and how such relationships alter according to season and the severity of climate is not yet clearly understood.

This present study was an attempt to provide some comparative data on relevant aspects of the biology of two of the commonest invertebrates associated with the macrophyte community. Such a habitat is not particularly easy to sample, either practically or statistically. Initial exploratory work at Borge Bay, Signy Island indicated that, although the extent and biomass of the macroalgal forest was less than in temperate seas, the habitat provided a valuable source of food and shelter to a wide variety of organisms. This paucity of macrophytes could be partly attributed to the mechanical attrition and shading of in-shore sea ice and to the lack of suitable colonising substrates for such plants. In addition, the diversity of species within the macrophyte community appeared to be less than that found in similar studies in temperate waters, (Moore, 1973). [It should be emphasised that in this current work complete extractions of the fauna associated with the macroalgae were not attempted].

The two invertebrates, the amphipod Pontogeneia antarctica and the benthic bivalve Lissarca miliaris have markedly contrasting life strategies. The crustacean migrated during the winter months to the undersurfaces of the sea ice, only returning to the benthos in spring but the bivalve remained throughout the year attached to the macroalgal fronds. These two poikilotherms were thus subjected to contrasting ecological, but not necessarily physiological régimes. Despite such differences, the two species exhibited some close similarities in their biology. Their rates of growth were slow, fecundity was reduced and the period of embryological development extended. In addition, the metabolism of P. antarctica, measured as respiration, was elevated over that expected for the low ambient temperature.

In the past, too much emphasis has been placed on the effect the rigorous climate and sea condition of the Antarctic have, per se, on its native fauna, without presuming that endemic organisms have adequately evolved to counter such stresses. Many polar animals have shown an appreciably higher 'standard metabolism' than might be expected at the prevailing low sea temperatures (Wohlschlag, 1960; McWhinnie, 1964 and Armitage, 1962). P. antarctica similarly demonstrated such metabolic 'cold adaptation' with correspondingly high Q_{10}'s. The fact that the movements and activity of high latitude poikilotherms, amphipods in particular, are certainly no slower than their temperate counterparts was remarked on by Bregazzi (1972) and indicates that comparable or elevated metabolisms are necessary if the rates of other vital processes, such as feeding, are not to be reduced. Conversely, unless the relative amount of energy ingested can be substantially increased then these high metabolic rates of antarctic invertebrates must produce reductions in other (less vital) energy consuming processes and Dunbar (1968) suggested that the slow growth rate of polar animals acould be attributed to this phenomenon.

Pelagic primary production in inshore antarctic waters has been reported as highly variable by Horne et al,(1969)and the chlorophyll values of Appendix II indicate that considerable diatom fluctuations were present in the plankton during 1972. My data suggested that although the rate of feeding of P. antarctica during the austral summer and on neritic diatoms was comparable to, but not particularly higher, than temperate species (Mathias, 1967), this rate could not be sustained throughout the extended winter when food supplies were limited.

A few antarctic invertebrates, such as Glyptonotus antarcticus, breed throughout the year (White, 1974), but the majority of species which have been studied in any detail possess synchronised breeding cycles, so that young are released during the late winter or spring when phytoplankton production, and thus a plentiful food supply, is at its peak. This synchrony of larval release is not necessarily confined solely to planktotrophic species for detritivores, relying on diatom 'fall-out' or predators feeding on the newly released larvae of diatomaceous species may synchronise to this same restricted period of the year. Unlike temperate species which can produce a number of broods during the long reproductive season, antarctic species are restricted to the production of a single or prehaps (as in the case of P. antarctica) two broods per year. To maintain adequate survival of the species with such reduced production, the mortality of embryos and young stages must be minimised. A means of achieving this is by increasing the degree of parental care during embryological development and by producing large eggs to release relatively large and well developed offspring. Such reproductive development has been identified in both P. antarctica and L. miliaris. The advantages of reduced fecundity, increased egg size and parental brooding have also been outlined in antarctic fishes by Marshall (1953) and Everson (1970). Such a strategy confers an immediate degree of independence on the young after their release. The mobility of young reduces potential predation and the increased size ensures that, due to weight related metabolism, the energy intake can be relatively reduced. It has also been shown in this study that young amphipods of P. antarctica need to achieve a certain minimum size to be able to utilise benthic food supplies.

With considerable fluctuations in food supply and feeding activity the construction of an energy budget for planktotrophic species poses problems. Some indications of the amount of energy available can however be determined. The feeding experiments (6.3.5. [b]) on the amphipod P. antarctica ($\bar{x}$ dry wt. 14.2 mg.) indicated a maximum cannibalistic feeding rate of 4.5 young amphipods per day. Such a level corresponds to an annual ingestion of between 2.59 and 3.25kJ. (depending on determined or estimated calorific values of the food supply). Presuming an assimilation efficiency of 60 percent (Clarke, pers. comm.) the amounts of energy available to the animal are substantially reduced to 1.55 to 1.95kJ. per year. An animal of 14.2 mg. produces on average 69 eggs in a brood, and since Maxwell (1976) demonstrated that the calorific value of fertilised and unfertilised eggs of the antarctic decapod (Chorismus antarcticus) remained the same the data of 7.3.4. (III) has been directly used.

Sampling evidence indicates that P. antarctica produces two broods within twelve months, the first clutch being considerably reduced. I have calculated the energy expended on egg production as 0.189 kJ. per year (i.e. a gross ash free weight egg production of 5.85 mg.) or 9.7 - 12.2 percent of the total annual energy input.

Additionally the oxygen consumed by this crustacean at the recorded level of 0.32 µl./mg./hr. would amount to 39.86 ml. per year, equivalent to 0.566 kJ. (for assuming an R.Q. value of between 0.7 and 1.0, a litre of oxygen ≙ 14.2 kJ.).

Food in the shallow-water benthos of the Antarctic is not a limiting factor during the spring and summer and most of the growth of polar organisms occurs during this short season (Rakusa-Suszczewski, 1972; Richardson, in press). The eggs of many species are also laid early in winter to fully utilise this substantial summer feeding. The percentage of the total assimilated energy channelled into metabolic maintenance and reproduction lay between 38.7 and 48.7 percent, (at the maximum feeding level). The data in this thesis have already indicated that the maximum feeding rates on which these calculations are based could not, in fact, with the limited food supplies, be sustained throughout the year. Consequently many of the charcterisic features common to the reproduction and rates of growth of antarctic invertebrates probably stem from the elevated metabolism which exists in many antarctic organisms coupled with the highly fluctuating primary production and its subsequent reduction in overall annual ingestion rates.

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Year 19/	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72
Duration (days)	144	169	241	84	161	70	177	130	125	228	113	104	164	135	113	211

$\bar{x}$ duration = 148 days ($\pm$ 49 S.D.)

Appendix I: Fast ice duration (days) for Borge Bay, Signy Island: (data from White, in press).

Appendix II: Sea water conditions at four depths, Signy Island, South Orkney Islands:

(a) 2m. depth Normanna Strait.

(b) 6m. depth Factory Cove, Borge Bay.

(c) 10m. depth Normanna Strait.

(d) 30m. depth Normanna Strait.

(data from J. Hoogesteger, 1973).

(a).

Date	Salinity	Ammonia	Nitrate	Nitrite	Phosphate	Silicate	Chlorophyll	Carotenoid
5.4.72	33.31	1.04	30.0	0.26	1.76	-	1.24	1.05
14.4.72	33.25	1.30	32.5	0.31	1.12	-	1.40	1.24
24.4.72	33.69	1.91	35.0	0.43	1.90	84.0	2.02	1.15
8.5.72	33.51	1.90	29.0	0.385	2.02	49.0	0.94	0.875
20.6.72	33.54	1.84	5.43	0.35	1.43	80.2	0.173	0.70
27.6.72	33.79	3.62	17.0	0.43	1.83	85.4	0.144	-
4.7.72	35.61	4.44	17.7	0.39	1.88	8.9	0.144	-
11.7.72	33.93	4.14	17.9	0.26	1.68	81.5	0.101	-
19.7.72	33.83	2.15	22.0	0.36	1.85	86.6	0.173	-
25.7.72	33.78	2.00	34.8	0.36	1.59	84.0	0.202	0.035
31.7.72	33.54	3.96	23.0	0.34	2.10	80.0	0.096	0.136
2.8.72	33.58	1.90	22.8	0.31	2.01	94.0	0.072	0.262
15.8.72	33.93	2.00	25.4	0.31	1.70	87.5	0.115	0.007
30.8.72	34.03	0.71	26.8	0.26	1.83	91.0	0.115	0.080
13.9.72	33.67	2.85	20.4	0.22	1.09	78.0	0.187	0.087
26.9.72	33.83	3.15	28.6	0.38	1.10	87.6	0.274	0.262
16.10.72	33.59	4.50	18.3	0.18	2.16	89.5	0.230	0.079
23.10.72	33.98	3.09	27.2	0.15	1.91	92.5	0.490	0.210
30.10.72	34.03	2.43	26.05	0.22	2.24	90.5	0.706	0.472
6.11.72	33.93	2.00	26.7	0.27	2.05	89.5	0.49	0.236
13.11.72	33.98	1.77	26.4	0.25	2.58	95.5	0.475	0.620
20.11.72	34.03	1.86	26.3	0.21	2.07	87.5	0.561	0.368
27.11.72	33.93	1.70	26.0	0.30	1.93	87.0	0.347	0.481
4.12.72	33.83	3.55	26.4	0.263	1.97	85.7	0.331	-
18.12.72	33.64	3.80	24.5	0.37	1.91	86.2	0.770	0.444
1.1.73	33.73	2.00	10.5	0.32	0.85	77.8	32.100	20.000
9.1.73	33.84	1.42	30.9	0.27	0.86	67.4	35.400	22.800
15.1.73	32.97	1.74	5.7	0.27	2.52	59.0	15.300	10.900
22.1.73	33.35	2.00	16.00	0.29	1.35	64.8	6.10	4.100
29.1.73	32.46	2.37	12.3	0.30	0.59	54.3	11.100	8.500
5.2.73	33.33	2.65	14.6	0.366	1.18	68.0	8.800	5.740
19.2.73	33.51	1.65	18.4	0.30	1.48	15.9	3.0	2.390
6.3.73	33.44	2.58	21.2	0.30	1.56	74.0	2.86	1.920
19.3.73	33.39	1.93	23.2	0.31	1.66	80.0	2.50	1.570

Data from J. Hoogesteger.

2m. Depth Station, Factory Cove, Borge Bay.

(b).

Date	Salinity	Ammonia	Nitrate	Nitrite	Phosphate	Silicate	Chlorophyll	Carotenoid
5.4.72	33.40	2.10	30.0	0.30	1.70	-	1.58	1.17
14.4.72	33.34	0.90	23.5	0.29	1.18	-	1.44	1.41
24.4.72	33.55	2.50	32.5	0.45	1.57	83.2	2.19	1.43
8.5.72	33.49	2.05	31.5	0.385	2.00	80.0	1.01	0.92
29.5.72	33.62	2.80	30.8	0.45	2.45	82.0	0.795	0.55
13.6.72	33.81	1.98	28.1	0.38	1.10	76.0	0.404	0.298
20.6.72	33.54	3.20	4.60	0.38	1.725	78.6	0.173	0.735
27.6.72	33.83	3.17	16.4	0.43	1.79	80.8	0.21	0.029
4.7.72	33.90	3.18	15.8	0.36	1.94	80.9	0.202	-
11.7.72	34.15	5.00	16.0	0.31	1.82	82.6	0.187	-
19.7.72	33.85	2.25	21.6	0.40	1.92	87.5	0.202	-
25.7.72	33.83	2.23	25.3	0.40	1.74	86.3	-	0.053
31.7.72	33.44	2.00	21.9	0.40	2.06	82.0	0.115	-
2.8.72	33.73	1.85	23.3	0.31	2.17	89.0	0.100	0.21
15.8.72	33.88	1.60	22.2	0.12	1.73	92.5	0.058	0.012
30.8.72	33.01	1.22	27.4	0.33	2.03	90.5	0.043	-
13.9.72	33.88	2.05	28.0	0.19	1.11	82.8	0.187	0.087
2.9.72	33.89	3.36	28.6	0.26	2.14	90.7	0.290	0.122
16.10.72	33.40	3.76	19.3	0.17	1.91	89.5	0.274	0.157
23.10.72	33.96	3.62	25.9	0.165	2.28	92.5	0.518	0.158
30.10.72	34.04	2.65	28.3	0.23	1.95	90.0	0.576	0.280
6.11.72	33.97	2.32	29.6	0.205	2.57	89.5	0.647	0.236
13.11.72	33.93	2.00	27.9	0.209	2.03	95.2	0.490	0.280
20.11.72	33.92	1.98	26.2	0.15	2.07	88.0	0.518	0.516
27.11.72	33.98	2.15	27.1	0.15	2.03	87.0	0.305	0.315
4.12.72	33.98	3.45	26.4	0.29	1.97	84.6	0.432	0.350
18.12.72	33.84	4.60	27.0	0.245	2.14	86.2	43.000	30.600
1.1.73	33.68	1.30	10.6	0.31	0.88	79.0	38.900	27.100
9.1.73	33.83	1.24	29.2	0.29	0.84	67.0	20.300	14.350
15.1.73	32.56	0.82	5.64	0.255	2.41	60.7	5.760	4.520
22.1.73	33.73	2.53	14.3	0.28	1.35	63.7	15.600	14.100
29.1.73	33.34	2.78	13.0	0.27	0.85	56.8	7.530	5.850
5.2.73	33.59	2.73	16.8	0.34	1.25	69.3	2.540	2.150
19.2.73	33.53	4.00	18.0	0.30	1.54	75.5	3.190	2.020
6.3.73	33.44	2.20	22.9	0.26	1.63	71.0	2.600	1.800
19.3.73	33.42	1.72	23.2	0.30	1.70	81.0	2.400	1.320

Data from J. Hoogesteger.

6m. Depth Station, Factory Cove, Borge Bay.

(c).

Date	Salinity	Ammonia	Nitrate	Nitrite	Phosphate	Silicate	Chlorophyll	Carotenoid
5.4.72	33.33	1.45	33	0.25	1.70	-	0.980	0.70
14.4.72	33.38	1.00	31	0.34	1.40	-	1.300	1.20
24.4.72	33.69	1.91	35	0.425	1.90	84.0	2.020	1.15
8.5.72	33.76	1.45	28	0.385	1.93	70.0	0.940	0.83
20.6.72	33.78	2.04	3.92	0.40	1.37	75.5	0.216	0.525
27.6.72	33.81	2.52	17	0.43	1.83	85.4	0.144	-
4.7.72	35.72	3.44	17.5	0.36	1.83	80.9	0.115	-
11.7.72	33.66	4.00	18.2	0.36	1.68	82.0	0.058	-
19.7.72	33.98	1.50	21.4	0.36	2.00	86.0	0.129	-
25.7.72	33.74	1.86	23.0	0.26	1.64	84.0	0.115	-
31.7.72	33.83	1.96	22.6	0.34	2.10	82.0	-	-
2.8.72	33.56	1.50	22.4	0.29	2.02	95.0	0.160	-
15.8.72	33.94	2.30	23.2	-	1.74	88.0	0.058	0.013
30.8.72	34.16	0.79	26.8	0.261	1.85	91.5	0.115	-
13.9.72	33.89	2.32	28.0	0.15	1.07	82.5	0.130	-
26.9.72	33.85	2.75	29.8	0.28	2.00	87.5	0.202	0.219
16.10.72	33.38	5.00	18.3	-	1.85	89.5	0.216	0.122
23.10.72	33.98	2.72	26.0	0.19	2.28	91.3	0.404	0.105
30.10.72	34.03	1.63	26.05	0.26	1.87	91.2	0.475	0.157
6.11.72	33.97	1.85	22.8	0.33	2.47	88.9	0.676	0.394
13.11.72	33.98	1.47	26.4	0.33	2.07	94.2	0.504	0.376
20.11.72	34.04	1.62	25.2	0.27	1.97	89.0	0.504	0.416
27.11.72	33.96	1.28	26.2	0.53	2.00	88.0	0.550	0.350
4.12.72	34.01	3.45	26.4	0.25	2.00	85.7	0.389	0.044
18.12.72	33.75	3.80	25.5	0.30	2.03	86.8	1.308	0.864
1.1.73	33.83	1.80	13.7	0.30	1.32	80.8	20.200	12.800
9.1.73	33.65	1.46	31.0	0.31	0.91	71.0	39.400	26.700
19.2.73	33.49	2.00	18.2	0.30	1.52	17.8	3.330	2.320

Data from J. Hoogesteger.

10 m. Depth Station, Normanna Strait.

(d).

Date	Salinity	Ammonia	Nitrate	Nitrite	Phosphate	Silicate	Chlorophyll	Carotenoid
5.4.72	33.50	1.50	31.0	0.25	2.02	-	0.99	0.65
14.4.72	33.35	1.06	30.0	0.31	1.34	-	1.24	1.11
24.4.72	33.44	1.91	32.5	0.38	1.81	81.5	1.51	1.37
8.5.72	33.50	1.91	29.5	0.33	2.18	79.0	0.87	0.665
20.6.72	33.81	2.80	6.0	0.35	2.12	80.1	0.36	0.613
27.6.72	33.83	2.93	16.4	0.45	1.60	83.0	0.26	-
4.7.72	34.70	3.64	16.3	0.22	2.00	80.9	0.130	-
11.7.72	33.71	4.65	20.3	0.36	1.73	82.0	0.28	-
19.7.72	33.93	1.59	21.6	0.35	1.96	87.0	-	-
25.7.72	33.74	2.34	24.4	0.32	1.57	84.7	0.173	-
31.7.72	33.79	2.00	22.0	0.325	2.10	83.0	-	-
2.8.72	33.54	2.08	23.0	0.25	2.12	95.5	0.10	0.08
15.8.72	33.99	1.40	24.2	0.14	1.69	89.0	0.10	0.016
30.8.72	34.03	0.85	26.6	0.20	1.95	90.0	0.014	0.079
26.9.72	33.88	2.82	28.6	0.14	1.91	88.9	0.187	0.096
16.10.72	33.39	5.45	16.4	-	1.88	90.0	0.26	0.149
23.10.72	34.02	2.96	23.0	0.15	2.23	92.5	0.504	0.219
30.10.72	34.05	2.73	27.8	0.20	1.93	92.4	0.317	0.123
6.11.72	33.99	2.08	27.0	0.20	2.47	89.5	0.518	0.044
13.11.72	33.98	1.77	27.8	0.209	2.02	95.2	0.374	0.446
20.11.72	34.03	2.20	27.2	0.20	2.00	90.0	0.475	0.402
27.11.72	33.98	1.40	26.3	0.19	2.08	87.0	0.305	0.315
4.12.72	34.01	3.45	26.4	0.24	2.04	86.8	0.404	0.193
18.12.72	33.88	3.82	27.6	0.263	2.13	86.6	0.864	0.595
1.1.73	33.90	1.03	20.4	0.29	1.64	85.0	24.800	17.700
9.1.73	33.50	0.68	30.9	0.345	1.05	71.0	37.500	27.800
19.2.73	33.53	3.85	18.4	0.26	1.58	21.2	6.650	4.700

Data From J. Hoogesteger.

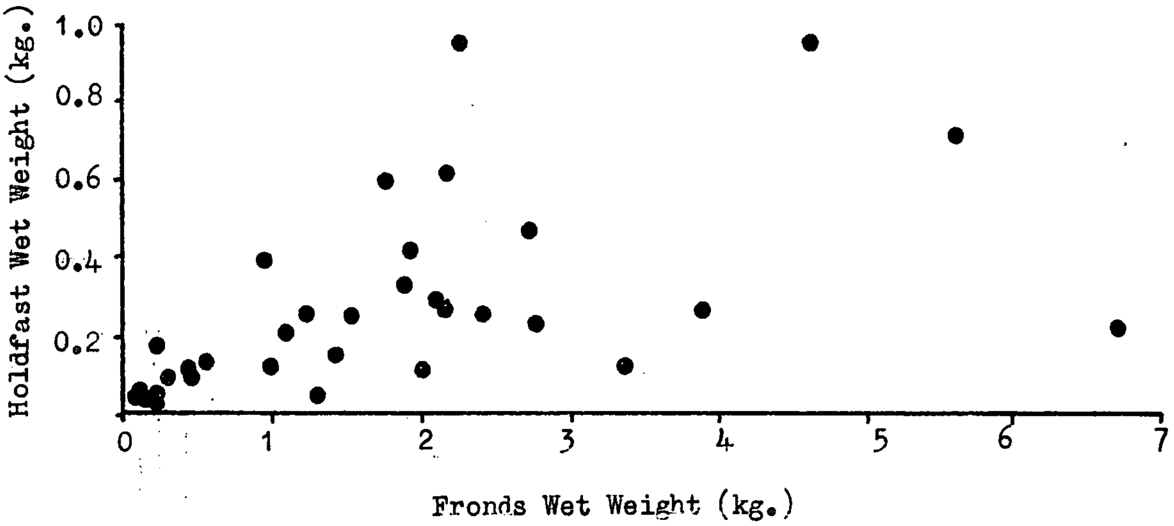
30 m. Depth Station, Normanna Strait.

Appendix III: The depth of 10% surface light conditions, Borge Bay Signy Island.

Date. (1972/73)	Depth (m).	Remarks
5.4.72	25	
11.4.72	26	
24.4.72	27	
8.5.72	33	
29.5.72	immediately under ice	15 cm. fast ice
13.6.72		20 cm.
20.6.72		15 cm.
27.6.72	Not detected	(-35° C. ambient)
4.7.72	1.6	
11.7.72	1.6	
19.7.72	3.0	
25.7.72	2.0	
31.7.72	2.0	
8.8.72	2.0	
13.9.72	0.5	75 cm. fast ice
26.9.72	0.5	
23.10.72	0.5	
30.10.72	0.75	
13.11.72	0.5	
20.11.72	0.3	
4.12.72	0.3	rotting ice
18.12.72	48	no ice, calm conditions.
1.1.73	9	phytoplankton bloom.
9.1.73	11.5	phytoplankton bloom.
15.1.73	18	
29.1.73	16	
5.2.73	16	
19.2.73	26	
6.3.73	35	
19.3.73	35	

Data from T. Whitaker.

Appendix IV:



(a): The relationship of D. anceps fronds weight (wet) to holdfast weight (wet).

(b): The percentage water content of D. anceps fronds.

	Frond Weight (g.)				
Date	Wet	Room Dry	Dry (100°C)	%H_2O	
18.2.72	1,254	244	219	82.5	
18.2.72	1,570	301	267	83.0	
19.2.72	642	174	114	82.2	
19.2.72	617	156	96	84.5	
20.2.72	217	79	49	81.9	
20.2.72	459	105	70	84.8	$\bar{x}$ = 83.2
4.4.72	68	11	9	86.4	
4.4.72	416	129	91	78.0	
4.4.72	332	114	70	79.0	
4.4.72	196	54	39	80.1	$\bar{x}$ = 80.9
13.7.72	5,962	1,341	1,187	80.1	
14.7.72	3,493	875	786	77.4	$\bar{x}$ = 78.8
3.8.72	10,053	2,162	1,925	80.9	
3.8.72	23,112	4,840	4,348	81.2	$\bar{x}$ = 81.1
11.10.72	6,731	1,185	1,086	83.9	
15.10.72	5,600	1,107	1,003	82.1	
15.10.72	1,897	219	198	89.6	
16.10.72	1,127	220	198	82.4	
16.10.72	1,306	224	204	84.4	$\bar{x}$ = 84.5
18.11.72	2,175	377	338	84.5	
18.11.72	858	130	120	86.0	
19.11.72	2,123	379	337	84.1	
19.11.72	875	192	168	80.8	$\bar{x}$ = 83.9

Appendix V: Species (excluding Amphipoda) recorded from *Desmarestia anceps* fronds.

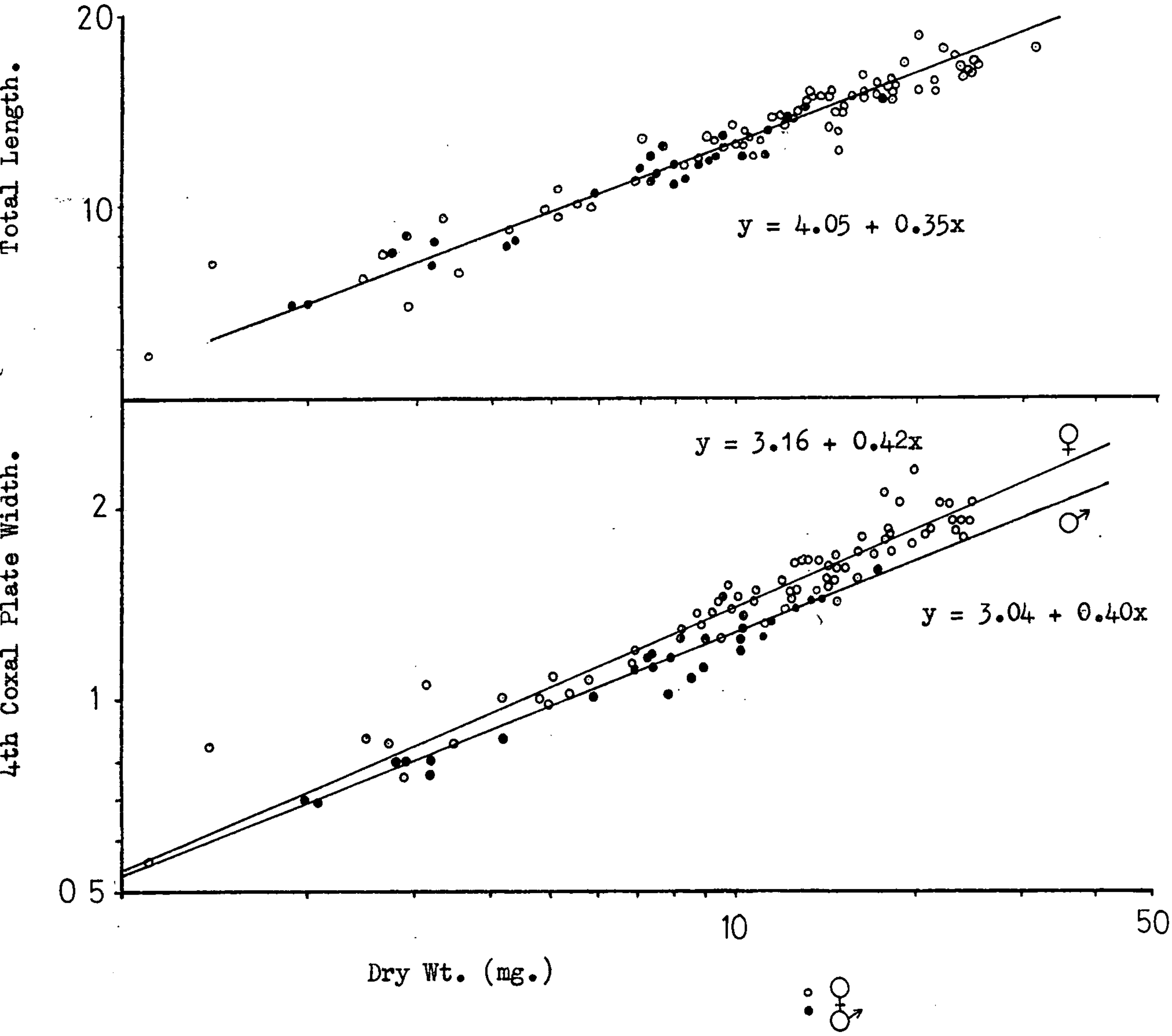
PLATYHELMINTHES		
	Turbellaria -	spp. not identified
NEMERTINI		
		Lineus corrugatus
		Tetrastemma validum
		Tetrastemma longistriata
		Tetrastemma spp.
		Amphiporous spp.
NEMATODA	-	spp. not identified
ANNELIDA	Polychaeta	*Ceratophale fauveli*
		Pionosyllis nutrix
		Pionosyllis spp.
		Potamilla antarctica
		Eulalia subulifera (?)
		Neanthes kerguelensis
		Terebellidae - spp. not identified
		Laena spp. (Hardy type spp. 58)
	Oligochaeta -	spp. not identified
ARTHROPODA	Crustacea	Ostraceda spp. not identified
		Copepoda spp. not identified
		Cumacea spp. not identified
		Tanaidacea
		Nototanias antarctica
		Amphipoda (see Table VIII)
		Isopoda
		Cymodocella tubicauda
		Paramunna gaini
		Pkakarthrium punctatissimum
		Gnathia spp. antarctica (?)
		Munna antarctica
		Glyptonotus antarcticus
		Serolis
		Antarcturus signiensis
		Pycnogonidae
		Nymphon australe
		Decalapoda antarctica
MOLLUSCA	Polyplacophora -	three spp. not identified
	Gastropoda	(see Table XIII)
		the following species were also recorded
		Microdiscus spp.
		Rissoa egariana
		Cyclostrema crassicostatus
		Diaphana antarctica
		Cerithiopsilla georgiana (?)
		Cerithiopsilla/Cerithiella spp
		Trophon minutus
		Prosiphon spp.
		Rissoa/Subnoba spp.
		Scissurella timora
	Bivalvia	*Lissarca milieris*
		Mysella charcoti
		Philcbrya spp. (2)
ECHINODERMATA	Echinoidea	*Sterechinus neumayeri*
	Holthuroidea	
	Asteroidea	*Crypostereas turqueti*
		Odontaster validus
VERTEBRATA	Pisces	*Notothenia coriiceps neglecta*
		Notothenia gibberifrons
		Notothenia rossii
		Notothenia nudifrons
		Trematomus newnesi
		Harpagifer bispinis

LYSIANASSIDAE:		
	Cheirimedon femoratus	(Pfeffer)
	Lepidepecreum cingulatum	Barnard
	Tryphosa kergueleni	
PHOXOCEPHALIDAE:		
	Heterophoxus videns	Barnard
AMPHILOCHIDAE:		
	Gitanopsis squamosa	(Thomson)
THAUMATELSONIDAE:		
	Thaumatelson walkeri	Chilton
	Prothaumatelson nasutum	(Chevreux)
STENOTHOIDAE:		
	Probolisca ovata	(Stebbing)
ACANTHONOTOZOMATIDAE:		
	Paraphimedia integricauda	Chevreux
	Gnathiphimedia fuchsi	Thurston
OEDICEROTIDAE:		
	Parhalimedon turqueti	Chevreux
PARAMPHITHOIDAE:		
	Epimeria monodon	Stephensen
CALLIOPIIDAE:		
	Oradarea bidentata	Barnard
	O. ocellata (?)	Thurston
	O. edentata	Barnard
	O. unidentata (?)	Thurston
	Metaleptamphopus pectinatus	Chevreux
EUSIRIDAE:		
	Atyloella magellanica	(Stebbing)
	Schraderia gracilis	Pfeffer
	Schraderia spp.	
	Schraderia spp. barnardi (?)	Thurston
	Djerboa furcipes	Chevreux
	Paramoera edouardi	Schollenberg
	Paramoera spp. (?)	
	Paramoera spp.	
	Paramoera hurleyi	Thurston
	Pontogeneia antarctica	Chevreux
	Pontogeneia redfearni	Thurston
	Prostebbingia gracilis	(Chevreux)
	Eurymera monticulosa	Pfeffer
	Pontogeniella brevicornis	(Chevreux)
	Bovallia gigantea	Pfeffer
GAMMARIDAE:		
	Paraceradocus miersi	(Pfeffer)
DEXAMINIDAE:		
	Paradexamine fissicauda	Chevreux
ISAEIDAE:		
	Haplocheira barbimanus	(Thomson)
ISCHYROCERIDAE:		
	Jassa falcata	(Montagu)
	Parajassa georgiana	Schollenberg
CAPRELLIDAE:		
	Caprellinoides mayeri	(Pfeffer)

Appendix VI: Amphipoda species recorded from *D. anceps* fronds.

Date	Fish species	(n)	Bottom type and plant association	Capture method	Depth (m).
4.5.71	*H. bispinis* *T. newnesi*	(14) (12)	Gravel, Rhodophyceae	I	7
8.4.72	*T. newnesi* *N. gibberifrons*	(1) (1)	Gravel/Boulder, *D. anceps*.	II	20
27.4.72	*T. newnesi* *N. larseni* *N. nudifrons*	(4) (1) (1)	Gravel with few boulders, *P. grandifolias* and mixed Rhodophyceae.	I	7
16.8.72	*N. c. neglecta*	(14)	Boulder/Rock, *D. anceps*.	V	15
10.11.72	*H. bispinis*	(1)	Gravel/Boulder, *D. anceps*.	III	3
20.11.72	*H. bispinis* *N. gibberifrons*	(2) (1)	Gravel/Boulder	III	20
23.11.72	*T. newnesi*	(1)	Gravel/Boulder	II	20
14.12.72	*T. newnesi* *N. larseni* *N. rossii* *N. gibberifrons*	(66) (2) (1) (11)	Gravel, Rhodophyceae.	I	12-20
22.12.72	*H. bispinis* *T. newnesi* *N. gibberifrons*	(9) (9) (2)	Gravel, Rhodophyceae.	I	14-20
2.1.73	*H. bispinis* *T. newnesi* *N. gibberifrons*	(10) (18) (6)	Gravel/Boulder, *D. anceps* and mixed Rhodophyceae.	I	12-20
16.1.73	*H. bispinis* *T. newnesi* *T. larseni* *N. gibberifrons*	(6) (1) (1) (4)	Pebbles/Silt	I	14-20
18.1.73	*N. c. neglecta*	(7)	Boulder/Rock, *D. anceps* and mixed Rhodophyceae.	V	1-3
20.1.73	*N. c. neglecta*	(13)	Boulder, *D. anceps* and mixed Rhodophyceae	V	2-3
8.3.73	*T. newnesi*	(4)	Pelagic	IV	5

Appendix VII : The total number of fish examined for stomach contents.

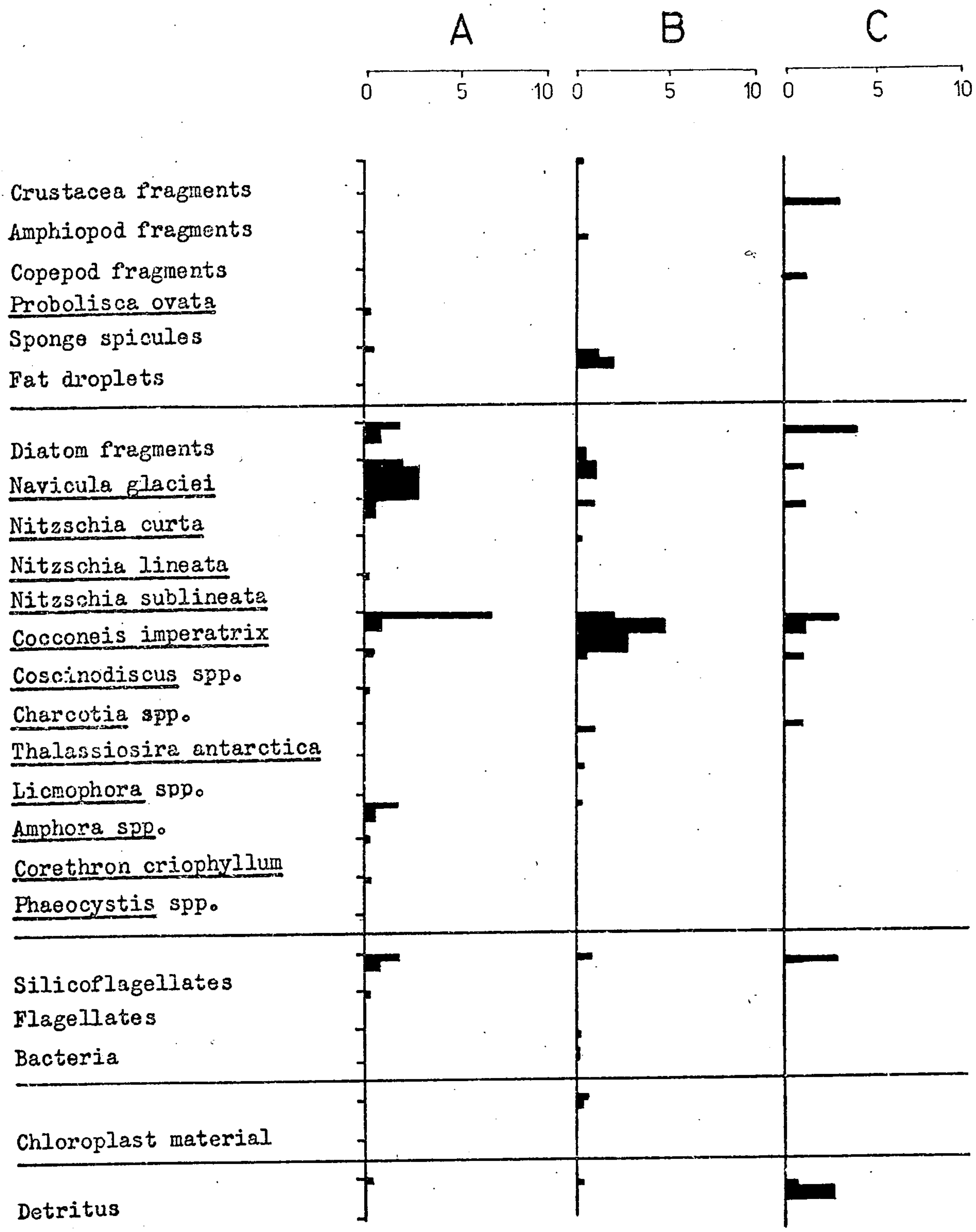


Appendix VIII: The relationships of various measurements to dry weight. (1) The width of the coxal plate 4. (mm.)
(2) Total length. (mm.)

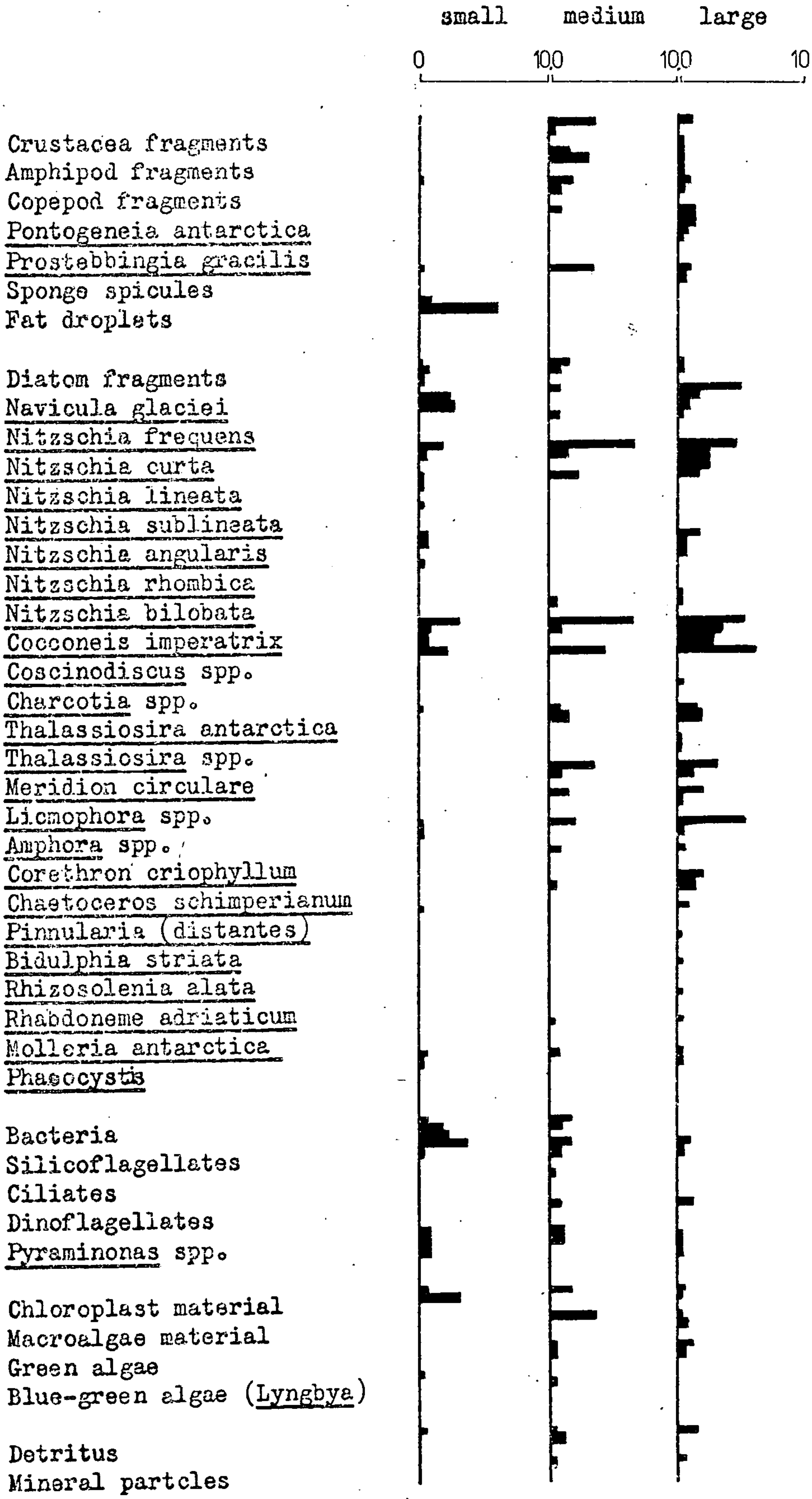
(data for <u>D. furcipes</u>)

Appendix VIII: (b). The Amphipods ivestigated for fecundity (see Fig. 22, Chapter 5.)

<u>Species No</u>. 1, <u>Proboilisca ovata</u>; 2, <u>Gitanopsis squamosa</u>; 3, <u>Parajassa georgiana</u>, 4, <u>Methalimedon nordenskjoldi</u>; 5, <u>Jassa falcata</u>; 6, <u>Monoculodes</u> spp. 7, <u>Paramoera</u> spp.; 8, <u>Metaleptamphopus pectinatus</u>; 9, <u>Haplocheira barbimanus</u>; 10, <u>Paramoera edouardi</u> (?); 11, <u>Schraderia gracilis</u>; 12, <u>Schraderia</u> spp.; 13, <u>Pontogeneia antarctica</u>, 14, <u>Djerboa furcipes</u>; 15, <u>Paradexamine fissicuadata</u>; 16, <u>Bovallia gigantea</u>.



Appendix IX : The dietary composition (per ten animals) of post-hatchling P. antarctica in three different habitats:
A. The Factory Cove ice foot.
B. The sea water laboratory.
C. The benthic environment (5m. depth).



Appendix X : The dietary composition (per ten animals) for three size categories of P. antarctica : small (2.0 - 4.9mm) medium (5.0 - 9.9mm) and large (10.0 +) from the benthic environment.

		Percentage dry material				Percentage ash-free dry material		
	Analyses	Temp. oC	Mean $\bar{x}$	s ±	n	Mean $\bar{x}$	s ±	n
Ash Weight	Elemental Analysis (HCN)	900-950	34.98	1.55	6	65.02	-	
"	Micro-bomb Calorimeter	900+	31.94	0.70	6	68.06	-	
"	Muffle Furnace Ashing	450	34.38	-	1	65.62	-	
	$\bar{x}$		33.77	-		66.23	-	
Total Lipid	Boehringer Total Lipid Kit		19.72	1.95	5			
Total Lipid	Bligh & Dyer Extraction (Freeze dried material)		23.89	-	1			
Hydrogen	Elemental Analyser	H	5.26	0.45	6	8.10	0.79	6
Carbon		C	34.01	2.46	6	52.51	4.39	6
Nitrogen		N	4.06	0.63	6	6.25	0.95	6
Total Phosphorus	Ammonium persulphate digestion		0.52	0.04	11	0.79		

			Parts per 10^6 (ppm) (dry material)	Parts per 10^6 (ppm) (ash-free dry)
Trace Elements	Flame Emission Photometer	Na	12,872	19,434
		K	8,076	12,193
		Fe	8,596	12,978
		Ca	2,698	4,073
		Mg	2,146	3,240
	Atomic Absorption Spectrometer	Al	1,682	2,540
		Zn	471	711
		Cu	357	539
		Pb	259	392
		Mn	100	151
		Cd	12.4	18.7
Caesium 137	Gamma Ray Emiss.	^{137}Cs	9.0 ± 2.2 x 10^{-12}	^{137}Cs/g. dry weight

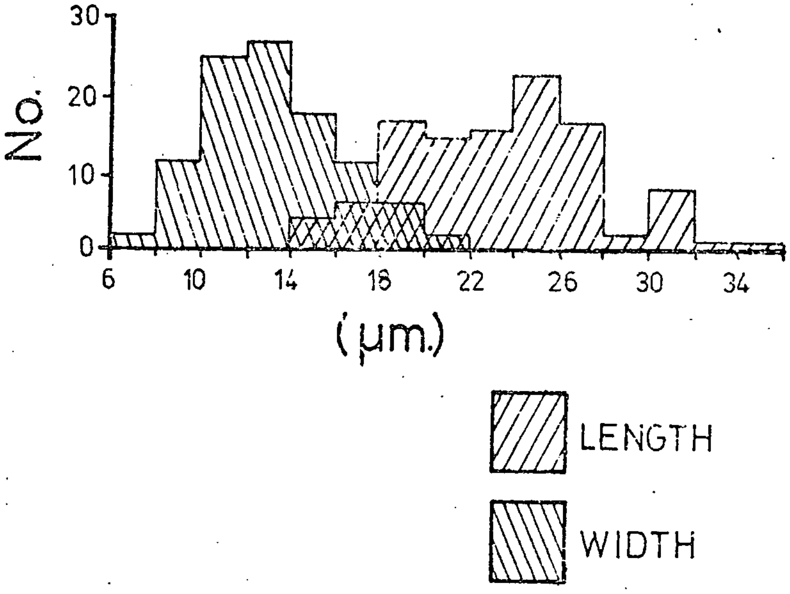
		calorific value	s ±	n	Calorific value	s ±
Calorific value	Micro-bomb calorimeter	3,675	395	6	5,427	527
		joules			joules	
		15,384	1,654		22,717	2,206

Appendix XI : Biochemical composition of *Navicula glaciei* Van Heurck.

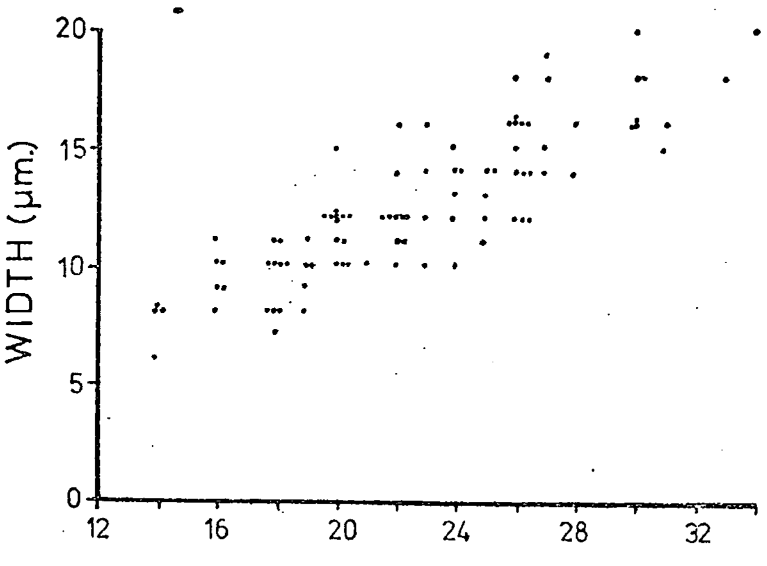
Mean percentage water content (dried at 60°C) = 68.5 ± 10.5

10^6 cells weigh 215 ug (dried at 60°C).

1 cell contains approx. 1.7 x 10^{-11} cals.



Appendix XII: The length and width distributions of the diatom *Cocconeis imperatrix*.



Appendix XIII: The relationship of length to width for *Cocconeis imperatrix*.

Elemental Analysis Results

Stage		% Total Dry Weight				% Ash-free Weight		
		H	C	N	Ash	H	C	N
I		7.78	60.13	7.91	5.63	8.24	63.72	8.38
		7.88	60.05	7.62	3.17	8.13	62.02	7.36
		7.72	59.88	8.07	3.47	8.00	62.04	8.36
	$\bar{x}$	7.79	60.02	7.87	4.09	8.12	62.59	8.20
	s ±	0.08	0.13	0.23	1.34	0.12	0.98	0.29
II		7.43	57.92	8.26	3.86	7.73	60.25	8.59
		7.14	50.13	(4.46)	(2.61)	7.33	51.47	(4.58)
		7.40	50.78	9.27	4.14	7.72	52.97	9.67
		7.20	50.34	9.26	3.91	7.49	52.38	9.64
	$\bar{x}$	7.34	53.01	8.93	3.97	7.64	55.20	9.30
	s ±	0.13	4.25	0.58	0.14	0.13	4.38	0.62
III		7.05	48.49	9.21	4.35	7.37	50.70	9.63
		7.26	48.79	9.30	4.75	7.62	51.23	9.76
		6.98	49.16	9.24	4.96	7.34	51.72	9.73
	$\bar{x}$	7.10	48.81	9.25	4.69	7.44	51.22	9.71
	s ±	0.15	0.34	0.05	0.31	0.15	0.51	0.07
IV		6.92	42.81	9.49	7.12	7.45	46.09	10.22
		6.94	46.91	10.39	5.78	7.37	49.79	11.02
		7.06	48.37	9.94	4.28	7.38	50.51	10.38
	$\bar{x}$	6.97	46.03	9.94	5.71	7.40	48.80	10.54
	s ±	0.08	2.88	0.45	1.44	0.04	2.37	0.42
V		7.26	41.36	8.79	8.93	7.98	45.42	9.66
		7.17	43.33	9.64	8.46	7.83	47.34	10.53
		7.15	45.15	9.01	8.76	7.95	49.49	9.87
		(6.18)	(38.18)	(8.51)	(6.74)	(6.92)	(40.94)	(9.12)
	$\bar{x}$	7.19	43.28	9.15	8.72	7.92	47.42	10.02
	s ±	0.06	1.90	0.44	0.24	0.08	2.04	0.45
VI		4.47	30.00	5.90	18.02	5.45	36.60	7.20
		4.51	33.59	6.21	18.38	5.53	41.16	7.61
		6.23	32.46	4.56	lost	----	----	----
		4.52	30.99	6.80	17.25	5.46	37.45	8.22
		(4.48)	(44.89)	(9.13)	(34.45)	(6.86)	(68.47)	(13.92)
	$\bar{x}$	4.52	31.76	6.29	17.88	5.48	38.40	7.68
	s ±	0.04	1.58	0.38	0.58	0.04	2.42	0.51

Appendix XIV: Percentage elemental composition of *Pontogeneia antarctica* eggs.

Stage	Total Dry Weight (µg)				Ash-free Weight (µg)		
	H	C	N	Ash	H	C	N
I	4.59	35.35	4.64	2.40	4.78	36.86	4.83
II	5.01	36.21	6.10	2.71	5.22	37.70	6.35
III	5.09	35.00	6.63	3.36	5.33	36.72	6.96
IV	5.70	37.65	8.13	4.67	6.05	39.91	8.62
V	not measured						
VI	5.22	36.65	7.26	20.63	6.32	44.31	8.86

Appendix XV: : The composition by unit weight (µg) of Hydrogen, Carbon, Nitrogen and Ash Weights for ova development stages of <u>Pontogeneia antarctica</u>.

Appendix XVI:

The numbers (with percentages) of the efficiency of runs achieved in respirometry methods (Chapter 8).

(I) Constant pressure respirometer (P.S. Davies)

Temp. $^{\circ}$C	Viable result (r 0.99)	Malfunctions	Deaths	Moults	Total runs
(a) Pontogenia antarctica					
- 1.5	41	not recorded			41
- 1.0	13(41)	19(59)	-	-	32
0.0	45(63)	21(30)	5(7)	-	71
2.0	48(70)	19(28)	1(2)	-	68
5.0	42(41)	57(56)	-	3(3)	102
$\bar{x}$ %	(54.2)	(42.5)	2.2	1.1	314
(b) Djerboa furcipes					
0.0	11(79)	1(8)	2(15)	-	14

(II) micro - Winkler

0.0	23(100)	-	-	-	23
2.0	21(100)	-	-	-	21
					44

[A] Pontogeneia antarctica

Temp °C	♀	♂	imm.	Total
Constant Pressure				
-1.5	23	9	9	41
-1.0	12	-	2	14
0.0	23	13	6	42
+2.0	28	10	10	48
+5.0	24	14	4	42
				189
Micro-Winkler				
0.0	16	2	5	23
+2.0	13	5	4	21
				44

[B] Djerboa furcipes

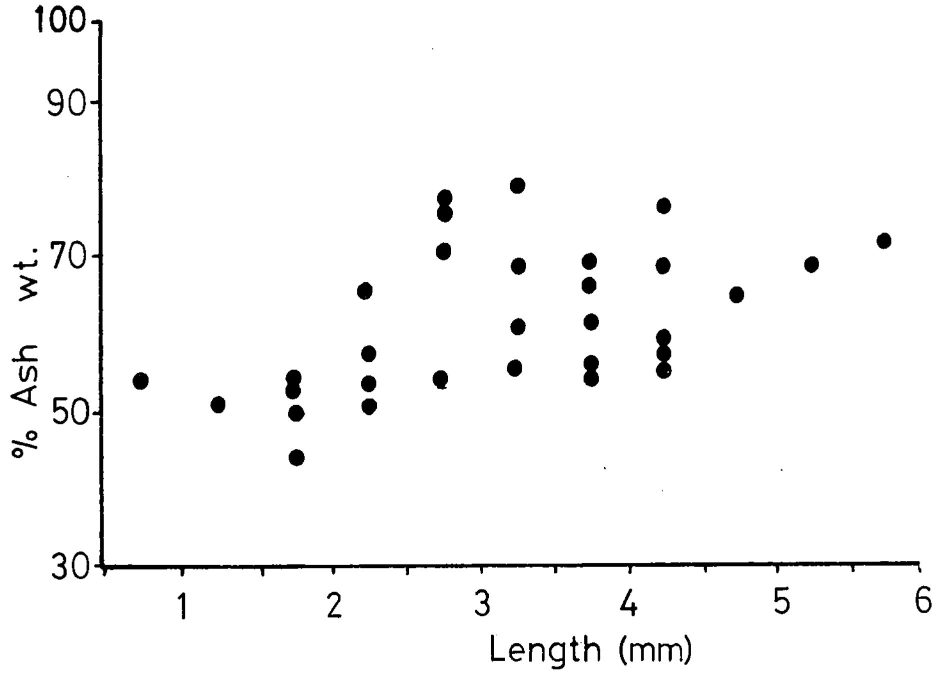
Constant Pressure				
0.0	9	2	-	11

Appendix XVII: The composition of Amphipoda used in respiration experiments at different temperatures.

L(mm)	Wt(mg)	H(mm)	B(mm)	Tissue Wt(mg)	Shell Wt(mg)
0.60	0.042	0.273	0.507	0.006	0.036
1.00	0.109	0.482	0.800	0.016	0.093
1.40	0.274	0.700	1.093	0.039	0.235
1.80	0.620	0.925	1.386	0.087	0.531
2.20	1.192	1.156	1.679	0.170	1.022
2.60	2.053	1.392	1.972	0.294	1.759
3.00	3.273	1.631	2.265	0.468	2.805
3.40	4.919	1.875	2.558	0.703	4.216
3.80	7.066	2.183	2.851	1.010	6.056
4.20	9.789	2.371	3.144	1.400	8.389
4.60	13.16	2.623	3.437	1.882	11.28
5.00	17.27	2.878	3.730	2.470	14.80
5.40	22.19	3.134	4.023	3.173	19.02

Appendix XVIII: Relative measurements of the bivalve <u>Lissarca miliaris</u>,

<u>Parameters</u>: Length (L), Total dry weight (Wt), Height (H), Breadth (B), Tissue weight (dry) and shell weight (dry).



Appendix XIX: The percentage ash weights of the bivalve *Lissarca miliaris*.

SAMPLE

Ring	13.1.72			19.2.72			9.5.72			9.6.72			10.7.72			16.8.72			11.9.72			9.10.72			10.11.72			29.12.72		
No.	n	$\bar{x}$	$s/\sqrt{n}$	n	$\bar{x}$	$s/\sqrt{n}$	n	$\bar{x}$	$s/\sqrt{n}$	n	$\bar{x}$	$s/\sqrt{n}$	n	$\bar{x}$	$s/\sqrt{n}$	n	$\bar{x}$	$s/\sqrt{n}$	n	$\bar{x}$	$s/\sqrt{n}$	n	$\bar{x}$	$s/\sqrt{n}$	n	$\bar{x}$	$s/\sqrt{n}$	n	$\bar{x}$	$s/\sqrt{n}$
0	1012	0.73	0.0016	515	1.01	0.0049	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	130	0.73	0.0047
1	156	1.50	0.0215	239	1.54	0.0113	436	1.25	0.0072	235	1.29	0.0099	213	1.26	0.0110	312	1.29	0.0100	904	1.36	0.0058	635	1.47	0.0122	197	1.46	0.0120	41	1.37	0.0292
2	217	2.42	0.0229	440	1.99	0.0093	435	2.18	0.0109	249	2.18	0.0157	301	1.96	0.0162	270	2.19	0.0152	337	2.33	0.0159	501	2.39	0.0150	65	2.15	0.0342	40	2.31	0.0389
3	185	3.21	0.0304	211	2.80	0.0200	355	2.83	0.0165	152	2.90	0.0273	369	2.62	0.0174	224	2.88	0.0247	325	2.89	0.0181	196	3.15	0.0289	83	2.74	0.0321	36	3.09	0.0450
4	39	4.05	0.0466	75	3.49	0.0406	99	3.75	0.0361	83	3.55	0.0273	212	3.33	0.0242	129	3.52	0.0268	171	3.71	0.0233	34	3.81	0.0907	23	3.55	0.0626	23	3.90	0.0676
5	6	4.51	0.1502	24	4.29	0.0861	26	4.40	0.0698	39	4.22	0.0484	44	4.29	0.0713	60	4.04	0.0473	33	4.30	0.0658	4	4.53	0.1040	8	4.63	0.1120	8	4.21	0.1170
6	3	5.03	0.1484	13	4.74	0.0982	9	4.86	0.1280	8	4.89	0.1370	14	4.91	0.1040	25	4.42	0.0510	11	4.97	0.1410	1	5.45	—	5	4.94	0.1650	3	4.72	0.1470
7	—	—	—	1	5.77	—	2	5.41	0.2450	—	—	—	2	5.12	0.2800	3	4.76	0.2150	—	—	—	—	—	—	—	—	—	—	—	—
Totals	1,618			1,518			1,360			766			1,155			1,023			1,781			1,369			381			281		

Total n = 11,252.

Appendix XX: Data of the age structure of the *Lissarca miliaris* population for each monthly sample, giving numbers, mean lengths with standard errors for the ring classes 0 - 7.