

# THE DISTRIBUTION OF ANTARCTIC MARINE MACRO-ALGAE RELATED TO DEPTH AND SUBSTRATE

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**ABSTRACT.** A survey of submarine macro-algal distribution, substrate and depth contouring was made over 4.22 hectares of Borge Bay, Signy Island, South Orkney Islands. The cover of plant material was related both to substrate and depth. Sub-littoral zonation of vegetation was apparent and four zones of Antarctic shallow-water phyto-benthos are described. Maximum biomass of the macro-algal genus *Desmarestia* occurred at 6-7 m. depth. *Phyllogigas grandifolius* had largest biomass at 8-12 m. Total plant material was greatest on a variable boulder bottom though *P. grandifolius* was present in greatest concentrations on finer pebble-cobble substrate. Measurements of standing crop (wet weight) for a limited number of quantitative samples are presented and the maximum floral biomass recorded was 2.05 kg. wet weight/m.<sup>2</sup>. Measurements of standing macrophyte stocks from other parts of the world are normally in excess of this figure and factors producing this depressed biomass are discussed in relation to other Antarctic benthic studies on zonation and biomass determinations.

MARINE biological studies carried out from the British Antarctic Survey's research station on Signy Island have been centred on Borge Bay, an area briefly described by Price and Redfearn (1968), and extensively investigated in the course of various ecological and physiological programmes. Recent biomass estimates (Hardy, 1972; White and Robins, 1972) have respectively compared the epifaunal and infaunal communities of some habitats in Borge Bay with estimates for benthic biomass from other sectors of the Antarctic region (Gallardo and Castillo, 1968, 1969; Propp, 1970). Evidence obtained so far by previous workers points to the diverse faunal nature of Antarctic benthos (Knox, 1970; Richardson and Hedgpeth, 1977) with standing crop figures in excess of temperate or tropical systems.

Faunal zonation has previously been described at McMurdo Sound by Dayton and others (1970), at other Antarctic localities (Hedgpeth, 1969a; Gruzov and Pushkin, 1970), and mentioned in passing by most authors on Antarctic benthos. The plant component of the bottom community presents a zonation similar to other less severe localities but the added limiting factors of ice, together with diminished light and a lower temperature, produce less extensive plant distribution and a decrease in standing crop. Several authors have described algal zonation in Antarctic waters (Delépine and Hureau, 1963; Arnaud, 1965; Neushul, 1965; Delépine, 1966; Delépine and others, 1966; Zaneveld, 1966a; Balech and others, 1968), whilst Stephenson and Stephenson (1972) discussed past results in this field. This paper is an attempt to quantify the distribution of macrophytes whose previous zonation patterns were expressed in purely qualitative terms.

One section of the epibenthos at present under review at the South Orkney Islands is the contribution by the marine macrophytes to the Antarctic shallow-water sub-littoral ecosystem. The dominant macro-alga extending to southern South America and the islands of the sub-Antarctic is the kelp *Macrocystis pyrifera*. This species is replaced in the South Orkney Islands by mixed forests of smaller *Phyllogigas grandifolius*\* and members of the genus *Desmarestia*. *Desmarestia ligulata* was found intermittently in shallow water (<5 m.), 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 sub-littoral zone and other algae including *Iridaea*, *Gigartina*, *Myriogramme* and *Phyllophora* compose an underflora to the larger plants.

The growths of macro-algae, especially *D. anceps*, provide shelter for some species of fish, *Notothenia coriiceps neglecta*, *Notothenia gibberifrons* and *Trematomus newnesi*, whilst commonly occurring invertebrates include the molluscs *Nacella concinna*, *Margarella antarctica*,

\* Now considered synonymous to *Himantothallus grandifolius* (A. & E. S. Gepp) Skott. (Moe and Silva, 1977, *Science*, N.Y., 196, 1206-08).

*Lissarca miliaris* and *Philobrya* spp. The isopods *Glyptonotus antarcticus*, *Munna antarctica* and *Antarcturus signiensis* are common and about 30 amphipod species notably *Bovallia gigantea*, *Oradarea* spp., *Pontogeneia* spp. and *Djerboa furcipes* are associated with *Desmarestia* fronds (Thurston, 1972). Biomass estimates for the macrophyte association will be presented in a future paper. Information obtained from previous research workers at Signy Island has been collated and is presented in Fig. 1 as a general flora distribution for the Borge Bay area.

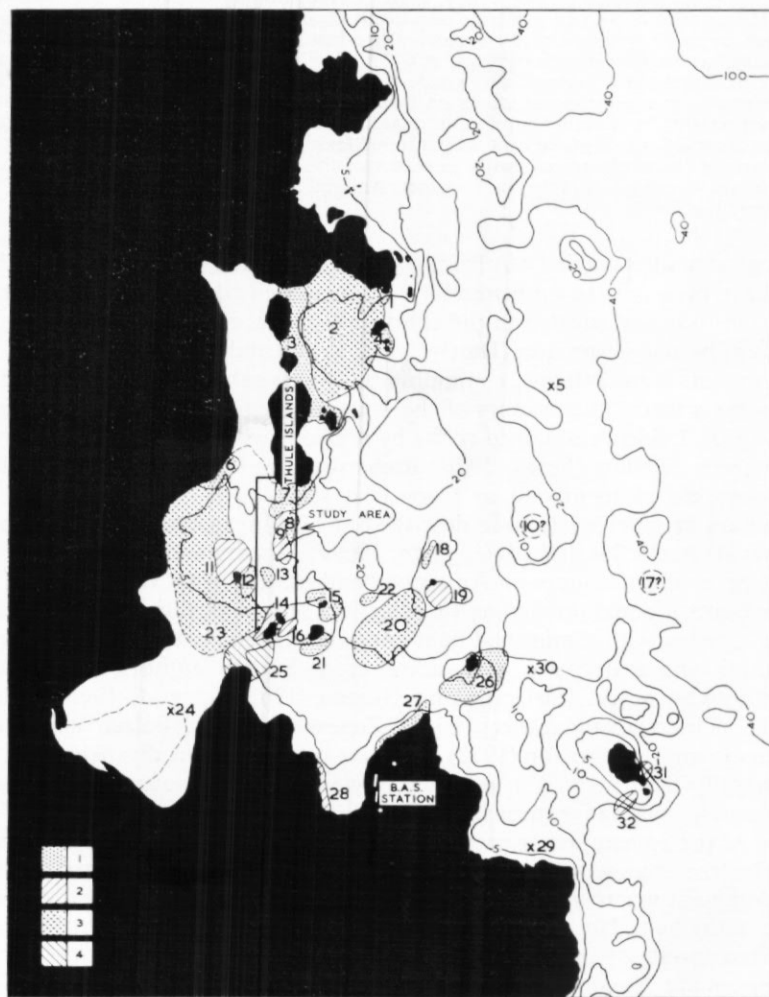


Fig. 1. Macro-algae distribution in Borge Bay, Signy Island.

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|---|--|
| 1. <i>Desmarestia</i> spp. beds   | Site Nos. 1, 3, 4, 6, 7, 8, 10, 12, 13, 15, 18, 21, 26, 27 and 30. |
| 2. <i>Phyllogigas grandifolius</i> beds   | Site Nos. 9, 11, 14, 16, 19, 28, 31 and 32.                        |
| 3. Impoverished areas, supporting diminished sparse flora of <i>Desmarestia</i> spp. and <i>P. grandifolius</i> | Site Nos. 2, 20, 23 and 29.  |
| 4. Shallow-water benthos supporting summer flora of <i>Adenocystis utricularis</i> and small Rhodophyceae       | Site No. 25.   |
| 5. Areas with no plants present   | Site Nos. 5, 17 and 24.  |

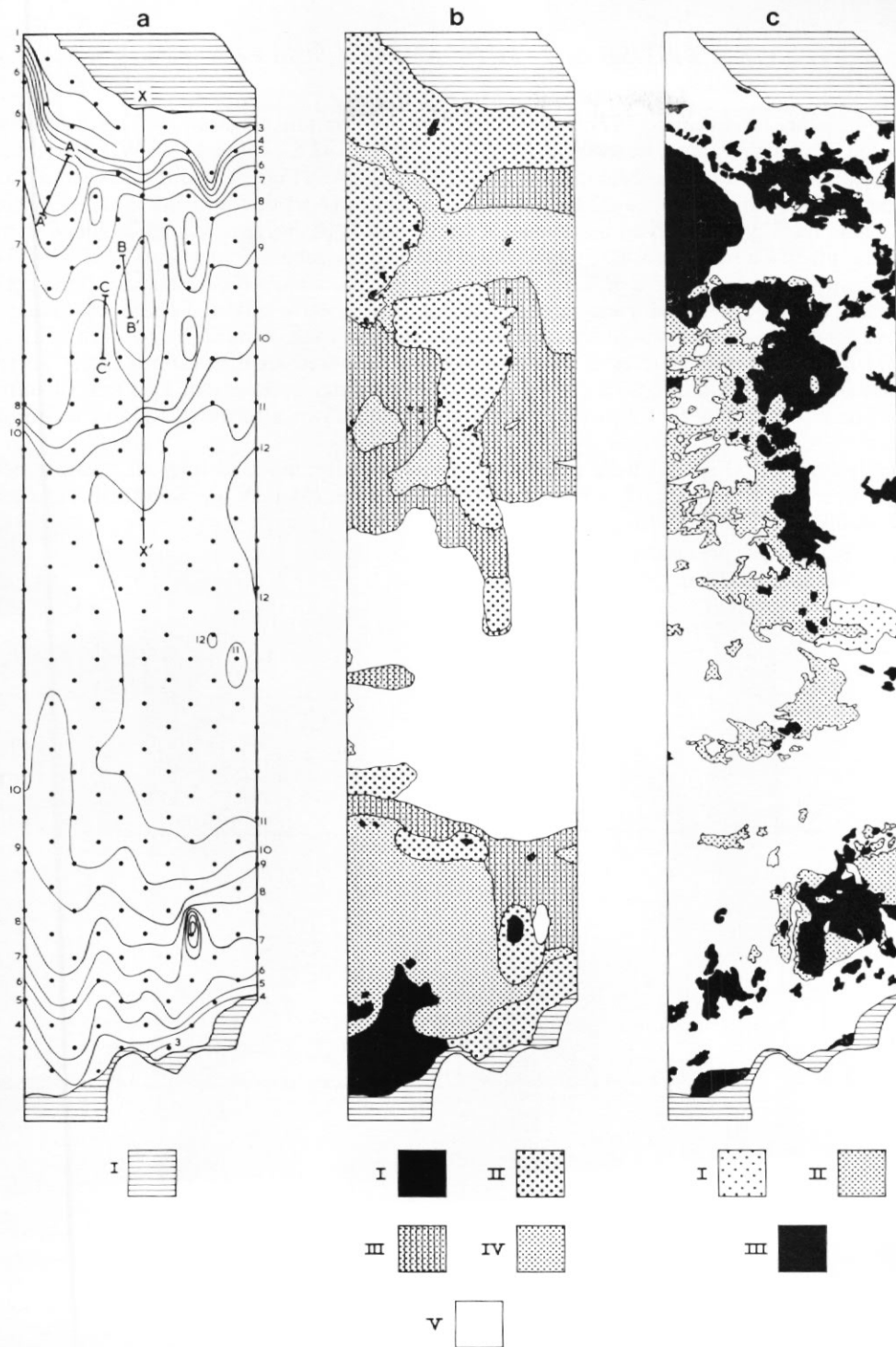


Fig. 2. Thule Islands-Billie Rocks transect survey.

a. Depth profile, showing the grid arrangement of ice holes, the sites of the three transects A-A', B-B' and C-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. Macro-algae distribution: I, decaying macro-algae; II, *Phyllogigas grandifolius*; III, *Desmarestia* spp.

## 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 (lat.  $60^{\circ}43'S.$ , long.  $45^{\circ}36'W.$ ) between the southernmost of the Thule Islands and inner Billie Rocks (Figs. 1 and 2). The study area measured 460 m. by 100 m. (4.22 hectares overall) and was divided into five 20 m. wide transects. This locality was chosen as typical of other nearby inshore areas and included depths from the littoral down to 13 m. Stable sea ice enabled an accurate survey to be made of the area which was divided into a grid of 20 m.<sup>2</sup> sub-units. The survey was restricted to the period when thin sea ice (30–50 cm.) 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.<sup>2</sup>. The position of each of the 231 holes used in the survey is shown in Fig. 2a. Coloured identification markers lowered through each hole produced a simple 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. 2a) 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. 2b):

- i. Solid rock, presumed bedrock.
- ii. Variable boulder pavement.

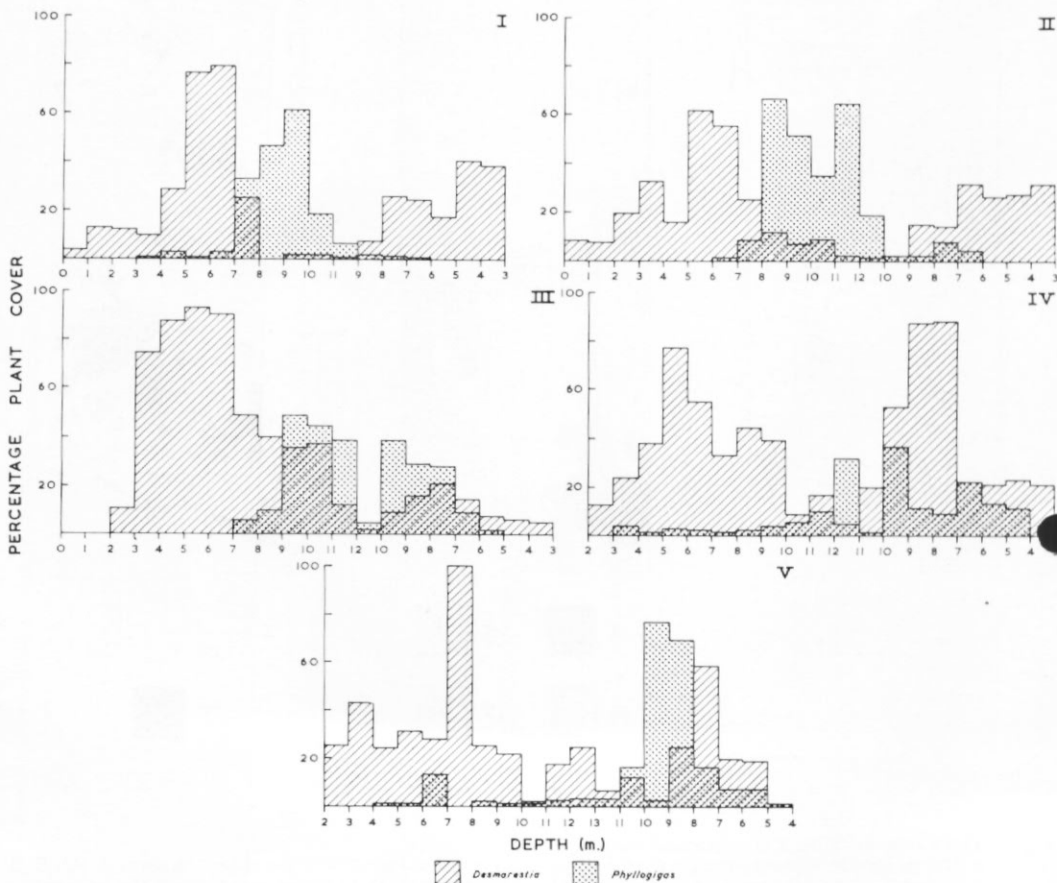


Fig. 3. The percentage plant cover with depths for transects I–V.

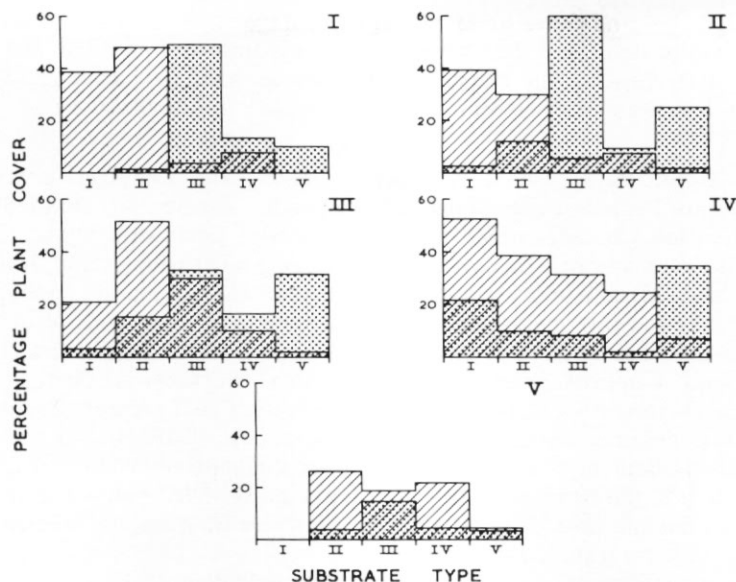


Fig. 4. The percentage plant cover with substrates for transects I-V. The shading is the same as in Fig. 3.

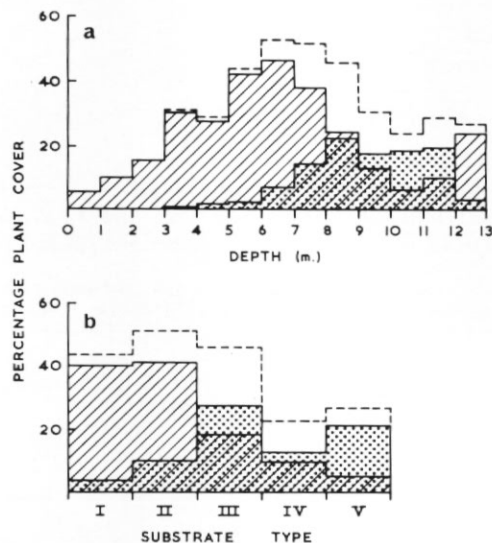


Fig. 5. The mean percentage plant cover for all transects: (a) with depths, (b) with substrates. The shading is the same as in Fig. 3.

- iii. Pebble-cobble.
- iv. Gravel.
- v. Sand-silt.

Fig. 2a, b and c shows the area in terms of depth, substrate and plant distribution.

Three transects 29 m. long were positioned at the northern end of the study area (Fig. 2a). The biomass (wet weight) of 30 1 m. squares was determined for three differing types of macro-algae (Table II).

Results in Figs. 3, 4 and 5 are presented as percentage cover of plant material related to either depth or substrate. These data were obtained by drawing Fig. 2a, b and c to 1 : 1,000 scale on paper and weighing the respective areas on an analytical balance. The error was estimated to be less than 2.5 per cent.

#### RESULTS

Most shores around Signy Island are steeply shelving and composed either of bedrock (predominantly quartz-mica-schists which can be highly fissured or abraded smooth), or composed of a variable boulder beach. Sediments became finer with depth. The immediate sub-littoral boulder-rock zone was replaced by smaller graded pebbles and gravels, whilst in deeper water, sand, silt and mud commonly occurred. The submarine topography, within the study area, followed this general pattern whilst north and south ends of the transect had similarities (Fig. 2b). The boulder-rock area nearer the shore occurred on a shelving beach extending to a depth of approximately 6 m.; at this contour the substrate altered to an irregular band of fine gravel. Large boulders, often 3 m. 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 a centrally running ridge of boulder pavement extending to the 10 m. contour by a narrow gravel-filled gully. The central bowl of the transect was a flat silt-sand plain 10-12 m. deep, where fragments of whalebone, 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

Macro-algae at Signy Island are present down to depths of 25-30 m. (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 13 m.

TABLE I. MODAL PEAKS FOR PLANT COVER WITH SUBSTRATES AGAINST THE DEPTH GRADIENT, SHOWING THE DEPTH RANGE ENCOUNTERED AND THE PERCENTAGE COVER OF PLANT MATERIAL

Species	Boulder		Pebble		Gravel	
	Depth (m.)	Percentage	Depth (m.)	Percentage	Depth (m.)	Percentage
<i>Desmarestia</i> spp.	7-8	75	5-6	56.5	7-8	22.4
<i>Phyllogigas grandifolius</i>	10-11	39	8-9	24.5	10-11	33.5

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 13 m. depth. Such habitats occur infrequently in Borge Bay.

Borge Bay is protected from severe surf action or heavy oceanic swell from all but south-easterly gales, whilst the main central ridge (300 m.) of Signy Island and Jane Peak give shelter from the prevailing north-westerly wind. Ice in the form of fast ice, brash ice, anchor ice and small and medium floes was a very common disruptive feature and reduced plant distribution both by its abrasive action and by diminishing light penetration. White (in press) has presented an analysis of sea-ice duration at Signy Island, indicating the extent of fast ice in Borge Bay during the years 1957-73. Fast-ice longevity has varied from 70 to 241 days and averages 149

days for the 16 years' observation. Records for pack ice at Signy Island are not so well documented though its presence may be extensive and occurring throughout the year. The total ice presence over the transect area during 1972 was 271 days (216 days' fast ice, 16 days' glacier brash, 12 days' pack ice (1–5/10), 27 days' pack ice (6–10/10).

The areas adjacent to the shoreline 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 sub-littoral to be totally barren of the larger species of macro-algae, though filamentous diatoms and smaller macrophyte species such as *Adenocystis utricularis* were found in the littoral during summer.

#### *Bathymetric plant distribution*

Data for the percentage cover of *Desmarestia* spp. and *P. grandifolius* are presented as histograms for each of the transects I–V (Fig. 3) and the mean for the whole area (Fig. 5a). Though variation between transects is present both in the amplitude and positioning of peaks, the fundamental pattern of the histograms is the same in all cases. The greatest percentage cover of *Desmarestia* spp. occurred in shallower water than the peak for *P. grandifolius*. The inter-transect modes for *Desmarestia* spp. vary from the 4–5 m. contour to the 7–8 m. depth line, whilst those for *P. grandifolius* are confined to depths of 9–10 m., or in the case of transect II, to depths of 8–12 m. Total plant cover (Fig. 5c) increased from the littoral area downwards and reached a peak of 53 per cent at 6–7 m. depth. The percentage cover then decreased with increasing depth and was only 27 per cent at 12–13 m. The greatest proportion of plant material within the upper 8 m. was composed of various species of *Desmarestia*, the maximum standing crop occurring within the 6–7 m. depth range. There was no rapid decline in the percentage cover of *P. grandifolius* after the mode indicating a greater potential bathymetric range. Maximum plant cover was present at 8–9 m. though the percentage cover varied little between 8 and 12 m. The apparent high figure of 24 per cent for *P. grandifolius* for the 12–13 m. range is a reflection of the small area sampled within that depth contour (483 m.<sup>2</sup>).

#### *Plant distribution with substrate*

The transitions between adjacent substrate types in Fig. 2b 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. 4 for all transects and the mean values are shown in Fig. 5b. The highest figures for *Desmarestia* distribution occurred on rock or boulder substrates whilst *P. grandifolius* showed greatest affinity for a pebble bottom. Transect IV, however, is an exception, since the greatest percentage cover of *Phyllogigas* occurred on sand.

Fig. 5b shows rock and boulder supporting a profuse covering of *Desmarestia* but less than 10 per cent of *Phyllogigas*. This situation is reversed on a pebble-cobble substrate with *P. grandifolius* becoming dominant. The dominance of *Desmarestia* spp. decreases markedly as the substrate becomes finer. Sand is an unsatisfactory substrate for macro-algal colonization 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 whalebone.

An area of detached seaweed, mainly *D. anceps*, occurred in the deepest section of the area and is indicated in Fig. 2c. 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) have remarked on these decaying algal masses.

#### *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 physio-chemical parameters contribute to differentiating plant systems. In

this paper only data for depth and substrate are presented and both play a major role in determining the niche separation of the two dominant algal components. Neither variable was entirely independent so that some correlation of depth and substrate was apparent. Whether one factor affected plant distribution only by reason of its association with the other factor needs assessing.

Fig. 6 shows the percentage cover of *Desmarestia* spp. and *P. grandifolius* for a particular substrate against the depth gradient. The means of all transects are expressed in the form of open histograms for the three substrates: boulder, pebble and gravel. 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) on any bottom formation varied appreciably with depth. The three substrates in Fig. 6 demonstrate the same pattern of weed distribution though to different depth profiles. In all cases the maximum biomass of *Desmarestia* spp. was present in water shallower than the maximum peak for *P. grandifolius*.

The high percentage cover of *Desmarestia* spp. on pebble substrate at 2–3 m. depth (46·5 per cent) and 12–13 m. depth (39 per cent) was due to a small number of samples. There is no decrease in the standing crop with depth of *P. grandifolius* on gravel substrates, indicating that its greatest biomass occurs in water deeper than that of the study area. The standing crop of *Desmarestia* spp. decreased with decreasing substrate particle size.

#### Biomass

The positions of the three transects A, B and C are shown in Fig. 2a. Depth range was limited (6–8 m.). The results in kg./m.<sup>2</sup> (wet weight) for the 30 quadrats examined are presented in Table II. Maximum biomass recorded was 2·05 kg./m.<sup>2</sup> with means for total plant material/m.<sup>2</sup> for transects A, B and C of 1·14, 0·74 and 1·03 kg./m.<sup>2</sup> (wet weight).

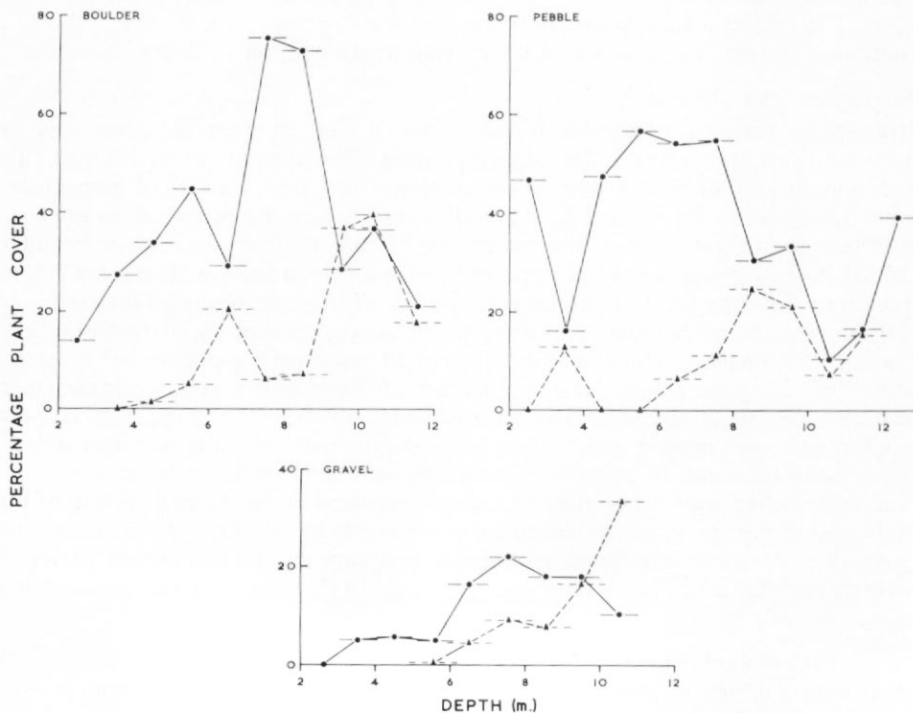


Fig. 6. The mean percentage plant cover for all transects against the depth profile. ●—● *Desmarestia* spp.; ▲—▲ *Phyllogigas grandifolius*.



TABLE II. MACRO-ALGAE STANDING CROP (kg./m.<sup>2</sup>, WET WEIGHT) FOR THREE TRANSECTS IN BORGE BAY, SIGNY ISLAND

<i>Transect number</i>	<i>Desmarestia spp.</i>			<i>Phyllogigas grandifolius</i>			<i>Rhodophyceae</i>			<i>Total plant</i>		
	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			
Standard deviation	0.32	0.37	0.69	0.27	0.38	0.60	0.21	0.16	0.05	0.37	0.61	0.52

## DISCUSSION

The contribution made by macrophytes to the primary production of inshore benthos has been shown to be a major energy input to the shallow-water community (Blinks, 1955; Teal, 1962; Marshall, 1970). Whilst the role of the macrophytes as a food source in Antarctic waters has not been widely investigated, gut analyses of weed-dwelling amphipods indicate that few species feed directly on macro-algae (paper in preparation by M. G. Richardson). Algal feeding was, however, observed in the polychaete worm *Neanthes kerguelensis*. Much of the organic component of algal matter is cycled via the decomposers, providing a ready food supply for the high biomass of diverse detrital feeders.

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 deep-water benthic biomass is comparatively increased (Belyaev, 1958; Ushakov, 1963; Andriashv, 1968; Hedgpeth, 1969b; Knox, 1970). The shallow-water communities are not afforded a similar stability but undergo greater light, salinity and temperature fluctuations, and are subjected to the mechanical disruptions of increased water movement, ice abrasion and anchor ice (White, 1977). The paucity of littoral and immediate sub-littoral fauna and flora has been remarked upon by previous authors (Dayton and others, 1970; White and Robins, 1972).

The action of ice scour, the light shading of the sub-ice water column, the disruptive effect of anchor ice and the cooling action in the proximity of ice particles all play a part in determining, and severely limiting, the colonization of the shallow-water environment. Only crevice dwellers or sessile colonies afforded protection from ice scour by cliff overhangs or caves can live in the immediate sub-littoral ice-abrasion zone (White and Robins, 1972).

The zonation of Antarctic plant benthos is correlated with many of the same factors found elsewhere in less severe environments. The effect of light penetration with depth is of prime importance. John (1971) demonstrated the effect of wave and surf action, light and depth on macrophyte biomass with standing crop and production per unit area was found to undergo a decrease with an increase in both depth and wave action. Interspecific competition is attributed to some of the community relationships found in Chilean waters (Dayton and others, 1973; Dayton, 1974) and at Macquarie Island (Kenny and Haysom, 1962). Lee (1973) suggested that ice is not the greatest physical disruptor in Arctic littoral waters but that air temperature and low salinity (due to ice melt) are the reasons for an impoverished flora.

Various zonal arrangements have been recognized by workers investigating southern cold waters (Kenny and Haysom, 1962; Delépine and Hureau, 1963; Arnaud, 1965; Dayton and others, 1973). At Signy Island four zones were recognized from the littoral down to the 13 m. depth contour. These are illustrated by a transect taken at points 'x-x' in Fig. 2a and Fig. 7.

*Sub-littoral zones from Borge Bay, Signy Island*

- I. Ice-abrasion zone: extending from the littoral down to 2 m. 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 to 8 m. The brown alga *A. mirabilis* is a species also common to this zone.
- III. *Phyllogigas*: pebble-cobble zone between the 8 and 11 m. depth contours.
- IV. Sand and mud zone carrying a diminished flora of *P. grandifolius*, *Desmarestia* spp. and Rhodophyceae. Most plants present are associated with sub-surface holdfast attachments.

The major factors influencing the variable distribution in the two genera investigated are depth, substrate and interrelationships with other plant types.

The greater diversity and high biomass attributed to Antarctic faunal benthos is not paral-

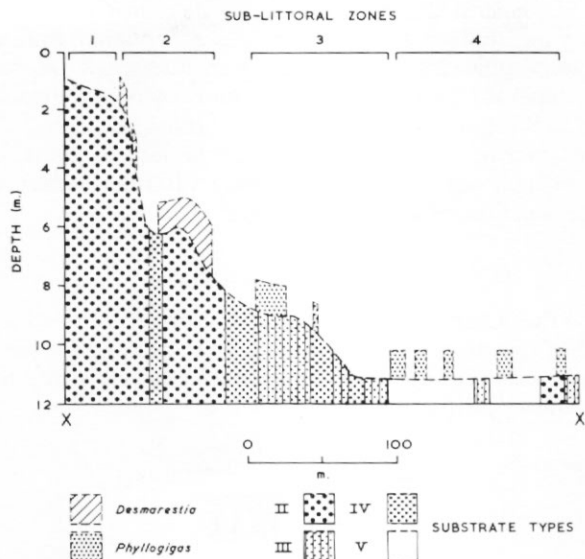


Fig. 7. Schematic transect from southern Thule Islands through the points  $\times-\times'$  (Fig. 2a).

led 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 climate and lack of suitable substrates. A variable bottom sediment, as found within Borge Bay, can never be fully utilized by macrophytes since much of the sea floor is unsuitable for colonization. From previous biomass figures for Antarctic benthic flora (White and Robins, 1972) and data introduced in this paper, standing crop per unit area in shallow seas is less than in cold-temperate or tropical systems. The maximum biomass recorded was 2.05 kg./m.<sup>2</sup> (wet weight), with a mean value for all 30 quadrats of 980 g. wet weight/m.<sup>2</sup>. Lüning (1969), working in the turbid waters off Helgoland, recorded biomass for *Laminaria* of 5.6–11.1 kg. wet weight/m.<sup>2</sup>, whilst similar order figures have been obtained from other localities (Norway: 8 kg./m.<sup>2</sup> (Grenager, 1953); Scotland: 6 kg./m.<sup>2</sup> (Walker, 1954); California: 14 kg./m.<sup>2</sup> (Blinks, 1955); Nova Scotia: average 3.8 kg./m.<sup>2</sup>, maximum 16 kg./m.<sup>2</sup> (Mann, 1972). Biomass values for the sub-littoral beds of the angiosperm *Zostera* in northern arctic waters was found to be as high as 1,150 g. dry weight/m.<sup>2</sup> (13.6 kg./m.<sup>2</sup> wet weight) (McRoy, 1969). McFarland and Prescott (1959) found that the biomass levels of *Macrocystis* forests in California were similarly high.

The paucity of an immediate sub-littoral biomass on an otherwise suitable substrate is a direct effect of abrasion and anchor-ice formation producing the pattern of isolated crevice-dwelling plant clumps rather than continuous forest growths. Since less than 1 per cent of incident light penetrates 1 m. of sea ice, and this situation is present for a large proportion of the year (White, 1977), we might expect a decrease in standing crop unless the species present are metabolically capable of fully utilizing the short photosynthetic period of ice-free summer. Productivity within algal species is not uniform; Joñsson (1970), working on the sub-littoral at Surtsey, noted that the rate of growth of the genus *Desmarestia* was more rapid than in laminarians. Benthic plants which extend their range to the unfavourable conditions of sub-ice situations are often capable of productivity under climatic extremes (McRoy, 1969).

Normally benthic algae of the temperate zones have a photosynthetic period in the summer. They then utilize the produced assimilation surplus in maximal winter growth (Lüning, 1971). Kanwisher (1966), working on arctic laminarians, emphasized the drastic effects of ice cover

on plant metabolism. *Laminaria* does not appear to be a metabolically adapted genus but relies on a diminishing 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 (1966b) observed photosynthetic production in Antarctic macro-algae subjected to a regime of 9–10 months/yr. under sea ice.

The comparative decrease in standing crop and the pattern of plant zonation in Antarctic waters are a function of light, ice, substrate and other variables; whether this low biomass is caused by decreased production requires further investigation.

## ACKNOWLEDGEMENTS

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