# A BIOLOGICAL STUDY of DESMARESTIA FIRMA (C.Ag.) Skottsb.

## (PHAEOPHYCEAE, DESMARESTIALES)

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## ABSTRACT

Several aspects of the biology of *Desmarestia firma* (C.Ag.) Skottsb., a common understorey alga in western Cape (Southern Africa) kelp beds, are investigated. The life-history of this species is described from culture. Zoospores from unilocular sporangia give rise to separate filamentous male and female gametophytes. Male gametophytes bear flask-shaped antheridia, each containing a single antherozooid. Female gametophytes bear club-shaped oogonia, each producing one or perhaps more eggs. Trichothallic sporophytes are fused to the female gametophytes. Specimens were cultured to a stage where they produced rhizoids and cortication became apparent. This is the first description of the life-history of a branched, ligulate *Desmarestia* species, and refutes the suggestion that in oppositely -branched species, gametophytes are monoecious.

Nomenclatural problems associated with *D. firma* are discussed, and the taxonomic relationships of *D. firma* and closely related species are investigated. Results show varying degrees of morphological overlap between this entity and certain others from North West America, South America and Morocco. Microscopic examinations show that sporophytes from New Zealand, Gough Island, South America and N.W. America have the same reproductive anatomy as *D. firma*, i.e. with sporangia scattered among, and similar in size and shape to the cells of the outer cortical layer. Material from the South Orkney Islands shows sporangia interspersed with sterile paraphyses and arranged in an elevated sorus. The taxonomic implications of these results are discussed, and the name *D. firma* is provisionally retained for the Southern African entity.

The distribution of *D. firma* at two levels is discussed. Geographically, this species is restricted to the cold waters of the west coast upwelling region of Southern Africa, and is found from Cape Point (34° 30'S 18° 29'E) northwards along the Atlantic coast to at least Luderitz Bay (26° 34'S 17° 04'E). Within the kelp bed, it is restricted to the sublittoral zone,

mg $O_2.g^{-1}$dry mass.$h^{-1}$, respectively. In both summer and winter plants the light compensation point lies between 10 and 20 $\mu E.m^{-2}.s^{-1}$, Pmax is reached at 300-400 $\mu E.m^{-2}s^{-1}$ (light saturation point), and Pmax does not decline at irradiance levels up to 2500 $\mu E.m^{-2}s^{-1}$. Pmax measured in the field in summer, using submarine perspex chambers is 1.9 mg $O_2.g^{-1}.h^{-1}$. The lower summer Pmax value obtained in the field is thought to be a result of inadequate stirring in the incubation chambers. Net photosynthetic rates in D. firma are compared with laboratory measurements obtained for other understorey algae from Oudekraal. Results indicate that the absence of D. firma in shallow water (less than 2m) cannot be related to excessively high irradiance, and that declining photosynthetic rates, combined with lower submarine irradiance levels, contribute to the decline in the standing crop of this species in winter. From P vs I curves, seasonal standing crop data, and measurements of submarine irradiance, the net production of D. firma during the 1978-1979 growing season is estimated as 15.4 g dry mass.$m^{-2}$. This value agrees fairly well with the estimate obtained using the Allen Curve method, and the implications and problems of this approach are discussed.

On the basis of alkali titration and gravimetric determination of total $SO_4$, D. firma is shown to contain approximately 18% $H_2SO_4$, per dry mass. This value is approximately the same in old and young plants, and does not vary with age. The palatability of D. firma is compared with 12 other common kelp bed algae, in 3 types of feeding experiment with the sea urchin Parechinus angulosus Leske. The algae are divided into three groups on the basis of the results: preferred, intermediate, and non-preferred, the latter group including D. firma. In order to explain these selection patterns, the relative astringencies of all of the algae, and the phenol contents (Folin-Denis method) of 4 (including D. firma) are measured. Results show that D. firma has a high relative astringency (0.75 on a scale 0 to 1) but low relative phenol content (0.04 on a scale 0 to 1). While high relative astringencies are thought to be directly related to high phenol levels in most of these

algae, in *D. firma* this is shown to be related to $H_2SO_4$ in the tissues. Simple rates of feeding by *Parechinus* show a statistically significant correlation ($r^2 = 0.58$) with the relative astringencies of the algae. It is concluded that in *D. firma*, $H_2SO_4$ acts as a secondary compound" in the sense that it discourages grazing by *Parechinus*. A final section discusses important questions raised by this entire study.

"I deny that the study of nature has in itself, an evil tendency. On the contrary, the study of organic nature ... ought to be one of the purest sources of intellectual pleasure. It places before us structures the most exquisite in form and delicate in material ... and if our minds are properly balanced ... reading in them the evidence of their relation to their Maker, we shall be led on to investigate our own."

W.H. HARVEY
(Nereis Boreali Americana)

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# CHAPTER 1

## INTRODUCTION and STUDY SITE

### 1.1 GENERAL INTRODUCTION

Productivity studies of kelp beds in the Northern Hemisphere have shown these systems to be of primary importance in inshore food chains (Mann, 1973; Chapman, 1974). Recently, the Ecklonia maxima (Osb.) Papenf. - Laminaria pallida (Grev.) J.Ag. beds of the south-western Cape coast have been the subject of a series of ecological studies, aimed primarily at an understanding of their structure and dynamics, (Field et al, 1977; Velimirov et al, 1977; Field et al, 1980a), particularly with relation to commercially valuable resources such as rock lobsters (Jasus lalandii), the kelps themselves, and possibly the coastal commercial fisheries. While these studies, and that of Dieckmann (1978) on Laminaria pallida, have dealt fairly comprehensively with the two major kelp species, they have only considered the smaller understorey algae in the broadest of terms. This present study of Desmarestia firma is the first detailed biological study of an understorey alga from these south-western Cape kelp beds.

Desmarestia firma was selected because it is common in these kelp beds, and was potentially interesting in that it appeared to be an annual and showed seasonal and spatial abundance, especially in areas from which kelp had been cleared (N. Jarman, pers. comm). Furthermore, this genus has recently received some taxonomic attention (e.g. Chapman, 1972; Moe & Silva, 1977) and it was felt that an investigation of its reproductive biology, as well as its taxonomic relationships with closely related species, might resolve some of the problems that these studies had raised.

The present study has two main objectives. The first is a taxonomic investigation of D. firma and closely related species, world wide. This is necessarily preceded by a study of the life cycle of the South African species, since Moe & Silva (1977) have pointed out that in the genus Desmarestia, evol-

utionary divergence may be primarily expressed by reproductive characteristics.

The second broad objective is an autecological study of *D. firma* in the Oudekraal kelp bed. To this end its spatial distribution in relation to other organisms and environmental factors, seasonal changes in standing crop , primary production and rates of photosynthesis have been studied. In addition, its sulphuric acid content was investigated, and its palatibility to the prominent kelp bed grazer *Parechinus angulosus* was compared with 13 other kelp bed algae. It was hoped that these studies would enable an understanding of the role and contribution of *D. firma* in these kelp beds.

## 1.2 STUDY SITE and ENVIRONMENTAL CONDITIONS

### 1.2.1 Location and General Description

The principal study site was a one hectare quadrat of Ecklonia and Laminaria kelp-bed at Oudekraal (34° 00'S, 18° 21'E) on the west coast of the Cape Peninsula, some 12 km south-west of Cape Town (Figs. 1.1, 1.2, 1.3). The centre of this quadrat was 350 metres offshore, and the area included the seaward margin of the kelp bed. The site lay within the boundaries of larger study areas described by Velimirov et al (1977) and Field et al (1980 b). Depths at low tide ranged from 0m (at the large rock known as the Pannekoek) to 15m, with an average depth of 9m.

The topography of the sea bed at this site is extremely variable, with areas of sand, flat rock, and boulders. In general, large granite boulders (often over 2m high) and deep crevices in the S.E. corner give way to flat rock in the north, and patches of sand, particularly in the south-west.

The distribution of plants and animals within kelp beds at Oudekraal is well described by Velimirov et al (1977), and is also discussed briefly in Chapter 4 of this study.

### 1.2.2 Local coastal hydrology

Oudekraal lies within a coastal region strongly influenced by the cool north-flowing Benguela current. In summer (September to March) prevailing south-easterly winds blowing offshore and roughly at right angles to the current, cause the cool (8 - 9°C) Benguela water on the continental shelf to upwell close inshore. This water is characterised by low temperatures, low salinities, low chlorophyll a content, low concentrations of dissolved oxygen, and high concentrations of silicate, phosphate, and nitrate (Andrews, 1974; Andrews & Hutchings, 1980). In winter (May - August), prevailing north-west and westerly winds drive relatively warm (18°C) oceanic water inshore and cause downwelling. This oceanic water is characteristically more saline,

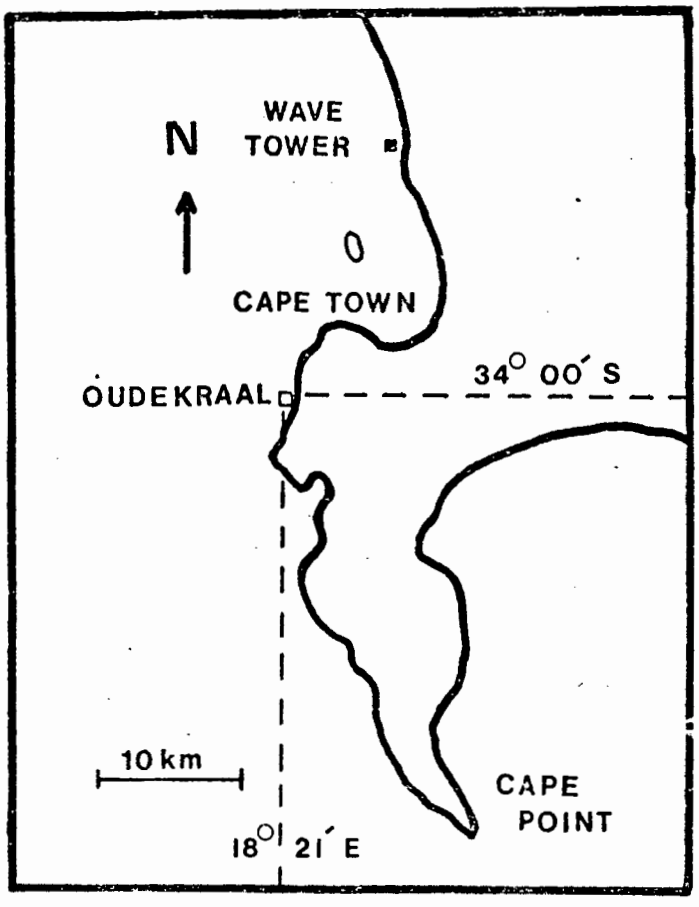



Fig. 1.1

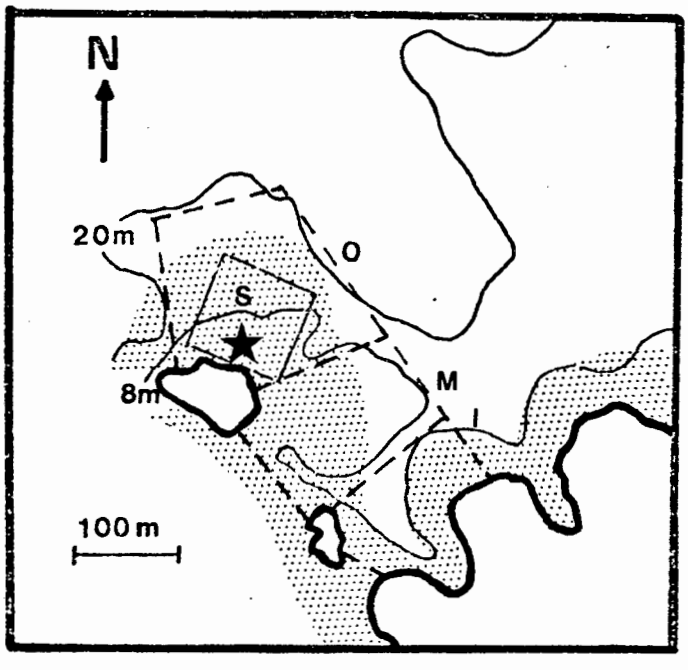



Fig. 1.2

Fig. 1.1 Map showing the location of the Oudekraal study area on the west coast of the Cape Peninsula. The position of the wave recording tower at Melkbosstrand is shown.

Fig. 1.2 Part of the Oudekraal kelp bed (stippled) showing the 1 ha study site (s), with position of thermoscript marked by star. The 8m and 20m depth contours are shown, as well as the Offshore, Mediate, and Inshore zones of Velimirov et al, 1977. (Broken lines).

Fig. 1.3. Oudekraal, Cape Peninsula, looking north-west. Position of study site arrowed. Distance from rocky point to study site approximately 300m.

better oxygenated, and has a higher chlorophyll a content than upwelled water. Nutrient levels, however, are much lower. Where the two water types meet and mix the water has an intermediate temperature (10 - 18°C) while levels of nutrients, chlorophyll a and dissolved oxygen are quite variable. Frequently "mixed water" supports dense blooms of phytoplankton. Although upwelling is most common in summer, it occasionaly occurs in winter. Conversely, downwelling occasionally occurs in summer.

At Oudekraal, south-east winds are funneled down the valleys of the mountain. Upwelling is therefore often rapid and intense, and during these conditions, the residence time of water within the area shown in Fig. 1.2 is only 3-8 hours (Field et al, 1980 b).

### 1.2.3 Temperature

Water temperature at Oudekraal was recorded continuously by a thermoscript (Fricke & Thum, 1975) positioned at 8m depth.

Mean monthly temperatures (Fig. 1.4) fail to show the rapid changes in sea surface temperature that occur within a 24 h period. A plot of daily temperature readings shows the frequent upwelling cycles in summer which cause large fluctuations in temperature that occur within a month (Fig. 1.5). In winter when upwelling is relatively uncommon, temperature fluctuations within a month are comparitively slight.

### 1.2.4 Nutrients

Dieckmann (1978) made monthly measurements of phosphate and nitrate concentrations at Oudekraal in 1975. He points out that daily measurements must be made for such data to be of use, because conditions change so rapidly during upwelling.

According to Andrews (1974), Andrews & Hutchings (1980), and Field et al (1980 b), water temperature is correlated with upwelling,

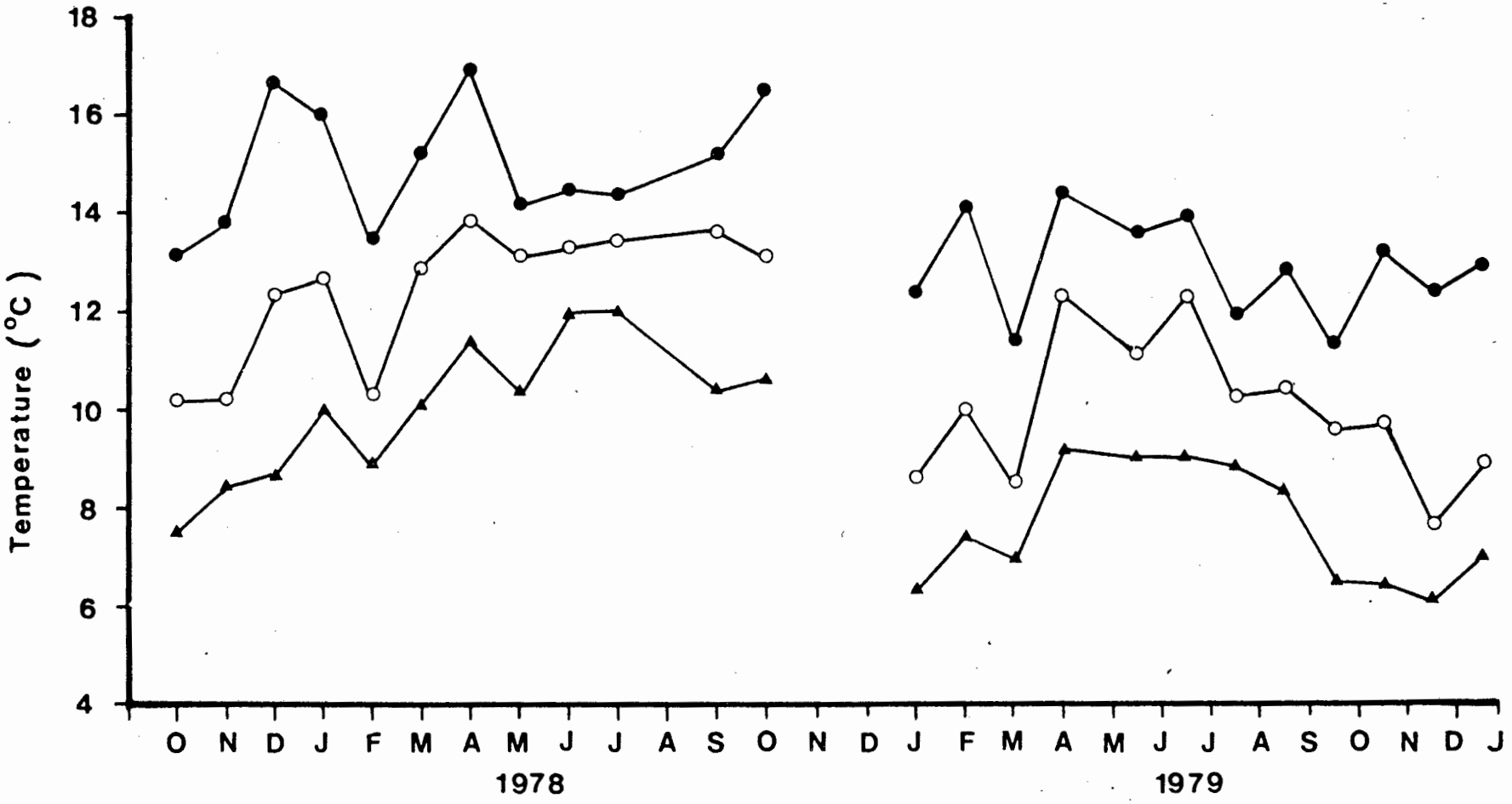



Fig. 1.4 Mean, maximum and minimum monthly water temperatures in the study site, Oudekraal, from October 1978 to January 1980. Data used by permission of R. Simons, Seaweed Unit, Sea Fisheries.

●—● - maximum; ○—○ - mean; ▲—▲ - minimum temp.

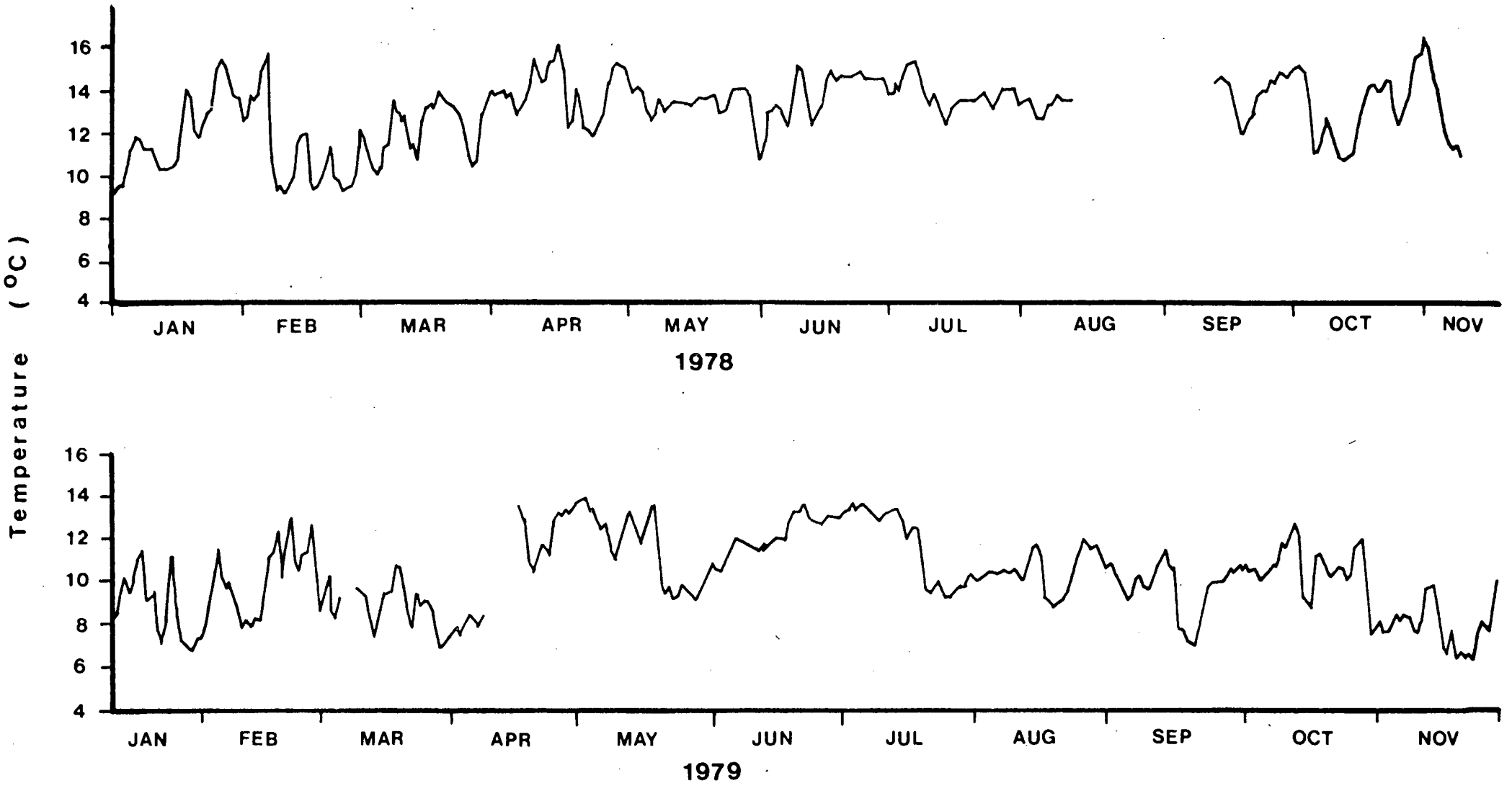



Fig. 1.5 Mean daily temperatures recorded on thermoscript, from January 1978 to November 1979. Data used with permision of R. Simons, Seaweed Unit, Sea Fisheries.

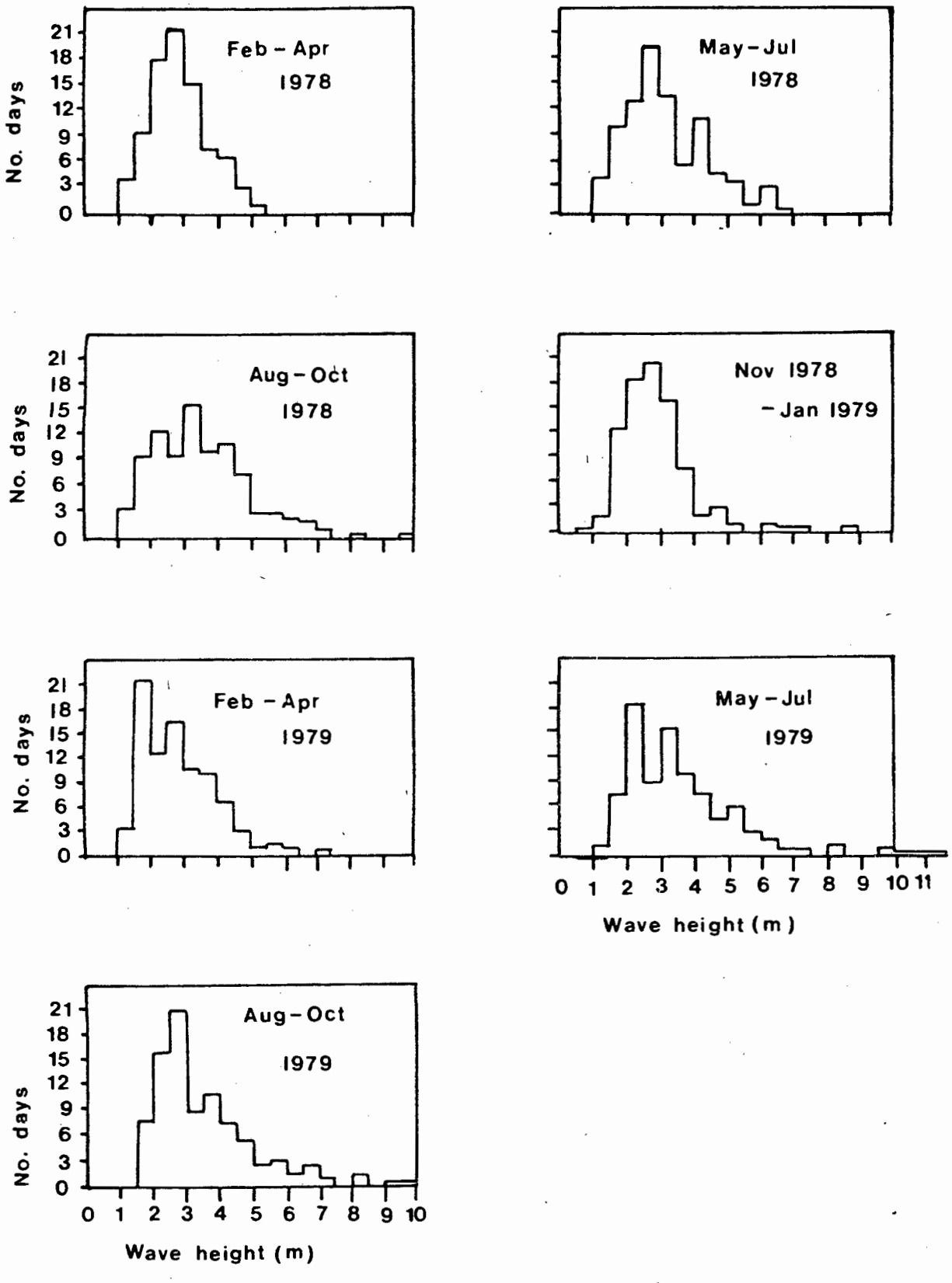



Fig. 1.6 Wave-height occurence histograms, obtained from wave-tower at Melkbosstrand. From Maxwell and Rattey, (1978, 1979), used with permission of E.S.C.O.M.

and therefore with the concentrations of nutrients. In general, temperatures of 10°C or lower may be taken as indicators of nutrient-rich water (maximum values of nitrate and inorganiic phosphate of 20 and 2.5 mg at. $l^{-1}$, respectively) while temperatures of 15 - 18°C indicate water with low nutrient levels (down to 1.0 and 0.5 mg at. $l^{-1}$ of nitrate and inorganic phosphate, respectively). During downwelling, nitrate at least may fall below levels limiting for the growth of phytoplankton and macrophytes (Field et al, 1980 b). These low levels are thought to be the result of depletion by blooms of phytoplankton, and they are often found in mixed as well as downwelled waters.

### 1.2.5 Wave Action

At Melkbosstrand, some 25 km north of the study site, wave heights are continuously recorded by a Wemelsfelder-type wave recorder on a sea tower 1 km offshore, in water 11m deep. All waves approaching between 202° and 312° E of N are detected, and this sector includes all possible directions of waves reaching Oudekraal. Data presented here (Fig. 1.6) are in the form of maximum wave height histograms (Maxwell and Rattey, 1978, 1979).

Swell height usually exceeds 1.5m, and may reach more than 10m (e.g. May - July 1979). In general, large swells are associated with westerly winds which prevail in winter. At Oudekraal, the Pannekoek defracts south-westerly swells and causes extremelypowerful bottom surges.

### 1.2.6 Submarine Irradiance

Light penetrates deepest when there is upwelling and little swell. Under these conditions visibility in the kelp bed can exceed 12m. When heavy swells coincide with upwelling, suspended particles and detritus reduce the visibility, often to less than 4 or 5m. In general, however, upwelling conditions are accompanied by very little swell action. In oceanic and mixed water, high standing crops of plankton discolour the

water, and reduce visiblity, sometimes to 2m or less.

Ideally, studies of growth or production should be accompanied by reliable data on submarine light conditions. Problems involved in the measurement of submarine light are discussed in Chapter 6, along with measurements of light penetration at Oudekraal.

# CHAPTER 2

## THE LIFE HISTORY of DESMARESTIA FIRMA (C.AG.) SKOTTSB. (PHAEOPHYCEAE, DESMARESTIALES)

This study is in press (Phycologia 21 (3), 1982, and is presented here in the form in which it was accepted for publication. The acknowledgements, abstract, and references are included in the corresponding sections for the thesis as a whole.

## 2.1 INTRODUCTION

The world-wide genus Desmarestia Lamouroux (Phaeophyta: Desmarestiales) comprises about 40 described species (Moe & Silva 1977), with life-cycle studies completed for: D. aculeata (L.) Lamour. (Schreiber, 1932; Chapman & Burrows, 1970), D. viridis (Müll) Lamour. (Abe, 1938; Kornmann, 1962) and D. tabacoides (Nakahara & Nakamura, 1971).

Taxonomic studies of this genus have been based almost entirely on morphological characters of the sporophyte. In their review of sporangia in Desmarestia, Moe & Silva (1977) stated that vegetative characters may be of secondary importance in expressing evolutionary divergence in this genus. It seems likely that the presently confused taxonomy of Desmarestia may only be resolved by comparing the life-cycles of putative species. A culture study of the South African entity Desmarestia firma (C. Ag.) Skottsb. was therefore made to compare this species with others whose life-cycles are known. In South Africa, D. firma is a common annual understorey species in Ecklonia maxima (Osb.) Papenf. and Laminaria pallida (Grev.) J. Ag. kelp beds and is distributed from Cape Point (34° 30'S 18° 29'E) northwards along the Atlantic coast to at least Luderitz Bay (26° 34'S 17° 04'E).

## 2.2 MATERIALS AND METHODS

### 2.2.1 Culture Methods

Mature sporophytes were collected in mid-July, 1980, at Kommetjie ($34^{o}8'S$ $18^{o}19'E$) and Bakoven ($33^{o}58'S$ $18^{o}22'E$), on the west coast of the Cape Peninsula, Republic of South Africa at depths of 20 and 10 m, respectively. Plants without visible epiphytes were selected. After examining sections to confirm the presence of sporangia, pieces of frond were rinsed in filtered sea-water, and suspended from corks above glass slides, in glass dishes containing 300 ml of filtered sea water (Millipore 0.45 $\mu$m membrane). The dishes were then placed either on a window-sill, in diffuse natural light, or in a cold room under fluorescent lights. On the window-sill, temperature varied from 14 to $22^{o}C$, and Photosynthetically Active Radiation (P.A.R.) never exceeded 60 uE $m^{-2}$ $sec^{-1}$, as measured with a Li-Cor 193s spherical quantum sensor connected to a LI 188 Integrating Quantum Meter (Lambda Instr. Corp.). The temperature in the coldroom was $11^{o}C$, and P.A.R. of the fluorescent lights 150 uE $m^{-2}$ $sec^{-1}$. After the spores had settled, the sea water was enriched by adding $NaNO_3$, $Na_2HPO_4$ and sterilised soil extract at concentrations of 1.5 mM, 100 $\mu$M and 50 ml per l respectively (Enriched Erdschrieber solution, from McLachlan, 1973). Culture media were changed weekly, and stages in the life-cycle were drawn and photographed. After three to five wk, the vegetative sporophytes in the window sill dishes were transferred to the coldroom and given new nutrient solutions.

### .2.2 Preparation of spores for scanning electron microscopy

Fertile, epiphyte-free material, cut into strips, was rinsed thoroughly and suspended from corks in filtered sea water in 250 ml flasks, for 6h. The frond material was then removed, and the spores which had been released were fixed by the addition of glutaraldehyde to a concentration of 2.5%. Two hours later, the samples were divided in half and filtered through 1 µm and 0.2 µm membrane filters. The membranes were then fixed between ring magnets, placed in artificial sea water, and transferred through decreasing salinities, ending with distilled water. Samples were then dehydrated through an increasing gradient, ending with 96% ethanol. Preparation was completed by critical point drying, mounting, and vacuum coating with gold-palladium.

## 2.3 RESULTS

### 2.3.1 The sporophyte

The sporophyte consists of secondary blades arranged pinnately on a single primary blade (Fig. 1). The secondaries often give rise to a third order of fronds. In the young sporophyte frond-margins are fringed with trichothallic hairs, giving the plant a feathery appearance (Fig. 2). Later in the growing season these hairs are lost. The plants are olive brown and membranous when young and become dark brown and leathery with age. In any area, the morphology of fronds is highly variable, and at any one time, the length of specimens may range from less than 5 cm to over 1.5 m, according to age and degree of damage. The holdfast is a disc from a few to over 15 mm in diameter. Composite holdfasts, giving rise to several plants, may be over 40 mm in diameter.

## 2.3.2 Sporangia and Spores

Sporangia, which appear in winter, are scattered throughout the superficial layer of cortical cells. Their dimensions are the same as those of the surrounding cortical cells i.e. about 15-20 µm long and 8-15 µm wide (Figs. 3,4). Mean dimensions of 20 sporangia were 17x10 µm. Sporangia are visible as dark cells in planar sections of the superficial cortex.

The sporangia of D. firma bear a striking resemblance to those of the Helgoland D. viridis (Kornmann, 1962), D. patagonica (Asensi & Carralves, 1972) and D. tabacoides (Nakahara & Nakamura, 1971). In terms of their development and disposition, they would belong to group 1 as proposed by Moe & Silva (1977) i.e. the sporangia are randomly scattered, and apparently develop from cells of the outer cortical layer.

The sporangia of D. firma are different in size and arrangement from those of a specimen from South Georgia initially described as D. firma by Skottsberg (1907). Significantly, he later (1921) re-identified that specimen as D. ligulata Lamour.

It was difficult to estimate the number of spores per sporangium, but 16 appears to be a likely number. The numbers of spores per sporangium in other species are given in the review of Moe & Silva (1977).

Zoospores are egg-shaped, with two laterally-attached flagella (Fig. 5). They are between 3.5 and 5 µm long, and 2 to 3 µm in diameter at the widest point. They are identical in appearance to, but smaller than those observed in other Desmarestia species: 6-7 µm in Helgoland D. viridis (Kornmann, 1962), 8-10 µm in Japanese D. viridis (Abe, 1938), 7-10 µm in D. aculeata (Schreiber, 1932; Chapman & Burrows, 1971) and about 9 µm in D. tabacoides (Nakahara & Nakamura, 1971). Both flagella appear to be of the whiplash type, but since they were invariably sucked through the pores in the membrane filters, the lengths could not be measured.

Copulation of spores was never observed, contrary to the observation in Japanese D. viridis (Abe, 1938).

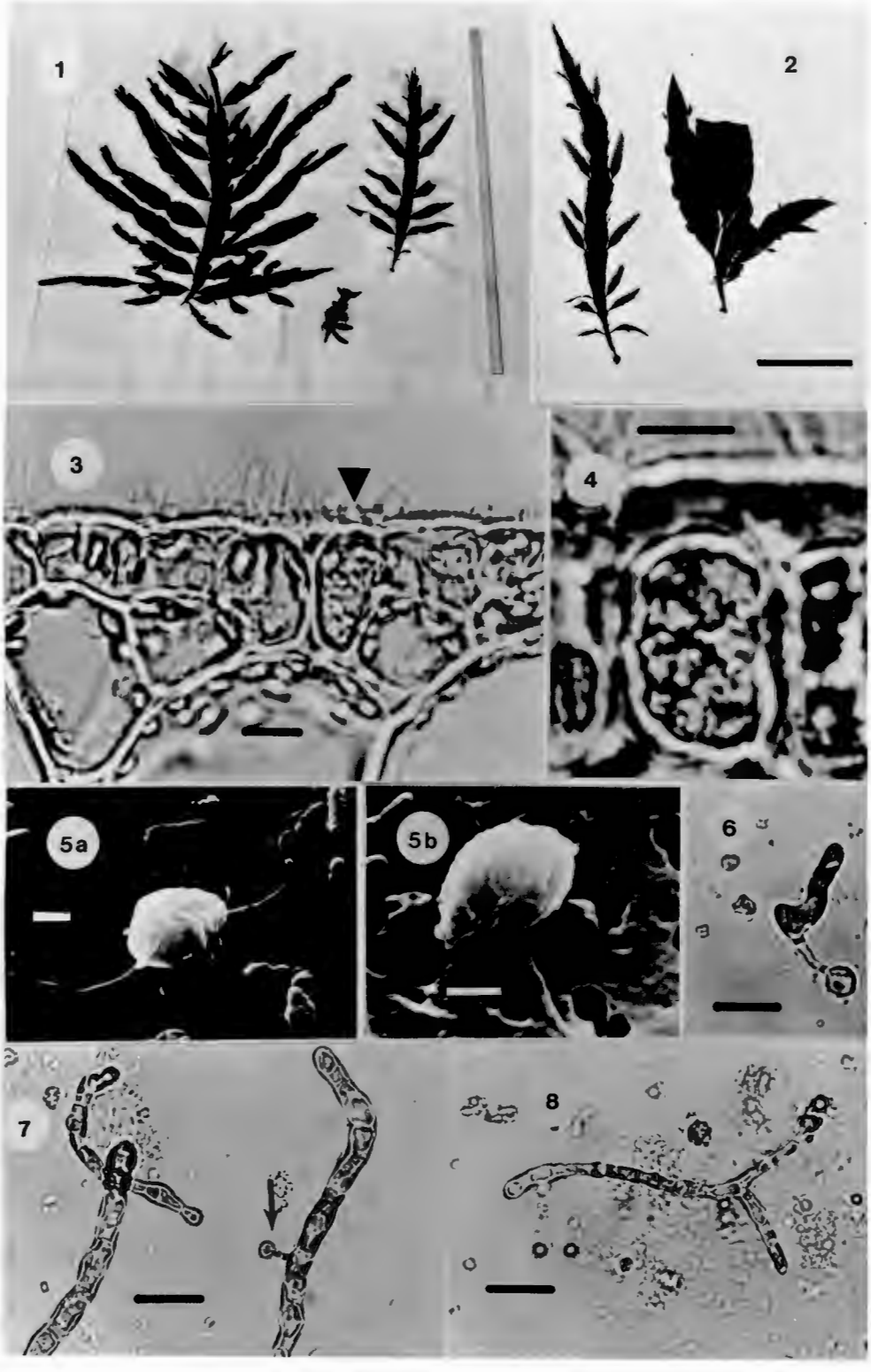
### 2.3.3 Growth and development of the gametophytes

Settled spores with germ tubes were observed approximately 72 h after spore release (Fig. 6). Within 10 days well-developed dioecious gametophytes were visible (Figs. 7,8), with the round, empty cell wall of the settled zoospore attached. Throughout the vegetative development of the gametophytes, those at 11°C, under fluorescent lighting grew markedly more slowly than those in natural light at 14-22°C.

The filaments of male gametophytes (Fig. 8) were initially 3-5 µm in diameter (mean of 10 = 3,5 µm), and between 5 and 8 µm wide at maturity, and at all stages showed very little pigmentation. Female gametophytes (Fig. 7) initially from 4,5 to 7 µm in diameter, increased to 7 to 12 um, and were more darkly pigmented than males. The gametophytes of other dioecious species described appear to be similar, with the males poorly pigmented and slightly over half the diameter of the females.

After approximately 30 days the culture vessels supported vegetative gametophytes forming clumps several millimetres across, often with male and female strands interwoven. At this stage, plants which were given new nutrient solutions and transferred to 11°C with fluorescent lighting, produced gametangia within two to three days. Gametophytes left at room temperature for 6 weeks remained vegetative. Kornmann (1962) found that fresh nutrient solution and a drop in temperature from 15 to 3-5°C appeared to cause sexual maturation and fertilization in D. viridis from Helgoland.

In D. tabacoides lower temperature and shorter photoperiod caused the formation of gametangia (Nakahara & Nakamura, 1971).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CAPTIONS TO FIGURES

FIG. 1. Mature sporophytes of *D. firma* at end of summer (May). Metre rule on right.

FIG. 2. Young sporophytes, collected in spring (September). Note trichothallic hairs on margins of fronds.
Scale bar = 10 mm.

FIG. 3. Section of frond, showing sporangium (arrowed) in superficial cortex.
Scale bar = 10 µm.

FIG. 4. Single sporangium.
Scale bar = 10 µm.

FIG. 5 a and 5 b. Scanning electron micrographs of zoospores.
Scale bar = 1 µm.

FIG. 6. Gametophyte, approximately 3 days after germination.
Scale bar = 10 µm.

FIG. 7. Female gametophytes, approximately 10 days old. Settled zoospore, and germination tube arrowed.
Scale bar = 20 µm.

FIG. 8. Male gametophyte, approximately 10 days old.
Scale bar = 20 µm.

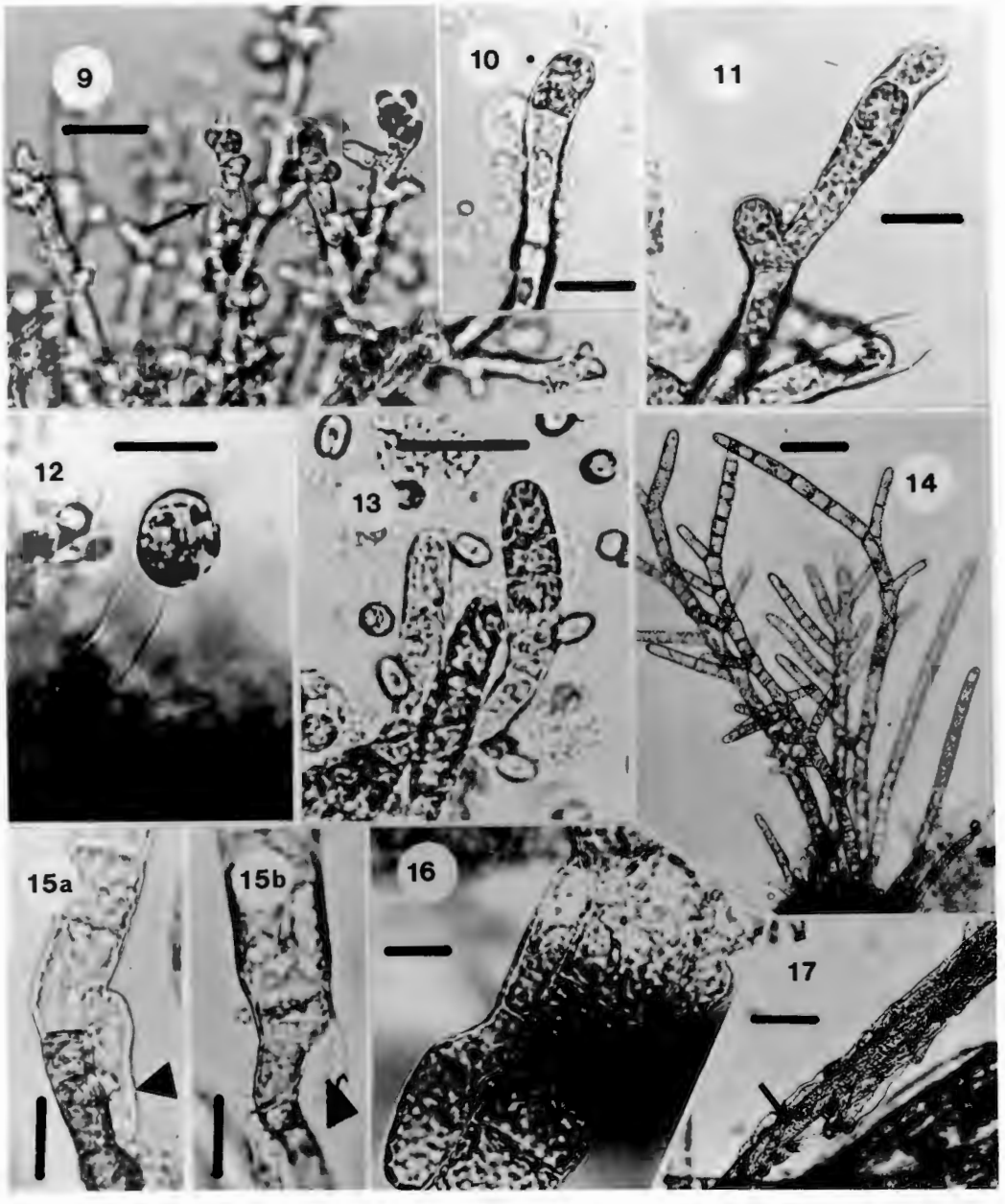
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FIG. 9. Mature male gametophyte bearing flask-shaped antheridia (arrowed).
Scale bar = 20 µm.

FIG. 10. Oogonium, on female gametophyte.
Scale bar = 20 µm.

FIG. 11. Oogonium, apparently with two eggs.
Scale bar = 20 µm.

FIG. 12. Egg or zygote at mouth of oogonium.
Scale bar = 20 µm.

FIG. 13. Sporophytes, approximately 5 days old.
Scale bar = 20 µm.

FIG. 14. Sporophytes, approximately 20 days old.
Scale bar = 100 µm.

FIG. 15 a & b Rhizoids (arrowed), growing down from the primary rhizoid cells, and closely abutting the darker cells of the female gametophyte.
Scale bar = 20 µm.

FIG. 16. Down growing corticating filaments, closely adhering to the axial strand cells.
Scale bar = 10 µm.

FIG. 17. Early stage of cortication. Central axial strand (arrowed) is becoming surrounded by corticating hyphae.
Scale bar = 30 µm.

### 2.3.4 The gametangia

Flask-shaped antheridia, 8-9 µm long, are clustered terminally on the male gametophytes (Fig. 9). Each contains a single antherozoid (Figs. 8,9). Release was observed on one occasion: the antherozooid emerged from a small pore in the antheridium, over a period of about one minute. Similar observations were made by Schreiber (1932) for D. aculeata.

Oogonia are club-shaped, 12-15 µm wide at their widest point, and 15-25 µm long (Figs. 10,11). In all cultures antheridia were far more numerous than oogonia. Eggs released when the tip of the oogonium ruptures (Fig. 11) often appear to remain attached to the mouth of the oogonium (Fig. 12). Fertilization was not observed, but presumably may occur while the egg is in the ruptured oogonium, since all the sporophytes observed were fused with female gametophytes (Figs. 15a,b). The same observation was made for D. viridis by Kornmann (1962) who suggested that this situation may not be as common in natural populations. In D. aculeata grown in culture, eggs were commonly dislodged from the oogonia (Chapman & Burrows, 1971).

In D. firma, many oogonia appeared large enough to accommodate more than one egg.

### 2.3.5 Growth of the young sporophytes

Within five days of the sexual maturation of the gametophytes, young sporophytes became visible as erect filaments, 2-4 cells long, 8-10 µm in diameter, and with abundant chloroplasts (Fig. 13). All were apparently firmly fused with the gametophytes, the zone of contact being marked by the darker pigmentation of the latter. No free sporophytes were found, but this may not reflect the situation in nature.

In all cultures, side branching of the monosiphonous thread began when it consisted of between 4 and 10 cells. Branching is opposite, distichous, but sometimes one of a pair fails to develop (Fig. 14). Rhizoids developed from the poorly pigmented basal cell of the sporophyte (the primary rhizoid cell) when there were between 3 and 10 pairs of side branches (Figs. 15a,b). Occasionally the tips of rhizoids attached to adjacent sporophytes. These observations agree closely with those made by Schreiber (1932) for D. aculeata zygotes which were attached to oogonia. However, he found that free zygotes produced rhizoids before the development of monosiphonous uprights. As Schreiber suggested, free zygotes are probably more common in nature where wave action would dislodge them from the mouth of the oogonium. Such developmental differences between free and attached zygotes may not occur in all species however, for Kornmann (1962) found that for D. viridis even in free zygotes the monosiphonous upright is formed before the primary rhizoid.

The next clear stage in the growth of the sporophyte is that of cortication. The first cortical initials arise just below the most basal pair of side branches. Swellings in the basal part of the parent cell develop as tubes which grow downwards, adhering closely to the central hypha (Fig. 16). Eventually, other corticating filaments arise from the basal cells of side branches further up the sporophyte. Within a few days, these hyphae form overlapping layers (Fig. 17). At this stage, the axial filament is still visible through the corticating filaments. No further growth could be observed, despite manipulations of the culture medium, and even transplanting the sporophytes into the sea.

## 2.4 DISCUSSION

Chapman & Burrows (1971) suggest that oppositely branched species of Desmarestia are monoecious and alternately branched species are dioecious. The former include Helgoland D. viridis (Kornmann, 1962) and the two Japanese species D. tabacoides (Nakahara & Nakamura, 1971) and D. ligulata (Nakamura, pers. comm. in Chapman & Burrows, 1971). The latter include D. aculeata (Schreiber, 1932, and Chapman & Burrows, 1971). However, the present study clearly shows that D. firma is oppositely branched and dioecious.

It seems that the D. firma gametophyte survives the winter, when conditions are unsuitable for the growth of sporophytes. The Western Cape winter is characterised by rough seas, low light and nutrient levels and warmer water temperatures. In this study sexual maturation of the gametophytes was induced when they were given new medium, the temperature was lowered, light levels increased, and the light quality altered. Precisely which of these conditions initiate maturation was not investigated. However, in Western Cape kelp beds similar conditions, favourable for the growth of sporophytes, occur in Spring and Summer, when upwelling brings cold, clear, nutrient-rich water inshore.

D. firma is reported from southern South America, various southern islands, and New Zealand. On morphological grounds at least, the New Zealand population appears to differ from that of South Africa. However, certain forms of D. ligulata from Chile, are morphologically very similar to D. firma from South Africa. The exact relationships between these southern hemisphere populations of ligulate Desmarestia will only become clear when their life-cycles have been described.

# CHAPTER 3

# NOMENCLATURE and TAXONOMY

## 3.1 INTRODUCTION

The genus Desmarestia was created by Lamouroux (1813), who recognised four species: D. aculeata L; D. viridis Muell.; D. ligulata Stackhouse (Fucus ligulatus Lightfoot nom. illeg.); and D. herbacea Lamouroux (Fucus herbaceus Turner nom. illeg.). Subsequently, Agardh (1824) grouped these species, along with several others, under the genus Sporochnus, which he divided into two groups: the filiform and the plane. Later writers have retained the name Desmarestia, but have followed the natural sub-division of Agardh (1824). The plane species include the branched ligulate forms examined in this study. The only described representative of this genus in Southern Africa is the branched ligulate Desmarestia firma (C. Ag.) Skottsb., which is found from Cape Point (34°30' S 18° 29' E) northwards to at least Luderitz Bay (26° 34' S 17° 04' E).

On the basis of morphological characters, Chapman (1972) combined 6 branched ligulate species from North-West America with an entity from Europe, under the name D. ligulata var. ligulata (Stackh.) Lamouroux. Desmarestia firma was not included within this group, but he pointed out that there was some morphological overlap between this species and specimens he had included in his new grouping, and suggested that the Desmarestia complex in the Southern Hemisphere is in need of examination.

In a review of patterns of sporangial development and disposition in the genus Desmarestia, Moe and Silva (1977) provided evidence that reproductive characters may be of primary importance taxonomically, and they strongly criticise the morphologically-based work of Chapman (1972).

The present study sets out to examine the gross morphology and reproductive anatomy of branched, ligulate Desmarestia, world-wide, in order to make taxonomic comparisons between

*D. firma* and entities which appear to be closely related to it. This is necessarily preceded by a discussion of nomenclatural problems in *D. firma*.

## 3.2 MATERIALS and METHODS

Over 1500 specimens of the South African *Desmarestia* population were examined, including routinely sampled material from Oudekraal, material collected during dives and from beach cast along the western coast of the Cape, and herbarium specimens. In accordance with the recommendation of Chapman (1972) mature specimens (those which had shed their trichothallic meristems) were measured.

Herbarium specimens of ligulate *Desmarestia* were borrowed from North American (MIN, DUKE, UBC, WTU), South American (SGO), and New Zealand (WELT) herbaria. The entire collections of ligulate *Desmarestia* were examined in BM, TCD, L and PCU. Additional pressed material was obtained from England, Chile, Argentina and Signy Island (South Orkneys). Fresh specimens of *Desmarestia* were collected using SCUBA at Gough Island (40° 21' S 9° 53' W) in the South Atlantic.

As full a range of morphological characters as possible was examined (although some are criticised by Chapman, 1972), since these have been used to define species in the past. In addition to characters illustrated in Fig. 3.1, observations were made on prominence of venation, degree of development of aculae, total number of fronds of respective orders per plant, and thallus texture. Material of juvenile plants was also examined for the purpose of general comparison. Formalin-preserved material was examined with respect to vegetative anatomy, in the search for taxonomically useful characters. When fertile material could be obtained, particular attention was paid to reproductive structure of the sporophytes. Cross-sections of material were cut on a freezing microtome for microscopic examination. Dried material was rehydrated in a weak detergent solution prior to sectioning.

Type descriptions of, and nomenclatural problems associated with entities which are similar to *D. firma* are provided in Appendix C, since they are referred to in this chapter.

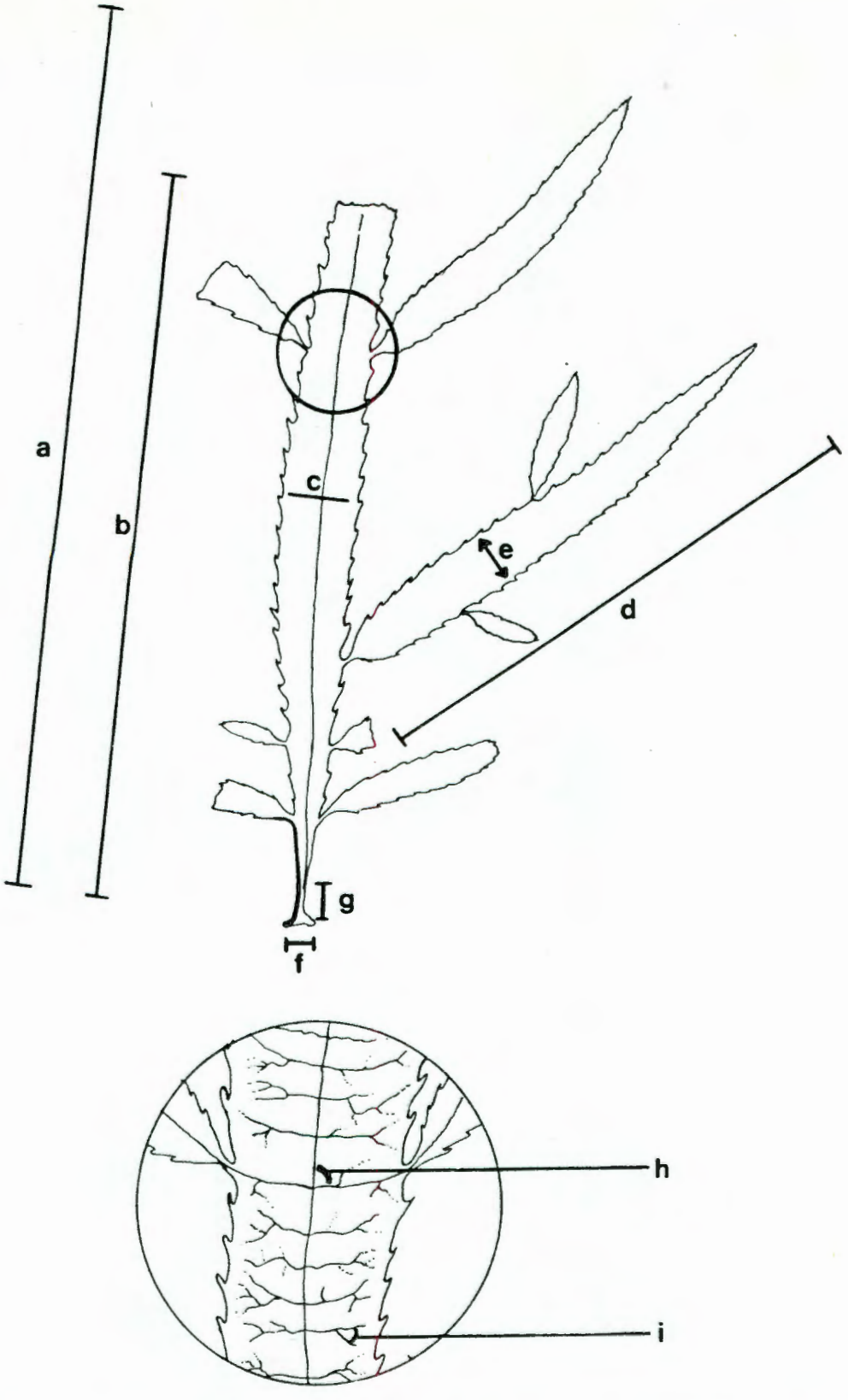



FIG. 3.1 Main characters used in studying morphological variation in ligulate Desmarestia species. a - overall length; b - axial frond length; c - maximum axial frond width; d - maximum primary frond length; e - maximum primary frond width; f - holdfast diameter; g - stipe length; h - angle of primary venation; i - angle of secondary venation. (After Chapman, 1972).

## 3.3 NOMENCLATURE in D. FIRMA

Accepted Name:

Desmarestia firma (C. Ag.) Skottsberg, Wiss. Ergebn. Schwed. Südpolar -Exped., 4 (6): 21, (1907).

Basionym:

Sporochnus herbaceus var. firma. C. Agardh, Systema Algarum: 261, (1824).

Type Description:

"Sp.herbaceus, fronde plana membranacea obsolete costata dentata bipinnata, pinnis pinnulisque oppositis ellipticus obtusis basi attenuatis.
Var. firma, fronde subcoriacea.
In mari Atlantica Gallia, ad cap b.spei".
"Sp. herbaceus, frond flat, membraneous, indistinctly mid-ribbed, dentate, bipinnate, pinnae pinnules opposite elliptical obtuse attenuated at base.
Var. firma, frond somewhat leathery.
From Atlantic France, to Cape of Good Hope".

Lectotype:
Papenfuss (1943) selected as lectotype specimen No. 49916, from C. Agardh's herbarium (LUND), which was collected at the Cape of Good Hope by Lalande.

Taxonomic Synonym:

Desmarestia herbacea f. latior Kutzing, Tabulae Phycologicae, 9:42, pl. 100, Fig. C, 1859.

Nomenclatural Synonym:

Desmarestia ligulata (Stackhouse 1809) Lamouroux 1813 var. firma (C. Agardh 1824). J. Agardh, Species Algarum, 1:169, 1848.

Discussion:

Skottsberg (1907:21) elevated Sporochnus herbaceus (C. Agardh) var. firma, Syst. Alg. 1824 to specific rank, but subsequently (Skottsberg 1921:21) considered this species to be synonymous with D. liqulata (Stackhouse) Lamouroux. However, Papenfuss (1943:82) claimed that D. firma (C. Agardh) Skottsb. should be retained, and several authors have evidently followed his advice; for example, Lindauer et al (1961) and Simons (1976). According to Chapman (1972:19), C.Agardh (1824) published the name of Sporochnus herbaceus var. firma as a substitute for another species Desmarestia dudresnayi Lamouroux in Leman 1819, but as varietal rank since he considered it as not worthy of species status. Chapman therefore contended that variety firma should be typified with D. dudresnayi[1].

"Desmarestia dresnaji[2], Lamour. ex. Leman in Dict. des Sci. Nat. cum icone". is listed as a synonym for Sporochnus herbaceus var. firma by C. Agardh in his 1824 publication, but he gave no reason for doing this.

Contrary to Chapman (1972) Sporochnus herbaceus var. firma C. Agardh does not have to be typified with the type specimen of D. dudresnayi Lamouroux and Leman. Only if C. Agardh listed

Footnotes:

1 Originally, Leman, following Lamouroux or causing the error, left the terminal "i" off the specific epithet. Art. 73.10 of the International Code of Botanical Nomenclature (Stafleu et al 1978) provides for the automatic correction of the ending (P.C. Silva, pers comm.30.1.80).

2 The 43rd plate of the Atlas accompanying Dictionnaire des Sciences Naturelle Vol. 13, 1819, bears the caption Desmarestia dresnayi. This is the usual spelling and is undoubtedly the origin of D. dresnayi in Agardh 1824. However, the date of this plate has never been established, though it appeared sometime between 1816 - 1829. Under these circumstances the correct spelling must be dudresnayi (P.C. Silva, pers. comm. 31.1.80.)

D. dudresnayi without additional material would Chapman be correct (Silva, pers comm. 30.1.80). However, C. Agardh listed two syntype localities for variety firma - the Atlantic Coast of France and the Cape of Good Hope - and previously D. dudresnayi had only been reported from the French coast (Lamouroux ex Leman 1819:106). It is worth noting that the syntype locality for Desmarestia ligulata var. firma J. Agardh (1848) was that of the Cape of Good Hope and no mention was made of France. However, the most important point is that the specimen from C. Agardh's herbarium selected by Papenfuss as the lectotype for D. firma(Fig. 3.2) was collected at the Cape of Good Hope by Lalande. This lectotype cannot be ignored and D. firma (C. Agardh) Skottsberg cannot be typified with D. dudresnayi.

## 3.4 RESULTS of EXAMINATIONS of WORLD-WIDE LIGULATE SPECIMENS and TAXONOMIC COMPARISONS

### 3.4.1 Southern Africa

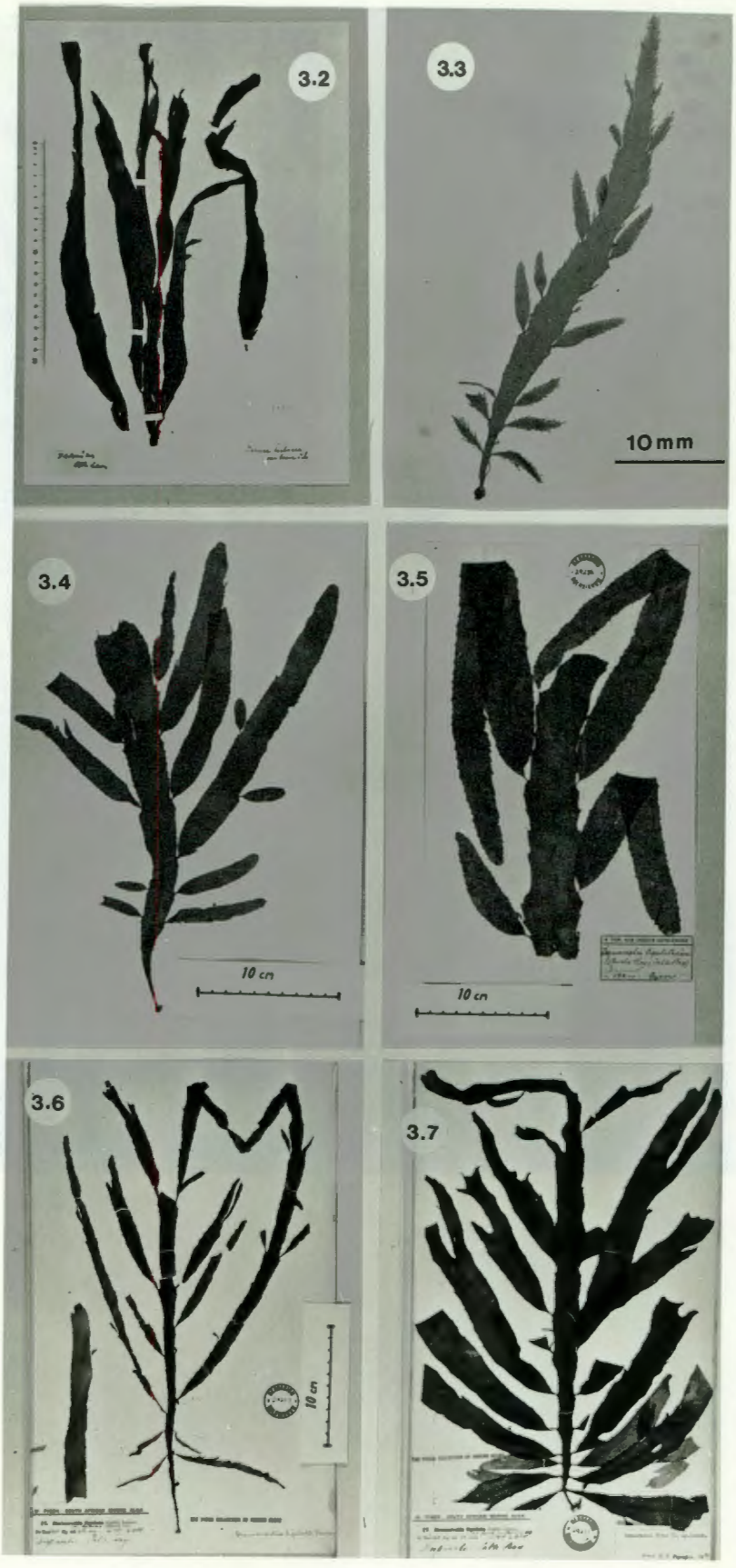
#### Morphology

South African *D. firma* is described as follows:

Fronds: Ligulate. In young plants thin, smooth and light yellowish-brown. Becoming thicker, leathery and dark-brown with age. In mature plants up to 90 cm long or longer, 1.5 to over 10 cm wide. Axial frond or central rachis increasing gradually in width from the base, attaining a maximum width more than 10 cm from its origin. Branches of 2, rarely 3, orders. The largest primary branches often as long as or longer than the axial frond, and often somewhat wider. Primary and secondary branches tapering abruptly to a short stipitate connection basally, distally tapering to a rounded or acuminate point. In mature plants fronds are generally between 10 and 50 mm apart, and the plants can be said to be fairly sparsely branched. Margins of young plants fringed with trichothallic hairs imparting a feathery appearance to smaller fronds or bearing spine-like teeth of variable length in older specimens. Lateral veins arising from midrib approximately at right angles, curving upwards and becoming indistinct towards frond margin. Holdfast: a parenchymatous disc or cone in young plants. In older specimens usually a calloused disc 1 - 3 mm thick and about 10 mm in diameter. Where several plants arise the diameter of the composite holdfast is commonly 20 - 30 mm. Stipe: Terete, 5 - 20 mm long, continuing in axial frond of mature plant as a distinct thick midrib, sometimes becoming indistinct distally. Habitat: Attached to rocks from a few metres below L.W.S. to at least 25 metres depth.

#### Phenotypic Variation of South African D. Firma

South African *D. firma* vary somewhat with respect to length, width (Table 3.1), and thickness of fronds, prominence of venation, and prominence of marginal teeth (see Figs. 3.3 - 3.9).


3.2
3.3
10 mm
3.4
10 cm
3.5
10 cm
3.6
10 cm
3.7

## Captions to Figs.

Fig. 3.2 Lectotype specimen of *D. firma* (C. Agardh's herbarium, No. 49916, LUND). Collected from Cape of Good Hope by Lalande, and bearing the name *D. herbacea* var. *firma* C. Ag.

Fig. 3.3 Juvenile *D. firma*, Oudekraal, Cape Peninsula.

Fig. 3.4 Mature *D. firma*, Oudekraal, Cape Peninsula.

Fig. 3.5 Part of mature *D. firma* plant. Coll. W. Tyson, Three Anchor Bay, Cape Town. (BOL 29283).

Fig. 3.6 Narrow-fronded, mature *D. firma*. Coll. W. Tyson, "Deep water, Table Bay". (BOL 29277). Some of primary fronds appear to have been truncated during mounting of specimen .

Fig. 3.8 Four young *D. firma* plants arising from single holdfast. Coll. W. Tyson, Table Bay. (BOL 29283).

Fig. 3.9 Apparently unbranched *D. firma* which has lost primary fronds as a result of grazing or erosion. Bakoven, Cape Peninsula.

Fig. 3.10 Cross-section of immature (approximately 2 month old *D. firma*.) c - cortical cells; g - parenchymatous ground tissue.

Fig. 3.11 Tip of primary branch of juvenile *D. firma*, showing trichothallic hairs and meristematic zone (m) of central filament.

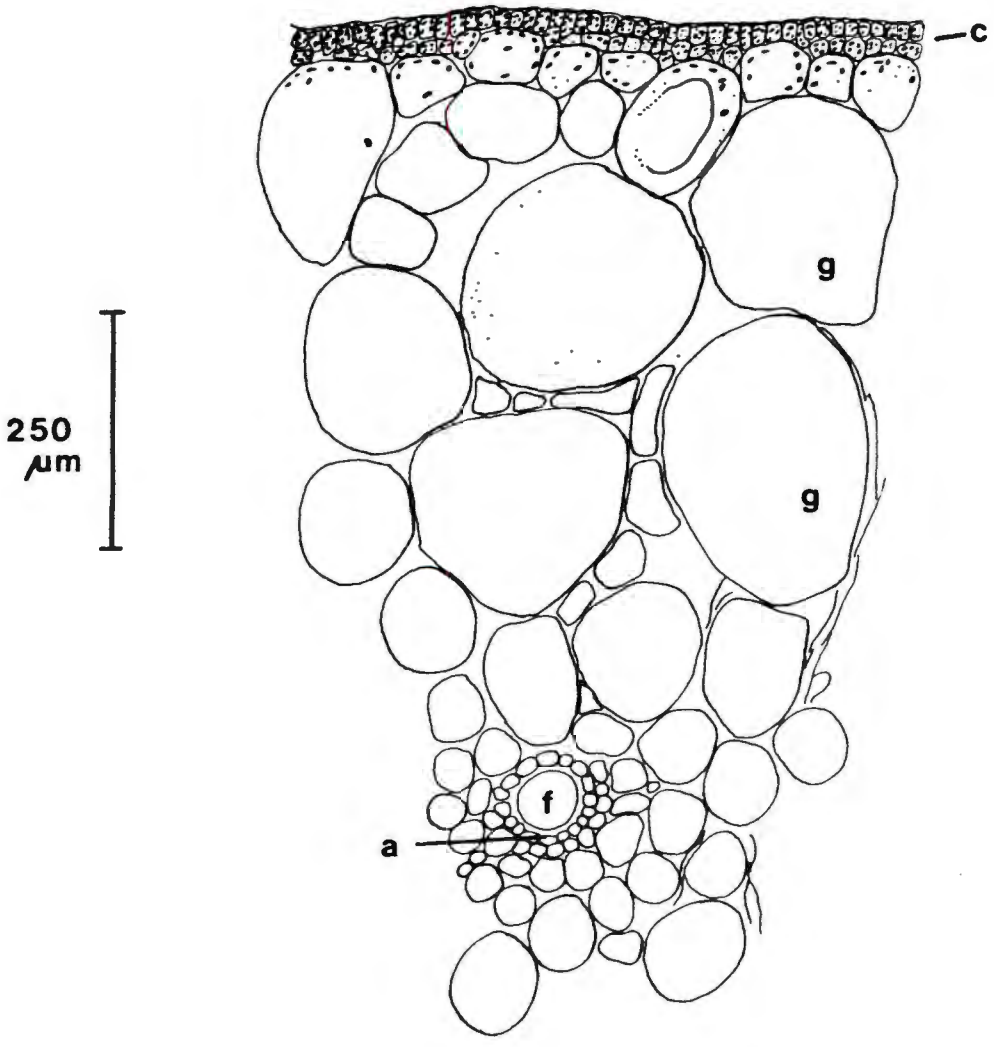



Fig. 3.12 Cross-section of axial frond of mature (approximately 12 months old) D. firma. c - cortical cells (containing chloroplasts); g - parenchymatous ground tissue; f - axial filament; a - assimilatory cells surrounding axial filament.

In March 1979, 195 mature specimens from Oudekraal were examined with respect to profusion of branching. Six percent of the specimens had only axial fronds, and 80% axial and primary fronds, and 14% axial, primary and secondary. None of the plants in this sample bore fronds of the 3rd order. In fact, out of approximately 1500 plants examined during the course of this study, only 3 specimens were found with 3rd order fronds, and there were only 1 - 2 3rd order fronds per plant. Mean, maximum and minimum numbers of primary and secondary branches in the March 1979 sample are shown in Table 3.2 Where several axial fronds arose from a single holdfast, they were regarded as separate plants, so that by definition no plant had more than one axial frond.

| Character | mean | 95% limits | max. | min. |
|---|---|---|---|---|
| Overall length (mm) | 484 | 81 | 1650 | ca 100 |
| Length axial frond (mm) | 296 | 65 | 1000 | ca 30 |
| Max. width axial frond (mm) | 33 | 7 | 90 | 10 |
| Max. l. primary frond (mm) | 306 | 60 | 1026 | ca 5 |
| Max. width prim. frond (mm) | 45 | 8 | 160 | 10 |
| Holdfast diam. (mm) | 6 | 1 | 38 | 2 |
| Stipe length (mm) | 12.4 | 1.3 | 24 | 5 |
| Angle of primary venation | ca 90° | | 100 | 60 |
| Angle of secondary venation | ca 70° | | 90 | 20 |

Table 3.1 Means and ranges for various morphological characters measured from a sample of 150 mature *D. firma* specimens. Maximum and minimum values express limits of ranges in sample.

| | $\bar{x}$ | max. | min. |
|---|---|---|---|
| Primary fronds | 8 | 24 | 1 |
| Secondary fronds | 6 | 32 | 1 |

Table 3.2 Numbers of primary and secondary fronds per plant in March 1979 sample. Means are based only on those plants which showed fronds of that respective order, i.e. not on the total sample of 195 plants.

Of all the plants examined during this study, the maximum number of primary fronds per plant was 31, and the maximum number of secondary fronds per plant was 38.

## Anatomy

The general anatomical features of ligulate Desmarestia species are comprehensively described and discussed by Pease (1920), and her observations were generally confirmed during this examination of the South African plants of different ages.

An axial filament runs through the centre of the frond (Fig. 3.12). This is surrounded by small cells, termed an "assimilation tissue" by Pease. A ground tissue of large parenchyma cells surrounds this, and forms the bulk of the thallus. Among these large cells is a network of ramifying filaments which run in all directions, and apparently serve to strengthen the tissue. A cortical layer, one to three cells deep, covers the ground tissue. The cortical and some of the outermost cells of the ground tissue contain chloroplasts forming a photosynthetic layer 2 - 4 cells deep.

Trichothallic hairs, lining the frond-margins of young plants, show essentially the same structure (Fig. 3.11) as those described for D. ligulata (Pease, 1920). The intercalary

meristematic zone, visible as the shortest (actively dividing) cells of the trichothallic filament, lies at its base, just above the junction of the filament and the thallus.

According to Pease (1920), in D. ligulata division is mostly proximal and rhizoidal cells are cut off from the branches of the filament and grow downwards, investing the filament with a cortical layer. In D. ligulata, this cortical layer divides to give rise to the outer cortical layer of the thallus, and the parenchymatous ground tissue. The latter gives rise to the inner assimilation tissue around the central filament (Pease, 1920). These details were not investigated in the present study, but development of these tissues is probably similar for South African D. firma. According to Harvey (1852), this cortical development extends "chiefly laterally, so as to form first a two-edged and then a flat or even leaf-like stem", in ligulate forms.

In South African D. firma, fronds appeared to thicken with age largely because of an increase in the number and size of the cells forming the parenchymatous ground tissue, while the chloroplast-containing cortical layer appeared to remain 2 - 3 cells thick in old as well as young plants (Figs. 3.12, 3.10): it was thus not clear whether there was continued meristoderm activity in D. firma.

Pease (1920) described two types of secondary growth in ligulate Desmarestia species. Filamentous "assimilatory cells" arising from the ground tissue grow down towards the base of the plant, by repeated cross-division near their tips. In the other type of secondary growth, intercalary filaments, made up of long repeatedly branched cylindrical cells, form a tangled network among the ground cells from which they arise (Pease 1920). These apparently bind the ground cells together, strengthening the lamina. These filaments were seldom clearly visible in cross-section, since sectioning obscures their ramified appearance.

Thus, there do not appear to be any clear differences in vegetative anatomy, between D. firma and North-American branched ligulate Desmarestia.

Details of the reproductive anatomy of D. firma are described in Chapter 2 (Life-History).

### 3.4.2 Europe and the British Isles

Ligulate Desmarestia material from France and the British Isles which I have examined, clearly represents two easily recognisable species; the profusely branched Desmarestia ligulata (Stackh.) Lamouroux, Ann. Mus. Hist. Nat. (Paris) 20:45, pl 8, Fig 1, (1813), and the predominantly unbranched Desmarestia dudresnayi Lamouroux ex Leman. Dict. Sc. Nat. 13:105 (1819), Planches: Botanique: Végétaux acotyldons : pl. (43), (1816 - 1819).

The majority of the approximately 90 French and U.K. branched ligulate specimens examined, including large collections in L, PCU, and BM, have 3 or 4 orders of fronds, excluding the axial frond. The axial, primary and secondary fronds may be between 1 and 10 mm wide, but are commonly between 3 and 6 mm wide. The 3rd order, and where present, 4th order, fronds are always somewhat narrower and considerably shorter than the first two orders of branches. Almost all of these specimens are very profusely branched with hundreds of fronds on each plant. The stipe continues in the axial frond as a thickened midrib, which becomes obsolete distally. Details of venation are often obscure, as might be expected in such narrow fronds. Where visible, the angles of both primary and secondary venation are between 45 and 90 .

Most of these plants clearly fit the type description and illustration of Lightfoot (1777), (F. ligulatus nom. illeg.) Those which differ do so only in terms of frond width (a minimum of 1 mm and maximum of 10 mm in all the specimens examined), but fit the type description and illustration in all other respects. I thus have no


3.13
10 cm


3.14
5 cm


3.15


3.16
10 cm


3.17
5 cm


3.18
30 mm
TANGER

## Captions to Figures

Fig. 3.13 *D. ligulata* from The Lizard, Cornwall, England. Coll. H. Becker, 1864 (BOL 29284). Typical specimen - note narrow, profusely-branched fronds.

Fig. 3.14 Typical European specimen of *D. ligulata*. From Cherbourg, France. Herb. A. le Jolis 144, now in TCD.

Fig. 3.15 Specimen of *D. dudresnayi* collected by Dudresnay and now in Lamouroux's collection at CN. I have designated this a lectotype specimen.

Fig. 3.16 Typical example of *D. dudresnayi*, showing unbranched and sparsely branched forms. From Roscoff, Britanny, Now in L.

Fig 3.17 *Desmarestia* specimen collected by Schousboe, in Tangiers, Morocco. Note forked axial frond. In Bornet's collection, PCU.

Fig. 3.18 *Desmarestia* specimen collected by Schousboe, in Tangiers, Morocco. Note truncated, broad fronds, and sparse branching (PCU).

hesitation in considering all of the branched ligulate specimens from France andthe U.K. to belong to D. ligulata . Harvey (1846) recorded some variation in frond width between populations of D. ligulata from various parts of the British coast.

Anatomically, European D. ligulata specimens examined were essentially similar to South African specimens. Cross-sections of the fronds of mature plants showed the same types of tissue as in D. firma (Fig. 3.12), except that there were fewer cells in each layer, and the parenchyma cells of the ground tissue were somewhat smaller, as might have been expected, since the fronds were thinner than those of mature South African plants.

Sporangia were not found in specimens examined during this study, but Johnson (1891) described sporangia in D. ligulata from Plymouth, England. In arrangement and shape, these appear to be strikingly similar to those in the Cape entity (this study), since they are apparently developed from scattered superficial cortical cells, but remain similar to those cells in size and shape. Johnson (1891) describes each sporangium as containing one spore only, or occasionally two to four, but this observation is challenged by Moe and Silva (1977). The former author may have observed these sporangia at a stage when nuclear division was incomplete.

The type description of D. ligulata (Stackh. ) Lamx., (Fucus ligulatus Lightfoot 1777, nom. illeg.) cannot be considered to fit South African D. firma. Lightfoot's (1777) illustration shows a plant with over 70 primary and over 250 secondary fronds, none broader than 6 mm, and numerous small 3rd order fronds. This is quite unlike D. firma, which is sparsely branched and when mature never has fronds narrower than about 10 mm.

All of the French and U.K. specimens of D. ligulata which I examined, are significantly narrower and more profusely branched than D. firma. Many show four orders of branches (quadripinnate, while in D. firma, 3rd-order fronds are extremely rare,

and 4th-order fronds were never found). These populations are thus considered to be morphologically quite distinct. Compare, for example, the illustrations of typical D. ligulata (Figs. 3.13, 3.14) with those of D. firma (Figs. 3.4 - 3.9).

Seven specimens of branched, ligulate Desmarestia from Spain and Portugal were examined (PCU, BM). All of these specimens bear the name D. ligulata. However, most are somewhat broader than indicated in the type description of this species, with fronds from 10 - 18 mm in width. Since they are profusely branched, with up to 3 and possibly 4 orders of fronds (tri- or quadri-pinnate), and morphologically resemble French and U.K. D. ligulata in all other respects, it seems likely that they represent a southern European form of this species. Matters are further complicated in that several of these specimens closely resemble certain New Zealand and North-West American entities, and fit the type description of Fucus herbaceus Turner 1809) (= D. herbacea Lamx.). These observations provide possible support for the Chapman's (1972) combination of European D. ligulata with D. herbacea and five other North-West American species, at least on morphological grounds.

While D. ligulata appears to be quite different from D. firma in terms of gross morphology, there do not appear to be any clear anatomical differences between these 2 entities, but more details of the reproductive anatomy, and a knowledge of the life-cycle of D. ligulata are necessary before clear taxonomic decisions can be reached.

Material of Desmarestia dudresnayi Lamour. ex Leman from France, England and Scotland (Oban), was examined, since this species was at one stage included with material from the Cape of Good Hope, under the combination Sporochnus herbaceus var. firma C. Agardh (1824).

This species is easily recognised, since it is unbranched or sparsely branched (with up to about 6 primary fronds) and

rather fragile, with a long, slender stipe (Figs. 3.15, 3.16). Two of the branched specimens in PCU had broad stipitate connections between the axial and primary fronds, quite unlike the narrow, petiolate connections in other species, including D. firma. None of the specimens examined had more than one order of branches. From the type description, the lectotype specimen (Fig. 3.15), and on the basis of examination of over 30 specimens of this species (PCU, BM, L, TCD, BOL), all of which conform to the type description, it is apparent that D. dudresnayi is distinctly different from D. firma.

The few unbranched specimens found among the South African Desmarestia population invariably appear to have lost their fronds as a result of damage (Fig. 3.9), and are tough and leathery, with a substantial, often short, stipe, and even young plants are considerably less fragile than the specimens of D. dudresnayi, the margins of which appear to be sinuate rather than dentate.

Chapman (1972) included D. dudresnayi, along with the North-West American D. foliacea Pease (and several other predominantly unbranched species) in his variety D. ligulata var. firma. Chapman's morphologically based work does not take into account ontogenetic patterns or sporangial development and arrangement. Details of the latter are not known at present, but Moe and Silva (1981) provide evidence that the patterns of growth are fundamentally different in branched and unbranched members of the genus Desmarestia. Although Moe & Silva (1981) did not deal with any of the species included in Chapman's D. ligulata var. firma, Silva (pers comm.) has pointed out that the predominantly unbranched entities included in this variety appear to have "an intermittently active (growth) pattern, with a large main blade and irregular production of secondary blades", which is fundamentally different to the open pattern found in the branched species such as D. ligulata and D. firma.

D. dudresnayi is recorded from the following localities: From Bretagne in France to San Sebastion, Spain, rare (Dizerbo, 1965); various localities in British Isles, rare (Blackler, 1961); Straits of Messina, Mediterranean (Drew and Robertson, 1974).

### 3.4.3 Tangiers, Morocco

There is a collection of branched, ligulate Desmarestia specimens from Tangiers, in the collection of E. Bornet (PCU) These plants were collected between 1815 and 1829 by the Danish Consul in Morocco, P.K.A Schousboe, and sent to Bornet in Paris. There are also several of these specimens in BM.

These plants (e.g. Figs. 3.17, 3.18) are relatively short (up to 35 cm total length) and broad with axial and primary fronds between 8 and 40 mm wide. Branching is fairly sparse, with two or occassionally 3 orders of fronds arising from the axial frond (bi- or tri-pinnate). In many plants the axial and primary fronds are truncated, and such fronds often appear to have become broad, so that they are wedge-shaped. This condition is never encountered in European D. ligulata, but is common in South African D. firma, which these Tangiers specimens resemble closely. The only morphological differences between D. firma and these Tangiers plants are that the latter often have branches of the third order (extremely rare in D. firma), and often have stipes or axial fronds which are forked, sometimes into three divisions, a condition rarely encountered in specimens from other areas. However, J.H. Price (pers. comm.) has observed forked stipes in certain local populations of British D. ligulata, and considers this phenomenon to be characteristic of specific areas, and taxonomically unimportant.

It should be borne in mind that much of Schousboe's material may have been collected in drift: certainly none of the Desmarestia specimens are annotated to the effect that they were attached to the substrate. In this case, they may well have originated from other coasts, particularly Spain, which lies only 50 km north of Tangiers.

There appears to be a gradient in the frond widths of branched, ligulate Desmarestia populations down a North-South axis along the Atlantic coast of Europe, with very narrow forms in France

and the British Isles (which clearly fit the type description of D. ligulata), somewhat broader forms in Spain and Portugal, and even broader specimens from Tangiers.

Sporangia were not found in the fragment of Tangiers specimen examined. Details of the vegetative anatomy were difficult to discern , since the material failed to re-hydrate completely. From the observations which were possible, these plants appear to be anatomically similar to D. firma, with a cortex 1 - 2 cells deep, underlain by large parenchyma cells.

Many of these Moroccan plants closely resemble D. firma, while others are morphologically indistinguishable from certain North-West American forms, particularly the entity previously described as D. herbacea. Certainly, they are morphologically more similar to these two entitues than to D. ligulata. The fact that these Moroccan plants might be expected to be closely related to, if not conspecific with, D. ligulata emphasises the problems in using morphological characters to define taxonomic relationships in this group.

Some of the Tangiers specimens bear the name Desmarestia tingitana, and have been re-labelled D. herbacea, presumably by Bornet. No reference could be found to the former name.

### 3.4.4 North-West America

Branched ligulate species described from North-West America, and which are apparently similar to South African D. firma, are Desmarestia herbacea Lamouroux Ann. Mus. Hist. Nat. (Paris), 20:45 (1813), D. latissima Setchell and Gardner ex Pease Pub. Puget Sound Biol. Sta., 2,53, p. 319, pl. 56, (1920), and D. munda Setchell and Gardner, Univ. Calif. Publ. Bot., 13:7, (1924). (Nomenclature and type descriptions in Appendix A). I have examined over 100 specimens from the Pacific coasts of the U.S.A., Canada and Alaska. Morphologically, these plants range from profusely-branched forms with 4 orders of 1 - 2 mm with fronds (e.g. the plant shown in Fig. 3.19, which closely resembles European D. ligulata) to extremely large sparsely branched forms with fronds over 20 cm wide (e.g. type specimen of D. latissima shown in Fig. 3.24). Most of the specimens have fronds of intermediate widths (e.g. Figs. 3.21 - 3.23).


3.19
10 cm

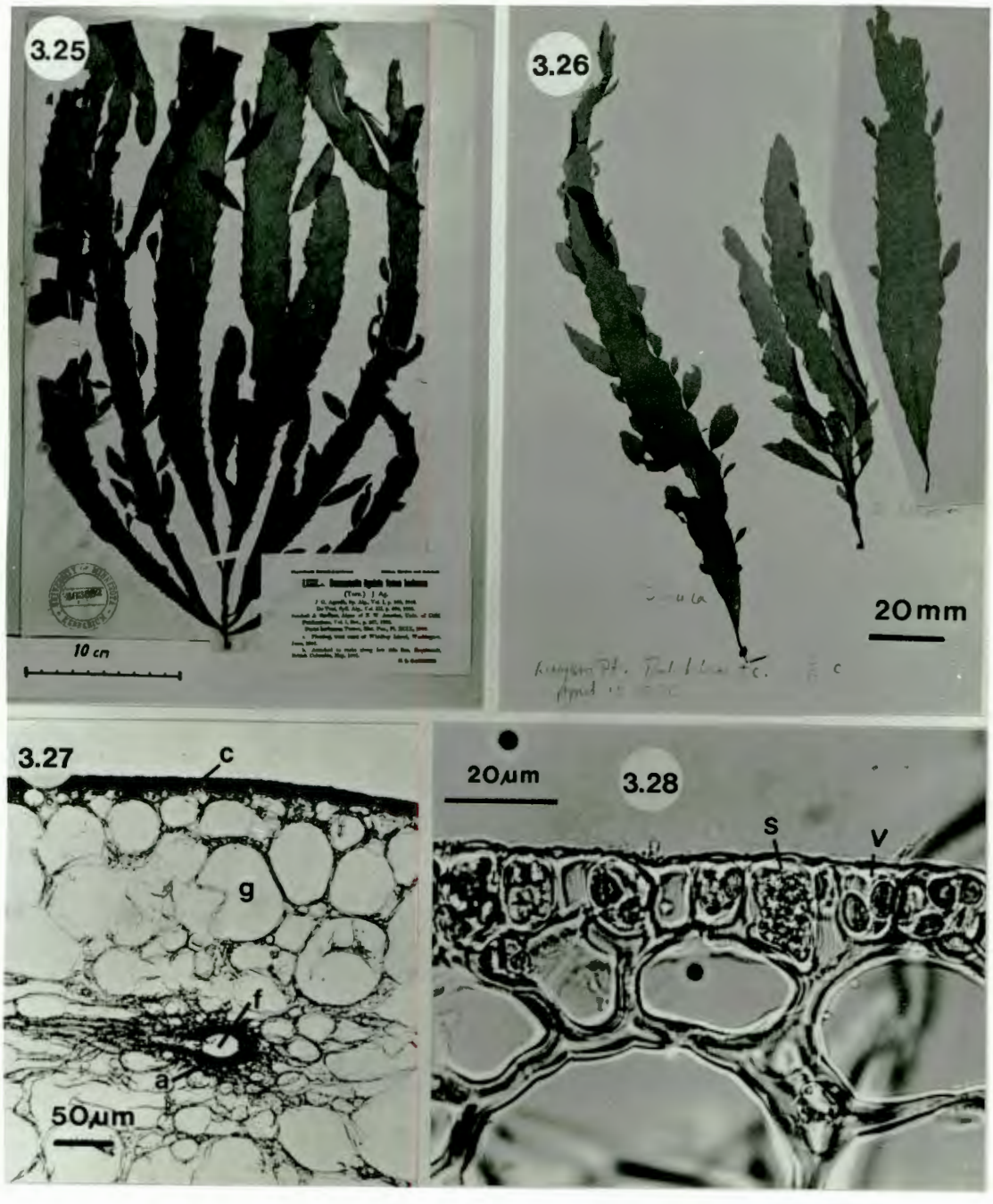

3.20
5 cm


10 cm
3.21


3.22
10 cm


10 cm
3.23


10 cm
3.24


3.25
10 cm
3.26
20mm
3.27
c
g
f
a
50µm
20µm
3.28
S
V

## Captions to Figs.

Fig. 3.19 Profusely-branched, narrow-fronded N.W. American form. Coll. V.A. Pease and labelled *D. ligulata*. San Juan Islands, Washington (MIN 589265).

Fig. 3.20 Lectotype specimen of *D. herbacea* Lamx. Coll. by A. Menzies, "North West America" (BM). This is the plant illustrated in Type Description of *Fucus herbaceus* Turner, *Hist. Fuc.*, 278, pl. 99, 1809.

Fig. 3.21 Broad-bladed specimen from Vancouver Island, B.C. Bears the name *D. munda*. This plant is morphologically identical to many South African plants.

Fig. 3.22 Specimen from Khantaak Island, Alaska (UBC 21073). Variously labelled *D. herbacea*, *D. munda* and *D. ligulata* var. *ligulata*. This plant is morphologically identical to many South African specimens.

Fig. 3.23 Type specimen of *D. latissima* (Setch. & Gard. ex Pease, 1970. (MIN 589279).

Fig. 3.24 Type specimen of *D. latissima* Setch. & Gard. ex Pease, 1920 (MIN 589282). Coll. V.A. Pease, San Juan Islands, Wash. Single extremely broad frond with one branch attached.

Fig. 3.25 Isotype specimen of *D. munda* Setch. & Gard. 1924. (Phycotheca Boreali Americana specimen LXXIX a) Coll. from Whidby Island, Wash.

Fig. 3.26 Juvenile specimens of ligulate N.W. American *Desmarestia*, from Balaklava Island, B.C. These juveniles are indistinguishable from those of South African *D. firma*.

Fig 3.27 Cross-section of frond of specimen from Vancouver Island, B.C., showing cortical layer (c), parenchymatous ground tissue (g), axial filament in centre of frond (f), and assimilatory cells (a).

Fig. 3.28 Cross-section of cortex of specimen from Vancouver Island, B.C., showing sporangium (S) and vegetative cortical cells (v) containing chloroplasts.

Profusion of branching is variable; the plants with narrow or medium width fronds have between 2 and 4 orders of branches, with varying numbers of fronds in each order. Only the extremely broad-bladed plants, e.g. D. latissima, differ in this respect, since they have one or rarely two branch orders, and branching is uniformly sparse.

Details of venation, holdfast shape and size, stipe length and diameter, and prominence of marginal spines were very similar within the range of plants examined. Where differences in these characters can be found, they are clearly related to the size of the plant. For example, large, broad-fronded plants have thicker stipes and larger holdfasts. These characters are thus of no more use than that of plant size, in discriminating between possible entities.

The vegetative anatomy of North-West American entities has been comprehensively described by Pease (1920). Specimens which I examined conformed to her descriptions, and were essentially similar to D. firma (shown in Figs. 3.10, 3.12).

In the present study, in a formalin-preserved specimen from Vancouver Island, B.C., sporangia were found in the superficial cortical layer of the frond (Fig. 3.28). Most of these cells were the same size and shape as the surrounding cortical cells, i.e. 7 - 9 um wide and 15 - 18 um long, but a few were slightly larger, up to 22 um long. These cells lacked chloroplasts and contained apparently dense granular cytoplasm, and in all respects resembled immature sporangia of the South African entity. Smith (1938 , Fig. 142 c) illustrated a sporangium in D. herbacea from California, which was flask-shaped and it may be that this author's illustration does not show a typical sporangium. Moe and Silva (1977 ) pointed out that if nuclear divisions were complete in the sporangium illustrated by Smith (1938), there would appear to be a total of 16 spores, since Smith illustrates 13 nuclei. It is important to note that the Vancouver Island plant fits the description of D. herbacea and is thus the same species as the plant which Smith (1938) illustrates.

Discrimination between North-West American branched ligulate species has in the past been based almost entirely on thallus size, and particularly on frond width. For example, Pease (1920), in her description of D. latissima, records that "the structure of the mature thallus does not differ from that of D. herbacea except in degree." In some cases (e.g. D. munda Setchell & Gardner, 1924) the species protologues give no indication of how the particular species differ from those to which they are closely related: this is no doubt because the differences are unclear in these morphologically variable populations. There has thus been considerable confusion in the taxonomy of branched, ligulate Desmarestia in North-West America (Scagel, 1957).

In an attempt to resolve this confusion, Chapman (1972) performed detailed biometric analyses of 26 populations of ligulate Desmarestia plants. Twenty-five of these populations were found between Calvert Island, British Columbia, and La Jolla, California, and one off the Isle of Man, U.K. From an examination of the morphological characters used to delimit taxa in the past, he reduced some 11 taxa to 3. His combination D. ligulata var. ligulata (Stackhouse) Lamouroux includes the above North-West American species, European D. ligulata, and several other species not dealt with here. While a detailed discussion of his work is inappropriate here, it is important in that it indicates that many of the previously used characters may be doubtful (e.g. size of thallus) or even untenable (e.g. holdfast shape, which is shown to be extremely variable, and thallus fragility, which appears to be largely environmentally induced.) Abbott and Hollenberg (1976) follow Chapman (1972) in referring branched ligulate entities found in North-West America to D.ligulata var. ligulata, but they extend the distribution of this variety to include similar forms from South America. Chapman's combination D. ligulata var. firma (C. Ag.) J. Agardh (1848), p. 169, which comprises predominantly unbranched entities, includes as synonym Sporochnus herbaceus var. firma C.Agardh (1824), p. 261. This combination is also followed by

Abbott and Hollenberg, (1976). To avoid confusion (since the South African entity was included in Agardh's (1824) variety) it must be pointed out that the South African entity is specifically excluded from Sporochnus herbaceus var. firma sensu Chapman (1972), since he based his name on the predominantly unbranched specimens from Atlantic France (see Section 3.3).

Many of the N.W. American plants which are intermediate in size (e.g. those shown in Figs. 3.21 - 3.23), are morphologically identical to South African D. firma, in terms of all the characters used in this study. Specimens which could not be distinguished from D. firma are listed in Table 3.3. Most of the South African plants fit the type description of D. munda, and are readily identified as this species using the key of Setchell & Gardner (1925). The only difference between these two entities appears to be that D. munda often has branches of the third order, whereas these are extremely rare in D. firma.

South African D. firma fits the type description of Fucus herbaceus Turner ( = D. herbacea Lamx. nom. nov.) well, with the exception that Turner describes fronds up to 1 inch (2.5 cm) wide, whereas, in D. firma, although the fronds may be as narrow as 1 cm, they are generally 3.5 cm wide, and may be as wide as 10 cm (Table 3.1). I have examined the lectotype specimen of F. herbaceus in BM (Fig. 3.15) and find it to be somewhat more profusely branched than D. firma, with approximately 23 primary and 45 secondary fronds (there were no third-order fronds). None of the D. firma plants examined during this study showed more than 38 secondary fronds. In all other respects, this specimen falls within the morphological range of D. firma. It is noteworthy that Papenfuss (1943) considered the South African entity to be closely related to D. herbacea, but regarded them as separate species on account of their geographical separation.

The type description of D. latissima does not correspond with any of the material of D. firma examined in this study, since

| Herbarium | Specimen No. | Additional Specimen No. | Collection Locality | Name (Prior to Chapman 1972) |
|---|---|---|---|---|
| Univ. of B.C. (UBC) | A 40707 | 25569 | Vancouver Island, B.C. | D. munda |
| | A 40713 | 25634 | Vancouver Island, B.C. | D. munda |
| | A 21073 | 10156 | Khantaak Island, Alaska | D. munda |
| | A 40910 | 25914 | Vancouver Island, B.C. | D. munda |
| | A 40170 | 24987 | Vancouver Island, B.C. | D. munda |
| | A 287 | | Monterey, California | D. munda |
| | Several - ARO Chapman | Unnumbered, 1970 | Cape Scott<br>Calvert Island | D. munda and<br>D. foliacea |
| Univ. of Minnesota. (MIN) | 589279 | | San Juan Island | D. latissima TYPE |
| | 589269 | | San Juan Island | D. latissima TYPE |
| | 363592 | | Washington | D. ligulata f. herbacea |
| Univ. of Wash. (WTU) | 244541 | Norriss 4638 | San Juan Island | D. munda |
| | 244540 | Harlin 762 | Thurston Co., Wash. | D. munda |
| | 637740 | Martin 349 | Friday Harbour, San Juan Island. | D. herbacea |

TABLE 3.3 List of N.W. American specimens which are apparently identical to plants of the South African population of Desmarestia.

the former species is indicated as "up to 8 m long, ...with few widely separated branches, only rarely of the second order." However, I have examined isotype specimens of D. latissima, and some of these, for example MIN 589279 (Fig. 3.23) are morphologically indistinguishable from certian large, sparsely-branched, sheltered-water specimens of D. firma. Thus there us clearly some morphological overlap between these two entities, but D. latissima is considered to be distinctly larger and more sparsely branched than D. firma.

These results show that in terms of anatomy and gross morphology, there are strong similarities between D. firma and certain N.W. American plants. If we consider the taxa which stood prior to the combination of Chapman (1972), D. munda, and possibly D. herbacea, might be considered to be conspecific with D. firma. However, the morphological range of Chapman's D. ligulata var. ligulata is far greater than that shown by D. firma. Furthermore, there are few reports of sporangia, and nothing is known of the life-cycles of the species included in Chapman's combination. The taxonomic implications of this are discussed in the final section of this Chapter.

### 3.4.5 South America

I have examined 24 apecimens of branched ligulate Desmarestia from localities from Valparaiso, Chile, around Cape Horn to the east coast of Argentina (DUKE, TCD, BM L, PCU, SGO). These plants vary in morphology from narrow-fronded, extremely profusely branched forms (e.g. Fig. 3.29), to sparsely branched forms with fronds 40 - 50 mm wide (Fig. 3.30). Most, however, have 2 - 3 orders of relatively narrow fronds (2 - 10 mm), for example Fig. 3.31. Several of the specimens examined show strong morphological similarities to South African D. firma. For example, a single frond (Fig. 3.30)collected from Puerto Aldea, Coquimbo, Chile (SGO 95693) is indistinguishable from fronds of many of the S.A. plants. Similarly, SGO 95711

collected from Bahaia de Arauco, Chile, falls within the morphological range of the South African species. It is therefore of great interest that M. Eliana Ramirez (pers. comm.) points out that many Chilean Desmarestia specimens (including SGO 95693, above) appear to be indistinguishable from the North-West American entity described as D. munda Setch. & Gard. (1924) which in turn, I consider to be morphologically very similar to D. firma.

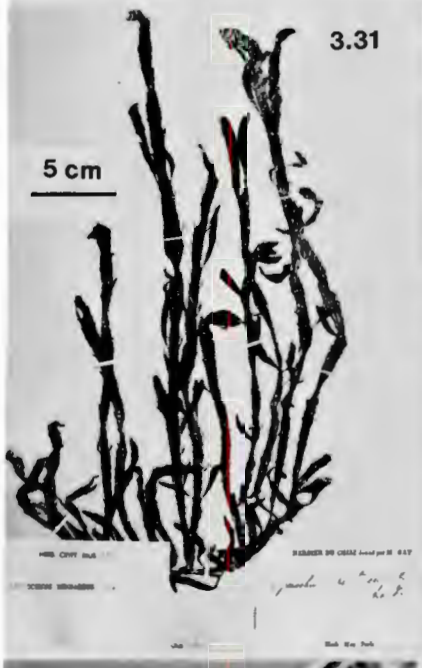
Some of the Desmarestia specimens (e.g. Fig. 3.32) collected from south Argentina and Chile during cruises of the research vessel "Hero" in 1972 and 1973 (now in the Duke University Algal Herbarium, DUKE) show a strong resemblance to South African specimens, but in general their fronds are narrower, and they are rather more sparsely branched. The axial fronds of these specimens, e.g. DUKE 16497 (Fig. 3.32) are invariably narrow (5 - 8 mm), and in many of the primary and secondary fronds the stipitate basal portion is longer than is common in South African plants. Details of venation are difficult to determine, since these specimens appear to have been preserved in formalin, but where visible venation is essentially the same as in the South African entity.

In terms of gross morphology, there are therefore strong similarities between the South African Desmarestia population and certain forms of the ligulate Desmarestia populations occuring in southern South America. It is therefore of note that Hooker (1847) and Skottsberg (1921) referred specimens from Fuegia, North-West America and South Africa to D. herbacea, and many of the older herbarium specimens of South African plants bear this name.

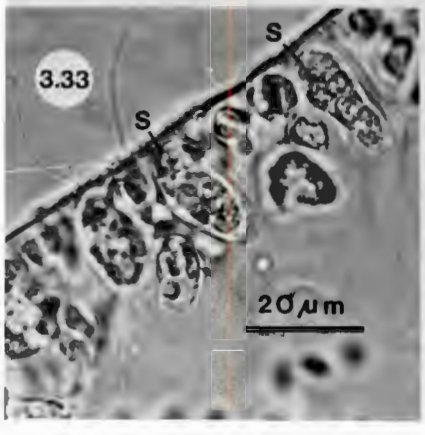
The cross-sectional anatomy of Chilean and Argentinian specimens is essentially the same as in South African D. firma with large (up to 200 µm diameter) parenchymatous cells making up the central ground tissue, interspersed with a network of filamentous strengthening cells. The cortex consists of 1 to 2 layers of chloroplast-containing cells which in cross-section vary in shape from round to rectangular. These cells are generally 10 to 16 µm long and 6 to 12 µm wide.

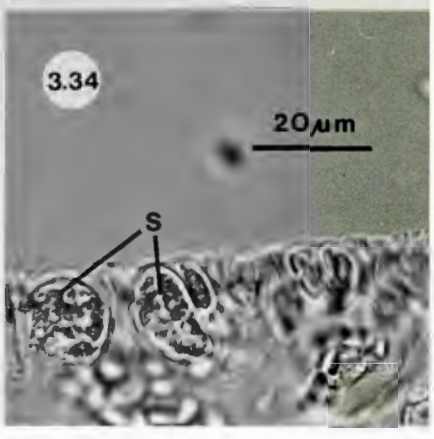

10 cm
3.29


10 cm
3.30


3.31
5 cm


3.32
10 cm


3.33
S
S
20 µm


3.34
20 µm
S

## Captions to Figs.

Fig. 3.29 Profusely branched, narrow-bladed specimen from Chiloe Island, Chile. This plant is morphologically identical to many specimens of European *D. liqulata*.

Fig. 3.30 Portion of broad-bladed specimen from Coquimbo, Chile (SGO 95693). This specimen is morphologically similar to South African *D. firma*.

Fig. 3.31 Specimen from Chile. Coll. by Gay. (PCU).

Fig. 3.32 Sparsely-branched form from Puerto Vancouver, Staten Island, Argentina. (DUKE 16497). This specimen is morphologically identical to many from Gough Island.

Fig. 3.33 Cross-section of cortex of specimen from Puerto Alert, Chile, showing sporangia (s).

Fig. 3.34 Cross-section of cortex of specimen from Staten Island, Argentina, showing sporangia (s).

Sporangia were found in specimens from Puerto Alert, Canal Trinidad, Chile, (DUKE 73-42-28) and from Puerto Vancouver, Staten Island, Argentina (DUKE 73-18-18). Both of these plants are morphologically identical to the Staten Island specimen shown in Fig. 3.32. There were no discernible differences in anatomy between these two specimens, and thus the following description applies to both (Figs. 3.33 and 3.34).

The sporangia are scattered among the superficial cortical cells, and are 10 to 20 µm long and 7 to 12 µm wide (mean dimensions of 20 sporangia were 18 x 9 µm). The sporangia vary somewhat in shape. Some are slightly longer than the vegetative cortical cells, and obclavate in shape (i.e. with the proximal end narrowing and slightly drawn out). Others are rectangular or almost round. There are 8 to 14 spores visible in one plane , indicating a total of 16, if nuclear division was complete at the time of observation.

It would thus appear that in terms of the shape and disposition of sporangia, these plants belong to Group I of Moe and Silva (1977), i.e. with "sporangia occurring singly or in small groups, *seemingly* randomly distributed, resulting from transformation of superficial cortical cells."

While these South American plants show some anatomical similarities to D. firma, their sporangia are often flask-shaped, and somewhat larger than in the South African entity. There may be some variability in the size and shape of sporangia in populations from different localities around the tip of South America, and it is unfortunate that sporangia could not be found in the Chilean specimens (e.g. SGO 95693) which were morphologically most similar to D. firma.

Records of branched , ligulate Desmarestia species from southern South America include D. ligulata (Gain, 1912; Hooker, 1846; Skottsberg, 1921; Reinsch, 1890) and D. herbacea (Montagne, 1845; Levring, 1960 in Kim, 1971). Specimens collected during the Duke University R.V. Hero expeditions to South America (e.g. Fig. 3.32) have been identified as D. ligulata var ligulata, evidently following Chapman(1972).

### 3.4.6 Gough Island

During a diving expedition to Gough Island (40° 21'S 9° 54'W) in September 1981, I collected material of a ligulate Desmarestia which comprises a new record from this island. Some 60 plants, from 4 populations, were examined, and typical specimens are illustrated in Figs. 3.35, 3.36. A general description of these plants is given as follows: Holdfast a rough disc or shallow cone; stipe terete, merging gradually into the axial frond where it is visible basally as a thickened midrib, becoming obsolete distally; up to 3 orders of branches in mature plant; axial frond increasing gradually in width, up to a maximum of about 15 mm (mean of 30 plants = 9 mm), truncated in many of the mature plants, otherwise up to 60 cm or more long, maximum of 15 mm wide, arising from short stipitate connection with axial frond, widening rapidly, then tapering very gradually to a point unless truncated; secondary and tertiary branches similar in shape, but smaller, up to about 7 and 3 mm wide, respectively; overall length of mature plants between about 20 and 120 cm (mean of 30 = 35 cm).

At the time of collection, about 50% of the plants had trichothallic hairs on the margins of terminal branches, indicating that they were not mature. In plants with truncated axial fronds, some of the primary fronds were often greatly lengthened.

The cross-sectional anatomy of these plants is illustrated in Fig. 3.39. Many of the mature plants bore sporangia (Figs. 3.37, 3.38) These were similar in size and shape to the surrounding outer cortical cells, i.e. approximately 12 - 17 µm long and 9 - 15 µm wide. Between 8 and 10 spores were visible in one plane, indicating a possible total of 16 per sporangium.

On Gough this species was found at four localities: Transvaal Cove, West of South Point, South of West Point, and in Baltic Bay. Plants were distributed from 3 m down to at least 12 m

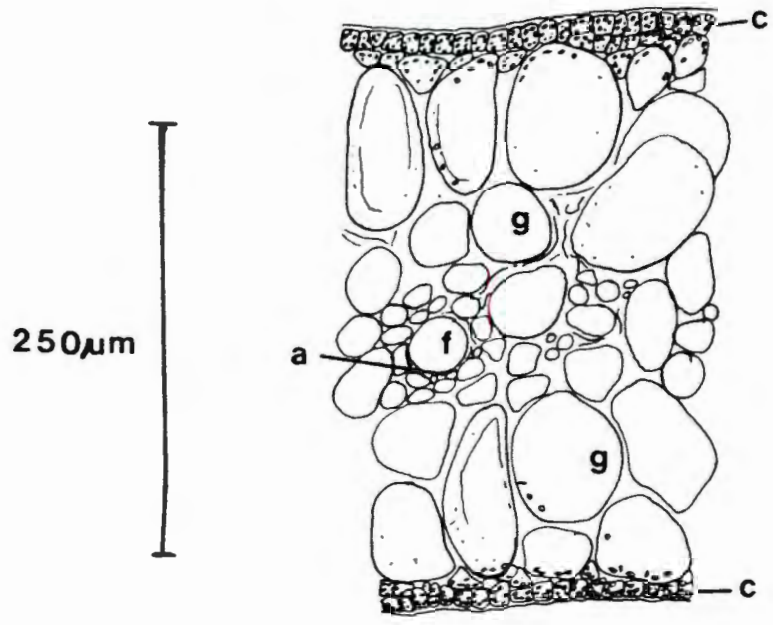



Fig. 3.39 Cross-section of frond of Desmarestia from Gough Island. c - superficial cortex; g - parenchymatous ground tissue; f - central axial filament; a - assimilatory cells.

depth, and grew on the tops of boulders, among young sporophytes of Macrocystis pyrifera and Laminaria sp. Many of the fronds of mature plants had 1 - 2 cm long folds, where the lamina had apparently been glued into a nesting tube by Amphipods, although the animals were not found. Similar observations have been made for South African Desmarestia plants (Appendix C). Morphologically, the plants from Gough Island, for example those shown in Figs. 3.33 and 3.34, appear to be distinct from the South African population, since their fronds are almost always narrower, and there are often 3 orders of branches. There may be some overlap between mature specimens of these 2 populations, with respect to frond width, since South African plants with uniformly narrow fronds (e.g. Fig. 3.6) are occassionally found, but this is only overlap at the extremes of the ranges of frond width, and none

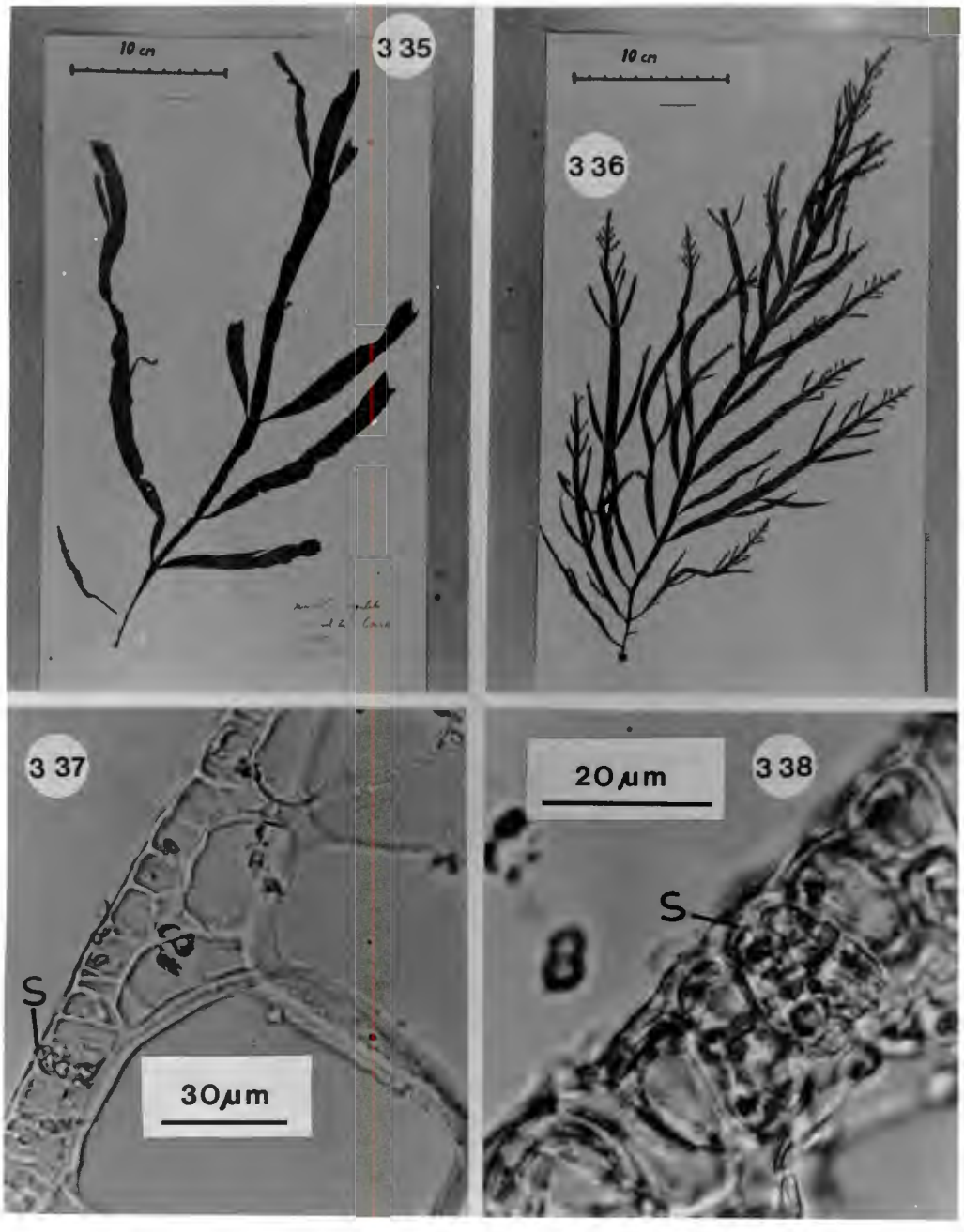
of the Gough specimens had fronds wider than about 15mm. Many mature Gough specimens were extremely profusely branched with more than 30 primary, 100 secondary and 50 tertiary fronds (one plant had over 250 tertiary branches). By contrast, the South African plants are relatively sparsely branched (see Table 3.2) and a maximum of 36 secondary fronds and 2 tertiary fronds were recorded in this study.

The holdfasts of mature S.A. plants are generally larger than those of mature Gough specimens, since the former plants are altogether more bulky, but there are no differences in shape and appearance. Patterns of venation are eseentially the same, except that secondary veins are seldom clearly visible in Gough specimens, as might be expected for narrower, slightly thinner fronds.

Anatomically, these two entities are similar (compare Figs. 3.10, 3.12, with Fig. 3.39), the relative thinness of Gough specimens being due to fewer and smaller cells of the parenchymatous ground tissue. Significantly, the shape and disposition of sporangia in these two entities is strikingly similar, and with respect to these characters, both the Gough and South African plants belong to GroupI of Moe and Silva (1977) i.e. with "sporangia occuring singly or in small groups, seemingly randomly distributed, resulting from transformation of superficial cortical cells".

The Gough Island population of branched, ligulate Desmarestia cannot be separated from South African D. firma in details of anatomy, but on morphological grounds the two populations appear separate. There is little or no overlap on the basis of frond width and many of the Gough Island plants are extremely profusely branched.

The Gough specimens fit the type description of D. ligulata (Fucus ligulatus Lightfoot, 1777, nom. illeg.). They also appear to be closely related to narrow-bladed forms from South America and New Zealand.


10 cm
3 35
10 cm
3 36
3 37
S
30µm
20µm
3 38
S

## Captions to Figs.

Fig. 3.35 Mature, sparsely-branched *Desmarestia* from Gough Island.

Fig. 3.36 Young Gough Island plant, with trichothallic hairs on terminal branches.

Fig. 3.37 Cross-section of superficial cortex of Gough specimen, showing arrangement of cortical cells and a sporangium (s).

Fig. 3.38 A sporangium (s) in the cortical layer of a Gough specimen. Outlines of some of the individual spores are visible.

### 3.4.7 The Falkland Islands and Crozet

I have seen two specimens of ligulate Desmarestia from the Falklands, both in BM. The first was collected by W.L. Schmitt (No. 120) during one of the two trips which he made to South America in 1925 - 27. The second bears the label "F.J.Hennis, West-Point Island, fragment of large specimen." Both plants have narrow fronds (1 - 3 mm), with 3 orders of branches of irregular length, arising from what is in each case part of an axial or primary frond. Neither specimen has a holdfast or stipe.

Morphologically these specimens closely resemble European D. ligulata and although they bear this name, an examination of reproductive material would be necessary to determine whether their sporangia are of the antarctic type (with raised sori) or are scattered among the superficial cortical cells.

Certainly, these Falkland specimens are significantly narrower and more profusely branched than South African D. firma.

I have not seen material from Crozet Island. Levring (1944) records D. ligulata, noting that the specimens appeared somewhat smaller than usual, and did not appear normally developed.

### 3.4.8 New Zealand and Neighbouring Islands

Lindauer et al (1961) describe the New Zealand entity as follows:

"Thallus up to 90 cm or more high, solid, cartilaginous and dark brown when fresh ... holdfast a compact disc, stipe and basal parts often woody, fronds erect, compressed, 3 - 4 oppositely pinnate in one plane ...; branches up to 4 cm wide, of same form as main rachis, often somewhat wider, linear-lanceolate in young plant, strap-like in older plant or broadly linear-lanceolate to oblong, tapering at both ends with a prominent proximal midrib forming a distinct pedicel, the branches of very irregular length but varying little in width, margins bearing more or less regular and close-set

series of fine teeth, somewhat aculeate, or small, flat proliferations..."

"New Zealand plants are extremely polymorphic, and although some plants resemble D. ligulata, a Northern Atlantic species others in a more pronounced form, closely resemble D. herbacea, a North-West American species ..."

I have examined approximately 40 herbarium specimens of New Zealand Desmarestia (BOL, TCD, PCU, L, BM, MIN) and 25 formalin preserved specimens from Kaikoura, on the west coast of South Island, were measured (Table 3.4).

Most New Zealand specimens are extremely profusely branched. An extreme example, a specimen collected by Lyall at Akaroa Harbour, 1850 (TCD), bears a total of over 1000 fronds, with 4 orders of branches, giving the pressed plant the appearance of a flattened bush (Fig. 3.42). None of the fronds are wider than 2 mm.

Most of the plants examined had fronds 5 - 10 mm wide (e.g. Figs. 3.40, 3.41) and in none were fronds wider than 25 mm. All of these specimens fitted the description of Lindauer and Chapman (1961).

There has been some confusion regarding the taxonomy of the ligulate Desmarestia species found in New Zealand and some neighbouring islands. Hooker (1867) records the occurrence of D. ligulata on the shores of New Zealand, from the East Coast (collected by Colenso) and from Akaroa (Lyall).

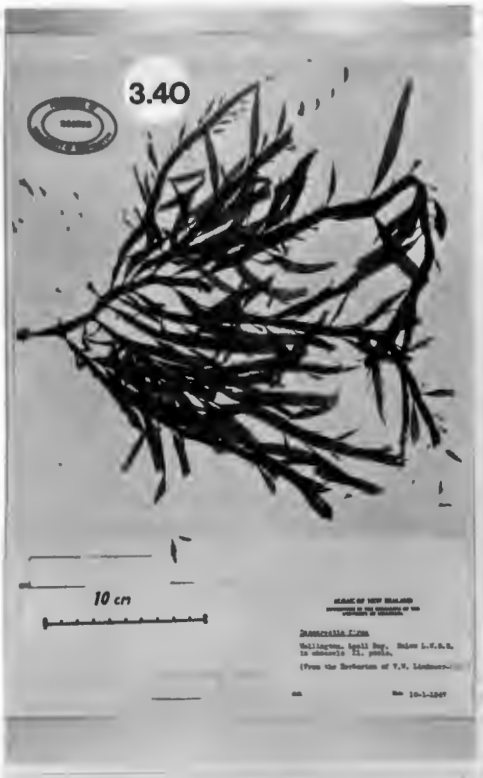
Lindauer et al (1961) follow Papenfuss (1943) in adopting the combination of Skottsberg (1907), and refer the New Zealand entity to D. firma (C. Ag.) Skottsb., although later Skottsberg (1921) discarded this combination. Evidently subsequent authors (e.g. Adams, 1972; South and Adams, 1976; Adams et al, 1974) continue to refer to the New Zealand species as D. firma, although Chapman (pers. comm., in South

| Character | Mean | Max. | Min. |
|---|---|---|---|
| Overall length (mm) | 674 ( 80) | 1030 | 330 |
| Length axial frond (mm) | 508 ( 100) | 95 | 9 |
| Max. width axial frond (mm) | 14 ( 2) | 20 | 7 |
| Max. length 1 frond (mm) | 400 ( 59) | 680 | ca 5 |
| Max. width 1 frond (mm) | 14 ( 2) | 26 | 8 |
| Holdfast diam. (mm) | 15 ( 5) | 42 | 5 |
| Stipe length (mm) | 14 ( 2) | 23 | 8 |
| Angle of 1° venation | ca 90° | 100° | 60° |
| Angle of 2° venation | ca 80° | 100° | 30° |

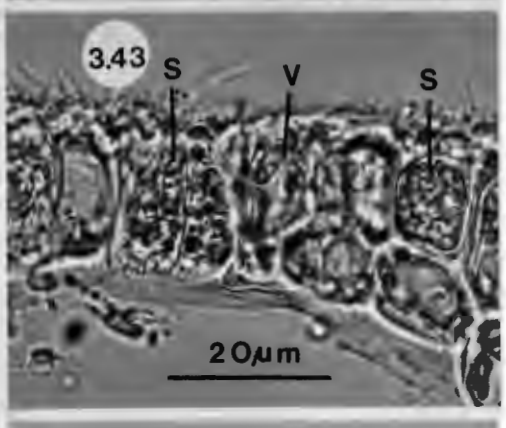
Table 3.4 Means and ranges of morphological characters measured in a sample of 25 mature Desmarestia plants. (Kaikoura, New Zealand, March 1982). Maximum and minimum values express limits of ranges in sample. 95% limits of means in parentheses.

| Frond Order | $\bar{x}$/plant | max./plant | n. |
|---|---|---|---|
| 1 | 40 | 65 | 25 |
| 2 | 83 | 7 250 | 25 |
| 3 | 30 | 7 100 | 13 |

Table 3.5 Numbers of first, second and third order branches per plant, in a sample of 25 mature Desmarestia plants (Kaikoura, New Zealand, March 1982). Means are based only on the plants which show fronds of that respective order (n).


3.40
10 cm


3.41


3.43
S
V
S
20µm


5 cm
3.42

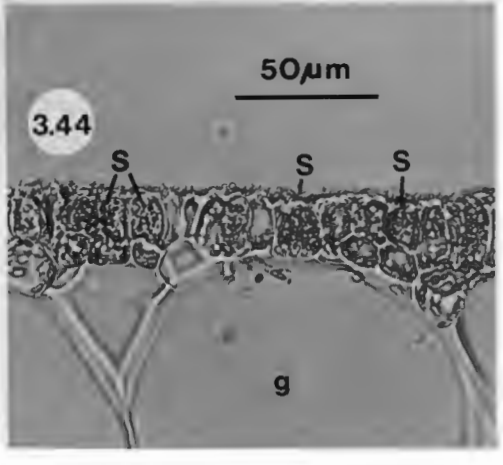

50µm
3.44
S
S
S
g

Fig. 3.40 New Zealand specimen showing intermediate frond width. From herbarium of V.W. Lindauer, collected in Lyall Bay, Wellington (WTU 244556).

Fig. 3.41 "New Zealand, Colenso". Herb. Hookerianum, BM.

Fig. 3.42 Extremely profusely-branched, narrow-fronded form, from Akaroa, N.Z. Coll. Lyall, 1850(TCD).

Fig. 3.43 Cross-section of cortical layer of specimen from Alkaroa, New Zealand, showing sporangia(s) among vegetative cortical cells (v).

Fig. 3.44 Cross-section of cortex and part of sub-cortical layer of specimen from Akaroa, New Zealand. Sporangia(s) visible in cortex, with underlying cells of parenchymatous ground tissue (g).

and Adams, 1976) points out that this entity may be properly referrable to D. ligulata.

Morphologically, the New Zealand plants differ from South African D. firma in the following respect: the former plants are markedly more profusely branched, and their fronds are narrower than is common in South African D. firma. The narrow-bladed New Zealand plants are strikingly similar to European D. ligulata and quite different to D. firma, while the broader N.Z. (e.g. Fig. 3.41) plants are morphologically identical to many N.W. American specimens which I have seen, particularly the entities previously described as D. herbacea Lamx.

The anatomy of the New Zealand entity is essentially the same as that of South African D. firma. In non-fertile material the cortex is 1 - 2 cells deep, underlain by parenchymatous ground tissue, the largest cells of which are up to 150 um in diameter. A network of transverse filaments is interwoven between the ground tissue cells.

In fertile material, sporangia are scattered among the cells of the outer cortical layer, which they resemble in size and shape (Figs. 3.43, 3.44). Sporangia range in size from 9 x 7 $\mu$m to 20 x 13 $\mu$m (mean of 15 sporangia was 18 x 11 $\mu$m). They vary in shape from rectangular to flask-shaped, and lack paraphyses or stalk-cells, although the appearance of stalk-cells is created when small sporangia overlie one layer of vegetative cortical cells. There are between 8 and 12 spores visible in one plane, suggesting a total of 16 spores per sporangium. Spores appear to be between 2 and 4 $\mu$m in diameter.

Thus, while the New Zealand Desmarestia is anatomically similar to South African D. firma, morphological differences preclude the combination of these two entities. From examinations of the material available, it is proposed that the New Zealand population should be regarded as D. ligulata (Stackh.) Lamx.but this

suggestion is open to some doubt, since the broader N.Zealand forms are somewhat wider than indicated in Lightfoot's (1777) type description.

Lindauer **et al** (1961) record the occurrence of the New Zealand entity "from Cook Strait southwards, rather spotwise; Stewart Island; Chatham Islands; Auckland Islands."

### 3.4.9 Australia and Tasmania

Womersley (1967)records D. ligulata from "Nora Creina, South Australia, to Phillips Island, Victoria". He further notes that this species is rare on those coasts, and known only from drift specimens. I have examined two Australian specimens, one in TCD (Fig. 3.45) and one in BM. Both were collected by Harvey, from Western Port, Victoria. The axial fronds of these specimens are 2 - 3 mm wide, primary fronds 1 - 2 mm, and there are several hundred second and third order fronds, and numerous very small fronds of the fourth order. These plants are similar in all respects to European D. ligulata, and narrower New Zealand specimens, and are distinctly different to South African D. firma, with respect to the width and profusion of fronds. It seems best to concur with Womersley (1967), and refer these specimens to D. ligulata.

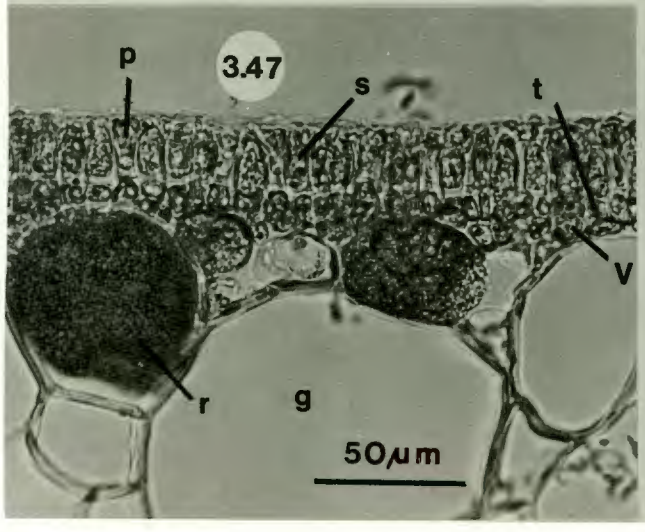
There is one specimen from "Mussel Roe Bay, East Tasmania", now in BM. This is a narrow-fronded, profusely branched plant, morphologically identical to Australian and European D. ligulata.

### 3.4.10 The Antarctic and the Islands of the Scotia Arc.

Specimens from Booth-Wandel Isle (PCU), Palmer Archipelago (BM) and the South Shetland Islands (BM) were examined, as well as a large collection of pressed and formalin-preserved material from Signy Island, South Orkneys (J,H, Price, BM). These plants have fronds 3 - 8 mm wide, with the exception of the larger Signy Island specimens, which have primary fronds up to 15 mm wide (Fig. 3.46). All were bi- or tri-pinnately branched (i.e. 2 to 3 orders of branches), and ranged from sparsely to extremely profusely branched, in the latter case


3.45
5cm


3.46


3.47
p
s
t
V
r
g
50µm

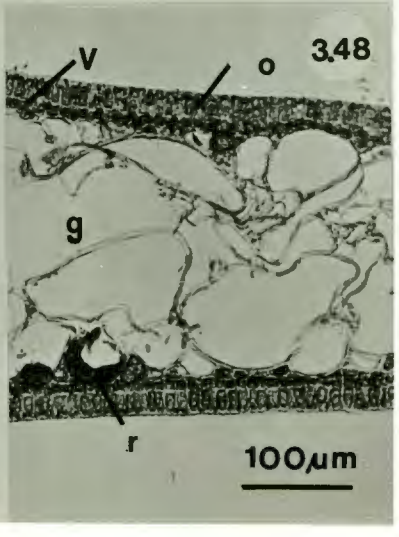

3.48
V
o
g
r
100µm

Fig. 3.45 Specimen collected in Western Port, Victoria, Australia (by W.H. Harvey), and named D.ligulata, in his handwriting. This specimen is identical to many of European D. ligulata.

Fig. 3.46 Specimen from Signy Island, South Orkneys (BM).

Fig. 3.47 Cross-section of part of frond of Signy Island specimen, showing sporangia (s), with stalk-cells (t), interspersed with sterile paraphyses (p), and forming a palisade-like sorus. Vegetative cortical cells (v) underlie the stalk-cells. Note parenchymal cells (r) with dense, granular contents.

Fig. 3.48 Cross-section of frond of Signy Island specimen, showing continuous sorus of palisade-like reproductive tissue ( o), overlying vegetative cortical cells(v), and parenchymatous ground tissue (g). Note densely pigmented cells (r) in periphery of ground tissue.

often with over 100 primary, and several hundred secondary branches. All of the South Orkney Desmarestia plants were growing epiphytically on Curdiea racovitzae ( J.H. Price, pers. comm.), as well as the Palmer Archipelago specimen, which is annotated to this effect by C. Skottsberg.

A notable characteristic of ligulate Antarctic and Signy Island Desmarestia specimens is the minutely speckled, reddish appearance of the pressed fronds. In addition, the frond margins are often dark, giving pressed specimens the appearance of being outlined in black. Morphologically, most of these specimens are similar to European D. ligulata (and most Antarctic specimens in herbaria bear this name), but the reddish speckling of the fronds may be diagnostic for Antarctic and Scotia Arc specimens, if this phenomenon occurs in South Georgia material (which I have not seen.)

The larger of the Signy Island specimens fall within the morphological range of South African D. firma, but in general the former plants are narrower, and more profusely branched than D. firma.

The vegetative anatomy of ligulate Signy Island Desmarestia is in most respects similar to non-Antarctic entities. Non-fertile fronds have 1 - 2 layers of cortical cells which are rectangular or round in cross-section and 7 - 12 µm long, and contain chloroplasts. The parenchymatous ground tissue consists of large (up to 150 µm diameter) cells, with few, if any, chloroplasts. However, the Signy material is unusual in one respect: scattered cells of the sub-cortical parenchyma have dense, granular contents (Figs. 3.47, 3.48) which are yellowish-brown or yellowish-red in colour, and are obviously responsible for the speckled appearance of the pressed fronds. The nature and function of these cells is not known, but they were not found in any non-Antarctic material examined during this study.

In fertile specimens, sori of a palisade-like layer of elongated flask-shaped sporangia cover all but the margins of fronds (fig. 3.47). The sporangia are 17 to 22 µm long and 7 - 10 µm in diameter. There appear to be between 8 and 10 spores per

sporangium, in one plane, indicating a total of 16.

This pattern of sporangial disposition is similar to that which Skottsberg (1907) illustrated in a specimen from South Georgia which he first called D. firma, then later (Skottsberg, 1921) identified as D. ligulata. The sporangia described by Skottsberg (1907) are somewhat longer (24 - 30 µm) than in the Signy Island plants. A similar pattern of sporangial disposition was reported for ligulate Desmarestia from Palmer Station, on the Antarctic Peninsula (Moe and Silva, 1977). These authors reported that sporangia in the Palmer Station plants were shorter and more rotund than those illustrated by Skottsberg (1907), and they point out that these size differences may reflect variations between the populations of different localities.

The Signy Island plants thus show the same type of sporangial development and disposition as the Antarctic entity, with "sporangia formed with paraphyses in an extensive sorus elevated above the vegetative surface" (Group 5 of Moe and Silva, 1977).

Although the narrower-fronded Antarctic plants are morphologically indistinguishable from European D. ligulata, it is clear that, as Moe and Silva (1977) pointed out, the former entity must by virtue of its reproductive structure, be given taxonomic recognition, at least at the species level. Biogeographically, it is significant that the Scotia Arc Desmarestia shows the same pattern of sporangial developement as the Antarctic entity, since Dell (1972) includes the Scotia Arc islands in the Antarctic Benthic Region.

### 3.4.11 Japan

The illustration of D. ligulata from Japan (Okamura, 1910, pl. 72. Fig. 1) shows a plant which is morphologically very similar to European D. ligulata. I have seen one specimen of Japanese D. ligulata (BM), which corresponds in all respects to the above illustration. However, the hemispherical sori

which Tokida (1954) illustrates in Japanese D. ligulata, are quite different to the type of sporangial development in Antarctic D. ligulata, or in the non-Antarctic branched ligulate specimens examined during the present study. Moe and Silva (1977) consider that, an ccount of these differences, Japanese material may represent a species distinct from European D. ligulata. I consider that the illustrations given by Tokida (1954) may show atypical sporangial structure in that the tissue may have been affected by a gall-producing agent. The only evidence I have for this suggestion comes from similar observatios in South African material, where apparent galls produced isolated nodules of elevated superficial cortex in a plant which otherwise showed sporangia scattered among the cortical cells. Further observations on Japanese material would be most useful in this respect.

## 3.5 DISCUSSION

These results and comparisions show clearly that in terms of morphology and anatomy there is very little difference between South African *D. firma* and populations of ligulate *Desmarestia* from northwestern America, particularly the entity described as *D. munda* by Setchell and Gardner in 1924. Specimens from Chile are also morphologically and anatomically similar to South African *D. firma*. It is possible, therefore, that all populations from these three regions belong to the same species.

South African *D. firma* is however, morphologically quite different from *D. ligulata* and *D. dudresnayi* from Europe and Britain. It also differs in its morphology from populations of ligulate *Desmarestia* from New Zealand and from Gough Island.

How then does this relate to the conclusions of Chapman (1972) who decided that all North American species of branched, ligulate *Desmarestia* and the European species *D. ligulata* belonged to the same variety: *D. ligulata* var. *ligulata*? Chapman argues that this variety exhibits a very wide range of morphologies which are to a large extent a phenotypic response to variations in the environment. Thus the very broad-bladed *D. latissima* Setch. and Gard. reflect extremely sheltered positions such as Puget Sound, while more finely divided *D. herbacea* is more typical of open coasts where wave action is stronger. It was largely on these grounds that Chapman felt it necessary to reduce the North American and European species to the same variety.

If we are to apply Chapman's reasoning to populations of ligulate *Desmarestia* in the Southern Hemisphere, then there can be little doubt that South African *D. firma*, together with New Zealand, Chilean and Gough Island ligulate populations would also fall within his concept of phenotypic range exhibited by the variety *ligulata*. The differences between *D. latissima* from northwestern America and *D. ligulata* from

Britain are, for example, much greater than the morphological differences between South African D. firma and the British D. ligulata. To adopt this procedure would effectively confer a world-wide range on the variety D. ligulata var. ligulata.

Although this would greatly simplify the taxonomy of ligulate Desmarestia species, it is a rather sweeping step to make without looking very critically at Chapman's reasons for reducing North American and European species to a single variety.

The six northwestern American species which Chapman synonymised with var. ligulata do show a very wide range of morphologies. The question which arises, however, is why do European D. ligulata var. ligulata fail to exhibit the same degree of variation. If the phenotype is largely governed by differences in wave action, then why, for example, are there no broad-bladed British D. ligulata in sheltered lochs and firths that are comparable with D. latissima, which occurs in sheltered waterways of Washington. If they are all the same variety, then presumably they would exhibit similar degrees of phenotypic plasticity.

Similarly, why does the South African population show a relatively narrow range of morphological variability, with none of the narrow-bladed, profusely-branched forms such as are found in America, Europe, or New Zealand? The answers to these questions cannot be found in the degree of exposure of the respective coasts, since many of the localities from which disparate forms have been collected, are similar with respect to exposure, for example, the Cape West coast, and The Lizard, Cornwall, England. Part of the explanation may lie in the evolutionary ages of these geographically distant populations, and in the size of the gene pool of the founding plants.

This is perhaps illustrated in the case of the Gough Island population of D. ligulata. This island is relatively young, with an age estimated at 1 million years (D. Reid, pers. comm.), and all of the four populations encountered at localities around the island were essentially identical, showing only a small range of morphological variability, accounted for by the ages of the plants. Similarly, the South African population may be young, in terms of evolutionary age, and descended from a few progenitors that were broader and less branched than the progenitors of the Gough population.

It is obvious that taxonomic problems pertaining to ligulate Desmarestia populations will not be resolved by discriminating between populations on purely morphological grounds. As Mathieson et al 1981 pointed out, the type method relies on the recognition of an entity based on relatively few specimens and often ignores the range of forms which may be encountered in living populations. This is certainly true for the branched, ligulate Desmarestia in North-West American populations, where taxa have been based essentially on the size of plants. This was one of the main reasons why Chapman combined North-Western American species with European D. ligulata.

Unfortunately, when using wide phenotypic variability as the basis for combining several species it is possible to err the other way, and combine populations which show little or no overlap in their morphological and anatomical features, and may even be reproductively isolated.

Thus when we interpret southern populations of ligulate Desmarestia in terms of the philosophy Chapman applied to European and North American populations, we then effectively lose sight of the rather distinct morphological differences that exist between widely separated southern populations. For example, the differences between South African and Gough Island Desmarestia. In addition there still remains the difficulty of explaining how South African D. firma is morphologically distinct from European D. ligulata var. ligulata,

but does show close morphological similarities with *D. munda* which is a species which Chapman recognises as being conspecific with variety *ligulata*.

Moe and Silva (1977) suggested that in the genus *Desmarestia*, which includes terete (filiform) and unbranched broad-bladed forms not investigated here, vegetative characters may be of secondary importance in expressing evolutionary divergence. This is strongly supported in the ligulate Antarctic entity, which is morphologically similar to European *D. ligulata* as well as entities from South America and New Zealand, and yet possesses an unique type of sporangial arrangement. However, the results of the present study indicate that, at least in the branched, ligulate forms examined here, there may be little variability in the arrangement and disposition of sporangia, even between geographically distant populations. Specimens from North-West America, South America, Gough Island, New Zealand and South Africa, as well as British *D. ligulate* (Johnson 1891) all have sporangia scattered among, and similar in size and shape to, the vegetative cortical cells. Although this might indicate that these entities are closely related (or even conspecific), the problem of morphological disparity between certain of these populations (e.g. South African *D. firma* and European *D. ligulata*) still arises and it is felt that such morphologically dissimilar and geographically distant populations should receive some taxonomic recognition if only at the varietal level.

Similarly, it is felt that caution must be exercised before including South American entities in *D. ligulata* var. *ligulata* sensu Chapman (1972), as Abbott and Hollenberg (1976) have done, since this variety is based on North West American and European material. Perhaps these problems will only be resolved by biochemical studies(electrophosesis), quantitative genetic evaluation, or hybridisation studies, as discussed by Mathieson *et al* (1981). Despite the contention of Moe and Silva (1977), it is not clear that diagnostic differences will arise from studies of the life-cycles of these closely related populations,

particularly those which have a similar reproductive structure, with sporangia scattered among vegetative cortical cells. In this respect, the only clear character which comes to mind is whether the gametophytes of a particular entity are monoecious or dioecious, and in view of the similarities in sporangial structure between many of these entities (South African, New Zealand, Gough Island, and North-West American specimens) which this study illustrates, there may be greater differences between these populations in terms of morphology, than in terms of their life cycle.

The final conclusion reached in this study is that, despite strong morphological and anatomical similarities with certain geographically distant Desmarestia populations and varying degrees of overlap with others, the South African population should provisionally retain the name D. firma (C.Ag.) Skottsb. While this conclusion is open to strong doubts, it is felt that taxonomic combination with North-West American and South American entities, on the limited anatomical and morphological information available, would be premature.

# CHAPTER 4

# DISTRIBUTION

## 4.1 INTRODUCTION

In this chapter the distribution of *Desmarestia firma* is described at two levels: 1) Its geographical distribution, and 2) Its distribution within the Oudekraal kelp bed. In addition, the worldwide geographical distribution of the branched ligulate *Desmarestia* complex is discussed, since although *D. firma* is provisionally regarded as being restricted to Southern Africa, its taxonomic position within this complex remains unclear (Chapter 3). Thus, any future taxonomic combination with other entities would alter its geographical range accordingly.

The distribution of understorey algae in Western Cape kelp beds has received little scientific attention. Velimirov *et al* (1977) have provided an account of faunal and floral boundaries within the Oudekraal kelp bed and briefly discussed the major organisms in the 3 zones which they recognised, namely the offshore, mediate and inshore zones (see Chapter 1, Fig. 1.2). They dealt only briefly with the understorey algae, but showed that the bulk of understorey algal standing crop is found in the mediate and inshore zones, while in the offshore zone (which largely includes the site of the present study), standing crops of understorey algae are lower, and animals (mainly detrital and filter feeders) are abundant. In an account of variations in the structure and biomass of 6 kelp beds (located between Cape Aghulas and Saldanha Bay), Field *et al* (1980 a) also dealt briefly with understorey algae, since they were concerned mainly with standing crops of the kelps and the standing stocks of the main animal species. Once again, it was found that inshore zones were relatively plant dominated and offshore zones relatively animal dominated. In the present study, the distribution of *D. firma* in the Oudekraal kelp bed is discussed with respect to biotic factors (animals and other plants), depth, and water movement.

## 4.2 MATERIALS and METHODS

### 4.2.1 Geographical Distribution

Records of D. firma on the Southern African coast are based on herbarium specimens, and on my own observations and collections from various localities along the coast between Eland's Bay (32° 18'S 18° 18'W) on the west coast and Cape Agulhas (34° 50'S 20° 0'W) in the south.

Information pertaining to the distribution of members of the branched, ligulate Desmarestia complex is derived from herbarium specimens, from freshly preserved material sent from overseas, and from published reports.

### 4.2.2 Distribution of D. Firma within the Oudekraal Kelp Bed

The distribution of D. firma within the study site was monitored at two-monthly intervals by plotting the position of specimens within four randomly placed 0.25m x 56.0m transects. Each transect was divided into 2m sections and the number of plants in each 2.0m x 0.25m quadrat was recorded. Results are illustrated in the form of distribution profiles (Figs. 4.3 - 4.8). The presence or absence of a kelp canopy, the abundance of other understorey algae, concentrations of the sea-urchin Parechinus angulosus, substrate type and slope, and depth (measured on a conventional divers' guage and later corrected to be expressed relative to L.W.S.), were recorded. These data are also included in Figs. 4.3 - 4.8. Between 25 March and 5 April 1979, eight additional transects of the same dimensions were placed in the "inshore" and "mediate" areas as described by Velimirov (1977), in order to plot the distribution of D. firma throughout the entire kelp bed. Results are illustrated in Fig. 4.7.

## 4.3. RESULTS

### 4.3.1 Geographical Distribution

#### D. firma in Southern Africa

Collection records for D. firma in Southern Africa are listed in Appendix B, and summarised in Fig. 4.1. All but two of the records lie along the Atlantic coast between Cape Point (34° 30'S 18° 29'E) and Luderitz Bay (26° 30'S 18° 04'E), within the west coast upwelling area.

There are only 2 records of this species east of Cape Point. One is from Seal Island, False Bay, collected by Sea Fisheries divers, 28.11.1967, and another is a specimen (in BM) bearing the label "Cape Agulhas, E. Thwaites, Received January 1819." It is not stated whether these specimens were collected among drift material, or whether they were attached to the substrate. These records are considered to be highly unusual, since there are no other records of this species, and I have never found it, east of Cape Point, either attached or in beach cast or drift.

#### Worldwide Distribution of Branched, Ligulate Desmarestia

Worldwide records of this group are summarised in Fig. 4.2. Off Europe, D. ligulata is recorded from the Faroes, Orkneys, Jersey, Scotland, England, Ireland, and Atlantic France (e.g. Turner, 1809; Kutzing, 1849; Lamouroux, 1813; Harvey, 1846; Le Jolis, 1880). In addition, branched, ligulate specimens are found on the Atlantic coast of Portugal and Spain (PCU) and Tangiers, Morocco (Schousboes' specimens in PCU, BM).

On the Pacific coast of North America, branched, ligulate Desmarestia (all previous entities in this group are included in the combination D. ligulata var. ligulata sensu Chapman, 1972) are recorded from Kodiak Island, Alaska (as D. herbacea) southwards to La Jolla, California (D. herbacea and D. munda)

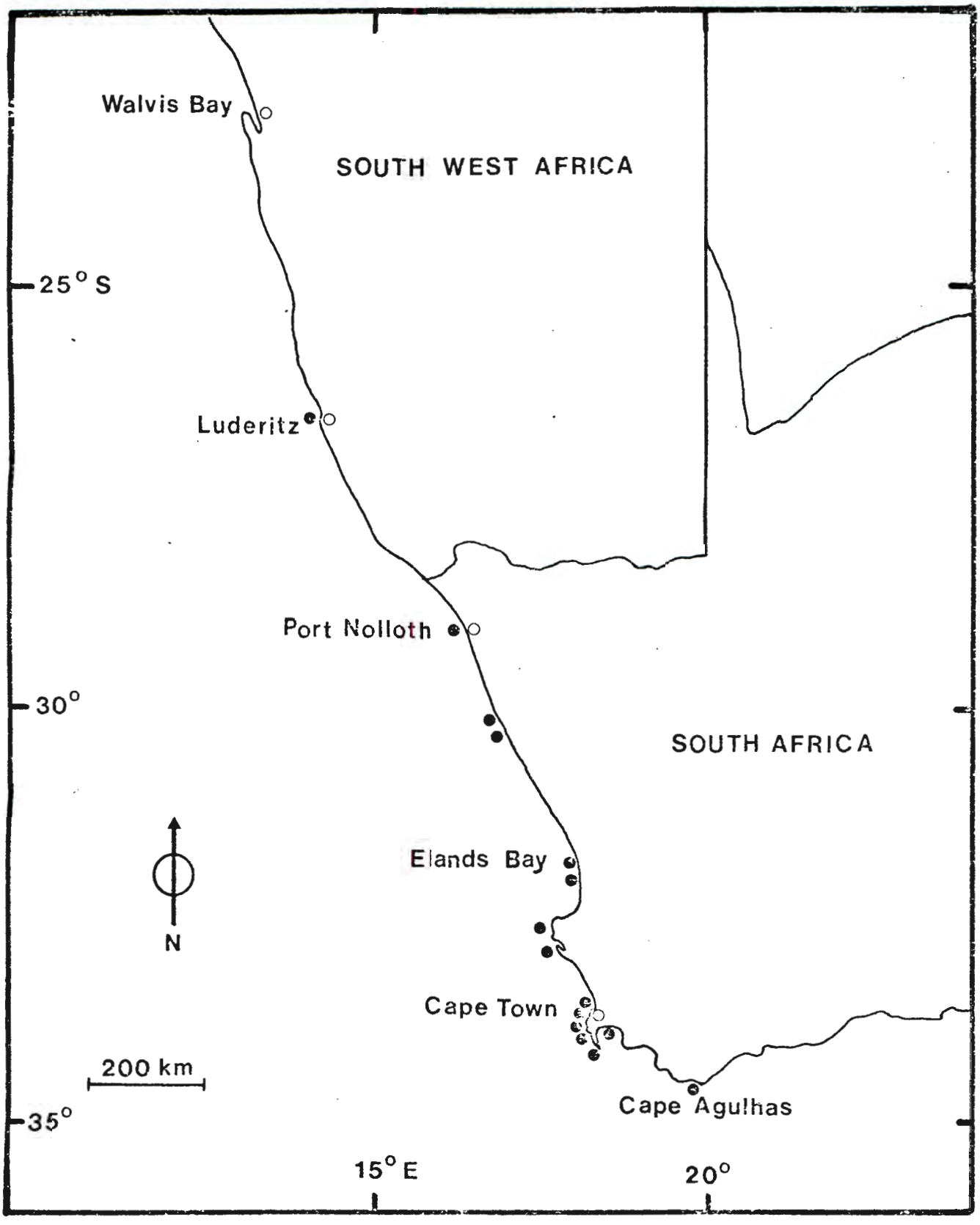



FIG. 4.1 The distribution of Desmarestia firma on the coast of Southern Africa. Closed circles indicate collection localities. For reasons of clarity some of the records from the Cape Peninsula are omitted.

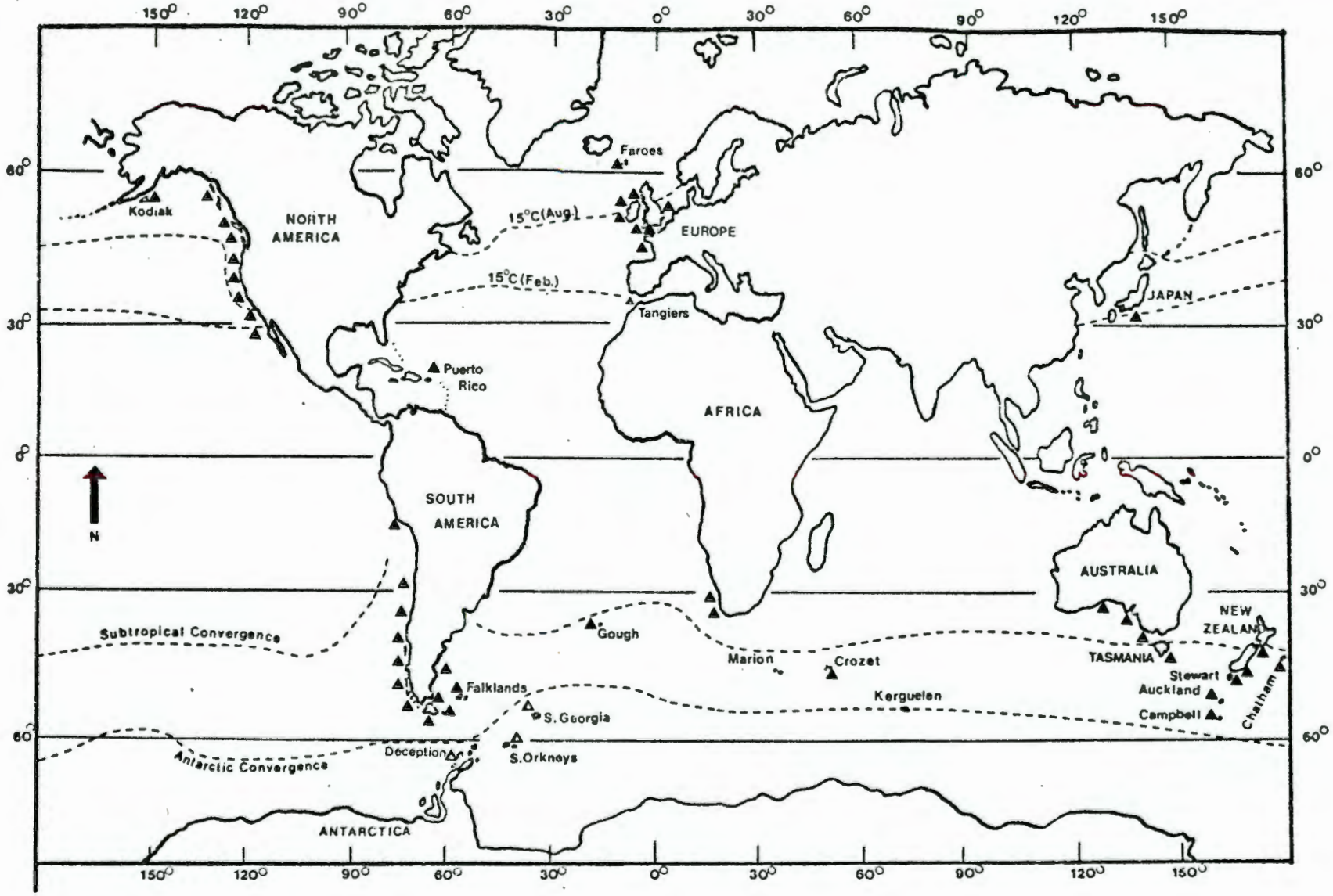



FIG. 4.2 Worldwide distribution of branched, ligulate Desmarestia. Open triangles indicate distribution of Antarctic entity, closed triangles indicate all others. Mean annual positions of Subtropical and Antarctic Convergences from Knox (1960), and August and February 15°C isotherms (Northern Hemisphere) from Sverdrup et al (1942).

(Setchell and Gardner, 1925). The collection localities of all of the North-West American herbarium specimens which I examined fell within this geographical range.

On the Pacific coast of South America, branched, ligulate specimens are recorded from as far north as "Southern Peru" (Cotton, 1915), with numerous records from about 35°S (Valparaiso) southwards, and from the Straits of Magellan (e.g. Taylor, 1938; Gain, 1912; Kim, 1971; Montagne, 1846; Piccone, 1886; Hooker, 1847; Skottsberg, 1907). In Argentina, this group is distributed northwards from Staten Island(e.g. Hooker, 1847) into the biogeographical area termed the "Patagonian Province", which extends from Rio Gallegos (approximately 52°S) to Punta Valdes (approximately 42°S) (Kuhnemann 1972). This author records that both D. ligulata and D. herbacea are abundant in this province. It is clear that this group extends further north along the western coast of South America than along the eastern coast.

Branched, ligulate Desmarestia is recorded from the Falkland Islands (Hariot, 1889; Bory de St. Vincent, 1826; Gain, 1912; Taylor, 1938; Cotton, 1915; Skottsberg, 1907), from Gough Island (present study), and from Crozet Island (Levring, 1944). This group has not been recorded from Tristan da Cunha (some 300 km N.W. of Gough), Marion and Prince Edward, and Kerguelen Islands, although terete and filiform Desmarestia are recorded from the latter 2 island groups, and an unbranched form is recorded from Tristan (Baardseth, 1941).

In New Zealand, branched, ligulate plants (which I regard as belonging to D. ligulata, see Chapter 3) are recorded from various localities, mainly on South Island (e.g. Hooker, 1867; Lindauer et al, 1961; Adams et al, 1974; Laing, 1909; South and Adams, 1972), and on the associated islands of the Aucklands (Gain, 1912; Lindauer et al, 1961; Laing, 1909), Campbell (Gain, 1912), Stewart (Lindauer et al, 1961) and the Chathams (Lindauer et al, 1961). In Australia, what is apparently the

same species is recorded from "Nora Creina, South Australia, to Philip Island, Victoria" (Womersley, 1967), and from Tasmania (BM).

Further records for this group come from Japan (Tokida, 1954; Cotton, 1915), and from deep water (50 - 70m) off the coast of Puerto Rico, in the Caribbean (Diaz-Piferrer, 1969).

The branched ligulate Desmarestia from the Antarctic and Scotia Arc Islands clearly represents an entity which is taxonomically different from all of the non-antarctic entities, on account of its unique sporangial structure (Moe and Silva, 1977; and present study, Chapter 3). This entity is recorded from Palmer Archipelago (Moe and Silva, 1977), the South Shetlands (Gain, 1912, as D. ligulata), the South Orkneys (BM), and South Georgia (Reinsch, 1890, as D. ligulata; Skottsberg, 1907, as D. firma then later as D. ligulata).

### 4.3.2 Distribution of D. Firma within the Oudekraal Kelp Bed

D. firma was scattered throughout the study site, from 2m down to 18m depth (the maximum depth in the study site). Outside the study site, in deeper water, specimens were found at approximately 25m depth.

The distribution of D. firma tended, in general, to be "clumped". That is, plants were usually found in patches, and seldom as randomly distributed individuals. This trend is particularly evident for new plants of each generation (Fig. 4.4, November 1978, transects 1 and 2; Fig. 4.5, January 1979, transects 1 and 3; Fig. 4.8, October 1979, transect 2). In these profiles high densities of small plants (sometimes over 50 plants.$m^{-2}$) were concentrated in a few areas, mostly in relatively shallow (2 - 5m) water. This clumping is also evident in the inshore and mediate zone profiles (Fig. 4.7) where no single individuals were encountered per quadrat.

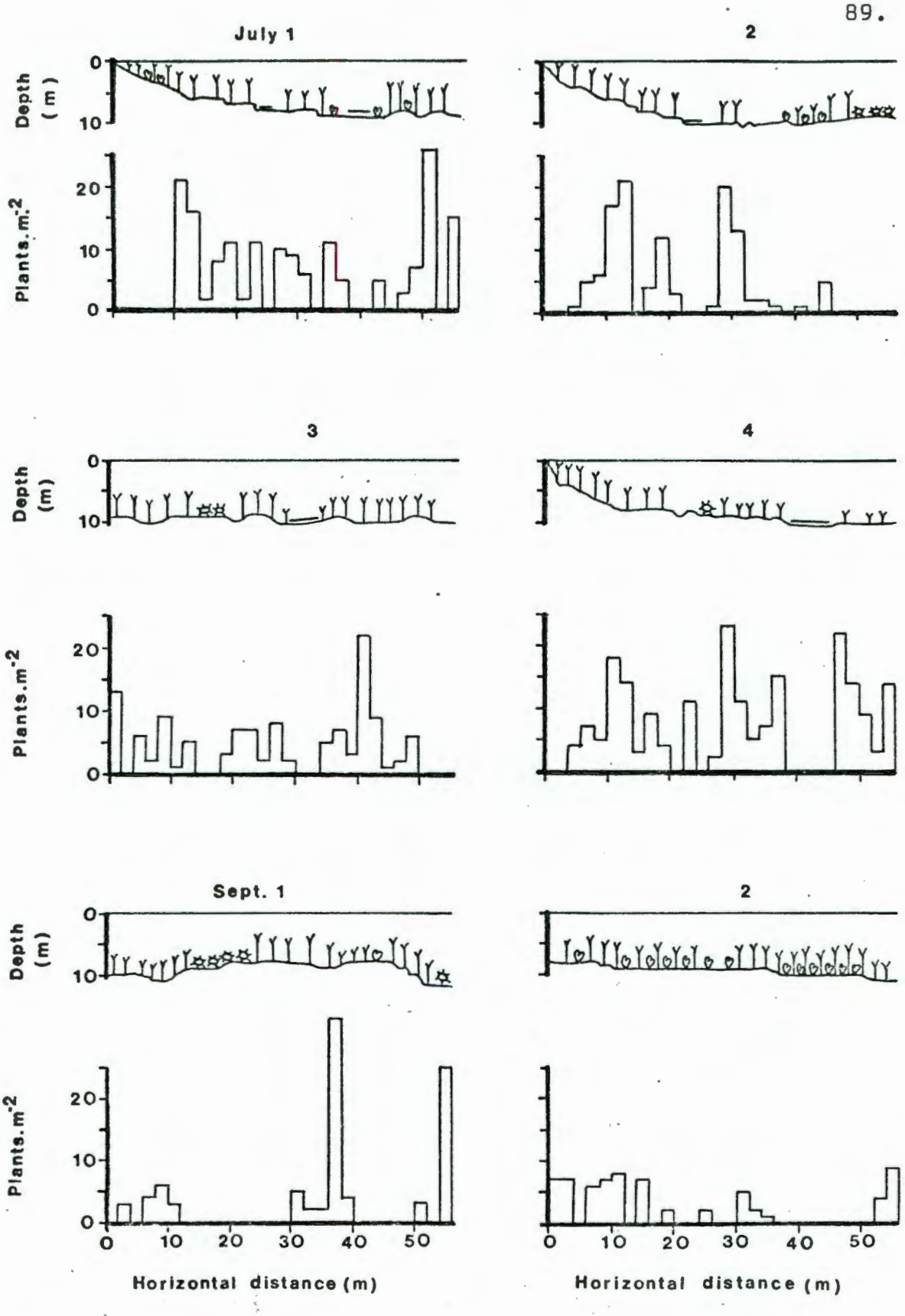



FIG. 4.3 Distribution profiles of D. firma in study site. July 1978, transects 1-4, September 1978, transects 1-2. No. of plants .$m^{-2}$ and depth (m) on vertical axes. Distance along profiles (m) on horizontal axes.

Key: Y - kelp; ✲ - urchin aggregates; ♡ - dense understorey algae; ═ - sand.
⊓ - Generation 1; ▨ - Generation 2;
▩ - Generation 3.

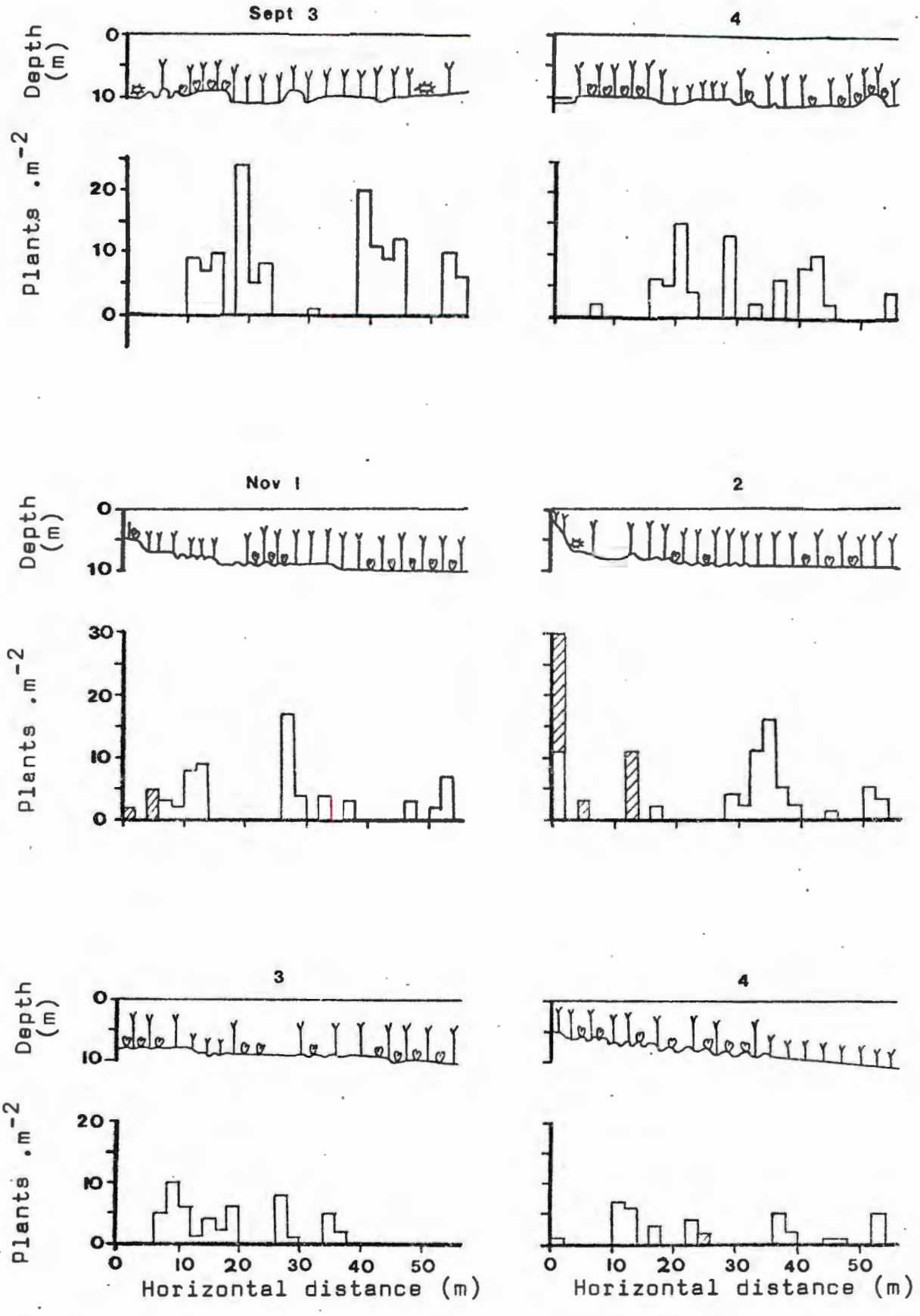



FIG. 4.4 Distribution profiles for D. firma in study site. September 1978 transects -34, November 1978 transects 1-4.

Key as in Fig. 4.3.

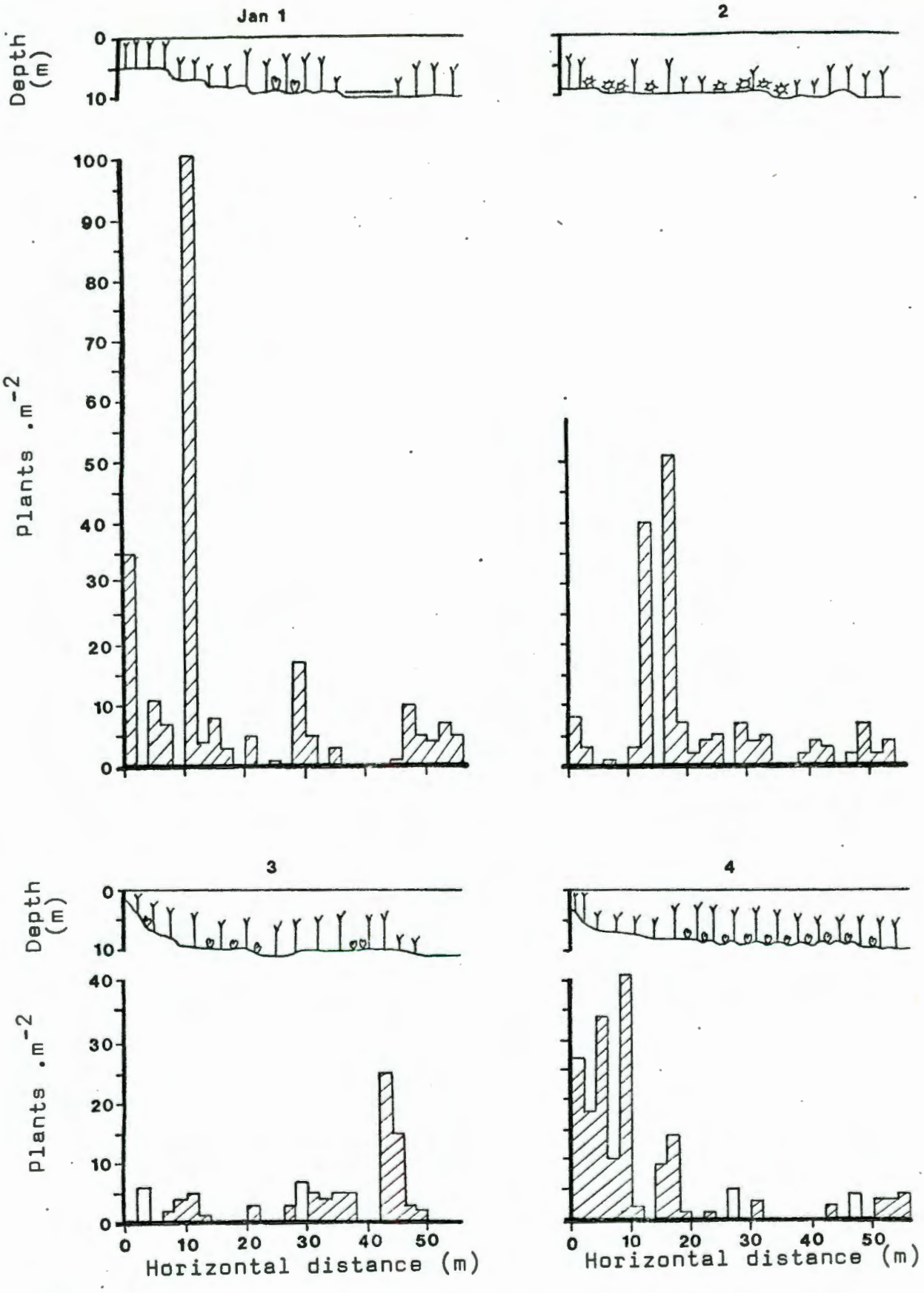



FIG. 4.5 Distribution profiles for D. firma in study site. January 1979 transects 1-4.

Key as in Fig. 4.3.

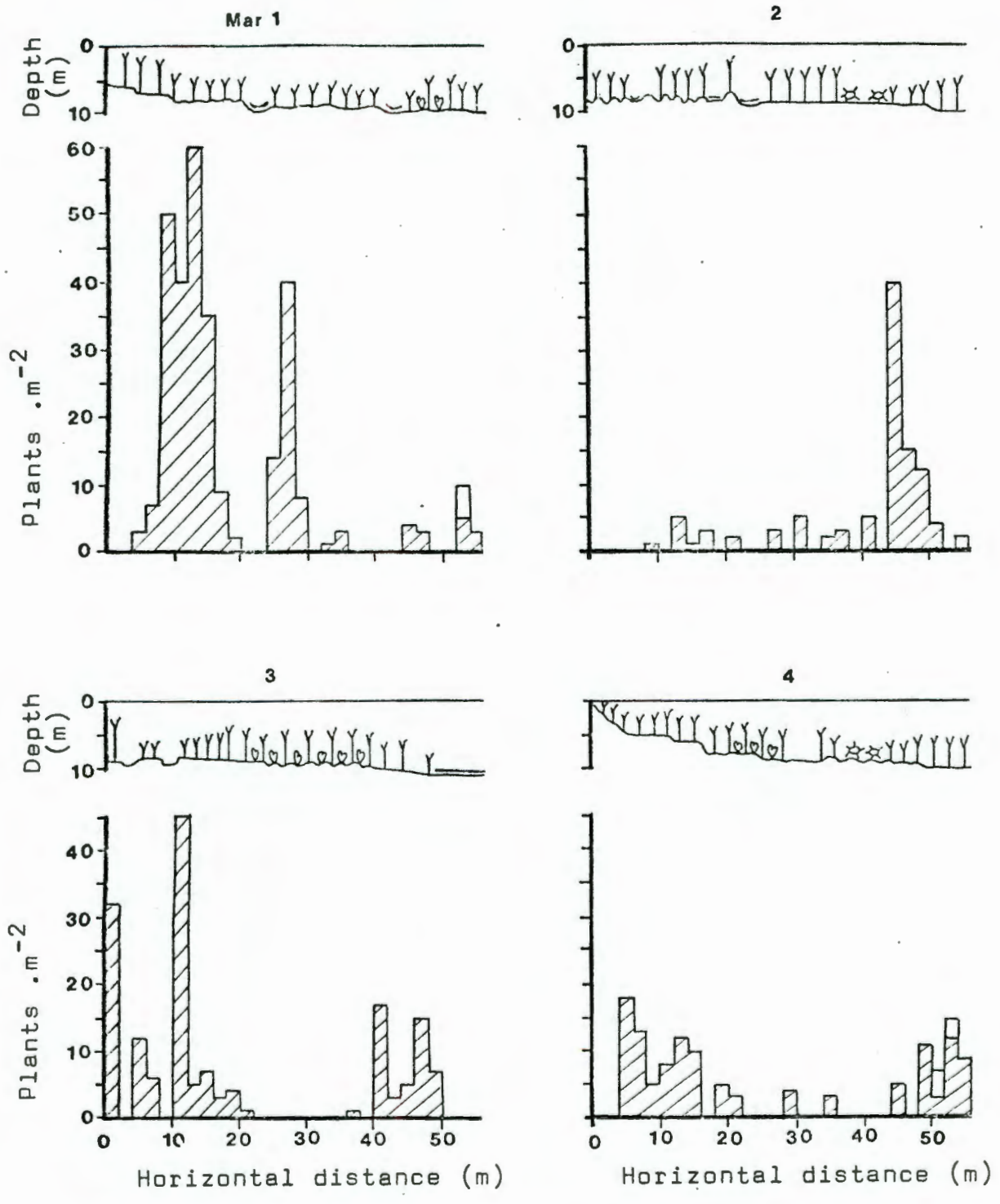



FIG. 4.6 Distribution profiles for D. firma in study site. March 1979 transects 1-4.

Key as in Fig. 4.3.

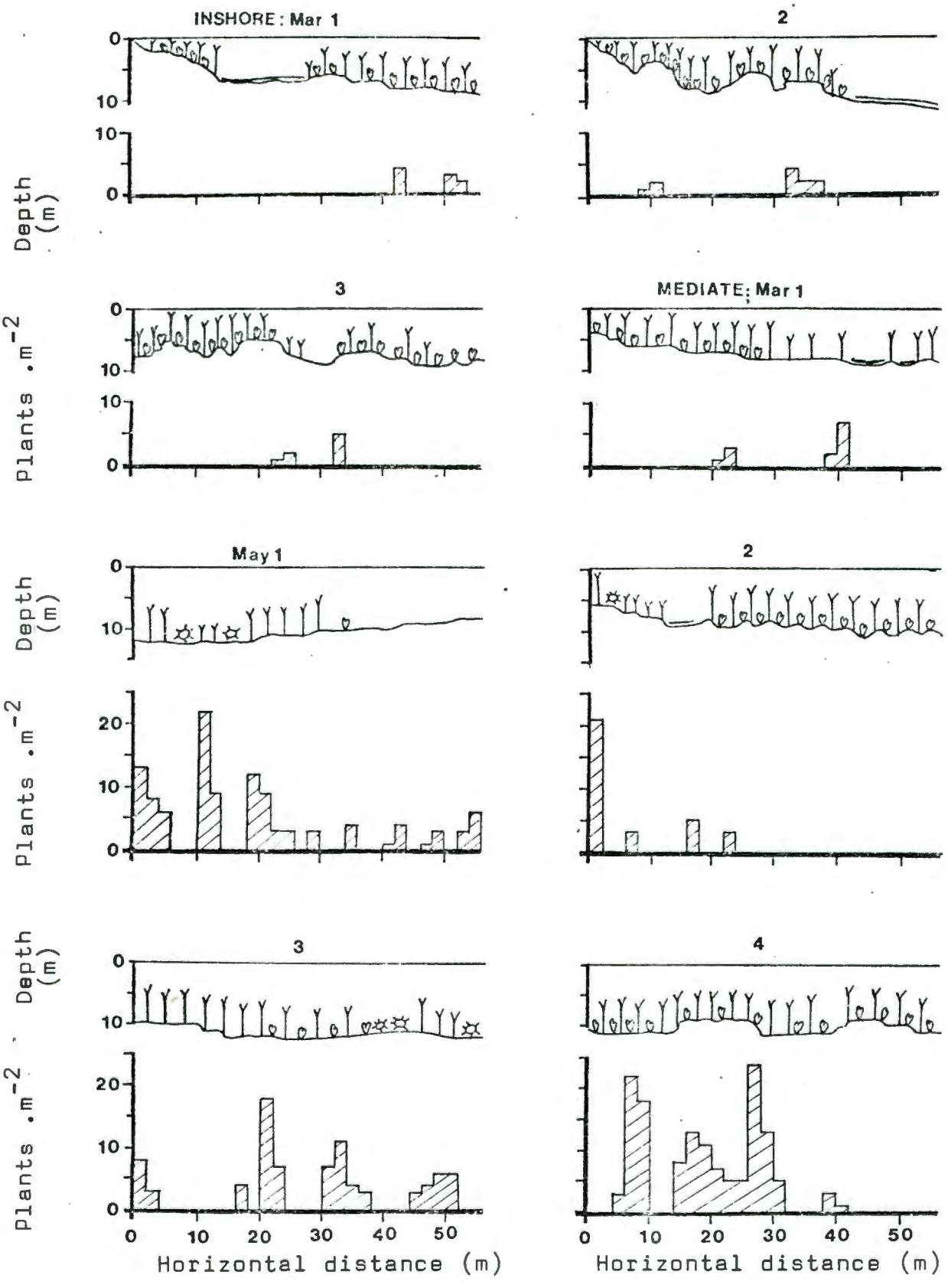



FIG. 4.7 Distribution profiles for D. firma. March 1979 transects in inshore zone 1- 3, and transect 1 in mediate zone. Inshore zone transect 4 and mediate zone transects 2-4 are omitted, since no D. firma was found. May 1979 profiles in study site, transects 1-4.

Key as in Fig. 4.3.

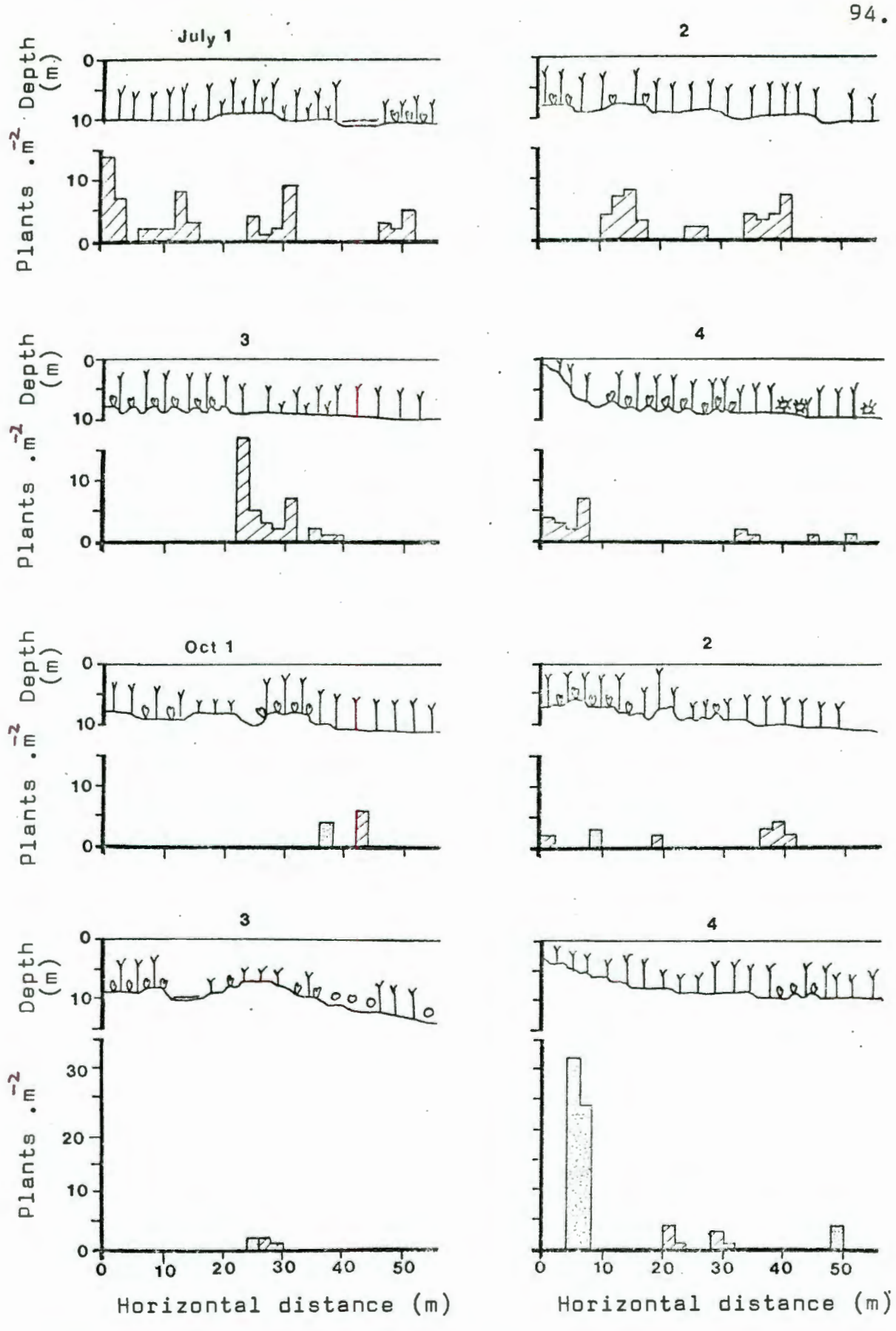



FIG. 4.8 Distribution profiles for D. firma in study site. July 1979 transects 1-4, October 1939 transects 1-4.

Key as in Fig. 4.3.

Areas with little or no D. firma fell into 3 categories. The first, bare sand, obviously supported no macroscopic algae. In the second type of area the sea urchin Parechinus angulosus was concentrated. These animals often form dense aggregates on the rock, sometimes several metres in extent, and with up to 240 urchins per $m^2$ of substrate. Here understorey algae in general were sparse or absent. The third category comprised areas of dense understorey algae, consisting of communities dominated by Hymenena venosa, Neuroglossum binderianum, Pachymenia cornea, P. carnosa, Gigartina clathrata, Botryoglossum platycarpum, and Botryocarpa prolifera.

Dense stands of understorey algae are characteristic of the 'mediate' and particularly the 'inshore' zone, where there is very little D. firma (Fig.4.7). One of the inshore and three of the mediate transects had no D. firma at all. In these zones the red algae listed above, as well as Bryopsis sp., Polyopes constricta and Thamnophyllis sp. completely cover most of the substrate. These zones are also characterised by the absence of urchin aggregates, and have a dense two-layered kelp canopy formed by Ecklonia maxima fronds at or near the surface, and L. pallida fronds at a few metres above the bottom. Large patches of D. firma (0.5 to 1.0 $m^2$ in extent), which were common in the study site, were never found in the 'inshore' or 'mediate' zones.

In the study site, clumps of D. firma were often adjacent to sand, where the clearing in the kelp canopy together with reflection from the sand combine to give relatively high levels of irradiance. Dense patches were also found , on occasion, adjacent to urchin aggregates and on bare rock where the kelp appeared to have been torn off by storms, often along with much of the associated animal and plant community.

An observation which was not apparent from the profiles was the apparent rapid colonisation of bare rock by D. firma sporophytes in spring. Areas denuded of kelp holdfasts during winter, often supported dense stands of small D. firma sporophytes, and recolonising sporophytes of L. pallida, and sometimes of E. maxima.

## 4.4 DISCUSSION

### 4.4.1 Geographical Distribution

#### D. firma in Southern Africa

D. firma , the sole representative of this genus in Southern Africa, appears to be restricted to the west coast upwelling region, from Cape Point northwards to at least Luderitz Bay, although it may very rarely be found east of Cape Point, as far as Agulhas. Sea temperatures in False Bay, and further east towards Agulhas are at least several degrees higher than on the west coast of the Cape. For example, at Millers' Point, on the east coast of the Peninsula, in False Bay, Fricke and Thum (1975) recorded a minimum temperature of 13°C (in winter) and a maximum of 23°C (in summer), which is approximately 6° C higher than the temperatures at Oudekraal (Figs. 1.4, 1.5). The shallow waters of False Bay are generally somewhat warmer than waters west of Cape Point and eastwards towards Agulhas, due to wind-induced currents and the effect of insolation. Silva (1959) points out that the west side of the Cape Peninsula thus has an essentially cold-water flora, with some south-coast species. Clowes (1950) showed that the region between Cape Agulhas and Cape Point receives a mixture of warm water from the Agulhas Current and cold water from the West Wind Drift. Thus Desmarestia and other cold temperate species may be periodically introduced to this region, but probably fail to become established east of Cape Point because of the warmer water. It is possible that the two anomalous records of D. firma, from this region, were plants which grew in deeper, colder water, or they may have originated from the west of Cape Point and been carried eastwards in coastal currents.

Although D. firma has not been recorded north of Luderitz Bay (26° 30'S 18° 04'E) on the west coast, this may simply reflect the paucity of collections from localities further north, since the area influenced by upwelling and the cold Benguela Current extends as far north as about 18°S (Knox, 1960). This cold temperate area, the West Africa Province of Knox (1960), supports many species of algae which do not occur on the warmer south and east coasts of Southern Africa.

## Worldwide Distribution of Branched Ligulate Desmarestia

Members of the branched ligulate Desmarestia complex are restricted to cold and temperate regions of the world's oceans, where surface temperatures are between 0°and about 12 - 13°C in the coldest months of the year, and do not rise above 20°C for long periods. In the Northern Hemisphere, this group is restricted to regions between about 25 N and 63 N (Fig. 4.2). The one anomalous record, that of D. ligulata dredged from the Caribbean, is explained on the basis of deep, cold-water currents (Diaz-Piferrer, 1969). Water temperatures off the West coast of North America range from 6°C off Kodiak Island, Alaska (winter), to about 18°C off Southern California (summer). (Sverdrup et al, 1942).

Water temperatures off England and Atlantic France range from about 8°C in winter to over 15°C in summer, while in Portugal and Atlantic Spain temperatures are somewhat higher, but nevertheless fall below about 13°C in winter (Sverdrup et al, 1942). Water temperatures on the Tangiers coast range between 15°C in winter and 20°C in summer (Sverdrup et al, 1942).

In the Southern Hemisphere, branched ligulate Desmarestia occur within the Antarctic, Subantarctic, and Transitional Cold Temperate Regions described by Knox (1960).

The Antarctic Region, which lies between the Antarctic continent and the Antarctic Convergence, is characterised by sea surface temperatures between -1.0°C in winter and 3.5°C in summer (Knox, 1960). It has been suggested that the Antarctic benthic region should include South Georgia (Hedgpeth, 1969; Dell, 1972). In this respect, it is interesting that there are striking similarities in the shape and arrangement of sporangia, between Desmarestia from the Antarctic and Scotia Arc islands, and that this entity is quite different to all non-Antarctic branched, ligulate entities.

The Subantarctic Region (cold temperate seas) extends from the Antarctic Convergence to the Subtropical Convergence, and is characterised by sea surface temperatures of 3.0 - 11.5°C in winter, and 5.5 to 14.5°C in summer (Knox, 1960). This region includes Southern South America (from 40°S), the Falklands, Gough, Marion and Prince Edward, Crozet, Kerguelen, and the New Zealand Subantarctic islands. Branched, ligulate Desmarestia are notably absent from Marion, Prince Edward, and Kerguelen Islands, for reasons which are not known. It should be borne in mind that more thorough SCUBA-aided collecting may reveal their presence at these localities. Members of this Desmarestia complex have not been recorded from New Amsterdam or St Paul Islands which lie north of the Subtropical Convergence (and consequently in warmer water) or from Tristan da Cunha, which lies on the mean annual position of the Subtropical Convergence.

The most northerly records of branched, ligulate Desmarestia in the Southern Hemisphere are all from areas which Knox (1960) has described as "Transitional Cold and Warm Temperate Regions". These include New Zealand, South Australia and Tasmania, South America, and South Africa. In these regions sea surface temperatures show a mean range of 12 - 20°C. Off western South America, the Peru current travels northwards from the West Wind Drift, and runs along the coasts of Chile and Peru to within 4°S of the Equator. This, in combination with upwelling, reduces coastal water temperatures to some 10°C lower than predicted for those latitudes (Knox, 1960). Cold temperate seaweeds, including members of this Desmarestia complex, are thus able to penetrate northwards along the coast of Chile and Peru. On the eastern coast of South America (Argentina), the Falklands Current extends northwards to about 30°S, its limits being correlated with the extent of southwards penetration of the warm Brazil Current. Thus the Patagonian coast has a 'Subantarctic' temperature regime (Knox, 1960), and members of this Desmarestia complex are found on these coasts.

The occurrence of branched, ligulate Desmarestia on the coasts of Tasmania and Southern Australia can be explained in terms of cold currents which reach these coasts. According to Knox (1960), a branch of the cold West Wind Drift travels eastwards along the southern coast of Australia during winter. Southern Australia has many species of algae in common with New Zealand (Womersley, 1959), so that it is likely the Australian Desmarestia population originated from New Zealand. Much of the New Zealand coast, in turn, particularly the south and east coasts of South Island, is directly influenced by the West Wind Drift (Knox, 1960). Thus, throughout the Antarctic and cold temperate regions of the Southern Hemisphere, the distribution of branched, ligulate Desmarestia is clearly related to areas influenced by the West Wind Drift currents, including their offshoots, for example the Peru and Benguela Currents.

## 4.4.2 Distribution of D. firma within the Oudekraal Kelp Bed

The clumped distribution of D. firma is probably the result of several interacting factors. Apart from sandy areas, rocky substrate for attachment and growth does not become uniformly available: kelp holdfasts are torn loose sporadically, other algae may be grazed off the rocks more or less randomly, and gaps in the kelp canopy create patches of relatively high illumination. An important factor is the dispersal range of spores of established D. firma plants. The motile zoospores are probably borne considerable distances in the strong water movement of the kelp beds, but densities of zoospore settlement are likely to be inversely proportional to the distance from the parent plant, in general. The zoospores are the only truly motile phase in the life cycle of the plant. Fertilised eggs may possibly break free from the gametophytes (Chapter 2) but their dispersal is likely to be extremely limited. Underwater observations showed that patches of young sporophytes were most often found around the old plants of the previous generation. This suggests the potential dispersal distance of zoospores may be largely responsible for the clumped distribution of the sporophyte.

The absence of D. firma and other algae from areas of urchin aggregates is doubtless due to grazing by these animals. These aggregates, often covering several square metres of rock, appear to move en masse, clearing patches of algae as they go.

The distribution of D. firma in areas of dense understorey algae is probably limited mainly by competition for space and light. In these dense stands in parts of the study site, and particularly in the 'Mediate' and 'Inshore' zones, D. firma, being an annual, would be at a competitive disadvantage compared with perennial species. The vast majority of understorey species in these zones are red algae, with diffuse meristematic tissue, e.g. Hymenena, exhibiting seasonal regeneration of new tissues from old stipes and holdfasts. Perennial species do not have

to find space with each annual cycle. Also, there are very few grazers in the mediate and particularly the inshore zones (Velimirov et al, 1977) so that stands of algae may persist, relatively undisturbed, and few new areas of substrate become available for colonisation. Under these conditions, D. firma, with an annual life cycle, is at a disadvantage. However, its apparently high growth rate, and ability to rapidly colonise cleared areas, may provide environmental advantages in the study site, and other parts of the offshore zone, where aggregates of urchins, possibly as well as other grazers (e.g. Turbo sp.), remove algae from the substrate. If these cleared areas are available in winter, when zoospore release is occurring, they can be settled by gametophytes, which in spring produce visible sporophytes. The growth of these plants is then further enhanced where clearing has reduced competition for light.

The opportunistic nature of D. firma is further evidenced by the rapidity with which it was observed to colonise rocks from which kelp holdfasts and associated fauna and algae had been removed by storms. These observations agree with theories of algal ecological strategy proposed by Dayton (1975) and developed further by Shepherd (1981). The latter author, in a study of a deep water red algal community, recognised three conditions (competition, stress and disturbance) which each invoke corresponding strategies, namely dominance, adaption to low light, and the ephemeral strategy, respectively. He broadly grouped the algae in this community according to these strategies, recognising that many species show strategies of two, or even three kinds. Littler and Littler (1980) recognised only the strategies of dominance and opportunism (the ephemeral strategy) but also recognised that these are extremes in a continuum of environmental adaption. These theories are closely linked to that of 'r'- 'K'-selection (MacArthur and Wilson, 1967) and it is tempting to speculate that from the point of view of the understorey algae at least, there may be a gradation within the Oudekraal kelp bed from an 'r-selected' environment in the offshore zone, to one that is relatively 'K-selected' inshore. These two terms

were coined by MacArthur and Wilson (1967), to describe theories of natural selection proposed largely by Dobzhansky (1950). Briefly, an 'r-selected' environment is unpredictable, and populations are subjected to non-directed, often catastrophic mortality (Pianka, 1970). Population size is variable in time, well below the carrying capacity of the environment, there is annual re-colonisation, and a high proportion of the organisms' energy is directed towards reproduction. Inter- and intraspecific competition is lax. The life of the population is short (annual or less), development is rapid and often associated with high productivity.

By contrast, the 'K-selected' environment is fairly constant. Mortality is directed and density-dependent. The population size is constant in time, at or near the carrying capacity of the environment, and there is strong inter- and intraspecific competition. The organisms live longer (e.g. perennial), develop more slowly, and have lower reproductive rates and lower productivity.

The concepts of r and K selection are comparative rather than absolute. That is, one species, or population, is only more or less of an r-strategist compared to other species or populations (Gadgil and Solbrig, 1972).

Considering the extremes of the inshore and offshore zones, it is apparent that, in terms of the understorey algae, the former is more a K-selected, and the latter more an r-selected, environment. The offshore zone is more exposed to swell action at Oudekraal. Catastrophic, non-directed mortalities of plants are visible in the form of storm-cleared areas, particularly the tops of boulders. In deeper water aggregates of urchins move and clear, in a similar non-directed manner, whole patches of understorey algae. Populations of understorey algae are variable and often sparse: in general the population size is well below the carrying capacity of the environment. Algae adapted to such an environment would be 'opportunistic' or 'fugitive' species (Dayton, 1975) or 'ephemerals' in the sense used by Shepherd (1981).

The inshore zone is more protected, at Oudekraal. Dense canopies of kelp reduce surge, and algae seldom appear to be torn off the substrate in large numbers. Grazer-induced mortality is selective, since it probably involves feeding by solitary animals. With dense understorey algae the environment is obviously near its carrying capacity, and there is little substrate for colonisation. This environment would appear to favour K-selection, and most of the algae appear to be "dominants" in the sense of Dayton (1975), Littler and Littler (1980), and Shepherd (1981).

D. firma, by contrast, shows many characteristics of a 'fugitive' or 'ephemeral' species, being largely restricted to an 'r'-selected environment, and showing a distinct annual cycle, populations which vary in density both spatially and seasonally, and the ability to rapidly colonise cleared areas. Insufficient is known of the understorey algal communities to make more than tentative suggestions in this respect, but these observations are felt to be important for future studies of the dynamics of these communities.

# CHAPTER 5

# POPULATION STUDIES

## 5.1 INTRODUCTION

The structure, mortality, growth rate and productivity of the Desmarestia population at Oudekraal form the basis of this chapter. Seasonal changes in population structure are described, together with changes in ash-free dry mass, calorific content, growth rates and standing crop. The effects of such environmental factors as swell action and light penetration on population structure are discussed. On the basis of these succesive measurements of population structure and size distribution it has been possible to estimate the net production of this species at Oudekraal. This study is the first in South Africa to provide such information for a small species of seaweed. Other South African studies have concerned the larger kelps (Dieckmann, 1978; Field et al, 1977; Field et al, 1980 a ). Similar studies of smaller brown seaweeds have been made of Fucus vesiculosis and F. serratus, (Knight and Parke, 1950) and Ascophyllum nodosum (David, 1943) in Britain, of Sargassum pteropleuron in the U.S.A. (Prince and O' Neal, 1979) and of Ascophyllum nodosum in Norway (Baardseth, 1970).

## 5.2 MATERIALS and METHODS

### 5.2.1 Field Methods

All data pertaining to this chapter were obtained from two-monthly collections of Desmarestia from the transects at Oudekraal described in the methods section of Chapter 4. Briefly, counts and collections of specimens were made every two months within 112 rectangular quadrats of 0.25 x 2.0 m, along four randomly placed transect lines; i.e. with 28 quadrats per line. When very large numbers of Desmarestia were present a sub-sample was taken from one-half or a quarter of the quadrat area. Specimens were transported to the laboratory in 20 l buckets of seawater, to prevent the acidic thalli from decomposing. Fresh mass was measured after mopping the specimens with paper towels. Frond lengths were measured to the nearest centimetre. Dry mass, used as a measure of size, was measured by drying the specimens to constant mass in a forced-draught oven at 75°C for 36 hours.

### 5.2.2 Population Structure

Size-distribution histograms were plotted for each two-monthly sample (Figs. 5.2, 5.3). Within one generation of plants it was sometimes difficult to separate, on a dry mass basis, juveniles from older plants which had a similar mass because they were damaged. However, specimens of Generation 1 could be visually distinguished from the older, second generation plants which were consistently thicker, darker, and more leathery.

### 5.2.3 Mortality

Seasonal changes in the numerical mean density of plants i.e. $\frac{\text{total no. of plants in 4 transects}}{\text{total area of transects (56 m}^2\text{)}}$ were used to estimate mortality. (Fig. 5.4).

### 5.2.4 Growth Rate

Growth as an increase in the number and size of cells in a plant is difficult to measure directly. In the laboratory increments in mass are the most practical measurements to make, but when diving it is essential to find some other measurement of growth which does not involve detaching the plants. Increments in the simple length of plants were found to give no

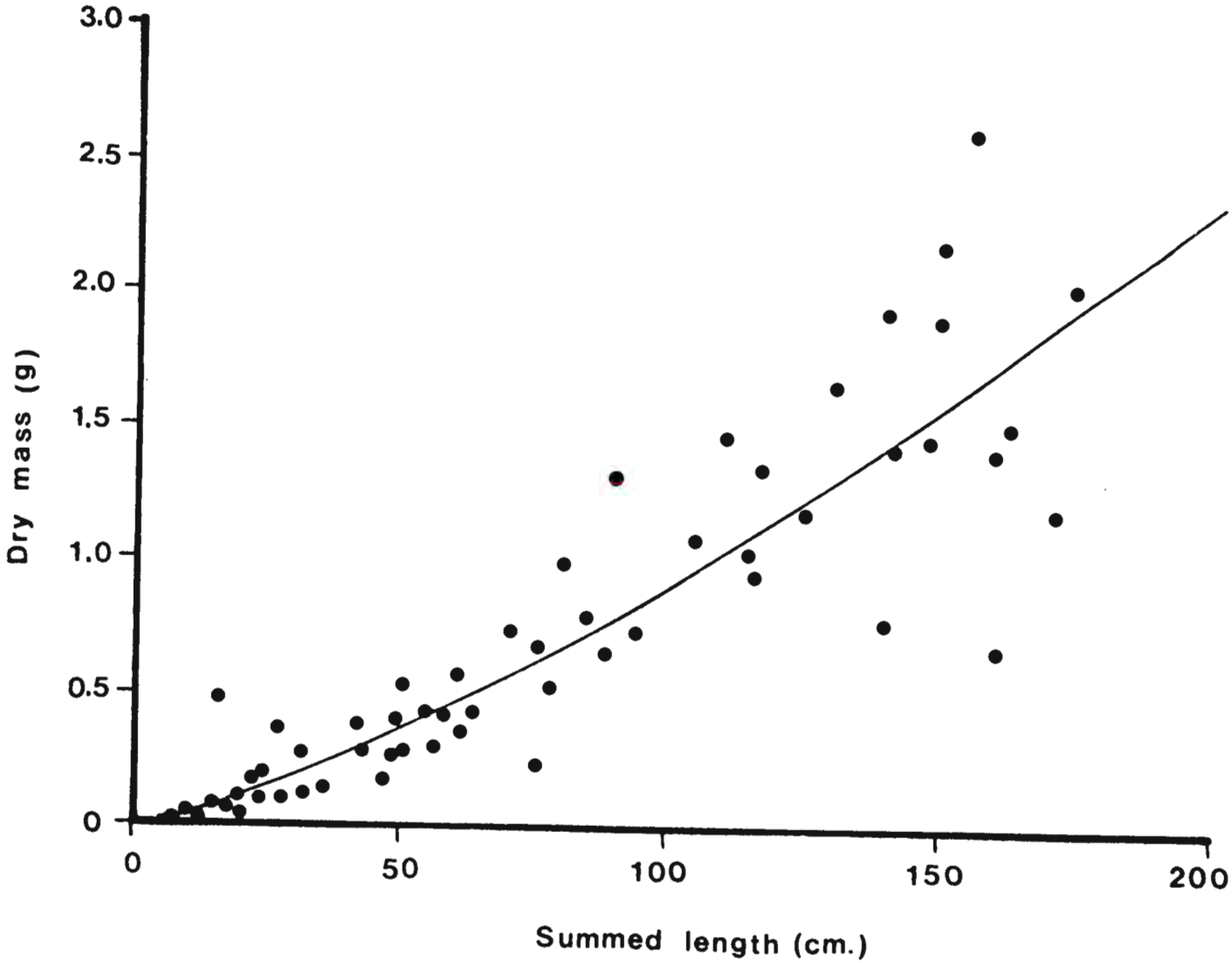



FIG. 5.1 Regression of dry mass on summed length for plants collected in March 1979. Power curve fitted by method of least squares. For reasons of clarity some points omitted. n = 90

reliable indication of increments in mass. This was mainly because the plants varied considerably with respect to their number and arrangement of fronds, and in the extent to which they were eroded or grazed. Therefore the sum of the lengths of all of the individual fronds on each plant was calculated. This measure, termed "summed frond length", was closely correlated with dry mass (Fig. 5.1). Correlation between the two variables was tested by Students' t-test (Zar, 1974) and was significant at the 99.9% probability level. With such a close correlation it is theoretically possible to indirectly measure growth underwater by successively measuring summed frond length of individual tagged specimens. This was attempted, but the project had to be abandoned because of difficulties in tagging the fragile plants and in relocating specimens. Growth is therefore estimated in terms of the change in summed frond length and mean dry mass values of all the plants in each 2-monthly sample (Figs. 5.5, 5.6, 5.7).

### 5.2.5 Percentage Dry Mass

The dry mass of Desmarestia, expressed as a percentage of its fresh mass (Fig. 5.8), was measured, to follow any seasonal changes in the content of water and volatile substances in the plants, relative to the amount of structural and stored material.

### 5.2.6 Ash Content

Ash content was determined by heating 15 - 20 samples in a muffle furnace for 4 hours at 540 - 550°C. Ash content is expressed as a percentage of dry mass. (Fig. 5.9).

### 5.2.7 Calorific Content

The calorific values for D. firma were determined with a Phillipson ballistic macro-bomb calorimeter according to methods described in Gentry Instruments Inc. Manual, and in the IBP Handbook No. 24 (Grodzinski et al, 1975). Samples were dried to constant

dry mass at 75°C then ground in a mill. After grinding the samples were dried at 60°C for 24 hours before being ignited in the bomb. Samples weighed approximately 300 mg before ignition. Seasonal calorific values are presented in Figs. 5.10, 5.11.

The energy contents of 12 - 15 individual plants in each sample were measured. Energy content is expressed both in terms of dry mass and ash-free dry mass. Because energy content expressed on a dry mass basis is generally inversely related to the inorganic content, energy is best expressed on an ash-free basis (Paine and Vadas, 1969).

### 5.2.8 Standing Crop

The standing crop of each two-monthly sample (representing $56m^2$) was calculated directly as the sum of the dry masses of all of the plants in each sample.

Between 25 March and 4 April, 1979, 8 additional transects were completed, but these were placed outside my study site, in areas of Oudekraal kelp bed described by Velimirov et al (1977) as "mediate" and "inshore" (Chapter 1, Fig. 1.2). The purpose of these transects was to estimate the Desmarestia standing crop for the entire Oudekraal kelp bed. The numerical densities of the plants were recorded, and the March 1979 value of mean dry mass per plant (Fig. 5.6) which had been obtained in the smaller study site was used to estimate standing crop for the mediate and inshore areas. The mean standing crop of D. firma in the whole kelp bed (March - April 1979) is summarised in Table 5.12.

### 5.2.9 Net Production

For the purpose of this study, net production is defined as the dry mass of plant material produced per unit area of substrate, over a certain period. This includes losses via grazers and erosion, mortality of whole plants, exudation of organic matter and spore production. If respiratory losses are added to the value obtained for net production, gross

production is obtained.

The sporophyte of D. firma is an annual, and becomes visible to the naked eye in Spring (September - November). The entire population can thus be treated as a "cohort" or "generation", and its net productivity may be estimated by the Allen curve method (Allen, 1951), successfully applied to plant populations by Matthews and Westlake (1969).

The net production equation can be summarised as follows (based largely on Westlake, 1963):

$$Pn = \Delta B + (G+D) + L + DOM + S$$

Where Pn = net production (g.dry mass. $m^{-2}$ unit $time^{-1}$).
$\Delta B$ = change in standing crop. unit $time^{-1}$).
(G + D) = losses by grazing and erosion. These are estimated as one value, since for practical reasons they cannot be separated.
L = mortality losses (entire plants)
DOM = "Dissolved Organic Matter" exuded by the living plant.
S = losses in spore release.

This study attempts to estimate the major components of this equation.

a) Change in standing crop ($\Delta B$):
By the Allen Curve method (Allen, ibid) the number of organisms per unit area is plotted against their mean dry mass at regular intervals throughout the life of a generation. The area under the curve then represents the dry mass of material produced in that period (Fig. 5.15). In the present study, the Allen Curve data were modified to obtain a "smoothed Allen Curve" (Peer, 1970). This involved calculating linear regressions for the density of plants against time of year (Fig. 5.13), and for mean dry mass of plants against time of year (Fig. 5.14). The regressive values for respective months are then plotted in an Allen Curve (Fig. 5.15).

b) Grazing and Erosion Losses

Losses to grazers and by erosion were estimated by comparing specimens which were obviously intact and undamaged with all the other specimens. Mean dry mass of the undamaged plants was compared with the mean dry mass of all the other plants comprising the sample. Relatively few of the routinely sampled plants were however intact. Additional intact specimens were therefore collected from areas adjacent to the quadrats so that at least thirty specimens comprised each "intact" sample. A second smoothed Allen Curve was constructed using the measurements of "intact" plants, and the same density data as for the routine samples (Fig. 5.15 curve b). The total area beneath this curve provides an estimate of potential production; that is, in the absence of grazing and erosion. Such an estimate is based on the assumption that, under these circumstances, the whole population would have been in the same state as these "intact" plants, and that mortality (whole plant) losses for a population of intact plants would be the same as for the sample as a whole. The difference in area between the two respective smoothed Allen Curves (Figs. 5.15 a and b) estimates losses by grazing and erosion.

c) Mortality (L)

Production lost by mortality is calculated directly from the Allen Curve (Fig. 5.15 curve a) and is represented by the approximately triangular, unstippled area. This area is the integral of mortality rate and the increase in mean dry mass of the plants, from November 1978 to July 1979. Ultimately (after October, 1979) all the plants were lost, so that there is 100% mortality.

d) Losses as Dissolved Organic Matter (DOM) and in the Form of Released Spores.

No attempts were made to measure either of these components which are assumed to be minor relative to erosion, grazing, and mortality.

## 5.3 RESULTS

### 5.3.1 Seasonal Size Distribution of Plants (Figs. 5.2, 5.3)

Between July 1978 (when sampling commenced) and mid-January, 1979, the mean dry mass of Generation 1 plants declined, as did the number of large plants (Figs. 5.2, 5.3). Generation 2 appeared early in summer (November, 1978) and by winter (May - July, 1979) there was a wide range of sizes in the population, but with the majority still of less than 1 g dry mass. Between November 1978 and March 1979 the two generations overlapped.

By comparing the size distributions of the two generations at the end of their respective growing seasons, it could be seen that the second generation population contained relatively fewer large plants (i.e. more than 5 g) than the first.

### 5.3.2 Mortality (Fig. 5.4)

The mortality rate of the first generation was steady between July 1978 and January 1979, and then declined slightly. The second generation exhibited a similar pattern, although densities of second generation plants were consistently lower. The majority of plants lost are thought to be torn off the substrate by wave action. Most of the *D. firma* plants collected in drift (an estimated 50 - 60%) still had holdfasts, and of these, many were attached to small mussels, while a few were even found with fragments of rock attached to their holdfasts.

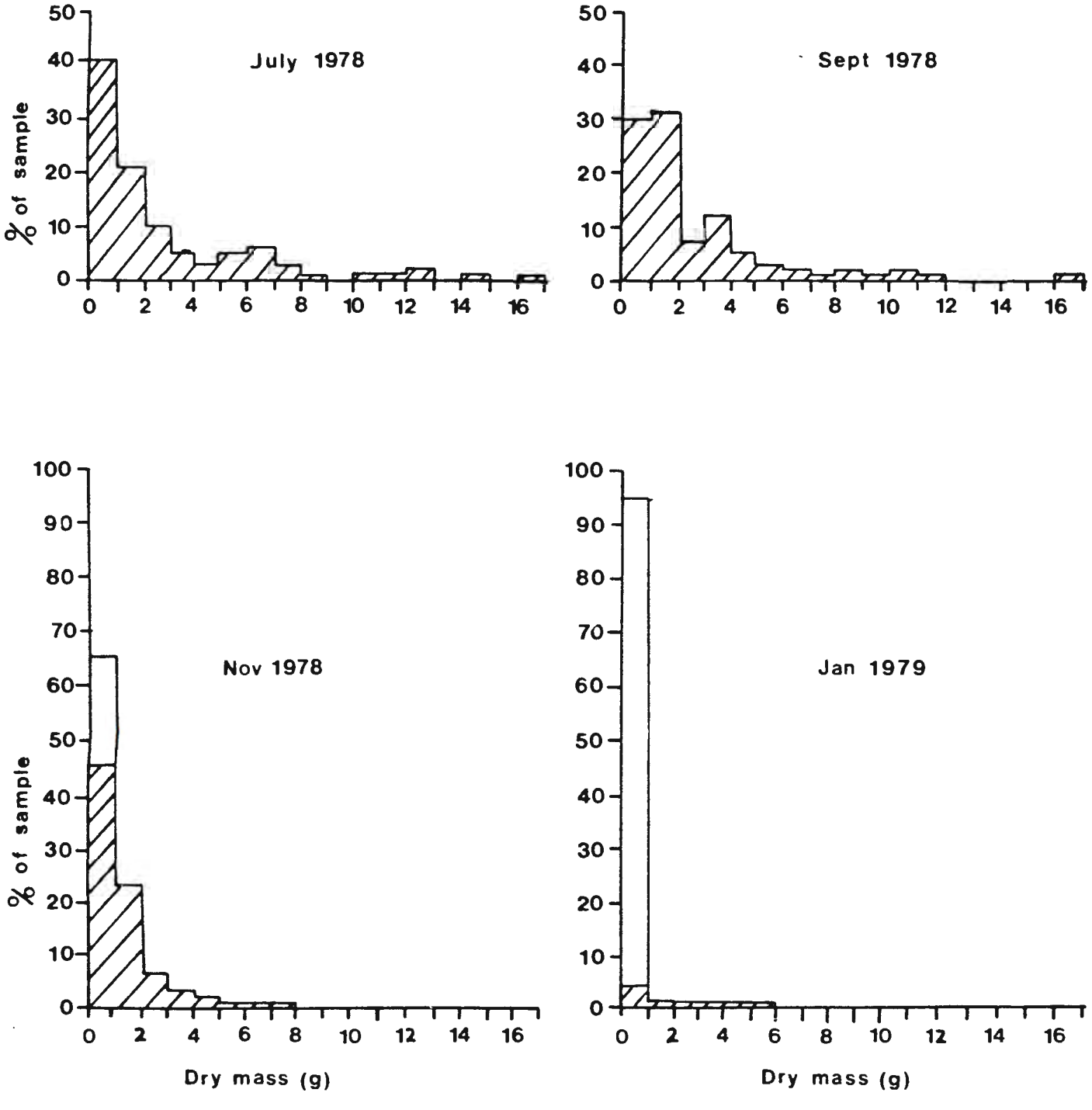



FIG. 5.2 Histograms showing size-distribution (g. dry mass) of plants in each sample, from July 1978 to January 1979. ▨ - Generation 1; ⊓ - Generation 2.

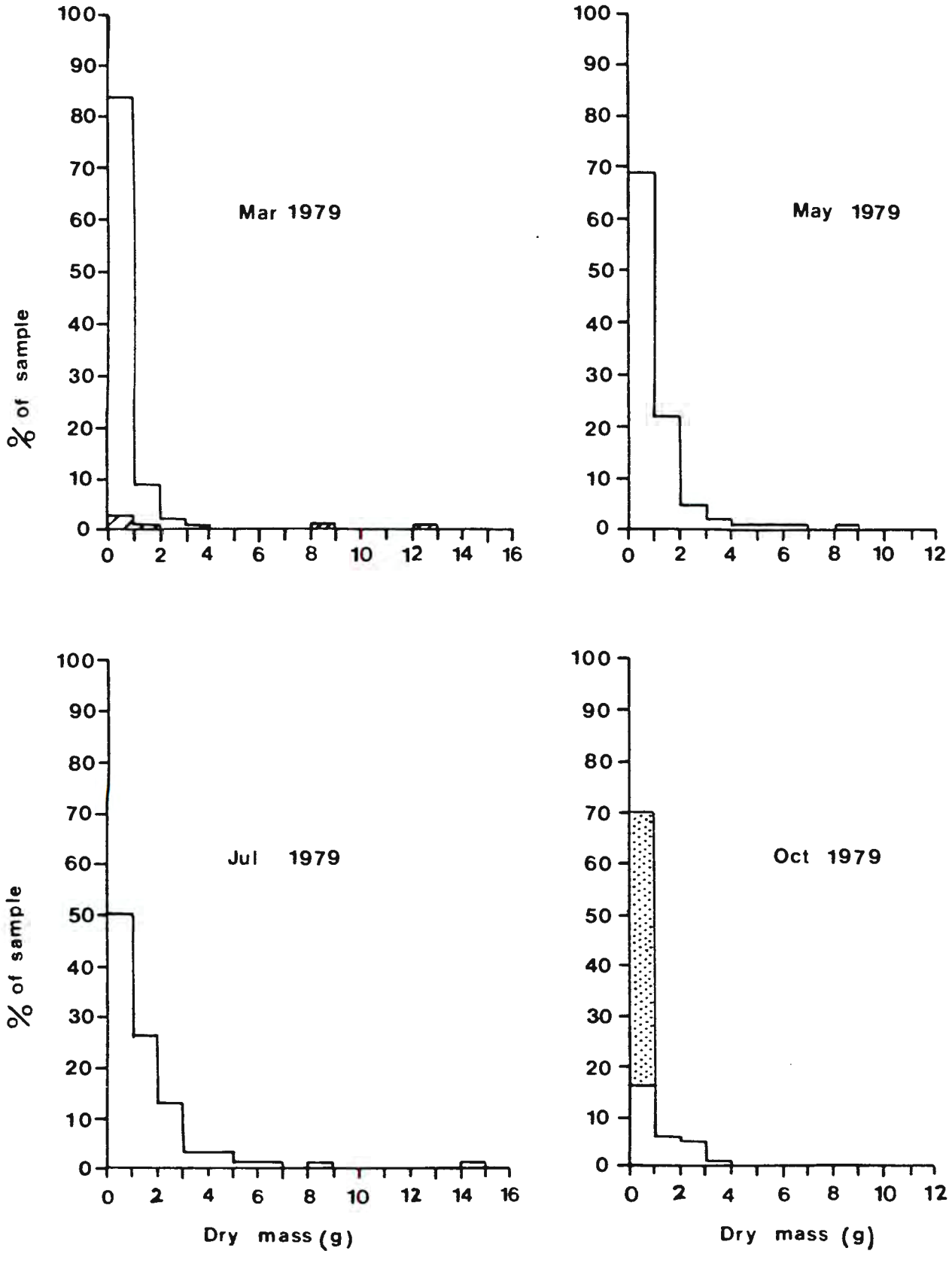



FIG. 5.3 Histograms showing size-distribution (g. dry mass) of plants in each sample, from March 1979 to October 1979. ⊓ - Generation 2; ⊡ - Generation 3.

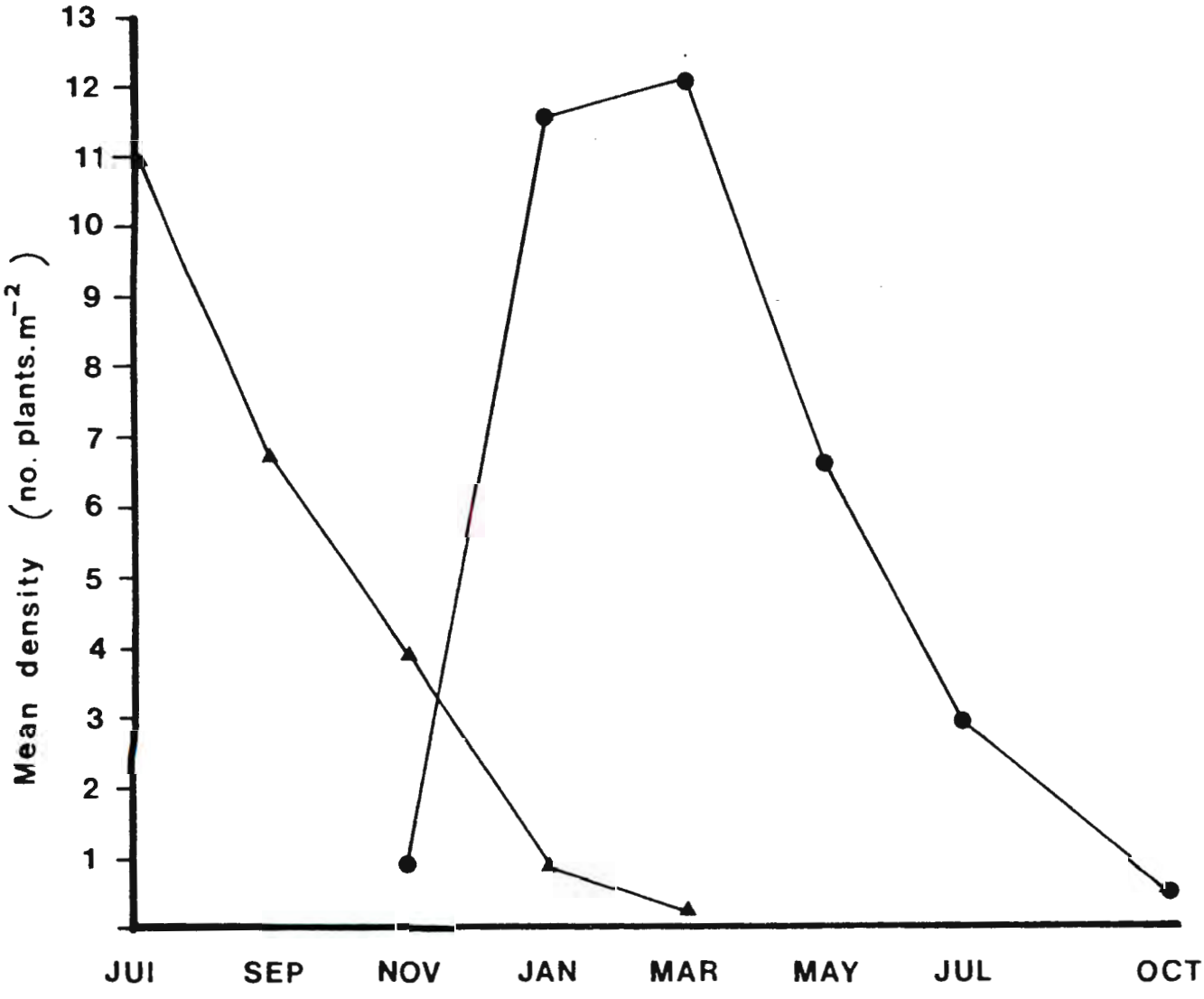



FIG. 5.4 Seasonal changes in mean density of *D. firma* in study site, from July 1978 to October 1979. ▲—▲ - Generation 1; ●—● - Generation 2.

## 5.3.3 Growth Rates (Figs. 5.5, 5.6, 5.7)

The mean dry mass and the mean summed length of plants increased steadily through summer, into early winter. Old plants showed no signs of regeneration in the following spring. The mean growth rate of "intact" plants (Figs. 5.5, 5.6 curve c) equals about 26 cm (in terms of summed frond length), or 0.5g dry mass, per month. Average values based on the entire sample (curve b) were of course much lower (10 cm per month; 0.2 g dry mass per month).

Growth may also be expressed in relative terms, as the percentage increase in dry mass of the plants, over each 2-monthly sampling period (Fig. 5.7). These results show that all plants of the population increased their mean dry mass approximately 700% during the period November 1978 - January 1978. In the subsequent period (January - March) this relative growth rate remains high (625%) in the intact plants, while it declines to 320% in the whole sample. In March to May all plants showed an approximate 230% increase in dry mass. In May - July this declined slightly (220%) in "intact" plants, and the mean value for *all plants* in the sample was 160%.

Thus, the relative growth rate of all plants in the population was highest at the start of the growing season, and thereafter declined steadily until winter, when growth apparently ceased.

During the first two months of growth of second generation plants (November to January), mean summed length increased by a factor of 6, while mean dry mass increased by a factor of 7 (Figs. 5.5 curve b and 5.6 curve b, respectively). Then from January until July, the rate of increase in mean summed length declined (an approximately fourfold increase in six months - Fig 5.5 curve b) while in the same period, mean dry mass increased some 14 times, from 0.1 to 1.4 g dry mass (Fig. 5.6 curve b).

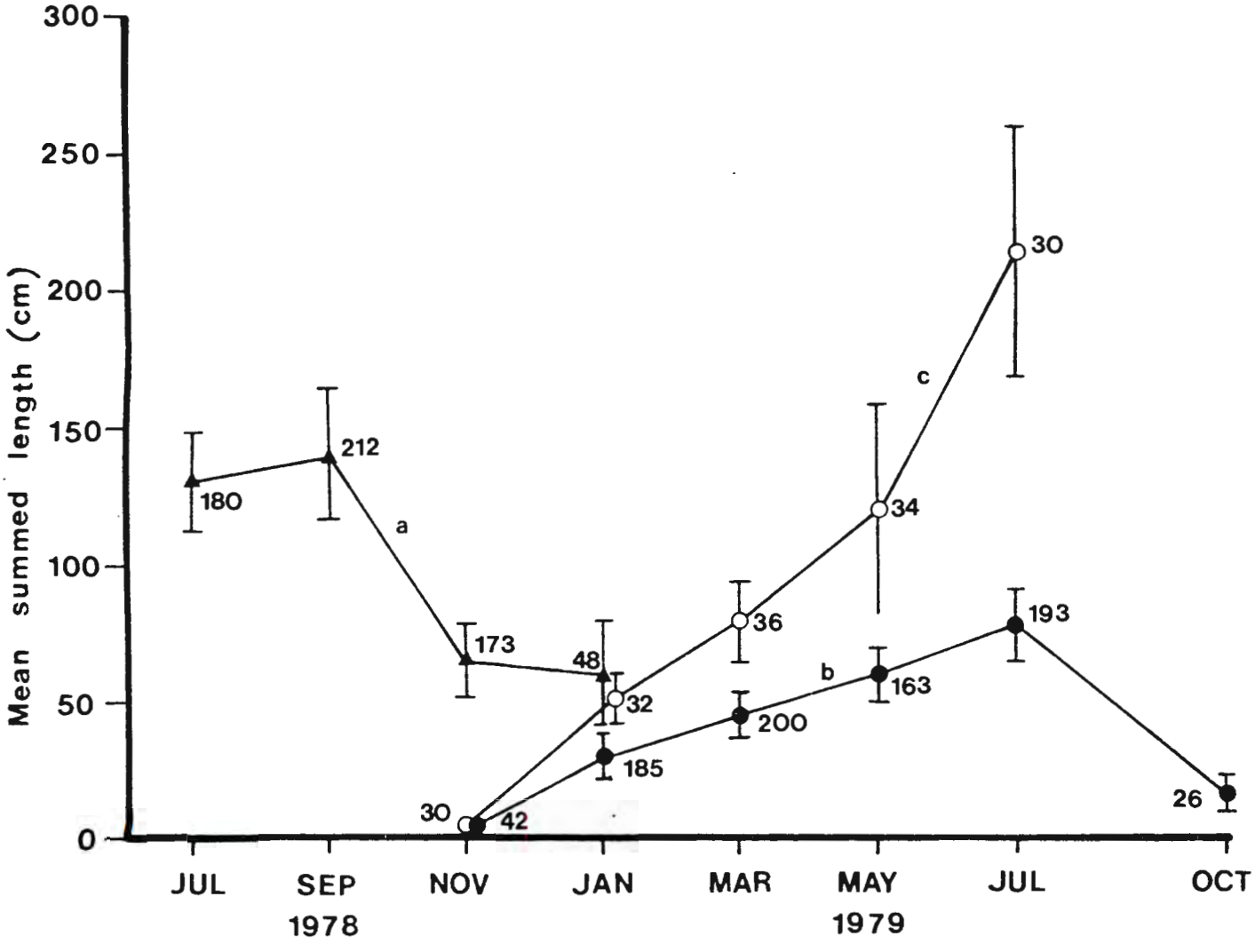



FIG 5.5 Mean summed lengths of D. firma plants, from July 1978 to October 1979. 95% confidence limits of means shown. ▲—▲ - Generation 1; O—O - Generation 2, entire sample; ●—● - Generation 2, intact plants only. Numbers of plants in each sample (n) adjacent to each point.

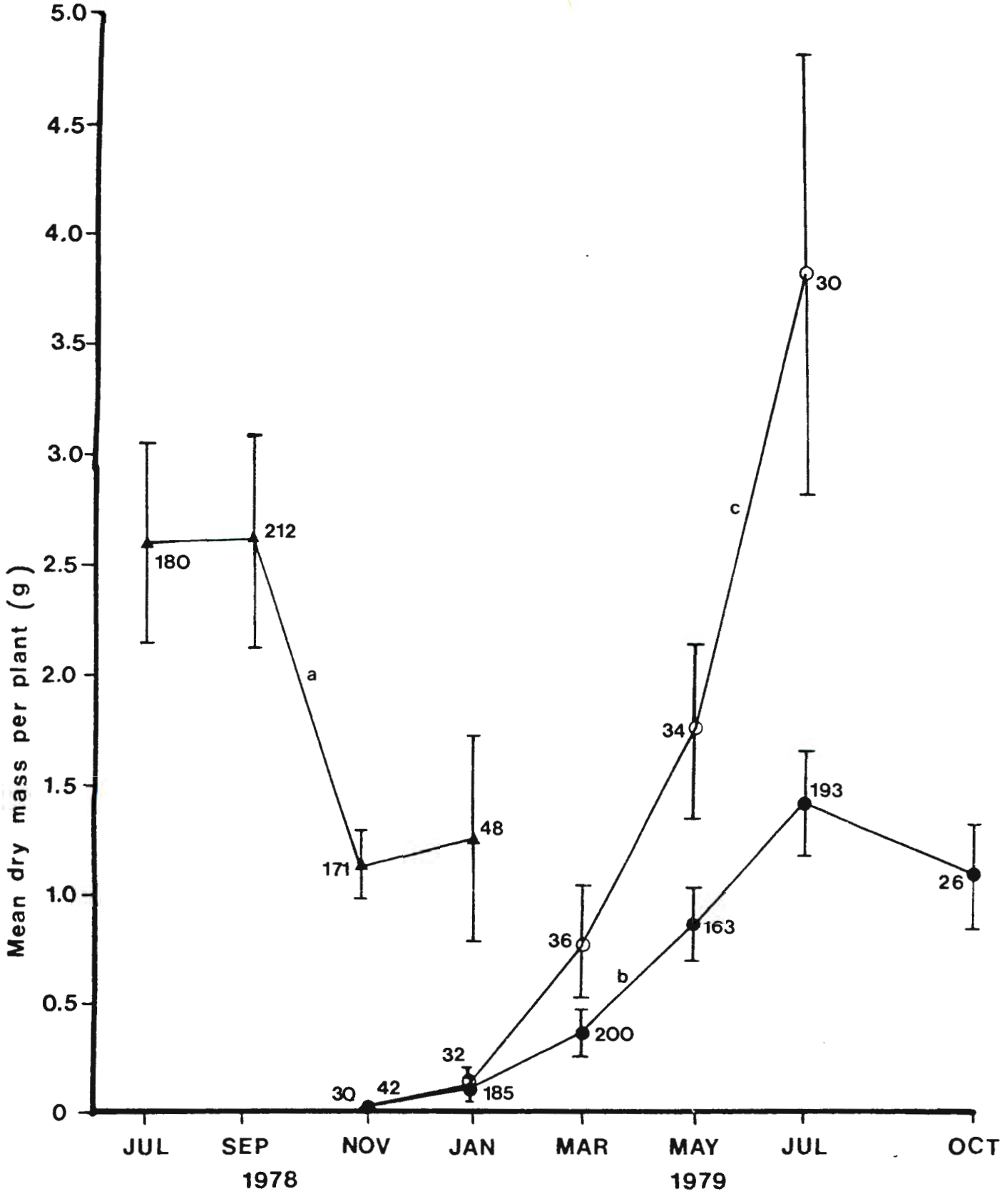



FIG. 5.6 Mean dry mass per plant (g) for each sample from July 1978 to October 1979. 95% confidence limits of means shown. ▲—▲ - Generation 1; O—O - Generation 2, entire sample; ●—● - Generation 2, intact plants only. Numbers of plants in each sample (n) adjacent to each point.

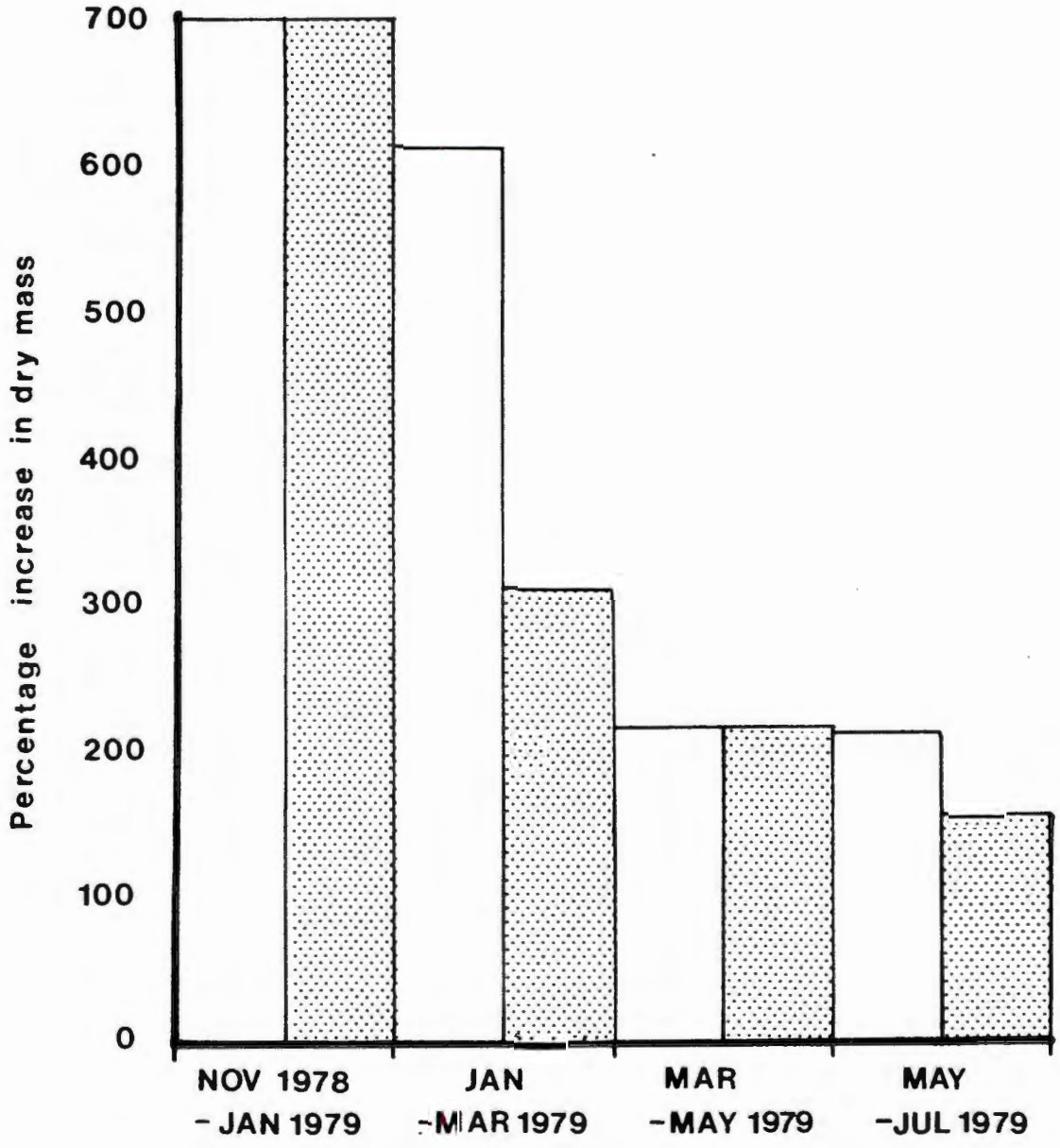



FIG. 5.7 Two-monthly percentage increase in dry mass of plants of Gen. 2 from November 1978 to July 1979.
▨ - entire sample; ⌜ ⌝ - intact plants only.

### 5.3.4 Dry Mass Expressed as a Percentage of Wet Mass (Fig. 5.8)

In January 1979, the old, first generation plants contained 3.5% less water and volatile substances than the young specimens of the second generation. Evidently as the plants aged there was an increase in their percentage dry mass. Second generation plants showed an increase from 9% in January 1979 to a stable value of 10.7 - 10.8% in July - October. There was a difference of approximately 2% in the percentage dry mass of plants in October of the respective seasons. The percentage dry mass of Generation 1 declined slightly after July, but this did not occur in Generation 2.

### 5.3.5 Ash Content (Fig. 5.9)

Between January and March the ash content of old, Generation 1 plants was approximately 3% lower than that of the younger Generation 2 plants. By following the ash content of Generation 2 plants a substantial decrease in percentage ash can be seen in winter (from 39.4% down to 33.8%). Both generations then show increases in late winter and spring (July to September). In plants of the first generation, the percentage ash declines during spring and summer, from over 40% (September 1978) to 35.2% in autumn (March 1979). Presumably a similar trend would have been observed for plants of the second generation, but insufficient plants remained after October 1979 to make the necessary analyses.

### 5.3.6 Calorific Content (Figs. 5.10, 5.11)

Seasonal trends in calorific content were similar whether expressed as per dry mass or per ash-free dry mass (Figs. 5.10, 5.11 respectively). Plants of Generation 1 showed a relatively low value (13.7 $K.J.g^{-1}$ a.f.d.m.) in July, increasing to between 15 and 17 $K.J.g^{-1}$ a.f.d.m. during spring and summer. The calorific content of plants of Generation 2 increased from January, when they first appeared, until March. From March until October, when sampling ceased, values were consistently in the 15 - 16 $K.J.g^{-1}$ a.f.d.m. range.

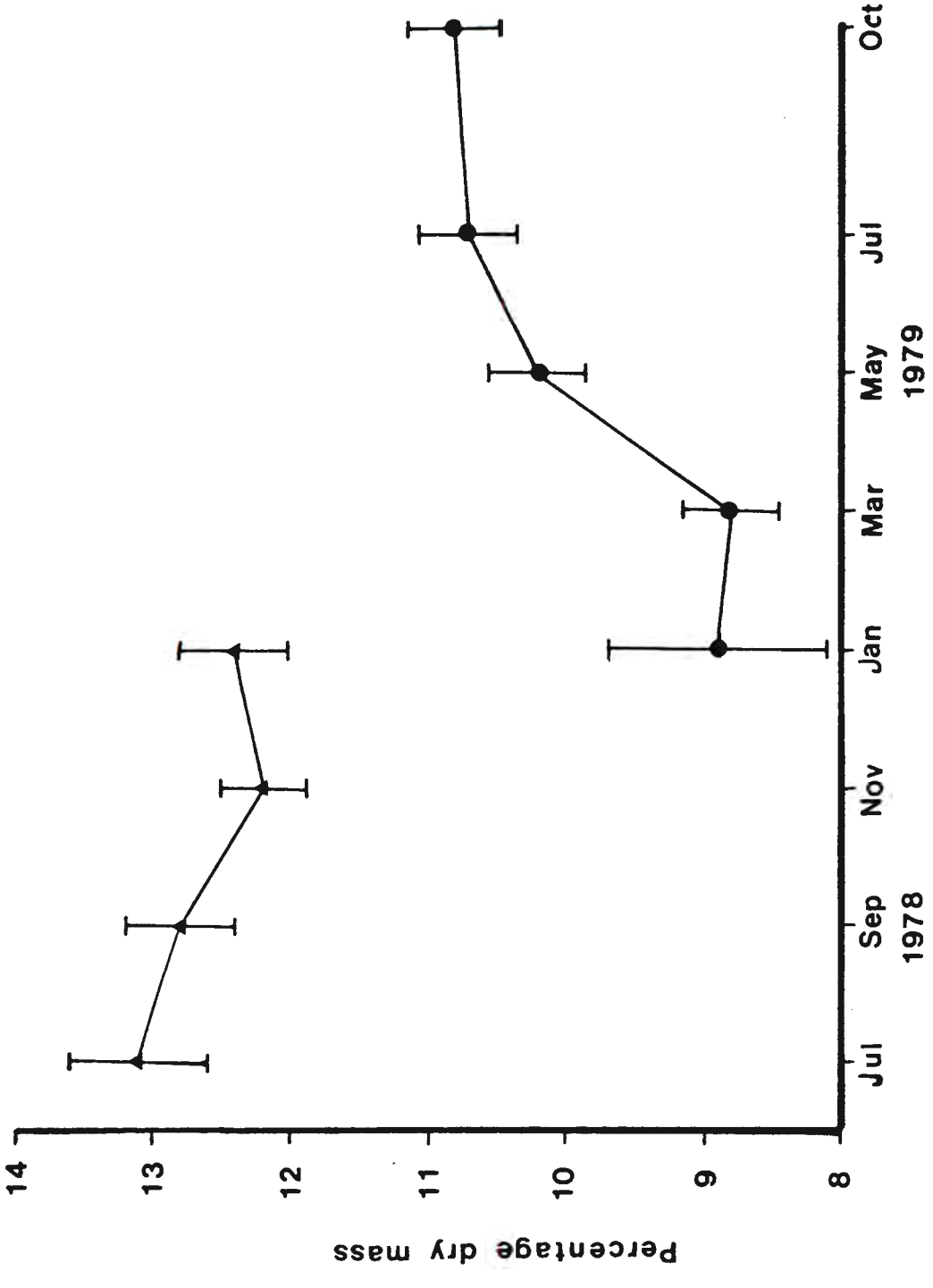



FIG. 5.8 Dry mass of D. firma expressed as a percentage of fresh mass. Each point is a mean of 40 specimens, with 95% confidence limits shown.
▲—▲ - Generation 1; ●—● - Generation 2.

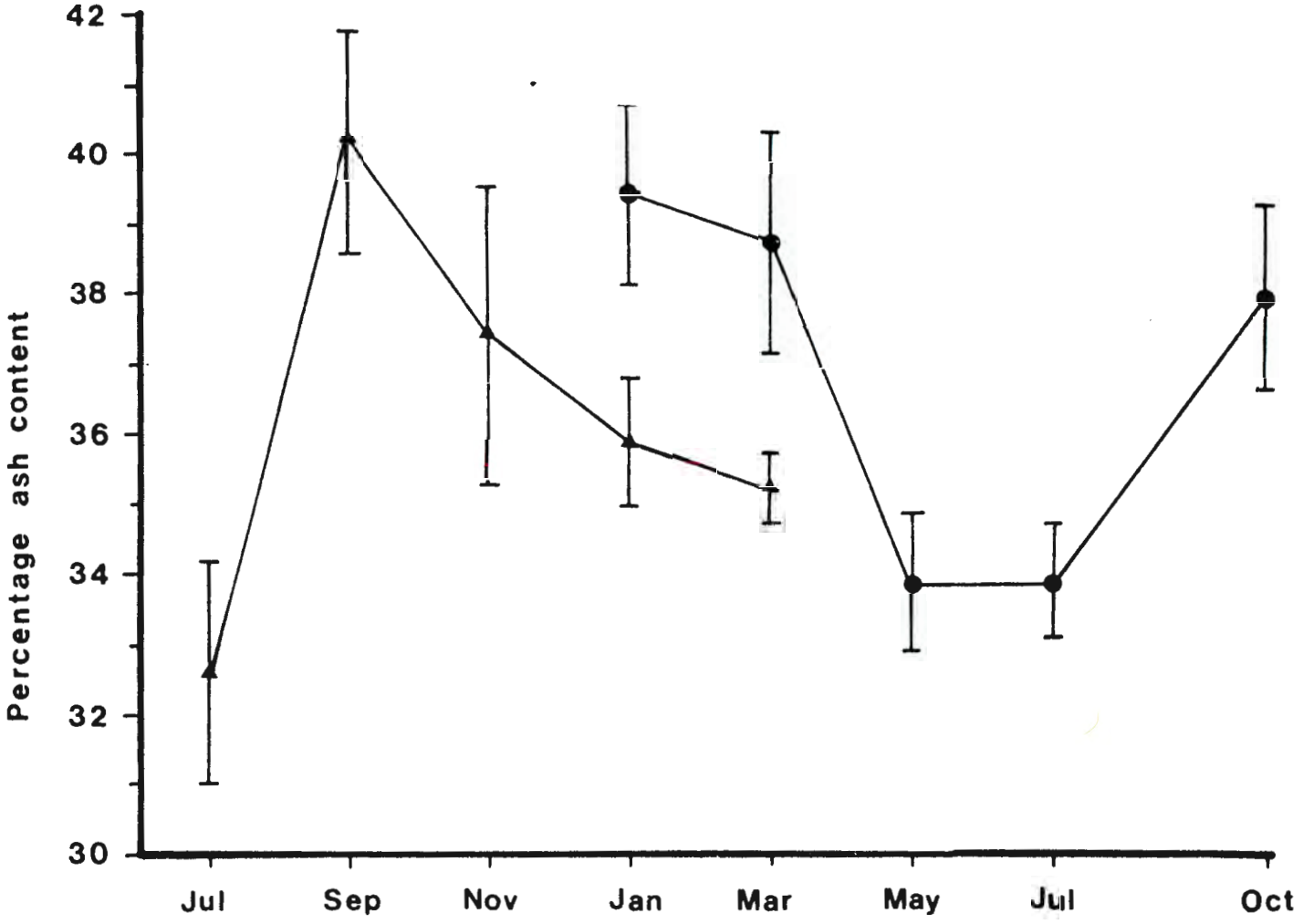



FIG. 5.9 Ash as a percentage of dry mass. Each point is the mean of 15 - 20 plants, with 95% confidence limits shown. ▲—▲ - Generation 1; ●—● -Generation 2.

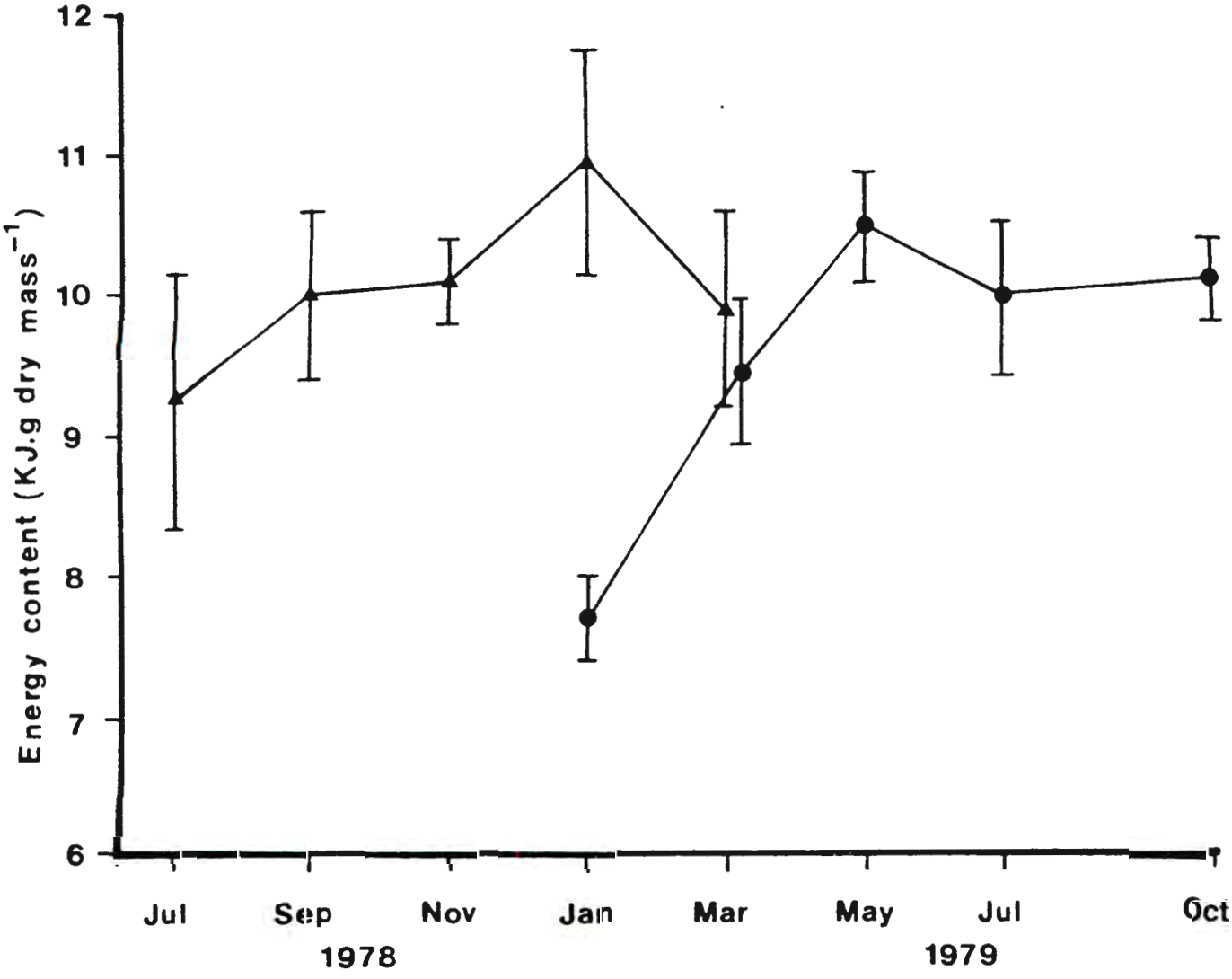



FIG. 5.10 Energy content of D. firma (kJ.g dry mass). Each point is mean of values for 12 - 15 plants with 95% confidence limits. ▲—▲ - Generation 1; ●—● - Generation 2.

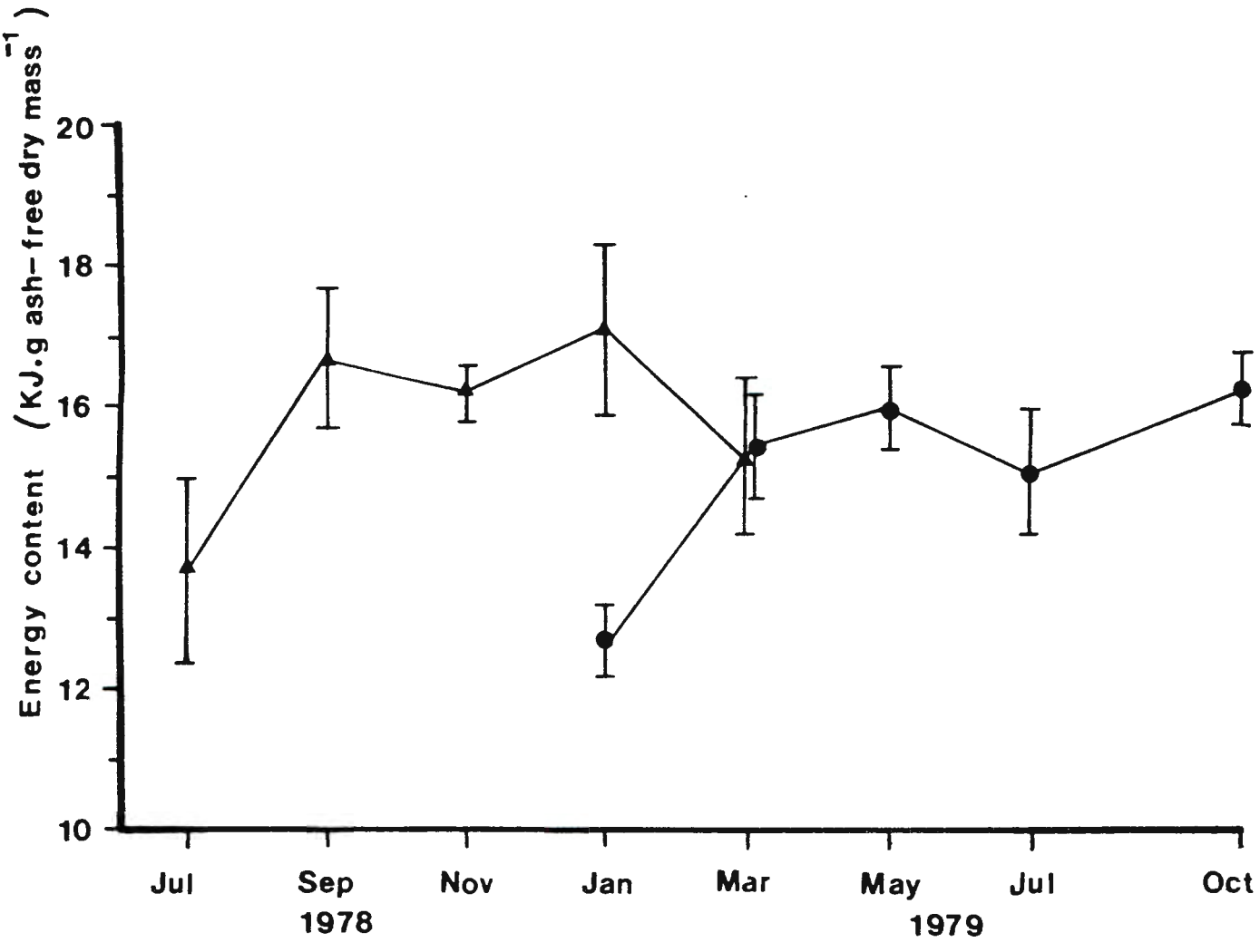



FIG. 5.11 Energy content of D. firma (kJ.g$^{-1}$ ash-free dry mass). Each point is mean of 12 - 15 plants with 95% confidence limits. ▲—▲ - Generation 1; ●—● - Generation 2.

## 5.3.7 Standing Crop (Fig. 5.12)

The standing crop of Generation 1 plants declined from a high value of 29 $g.m^{-2}$ in July 1978 to a low value of 0.5 $g.m^{-2}$ in March, 1979, when only remnants of plants persisted.

The maximum standing crop of Generation 2 (approximately 6.5 $g.m^{-2}$ in March 1979) was relatively low compared with that of Generation 1. The standing crop of Generation 2 increased symmetrically through early summer to the onset of winter, and thereafter declined. In October 1979 the first plants of a third generation had begun to appear. Their appearance was thus one month earlier than the arrival of Generation 2 plants, and indicates year-to-year differences in the time of appearance of the first sporelings of the *D. firma* population.

The March/April 1979 standing crop of *D. firma* in the entire kelp bed was 1.5 g dry mass.$m^{-2}$ (Fig. 5.12) or approximately 14.9 $kJ.m^{-2}$. This standing crop is considerably lower than that in the offshore zone (study site) only, in May 1974 (6.5 $g.m^{2}$ or 68.3 $kJ.m^{-2}$).

From observations made during the course of dives along the west coast of the Cape Peninsula, it was noted that standing crops of *D. firma* varied considerably from place to place. Furthermore, extensive observations on drift material showed that this species may be absent from drift in certain areas, while in others it may be abundant. On one occasion, at Scarborough, on the Cape Peninsula, *D. firma* made up more than 90% of the weight of drift algae. Large amounts of drifting *D. firma* (and other algae) are typically found after storms.

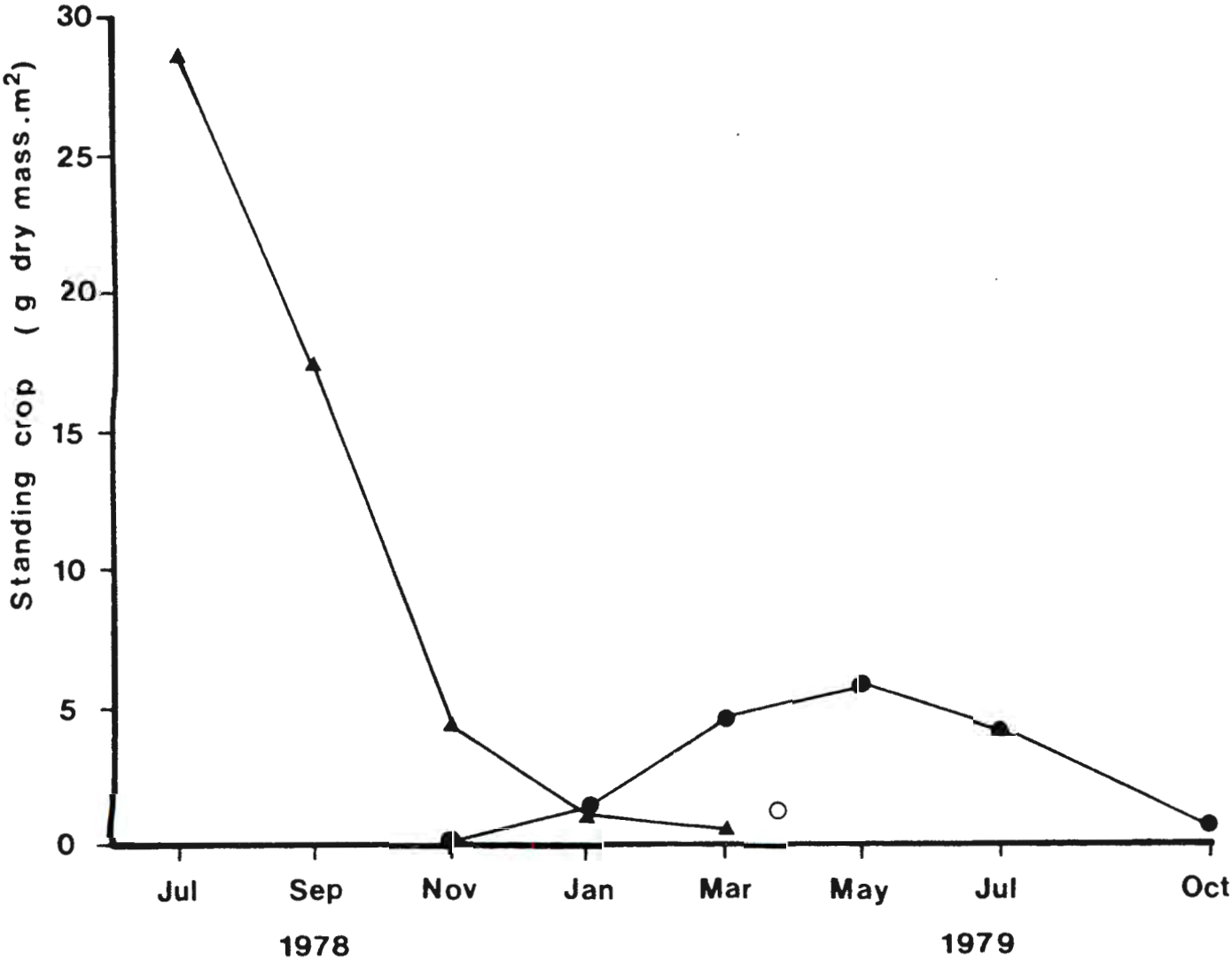



FIG. 5.12 - Seasonal changes in standing crop of D. firma in study site. ▲—▲ - Generation 1; ●—● - Generation 2; O - standing crop of D. firma in whole kelp bed, Oudekraal, March/April 1979.

## 5.3.8 Net Production

The high coefficient of determination ($r^2$) obtained for the 3 regression curves (Figs. 5.13, 5.14 A, B) indicated that unsmoothed Allen Curves would have differed little from these smoothed ones (Fig. 5.15 A, B). The area under Allen Curve A (Fig. 5.15) provided estimates for two components in the primary production equation, for the period November 1978 to July 1979:

Standing crop (B) = 5.7 g. dry mass. $m^{-2}$
Mortality losses (L)= 5.1 g. dry mass. $m^{-2}$
The sum of these, here denoted as $P_1 = (B + L)$
$= 10.8$ g dry mass. $m^{-2}$

The curve based on intact plants (Fig. 5.15, curve B) yielded an estimated "potential" production, "$P_2$" = 23.4 g dry mass. $m^{-2}$ (represented by the total area under the curve). The difference between the areas under the two curves, i.e. the difference between the actual production and the "potential" production ($P_2 - P_1$), from November 1978 to July 1979, is therefore equal to the estimate of grazing and decay (G + D), and equals 12.6 g dry mass. $m^{-2}$.

Between November 1978 and July 1979, a summary of the estimated net productivity was

$$Pn = 5.7 + 5.1 + 12.6 + DOM\ ? + S\ ?\ g.m^{-2}$$
$$= 23.4 + DOM\ ? + S\ ?\ g.m^{-2} \text{ (Fig. 5.16)}$$

At the end of the growing season (approximately in July) the production:standing crop ratio was therefore $\frac{23.4}{5.7} = 4.1$. Between July and October 1979, tissue was lost to erosion and grazing faster than it could be produced and this is reflected in the negative production values for this period.

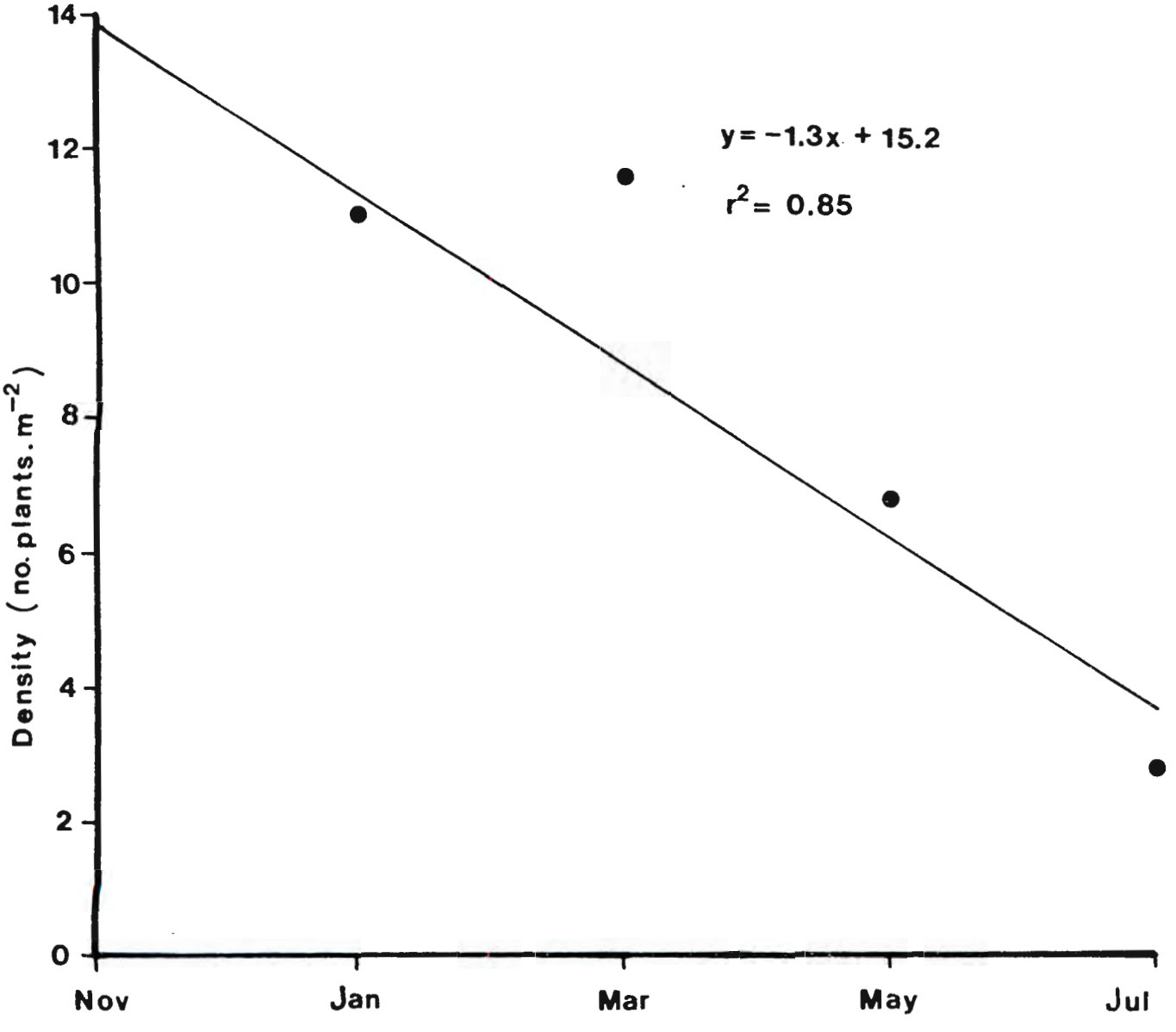



FIG. 5.13 Linear regression: mean density of Generation 2 plants against time (2 monthly intervals).

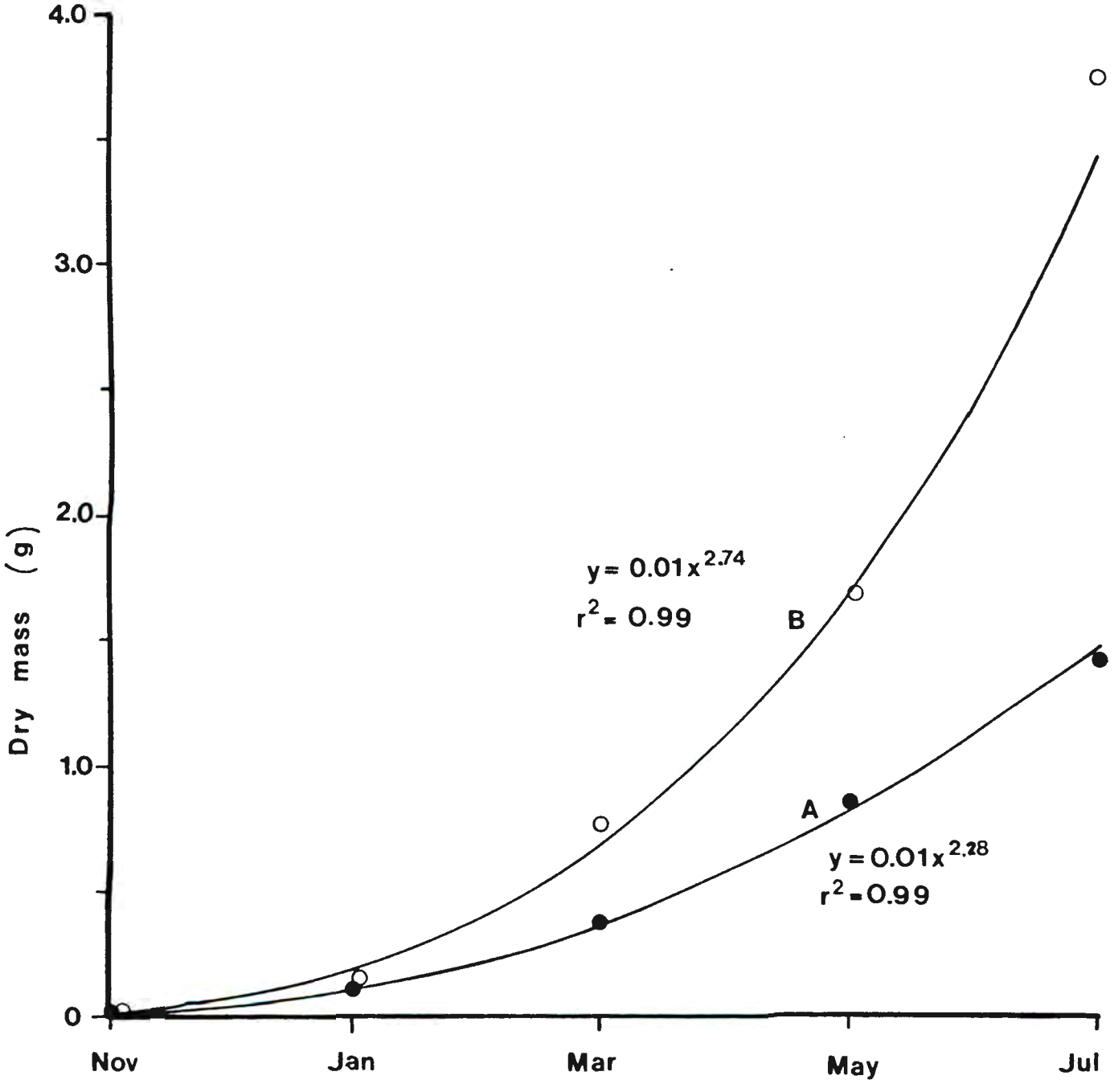



FIG. 5.14 Relationship between mean dry mass of plants in each sample (g.) and time of sampling for Generation 2.
Power curves fitted by method of least squares.
A - entire sample; B - intact plants only.

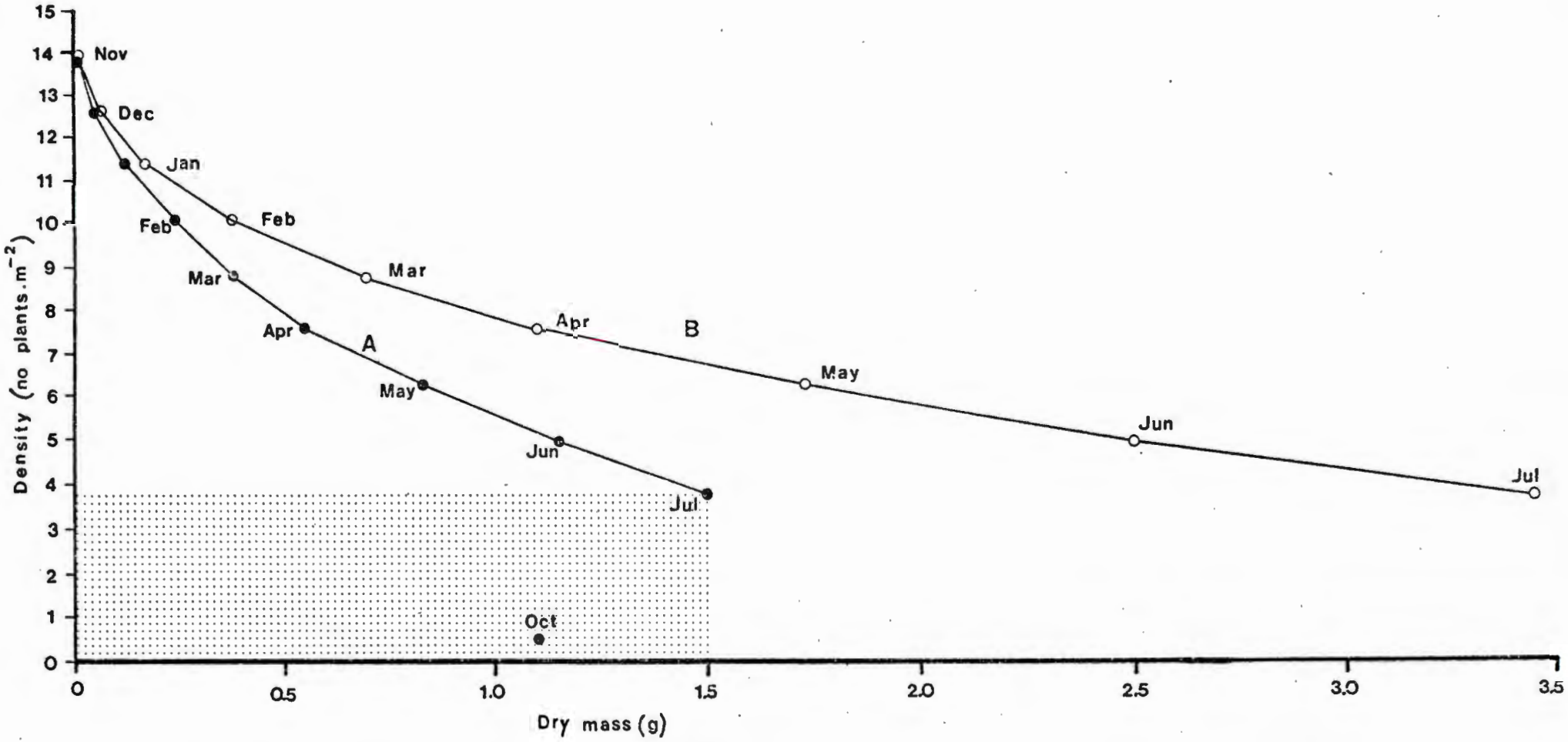



FIG. 5.15 Smoothed Allen Curves, for plants of Generation 2. A- (-●-) entire sample; B- (-o-) intact plants only. Stippled rectangle under Curve A represents the July 1979 standing crop of the entire sample. (See text, pages 109 – 110).

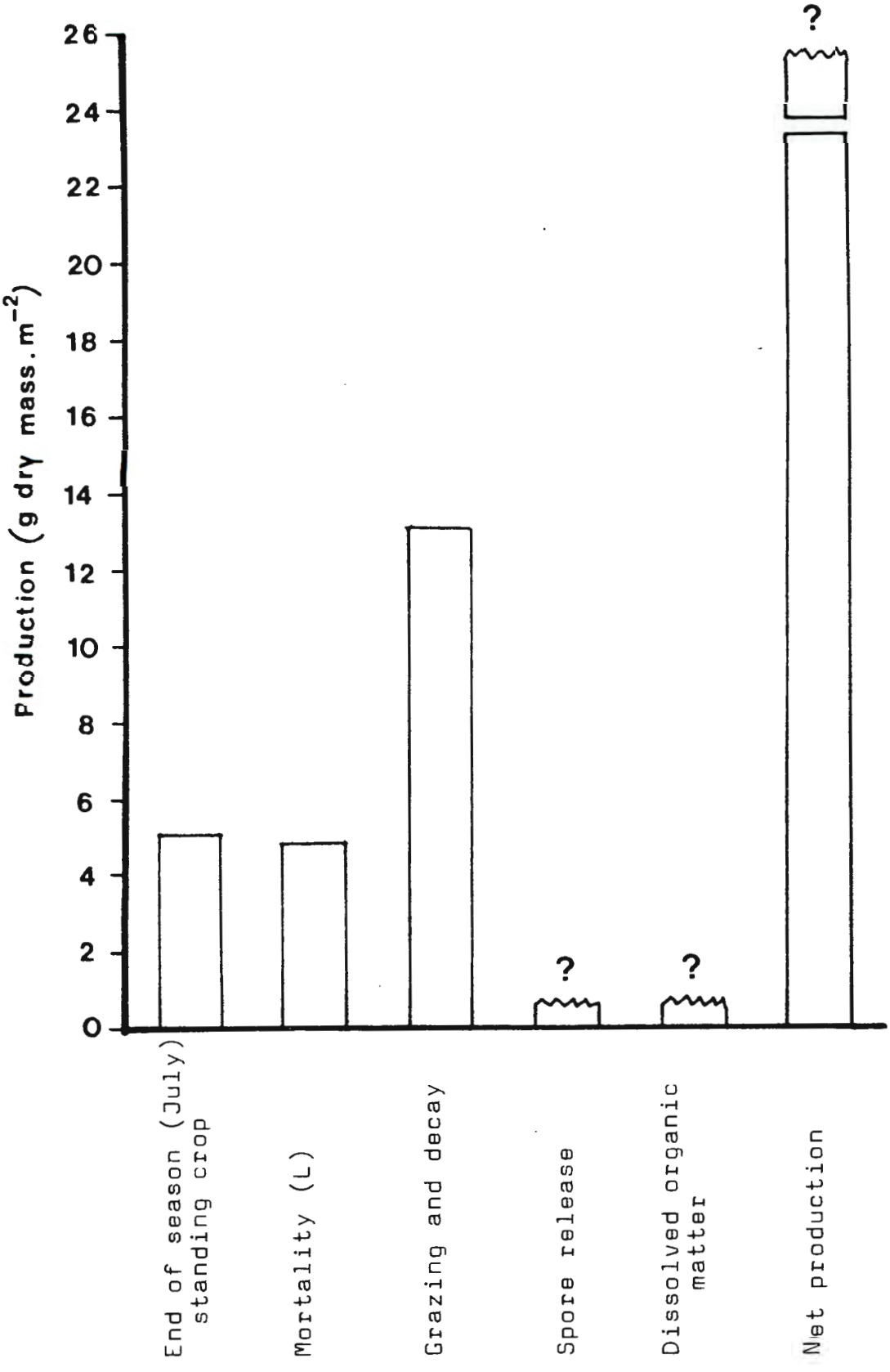



FIG. 5.16 Bar-graph summarizing the net production of D. firma in the study site from November 1978 to July 1979.

## 5.4 DISCUSSION

### 5.4.1 Seasonal Size Distribution of Plants

The decline in the size of plants, during winter (Figs. 5.2, 5.3) may be a result of the erosion of plants, and senescence and a decline in growth caused by lower light and nutrient levels accompanying downwelling. Also, this effect may be an artifact caused by a lowering of the mean values by disproportionately high mortality among large specimens. Probably a combination of all of these factors accounts for the decline in the size of plants.

The persistence of relatively more large plants in Generation 1 (July - September 1978) compared to Generation 2 (July - October 1979) may be related to annual variations in grazer pressure, or light penetration, or swell action. Certainly, swells were larger and more frequent during February - July 1979 than during the same period of the previous year (Fig. 2.6). Heavy swells are generally accompanied by downwelling conditions, so in terms of underwater illumination and the availability of nutrients, the 1979 summer season would have been less favourable for the growth of macrophytes, than that of 1978.

The high percentage of small plants (0.01 - 1.0 dry mass) present throughout the sampling period does not indicate constant settlement and recruitment. Young and heavily eroded plants are not separated on the basis of their mass, so that as the season progresses, the percentage of 'small' plants is kept fairly high by the inclusion of damaged individuals.

Although some new sporelings were found as late as March, 1979, the great majority settled in spring and early summer (October - December 1978). Nevertheless the presence of occasional new juvenile plants in the summer months shows that persistent old plants of the previous generation remain sporogenous well into their second summer, or that fertile gametophytes may be present in summer.

### 5.4.2 Mortality

A number of factors cause mortality, but grazing and detachment during large swells are likely to be the most important. High mortality rates of first generation plants during July - September 1978 and second generation plants during March - May 1979 (Fig. 5.4) coincided with periods when large swells were frequent (Fig. 1.6). During January - March 1979 when there was very little swell the rates of mortality were relatively low.

### 5.4.3 Growth Rates

Expressed in terms of percentage increase in dry mass (Fig.5.7), maximum growth rates which occurred during the first four months of the growing season (November - March) corresponded with a period when upwelling was most frequent.

It is difficult to compare these absolute growth rates of *D. firma* with results obtained for other species of *Desmarestia* or for other species of understorey algae which inevitably have markedly different morphologies. Also, different workers use different methods of measuring growth. Measurements of *D. aculeata* from the Isle of Man (Chapman and Burrows 1971) have shown a 3.5-fold increase in overall length during a month of peak growth. This value is similar to *D. firma* growth rates between November and January, when there was an approximately 3-fold increase in summed length per month. But such comparisons must be treated cautiously because *D. aculeata* is described by the authors above as a "bunch of knotted string", and is therefore quite unlike ligulate *D. firma*.

A slower increase in summed length relative to the increase in dry mass after Janury 1979, indicates that growth effort is going into increasing the width and thickness of the fronds. Microscopic examination showed that the number and size of the cells of the parenchymatous ground tissue increased with age.

The decrease in mean summed length and dry mass of plants, after July, showed that losses to grazing and erosion exceed the tissue produced. Presumably this is because plants grew more slowly during this period, possibly in response to downwelling conditions and lower levels of irradiance at this time of year. Since the plants are annuals it is also possible that a slower growth rate at this stage of the life cycle is an endogenous feature. Good evidence for this is found in the fact that winter plants showed a rate of light-saturated photosynthesis (1.6 mg $O_2$.g dry mass$^{-1}$.h$^{-1}$.) substantially lower than the rate in summer (2.7 mg $O_2$.g dry mass$^{-1}$.h$^{-1}$), under the same experimental conditions (Chapter 6).

### 5.4.4 Percentage Dry Mass

Seasonal variation in the percentage of dry matter, with low values in summer and relatively high values in winter, has been observed for other brown algae; for example, Ascophyllum nodosum (Baardseth 1970), Lessionopsis littoralis and Hedophyllum sessile (Himmelman and Carefoot 1975), Laminaria saccharina (Black 1948), L.digitata and L. longicruris (Mann 1972), and L. pallida (Dieckmann 1978). As winter approaches D. firma sporophytes become thicker and more rigid because of the development of secondary tissue consisting of thick-walled cells. This causes an increase in the percentage of dry matter. D. aculeata also produces secondary tissue towards the end of the growing season (Chapman and Burrows 1971). According to Pease(1920) the thick-walled secondary tissue of ligulate Desmarestia species is concentrated mainly in the basal portions of the plants. Mann (1972) attributed the seasonal increase in the percentage dry mass of two Laminaria species to a decrease in nitrogen relative to carbon, and perhaps this applies to Desmarestia.

## 5.4.5 Percentage Ash Content

The decline in the percentage of ash content in Generation 1 from September 1978 to March 1979, and in Generation 2 from January to July 1979 (Fig. 5.9), may be caused by thickening of cell walls, which chiefly comprise cellulose and alginic acid. In *D. firma* plants collected in March 1975, alginic acid content comprised 17 to 23% of the total dry mass of the plants (Carlberg *et al*, 1978).

During the period of overlap between Generation 1 and Generation 2 (January to March 1979) the lower ash content of the old plants may reflect their high organic content, since they had relatively thick cell walls.

The increase in ash content in Generation 1 between July and September 1978, and in Generation 2 between July and October 1979, is difficult to explain, but may be related to a build-up of diatoms on the surface of the fronds, since large numbers of silicaceous frustules may have appreciably increased the measured ash content of samples. If this was the case, it becomes difficult to explain why the ash content of Generation 1 declined after September 1978, since these old, senescent plants appeared to be heavily epiphytised by diatoms, although the extent of epiphytism was not quantified.

This seasonal pattern in *D. firma* with low levels of ash at the beginning of winter (May to July 1979) is similar to results obtained by Himmelman and Carefoot (1975) for the intertidal algae *Iridaea cordata*, *Hedophyllum sessile*, and *Lessoniopsis littoralis*, but is however opposite to the pattern observed in *Ascophyllum*, when ash values were lowest in summer (Baardseth, 1970).

## 5.4.6 Calorific Content

The lower calorific value of young plants (January - March) of Generation 2, does not represent a truly seasonal phenomenon, since old plants (Generation 1) showed no significant change in calorific value during the same period(Fig. 5.10, 5.11). Paine and Vadas (1969) performed calorific determinations on 70 species of marine algae, and found that in general there were no significant seasonal variations in calorific content. Similarly 2 out of 3 algae investigated by Himmelman and Carefoot (1975) showed no significant seasonal energy changes, on an ash-free basis, but the third, Lessionopsis littoralis, showed a higher energy content in the autumn. In Laminaria pallida, Dieckmann (1978) noted that calorific content showed no significant seasonal variations.

The energy content of young plants may be lower than that of older plants because of changes in the relative proportions of carbohydrates, proteins and lipids. If, for example, the lipid content of older plants increased, the calorific values would increase due to the relatively high calorific value of lipids. Increases in organic cell-wall constituents in older plants (and therefore lower ash, measured as a percentage of total dry mass - Fig. 5.9) and in stored high-energy compounds (e.g. lipids), may thus be responsible for the high calorific levels in old plants. The relatively fragile young plants have thin cell walls, and are growing rapidly. Paine and Vadas (1969) noted that the extremely fast growing giant kelp Nereocystis has a low calorific value compared to slower growing algae.

In D. firma it is also possible that the appearance of numerous sporangia in the fronds, from autumn (April - May) onwards, may contribute to the energy content of the plants as a whole, since the motile zoospores are likely to be energy-rich.

## 5.4.7 Standing Crop

The standing crop of the second generation was much smaller than that of the first because second generation plants were both smaller and less abundant.

The relatively low densities of the second generation plants may have been caused by several factors: Spore production by the previous generation could have been low, conditions could have been unfavourable for the settlement of spores and hence the development of gametophytes, gametophytes may have been grazed heavily by molluscs and echinodermsand conditions may have been unfavourable for the release of gametes for fertilisation or for the early development of germling sporophytes. Germling sporophytes may also have had to compete for space with other organisms such as the mussel Aulacomya ater which in certain years (1981 for example) almost totally covered large areas of rock within these kelp beds. All or just one of these factors may have been responsible for the lower rate of recruitment of the second generation. Unfavourable environmental conditions may also have been responsible for the smaller mean size of Generation 2 plants (Figs. 5.5, 5.6).

After January 1979, the increase in standing crop of Generation 2 reflected increases in mean plant mass (Fig. 5.6) rather than a significant increase in numerical density (Fig. 5.4). From May to July 1979 the decline in this standing crop reflected a decline in numerical density (Fig. 5.4),which overrides the growth of the remaining plants.

The steady decline in the standing crop of D. firma, from midwinter onwards, appeared to be a result of storm and grazing damage, and declining growth rates due to low light and nutrient levels associated with winter downwelling.

The standing crop of D. firma varied markedly in different zones of the Oudekraal kelp bed. The high standing crop within the 1 ha study site, as compared to the entire kelp bed (Table 5.1)

was to be expected, since this site was chosen on account of the abundance of D. firma. It is worth emphasising, however, that even during months when D. firma was most abundant (May - July, at the end of the growing season) very little grew in the mediate and inshore zones at Oudekraal. The possible reasons for this are discussed, together with factors influencing the distribution of the species locally, in Chapter 4.

In a study of standing crops of plants and animals in six kelp beds between Cape Aghulas and Saldanha Bay, the proportions of understorey algae relative to kelps, were shown to vary considerably between different localities (Field et al, 1980 a). Thus at Kreeftebaai, near Saldanha, understorey algae accounted for 37% of the total plant standing crop, while, according to Velimirov et al (1977) these algae accounted for only 0.7% of the total algal standing crop at Oudekraal. It is noteworthy that at Sea Point, Cape Town, although understorey algae accounted for only 4.5%of the total algal standing crop on a wet mass basis (or 10% on the basis of $kJ.m^{-2}$), D. firma was one of the three understorey species which together accounted for more than 1% of the total algal standing crop (Field et al, 1980 a). This regional variability in the standing crops of D. firma was borne out by observations on beach cast, where the fractions of D. firma in drift varied considerably from place to place.

The maximum standing crops of D. firma in the study site and throughout the Oudekraal kelp bed are compared with data for the kelps in Table 5.1.

In July 1978 and May 1979, when relatively large standing crops of D. firma were present in the study site (28.0 and 6.5 $g.m^{-2}$ respectively) the standing crops of Laminaria pallida were greater by approximately 40 and 175 times, respectively. The standing crop of L. pallida plus Ecklonia maxima in the Oudekraal kelp bed as a whole, 816.6 $g.m^{-2}$ (Velimirov et al, 1977) is 544 times greater than that of D. firma in March/ April 1979 (1.5 $g.m^{-2}$ (Table 5.1).

## 5.4.8 Net Production

Since there are no data available on the productivity of other understorey algae of these kelp beds, comparisons with D. firma cannot be made. By comparison with the two kelp bed species which dominate these beds, the production of D. firma during the 1978 - 1979 growing season (approximately 23 g dry mass.$m^{-2}$. $year^{-1}$ was slight. Annual production of L. pallida is in the order of 2100 g dry mass.m (calculated mean of stations in the mediate and offshore zones, from Dieckmann, 1978). In climax stands of E. maxima , which dominate shallower areas of the kelp bed, annual production is in the order of 7.8 kg dry mass.m. year (Newell et al, 1982).

The production: standing crop ratio for D. firma (4.1) was slightly higher than the value of 3.49 given for L. pallida (Dieckmann, 1978), implying slightly higher rates of production in the former species. By the end of the growing season, as much D. firma material had been lost in the removal of decay of whole plants (mortality) as was left on the substrate (July standing crop). The estimate of grazing and decay losses was approximately double the end of season standing crop. The estimates of losses would presumably be increased if release of spores and possibly dissolved organic material could be measured. Estimates of dissolved organic carbon losses for brown algae vary from about 40% of gross production (Khailov and Burlakova, 1969; Sieburth, 1969) to as little as 1.1 - 3.8% (Brylinsky, 1977.

As it is, total losses of D.firma material amounted to over 3 times the end of season standing crop. If all understorey algae are subject to similar losses then a considerable amount of organic material must enter the kelp bed ecosystem from these algae alone. For example, a mean standing crop of understorey algae in the kelp bed at Olifantsbos, Cape Peninsula, of 1.234 kg wet mass.$m^{-2}$ (calculated from Field et al, 1980 a) would indicate annual losses into the ecosystem of over 3.7 kg wet mass.$m^{-2}$.

| Source of data and locality | Species | Date Measured | Standing Crop $g.m^{-2}$ | Standing Crop $kJ.m^{-2}$ |
|---|---|---|---|---|
| Present study - study site | *D. firma* | July '78 | 27.0 | 249.8 |
| Present study - study site | | May '79 | 6.5 | 68.3 |
| Present study - whole kelp bed | | Mar/Apr '79 | 1.5 | 14.9 |
| Dieckmann 1978: mean of stations B,C at Oudekraal (sites of optimal standing crop). | *Laminaria pallida* | '75 - '77 | 1150.0 | 10646.0 |
| Velimirov *et al* 1977: Whole kelp bed, Oudekraal. | Total kelp: *L. pallida* & *E. maxima* | Not given | 816.6 | 9128.4 |

TABLE 5.1 Selected standing crop data for *D. firma* and for the dominant kelp species at Oudekraal. $kJ.m^{-2}$ standing crops for *D. firma* calculated from standing crop data (Fig. 5.12) and calorific values (Fig. 5.10). Values for *D. firma* in the whole kelp bed are based on 4 transects placed in each of the Inshore and Mediate Zones, in March/April 1979.

In July 1978 and May 1979, when relatively large standing crops of *D. firma* were present in the study site (28.0 and 6.5 $g.m^{-2}$ respectively) the standing crops of *Laminaria pallida* were greater by approximately 40 and 175 times, respectively. The standing crop of *L. pallida* plus *Ecklonia maxima* in the Oudekraal kelp bed as a whole, 816.6 $g.m^{-2}$ (Velimirov *et al*, 1977) is 544 times greater than that of *D. firma* in March/April 1979 (1.5 $g.m^{-2}$) (Table 5.1).

The understorey algae, of which *D. firma* is one variable component, may therefore form only a minor fraction of the total standing crop of a west coast kelp bed. Nevertheless, they are an ecologically important component since they provide food and shelter for a wide range of kelp bed animals which are largely concentrated on the sea floor rather than within the kelp canopy.

# CHAPTER 6

# PHOTOSYNTHESIS in DESMARESTIA FIRMA

## 6.1 INTRODUCTION

This chapter largely concerns the photosynthetic rate of *D. firma* with respect to different levels of irradiance and to season. The rationale for this work was that information concerning the relationship between photosynthetic rate and irradiance may be very relevant when discussing the local distribution of the species in kelp beds. For example, from photosynthetic light response of this species it was hoped to test whether an intolerance of high light levels might account for the scarcity of this species in shallow water. Also, by comparing the photosynthetic rates of young and old plants it may be possible to determine if the diminishing standing crop of *Desmarestia* in autumn is in any way related to a slowing down in metabolic rate.

Several experiments were therefore conducted both **in situ** and in the laboratory to obtain the necessary information. In doing so it became clear that monitoring the photosynthetic rate of large seaweeds is not without a number of practical problems, and there can be little doubt that the techniques employed greatly influence the sort of results that are obtained. It is pertinent here to list some of the more important problems that must be overcome in order to make realistic measurements of the photosynthetic rates of seaweeds in the field and in the laboratory.

There are numerous problems associated with the measurement of irradiance. The use of the photometric units lux and foot-candles (e.g. Brinkhuis and Jones, 1974; Mathieson and Burns, 1971) has been severely criticised by Tyler (1973) and Chapman and Campbell (1975) on the grounds that these methods are based on the spectral sensitivity characteristics of the human eye, and measure predominantly green wavelengths. While Tyler (ibid) recommends that irradiance be measured either in terms of power available (watts or g. cal.cm$^{-2}$) or quanta, over the photosynthetically useful wavelengths 400 - 700 um, Chapman and Campbell

(ibid) provide evidence that in the Phaeophyta, the important parameter which must be measured is total quanta, rather than power available.

Ideally, measurements of photosynthetic rate should be made *in situ*, but there are problems in constructing light gradients in the field. Firstly, the light source is not constant, and secondly, it is difficult to create a light gradient. One method is to suspend incubation chambers at different depths in the water column; however, in this case, the spectral composition as well as the level of irradiance changes with depth. Alternatively the incubation chambers may be shaded to varying degrees. Light gradients set up in the laboratory, despite the disadvantage of using an artificial light source, provide light of a constant spectral composition, and are easy to set up. Furthermore, the spectral quality of the light source can, if necessary, be adjusted with the aid of filters, and instantaneous (short term) incubation can be performed in the field to test whether photosynthesic rates *in situ* and in the laboratory are similar at the same level of irradiance.

Other problems are the so-called 'bottle effects' which result from enclosing a seaweed sample in a small container. During incubation within such an enclosed environment, there are changes in seawater chemistry which may significantly affect photosynthetic rate. For example, oxygen tension increases as a result of photosynthesis, and several workers have shown that apparent photosynthesis in marine plants as well as dark respiration, are sensitive to oxygen concentration (Black *et al*, 1976; Downton *et al*, 1976; Burriss, 1977; Dromgoole, 1978; Littler, 1979). pH may also increase rapidly and exert an influence, and it is possible that some nutrients may become limiting.

Another bottle effect is that the rate of flow of water over the surface of the seaweed is greatly diminished inside an incubation chamber, unless a stirring or mixing process is incorporated into the design. For example, Buesa (1977) reported a 34% reduction in photosynthetic rate, in non-mixed versus mixed bottles

containing macroalgae. In Ulva absence of stirring caused a 73% reduction in photosynthetic rate (Littler, 1979), which was attributed to a buildup of concentration gradients within the system, and diffusion barriers at the plant/water interface. Kanwisher (1966) observed a doubling of photosynthetic oxygen production following shaking, during respirometer studies of marine macroalgae.

A further problem is that of the ratio of algal mass to water volume, which a number of studies have revealed as an important factor in influencing photosynthetic rates. Wood(1968) showed that the photosynthetic rate of Cladophora decreased as the mass of samples increased over the range of 0.1 to 1.4 dry mass per litre, and attributed this to self shading. Buesa (1977) found similar variations with several species of tropical algae, and obtained the highest values for both photosynthesis and respiration when mass/volume ratios were between 0.02 and 0.195 $g.l^{-1}$. Clearly the samples in the incubation chambers must be very small to obtain such low ratios, or alternatively the chambers must be very large and thus cumbersome. With large seaweeds it is therefore necessary to resort to the use of fragments, but this has been shown (UNESCO, 1973) to lower production rates in some marine algae. Dromgoole (1978) found that to avoid inordinately high measurements of dark respiration, it was necessary to wash cut thalli for several hours prior to incubation. All of the above bottle effects will be influenced by the period over which incubations are carried out, and Buesa (1977) has pointed out that prior to measurements of photosynthetic rate, the optimum incubation duration should be determined for the particular algae and experimental conditions in use.

Finally there are several problems in using measurements of photosynthetic rate to estimate the net productivity of seaweeds. There is the obvious problem of extrapolating from what are essentially 'instantaneous' measurements obtained from a few hours incubation to net productivity over a period of a month or a year (Morris, 1974). Day to day variations in irradiance, and diurnal variations in photosynthetic rates (Ramus and Rosenberg,

1980), mean that a single incubation is by no means indicative of mean photosynthetic rate over a much longer period.

More important is the well-debated problem of estimating net production from measurements which are not truly representative of net photosynthetic rate. A problem common to techniques that measure $O_2$ production or the rate of uptake of $^{14}C$ labelled bicarbonate is that neither technique is able to account for photorespiration. Unlike terrestrial plants, algae may excrete glycolate, and there is evidence that this excretion is particularly active under low nutrient (Berman, 1976) and high light conditions (Fogg, 1966; Watt, 1966). According to Peterson (1980), in an excellent summary of problems in estimating aquatic primary productivity on the basis of $O_2$ and $^{14}C$ methods, the glycolate not excreted may be photorespired. There is thus a tendency for both methods to underestimate overall respiration rate with the result that they measure somewhere between net and gross photosynthesis, and in view of the rather contradictory literature on the subject, we cannot be sure where, between the extremes. Ryther (1954, 1956), for example, contended that the $^{14}C$ method measured close to net, but Steeman Nielsen and Al Kholy (1956) showed that it was closer to gross for phosphorus and nitrogen deficient algae.

The problems briefly discussed above mean that it is virtually impossible to make direct comparisons between the photosynthetic rates of different species of algae which have been studied by different workers using a range of equipment and methods. At best, one can try to reduce these various problems to a minimum and obtain measurements that come close to estimating photosynthetic rate under entirely natural conditions. In the case of autecological studies such as this one, relative measurements of photosynthetic rate are valid and satisfactory, as long as the apparatus and methods are kept constant throughout the course of the study.

## 6.2 METHODS and MATERIALS

### 6.2.1 Measuring Irradiance

In both the field and in the laboratory irradiance was measured as "Photosynthetically Active Radiation (P.A.R.), with a LiCor 193s spherical quantum sensor, connected by waterproof cable to a Licor 189 Integrator (Lambda Instrument Corporation). This system measures total quanta incident per unit area per unit time ($\mu E.m^{-2}s^{-1}$) between the wavelengths 400 and 700 nm. In the field, surface irradiance was measured with a LiCor 190s quantum sensor connected to the same integrator. The spectral composition of the tungsten-halogen lamps used in the laboratory was measured using a spectraradiometer (Scientific Instruments, Rayleigh, Essex).

To obtain measurements of typical light levels in the Oudekraal kelp bed irradiance was measured at 6m depth, on exactly the same location, during a day of downwelling (28.11.1979; Fig. 6.5) and during a day of active upwelling (12.12.1979; Fig. 6.6). At this location, a partial canopy of Laminaria pallida provided about 30% cover. Surface and underwater P.A.R. levels were measured every half hour, from first light to dusk. In the laboratory experiments, P.A.R. measurements were made by placing the 193s quantum sensor in a water-filled incubation jar, at the appropriate distance from the light source.

### 6.2.2 Collection of Material and General Laboratory Methods

Specimens were collected at Oudekraal in June and July (winter) and December (summer) 1981, from depths of 4 - 10m, and transported to the laboratory in 20l buckets of sea-water. Here they were stored in running-water aquaria, in aerated water circulated from a reservoir containing 3 tonnes. The plants were kept at 11 - 13°C in a daily 12h light, 12h dark cycle. Mercury vapour lamps provided the light, and P.A.R. levels were approximately 300 $\mu E.m^{-2}.s^{-1}$. All material was used within 3 days of collection. Apparently healthy plants of small to medium size were selected for incubation, and only entire plants were used, i.e. not strips, discs, or single fronds.

Sea-water for the experiments run in winter was obtained from below the 12°C thermocline, several km off the west coast of the Cape Peninsula, using 18 l hydrographic bottles. This is essentially "pre-upwelled" water, and was assumed to contain the high nutrient levels associated with upwelling (see Chapter 1). Prior to use in experiments, levels of nitrate, nitrite, ammonium and phosphate were determined using a Technikon Antoanalyser (Swords Co., Dublin). Water samples for nutrient determinations were frozen in 100 ml plastic bottles, since it has been shown (De Gobbis, 1973) that this is an effective method of stabilizing ammonia levels. Nutrient levels were as follows: phosphate = 1.3 µg. at P/l, nitrate = 6.0 µg at N/l. These levels are considered to be relatively high, and it is unlikely that any of these macronutrients would become limiting during incubation.

Water for use in summer experiments was collected at Oudekraal during active upwelling in December 1981. It was assumed that this water would contain high nutrient levels.

Prior to use, all water was filtered through 0.45 um micropore filters at a pressure of 0.5 atmospheres. Photosynthetic rate was measured in terms of increase in the concentration of dissolved oxygen. Oxygen levels before and after each incubation were initially measured according to the Winkler titration method for total $O_2$ (Strickland and Parsons, 1968) and later using a Schott-Gerate CG867 portable oxygen meter, calibrated against Winkler-titrated water. Incubations were carried out in 1 litre glass jars with ground glass lids coated with silicone grease. The algae were attached to the lids by means of hooks (Fig. 6.1). Stirring was provided by magnetic stirrers, adjusted so that plants in replicate bottles revolved at similar rates. Prior to all incubations, specimens were left in beakers of the incubation sea-water for 20 minutes, to allow oxygen levels in the tissues to equilibrate with those in the incubation water.

Irradiance was provided by EMM/EKS 250W - 24V 'Sylvania" tungsten halogen projector lamps with dichroic filters, and intensity was varied by simply moving the incubation jars further

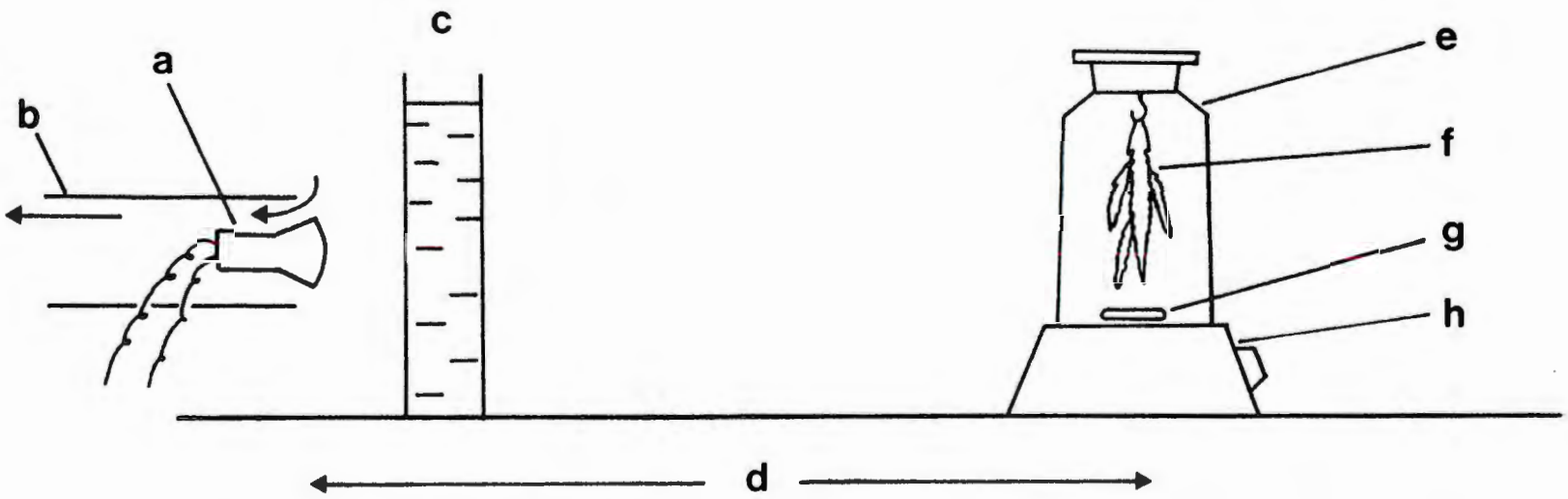



FIG. 6.1 Laboratory apparatus used to measure rates of net photosynthesis in D. firma. a - light source; b - vacuum system for cooling of lamps (direction of air flow shown); c - water trough; d - variable light-path length; e - incubation jar; f - alga suspended from hook; g - magnetic stirring bar; h - magnetic stirrer.

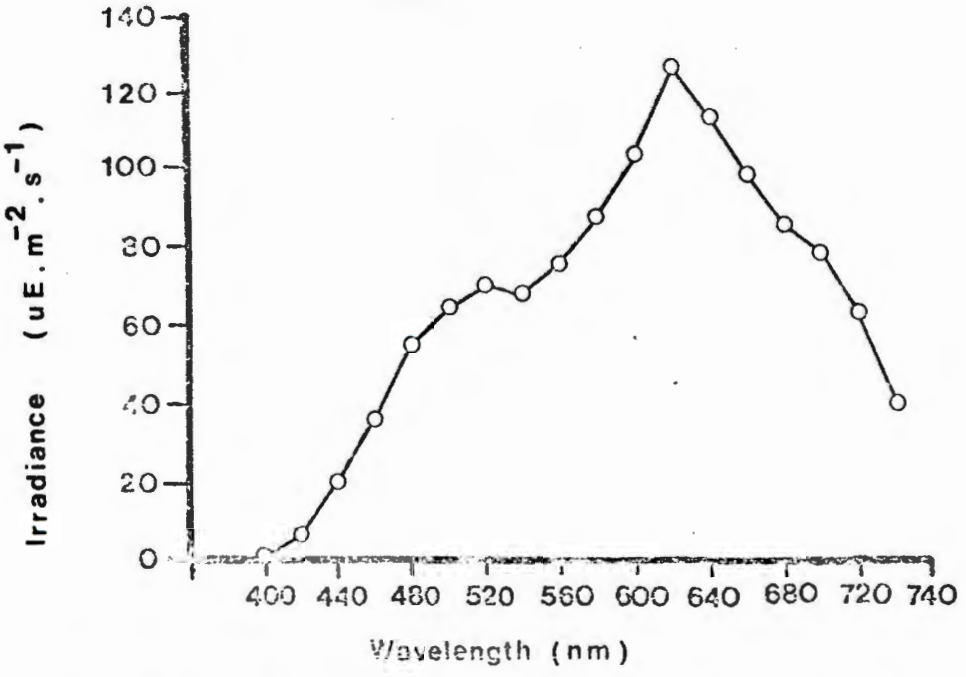



FIG. 6.2 Spectral composition of natural sunlight at noon, in summer (Dec. 1981), through glass and water.

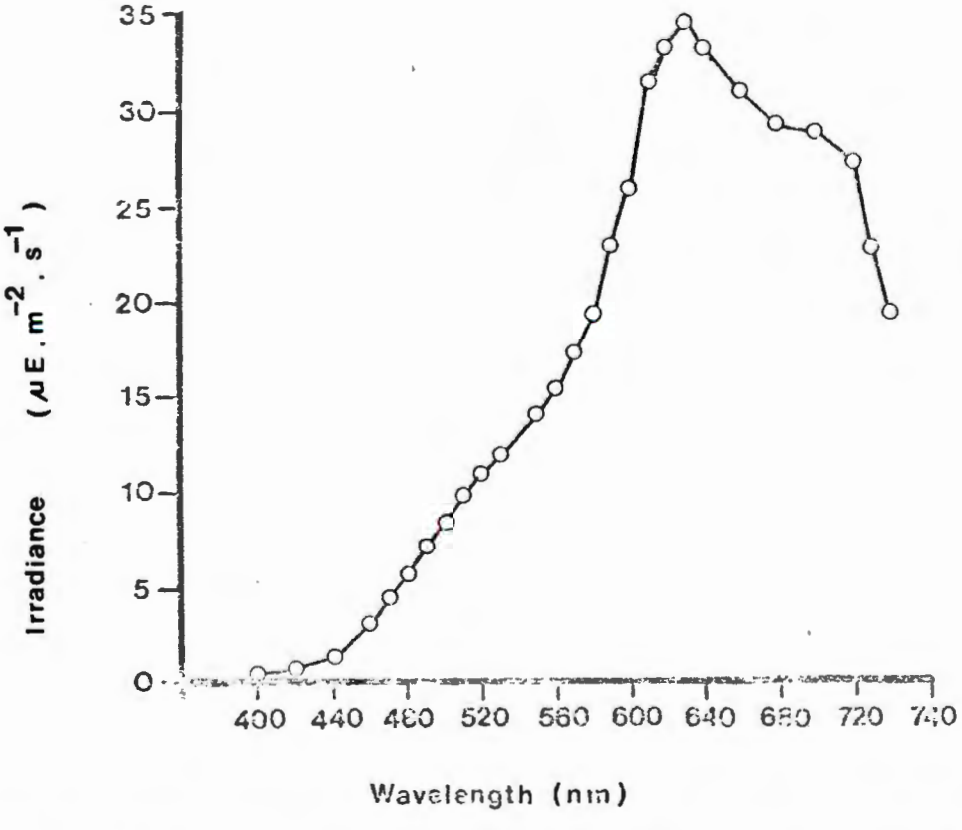



FIG. 6.3 Spectral composition of light from tungsten-halogen lamps used in laboratory experiments, through glass and water.

from the light source. Very low P.A.R. levels were obtained by placing several layers of black shade netting in the light path. A 10 cm wide glass trough, filled with fresh water, provided a heat and ultra-violet radiation screen. Air pumps drew cold air over the lamps to prevent overheating. The spectral composition of sunlight, through glass and water (Fig. 6.2), and spectral composition of this experimental light source (Fig. 6.3) show only slight differences, mostly in the 480 - 520 nm region. The apparatus was housed, and all experiments run, in a cold-room at 12 - 13°C.

Before measuring the response of photosynthetic rate to P.A.R. levels, three types of preliminary experiments were conducted, to investigate possible effects of duration of incubation, seaweed mass/sea-water volume ratio, and initial $O_2$ levels. All of these experiments were run in June and July, 1981.

### 6.2.3 *Effects of Experimental Conditions on Photosynthetic Rates*

#### 6.2.3.1 *Period of Incubation*

Before constructing photosynthesis vs irradiance curves the effect of incubation time on the photosynthetic rate of D. firma was investigated. Measurements were made over periods of 0.5, 1.0, 1.5, 2.0, 3.0 and 4.25 hours, to establish the optimum incubation time under these experimental conditions. There were four replicates for each time period, and all incubations were run at 12 - 14°C, at 500 $uE,m^{-2}.s^{-1}$. Plants of similar size were selected, and initial $O_2$ level was 7.2 mg $O_2.l^{-1}$. Results (Fig. 6.7) were subjected to a one-way analysis of variance (Zar, 1974) to test the null hypothesis that there were no significant differences between mean rates of photosynthesis for the 6 experimental incubation periods.

#### 6.2.3.2 Initial Oxygen Levels

The effect of initial $O_2$ concentration on photosynthetic rate was investigated by incubating specimens for 1 hour at $O_2$levels of 1.5, 3.7,6.6,8.4,10.2 $mgO_2.l^{-1}$. Dissolved oxygen concentration was lowered artificially by bubbling nitrogen gas through

filtered sea-water for various periods. An apparently saturated level of 10.2 mg $O_2.l^{-1}$ was obtained by repeatedly pouring the water back and forth between buckets, and then vigorously stirring. Specimens were then allowed to equilibrate in containers of the respective $O_2$ levels for 20 minutes. This minimised the possibility that changes in $O_2$levels in the incubation water could be caused by passive diffusion from oxygen-rich tissues to oxygen-poor water, or vice-versa (Dromgoole, 1978). After this period, the plants were placed in incubation jars containing water of the respective $O_2$ concentrations, and allowed to photosynthesize for 1 hour at 440 uE.$m^{-2}$.$s^{-1}$. After incubation specimens were oven dried at 75°C and weighed. Results (Fig. 6.8) were subjected to a one-way analysis of variance(Zar, 1974) to test the null hypothesis that there was no significant difference between the mean rates of photosynthesis, at various initial $O_2$levels.

### 6.2.3.3 *Seaweed Mass: Sea-Water Volume Ratio*

The effect of this ratio on photosynthetic rate was investigated by incubating sea-weed samples with dry masses ranging from 0.1 - 5.0 g, in a litre of seawater. Plants were selected by fresh mass, assuming a dry mass: fresh mass ratio of 1:10. Irradiance was 440 uE.$m^{-2}$.$s^{-1}$, incubation time 1 hour, and the initial $O_2$ level 6.3 mg $O_2.l^{-1}$. Oxygen measurements were made by the Winkler method. After incubation, plants were oven dried at 75°C and weighed. Results, summarised in Fig. 6.9, were divided into 2 groups on the basis of dry mass: those from 0.09 to 1.1g, and those from 1.5 to 2.7 g dry mass. These two groups were then compared with respect to their mean photosynthetic rate, using Students' t-test (Zar, 1974).

## 6.2.4 Laboratory Measurements of Photosynthetic Light Response

Based on the results of the preceding experiments, all specimens were incubated for 1 hour, and initial $O_2$ levels were between 6 and 8 mg$O^2.l^{-1}$. Plant dry mass was kept between 0.30 and 0.52 g. Plants were selected on the basis of fresh mass using a dry mass : fresh mass ratio of 1:10. Results are presented in the form of winter (June - July) and summer (December) light curves (Fig. 6.10). Plants

used to measure dark respiration were allowed to equilibrate for 1 hour in the dark, then transferred to fresh incubation medium with the same initial $O_2$ levels.

### 6.2.5 Incubation Experiments In Situ

Rates of photosynthesis were measured over two days in January 1982, at Bakoven, on the west coast of the Cape Peninsula. For these experiments, 6 perspex incubation chambers, each with a built-in circulation system, were designed and constructed (Fig. 6.4). Incubation volume in the chambers was 1.9 litres, to *accomodate* larger specimens than were used in the laboratory experiments. The procedure for filling the chambers and running the experiment was as follows: Chambers were held vertically and filled with pre-filtered sea water. The seaweed specimen was added and initial $O_2$ level measured before the lid was fitted. Whilst fitting the lid, the clamp on the overflow tube was left open. By tapping the sides of the chamber, air bubbles were released via the concave lid and overflow tube. The clamp was then closed and the chamber suspended horizontally between a transparent plastic buoy and an anchor. Circulation within the chamber was provided by a small gear-driven electric pump (Mitsubishi Ltd, Japan). Flow rate from these pumps were approximately 1.5 litres per minute. The tube drawing water into the pump was perforated to prevent blockage by algal fronds. Water movement was just sufficient to agitate the fronds, and some additional agitation came from wave-induced movements of the whole apparatus. Sealed wires ran from the chambers to a 6 volt car battery in a dinghy on the surface.

A total of seven 1.5 hour incubations were performed, using 5 replicate chambers suspended 1m apart, at a depth of 2m. Water temperature was 13 - 14°C, and visibility approximately 10m. Desmarestia plants were collected prior to the experiment in an adjacent kelp bed. Only intact plants, free of visible epiphytes, were used. Upwelled sea-water, filtered through 0.45 um microspore filters, and with initial $O_2$ levels between 7.7 and

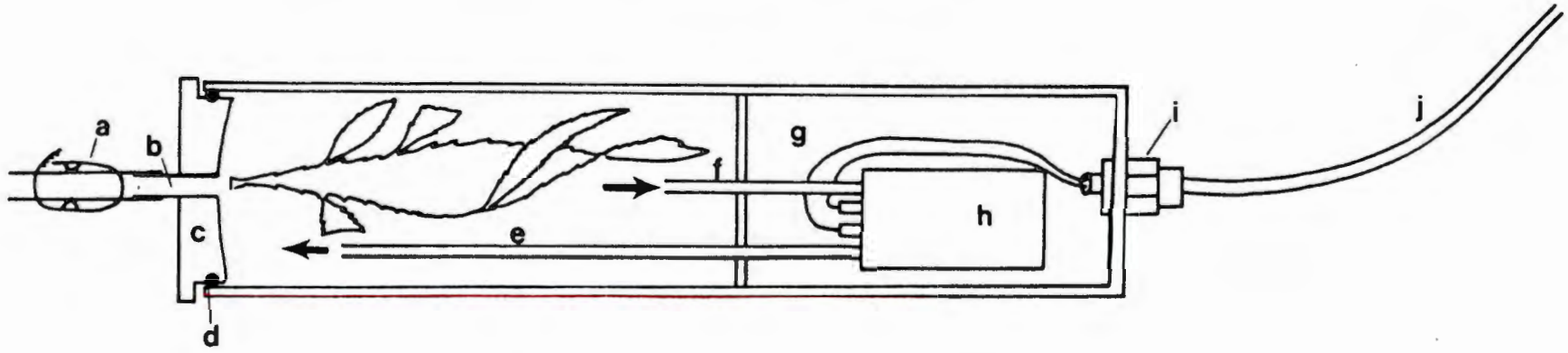



FIG. 6.4 Perspex underwater incubation chamber used for *in situ* measurement of photosynthesis. a - sealing clip; b - overflow tube; c - lid; d - o - ring; e - pump outflow tube; f - pump inlet tube; g - air-filled chamber; h - electric pump; i - sealing nut; j - waterproof electric cable to 6v battery on the surface.

8.0 mg.$l^{-1}$, was used. P.A.R. at the surface and at the incubation depth was measured at 15 minute intervals throughout the course of the experiment. The 193s spherical quantum sensor was placed inside a perspex chamber when making the submarime measurements. Results of 6 sets of incubations are presented in Fig. 6.10. Day 1 was completely cloudless, and incubations were run from 1430h to 2000h. Day 2 was completely clouded, and incubations were run from 0800h to 1100h.

## 6.3 RESULTS

### 6.3.1 In Situ P.A.R. Levels during Upwelling and Downwelling

During the day of downwelling conditions (28.11.1979, Fig. 6.5) there was a light north-westerly wind, the sky was cloudy , with rain, water temperature was 14°C, and swell height about 1m. Underwater visibility was 4 - 5m, and the water was dark green with phytoplankton. On 12.12.79, during active upwelling (Fig. 6.6) there was a south-easterly breeze, visibility was 10 -12m, water temperature 10°C, and swell height about 1m. The sky was clear throughout the day.

Results of light measurements (Figs. 6.5, 6.6) show that P.A.R. levels at 6m are far higher during upwelling (maximum of 600 $\mu E.m^{-2}.s^{-1}$) than during downwelling (maximum of 200 $\mu E.m^{-2}.s^{-1}$) conditions. From the areas under the respective curves, the total no. of quanta can be claculated. On the day of downwelling, the total number of quanta incident at 6m was only 17% of the number incident at the same depth during upwelling. Similar calculations show that during the day of upwelling, the total number of quanta incident at 6m was equivalent to 26% of quanta incident at the surface, while during downwelling, light is attenuated more rapidly and irradiance at 6m amounted to only 9% of surface irradiance.

### 6.3.2 Effects of Experimental Conditions on Photosynthetic Rates

#### 6.3.2.1 Period of Incubation

Results (Fig. 6.7) showed an optimum photosynthetic rate of 1.64 mg $O_2.g^{-1}$ dry mass.$h^{-1}$ after an hour's incubation and slightly lower values after 0.5, 1.5, and 2.0 hour periods. Apparent photosynthesis dropped to 1.35 and 1.3. mg $O_2.g^{-1}.h^{-1}$ for 3.0 and 4.25 hour periods, respectively. However, a one-way analysis of variance supported the null hypothesis that there is no difference between the means, at the 95% confidence level. (A calculated F value of 0.773 was obtained which is lower than the tabulated critical value of F (0.05, 5, 18) = 2.80. **Nevertheless,** all subsequent laboratory incubations were run for 1 hour.

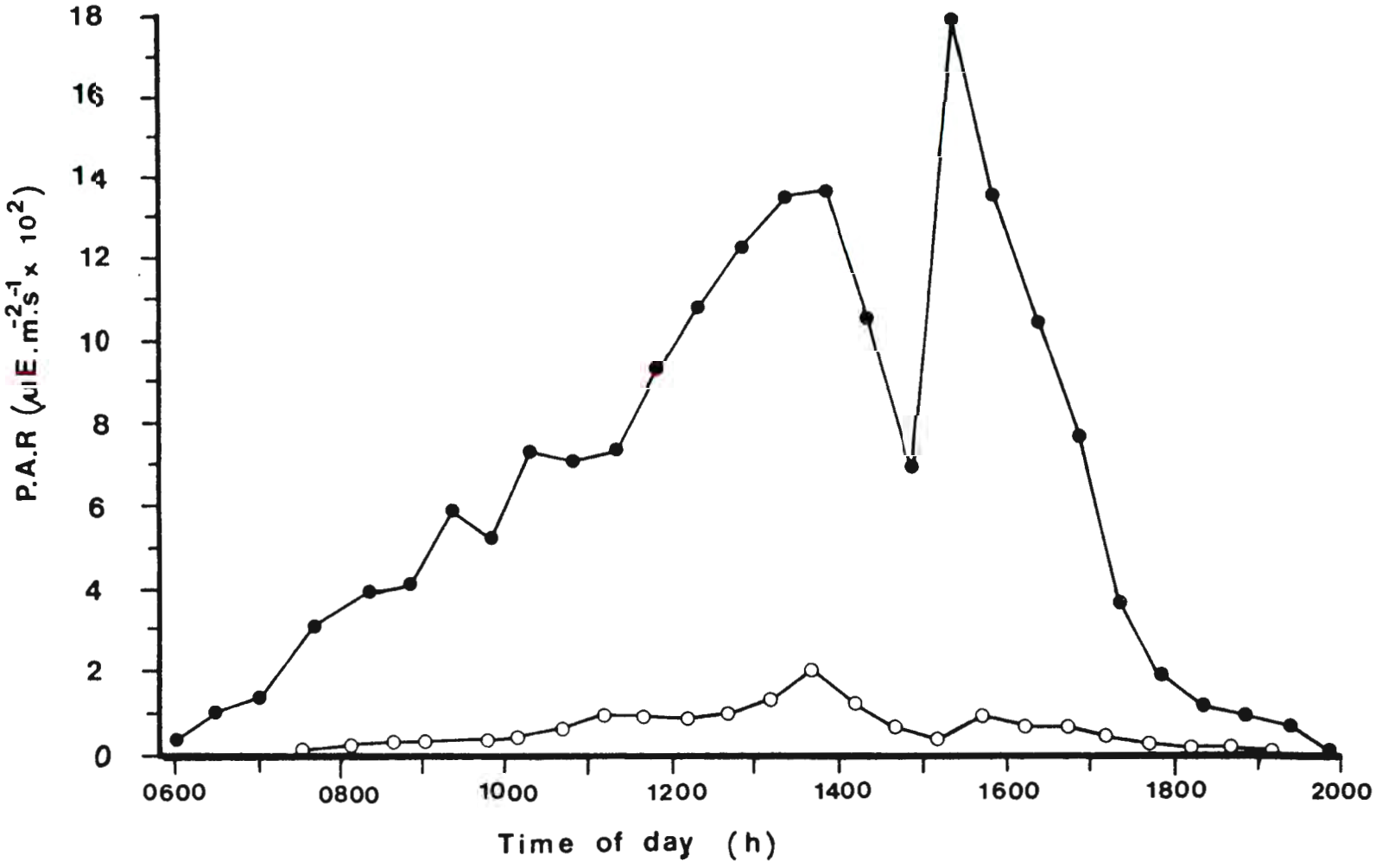



FIG. 6.5 Photosynthetically active radiation during a day of downwelling, at Oudekraal (28 Nov. 1979). ●—● - at surface; o—o - at 6m depth.

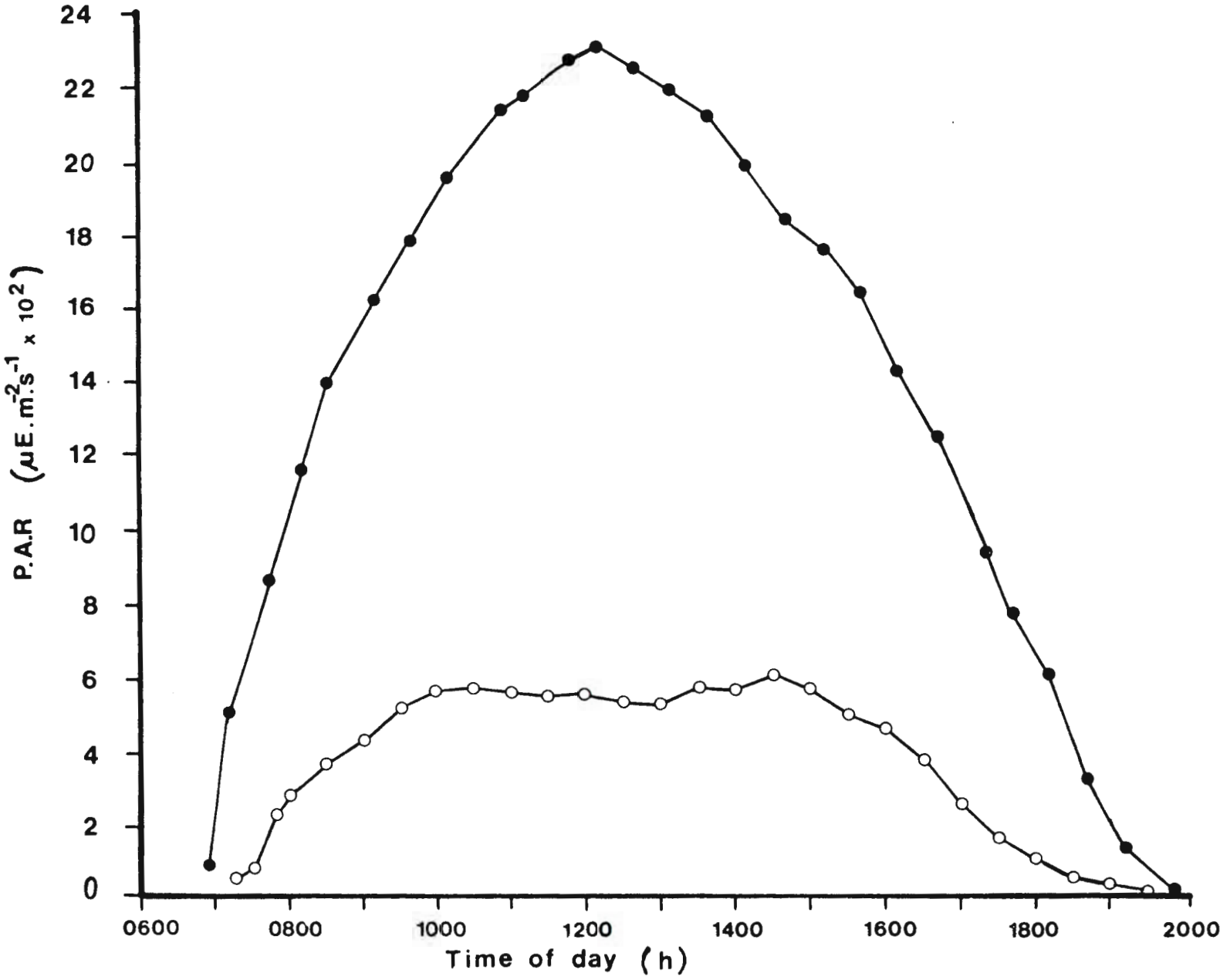



FIG. 6.6 Photosynthetically active radiation during a day of active upwelling at Oudekraal (12 Dec. 1979). ●—● - at surface; o—o - at 6m depth.

### 6.3.2.2 Initial Oxygen Levels

Results (Fig. 6.8) suggested a weak negative relationship between photosynthetic rate and initial dissolved $O_2$ concentration. A one-way analysis of variance yielded an F value of 2.28, which is lower than the critical value of F(0.05,4,15) = 3.10. Statistically, therefore, there is no difference between rates of photosynthesis at $O_2$ levels between 1.5 and 10.4 mg $O_2.l^{-1}$, in *D. firma*, using this apparatus. For all subsequent experiments, initial $O_2$ levels of between 6 and 8 mg $O_2.l^{-1}$ were used, since these are consistent with average values for upwelled water at Oudekraal (R. Carter, *pers. comm.*).

### 6.3.2.3 Seaweed Mass: Incubation Volume Ratios

A linear regression of photosynthetic rate against thallus mass (Fig. 6.9) suggested a weak negative relationship between these two variables ($r^2$ = 0.16). However, the coefficient of correlation, r = 0.13, fell below the tabulated critical value r/0.05,21) = 0.381. Statistically, therefore, there is no correlation between the two variables at the 95% confidence level. Also, the results of a Students' t-test showed that there is no significant difference, at the 95% confidence level, between the mean photosynthetic rates of plants of 0.09 to 1.1g dry mass, and plants of 1.5. to 2.7g dry mass. Under these experimental conditions, photosynthetic rate appears to be unaffected by tissue mass/incubation volume ratios up to at least 2.7g dry mass.$l^{-1}$.

### 6.3.3 Photosynthetic Light Response in D. firma

Photosynthetic rate versus irradiance curves for *D. firma* specimens collected in summer and winter and measured in the laboratory, together with a photosynthesis vs irradiance curve measured *in situ*, are shown in Fig. 6.10.

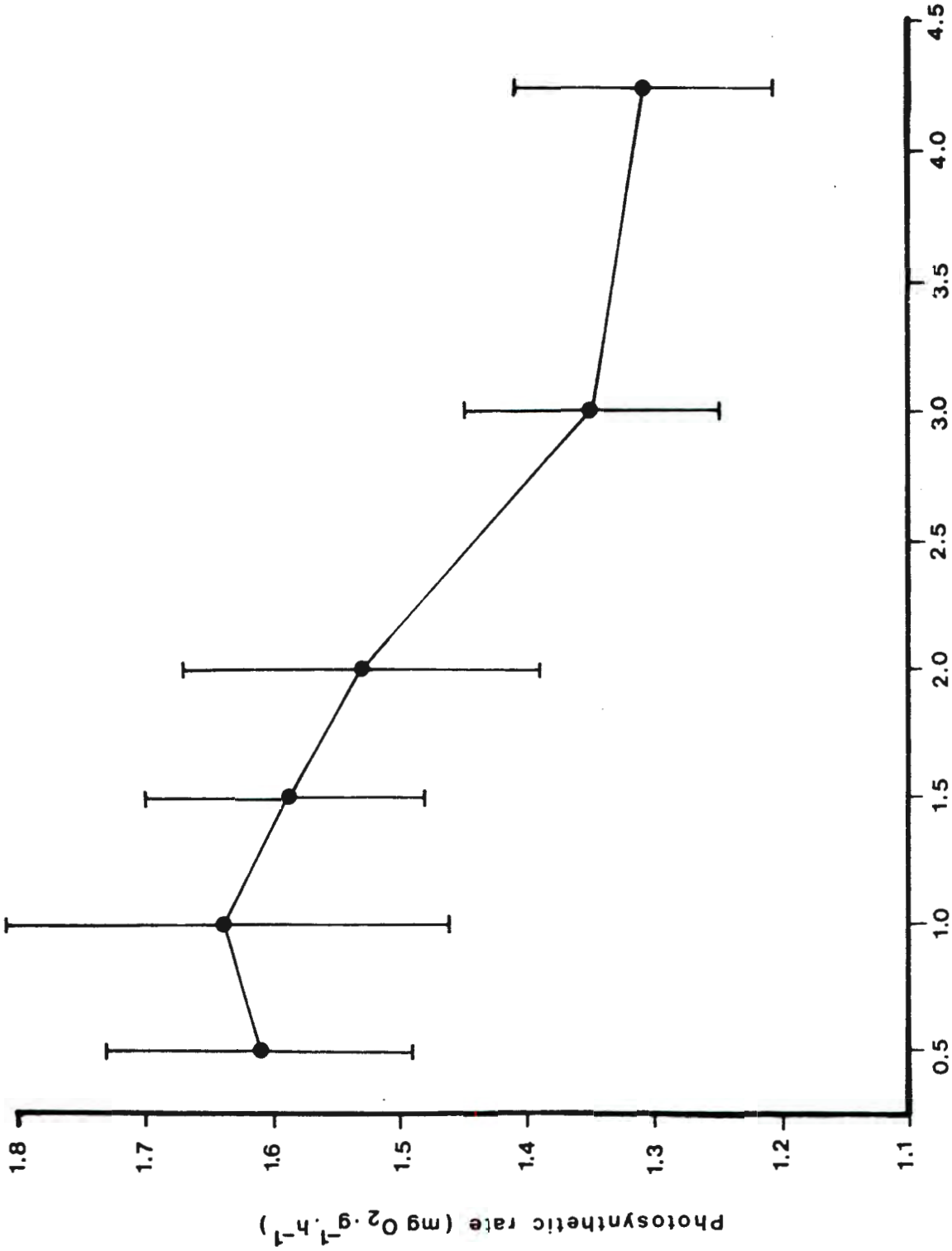



FIG. 6.7 Rates of photosynthesis over varying incubation periods. Each point is a mean of 4 replicate incubations. 95% confidence limits of means shown.

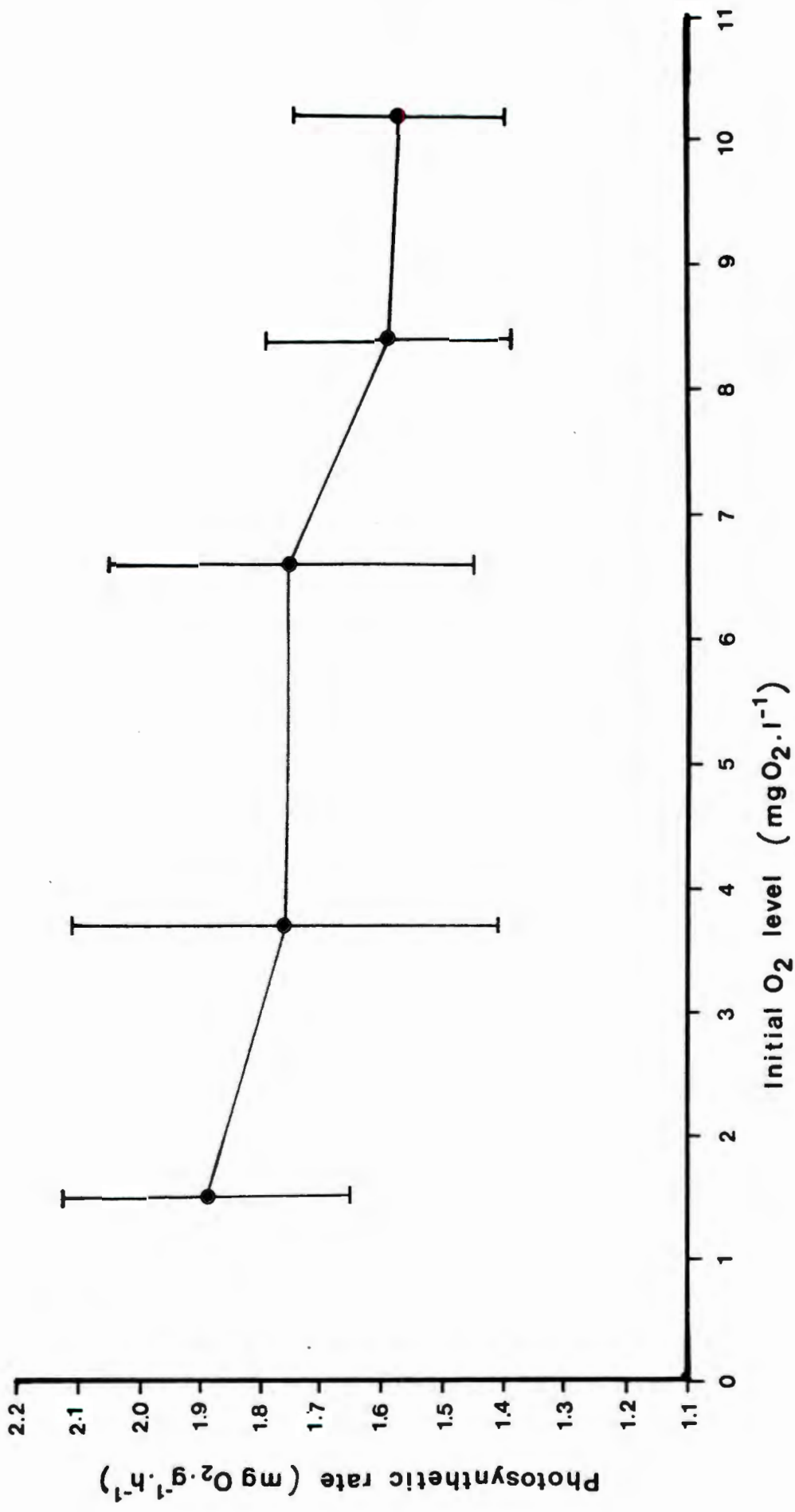



FIG. 6.8 Rate of photosynthesis versus initial oxygen level in incubation medium. Each point is mean of 4 replicate incubations. 95% confidence limits of means shown.

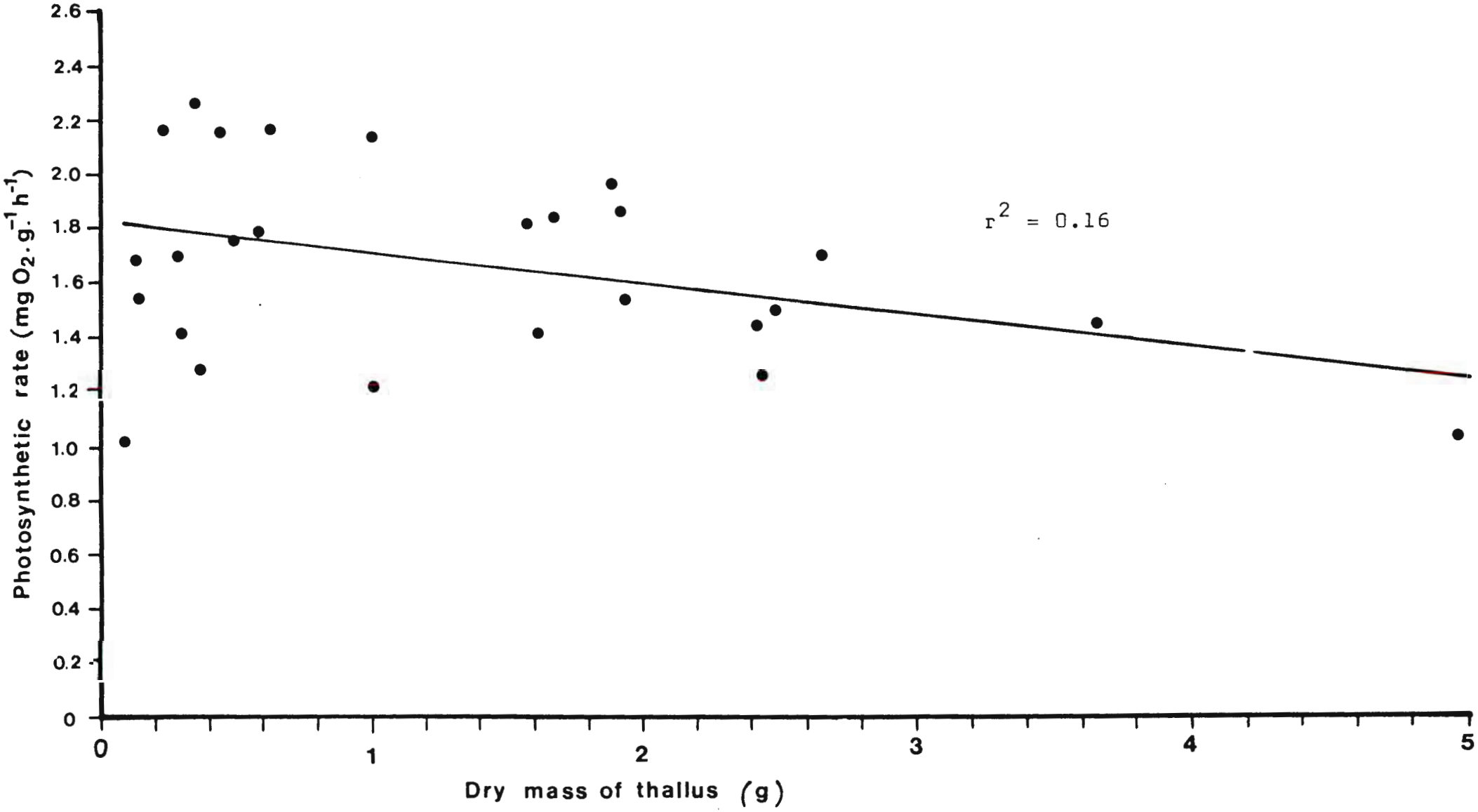



FIG. 6.9 Rate of photosynthesis versus dry mass of thallus, in 1 litre incubation chambers. Each point is result of a single incubation. Linear regression line shown.

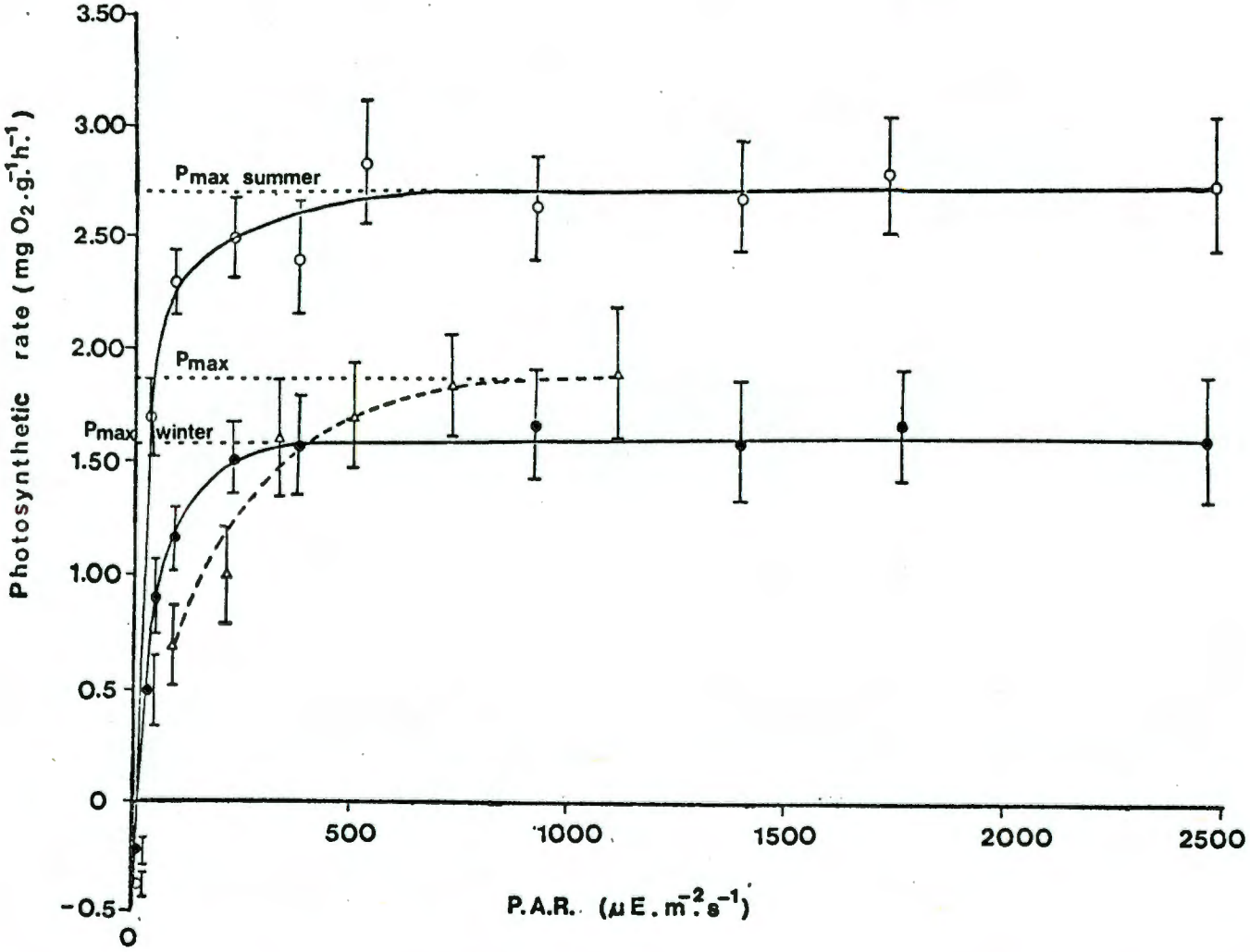



FIG. 6.10 Photosynthetic light response curves for D. firma, obtained in the laboratory (solid lines) and in situ (broken line). o—o - summer plants; ●—● - winter plants. Each point in laboratory data is mean of 4 replicate incubations (95% confidence limits shown). Each point in in situ curve is mean of 5 replicate incubation (95% confidence limits shown).

The results from the laboratory incubations show a marked difference between light saturated rates (Pmax.) in summer (2.75 mg $O_2.g^{-1}.h^{-1}$) and those in winter (1.6 mg $O_2.g^{-1}h^{-1}$). In both cases saturated levels are reached at about 300 - 400 $\mu E.m^{-2}.s^{-1}$. The light compensation point(P.A.R. level at which respiratory $O_2$ uptake equals photosynthetic $O_2$ production) appears to be similar for summer and winter plants (between 10 and 20 $\mu E.m^{-2}.5^{-1}$).

Neither summer nor winter plants showed any decline in photosynthetic rate at P.A.R. levels exceeding the light saturation point, even up to 2.500 $\mu E.m^{-2}.s^{-1}$. Summer plants showed a higher rate of dark respiration (0.38 mg $O_2.g^{-1}.h^{-1}$). However, the ratios of Pmax/dark respiration remained essentially the same (approximately 7.2).

The maximum rate of photosynthesis measured *in situ* (approximately 1.9 mg $O_2.g^{-1}.h^{-1}$) was about 30% lower than the summer value obtained in laboratory measurements.

## 6.4 DISCUSSION

### 6.4.1 In Situ P.A.R. Levels During Upwelling and Downwelling

These results are consistent with accepted ideas that downwelling is accompanied by low underwater light levels. On the day on which the downwelling measurements were made, underwater irradiance was reduced partly by cloud cover and partly by phytoplankton and suspended material in the water column, since only 9% of the surface illumination reached 6m, whereas during upwelling 26% of surface illumination reached this depth. The effects of these light reductions in photosynthesis are discussed in Section 6.4.3.

### 6.4.2 Effects of Experimental Conditions on Photsynthetic Rates

#### 6.4.2.1 Period of Incubation and Seaweed Mass: Sea-water Volume Ratio

The finding that photosynthetic rate in D. firma did not decline significantly with incubation periods up to 4.25 hours (Fig 6.7) is in agreement with results obtained for the 5 species of algae (Acetabularia crenulata, Batophora oerstedii, Caulerpa cupressoides, C. paspaloides, and Penicillus capitatus) investigated by Buesa (1977). Using dry mass/volume ratios of 0.02 - 0.20 $g.l^{-1}$, he found that photosynthetic rate did not differ significantly for periods between 0.5 and 24 hours. Other workers have used incubation periods longer than the 1 hour period used in the present study, e.g. 4.5 - 6 hours (Littler, 1979) and 3.5 hours (Littler and Arnold, 1980).

It is noteworthy that in D. firma, thallus mass/incubation volume ratios as high as 2.7$g.l^{-1}$ did not significantly affect photosynthesis (Fig. 6.9), since other workers have shown strong effects for ratios higher than about 2.0 $g.l^{-1}$. Buesa (1977) investigated the effect of thallus dry masses from 0.004 - 3.80 $g.l^{-1}$ in 10 species of algae and a marine grass, and found that the highest rates of photosynthesis and respiration were obtained with ratios between 0.02 and 0.195 $g.l^{-1}$. If his incubations were performed over long periods (the time is not stated), then

this could partly explain these effects. Similarly, the results of Littler (1979), which showed significant mass/volume effects within the range of 0.036 to 0.128 g dry mass.$l^{-1}$, may be partly accounted for by the relatively long incubation periods (4.5 - 6 hours).

In these closed experimental systems, it is obvious that the effects of duration of incubation and thallus mass/incubation volume vary according to experimental nutrient conditions, and the morphology and physiology of the algae involved. Reduction in photosynthetic rate could be caused by several factors. The most likely of these is a depletion of nutrients or $CO_2$. Johnston (1969) showed that if tissue dry mass/incubation volume ratios are kept below 0.3 g.$l^{-1}$, there were no nutrient deficiencies for periods up to 24 hours. Most workers (e.g. Littler, 1979; Buesa, 1977; Littler and Arnold, 1980) do not provide data on nutrient levels, so that it is difficult to compare their thallus mass/volume and incubation period results with those of the present study. The initial levels of $NO_3$, $NO_2$, $NH_4$ and $PO_4$ in this study were reasonably high (6.0, 0.2, 12.0, and 1.3 ug at.$l^{-1}$, respectively), so that the absence of significant tissue mass and incubation period effect may indicate that there was no significant nutrient depletion.

Self-shading is an important cause of reduced photosynthetic rates when large tissue masses are used. Littler (1979) showed that higher photosynthetic rates were obtained with few macroalgal individuals in small bottles rather than more numerous thalli of the same species in large bottles, even though in the large bottles there were relatively greater volumes of seawater per dry mass of algal tissue. He attributed this effect to competition for $CO_2$ and self-shading of thalli, even when they were surrounded by a relatively large volume of seawater. The *D. firma* plants used in the present study tended to hang with the fronds open and flat in one plane, so there was little self-shading, compared with what would be obtained in a 'bushy' thallus such as certain Cladophora species (e.g. as used by Wood, 1968).

This may contribute to the sustained rates of photosynthesis of D. firma, even at high thallus mass/incubation volume ratios. Only in the largest plant used (4.96 g dry mass) was there obvious self-shading, and this plant showed a reduced rate of photosynthesis (1.3 mg $O_2.g^{-1}.h^{-1}$) compared to an average rate of about 1.6 mg $O_2.g^{-1}.h^{-1}$ for the other specimens (Fig. 6.9). The important point is that these effects should be established experimentally for each species before determining light curves or estimating production rates from closed incubation systems.

### 6.4.2.2 Initial Oxygen Levels

These results, which showed there was no statistical difference between photosynthetic rates in D. firma over a gradient of initial oxygen concentration of 1.5 to 10.2 mg $O_2.l^{-1}$, are at variance with results from several similar investigations of other marine algae. In Carpophyllum flexuosum, apparent photosynthesis in various parts of the plant was reduced by values between 17 and 50%, as oxygen levels increased from 1.7 to approximately 8.3 mg $O_2.l^{-1}$ (Dromgoole, 1978). In the same study, a corresponding increase in oxygen levels caused a 33% reduction in apparent photsynthesis in Ecklonia radiata. Several hypotheses have been proposed to explain oxygen inhibition of apparent photosynthesis (the Warburg effect) in plants (Turner and Brittain, 1962). In many marine algae high external oxygen levels effect an increase in rates of dark respiration, which may contribute to the Warburg effect (Dromgoole, 1978). This effect cannot be easily assessed in the light since $O_2$ produced by photosynthesis may be directly used in the biochemical pathway of dark respiration. However, in Carpophyllum, photosynthesis was shown to be reduced by $O_2$ levels which exceed saturation levels for dark respiration, so that there appears to be either a direct $O_2$ inhibition of photosynthesis, or a photorespiratory pathway which is sensitive to high oxygen (Dromgoole, 1978). It is difficult to explain why high oxygen effects should be insignificant in photosynthesis in D. firma, other than to suggest that photorespiration in this species may be minimal, or even absent, although this was not specifically investigated.

In experimental measurements of photosynthesis , it is clear that oxygen levels should be kept close to those that the plant is likely to experience in nature. In the Oudekraal kelp beds, upwelling is accompanied by low $O_2$ levels in the water, from 8 down to approximately 4-5 mg $O_2.l^{-1}$ (R. Carter, pers comm) while downwelling water may have levels as high as 10.5 mg $O_2.l^{-1}$ (Field et al, 1980 b). For the purpose of this study, oxygen levels were therefore kept between 6 and 8 mg $O_2.l^{-1}$, although oxygen effects on photosynthesis were shown to be insignificant.

### 6.4.3 Photosynthetic Light Response in D. firma

The lower rates of photosynthesis of D. firma in winter agree (Fig. 6.9) well with the findings in other studies of benthic marine algae. In Ascophyllum nodosum, for example, maximum rates of photosynthesis $^{14}C$ incorporation were measured during spring, and variations in photosynthetic potential corresponded to seasonal changes in field standing crops (Brinkhuis, 1977). In a study of photosynthetic rates in 22 species of Baltic algae, King and Schramm (1976) showed that in general, most species showed highest values in spring and summer, corresponding to their seasonal growth pattern, and that the highest production rates were shown by annual or short-lived algae, and those with sheet-like thalli. Similar seasonal photosynthetic effects were shown in most of the 10 species of Baltic algae investigated by Wallentinus (1978). This author pointed out that differences between species and between the same species in different ambient conditions were largely eliminated when photosynthetic rates were expressed on the basis of chlorophyll a content. In D. firma the seasonal differences which were measured may be due to several factors. The most likely of these is simply that the old fronds of the winter plants are thicker and contain proportionately more non-chlorophyllous cells to chlorophyllous cells than the young (summer) plants. If the chlorophyll a content of chlorophyllous cells in old and young plants is more or less constant then photosynthetic rates, expressed in

terms of dry mass tissue, would be lower in winter. If rates had been expressed per unit of chlorophyll a, then these differences may have been eliminated. Although microscopic examination of the tissues showed that there is little change in the numbers of layers of the chlorophyll-containing cells which comprise the superficial cortex of these plants, it is possible that the amounts of chlorophyll, or numbers of chloroplasts per cell, may increase in winter, since the plants certainly become darker during this season. However, the darkening of the fronds may simply be a result of their increase in thickness, which is caused by an increase in the number and size of the parenchyma cells which make up the bulk of the thallus tissue. These seasonal differences in net photosynthesis per dry mass are thus considered to be largely attributed to the increase in non-photosynthetic tissue in the old plants. Apparent differences in net photosynthesis may have been largely or even entirely eliminated had photosynthesis been expressed in terms of chlorophyll a content, as recommended by Wallentinus (1978).

It is also possible that old, winter plants are metabolically less active than juveniles which grow rapidly during summer. The presence of epiphytes (see Apendix C ) on the old plants may also lower photosynthetic rates by shading. However, the opposite effect was shown in the case of the red alga Ceramium tenuicorne, where plants with a covering of rapidly growing epiphytic green algae showed higher rates of photosynthetic $^{14}C$ assimilation than those without epiphytes (Wallentinus, 1978).

It is interesting that the light compensation points in summer and winter D. firma plants are the same (10 - 20 $\mu E.m^{-2}.s^{-1}$), as are the light saturation levels (300 - 400 $\mu E.m^{-2}.s^{-1}$). In 22 species of algae investigated by King and Schramm (1976), light compensation points were lower in winter than in summer. Light saturation levels were lower in only some of the species which they examined, e.g. Laminaria saccharina and L. digitata.

In D. firma, maximum levels of photosynthesis (light saturated photosynthesis), in both summer and winter plants, showed no decline, up to P.A.R. levels of 2,500 $\mu E.m^{-2}.s^{-1}$. It is known that different algae exhibit different photosynthetic responses to high light levels (Hellebust, 1970). For example, King and Schramm (1976) showed that, of the 7 brown algae which they investigated, only Ectocarpus confervoides showed a decline in photosynthesis with high light levels, in spring. In Laminaria saccharina and L. digitata, photosynthesis was inhibited by high light levels in winter, but remained unaffected in spring and summer.

Of the 8 species from Oudekraal which Hay and Pope (unpublished) examined, sustained light saturated rates of photosynthesis, up to 2.500 $\mu E.m^{-2}.s^{-1}$, were shown for Botryocarpa prolifera, Neuroglossum binderianum, Epymenia obtusa, Axillariella constricta, and Suhria vittata. By contrast, Gelidium sp., and Cladophora sp., from the same algal community, showed declining rates of photosynthesis at P.A.R. levels in excess of 2,000 $\mu E.m^{-2}.s^{-1}$.

However, the incubations performed in the present study, and those of Hay and Pope, were run for 1 hour at a time, and it is possible that longer periods of exposure to strong light could result in reduced rates of photosynthesis even at levels well below 2500 $\mu E.m^{-2}.s^{-1}$. Lowered rates of photosynthesis at high light levels may be caused by an increase in photorespiration relative to photosynthesis, since high light levels have been shown to stimulate photorespiration in land plants (Zelitch, 1968 in Hough, 1974), and the presence of photorespiration in at least some algae is well known (Burriss, 1977; Black et al, 1976; Burris et al, 1976; Tolbert and Garey, 1976; Hough, 1976). In D. firma and other algae which show sustained photosynthesis at high light levels, photorespiration may thus be negligible, or absent. This is borne out by the negligible inhibitory effect of high $O_2$ levels on photosynthesis in D. firma, since high $O_2$ levels are known to stimulate photorespiration.

The higher rate of dark respiration in summer as opposed to winter (0.38 and 0.22 mg $O_2.g^{-1}h^{-1}$ respectively) is probably a result of the rapid growth of the former young plants, with cells of all the tissues increasing in size, and actively dividing.

The ratio of net photosynthetic rate to dark respiration (= 7.2) remained essentially the same in summer and winter, and is slightly higher than an average value of 6.03 obtained for Sargassum sp., Chaetomorpha sp, Enteromorpha sp., and Asparagopsis taxiformis (Burriss, 1977). Most of the marine algae investigated by Downton et al (1976) showed photosynthesis /dark respiration ratios of less than 10, and low ratios are suspected to be related to low growth rates in certain algae (Brown and Tregunna, 1967, in Burriss, 1977). In general, these ratios in marine algae are lower than reported for terrestrial plants (Burriss, 1977).

The light saturated rate of photosynthesis measured in the field (1.90 mg $O_2.g^{-1}.h^{-1}$), in summer, is significantly lower than the summer rate measured in the laboratory (2.75 mg $O_2.g^{-1}.h^{-1}$). Both curves are based on data from young plants which had not shed their trichothallic meristems, and were apparently healthy and epiphyte-free. The lower in situ rate of photosynthesis is expected to be an experimental artifact caused by lower rates of stirring in the chamber used in the field. The pumps in these chambers only provided sufficient water movement to slightly agitate the fronds, whereas the magnetic stirrers used in the laboratory provided virorous agitation. This concurs with the findings of Buesa (1977), who showed that stirring was a significant factor when measuring photosynthetic rates. It is concluded that the laboratory measurements give a more realistic estimate of photosynthesis in the natural environment, where water movement is invariably vigorous.

It is difficult to compare absolute rates of net photosynthesis in D. firma with results obtained using other species of seaweed

from elsewhere. There have been numerous studies of the relationship between light intensity and photosynthesis in marine algae, both using $O_2$ methods (e.g. Johston and Cook, 1968; King and Schramm, 1976; Brinkhuis, 1977; Hatcher *et al*, 1977; Littler, 1980; Arnold and Murray, 1980) and using $^{14}C$ assimialtion methods (e.g. Wallentinus, 1978; Brinkhuis and Jones, 1974; Mathieson and Burns, 1971; Smith, 1981). However, differences in experimental methods (e.g. light source and method of measurement, water movement, incubation period, etc) and differences inherent in the wide range of algae used, make comparisons of absolute rates of photosynthesis dubious, at best. The subtidal algae from Oudekraal which Hay and Pope (unpublished) studied under the same experimental conditions as used in the present study, showed a wide range of maximum (light saturated) photosynthetic rates. *Botryocarpa prolifera*, *Neuroglossum binderianum* and *Epymenia obtusa* showed rates which were similar to (2.0 to 2.7 mg $O_2.g^{-1}.h^{-1}$) but slightly lower than *D. firma* (2.75 mg $O_2.g^{-1}h^{-1}$). *Suhria vittata*, *Cladophora sp.* and *Hymenena venosa* showed somewhat higher maximum rates of net photosynthesis (4.5 to over 6.0 mg $O_2.g^{-1}.h^{-1}$), and *Gelidium sp.*, *Axillariella constricta*, *Trematocarpus sp.*, and *Heringia sp.* showed considerably lower rates (o.5 to 1.5 mg $O_2.g^{-1}.h^{-1}$). Since nothing is known of the growth rates of the algae used by Hay and Pope, a possible correlation between growth rate and maximum photosynthesis rate cannot be established. However, it is clear that some of the most bulky algae (e.g. *Axillariella*) show the lowest rates of maximum photosynthesis. Net and gross production rates, per dry mass, were shown to correlate well with thallus form, in 45 species of marine macroalgae investigated by Littler (1980). The highest per dry mass production rates were shown by thin, sheet-like and finely branched forms, followed by coarsely branched forms, with the lowest rates shown by articulated corallines, cushion-like forms, and thick sheet-like forms.

Several conclusions emerge from this study. Firstly, the fact that *D. firma* is most abundant in deeper zones in the

Oudekraal kelp bed, and is almost absent from depths of less than 2m below L.W.S., cannot be related to high light levels in the shallow water, because photosynthesis in this species is not inhibited even by light levels approaching those of full sunlight. In any case, there is evidence that seaweeds are capable of modifying both their absolute pigment levels and the relative levels of different pigments in response to ambient light levels, in order to optimise rates of photosynthesis (Ramus et al, 1976 a, b; Ramus et al, 1977). The reasons for D. firma being most abundant in water deeper than 2-3m are thought to be related to biotic factors, such as competition for space (see Chapter 4).

During summer upwelling, D. firma plants can show maximum rates of photosynthesis for a large part of each day. For example, plants at 6m depth, where P.A.R. was measured (Fig. 6.6), would show maximum rates for 8-9 hours. However, during winter downwelling, when surface, and particularly submarine irradiance levels are far lower, it is unlikely that the plants ever show maximum photosynthesis rates, and as a result their daily production must decline. It is therefore very likely that the winter decline in growth rates and standing crop of D. firma is directly related to low ambient light levels.

Maximum rates of photosynthesis in D. firma are similar to those in most of the other subtidal algae from Oudekraal for which data are available. Thus, this species, despite its annual nature, does not appear to be inherently more productive than many of its neighbours.

Finally, it seemed logical to use the data on photosynthetic rates (Fig. 6.10), submarine irradiance (Figs. 6.5, 6.6) and data on seasonal standing crops of Generation 2 plants in 1978 - 1979 (Chapter 5, Fig. 5.12), and, making several broad assumptions, to estimate the net primary production of D. firma in the study site and to compare this estimate with the value obtained by the Allen Curve method (Chapter 5).

Assuming that upwelling occurs continuously during spring and summer (September - March), and that during a day of upwelling, D. firma shows a sustained rate of maximum gross photosynthesis (maximum net photosynthesis plus dark respiration) of 3.08 mg $O_2.g^{-1}h^{-1}$ for 9 hours, then total gross photosynthesis during this period equals $5.82 \times 10^3$ mg $O_2.g^{-1}$ dry mass. During the same period $1.9 \times 10^3$ mg $O_2.g^{-1}$ are lost during dark respiration (assuming that this occurs continuously at the rate of 0.38 mg $O_2.g^{-1}.h^{-1}$, shown in Fig. 6.10). Thus, net photosynthetic production during this period was approximately 2.3 $g.m^{-2}$, and thus in September-March, net production per unit area = $9.02 \times 10^3$ mg $O_2.m^{-2}$. To convert this value to total carbon fixed, a photosynthetic quotient of 1.25 was used, since Westlake (1963) suggests that this is applicable to plant populations growing in optimal nutrient conditions. Thus net production = 2.71 $gC.m^{-2}$. Assuming that carbon comprises 25% of the dry mass of the tissues (the value obtained in Laminaria pallida fronds, by Dieckmann, 1978), the net production of D. firma during this period, in terms of dry mass would be 10.84 g dry $mass.m^{-2}$. A similar calculation for the period April-August, assuming uniform downwelling conditions with a daily mean of 8 hours light at 100 $nE.m^{-2}.s^{-1}$ (from Fig. 6.5), a gross photosynthetic and dark respiration rate of 1.47 and and 0.22 mg $O_2.g^{-1}$ dry $mass.h^{-1}$ respectively (Fig. 5.12), and a photosynthetic quotient of 1.2 for unfavourable nutrient conditions (Westlake, 1963), yields a net production value of 5.56 g dry $mass.m^{-2}$. The sum of these summer and winter estimates equals 16.4 g dry $mass.m^{-2}$.

While this value compares well with that obtained from seasonal changes in standing crop, using the Allen Curve method (approximately 23 g dry $mass.m^{-2}$), it is clear that because of the assumptions made in the former case, the production value (16.4 g dry $mass.m^{-2}$) can only be treated as a very general estimate. There may be important errors in the assumptions made in this estimate, particularly those pertaining to submarine irradiance. Depths at which D. firma is found in the study

site vary from 0 to 14m, with concurrent variation in the quantity and spectral quality of submarine irradiance. The assumption that upwelling occurs for 7 months (58%) of the year agrees fairly well with data obtained by Carter (1982), who showed that upwelling occured 52% of the time, during four seasonally-spaced surveys, each of 8 - 10 days duration, in 1979. However, the time of the year during which upwelling occurs may be important when related to the seasonal standing crop of D. firma. For example, protracted upwelling at the beginning of spring (August), when the standing crop of D. firma is minimal, would not immediately enhance production rates as much as protracted upwelling in April, when standing crops are high. Furthermore, it may be misleading to assume that the maximum photosynthetic rate is sustained throughout most of a day of upwelling, since Ramus and Rosenberg (1980), using 5 species of intertidal marine algae, have shown that there are considerable diurnal fluctuations in photosynthetic rate, particularly under conditions of high illumination. Under these conditions, diurnal rates did not symmetrically correspond to diurnal fluctuations in irradiance, and in most of these species (e.g. Codium decorticatum, Ulva lobata, and Gracilaria foliifera) photosynthetic rates were highest in the morning, and then declined throughout the day. These authors suggest that this decline may be due to a number of factors, including an inherent circadian periodicity, photoinhibition, photorespiration, and an increase in dark respiration. They conclude that maximum photosynthesis values derived from instantaneous measurements in the laboratory cannot provide an accurate estimate of diurnal production.

From the preceding observations it is clear that reliable estimates of primary production from photosynthesis measurement take into account possible diurnal fluctuations in photosynthetic rate, and include reliable field data on submarine irradiance, and on seasonal standing crops of the alga concerned. Although this study did not specifically set out to estimate production in the field from P vs I curves, it provides evidence that this approach may be most useful, particularly when the above criteria are met.

# CHAPTER 7

## ACIDITY of DESMARESTIA FIRMA and the PALATABILITY of THIS ALGA to the URCHIN PARECHINUS ANGULOSUS

### 7.1 INTRODUCTION

The acidity of certain Desmarestia species is well-known to collectors of algae, since these plants turn light green after removal from sea water, and will discolour and destroy other specimens with which they come into contact. During this study it was found that D. firma bleached rocks in the supra-littoral zone, when cast ashore and left drying in the sun. White Desmarestia-shaped marks indicated where the acid had removed the brown organic coating on sandstone rocks.

Various authors have investigated the acidity in Desmarestia species (Kylin, 1931; Wirth and Rigg, 1937; Miwa, 1953; Meeuse, 1956; Eppley and Bovell, 1958; Carlberg et al, 1978), which occurs as a result of high levels of $H_2SO_4$ (in the vacuoles of the cells) and possibly small quantities of organic acids. In the present study both total acidity and sulphate levels were compared with those in the non-acid Desmarestia rossii J.D. Hooker et Harvey.

During the course of this thesis, the question arose as to whether the acidity may act as a deterrent to potential grazers of D. firma. It has been shown that urchins fed only D. ligulata (another acid containing species) suffered eroded teeth (Irvine, 1973).

A variety of marine herbivores have been shown to have distinct preferences for certain algae, while avoiding others (Leighton and Boolootian, 1963; Vadas, 1977; Ogden, 1976; Paine and Vadas, 1969; Leighton, 1966; Lawrence, 1975). Many of these authors suggest that negative preferences may be associated with chemical deterrents in certain algae (e.g. Vadas, 1977).

Paech (1950) discussed the wide group of compounds which do not appear to be involved in the primary metabolism of plants, and termed them "secondary substances". These, by definition,

occur sporadically in various groups of plants, show a wide range of chemical constitutions, and appear to provide the plant with some sort of environmental advantage, for instance by discouraging grazers (Fraenkel, 1959) or micro-organisms. Secondary substances include glucosides, saponins, phenols, alkaloids and many other compounds. By contrast, "primary" substances (for example starch, vitamins, and amino acids) occur in all living matter, and are unlikely to specifically influence predation by grazers. Recently there is evidence that many of the "secondary chemicals" in plants are in fact involved in primary metabolic processes (Seigler & Price, 1976; Seigler, 1977). Nevertheless, it is indisputable that certain compounds provide chemical defense mechanisms in some plants, and the term "secondary substances" is used here in this sense.

Among algae, these secondary substances include phenols, which have been shown to have antibiotic effects (Sieburth and Conover, 1965; Martinez Nadal et al, 1965) and the halogenated compounds shown to be present in many of the Rhodophyta (Fenical, 1975). Anti-bacterial effects were shown for many of the 151 British algae investigated by Hornsey and Hide (1974) but they made no attempt to isolate the chemical compounds responsible. Certain simple phenols from macro-algae have been shown to adversely affect unicellular algae, and they are implicated in the regulation of endo and epiphyte build-up (McLachlan and Craigie, 1966). Physodes, which are small sub-cellular bodies present in the cells of brown algae, have been shown to contain phenolic compounds, and their occurence is reviewed by Ragan (1976). More recently, Polyphenols in the brown algae Fucus vesiculosus and Ascophyllum nodosum have been shown to inhibit feeding by the major herbivore found in their community, the snail Littorina littorea (Geiselman and McConnel, 1981).

The present study has two aims. First to measure the total acidity in the thallus of D. firma and to determine whether this varies with the age of the plant or between different parts of the plant. The second aim is to examine the relative palatability of D. firma, compared to 12 other common kelp bed algae, in order to determine whether the acid content may function as a "secondary compound" in the sense that it makes the

plant unattractive to the grazing animal Parechinus angulosus Leske. These sea urchins were used as the experimental grazer because they are one of the most prominent herbivores in local kelp beds (Velimirov et al, 1977), they are easy to collect and maintain in the laboratory, and they have been studied in some detail (Greenwood, 1974). In addition, a great deal of work has been done on food selection in other species of urchins, and is reviewed by Lawrence (1975).

In an effort to further explain the patterns of choice which were shown, the relative astringency values (Bate-Smith, 1973) of the experimental algae were measured, and the phenol contents of selected species were estimated by the Folin-Denis method (Folin and Denis, 1915; Swain and Hillis, 1959).

## 7.2 MATERIALS and METHODS

### 7.2.1 Determination of Acid Content in D. Firma

#### 7.2.1.1 Estimation of Total Acidity by Alkali Titration

Plants were collected from the study site in March 1979, and kept in running water aquaria overnight. Fronds were lightly mopped with paper towels, and divided into 3 categories: entire axial frond, basal half of primary frond, and distal half of primary frond. The secondary fronds were not used. These 3 categories of tissue were treated separately for comparative purposes. The fronds were cut into peices and 8g amounts of tissue weighed into conical flasks containing 150 ml of distilled water. The tissue was then macerated with a high-speed blender until it consisted of uniform fine pieces less than 1 mm in size. The volume of each flask was then made up to 200 ml and the flasks sealed and left at $10^{o}$C overnight.

From each flask two 25 ml aliquots of the clear supernatant were removed for titration with standard 0.1N NaOH, to an end point of pH7, using a Beckman pH meter. Each final titre value was a mean of the 3 aliquots.

Assuming that the only acid present was $H_2SO_4$, the mass of $H_2SO_4$ was then calculated. Results are expressed as mg. of $H_2SO_4$ per g. fresh mass, and using a ratio of dry mass = 8.8% of fresh mass (March '79 population data, Fig. 5.8), results are expressed on a dry mass basis as well (Table 7.1).

#### 7.2.1.2 Gravimetric Determination of Sulphate Content

D. firma material was collected in November 1979 at Oudekraal, placed in an aquarium, and processed the following day. Material of D. rossii, a non-acid species, was collected from Ship's Cove, Marion Island ($46^{o}$ 54'S $37^{o}$ 45'E) and kept frozen until analysed.

Sulphate content was determined by precipitation with excess

barium chloride according to Vogel (1961). Three categories of tissue were analysed for comparative purposes; young D. firma (approximately 2 months old), old D. firma (approximately 12 months old), and D. rossii (of unknown age). Fifteen replicates of each category were used.

Approximately 10g of fresh tissue were blotted dry, weighed and macerated in 100 ml of distilled water, using a high-speed blender, then left to stand for 24 hours at 10°C. Samples were then filtered through Whatman No. 1 paper. The filtrate was then neutralised where necessary, with 0.1N NaOH, and made up to 200 ml with distilled water. 1 ml of concentrated HCl was added to each sample, and it was heated to boiling point.

With the sample on a hotplate/magnetic stirrer, 10 ml of warm 10% $BaCl_2$ was added drop-wise from a burette. The precipitate was allowed to settle for a few minutes. The supernatant was tested with a few drops of $BaCl_2$. In no cases did further precipitate form, indicating that excess $BaCl_2$ had been added initially.

The solution was kept at 80°C for 1 hour, and the volume was kept at 200 ml by adding distilled water. The supernatant was tested once more with a few drops of $BaCl_2$, and the solution left to stand overnight to obtain a coarse precipitate.

Solutions were then filtered through No. 42 Whatman paper, washing with hot distilled water, until the wash ceased to show opalescence, when tested with silver nitrate. The filter was transferred to a crucible which had previously been heated to 400°C, cooled in a desiccator and weighed.

The samples were first dried at 80°C then placed in a muffle furnace with the door open, and the temperature increased until the papers were ashed, taking care that they did not burst into flames. The furnace was then closed and the temperature raised to 900°C for 15 mins. The crucibles were transferred to a desiccator, allowed to cool, and weighed.

The total sulphate content of each sample was calculated as follows: $BaSO_4$ contains 41.16% $SO_4$, therefore

$$\text{mg. } SO_4.g^{-1} \text{ fresh mass} = \frac{\text{mass of ppt (g)} \times \frac{41.16}{100}}{\text{fresh mass of sample (g)}}$$

## 7.2.2 Astringency and Phenol Content of Algae

### 7.2.2.1 Collection of Material and Extraction of Astringent Compounds

All of the algae used in the feeding experiments were subjected to a relative astringency test, and four of these were selected and tested for phenols, using Folin-Denis reagent. The methods of extraction were the same in both cases.

Plants for the relative astringency test were collected at Oudekraal, at depths of from 3 - 10m in August (late winter). Material was frozen and the extraction and relative astringency analyses performed one month later. Plants for the Folin-Denis test were collected in January (summer) from 5 - 10m depth at Bakoven, near Oudekraal, and fresh material used for extractions.

In neither case was oven-dried material used, since drying may polymerize phenols (Goldstein and Swain, 1963).

Several plants of each species were cut into strips, the strips were mixed, mopped with paper towel, and 3g samples weighed out. Duplicate samples were extracted for each species.

The samples were homogenized in pure (98%) methanol using a high-speed blender. The homogenate was made up to about 50ml with methanol, and extraction was completed by the method of Swain and Hillis (1959). This involves four 5-minute washes in boiling pure methanol (70°C) and four 5-minute washes in boiling 50% methanol (80°C). The pure and 50% extracts were kept separate, and evaporated down to about 20ml. They were

then filtered through Whatman No.1 cellulose filter paper which had been wetted with the relevant solvent to minimise absorption of the extract, and the volumes were made up to 25 ml. The extracts were stored in air-tight vials and refrigerated until they were analysed.

### 7.2.2.2 Measurement of Relative Astringency

The method of Bate-Smith (1973) was followed. This is based on the precipitation of haemoglobin by phenolic compounds. The degree of precipitation is determined colourimetrically, and related to a standard curve of a reference compound (in this case tannic acid) of known concentrations.

Fresh venous human blood was obtained with a hypodermic syringe, mixed with a small amount of sodium citrate buffer/ anticoagulant, and stored overnight at $2^{o}C$.

The blood was then diluted 50 times with cold distilled water, kept chilled and used within 38 hours.

2 ml aliquots of the haemalyzed blood were mixed with 2 ml aliquots of each extract, centrifuged at 3000 r.p.m. for 5 minutes, and the absorbance of the supernatant read at 578 nm., on a Beckman automatic spectrophotometer.

Controls consisted of 2 ml of the relevant extract and 2 ml of distilled water, subjected to the same centrifugation as the experimental samples. The absorbance value for the control supernatant was subtracted from that of the reaction, in each case.

In some cases it was necessary to dilute the algal extract to allow comparision with the standard curve.

Fresh tannic acid solutions (0 - 0.9 mg. $ml^{-1}$) were used to construct a standard curve (Fig. 7.1). This range of concentrations is slightly greater than that recommended by Bate-Smith (1973) or Glyphis (unpublished, 1980), but a good linear fit was

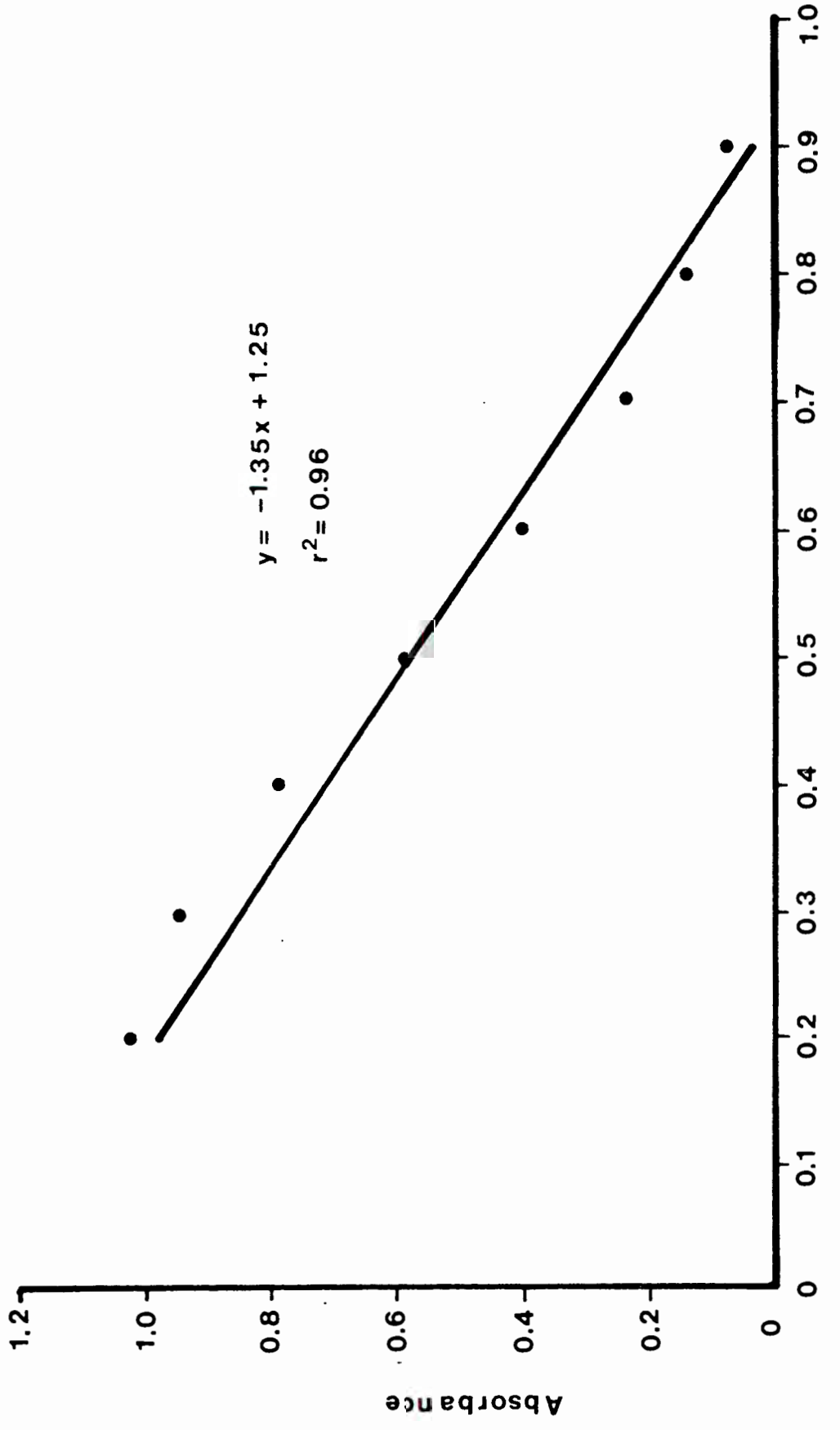



FIG. 7.1 Standard curve: absorbance at 578 nm of haemoglobin solutions after precipitation with varying concentrations of tannic acid.

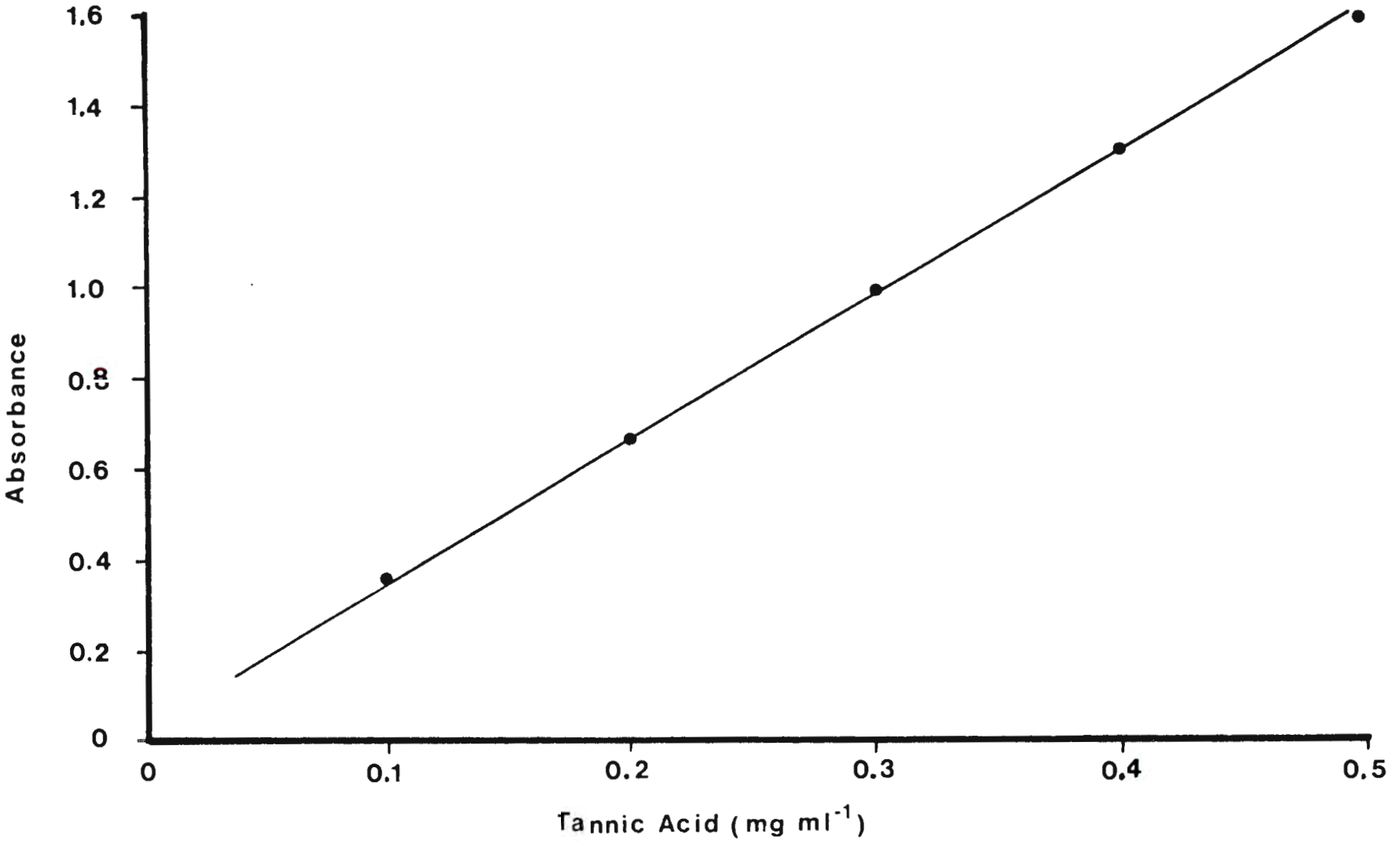



FIG. 7.2 Standard curve: Absorbance at 725 nm of tannic acid solutions subjected to Folin-Denis reaction.

obtained ($r^2$ = 0.96).

The results for the 98% and 50% methanol extracts, estimated as "equivalent tannic acid" ($mg.g^{-1}$ fresh mass), are presented in Table 7.3. In the final column of this table, astringency results are expressed on a relative scale, taking the highest total astringency, that of Ecklonia maxima as 1.

Since D. firma was found to contain approximately 16.0 $mg.g^{-1}$ fresh mass of $H_2SO_4$ a solution of $H_2SO_4$ of the relevant concentration (1.92 mg $H_2SO_4$ $ml^{-1}$, assuming all the acid is extracted) was tested for relative astringency in the same way as the algal extracts. In this case the control was distilled water.

In order to investigate the possible relationship between relative astringency of the algae and the feeding rates of urchins, a linear regression of feeding rates (Fig. 7.2) against relative astringency (Table 7.3) was performed, and is presented in Fig.7.4.

### 7.2.2.3 Folin-Denis Test for Phenols

The Folin-Denis method was used to determine "total phenols" (Folin and Denis, 1915). Methods used were modified according to Glyphis (unpublished, 1980), Swain and Hillis (1959) and Goldstein and Swain (1963). Four of the 13 algae were used: D. firma, Ecklonia maxima, Laminaria pallida and Gigartina clathrata. This method measures the concentrations of total polyphenols with molecular weights in the approximate range 1000 - 3000, since these are extracted using methanol and aqueous methanol.

1 ml of each extract was pipetted into each test tube, and 1 ml of 0.25N Folin-Denis reagent (complex phosphotungstomolybdate) added, and the test tubes shaken, and left to develop for 1 hour.

The tubes were then centrifuged at 2000 r.p.m. for 2 minutes, and the supernatant drawn off. Clear yellowish rings were present in the supernatant of the Gigartina, and to a slight degree in the Laminaria and Ecklonia. These rings were not included in the fraction used to measure absorbance. It is thought that they may result from reactions of polypeptides with the Folin-Denis reagent. Absorbance of the supernatant fractions was read in a Beckman model 25 spectrophotometer at a wavelength of 725 um. The control consisted of a distilled water blank, subjected to the addition of Folin-Denis reagent, $Na_2CO_3$, and to centrifugation.

Fresh tannic acid solutions, in the range 0.0-05 mg. $ml^{-1}$ were used to construct a standard curve (Fig. 7.2).

Results for the 98% and 50% methanol extracts are expressed as equivalent tannic acid (mg.$g^{-1}$ fresh mass) and the totals are also expressed on a relative scale, taking the value for Ecklonia as 1. (Table 7.4).

It is recognised that this method does not provide an absolute measure of phenol content, since values are based on a colourimetric reaction, and related to a standard curve of an arbitrarily chosen phenol, tannic acid. However, they provide an estimate of the relative phenol levels in the 4 species investigated.

### 7.2.3 Feeding Experiments

#### 7.2.3.1 Collection of Material

Sea urchins Parechinus angulosus were used as the experimental grazing animal. It was initially intended to use other grazers as well but problems led to these attempts being abandoned. The abalone Haliotis midae proved to be a somewhat erratic feeder and the isopod Paridotea reticulata was difficult to collect in sufficient numbers.

Urchins and 13 common subtidal algae were collected from depths of 3 - 10 metres at Oudekraal. Urchins were starved for 10 days before use, and algae always used within 2 days of collection. Material was stored and experiments carried out, in running-water aquaria at 12°- 14°C. Urchins of 2.5 - 4 years old were selected on the basis of test diameters (Greenwood, 1974) to ensure some uniformity in feeding rates. New sets of animals were used for each experiment to avoid conditioning them to certain diet algae.

The following algae were used (order and family in parentheses):

Phaeophyta:
Desmarestia firma (Desmarestiales, Desmarestiaceae)
Ecklonia maxima (Laminariales, Alariaceae)
Laminaria pallida (Laminariales, Laminariaceae)
Macrocystis angustifolia (Laminariales, Lessoniaceae)
Axillariella constricta (Fucales, Fucaceae)

Rhodophyta:
Gelidium sp. (Gelidiales, Gelidiaceae)
Suhria vittata (Gelidiales, Gelidiaceae)
Pachymenia cornea (Cryptonemiales, Cryptonemiaceae)
Gigartina clathrata (Cigartinales Gigartinaceae)
Botryocarpa prolifera (Ceramiales, Delesseriaceae)
Neuroglossum binderianum (Ceramiales, Delesseriaceae)
Hymenena venosa (Ceramiales, Delesseriaceae)
Carradoria virgata (Ceramiales, Rhodomelaceae).

The three types of feeding experiments are described below:

### 7.2.3.2 Rate of Feeding on Single Species of Algae.

Algae were cut into strips, mopped with paper towel and about 20 g of each species weighed out into each tank. There were 4 urchins per tank, and 6 replicate tanks were used for each algal species. Urchins were allowed to feed for 72 hours and

then the strips were removed, mopped and re-weighed. Control tanks contained no urchins and were used to provide estimates for non-grazing weight loss. Since feeding rates on a single species of algae may not give a good indication of preferences (Vadas, 1977), additional experiments were performed which involved selection and feeding on a range of algae.

### 7.2.3.3 Multiple Choice Feeding Experiments

In these experiments, urchins were allowed to select and feed on various algal species simultaneously to investigate whether the algae could be ranked according to palatibility. Vadas, (1977), and Leighton, (1966), consider this type of experiment to be the best test of algal palatibility since it involves selection and feeding, both of which are necessary requisites for animal survival. Four of these selection experiments were performed, and in each experiment 5 species of algae were used simultaneously, since a larger number may have obscured measurable preferences.

The algae were cut into strips, mopped with paper towel, and approximately equal masses of each species mixed into each of 3 replicate tanks, and into one control tank. Eight pre-starved urchins were placed in each tank except the control and allowed to feed for 72 hours. The algae were then removed, sorted into species, mopped dry, and re-weighed. Final fresh-mass grazing losses were corrected for non-grazing losses, which in all species were less than 4%.

Results were subjected to Analysis of Variance to test the null hypothesis that there was no difference between the mean masses of the various algae eaten. All possible comparisons of means were then made by the Student Newman Keuls test (Zar, 1974).

### 7.2.3.4 Paired Algae Feeding Experiments

To clarify some of the relative preference results from the rate of feeding and the multiple choice experiments, urchins were given pairs of algal species to select and feed from.

Weighed strips of 2 species of algae were mixed into each replicate tank, and 4 pre-starved urchins placed in each tank, and allowed to feed for 72 hours. Once again corrections were made for non-grazing losses. The number of replicates for each species pair varied between 4 and 8.

The fresh masses of algae consumed in each species pair were compared by Mann-Whitney U test, and the results are presented in Table 7.6.

## 7.3 RESULTS

### 7.3.1 Acidity in D. firma

#### 7.3.1.1 Estimation of Total Acidity by Alkali Titration

The results of total acid determinations are presented below. Results on dry mass basis are estimated from 'per fresh mass' values, using a ratio of dry mass = 8.8% fresh mass, from March 1979 population data.

| Portion of thallus | No. of Samples | $H_2SO_4$ per fresh mass | | Total $H_2SO_4$ per dry mass | |
|---|---|---|---|---|---|
| | | % | $mg.g^{-1}$ | % | $mg.g^{-1}$ |
| Axial fronds - basal | 10 | 1.6 | 16.0 ( 2.1) | 18.3 | 183 ( 24) |
| Axial fronds - distal | 10 | 1.6 | 16.0 ( 1.2) | 18.3 | 183 ( 13) |
| $1^{O}$ fronds - entire | 20 | 1.6 | 16.4 ( 0.8) | 18.7 | 187 ( 10) |

Table 7.1 Total acid content of *D. firma* fronds, assuming all $H^+$ ions from $H_2SO_4$. 95% confidence limits of means shown in parentheses.

These results indicate that there is no difference in total acidity between basal and distal portions of the axial frond, and primary fronds. The whole thallus of these plants (approximately 4 months old) showed a mean acid content of 1.6% of fresh mass, or about 18% of dry mass.

#### 7.3.1.2 Gravimetric Determination of Sulphate Content

The results of sulphate determinations are presented below. Results expressed on a per dry mass basis are estimated from the results per fresh mass and the relevant percentage dry mass.

| Plant | % dry mass | $SO_4$ per fresh mass | | $SO_4$ per dry mass | |
|---|---|---|---|---|---|
| | | % | $mg.g^{-1}$ | % | $mg.g^{-1}$ |
| D. firma approx. 2 mo old | 9 | 2.5 | 24.5 ( 1.5) | 27.2 | 272 ( 17) |
| D. firma approx. 12 mo old | 12 | 2.3 | 23.3 ( 1.3) | 19.3 | 193 ( 12) |
| D. rossi (unknown age) | 35 | 0.2 | 1.8 ( 0.3) | 0.5 | 5 ( 1) |

Table 7.2 Total sulphate content of D. firma and D. rossi. Values are means of separate determinations on 15 samples each, D. firma from separate plants, D. rossi from one plant. 95 % confidence limits of means in parentheses.

There was no difference in sulphate content per fresh mass between 2 and 12 months old plants (Students't-test).

There is a significant difference even at the 99% probability level, between sulphate content of 2 and 12 month old plants expressed on a dry mass basis (Students' t-test). However this is because the % dry mass values of the young and old plants differ, and if the percentage dry mass value of old plants (12%) is used to calculate sulphate per dry mass for the young plants, a value of 204 ± 13 mg $SO_4$ $.g^{-1}$ dry mass is obtained, which does not differ statistically from the value of 193 ± 12 mg $SO_4$ $.g^{-1}$ for old plants. In any case, to a grazing animal, acidity is effective on the basis of the fresh mass of material ingested.

The non-acid forming D. rossii shows $SO_4$ levels of about 2.5% of those in D. firma, per unit dry mass of tissue.

### 7.3.2 Astringincy and Phenol Content of Algae

#### 7.3.2.1 Measurements of Relative Astringency

Tannic acid standard curve shown in Fig. 7.1

| Source | Astringency | | | Relative scale |
|---|---|---|---|---|
| | 98% MeOH | 50% MeOH | Total | |
| Pachymenia cornea | 0.42 | 1.50 | 1.92 | 0.07 |
| Gigartina clathrata | 2.50 | 0.67 | 3.17 | 0.12 |
| Carradoria virgata | 1.17 | 2.00 | 3.17 | 0.12 |
| Laminaria pallida | 4.17 | 2.33 | 6.50 | 0.24 |
| Gelidium sp. | 5.41 | 2.00 | 7.41 | 0.27 |
| Suhria vittata | 5.00 | 2.67 | 7.67 | 0.28 |
| Macrocystis angustifolia | 7.49 | 2.00 | 9.49 | 0.35 |
| Botryocarpa prolifera | 6.66 | 2.83 | 9.49 | 0.35 |
| Hymenena venosa | 8.16 | 9.60 | 17.76 | 0.65 |
| Desmarestia firma | 12.50 | 8.00 | 20.50 | 0.75 |
| Axillariella constricta | 18.74 | 4.75 | 23.49 | 0.87 |
| Neuroglossum binderianum | 22.49 | 2.33 | 24.82 | 0.91 |
| Ecklonia maxima | 23.32 | 3.83 | 27.15 | 1.00 |

Table 7.3 The relative astringencies of 98% and 50% methanol extracts of experimental algae. Astringency values are expressed as estimated equivalent tannic acid ($mg.g^{-1}$ fresh mass alga). The relative scale is based on the highest total astringency measured, that of *E. maxima*.

The results show a range of relative astringencies in the experimental algae, with the highest, *Ecklonia*, some 14 times higher than the lowest, *Pachymenia*.

An important result is that a sulphuric acid solution of the same concentration as that which is found in *D. firma*, has an apparently high astringent effect (0.66 on a relative scale), which would account for 88% of the measured astringency of this alga.

### 7.3.2.2 Phenol Content of Selected Algae

The standard curve in Fig. 7.2 was used to estimate the phenol content of the samples, expressed as equivalent tannic acid (mg. $ml^{-1}$).

| Algal Species | Equivalent tannic acid (mg.$g^{-1}$ fresh mass) | | | Relative scale |
|---|---|---|---|---|
| | 98% MeOH | 50% MeOH | Total | |
| *Ecklonia maxima* | 3.69 | 0.23 | 3.92 | 1.00 |
| Desmarestia firma | 0.16 | 0.00 | 0.16 | 0.04 |
| Laminaria pallida | 0.25 | 0.01 | 0.26 | 0.06 |
| Gigartina clathrata | 0.12 | 0.00 | 0.12 | 0.03 |

Table 7.4 Estimated phenolic contents of 4 species of algae used in feeding experiments, determined by Folin-Denis method. Results are expressed as equivalent tannic acid (mg.$g^{-1}$ fresh mass) and on a scale relative to the highest value (that of Ecklonia.)

These results indicate that phenol levels in Ecklonia are approximately 20 times higher than in the other 3 species tested.

It is important to note that phenol levels in Desmarestia appear to be low, and comparable to Laminaria and Gigartina.

There is a marked difference between directly measured phenol levels, as estimated by the Folin-Denis method, Table 7.4, and the relative astringencies of these algae (Table 7.3). For example, measurement of relative astringency in Ecklonia would imply a phenol content some 7 times higher (27.15 mg.$g^{-1}$ fresh mass) than that measured using the Folin-Denis method (3.92 mg.$g^{-1}$ fresh mass). However within the values obtained by

each of the two methods, the differences bwtween species i.e. the relative differences, appear to be fairly consistent.

## 7.3.3 Feeding Experiments

### 7.3.3.1 Rate of Feeding on Single Species of Algae

In Fig. 7.3 feeding rates of urchins are presented, ranked from highest to lowest fresh masses eaten. There are clear differences in the amounts of the various species eaten, from the apparently most favoured, P. cornea to the least favoured H. venosa. The mean mass of D. firma eaten is intermediate between these, but relatively low.

### 7.3.3.2 Relationship Between Urchin Feeding Rates on Single Species and Astringency of Algae

This relationship was tested directly by simply plotting a regression of feeding rate by urchins (Fig. 7.3) against relative astringency (Table 7.3), for the 13 algae used (see Fig. 7.4).

The correlation coefficient, r, was then tested for significance (two-tailed test).

$r^2 = 0.58$

$r = 0.76$

$r_{0.01, 13} = 0.641$ (critical value of r)

Since the calculated value of r (0.76) exceeds the critical value, at the 99% probability level (0.641), it is concluded that there is a significant linear relationship between relative astringency and urchin grazing rates.

However, the low coefficent of determination, $r^2$ limits the predictive value of the correlation. In other words, while this regression shows a trend that urchin feeding rate is inversely proportional to the astringency of the algal prey, feeding rates cannot be quantitatively predicted from the relative astringency of the algae.

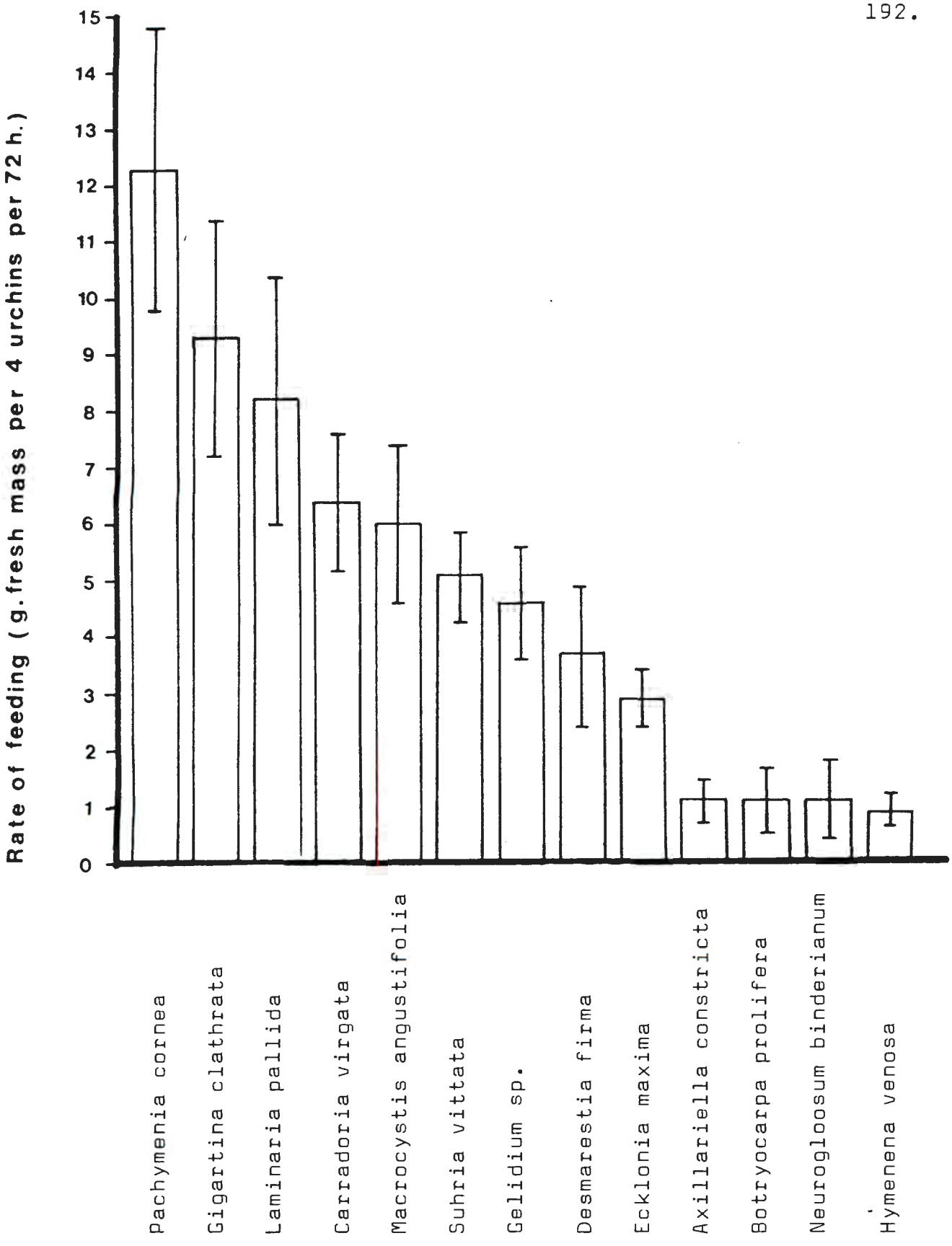



FIG. 7.3 Rates of urchin feeding on single species of algae.
Values are means of 6 replicates.
95% confidence limits of means are shown.

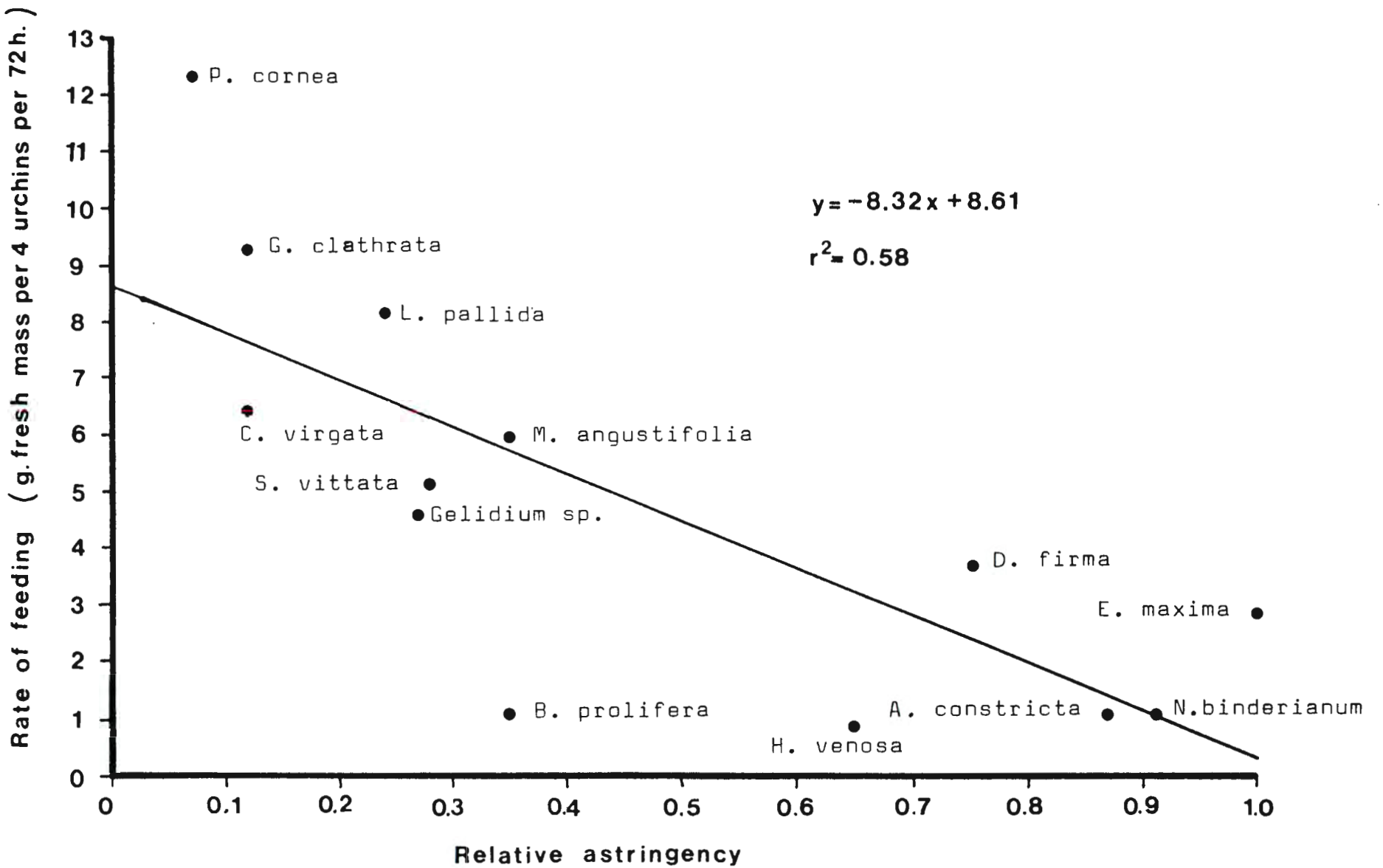



FIG. 7.4 Linear regression showing relationship between feeding rate of urchins on single species of algae and relative astringency of species.

It is noteworthy that D. firma falls with Ecklonia, Axilariella, Neuroglossum, Hymenena and Botryocarpa both in terms of high relative astringencies, and low rates of feeding by urchins. Pachymenia, Gigartina, Laminaria, Carradoria, Suhria, Gelidium and Macrocystis form a second group, with lower relative astringencies and higher urchin feeding rates.

### 7.3.3.3 Multiple Choice Feeding Experiments

Results of the four multiple choice experiments are summarised in Table 7.5.

**Experiment 1**

| | |
|---|---|
| Gigartina clathrata | 8.4 |
| Pachymenia cornea | 7.1 |
| Laminaria pallida | 1.2 |
| Ecklonia maxima | 1.1 |
| Desmarestia firma | 0.9 |

**Experiment 2**

| | |
|---|---|
| Suhria vittata | 5.2 |
| Gelidium sp. | 3.3 |
| Hymena venosa | 1.0 |
| Desmarestia firma | 0.6 |
| Axillariella constricta | 0.3 |

**Experiment 3**

| | |
|---|---|
| Pachymenia cornea | 5.2 |
| Gelidium sp. | 3.4 |
| Gigartina clathrate | 2.6 |
| Botryocarpa prolifera | 1.3 |
| Macrocystis angustifolia | 1.3 |

**Experiment 4**

| | |
|---|---|
| Carradoria virgata | 7.8 |
| Neuroglossum binderianum | 4.1 |
| Ecklonia maxima | 2.8 |
| Botryocarpa prolifera | 1.7 |
| Desmarestia firma | 1.5 |

Table 7.5 Overall results of multiple choice experiments. Values are g. fresh mass eaten per 8 urchins per 72 hours (means of 3 replicates). Solid lines indicate significant differences at 95 % confidence level or higher (Student Newman-Keuls test). Broken lines indicate difference at 90% confidence level according to Student Newman-Keuls test, between all possible pairs within each experiment.

Within each of the above experiments, analyses of variance showed that, at the 95% confidence level, there were significant differences between the amounts of the various algae eaten. The Student Newman-Keuls test then provided species-by-species comparisons.

Experiment 1: Urchins showed a significant preference for G. clathrata and P. cornea, while L. pallida, D. firma and E. maxima were non-preferred.

Experiment 2: S. vittata was most preferred, followed by Gelidium sp. and D. firma, A. constricta and H. venosa were equally unfavoured.

Experiment 3: Significantly more P. cornea was eaten, than was Gelidium sp., G. clathrata, M. angustifolia and B. prolifera, at the 95% confidence level. At the 90% confidence level, Gelidium sp was eaten in larger amounts than the three species ranked below it.

Experiment 4: The results of this experiment were less clear-cut. Carradoria was clearly preferred, while B. prolifera, D. firma and E. maxima appeared to be least preferred, with N. binderianum intermediate in ranking.

## 7.3.3.4 Paired Algae Feeding Experiments

| Species Pair | Mass eaten (g) | Replicate No. | U Value | Probability | Conclusion |
|---|---|---|---|---|---|
| L. pallida<br>D. firma | 3.9<br>1.1 | 7 | 0 | 0.000 | L. pallida preferred |
| G. clathrata<br>D. firma | 5.5<br>0.6 | 6 | 0 | 0.002 | G. clathrata preferred |
| P. cornea<br>D. firma | 4.1<br>0.6 | 4 | 0 | 0.028 | P. cornea preferred |
| E. maxima<br>D. firma | 1.5<br>1.5 | 7 | 24 | 1.000 | No difference |
| D. firma<br>A. constricta | 2.6<br>0.2 | 6 | 0 | 0.002 | D. firma preferred |
| E. maxima<br>A. constricta | 2.5<br>0.2 | 6 | 0 | 0.002 | E. maxima preferred |
| D. firma<br>H. venosa | 2.9<br>0.7 | 6 | 1 | 0.004 | D. firma preferred |
| P. cornea<br>Gelidium sp. | 2.8<br>2.5 | 6 | 17 | 0.930 | No difference |
| L. pallida<br>M. augustifolia | 5.1<br>1.8 | 6 | 1 | 0.004 | L. pallida preferred |
| L. pallida<br>E. maxima | 6.8<br>2.4 | 6 | 0 | 0.001 | L. pallida preferred |
| D. firma<br>N. binderianum | 3.0<br>1.4 | 6 | 0 | 0.002 | D. firma preferred |

Table 7.6 Results of paired algae feeding experiments. Mass eaten expressed as g fresh mass per 4 urchins per 72 hours. Probability is that associated with the Mann-Whitney statistic (2-tailed test).

On the basis of the above three types of feeding experiment, the 13 species of algae are divided into three arbitrary groups, according to their apparent palatibility to the urchin P. angulosus. These three groups are defined as follows:

Preferred: Algae which urchins appear to select and eat in relatively large amounts. This group includes Pachymenia cornea, Gigartina clathrata, Carradoria virgata, Suhria vittata and Gelidium sp.

Non-preferred: These algae are eaten in small amounts, particularly when other more palatable species are available. This group includes Hymenena venosa, Botryocarpa prolifera, Ecklonia maxima, Axillariella constricta, and Desmarestia firma.

Intermediate: These algae are eaten in variable amounts, but urchins do not appear to show any strong preference or dislike for them. These would include Laminaria pallida, Macrocystis angustifolia and possibly Neuroglossum binderianum.

## 7.4 DISCUSSION

### 7.4.1 Acidity in D. Firma

The first quantitative estimates of acidity in the genus Desmarestia were made by Kylin (1931), who concluded that D. viridis contains 3.96% of Malic acid. Later investigation challenged his findings, however. In three acid-forming species, Wirth and Rigg (1937) investigated H-ion concentration, total acidity, chloride, and sulphate content of pressed juice, and concluded that the acidity was due to $H_2SO_4$ rather than any organic acid, and that the $H_2SO_4$ was present in amounts comprising up to 20% of the solid material in the juice.

These results were confirmed by Miwa (1953). In an investigation of D. tabacoides, and dried specimens of D. viridis and D. ligulata, he obtained only faintly positive results for tests of malate, while sulphuric acid was directly precipitated in amounts up to 25% of the dry mass of these algae.

Meeuse (1956) carried out filter paper chromatography, total carbon analyses, enzyme tests for malate, and constructed titration curves, using extracts of acid-forming species; mainly D. munda, a form morphologically very similar to D. firma. A balance sheet for the main ions showed that, among the anions available to match the free hydrogen ions, sulphate is the most important. However, he cautioned against the statement that Desmarestia produces free sulphuric acid, since other cations, e.g. Na, K, Ca, and Mg are present to balance the $SO_4$ anion.

According to Eppley and Bovell (1958), $H_2SO_4$ is located within the vacuoles of D. munda and is present in amounts up to 0.44N.

In this study, a uniformly high level of acidity is shown to be present in all parts of the D. firma plant. Gravimetric sulphate determinations show high levels of this anion, in both young and old plants. By comparison; D. rossii, a non acid-forming species, has sulphate levels some 40 times lower than

D. firma. It cannot be assumed that all the $SO_4$ present in D. firma is derived from $H_2SO_4$. Other sources of $SO_4$ probably include sulphate-linked polysaccharides. Sulphate comprises approximately 0.2% of the dry mass of D. rossii, but in D. firma there may be a pool of'non-acid' sulphate metabolically associated with the $H_2SO_4$, and balanced by cations other than H+. Alkali titration would measure only free H anions. The situation is further complicated by the probable presence of small amounts of organic acids (e.g. Malic acid), which would contribute to the total acidity of D. firma. However the high sulphate levels in D. firma are consistent with the view that most of the acidity in the thallus is due to high levels of $H_2SO_4$.

In a study of the carbohydrate composition of D. firma and a closely related species, D. ligulata, Carlberg et al (1978) showed that the presence of sulphuric acid has no apparent effect on the carbohydrate metabolism of these species. From determinations based on dried material, they reported a value of 5.8% $H_2SO_4$ by dry mass in D. firma. This value is lower than that of approximately 18% obtained in this study, using fresh material. It is likely that Carlberg et al (1978) lost much of the acid during the drying of their specimens.

It is interesting that among animals, certain ascidians are known to contain free $H_2SO_4$, which is thought to be connected with their high vanadium contact (Webb, 1939). Quantities of vanadium in D. firma and D. ligulata are similar to those in other algae which do not contain $H_2SO_4$, suggesting that there may not be any similarities between acid matabolism in Desmarestia and these ascidians (Cockerill et al, 1978).

The biochemical path-way of acid metabolism in Desmarestia is unknown, but the well-documented acidity of the thallus is the result of high levels of $H_2SO_4$. As far as grazers are concerned, total acidity per unit fresh mass would presumably determine any deterrent effect.

## 7.4.2 Relative Astringency and Relative Phenol Levels

The high estimate of relative astringency and phenol content in Ecklonia maxima is in agreement with data for Ecklonia bicyclis and E. cava, which showed higher phenol levels than any of the other 28 species of brown algae listed (Katayama, 1951 , in Ragan and Jensen, 1977). This finding may have important implications in biochemical interactions in Cape kelp beds, since Ecklonia, along with Laminaria, dominates the ecosystem and must release large quantities of phenols into the water, during decay. It is also possible that light-induced exudation of polyphenols occurs in this species, as has been shown to be the case in Ascophyllum nodosum (Ragan and Jensen, 1979).

The high relative astringency value obtained for Hymenena venosa, Neuroglossum binderianum, and to a lesser degree, Botryocarpa prolifera, are interesting since Fenical (1975) points out that many members of the Rhodomelaceae (Ceramiales) are among the most prolific red algal producers of halogenated metabolites, especially bromophenolic compounds.

Axillariella constricta is shown to exhibit a high relative astringency. Fucus vesiculosus, another member of the Fucaceae, has been shown to produce extracellular phenolic substances which are toxic to unicellular algae (McLachlan and Craigie, 1964).

Furthermore, Fucus vesiculosus and Ascophyllum nodosum have been shown to contain polyphenols which actively inhibit feeding by the snail Littorina littorea. (Gieselman and McConnell, 1981).

The other brown algae investigated in this study, Macrocystis angustifolia and Laminaria pallida, show intermediate relative astringencies.

The four other Laminaria species on which data are available, show a range of phenol contents from 0 to a relatively high value (Haug and Larsen, 1958, and Munda, 1962, in Ragan and Jensen, 1977). This indicates a large degree of variability in phenol content, within the genus.

The remaining red algae, Suhria, Gelidium, Carradoria, Gigartina and Pachymenia show a small range of low relative astringency values. Fenical (1975) found no significant formation of halogenated metabolites in those members of the genera Gelidium and Gigartina which he investigated. This work on Desmarestia firma provides evidence that, while relative astringency is essentially a test for measuring phenols, it also indicates the presence of other extractable compounds which will precipitate haemoglobin. The phenol levels in D. firma were shown to be low, and comparable to Laminaria pallida, and yet extracts indicate a high relative astringency. However, most of this effect can be ascribed to the $H_2SO_4$ in D. firma.

It is important to note that neither relative astringency nor relative phenol levels measured in this study provide absolute values: both are based on standard curves for tannic acid and the phenols in the plants may be present in a number of forms, with different structures and molecular weights (Ragan and Jensen, 1977). These authors also point out that the Folin-Denis method is affected by interference of polypeptides, urea, and other compounds and that absolute phenol levels can only be measured gravimetrically. However, it is felt that for the purposes of this study, the relative astringency method provides adequate comparative data for the algae investigated.

### 7.4.3 Urchin Feeding Preferences

The results of these feeding experiments show that Desmarestia firma, along with Botryocarpa prolifera, Ecklonia maxima, Axillariella constricta, Hymenena venosa and probably Neuroglossum binderianum, appear to be relatively unpalatable to Parechinus angulosus. All of these algae except Botryocarpa had high relative astringencies which, except in the case of

Desmarestia, are probably related to high phenol levels, since the relative astringency method essentially tests for phenols. High phenol levels in Ecklonia are confirmed by results of the Folin-Denis test. The high relative astringency of D. firma is shown to be caused by its high $H_2SO_4$ content. It seems reasonable to conclude therefore, that the high $H_2SO_4$ content of D. firma may be responsible for its relatively low palatibility to Parechinus.

However, D. firma may not be unpalatable to other kelp bed grazers. In a study in California, a range of grazing invertebrates (echinoids, gastropods and crustaceans) were fed seven species of algae, and the preferences shown were not always consistent for different grazing groups (Leighton 1966).

Feeding preferences of any grazer are likely to be determined by many factors besides the presence of deterrent compounds. In nature, the most obvious of these is availability of the prey algae. It is well-known that urchins will eat most algae when starved, and Vadas (1977) has shown in field experiments that feeding of urchins is a compromise between the availability of the algae and the preference of the urchin. In a comprehensive study of feeding in Strongylocentrotus drobachiensis and S. franciscanus, it was found that these urchins would actively select preferred algae even if they were not abundant in the field, while algae of intermediate preference (as determined in laboratory experiments) were eaten in proportion to their availability (Vadas, 1977). These urchins would actively avoid certain algae, and this author suggests that these algae had evolved chemical or physical defence mechanisms.

In the present study site at Oudekraal, urchins were only observed feeding on drift algae and algal debris, although the presence of large aggregates of urchins in more or less sea-weed-free areas indicates that they do periodically graze stands of understorey algae.

Of the thirteen algae used in this study, Suhria and Carradoria grow almost exclusively as epiphytes on the kelp Laminaria, where they would be unavailable to urchins except when detached or in drift. It is possible that other epiphytes on the kelps (e.g. Carpoblepharis flaccida) are highly palatable to grazers, which would suggest that this epiphytism could be a grazer-avoidance mechanism. The older kelp plants are probably unavailable to urchins except when dislodged from the substrate during periods of high swell action. If small Ecklonia plants contain high phenol levels, similar to the older individuals, they would have some protection from urchins.

The remaining nine species used in this study, including D. firma, were found to occur more or less throughout the understorey of kelp beds at Oudekraal.

If the availability of the prey algae is equal, then grazer preference must be a result of factors endogenous in the grazer-prey relationship. In algae, endogenous factors include texture and food value.

The algae used in this study showed a range of textures. Axillariella has a tough almost gritty composition when cut or chewed. However, the branched strands of Gelidium are equally tough, and this species was shown to be highly preferred. Similarly, Carradoria has a thallus of thin tough strands, and was apparently highly palatable to Parechinus. The kelps Laminaria and Ecklonia have thick, leathery fronds, yet the former was preferred and the latter avoided. The texture of the other species used are comparable. It seems unlikely that the texture of the algae has a significant effect on their selection by grazers, a contention that is borne out by results obtained by Leighton (1966), in feeding experiments with eleven invertebrates and seven algae in California.

It is difficult to directly measure the food value of algae, with respect to grazers, since it may be determined by the levels of many specific compounds, (e.g. carbohydrates, proteins, fats, vitamins), and different species of grazers may have different nutritional requirements.

An approach which attempts to estimate food value indirectly is that of measuring the calorific value of prey algae. Paine and Vadas (1969) attempted to explain the results of three algae/herbivore experiments on the basis of calorific values of the algae, but they found little correlation between feeding rate and the calorific values of the algae. Similar attempts to correlate calorific values of algae with feeding rates, for a number of grazers, indicated that there is no simple relationship (Himmelman and Carefoot 1975; Vadas 1977). Differences in the enzyme systems of various grazers may account for their different algal preferences (Vadas 1977). In a comprehensive experimental study of algal preferences in two species of American sea urchin, this author provides good evidence that these animals feed preferentially on algae which promote optional "fitness", measured in terms of growth and reproductive capacity. Clearly then, among algae which do not possess strong chemical or physical grazer deterring mechanisms, preferences shown by grazers may be based on relative food values of the algae.

The present study investigated the palatability of D. firma relative to other algae, and suggests that high $H_2SO_4$ levels make it unattractive to the grazer Parechinus, so that in this sense the $H_2SO_4$ could be considered a "secondary substance". However, one of the most frequently suggested functions for these compounds as a group, is that they have antibiotic effects, or discourage the growth of endo- or epiphytes, or the settlement of epiphytic animals. Extracts from many algae have been shown to have antibacterial effects (Martinez, Nadal et al 1965; Hornsey and Hide 1974), antialgal effects (McLachlan and Craigie 1964, 1966) and extracts of Sargassum tannin have been shown to immobilize fouling epifauna (Sieburth and Conover, 1965). However, a major drawback of using algal extracts is that the extracted substances may not normally be released from the living plant. In this respect, it is interesting that polyphenolic compounds have been found to be released by a variety of algae, under various environmental conditions (Sieburth 1969), and that light-mediated exudation of polyphenols has been demonstrated in

Ascophyllum nodosum (Ragan and Jensen 1979).

These exuded polyphenols could play a role in discouraging attack by bacteria, settlement of epiphytic organisms, or in calm water or tide-pools, may inhibit settlement of other algae or sessile animals in the vicinity of the exuding species. Whether the astringent compounds present in the algae used in this study are normally released into the water is unknown, but it is possible that, at least in Ecklonia, which contains very high levels of phenols, some exudation may occur.

In D. firma, plants up to a few months old are epiphyte-free, but old plants (which have the same $H_2SO_4$ content as young ones) are coated with diatoms and other unicellular algae. The basal parts of these old specimens often support hydrozoans and barnacles. Even in relatively young plants Amphipods (Ampithoe humeralis) form nesting tubes, around which the surface of the frond may be grazed (see Appendix C). The occurence of the epiphytic plants and animals suggests that $H_2SO_4$ has little effect in discouraging their settlement.

The pH of buckets of sea water containing D. firma only changed measurably once the fronds began to lose their natural colour and turn green, indicating that significant acid release only occurs when the cells undergo lysis. Considering the buffering quality of sea water, it seems unlikely that the release of $H_2SO_4$ could have any effect on nearby organisms. Litmus paper held on the surface of fronds only indicated acid release when the fronds were beginning to become soft and green, showing lysis of the cells.

Desmarestia ligulata, another acid species, was shown to have a strong antibiotic effect when tested on five species of bacteria (Hornsey and Hide 1974). This test was based on the width of the inhibition zone produced by pieces of thallus placed on agar plates, so that degradation of the tissue must

certainly have occured, which would have released $H_2SO_4$ into the agar, and once again no inference can be made concerning antibiotic effects in nature. Possibly the only way to compare relative antibacterial or anti-epiphyte properties of algae would be to perform extensive quantitative estimates on a large number of algae, and this has not been attempted so far. Relative grazer preferences are far easier to measure, and involve the destruction and digestion of the algal tissue, so that estimates of chemical deterrence, based on tissue extracts, can be invoked to explain feeding patterns.

It is concluded that at this stage no inferences can be made concerning anti-bacterial or anti-epiphyte properties of acid containing Desmarestia. Furthermore, nothing is known of the synthesis of $H_2SO_4$ in Desmarestia, of its possible role in the primary metabolism of the plant. Whether the $H_2SO_4$ in D. firma is a by-product of an undiscovered primary metabolic process, or has evolved specifically for the purpose of grazer deterrence which would make it a true "secondary compound" is unknown, but it appears to discourage grazing by the urchin Parechinus.

# CHAPTER 8

## GENERAL DISCUSSION

It is perhaps inevitable that a diverse study of this sort raises more questions than it answers. In this section some of these questions are briefly examined, and future directions for research are suggested.

The most fundamental problem to arise from the systematic examination, is that the taxonomy of branched, ligulate Desmarestia remains confused. Although Chapman's (1972) treatment of N.W. American and European populations greatly simplifies the taxonomy of this group, it remains unsatisfactory, for reasons discussed in Chapter 3. In reducing 7 branched ligulate species to 1 variety (D. ligulata var. ligulata) Chapman has left the taxonomist working with Southern Hemispere populations of this group little room to manoeuvre. For example, if on grounds of morphology and reproductive anatomy, Southern African D. firma is considered to be conspecific with certain N.W. American forms (e.g. D. munda), their combination would imply that D. firma is also conspecific with European D. ligulata, which on morphological grounds would be difficult to defend. For these reasons, it is felt that a new approach to the taxonomy of southern populations of branched, ligulate Desmarestia is required. It seems likely that populations which are more or less morphologically distinct may be most usefully treated as varieties, in the sense that they represent morphologically distinct local facies of a species which occupy a particular geographical area (Du Reitz, 1930), or as subspecies, in the sense that they may represent a portion of a species with a distinct area and a more or less distinct morphology (Hedberg 1958). The chief difference between these categories is that a subspecies may include several varieties: the former category implies a larger, more regional distribution (Davis and Heywood, 1963). Central to this approach is the need for more comprehensive collections,

particularly from South America. Among the specimens which I examined from those coasts, there was a wide range of morphological variability, but it is not clear whether different morphological forms from the same area represent sympatric populations or randomly collected individuals from along a morphological gradient. While biochemical studies (electrophoresis) and quantitative genetic evaluation (e.g. Chapman, 1975) may alleviate confusion in this group, perhaps only hybridisation studies, such as those employed by Luning et al, (1978), in North Atlantic Laminaria, may finally resolve these problems.

While, on morphological grounds, Chapman (1972) has reduced some 11 ligulate (branched and unbranched) taxa to 3, Moe and Silva (1981) suggest that on the grounds of ontogenic patterns in the sporophytes, the genus Desmarestia (including terete and unbranched and branched ligulate forms) may require subdivision into segregate genera. These authors have shown that the ligulate species which are unbranched (e.g. D. tabacoides Okamura) show a closed growth pattern which is fundamentally different from the open pattern shown in branched ligulate forms (e.g. D. ligulata). It is tempting to speculate that on these grounds, the 'natural' division of this genus into filiform and plane groups (Agardh, 1824) may be misleading, since branched ligulate forms may be more closely related to branched terete forms than to unbranched ligulate forms. It is clear that details of ontogeny are of fundamental importance in the taxonomy of this genus.

The rather qualitative nature of the life-cycle study of D. firma means that no precise inferences can be made concerning the effects of environmental factors (particularly temperature and light) on the possible distribution of the gametophyte, and consequently on the distribution of the sporophyte. An important question is whether it may be the effect of temperature on the gametophyte rather than on the sporophyte, which limits this species to the west coast upwelling region of Southern Africa.

An experimental investigation of the controlling effects of temperature and possibly light, on the development of the gametophyte and sporophyte phase of D. firma may lead to a satisfactory explanation of its geographical distribution.

It is difficult to speculate on possible centres of distribution of the genus Desmarestia, since taxonomic relationships within this group are largely unresolved. South (1979) has pointed out that although a Southern Hemisphere centre of distribution may be inferred, on the grounds that 11 species of Desmarestia are listed for Antarctic and Sub-Antarctic waters (Papenfuss, 1964), the status of 5 of these is in doubt, and such inferences must await better taxonomic information. Among the branched ligulate group the widest range of morphological forms are encountered in N.W. America, which may suggest this region as their centre of distribution. It is useful to compare Desmarestia with Macrocystis since it is only in these 2 genera that bipolar distribution can be suggested (South, 1979). A northern origin has been suggested for Macrocystis on the basis of fossil records, the origin of related genera, and the palaeogeography of the Northern and Southern Hemispheres (Nicholson, 1979). Whether the same reasoning can be applied to Desmarestia is speculative: in view of the numbers of forms in North West and South America, it seems that the genus Desmarestia may have originated in either of these regions.

The population studies highlighted many areas where future research is needed. Firstly, it became obvious that almost nothing is known of the understorey algae in Western Cape kelp beds: most species have been named, and little more. Autecological studies of the major species would yield valuable information. As far as their productivity is concerned, this study indicates that it may be most practical to estimate their net annual production from instantaneous measurements of photosynthetic rate vs irradiance, if the conditions discussed in Chapter 6 are met. This method has been used by other workers (e.g. Smith, 1981) and would be particularly useful in perennial species, where, unlike the annual D. firma, the Allen Curve method cannot be used. Productivity studies of these or similar kelp bed systems may be advised to use this method: all

that is necessary are reliable (preferably continuous) data on submarine irradiance, seasonal estimates of standing crops, and P vs I curves for the major species, bearing in mind that the algae may show diurnal fluctuations in photosynthetic rate (Ramus and Rosenberg, 1980).

An important point to emerge from field observations during the present study, is that standing crops of the major understorey algae, and standing stocks of animals (e.g. mussels) may vary significantly over periods longer than 1 or 2 years. This is a problem in productivity studies (which for practical reasons have to be limited to a few years duration), since it means that the contributions of the major functional groups may be misrepresented, but for the community ecologist these fluctuations could provide a wealth of study material. For example, the vast settlement of the filter-feeding mussel Aulacomya, which covered several hectares of substrate in and adjacent to the Oudekraal study site in 1981 must have had a significant effect on other animals and on the understorey algae, with which they must compete for substrate space. Another example is the movement of large urchin aggregates, which cause major and apparently random disturbances as they move. These, and storm-induced disturbances obviously have a major structuring effect on the understorey community.

Besides the general information given by Velimirov et al (1977) and Field et al (1980 a) there are no descriptive data on algae, and virtually nothing is known of their relationships with animals, particularly with respect to grazers. This study provides evidence that 'secondary substances' (mainly phenols) may protect certain of these algae from grazers, but leaves important questions unanswered: do urchins select certain algae in the field while avoiding others, and do these 'secondary substances' deter grazing by other animals, for example the mollusc Turbo or the isopod Paridotea? It is clear that both laboratory experiments and simple field observations would be useful, and that further information on animal/plant relationships is necessary before energy flow models of the type proposed for

these kelp beds by Field *et al* (1977) can be constructed.

While the present study provides evidence that the acid in *D. firma* functions as a 'secondary compound' in that it discourages grazing by *Parechinus*, a fundamental question remains unanswered: why is $H_2SO_4$ accumulated in the vacuoles of *Desmarestia*? The answer to this must be found in biochemical studies, possibly by following the path of incorporation of $^{35}S$ labelled sulphate.

In a critical examination of the aims and methods of ecologists working in coastal marine systems, Lewis (1980) pointed out two clear phases in such studies: the descriptive and the dynamic phases. The former shows patterns of distribution and its methods involve surveys of some sort. The latter, dynamic phase seeks to explain these patterns in terms of the physical and biological environment, and its methods involve studies of seasonal and annual changes, life histories, and relationships between organisms. I feel that the present study avoids the lack of "natural history awareness" which this author decries, and in invoking both of these approaches, provides a fuller understanding of the autecology of *Desmarestia firma*, and a fuller understanding of some of the processes in the kelp bed ecosystem.

# REFERENCES

ABBOTT, I.A. & HOLLENBERG, G.J., 1976. Marine Algae of California. Stanford Univ. Press, 827 pp.

ABE, K., 1938. Entwicklung der Fortpflanzungsorgane und Keimungsgeschichte von Desmarestia viridis (Müll.) Lamour. Sc. Rep. Tohoku Univ., Biol., 12:475-482.

ADAMS, N.M., 1972. The marine algae of the Wellington area. A list of species. Rec. Dom. Mus., Well., 8 (4): 43 - 98.

ADAMS, N.M., CONWAY, E., & NORRIS , R.E., 1974. The marine algae of Stewart Island. A list of species. Rec. Dom. Mus.,. Well., 8 (14):185 - 245, 1 pl., 1 map.

AGARDH, C.A., 1824. Systema Algarum. Lundae xxxviii - 312 pp.

AGARDH, J.G., 1848. Species Genera et Ordines Algarum ..., Vol. 1, Lundae, viii - 363 pp.

ALLEN, K.R., 1951. The Horokiwi Stream: a study of a trout population. Fish. Bull. Well., N.Z. 10: 1 - 238.

ANDREWS, W.R.H., 1974. Selected aspects of upwelling research in the southern Benguela Current. Tethys, 6:327 - 340.

ANDREWS, W.R.H. & HUTCHINGS, L., 1980. Upwelling in the southern Benguela current. Progr. Oceanogr., 9 : 1 - 81.

ARNOLD, K.E. & MURRAY, S.N., 1980. Relationships between irradiance and photosynthesis for marine benthic green algae (Chlorophyta) of differing morphologies. J. Exp. Mar. Biol. Ecol., 43: 183-192.

ASENSI, A.O. & CARRALVES, M.G., 1972. Una nueva especie de alga parda: Desmarestia patagonia ASENSI sp. nov. (Phaeophyta - Desmarestiales). Darwiniana, 17: 378-383.

BAARDSETH, E., 1941. The marine algae of Tristan da Cunha. Res. Norw. Sci. Exped. Tristan da Cunha 1937-1938, Oslo: 9: 173 pp., 1 map.

BAARDSETH, E., 1970. Seasonal variation in Ascophyllum nodosum (L.) Le Jol. in the Trondheimsfjord with respect to the absolute live and dry weight and the relative contents of dry matter, ash and fruit bodies. Bot. Mar., 13: 13-22.

BATE-SMITH, E.C., 1973. Haemanalysis of tannins: the concept of Relative Astringency. Phytochem., 12: 907 - 912.

BERMAN, T. 1976. Release of dissolved organic matter by photosynthesizing algae in Lake-Kinneret Israel. Freshw. Biol. 6: 13 - 18.

BLACK, C.C., BURRISS, J.E. & EVERSON, R.G., 1976. Influence of oxygen concentration on photosynthesis in marine plants. Aust. J. Plant Physiol., 3: 81 - 86.

BLACK, W.A.P., 1948. The seasonal variation in chemical constitution of some of the sublittoral seaweeds common to Scotland. J. Soc. Chem. Ind., 67: 165 - 175.

BLACKLER, H., 1961. Desmarestia dudresnayi Lamouroux in Britain. Br. Phycol. Bull., 2: 87.

BORY DE SAINT-VINCENT, J.B., 1826. Cryptogamia. In Dumont-D'Urville, J., Flore des Malouines. Soc. Linn. Paris. 4: 573-621.

BRINKHUIS, B.H., 1977. Seasonal variations in salt-marsh macroalgae photosynthesis. I. Ascophyllum nodosum ecad scorpioides. Mar. Biol., 44: 165-175.

BRINKHUIS, B.H. & JONES, R.F., 1974. Photosynthesis in whole plants of Chondrus crispus. Mar. Biol., 27: 137-141.

BROWN, D.L. & TREGUNNA, E.B., 1967. Inhibition of respiration during photosynthesis by some algae. Can. J. Bot., 45: 1135-1143. In Burriss, J.E., 1977. Photosynthesis, photorespiration and dark respiration in eight species of algae. Mar. Biol., 39: 371-379.

BRYLINSKY, M., 1977. Release of dissolved organic matter by some marine macrophytes. Mar. Biol., 39: 213-220.

BUESA, R.J., 1977. Photosynthesis and respiration of some tropical marine plants. Aquat. Bot., 3: 203-216.

BURRISS, J.E., 1977. Photosynthesis, photorespiration and dark respiration in eight species of algae. Mar. Biol., 39: 371-379.

BURRISS, J.E., HOLM-HANSEN, O., & BLACK, C.C. 1976. Glycine and serine production in marine plants as a measure of photorespiration. Aust. J. Plant Physiol., 3: 87-92.

CARLBERG, G.E., PERCIVAL, E., & RHAMAN, M.A., 1978. Carbohydrates of the seaweeds Desmarestia ligulata and D. firma. Phytochem., 17: 1289-1292.

CARTER, R.A., 1982. Phytoplankton biomass and production in a southern Benguela kelp bed system. Mar. Ecol. Progr. Ser., 8: 9-14.

CHAPMAN, A.R.O., 1972. Morphological variation and its taxonomic implications in the ligulate members of the genus Desmarestia occurring on the west coast of North America. Syesis, 5: 1-20.

CHAPMAN, A.R.O., 1974. The ecology of macroscopic marine algae. Ann. Rev. Ecol. Syst., 5: 65-80.

CHAPMAN, A.R.O., 1975. Inheritance of mucilage canals in Laminaria Lamour. (Section Simplices) in eastern Canada. Br. Phycol. J., 10: 219-223.

CHAPMAN, A.R.O. & BURROWS, E.M., 1970. Experimental investigations into the controlling effects of light conditions on the development and growth of Desmarestia aculeata (L.) Lamour. Phycologia, 9: 103-108.

CHAPMAN, A.R.O. & BURROWS, E.M., 1971. Field and culture studies of Desmarestia aculeata (L) Lamour. Phycologia, 10: 63-76.

CHAPMAN, A.R.O. & CAMPBELL, C.C.M., 1975. Quanta vs Watts Limnol Oceangr., 20(3): 496.

CLOWES, A.J., 1950. An introduction to the hydrology of South African waters. Rep. S. Afr. Fish. Mar. Biol. Surv., 12: 1-42.

COCKERILL, B.M., FINCH & PERCIVAL, E., 1978. Vanadium in the brown seaweed Desmarestia firma. Phytochem., 17: 2129.

COTTON, A.D., 1915. Cryptogams from the Falkland Islands collected by Mrs Vallentin, and described by A.D. Cotton, F.L.S. J. Linn. Soc. Bot., 43: 137-231.

DAVID, H.M., 1943. Studies on the autecology of Ascophyllum nodosum Le Jol. J. Ecol., 31: 178-198.

DAVIS, P.H., & HEYWOOD, V.H., 1963. Principles of Angiosperm Taxonomy. Oliver and Boyd. Edinburgh and London. xx + 558 pp.

DAYTON, P.K., 1975. Experimental evaluation of ecological dominance in a rocky intertidal algal community. Ecol. Monogr., 45: 137-159.

DE GOBBIS, D., 1973. On the storage of seawater samples for Ammonia determination. Limnol Oceanogr. 18: 146-150.

DELL, R.K., 1972. Antarctic benthos. Adv. Mar. Biol., 10: 1-216.

DIAZ-PIFERRER, M., 1969. Distribution of the marine benthic flora of the Caribbean Sea. Carib. J. Sci., 9: 151-178.

DIECKMANN, G.S., 1978. Aspects of growth and production of Laminaria pallida (Grev.) J.Ag. off the Cape Peninsula. M.Sc. thesis, University of Cape Town, Botany Department, 98 pp.

DIZERBO, A.H., 1965. Desmarestia dresnayi Lamour. ex Leman in France and Spain. Br. Phycol. Bull., 2: 504.

DOBZHANSKY, T., 1950. Evolution in the tropics. Amer. Sci., 38: 209-221.

DOWNTON, W.J.S., BISHOP, D.G., LARKUM, A.W.D. & OSMOND, C.B., 1976. Oxygen inhibition of photosynthetic oxygen evolution in marine plants. Aust. J. Plant Physiol., 3: 73-79.

DREW, E.A., & ROBERTSON, W.A.A., 1974. Direct observation of Desmarestia dresnayi Lamour. ex Leman in the British Isles and in the Mediterranean. Br. Phycol. J., 9: 195-200.

DROMGOOLE, F.I., 1978. The effects of oxygen on dark respiration and apparent photosynthesis of marine macroalgae. Aquat. Bot., 4(3): 281-298.

DU REITZ, G.E., 1930. The fundamental units of biological taxonomy. Bot. Tidskr., 24: 233-428.

EPPLEY, R.W. & BOVELL, C.R., 1958. Sulfuric acid in Desmarestia. Biol. Bull., 115: 101-106.

FENICAL, W., 1975. Halogenation in the Rhodophyta: A review. J. Phycol., 11:245-259.

FIELD, J.G., JARMAN, N.G., DIECKMANN, G.S., GRIFFITHS, C.L. VELIMIROV, B., & ZOUTENDYK, P., 1977. Sun, waves, seaweed and lobsters: the dynamics of a west coast kelp bed. S. Afr. J. Sci., 73: 7-10.

FIELD, J.G., GRIFFITHS, C.L., GRIFFITHS, R.J., JARMAN, N., ZOUTENDYK, P., VELIMIROV, B., & BOWES, A., 1980 (a). Variation in structure and biomass of kelp communities along the south-west Cape coast. Trans. Roy. Soc. S. Afr., 44(2): 145-203.

FIELD, J.G., GRIFFITHS, C.L., LINLEY, E.A., CARTER, R.A. & ZOUTENDYK, P. 1980 (b). Upwelling in a nearshore marine ecosystem and its biological implications. Estuar. Coast Mar. Sci., 2: 133-150.

FOGG, G.E., 1966. The extracellular products of algae. Oceanogr. Mar. Biol. Ann. Rev., 4: 195-212.

FOLIN, O., & DENIS, W., 1915. A colorimetric method for the determination of phenols (and phenol derivatives) in urine. J. Biol. Chem., 22: 305-308.

FRAENKEL, G., 1959. The raison d'etre of secondary plant substances. Science,129: 1466-1470.

FRICKE, A.H., & THUM, A.B., 1975. Temperature recording in shallow marine environments. Trans. Roy. Soc. S. Afr., 41: 351-357.

GADGIL, M., & SOLBRIG, O.T., 1972. The concept of r- and K-selection: evidence from wild flowers and some theoretical considerations. Amer. Nat., 106 (947): 14-31.

GAIN, L., 1912. La flore algologique des régions antarctique et sub-antarctique. In: Charcot, J. Deuxième Expédition Antarctique Francaise (1908-1910), Sc. Nat. , Paris, 218 pp., 98 figs., 5 pls.

GEISELMAN, J.A., & McCONNEL, O.J., 1981. Polyphenols in the brown algae Fucus vesiculosus and Ascophyllum nodosum: Chemical defences against the marine herbivorous snail, Littorina littorea. J. Chem. Ecol., 7 (6): 1115 - 1133.

GLYPHIS, J., 1980. Chemical methods for analysing secondary compounds. In: Puttick, G., & Glyphis, J., Herbivory studies in a strandveld community. Unpubl. report, Zoology Dept., University of Cape Town, pp 13-38.

GOLDSTEIN, J.L., & SWAIN, T., 1963. Changes in tannins in ripening fruits. Phytochem., 2: 371-383.

GREENWOOD, P.J., 1974. The population dynamics and ecological energetics of Parechinus angulosus at Robben Island and in False Bay, South Africa. M.Sc. Thesis, University of Cape Town, Zoology Department. 97 pp.

GRODZINSKI, W., KLEKOWSKI, R.Z., AND DUNCAN, A., 1975. Methods for ecological bioenergetics. In: IBP Handbook No. 24., Blackwell Scientific Publications, Oxford, 367 pp.

HARIOT, P., 1889. Algues. Mission scientifique du Cap Horn, 1882-1883. Vol. 5. Botanique. Gauthier-Villars et Fils, Paris. Pp. 3-400, 3 maps, 12 pls.

HARVEY, W.H., 1846. Phycologia Britannica, Vol. 1: Melanospermeae. London. 120 pls.

HARVEY, W.H., 1852. Nereis Boreali-Americana, Vol 1: Melanospermeae. London. 149 pp., 12 pls.

HATCHER, B.G., CHAPMAN, A.R.O., & MANN, K.H., 1977. An annual carbon budget for the kelp Laminaria longicruris. Mar. Biol., 44: 85-96.

HAUG, A., & LARSEN, B., 1958. Brunfarging av tangmel og tangestrakter. Norsk Inst. for Tang-og Tareforsk. Rapp. No. 22, 18 pp. In Ragan, M.A. & Jensen, A., 1977. Quantitative studies on Brown Algal phenols. I. Estimation of absolute polyphenol content of Ascophyllum nodosum (L.) Le Jol and Fucus vesiculosus L. J. Exp. Mar. Biol. Ecol., 30: 209-221.

HEDBERG, O., 1958. The taxonomic treatment of vicarious taxa. Uppsala Univ. Arsskr., 6: 186-195.

HEDGPETH, J.W., 1969. Introduction to Antarctic zoogeography. Amer. Geog. Soc. Antarctic Map Folio Ser. 11: 1-9.

HELLEBUST, J.A., 1970. Light-Plants. In Kinne, O. (Ed.) Marine Ecology, Vol. 1. Wiley - Interscience, New York. Pp. 125 - 158.

HIMMELMAN, J.H., & CAREFOOT T.H., 1975. Seasonal changes in calorific value of 3 Pacific coast seaweeds, and their significance to some marine invertebrate herbivores. J. Exp. Mar. Biol. Ecol., 18: 139-151.

HOOKER, J.D., 1845-1847. Flora of Fuegia, the Falklands, Kerguelen's Land etc., Part 2. In: The Botany of the Antarctic Voyage of H.M. Discovery ships Erebus and Terror in the years 1839-43. Flora Antarctica I. Reeves, London. Pp. 454-502., pls. 165-194.

HOOKER, J.D., 1867. Handbook of the New Zealand Flora ... Part II. Algae, pp. 638-721. London.

HORNSEY, I.S., & HIDE, D., 1974. The production of antimicrobial compounds by British marine algae: I . Antibiotic-producing marine algae. Br. Phyc. J., 9: 353-361.

HOUGH, R.A., 1976. Light and dark respiration and release of organic carbon in marine macrophytes of the Great Barrier Reef region. Aust. J. Plant Physiol., 3: 63-68.

HUDSON, G., 1778. Flora Anglica. (Ed. 2) London, xxxviii-690 pp.

IRVINE, G.V., 1973. The effect of selective feeding by two species of sea urchins on the structuring of algal communities. (Abstract). Amer. Zool., 13: 1315.

JOHNSON, T., 1891. Observations on Phaeozoosporeae. Ann. Bot., 5: 135-144.

JOHNSTON, C.S., 1969. Studies on the ecology and primary production of Canary Islands marine algae. In: Margalef, R. (Ed.), Proc. 6th Intl. Seaweed Symp., pp. 213-222.

JOHNSTON, C.S., & COOK, J.P., 1968. A preliminary assessment of the techniques for measuring primary production in macrophytic marine algae. Experientia 24: 1176-1177.

KANWISHER, J.W., 1966. Photosynthesis and respiration in some seaweeds. In: Barnes, H., (Ed.), Some contemporary studies in marine science. Allen &Unwin. London. Pp. 407-420.

KATAYAMA, T., 1951. Tannins of seaweeds. J. Chem. Soc. Japan, Ind. Chem. Sect., 54: 603-604.

KHAILOV, K.M., & BURLAKOVA, Z.P., 1969. Release of dissolved organic matter by marine seaweeds and distribution of their total organic production to inshore communities. Limnol. Oceanogr., 14: 521-527.

KIM, D.H., 1971. A guide to the literature and distribution of the benthic algae in Chile. Part I. Chlorophyceae - Phaeophyceae. Gayana, Bot., 1: 3-82.

KING, R.J., & SCHRAMM, W., 1976. Photosynthetic rates of benthic marine algae in relation to light intensity and seasonal variations. Mar. Biol., 37: 215-222.

KNIGHT, M., & PARKE, M., 1950. A biological study of Fucus vesiculosus L. and F. serratus L. J. Mar. Biol. Assoc. U.K., 29: 439-514.

KNOX, G.A., 1960. Littoral ecology and biogeography of the Southern Oceans. Proc. Roy. Soc. Lond., B, 152: 577-624.

KORNMANN, P., 1962. Der Lebenszyklus von Desmarestia viridis. Helgoländer wiss. Meeresunters., 8: 287-292.

KUHNEMANN, O., 1972. Bosquejo fitogeografico de la vegetacion marina del litoral Argentino. Physis, 31: 117-325.

KÜTZING, F.T., 1849. Species Algarum. Leipzig. vi + 922 pp.

KÜTZING, F.T., 1859. Tabulae Phycologicae .... Vol. 9. Nordhausen. viii + 42 pp., 100 pls.

KYLIN, H., 1931. Apfelsaure in einer Braunalge. Zeitschr. Physiol. Chem., 197: 7.

LAING, R.M., 1909. The marine algae of the subantarctic islands of New Zealand. In: Chilton, C. (Ed.), The sub-antarctic islands of New Zealand. Vol. 2. Wellington. Pp. 493-527, pls. 21-24.

LAMOUROUX, J.V., 1813. Essai sur les genres de la famille des Thalassiophytes non articulées. Ann. Mus. d'Hist. Nat., 20: 21-47, 115-139, 267-293, pls. 7-13.

LAWRENCE, J.M., 1975. On the relationship between marine plants and sea urchins. Oceanogr. Mar. Biol. Ann. Rev. 13: 213-286.

LEIGHTON, D.L., 1966. Studies of food preferences in algivorous invertebrates of southern California kelp beds. Pacific Sci., 20: 104-113.

LEIGHTON, D.L., & BOOLOOTIAN, R.A., 1963. Diet and growth in the Black Abalone, Haliotis cracherodii. Ecol., 44 (2): 227-238.

LE JOLIS, A., 1880. Liste des algues marines de Cherbourg. Mém. Soc. Imp. Sci.Nat. Cherbourg, 10 (1): 1-168.

LEMAN, D.S., 1819. In: Levrault, F.G. (Ed.) Dict. Sc. Nat. Paris. 13: 104-106. Planches: Botanique: Vegétaux acotylédons, pl. (43), 1816-1819.

LEVRING, T. 1944. Meeresalgen van den Crozet-Inseln und Kerguelen. Arkiv. Bot., 31 A (8): 31pp, 19 figs.

LEVRING, T., 1960. Contributions to the marine algal flora of Chile. Lunds. Univ. Arsskr. N.F., Avd. 2, 56 (10): 1-84. In: Kim, D.H., 1971. A guide to the literature and distribution of the benthic algae of Chile. Part I. Chlorophyceae - Phaeophyceae. Gayana, Miscelanea No. 1, Concepcion, Chile, 82 pp.

LEWIS, J.R., 1980. Objectives in littoral ecology - a personal viewpoint. In: Price, J.H., Irvine, D.E.G., & Farnham, W.F. The Shore Environment, Vol. 1, Methods. Academic Press, London. Pp. 1-18.

LIGHTFOOT, J., 1777. Flora Scotica Vol. 2. London. 531-1151 + (24) pp.

LINDAUER, V.W., CHAPMAN, V.J., & AIKEN, M., 1961. The marine algae of New Zealand. II. Phaeophyceae. Nov. Hedwig. 3: 129-350.

LITTLER, M.M., 1979. The effects of bottle volume, thallus weight, oxygen saturation levels, and water movement on apparent photosynthetic rates in marine algae. Aquat. Bot., 7: 21-34.

LITTLER, M.M., 1980. Morphological form and photosynthetic performance of marine macroalgae: Tests of a functional/form hypothesis. Bot. Mar., 22: 161-166.

LITTLER, M.M., & ARNOLD, K.E., 1980. Sources of variability in macroalgal primary productivity: sampling and interpretive problems. Aquat. Bot., 8: 141-156.

LITTLER, M.M., & LITTLER, D.S., 1980. The evolution of thallus form and survival strategies in benthic marine macroalgae: field and laboratory tests of a functional form model. Amer. Nat., 116: 25-44.

LÜNING, K., CHAPMAN, A.R.O., & MANN, K.H., 1978. Crossing experiments in the non-digitate complex of Laminaria from both sides of the Atlantic. Phycologia, 17: 293-298.

MACARTHUR, R.H., & WILSON, E.O., 1967. The Theory of Island Biogeography. Princeton Univ. Press, Princeton, N.J. 203 pp.

MANN, K.H., 1972. Ecological energetics of the seaweed zone in a marine bay on the Atlantic coast of Canada. II. Productivity of the seaweeds. Mar. Biol., 14: 199-209.

MANN, K.H., 1973. Seaweeds: Their productivity and strategy for growth. Science, 182 (4116): 975-981.

MARTINEZ NADAL, N.G., RODRIGUEZ, L.V., & DOLAGARAY, J.I., 1966. Low toxic effect of antimicrobial substances from marine algae. Bot. Mar., 9:62-63.

MATHEWS, C.P., & WESTLAKE, D.F., 1969. Estimation of production by populations of higher plants subject to high mortality. Oikos, 20: 156-160.

MATHIESON, A.C., & BURNS, R.L., 1971. Ecological studies of economic red algae. I. Photosynthesis and respiration of Chondrus crispus Stackhouse and Gigartina stellata (Stackhouse) Batters. J. Exp. Mar. Biol. Ecol., 7: 197-206.

MATHISON, A.C., NORTON, T.A., & NEUSHUL, M., 1981. The taxonomic implications of genetic and environmentally induced variations in seaweed morphology. Bot. Rev., 47: 313-347.

MAXWELL, C.D., & RATTEY, D., 1978, 1979. E.S.C.O.M. Oceanographic Investigations for the Koeberg Nuclear Power Station, Internal Progress Reports, Nos. 4-11.

MCLACHLAN, J., 1973. Growth-media - marine. In: Stein, J.R. (Ed.). Handbook of Phycological Methods, Culture Methods and Growth Measurements. Cambridge Univ. Press, pp 25-52.

MCLACHLAN, J., & CRAIGIE, J.S., 1964. Algal inhibition by yellow ultraviolet-absorbing substances from Fucus vesiculosus. Can. J. Bot., 42 (3): 287 -292.

MCLACHLAN, J., & CRAIGIE, J.S., 1966. Antialgal activity of some simple phenols. J. Phycol., 2: 133-135.

MEEUSE, B.J.D., 1956. Free sulfuric acid in the brown alga, Desmarestia. Biochim. Biophys. Acta, 19: 372-374.

MIWA, T., 1953. Occurrence of abundant free sulphuric acid in Desmarestia. Proc. 7th Pac. Sci. Congr., Pac. Sci. Assoc., 5: 78-80.

MOE, R.L. & SILVA, P.C., 1977. Sporangia in the brown algal genus Desmarestia with special reference to Antarctic D. ligulata. Bull. Jap. Soc. Phycol. 25 Suppl. (Mem Iss. Yamada): 159-167.

MOE, R.L., & SILVA, P.C., 1981. Morphology and taxonomy of Himantothallus (including Phaeoglossum and Phyllogigas), an Antarctic member of the Desmarestiales. (Phaeophyceae). J. Phycol., 17: 15-29.

MONTAGNE, (J.F.)C., 1845. Plantes cellulaires. Voyage au Pole Sud ...sur ... l'Astrolabe et la Zélée ...pendant 1837-1838-1839-1840. Botanique, Vol. I. Paris. xiv + 349 pp, 20 pls.

MONTAGNE, C., 1846. Phyceae. In Gaudichaud, C., Voyage autour du monde exécuté pendant les années 1836 et 1837 sur la corvette La Bonité ... Botanique. Vol. I: Cryptogames cellulaires et vasculaires .... Paris. Pp. 1-112.

MORRIS, I., 1974. The limits to the productivity of the sea. Sci. Progr. Oxford, 61: 99-122.

MUNDA, I., 1962. Odnos sadrzaja fizoda i reduktivnih supstanca u nekim jadranskim smedjim algama. Acta Adriat., 10: 3-11. In: Ragan, M.A., & Jensen, A., 1977. Quantitative studies on brown algal phenols. I. Estimation of absolute polyphenol content of Ascophyllum nodosum (L.) Le Jol. and Fucus vesiculosus L. J. Exp. Mar. Biol. Ecol. 30: 209-221.

NAKAHARA, H. & NAKAMURA, Y., 1971. The life history of Desmarestia tabacoides Okamura. Bot. Mag. Tokyo, 84: 69-75.

NEWELL, R.C., FIELD, J.G., & GRIFFITHS, C.L., 1982. Energy balance and the significance of microorganisms in a kelp bed community. Mar. Ecol. Progr. Ser. (In Press).

NICHOLSON, N.L., 1979. Evolution within Macrocystis: Northern and Southern Hemisphere taxa. Proc. Intl. Symp. Mar. Biogeogr. Evol. S. Hemisphere, Auckland, New Zealand, 1978, 2: 103-441.

OGDEN, J.C., 1976. Some aspects of herbivore-plant relationships on Caribbean reefs and seagrass beds. Aquat. Bot., 2: 103-116.

OKAMURA, K., 1910. Icones of Japanese Algae. Vol. 2, Fasc. 5.

PAECH, K., 1950. Biochemice und Physiologie der Sekundären Pflanzenstoffen. Springer, Berlin, 334 pp.

PAINE, R.J., & VADAS, R.L., 1969. Calorific values of benthic marine algae and their postulated relation to invertebrate food preferences. Mar. Biol., 4: 79-86.

PAPENFUSS, G., 1943. Notes on South African marine algal II. J.S. Afr. Bot., 9: 79-92.

PAPENFUSS G., 1964. Catalogue and bibliography of Antarctic and Subantarctic benthic marine algae. Antarctic Res. Ser. Washington, 1: 1-76.

PEASE, V.A., 1920. Taxonomy and morphology of the ligulate species of the genus Desmarestia. Publ. Puget Sound Mar. Biol. Sta., 2: 313-367.

PEER, D.L., 1970. Relation between biomass, productivity, and loss to predators in a population of a marine benthic polychaete, Pectinaria hyperborea. J. Fish. Res. Bd. Can. , 27 (12): 2143-2153.

PETERSON, B.J., 1980. Aquatic primary productivity and the $^{14}C - CO_2$ method: A history of the productivity problem. Ann. Rev. Ecol. Syst., 11: 359-385.

PIANKA, E.R., 1970. On r- and K-selection. Amer. Nat. 104: 592-297.

PICCONE, A., 1886. Alghe del viaggio di circumnavigazions della vettor Pisani. Genoa. 97 pp., 2 pls.

PRINCE, J.S., & O'NEAL, S.W., 1979. The ecology of Sargassum pteropleuron Grunow (Phaeophyceae, Fucales) in the waters off South Florida. I. Growth, reproduction and population structure. Phycologia, 18: 109-114.

RAGAN, M.A., 1976. Physodes and the phenolic compounds of Brown Algae. Composition and significance of physodes in vivo. Bot. Mar., 19: 145-154.

RAGAN, M.A. & JENSEN, A., 1977. Quantitative studies on Brown Algal phenols. I. Estimation of absolute polyphenol content of Ascophyllum nodosum (L.) Le Jol. and Fucus vesiculosus L. J. Exp. Mar. Biol. Ecol., 30: 209-221.

RAGAN, M.A. & JENSEN, A., 1979. Quantitative studies on Brown Algal phenols. III. Light-mediated exudation of polyphenols from Ascophyllum nodosum (L.) Le Jol. J. Exp. Mar. Biol. Ecol., 36: 91-101.

RAMUS, J., BEALE, S.I. & MAUZERALL, D., 1976 (a). Correlation of changes in pigment content with photosynthetic capacity of seaweeds as a function of water depth. Mar. Biol., 37: 231-238.

RAMUS, J., BEALE, S.I., MAUZERALL, D., & HOWARD, K.L., 1976 (b). Changes in photosynthetic pigment concentration in seaweeds as a function of water depth. Mar. Biol., 37: 223-229.

RAMUS, J., LEMONS, F., & ZIMMERMAN, C., 1977. Adaptation of light-harvesting pigments to downwelling light and the consequent photosynthetic performance of the eulittoral rockweeds Ascophyllum nodosum and Fucus vesiculosus. Mar. Biol., 42: 293-303.

RAMUS, J., & ROSENBERG, G., 1980. Diurnal photosynthetic performance of seaweeds measured under natural conditions. Mar. Biol., 56: 21-28.

REINSCH, P.F., 1890. Zur Meeresalgen von Süd-Georgien. In: Neumayer, G., Internationale Polarforschung, 1882-1882. Die Deutschen Expedition und ihre Ergebnisse. Vol. 2. Beschreibende Naturwissenschaften. Hamburg. Pp. 366-449, pls. 1-19.

RYTHER, J.H., 1954. The ratio of photosynthesis to respiration in marine plankton algae and its effect upon the measurement of productivity. Deep Sea Res., 2: 134-139.

RYTHER, J.H., 1956. Interrelation between photosynthesis and respiration in the marine flagellate, Dunaliella euchlora. Nature, 178:861-62.

SCAGEL, R.F., 1957. An annotated list of the marine algae of British Columbia and Northern Washington. Bull. Nat. Mus. Can. , 150: vi - 289 pp.

SCHREIBER, E., 1932. Uber die Entwicklungsgeschichte und systematische Stellung der Desmarestiaceen. Zeitschr. Bot., 25: 561-582.

SEIGLER, D.S., 1977. Primary roles for secondary compounds. Biochem. Syst. Ecol., 5:195-199.

SEIGLER, D.S., & PRICE, P.W. 1976. Secondary compounds in plants: primary functions. Amer. Nat., 110: 101-105.

SETCHELL, W.A., & GARDNER, N.L., 1925. The marine algae of the Pacific coast of North America. III. Melanophyceae. Univ. Calif. Publ. Bot., 8: 383-898.

SETCHELL, W.A., & GARDNER, N.L., 1924. Phycological contributions, VIII. Univ. Calif. Publ. Bot., 13: 1-13.

SHEPHERD, S.A., 1981. Ecological strategies in a deep water red algal community. Bot. Mar., 24: 457-463.

SIEBURTH, J. MCN., 1969. Studies on algal substances in the sea. III. The production of extracellular organic matter by littoral marine algae. J. Exp. Mar. Biol. Ecol., 3: 290-309.

SIEBURTH, J. MCM., & CONOVER, J.T., 1965. Sargassum tannin, an antibiotic which retards fouling. Nature,208 (5005): 52-53.

SILVA, P.C., 1959. The genus Codium (Chlorophyta) in South Africa. J. S. Afr. Bot., 25: 103-165, pls. 2-16.

SIMONS, R.H., 1976. Seaweeds of Southern Africa: Guidelines for their study and identification. Fish. Bull. S. Afr., 7: 1-113.

SKOTTSBERG, C., 1907. Zur Kenntis der subantarktischen und antarktischen Meeresalgen. I. Phaeophyceen. Wiss. Ergebn. Schwed. Sudpolar -Exped. 1901-1903, 4: 1-172.

SKOTTSBERG, C., 1921. Botanische Ergebnisse der Schwedischen Expedition nach Patagonica und dem Feuerlande 1907-1909. VIII. Marine algae 1. Phaeophyceae. K. Svenska Vet.-Akad. Handl., 61: 1-56.

SMITH, G.M., 1938. Cryptogamic Botany. Vol. 1. Algae and Fungi. New York. viii + 545 pp.

SMITH, W.O., 1981. Photosynthesis and productivity of benthic macroalgae on the North Carolina continental shelf. Bot. Mar., 24: 279-284.

SOUTH, G.R., 1979. Biogeography of benthic marine algae of the southern oceans. Proc. Intl. Symp. Biogeog. Evol. S. Hemisphere, Auckland, N.Z., 1: 85-108.

SOUTH, G.R., & ADAMS, N.M., 1976. Marine algae of the Kaikoura coast. A list of species. Nat. Mus. N.Z. Misc. Ser., 1:1-67 + 1 map.

STACKHOUSE, J., 1809. Tentamen marino-cryptogamicum. Mem. Soc. Imp. Nat. Moscow, 2: 50-97.

*STAFLEU,F.A. (Ed.),1978. See bottom of page.

STEEMAN NIELSEN, E., & AL KHOLY, A.A., 1956. Use of the $^{14}C$ technique in measuring photosynthesis of phosphorus or nitrogen deficient algae. Physiol. Plant., 9: 144-153.

STRICKLAND, J.D.H., & PARSONS,, T.W., 1968. A practical handbook of seawater analysis. Bull. Fish. Res. Bd. Can., 167: 1-311.

SVERDRUP, H.U., JOHNSON, M.W., & FLEMING, R.H., 1942. The Oceans. Their physics, chemistry and general biology. Prentice-Hall, N.J. X + 1087 pp., 7 maps.

*STAFLEU,F.A. (Ed.),1978. International Code Of Botanical Nomenclature. Bohn, Scheltema & Holkema, Utrecht, 457 pp.

SWAIN, T., & HILLIS, W.E., 1959. The phenolic constituents of Prunus domestica. I. The quantitative analysis of phenolic constituents. J. Sci. Food Agric., 10: 63-68.

TAYLOR, W.R., 1938. Algae collected by the "Hassler", "Albatross", and Schmitt expeditions. II. Marine algae from Uruguay, Argentina, the Falkland Islands, and the Strait of Magellan. Papers Mich. Acad. Sci. Arts. Lett., 24: 127-164, pls. 1-7.

TOKIDA, J., 1954. The marine algae of Southern Saghalien. Mem. Fac. Fish. Hokkaido Univ., 2: 1-264.

TOLBERT, N.E., & GAREY, W., 1976. Apparent total $CO_2$ equilibrium point in marine algae during photosynthesis seawater. Aust. J. Plant Physiol., 3: 69-72.

TURNER, D., 1809. Fuci sive plantarum fucorum generi a botanicis ascriptarum icones descriptiones et historia. Vol. 2. London. 162 pp., 134 pls.

TURNER, J.S., & BRITTAIN, E.G., 1962. Oxygen as a factor in photosynthesis. Biol. Rev.. (Camb.), 37: 130-170.

TYLER, J.E., 1973. Lux vs quanta. Limnol. Oceanogr., 18 (5): 810.

UNESCO, 1973. A Guide to the Measurements of Marine Primary Production Under Some Special Conditions. Paris. 73 pp.

VADAS, R.L., 1977. Preferential feeding: An optimization strategy in sea urchins. Ecol. Monogr., 47: 337-371.

VELIMIROV, B., FIELD, J.G., GRIFFITHS, C.L., & ZOUTENDYK, P., 1977. The ecology of kelp bed communities in the Benguela upwelling system. Analysis of biomass and spatial distribution. Helgol. Wiss. Meeresunters., 30: 495-518.

VOGEL, A.I., 1961. A textbook of quantitative inorganic analysis. 3rd edition, Longmans, London. 1216 pp.

WALLENTINUS, I., 1978. Productivity studies on Baltic macroalgae. Bot. Mar., 21: 365-380.

WATT, W.D., 1966. The release of dissolved organic material from the cells of phytoplankton. Proc. Roy. Soc. Lond., Ser. B, 164: 521-551.

WEBB, D.A., 1939. Observations on the blood of certain ascidians, with special reference to the biochemistry of vanadium. J. Exp. Biol., 16: 499-523.

WESTLAKE, D.F., 1963. Comparisons of plant productivity. Biol. Rev., 38: 385-425.

WIRTH, H.E., & RIGG, G.B., 1937. The acidity of the juice of Desmarestia. Amer. J. Bot., 24: 68-70.

WOMERSLEY, H.B.S., 1959. The marine algae of Australia. Bot. Rev., 25 (4): 545-614.

WOMERSLEY, H.B.S., 1967. A critical survey of the marine algae of Southern Australia. II. Phaeophyta. Aust. J. Bot., 15: 189-270.

WOOD, K.G., 1968. Photosynthesis of Cladophora under unnatural conditions. In: Jackson, D. (Ed.) Algae, Man and Environment. Syracuse Univ. Press, N.Y. Pp. 221-133.

ZAR, J.H., 1974. Biostatistical Analysis. Prentice-Hall, Inc., N.J. 620 pp.

ZELITCH, I., 1968. Investigations on photorespiration with a sensitive $^{14}C$-assay. Plant Physiol., 43: 1829-1837. In: Hough, R.A., 1976. Light and dark respiration and release of organic carbon in marine macrophytes of the Great Barrier Reef region. Aust. J. Plant. Physiol., 3: 63-68.

# APPENDIX A

## Nomenclature and Type Descriptions of Species Compared with D. Firma

This Appendix provides type descriptions and information pertaining to the types, for species which are compared with South African *D. firma* (Chapter 3).

1) Desmarestia ligulata (Stackhouse) Lamouroux, Ann. Mus. Hist. Nat. (Paris) 20:45, pl. 8, Fig. 1,(1813)
Basionym: Herbacea ligulata Stackhouse Mem. Soc. Imp. Naturalistes Moscou 2:89, (1809).

Type specimen:

Lightfoot's illustration (Fig. 29 in Vol. 11 of his Flora Scotia, 1777) of Fucus ligulatus was designated as the lectotype by Chapman (1972), since no specimen of D. ligulata was found in Lightfoot's collection in the British Museum (Natural History).

Type description:

Lightfoot's original description of Fucus ligulatus reads as follows: "F. fronde membranacea lineari bipinnato - ligulata ligulis ensiformis ciliatis."
(Frond membranceous, linear bipinnate - ligulate, ligule sword-like, ciliate".)

"The colour of this is a dull green; the substance membranaceous and pellucid, without rib or nerve, but the central stalk slightly cartilaginous; the height of the whole plant two or three feet; its width, including the branches fairly expanded, six or eight inches. The middle stalk is flat and linear, about one-fifth of an inch wide, and continued from the base to the summit of the plant, ending acutely. This stalk is doubly proliferous; for out of the edges in a distichous and oppositely pinnate order, grow narrow sword-shaped, leafy ligaments, from three to eight inches long, which are again pinnated with shorter but similar ligaments, ciliated on the margins with the rudiments of others, not much bigger than hairs. The primary ligaments are for the most part gradually shortened towards the summit of the stalk, so as to leave it at last simply pinnated, and thereby give to the plant a nearly conical form.

The fructification we have never observed, but suppose they must reside in the minute cilia or marginal ligaments."

Type locality:

"In the Firth of Forth, about New-Haven, and other places, but not common".

Synonymy:

D. ligulata (Stackhouse) Lamouroux is included in D. ligulata var ligulata (Stackh.) Lamx. sensu Chapman (1972).

Discussion:

D. ligulata (Lightfoot) Lamouroux was ostensibly a new combination of Fucus ligulatus Lightfoot, Fl. Scot. 946, pl. 29 (1777), but that name is illegitimate since it is a later homonym of Fucus ligulatus S.G.Gmelin, Hist. Fuc. 178, pl. 21. fig. 3, 1768)(which is probably a later taxonomic synonym of Fucus ciliatus Hudson (1762) = Calliblepharis ciliata (Hudson) Kutzing. The earliest use of the name ligulata in another genus (thus creating a new name in accordance owth ICBN Article 72, Note 1) is Herbacea ligulata Stackhouse 1809 (who made the combination H. ligulata (Lightfoot) Stackhouse). Thus the basionym of D. ligulata is Herbacea ligulata Stackhouse. (Pers comm., P.C. Silva, 30.1.80).

Since Stackhouse based his combination H. ligulata on Fucus ligulatus Lightfoot, the type remains that of Lightfoot (1777).

2) Desmarestia dudresnayi Lamouroux ex Leman. Dict. Sc. Nat. 13:105 (1819). Planches: Botanique: Végétaux acotylédons: pl. (43). (1816 - 1819).

Type specimen: A specimen labelled D. dudresnayi by Lamouroux, which was collected in N.W. France by Dudresnay, and is now in Lamouroux's collection at Caen (CN) (Fig. 3.15) is further annotated by Sauvageau to the effect that it does not correspond with the illustration in pl. 43, accompanying Lamouroux's protologue, As Chapman (1972) points out, it cannot therefore be recognised as the Holotype. I have therefore recognised it as a Lectotype.

Type description:

"Fronde plane, membraneuse, foliacée,très large, légèrement pédiculée, divisée dès l'origine en trois frondules lancéolées, trés longues, pointuess, traversées dans le milieu par une nervure longitudinale d'où partent un grand nombre de veines transversales opposées, simples, rarement bifurquées à l'extrémité; bord des frondules sinueux, ondulé marqué de denteleures écartées qui se changent quelquefois en petites feuilles de même forme que les frondules.

Cette plane est d'un vert brun, et longue de près de deux pieds; ses frondules ont d'un à deux pouces et plus de largeur dans presque toute leur longeur. Celle a été découverte en France sur les côtes de l'Ocean, par M. Dudresnay ..."

"Frond flat, membranous, foliaceous, very large, gradually pediculate, divided from the origin into three lanceolate fronds, very long, pointed, traversed along the middle by a longitudinal nerve from which arises a large number of transverse, opposite, simple veins, rarely branched at the extremity; edges of the fronds sinuate, undulate, marked with remote teeth which change occasionally into small leaves of the same form as the fronds.

"This plant is greenish brown and about two feet long, the fronds are one or two inches wide along their whole length. It was discovered in France, along the coast, by M. Dudresnay ..."

Type locality:

The specimen which I have designated as the lectotype (in Lamouroux's collection at CN) was collected by Du Dresnay near St Pol-de-Leon, Finistère, Brittany. (Dizerbo, 1965).

3) Desmarestia herbacea Lamouroux, nom. nov. Ann. Mus. Hist. Nat. (Paris) 20:45 (1813).

Basionym: Fucus herbaceus Turner, Hist. Fuc. 2:78, pl. 99 (1809). This name is illegitimate since it is a later homonym of F. herbaceus Hudson, Fl. Angl. ed. 2:582 (1778), which is a later taxonomic synonym of F. ligulatus Lightfoot (Silva pers comm.). However, in the case of Desmarestia herbacea Lamx., the specific epithet is used in another genus, hence legitimizing it in terms of ICBN Art. 72, Note 1.

Type specimen:

Chapman (1972) designated a specimen in the British Museum (Natural History) which corresponds to Turner's original illustration,as the lectotype for Turner's Fucus herbaceus (Fig. 3.20). This specimen is annotated "North West Coast of America" in what is thought to be Menzies' hand (Chapman 1972).

Type description:

"Fucus herbaceus, frond membranaceous, flat, obsoletely mid-ribbed, bipinnate; segments opposite, elliptical, attenuated at their bases, blunt at their apices, toothed as if with spines at their margins.

"Frond, flat, two feet or more long, rising with a single undivided stem, at its base nearly cylindrical, and as thick as a crow's quill, but almost immediately becoming flat, and gradually widening to the height of a few inches, where it aquires the width of half an inch, or three-quarters of an inch, after which it continues linear, till, on approaching the extremity, it is again slightly narrowed, and terminates in a rounded apex; the margins are throughout the whole length serrated, with small spiniform, rather remote teeth; the stem, from root to summit, is pinnated with opposite, distichous branches, of the same substance as itself, between horizontal and patent, separated by intervals of about half an inch, a foot or a foot and a half long, and the middle ones, apparently the longest, their greatest width nearly an inch, attenuated at their bases into very short sub-cylindrical petioli, rounded at their apices, toothed at their margins, and in their turns

pinnated with a series of others, similar to them in every particular, except their small size:- throughout the whole frond runs a midrib, thick and rather wide in the stem, but in the branches thin and faint, so as scarcely to be visible, unless the plant is held to the light, and appearing only like a dark line." He further gives his reasons for considering this a species distinct from D. ligulata, based largely on the size, shape and colour of the fronds.

Type locality:

"North-West coast of America. Mr Menzies."

4) Desmarestia latissima Setchell and Gardner ex Pease sp. nov., Pub. Puget Sound Biol. Sta. 2.53 p 319, pl. 56, (1920).

Type specimen:

Pease's isotype specimens of this species are in the Algal Herbarium of the University of Minnesota (MIN). Two of these are illustrated in Figs. 3.23 and 3.24.

Type description:

"Fronde magna, foliacea, latissima, inferne sub-coriacea et evidenter costata; pinnis distantibus, margine dentis distantibus".

(Frond large, foliaceous, broad, lower parts almost leathery and with visible veins; branches distant, marginal teeth distant).

Pease (1920) further describes the plants as very large, up to 8m long, fronds 4 - 100 cm wide, with few widely separated branches, only rarely of the second order.

Type locality:

San Juan Islands, Washington.

5) Desmarestia munda Setchell and Gardner, sp. nov., Univ. Calif. Publ. Bot. 13:7, (1924).

Type specimen:

According to Silva (pers. comm. in Chapman, 1972) the Phycotheca Boreali-Americana distribution of this species can be considered as the lectotype collection, with the specimen U.C. 809472 (Herbarium of the University of California, Berkley) as the lectotype.

Type description:

"Frondibus per disco firmo parenchymatoideoque affixis, ligulatis comparate rigidis et coriaceous, usque ad. 8m longis, 4 - 10 cm latis, nitentibus et luteofuscis, maturitate sparse ramosis; costa in stipite et partibus inferioribus valde conspicua aut superne ut nervo indistincto ostendente; ramis vulgo 2-, sed partim 3- ordinatus, ramis maximis, prope basim oriendis et axim primarium aequantibus, aliquando latioribus quam axi primaria sed basim ad connectioneus parvam cylindraceamque attenuatis, superne acuminatis aut rotundatis, marginibus ubique projectiones spinuliforme remotas cum angulis supernia rotundatis ostendentibus; stipitibus fere ad basim complanatis."

("Fronds attached by a firm parenchymatous disc, ligulate relatively rigid and coriaceous, up to 8m long, 4 - 10 cm wide, glossy, yellowish-brown in colour, sparingly branched at maturity; midrib prominent in the stipe and lower parts, becoming inconspicuous or appearing only as a mere nerve above; branches usually of 2 but in part 3 orders, the largest primary branches arising near the base at times as long as the central rachis, and even wider in part, tapering rather abruptly to a small cylindrical connection at the base, acuminate or rounded above, the margins of all bearing very prominent, rather distant, spine-like projections with more or less rounded angles above; stipe flattened almost to the base."

Type locality:

"Growing principally on rocks in the sub-littoral belt. Puget Sound, Washington, to southern California (San Pedro)" (Setchell and Gardner 1924). According to Chapman (1972) the collection data for the lectotype are "Floating, west coast of Whidby Island, Washington, June 1901 N.L. Gardner".

Synonymy:

According to Chapman (1972), D. munda Setchell and Gardner (1924) is a taxonomic synonym of D. ligulata (Lightf.) Lamouroux.

# APPENDIX B

## South African Distribution Records for *D. firma*

## Appendix B - List of Southern African Localities from which D. firma is Recorded.

Cape Point, 14.2.1973, Sea Fisheries Divers. Olifantsbos, 5.2.1954, W.E. Isaac (L). Kommetjie,(drift), 20.3.1970, M.L. Branch. Camps bay, W. Tyson (PRE). Sea Point, W. Tyson (PRE). Three Anchor Bay, W. Tyson (L, BOL). Table Bay, April 1869, H. Becker (BOL), W. Tyson (PRE), C.B.S. (TCD), E.M. Hol (BM). 'Deep water', Table Bay, W. Tyson (PRE, BOL). Mouille Point, (drift), 12.1.1967, R.H. Simons. Cape Columbine, January 1982, N. Jarman. Port Nolloth, 26.10.1935, J.A. Stephenson (BM), 22.1.1958, R.H. Simons and J.M. Graves. Luderitz Bay, 26.7.1959, W.E. Isaac (PRE). Seal Island, False Bay, 28.11.67, Sea Fisheries divers (Seaweed unit). Cape Agulhas, E. Thwaites(received January 1891, BM).

In addition to the above records, I have observed or collected D. firma at the following localities:

Maclear's Beach, Olifantsbos, Scarborough, Witsand, Kommetjie, Noordhoek, Hout Bay, Llandudno, Oudekraal, Bakoven, Sea Point, Bloubergstrand, Marcus Island (Saldanha Bay), Elands Bay, and Hondeklip Bay.

# APPENDIX C

## Organisms Found on D. Firma

This Appendix provides a brief description of the major organisms growing epiphytically on, or in close association with the fronds of, *D. firma*.

1) Observations

a) Epiphytic Algae

There was a steady increase in the microflora on the surface of fronds, throughout the life of D. firma plants. Young plants, in spring or summer, had little or no epiphytic microflora (Fig. 3 ), but by the end of winter dense aggregates of diatoms, as well as several species of filamentous red and green algae covered the surfaces of all D. firma plants collected during routine sampling (Fig. 1 and 2 ). Plants with Ectocarpus sp. growing on their fronds were found in drift at several localities on the Cape Peninsula.

b) Macroscopic Epifauna

Three macroscopic animals were found on the fronds of D. firma. Two of these, the barnacle Balanus amphitrite and an Electra-like hydroid, were attached to the holdfast, stipe and axial fronds of plants, while the amphipod Ampithoe humeralis formed nesting tubes in the fronds of plants (Fig. 4).

| Animal | Nov | Jan | Mar | May | July | Oct |
|---|---|---|---|---|---|---|
| Ampithoe humeralis tubes | 2 | 12 | 17 | 7 | 4 | 7 |
| Balanus amphitrite | 0 | 0 | 0 | 3 | 1 | 0 |
| Hydroid | 0 | 0 | 0 | 4 | 3 | 3 |
| Total no. of plants sampled | 150 | 200 | 150 | 150 | 170 | 26 |

TABLE C.1 Percentage of plants (Generation 2) supporting epyphytic Hydroids, Barnacles and amphipod nesting tubes.

The percentage of plants with amphipod nesting tubes increased from 2% in November 1978 to a maximum of 17% of the population in March 1979, then declined to 4% in July 1979. The apparent increase in October may be an artifact of the small number (26) of Generation 2 plants in that sample.

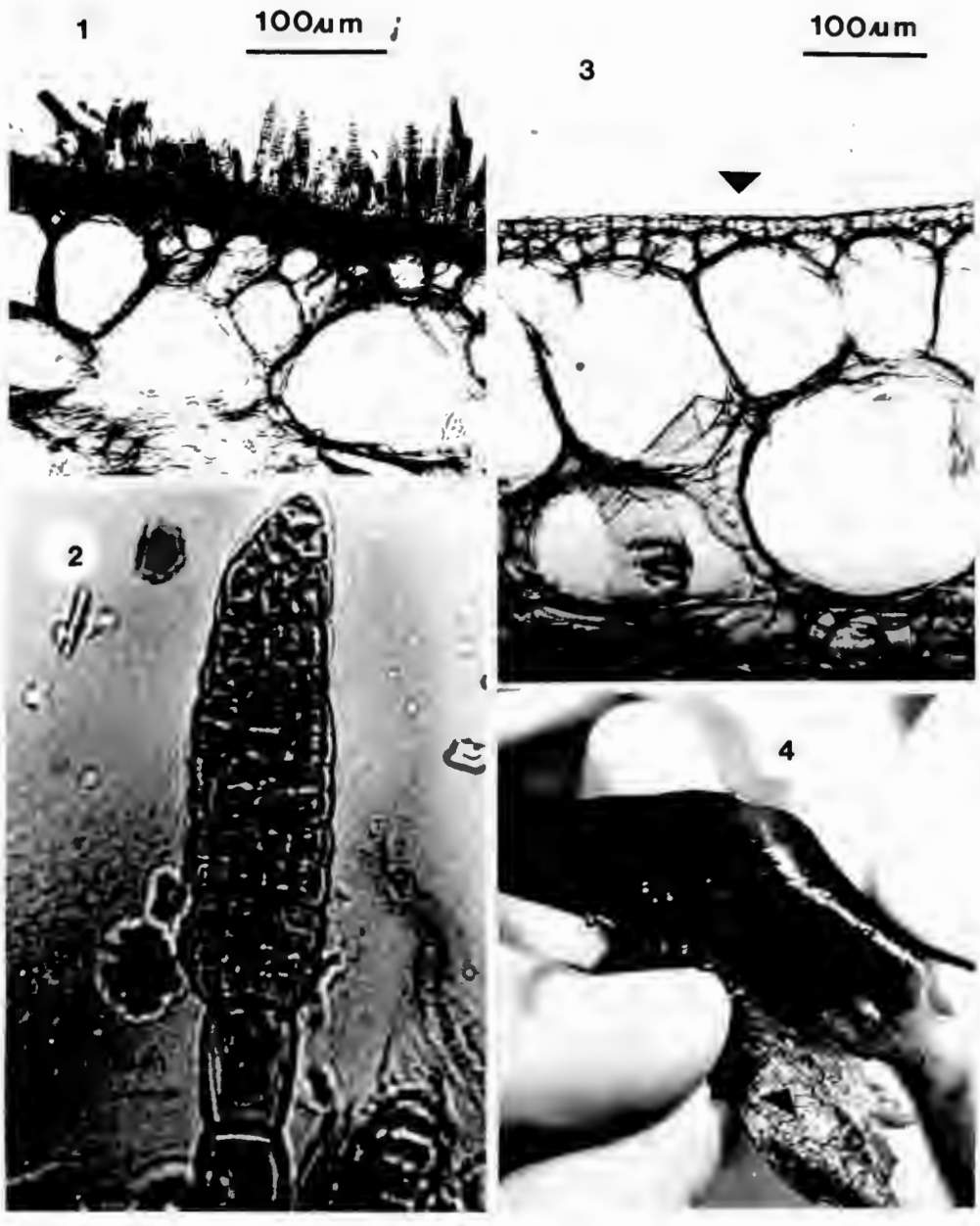
A small percentage of plants, from March 1979 onwards, supported barnacles and hydrozoans. These organisms always grew on the basal portion of the axial frond, just above the stipe.

2) Discussion

The buildup of epiphytic algae, hydrozoans and barnacles appears to be a simple increase with time, as the plants become older. The amphipods appeared to occupy nesting tubes as soon as the plants were large enough to support them. The decline in the percentage of plants with nesting tubes, after March 1979, is probably related to seasonality in the life-cycle of these animals, since there is no indication that the plants become less suitable for settlement, later in the season. It is interesting that a specimen of Desmarestia collected from Wellington, New Zealand, now in MIN (No. 554871) also bears tufts of Ectocarpus sp.

The progressive increase in the microscopic flora on the surfaces of the fronds presumably has several harmful effects. Firstly, penetration of light into the cortical cells is reduced. Secondly, the epiflora presumably impedes the flow of water over the frond surface, and the microscopic algae may compete with the host plant for nutrients. Old fronds are palpably rougher than young specimens: increasing water resistance presumably places a greater tensile strain on the plant when surge action is strong. It is possible that carpets of epiphytes may attract grazers, which would damage the tissue of the host during feeding, although there is no evidence for this.

There can be little doubt that towards the end of summer, the abundant epiphytic algae must promote the senescence of the Desmarestia population as a whole.


1
100μm
3
100μm
2
4

## Appendix Figs.

Fig. 1 Cross-section of old (approximately 1 year) *D. firma* plant showing epiphytes.

Fig. 2 Plurilocular sporangium of epiphyte, common on old *D. firma*.

Fig. 3 Cross-section of frond of young (approximately 2 month old) *D. firma*, showing epiphyte-free surface (arrowed).

Fig. 4 Tube in old *D. firma* frond, formed by the amphipod *Ampithoe humeralis*. The grazed surface of the frond, adjacent to the tube, is arrowed.