STUDIES ON THE BIOLOGY OF THE ECONOMIC MARINE RED ALGA *GELIDIUM PRISTOIDES* (TURNER) KUETZING (GELIDIALES: RHODOPHYTA)

THESIS

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DECLARATION OF ORIGINALITY

The information presented in this thesis represents the original work of the candidate, conducted in consultation with his supervisors. A limited part of the information presented in Chapters 4 and 7, was obtained with the assistance of two Honours students in the Department of Plant Sciences during 1984 and 1985, who used the information as part of their honours projects. This thesis, or any part hereof, has not been submitted by the candidate for a degree in any other university.

A.R. CARTER
CAPE TOWN
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ABSTRACT

Various aspects of the biology of the intertidal agarophyte, Gelidium pristoides, were investigated, with the aim of providing information that would assist in formulating a management policy for this economic seaweed resource.

G.pristoides occurs as tufts comprising as many as 40 individual plants, representing all three conspicuous life history stages, that are linked by the intertwining of their basal creeping axes. Individual plants consist of a system of branched creeping axes, which is largely responsible for colonizing surrounding substrata, from which one or more erect flattened fronds arise. These erect fronds may reach a height of 15 cm, and are irregularly bipinnately branched. Internal vegetative anatomy is generally typical of the genus. Morphological variation in mature plants is limited to increased plant height and branch density during the summer season. A dorso-ventrally flattened creeping habit was seen during early recruitment on flat rock surfaces and limpet shells within grazer exclusion plots, which developed into typical erect plants. Although there is a close taxonomic affinity between G.pristoides and the low-growing Gelidium turf, which occurs on wave-cut platforms in the eastern Cape (both produce bispores), the turf appears to represent a genetically divergent ecotype of the typical G.pristoides habit. In the light of present observations, it is suggested that the recent inclusion of G.pristoides in the new Onikusa genus should be questioned.

Reproduction in G.pristoides is typical of the genus, except for the production of bispores, instead of tetraspores, in the sporophyte generation. The smaller nuclei in the binucleate bispores, in comparison to carpospores, suggested they are the product of normal meiosis (meiospores). This was confirmed by chromosome counts of germlings derived from bispores ($n = 13-17$) and carpospores ($2n = 28-33$). Throughout the geographical range of the seaweed, the bisporophyte generation is dominant over the combined male and female gametophyte generation by a ratio of about 3 : 1. This imbalance may be due to a greater germination success of carpospores over bispores. G.pristoides plants are fertile throughout the year, while at Port Alfred there is no apparent seasonality in spore release. Growth of carpospore and bispore germlings is similar under various temperature treatments in culture. Optimum temperatures for growth were from 15-23°C, which corresponds with the sea temperatures experienced within the geographical range of the species.

At Port Alfred, growth (linear frond elongation) and standing crop levels were maximal during summer. Dry weight levels were significantly inversely related to both growth and ash levels. Agar contents (% of dry weight) were generally greater in summer (48%) than in winter (30%), and were inversely correlated with thallus nitrogen levels. Agar contents of distal plant halves were higher (8-15%) than in proximal halves.

Regrowth of G.pristoides to original biomass or standing crop levels after harvesting, is similar for plucking and shearing at different times of the year. Regrowth is more rapid after spring and summer harvests (2-3 months) than after winter harvests (4-5 months). During the summer season, harvesting at monthly intervals showed significantly greater total yields, and production rates (e.g. 3.13 g. dry wt./m^2/day for plucking) than under 3-monthly intervals (1.42 g. dry wt./m^2/day for plucking). In contrast, average yields per harvest were significantly greater when recovery period was longer (e.g. 3 months). Quadrats that were completely denuded failed to recover after a year, while regrowth was also retarded with increased elevation on the shore. Agar contents did not differ significantly between plucked (38%) and sheared (42%) plant material.

G.pristoides is distributed from about 0.2-0.75 m above MLWS, with a reduction in stature and frequency corresponding to increased elevation on the shore. Frond elongation rates, germling survival and recruitment within grazer-exclusion plots, is retarded with increased elevation level. Plants transplanted above the normal vertical range of the seaweed became severely bleached and died, while plants transplanted below the normal range of the seaweed (sublittoral fringe) senesced due to overgrowth by the epiphytic encrusting coralline, Polyporolithon patena (Hook. et Harv.) Mason. G.pristoides recruitment in the sublittoral fringe was enhanced with the exclusion of grazers. However, successful recruits were displaced

due to smothering by articulated corallines (e.g. *Corallina* sp. and *Jania* sp.).

G.pristoides is largely restricted to cracks and crevices in the rock, and also occurs on a large proportion of the available shells of the limpet *Patella oculus* Born., and to a lesser extent, shells of the barnacle *Tetraclita serrata*. *G.pristoides* recruitment was significantly enhanced by the exclusion of grazers (using toxic antifouling paint barriers). *G.pristoides* recruitment within the exclusion plots was significantly greater on artificially attached limpet shells (almost 100% cover) than on rock surfaces (20-30% cover), which occurred largely within cracks and crevies in the rocky substratum. *G.pristoides* plants are significantly more strongly attached to limpet and barnacle shells than to rock and epilithic encrusting corallines (*Lithothamnion* sp.). Removal of *G.pristoides* from limpet shells revealed pits of a uniform size in the surface of the shells, into which the rhizoidal attachment organs of the seaweed penetrate. It is concluded that the horizontal distribution of *G.pristoides* is largely controlled by grazers (and "escapes" from grazing) and resistance to dislodgement by wave action.

Based on present results, and considering some of the socio-economic factors associated with the *Gelidium* industry in South Africa, suggestions are made concerning the management and long-term maintenance of *G.pristoides* resources in the eastern Cape.

CHAPTER 1

GENERAL INTRODUCTION

Gelidium pristoides (Turner) Kuetzing (Fig. 1.1) is an intertidal red alga which is endemic to South Africa, and occurs from Kommetjie on the west coast of the Cape Peninsula to Port Edward, just south of Durban, on the east coast of Natal (Day 1969). It is particularly abundant on the southern and eastern rocky shores of the Cape Province where it is harvested for the extraction of agar. (Fig. 2.1).

Agar is a polysaccharide located within the cell walls and intercellular matrices of the thalli of certain algae (Akatsuka and Iwamoto 1979). It is produced by a number of red algae, but for commercial purposes is obtained primarily from species of Gelidium, Pterocladia (Gelidiaceae, Gelidiales) and Gracilaria (Gracilariaceae, Gigartinales) (Santos and Doty 1983). Agar comprises two polysaccharides, Agarose and Agaropectin, and the quality of agars from different algal species is determined largely by the proportion of sulphate groups attached to the Agaropectin polymer (Percival 1968, Whyte and Engler 1981, Miller and Furneaux 1982).

The unique structure of agar gives it special physical qualities which no synthetic substitute can emulate. In solution it produces high gel strengths at very low concentrations, has a low viscocity and may persist in either a liquid or gel state under a wide range of temperatures (Silverthorne 1977). Agar is widely used for making detailed casts of objects in dentistry, criminology and plastic surgery, while in the food processing

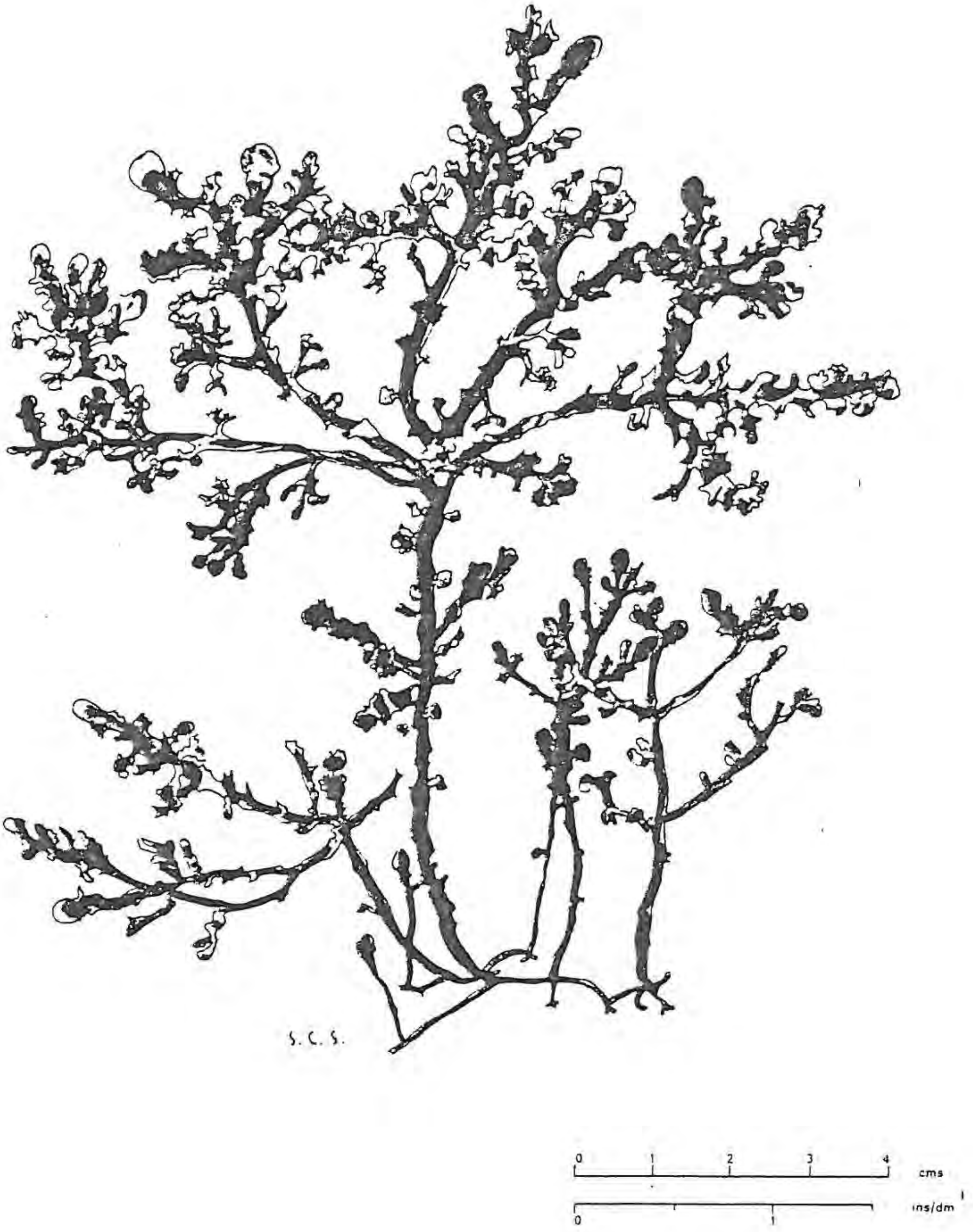

Fig. 1.1 <u>Gelidium pristoides</u> (Turner) Kuetzing (after Seagrief 1967).

industry it is used extensively as an emulsifier, stabilizer, gelling agent and thickener (Chapman 1970, Silverthorne 1977). In medicine it is also used as a laxative due to its capacity for absorbing water, but agar is probably best known for its use a microbiological culture medium.

According to Doty *et al.* (1983), although *Gracilaria* species are becoming increasingly important for meeting worldwide agar requirements, there is still a high demand for agar-producing Gelidiaceae, which generally produce agars of a superior quality (Patwary and v.d. Meer 1983). *Gelidium* agars are usually desired either for specific applications, or to blend with the lower quality gels obtained from most *Gracilaria* species.

In South Africa, *G.pristoides* makes up about 80%, by weight, of the *Gelidium* species that are harvested. The remaining 20% comprises *Gelidium amansii* (Lamour.) Lamour. and *Gelidium versicolor* (Gmel.) Lamour. According to K.W. Rotmann of Taurus Products (Pty) Ltd (pers. comm.), *G.pristoides* yields greater quantities of agar, and of a higher quality than the other two local species, which are harvested primarily in the Republic of Transkei. During 1984, 54 tonnes of *Gelidium* species, consisting mostly of *G.pristoides*, were harvested from the South African coast and exported to Japan for agar extraction (Anonymous 1984).

G.pristoides has been harvested commercially on the eastern and southern Cape coast since 1951 (Isaac and Molteno 1953) and, as one of the most common and abundant intertidal seaweeds, is of obvious ecological importance (Eyre *et al.* 1938, Stephenson *et al.* 1938, Eyre 1939). However, harvesting in the eastern Cape in particular, has come to the attention of both the public and local authorities, who have expressed some concern regarding the possible detrimental effects of this practice on the ecology of the local rocky shores.

There has been surprisingly little research done on G.pristoides. It was first examined as a source of agar during World War II, when this commodity became unavailable from Japan. But these early reports (Fox and Stephens 1943, Isaac 1942, Isaac et al. 1943) provided no quantitative measurements of agar content, and the present study is the first to do so. Furthermore, the only information available on standing crops of this seaweed is provided for Dalebrook in the Cape Peninsula (McQuaid 1985), which is now a protected area, and St. Croix Island, near Port Elizabeth (Beckley and McLachlan 1979, Beckley 1982), which is inaccessible to harvesters. Neither of these studies dealt with G.pristoides in any depth.

The aim of this study was to give a comprehensive account of the biology of G.pristoides, and is largely aimed at providing information that will assist in the formulation of a rational management policy for this South African seaweed resource. The study has been organized into nine chapters: a description of the study site; taxonomy and morphology; reproduction and cytology; seasonal growth and agar contents; regrowth after harvesting; factors affecting distribution in the intertidal; socio-economic factors associated with the Gelidium harvesting industry; and a final discussion.

This study is thus mainly autecological in nature, but necessarily diverse in scope. It makes no attempt to separate "applied" from "academic" aims, but rather hopes to demonstrate that these aspects are interdependant, and in fact, inseparable.

CHAPTER 2

DESCRIPTION OF THE STUDY AREA

All field experiments and most G.pristoides collections were carried out on rocky shores in the vicinity of Sharks Bay, which is located about 1 km south of the Kowie River mouth in Port Alfred (Fig. 2.1). Port Alfred (26°55'E, 33°36'S) lies halfway between East London and Port Elizabeth and on the south east coast of South Africa. This location was chosen as a study site because it is situated near the centre of the geographical distribution of G.pristoides, and is an area that is regularly exploited by commercial harvesters.

2.1 PHYSICAL FEATURES OF THE STUDY AREA

The exposed rocky shores in the vicinity of Sharks Bay (Fig. 2.2 a) consist mainly of folded and jointed quartzitic sandstones of the Table Mountain series, which lie in ridges perpendicular to the shoreline (Fig. 2.2 b). The ridges are arranged either to produce vertical faces or gently sloping north facing surfaces. Movable boulders occur in the gulleys between adjacent ridges. The width of the rocky tract at LWS is about 80 m.

The rocky shore at Sharks Bay is somewhat protected from severe wave action (except during exceptionally high seas) by a reef lying about ½ km offshore. The main deep-sea waves in the area originate from a sector between ESE and SSW, with maximum frequency from the south during winter, when south westerly winds predominate (Heydorn and Grindley 1982). During summer,

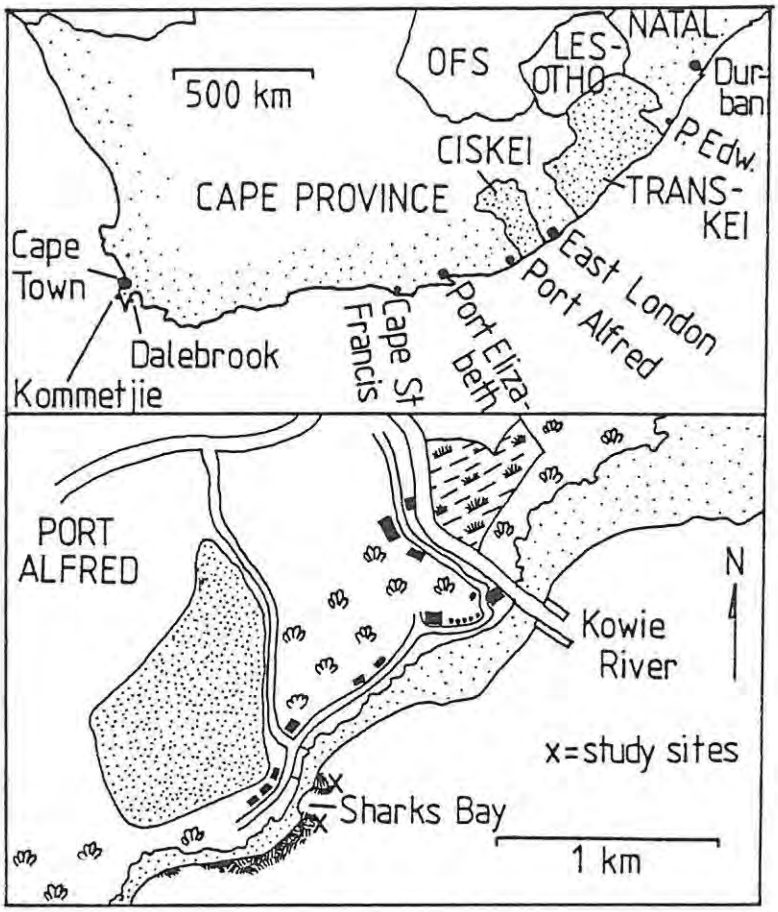

Fig. 2.1 Location of study sites.

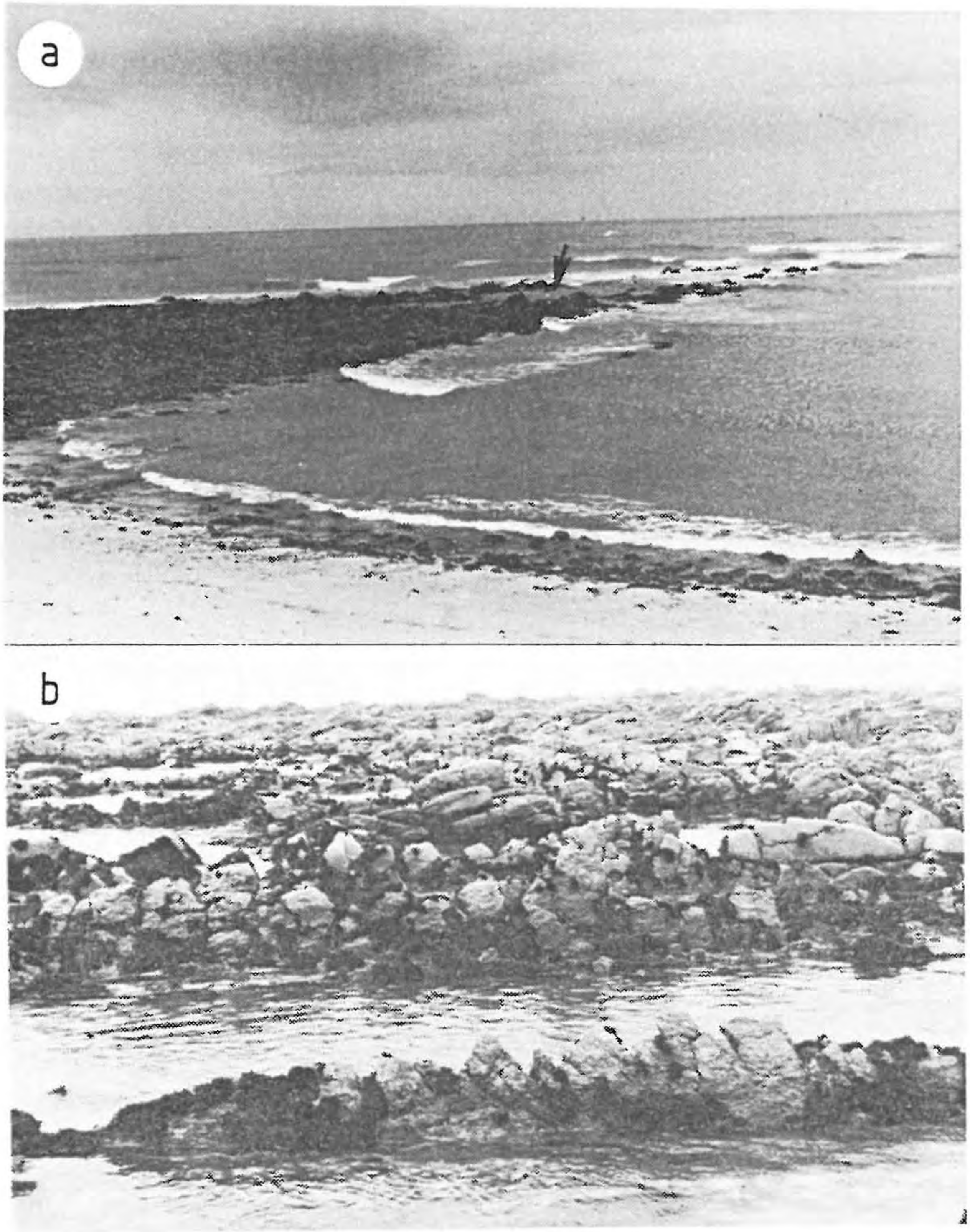

Fig. 2.2 a) Sharks Bay, Port Alfred, with a study site arrowed.
b) Sandstone ridges of the Table Mountain series running perpendicularly to the shoreline just south of Sharks Bay.

winds blow mainly from the ENE sector.

Sea temperatures at Port Alfred range from 14-22°C (Heydorn and Grindley 1982). Data from East London and Port Elizabeth (Fig. 2.3) show that sea temperatures in the eastern Cape area are seasonal (which is somewhat more marked at Port Elizabeth), with warmer temperatures occurring during summer. Local sea temperatures, however, tend to be strongly affected by prevailing wind directions, with easterly and north-easterly winds during summer frequently causing upwelling and a dramatic drop in inshore temperatures (to a minimum of 14°C). This effect is clearly seen by the low minimum temperatures during December at East London. There is no information available on nutrient levels associated with upwelling.

Since Port Alfred is situated midway between East London and Port Elizabeth, tidal data for the study area is given as mean values for these two ports (S.A. Tide Tables 1983).

MEAN HIGH WATER SPRING	1.95 m (above chart datum)
MEAN LOW WATER SPRING	0.33 m (above chart datum)
MEAN TIDAL LEVEL	1.14 m (above chart datum)
TIDAL RANGE	1.62 m

2.2 BIOLOGICAL FEATURES OF THE STUDY AREA

Stephenson (1948) considers the eastern Cape area to have a warm-temperate biota, which is characteristic of the south coast shores of the Cape Province. According to Seagrief (1986) 267 algal species are represented

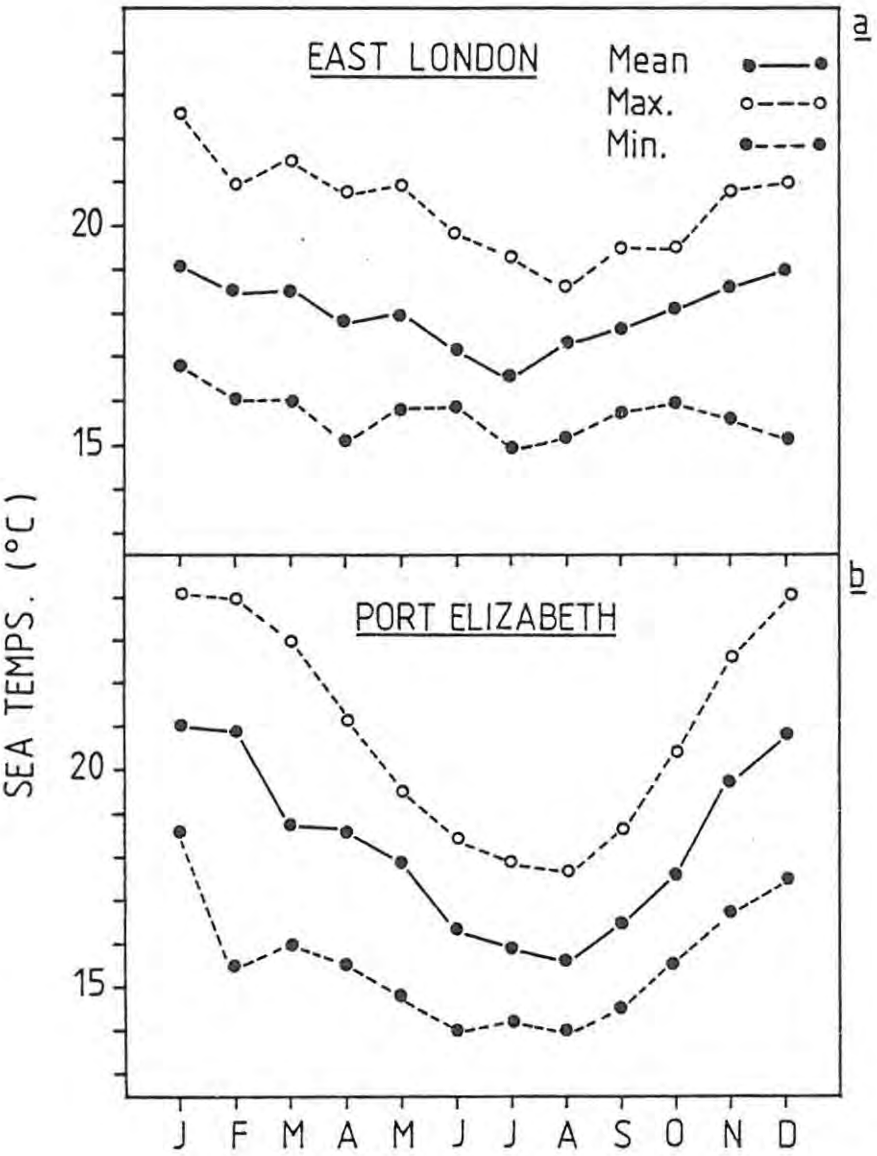

Fig. 2.3 Monthly mean, maximum and minimum sea temperatures for a) East London and b) Port Elizabeth, given as averages over the period 1973-1983 (supplied by the S.A. Maritime Weather Office).

in this area.

The biological zonation in the intertidal zone at Sharks Bay corresponds to a certain extent with that seen in the East London (Eyre et al. 1938) and Port Elizabeth areas (Stephenson et al. 1938). Biological zones which are similar, include: a) the sublittoral fringe comprising a mixed algal community of Hypnea spicifera (Suhr) Harv. in J.Ag. and an abundance of turf-forming corallines, mainly species of Corallina and Jania; b) upper and lower barnacle dominated Balanoid zones, with G.pristoides being the most common alga in the lower zone; c) Littorina zone, which is the highest zone and is largely bare except for species of the small gastropod snail, Littorina.

One aspect, however, where zonation differs, is in the absence of a typical Cochlear zone at Sharks Bay. The Cochlear zone seen elsewhere comprises a characteristic mosaic-like arrangement of the limpet Patella cochlear L. At approximately the same elevation of the Cochlear zones seen at Kenton-on-Sea (about 30 km south of Port Alfred) and Dalebrook in the Cape Peninsula (McQuaid 1985), there is instead at Port Alfred a zone in which the limpet Patella oculus Born. is common and G.pristoides forms a distinct band (Fig. 2.2). However, the term "Cochlear zone" has been retained in later discussion to avoid terminological confusion.

CHAPTER 3

Vegetative morphology, habit and taxonomic studies of Gelidium pristoides.

3.1 INTRODUCTION

Due to the uniformity in reproduction seen in members of the Gelidiaceae, generic and specific distinctions have tended to rely heavily upon vegetative morphological characteristics (e.g. Fan 1961, Kraft 1976, Santelices 1976, 1978, Silva 1978, Santelices and Montalva 1983). However, as Santelices (1978) pointed out, owing to the considerable degree of morphological variation shown by numerous gelidiaceous algae (as fully referenced in the discussion), morphology as an absolute taxonomic criterion should be used with caution in the absence of extensive field surveys. As a result of inadequate field observations in the past, and a failure to recognise morphological variants, there is a trend now towards the merging of certain species of the Gelidiaceae that were previously considered to be taxonomically distinct (e.g. Silva 1978, Santelices and Montalva 1983).

In Fan's (1961) morphological survey of 14 gelidiaceous species, including G.pristoides collected from Dalebrook in the Cape Peninsula, neither morphological variation within species nor habit features were considered. There are no other published accounts giving any useful information on the morphology of this economically important species. A knowledge, particularly of morphology would be of value in understanding the ecology of natural populations and hence the management necessary for the maintenance of G.pristoides resources.

Recently, Akatsuka (1986) established a new genus, Onikusa, to include G.pristoides (O.pristoides) and Gelidium japonicum (Harv.) Okam. However, he apparently only examined a single sheet of G.pristoides specimens from Kommetjie, very close to the westernmost extent of the distribution range of this species. Therefore, the inclusion of G.pristoides in the new genus Onikusa was examined in the light of present results.

In addition, the taxonomic relationship between G.pristoides and a low-growing Gelidium turf, that occurs on wave-cut platforms in the vicinity of Port Alfred, and also in the East London area (Eyre et al. 1938), was investigated. This problem also carries certain management implications, since although the turf itself cannot be readily harvested, it may present a potentially important source of reproductive propagules for long-term recruitment of G.pristoides, should it in fact represent an environmentally induced variation of the species. The turf-forming habit in various algae has previously been associated with physical stress (Hay 1981), grazing (Hay 1981, Underwood and Jernakoff 1981) and the accumulation of sediments (Stewart 1983).

3.2 MATERIALS AND METHODS

Morphological examinations were made of G.pristoides from: Sharks Bay (Port Alfred), Kenton-on-Sea (about 30 km south west of Port Alfred), Seal Point (Cape St. Francis), and Dalebrook in the Cape Peninsula. The average height of 50 plants collected from each locality during January

1984 was determined. In addition, the average heights of 10 permanently marked G.pristoides tufts (based on 5 random measurements of each tuft) at Port Alfred, were monitored at about monthly intervals during most of 1983 and 1984.

Ten entire G.pristoides tufts were carefully removed from rocky substrata at Port Alfred using a fine scraper and scalpel so that the holdfasts were largely undamaged. The holdfast portions were carefully dissected to separate individual plants, of which respective sizes and reproductive states were determined. In addition, 240 upright fronds representing all size classes were excised and dried separately to constant weight at 70°C, and their dry weights determined. The size distribution and reproductive state of 100 Gelidium turf plants obtained from Kenton-on-Sea, was also determined.

Observations were made of the anatomy of G.pristoides plants collected from Port Alfred, and Gelidium turf collected from Kenton-on-Sea. Sections of plant material were cut on a Reichert freezing microtome, stained with aniline blue and mounted in 25% glycerine. Measurements were also made of surface or cortical cell widths from sections of the middle regions of both mature G.pristoides and Gelidium turf thalli.

Rock fragments bearing Gelidium turf or G.pristoides (control) were chiselled from a wave-cut platform at Kenton-on-Sea and affixed (using quick-setting epoxy adhesive) within the zone of maximum G.pristoides density at Port Alfred. The transplants were monitored periodically from June to November 1984, to see whether the turf grew up to resemble typical

G.pristoides in a habitat where only typical G.pristoides plants are found.

In order to test whether the removal of grazing pressure would cause the Gelidium turf to grow into typical large G.pristoides plants, ten centimetre wide bands surrounding five homogeneous areas of Gelidium turf (0.7 x 0.4 m^2) were stripped of all algal growth (using a scraper and gas blow lamp) and painted with toxic marine antifouling paint (the use of toxic antifouling paint barriers in grazer-exclusion experiments is described in Chapter 7). All grazing animals, primarily the gastropod Siphonaria deflexa (Helblinge), were removed from the antifouling-paint-enclosed plots, and subsequent limpet colonizers were removed during later visits to the experimental sites, when fresh paint was also applied around the five exclusion plots. Unenclosed adjacent plots constituted controls. The morphology of the Gelidium turf was monitored throughout 1984.

3.3 OBSERVATIONS AND RESULTS

3.3.1 External vegetative morphology and habit features of G.pristoides

A single G.pristoides tuft may comprise up to 40 individual plants showing varying stages of development (Fig. 3.1), which are connected by the intertwining of their basal creeping axes (Fig. 3.2 a). These creeping axes are irregularly branched with the apical tip of each axis possessing a single apical cell (Fig. 3.2 c). At intervals along the creeping axes, disc-like rhizoidal attachment organs are produced (Fig. 3.2 b-f and Fig. 3.9 b), which serve to attach the axes to the substratum. The attachment organ is made up of rhizoidal filaments which develop from

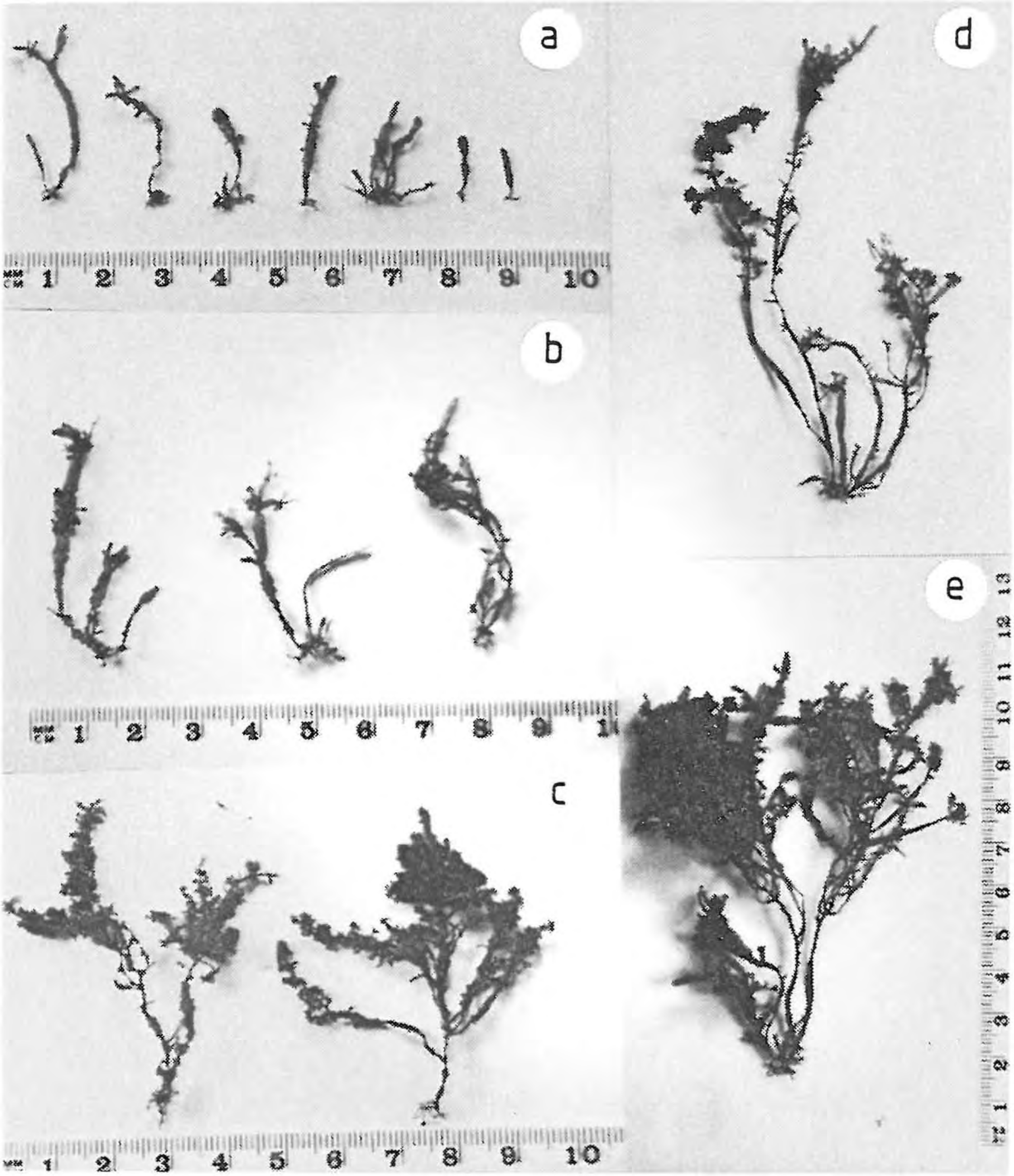

Fig. 3.1 a) Immature sterile G.pristoides plants.
b-e) Fertile G.pristoides plants at various stages of development, showing a wide range of form and branching. d) shows eight erect fronds issuing from a single system of creeping axes or holdfast.

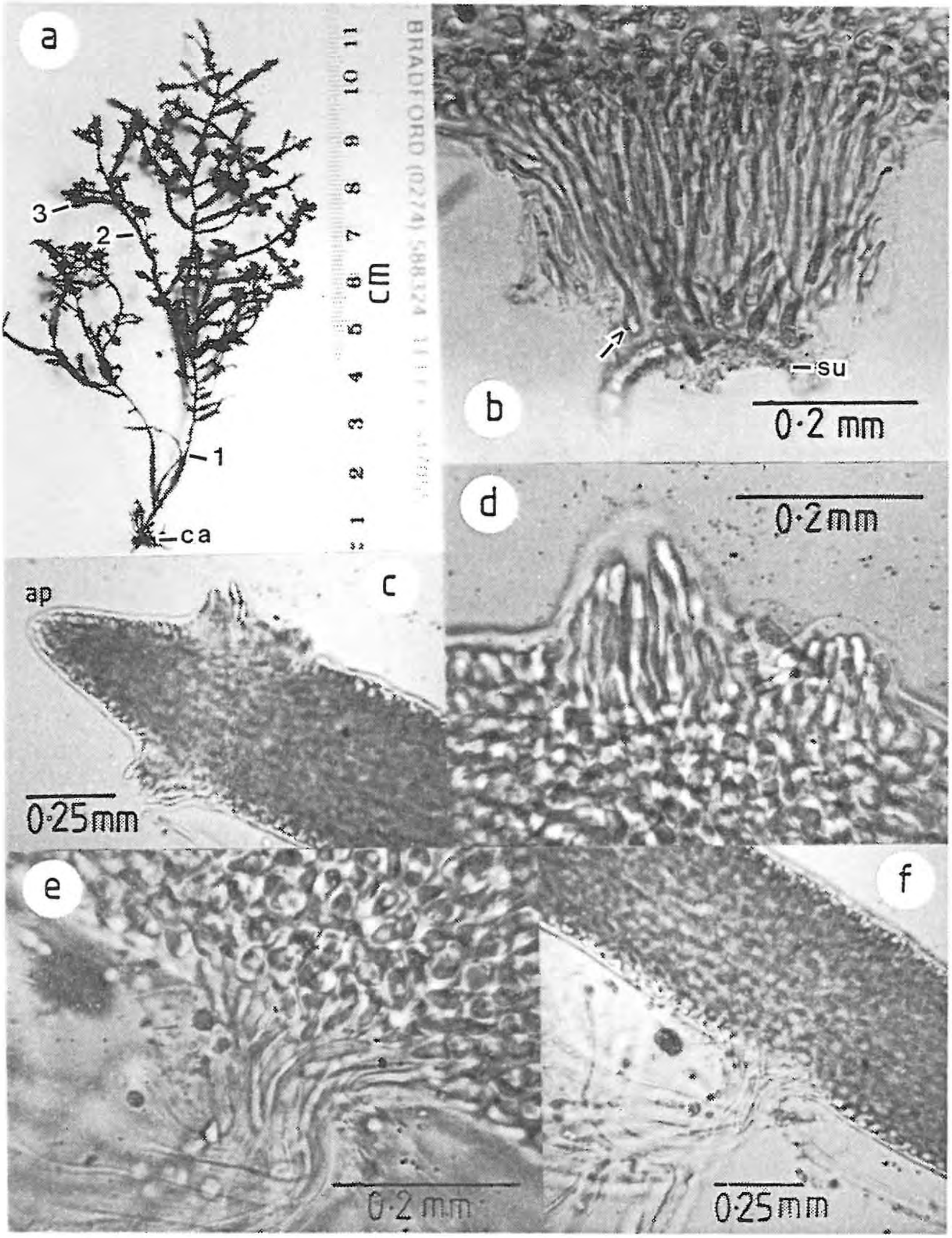

Fig. 3.2 a) A typical individual G.pristoides plant with a holdfast comprising a system of creeping axes (ca) and numerous erect fronds showing an irregular bipinnate branching pattern. 1, 2 and 3 = first, second and third order branches. Note absence of proximal branches (sloughed-off).

b) Transverse section through a rhizoidal attachment organ showing rhizoidal filaments originating from outer cortex and giving rise to bulbous tips (arrowed), which adhere to the substratum (su).

c-f) Development of rhizoidal attachment organs along the length of a creeping axis. c) shows a single apical cell (ap) at the tip of the axis.

the outermost layer of cortical cells (Fig. 3.2 b). A bulbous 'head' at the tip of each filament seems to effect the actual attachment process.

Numerous flattened erect fronds arise at intervals along the length of a single system of creeping axes (Fig. 3.1 d). Most new tuft growth is the result of the outward propagation of the creeping axes with younger and shorter upright fronds usually occurring towards the periphery of the tuft. While individual plants show a wide range of sizes, some reaching a height of 15 cm, plants generally only become reproductively mature above a height of 3 cm (Fig. 3.3 a). All three conspicuous life history stages (male, female and bisporic) were represented in some of the tufts examined. However, most tufts comprised only bisporic plants (see Chapter 4).

The pattern of branching in upright G.pristoides thalli is irregularly bipinnate (Fig. 3.2 a). The main upright fronds of indeterminate growth produce from their margins second and third order branches also of indeterminate growth. The pattern of branching is often obscured due to irregular regeneration from damaged meristematic apices, often the result of epifaunal grazing. Although there is a good deal of variation in the biomass levels for the various G.pristoides frond size classes (due to the irregular pattern of branching), the relationship between these two parameters becomes asymptotic, with plant sizes greater than 8 cm showing relatively uniform mean biomass levels (Fig. 3.4). This appears to be primarily due to the biomass contribution of distal branching being negated by the sloughing-off of branches in the proximal regions of erect fronds.

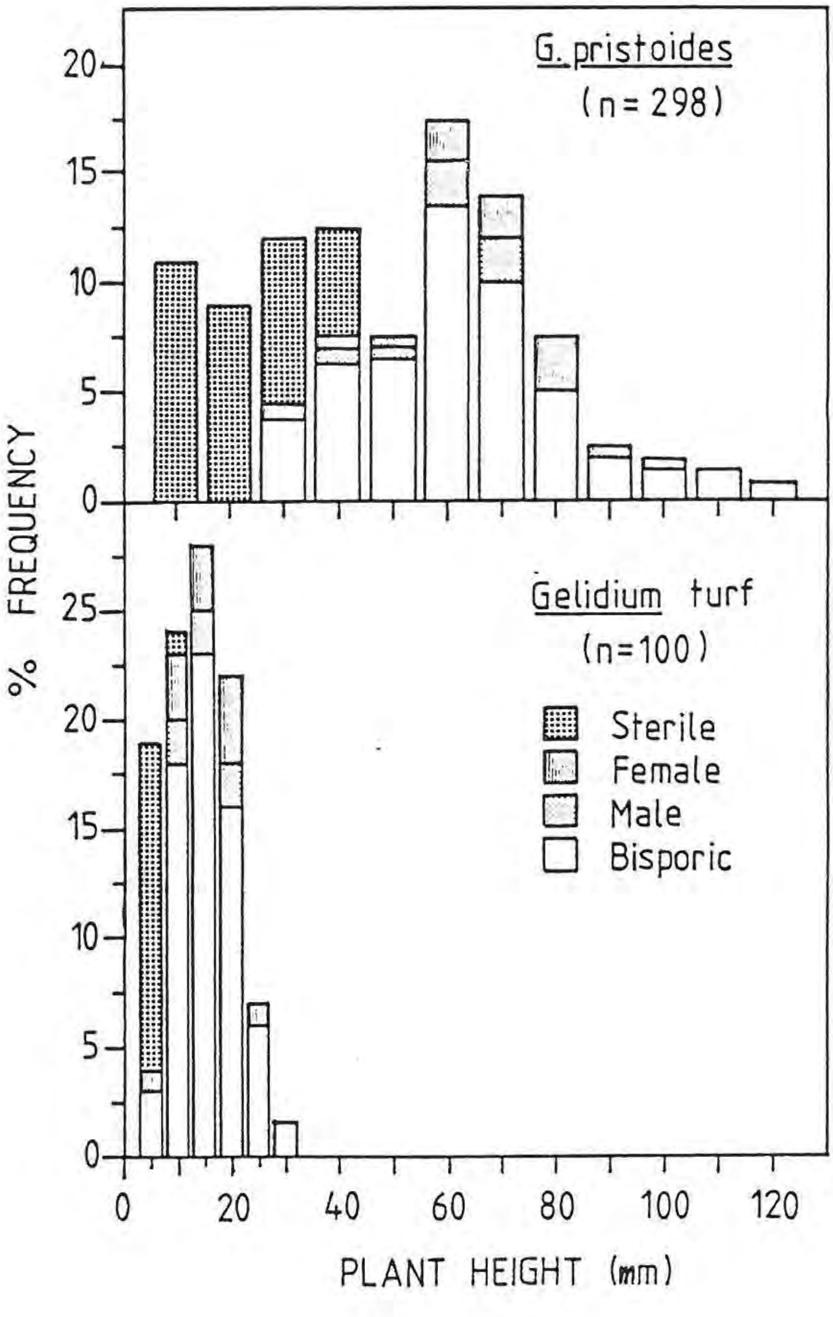

Fig. 3.3 Size distribution of sterile and fertile plants of: a) G.pristoides, b) Gelidium turf.

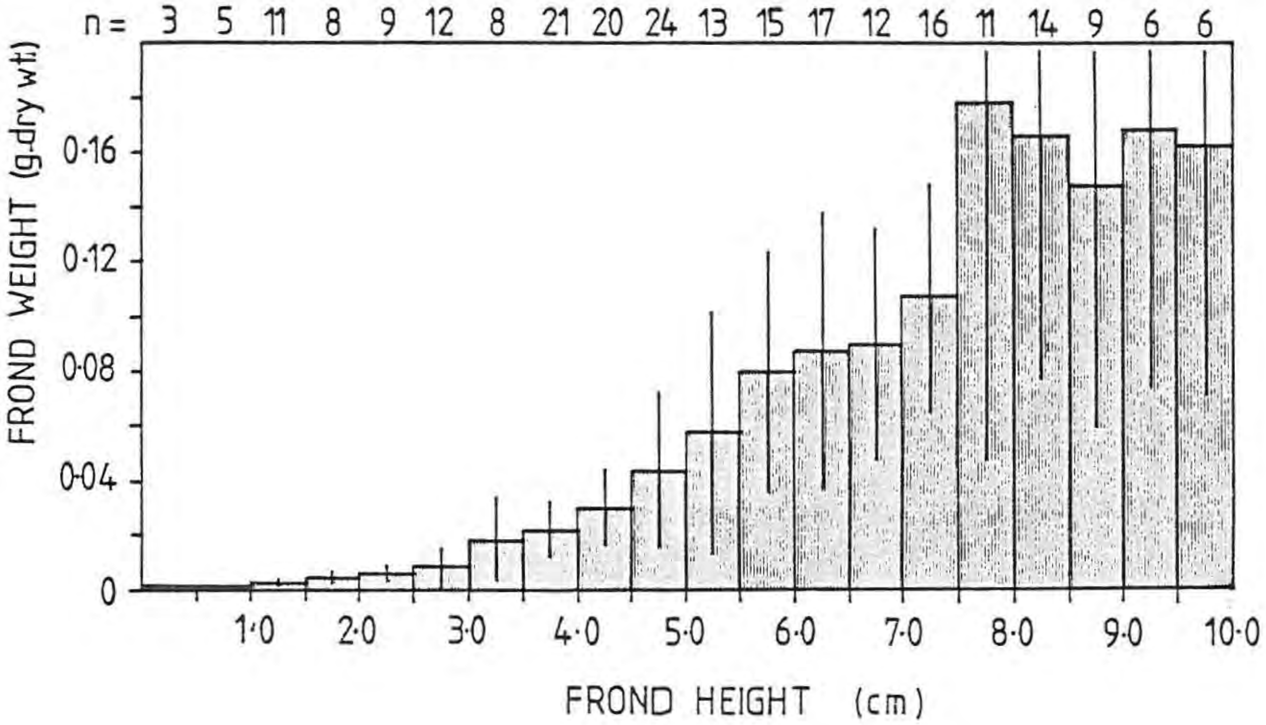

Fig. 3.4 Relationship between height and biomass (g dry wt) of erect <u>G.pristoides</u> fronds. Bars = SD, n = number of fronds measured for each size class.

First and second order branchlets of determinate growth (ramuli) issue from both the surfaces and margins of indeterminate axes, and reproductive organs are restricted to these (details in Chapter 4). All flattened fronds, whether determinate or indeterminate, have tooth-like serrations (serrulae) along their margins (Fig. 3.5 b). Each serration has an apical cell.

3.3.2 Vegetative anatomy of G.pristoides

A number of apical cells are dispersed over the margins of apical meristematic regions of fronds showing indeterminate growth (Fig. 3.5 b). Each dome-shaped apical cell divides transversely to produce a central axial filament and pericentral derivatives (Fig. 3.5 a), similar to that seen in other Gelidium species (Dixon 1958, Fan 1961). These uninucleate filament-forming cells are elongated and produce 'arms', which form secondary pit connections with the cells of adjacent filaments, thus producing a net-like cellular arrangement (Fig. 3.5 c).

The peripheral region of mature thalli (cortex), comprises 5-6 layers of deeply pigmented cells (Fig. 3.6 b). The inner cortical cells show a mean width of 5.2 um, and surface cells a mean width of 2.6 um (Table 3.1). The surface cortical cells vary in shape throughout the thallus. Cells tend to be ovoid in the lower, older thallus regions, becoming increasingly more elongate or columnar in shape towards the apical meristem (see Figs. 3.5 a, 3.6 e). The central region of the thallus (medulla) comprises less deeply pigmented and elongate cells, which appear to contribute the greatest bulk to the formation of the midrib (Fig. 3.6 a

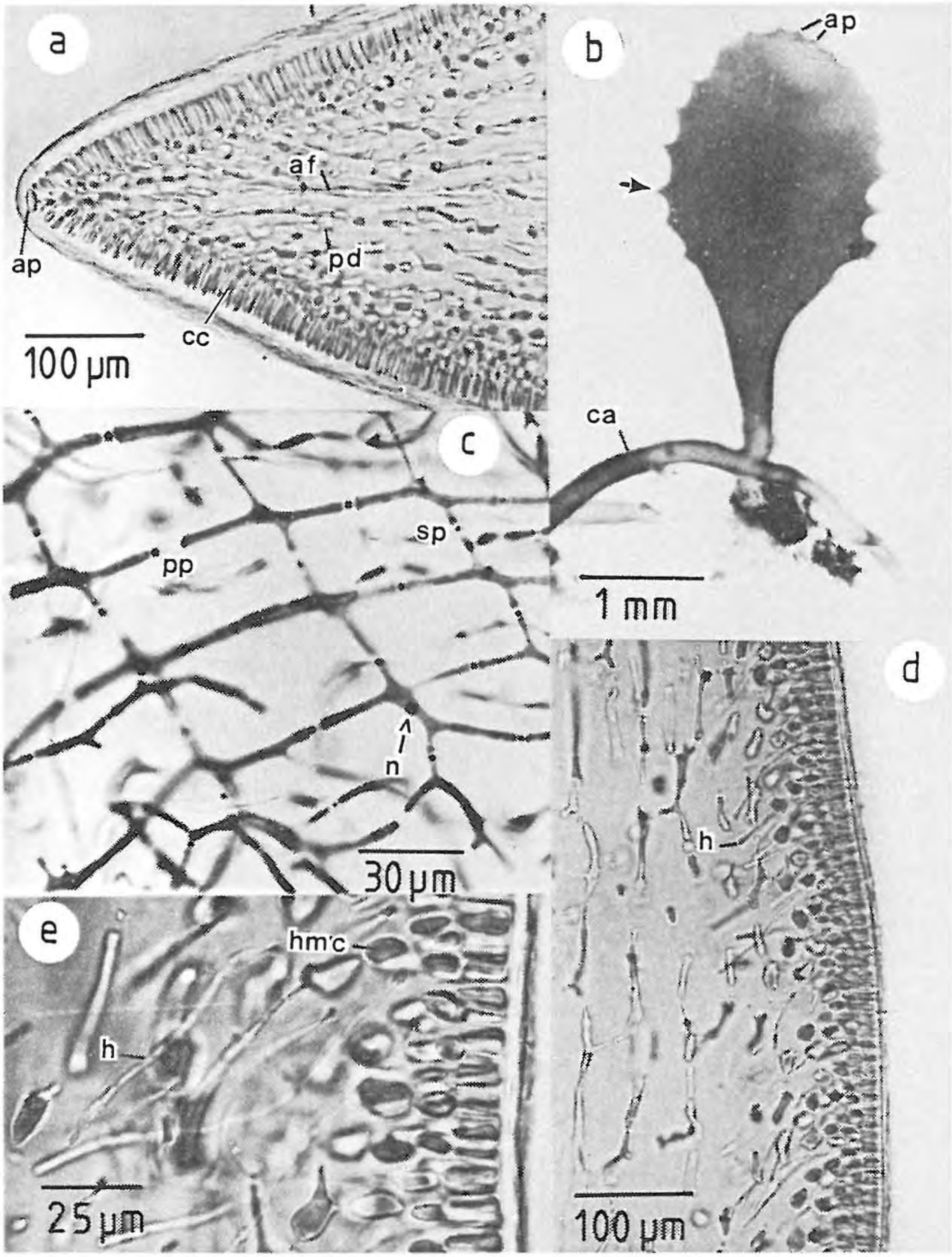

Fig. 3.5 G.pristoides

a) Longitudinal section through the apex of an indeterminate frond showing: dome-shaped apical cell (ap); central axial filament (af); pericentral derivatives (pd) forming adjacent filaments; columnar outer cortical cells (cc).

b) A newly formed erect frond of indeterminate growth issuing from a creeping axis (ca), showing tooth-like serrations (arrowed) and a number of apical cells (ap) dispersed over the margin of the frond apex.

c) Uninucleate (n) cells of adjacent medullary filaments forming a net-like cellular arrangement (pp = primary pit connection, sp = secondary pit connection).

d & e) Internal hyphae (h) produced about 3 mm below a frond apex and developing downwards between the medullary cells of the thallus. The hyphal mother cell (hmc, in e) is an inner cortical cell.

Table 3.1

Surface cell widths measured in the middle regions of mature G.pristoides thalli from Port Alfred and Kommetjie in the Cape Peninsula, and Gelidium turf from Kenton-on-Sea.

SPECIMEN	MEAN SURFACE CELL WIDTH (um) +/- SE
G.pristoides (Port Alfred)	2.6 +/- 0.1
G.pristoides (Kommetjie)	5.4 +/- 0.3 (Akatsuka 1986)
Gelidium turf (Kenton-on-Sea)	3.5 +/- 0.1

and b).

Within 3-4 mm of the frond apex, many thick-walled filaments (Fig. 3.6 e), referred to as either hyphae (Fan 1961) or hairs (Dixon 1973), are produced (Fig. 3.5 d). The mother cell of a hyphal filament is an inner cortical cell which cuts off a lateral protuberance, which in turn elongates and develops downwards within the thallus between the cells of the medulla (Fig. 3.5 e). Hyphae are distributed throughout the medulla of mature flattened G.pristoides fronds, but are more concentrated within the outer medullary region, forming a definite zone (Fig. 3.6 b). In older and more terete basal frond regions (Fig. 3.6 c), and in creeping axes (Fig. 3.6 d and e), hyphae tend to be evenly distributed throughout the medulla. It was also noted that in the apex of actively growing fronds, hyphal production only occurred subsequent to the formation of the midrib, or the production of wing-like parts (Fig. 3.6 a).

3.3.3 Variations of the typical G.pristoides growth form

Morphological and habit features of the typical G.pristoides growth form showed no apparent variation between the various life history stages (male, female and bisporic), and were uniform at the different geographical localities sampled. However, there were differences in the average heights of plants at these various localities, with plants being significantly shorter at Dalebrook than at Port Alfred (Table 3.2).

The only features which varied seasonally in G.pristoides at Port Alfred were mean plant height and branch density. Increased plant heights

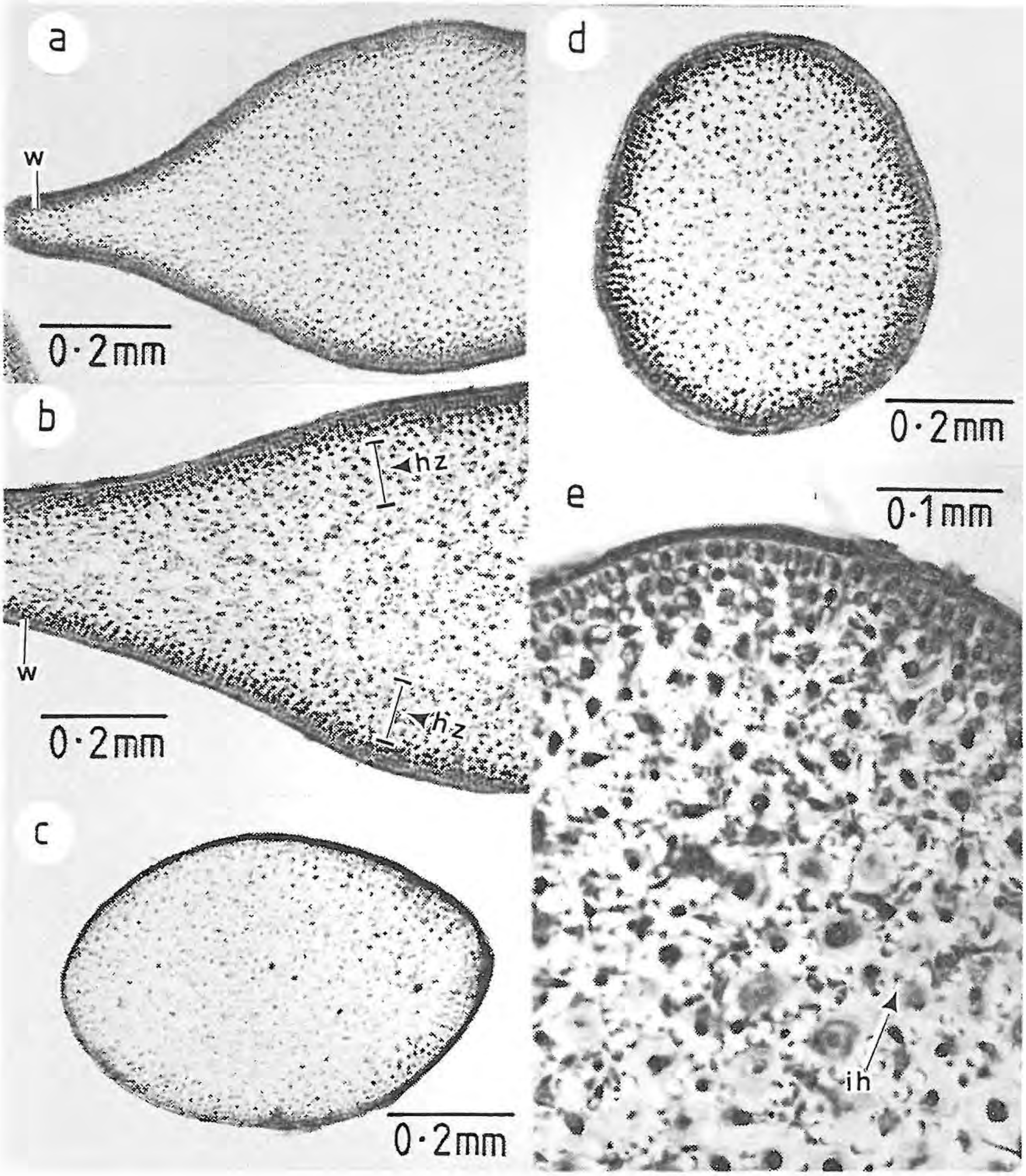

Fig. 3.6 G.pristoides. Transverse sections of:

a) The region of an apical meristem. Internal hyphae are absent, while the formation of a midrib and production of wing-like (w) parts is apparent.

b) The middle region of a mature flattened frond. Hyphae form a dense zone in the outer medulla (nz = hyphal zone).

c) The basal region of an erect frond tending to be more terete, with hyphae distributed evenly throughout the medulla.

d & e) A cylindrical creeping axis. Thick-walled internal hyphae (ih) are distributed evenly throughout the medulla.

Table 3.2

The mean height of 50 G.pristoides plants collected from various geographical localities in January 1984.

LOCALITY	MEAN PLANT HEIGHT	+/- SD	(SE)
Sharks Bay, Port Alfred	7.8	+/- 2.1	(0.3)
Kenton-on-Sea	5.7	+/- 1.3	(0.2)
Seal Point, Cape St. Francis	6.7	+/- 2.1	(0.2)
Dalebrook, False Bay, Cape	5.3	+/- 1.6	(0.2)

during summer (Fig. 3.7) corresponded to prolific distal branching and an abundance of actively growing frond apices (Fig. 3.8 a and b). Reduced plant heights during winter corresponded to a sloughing-off of distal branches and a scarcity of apices (Fig. 3.8 c and d). These seasonal variations have a significant effect on standing crop levels (Chapter 5).

A major variation in the typical G.pristoides growth form was seen during recruitment on artificially attached limpet shells and flat rock surfaces within the limpet exclusion plots described in Chapter 7. These plants comprised a system of dorso-ventrally flattened creeping axes with a single apical cell per axis, and rhizoidal attachment organs identical to those seen in the cylindrical creeping axes of typical G.pristoides plants (Fig. 3.9). These plants adhere very closely to the substratum surface, and may produce typical erect fronds with serrated margins, which themselves may possess rhizoidal attachment organs (Fig. 3.9 c). In the exclusion experiments (Chapter 7), this dorso-ventrally flattened growth form, occurring on both rock and limpet shells, eventually developed into typically erect G.pristoides plants.

3.3.4 Vegetative morphology and habit features of the Gelidium turf

At Kenton-on-Sea the low-growing Gelidium turf is restricted to wave-cut platforms where it forms a dense carpet-like covering over the rock (Fig. 3.11 a). Although typical G.pristoides plants frequently occur together with the Gelidium turf, under apparently identical environmental conditions, the turf is not found at Sharks Bay.

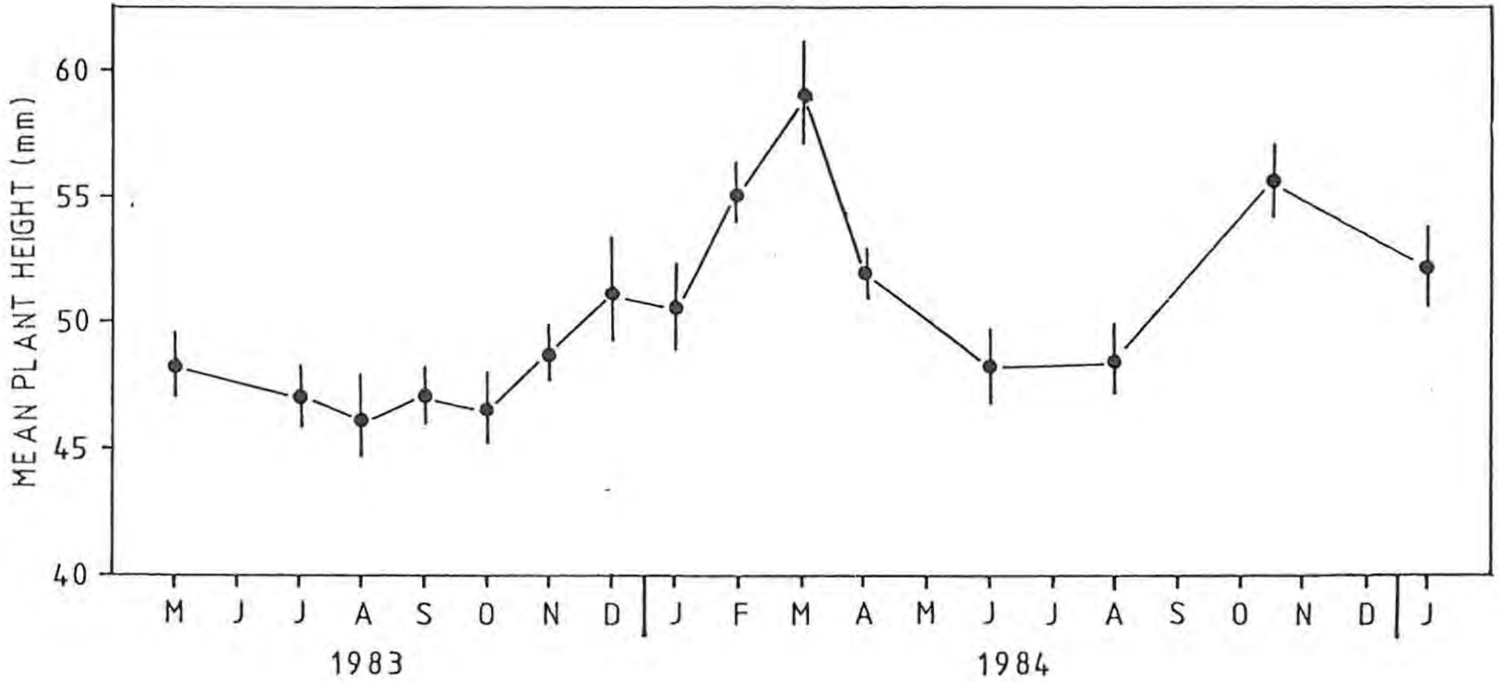

Fig. 3.7 Seasonal variation in mean G.pristoides plant height at Port Alfred. Bars = SE.

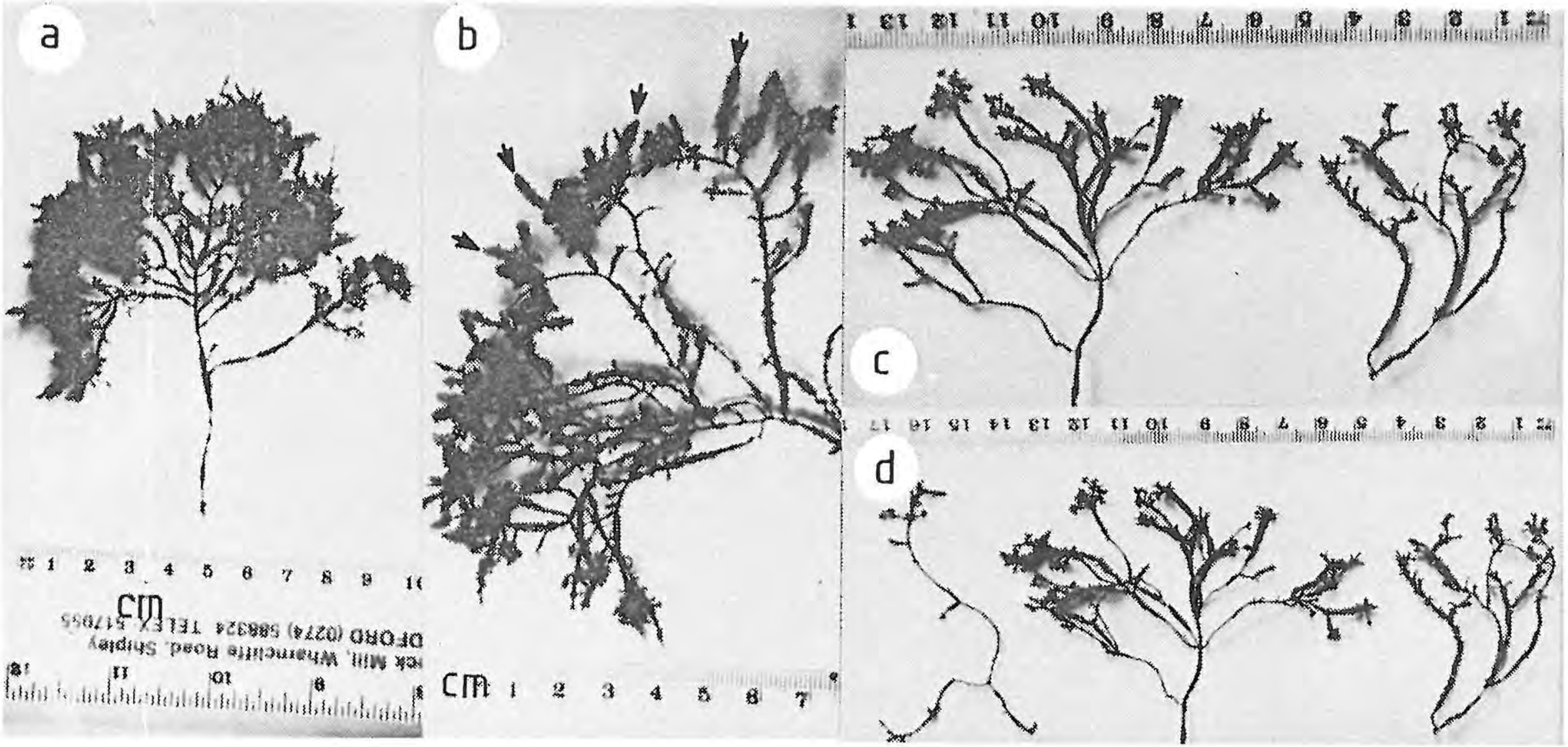

Fig. 3.8 G.pristoides.
a & b) Plants collected in summer showing prolific branching and abundant actively growing frond apices (arrowed).
c & d) Plants collected in winter clearly showing deterioration in condition.

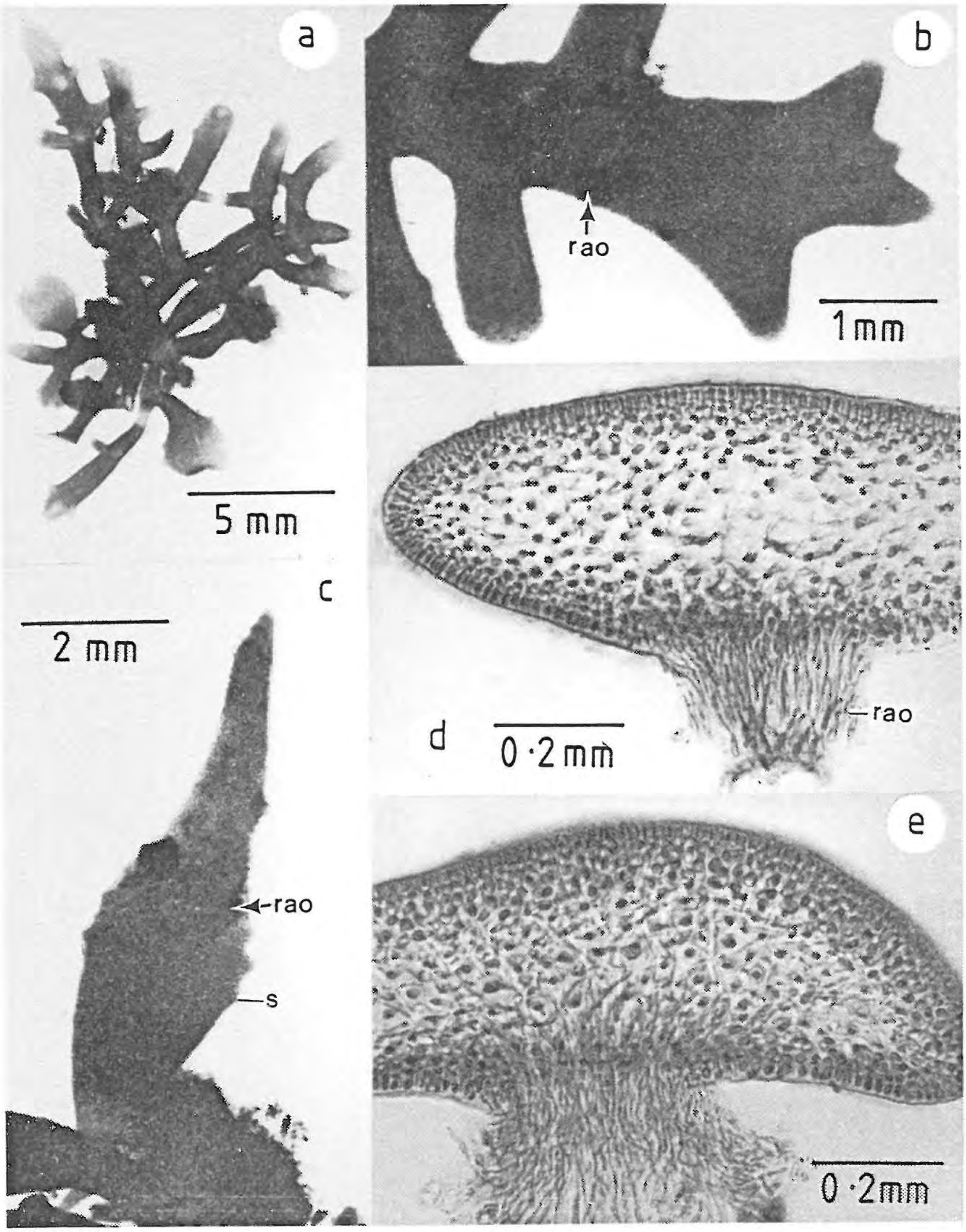

Fig. 3.9 Creeping G.pristoides growth form showing:
- a) dorso-ventrally flattened system of creeping axes,
- b) disc-shaped rhizoidal attachment organ (rao),
- c) erect frond with serrated margins reverting back to creeping habit (rao).
- d & e) Transverse section through the rhizoidal attachment organs (rao) of flattened creeping axes.

Individual plants of the Gelidium turf are much smaller in stature than G.pristoides, reaching a maximum height of about 3 cm (Fig. 3.3 b). Plants also reach reproductive maturity at a smaller size than G.pristoides plants, with the greater proportion of plants being bisporic. Individual plants comprise one or more erect flattened fronds arising from a system of cylindrical creeping axes (Fig. 3.10 b). Fronds tend to be more membranous in texture than in G.pristoides and a midrib is lacking.

The branching pattern of erect thalli is bipinnate, with second order branches always issuing from the margins of first order fronds. Reproductive structures are limited to first and second order branchlets of determinate growth that always issue from the margins of vegetative axes. Although all fronds and branches have tooth-like serrations along their margins (Fig. 3.10 b) they are not as well developed as the serrations seen in G.pristoides.

In transverse sections of mature thalli, a distinct cortex and medulla is apparent, with hyphae being distributed evenly throughout the latter (Fig. 3.10 c). The cortex comprises 3-4 layers of ovoid cells showing a larger size than those seen in sections of mature G.pristoides thalli (Table 3.1). The absence of a midrib is also apparent in transverse section (Fig. 3.10 c).

Reproductive structures are identical to those seen in G.pristoides (Chapter 4), including the production of bispores by the sporophyte generation (Fig. 3.10 d).

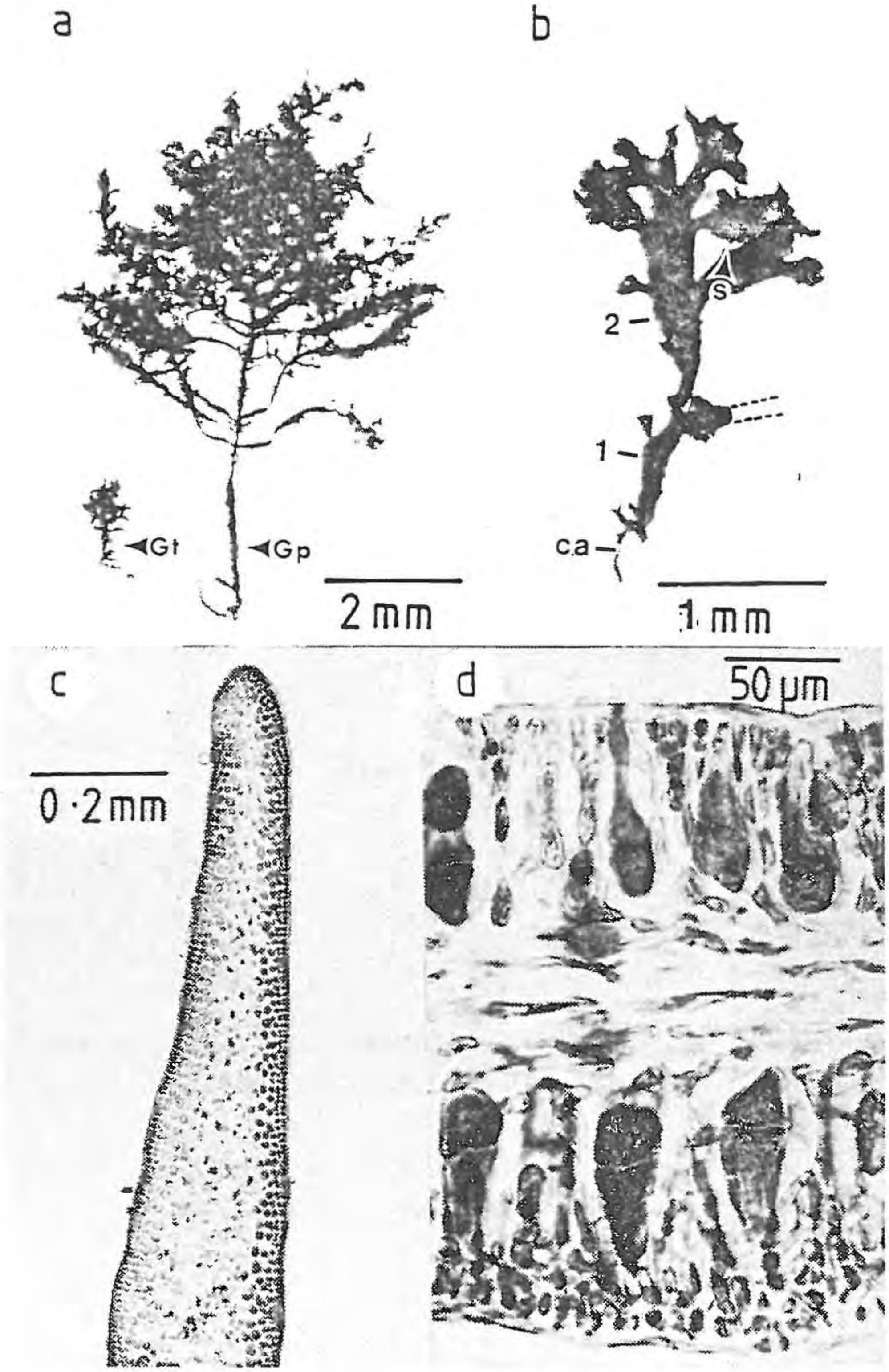

Fig. 3.10 Gelidium turf:

a) Reduced stature of turf-forming Gelidium (Gt) in comparison with a typical G.pristoides (Gp) plant.

b) Plant showing creeping axis (ca), first (1) and second (2) order branching, and tooth-like serrations (s) on a fertile ramulus.

c) Transverse section through the middle region of a mature plant showing the absence of a midrib and 3-4 layers of cortical cells.

d) Bisporangium formation in the sporophyte generation.

3.3.5 Gelidium turf transplants and grazer exclusions

Gelidium turf transplanted into typical G.pristoides stands at Sharks Bay, Port Alfred, did not show any transformation in morphology or change in stature. Eventually, after four months, the Gelidium turf was lost from the artificially attached rock fragments while the G.pristoides controls persisted.

The exclusion of grazers such as the gastropod Siphonaria deflexa, did not affect the morphology or stature of Gelidium turf at Kenton-on-Sea over a period of about a year (Fig. 3.11 b).

3.4 DISCUSSION

Present observations confirm the earlier findings of Fan (1961) that the general vegetative structure of G.pristoides is similar to that of other members of the Gelidiaceae (Dixon 1958, Fan 1961, Silva 1978, Santelices and Montalva 1983, Akatsuka 1983, 1986). One aspect, however, where present observations differ from those of Fan, is that relating to the formation of the midrib in G.pristoides. The presence of a midrib is also a feature of Suhria vittata (L.) J.Ag., Pterocladia lucida (Turn.) J.Ag and G.japonicum, in addition to G.pristoides, and which according to Fan (1961) is formed mainly due to the production of internal hyphae. By this it is implied that the midrib is a derived character having a structural function. However, present observations clearly show that the midrib of G.pristoides is formed in the region of the apical meristem prior to the production of hyphae. The production and distribution of hyphae,

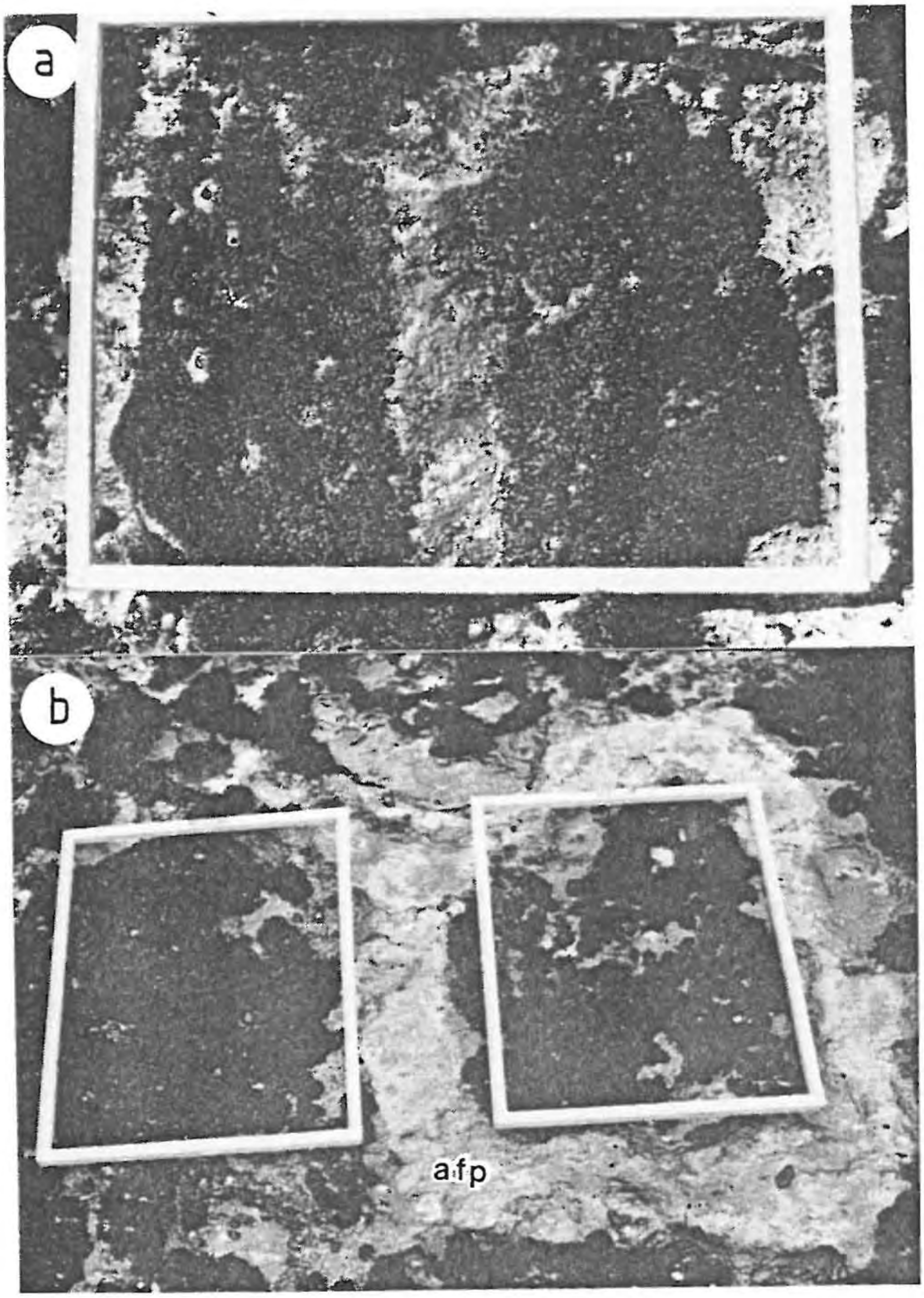

Fig. 3.11 a) Gelidium turf forming a dense carpet-like covering upon rock platforms at Kenton-on-Sea.
b) Grazer-exclusion plots at Kenton-on-Sea (afp = antifouling paint barrier). There was no apparent change in the morphology of the Gelidium turf within the exclusion plots after a year.

therefore, in no way contributes to the formation of the midrib in this species. It is suggested that the midrib is a remnant feature of an ancestral terete growth form which has evolved to produce wing-like parts. The evolution of this flattened growth form is possibly associated with desiccation resistance and survival in an intertidal habitat. It is also interesting to note that a midrib is absent in the Gelidium turf, which appears to be an ecotype of G.pristoides (discussed later).

Taxonomic distinctions in the Gelidiaceae at the generic level have been based largely on the distribution and presence or absence of internal hyphae in mature thalli. In the majority of Gelidium species hyphae are confined to the cortex, whereas in most Pterocladia species they occur mainly in the centre of the medulla. However, Fan (1961) rejects this as a valid distinguishing criterion since species of both the above genera show anatomical features intermediate between the two extremes. Such is the case in G.pristoides, where hyphae occur throughout the medulla but form a more compact zone in the outer medullary region.

The colourless, thick-walled internal hyphae or hairs are common among the Florideophyceae and typically emerge from the cells of the cortex. The function of these hyphae is unknown, although it has been suggested that they may serve to protect the alga from excessive illumination or have a nutrient absorbing function (Dixon 1973, Bold and Wynne 1978).

A single G.pristoides tuft may comprise as many as 40 individual plants of varying ages and life history stages, linked by the intertwining of their creeping axes. This holdfast system of numerous creeping axes is an important feature of the species since it is capable of colonizing surrounding substrata and of producing new erect fronds. Holdfasts are considered to be the most important plant portion effecting the regeneration and maintenance of economic red algae harvested in other parts of the world (Marshall et al. 1949, Dawes et al. 1974a, Fralick and Andrade 1981), and they appear to be no less important in the short term maintenance of harvested G.pristoides populations at Port Alfred, where germlings are rare in natural populations (see Chapter 6). A general dearth of germlings has also been reported for other gelidiaceous algae (Montalva and Santelices 1981, Jernakoff 1986). Similarly, Dixon (1958) reported a lack of recruitment of two British Gelidium species from propagules, and that all new growth could be traced back to the creeping axes of already well established plants.

Morphological variation is widespread among the Gelidiaceae. Dixon (1958) reported a correlation of morphological variation in Gelidium latifolium (Grev.) Born. et Thur. with variations in substratum size and stability in Britain, where Gelidium pusillum (Stackh.) Le Jol is also known to occur in a variety of forms (Dixon and Irvine 1977). In addition, morphological variation has been reported in Pterocladia caerulescens (Kütz.) Santl. in Hawaii (Santelices 1978) and in other Gelidiaceae (Dixon 1966, Stewart 1968) in response to ecological environmental gradients, while seasonal variants have been described for Pterocladia capillacea (Gmel.) Born. et Thur. in New Zealand (Dixon 1970) and Gelidium sesquipedale (Clem.) Thur. in Spain (Seone-Camba 1969).

While the morphology of G.pristoides is uniform at the various geographical localities sampled, minor seasonal variations, reflected mainly in plant heights and branching density, were observed at Port Alfred. A reduction in plant stature with increased intertidal elevation is also apparent (Chapter 7). A major variation in the growth form of *G.pristoides* is found in the plants colonizing limpet shells and flat rock surfaces, which have dorso-ventrally flattened creeping axes adhering closely to the substratum. These grow into typical *G.pristoides*, but in their younger state appear to be well adapted to withstanding dislodgement by waves.

Certain anatomical features which are common to the *Gelidium* turf and typical *G.pristoides* plants, clearly indicate that the two growth forms are closely related. The most important of these is the presence of bisporangia in the sporophyte generations. Bispores are produced in only one other species in the Gelidiaceae, *Suhria vittata* (L.) J.Ag., which is largely limited to the west coast of South Africa (Anderson and Bolton 1985) (Hommersand 1986, believes that *G.pristoides* and *S.vittata* may be closely related). Furthermore, populations of the typical and turf *Gelidium* growth forms show a significant dominance of the bisporophytic generation over gametophytes. This disproportionate representation of life history stages appears to be biologically determined (as discussed in Chapter 4) thus pointing to a genetic similarity between the two *Gelidium* populations. Both plants also possess characteristic tooth-like serrulae along the margins of their respective flattened fronds.

Despite the apparent close taxonomic affinity between the *Gelidium* turf and *G.pristoides*, the present study also shows that morphological, size and ecological differences exist between the two plants. While a midrib, which is present in *G.pristoides*, is lacking in the turf, there are also differences in the origin of branches. In the *Gelidium* turf, branches always arise from the margins of lower order axes, whereas branches of indeterminate growth arise from the surfaces of flattened lower order *G.pristoides* fronds.

The *Gelidium* turf has a greatly reduced stature and a smaller size of reproductive maturity in comparison to *G.pristoides*. According to Grime (1979) reduced stature may reflect a high degree of habitat disturbance in plants. Hay (1981) suggested that a low growing turf-like habit may be a response to both physical stress and grazing pressure. Underwood and Jernakoff (1981) showed that cropping by a *Siphonaria* species reduced the stature of algae growing on the N.S.W. shores of Australia. The removal of grazers over a period of about a year, had no effect on the morphology of the established *Gelidium* turf at Kenton-on-Sea. It is possible that physical conditions at certain localities in the eastern Cape (Kenton-on-Sea) present sufficient selection pressure for the morphological divergence seen in the *Gelidium* turf. One possible source of pressure might be the accumulation of sandy sediments among plant thalli, due to slow water run-off. Stewart (1983) showed that the structure of turf-forming seaweeds on rock platforms in California, including *Pterocladia capillacea* (Gmel.) Born. et Thur. (Gelidiaceae), is influenced by sand accumulation.

Whatever the cause of the morphological divergence between the *Gelidium* turf and typical *G.pristoides*, the important question is the extent to which this represents genetic divergence. The fact that both plants remain distinctive while occurring together under apparently identical conditions on the rock platforms at Kenton-on-Sea, would suggest that the morphological variation between the two plants (particularly in terms of stature) has a genetic basis. A further indication of this was the maintenance of the morphological features and eventual death of *Gelidium* turf that was transplanted into a habitat characteristic of the typical *G.pristoides* growth form. It is believed, therefore, that while showing a close taxonomic affinity with *G.pristoides*, the *Gelidium* turf represents a genetic divergence of locally adapted populations. Recently, Cheney and Mathieson (1979) reported genetic divergence in locally adapted populations of *Chondrus crispus* Stackh. in New Hampshire over very short distances, even in the presence of gene flow between divergent populations. It is not known whether the two *Gelidium* growth forms are reproductively compatible, or whether spores from the turf could result in typical *G.pristoides*. This requires further investigation. It is suggested, however, that since the *Gelidium* turf appears to represent a genetically divergent ecotype of *G.pristoides*, it should perhaps be treated as a subspecies.

Akatsuka (1986) distinguishes the proposed new genus *Onikusa* from other Gelidiaceae on the presence of serrulae along the margins of flattened fronds, the presence of a midrib, and the shape and size of surface cells in the middle region of mature thalli. Akatsuka tends to place a great deal of emphasis on the latter characteristic, having measured both the length and width of surface cells in surface view (surface cells tend to be elliptical in shape in surface view). In addition, a significant difference in width was also seen in thalli of *Gelidium* turf, which appears to be merely an ecotype of *G.pristoides*. Hence, due to the variation seen in surface cell widths alone (50% in *G.pristoides* from different areas), surface cell dimensions cannot be regarded as a sound criterion for making taxonomic distinctions, particularly at the generic level. Furthermore, the presence or absence of a midrib should also be viewed with caution, since while it is present in typical G.pristoides plants, it is absent in the closely related turf-like ecotype of the species.

Akatsuka's results are based on eight specimens on a single sheet (PRE 2344) collected from Kommetjie on the west coast of the Cape Peninsula in 1957. Basing a new genus on such a small sample is in itself questionable, particularly in the light of the high degree of morphological variation seen in members of the Gelidiaceae. Considering all the above, the proposed inclusion of G.pristoides in the genus Onikusa must be questioned.

CHAPTER 4

Reproductive morphology, and phenology, growth in culture and cytological studies of Gelidium pristoides*.

4.1 INTRODUCTION

The reproductive morphology of the carposporophyte, bisporophyte and female gametophyte generations in the life history of G.pristoides has already been described by Fan (1961) for material collected at St. James near Cape Town. Reproductive structures are typical of the genus except for the production of bispores rather than tetraspores in the sporophyte generation. Male plants have not previously been examined and have often been confused with vegetative plants due to the inconspicuous nature of the reproductive structures. There is no information available on the reproductive ecology and phenology of G.pristoides, and neither has any attempt been made to grow this seaweed in culture from spores.

The present study describes the reproductive phenology and morphology of bisporophytic and gametophytic life history stages of a G.pristoides population at Port Alfred. Phenological information has practical implica-

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*Part of this chapter has previously been published by Carter (1985).

tions, in that harvesting activities should take into account seasonality in reproductive activity. I also examined the proportions of G.pristoides life history stages occurring at various localities within its geographical range, namely, Kenton-on-Sea, Cape St. Francis and Dalebrook in the Cape, in order to determine whether reproductive phenology is uniform throughout its geographical range. Furthermore, although Guiry (1978) suggested that the bispores in G.pristoides are probably the product of normal meiosis, following his recommendation, the cytology and behaviour of nuclei in germinating spores was investigated. The growth of G.pristoides germlings in culture at various temperatures was measured in order to gain some understanding of the factors controlling its geographical distribution, as well as for future possible mariculture of the seaweed.

4.2 MATERIALS AND METHODS

All G.pristoides plant material, unless otherwise stated, was collected from Sharks Bay, Port Alfred.

4.2.1 Reproductive morphology and cytology.

Sections of fertile fronds were cut on a Reichert freezing microtome. Nuclei of released spores and bisporangia were stained with Aceto-iron-haemotoxylin-chloralhydrate (Whittman 1965) according to the method used by Hommersand (pers. comm.). Spores were allowed to release and attach to glass slides. After fixation in a 3:1 alcohol/acetic acid solution, the spores were stained for an hour, a coverslip applied and then gently heated on a hot-plate until the stain changed colour from dark brown to burnt amber. Nuclei tended to stain better if the plant material was treated with 4% KOH for 10 minutes following fixation. The spores were destained with 45% acetic acid for a few minutes, washed in distilled water and mounted in glycerol. Care was taken at all times not to dislodge the attached spores. The identical staining procedure was used for examining bisporangia except that prior to fixation, bisporangial plant fragments were bleached in 10% formalin and seawater under lamp-light until most pigment had disappeared. The material was also squashed on application of the coverslip. Measurements were made of; the diameters of unstained carpospores and bispores, the diameters of stained carpospore and bispore nuclei, and the diameters of different bispore types.

Dixon (1966a) indicated that the nuclear behaviour in sporangia (e.g. bispores) can be deduced from cytological examinations of spores released by the sporangia. Aceto-iron-haemotoxylin-chloralhydrate was also used for studying the chromosomes of germlings derived from bispores and carpospores. Iron-alum aceto-carmine (Austin 1959) was also used, but with less success. All plant material was collected from Dalebrook on the Cape Peninsula. Fertile bisporic and cystocarpic fronds were excised, and washed in millipore-filtered seawater (pore size = 0.45 um) (washing in distilled water tended to reduce bispore germination). The fronds were placed over glass slides within petri-dishes containing filtered seawater. The following day, the fronds were removed and the released spores allowed to germinate to the 1-4 cell stage. The germlings, now attached to the glass slides, were fixed in 3:1 alcohol/acetic acid for an hour, thoroughly washed in distilled water and then stained for half an hour. The next procedure involved careful heating over a steam bath, and was crucial in obtaining good clearing of the cytoplasm and well-stained chromosomes. Regular short exposures to heat produced the best results, as against underheating and overheating. Destaining was not carried out, because it frequently resulted in a deterioration in clarity and the visibility of chromosomes. Between 10-15 chromosome counts were made of each germling-type. Photographs were taken using Ilford Pan F (ASA 50) and FP 4 (ASA 125) black and white film.

4.2.2 Germination experiments.

Germination experiments were conducted in the laboratory at ambient room temperature (15-23°C) and in diffuse natural light. Fertile bisporophytic and cystocarpic fronds were placed over glass slides within petri-dishes containing millipore-filtered seawater (pore size = 0.45 um). The glass slides had grids with 9 mm^2 blocks scratched into them. Attached spores were counted in randomly selected squares, their grid co-ordinates noted, and the germination success of carpospores and bispores determined after two days. Five replicates were prepared for each spore-type, and the experiment repeated four times.

In addition, during one of the above experiments, the size range of bispores in certain blocks was measured. After germination, the sizes of the evacuated spore capsules (Fig. 4.2 e) belonging to successful bispore germlings was recorded. Thus, assuming that spore capsules did not change in size after germination, an indication of germination success in relation to bispore size, was obtained.

4.2.3 Culture experiments.

Culture experiments were conducted in constant environment growth rooms with a photoperiod of 16:$\overline{8}$h (light:dark). Light was supplied by fluorescent cool-white light tubes. Culture dishes were arranged so that the photon flux density above each dish was in the region of 50 umol. quanta./m^2/sec. Light measurements were obtained with a Li-Cor LI-1888 integrating quantum/photometer. Fertile bisporophytic and cystocarpic fronds (collected from Dalebrook) were suspended over glass slides in Pyrex, glass culture dishes (200 ml) containing 100 ml of Provasoli's Enriched Seawater Medium (McLachlan 1973). The following day, fronds were removed and culture dishes were placed in water-baths at 8, 12, 15, 19, 23, 27 and 30°C, respectively. Three replicate dishes were set up for each spore type and temperature treatment. The growth of randomly selected germlings was measured in terms of increase in germling length. Measurements were made at 2-3 day intervals over a period of 12 days. Culture media were changed on the seventh day.

4.2.4 Seasonal plant fertility and spore release.

At monthly intervals from February 1983 to January 1984, a sample of 50 mature <u>G.pristoides</u> plants (greater than about 30 mm in height) was randomly collected from Sharks Bay. On returning to the laboratory, each plant was examined for reproductive structures. Three samples of 50 plants each were also collected from Kenton-on-Sea (about 30 km south of Port Alfred), Seal Point at Cape St. Francis, and Dalebrook near Cape Town during January 1984. Plants from these samples were also examined for reproductive structures. Numbers of male, female and bisporophytic plants were expressed as percentages of the total number of plants in each sample.

Carpospore and bispore release was monitored at monthly intervals from April to November 1984. Fertile bisporic and cystocarpic fronds were excised, washed in distilled water and suspended over a petri-dish having a calibrated grid marked on it, and within a plastic dish containing filtered seawater . Fronds were allowed to release spores for exactly 24 hours, after which the petri-dishes were removed and settled spores counted in random blocks of the grid. Total spore release was extrapolated. The fronds were dried to constant weight and spore release was calculated in relation to plant dry weight (spores/g.dry wt. x 10^3). Five replicates were prepared for each spore type.

4.3 RESULTS

4.3.1 Reproductive morphology.

The life history of G.pristoides consists of alternating bisporophytic and dioecious gametophytic plants which are morphologically similar except for reproductive structures. These occur on first and second order flattened determinate branches or ramuli (Figs. 4.1 a and e) that are borne either along the margins or on the surfaces of flattened axes of indeterminate growth.

Male plants are distinguished by the presence of superficial colourless patches on the surfaces of fertile branches (Fig. 4.1 a). A cortical

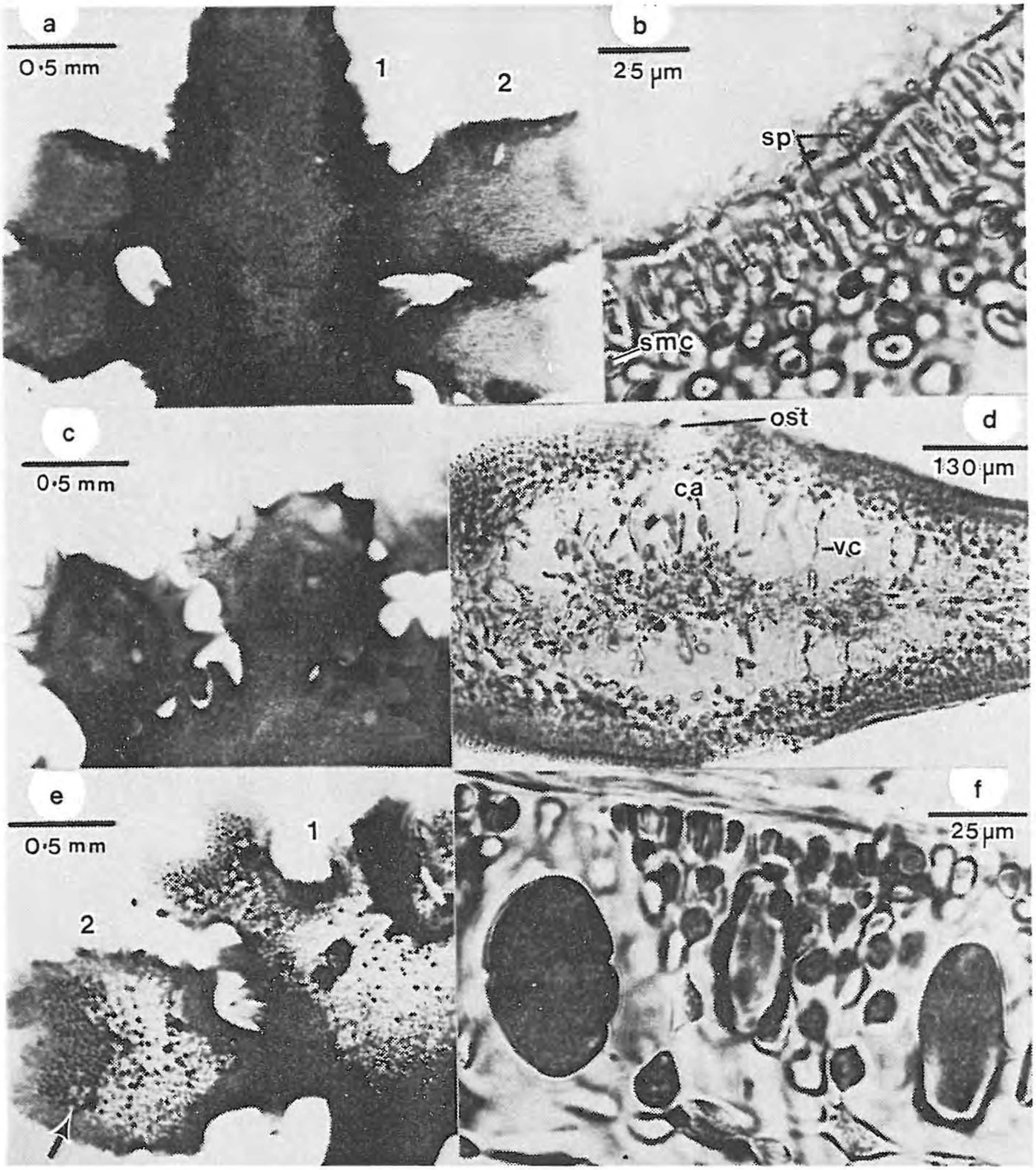

Fig. 4.1 Reproductive morphology of G.pristoides:

a) Male plant with superficial colourless patches on first (1) and second (2) order determinate branches.

b) Transverse section through the fertile region of a male plant showing spermatangial mother cells (smc) and spermatangia (sp).

c) Female plant with bilocular cystocarps.

d) Transverse section through a cystocarp showing elongated vegetative cells (vc) and club-shaped carposporangia (ca). An ostiole (ost) is present on each surface of the cystocarp.

e) Bisporophytic plant with clearly visible sporangia (arrowed) and vacant soral regions within first (1) and second (2) order determinate branches.

f) Transverse section through a fertile sporophytic branch showing bisporangial development.

cell produces two or more colourless elongated spermatangial mother cells (Fig. 4.1 b). A transverse division of the spermatangial mother cell results in the formation of a terminal spermatangium which is released from the fertile region.

Female plants possess bilocular cystocarps (Fig. 4.1 c) in which gonimoblast filaments are produced in abundance by the carposporophyte generation. Club-shaped carposporangia are cut-off towards both surfaces of the fertile branch (Fig. 4.1 d). Elongated vegetative cells extend from the region of the developing carposporophyte to the surface walls of the cystocarp. Carpospores are released through ostioles which occur on both surfaces. Diameters of released carpospores ranged from 27-34 um (Fig. 4.4), while their nuclei showed a range from 6.5-7.7 um (mean diameter = 7.3 um, n = 30) (Fig. 4.2 a). The occasional binucleate carpospore was also seen (Fig. 4.3 a).

Bisporangial plants possess clearly visible sporangia with vacant soral areas often evident in the proximal regions of the fertile branches (Fig. 4.1 e). The bisporangial initial is cut-off laterally from the apical cell of a cortical filament by an anticlinal division. The apical initial continues to divide and branch while the sporangium enlarges considerably (Fig. 4.1 f). At maturity the sporangium thus appears as a one celled lateral filament immersed within the cortex. A single transverse division of the sporangium mother cell results in the formation of a tetranucleate bisporangium (Fig. 4.2 b). Three types of released bispores were seen: mononucleate, binucleate (Fig. 4.2 c) and tetranucleate bispores (Fig. 4.2 d). Binucleate bispores were by far the most abundant

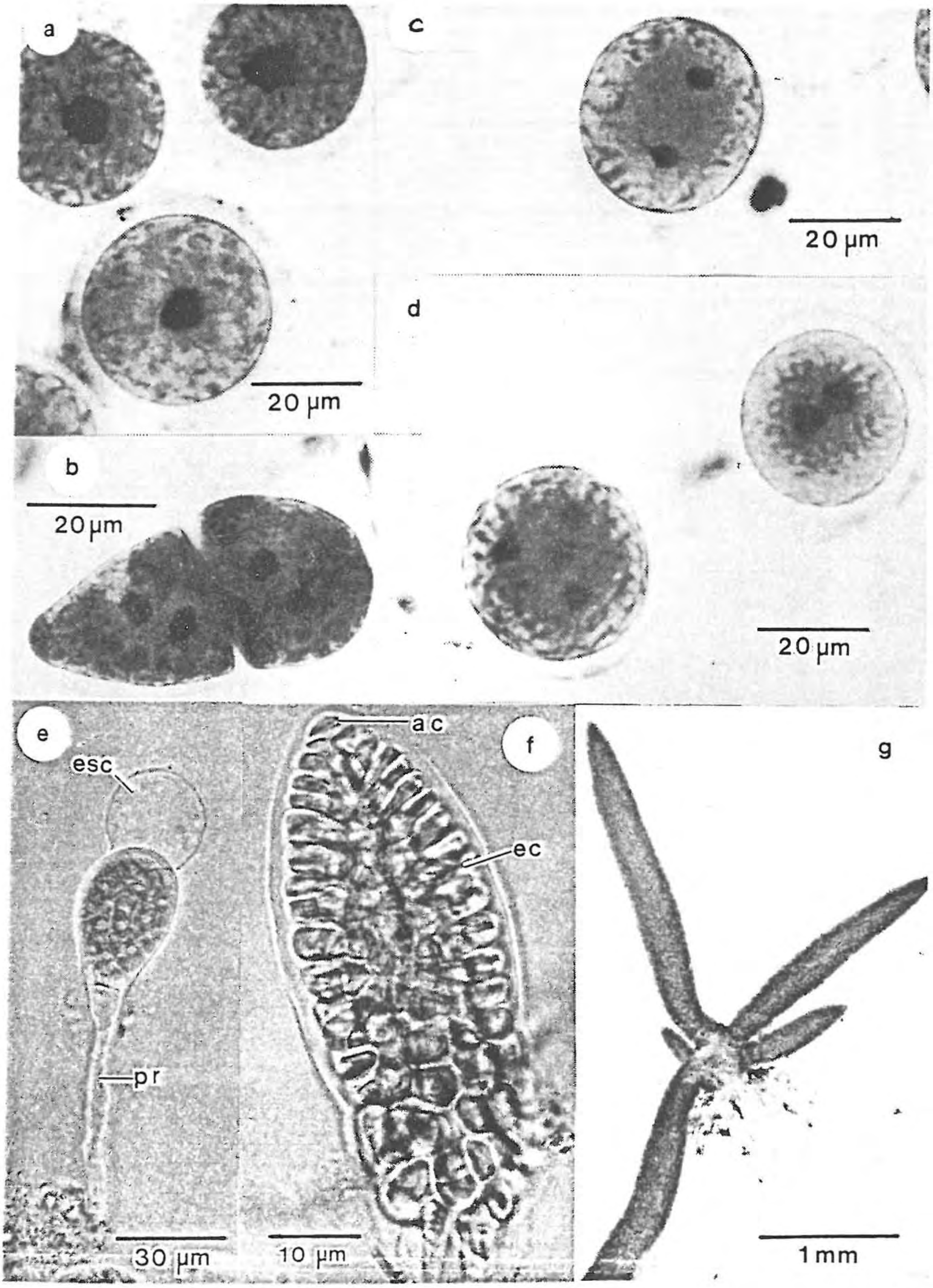

Fig. 4.2

a) Large single nuclei of released carpospores.
b) A tetranucleate bisporangium.
c) Smaller nuclei of released binucleate bispore.
d) Similar nuclei sizes in binucleate and tetranucleate bispores.
e) Two day old bispore germling showing the evacuated spore capsule (esc) still attached, and primary rhizoid (pr) development.
f) Ten day old carpospore germling with a dome-shaped apical cell (ac) and showing early cortication (ec).
g) One month old bispore germling with cylindrical creeping axes.

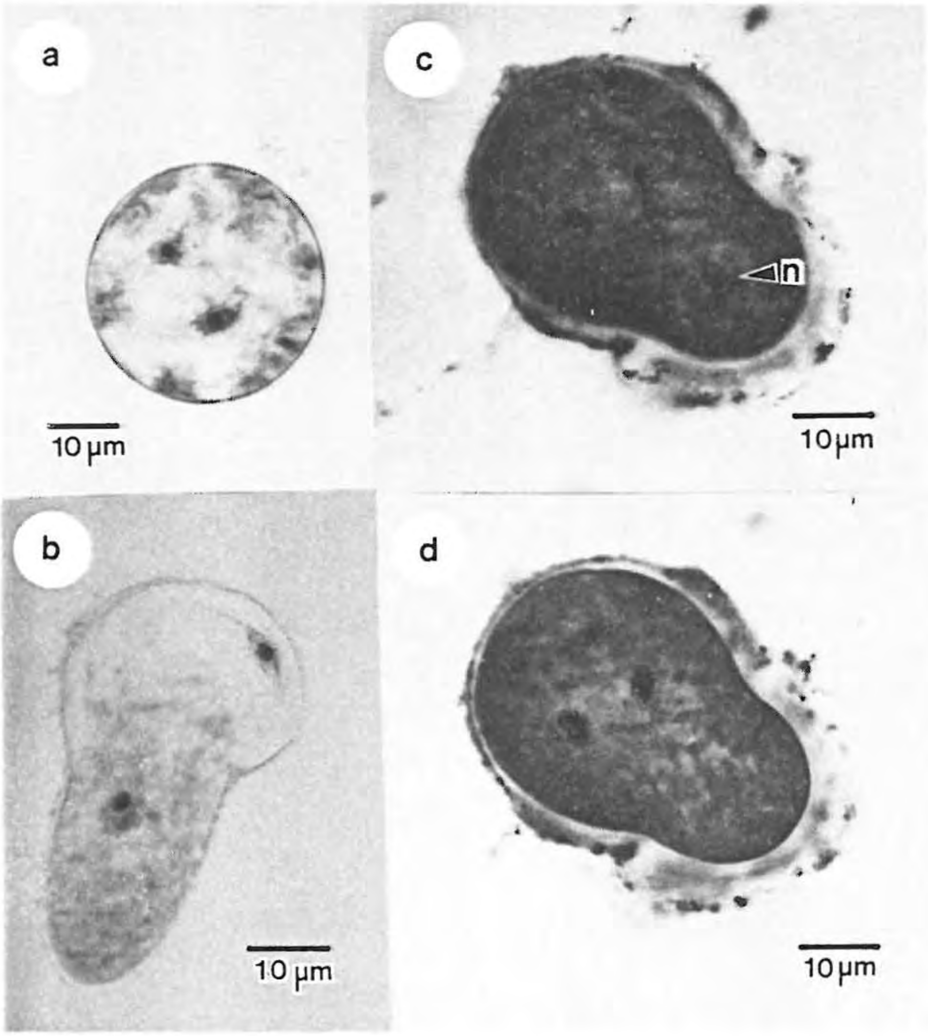

Fig. 4.3 a) Released binucleate carpospore.
b) Migration of a single nucleus of a binucleate carpospore into the germination tube.
c & d) Migration of a single nucleus of a tetranucleate bispore into the germination tube.

spore-type produced and ranged in diameter from 23-38 um (Fig. 4.4). Tetranucleate and mononucleate bispores showed a similar size range to binucleate spores (Fig. 4.5), but both (especially the mononucleate type) were relatively scarce in occurrence. The proportions in which the different bispores occurred, are illustrated to a certain extent in Figure 4.5. The nuclei of the binucleate and tetranucleate bispores were of a similar size (mean diameter = 4.1 um, n = 35) (Fig. 4.2 d), almost half the size of carpospore nuclei. Only a few nuclei of mononucleate bispores were measured, but showed a larger diameter than the other bispore types (5.4-6.6 um).

4.3.2 Chromosome numbers in carpospore and bispore germlings

Counts were made of chromosomes in mitotic metaphase during the early development of germlings derived from carpospores and bispores. Chromosomes were best seen during the early 1-4 celled stages of germling development. Chromosome numbers in bispore germlings ranged from 13-17 (Figs. 4.6 a and b; 4.7 a and b) and carpospore germlings from 28-33 (Figs. 4.6 c and d; 4.7 c and d). Chromosomes appeared to be about 0,5 um in diameter and could be clearly distinguished.

4.3.3 Spore germination and related experiments.

The general pattern of germination is similar for both bispores and carpospores, where the contents of the spore are evacuated, leaving an empty spore wall which remains attached indefinitely (Fig. 4.2 e). The various stages of spore germination and early germling development are shown in

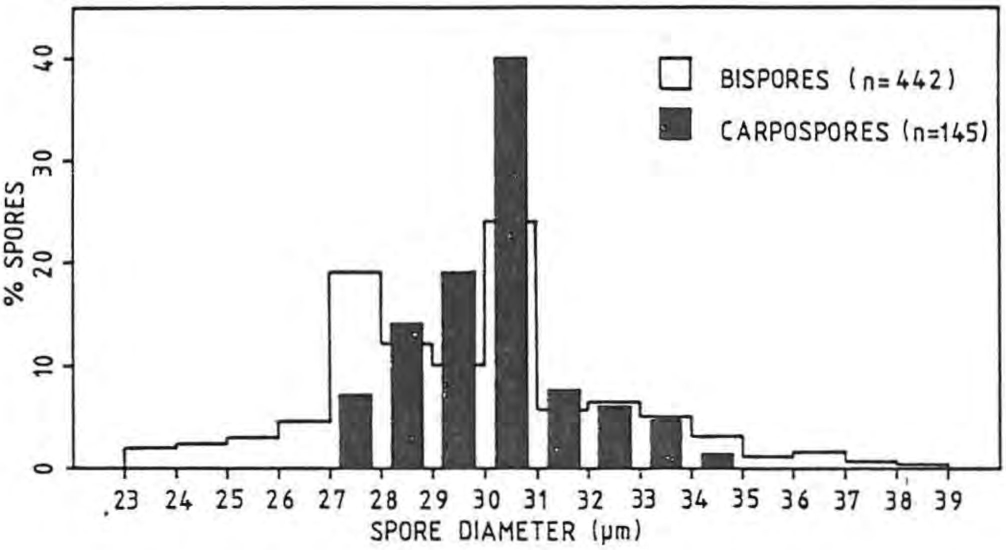

Fig. 4.4 Bispore and carpospore size distributions given as percentages of the total number of spores measured for each type (n = numbers measured of each type).

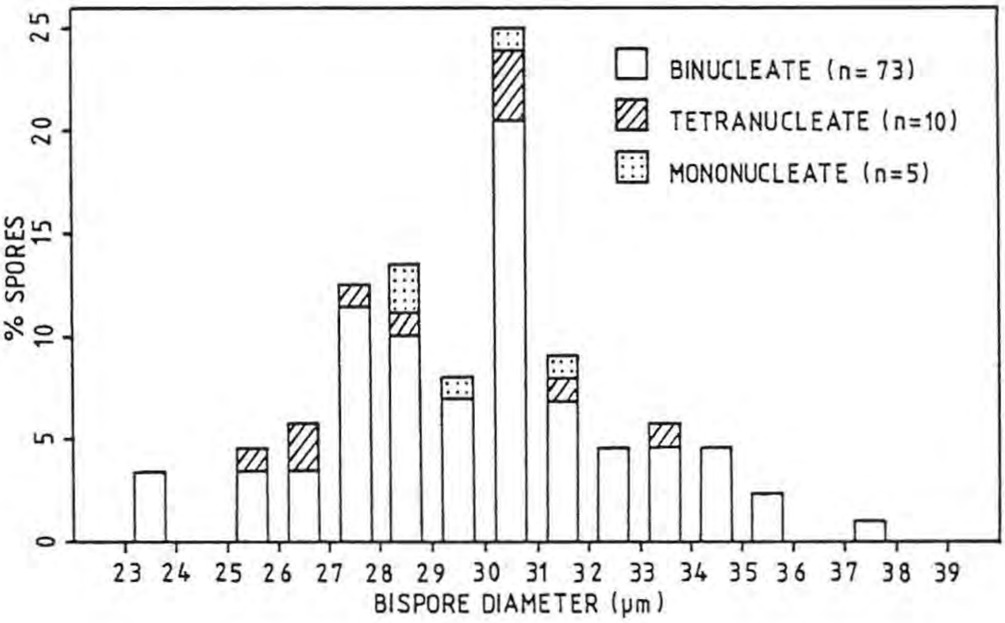

Fig. 4.5 Size distributions of binucleate, tetranucleate and mononucleate bispore types, given as percentages of the total number of bispores measured (n = numbers measured of each type).

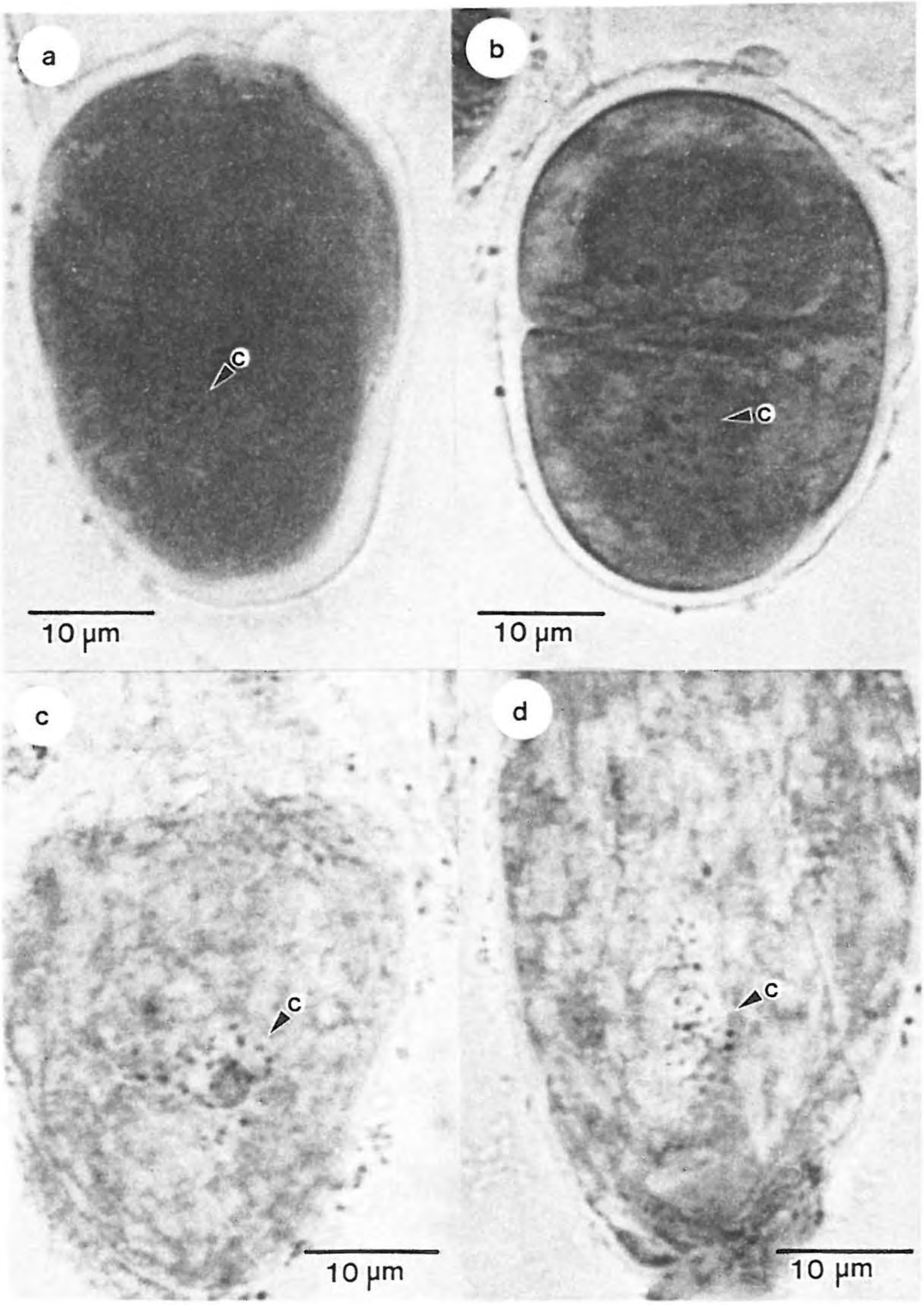

Fig. 4.6 Mitotic metaphase chromosomes (c) in a:
a) single celled bispore germling (n = 14)
b) two celled bispore germling (n = 15)
c) single celled carpospore germling (n = 30)
d) four celled carpospore germling (n = 33).

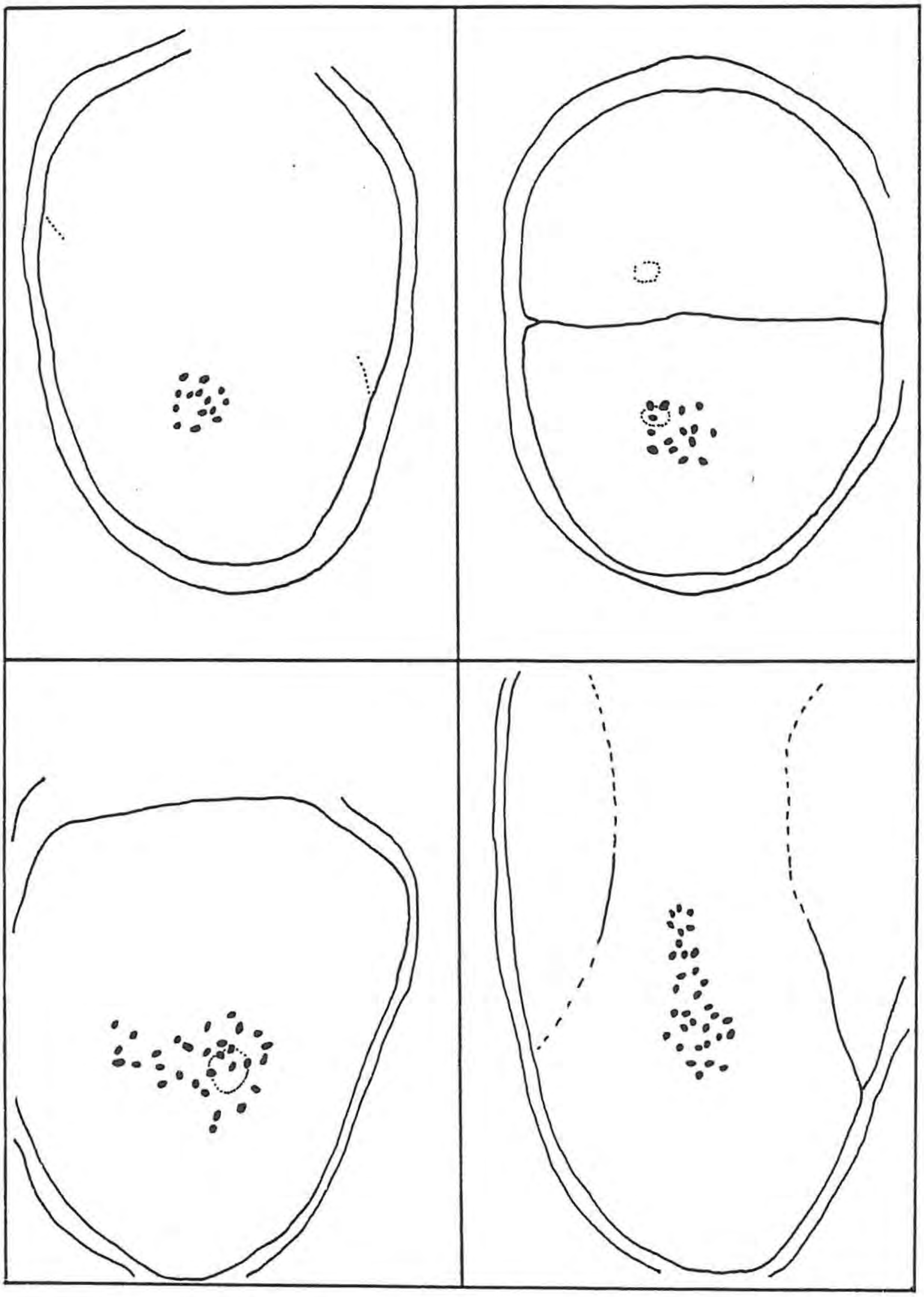

Fig. 4.7   Map of chromosomes seen in Fig. 4.6

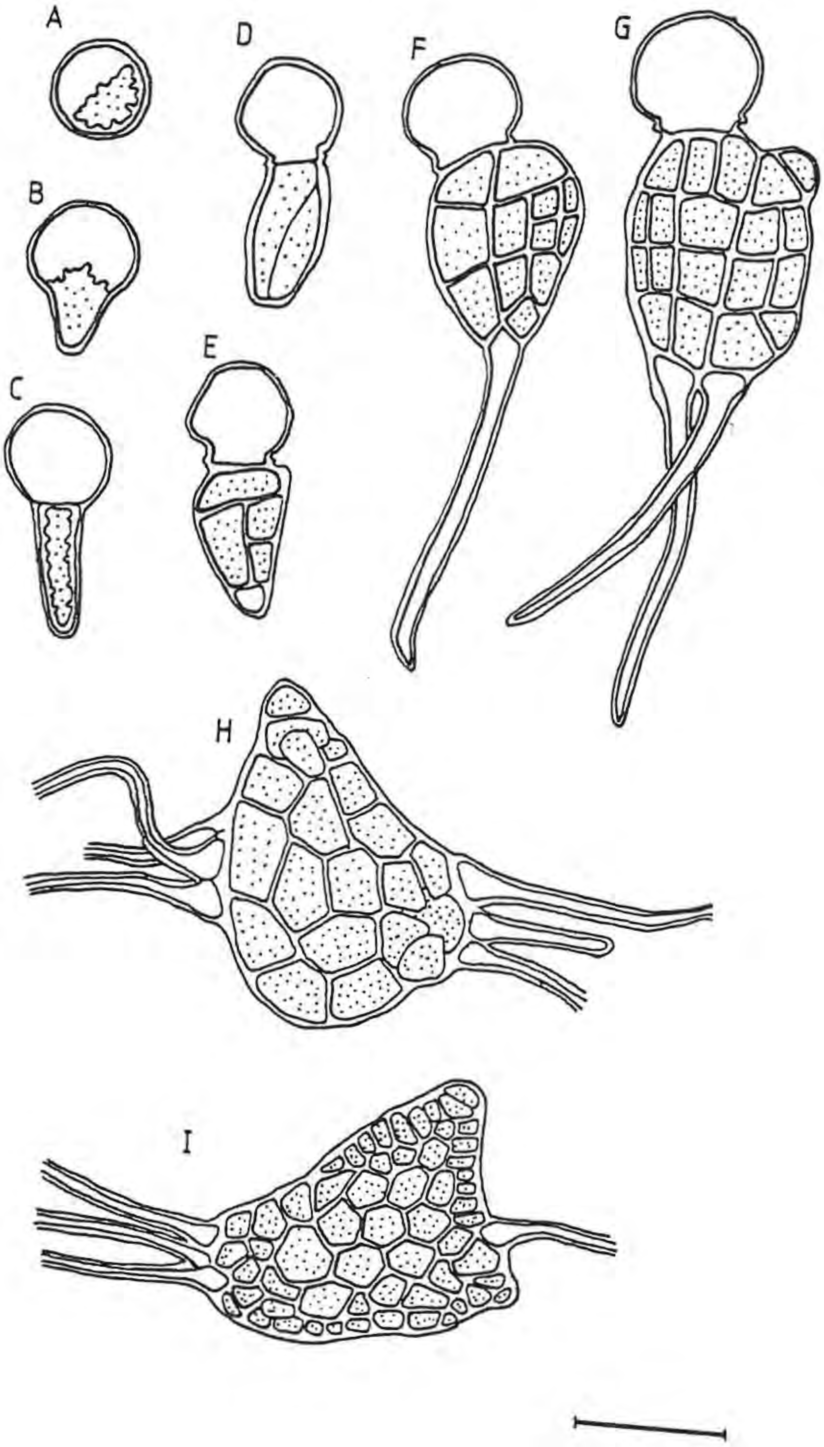

Fig. 4.8 Stages of spore germination (A-G), and early cortication (H & I) in G.pristoides. Scale = 50 mm.

Figure 4.8. Just prior to spore germination, binucleate bispores and uninucleate carpospores appear to undergo a mitotic nuclear division resulting in tetranucleate bispores (Fig. 4.2 d) and binucleate carpospores (Fig. 4.3 a). However, only one of these nuclei enters the germination tube (Fig. 4.3 b for carpospores; Fig. 4.3 c and d for bispores), and is cut off from the spore capsule and remaining nuclei. Nuclei remaining within the spore capsule continue to divide in synchrony with the divisions in the newly formed germling. As a result, numerous nuclei may be seen within spore capsules after germination.

Results indicate that the germination success of carpospores is significantly greater than for bispores (Table 4.1). Furthermore, there is some indication that among bispores, the larger representatives germinate more readily than those smaller in size (Fig. 4.9).

4.3.4 Culture experiments.

Although there was no significant difference in the growth rate between carpospore germlings (bisporophyte) and bispore germlings (gametophyte), growth showed marked variation with temperature treatment. There was no growth at 8 and 30°C, while maximum growth occurred at 23°C (Fig. 4.10). Good germling growth was also recorded at 15 and 19°C. Figure 4.2 f shows a carpospore germling after 6 days in culture at a temperature of 23°C. Germlings maintained in culture for longer than a month failed to develop into plants resembling those found in nature, which have flattened upright fronds. The cultured plants persisted as terete horizontally creeping axes (Fig. 4.2 g). (As a result, mature plants were not produced under

TABLE 4.1

Percentage germination success of carpospores and bispores of <u>G.pristoides</u>. The standard deviation is given for the mean percentage germination of each spore type.

SPORE TYPE	% GERMINATION	NO. SPORES	MEAN % GERMINATION
BISPORE	11.4	3053	10.9 ± 3.5
	5.4	2013	
	14.9	2836	
	11.9	1633	
CARPOSPORE	31.5	1537	29.7 ± 8.4
	35.4	1365	
	15.4	2870	
	36.6	1950	

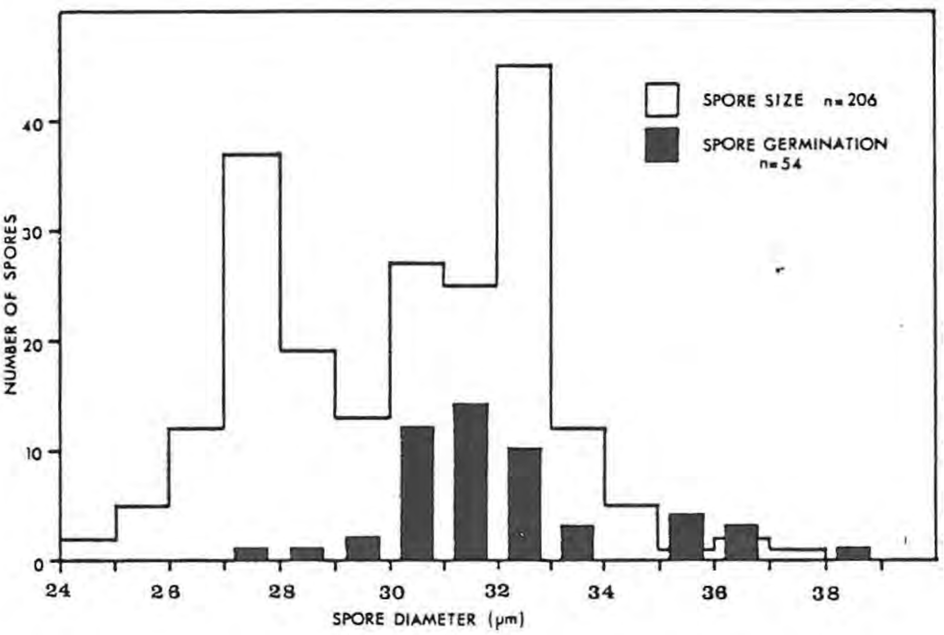

Fig. 4.9 Bispore size distribution and germination success based on measurements of evacuated spore capsules.

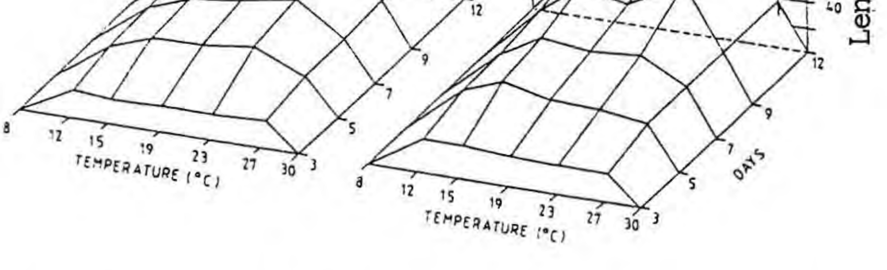

Fig. 4.10 Growth of bispore germlings (A) and carpospore germlings (B) of G.pristoides in response to temperature treatment. Bars = SE.

the culture conditions described here.) Cultures were not maintained for longer than about four months.

4.3.5 Reproductive phenology and spore release.

Since G.pristoides plants smaller than about 30 mm rarely possess reproductive organs (Chapter 3), only plants larger than this were considered to be mature or potentially reproductive. Throughout the year at Sharks Bay, bisporophytic and male and female gametophytic plants were present in proportions that showed no apparent seasonal fluctuations (Fig. 4.11). Furthermore, all plants examined (greater than 30 mm in height) possessed reproductive structures, i.e. none were sterile at any time of the year. There was also no apparent seasonal fluctuation in spores released by either bisporic or cystocarpic plants (Fig. 4.12), while routine culturing of bispores and carpospores indicated that they are viable throughout the year.

Within the G.pristoides population at Sharks Bay, the bisporophytic generation dominates the combined gametophytic generations by a ratio of about 3:1 (Fig. 4.11). Similar ratios were observed in the populations sampled at Kenton-on-Sea, Cape St. Francis and Dalebrook (Table 4.2). During the spore release experiments, carpospore release always exceeded that of bispores (although the difference was not always significant) (Fig. 4.12), sometimes by up to 20% (mean = 10.6%).

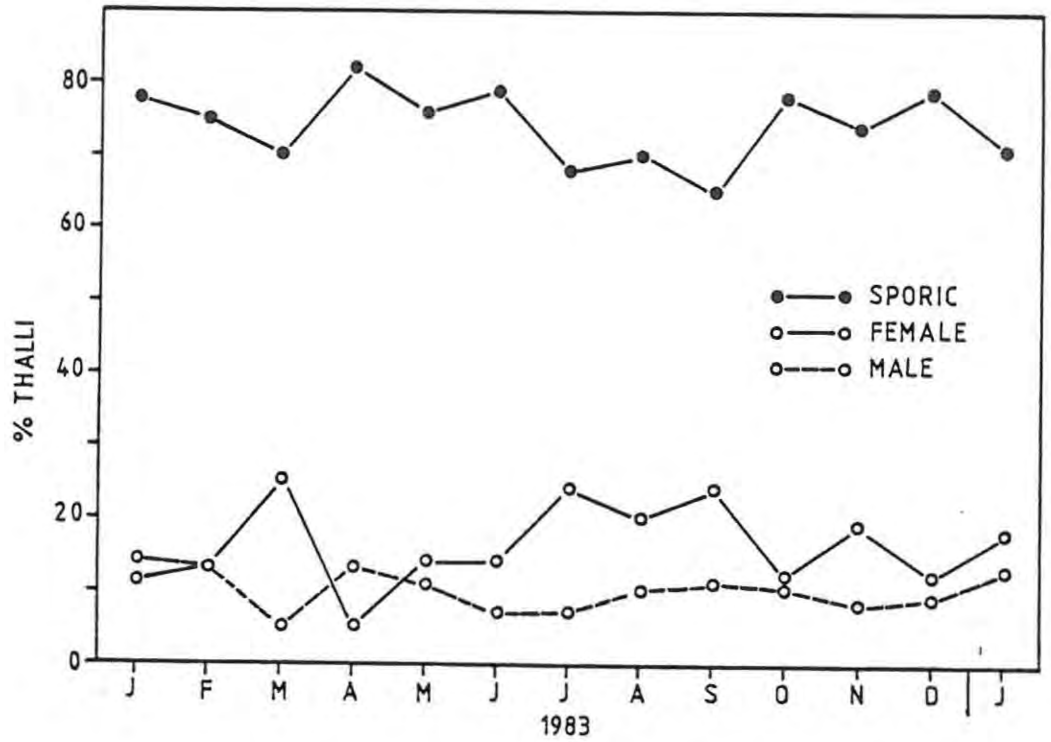

Fig. 4.11 Seasonal proportions of male, female and bisporophytic G.pristoides plants at Sharks Bay, Port Alfred.

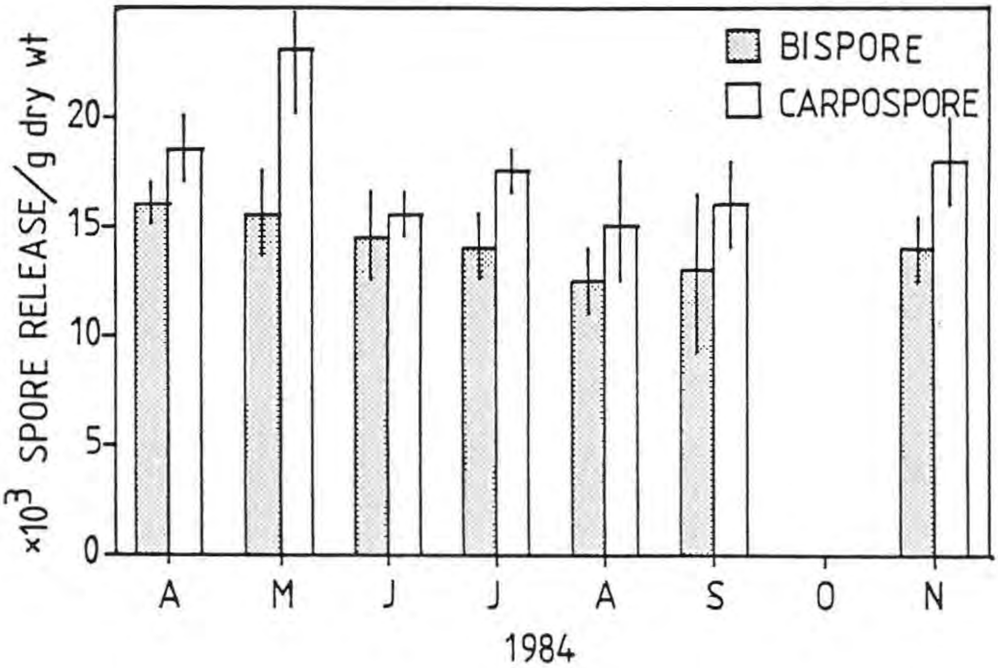

Fig. 4.12 Seasonal bispore and carpospore release. Bars = SE.

TABLE 4.2

Percentage occurrence of male, female and bisporic <u>G.pristoides</u> plants at various geographical localities.

LOCALITY	MALE (%)	FEMALE (%)	BISPORIC (%)	SAMPLE SIZE
SHARKS BAY	8.9	16.6	74.5	600
KENTON-ON-SEA	6.6	16.5	76.7	50
CAPE ST. FRANCIS	12.2	14.1	73.7	50
DALEBROOK	13.3	17.8	71.1	50

4.4 DISCUSSION

4.4.1 Reproductive morphology and cytology.

The reproductive morphology of the female gametophytic and bisporophytic life history stages of G.pristoides collected at Port Alfred, is similar to that described by Fan (1961) for material collected at St. James on the Cape Peninsula. Male plants have not previously been reported. This may be due to the inconspicuous nature of male reproductive organs, thus having been confused with vegetative plants. However, the male reproductive structures presently seen in G.pristoides appear to be identical to those described for other Gelidium species (Dixon 1959, Fan 1961).

This is the first attempt to culture G.pristoides from spores. The pattern of germination is similar for both carpospores and bispores and is typical of the Gelidiales, where the spore contents are evacuated into a germ tube leaving an empty spore cell wall (Chihara and Kamura 1963, Guzmán del Proó et al. 1972, Bold and Wynne 1978).

Although Fan (1961), reported the presence of tetranucleate bisporangia in G.pristoides, the present study has shown that in addition to binucleate bispores, mononucleate and tetranucleate bispores are also produced by the bisporophyte generation (but at much lower frequencies). Since both additional spore types show a similar size range to the typical binucleate type, it is likely that they too are the products of a single cytoplasmic cleavage of the sporangium mother cell (i.e. they are also types of bispore).

Sporangia with two spores have been widely reported in the Corallinaceae (particularly the crustose species) and in other members of the Florideophyceae (Guiry 1978), including *Rhodochorton purpureum* (Lightf.) Rosen. (Knaggs 1967) and *Suhria vittata* (L.) J.Ag. (Fan 1961). However, there appear to be only two published accounts (both in corallines) where the mode of bispore formation has been positively identified. Suneson (1950) showed that the binucleate bispores of *Dermatolithon corallinae* (Crouan frat.) Foslie are the product of normal meiosis, while Chamberlain (1977) demonstrated that the mononucleate bispores of *Fosliella farinosa* (Lamour.) Howe are apomeiotically derived. Based on these and other observations, Guiry (1978) suggested that the binucleate bispores of *G.pristoides* and *S.vittata* (also Gelidiaeceae) are probably homologous with the meiotically produced tetraspores seen in other red algal species.

More recently, Goff (1981) reported a difference in nuclear size between mononucleate and binucleate bispores in *Gardneriella tuberifera* Kylin (Gigartinales) and suggested that this may reflect ploidy differences. If this criterion were to be used as an indication of ploidy level in *G.pristoides*, the smaller nuclei of the binucleate and tetranucleate bispores, in comparison to those in carpospores, would suggest that they are the products of reduction divisions (meiospores). The fact that sexual plants are present in natural populations would also tend to indicate that meiosis is normal in *G.pristoides*. This was confirmed by subsequent chromosome counts, where germlings that were derived from bispores had half the number of chromosomes (n = 13-17) than germlings derived from carpospores ($2n$= 28-33), implying that reduction division occurs during bispore formation. The binucleate bispores of G.pristoides (and probably S.vittata as well) are, therefore, homologous to the tetraspores produced by most other members of the genus.

It is not known whether mononucleate bispores are apomeiotically produced. However, their extreme scarcity would suggest that their origin is accidental and that they are not important in the life history of G.pristoides. The tetranucleate state of some bispores is probably the result of a mitotic nuclear division following normal meiosis, and is perhaps a prerequisite for successful germination. This would account for the binucleate state seen in some carpospores. In both instances, whether a binucleate carpospore or tetranucleate bispore, only one nucleus enters the germ tube.

The bispores of G.pristoides also show a wide range of sizes (due to uneven cleavages of the bisporangium mother cell), which are generally larger than the tetraspores produced by the subtidal gelidiaceous species, G.amansii (Fig. 4.13). Furthermore, there is some indication that the larger bispores germinate more readily than the smaller ones. Van der Meer (1977) suggested that larger spores are perhaps better able to survive under certain environmental conditions, while Okuda and Neushul (1981) went a step further to suggest that some species might produce larger spores that are better able to survive in habitats that are only intermittently suitable for germling growth. Since bispores in G.pristoides are probably larger than tetraspores would have been, perhaps bisporophytic plants producing larger bispores achieved greater success in the intertidal habitat, and were therefore selected over plants producing smaller tetraspores.

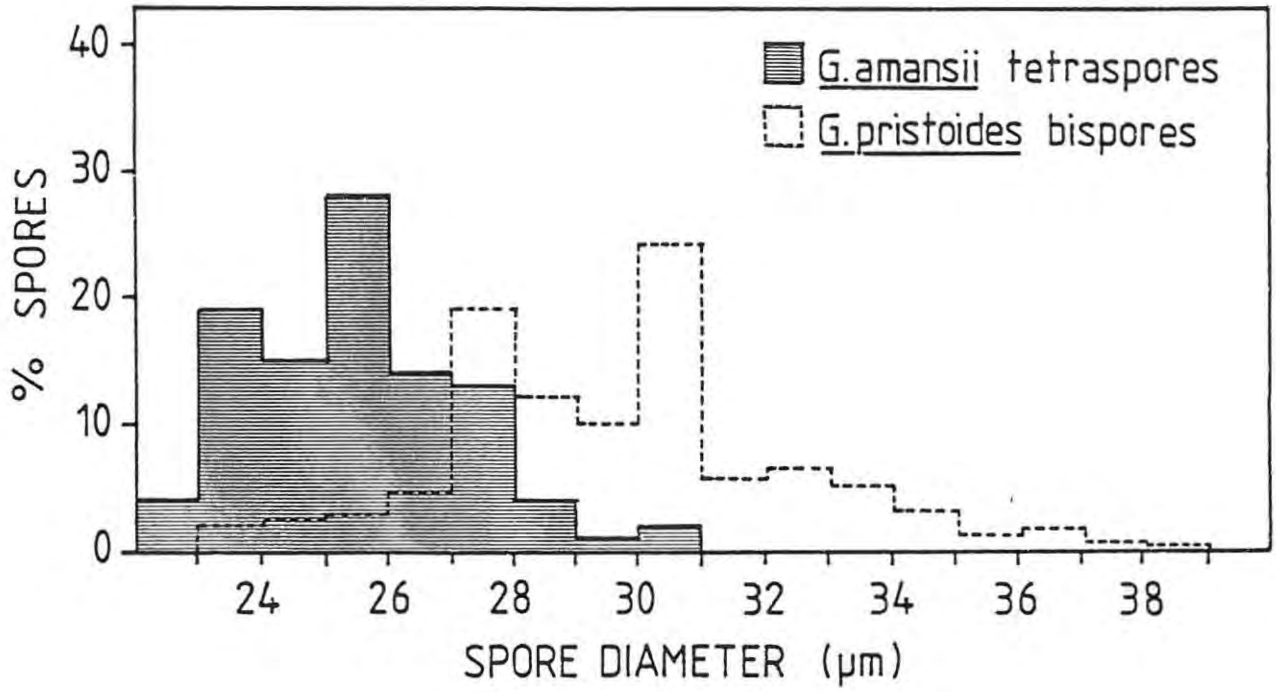

Fig. 4.13 Comparative size ranges of tetraspores from Gelidium amansii and bispores from G.pristoides.

There appears to be some discrepancy regarding chromosome numbers previously reported for Gelidium species. The numbers reported by Dixon (1954) for G.latifolium (Grev.) Born. et Thur. and G.corneum (in both: n = 4-5; 2n = 9-10) are very much lower than were reported for G.latifolium var. luxurians (n or 2n = 25-30, Magne 1964). Is such a disparity likely to occur within the same genus, let alone in closely related species as above? Hommersand (pers. comm.) believes that exceedingly high counts may be due to single chromosomes appearing as two or more individuals under a microscope as a result of chromosome tortions. However, even bearing this possibility in mind, I believe that the numbers recorded here are a true indication of the situation in G.pristoides (n = 13-17, 2n = 28-33). Since these are in accord with the results of Magne, the results of Dixon (1954) remain difficult to explain.

4.4.2 Growth of germlings in culture.

Culture experiments showed that the optimum temperature for the growth of G.pristoides germlings is between 15 and 23°C (maximum growth occurring at 23°C). While similar growth optima have been reported for other economic red algae (Burns and Mathieson 1972 a, Braud and Delépine 1980, Fralick and Andrade 1981), Fralick and Mathieson (1975) showed that four Polysiphonia species could be separated into two distinct categories based on natural distributions and temperature optima. Cold water species exhibited active photosynthesis at temperatures as low as 5°C, while species with warm water affinities showed little or no photosynthetic activity below 10°C. In addition, Mshigeni (1976 b) showed that the slow growth of the carposporelings of two Hypnea species at 20°C, agreed with their primarily tropical geographical distribution. He suggested that their absence in higher latitudinal regions, might reflect the inability of their spores to develop at colder temperatures. Although Anderson and Bolton (1985) showed that optimum temperatures for growth in S.vittata were higher than the temperatures recorded in its natural environment, growth optima shown by G.pristoides germlings correspond well with sea temperatures experienced over its geographical range. The species is most abundant in the eastern Cape Province where temperatures range between 14 and 22°C (Heydorn and Grindley 1982), whereas its distribution limits on the west coast of the Cape Peninsula, and towards Natal on the east coast of South Africa, are characterised by temperatures less than 10°C and exceeding 27°C, respectively (Heydorn and Tinley 1980). G.pristoides plants at Dalebrook on the Cape Peninsula are significantly smaller than at Port Alfred (see Chapter 3), possibly as a result of reduced growth in response to lower sea temperature at the former site.

It has been suggested that the culturing of seaweed spores in the laboratory for subsequent transplantation to the field, might be a possible means for increasing the production of economically important seaweeds (Krishnamurthy 1965). In the case of G.pristoides this could perhaps be done by seeding rope nets and attaching them in the rocky intertidal zone. At the present time (due to the abundance of natural populations) mariculture of this species is not economically feasible, but before it could be considered, effects of other factors such as nutrients, illumination etc. on the growth in culture of G.pristoides, would have to be examined. Furthermore, no success has yet been achieved in raising sporelings of any member of the Gelidiales to maturity in culture (Chihara and Kamura 1963, West and Hommersand 1981). The present study proved no exception. Therefore, further study is required in order to determine the culture conditions in which mature G.pristoides plants may be obtained.

4.4.3 Bisporophyte dominance.

The presence of vegetatively morphologically similar bisporophytic and gametophytic generations, in addition to normal meiosis occurring during bispore formation, indicates that G.pristoides possesses a typical Polysiphonia-type life history. Under normal circumstances one would expect the two generations to be present in similar proportions (Hoyle 1978 a, Kain 1982). However, it is evident that in G.pristoides these life history stages are disproportionately represented, where the bisporophyte generation is dominant over the combined gametophyte generation by a ratio of about 3:1. A similar degree of imbalance persists throughout the geographical range of the species, thus imlying that bisporophyte dominance in G.pristoides is biologically determined.

The most obvious explanation for bisporophyte dominance in G.pristoides would be that the prediction for equal proportions is based on the assumption that tetraspores are the product of meiosis in the sporophyte generation, as in most Florideophyceae. Since bispores are produced in G.pristoides (therefore, half as many spores than tetrasporophytes), one might then expect some disparity in the proportions of bisporophytic and gametophytic plants in natural populations. Results show that more carpospores than bispores are shed in G.pristoides. This difference (about 10%), however, would not account for the much larger disparity in the generations. Furthermore, in S.vittata, which also produces bispores, all generations are equally represented in natural populations (Anderson and Bolton 1985). Therefore, bispore production is probably not the primary factor causing bisporophyte dominance in G.pristoides.

Dominance of tetrasporophytes has been reported for many red algae (Hansen and Doyle 1976, Mshigeni 1976 a, Rama Rao 1977, Hoyle 1978 a, Kain 1982) including species of Gelidiales (Johnstone and Feeney 1944, Guzmán del Proó and de la Campa de Guzmán 1978, Fralick and Andrade 1981, Montalva and Santelices 1981). Various explanations for this phenomenon have been proposed. Kain (1982) suggested that since the diploid state usually dominates, there might be inherent advantages of diploidy over haploidy with regard to a greater success rate of sporophytic plants in natural populations. Increased vigour of sporophyte germlings might be advantageous to successful recruitment, particularly in an intertidal habitat as seen in G.pristoides. While Anderson and Bolton (1985) showed that bisporophyte germlings of S.vittata grow at a 25% faster rate than gametophytes, the situation in G.pristoides is similar to that described for two Hypnea species (Mshigeni 1976 b), where the growth response of sporophytic and gametophytic germlings is very much the same under a wide range of culture conditions.

It has also been suggested that a higher percentage of carpospores survive to produce sporophytic plants (Johnstone and Feeney 1944, Hansen and Doyle 1976, Hoyle 1978 a, Kain 1982). Present results showed a 60% greater germination success rate in carpospores than bispores of G.pristoides.

Although ultrastructural studies have revealed the exclusive presence of fibrilar vesicles in carpospores of G.pristoides (Young 1984) their significance is unknown, and, the reason for greater carpospore germination success still remains unclear, and should receive further attention.

4.4.4 Phenology.

Results show that G.pristoides is fertile throughout the year at Port Alfred. However, Kain (1986) suggested that seasonal growth patterns may induce seasonality in reproductive activity. This is supported by the results of Guzmán del Proó et al. (1972), showing maximal spore expulsion in Gelidium robustum (Gardn.) Hollenb. et Abb. corresponding with increased growth during the Mexican summer. Spore release in G.pristoides, however, showed no obvious seasonal trend even though growth rates show clear seasonality. Carpospores and bispores also appear to be viable throughout the year.

Kain (1982) also suggested that seasonality in reproduction may be related to the geographical distribution of a species, becoming more marked towards distribution limits. Conditions at Port Alfred are probably suitable for all-year-round reproductive activity in G.pristoides since it is near the centre of the geographical range of the species. Although seasonality in reproductive activity was not monitored at the extreme limits of its range, more recent observations indicate that G.pristoides is also fertile throughout the year at Dalebrook in the Cape. Therefore, it is probable that seasonality in reproductive activity in G.pristoides is minimal, if not entirely lacking, throughout its relatively short geographical range, and therefore, need not be considered in the timing of harvesting of natural populations.

CHAPTER 5

Seasonal growth and agar contents in Gelidium pristoides*.

5.1 INTRODUCTION

Two important considerations when formulating a rational management policy for a seaweed resource such as G.pristoides are; the time of the year when plant productivity (growth), and the levels of the sought-after economic product (e.g. agar), are maximal. This information would assist both in the optimal utilization and conservation of the natural resource.

Seasonal growth patterns and product levels have been reported for a wide range of economic red algae in other parts of the world (as referenced in the discussion). However, there is a dearth of useful published information on South African species including G.pristoides. Although there are some early reports on the agar contents of several South African algae (Isaac 1942, Isaac et al. 1943, Fox and Stephens 1943, Isaac and Molteno 1953), including G.pristoides, this information is of limited practical value since the authors do not provide quantitative data nor do they examine possible seasonal fluctuations in agar contents.

In the present study of a natural G.pristoides population at Port Alfred, seasonal growth (linear frond elongation rate), agar contents and other

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*Part of this chapter has previously been published by Carter and Anderson (1986).

related parameters including standing crops, thallus nitrogen, dry weights and ash levels, were monitored over a two year period. In addition, agar contents and biomass yields were compared between distal and proximal halves of plant tufts in order to determine whether either of these portions should be selected by commercial harvesters.

5.2 MATERIALS AND METHODS

All experimental studies were conducted, and plant collections taken at Sharks Bay, Port Alfred, from March 1983 to April 1985.

5.2.1 Linear frond growth.

Growth of individually tagged fronds was measured in terms of linear elongation. Numbered "Dymo" tags were attached near the tips of actively growing fronds using 2 kg fishing nylon which was sewn through the midrib of the frond (Fig. 5.1). Since growth in G.pristoides is apical, elongation rates were measured as the increase in distance from the point of attachment of the tag to the frond apex, and were expressed as mm/day. Initially, 40 fronds were tagged, but due to losses, additional fronds were tagged every month to maintain a sample size of 15-25 fronds. Some fronds were tagged twice along the same axis in order to determine whether any intercalary elongation occurred. Percentage tag losses were also calculated for every month from March 1983 to December 1984.

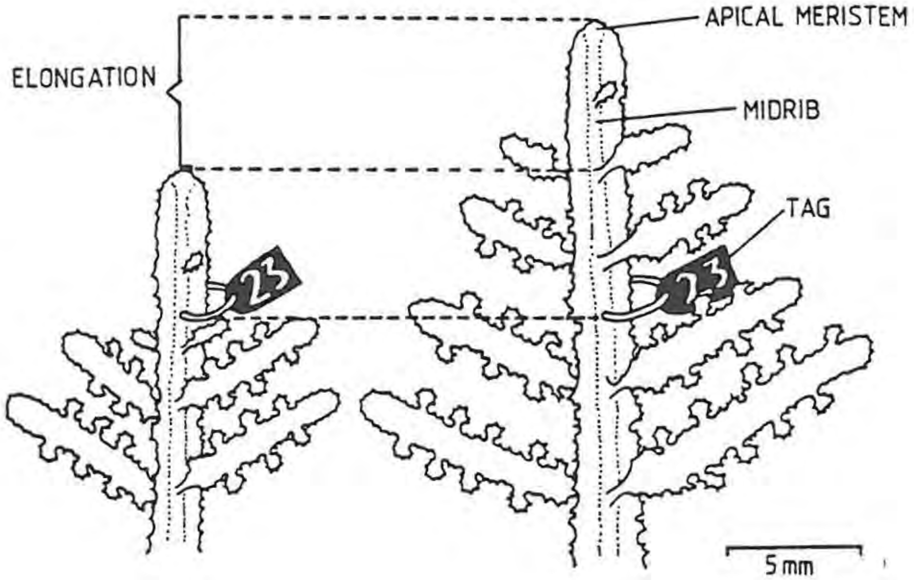

Fig. 5.1 Method of tagging G.pristoides fronds for determining seasonal elongation.

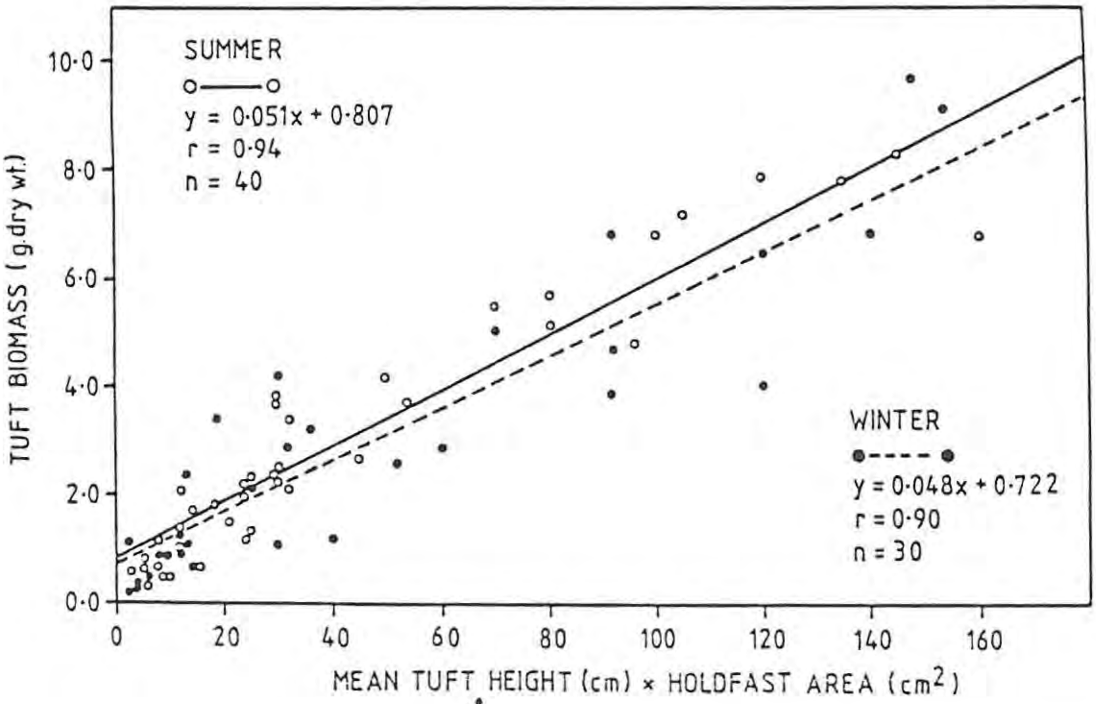

Fig. 5.2 Enumerations used for estimating seasonal standing crops of G.pristoides.

5.2.2 Standing crops.

Estimations of the biomass of individual G.pristoides tufts were made from a summer (February 1983, n = 40 tufts) and a winter (July 1984, n = 30 tufts) enumeration of biomass (g dry wt) and the product of mean tuft height and holdfast area (cm.cm^2). The mean height of each tuft was determined from five random measurements, and the holdfast area was measured by encircling the base of the tuft with wire, then placing the shaped wire over a calibrated grid. Individual tufts were then removed and dried to constant weight at 70°C.

Seasonal standing crop levels are based on extrapolations of biomass values from the above two relationships (Fig. 5.2), by measuring the size changes (tuft height and holdfast area) of 26 individual tufts distributed within seven 0.075 m^2 permanent quadrats. Biomass values from the months October to March, and April to September, were extrapolated from the summer and winter enumerations, respectively. Standing crop levels are expressed as grams dry weight of G.pristoides per square metre of substratum area (g dry wt/m^2).

5.2.3 Agar content.

Agar contents were determined monthly as follows: 10 g of oven dried plant material, obtained by mixing at least 20 randomly collected plant tufts, were added to 400 ml of boiling distilled water. The solution was maintained at boiling point and evaporated water replaced, for 1 hour. The hot suspension was then centrifuged at 2 000 rpm for 20 minutes. The supernatant was poured off and the pelleted material re-extracted as above. The supernatants were frozen overnight then thawed in tap water. The agar flock was removed by filtering through fine muslin cloth and then dried at 70°C to constant weight. Agar content is expressed as a percentage of dried seaweed weight. Extractions were conducted in triplicate.

The above method was also used for comparing the agar contents of proximal and distal plant portions. Entire plant tufts were randomly collected at 2-3 month intervals throughout 1984 and separated into distal (upper) and proximal (lower) halves with shears. Extractions were conducted in duplicate. The plant biomass (g dry wt) yielded from distal and proximal halves was determined from samples collected in summer (February 1984) and winter (July 1984) and the ratio of distal/proximal biomass yield was determined for each sample.

5.2.4 Thallus nitrogen.

The Micro-Kjeldahl method described by Hasses (1971), involving titration against a boric acid indicator after extraction of 100 mg samples of dried seaweed sample using sulphuric acid, was used to determine seasonal thallus nitrogen levels. Determinations were conducted in triplicate on homogeneous seaweed powder (dried to constant weight at 70°C) obtained from milling at least 20 plants per month collected from the study site. Thallus nitrogen levels are expressed as a percentage of dried seaweed weight.

5.2.5 Dry weights.

Twenty entire G.pristoides tufts were selected at random from a larger monthly collection. Plants were washed in tap water to remove sand and other debris, shaken vigorously and blotted on newsprint to remove excess water, weighed, dried to constant weight at 70°C, and then reweighed. Dry weight is expressed as a percentage of wet weight.

5.2.6 Ash.

Monthly ash levels were determined by heating 2.0 g of dried homogeneous powdered seaweed in a muffle oven at 500°C for 24 hours. Five replicates were analysed from a combined monthly seaweed sample. Ash levels are expressed as a percentage of dried seaweed sample.

5.2.7 Correlation analysis.

The correlation coefficient (r) was determined between seasonal variations of: frond elongation rate, agar content, thallus nitrogen, dry weight and ash levels (Table 6.1).

5.3 RESULTS

5.3.1 Seasonal growth

Rates of elongation of tagged G.pristoides fronds varied with season (Fig. 5.3). Highest values were recorded during mid to late summer

TABLE 5.1

Correlation coefficients (r) between seasonal growth and various physiological parameters in G.pristoides. Significant correlations are marked ** if significant at the 1% level ($P < 0,01$), and * if significant at the 5% level ($P < 0,05$). All other combinations were not significant ($P > 0,05$) (d.f = 24).

	GROWTH	% AGAR	% NITROGEN	% DRY WT	% ASH
GROWTH					
% AGAR	0.36				
% NITROGEN	-0.12	-0.23			
DRY WT	-0.48*	0.17	0.26		
ASH	0.27	-0.42*	-0.11	-0.58**	

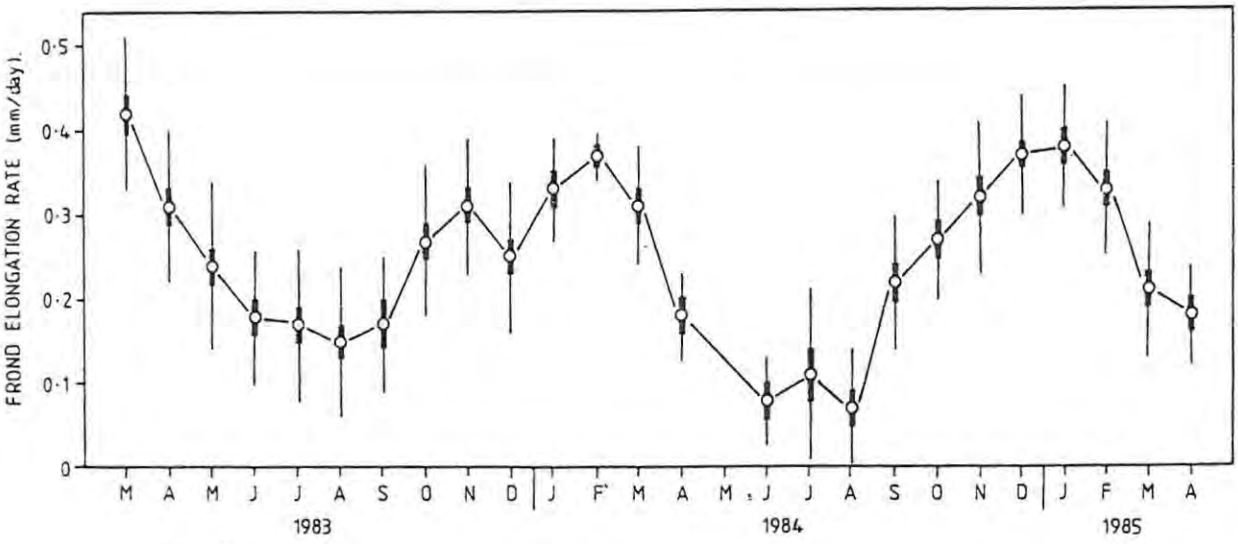

Fig. 5.3 Seasonal frond elongation rates of G.pristoides at Sharks Bay, Port Alfred. Thin bars = SD, thick bars = SE.

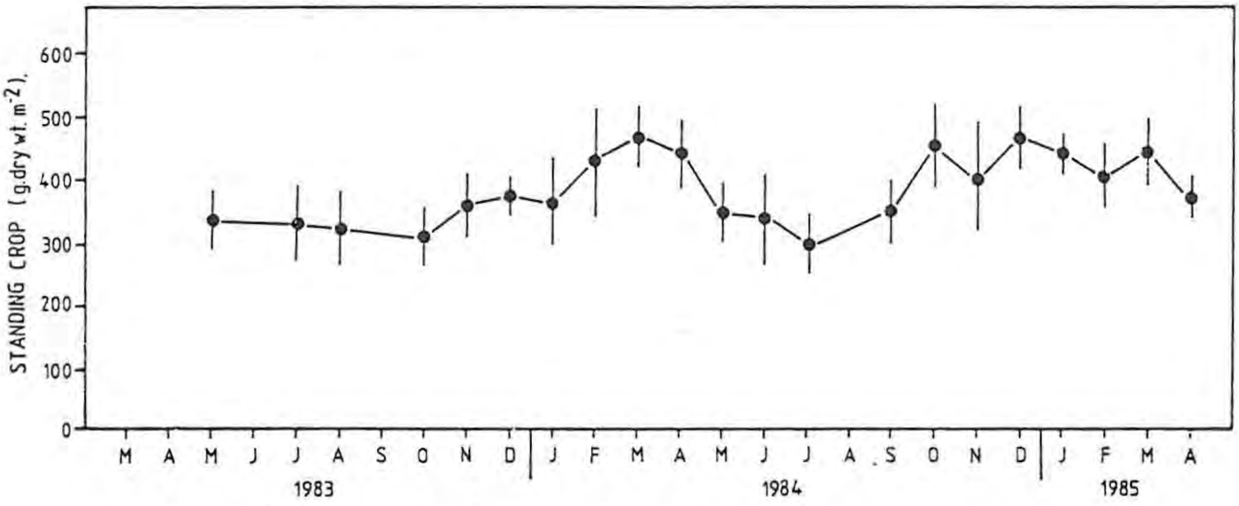

Fig. 5.4 Seasonal standing crops of G.pristoides at Sharks Bay, Port Alfred. Bars = SE.

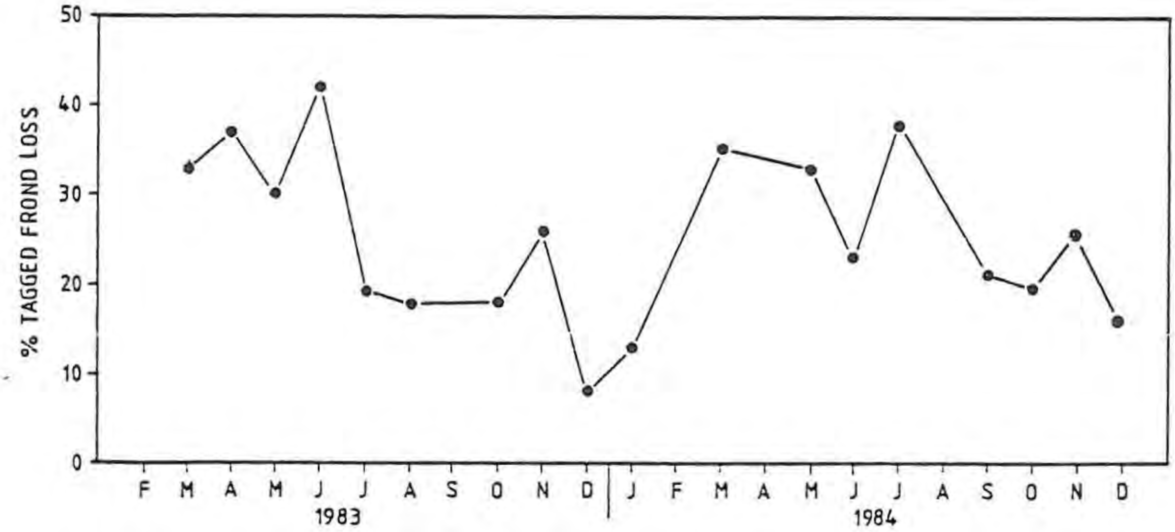

Fig. 5.5 Seasonal percentage loss of tagged G.pristoides fronds at Sharks Bay, Port Alfred. Monthly sample sizes ranged from about 20-30 fronds.

(0.42 mm/day in March 1983; 0.38 mm/day in February 1984; 0.37 mm/day in January 1985) and the lowest values during winter (0.15 mm/day in August 1983; 0.07 mm/day in August 1984). The total frond elongation for the period March 1983 to February 1984 was 90.3 mm, and for the period March 1984 to February 1985, 83.7 mm. No intercalary elongation was recorded.

The summer and winter enumerations of biomass and tuft size (mean tuft height x holdfast area) varied slightly, with greater biomass levels being recorded during summer (Fig. 5.2). Due to the consistancy of the relationships, they were considered to be an accurate means of estimating tuft biomass, therefore suitable for determining seasonal standing crop levels.

Standing crop levels showed significant seasonal variation (Fig. 5.4) which was mainly due to changes in mean tuft height. Maximum values during late summer and early autumn coincided with increased frond elongation rates and prolific branching (see Fig. 3.8 a and b, Chapter 3). Reduced standing crop levels during autumn and winter corresponded to a reduction in frond elongation rates and the sloughing-off of branches (Fig. 3.8 c and d).

There was also a tendency for a greater loss of tagged fronds during winter (Fig. 5.5).

5.3.2 Seasonal agar content and thallus nitrogen levels.

Both agar content and thallus nitrogen levels varied seasonally (Fig. 5.6), and were generally inversely related, although not significantly

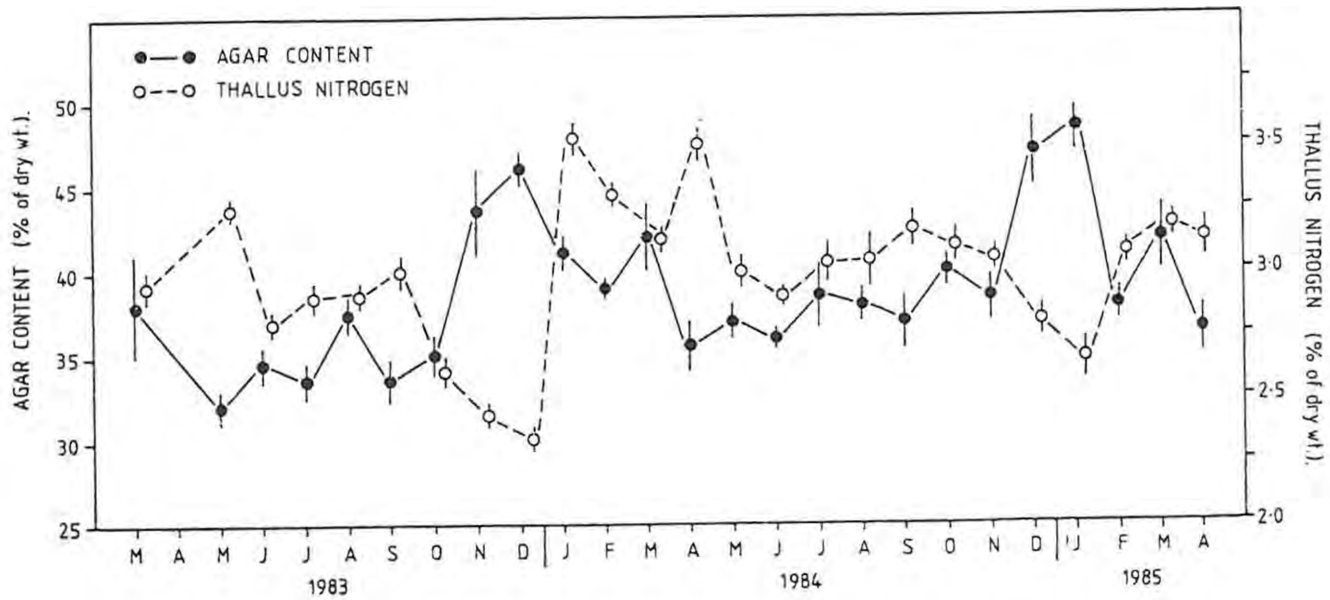

Fig. 5.6 Seasonal agar contents and thallus nitrogen levels of G.pristoides at Sharks Bay, Port Alfred. Bars = SD.

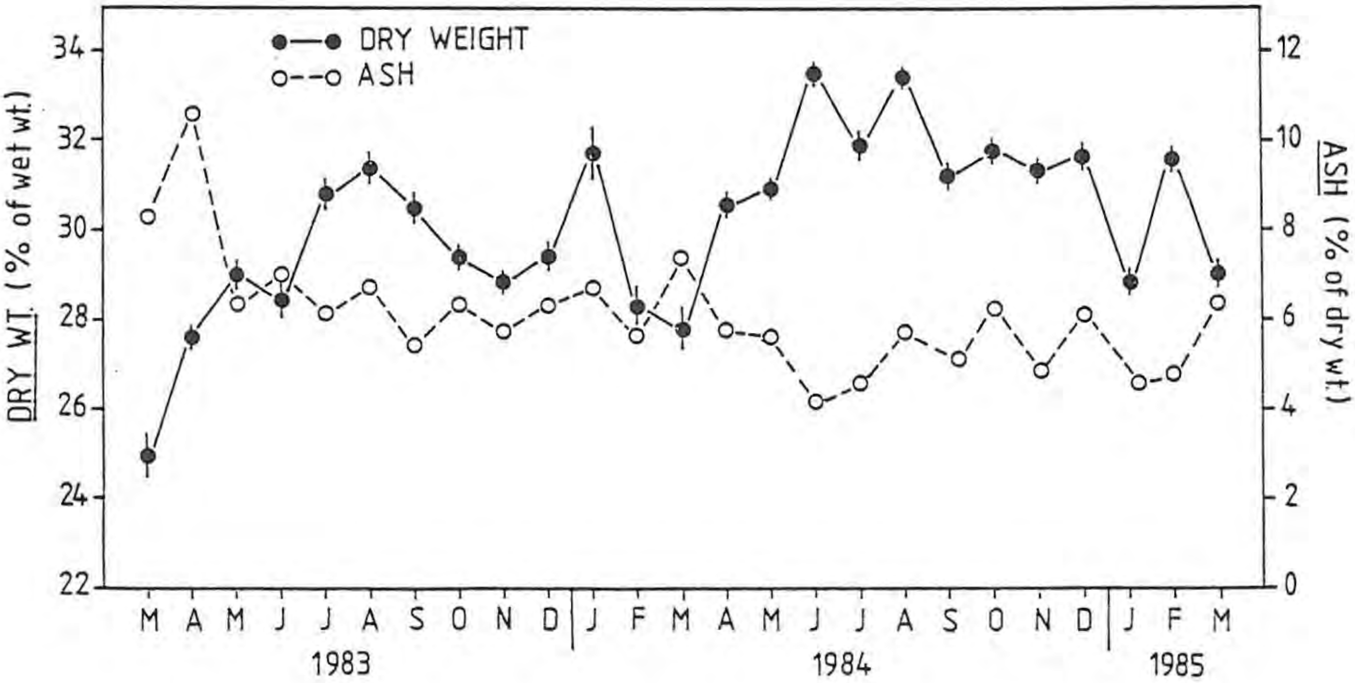

Fig. 5.7 Seasonal dry weight and ash levels of G.pristoides at Sharks Bay, Port Alfred. Bars = SE.

(Table 5.1). High agar contents in summer corresponded to a decline in thallus nitrogen levels. Throughout the entire study period, agar contents ranged from 30% (April 1983) to 48% (January 1985) (Table 5.2). Thallus nitrogen levels ranged from 2.3 to 3.5%. Agar contents were also significantly inversely related to ash levels ($r = -0.42$, $P < 0{,}05$).

5.3.3 Seasonal dry weight and ash levels.

Both dry weight and ash levels showed seasonal variation (Fig. 5.7), and were significantly inversely related ($r = -0.58$, $P < 0{,}01$). Dry weight was also significantly inversely related to frond elongation rate ($r = -0.48$, $P < 0{,}05$). It is interesting also to note that an inexplicable drop in growth during the month of December 1983, corresponded to a sharp drop in thallus nitrogen and was followed by a sharp peak in dry weight level.

5.3.4 Agar contents in distal and proximal plant portions.

Agar contents were between 8 and 15% higher in distal than in proximal plant halves throughout 1984 (Fig. 5.8). Ratios of the biomass of distal to proximal plant halves were 2.8 during summer (February) and 2.1 during winter (July). Therefore, absolute yields of agar from distal plant halves would be very much greater (approximately three times) than those from proximal plant halves, per unit weight of whole plant tuft.

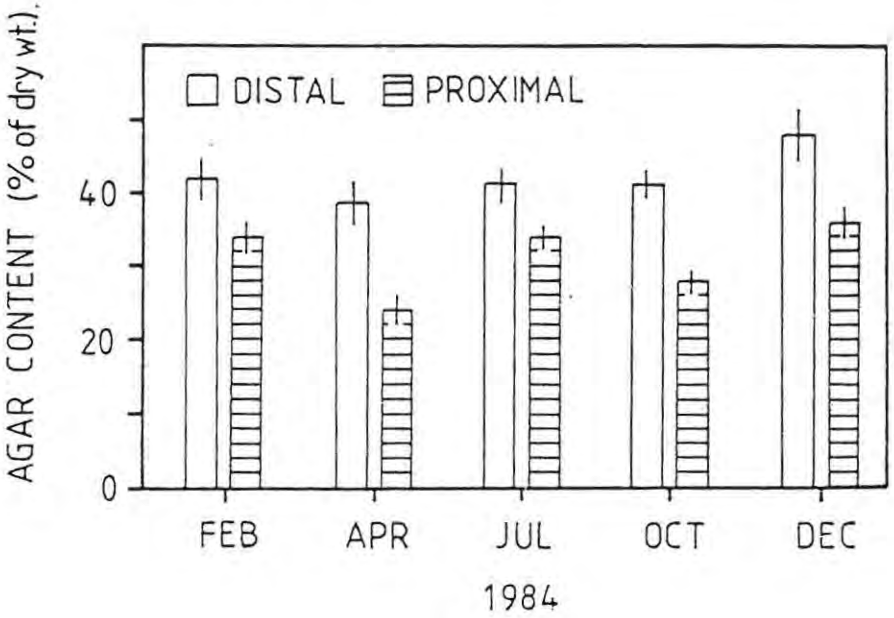

Fig. 5.8 Agar contents of distal (upper) and proximal (lower) plant halves during 1984. Bars = SD.

5.4 DISCUSSION

The annual frond elongation rates of 90.3 mm and 83.8 mm recorded for G.pristoides at Port Alfred, are very similar to the value of 90.0 mm reported for the morphologically similar Gelidium robustum (Gardn.) Hollenb. et Abb. in California (Barilotti and Silverthorne 1972). Frond elongation rates showed clear seasonality with maximum rates during the summer season corresponding to increased standing crops.

The slight variation in the two enumerations used for estimating seasonal standing crops may also reflect seasonal growth in G.pristoides. The greater plant biomass relative to plant size (tuft height x holdfast area) for the summer enumeration probably reflects increased branch density during the summer season. Guzmán del Proó and de la Campa de Guzmán (1978) showed a seasonal variation in enumerations of fresh weight and main axis length for G.robustum in Mexico, and which closely correlated with seasonal growth rates.

Similar seasonal patterns of growth to G.pristoides, with higher values recorded summer, have been reported for other economically important red algae (Barilotti and Silverthorne 1972, Guzmán del Proó and de la Campa de Guzmán 1978, Thomas et al. 1978). Peak summer growth has been correlated with increased solar radiation and day length (Bidwell et al. 1984, Saunders and Lindsay 1978, Whyte et al. 1981), and with increased sea temperatures (Mathieson and Burns 1971, Fralick and Andrade 1981).

Growth rates have also previously been correlated with nutrients available to natural seaweed populations (Rosenberg and Ramus 1982, Dawes et al. 1974 a), while nitrogen enrichment has been reported to enhance the growth of numerous red algae in culture (Neish et al. 1977, De Boer 1978, De Boer et al. 1978, Dawes et al. 1984). However, in the absence of nutrient data for the eastern Cape, the relative importance of seasonal factors such as total daily irradiance and temperatures, and nutrient availability in determining the growth rates of G.pristoides, is unclear.

Seasonal dry weight and ash levels were significantly inversely related, while dry weights also showed a significant inverse relationship with frond elongation rates. Increasing and decreasing dry weights corresponded to periods of minimum and maximum growth, respectively, an observation also previously reported for other red algae (Zavodnick 1973, Dawes et al. 1974 b, Neish et al. 1977, Thomas et al. 1978). Dry weight values, being the reciprocal of water content, reflect the cellular condition of plants (possibly the cytoplasmic content of cells). Therefore, low dry weights (or higher water content) during the summer season would imply that plant cells are in good condition. Although both dry weights and ash levels have been used to monitor growth patterns in other seaweeds, dry weights showed a significant inverse relationship with frond growth and clearer seasonal variations in G.pristoides and would therefore appear to be a more reliable means of monitoring growth in this species.

Agar contents in G.pristoides also varied seasonally, with highest values during summer corresponding to maximum growth. A similar correlation has been reported for Gracilaria coronopifolia J. Ag. in Hawaii (Hoyle 1978 b), and Gelidium cartilageneum (L.) Gaill in California (Cooper and

Johnstone 1944), while low agar yields from *Gracilaria dentata* J. Ag. coincided with a reduction in standing crop levels during the Ghanaian wet season (John and Asare 1975). In contrast, inverse relationships between phycocolloid content and growth have been reported in some economic red algae (Dawes *et al.* 1974 b, Fuller and Mathieson 1972, Mathieson and Tveter 1975, Whyte *et al.* 1981), thus suggesting that seasonal fluctuations in growth and phycocolloid content are influenced by different factors in different areas, or different species.

The inverse relationship between agar content and thallus nitrogen levels shown here in *G.pristoides*, is well known for other economic red algae (Dawes *et al.* 1974 b, Mathieson and Tveter 1975, 1976, Hoyle 1978 b, Durako and Dawes 1980, Dawes *et al.* 1984), while there is also good evidence of an inverse relationship between phycocolloid content and nitrogen availability in the surrounding seawater of both species growing *in situ* (Fuller and Mathieson 1972, Mathieson and Tveter 1975, 1976, Hoyle 1978 b, Mathieson *et al.* 1984) and in culture (Neish *et al.* 1977, De Boer 1978).

Fogg (1964) suggests that in algae growing under conditions of nitrogen deficiency, photosynthetic intermediates may be diverted from protein synthesis to other metabolic pathways including that of carbohydrate synthesis. Higher agar contents during the summer season at Port Alfred, may afford *G.pristoides* plants greater protection against more severe irradiation levels and desiccation stress experienced during this season. However, one might speculate that the high demand for nitrogenous compounds during increased summer growth might deplete the thallus nitrogen reserves, and based on Fogg's hypothesis, result in increased agar production. This explanation would account for the unexpected slump in growth during December 1983, which corresponded with a marked decline in thallus nitrogen and a dramatic rise in agar content. Whatever the cause of seasonal fluctuations in the agar content of G.pristoides, the range of yields measured in this species (30-48% of dry wt) compares very favourably with those reported for other agarophytes (Table 5.2), and confirms its value as an economic source of agar.

Since agar content is higher in distal than proximal plant halves, and agar yields relative to the amount of plant biomass in each region are considerably higher from distal halves, it is suggested that commercial harvesters should consider shearing of distal portions of tufts rather than the plucking of whole tufts. Shearing may have two advantages. It would allow for selection of agar-rich distal plant portions, and it would reduce damage to the regenerative holdfast region of G.pristoides tufts.

On the basis of present results, it is suggested that commercial harvesting of G.pristoides should be concentrated during the summer season when plant growth is maximal, and hence regrowth after harvesting will be more rapid, thus allowing more frequent harvesting without having any serious effect on the environment. Furthermore, the tendency for greater agar contents and standing crop levels during the summer season, would imply that maximum returns from the resource (both in terms of agar yield and harvesting effort) may be obtained during this time of the year.

TABLE 5.2

Agar contents (% of dry wt) reported for other economically important agarophytes.

Species	Locality	% Agar	Source
Gracilaria follifera (Forssk.) Børg.	Cape Cod	25–45	De Boer 1978
G. cylindrica Børg	Hawaii	24–40	Doty *et al.* 1983
G. bursapastoris (Gmel.) Silva	Hawaii	16–20	Hoyle 1978b
G. coronopifolia J. Ag.	Hawaii	22–26	Hoyle 1978b
G. dentata J. Ag.	Ghana	15–30	John and Asare 1975
G. verrucosa (Huds.) Papenf.	Chile	17–26	Kim and Hendriquez 1978
G. (*verrucosa* type)	Canada	13–32	Whyte *et al.* 1981
Gelidium cartilagineum (L.) Gaill	California	12–23	Cooper and Johnstone 1944
G. robustum (Gardn.) Hollenb. et Abb.	California	25–30	Silverthorne 1977
G. purpurascens Gardn.	Canada	18	Whyte and Engler 1981
Gelidiella acerosa (Forssk.) Feld. et Hamel	India	20–32	Thomas *et al.* 1978
Gelidium pristoides (Turn.) Kütz.	P. Alfred S. Africa	30–48	Present study

CHAPTER 6

Regrowth and production of Gelidium pristoides after experimental harvesting*.

6.1 INTRODUCTION

G.pristoides has been harvested along the southern and eastern Cape coastlines of South Africa for the past 30 years without any obvious signs of damage to the condition of natural populations. However, with the recent expansion of the local seaweed industry, the demand for agar producing seaweeds, particularly G.pristoides, has greatly increased, with populations such as those at Port Alfred being subjected to harvesting on a much more regular basis. As a result, some concern has been expressed by local authorities regarding the method of plant removal (plucking) and the effects of frequent harvesting on the maintenance of natural stocks and on the general ecology of these rocky shores. In this regard, Beckley (1979, 1982) has indicated that harvesting of G.pristoides could be detrimental to the recruitment of littoral animals which live among its fronds.

Although previous studies of economic red algae in other parts of the world (Marshall et al. 1949, Barilotti and Silverthorne 1972, Burns and Mathieson 1972 b, Mathieson and Burns 1975) have shown that recovery after

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*Parts of this chapter have previously been published by Carter and Anderson (1986) and Carter and Simons (1986) harvesting is usually more rapid during summer than in winter, actual recovery rates and the effects of different harvesting methods may vary considerably between species and geographical localities. Hence the need for an independent study on the G.pristoides population at Port Alfred.

Harvesting experiments were first initiated in 1983 when regrowth after single shearing and plucking treatments were compared at different times of the year, as was recovery after shearing at different elevations on the shore. Subsequently, however, the frequency of harvesting that will sustain the natural resource (Caddy and Fischer 1984), and the effects of repeated harvesting on the regenerative capacity of the seaweed (Santelices et al. 1984) were examined. These later experiments were timed to coincide with the summer season of 1985/86, when plant growth and agar contents are highest (Chapter 5). In addition, because results obtained in the previous chapter also showed that upper distal plant portions produce greater quantities of agar than proximal portions, the respective agar contributions from sheared and plucked plants were compared, since shearing removes distal portions, while plucking removes whole plants from each tuft.

The present chapter is essentially a synthesis of two independent studies, with different methodological approaches. However, both aim to assist in formulating a policy for the best method and season for harvesting.

6.2 MATERIALS AND METHODS

All harvesting experiments were conducted at Sharks Bay, Port Alfred.

The study was done in two phases: May 1983-April 1984, when regrowth at different times of the year, and different elevations on the shore were monitored; October 1985 to April 1986, when regrowth and production capacity were monitored under various harvesting periodicities.

6.2.1 Effects of harvesting method and seasonality on regrowth (1983/84).

Regrowth of G.pristoides was monitored after single shearing and plucking treatments in late autumn (May 1983) and early spring (September 1983). Estimations of regrowth of sheared and plucked tufts in terms of biomass, were extrapolated from two different enumerations of biomass and tuft size.

The enumeration of biomass and the product of mean tuft height and holdfast areas of 45 randomly selected G.pristoides tufts provided estimates of regrowth in terms of biomass after shearing (Fig. 6.1 a). The mean height of each tuft was determined from five random measurements of upright fronds, while holdfast area was determined by encircling the base of each tuft with wire, then placing the shaped wire over a calibrated grid. The individual tufts were removed and dried to constant weight at 70°C. Biomass was then regressed on the product of the two tuft-size parameters.

The enumeration between biomass and the cover area of 35 G.pristoides tufts provided estimates of regrowth in terms of biomass after plucking (Fig. 6.1 b). The area covered by each tuft was measured with a grid as the tuft fell naturally over the rock substratum and biomass was regressed with cover.

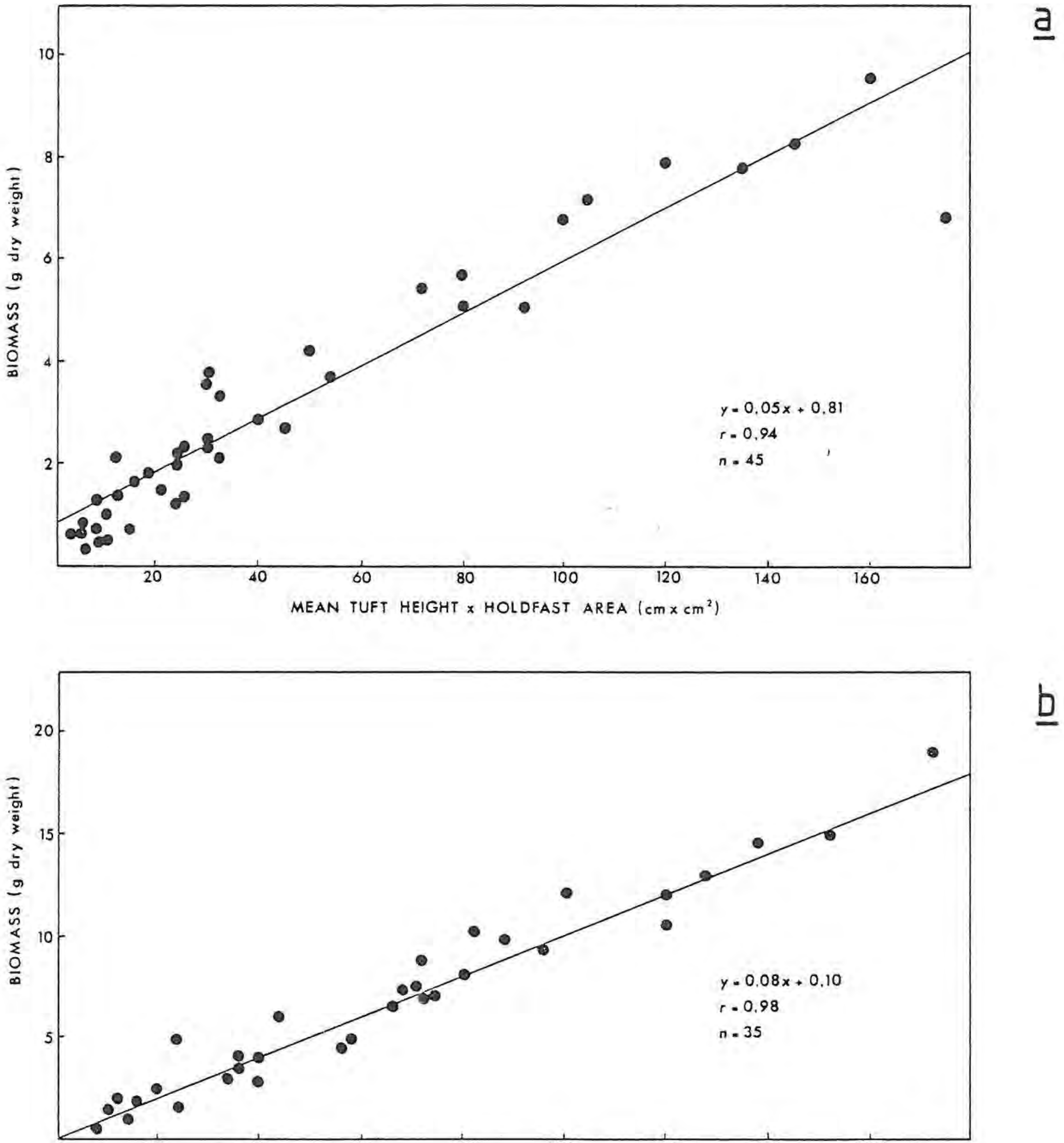

Fig. 6.1 Enumerations of <u>G.pristoides</u> biomass and tuft size.
(a) Biomass and mean tuft height x holdfast area.
(b) Biomass and tuft cover.

For the shearing experiments, 30 G.pristoides tufts attached to immobile substrata such as rock, were cut with shears to a height of 10 mm, avoiding damage to the holdfasts. At about monthly intervals, mean plant height and holdfast area of each tuft were measured, and biomass values extrapolated from the appropriate enumeration (Fig. 6.1 a). Regrowth was expressed as grams dry weight of G.pristoides per square metre of substratum area (g dry wt./m^2). Twenty unsheared tufts constituted the controls.

About 30 G.pristoides tufts situated within seven 0.075 m^2 quadrats, were plucked by hand to simulate the method presently employed by commercial harvesters. This involved a single hand-grab or snatch at each tuft which resulted in the removal of most upright fronds and some holdfast material. At monthly intervals the cover of individual tufts was measured from photographic slides projected onto a calibrated screen, and biomass values estimated from Figure 6.1 b (g dry wt/m^2). Five unplucked quadrats comprising about 15 tufts constituted the controls.

Since estimates of biomass for sheared and plucked treatments were derived from two different relationships, comparability was determined by applying a t-test to the two sets of control data for which each enumeration was used. As a further check, control tufts were removed from the substratum at the end of the experiment, and in all cases their dry masses corresponded closely with their predicted dry masses.

6.2.2 Recovery after complete plant removal (1983/84).

In addition to the plucking and shearing experiments in May 1983, all visible plant material was removed from seven 0.05 m^2 quadrats by burning, scraping and brushing with a wire brush. Unharvested quadrats adjacent to each experimental plot constituted controls. Recovery of the denuded quadrats was monitored photographically at about two-monthly intervals.

6.2.3 Effects of elevation on regrowth.

Experiments comparing the regrowth of sheared G.pristoides tufts in the upper and lower regions of its vertical intertidal range were carried out from February to August 1980. Fifteen tufts in the upper barnacle-dominated zone (about 0.45-0.75 m above MLWS) and 25 tufts in the lower limpet-dominated zone (about 0.20-0.45 m above MLWS) were cut to a height of 10 mm. At monthly intervals, the mean heights of the tufts were determined from five random measurements. No attempt was made to express regrowth as biomass, and mean tuft height was used as an indication of recovery rate.

6.2.4 Effects of harvesting periodicity on regrowth and production capacity (1985/86).

During October 1985 (spring), five topographically similar localities on the shoreline at Sharks Bay were selected (each consisted of gently sloping, north-facing sandstone surfaces, representing five replicates for each experimental treatment). At each site, five adjacent pairs of quadrats (0.3 x 0.4 m^2) were marked out using quick-set epoxy putty within well-established homogeneous stands of G.pristoides (about 0.2-0.45 m above MLWS). All G.pristoides tufts occurring on mobile animals such as limpets, were removed during every visit to the experimental plots.

In one plot of each of the five pairs, all tufts were sheared at regulated intervals, while in the second plot of each pair, all tufts were plucked at corresponding intervals. Shearing consisted of cutting tufts down to a height of 30 mm using shears, and avoiding damage to the holdfasts. Plucking, once again, involved a single hand-grab or snatch at each tuft. Both methods were applied uniformly throughout the study so that a similar amount of plant material remained in each plot (remnant) after each subsequent treatment.

One pair of plots was treated at regular 4-week intervals; the second, every six weeks; the third, every eight weeks; the fourth at 12-week intervals; and the fifth with an initial 8-week gap, followed by two harvests at 4-week intervals, followed by a final harvest after eight weeks. Thus between October and April, periods allowed for regrowth varied between four and 12 weeks.

After drying to constant weight at 70°C, the weight of the plant material harvested from each plot was recorded and expressed as dry weight per square metre of substratum area (g dry wt./m^2). Production rates (g dry wt./m^2/day) for the various harvesting treatments (except under the varied time regime) were calculated by dividing mean yields for each treatment by the time interval allowed for regrowth between successive harvests (i.e. 30, 45, 60 and 90 days). At the termination of the experiments, aggregate and mean yield per harvest for each treatment was also determined. Each harvest aggregate was analysed for agar content by the method described in Chapter 5.

After the final harvests at the beginning of April, all G.pristoides plant material remaining within each quadrat (remnant) was carefully scraped from the rocky substratum and dried to constant weight. Standing crop (biomass) present in each quadrat at the beginning of the experiment was estimated by adding together the weights of the respective remnants and the yields from the first harvests in October (which were previously undisturbed). Based on these values, a measure of plucking and shearing efficiency was determined.

6.3 RESULTS

6.3.1 Enumerations of tuft size and biomass.

The two tuft-size parameters used for estimating regrowth in terms of biomass after shearing and plucking (Fig. 6.1 a and b), both showed good linear relationships with biomass (for tuft height x holdfast area and biomass, $r = 0.93$, $P > 90\%$; for cover and biomass, $r = 0.98$, $P > 90\%$). The t-test showed no significant difference between the biomass values of the controls that were extrapolated from the two relationships. Furthermore, the dry masses of the control tufts that were removed from the substratum at the end of the harvesting experiments corresponded closely with their predicted dry masses. Thus, although derived from two different enumerations, rates of regrowth estimated as biomass after shearing and plucking are comparable. Because of their similarity, the two sets of control values were combined (Fig. 6.2).

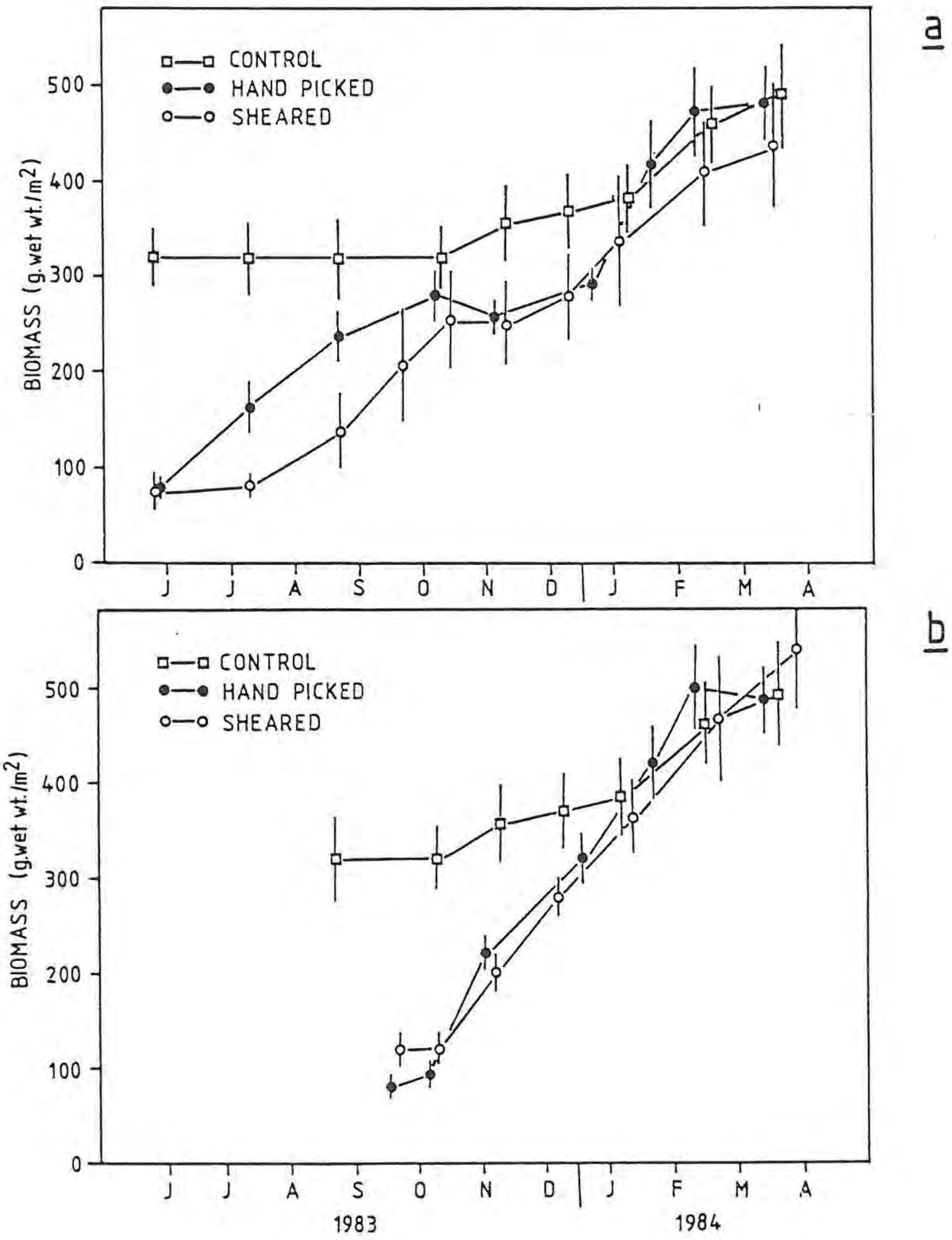

Fig. 6.2 Regrowth of G.pristoides after shearing and plucking in (a) late autumn (May 1983) and (b) early spring (September 1983). Bars = SE.

6.3.2 Effect of harvesting method on recovery rate.

Regrowth of G.pristoides tufts following single plucking or shearing treatments in late autumn (May 1983) and early spring (September 1983) is shown in Figure 6.2 a and b. Apart from an initial lag in regrowth shown by tufts sheared in May, recovery rates were significantly similar for both shearing and plucking treatments.

Similar results were obtained in the more recent harvesting experiments. First plucks in October 1985 yielded significantly greater quantities of G.pristoides than did first shearings (Table 6.1) (i.e., simply more was plucked than cut). However, these differences were not apparent in subsequent uniform treatments, with generally similar yields being obtained for pluckings and shearings under all five harvesting periodicities (Fig. 6.5 a-e). In these experiments, repeated shearing treatments, unlike plucking, resulted in atypical prolific branching in the upper distal regions of plants, thus raising yields beyond those which would be expected had normal linear frond growth occurred.

Quadrats that were completely cleared in May 1983 failed to recover at all (Fig. 6.3 a and b). There was no sign of colonization by juvenile G.pristoides plants at the termination of the other experiments 12 months later.

6.3.3 Effect of elevation on regrowth.

The regrowth of sheared G.pristoides tufts over a period of six months

TABLE 6.1

Partition of the estimated G.pristoides standing crops at all first October plucking and shearing treatments. Values are given as g dry wt/m². Brackets give percentages.

	PLUCKED			SHEARED		
	$\bar{x}$	SE	(%)	$\bar{x}$	SE	(%)
Remnant	22.4	+/- 6.8	(19.1)	41.5	+/- 5.3	(38.8)
First Harvest	94.8	+/- 5.8	(80.9)	65.5	+/- 4.8	(61.2)
Standing crop	117.3	+/- 6.3	(100)	107.0	+/- 5.1	(100)

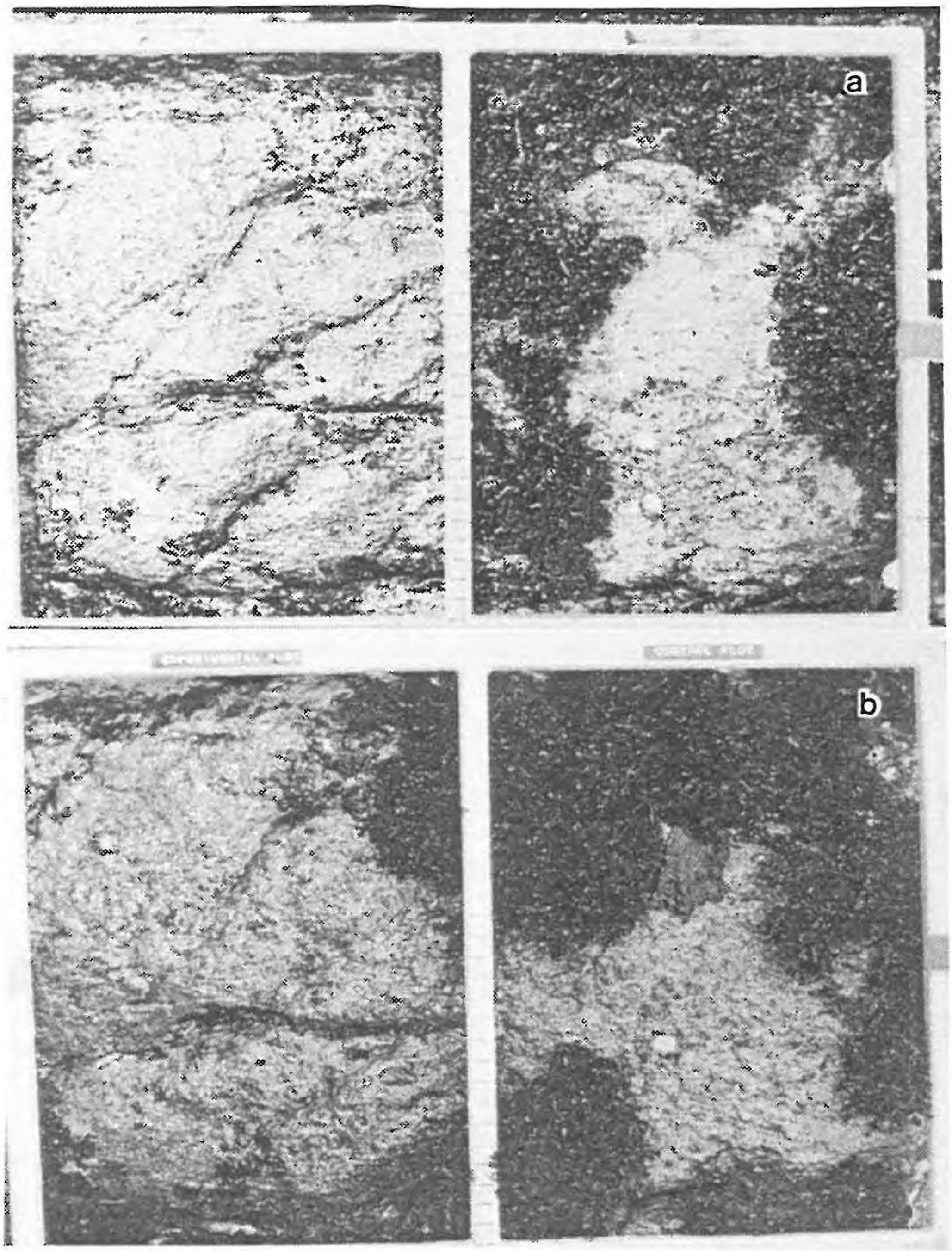

Fig. 6.3 Quadrat completely denuded of <u>G.pristoides</u> growth (a) in May 1983, and (b) a year later.

(February to August 1980) was four times more rapid in the lower intertidal range of the seaweed than in its upper range (Fig. 6.4). Furthermore, two quadrats that were plucked in May 1983 and which were positioned slightly higher up in the intertidal zone than the rest, failed to recover to their original state. These were not included in the results in Fig. 6.2 a, and subsequently all experimental plots were positioned at similar elevations and within the zone of maximum G.pristoides density, about 0.20-0.45 m above MLWS.

6.3.4 Effects of seasonality on regrowth and production capacity.

Results show that recovery from harvesting occurs more rapidly during the summer season than during winter. The biomass levels of G.pristoides tufts harvested in late autumn (May 1983), closely approached control levels (of standing crop) after 4-5 months (Fig. 6.2 a). However, as a result of a slump in regrowth during October, actual control levels were only reached after eight months. In comparison, a more rapid 3-4 month recovery rate was observed after harvesting in early spring (Fig. 6.2 b).

The effect of seasonality on regrowth and production capacity was also seen during the more recent summer harvesting experiments (1985/1986). Production rates, particularly under plucking and shearing treatments at monthly intervals (Fig. 6.5 a and b), showed clear seasonal variation with highest values occurring during the midsummer months of January and February. Biomass yields virtually identical to the original October harvests were obtained after the first two months (Fig. 6.5 a and e).

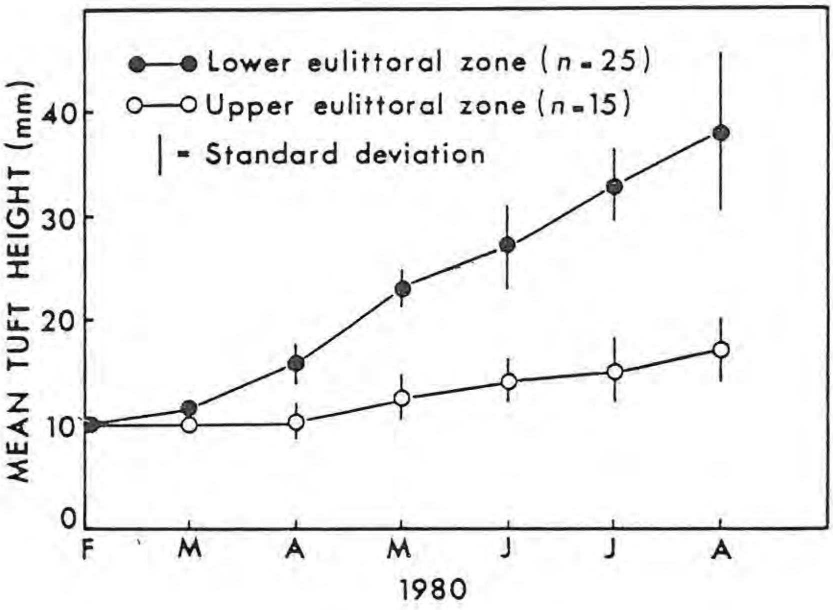

Fig. 6.4 Regrowth of sheared G.pristoides tufts in the upper and lower regions of its intertidal range. Bars = SD.

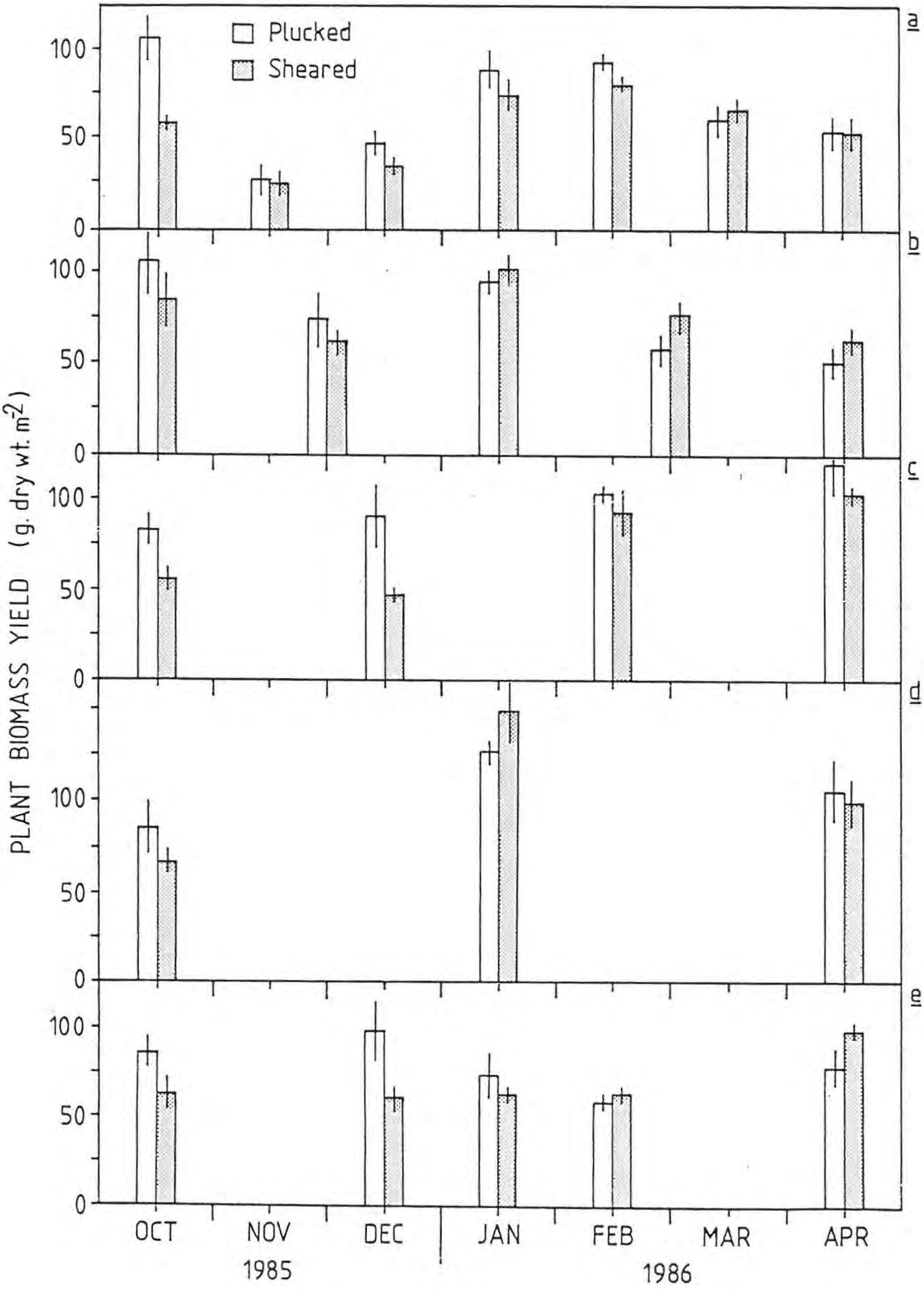

Fig. 6.5 G.pristoides biomass yields from plucking and shearing at various time intervals: a) 4-weekly; b) 6-weekly; c) 8-weekly; d) 12-weekly; e) varied. Bars = SE.

Those after the first six weeks closely approached the original harvest values (Fig. 6.5 b), while uninterrupted growth through an interval of three months yielded significantly greater harvests than in October (Fig. 6.5 d).

6.3.5 Effects of harvesting periodicity on regrowth and production capacity.

During the summer experiments, repeated harvesting at regular monthly intervals (Fig. 6.5 a) resulted in yields that, though small at first, were successively greater until January, when they were similar to the original October yields. In addition, production rates were generally significantly greater under shorter harvesting periodicities. For example, the highest value calculated for plucking at monthly intervals was 3.13 g.dry wt./m^2/day, while that under the 3-monthly intervals was 1.42 g.dry wt./m^2/day (Fig. 6.6 a).

Greater productivity under shorter harvesting periodicities is again evident when aggregate yields are compared (Fig. 6.7 a). Monthly harvesting produced the greatest total quantities of G.pristoides at 372 and 335 g.dry wt./m^2 for plucking and shearing, respectively. In comparison, a periodicity of three months yielded the lowest aggregate totals of 233 and 250 g.dry wt./m^2 for plucking and shearing, respectively. However, taking into consideration harvesting effort, expressed here as mean biomass yield per harvest (Fig. 6.7 b), longer intervals between successive harvests carry obvious advantages.

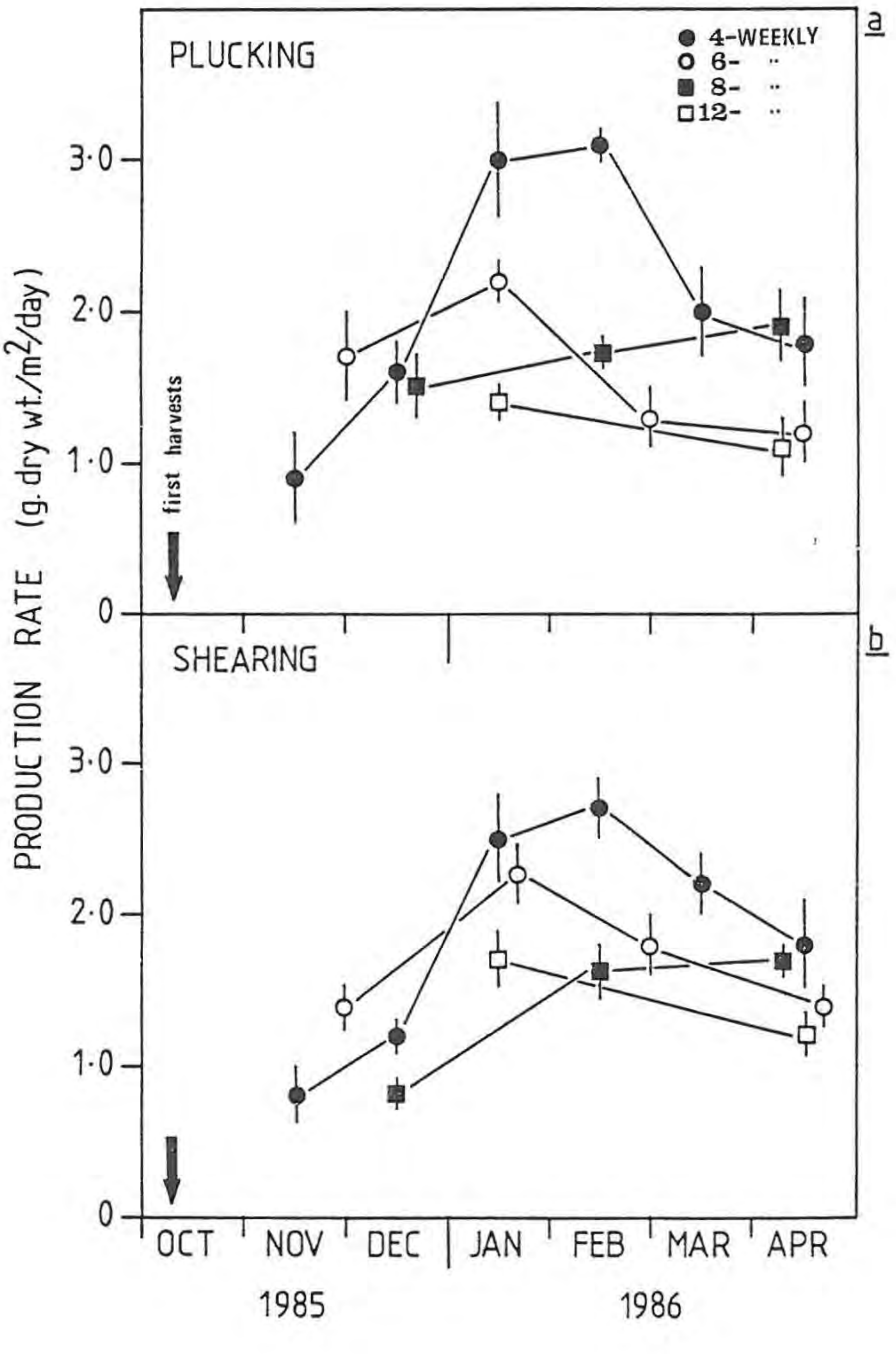

Fig. 6.6 G.pristoides production rates after (a) plucking and (b) shearing. Bars = SE.

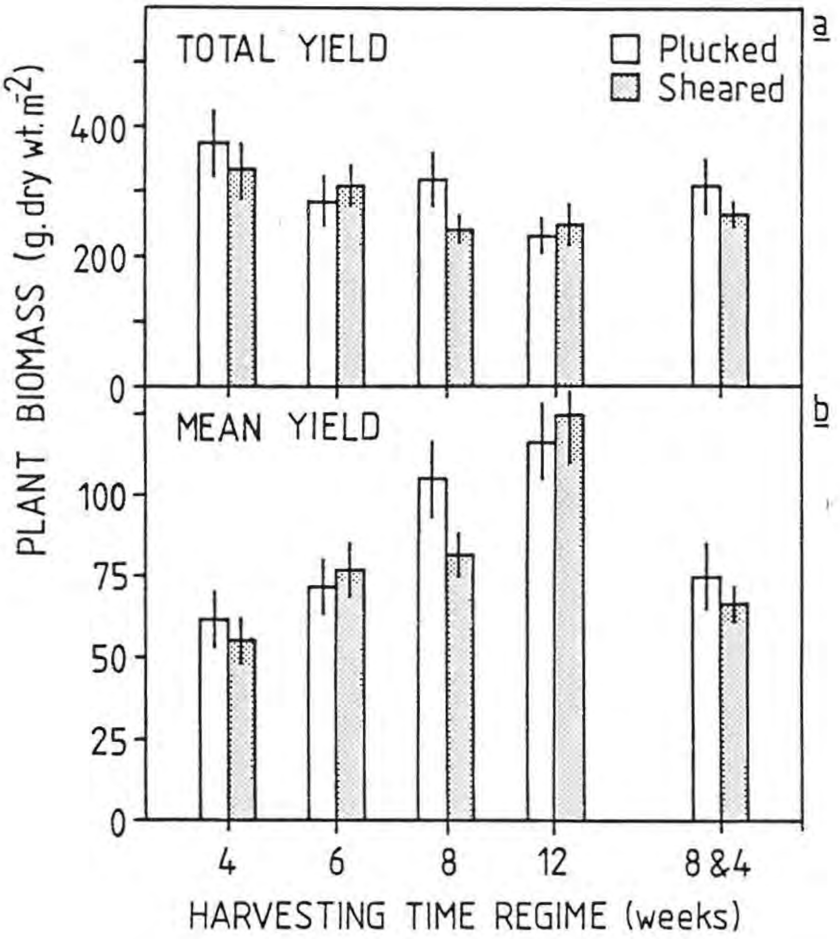

Fig. 6.7 (a) Aggregate yields and (b) mean yield of G.pristoides per harvest from plucking and shearing at various time intervals. Bars = SE.

6.3.6 Agar contents of sheared and plucked plants.

Agar contents, although slightly higher in sheared plant material ($\overline{x}$ = 42.8%, SE = 1.8), did not differ significantly from plucked plant material ($\overline{x}$ = 38.8%, SE = 2.1).

6.4 DISCUSSION

The present experimental results show clear trends regarding the regrowth and production capacity of G.pristoides tufts after harvesting at Port Alfred. The first point of interest is that regrowth and production rates are more rapid during the summer season. This corresponds with the results of the previous chapter showing peak frond elongation rates and standing crop levels during the summer months. Enhanced regrowth during the summer has also been reported for economic red algae harvested in other parts of the world (Marshall et al. 1949, Barilotti and Silverthorne 1972, Burns and Mathieson 1972 b, Mathieson and Burns 1975).

The more recent harvesting experiments carried out during the summer of 1985/86, showed that G.pristoides biomass yields subsequent to the initial spring harvests (October) were very much the same for shearing and plucking, regardless of harvesting periodicity. This was also reflected in the similar production rates that were calculated for the two harvesting methods, and confirmed the results of the 1983/84 experiments. These findings, however, contrast with the results obtained for other economic species. In the case of Gelidium robustum (Gardn.) Hollenb. et Abb., a subtidal agarophyte in Baja California, regrowth was more rapid after shearing than plucking (Guzmán del Proó and de la Campa de Guzmán 1969), while the converse was true in England (Marshall et al. 1949) for the intertidal carrageenan-producing red alga, Gigartina stellata (Stackh.) Batt. (now known as Mastocarpus stellatus, Guiry et al. 1984).

Although these varying responses to plucking and shearing treatments probably reflect morphological and habitat differences between the species (and also perhaps different applications of the same method), it was expected that regrowth of G.pristoides would be more rapid after shearing, because this treatment causes minimal damage to the regenerative holdfast regions. Harvesting by plucking, on the other hand, carries an inherent danger of causing damage to the holdfast region. Observations of other perennating economic red algae (Marshall et al. 1949, Fralick and Andrade 1981) have stressed the importance of holdfasts in maintaining successful vegetative regeneration after harvesting of natural stocks.

The need to avoid excessive damage to vegetative holdfasts should, therefore, be of primary concern. The fact that the quadrats which were completely denuded of G.pristoides failed to show any sign of recovery after a year, stresses the importance of vegetative regeneration in the maintenance of harvested natural populations. Since present results show that regenerative capacities do not differ for the two harvesting treatments applied here, a single hand-grab or snatch at a tuft appears to have no obvious detrimental effect on the regenerative capacity of this seaweed. During plucking, some of the upright fronds remain intact and may afford the regenerative holdfasts some protection against desiccation stress, as was suggested for G.stellata by Marshall et al. (1949).

Results showed that the regrowth of sheared G.pristoides tufts was four times slower in the upper barnacle-dominated zone than in the lower limpet-dominated zone. In addition, the two quadrats that failed to recover after plucking in late autumn, were situated at slightly more elevated levels where desiccation stress would be greater. These observations clearly indicate that harvesting should be avoided in the upper intertidal range of this seaweed, where damage due to harvesting could be detrimental to the maintenance of natural stocks.

In the previous chapter it was shown that more agar tends to be located in upper distal portions of G.pristoides fronds, and was suggested that shearing-off of these agar-rich distal portions might be both a conservative and economically feasible method of harvesting. Present results, however, show no significant difference between agar yields arising from the use of the two harvesting methods (plucking and shearing). Even though successive shearing treatments, through a coppicing effect, markedly increased the relative biomass of distal tuft regions, this still did not enhance agar yields. It should be noted, however, that the present results were obtained from the aggregate yields from the same plant tufts, and not from random collections of previously undisturbed plants as in the previous chapter. Perhaps a difference in the manner of regrowth between sheared and untreated plants would account for this discrepancy in results.

While the earlier harvesting experiments (1983/84) indicated that recovery takes 3-4 months after harvesting in spring (September), the more recent results show that G.pristoides tufts are capable of restoring material lost during a spring (October) harvest within two months. This small variation may reflect slight seasonal differences (harvesting in September as opposed to October), or the different methodologies used to measure regrowth. It is difficult to compare recovery rates of harvested red algae from various parts of the world due to often vastly differing morphologies and prevailing climatic conditions (e.g. in New Hampshire, U.S.A., where conditions are more severe than at Port Alfred, regrowth of *G.stellata* takes about 12 months after harvesting in summer; Burns and Mathieson 1972 b). However, a similar recovery rate to *G.pristoides* has been reported for *Gracilaria secundata* Harv. in New Zealand (Luxton 1981), while a slightly faster recovery rate of 1-2 months has been reported for *Gelidium amansii* (Lamour.) Lamour. in Japan (Nonaka *et al.* 1962).

Although the recent experiments showed that increased *G.pristoides* yield and production concided with maximum midsummer frond elongation rates, the reason for greater production and yield with shorter intervals between successive plucking and shearing treatments is less clear. While Santelices *et al.* (1984) demonstrated that harvesting frequency had minor effects on the production capacity of *Gracilaria lemaneiformis* (Bory) Weber-van Bosse, in central Chile, Katada (in Katada and Satomi 1975) reported that repeated harvesting resulted in increased yields from a *Gracilaria* species in Japan. In *G.pristoides*, this effect might in the case of successive shearing be attributed to the coppicing effect already described, while in the case of plucking, moderate disturbance to the holdfast region caused by this method may somehow stimulate frond production. Although neither method of harvesting appears to present advantages in terms of production capacity or agar yield, it is recommended that plucking by a single hand-grab of tufts would be the most effective method for harvesting *G.pristoi-*

des, as it is a less time consuming and therefore a more cost-efficient method than shearing.

Owing to increased production rates, aggregate yields from plucking G.pristoides at 4-weekly intervals were significantly greater than under the 12-weekly regime. However, aggregate yield from the 8-weekly (bi-monthly) treatment were similar to those recorded for the 4-weekly treatment (Fig. 6.7 a). Furthermore, taking into consideration harvesting effort (expressed here as mean yield per harvest, Fig. 6.7 b), plucking at bi-monthly intervals during the summer season seems ideal, since it combines the advantages of both frequent harvesting, and yield as a function of harvesting effort.

It should be noted that since the present experiments involved the repeated cropping of the same G.pristoides tufts, the results recorded need to be related to the present commercial harvesting practice. The plucking intensity of about 80% of the standing stock shown here (Table 6.1), must be compared with that of 20-30% plucking efficiency (an effective one tuft in five) which has been estimated for the commercial pluckers (Simons pers. comm.). Present results represent what might be described as "worse case cropping". Therefore, recommendations for the management of natural G.pristoides populations, based on trends seen here, should also take this into account. For example, a 6-weekly (or even a monthly) plucking periodicity, may not be as inefficient or destructive as would appear from present results.

While present observations showed that regrowth was slower after a single harvest in autumn than in spring, Simons (pers. comm.) recorded a severe depression of G.pristoides standing stocks with winter harvesting. Therefore, based on these results, it would seem that harvesting should be avoided during the winter months. It is suggested that a reasonable harvesting strategy at any one site might be five consecutive 6-weekly harvests beginning in October and ending in April, and allowing recovery from contingency damage during winter. Such a strategy would probably prevent irreversible damage to the natureal seaweed stocks, and yet, would ensure a regular and predictable optimal yield from the resource.

CHAPTER 7

Factors affecting the vertical and horizontal distribution patterns of Gelidium pristoides.

7.1 INTRODUCTION

An understanding of the structure of intertidal communities has long been a major goal of marine ecologists. Most of the pioneer work in this area of research has taken the form of descriptive and quantitative surveys, identifying patterns of distribution and comparing them with other localities or geographical areas. There are numerous South African examples (Bokenham and Stephenson 1938, Eyre et al. 1938, Eyre 1939, Stephenson et al. 1937, 1938), while most of the early work has been reviewed by Stephenson and Stephenson (1949) and Southward (1958). However, this type of information is of limited value in attempting to understand the mechanisms of intertidal population and community dynamics (e.g. Dayton 1971, 1975, Menge 1976, Crawley 1983).

During the past two decades there has been a major change in emphasis from density-type surveys to experimental analyses of the interactions that determine the structure of intertidal communities (as reviewed by Connell 1972, Lubchenco and Gaines 1981, Hawkins and Hartnoll 1983). These experiments have usually taken the form of manipulations, where, by various means (e.g. transplantations or predator/herbivore exclusions), an organism is subjected to abnormal environmental conditions (biotic or abiotic). These experimental studies have made a significant contribution to our present knowledge and understanding of ecological systems in general. Intertidal habitats are well suited to manipulation experiments since they normally involve small areas over which environmental gradients are clearly defined (e.g. tidal rhythms), and the response to manipulative changes is relatively rapid in comparison to most terrestrial situations. Furthermore, the organisms under study are usually relatively easy to monitor and control.

Gelidium pristoides is the dominant intertidal alga on the rocky shores at Port Alfred. This species has also been described as a characteristic intertidal alga in the Port Elizabeth and East London areas (Stephenson et al. 1938, Eyre et al. 1938, Beckley and McLachlan 1979, Beckley 1982), while McQuaid (1985) also regarded it as a dominant midshore species at Dalebrook in the Cape Peninsula. When considering the structure and dynamics of an intertidal alga such as G.pristoides, there are two questions that are usually asked: What are the factors that determine;

a) the vertical distribution (i.e. upper and lower limits) and

b) the horizontal pattern of distribution of the species?

Numerous studies have examined the factors determining the vertical distribution of intertidal algae, and it is generally agreed that physical factors such as desiccation determine upper limits, while competition and herbivory are important in setting lower limits (as fully referenced in the discussion). Although previous studies have reported variations in the width and elevation of G.pristoides belts in response to varying exposure to wave action (Beckley 1982), and seasonal variations in the zone of maximum density (McQuaid 1985), the question as to what factors actually determine the upper and lower limits of this seaweed still remained unanswered.

Herbivory is regarded as both the most important factor determining the horizontal distribution patterns and the major source of patchiness in intertidal algal populations. Although there are probably numerous grazing species concurrently influencing algal recruitment, Paine (1980) stressed that when dealing with complex intertidal communities, emphasis should be placed on examining the community links that have a major influence on the community organization, and that interaction strength is more important than trophic complexity.

At Port Alfred, G.pristoides plants tend to occur in cracks and crevices in the rocky substratum where germlings would be immune to grazing. Furthermore, the dominant herbivores in the G.pristoides zone, the limpets Patella oculus Born. are frequently surrounded by large areas of bare flat rock while having heavy G.pristoides growth on their shells (Fig. 7.1). Commenting on the lack of macroalgal cover in South African intertidal communities in general, Branch (1971) suggested that grazing by limpets has a profound influence on algal recruitment by eradicating all the spores that settle on accessible substrata. Similar situations have been confirmed by experimental analysis in other parts of the world (see reviews by Connell 1972, Lubchenco and Gaines 1981, Hawkins and Hartnoll 1983, and also Jernakoff 1983, 1985, Lubchenco 1983, Menge et al. 1985, Underwood and Jernakoff 1984), while the importance of local refuges or "escapes" from herbivory as a cause of patchiness in algal populations has also been emphasised (e.g. Menge 1976, Menge and Lubchenco 1981, Hawkins 1981, Lubchenco 1983).

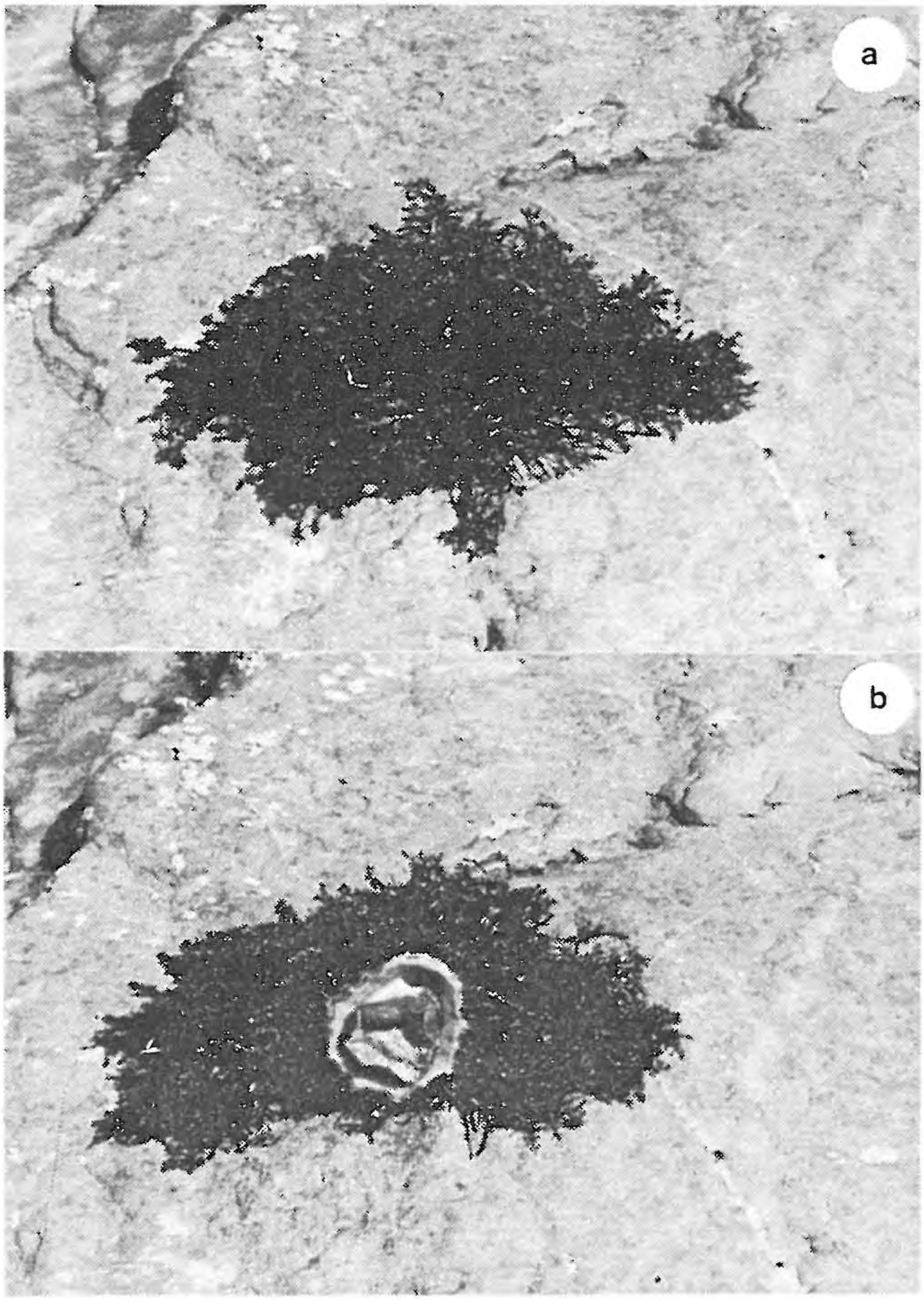

Fig. 7.1 Heavy G.pristoides growth on the shell of a limpet (P. oculus), surrounded by bare rock.

Major similarities exist between intertidal communities that have so far been studied (mainly in the U.S.A., Britain and Australia). However, differences have also been recognised, and according to Underwood and Denley (1984), currently accepted models and generalizations regarding the structure of intertidal communities, should receive more critical testing in other parts of the world. Information on the dynamics of South African intertidal communities is limited, although Branch (1981) has performed some limpet manipulation experiments at Dalebrook in the Cape.

The aims of this study were:

1) To describe the vertical and horizontal distribution patterns of *G.pristoides* at Port Alfred.

2) To try and understand some of the factors influencing these distributions patterns by experimentally examining:

a) Factors determining the vertical distribution of *G.pristoides*, i.e. the upper and lower intertidal limits of the species.

b) Factors determining the horizontal distribution of *G.pristoides*. With regard to this latter objective, the effect of the limpet *P.oculus* on the recruitment of *G.pristoides* was investigated by using toxic antifouling paint barriers to control the movement of limpets, a method which has been used successfully in the past to control both limpets and sea urchins (Hawkins and Hartnoll 1983) (see also Appendix I). The importance of refuges or "escapes" from grazing, on *G.pristoides* distribution patterns, was also investigated.

7.2 MATERIALS AND METHODS

All experiments were carried out at Sharks Bay, Port Alfred, from February 1985 to April 1986. Heights of elevation within the intertidal zone are based on an approximation of the mean low water spring tidal level (MLWS) seen during the study period.

7.2.1 Vertical and horizontal distribution patterns

The vertical frequency and size distribution of G.pristoides was measured by placing a 1 m^2 grid (comprising 169 evenly spaced intersects) against 10 vertical rock faces, which showed the entire intertidal range of the seaweed (Fig. 8.3 a). At each elevation level of grid intersects, the presence/absence, and height of each G.pristoides tuft was recorded. At the same time, the availability and the occurrence of G.pristoides on various substratum types was noted. Percentage substratum availability, occurrence of G.pristoides on substratum-types, and occurrence of G.pristoides relative to the total availability of each substratum-type, was calculated for each elevation level. An additional 10 grids were also sampled in a similar manner upon horizontal rocky surfaces within the zone of maximum G.pristoides density.

7.2.2 Transplantation experiments (growth and germling survival)

a) Frond growth

Limpets (P.oculus) with G.pristoides growing attached to their shells were collected and the living flesh portion removed. A hole was drilled through the centre of each shell, and three G.pristoides fronds on each shell were tagged so that frond elongation rates could be measured (see Chapter 5). Five prepared limpet shells were transplanted into the following intertidal regions: Sublittoral fringe (below the normal vertical range of G.pristoides), upper Balanoid zone (above the normal vertical range), and the Cochlear and lower Balanoid zones (both within the normal vertical range of the seaweed). The shells were attached by means of stainless-steel screws to plastic wall-plugs inserted into pre-drilled holes in the rock. For the sublittoral fringe transplants, shells were attached to loose boulders which were then placed at the required level. Lengths of tagged fronds were recorded at monthly intervals from February to June 1985, and elongation rates were calculated in mm/day. Additional fronds were tagged every month to replace those lost, and to maintain a sample size of 10-15 fronds. The average heights of the G.pristoides tufts attached to the limpet shells were also measured, in addition to heights of the tagged fronds.

b) Germling survival

Clean limpet shells (after removal of the fleshy portion and all algal growth, and sterilization at 100°C) were placed in aquaria containing half-strength Erdschreiber culture medium (McLachlan 1973). Fertile G.pristoides fronds were suspended above the limpet shells so that the spores being shed would settle and attach to the shell surfaces. After spore germination, the culture media were aerated continuously at a temperature of 20°C and a photoperiod of 16:8h (light:dark). Light was supplied by fluorescent cool-white light tubes providing a photon flux density of about 40 umol quanta/m^2/s. Culture media were changed every two weeks. After two months growth in culture, the germlings on the limpet shells were transplanted into the four intertidal zones described. In each zone, three sets of shells, each consisting of three shells with germlings (treatment) and three sterilized shells without germlings (control), were screwed to the rock. Barriers of antifouling paint were applied around each set. Survival of germlings was monitored every two weeks from September to November 1985. Since germling survival proved to be difficult to quantify, shells were placed in one of the following categories: good, fair or poor germling survival.

7.2.3 Grazer exclusion and colonization experiments

a) At each of three topographically similar localities on the shoreline (gently sloping, north facing rock surfaces, representing three replicates for each experimental treatment) situated well within the zone of maximum G.pristoides density, three adjacent plots (1.0 x 0.75 m^2) were cleared of all animals (mobile and sessile) and most plant growth. Clearing of the rock surfaces was done both by scraping and burning using a gas torch. Dayton (1971) showed that burning is the most effective method of denuding intertidal surfaces, killing most algal growth.

Seven holes were drilled into the rock in each of the three adjacent plots. Clean limpet shells were then attached using the method already described. A 10 cm wide band of "Viking" marine-antifouling paint was applied around two of the three plots. Into one of these, a fertile G.pristoides tuft on a limpet shell was transferred. The plot without the antifouling paint barrier constituted the control (see Fig. 7.11 for a diagram showing the arrangement of the plots). At intervals of two months, algal recruitment (cover) on rock surfaces was measured with the aid of a metre squared grid, while on the artificially attached limpet shells, cover was estimated visually.

b) Similar exclusion and non-exclusion (control) plots (0.4 x 0.4 m^2) were also set up on two vertical rock faces and at the four elevation levels already described, namely, sublittoral fringe, Cochlear, and upper and lower Balanoid zones. Loose boulders were used for the sublittoral fringe plots. Algal recruitment (cover) was monitored from July 1985 to April 1986, with the aid of a grid (Fig. 7.7 shows the arrangement of plots at one of the two sites). Since results were based on the mean of only two replicate treatments, standard errors were not calculated.

7.2.4 Strength of G.pristoides attachment to various substrata

An apparatus comprising a length of elastic, a rule and pinch-clamp was used to measure the strength of attachment of G.pristoides fronds to four common substratum-types, namely, rock, lithothamnia, and barnacle and limpet shells. The clamp was attached close to the bases of five upright fronds at a time. Tension was applied in such a way that when the fronds were torn from the substratum, the degree of extension of the elastic could be noted by reference to the rule. Twenty measurements were taken for each substratum-type. Measurements were then calibrated using various weights of known mass, and the force required to remove the fronds was expressed in Newtons (N).

7.3 **RESULTS**

7.3.1 Vertical distribution of G.pristoides

At Port Alfred, G.pristoides is distributed from about 0.2 m to 0.75 m above MLWS (Fig. 7.2). In terms of biological zones, the vertical distribution of the seaweed corresponds to the zone dominated by the limpet P.oculus (0.2-0.45 m above MLWS) and extends upward into the lower region of the barnacle dominated Balanoid zone (Fig. 7.3 a). The P.oculus zone corresponds to the approximate elevation of the Cochlear zone seen at other nearby localities (e.g. Kenton-on-Sea, about 30 km south of Port Alfred), where the limpet Patella cochlear shows a typical mosaic-like arrangement. Although there is not a P.cochlear community at Port Alfred, the term Cochlear zone has been retained to prevent terminological confusion.

G.pristoides tufts occur less frequently and show a reduction in stature with increased elevation (Fig. 7.2). In the lowest range of its vertical distribution, G.pristoides tufts ranged in height from 1.0 to 12.0 cm, and in the highest zone from 0.5 to 5.0 cm.

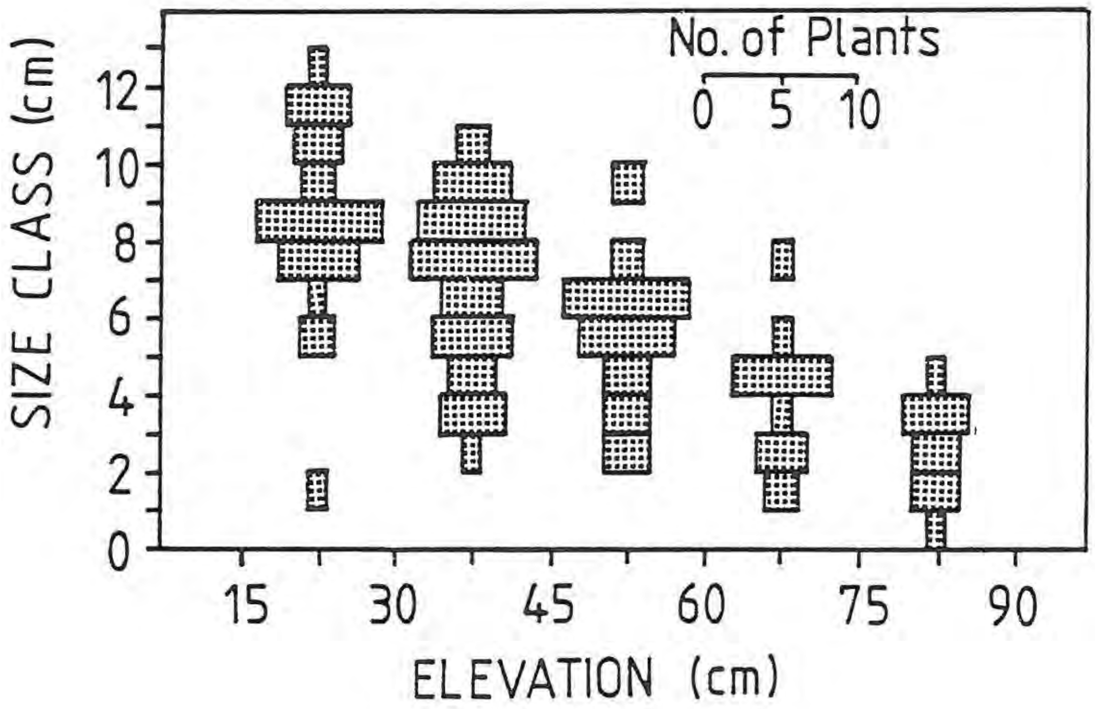

Fig. 7.2 Frequency and size distribution of G.pristoides plants relative to elevation (given as height above MLWS) at Sharks Bay, Port Alfred.

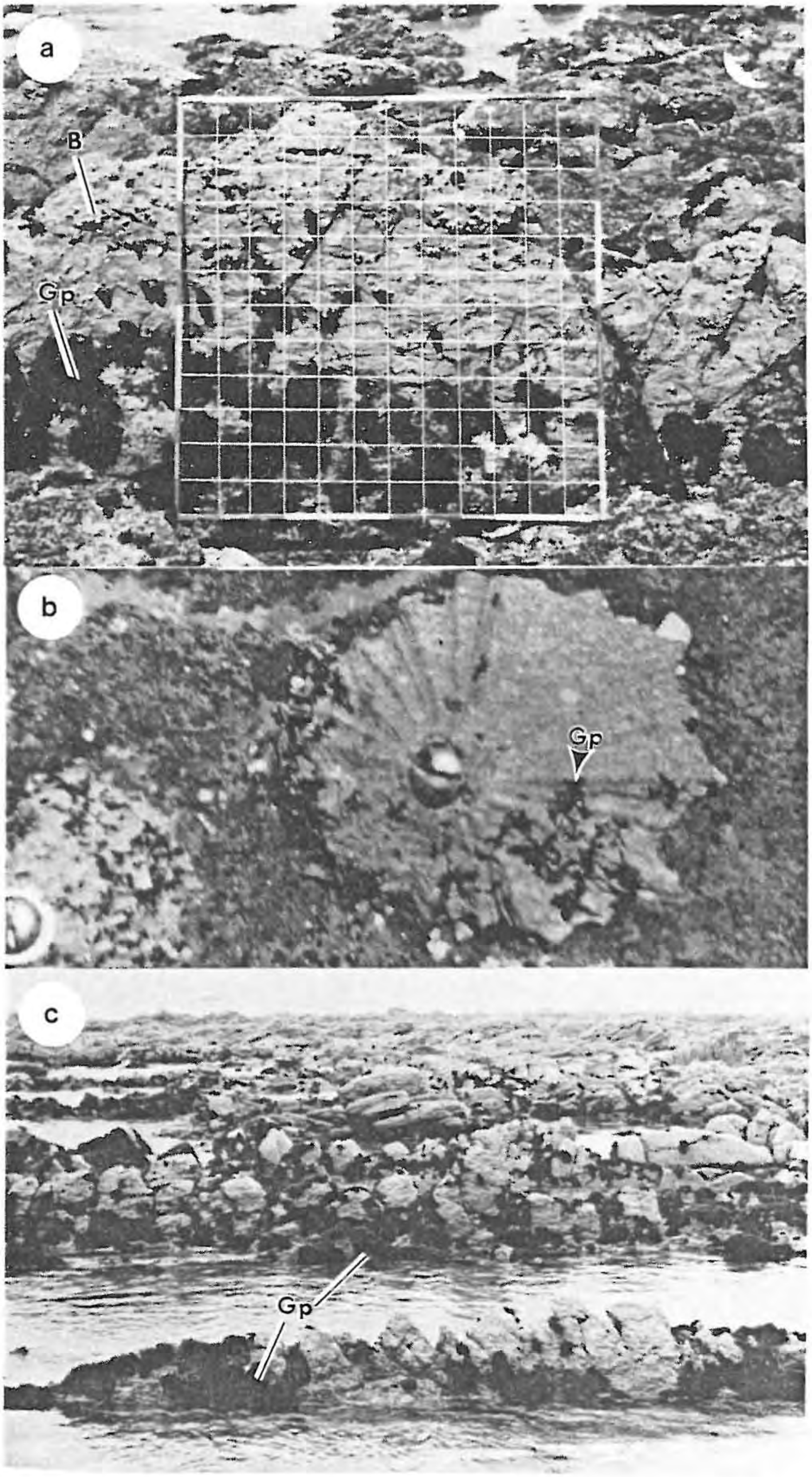

Fig. 7.3 a) Metre squared grid used to sample vertical rock faces. The band of G.pristoides (Gp) in the Cochlear zone is clear, with a lower frequency of plants occurring in the lower Balanoid zone (B = barnacle).

b) Juvenile G.pristoides (Gp) plants that developed from germlings cultured on limpet shells in the laboratory and transplanted into the sublittoral fringe.

c) Patchy distribution of G.pristoides (Gp) at Port Alfred.

7.3.2 Transplantation experiments

a) Frond growth

Elongation rates of G.pristoides fronds generally decreased with increased elevation (Fig. 7.4). While growth in the lower Balanoid zone was always significantly lower than in the Cochlear zone, growth was completely retarded (except in February) when plants were transplanted above the normal range of the seaweed (upper Balanoid), where severe bleaching, and senescence of tufts was also observed.

In the sublittoral fringe, where transplants were only emersed for short periods during spring low tides, growth rates were consistently comparable to those in the Cochlear zone of maximum G.pristoides density. However, plants that were transplanted into the sublittoral fringe became overgrown within a matter of weeks by the epiphytic encrusting coralline Polyporolithon patena (Hook. et Harv.) Mason (Fig. 7.5 c and d), eventually causing the Gelidium plants to senesce and die (Figs. 7.5 a and 7.6). Prior to complete senescence, however, some of the epiphytized G.pristoides plants (attached to limpet shells), were transplanted back into the normal Cochlear zone of the seaweed. Some plants recovered from the epiphytic growth while others failed to do so (Figs. 7.5 a and 7.6).

b) Germling survival

G.pristoides germling survival decreased with increased elevation (Table 7.1). Germlings that had been transplanted into the lower (normal)

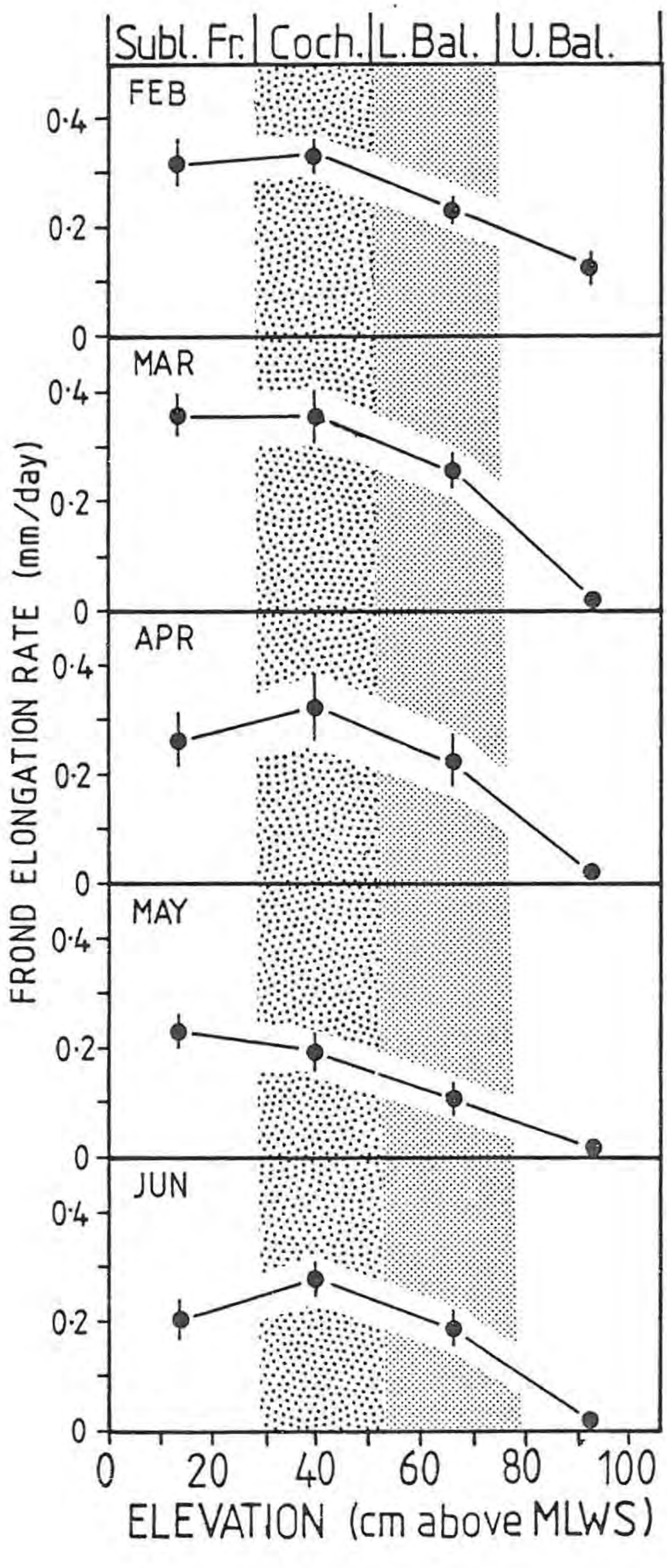

Fig. 7.4 G.pristoides frond elongation rates at various elevations on the shore. Shaded areas represent the normal intertidal range of the seaweed. Bars = SE.

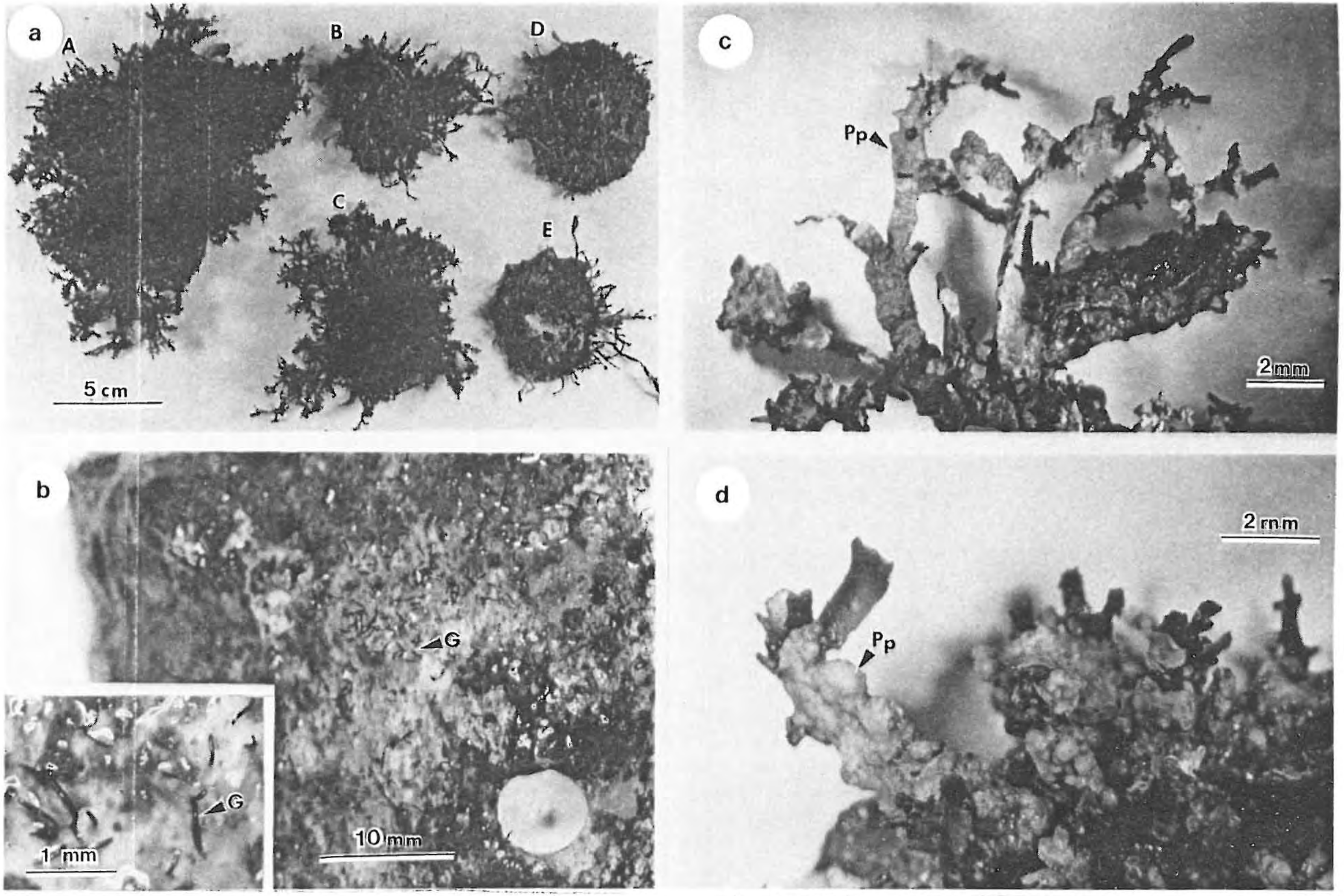

Fig. 7.5 a) G.pristoides transplants: (A) no P.patena epiphytic growth and damage in normal zone (control); (B & C) after transplantation back into normal zone following P.patena epiphytization in sublittoral fringe (B - irreversibly damaged; C - recovered); (D & E) almost complete senescence due to P.patena epiphytization in the sublittoral fringe.

b) G.pristoides germlings (G) cultured from spores on limpet shells for transplantation into the shore at Port Alfred (inset = close-up of germlings).

c & d) Overgrowth of G.pristoides plants transplanted into the sublittoral fringe, by the encrusting epiphytic coralline, Polyporolithon patena.

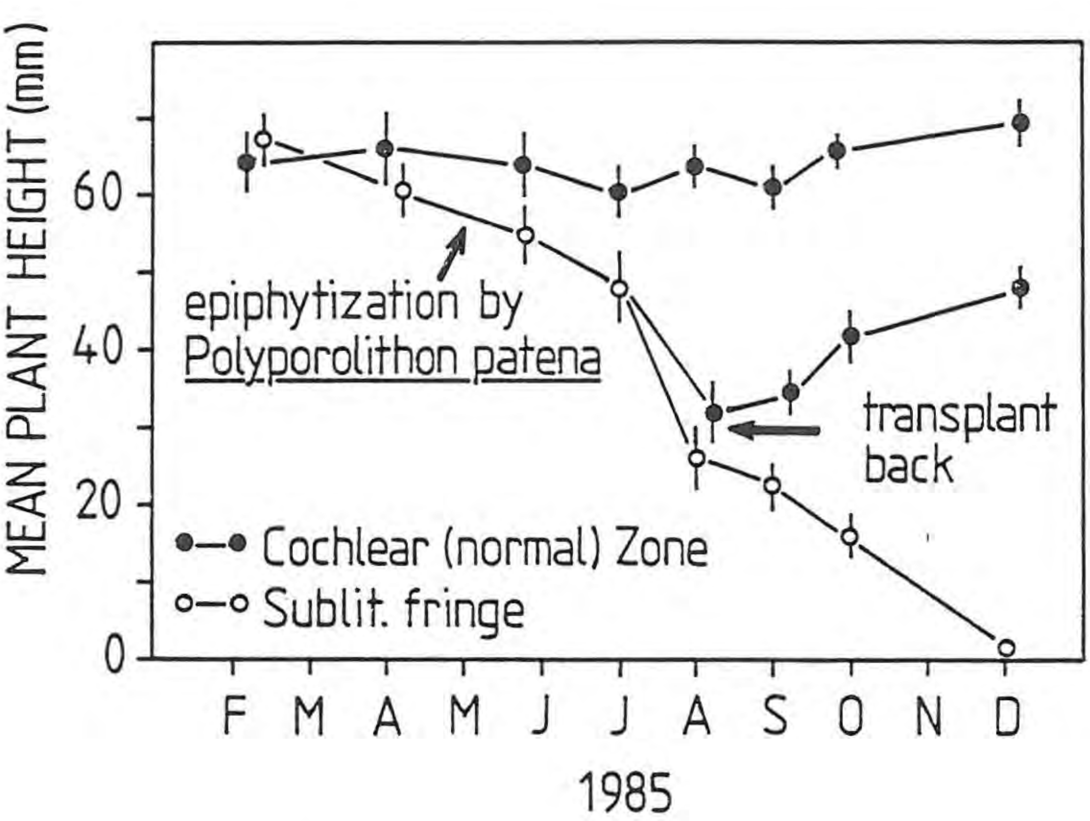

Fig. 7.6 Change in mean height of <u>G.pristoides</u> tufts transplanted within the normal <u>G.pristoides</u> band in the Cochlear zone (control), and into the <u>sublittoral</u> fringe, below its normal vertical range.

and upper (above normal) Balanoid zones disappeared within two weeks. Germlings within the Cochlear zone disappeared within six weeks, while those in the sublittoral fringe developed into small but normal *G.pristoides* plants (Fig. 7.3 b). However, they too were subjected to *P.patena* overgrowth, and died after 10 weeks.

7.3.3 Colonization of grazer exclusion plots at various elevations

While colonization was somewhat better in grazer exclusion areas in comparison to non-exclusion plots (described later in 7.3.6), algal recruitment, including that of *G.pristoides*, was inversely related to elevation (Figs. 7.7 and 7.8). Colonization was completely retarded in both the exclusion and non-exclusion plots situated in the upper Balanoid zone (above the normal *G.pristoides* range), with the best *G.pristoides* recruitment occurring within the Cochlear zone, particularly on limpet shells.

In the sublittoral fringe, *G.pristoides* colonized both rock and limpet shells within the grazer exclusion plots, and limpet shells within the non-exclusion plots. However, it was absent on rock surfaces from which grazers were not excluded. All recruited *G.pristoides* plants eventually became heavily infected by *P.patena* growth. Both encrusting (*Lithothamnion* sp.) and articulated corallines (*Corallina* sp. and *Jania* sp.) showed rapid recruitment in both exclusion and non-exclusion plots within the sublittoral fringe and eventually dominated most of the available space.

TABLE 7.1

Survival of <u>G.pristoides</u> germlings which were cultured on limpet shells and transplanted at various levels of elevation on the shore (degree of germling survival; xxx = good; xx = fair; x = poor; / = none).

ZONE	WEEKS					
	0	2	4	6	8	10
Upper Balanoid	xxx	/	/	/	/	/
Lower Balanoid	xxx	/	/	/	/	/
Cochlear	xxx	x	x	/	/	/
Sublitt. fringe	xxx	xxx	xx	xx	x	/

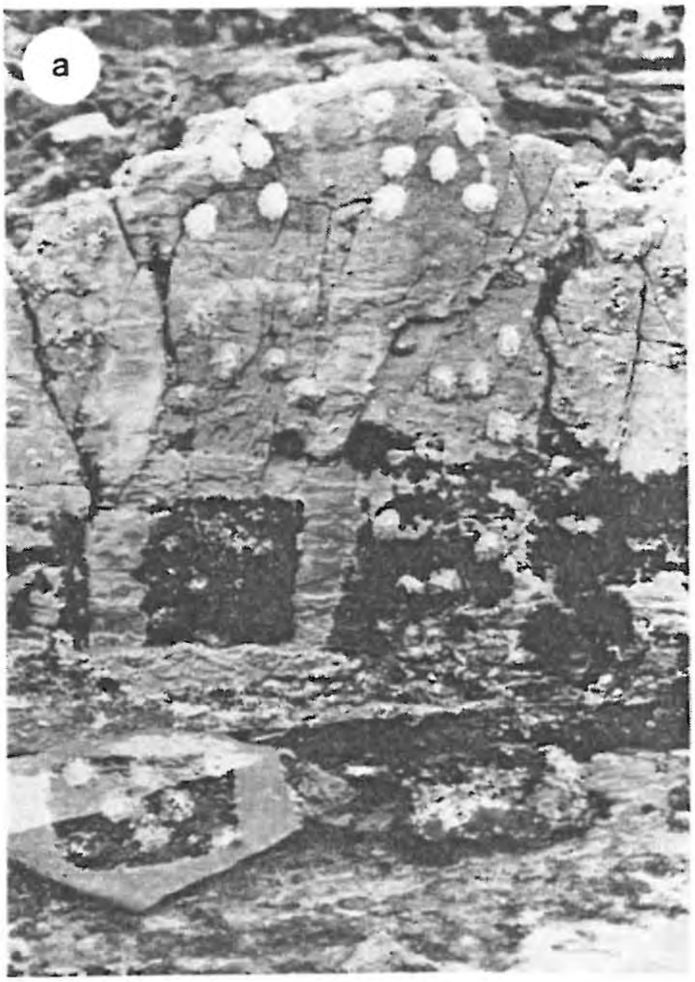

Fig. 7.7 Arrangement of exclusion and non-exclusion plots at various elevations on the shore.

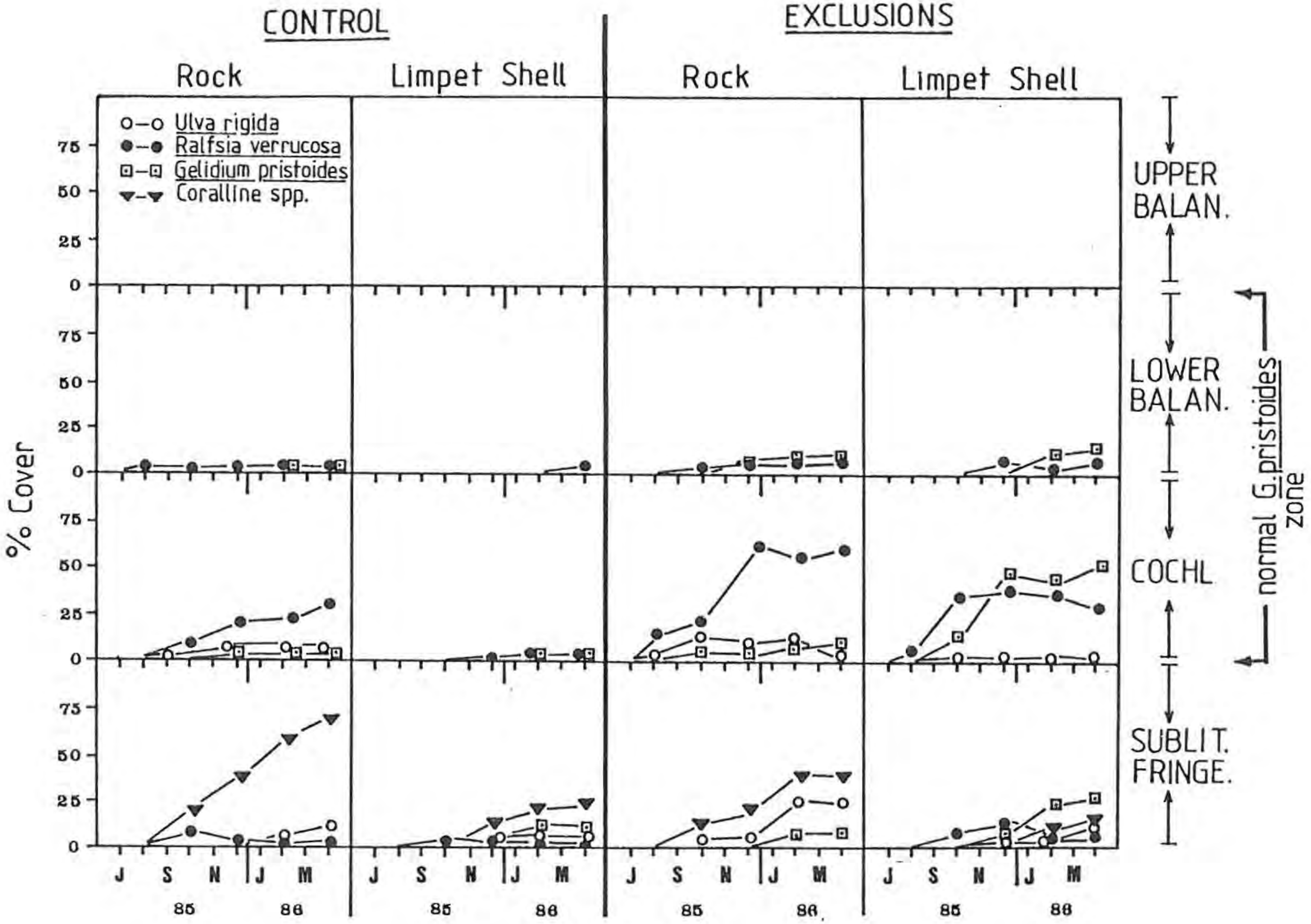

Fig. 7.8 Colonization (% cover) of cleared rock surfaces and artificially attached limpet shells, with (control) and without (exclusions) the effects of grazers, and at various elevations on the shore.

7.3.4 Horizontal distribution of G.pristoides and occurrence on various substrata

G.pristoides shows a patchy distribution within its normal vertical range at Port Alfred (Fig. 7.3 c). While most plants are found attached to the sandstone rocky substratum, the greater proportion of these plants occur in, or originate from, cracks and crevices in the rock surface (Figs. 7.9 b and 7.10 b). Furthermore, when the frequency of G.pristoides occurrence on various substrata is related to substratum availability (Fig. 7.9 c), rock takes on a much lower significance, while limpet shells become the most important substratum, particularly in the Cochlear zone where G.pristoides occurred on 97% of the limpets encountered (Fig. 7.10 c). Barnacle shells (Tetraclita serrata Darwin) show some importance as a substratum for G.pristoides attachment in the Balanoid zone, about 45-75 cm above MLWS (Fig. 7.9 c).

7.3.5 Effect of the limpet P.oculus on algal recruitment and succession

Exclusion of the limpet P.oculus from cleared rocky surfaces resulted in significantly greater algal recruitment compared to non-exclusion plots, which remained almost completely clear of algal growth, even after a year (Figs. 7.11 and 7.12). There was no obvious difference in recruitment between exclusion plots containing an artificially attached fertile G.pristoides tuft, and those without (i.e. experiments 1 and 2).

A clear trend seen within the exclusion plots was a significantly greater recruitment of G.pristoides plants on limpet shells, as opposed to rock

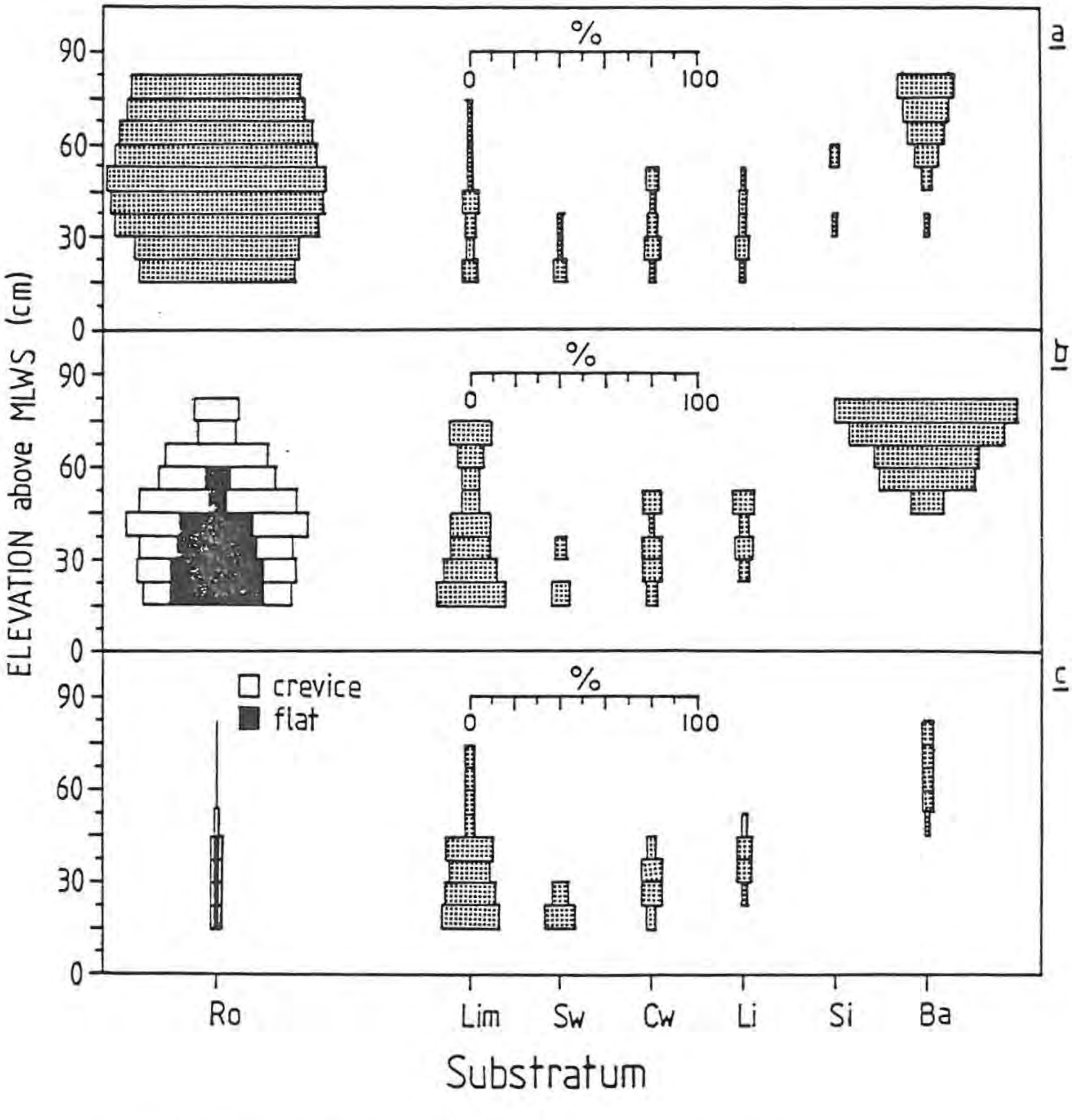

Fig. 7.9 Percentage occurrence at various elevation levels of:
a) available substrata,
b) *G.pristoides* on each substratum-type,
c) *G.pristoides* relative to the total availability of each substratum-type.
(Ro = rock; Lim = limpet, *P.oculus*; Sw = sandworm, *Gunnarea capensis* (Schm.); Cw = coralworm, *Pomatoleios krausii* (Baird); Li = encrusting coralline, *Lithothamnion* sp.; Si = limpet, *Siphonaria deflexa*; Ba = barnacle, *Tetraclita serrata* Darwin)

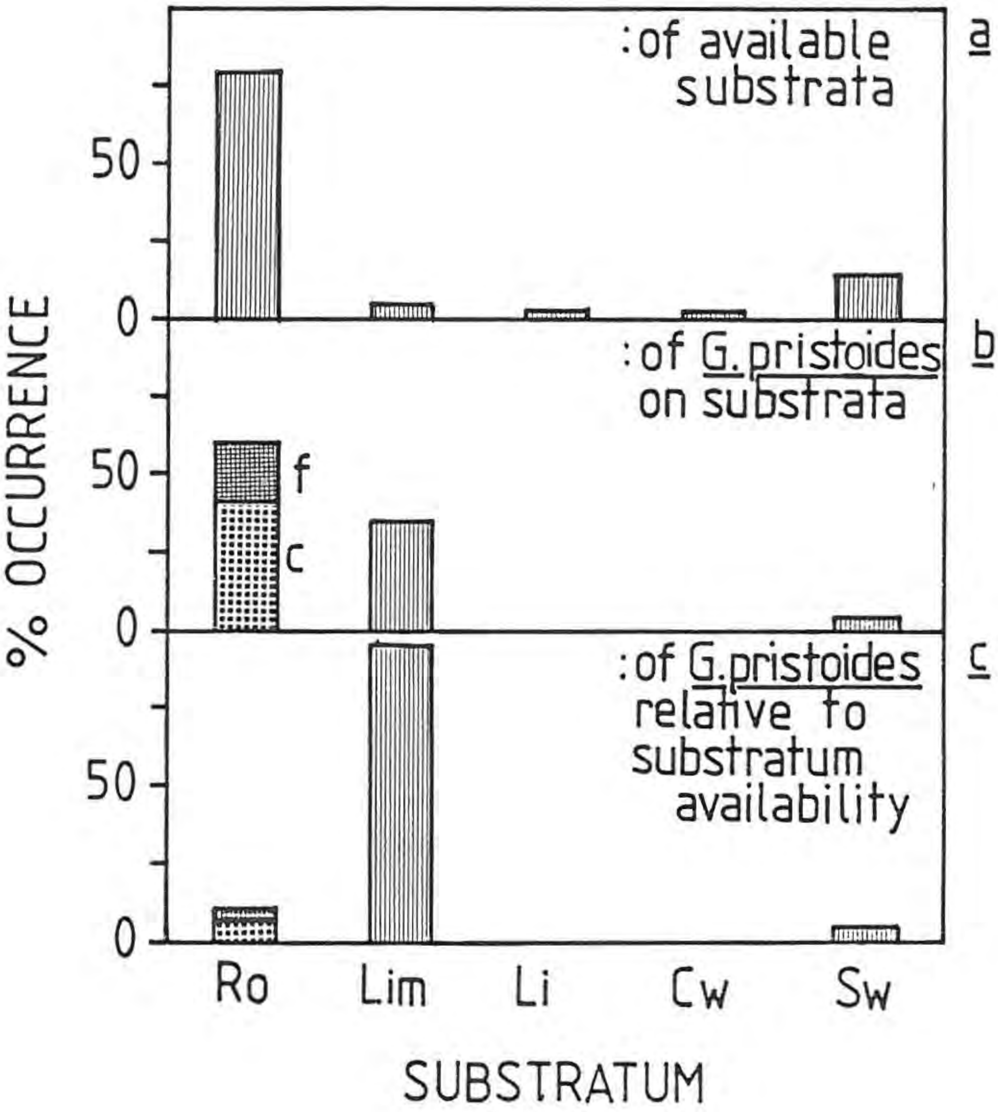

Fig. 7.10 Percentage occurrence in the Cochlear zone of:
a) available substrata,
b) *G.pristoides* on each substratum-type,
c) *G.pristoides* relative to the availability of each substratum-type.
(Key to substrata as before)

(Figs. 7.11 and 7.12). After 13 months, the Gelidium cover on limpet shells was nearly 100%. By contrast, although total algal cover on rock surfaces amounted to about 80%, the cover by G.pristoides was only in the region of 20-30%.

Observations (Fig. 7.14) also clearly indicated that successful recruitment by G.pristoides plants was largely restricted to cracks and crevices in the rock, within the limpet exclusion plots. When colonization of flat rock surfaces was successful, this was achieved by plants that initially showed the dorso-ventrally flattened creeping habit (described in Chapter 3), where plants adhere very closely to the rock surface. Typical foliose plants subsequently developed.

Although Ulva rigida C.Ag. was always the first alga to colonize the exclusion plots, its early arrival appeared not to influence the success and sequence of subsequent arrivals. Both Ralfsia verrucosa (Aresch.) J.Ag. and G.pristoides successfully colonized bare primary rock surfaces. However, in some instances, the detachment of Ralfsia crusts (probably due to drying-out, Fig. 7.16 a and b) did appear to facilitate recruitment by Ulva, followed by Gelidium. On all substrata (including limpet shells) where initial Ulva and Ralfsia recruitment was followed by Gelidium, Ulva and Ralfsia were displaced.

In addition to Ulva, Ralfsia and Gelidium, various other algae were also recorded within the limpet exclusion plots, but often in negligible amounts. An indication of the frequency at which they occurred is given in Table 7.2.

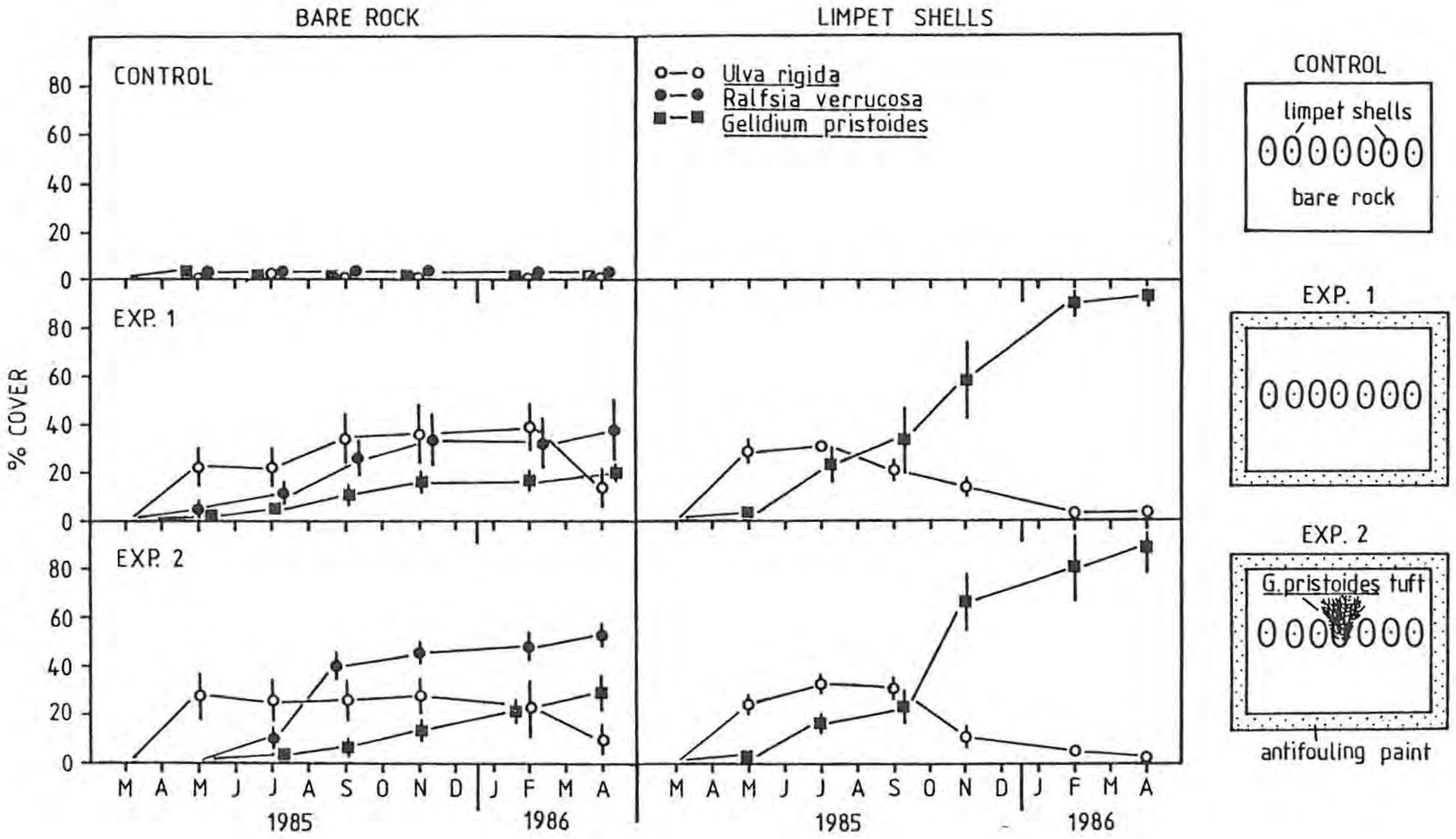

Fig. 7.11 Effects of limpet herbivore (P.oculus) on the recruitment of macroalgae, including G.pristoides, on bare rock and artificially attached limpet shells (Bars = SE).

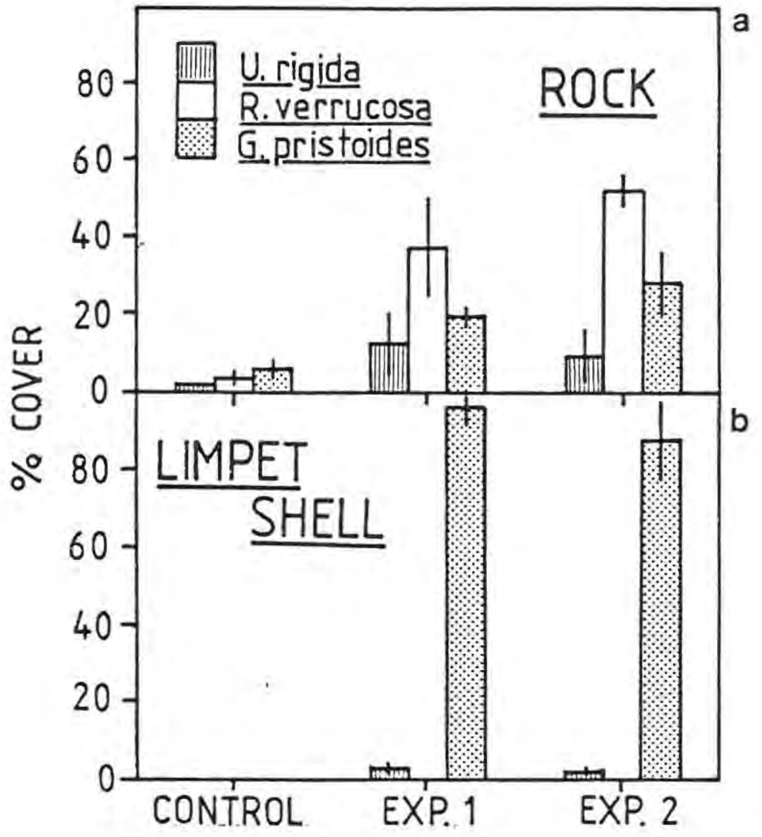

Fig. 7.12 Major changes in algal recruitment (after 13 months) within P.oculus exclusion (Exps. 1 and 2) and non-exclusion plots (control).

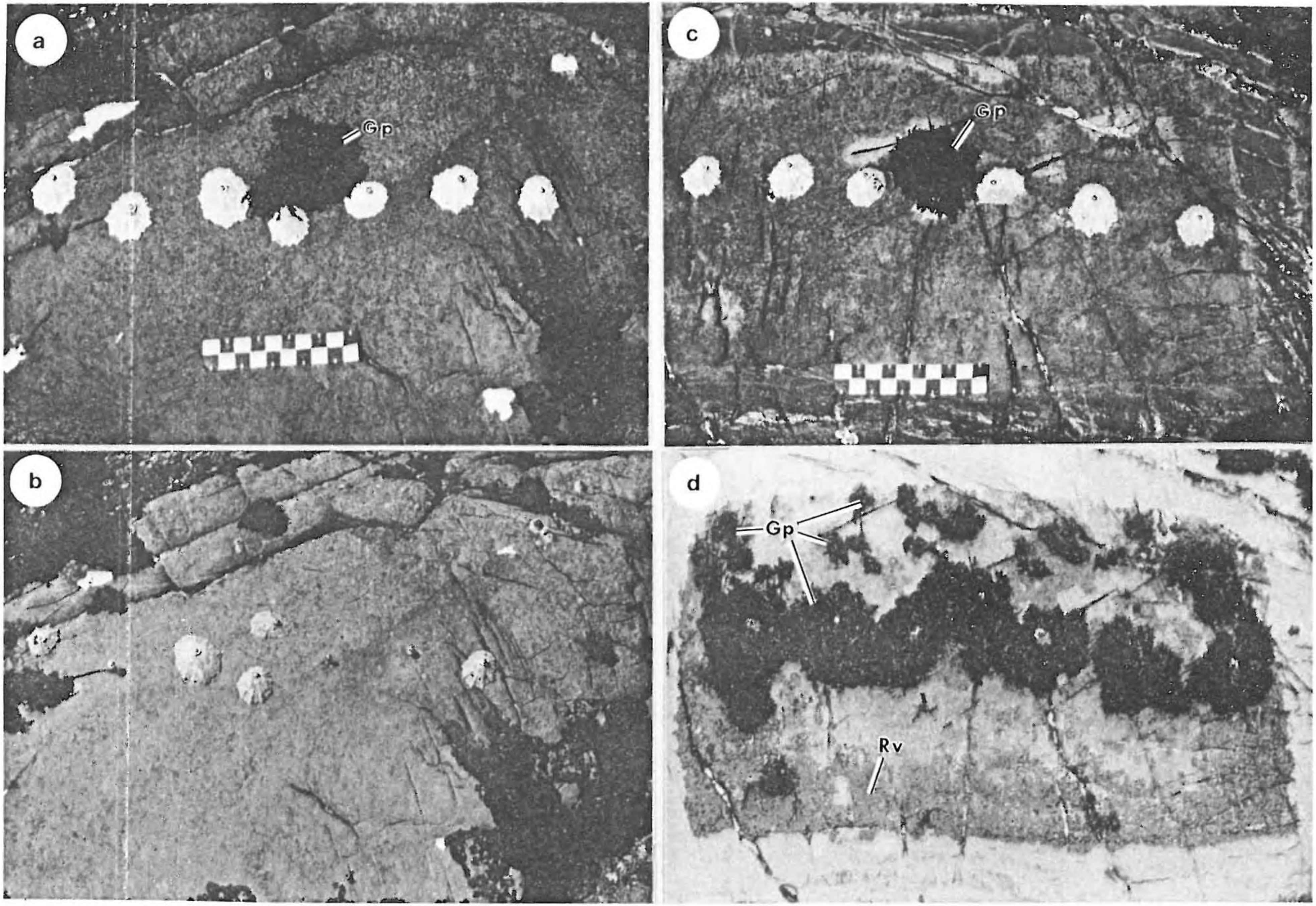

Fig. 7.13 Non-exclusion plots:
a) after initial clearing,
b) after 13 months.

Herbivore exclusion plots:
c) after initial clearing,
d) after 13 months.
(Gp = *G.pristoides*, Rv = *Ralfsia verrucosa*)

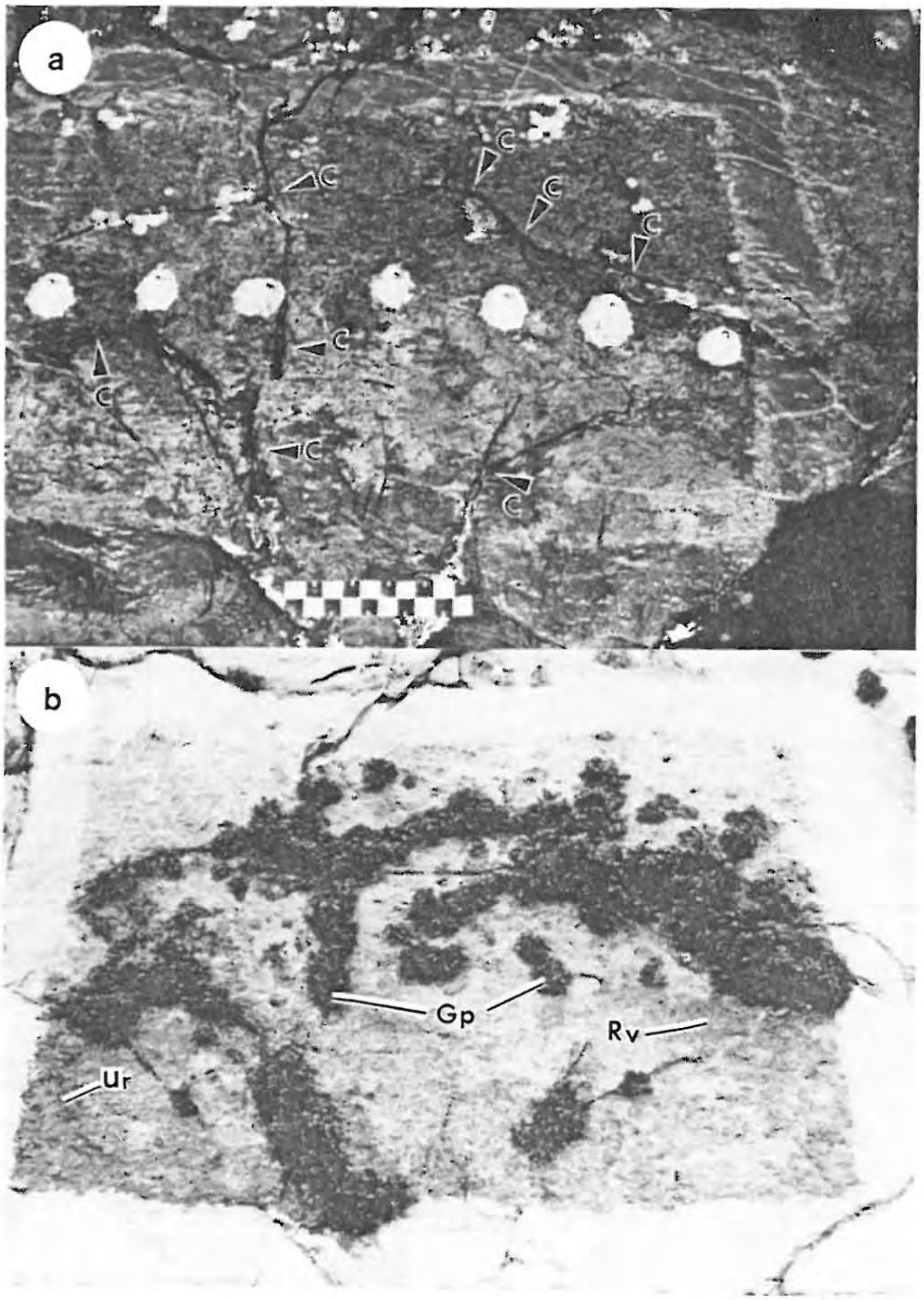

Fig. 7.14 A herbivore exclusion plot showing:
a) cracks and crevices (c) in the rock surface after initial clearing, and
b) 13 months later with *G.pristoides* recruitment largely restricted to where cracks and crevices occur (Gp = *G.pristoides*, Ur = *Ulva rigida*, Rv = *Ralfsia verrucosa*).

TABLE 7.2

Algal species recorded within herbivore exclusion plots in the Cochlear zone at Port Alfred (xxx = common and significant contribution to total cover; xx = common, but little contribution to total cover; x = occasionally present).

ALGAL SPECIES	SIGNIFICANCE
G.pristoides	xxx
R.verrucosa	xxx
U.rigida	xxx
Chaetangium erinaceum (Turn.) Papenf.	xx
Gigartina minima Kylin	xx
Hildenbrandtia sp.	xx
Iyengaria stellata (Börg.) Börg.	xx
Caulacanthus divaricatus (Suhr) Papenf.	x
Splachnidium rugosum (L.) Grev.	x

7.3.6 Strength of *G.pristoides* attachment to various substrata

During routine collections of *G.pristoides* plant material, it was noted that plants could be more easily plucked from rock substrata than from limpet shells. This was confirmed by measurements of attachment strength, which showed that a significantly greater force was required to remove *G.pristoides* fronds from limpet and barnacle shells than from rock and encrusting corallines e.g. *Lithothamnion* (Fig. 7.15).

Close examination of limpet shells bearing *G.pristoides* growth, revealed pits in their surfaces (Fig. 7.16 c and d) into which the rhizoidal attachment organs of the *Gelidium* holdfasts were seen to penetrate. The pits are uniform in size and appear to be produced by the rhizoidal organs of the seaweed.

A summary of the results and observations in this chapter is given in Figure 7.17.

7.4 DISCUSSION

7.4.1 Factors determining the vertical distribution of *G.pristoides*

At Sharks Bay, Port Alfred, *G.pristoides* growth is restricted to a vertical range of about 0.2 to 0.75 m above MLWS, which corresponds to the range reported for the seaweed at Dalebrook in the Cape Peninsula (McQuaid 1985). In terms of biological zones, this vertical distribution pattern at Port Alfred corresponds to a zone dominated by the limpet *P.oculus* (having

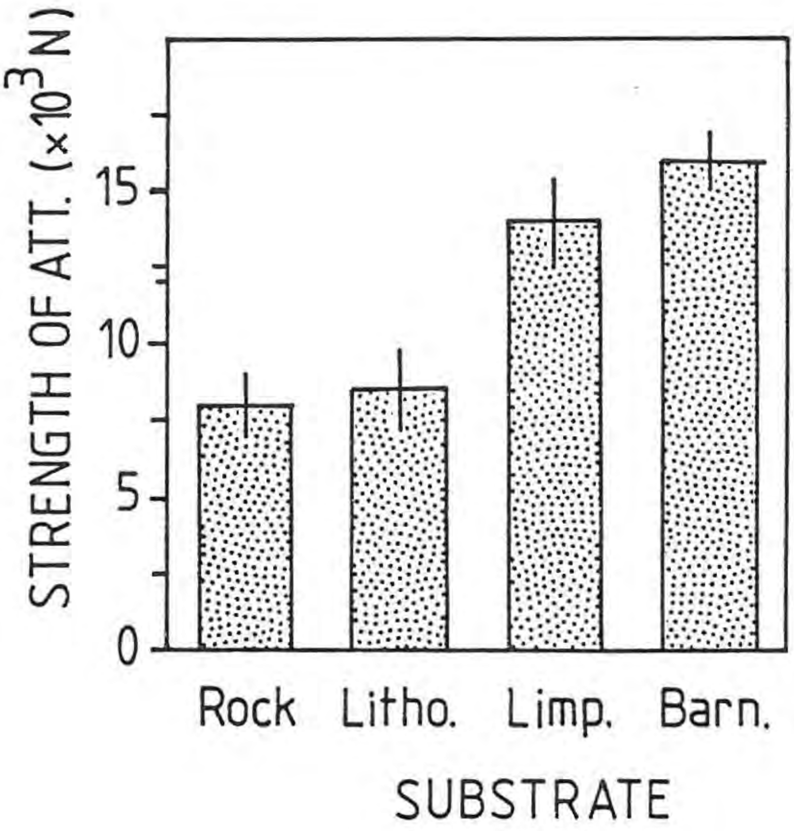

Fig. 7.15 Strength of G.pristoides attachment to four common substrata: Rock; Lithothamnion sp. (Litho.); limpet P.oculus (Limp.); and barnacle Tetraclita serrata (Barn.).

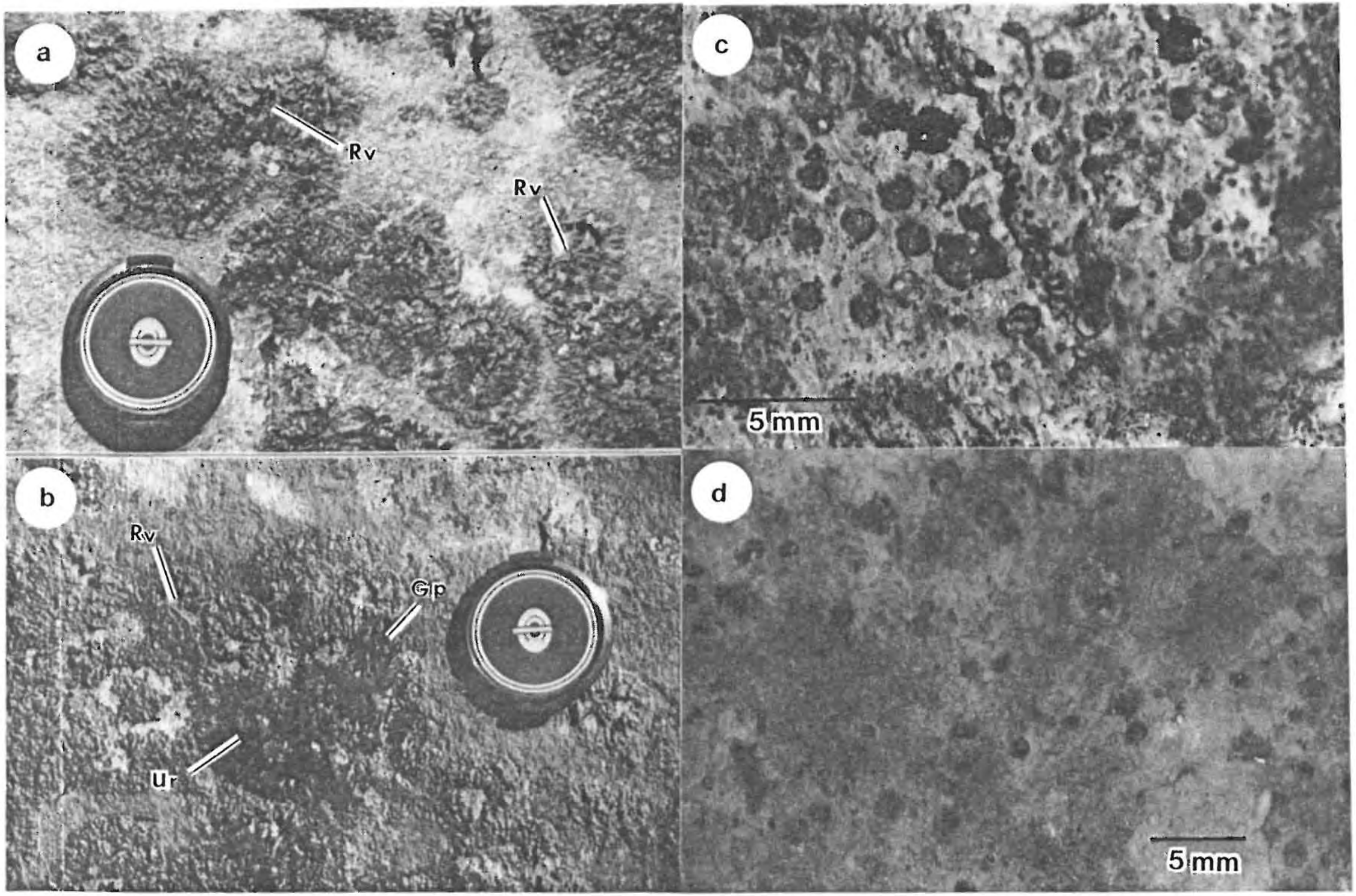

Fig. 7.16 a & b) Algal succession on bare rock within limpet exclusion plots in the Cochlear zone. a) Detachment of Ralfsia verrucosa (Rv) crusts, b) colonization of detached crust by Ulva rigida (Ur) and G.pristoides (Gp).

c & d) Pits in P.oculus shells, into which G.pristoides rhizoidal attachment organs actually penetrate.

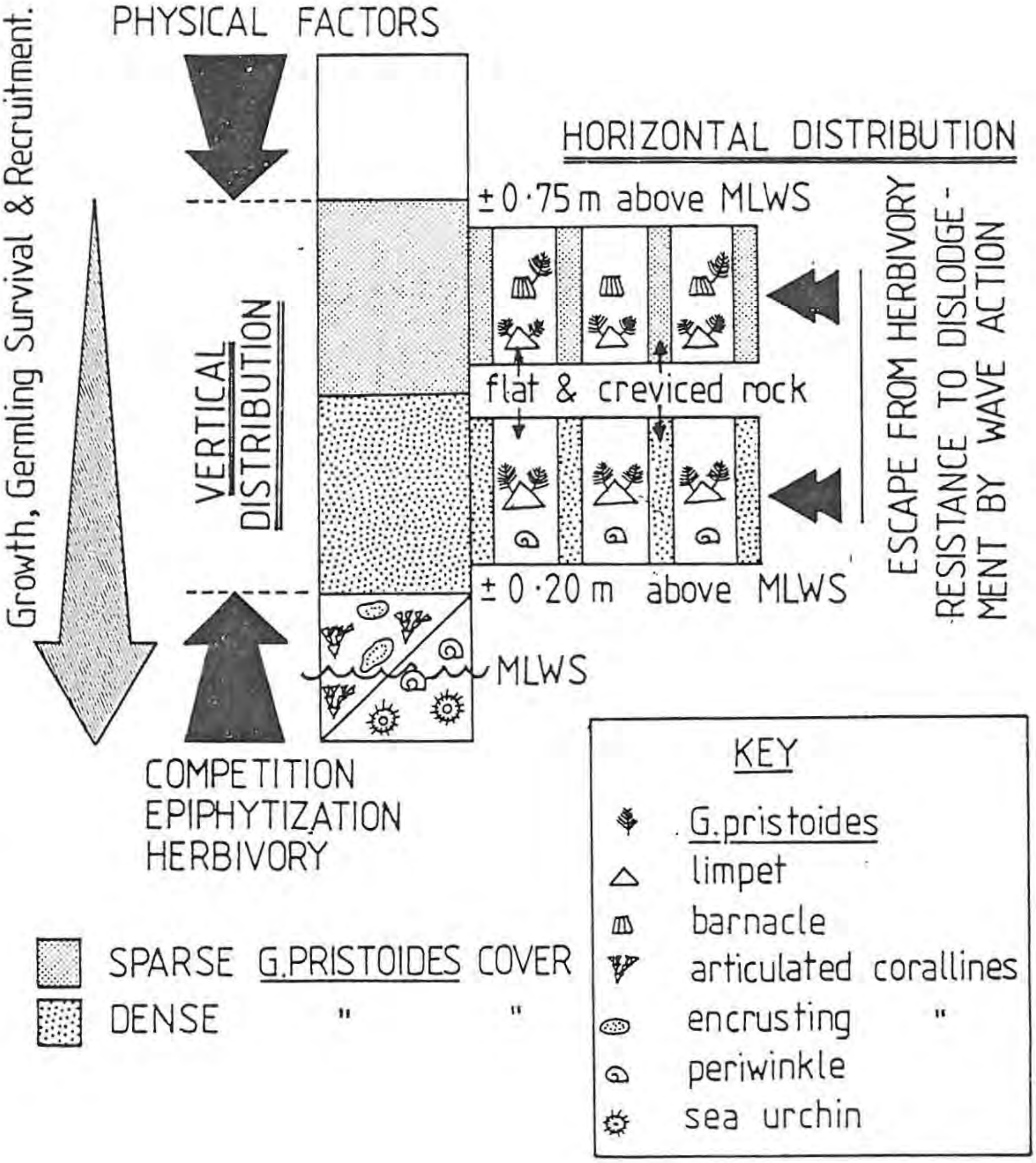

Fig. 7.17 A summary of the major factors influencing the intertidal distribution of G.pristoides at Port Alfred. The seaweed is distributed from about 0.20-0.75 m above MLWS. Frond growth, germling survival and recruitment from spores decreases with increased elevation, thus physical factors associated with prolonged emersion appear to set the upper limits of the species. The lower limits are determined by a combination of biological agents, including; competition for space with epilithic articulated (e.g. Corallina sp. and Jania sp.) and encrusting corallines (Lithothamnion sp.); epiphytization by the encrusting coralline P.patena; herbivory by the sea urchin P.angulosus, and the periwinkle O.tigrina. Plants are largely restricted to cracks and crevices in the rocky substratum and also to limpet (P.oculus) and barnacle (T.serrata) shells. This appears to be the combined result of escape from herbivory, mainly from the limpet P.oculus, and resistance to dislodgement by wave action, which on shell substrata, is enhanced by a strong attachment.

a similar elevation to the Cochlear zone seen elsewhere; Eyre et al. 1938, Stephenson et al. 1938, McQuaid 1985), and the lower Balanoid zone. G.pristoides is absent from the coralline-dominated sublittoral fringe, immediately below the Cochlear zone, and from the upper region of the Balanoid zone.

a) Upper limits

It is generally accepted that physical factors associated with prolonged periods of emersion are responsible for setting the upper limit of most intertidal macroalgae (as reviewed by Connell 1972, Lubchenco and Gaines 1981, Hawkins and Hartnoll 1983), and this has recently been confirmed for various littoral fringe algae in Britain (Hawkins and Hartnoll 1985).

Physical factors associated with increased levels of intertidal elevation appear to be important in determining the upper limits of G.pristoides at Port Alfred. Frond growth was clearly retarded while germling survival was extremely poor above the normal range of the seaweed. G.pristoides plants also became severely bleached and did not survive transplantation above the normal vertical range. Further evidence of the influence of prolonged periods of emersion on setting the upper limits of G.pristoides is the tendency for a reduced frequency and decreased stature of plants with increasing elevation. The bleaching of plants suggests that desiccation stress and solar damage are the actual limiting factors: heating caused by insolation (Schramm 1968) and nutrient shortage (Schonbeck and Norton 1979) have been sited as important limiting factors in other intertidal algae.

In addition to physical stress, competition and herbivory have been shown to affect the upper limits of some intertidal macroalgae. For example, Hawkins and Hartnoll (1985) demonstrated that certain British intertidal fucoids were able to extend their range upshore when species zoned immediately above each, were experimentally removed. The removal of herbivores has been shown to have a similar effect on intertidal macroalgae in Britain (Southward and Southward 1978), Australia (Underwood 1981, Underwood and Jernakoff 1984) and Panama (Sousa et al. 1981), while both competition and herbivory appear to influence the upper limits of Iridaea boryana (Setch. et Gardn.) Skottsb. in Chile (Jara and Moreno 1984).

Present results show that neither herbivory nor competition with other algae influence the upper limits of G.pristoides. Grazer exclusion plots situated above the normal range of the seaweed were not colonized by any algae. Here again, G.pristoides recruitment correlated with elevation and immersion time, with maximum recruitment occurring at lower elevations within the normal range of the seaweed. Furthermore, since no other algal species occupies any appreciable amount of space towards the upper limits of G.pristoides distribution, competition can, with reasonable certainty, be excluded as a possible factor influencing the upper limits of the seaweed at Port Alfred. It is therefore concluded that the upper limits of G.pristoides populations at Port Alfred are determined solely by physical factors associated with elevation and prolonged emersion (Fig. 7.17).

b) Lower limits

Numerous studies have demonstrated that the growth of intertidal macroalgae is either unaffected when they are transplanted below their normal vertical ranges (Hruby 1976, Lubchenco 1980) or enhanced when they are subjected to longer than normal periods of submergence in culture (Edwards 1977) and _in situ_ (Schonbeck and Norton 1980). The present study showed similar results for _G.pristoides_, where frond growth was unaffected and germling survival was enhanced in the sublittoral fringe, below the normal vertical range of the seaweed. However, _G.pristoides_ is completely absent from the sublittoral fringe.

A further generalization that has emerged regarding vertical patterns of algal distribution, is that biological interactions, including competition and herbivory, are largely responsible for setting the lower limits of intertidal macroalgae. Competition for space apparently determines the lower limits of _Iridaea cordata_ (Turn.) Bory (Hruby 1976) and five fucoid species in Britain (Hawkins and Hartnoll 1985), while grazing by sea urchins is believed to prevent the downward extension of _Laminaria hyperborea_ (Gunn.) Fosl. in Britain (Jones and Kain 1967) and various foliose species in Australia (Underwood and Jernakoff 1981). A combination of competition and herbivory effect the lower limits of _Fucus_ species on New England rocky shores, where competition by _Chondrus crispus_ Stackh. is facilitated by the activities of grazers such as _Littorina littorea_ L. (Menge 1976, Lubchenco 1980).

At Port Alfred, a combination of biological factors also appears to prevent the downward extension of _G.pristoides_ into the sublittoral fringe (see Fig. 7.17). Firstly, the negative affect of grazing on _Gelidium_ recruitment in the sublittoral fringe was evident from the absence of plants in non-exclusion plots, whereas successful recruitment occurred where grazers were excluded. Two common herbivores occurring in this zone are the sea urchin Parechinus angulosus (Leske) and the periwinkle Oxystele tigrina (Chemn.), and which are often associated with boulders and flat rock surfaces that are completely clear of algal cover, inluding G.pristoides. The maintenance of similar clear areas has been attributed to urchin grazing on rocky shores in both the U.S.A. (Paine and Vadas 1969, Dayton 1975) and Australia (Underwood and Jernakoff 1981).

Secondly, epiphytization (by Polyporolithon patena) and competition with various coralline algae (Corallina sp. and Jania sp.), which normally dominate the sublittoral fringe, apparently also prevents the downward extension of G.pristoides into this zone. Rapid coralline recruitment has also been reported on the rocky shores of Oregon, U.S.A. (Padilla 1984). The way in which the epilithic corallines competitively exclude G.pristoides is unclear. Articulated forms did, however, tend to smother and interfere with the Gelidium recruits within the exclusion plots, while encrusting forms are well known for their ability to slough epithelial cells, thus preventing overgrowth by other macroalgae (Masaki et al. 1984, Johnson and Mann 1986).

c) Vertical distribution and the niche width concept

As a result of the clearly defined environmental gradients associated with intertidal habitats, studies on the vertical distribution patterns of intertidal organisms have made a significant contribution to the current understanding of the niche width concept. Hutchinson (1958) originally drew the distinction between the concepts of "fundamental" niche (the resources available to an organism in the absence of biotic interference) and "realized" niche (where limiting biotic factors are considered). However, instead of focusing on the differences between these two types of niche, Lubchenco (1980) suggests that the emphasis should be on the factors determining the width of the "realized" niche, since this is where all natural selection takes place. In this regard, Lubchenco suggests that one should attempt to identify, in addition to the limiting factors (i.e. biotic and abiotic influences), the adaptations and "trade-offs" that define the realized niche width of a particular organism.

In evaluating the results of the present and previous chapters (3 and 4) several speculations can be made concerning possible adaptations and "trade-offs" in G.pristoides, in relation to its vertical pattern of distribution. While being subjected to greater physical stress, the occupation of more elevated positions in the intertidal zone carries obvious benefits, e.g. less competition and herbivore pressure. The abundant G.pristoides growth in the intertidal zone in comparison to the low frequency of other Gelidium species (e.g. G.amansii) in the sublittoral, where emersion related stress is lower, but competitive stress higher, is perhaps indicative of this. However, survival in an intertidal habitat depends on the degree of success achieved in adapting to harsher physical conditions. One possible adaptation in G.pristoides is the production of bispores, which tend to be larger than the tetraspores produced by other Gelidium species, and can perhaps better survive prolonged emersion. However, here a "trade-off" (in the sense used by Lubchenco 1980) occurs, since recruitment of G.pristoides from spores and germling success, is greatly retarded in the intertidal environment.

A further possible trade-off mentioned by Lubchenco is the occupation of intertidal habitats at the expense of growth capacity. It has been demonstrated that algae which grow higher on the shore are better able to withstand desiccation, but have slower growth rates than algae growing lower down (Schonbeck and Norton 1978). However, the similar growth rates that G.pristoides exhibited within its normal intertidal range, in comparison to that in the sublittoral fringe, is perhaps indicative of the success that the species has achieved in adapting to an intertidal existence. It is presently suggested that this has been achieved primarily through the evolution of wing-like parts (from an ancestral terete form), resulting in flattened fronds, which are somehow advantageous for withstanding desiccation.

7.4.2 Factors determing the horizontal distribution of G.pristoides

G.pristoides shows a patchy distribution within its normal intertidal range, with most of the available rocky substratum remaining completely devoid of algal growth. Furthermore, juvenile Gelidium plants are rare, and the maintenance of natural stocks occurs largely by vegetative propagation of existing tufts (see Chapters 3 and 6). The frequent occurrence of limpets with heavy algal growth on their shells, surrounded by bare rock surfaces (Fig. 7.1), led Branch (1971) to suggest that limpet grazing is a major factor influencing algal recruitment on South African rocky shores.

a) The effect of herbivory on G.pristoides recruitment

The limpet P.oculus is the most common herbivore occurring within the G.pristoides belt at Port Alfred, and is considered to be both highly mobile and an active grazer (Branch 1975, Branch and Newell 1978). Exclusion experiments, using antifouling paint barriers, showed that this limpet has a profound negative effect on the successful recruitment of rocky substrata by various macroalgae, including G.pristoides. After a period of 13 months, the total algal cover within the exclusion plots amounted to 80% (20-30% G.pristoides), while non-exclusion plots remained comparatively bare. Limpets have also been shown to be important regulators of algal recruitment in other parts of the world (e.g. Dayton 1971, Southward and Southward 1978, Hawkins and Hartnoll 1981, Underwood and Jernakoff 1981, Jernakoff 1983, 1985).

In addition to the grazing activities of P.oculus, other herbivores such as the periwinkle O.tigrina probably also influence algal recruitment within the G.pristoides zone at Port Alfred. Toxic antifouling paints do not tend to restrict the movement of these gastropod snails (Hawkins and Hartnoll 1983, and pers. obs.), therefore, the total exclusion of all herbivores might have produced even more dramatic results. Poor algal recruitment has previously been associated with grazing by various other intertidal animals including snail-like gastropods (Lubchenco 1982, 1983, Jernakoff 1983), sea urchins (Jones and Kain 1967, Paine and Vadas 1969, Dayton 1975, Menge 1976, Sousa et al. 1981) and inshore reef fish (John and Pople 1973, Joubert and Hanekom 1980).

The sequence of algal succession within the limpet exclusion plots followed a pattern which has been seen in most previous colonization (Bokenham and Stephenson 1938, Northcraft 1948, Hruby and Norton 1979) and exclusion studies (e.g. Sousa 1979, Hawkins 1981, Lubchenco 1983). Fast growing ephemerals (Ulva rigida) were followed by slower growing perennials (mainly Ralfsia verrucosa and G.pristoides). Early colonists generally did not determine the sequence of subsequent arrivals, and all the major colonizers were capable of successful recruitment on bare primary substrata. Occasionally, however, Ralfsia crust became partially detached, apparently due to drying-out, and both Ulva and G.pristoides recruitment tended to be enhanced among the detached crusts, which probably trap water-borne spores and provide shade, moisture and protection from dislodgement by wave-wash. On all occasions where G.pristoides recruitment was preceded by Ulva or Ralfsia, the latter two algae became overgrown by G.pristoides and were displaced. This was particularly evident on limpet shells, and demonstrates a high competitive ability in G.pristoides.

b) The importance of refuges in the horizontal distribution of G.pristoides

Refuges or "escapes" from grazing are considered to be major sources of patchiness in the distribution of intertidal algae (Dayton 1971, Menge 1976, Menge and Lubchenco 1981). Refuges from grazers may for instance include cracks and crevices in rock surfaces and even plant size. For example, Lubchenco (1983) showed that the gastropod Littorina littorea L. only regulates the recruitment of Fucus on flat rock surfaces on New England shores. Cracks and crevices, and inaccessible spaces between barnacles provide refuges for small grazer-vulnerable Fucus germlings, which after attaining a certain size, become less susceptible to grazing pressure.

At Port Alfred, G.pristoides plants tend to occur more frequently in cracks and crevices than on flat rock surfaces. This probably to a large extent reflects the recruitment of grazer-free refuges that are inaccessible to P.oculus. However, present observations showed that even within the grazer exclusion plots, G.pristoides recruitment was still largely restricted to cracks and crevices, suggesting therefore that they provide additional conditions that facilitate G.pristoides recruitment. Cracks and crevices undoubtedly provide shaded and moist conditions under which spore germination and germling growth would be enhanced, while they may also afford juvenile stages some protection from dislodgement by wave action until holdfasts are established. G.pristoides plants that do occur on flat rock surfaces were obviously missed during the grazer-vulnerable germling stage, and with increased size and development have become immune to grazing and more resistant to dislodgement by wave action. It is interesting that during initial recruitment on flat rock surfaces and limpet shells, G.pristoides plants took the form of dorso-ventrally flattened creeping axes (see Chapter 3) that adhered very closely to the substratum, and perhaps represent an adaptation for recruitment on these exposed and vulnerable substrata.

The refuge concept may also partly explain the high incidence of G.pristoides growth on the shells of P.oculus at Port Alfred, and elsewhere on the eastern Cape coast. P.oculus is known to exhibit intraspecific aggression and territorial behaviour (Branch 1975, and pers. comm.), thus their shells would not be grazed by other individuals and would provide refuges for algal recruitment. Evidence for this is provided by the fact that artificially attached, dead limpet shells within the non-exclusion plots, remained completely bare of algal growth (since grazing on the shells was unrestricted), while shells in the exclusion plots were readily colonized. Barnacles situated higher up in the G.pristoides zone appear to provide similar refuges, their shells not being easily traversible by grazers. Hawkins (1981) reported that both barnacle shells and the narrow gaps between individuals, provide grazer-free refuges for certain macroalgae on British shores. In contrast, however, Jernakoff (1983, 1985) found that algal recruitment on rocky shores of N.S.W., Australia, was not determined by the availability of grazer-free refuges among barnacles. He further pointed out that previous studies (e.g. Hawkins 1981) did not attempt to distinguish between recruitment due to "escapes from grazing", and that reflecting resistance to dislodgement by wave-wash as a result of secure attachment.

Present results showed that within the grazer exclusion plots, G.pristoides recruitment was significantly greater on artificially attached limpet shells (almost 100% cover) than on rocky substrata (about 30% cover). The fact that limpet shells in the non-exclusion control plots remained completely bare of algal growth indicates that the high recruitment on limpet shells within the exclusion plots is not an artifact resulting from the method of shell attachment, but rather reflects some biological process. Cullinane et al. (1984) reported that Gracilaria verrucosa (Huds.) Papenf. in Ireland is also more frequently attached to shells and shell fragments than any other substrata.

Substratum surface relief is considered to be an important factor that regulates algal recruitment (Pomerat and Weiss 1946, Harlin and Lindbergh 1977). Jernakoff (1986) demonstrated that barnacles were crucial for the recruitment of <u>Gelidium pusillum</u> (Stackh.) Le Jol., and suggested that the texture of the barnacle shells may provide a better site for attachment than bare rock. Measurements revealed that <u>G.pristoides</u> plants are attached more securely to limpet and barnacle shells than to rock and encrusting coralline thalli. Therefore, limpet and barnacle shells appear to be providing, in addition to refuges from grazing, substrata on which a secure attachment can be achieved, thus enhancing resistance to dislodgement by wave action. While the ribbed shells of the barnacle <u>T.serrata</u> probably enhances the strength of attachment by <u>G.pristoides</u> at Port Alfred, <u>P.oculus</u> shells are generally smooth by comparison. Observations indicate, however, that the secure attachment to limpet shells is achieved by the presence of pits in the shell surface, into which the rhizoidal attachment organs of <u>G.pristoides</u> penetrate. Since the pits are regular in size and only occur in association with rhizoidal organs, it seems certain that they are produced by the rhizoidal organs themselves, perhaps by the release of a substance that dissolves calcium carbonate. Certain green algal species are also known to bore into shell substrata (Wilkinson and Burrows 1972, Harris <u>et al</u>. 1986). It is not known whether this apparent ability of <u>G.pristoides</u> to form rhizoidal pits in limpet shells is merely coincidental, or whether it represents a feature derived through a process of natural selection. Whatever the origin, it would appear that the resultant secure attachment to limpet shells and greater resistance to wave dislodgement, contributes to the success of the seaweed in the intertidal zone, particularly under conditions of severe herbivore pressure.

CHAPTER 8

Some socio-economic aspects of the Gelidium harvesting industry in southern Africa.

8.1 INTRODUCTION

Since the Gelidium harvesting industry in southern Africa relies heavily on a suitable labour force, socio-economic as well as biological factors must be considered in the formulation of management policies governing the use of this resource. Economic development, as Cherns (1980) points out, cannot be justified without a corresponding enhancement of the quality of human life, and the importance of socio-economic factors in development is stressed by modern workers in this field (e.g. Laker 1981). The aim of this chapter is simply to draw attention to some of these factors which have, and will continue to influence the development of the Gelidium industry in southern Africa.

Approximately 80% of harvested G.pristoides is obtained from South African shores, and the remainder from the Transkei, which is the major source of G.amansii and G.versicolor. The Transkei has therefore been included in this part of the study, although harvesting practices differ between the two countries (as described later).

8.2 REGULATIONS GOVERNING SEAWEED HARVESTING

In South Africa, seaweed harvesting is controlled by the Sea Fisheries

Act of 1973 (Act 58), the provisions of which are enforced by the Marine Development Branch of the Department of Environment Affairs. In terms of this Act, the southern and eastern shores of the country are divided into five concession areas and permits to harvest seaweed in each area are awarded on a tender basis, and are renewable every 5 years. The permit-holder has the exclusive right to remove seaweeds from the shore, subject to certain conditions, including: that no shellfish or organisms other than seaweeds are to be disturbed or removed; that seaweeds are to be removed by plucking (since the use of implements is considered to encourage the removal of shellfish); and that harvesters must be registered with the permit-holder and wear identification bearing details of the permit-holder. The Minister of Environment Affairs may at any time withdraw the permit in respect of part or all of the concession area.

In the Transkei, access to the marine resource is open, except in Nature Reserves, and anyone may collect seaweeds. There are no regulations concerning the method of plant removal, and collection of Gelidium species (mainly G.amansii and G.versicolor) is both uncontrolled and uncoordinated.

At present, harvesting operations in South Africa and Transkei are conducted by a single company, Taurus Products (Pty) Ltd, who, until recently, carried out the processing of Gelidium for export (final drying, sorting and packing) at a factory in Butterworth, Transkei. This company has now built an agar processing plant in Lüderitz, S.W.A. (discussed later).

8.3 THE LABOUR RESOURCE (HARVESTERS)

Between 60 and 100 seaweed harvesters are employed in South Africa. Harvesters operate in teams of 10-15, and are transported to collection sites over the 5-6 days during each spring tide. Collection is carried out under the direction of a supervisor. Harvesters are recruited from areas close to the collection sites, and the numbers from each area vary according to their availability and the extent of the seaweed stocks. In the Transkei, most of the 600-1 000 harvesters operate independently, having no formal association with the company.

The vast majority of the African harvesters are from a rural and illiterate background, most of whom were previously employed as farm labourers. African tribal culture still plays an important role in the lives of the rural Africans in South Africa and Transkei, in which aspirations for self-fulfilment are low and the good of the family and community is stressed (McWilliam-Smith 1981).

Women constitute most of the seaweed harvesting work-force. In the Transkei, in particular, women are the major source of labour due to the migration of adult males to the urban centres and mines in the Transvaal in search of work. Women are also the prime decision makers in the household and often contribute substantially to the total family income. According to Bembridge (1984), the role of women in the economic development of the Transkei has, thus far, not been fully recognised.

In South Africa, the harvesters are employed throughout the year on a "casual" basis, and are remunerated according to the amount of seaweed that they collect. At present, an average of R0.53 is paid per kg dry weight of Gelidium. Over a period of 5-6 days during low spring tides, when G.pristoides can be picked, a single harvester may earn in the region of R50.00 to R60.00, giving an average monthly income of R100.00 to R120.00. The harvesters are also given cash bonuses for continued good quality pickings (i.e. absence of unwanted species and impurities) and on consistently good production. Other benefits include a limited range of basic commodities, e.g. tea, coffee, sugar, salt etc.

In the Transkei, however, where there is a "wild" staff rotation, and the bulk of production comprises the subtidal species G.amansii and G.versicolor, seaweeds can only be collected in significant quantities during Equinox spring tides twice a year. During this period a harvester may earn up to R100.00. Seaweed collecting during the rest of the year is hampered by rough surf and tides that are not sufficiently low for collecting. Therefore, in contrast with the situation in South Africa, Transkei harvesting and remuneration is more seasonal and less predictable. As a result of the "wild" staff rotation, no figures are available on the per capita income of labourers in the Transkei.

One of the controversies surrounding the collection of seaweeds is the concurrent removal of other intertidal organisms. Shellfish are removed either accidentally (i.e. G.pristoides attached to limpet shells) or deliberately to supplement income or diet. In the Port Elizabeth area recently, harvesting was temporarily halted in response to public outcry against the removal of shellfish. The seaweed company attributed this breach in the permit regulations to poor supervision. The supervisor concerned was duly dismissed.

8.4 ECONOMIC FACTORS

Gelidium production figures for South Africa during the past 20 years (mainly G.pristoides), are given in Figure 8.1. In the past 10 or so years, Gelidium yields have increased dramatically, coincident with the establishment of the company now responsible for most of the seaweed harvesting in South Africa. Combined annual Gelidium yields for South Africa and the Transkei are now in the region of 100 tonnes dry weight, which up until recently, was all exported to Japan for processing. Prices obtained for the dried seaweed depend on yields in Japan, Chile and Argentina, and may vary between US$600 and US$2300 per dry tonne. The quality of the product, i.e. agar yield, gel strength, gel clarity, is also important in determining prices.

Prior to 1980, agar producing seaweeds, including species of both Gelidium and Gracilaria, were processed locally and the agar exported to Germany, Finland and Italy (the local demand for agar was at that time comparatively small, at about 3-12 tonnes per annum). With the subsequent economic boom in the early 1980s and the strong Rand against foreign currencies, it was no longer economically viable to process locally for export. However, with the situation presently being the reverse (i.e. a weak Rand and depressed economy), local processing has again become viable and a processing plant has just recently gone into operation at Lüderitz in South West Africa (where Gracilaria is collected), at an estimated construc-

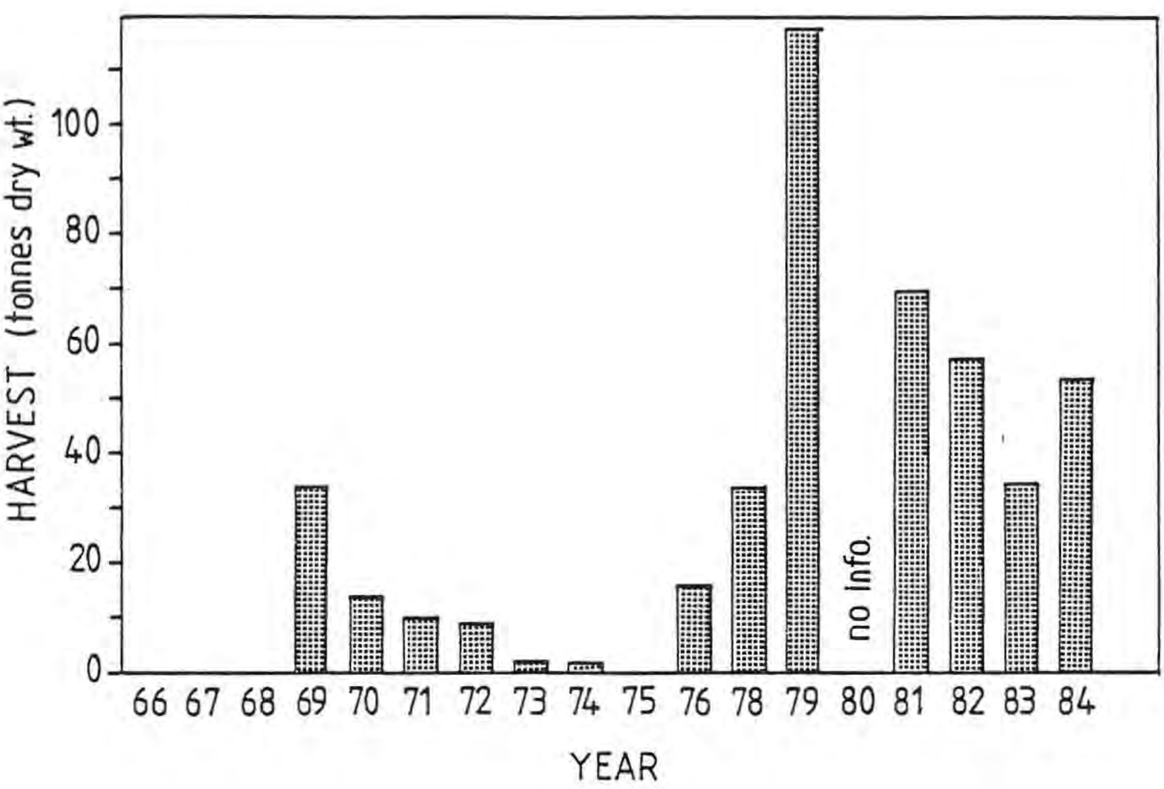

Fig. 8.1 *Gelidium* harvest figures for South Africa during the past 20 years (values obtained from annual reports of the Department of Environment Affairs, Marine Development Branch).

tion cost of R1 million.

Present agar prices range between US$10 and US$32 per kilogram, depending once again on market conditions and agar quality. Assuming an average agar yield of 20% (per g. dry wt. of seaweed) and present market values, it is estimated that the agar produced locally may yield a financial return that is three times greater (R10 000 - 32 000 per tonne) than that which is obtained from exporting sufficient seaweed to produce the same quantity of agar (R3 000 - 11 500 per tonne). Against these increased returns, the cost of building and running the agar plant must be offset. It is estimated (Taurus Products, pers. com.) that this plant will provide employment for 60-100 workers.

8.5 DISCUSSION

Probably the most contentious issue surrounding the Gelidium harvesting industry in South Africa is the simultaneous removal of shellfish by the harvesters, to supplement their diet and income. The removal of shellfish is also a problem in the Transkei, where the intensity of removals has increased dramatically over the past 15 years, due to human population pressure and other factors such as drought and crop failure (Hockey and Bosman 1986). The most important single prey item is the brown mussel Perna perna (L.), while mobile gastropods, including numerous limpet species, are also removed in large amounts.

As aforesaid, harvesting of G.pristoides was recently temporarily halted at Port Elizabeth, on the eastern Cape shore of South Africa, as a result of public outcry against the removal of shellfish. Although harvesting was resumed after a few months, the temporary halt in operations meant that seaweed production during this period was below optimum, and the harvesters received less income. If the harvesters, the harvesting industry and the public are to be satisfied, the aim should be to establish a stable, well-trained and reliable work-force who will have no incentive to remove shellfish. To this end, careful selection of labourers is important, and consideration should perhaps be given to employing relatives or close associates of presently reliable workers, to create a cohesive work-force where self-restricting influences will discourage shellfish removal. The current system of awarding bonuses for good work (a recognised method of increasing reliability and efficiency) is creditable, in this regard.

According to Thomas (1982), about 20% of the 970 000 Transkeian work-force are unemployed, while 69% of the rural population live below the Minimum Level of Living (MLL) (Bembridge 1984), which for a rural family of six is considered to be a total monthly income of R188.00 (De Klerk 1984). However, nutritional habits, together with the system of communal family kinship obligation, tends to cushion the effects of poverty (Bembridge 1984). Although the harvesting of predominantly subtidal Gelidium species is largely seasonal and unpredictable, seaweed collecting at least provides an alternative source of income for the 600-1000 "wild" staff in the Transkei.

In South Africa, it is possible for a harvester to receive a regular income of about R100 to R120 per month, since the harvesting of the intertidal G.pristoides can be conducted throughout the year, albeit for only 10-12 days during the two spring tides of each month. Although the remuneration received would make a significant contribution to the family income, perhaps raising it above the MLL, De Klerk (1984) indicated that the financial stability of rural workers is greatly dependent on permanent wages and the number of permanent workers in a family. It is suggested that once a suitable work-force has been established, the seaweed company should seriously consider adopting a system whereby a proportion of the predicted income of a harvester is guaranteed. Other permanent employment benefits such as unemployment insurance and some form of medical aid should also be considered.

Obviously, for the seaweed company to consider the long-term interests of the harvesters, it must assured of access to the seaweed resource in the long-term. Presently, the permit to harvest is renewable every five years, and may be withdrawn at any time by the issuing authorities. While is recognised that proper leasing arrangements are essential for controlling poor management and over-exploitation of the Gelidium resources, it is suggested that some consideration be given to increasing the duration of the permit, or by some other agreement, guarantee the company future access to the resource, thus enabling it to make long-term plans for the development of the industry.

The construction of an agar processing plant at Lüderitz, at a cost of approximately R1 million, is evidence of a commitment by Taurus Products (Pty) Ltd to the long-term development of the southern African agar industry. At present, most agarophytes are processed in Japan (McHugh 1984). Besides creating employment, and other economic benefits, the opportunity will exist for southern Africa to become self-sufficient in terms of agar, an important consideration with the current threat of increased economic sanctions against South Africa. Furthermore, Taurus Products (Pty) Ltd will be able to extract carrageenans at this factory, using a method similar to that for agar extraction. This creates the opportunity to develop a carrageenan industry in southern Africa, which could initiate the commercial exploitation of the common carrageenophytes that occur on these coasts (eg. Gigartina radula (Esper.) J.Ag. and Hypnea spicifera (Suhr) Harv.).

Although the above economic considerations are important for the development of the local Gelidium harvesting industry, the industry is fortunate in having a local rural population to provide a suitable labour resource for collecting the seaweeds. It is therefore imperative that, in the course of further development, cognizance be taken of the needs and well-being of these people.

CHAPTER 9

GENERAL DISCUSSION

The commercial exploitation of renewable marine resources has frequently resulted in a severe depletion or even extinction of the resource itself (Crutchfield 1982). Since resources of the sea are common property, society has the right to expect that they are properly managed and conserved for future prosperity. According to Huftschmidt and Carpenter (1982), the key to reconciling the objectives of commercial exploitation with those of conservation, lies in the formulation of a management plan that is geared towards the long-term maintenance of the resource. Since the present study is essentially biological in nature, a summary of findings which are relevant to the management and long-term maintenance of the G.pristoides resource in the eastern Cape is provided here.

Reproduction in G.pristoides is similar to that seen in most other Gelidiaceae (with a Polysiphonia-type life history), and although bispores rather than tetraspores are produced, they are the products of normal meiosis. There is no seasonality in the proportions of gametophytes and bisporophytes, which are present and produce viable spores throughout the year. However, whether these spores are likely to survive and produce new plants throughout the year, would be difficult to measure, and remains unknown. What is important in management is that short-term recovery in natural populations is chiefly by vegetative regeneration, and recruitment by spores appears to be relatively unimportant. Furthermore, the Gelidium turf, although closely related to G.pristoides, cannot be considered as a source of spores for the long-term maintenance of G.pristoides populations.

This study clearly shows that the upper and lower limits of vertical distribution of G.pristoides are determined, respectively, by physical factors (desiccation stress etc.) and biological factors (herbivory and competition), confirming the recent general hypothesis of Hawkins and Hartnoll (1983) for most intertidal algae. However, this is the first study to clearly implicate epiphytic growth as having a major influence in setting the lower distribution limits of an intertidal alga. The importance of grazers (in this case mainly the limpet P.oculus) in determining the horizontal distribution pattern of G.pristoides, is clearly shown from the results of experimental exclusion plots, and it is tempting to suggest that removal of limpets may be a means of increasing G.pristoides standing crops. However, this would almost certainly arouse controversy, and requires further study.

Summer would appear to be the best time for harvesting G.pristoides, since agar content is highest (up to 48% per dry weight), standing crops are maximal, and both normal growth and recovery after harvesting are most rapid. In terms of rate of recovery alone, a period of only two months would appear to be necessary for a harvested G.pristoides tuft to grow back to its original level of biomass. However, harvesting frequency (at any one site) must take other factors into account. The most obvious is that commercial harvesters only remove an estimated 20-30% of the standing crop (Simons pers. comm.), or an effective one tuft in five, during a single visit to one site. This would tend to imply that harvesting at intervals even shorter than two months may not be inefficient or destructive to the stocks. However, greater G.pristoides yields from any one site, derived from harvesting more frequently, must be offset by the increased time and effort that will be expended in seeking out those tufts that were either missed on a previous visit, or which to the harvester will present worthwhile pickings.

To concentrate harvesting effort in the summer months would, however, have practical disadvantages. Firstly, a larger work-force would be required in order to maintain present annual yields, since harvesting would need to be both more extensive (cover more collecting sites), and intensive (more frequent visits to each site). This would then require a greater capital outlay (transport, accommodation etc. for the labourers), while facilities would be unused, and the labourers unemployed, during winter.

Harvesting by shearing has been suggested as a possible means of preventing damage to the regenerative holdfast portion of G.pristoides tufts. Present results, however, indicate that recovery after shearing is not significantly more rapid than after plucking, and the former method has no obvious biological advantages. Furthermore, although Beckley (1982) suggested that the harvesting of the holdfast region could be detrimental to the recruitment of surrounding littoral animals, whose early life-stages depend on the seaweed as a nursery, recent research (Jarman pers. comm.) indicates that a very small proportion of the total intertidal epifauna occurs on G.pristoides, and none are specific to this alga. The main practical disadvantage of shearing is that it takes longer than plucking, and is therefore less cost-efficient. It is considered unlikely that pickers will remove too much material from any one tuft of G.pristoides: the effort required to remove more than the first handfull or two is not justified, as the next tuft has more to offer.

So far, the media exposure on G.pristoides harvesting (see examples in Appendix II) appears to have been negative. Properly controlled, this industry is no more likely to present a threat to natural marine resources than other "acceptable" human activities, for example, bait collection and sport angling. It is suggested, therefore, that the industry should consider embarking on some form of publicity campaign to counter some of the current negative publicity which it receives.

In order for the development of the agar industry in South Africa, the commercial companies concerned must be guaranteed future access to the Gelidium resources. However, it is essential that the exploited seaweed stocks are periodically assessed for contingency damage resulting from year-to-year harvesting. Perhaps a suitable time for doing this would be immediately prior to the date on which the permit to harvest is due for renewal, which at present is every five years. This continuing assessment should be conducted in such a way that changes in the seaweed populations under natural and exploited conditions may be compared. A method using permanent transects is currently employed to monitor harvested Chondrus crispus populations in Canada (Taylor 1981).

The agar industry in South Africa is fortunate in having an abundant resource in the form of G.pristoides, which can be harvested with relative ease, and a suitable labour resource for collecting the seaweed. However, it is in the interests of all concerned, that the resource is properly managed. It is hoped that the present investigation will assist in the formulation of such a rational management policy, and that it might encourage further research on other neglected economic seaweeds which occur locally.

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Appendix I Results of preliminary limpet exclusion experiments conducted at Port Alfred, which appeared in Newsletter No. 14 (December 1985) of the Phycological Society of South Africa.

PRELIMINARY OBSERVATIONS ON THE COLONIZATION OF BARE ROCKY SUBSTRATA BY *GELIDIUM PRISTOIDES* (GELIDIALES,. RHODOPHYCEAE) WITHIN LIMPET EXCLUSION AREAS AT PORT ALFRED

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Most intertidal gastropods feed primarily on microalgae, diatoms and macroalgal spores (Underwood, 1979). Consequently, the grazing activities of these animals may have a profound effect on the settlement and subsequent estabishment of a number of macroalgae on bare rock surfaces. The grazing activities of *Patella vulgata* in England have been shown to have an inhibitory effect on the colonization of bare rocky surfaces by *Fucus* populations (Hawkins, 1981). Branch (1971) suggested that the grazing activities of limpets on South African rocky shores results in the eradication of all algal spores thus preventing the establishment of several algal species including *Gelidium pristoides*.

At Port Alfred, *G. pristoides* plants tend to be restricted to cracks and crevices in rock surfaces, and to barnacle and limpet shells (fig. 1) where sporelings would be less vulnerable to predation by limpets. These observations seem to point to the complicity of limpets such as *P. granularis* in determining the spatial distribution and consequently the standing crops of *G. pristoides* populations at this locality. Preliminary experiments were conducted using ship anti-fouling paint to exclude grazing limpets from rocky areas.

The exclusion of limpets resulted in the colonization of the bare rocky surfaces by various macroalgae (figs. 2 and 3). An initial rapid colonization by *Ralfsia verrucosa* (reaching 80% cover after five months) was followed by the appearance of *Ulva rigida*, and finally *G. pristoides*, during the summer period 1984/85 (fig. 4). Other species recorded within the exclusion areas were *Gigartina minima* and *Gigartina sp.*, which occured at densities too low to include in figure 4. In all control areas where the movement of limpets was not impeded, there was little or no sign of colonization by *G. pristoides* or other macroalgae. The close proximity of the anti-fouling paint barrier, thus restricting the movement of limpets, is a likely explanation for the appearance of *G. pristoides* in the crevice adjacent to the exclusion plot in figure 3 (arrowed).

Our present observations clearly indicate the inhibitory effect of limpet grazing on the colonization of rocky substrata by various macroalgae, including the economically important agarophyte, *G. pristoides*. While this information should be of some interest to commercial harvesters of this seaweed, it also raises the following questions: 1) What is the propagative potential of *G. pristoides* by spores in the absence of limpet grazers, and 2) of what importance is substrate-type in the settlement and recruitment of plants by spores? The second aspect is of particular interest, since, in addition to the probability that sporelings on limpet shells are less vulnerable to predation by other limpets, *G. pristoides* plants seem to show a preference for limpet shells as a substrate for colonization. Experiments are presently in progress to examine the above questions.

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Figure 1. *Gelidium pristoides* tuft attached to limpet shell.
Figure 2. Limpet exclusion area after six months.
Figure 3. Limpet exclusion area after a year.

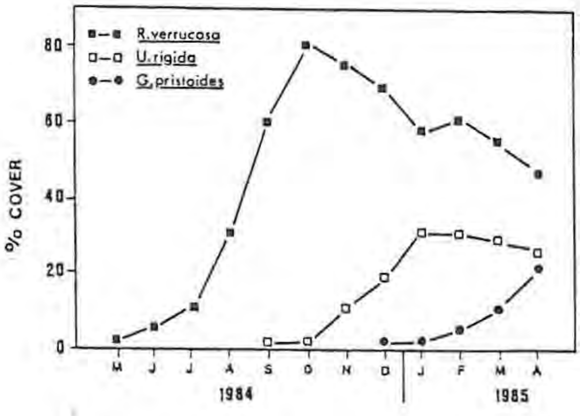

Figure 4. Percentage cover of algae in exclusion areas.

Appendix II Articles on Gelidium harvesting which appeared in the local press during 1983-1985.

4 EVENING POST, WEDNESDAY, MAY 1, 1985

Mr COLIN McDONALD, a committee member of the Seaview Ratepayers' Association, holds a bunch of seaweed which was discarded by a gang of workers employed by Taurus Products, Transkei, who decended over the weekend and scoured the plants off the coastline. The seaweed pictured was thrown aside because it was attached to the back of a limpet shell.

Seaweed stripping halted after outcry

Post Reporter

A PUBLIC outcry has stopped a Transkei company tearing seaweed from the rocks at Seaview, near Port Elizabeth.

Gangs of workers have been bagging truckloads of seaweed and dispatching it for processing to a factory in Butterworth.

Concerned for the ecology of the coastline, local residents have voiced a strong protest and the company has pulled out — for the time being.

The company, Taurus Products Transkei Ltd, was operating on a permit granted by the Department of Environment Affairs and Tourism and administered by Dias Divisonal Council.

It blamed its "unskilled" locally recruited workers and the length of the Eastern Cape seaweed for any loss of shellfish that might have occurred.

Some of the workers may face charges brought by the Directorate of Marine Development.

Mr Mark Weber, manager of the Butterworth company, said two 30-man teams had been withdrawn as a sign of "the company's sensitivity to public feeling".

However, he said the company was planning a "more intensive move into the area around PE" after discussions with the residents.

The company was sent packing from Gonubie near East London recently.

The Secretary of the Dias Divisonal Council, Mr N W Anderson, has promised the ratepayers an intensive and top priority investigation.

Seaview residents were horrified when the workers moved in and began stripping by the handful.

A delegation, consisting of a committee member on the Seaview Ratepayers' Association, Mr Colin McDonald, a resident, Mrs Di Matlock, municipal ranger Mr Noel Roberts and a traffic officer approached the supervisor of the harvesting team, a Mr Scheepers, demanding to know what was going on.

Mr McDonald said Mr Scheepers showed them a copy of the permit, but members of the group asked to inspect the bags.

Mr McDonald said he found that one bag was about one-fifth full of seaweed which still had roots attached.

"But any seaweed which is growing on the back of limpets is discarded if plucked. I am sure it will never be able grow again."

"If you part seaweed with your hand, you can always see lots of little shrimps, worms and shellfish living in it. I am convinced that stripping this will create an imbalance in the close inshore ecology."

Mr T M Cronje, the principal fisheries officer for the Directorate of Marine Development, confirmed he was investigating the complaint and said that a docket involving criminal charges was being investigated.

"The permit was not given lightly and a number of stringent conditions were attached — some may not have been complied with and we are investigating."

It is known that the charges related to an undisclosed number of bags of black mussels found in the employee's possession.

Mr Weber said: "It was possible shellfish were collected in the operation.

"But this is because in the Eastern Cape the length of the seaweed is very long and because a number of workers recruited in PE were unskilled in the job.

"The management had difficulty in achieving a perfect harvesting situation, which we want to achieve as soon as possible.

"Workers used their hands and not implements — to discourage them from taking shell fish, such as the black mussel."

Seaweed is either exported or crushed to extract a gelatinous substance called Agar used in medicines and food products.

● Mr Alan Carter, a PhD student at Rhodes University, who is near to completion of a thesis on the regeneration of Gelidium *Pristoides*, the most common species of seaweed found on the Eastern Cape coast, said his research showed that seaweed harvested in winter, or picked in the upper inter-tidal zone (nearest the shore), took twice a. long (five to six months) to regenerate.

Albany M.P. expresses further concern at Seaweed Harvesting

During a recent parliamentary debate, Mr Errol Moorcroft (PFP, Albany) expressed further concern about the uncontrolled harvesting of seaweed along the Eastern Cape coast. Collectors harvested the weed in a manner which prevented further growth.

Mr Moorcroft called for a scientific study on seaweed harvesting, and recommended that all harvesting outside the kelp beds should cease until the results of such a study were available. He also pressed for the abolition of commercial concessions until more information was available.

There was also reason to believe that the collectors of seaweed were not properly supervised, and that they were guilty of the large-scale collecting of shell-fish from the rocks. Mr Moorcroft stated that he had received numerous representations from organisations requesting that something be done about the widespread destruction currently being wreaked along our unique coastline.

Seaweed debate: pluck or cut?

EAST LONDON — Debate on the rights and wrongs of seaweed harvesting on the south-east coast has begun again after a statement by Professor Margaret Smith on the implications of pulling up, rather than cutting, the seaweed.

Prof Smith, of the Department of Ichthyology at Rhodes University, said that the seaweed stood a much better chance of healthy regrowth if it was cut rather than plucked.

"Studies made overseas have shown that cut seaweed grows back very quickly. In a period of about three months in fact.

"Pulling up the seaweed by the roots not only endangers regeneration but it completely disrupts the environment of inshore marine life," Prof Smith said.

Mr R. Simons of the marine research unit at the University of Cape Town, who is currently conducting a study of the harvesting of kelp for the Department of Environment Affairs and Fisheries, confirmed that at present harvesters were plucking the weed.

"Under the terms of the permit issued to gathers, the weed is to be plucked rather than cut. I would like to know on what Prof Smith bases her hypothesis.

"Seaweed has been harvested for the past 50 years on the western Cape coast, and it is certainly not in short supply," Mr Simons said. — DDR.

Seaweed collection control

In an attempt to regulate the collection of seaweed in our area, the Port Alfred Municipality recently held meetings with the Department of Fisheries and a company concerned.

As a result, stricter control will be exercised and collectors for authorised companies will have to wear easily identifiable vests.

Now, as a result of the Marine Development Branch's recent investigational visit to Port Elizabeth, East London and the vicinity, the first report regarding exploitation has been compiled.

It appears in South Africa we are blessed with sometimes copious supplies of seaweeds with established uses and these resources are crying out to be tapped.

At first concessions for the harvesting of seaweed were granted by the Department of Agricultural Credit and Land Tenure, which often delegates the administration to local authorities. The responsibilities in 1971 were transfered to the Sea Fisheries Institute, then to the Department of Industries, and now to the Department of Enviroment Affairs.

In the early history of this activity, concessions were granted to exploiters for a nominal fee without stipulating any special conditions and procedures; collectors were free to operate as they wished. Soon after, Sea Fisheries (Now the Marine Development Branch) granted concessions on the basis of the highest tender.

For the efficient management of the industry, the Coast of South Africa has now been divided into 17 seaweed exploitation areas and the concession permits contain stringent conditions and monitoring procedures.

Now all seaweed collectors who have received authorisation for gathering seaweed are easily identified and anyone not conforming to the standards should immediately be reported to the relevant authorities.

All collectors will wear bright vests identifying the company for which they work and will also bear some number on his or her vest for easy identification.

The Port Alfred Town Council, having been included on a list of local authorities who have delegated powers to control the collection of seaweed within their area of jurisdiction, will be kept informed on the situation along the East Cape Coast and will receive reports from the Marine Development Branch.