STUDIES ON CARRAGEENOPHYTES OF THE WESTERN CAPE, SOUTH AFRICA: ECOLOGY, MANAGEMENT AND SYSTEMATICS

Graham Julian Levitt

Submitted in fulfilment of the
requirements for the degree of
Doctor of Philosophy
in the
Department of Botany
Faculty of Science
University of Cape Town

August, 1998

ABSTRACT

Four species of carrageenophytes were surveyed to determine the harvestable biomass of populations, between the areas of Cape Columbine and Cape Agulhas, in the southern Western Cape Province, South Africa. Three species, *Aeodes orbitosa*, *Gigartina polycarpa* and *Sarcothalia stiriata* occur in sufficient quantities to be harvested, with summer fresh weight standing stocks of 193.5, 154 and 104 tons respectively. The summer standing stock of *Mazzaella capensis* (33.5 tons) was too low to warrant exploitation, as was the winter standing stock (10 tons) of *A. orbitosa*. Biomass of *G. polycarpa* and *S. stiriata* fluctuated seasonally, being maximum (2.9 and 3.0 $kg.m^{-2}$ respectively) in summer and minimum (0.8 and 1.2 $kg.m^{-2}$ respectively) in winter although seasonal data were not statistically different. The lower biomass of these two species during winter may limit their harvesting potential during that season. The mean carrageenan content (as percentage of dry weight) of *G. polycarpa* and *S. stiriata* was 44-49% (gametophytes) and 39-41% (tetrasporophytes). The estimated carrageenan yield from a summer harvest of *A. orbitosa*, *G. polycarpa* and *S. stiriata* would be approximately 29.3 tons.

Demographic parameters of phenology, plant density and fertility of intertidal populations of *Gigartina polycarpa* and *Sarcothalia stiriata* were investigated. Life-history phases were present in the ratio of 0.9:0.9:1.1 and 2.8:2.5:1 male gametophyte : female gametophyte : tetrasporophyte respectively for *G. polycarpa* and *S. stiriata*, with no clear seasonal variation. Juveniles not identifiable to species were numerically dominant, with no apparent seasonal recruitment pattern. Recruitment data for identifiable juveniles of *S. stiriata* and *G. polycarpa* were similarly variable. It is likely that vegetative regrowth provides a significant portion of new plant biomass. Female gametophytes of *S. stiriata* displayed a significant seasonal pattern of reproductive weight of fertile plants with a summer maximum, implying that the following winter's macroscopic sporelings are the progeny of a summer spore release. No seasonal pattern of reproductive weight of fertile plants was apparent in any phase of *G. polycarpa* or in male gametophytes of *S. stiriata*. Fertile material accounts for significantly more biomass in gametophytes as opposed to tetrasporophytes in both *G. polycarpa* and *S. stiriata*. Populations of both species were gametophyte dominated, differential spore survival and/or regrowth of existing plants from perennial holdfasts probably favouring the gametophyte.

The seasonal growth rates of *Gigartina polycarpa* and *Sarcothalia stiriata* were also investigated. *G. polycarpa* displayed a summer maximum and a winter minimum in growth rate, whereas a spring maximum and autumn minimum was apparent in *S. stiriata*. In *G. polycarpa*, these seasonal patterns correlated reasonably well with seasonal biomass observations, with little or no lag between the two. In *S. stiriata* maximal biomass lagged behind maximal growth, possibly as a result of greater wave action in the habitat occupied by this species.

The effects of different conditions of wave exposure in adjacent stands of *Gigartina polycarpa* and *Sarcothalia stiriata* were tested by transplanting the different life-history phases during spring/summer and winter. Female gametophytes and tetrasporophytes of *G. polycarpa* and female gametophytes of *S. stiriata* were transplanted to areas of greater wave action, whereas tetrasporophytes of *S. stiriata* were transplanted to less exposed areas. Spring/summer transplants of female gametophytes of *G. polycarpa* displayed enhanced growth rates, whereas the growth rate of tetrasporophytes transplanted during this period was reduced. No differences in growth rate were evident in winter transplants of *G. polycarpa* female gametophytes and tetrasporophytes. Reduced growth rates were also apparent in spring/summer transplants of *S. stiriata* female gametophytes, whereas growth of winter transplants was unchanged. Increased growth was apparent in transplants of *S. stiriata* tetrasporophytes in both winter and spring/summer. Enhanced growth rates are possibly the result of a more favourable environment after transplanting. Reduced growth rates of winter transplants are most likely the result of physical damage arising from increased hydrodynamic forces, such damage being clearly visible.

Drag coefficients of both *Gigartina polycarpa* and *Sarcothalia stiriata* decreased with increasing water velocity. In both species, drag coefficients of tetrasporophytes were lower than male and female gametophytes. The two species responded differently to increased hydrodynamic forces, these responses being both morphological and physical. Both *G. polycarpa* and *S. stiriata* displayed evidence of streamlining to reduce hydrodynamic loading, it being possible that *G. polycarpa* is adapted to survive in different hydrodynamic habitats through morphological plasticity. Differential spore survival as a response to wave action is also a possible factor affecting the distribution of these species on exposed and sheltered shores.

Commercial harvesting of *Gigartina polycarpa* and *Sarcothalia stiriata* is a likely prospect, with a consequent requirement for ecological information for use in the formulation of rational harvesting practices. Field experiments indicate that harvesting of these two species would be most economically and ecologically viable at four-monthly intervals. This harvesting interval results in a maximum yield per harvest of 0.73 and 3.01kg.m^{-2} respectively, with no negative effects on the amount of fertile frond material (i.e. reproductive capacity) over a one-year period. The method of harvesting has a major effect on regeneration, harvesting by cutting yielding on average 80% less material than the use of hand-plucking. Hand-plucking has little or no effect on the phenological composition of subsequent harvests. Patch stability is characteristic of harvested stands of *G. polycarpa* and *S. stiriata*, changes in species diversity after disturbance being of short-term duration (< 1yr). Removal of grazing pressure by limpets promotes interspecific algal competition, and allows the invasion of opportunistic species in floristically-disturbed localities. Recovery to a community state similar to that observed before disturbance takes place within a year.

Vegetative development of germlings produced from carpospores and tetraspores of *Gigartina polycarpa* and *Sarcothalia stiriata* were studied *in vitro* under a range of light and temperature conditions, and the results related to the natural environment over the range of ditribution of the two species.

Initial vegetative growth of carpospore and tetraspore germlings of both species was light saturated at 50μmol.m^{-2}.s^{-1}, germlings persisting for at least five weeks at 0.5μmol.m^{-2}.s^{-1}. It is concluded that germlings of both species are adapted to survive transient periods of near-darkness and to grow under low irradiances typical of the eulittoral understorey.

Germlings of *Sarcothalia stiriata* survive temperatures of 5-15°C but not 0° or 20°C, with a growth peak at 15°C, typical of cold-temperate species. In contrast, germlings of *Gigartina polycarpa* display temperature tolerances consistent with warm-temperate species, surviving in the range 5-20°C (dying at 0° and 25°C), with a broad growth peak of 15-20°C.

Gametophyte dominance of mature populations of either species cannot be attributed to differential spore survival resulting from differing light and temperature tolerances of carpospore and tetraspore germlings, these being non-significant within each species. However, differential spore release is a possible factor, *in vitro* release of tetraspores being easier to stimulate than carpospores in both species. It is also possible that invertebrate grazing

in the wild may be a factor assisting carpospore release, carpospore release in the laboratory by surface-sterilized cystocarpic material being poor in comparison with tetrasporic material. Temperature tolerances displayed by *Sarcothalia stiriata* place this species firmly within the range of temperatures typical of the west coast, this being suppported by the fact that *S. stiriata* is locally confined to the region known as the Benguela marine province. In contrast, the wider temperature tolerances displayed by *G. polycarpa* germlings correlates well with its broader geographic distribution within both the Benguela and Agulhas marine provinces.

In a recent revision of the classification of the marine red algal family Gigartinaceae, seven genera were proposed for the family based upon observations of characters of vegetative morphology and reproductive development. Previously, four South African members of the Gigartinaceae had been examined to assess their position within the revised classification, namely *Sarcothalia stiriata*, *Sarcothalia scutellata*, *Gigartina polycarpa*, *Gigartina clathrata* and *Mazzaella capensis*. Using the revised classification, the taxonomic position of the entity presently known as *Gigartina paxillata* Papenfuss has been determined .

Morphologically, *Gigartina paxillata* has large sub-terminal cystocarps which are formed either on papillae or adventitious branches, with an obvious ostiole present in mature cystocarps. Microscopically, the auxiliary cell becomes surrounded by a compact envelope during development, the envelope becoming penetrated by gonimoblast filaments which link to the envelope by cell fusion. Carposporangia are formed in chains which link to each other and to the sterile cells of the placenta by broadened pit connections. Mature carposporangia form grape-like clusters which are separated by the placenta and surrounded by the envelope. Tetrasporangial sori are raised and mainly elliptical. Mature tetraspores are released by excision of the entire sorus.

Based upon these observations, it is concluded that *Gigartina paxillata* is correctly positioned within the genus *Gigartina*.

CHAPTER 1

GENERAL INTRODUCTION

1.1 RATIONALE

In the Benguela marine province on the west coast of Southern Africa two morphologically different species of the Gigartinaceae are commonly abundant. *Gigartina polycarpa* (Kützing) Setchell *et* Gardner and *Sarcothalia stiriata* (Turner) Leister co-occur on rocky shores from depths of *ca.* 7m and 2.5m, respectively, in the sublittoral (Jackelman, 1996) through to the mid-eulittoral (Levitt and Bolton, 1990; Jackelman, 1996). Both species occur on relatively sheltered and semi-exposed shores. *Sarcothalia stiriata* can occupy sites directly exposed to breaking waves as well as more sheltered sites such as ledges protected behind rocky outcrops. These ledges are also commonly occupied by *G. polycarpa*, which is more common than *S. stiriata* on more sheltered shores.

Morphologically *Gigartina polycarpa* has a thallus of flat, leathery blades which average 15-20cm in length with a maximum of up to 45cm. The gametophytes and tetrasporophytes are isomorphic (Guiry *et al*, 1984; Guiry and Garbary, 1990), there being no separate crustose phase such as is found in the genus *Mastocarpus*. The male gametophytes (fig. 1.1) are characterized by numerous papillae on the thallus and the female gametophytes (fig. 1.2) by numerous protruding cystocarps. Mature tetrasporophytes (fig. 1.3) of *G. polycarpa* have thinner thalli with numerous visible, embedded tetrasporangial sori. *Sarcothalia stiriata* is a smaller plant, with an average length of 10-15cm and a maximum of 30cm. The male (fig. 1.4) and female (fig. 1.5) gametophytes are indistinguishable until reproductively mature, the multiple branches of the female thallus bearing numerous rounded swellings containing the cystocarps. Although *S. stiriata* has been characterized (Hommersand *et al.* 1993, 1994) as having a dimorphic thallus with proliferously branched gametophytes and smooth tetrasporophytes (the tetrasporophyte (fig. 1.6) having once been separately described as *Gigartina burmanii* (C. Ag.) J. Ag. (Seagrief, 1984)), it can be considered to be isomorphic because the gametophyte and tetrasporophyte are morphologically similar in thallus shape and size, there being no alternate crustose or microscopic phase.

Of the carrageenophyte species common to the south Western Cape, only *Gigartina polycarpa*

Figure 1.1 *Gigartina polycarpa* male gametophyte.

Figure 1.2 *Gigartina polycarpa* female gametophyte.

Figure 1.3 *Gigartina polycarpa* tetrasporophyte.

Figure 1.4 *Sarcothalia stiriata* male gametophyte.

Figure 1.5 *Sarcothalia stiriata* female gametophyte.

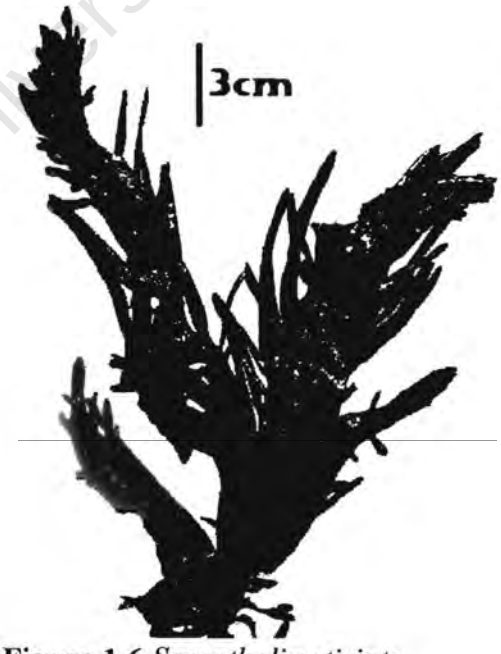


Figure 1.6 *Sarcothalia stiriata* tetrasporophyte.

has previously been commercially exploited (Anderson *et al.* 1989). No carrageenophyte species are presently harvested within the region, although interest in *G. polycarpa*, *Sarcothalia stiriata*, *Aeodes orbitosa* (Suhr) Schmitz and *Mazzaella capensis* (J. Agardh) Fredericq has been expressed by local and international entrepreneurs. In view of their economic potential, the formulation of a rational management policy for these resources is essential. A prerequisite to the formulation of such a policy is the acquistion of basic information regarding biomass, demographics and population biology of the target species. The magnitude of each resource can be determined by estimation of the seasonal harvestable biomass along the exploited coastline. In this dissertation, such information is presented in respect to *Gigartina polycarpa*, *Sarcothalia stiriata*, *Aeodes orbitosa* and *Mazzaella capensis*. Determination of age-class structures within populations of *Gigartina polycarpa* and *Sarcothalia stiriata* is impractical due to logistical problems involved in tagging many thousands of individuals on an ongoing basis, this being further complicated by difficulties in identifying individual plants - both species are clonal (*sensu* Scrosati, 1996), the basic population unit being the ramet. Therefore, demographic parameters of phenology, fecundity and growth rate are used to elucidate the population biology of these two species.

The most appropriate management strategy must be formulated so as to ensure optimal utilization of resources, specifically the determination of a sustainable optimal harvest, as well as harvesting methods and their effects on reproductive capacity. Harvest yields under a variety of harvesting regimes are assessed in terms of these criteria. However, the ecological consequences of such disturbance on community structure must also be taken into account to ensure long-term management success: the possibility of longer term effects on populations resulting from, for example, the establishment of alternate communities following disturbance, need to be considered. Information is presented in respect of changes in community structure following disturbance (removal of algal flora and/or molluscan grazers) of communities dominated by populations of *Gigartina polycarpa* and *Sarcothalia stiriata*.

Factors influencing demographic factors such as growth rate include selective forces such as wave action, which plays a major role in maintaining habitat diversity (Shaughnessy *et al.* 1996). Seasonal growth rate and occupied habitat are two factors which typically may be influenced by wave action, through the mechanism of differing response of thallus morphology to hydrodynamic force. Empirical measurements of growth and drag observed in the various

life-history phases of both *Gigartina polycarpa* and *Sarcothalia stiriata* are used to assess the importance of wave action as a factor selecting the habitats of populations of these two species. In the Benguela and Agulhas marine provinces, temperature is the most significant factor affecting seaweed biogeography (Bolton, 1986), a significant discontinuity in species composition occurring at Cape Agulhas, the geographic locality where the warm Agulhas current meets the cold Benguela current (fig. 2.1). The geographic distribution of seaweeds can be expected to be related to their temperature tolerances for growth and reproduction. Light can also be a factor controlling marine algal shore zonation though the mechanisms of shading or photoinhibition; different species may be adapted to occupy differing ecological niches as a consequence of their ability to grow in high or low irradiance environments. Thus, the light and temperature tolerances for growth of *Gigartina polycarpa* and *Sarcothalia stiriata* sporelings are determined in order to assess the importance of these two factors in ecologically separating populations of these two species, the extent to which they determine their geographic distribution, as well as to speculate on their respective biogeographic origins.

The systematics of the Gigartinaceae has recently undergone a revision (Hommersand *et al.* 1993, 1994), with a consequent change in the classification of three of the four carrageenophytes common to the South African west coast, namely *Gigartina polycarpa*, *Sarcothalia stiriata* and *Mazzaella capensis* (*Aeodes orbitosa* belongs to the Halymeniaceae). The taxonomic position of three other *Gigartina* species found in the south Western Cape were not addressed in the revised classification, namely, *Gigartina insignis*, *Gigartina minima* and *Gigartina paxillata*. The latter species is common in the south Western Cape and the Eastern Cape, co-occurring with *G. polycarpa* within the western overlap region. The characters defined by Hommersand *et al.* (1993) are used to clarify the taxonomic position of *G. paxillata* within the Gigartinaceae.

1.2 STUDY SITE

The field experiments described in chapters 2 to 5 of this dissertation were conducted at Kommetjie (34°08.1'S,18°18.6'E, approximately 30km from Cape Town) on the west coast of the Cape Peninsula, in the southern Western Cape, South Africa. Topographically the shore comprised a flat, rocky ledge (*ca.* 90m²) of Table Mountain Sandstone with a perimeter of medium-sized (*ca.*1m diameter), immoveable boulders (fig. 1.7). The boulders were directly exposed to the prevailing south-westerly swell and provided a barrier which provided some

Figure 1.7 Main study site at Kommetjie comprising flat ledge of Table Mountain Sandstone with perimeter of medium-sized boulders. View facing directly west. The mixed community of *Gigartina polycarpa* and *Sarcothalia stiriata* is clearly visible in the foreground.

shelter to the ledge. Both *Gigartina polycarpa* (all life history phases) and *Sarcothalia stiriata* (male and female gametophytes only) occurred on the ledge, whereas the boulders were occupied predominantly by *S. stiriata* tetrasporophytes together with a few *S. stiriata* female gametophytes.

CHAPTER 2

POTENTIAL HARVESTABLE BIOMASS AND CARRAGEENAN YIELD OF *AEODES ORBITOSA*, *GIGARTINA POLYCARPA*, *MAZZAELLA CAPENSIS* AND *SARCOTHALIA STIRIATA* IN THE WESTERN CAPE, SOUTH AFRICA

2.1 INTRODUCTION

The collection and harvesting of carrageenophytes in the Western Cape Province, South Africa, was historically of minor economic importance compared to that of alginate-producing kelps. The economic potential of the carrageenan-yielding seaweeds of the Western Cape was first recognized during World War 2 (Isaac, 1942; Isaac *et al.* 1943) when wartime shortages caused industries to seek local replacements of seaweed products (mainly agar) traditionally obtained from the Far East. After the war, interest in the potential use of seaweed polysaccharides was still evident (Isaac and Molteno, 1953), although the then renewed availability of Japanese material made local demand less urgent. As a result, the South African carrageenan industry developed from the sporadic harvesting of predominately *Gigartina polycarpa* (Kützing) Setchell *et* Gardner (formerly *Gigartina radula* (Esper) J. Agardh - Hommersand *et al.* 1994) mixed with some *Sarcothalia stiriata* (Turner) Leister (formerly *Gigartina stiriata* (Turner) J. Agardh - Hommersand *et al.* 1994). Harvested species were not processed locally for extraction of carrageenan but were exported as dried raw material.

Between 1956 and 1978 small and variable quantities of mainly *Gigartina polycarpa*, ranging from 0.4 to 54.4 tons dry weight.year^{-1}, were harvested (Anderson *et al.* 1989), the total harvest during those years amounting to 149.9 tons dry weight. More recently, commercial interest in South African carrageenophytes has been revived as a combined result of the decline in the exchange rate, which raised the local price for exported material, and the interest shown by multi-national corporations in new sources of carrageenan. This interest has not been confined to *G. polycarpa* and *Sarcothalia stiriata*, because it is thought that simultaneous collections of *Aeodes orbitosa* (Suhr) Schmitz and *Mazzaella capensis* (J. Agardh) Fredericq, formerly *Iridaea capensis* J. Agardh (Hommersand *et al.* 1994), may prove to yield a greater harvest per unit effort, making the harvesting of Western Cape carrageenophytes economically viable.

Seaweeds in South Africa are commercially exploited solely off the Western Cape and Eastern Cape coasts. Surface temperatures along this coastline are temperate: the cool West Coast (12-15.8°C mean annual temperature) which extends from the Namibian border to the Cape Peninsula, and the warmer South Coast (17.2-18.2°C) from Cape Agulhas to the Kei River on the East Coast (Bolton, 1986). These regions are phytogeographically distinct, except for an area of overlap between the Cape Peninsula and Cape Agulhas, and have been designated the Benguela and Agulhas marine provinces respectively (Bolton and Anderson, 1997). Of the potentially economically viable and commercial seaweeds, the alginophytes *Ecklonia maxima* (Osbeck) Papenfuss, *Laminaria pallida* Greville ex J. Agardh, *Laminaria schinzii* Foslie, the agarophyte *Gracilaria gracilis* (Stackhouse) Steentoft, Irvine *et* Farnham, and the carrageenophytes *Gigartina polycarpa*, *Sarcothalia stiriata*, *Aeodes orbitosa* and *Mazzaella capensis* are more abundant on the West Coast. On the South and East coasts, the agarophyte *Gelidium pristoides* (Turner) Kützing and the carrageenophyte *Hypnea spicifera* (Suhr) Harvey are the most important species (Bolton and Stegenga, 1990). Because of the different phytogeographical distributions in seaweed species, economic activity is concentrated at two centres, Cape Town in the Western Cape and East London in the Eastern Cape, which are approximately 1000km apart. Present exploitation has revolved around *Gracilaria*, *Gelidium*, *Ecklonia* and *Laminaria*, but the existence of four currently unexploited carrageenophytes, which are perceived to be abundant in the Western Cape, has prompted renewed interest from entrepreneurs.

Gigartina polycarpa occurs from Lüderitz (26°38.1'S, 15°09.2'E) in southern Namibia southwards past Cape Agulhas (34°49.8'S,20°01.00'E) at the southern tip of Africa, and extends as far east as Three Sisters (33°35.5'S, 26°55.4'E) near Port Alfred in the Eastern Cape province (H. Stegenga, Rijksherbarium Leiden, *pers. comm.*). *Sarcothalia stiriata* co-occurs with *G. polycarpa* in the eulittoral zone of West Coast rocky shores between Lüderitz and Cape Agulhas. *Mazzaella capensis* is also common on the west coast of southern Africa between Cape Frio (18°28.4'S, 12°01.2'E) in northern Namibia (H.R. Engledow, University of Cape Town, *pers. comm.*) and Cape Agulhas (Stephenson, 1948). *Mazzaella capensis* is particularly prevalent on sand-affected shores (Bolton and Joska, 1993). Somewhat similar in external appearance to *M. capensis*, *Aeodes orbitosa* co-occurs with that species on West Coast rocky shores, having been recorded from Cape Frio (Simons and Hewitt, 1976) and Rocky

Point (18°59.4'S, 12°28.6'E) in northern Namibia (Penrith and Kensley, 1970) to as far south as Danger Point (34°35.4'S, 19°18.4'E) near Cape Agulhas (this study). Neither *M. capensis* nor *A. orbitosa* have been exploited by the seaweed industry, and apart from some general biomass information which suggests that these species have a summer maximum and a winter minimum (Bolton and Levitt, 1992; Bolton and Joska, 1993), no data are available on their exploitation potential on the South African west coast.

Yaphe (1959) reported that both *Gigartina polycarpa* and *Sarcothalia stiriata* contain κ-carrageenan. Anderson *et al.* (1968) analysed the structure of carrageenan from *G. polycarpa* and Furneaux and Miller (1986) reported a 3:1:1 mixture of κ-,ι-, and μ-/ν-carrageenans for *S. stiriata*, similar to *Gigartina canaliculata* (Lawson *et al.* 1973) and *Gigartina chamissoi* (Penman and Rees, 1973), with a yield of 46% (of dry weight). The absence of λ-carrageenan in the samples analysed by Anderson *et al.* (1968) and Furneaux and Miller (1986) indicates that they consisted of gametophytic material, λ-carrageenan being characteristic of the sporophyte phase in members of the Gigartinaceae (Peats, 1981; McCandless *et al.* 1983). *Gigartina polycarpa* gametophytes contain a 40:45:15 mixture of κ-,ι-, andν-carrageenans, whereas the tetrasporophytes contain λ-carrageenan (R.H. Furneaux, DSIR, New Zealand, *pers. comm.*). A variable carrageenan content of 30-42% of dry weight was reported by Bolton and Joska (1993) for *Mazzaella capensis*, with a late-winter/spring maximum and a summer/autumn minimum.

The polysaccharide extracted from *Aeodes orbitosa* (termed "aeodan") is considerably more viscous than that from *Gigartina polycarpa* (Molteno *et al.* 1953), consisting of highly sulphated D-galactose residues (Nunn and Parolis, 1968), the structure of which has been further elucidated (Allsobrook *et al.* 1969) as 1-3 and 1-4 linked galactose, the 1-4 links being sulphate-free. A carrageenan content of 45 and 30% of dry weight was measured in mature and juvenile plants of *A. orbitosa* respectively (J.J. Bolton and M.A.P. Joska, University of Cape Town, *pers. comm.*).

In order to determine the extent of the carrageenophyte resource along the coast of the southern Western Cape, a biomass survey of the four major species was undertaken. The biomass and carrageenan content of *Gigartina polycarpa* and *Sarcothalia stiriata* were investigated to determine the phycocolloid yield and the economic viability of their exploitation.

2.2 METHODS

The area surveyed for carrageenophyte biomass extended from the mouth of the Berg River (32°46.4'S,18°09.0'E) and Cape Agulhas, a length of shoreline of *ca.* 820km. An initial, aerial survey of the coast by helicopter, with spot-landings made *en route*, helped to distinguish areas where carrageenophytes were scarce or absent; those areas were excluded from the follow-up ground survey. The survey area was separated into six sectors: Cape Columbine, the Cape south-west coast, Cape Peninsula, Cape Hangklip, Mudge Point and Danger Point. A summer ground survey of *Gigartina polycarpa* and *Sarcothalia stiriata* was undertaken during November 1987 and winter and summer ground surveys of *Aeodes orbitosa* and *Mazzaella capensis* were undertaken during July and December 1989. Totals of 32 sites for *G. polycarpa* and *S. stiriata* and 35 sites for *A. orbitosa* and *M. capensis* were surveyed. Estimates of standing stock were made at sites where populations of the four species were present using the following methods.

i). The widths of zone occupied by each species were measured at various points along the shore (usually *ca.* 50m apart). The number of measurements varied between six and sixteen, depending on the amount of rocky shore. All measurements were then averaged for each particular length of shore.

ii). The biomass ($kg.m^{-2}$) of each species was measured by harvesting and weighing the seaweeds in a minimum of nine 50 x 50cm quadrats at each point along the shore where the zone width was measured. Quadrat size was the maximum allowed, given the constraints of shore topography, and each quadrat enclosed numerous individual plants. Seaweeds were harvested by plucking in order to emulate a commercial harvest. No attempt was made to remove the firmly attached remaining small plants or holdfasts.

iii). The shoreline adjacent to the sample site was then inspected to ascertain the length of similar habitat occupied by the target species.

iv). The standing stock for each shore visited was estimated as the product of shoreline length (km), zone width (m) and mean biomass in the quadrats ($kg.m^{-2}$).

As the biomass of *Gigartina polycarpa* and *Sarcothalia stiriata* was surveyed only once along the coast, a fixed site at Kommetjie (34°08.1''S,18°18.6'E) on the west coast of the Cape Peninsula was chosen to investigate seasonal variations in biomass of those two species. A flat,

rocky ledge (*ca.* 90m²) of Table Mountain Sandstone bearing a mixed population of *G. polycarpa* and *S. stiriata,* was sampled monthly between May 1987 and June 1988. To facilitate comparability with the estimates of standing stock, the biomass at this site was measured by means of harvesting (plucking) the plants in three 50 x 50cm quadrats, each placed at random within the population. Areas which had previously been plucked were excluded from further sampling. Biomass data were analyzed for seasonal variation (monthly data combined for season in the following manner: December, January, February = summer; March, April, May = autumn; June, July, August = winter; September, October, November = spring) by one-way ANOVA using the Student-Newman-Keuls multiple range test for differences between treatments (α=0.05). In all the ANOVAs performed throughout this dissertation, it was assumed that samples were from normal populations. Although it is possible to use Bartlett's test for homogeneity to test whether the assumption of equal variances is met, it is generally not worthwhile to use it in conjunction with ANOVA since it is inefficient and badly affected by nonnormality (Zar, 1984). Fortunately, ANOVA is robust, and operates well even with considerable heterogeneity of variances and considerable skewness or kurtosis in the underlying populations' normality (Zar, 1984).

The macroscopic phases of the life-history of *Gigartina polycarpa* and *Sarcothalia stiriata* were distinguished by identification of reproductive structures in female gametophytes and tetrasporophytes. As only mature plants were studied and because mature female gametophytes and tetrasporophytes are fertile year-round, the remaining adult plants, with a clearly different morphology to that of tetrasporophytes and gametophytes and without obvious reproductive structures, were assumed to be male gametophytes. The acetal-resorcinol method used to identify life-history phases (Craigie and Leigh, 1978) can only differentiate between gametophytes and tetrasporophytes, and since these could be differentiated morphologically, use of the test was considered to be redundant. Each month, eight plants of each life-history phase of *G. polycarpa* and *S. stiriata* were analysed individually for carrageenan content (without alkali modification), using a method derived from that of Santos and Doty (1975). Freshly collected plants from the biomass study were oven-dried for 48h at 60°C. Plants were not rinsed prior to drying in order to prevent loss of carrageenans. Clean samples (8g) were selected from the dry plant material, milled coarsely, and heated in a water bath at 85°C in 250mℓ aliquots adjusted to pH 9 by the addition of 2% NaOH. Alkali modification (the

addition of KOH or NaOH) does not affect total carrageenan yield (Santos and Doty, 1975) but reduces the amount of SO_3Na attached to the carrageenan molecule, often resulting in an increase in ι-type carrageenan (Zinoun *et al.* 1993) at the expense of other carrageenan types. Alkali modification is used mainly to improve gel strength (Istini *et al.* 1994). Since gel strength was not tested in this study, alkali modification was not considered necessary. The optimum extraction period was determined by comparing carrageenan yield against extraction time in tetrasporophytes and female gametophytes of *G. polycarpa*: three replicate samples of each of these life-history phases were extracted at each hourly interval between one and twelve hours. To ensure complete separation of the plant material from the colloidal solution, centrifugation at 10 000G for 30 minutes was used, rather than pressure filtration recommended in the method of Santos and Doty (1975). Carrageenan was precipitated by means of rapid stirring, using a double volume of 85% isopropanol. The precipitate was strained through a nylon cloth, rinsed twice with isopropanol and oven-dried at 60°C. Where conversion from wet weight to dry weight was required, water contents of 83.6% for *G. polycarpa* and *S. stiriata* (Levitt, 1987) and 88% for *Aeodes orbitosa* and *Mazzaella capensis* (M.A.P. Joska, *pers. comm.*) were used. Carrageenan yields (% dry weight) of 45% for *A. orbitosa* (M.A.P. Joska, *pers. comm.)* and 34.4% for *M. capensis* (Bolton and Joska, 1993) were used in the calculation of total harvestable carrageenan for these two species.

2.3 RESULTS

The aerial and ground surveys showed that *Gigartina polycarpa* and *Sarcothalia stiriata* were present at 22 of the 32 sites surveyed. *Aeodes orbitosa* was present at 29 (winter) and 30 (summer) sites and *Mazzaella capensis* at 21 (winter) and 27 (summer) sites, from a total of 35 sites surveyed (fig. 2.1).

The biomasses ($kg.m^{-2}$) and the standing stocks (kg fresh weight) of *Gigartina polycarpa* and *Sarcothalia stiriata* at the 22 sites during the November survey are listed in table 2.1. Biomass of *G. polycarpa* and *S. stiriata*, respectively, ranged from 0.75 to 5.96 $kg.m^{-2}$ and from 0.15 to 5.49 $kg.m^{-2}$, with means of 2.94 (S.E. 0.27) and 1.45 (S.E. 0.29) $kg.m^{-2}$. These values equate to standing stocks of *G. polycarpa* and *S. stiriata*, respectively, of 40.6 and 51.1 tons of male gametophytes, 56.0 and 38.9 tons of female gametophytes and 57.5 and 13.9 tons of tetrasporophytes along the south Western Cape coast. The largest populations (87.9 tons of *G.*

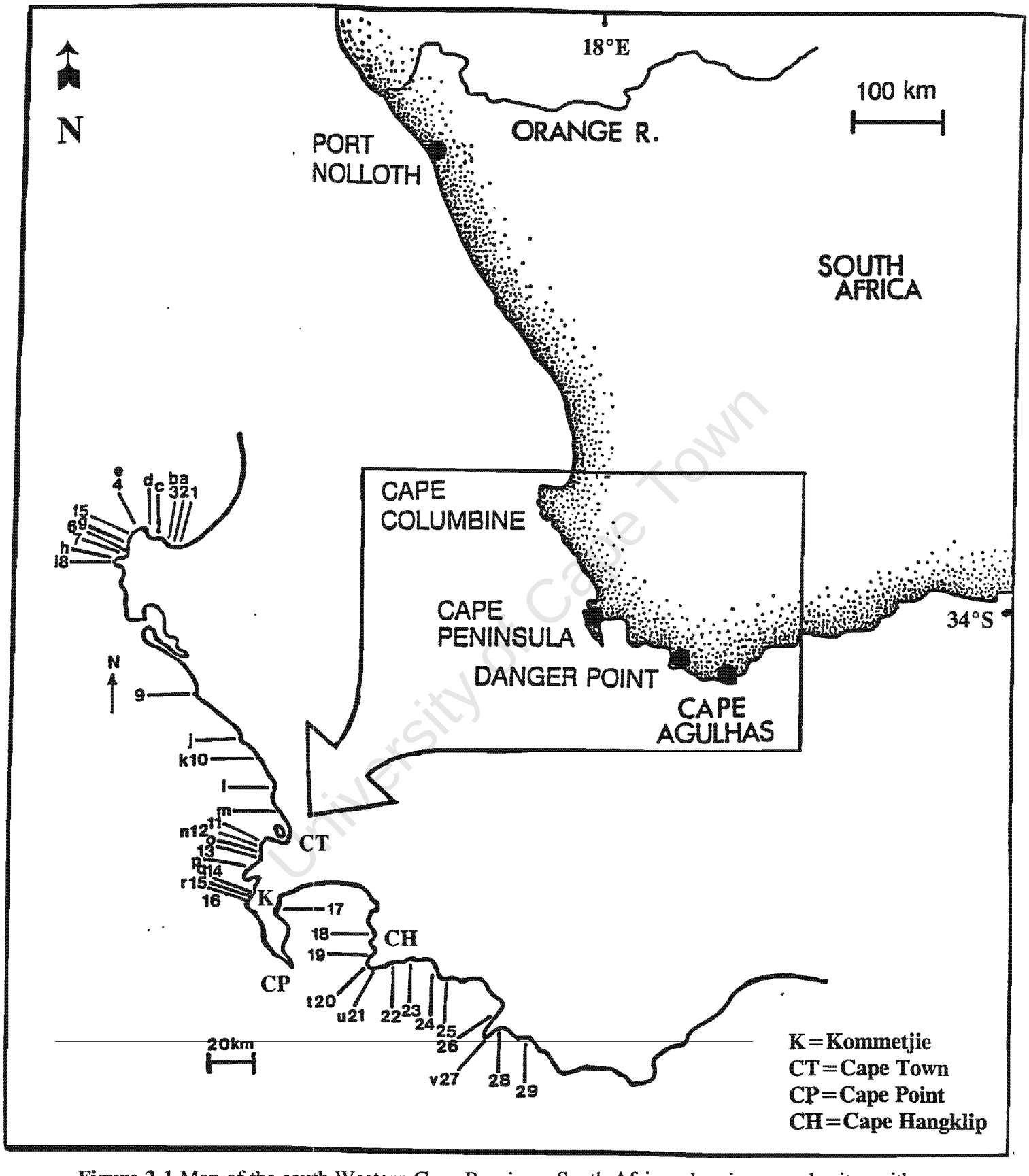


Figure 2.1 Map of the south Western Cape Province, South Africa, showing sample sites with harvestable amounts of *Aeodes orbitosa*, *Gigartina polycarpa*, *Mazzaella capensis* and *Sarcothalia stiriata*.

polycarpa and 63.2 tons of *S. stiriata*) were concentrated at Cape Columbine, with sizeable populations in the Cape Peninsula (22.9 and 33.1 tons, respectively) and at Cape Hangklip (27.1 tons of *G. polycarpa*). The total standing stocks of *G. polycarpa* and *S. stiriata* during November 1987 were 154.1 and 104.0 tons, respectively.

The biomasses ($kg.m^{-2}$) and the standing stocks (kg fresh weight) of *Aeodes orbitosa* and *Mazzaella capensis* during the summer and winter surveys are given in table 2.2. Biomass of *A. orbitosa* ranged from zero to 19.37 $kg.m^{-2}$ in summer and from 0.01 to 0.68 $kg.m^{-2}$ in winter, with means of 2.43 (S.E. 0.77) and 0.12 (S.E. 0.03) $kg.m^{-2}$, respectively. Biomass of *M. capensis* ranged from zero to 1.87 $kg.m^{-2}$ in summer and from zero to 1.14 $kg.m^{-2}$ in winter, with means of 0.41 (S.E. 0.10) and 0.07 (S.E. 0.04) $kg.m^{-2}$, respectively. Standing stocks were greater in summer than in winter, respective values of *A. orbitosa* and *M. capensis* being 193.6 and 33.6 tons (summer) and 10.0 and 4.5 tons (winter).

The largest standing stock of *Aeodes orbitosa* was found on the Cape Peninsula (129.8 tons), with lesser amounts at Cape Columbine (22.5 tons), Danger Point (18.1 tons), Mudge Point (13.0 tons), the Cape south-west coast (5.4 tons) and Cape Hangklip (4.8 tons). The relative proportion of standing stock distribution in winter was similar to that in summer, but the biomass was greatly reduced, the largest quantity being 6.0 tons on the Cape Peninsula. The largest summer standing stock of *Mazzaella capensis* was found at Danger Point (14.5 tons) and off the Cape Peninsula (12.2 tons), stocks at other sites ranging from 2.4 tons at Cape Columbine to 0.7 tons at Cape Hangklip. The winter standing stock of *M. capensis* was negligible, except off the Cape south-west Coast, which yielded 2.5 tons.

Seasonal variations in biomass of the various life history phases of *Gigartina polycarpa* and *Sarcothalia stiriata* at Kommetjie are shown in figs 2.2 and 2.3, respectively. A trend for a greater biomass in late-summer (February) and low biomass in winter (June and July) was evident in all three life-history phases of *G. polycarpa*, although seasonal data were not statistically significantly different (see chapter 3, section 3.3.2). Biomass was highest in female gametophytes, ranging from 0.2 to 1.5 $kg.m^{-2}$ (fig. 2.2b), followed by tetrasporophytes (0.4 to 0.9$kg.m^{-2}$, fig. 2.2c) and male gametophytes (0.15 to 0.5$kg.m^{-2}$, fig. 2.2a). The biomass of *S. stiriata* was greater than that of *G. polycarpa*, with a trend toward greater values in mid-summer (November to January) and lower values in winter (June), with no statistically significant differences between seasons (see 3.3.2). Male (fig. 2.3a) and female (fig. 2.3b)

		Gigartina polycarpa				*Sarcothalia stiriata*			
		Biomass	Standing stock kg			Biomass	Standing stock kg		
Region & locality	Shore length m	kg.m^{-2}	♂	♀	⊕	kg.m^{-2}	♂	♀	⊕
Cape Columbine									
a. Vioolbaai / Brandbaai	2250	2.28	811	1119	1148	0.28	186	141	51
b. Noordbaai / Hannasbaai	2700	3.29	6977	9624	9871	3.64	14409	10953	3925
c. Klipbank - Middle Bay	1500	3.75	4284	5910	6062	0.15	320	243	87
d. Rocky Point (S. of Stompneus Point)	350	4.14	183	253	259	0.55	45	35	12
e. Shell Bay	1750	1.09	960	1325	1359	5.49	9028	6863	2459
f. Britannia Bay	300	2.90	92	127	130	1.48	87	66	24
g. Cape St Martin - Duiker Island	1340	2.25	890	1228	1259	3.48	2570	1953	700
h. Lizaseklip - Bekbaai	830	3.58	1934	2668	2737	1.18	1190	905	324
i. Trappiesklip - Cape Columbine	2250	5.07	7035	9705	9954	1.26	3264	2481	889
Cape south west Coast									
j. Kabeljoubank - Die Skaapwas	1170	2.16	719	992	1018	1.17	727	553	198
k. Grotto Bay	860	1.96	355	490	503	0.69	234	178	64
l. Melkbos	750	3.59	1135	1566	1606	2.67	1576	1198	429
m. Blouberg / Haakgat	2000	3.40	1631	2250	2307	0.41	367	279	100
Cape Peninsula									
n. Sea Point - Mouille Point	4650	3.11	1029	1420	1456	1.00	618	470	168
o. Bakoven	250	2.22	234	323	331	1.48	291	221	79
p. Oudekraal	320	1.87	391	540	553	1.29	504	383	137
q. Kommetjie	820	1.24	3149	4344	4455	2.01	9528	7243	2596
r. Soetwater	2240	0.75	1235	1704	1748	1.74	5350	4067	1457
Cape Hangklip									
s. Pringle Bay	220	3.23	243	336	344	0.37	52	40	14
t. Skuitbaai	1200	5.96	6673	9205	9441	0.24	502	381	137
u. Maasbaai	1750	3.68	221	304	312	0.23	26	20	7
Danger Point									
v. Kruismansbaai	310	3.09	437	602	618	1.04	274	209	75
Totals (∑) and means ($\bar{t}$)	∑	$\bar{t}$	∑	∑	∑	$\bar{t}$	∑	∑	∑
	29810	2.94	40618	56035	57471	1.45	51148	38882	13932

Table 2.1: Biomass and standing stock of *Gigartina polycarpa* and *Sarcothalia stiriata* in the south Western Cape, November 1987 (fresh weight).

Region & locality	Shore length m	*Aeodes orbitosa* Biomass kg.m^{-2} Summer	*Aeodes orbitosa* Biomass kg.m^{-2} Winter	*Aeodes orbitosa* Standing stock kg Summer	*Aeodes orbitosa* Standing stock kg Winter	*Mazzaella capensis* Biomass kg.m^{-2} Summer	*Mazzaella capensis* Biomass kg.m^{-2} Winter	*Mazzaella capensis* Standing stock kg Summer	*Mazzaella capensis* Standing stock kg Winter
Cape Columbine									
1. Soldatepos	2950	2.71	0.13	7991	396	0.01	0.00	40	0
2. Vioolbaai	700	2.47	0.33	1731	231	1.16	0.09	809	63
3. Hannasbaai	850	0.96	0.00	816	0	0.21	0.00	179	0
4. Shell Bay Point	450	0.86	0.18	386	79	0.06	<0.01	26	2
5. Britannia Bay	750	1.70	0.12	1273	88	0.01	0.01	11	10
6. Patemoster	900	1.99	0.08	1789	73	0.46	0.16	410	142
7. Abdolsbaai	1050	3.68	0.16	3868	169	0.89	0.15	933	162
8. Cape Columbine	7900	0.58	0.06	4614	452	<0.01	0.05	22	376
Cape south west Coast									
9. Yzerfontein	2200	0.36	0.17	797	374	0.91	1.14	1996	2503
10. Grotto Bay	4150	1.11	0.11	4598	467	<0.01	0.00	30	0
Cape Peninsula									
11. Mouille Point	2350	11.93	0.18	28026	427	0.00	0.00	0	0
12. Sea Point	2600	2.04	0.09	5316	236	1.60	0.11	4260	280
13. Oudekraal	6458	1.19	0.17	7709	1067	0.03	<0.01	164	22
14. Kommetjie	3350	19.37	0.60	64888	2016	1.29	<0.01	4323	8
15. Soetwater	3200	7.06	0.68	22579	2171	0.04	<0.01	128	2
16. Scarborough	1800	0.73	0.01	1311	19	1.87	<0.01	3356	16
17. Sunny Cove	2600	0.00	0.03	0	73	0.00	0.00	0	0
Cape Hangklip									
18. Rooi Els	2000	0.06	0.00	113	0	0.08	0.00	163	0
19. Pringle Bay	1700	0.10	0.00	177	0	<0.01	0.00	1	0
20. Cape Hangklip	1450	0.56	0.00	805	0	0.09	0.00	135	0
21. Maasbaai	4500	0.75	0.02	3361	68	0.00	<0.01	0	20
22. Kleinmond	1250	0.25	0.08	308	96	0.29	<0.01	359	4
Mudge Point									
23. Harry's Bay	2150	1.35	0.04	2891	75	0.07	<0.01	142	4
24. Sandbaai	6250	0.73	0.04	4545	249	0.05	0.01	341	85
25. Hermanus	4250	1.31	0.01	5556	34	0.29	0.00	1223	0
Danger Point									
26. Stanford's Cove	600	4.13	0.07	2480	40	0.00	0.00	0	0
27. Kruismansbaai	9250	1.10	0.10	10145	927	0.77	0.05	7122	502
28. Franskraal	6250	0.36	<0.01	2261	36	0.68	0.03	4272	160
29. Pearly Beach	3550	0.91	0.03	3227	118	0.88	0.04	3106	140
Totals ($\sum$) and means ($\bar{t}$)	$\sum$	$\bar{t}$	$\bar{t}$	$\sum$	$\sum$	$\bar{t}$	$\bar{t}$	$\sum$	$\sum$
	87458	2.43	0.12	193561	9981	0.41	0.07	33551	4501

Table 2.2: Summer/winter biomass and standing stock of *Aeodes orbitosa* and *Mazzaella capensis* in the south Western Cape, July (winter) and December (summer) 1989 (fresh mass).

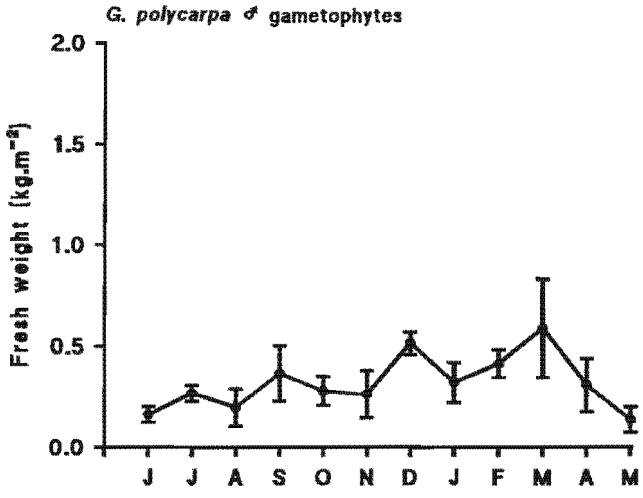


Fig. 2.2a

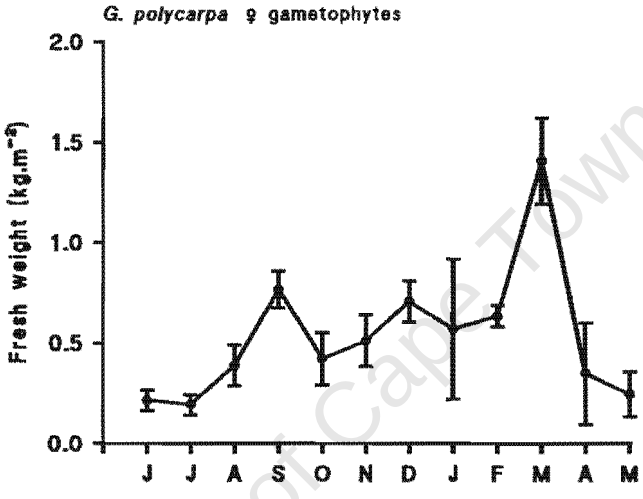


Fig. 2.2b

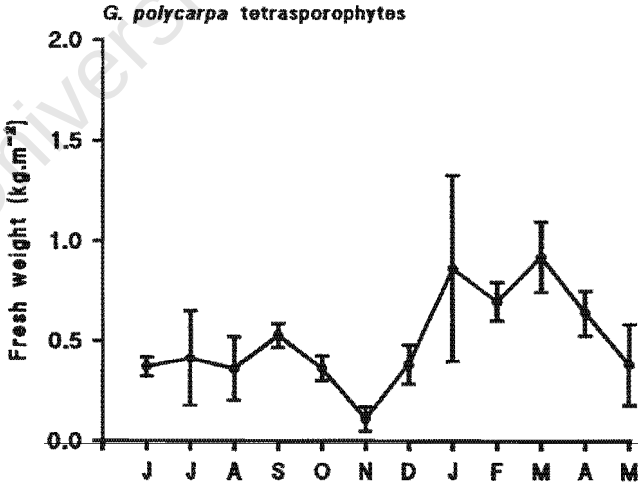


Fig. 2.2c

Figure 2.2 Seasonal variation in biomass ($kg.m^{-2}$) of different life-history phases of *Gigartina polycarpa* at Kommetjie, Cape Peninsula (1987/88): a) ♂ gametophytes; b) ♀ gametophytes; c) tetrasporophytes; 95% confidence limits indicated.

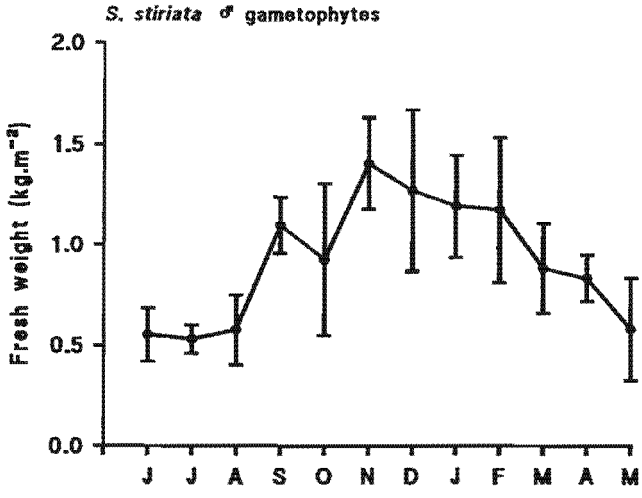


Fig. 2.3a

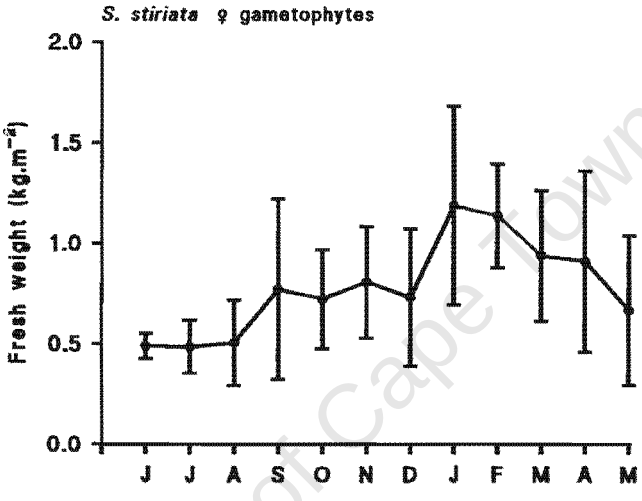


Fig. 2.3b

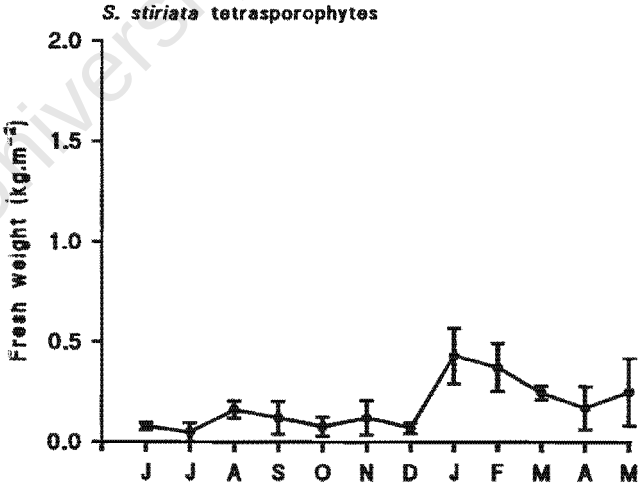


Fig. 2.3c

Figure 2.3 Seasonal variation in biomass ($kg.m^{-2}$) of different life-history phases of *Sarcothalia stiriata* at Kommetjie, Cape Peninsula (1987/88): a) ♂ gametophytes; b) ♀ gametophytes; c) tetrasporophytes; 95% confidence limits indicated.

gametophytes dominated the biomass, ranging from 0.55 to 1.5 $kg.m^{-2}$ and from 0.55 to 1.1$kg.m^{-2}$, respectively. Tetrasporophytes of *S. stiriata* (fig. 2.3c) were much less abundant (0.05 to 0.4$kg.m^{-2}$) than those of *G. polycarpa*.

Carrageenan yield, expressed as a percentage of dry weight against extraction time (h), is shown for *Gigartina polycarpa* female gametophytes (fig. 2.4a) and tetrasporophytes (fig. 2.4b). Results of one-way analysis of variance and the Student-Newman-Keuls test showed a significant difference ($F_{0.05(2),11,35} = 15.77 > 2.39$) between female gametophytes incubated for less than 4h and those incubated for 4h or more. There was no significant difference in carrageenan yield in tetrasoprophytes incubated for 5h or more, but a significant difference was found ($F_{0.05(2),11,36} = 38.62 > 2.39$) from those incubated for 4h or less. The optimum extraction period which allowed a standardization of methods for both female gametophytes and tetrasporophytes was therefore 5h. Seasonal variations in carrageenan yield of the different life-history phases of *G. polycarpa* are shown in fig. 2.5; mean yields of 46.10, 49.39 and 41.02% of dry weight were found in male and female gametophytes and tetrasporophytes, respectively. In *Sarcothalia stiriata* (fig. 2.6), the mean carrageenan yield was 44.37, 43.64 and 39.10% of dry weight in male and female gametophytes and tetrasporophytes, respectively. Although carrageenan content varied monthly in all life-history phases of the two species (figs 2.5 and 2.6), no significant seasonal differences were apparent ($p>0.05$: $F_{0.05(2),3,14} < 4.24$, all phases).

Summarizing the summer harvest of the four species from the south Western Cape (table 2.3), *Gigartina polycarpa* was estimated to yield the most carrageenan (11.5 tons), followed by

Species	♂ Gametophytes (kg)	♀ Gametophytes (kg)	⊕ Tetrasporophytes (kg)
Gigartina polycarpa	3071	4539	3866
Sarcothalia stiriata	3722	2783	893
Aeodes orbitosa	10452 (no division into life-history phase)		
Mazzaella capensis	1386 (no division into life-history phase)		

Table 2.3: Estimated carrageenan yield (dry weight) from a summer harvest of *Gigartina polycarpa*, *Sarcothalia stiriata*, *Aeodes orbitosa* and *Mazzaella capensis* in the south Western Cape.

Aeodes orbitosa (10.5 tons) and *Sarcothalia stiriata* (7.4 tons). *Mazzaella capensis*, would yield just 1.4 tons of carrageenans.

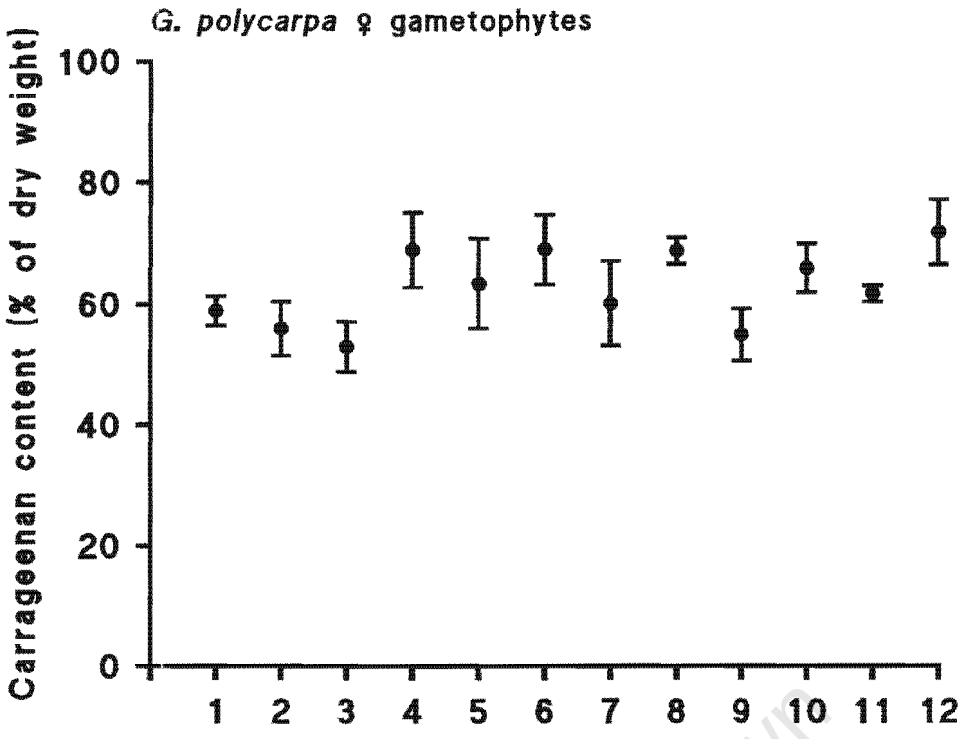


Fig. 2.4a

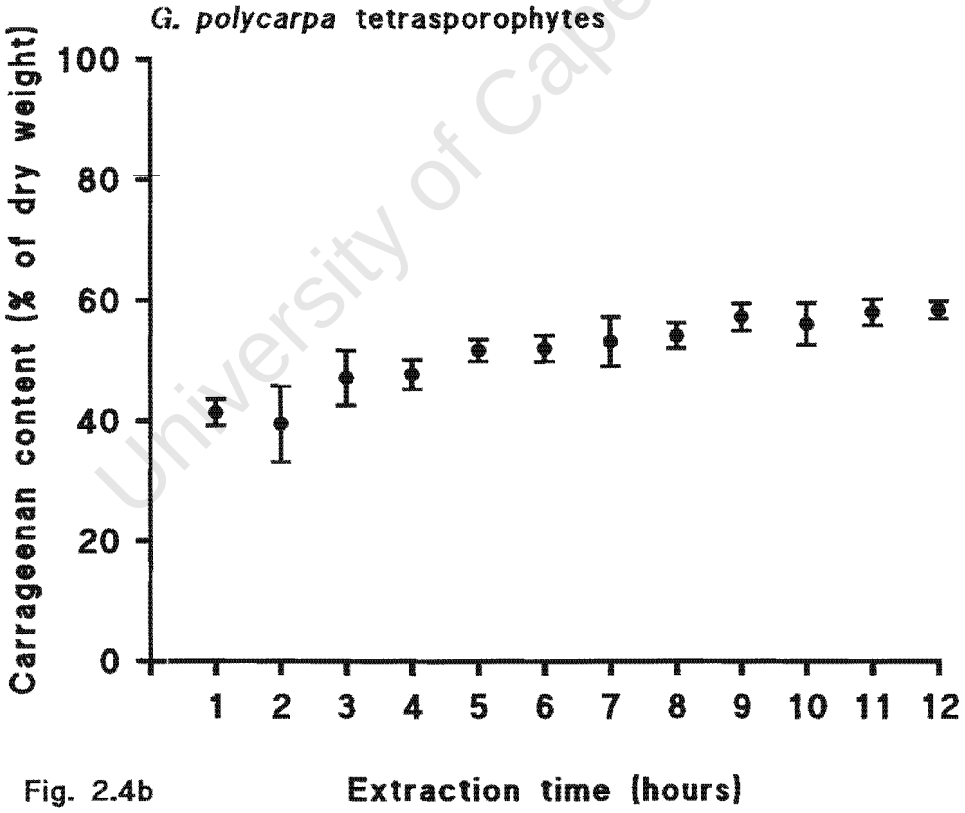


Fig. 2.4b

Figure 2.4 Carrageenan yield (% of dry weight) versus extraction time at 85°C (hrs) of *Gigartina polycarpa* a) ♀ gametophytes; b) tetrasporophytes; 95% confidence limits indicated.

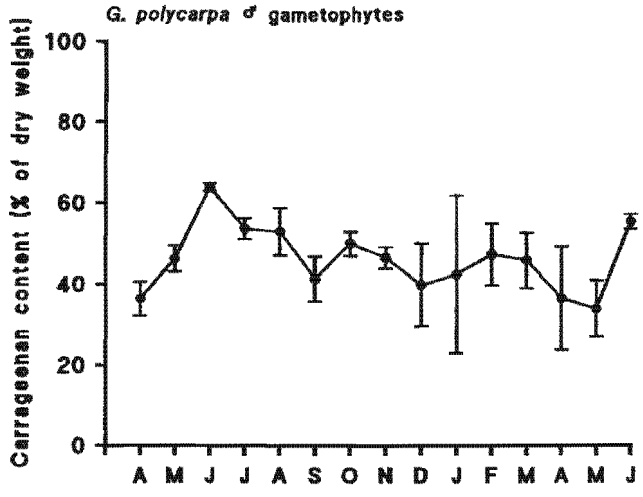


Fig. 2.5a

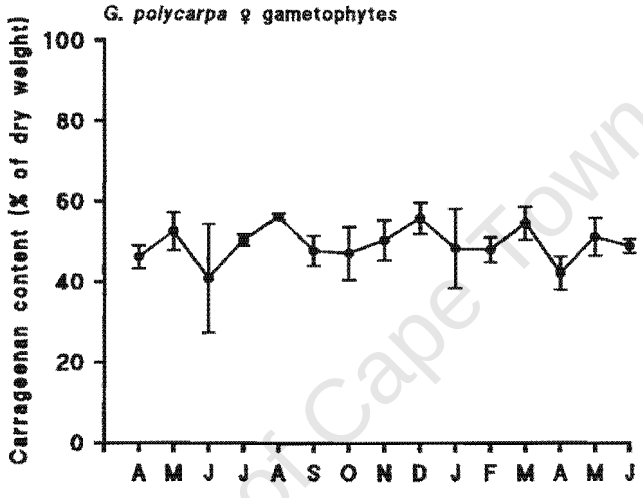


Fig. 2.5b

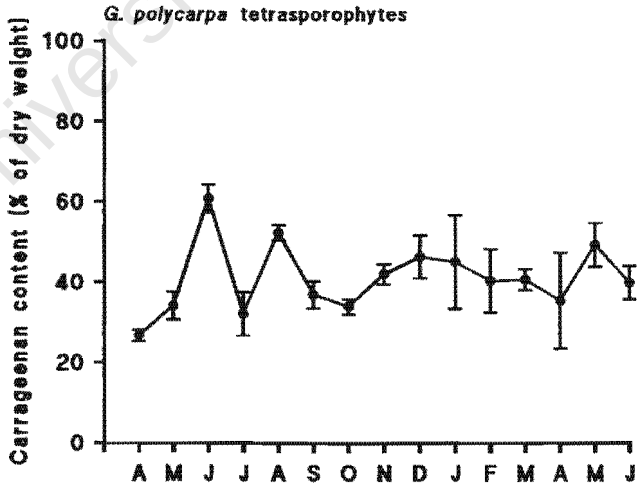


Fig. 2.5c

Figure 2.5 Seasonal variation in carrageenan content (% of dry weight) of different life-history phases of *Gigartina polycarpa* at Kommetjie, Cape Peninsula (1987/88): a) ♂ gametophytes; b) ♀ gametophytes; c) tetrasporophytes (⊕); 95% confidence limits indicated.

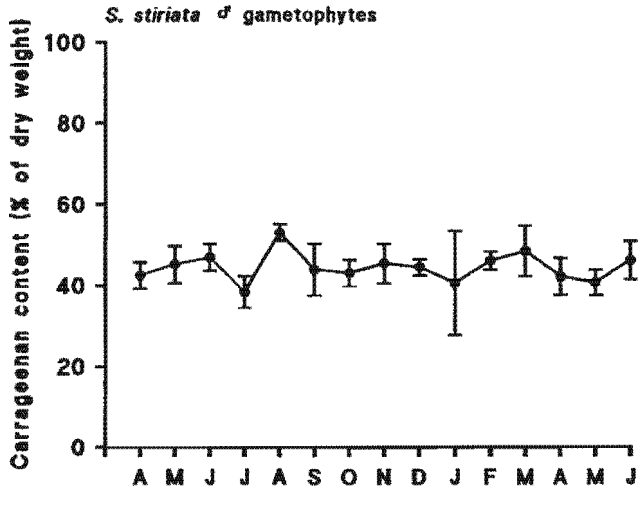


Fig. 2.6a

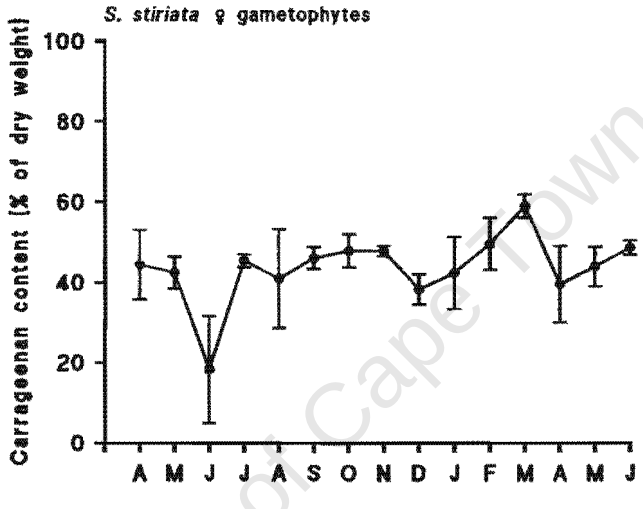


Fig. 2.6b

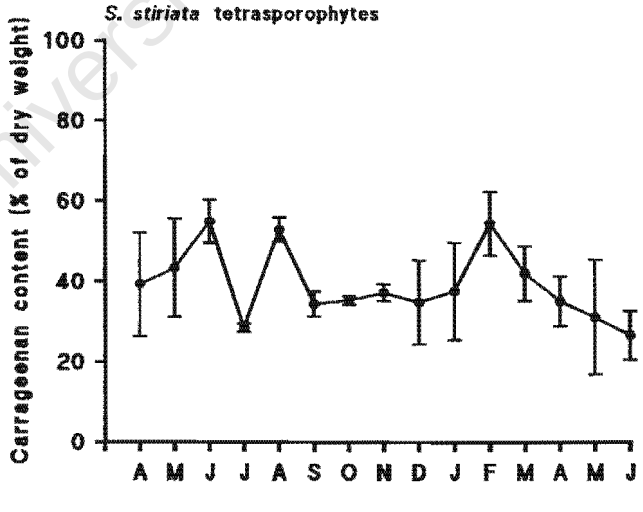


Fig. 2.6c

Figure 2.6 Seasonal variation in carrageenan content (% of dry weight) of different life-history phases of *Sarcothalia stiriata* at Kommetjie, Cape Peninsula (1987/88): a) ♂ gametophytes; b) ♀ gametophytes; c) tetrasporophytes (⊕); 95% confidence limits indicated.

2.4 DISCUSSION

The spring/summer (November/December) fresh weight standing stocks of *Gigartina polycarpa* (154 tons), *Sarcothalia stiriata* (104tons), *Aeodes. orbitosa* (194 tons) and *Mazzaella. capensis* (34 tons) amount to a total standing stock of 486 tons on the south Western Cape coast. This quantity is equivalent to approximately 69.6 tons dry weight of carrageenophytes, of which *G. polycarpa* and *S. stiriata* constitute 42.3 tons. This amount is comparable to the standing stock estimate 39 tons for the Eastern Cape carrageenophyte *Hypnea spicifera* between the Kei River and Cape St Francis (van Zyl, 1993), a similar length of coastline to that surveyed in the present study. Individually, none of the Western Cape carrageenophyte species was as abundant as *H. spicifera*. With the exception of *M. capensis*, carrageenophytes were more abundant in the northern region of the study area (Cape Point to Cape Columbine), occurring in relatively small quantities from Cape Hangklip to Cape Agulhas. This regional difference in biomass may be attributed to the high nutrient levels of the Benguela upwelling system on the West Coast promoting algal growth, particularly in the region between Cape Point and Cape Columbine (Andrews and Cram, 1969; Andrews, 1974; Andrews and Hutchings 1980). Temperature differences between the West Coast and the South Coast overlap region are more likely to determine biogeographical distributions on a regional level (see chapter 6), physical and biotic factors probably causing distributional differences at a local level (see chapter 4). The greater abundance of *M. capensis* at Danger Point may be a result of a combination of physical factors such as wave action and sand scouring, which tend to be greater there than elsewhere on the south Western Cape coast. *Mazzaella capensis* is psammophilic and tolerant of extreme wave action, whereas *Aeodes orbitosa* is relatively psammophobic (Bolton and Levitt, 1992; Bolton and Joska, 1993). *Gigartina polycarpa* is tolerant of sand inundation (Jackelman and Bolton, 1990), *S. stiriata* less so (Bolton and Levitt, 1992). *Gigartina polycarpa* is absent in areas of extreme wave action, whereas *S. stiriata* may persist in such localities (see chapter 4). The observed distribution of these species in the present study reflects the importance of these factors in determining their distributions. Compared to other countries, the standing stock of Western Cape carrageenophytes is extremely low. Hannach and Waaland (1986) reported a fresh weight standing stock of 2600 tons of *Iridaea cordata* (Turner) Bory along 70km of shore in British Columbia, and Santelices and Norambuena (1987) reported exports exceeding 5000 tons dry weight of *Mazzaella*

laminariodes (Bory) Fredericq (formerly *Iridaea laminariodes* - Hommersand *et al.* 1994) collected from natural populations in Chile. The mean fresh biomass of 2.94 and 1.45kg.m^{-2} (470 and 238g.m^{-2} dry weight) for *Gigartina polycarpa* and *Sarcothalia stiriata*, respectively, estimated for the south Western Cape, were similar to that found on the Eastern Cape for *Hypnea spicifera*, where a dry biomass of *ca.*385g.m^{-2} was recorded (van Zyl, 1993). For the west coast of North America, Hannach and Waaland (1986) reported values of *ca.* 400g.m^{-2} dry weight for *I. cordata*. The considerably smaller standing stock of the South African carrageenophytes relative to that of other countries may be attributed to the substantially smaller areas occupied by these species as a result of environmental conditions such as the relatively small tidal range (*ca.* 2m).

The optimum heated-water immersion time of 4-5h for the extraction of carrageenan from *Gigartina polycarpa* and *Sarcothalia stiriata* is similar to the estimate of 3-5h which produced the highest carrageenan yield, gel strength and viscosity in *Eucheuma isiforme* (Dawes *et al.* 1977). Other workers have used similar extraction periods to determine carrageenan content *e.g.* 4-5h for *Eucheuma nudum* and *E. isiforme* (Dawes *et al.* 1974b), 4h for *Ahnfeltia concinna* (Santos and Doty, 1975), 4h for South African *S. stiriata* and *Hypnea spicifera* (Furneaux and Miller, 1986), and 4h for 24 species of the Phyllophoraceae (McCandless *et al.* 1982). The method devised by Santos and Doty (1975) is the most widely used method of carrageenan extraction (*e.g.* Semesi and Mshigeni, 1977; Mshigeni and Semesi, 1977; Mshigeni *et al.* 1979; Bolton and Joska, 1993), and an extraction period of about 4h is generally accepted. Carrageenan content of *G. polycarpa* and *S. stiriata* was similar to that of other South African carrageenophytes (*e.g. ca.*43% for *H.spicifera*, van Zyl (1993), *ca.*36% for *Mazzaella capensis*, Bolton and Joska (1993)), but considerably less than the 70% recorded for *Gigartina teedii* from France (Zinoun *et al.* 1993).

In contrast to the lack of seasonality found in carrageenan content of *Gigartina polycarpa* and *Sarcothalia stiriata* off the south Western Cape, Dawes *et al.* (1974b,1977) and Chopin *et al.* (1987) showed distinct seasonal patterns in *Eucheuma isiforme*, *Eucheuma nudum* and *Chondrus crispus*, with summer maxima and autumn/winter minima in carrageenan content. Carrageenan levels in *Eucheuma* spp. are low when new plants recruit into the population and are growing actively (Dawes *et al.* 1974b), a feature also found in *Aeodes orbitosa* (J.J. Bolton and M.A.P. Joska *pers. comm.*), and also when plants lose structural material during the

breakdown of tissue to release spores during reproduction (Dawes *et al.* 1977). High levels of carrageenan are found in mature plants until the onset of reproduction (Dawes *et al.* 1977). As large, mature thalli of *G. polycarpa* and *S. stiriata* were used in the present study, this may explain the lack of seasonality found in carrageenan content. In contrast, Bolton and Joska (1993) observed a reverse pattern in *Mazzaella capensis*, with a summer minimum and winter maximum in carrageenan content and a positive correlation between carrageenan content and recruitment of new plants in winter/spring. Bolton and Joska (1993) hypothesized that low carrageenan levels may be a result of high concentrations of nutrients during summer. In *C. crispus*, an inverse correlation between nitrogen concentration and carrageenan content was demonstrated by Neish *et al.* (1977), as was an inverse correlation between phosphorus concentration and carrageenan content (Chopin *et al.* 1990; Chopin *et al.* 1995). Juveniles of *G. polycarpa* and *S. stiriata* recruit into the population between August and December (see chapter 3), and it is likely that these plants have low levels of carrageenans. The inverse correlation between carrageenan content and growth rate was also observed in *Hypnea spicifera* on the Eastern Cape coast (van Zyl, 1993). Because of the lack of seasonality in carrageenan content in mature thalli of *G. polycarpa* and *S. stiriata* it may be that seasonal fluctuations in nutrient levels are not solely responsible for changes in carrageenan content, but rather that they are the result of a complex interaction of many factors, of which nutrients (Fuller and Mathieson, 1972) is one component. Seasonality may also have been masked by the use of isopropanol to precipitate the carrageenan. Chopin *et al.* (1991) showed that precipitation by alcohol resulted in the simultaneous precipitation of floridean starch, especially in conditions of phosphorus enrichment. Chopin *et al.* (1990) recommend the use of hexadecyltrimethylammonium bromide (CTAB) as a substitute for alcohol.

In conclusion, Western Cape carrageenophytes are capable of supporting an industry at a low level of exploitation. Populations of *Gigartina polycarpa*, *Sarcothalia stiriata* and *Aeodes orbitosa* are sufficiently large to be exploited at Cape Columbine and the Cape Peninsula, and at Danger Point for *A. orbitosa* only. Populations of *Mazzaella capensis* are too scattered to be economically useful and, being subject to periodic sand inundation (Bolton and Joska, 1993), of limited harvesting potential. However, it would be possible to harvest *M. capensis* together with the other species where they occur in sufficient quantities. The expected carrageenan yield from a combined summer harvest of the three exploitable species is

estimated at 29.3 tons. Since commercial use may require either pure carrageenan types, or blends of carrageenan types in specified proportions, the life-history phases of each species would have to be individually harvested and sorted, although such harvesting could be simultaneous. This may affect the economic viability of harvesting, but this could be offset by better prices obtained for quality carrageenan blends or pure carrageenans. Although the carrageenan extracted from *A. orbitosa* is similar to λ-carrageenan in structure, it has a low level of sulphation (Nunn and Parolis, 1968) which renders the species unattractive to the industry. Because *A. orbitosa* is an annual, it should be harvested only once per year. Small plants recruit in winter, grow to a large size by early summer and thereafter become reproductive and survive until autumn (Bolton and Levitt, 1992). Harvesting may therefore have a considerable detrimental effect on future recruitment, which in turn may have serious implications for future harvests. Although individual plants are short-lived, *M. capensis* is probably less susceptible to recruitment failure following harvesting because reproductive plants are present throughout the year (Bolton and Levitt, 1992). Upright thalli of *G. polycarpa* and *S. stiriata* are fertile all year round (Bolton and Levitt, 1992). Holdfasts of these two species appear to be perennial, which makes them least susceptible to harvesting. They are suitable for exploitation both in terms of biomass and usefulness of the phycocolloid. However, the overall economic viability of exploiting such limited resources seems doubtful, and future economic exploitation is more likely to depend on mariculture than on the use of natural populations, as has been proposed for *Iridaea cordata* (Hannach and Waaland, 1986).

CHAPTER 3

SEASONAL DEMOGRAPHIC PATTERNS IN POPULATIONS OF *GIGARTINA POLYCARPA* AND *SARCOTHALIA STIRIATA*

3.1 INTRODUCTION

Because of the economic potential of *Gigartina polycarpa* and *Sarcothalia stiriata* as carrageenophytes, it is desirable to understand the seasonal patterns of development of populations of these two species. Since sympatric biota cannot be occupying the same ecological niche, the co-occurrence (no apparent spatial separation) of multiple life-history phases of a species in one geographical locality is generally understood to be an adaptation to a seasonally variable environment or that containing differing environmental characteristics (Santelices, 1990). This is thought to explain the occurrence of species with a heteromorphic alternation of generations - differential effects of factors such as growth, reproduction and mortality permitting the exploitation of seasonally or spatially dissimilar niches within the same habitat. Ecological dissimilarities may result in bimodal selection pressures with the separate phases evolving towards opposite life styles (Vadas, 1979). However, many seaweeds (including the subjects of this study) are isomorphic, the reproductive phases possessing highly similar forms, and the adaptive advantages and disadvantages of the various ploidy levels in these species has been the subject of speculation (Santelices, 1990). Ecological differences between life-history phases in isomorphic seaweeds appear to be more subtle than in heteromorphic species, and this poses questions as to the adaptive value of an alternation of generations, which is supposed to lie in the enhanced fitness resulting from heterosis in the diploid genome (Hansen and Doyle, 1976). The relative abundance of isomorphic life-history phases is closely related to the adaptive value (i.e. enhanced fitness) of an alternation of generations, and is often used as indirect evidence of a species life history strategy: when life-history phases are unequally represented (*i.e.* gametophyte : sporophyte ratio ≠ 1:1), it is assumed that a strict alternation of generations is of less importance than other regenerative means (Dawes *et al.* 1974a; Hansen and Doyle, 1976). Both *G. polycarpa* and *S. stiriata* display the common *Polysiphonia*-type life history pattern, which is karyologically trigenetic and has two free-living isomorphic generations: a dioecious haploid gametophyte generation

and a diploid sporophyte generation (Hawkes, 1990). Various studies have shown variation in gametophyte : sporophyte ratios, as well as deviation from a 1:1 gametophyte sex ratio in dioecious taxa (De Wreede and Klinger, 1988). Sporophyte dominance has been recorded in populations of a member of the Gigartinaceae, *Iridaea cordata* (Turner) Bory (Hansen and Doyle, 1976), whilst May (1986) and Luxoro and Santelices (1989) have observed gametophyte dominance in *I. cordata* and *Mazzaella laminarioides* (Bory) Fredericq, respectively. They suggested that the dominance of gametophytes over sporophytes of *M. laminarioides* at the uppermost limits of this species' distribution was due to the gametophytes higher desiccation tolerance and better growth rate, which casts doubt on arguments invoking increased adaptive benefit of diploidy over haploidy. Also, Abbott (1980) observed gametophyte dominance in a population of *Gigartina leptorhyncos* J. Agardh, whilst De Wreede and Green (1990) observed a seasonal alternation of gametophyte dominance in *Mazzaella splendens* (Setchell *et* Gardner) Fredericq. An example of an environmentally induced alternation of generations has been observed by Bolton and Joska (1993) who, in observing an alternation from sporophyte to gametophyte dominance in a population of the S. African carrageenophyte *Mazzaella capensis* (J. Agardh) Fredericq, concluded that periodic sand inundation was a factor complicating the alternation of generations.

Variations from the theoretical life history may be attributable to greater fecundity and survivorship of one phase, or to asexual reproduction via vegetative propagation or apomixis (Hawkes, 1990). For example, some Gigartinaceae possess both sexual and asexual reproductive modes in their life history utilizing various sexual and asexual reproductive pathways to maintain themselves throughout their range and under different environmental conditions (Hawkes, 1990). For example, *Mastocarpus papillatus* (C. Agardh), Kützing displays both sexual (foliose haploid gametophytes alternating with crustose diploid sporophytes) and asexual (gametophytes cycling directly) life-histories, the proportion of these two pathways within populations varying with latitude (Zupan and West, 1988). Also, Hansen (1977) concluded that plants of *I. cordata* grow from long lived crusts rather than spore re-establishment, whilst May (1986) proposed that vegetative perennation and better survival of gametophyte spores and sporelings maintained gametophyte dominance. However, vegetative perennation requires a high investment of resources (Santelices, 1990), whilst asexual reproduction via small propagules is more economical. Asexual phenomena may be

obligate or facultative (Hawkes, 1990), occurring in some or all individuals of a population (*e.g. Mastocarpus papillatus*; Polanshek and West, 1977) , or in some or all populations of a species *e.g. Mastocarpus stellatus* (Stackhouse) Guiry, where some populations display a sexual heteromorphic life history, some display a direct development and cycling of female gametophytes, and others a mixture of both pathways (Guiry and West, 1984). Asexual propagules supposedly produce populations with less genetic flexibility than sexually produced populations, and are more susceptible to environmental changes (Santelices, 1990). For example, Dyck *et al.* (1985) suggested that wave exposure was a contributing factor on shores where sporophytes of *I. cordata* dominated. They also observed local variability in the dominant life history phase of *I. cordata*, with sporophyte dominance in northerly populations and gametophyte dominance in southerly populations on the North American west coast, which implies that sporophytes were better suited to the more environmentally variable higher latitudes. Sporophyte dominance has also been recorded in carrageenophytes from other families (*e.g. Hypnea musciformis* (Wulf.) Lamour. (Rao, 1970), *Eucheuma isiforme* (C. Ag.) J. Ag. (Dawes *et al.* 1974a) and South African *Hypnea spicifera* (Suhr) Harv. (van Zyl, 1993)).

Dyck *et al.* (1985) hypothesized that if one particular life-history phase was dominant, an event which subsequently causes removal (*e.g.* very low tides combined with hot weather) would enable spores to settle and grow into the alternate phase which would then dominate until the next catastrophe. The alternation of generations of *Mazzaella capensis* appears to be via such a mechanism (Bolton and Joska, 1993). Whilst such an alternation of generations may occur when a catastrophe opens sites for spore colonization, perennation from basal systems (if these remain after the catastrophe) may result in a regular alternation of generations being less common than expected. Hansen and Doyle (1976) observed that adult plants of *I. cordata* were reduced to "stubs" in winter by the mechanical shearing of storm action, these producing new thalli in the spring. Clonal propagation via ramets thus allows continued occupation of space and more rapid regrowth in the population. In clonal red algae, such as members of the family Gigartinaceae, the genet is the entire thallus which arises from a single spore, whereas the foliose fronds which make up the genet are individually considered to be ramets (Scrosati, 1996). According to Scrosati and De Wreede (1997), ramets of clonal plants have different growth dynamics to the genets of non-clonal plants - small, non-clonal genets dying as a result

of overcrowding due to biomass accumulation (self- thinning) whereas clonal plants do not undergo self-thinning as a result of frond crowding due to the physical integration that exists between ramets (Martínez and Santelices, 1992; Scrosati, 1996). Fronds of clonal red algae arising from the same holdfast may have a certain degree of physiological integration (Maggs and Cheney, 1990) whereby assimilates are translocated from large to small ramets to ensure the survival of the latter. Therefore, the occurrence of self-thinning can be determined by examining the relationship between stand biomass and frond density - stands of plants which undergo self-thinning exhibit a negative slope when plotted on a bi-logarithmic scale (Scrosati, 1996). This negative relationship indirectly indicates the existence of competition among plants in the stand through density-dependent mortality as the stand ages. A hypothetical line, the ultimate-biomass density line describes the maximum mean biomass possible for any plant density, and is thought to constrain all plant populations, including those that do not undergo self-thinning (Weller, 1989). This line, with a slope of -1.5 and a maximum y-intercept of 4.3, is referred to as the "-3/2 power law" or "self-thinning law" (Martínez and Santelices, 1992). Theoretically, greatest mean biomass of non self-thinning ramets would be attained at the ultimate biomass-density line, growth ceasing at this point simultaneously with the onset of sexual reproduction and senescence.

The importance of facultative asexual reproduction as an alternate pathway in sexual life-histories has been largely ignored (Dixon, 1965), yet vegetative reproduction is probably more widespread and more important in maintaining populations than currently recognized (Hawkes, 1990). For example, Woodward (1988) observed that sporophyte dominance in Californian populations of *Endocladia muricata* (Post. and Rupr.) J. Ag. was due to better sporophyte growth and survivorship (by vegetative secondary attachment), rather than better sporophyte recruitment. A further advantage is that when environmental conditions are not favourable for sexual reproduction or sporeling recruitment, asexual reproduction allows for persistence of the species (Templeton, 1982).

The aim of this investigation was therefore to investigate the seasonal demography and reproductive phenology of *Sarcothalia stiriata* and *Gigartina polycarpa* and to assess their population dynamics with special reference to any imbalance in sporophyte : gametophyte ratios which may occur. Different gametophyte : sporophyte ratios of these two related, co-occurring members of the Gigartinaceae would imply differing adaptive strategies to ensure

niche separation, and this could well be a means of ensuring survival of populations of each species within the same habitat. An understanding of population structure and development under field conditions is required for the management and manipulation of natural populations, especially if they are to be exploited. Within the Gigartinaceae, λ-type carrageenans occur solely in the sporophyte generation and κ-type carrageenans are characteristic of the gametophyte (McCandless *et al.* 1973). Both species also have differing proportions of other (ι,μ andν) carrageenan types (Furneaux and Miller, 1986) in the gametophyte phase. Thus, the relative abundance of life-history phases is of importance since changes in population structure would affect both carrageenan yield and quality.

3.2 METHODS

3.2.1 Study site

With the exception of the studies on fecundity which took place between July 1991 and January 1992, these investigations were carried out over a 16 month period between February 1987 and May 1988. Plants of *Gigartina polycarpa* and *Sarcothalia stiriata* were collected at Kommetjie on the west coast of the Cape Peninsula (34°08.4'S, 18°19.4'E). The site at Kommetjie consisted of a semi-exposed ledge of Table Mountain Sandstone bounded on the west, sea-facing side by immoveable, medium-sized boulders (*ca.*1m diameter). The ledge was occupied by a mixed population of *G. polycarpa* and *S. stiriata*, sheltered crevices being populated by *G. polycarpa* and *S. stiriata* solely occupying exposed boulder edges.

3.2.2 Phenology, thallus weight and reproductive weight

The phenology of both species was investigated monthly using a point system. A line marked at 10cm intervals was laid randomly through a mixed community of *Gigartina polycarpa* and *Sarcothalia stiriata*. Where a mark touched a plant the life history phase of that species was noted until a total of 300 plants of both species had been recorded. Phenology data were analyzed for seasonal variation (monthly data combined for season in the following manner: December, January, February = summer; March, April, May = autumn; June, July, August = winter; September, October, November = spring), and for differences between life-history phases over the entire experimental period, by one-way ANOVA on arcsin-transformed percentage data using the Student-Newman-Keuls multiple range test for differences between treatments (α=0.05).

Seasonal biomass was determined by a monthly collection of all plants in a minimum of three 50 x 50cm quadrats, these being cleared by scraping with a steel abalone lever. Plants were divided into species and life-history phase and the total fresh thallus weight recorded. Vegetative plants without visible reproductive structures were identified visually by observation of their gross morphology - *i.e.* strongly papillate individuals of *G. polycarpa* and very fleshy individuals of *S. stiriata* were classed as male gametophytes, stringy individuals of *S. stiriata* were identified as female gametophytes and smooth thalli of both species were considered to be tetrasporophytes. Areas of the thallus containing visible cystocarps or tetrasporangial sori were excised and weighed separately to give a figure for total reproductive thallus weight (female gametophytes and tetrasporophytes only). Biomass data were analyzed for seasonal variation by one-way ANOVA on a similar basis to the phenology data, but without arcsin transformation (data were empirical).

3.2.3 Population demography

According to Ang and De Wreede (1990) it is likely, given the modular character of many algae, that algal demographic studies are best described based on size. Accordingly, demography data were collected monthly by weighing individually all plants collected from four 25 x 25cm quadrats. Six weight classes were chosen for ease of data interpretation and the data was converted to frequency in size class per m^2. Plants were grouped according to life-history phase and whether they could be macroscopically identified to species, the groups being: unidentifiable *Gigartina* sp. juveniles, identifiable juveniles of *Gigartina polycarpa* and *Sarcothalia stiriata* and male or female gametophytes and tetrasporophytes of both species. Frond biomass versus frond density relationships were calculated by plotting the $\log_{10}$ (biomass per m^2) against the $\log_{10}$ (density per m^2) for the combined life-history phases of both species, and comparing the results with the ultimate biomass-density line as described by Scrosati and De Wreede (1997). The data used in this analysis was for the period July 1987 to May 1988. In order to determine the proportion of gametophytes to tetrasporophytes where these could not be visually distinguished, a separate study where all the juvenile plants from three 10x10cm quadrats were removed at monthly intervals from July 1991 to June 1992 was conducted. Each individual plant was analysed (after oven-drying at 60°C for 72 hours) for the presence of 3,6-anhydrogalactose using the acetal-resorcinol method described by Craigie and Leigh (1978), as modified by Dyck *et al.* (1985), and with further modification by

Shaughnessy and De Wreede (1991) using 1.0 ml of resorcinol solution for two minutes at 85°C. In order to determine the reliability of this method in distinguishing between diploid and haploid *Gigartina polycarpa* and *Sarcothalia stiriata*, five replicates of each of four different-sized portions of known life-history phases (i.e. reproductive adults) of these two species were assayed using this test.

3.2.4 Fecundity

The number of cystocarps/tetrasporangial sori per g fresh weight of reproductive plant material in both species was determined by counting the number of cystocarps/tetrasporangial sori in five tissue subsamples from 10 plants of each life history phase. Five cystocarps/tetrasporangial sori per subsample were subsequently examined microscopically to determine the number of spores in each, using both counting and measuring techniques: the number of spores visible in a cross-section of either a cystocarp or tetrasporangial sorus was multiplied up using a constant obtained from dividing the mean volume of a cystocarp (n=66, *Gigartina polycarpa*; n=34, *Sarcothalia stiriata*) or tetrasporangial sorus (n=90, *G. polycarpa*; n=30, *S. stiriata*) by the mean volume of a carpospore (n=30, *G. polycarpa*; n=34, *S. stiriata*) or tetraspore (n=58, *G. polycarpa*; n=30, *S. stiriata*) in order to obtain an estimate of the no. of spores per cystocarp or tetrasporangium. This was performed during December/January (austral summer) and July/August (austral winter) and an estimate of the number of spores per g fresh weight (fw) was then calculated and combined with the data for total reproductive thallus weight to give an estimate of spore production for each phase of both species during summer and winter. These calculations assumed that the total volume of the cystocarp was occupied by carpospores. No allowance was made for the volume occupied by supporting tissue or for interstitial spaces between carpospores.

3.3 RESULTS

3.3.1 Phenology

Monthly variability in proportions of the life history phases of *Gigartina polycarpa* and *Sarcothalia stiriata* was evident (fig. 3.1). In *G. polycarpa*, the proportion of male gametophytes in the population (table 3.1) was significantly greater during winter (40%) when compared with spring (30%) and summer (27%). A trend for an increase in the proportion of male gametophytes was observed in autumn and winter (35-50%), but this was not statistically

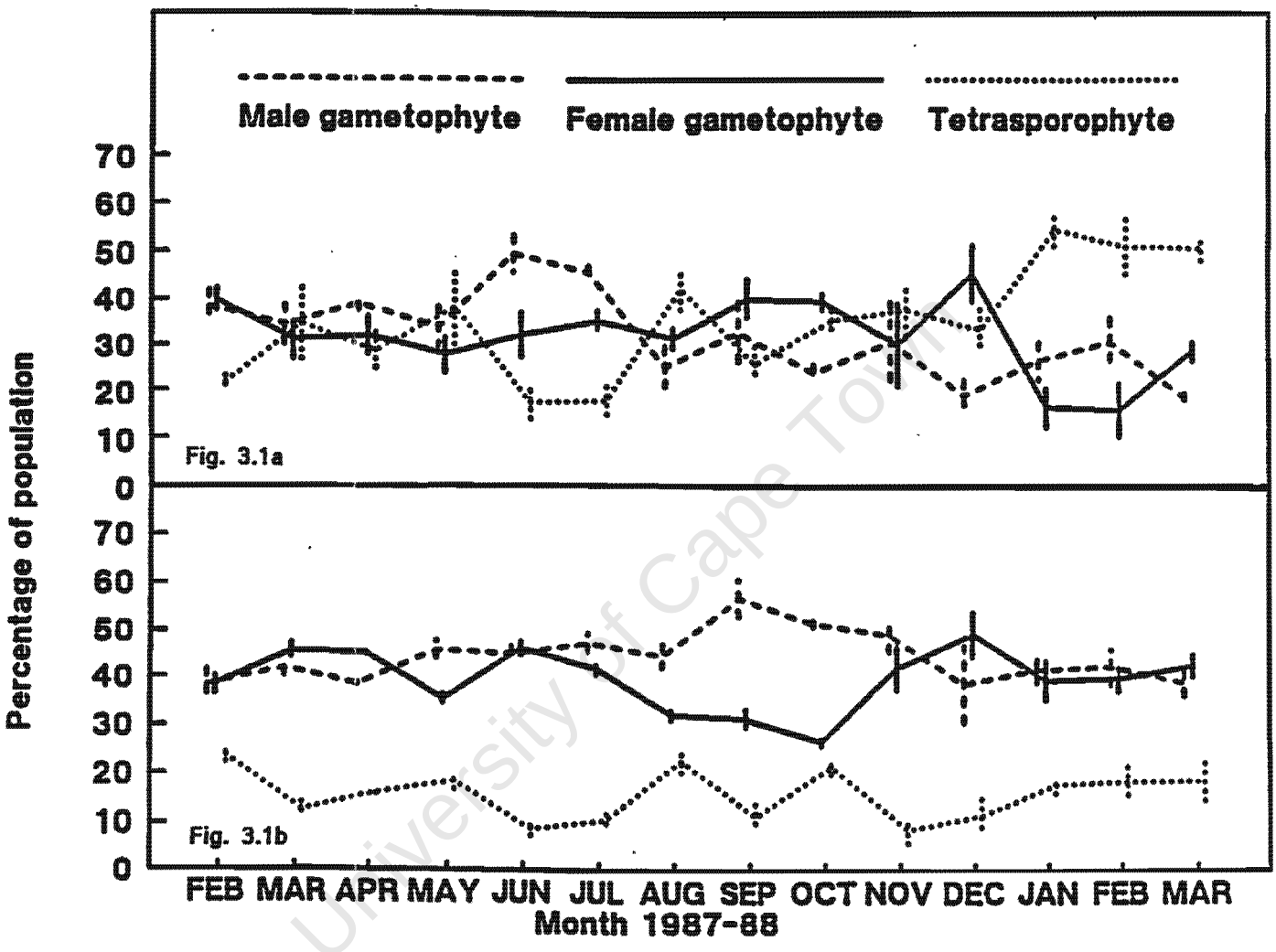


Figure 3.1 Seasonal phenology expressed as percentage composition of population by male and female gametophytes and tetrasporophytes of a) *Gigartina polycarpa* and b) *Sarcothalia stiriata* at Kommetjie, 1987-88. Standard errors indicated.

G. polycarpa ♂ gametophyte $F_{0.05(2),3,52} = 4.55 > 3.39$ significant	Percentage of population (mean)	SNK - grouping
Spring	29.52	B
Summer	27.27	B
Autumn	35.60	A B
Winter	40.36	A

Table 3.1 Analysis of variance and Student-Newman-Keuls test results for arcsin-transformed phenology data: Percentage of population of *Gigartina polycarpa* accounted for by male gametophytes on a seasonal basis. Means with the same letter are not significantly different.

G. polycarpa tetrasporophyte $F_{0.05(2),3,52} = 4.14 > 3.39$ significant	Percentage of population (mean)	SNK - grouping
Spring	33.52	A B
Summer	42.83	A
Autumn	33.99	A B
Winter	26.41	B

Table 3.2 Analysis of variance and Student-Newman-Keuls test results for arcsin-transformed phenology data: Percentage of population of *Gigartina polycarpa* accounted for by tetrasporophytes on a seasonal basis. Means with the same letter are not significantly different.

G. polycarpa ♀ gametophyte $F_{0.05(2),3,52} = 1.19 < 3.39$ not significant	Percentage of population (mean)	SNK - grouping
Spring	36.95	A
Summer	29.89	A
Autumn	30.42	A
Winter	33.23	A

Table 3.3 Analysis of variance and Student-Newman-Keuls test results for arcsin-transformed phenology data: Percentage of population of *Gigartina polycarpa* accounted for by female gametophytes on a seasonal basis. Means with the same letter are not significantly different.

S. stiriata ♂ gametophyte $F_{0.05(2),3,52} = 9.87 > 3.39$ significant	Percentage of population (mean)	SNK - grouping
Spring	52.46	A
Summer	39.84	B
Autumn	41.91	B
Winter	45.70	B

Table 3.4 Analysis of variance and Student-Newman-Keuls test results for arcsin-transformed phenology data: Percentage of population of *Sarcothalia stiriata* accounted for by male gametophytes on a seasonal basis. Means with the same letter are not significantly different.

S. stiriata tetrasporophyte $F_{0.05(2),3,52} = 1.50 < 3.39$ not significant	Percentage of population (mean)	SNK - grouping
Spring	14.01	A
Summer	18.26	A
Autumn	16.02	A
Winter	14.14	A

Table 3.5 Analysis of variance and Student-Newman-Keuls test results for arcsin-transformed phenology data: Percentage of population of *Sarcothalia stiriata* accounted for by tetrasporophytes on a seasonal basis. Means with the same letter are not significantly different.

S. stiriata ♀ gametophyte $F_{0.05(2),3,52} = 4.40 > 3.39$ significant	Percentage of population (mean)	SNK - grouping
Spring	33.53	B
Summer	41.9	A
Autumn	42.07	A
Winter	40.16	A

Table 3.6 Analysis of variance and Student-Newman-Keuls test results for arcsin-transformed phenology data: Percentage of population of *Sarcothalia stiriata* accounted for by female gametophytes on a seasonal basis. Means with the same letter are not significantly different.

significant. Conversely, there was a significant decrease (table 3.2) in the proportion of tetrasporophytes of *G. polycarpa* during winter (26%) when compared with summer (43%). There were no significant seasonal fluctuations in the proportion of female gametophytes of *G. polycarpa* (table 3.3), although there was a noticeable decrease from mid- to late-summer (January/February, fig. 3.1). The phenological composition of *G. polycarpa* populations appears more variable than that of *S. stiriata*, as evidenced by the marked differences observed in the proportions all life-history phases in the year from February 1987 to February 1988 (fig3.1). In *Sarcothalia stiriata,* the proportion of male gametophytes (table 3.4) was significantly greater in spring (52%) than in summer (40%), autumn (42%) or winter (46%). No significant seasonal fluctuations (table 3.5) in the proportion of tetrasporophytes (14-18%) were apparent. A significant difference in the proportion of female gametophytes (table 3.6) was also apparent (corresponding inversely with that of male gametophytes), being considerably less in spring (34%) when compared with summer (42%), autumn (42%) and winter (40%). *Gigartina polycarpa* displayed no significant difference in the overall proportions of male gametophytes : female gametophytes : tetrasporophytes (table 3.7). The ratio of *G. polycarpa* life history phases were approximately equal, comprising 0.9:0.9:1 male gametophytes : female gametophytes: tetrasporophytes. The overall proportions of male gametophytes : female gametophytes : tetrasporophytes of *Sarcothalia stiriata* (table 3.8) were significantly different, the respective phases being present in the ratio 2.8:2.5:1. Populations of both species were therefore gametophyte dominated, *G. polycarpa* displaying a gametophyte : sporophyte ratio of 1.8:1 and *S. stiriata* a ratio of 5.3:1.

Species / life-history phase $F_{0.05(2),2,165} = 1{,}01 < 3.78$ not significant	Percentage of population (mean)	SNK - grouping
G. polycarpa ♂ gametophyte	32.34	A
G. polycarpa ♀ gametophyte	32.23	A
G. polycarpa tetrasporophyte	35.42	A

Table 3.7 Analysis of variance and Student-Newman-Keuls test results for arcsin-transformed phenology data: Percentage of population of *Gigartina polycarpa* accounted for by the various life history phases during this study. Means with the same letter are not significantly different.

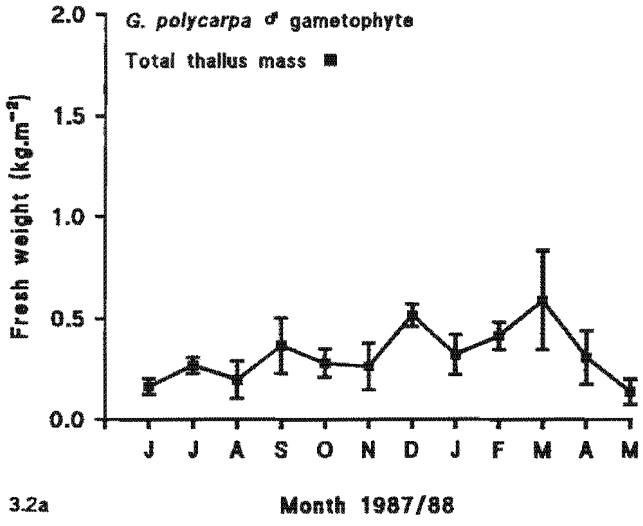
Species / life-history phase $F_{0.05(2),2,165} = 234.99 > 3.78$ significant	Percentage of population (mean)	SNK - grouping
S. stiriata ♂ gametophyte	44.24	A
S. stiriata ♀ gametophyte	39.77	B
S. stiriata tetrasporophyte	15.99	C

Table 3.8 Analysis of variance and Student-Newman-Keuls test results for arcsin-transformed phenology data: Percentage of population of *Sarcothalia stiriata* accounted for by the various life history phases during this study. Means with the same letter are not significantly different.

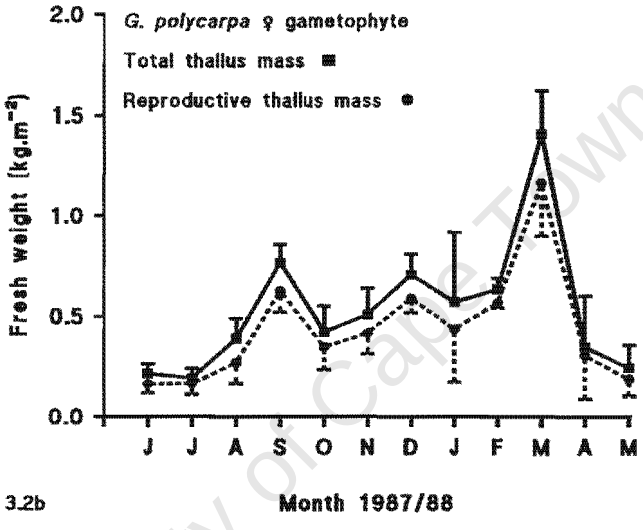
3.3.2 Thallus weight and reproductive weight

A seasonal trend of increased thallus weight in late-summer and decreased thallus weight in winter was apparent in *Gigartina polycarpa* male gametophytes, female gametophytes and tetrasporophytes, although these data were not significant (male gametophytes $F_{0.05(2),11,24} = 2.24 < 2.59$; female gametophytes $F_{0.05(2),11,24} = 1.38 < 2.59$; tetrasporophytes $F_{0.05(2),11,24} = 1.34 < 2.59$). Male gametophytes contributed least to the biomass of *G. polycarpa*, averaging 0.32kg.m^{-2} during the study period (fig. 3.2a), with maximum biomass during late-summer and early autumn (0.41-0.59kg.m^{-2}, February/March) and minimum biomass during late autumn and winter (0.14-0.16kg.m^{-2}, May/June). The greatest contribution to *G. polycarpa* biomass during the study period was by female gametophytes with a mean of 0.53kg.m^{-2} (fig. 3.2b). Maximum biomass was during late-summer and early autumn (0.64-1.41kg.m^{-2}, February/March) with a secondary peak during early spring (0.77kg.m^{-2}, September). Minimum biomass was observed during winter (0.22-0.19kg.m^{-2}, June/July). Tetrasporophytes of *G. polycarpa* (fig. 3.2c) contribute a similar amount to the total biomass as female gametophytes, averaging 0.50kg.m^{-2} during the study period. Maximum biomass was attained from mid-summer through early autumn (0.86-0.92kg.m^{-2}, January/March). Biomass during winter was low during the period June - August (0.37-0.36kg.m^{-2}), but the minimum biomass observed was during late-spring (0.11kg.m^{-2}, November).

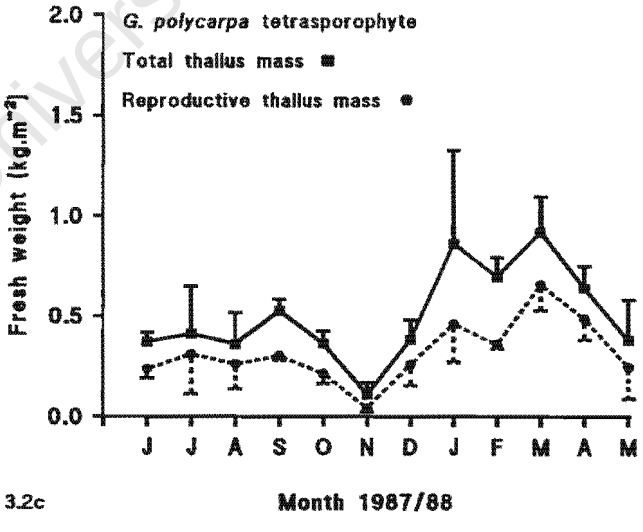
Reproductive weight of *Gigartina polycarpa* (fig. 3.2b,c) followed a similar, non-significant (female gametophytes $F_{0.05(2),11,24} = 1.38 < 2.59$; tetrasporophytes $F_{0.05(2),11,21} = 1.69 < 2.68$) trend to that of thallus weight, with greater values during late-summer and smaller values during winter. There was also no significant seasonal pattern in fertile weight as a percentage



3.2a



3.2b



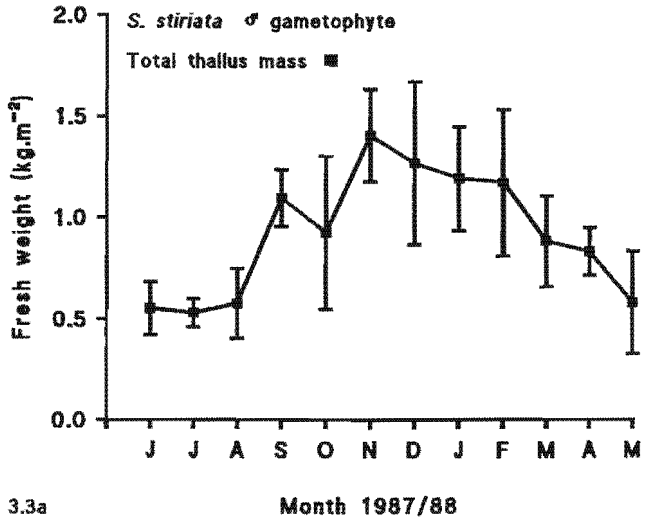
3.2c

Figure 3.2 Seasonal total fresh weight and reproductive fresh weight of *Gigartina polycarpa* at Kommetjie 1987-88: a) male gametophytes; b) female gametophytes; c) tetrasporophytes. Standard errors indicated.

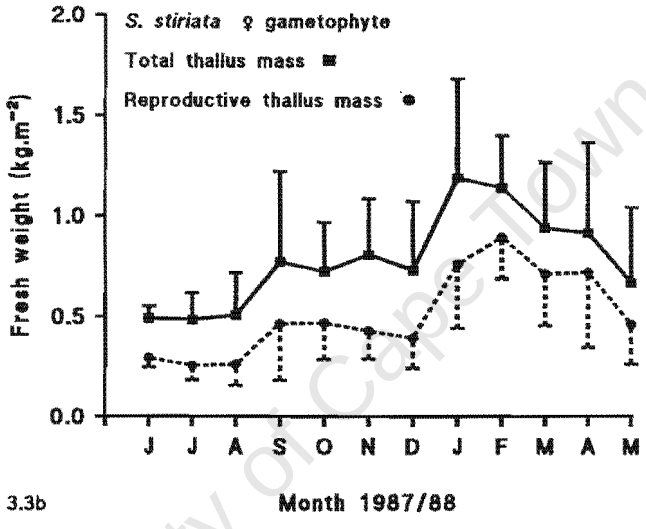
of total weight in either female gametophytes ($F_{0.05(2),11,17}$= 2.37 < 2.87) or tetrasporophytes ($F_{0.05(2),11,21}$= 1.69 < 2.68) of *G. polycarpa*, the proportion of fertile weight remaining relatively constant throughout the study period. The mean percentage fertility (total reproductive weight as a proportion of total thallus weight) of *G. polycarpa* was 71.5% (female gametophytes) and 56.3% (tetrasporophytes).

A seasonal pattern of summer maxima and winter minima was evident in thallus weight of *Sarcothalia stiriata* male gametophytes ($F_{0.05(2),11,24}$= 2.30 < 2.59), female gametophytes ($F_{0.05(2),11,24}$= 4.13 > 2.59) and tetrasporophytes ($F_{0.0521),11,24}$= 3.44 > 2.59), this being significant for the latter two life-history phases. In contrast with the situation with *Gigartina polycarpa*, male gametophytes contributed most to the biomass of *S. stiriata*, averaging 0.92kg.m^{-2} during the study period (fig. 3.3a), with maximum biomass over a broad period from late-spring through late summer (1.40-1.17kg.m^{-2}, November/February) and minimum biomass during winter (0.55-0.53kg.m^{-2}, June/July). Female gametophytes of *S. stiriata* contributed almost as much as male gametophytes to the total biomass of this species, with a mean of 0.78kg.m^{-2} during the course of this study. Maximum biomass was attained during mid- to late-summer (fig. 3.3b) with a slow decline beginning during autumn (1.19/1.14/0.94kg.m^{-2}, January/February/March). As in *G. polycarpa* female gametophytes, an increase in biomass was also observed during spring (0.77kg.m^{-2}, September), this increase being maintained until the enhanced summer biomass-increment became evident. Minimum biomass was observed during winter (0.22-0.19kg.m^{-2}, June/July). Tetrasporophytes of *S. stiriata* contributed substantially less to the total biomass than tetrasporophytes of *G. polycarpa*, averaging just 0.18kg.m^{-2} during the study period (fig. 3.3c). Maximum biomass was attained during mid-summer (0.43-0.37kg.m^{-2}, January/February), whilst minimum biomass was observed during mid-winter (0.05kg.m^{-2}, July). As in *G. polycarpa*, there was no seasonal pattern in reproductive weight as a percentage of thallus weight in either female gametophytes ($F_{0.05(2),11,23}$= 2.23 < 2.62) or tetrasporophytes ($F_{0.05(2),11,17}$= 0.94 < 2.87) of *S. stiriata* (fig. 3.3b,c). The mean proportions of fertile weight as a percentage of total thallus weight in *S. stiriata* were 67.4% (female gametophytes) and 52.7% (tetrasporophytes).

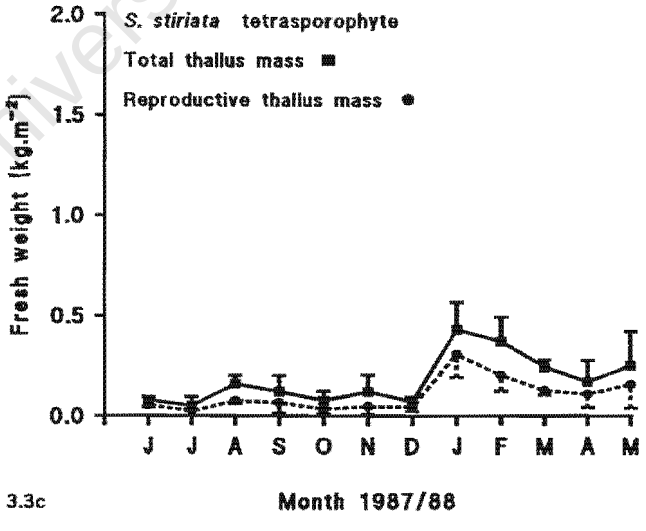
Tetrasporophytes of both *Gigartina polycarpa* ($F_{0.05(2),1,60}$= 19.47 > 5.29, fig. 3.2c) and *Sarcothalia stiriata* ($F_{0.05(2),1,62}$= 8.07 > 5.29, fig. 3.3c) were significantly lower in percentage fertility from their respective female gametophytes (figs 3.2b, 3.3b). There was no



3.3a



3.3b



3.3c

Figure 3.3 Seasonal total fresh weight and reproductive fresh weight of *Sarcothalia stiriata* at Kommetjie 1987-88: a) male gametophytes; b) female gametophytes; c) tetrasporophytes. Standard errors indicated.

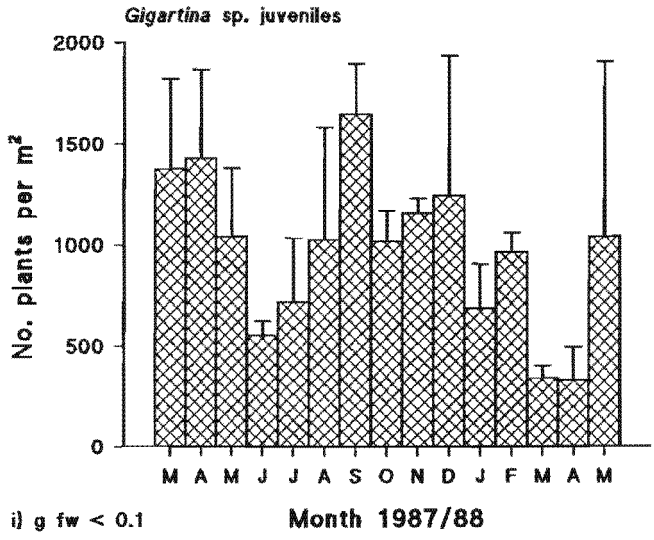
significant difference in fertility between tetrasporophytes of *G. polycarpa* (fig. 3.2c) and *S. stiriata* (fig. 3.3c) ($F_{0.05(2),1,60} = 0.87 < 5.29$), but female gametophytes of *G. polycarpa* (fig. 3.2b) were significantly more fertile than those of *S. stiriata* (fig. 3.3b) ($F_{0.05(2),1,62} = 12.14 > 5.29$).

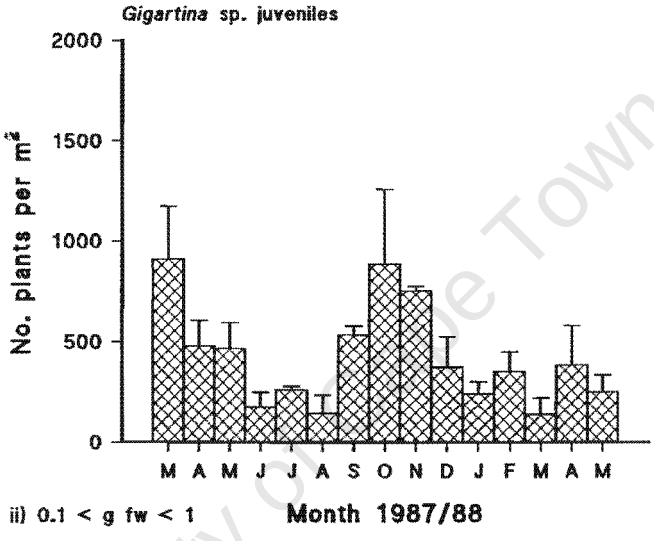
3.3.3 Population demography

A large number (>500 plants.m^{-2}) of juvenile members of *Gigartina* sp. macroscopically unidentifiable to species were present almost all year round in the <0.1g fw weight class (fig. 3.4a-i), the monthly average being 972 plants.m^{-2}. Due to extreme variability in the data , no seasonal pattern in the frequency of these juveniles was apparent. The greatest number of juveniles in this weight class were observed during early-spring (1648 plants.m^{-2}, September) and the least number were noted during autumn (331 plants.m^{-2}, April). This pattern is partially reflected in the next weight class (0.1-1g fw, fig. 3.4a-ii), but with less amplitude as the juveniles become more easily identifiable, plant density averaging 423 plants.m^{-2}. A spring peak in plant density was observed (885 plants.m^{-2}, October), and a second, slightly larger peak, was also noted during March 1987 (912 plants.m^{-2}). Extreme variability in the data was apparent, a low plant density of just 138 plants.m^{-2} being observed one year later (March 1988). Once juvenile plants exceeded 1g fw they were almost completely identifiable to species level (fig. 3.4a-iii), this being the reason for the very few unidentifiable juveniles of *Gigartina* sp. noted in this weight class.

The density of macroscopically identifiable juveniles of *Sarcothalia stiriata* (fig. 3.4b) also displayed a variable pattern. In juveniles with a fresh weight of less than 0.1g (fig. 3.4b-i), plant density averaged 342 plants.m^{-2}, the difference between the highest and lowest recorded values being 624 plants.m^{-2}. In plants with a fresh weight between 0.1 and1g (fig. 3.4b-ii) this density variation was extremely high (1722 plants.m^{-2}), with a mean plants density of 948 plants.m^{-2}. In larger plants (1-4g weight class, fig. 3.4b-iii), the data were less variable, the difference between the highest and lowest recorded values being 272 plants.m^{-2} with a mean density of 165 plants.m^{-2}. No seasonal pattern of plant density was apparent. The majority of individuals occurred in the 0.1-1g weight class. By the time individuals exceeded a weight of 4g, they were almost entirely reproductively mature, and could no longer be classed as juveniles (fig. 3.4b-iv).

Gigartina polycarpa juveniles (fig. 3.4c) also displayed a variable pattern of plant density,





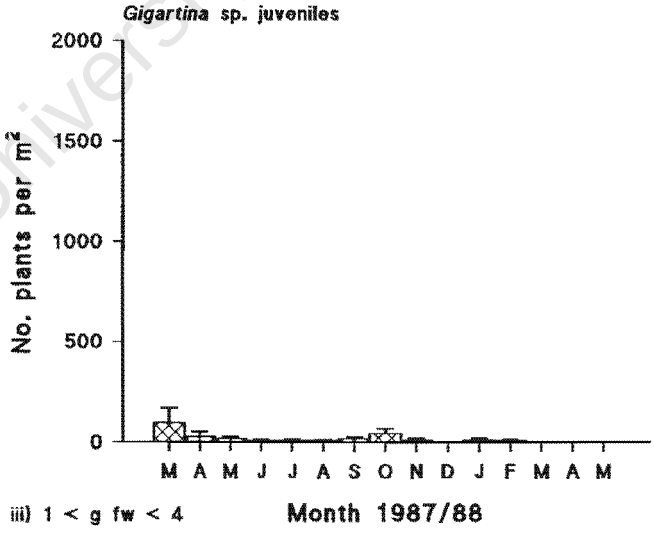


Figure 3.4a Seasonal demography of unidentifiable juvenile members of *Gigartina* sp.: numbers of plants in different weight classes, 1987-88: i) g fw < 0.1g; ii) 0.1g < g fw < 1g; iii) 1g < g fw < 4g. Standard errors indicated.

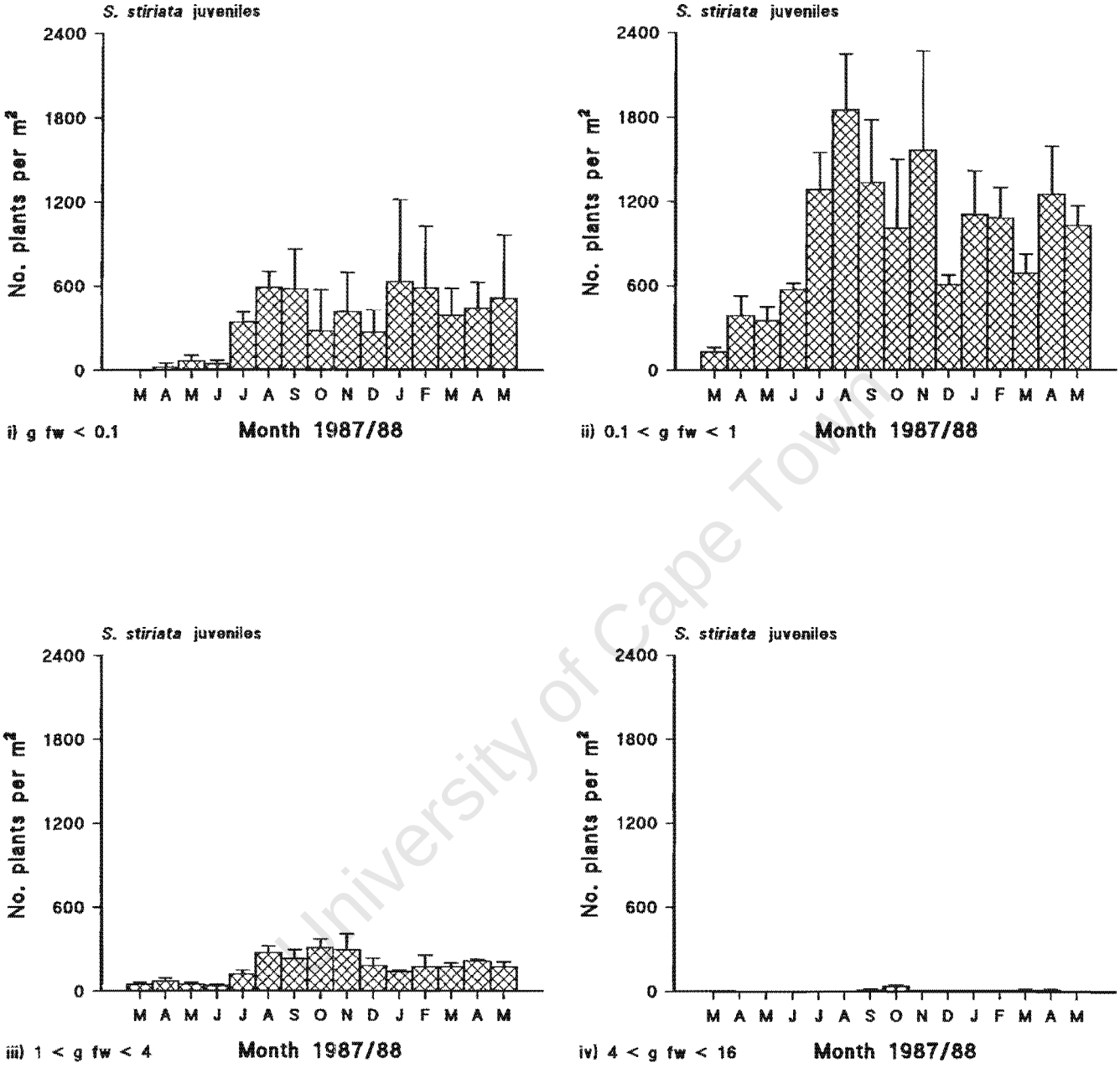


Figure 3.4b Seasonal demography of juvenile *Sarcothalia stiriata*: numbers of plants in different weight classes, 1987-88: i) g fw < 0.1g; ii) 0.1g < g fw < 1g; iii) 1g < g fw < 4g; iv) 4g < g fw <16g. Standard errors indicated.

with no evident seasonal pattern. In the less than 0.1g weight class (fig. 3.4c-i), plant density averaged 55 plants.m^{-2}, with a density variation of 181 plants.m^{-2}. Like *Sarcothalia stiriata*, the majority of individuals occurred in the 0.1-1g weight class (fig. 3.4c-ii), with a mean of 348 plants.m^{-2}, the difference between the highest and lowest recorded values being 672 plants.m^{-2}. Also like *S. stiriata*, the data were less variable in larger plants (1-4g weight class, fig. 3.4c-iii), the difference between the highest and lowest recorded values being 154 plants.m^{-2} with a mean density of 99 plants.m^{-2}. Similarly, by the time individuals exceed a weight of 4g, they were almost entirely reproductively mature and no longer classed as juveniles (fig. 3.4c-iv).

Juvenile plants of *Sarcothalia stiriata* comprised a considerably larger proportion of the total juvenile population (fig. 3.4b) than juveniles of *Gigartina polycarpa* (fig. 3.4c). Identifiable plants of *S. stiriata* (fig. 3.4d-f) were also more abundant than *G. polycarpa* (fig. 3.4g-i). Reproductive structures were observed on nearly all individual tetrasporophytes and female gametophytes of both species heavier than 4g fresh weight. *S. stiriata* male gametophytes (fig. 3.4d) were numerically dominant in the 1-4g weight class (mean density 213 plants.m^{-2}), with fewer plants in the 0.1-1g (65 plants.m^{-2}), 4-6g (121 plants.m^{-2}) and 16-64g (20 plants.m^{-2}) weight classes. *Sarcothalia stiriata* female gametophytes (fig. 3.4e) were numerically dominant in the 1-4g (110 plants.m^{-2}) and 4-16g (93 plants.m^{-2}) weight classes, with considerably fewer plants in the 0.1-1g (15 plants.m^{-2}) and 16-64g (22 plants.m^{-2}) weight classes. *Sarcothalia stiriata* tetrasporophytes (fig. 3.4f) numerically dominated the 1-4g (23 plants.m^{-2}) and 4-16g (25 plants.m^{-2}) weight classes, with fewer plants in the 0.1-1g (2 plants.m^{-2}) and 16-64g (8 plants.m^{-2}) weight classes. There were no individuals of any life-history phase heavier than 64g fresh weight. Density data for all three life-history phases were extremely variable, with no clear seasonal pattern. The apparent lack of any seasonal patterns may be an artifact of the analysis, the weight-class groupings resulting in heterogenous samples of plants of different weight, size and age.

The data for *Gigartina polycarpa* also showed considerable variation, with no clear seasonal patterns displayed by any life-history phase (fig. 3.4g-3.4i). *Gigartina polycarpa* male gametophytes (fig. 3.4g) were numerically dominant in the 1-4g and 4-16g weight classes (mean density 22 and 27 plants.m^{-2} respectively), with fewer plants in the 0.1-1g (6 plants.m^{-2}) and 16-64g (7 plants.m^{-2}) weight classes. Plant densities were more evenly distributed in *G.*

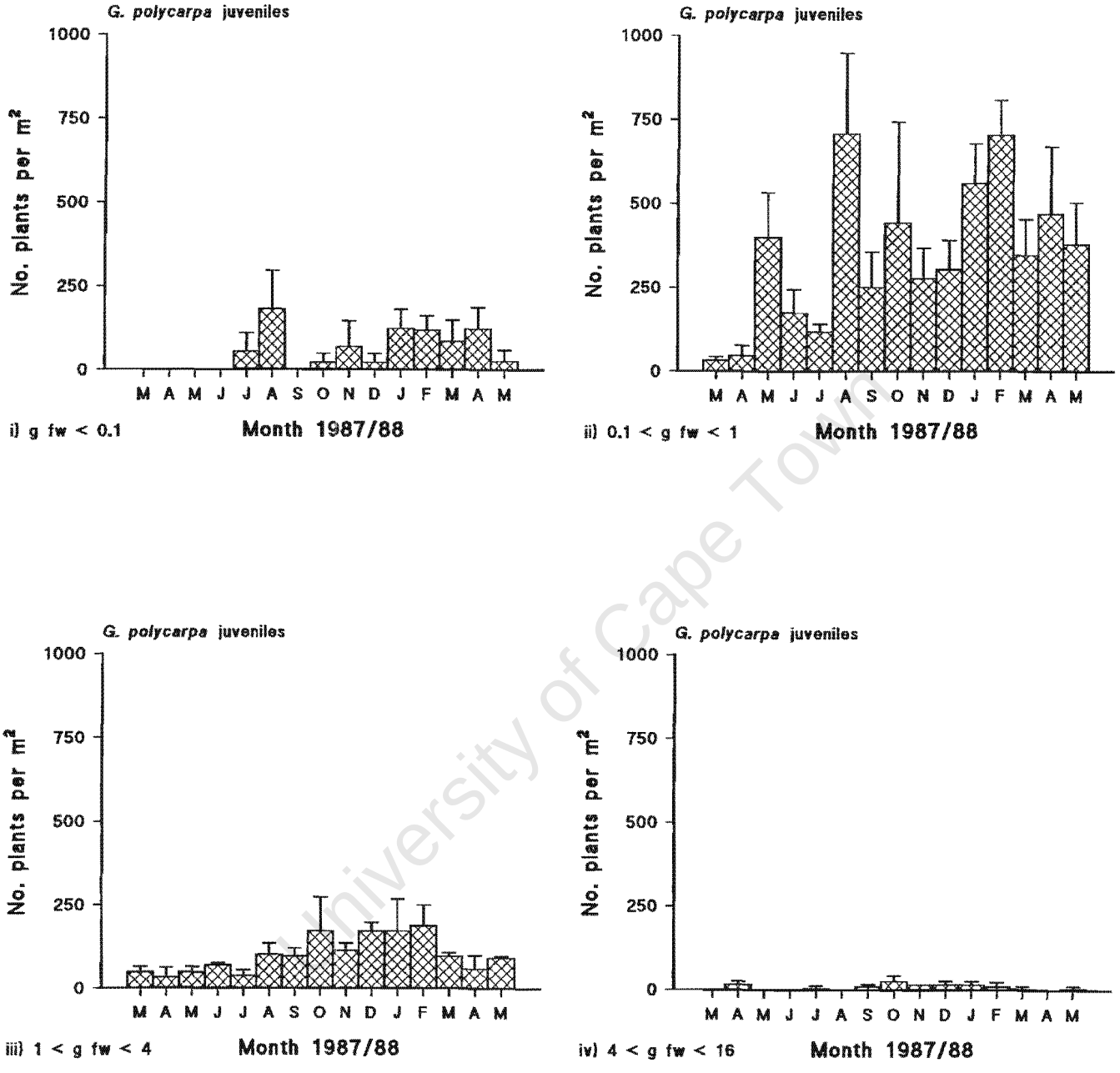


Figure 3.4c Seasonal demography of juvenile *Gigartina polycarpa*: numbers of plants in different weight classes, 1987-88: i) g fw < 0.1g; ii) 0.1g < g fw < 1g; iii) 1g < g fw < 4g; iv) 4g < g fw <16g. Standard errors indicated.

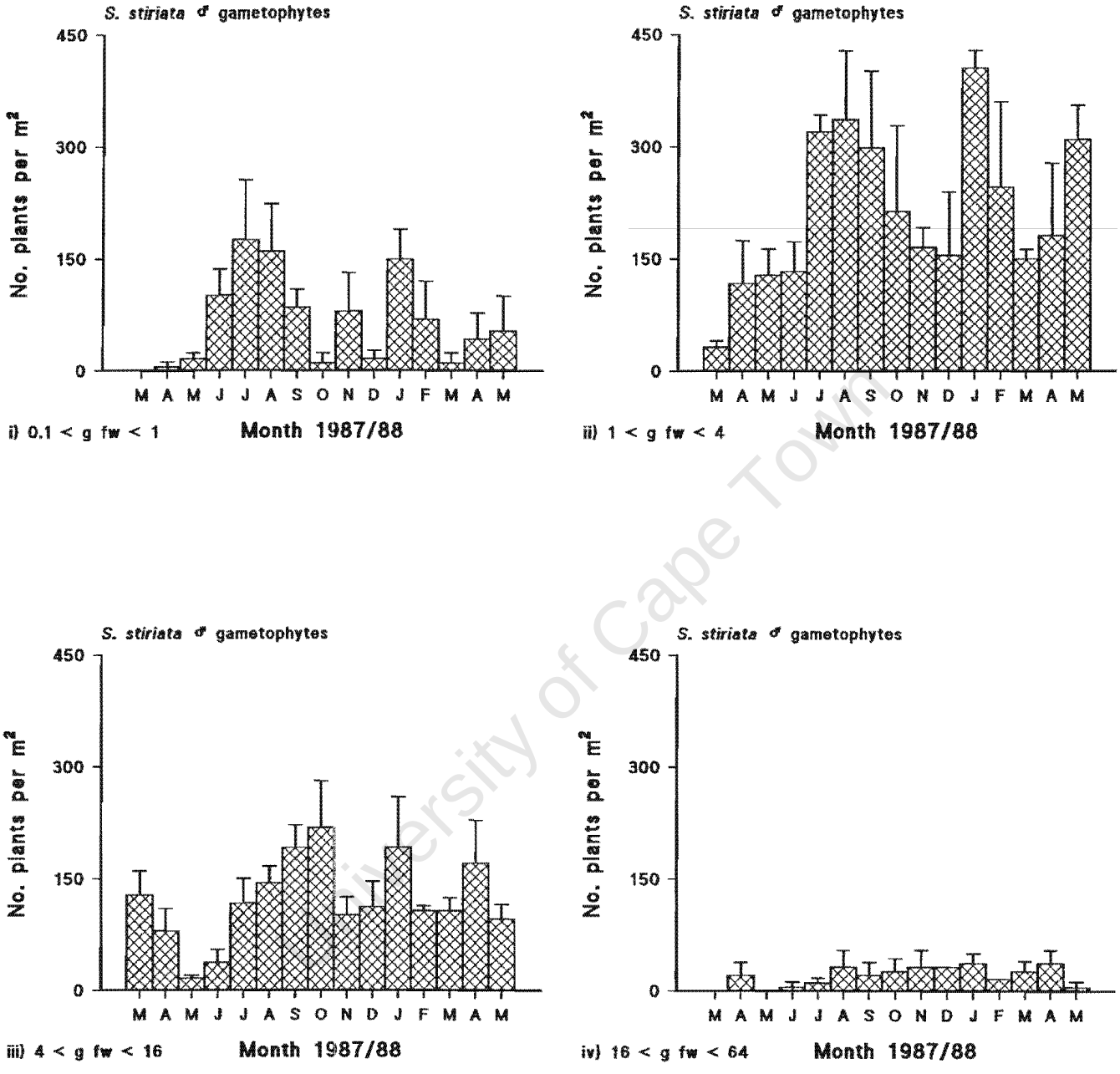


Figure 3.4d Seasonal demography of *Sarcothalia stiriata* male gametophytes: numbers of plants in different weight classes, 1987-88: i) 0.1g < g fw < 1g; ii) 1g < g fw < 4g; iii) 4g < g fw <16g; iv) 16g < g fw < 64g. Standard errors indicated.

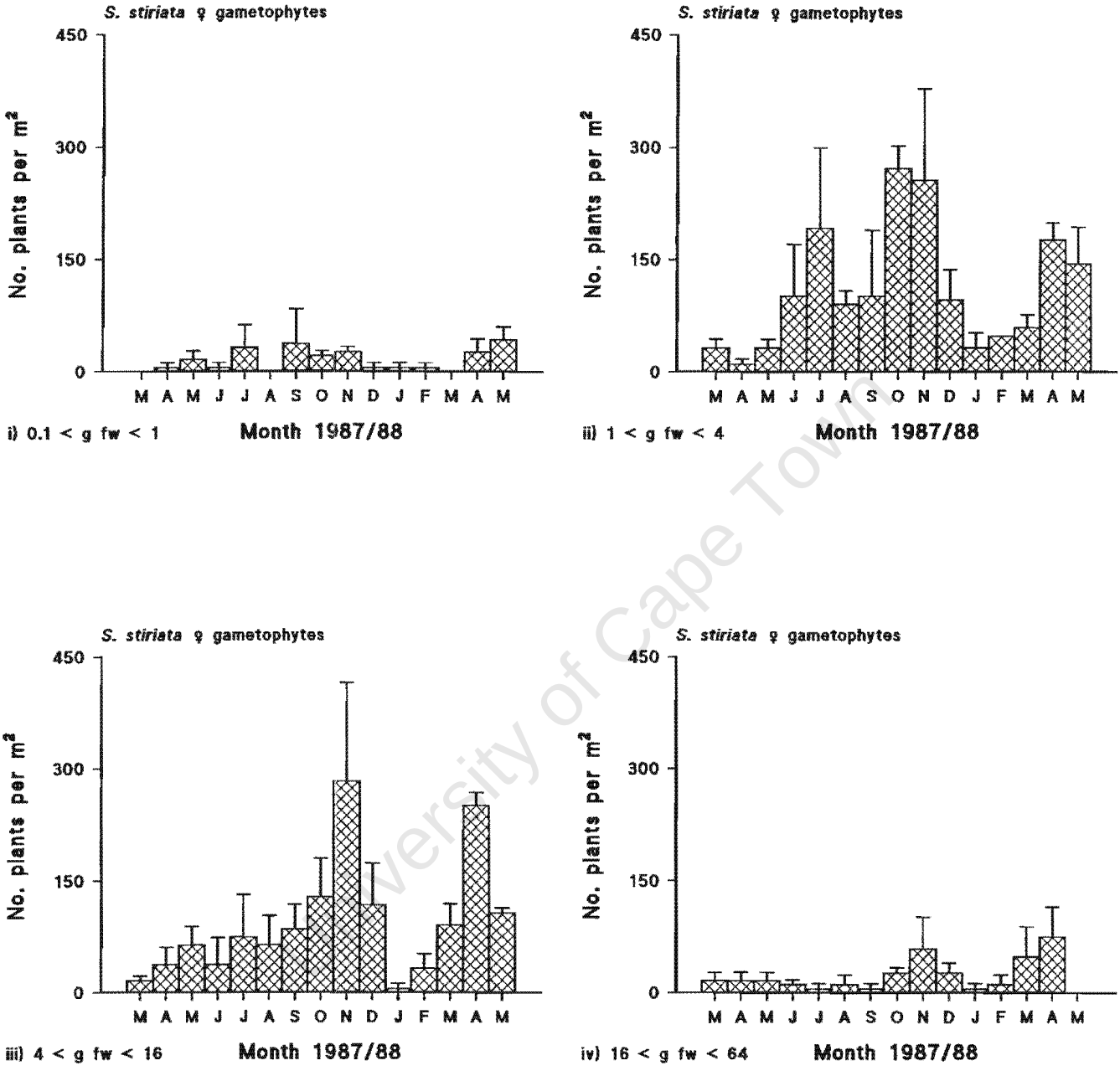


Figure 3.4e Seasonal demography of *Sarcothalia stiriata* female gametophytes: numbers of plants in different weight classes, 1987-88: i) 0.1g < g fw < 1g; ii) 1g < g fw < 4g; iii) 4g < g fw <16g; iv) 16g < g fw < 64g. Standard errors indicated.

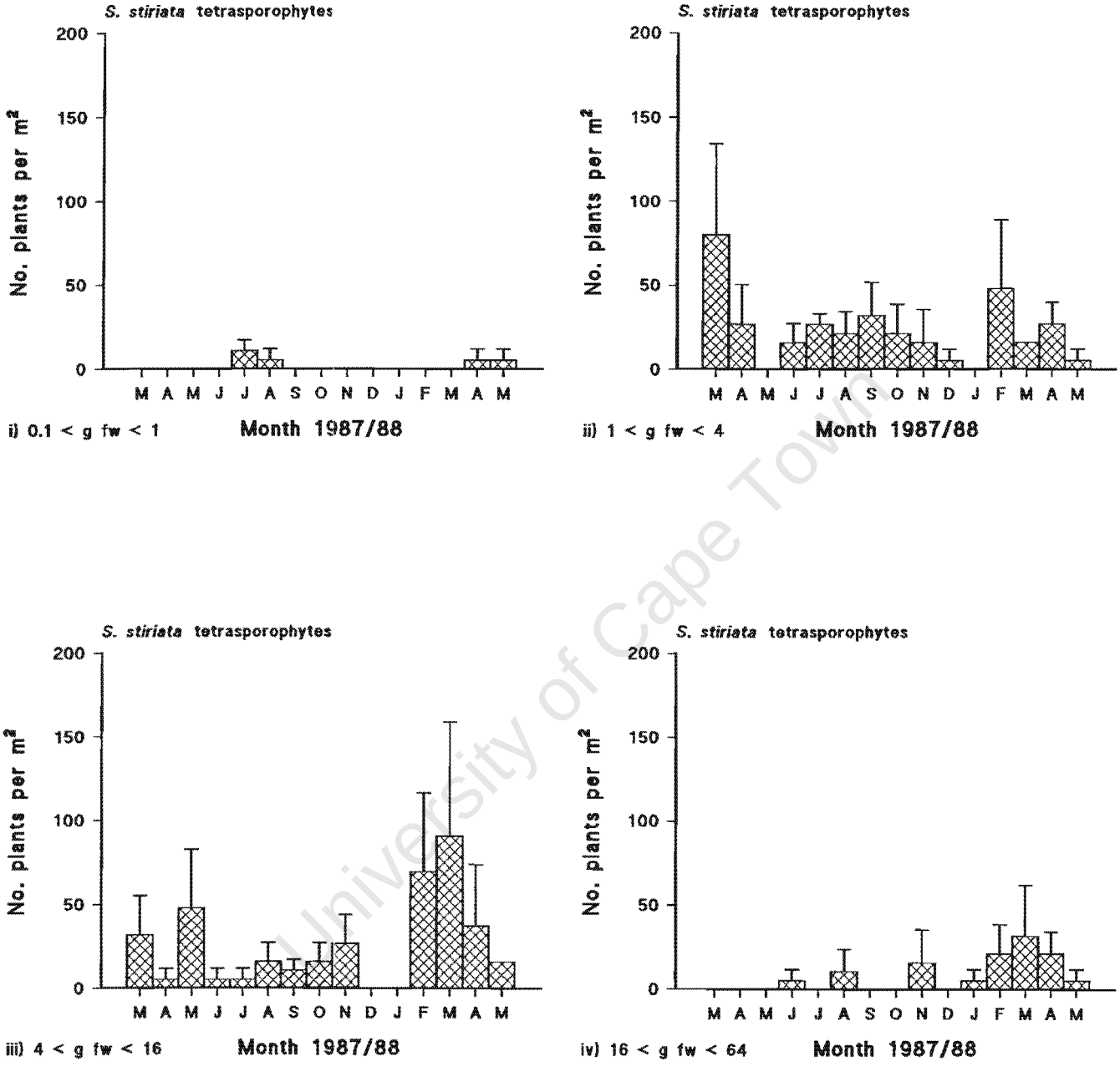


Figure 3.4f Seasonal demography of *Sarcothalia stiriata* tetrasporophytes: numbers of plants in different weight classes, 1987-88: i) 0.1g < g fw < 1g; ii) 1g < g fw < 4g; iii) 4g < g fw <16g; iv) 16g < g fw < 64g. Standard errors indicated.

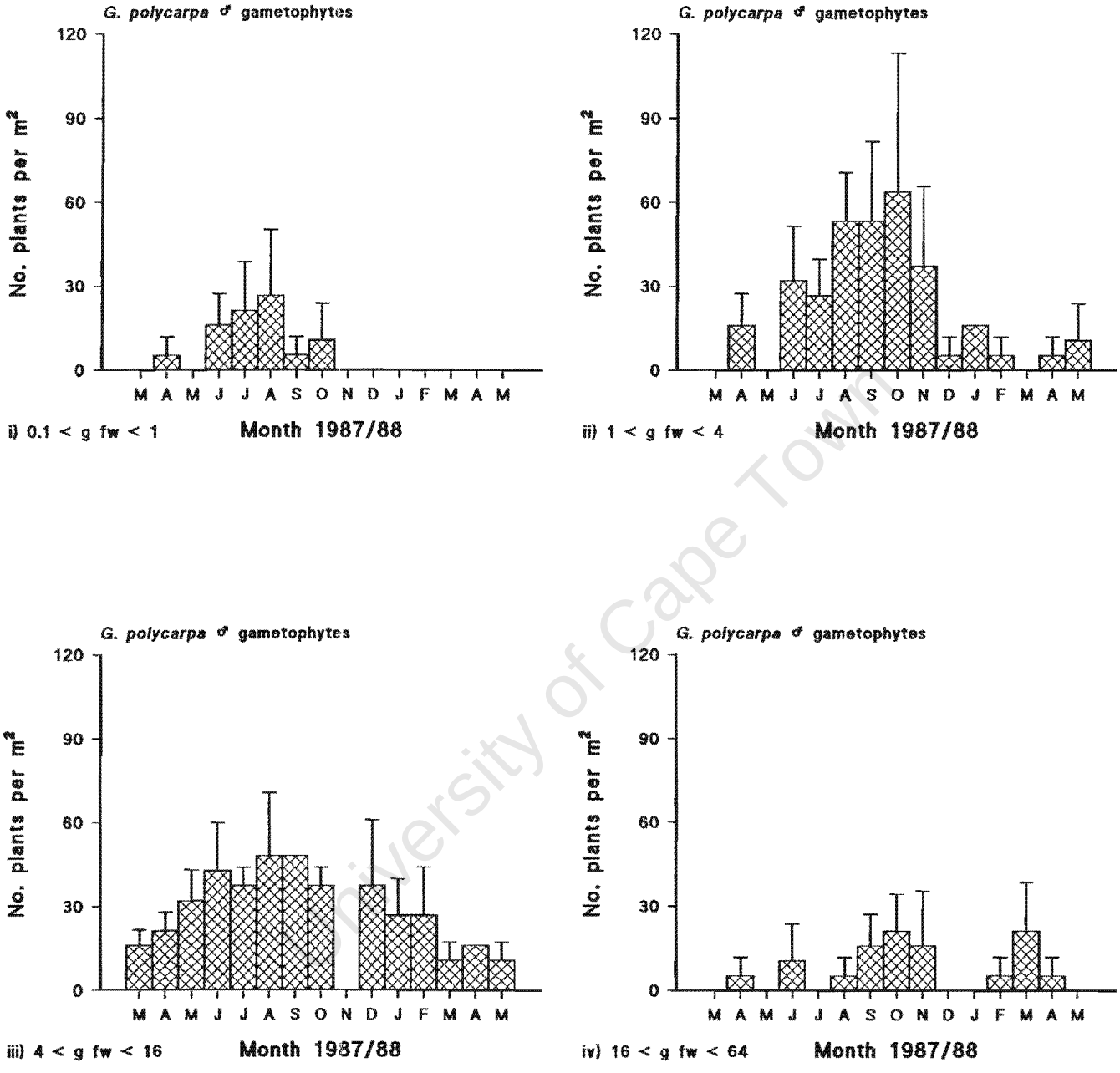


Figure 3.4g Seasonal demography of *Gigartina polycarpa* male gametophytes: numbers of plants in different weight classes, 1987-88: i) 0.1g < g fw < 1g; ii) 1g < g fw < 4g; iii) 4g < g fw <16g; iv) 16g < g fw < 64g. Standard errors indicated.

polycarpa female gametophytes (fig. 3.4h), with a maximum plant density of 23 plants.m^{-2} in the 4-16g weight class. Plant densities were slightly less in the 1-4g (15 plants.m^{-2}) and 16-64g (13 plants.m^{-2}) weight classes, and reached a minimum in the 0.1-1g weight class (4 plants.m^{-2}). *Gigartina polycarpa* tetrasporophytes were numerically dominant in the 1-4g (28 plants.m^{-2}) and 4-16g (35 plants.m^{-2}) weight classes (fig. 3.4i), with fewer plants in the 0.1-1g (5 plants.m^{-2}) and 16-64g (9 plants.m^{-2}) weight classes. Gametophytes and sporophytes of *G. polycarpa* only rarely achieved a weight exceeding 64g fw (fig. 3.5).

The average abundance (over 13 months) for combined life-history phases of *Gigartina* sp., *Sarcothalia stiriata* and *Gigartina polycarpa* in each size class (fig. 3.5) emphasizes the numerical dominance of unidentifiable juveniles. Most juveniles were identifiable once they reach the 0.1-1g weight class. Of the original number of unidentifiable juveniles (0.0-0.1g weight class, fig. 3.5a), there were 68.5% in the 0.1-1g weight class, 17.2% in the 1-4g class, 13.7% in the 4-16g class and 3.1% in the 16-64g class. This reduction was due to mortality as well as growth into size classes where they can be identified to species and life-history phase. The majority of identifiable individuals of *G. polycarpa* (fig. 3.5b) and *S. stiriata* (fig. 3.5c) were concentrated in the 1-4g and 4-16g weight classes. Both *G. polycarpa* and *S. stiriata* tetrasporophytes were slightly more abundant in the 4-16g weight class, but these data were not significantly different from density data from the 1-4g weight class in either species ($F_{0.05(2),1,15} = 2.35 < 6.20$; $F_{0.05(2),1,15} = 1.78 < 6.20$ respectively). *Sarcothalia stiriata* gametophytes were more abundant in the 1-4g weight class, but this was again not significantly different from the 4-16g weight class ($F_{0.05(2),1,15} = 4.73 < 6.20$). Similarly, *G. polycarpa* gametophyte densities were higher in the 4-16g weight class, but this was not significantly different to the 1-4g weight class ($F_{0.05(2),1,15} = 3.69 < 6.20$).

In both *Gigartina polycarpa* (fig. 3.6a) and *Sarcothalia stiriata* (fig. 3.6b), the relationship between $\log_{10}$ frond biomass and $\log_{10}$ frond density was positive, biomass increasing with density. The biomass-density relationship of both species was also positive with respect to the ultimate biomass-density line (fig. 3.6c), proposed as universal for the plant kingdom (Weller, 1989), observed frond weight being higher than values expected from observed densities under the self-thinning law.

The assay of known life-history phases of *Gigartina polycarpa* and *Sarcothalia stiriata* (table 3.9) showed that the resorcinol method could be accurately used to determine the

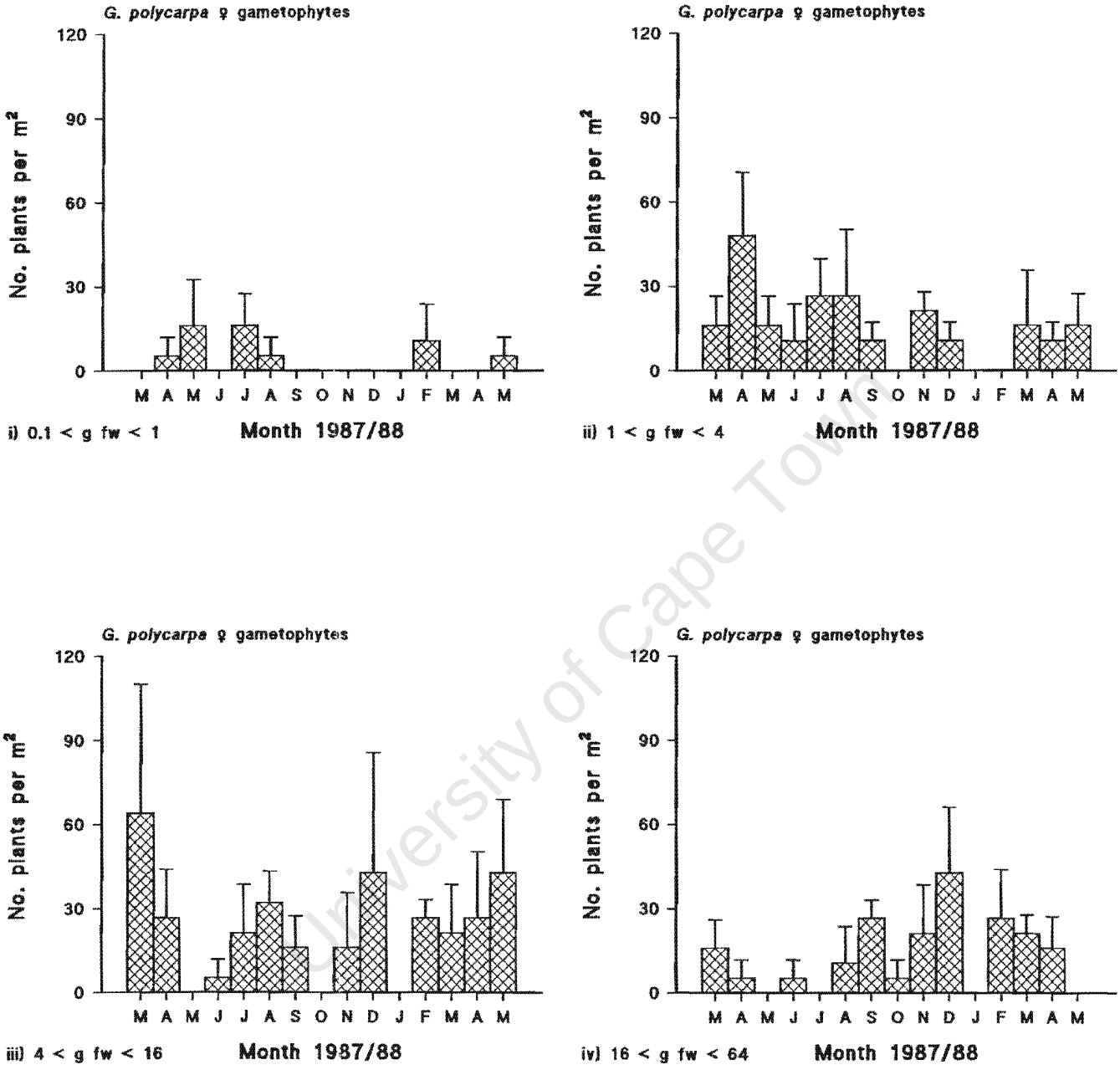
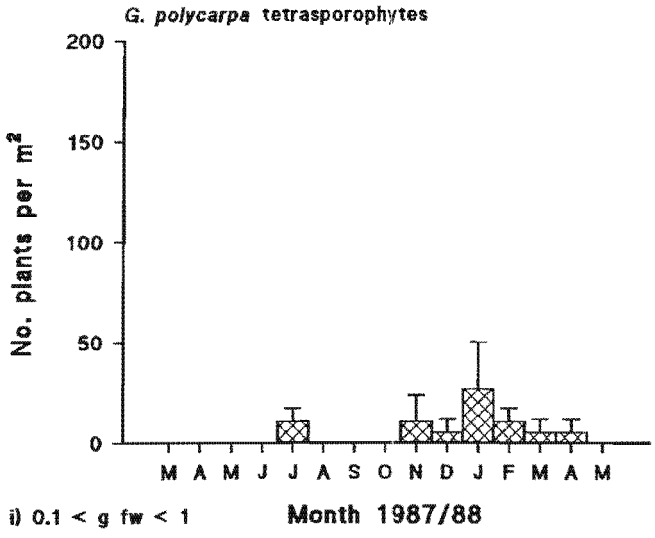
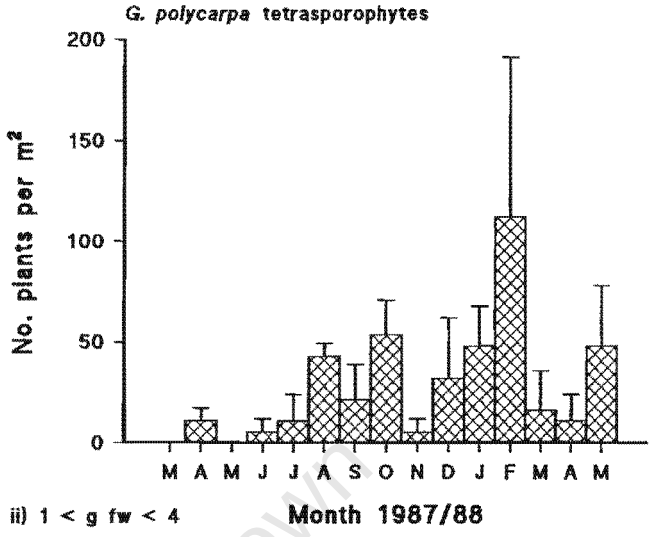
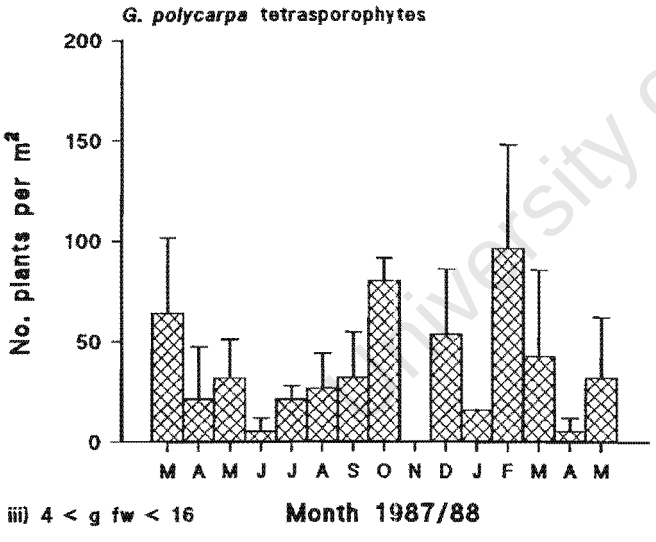


Figure 3.4h Seasonal demography of *Gigartina polycarpa* female gametophytes: numbers of plants in different weight classes, 1987-88: i) 0.1g < g fw < 1g; ii) 1g < g fw < 4g; iii) 4g < g fw <16g; iv) 16g < g fw < 64g. Standard errors indicated.







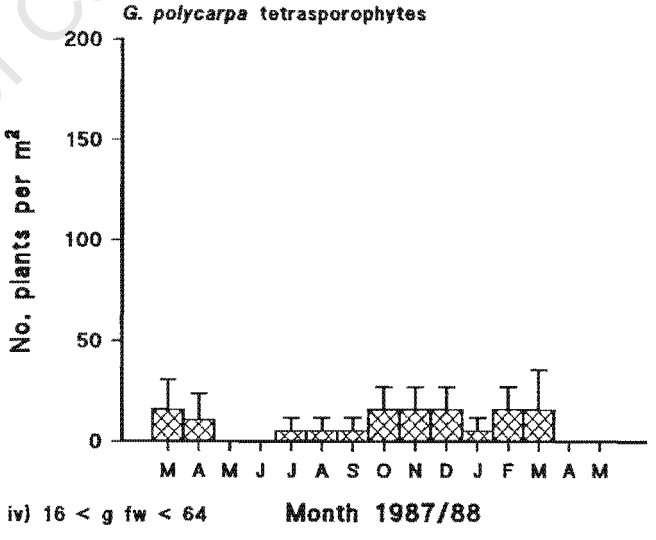


Figure 3.4i Seasonal demography of *Gigartina polycarpa* tetrasporophytes: numbers of plants in different weight classes, 1987-88: i) 0.1g < g fw < 1g; ii) 1g < g fw < 4g; iii) 4g < g fw <16g; iv) 16g < g fw < 64g. Standard errors indicated.

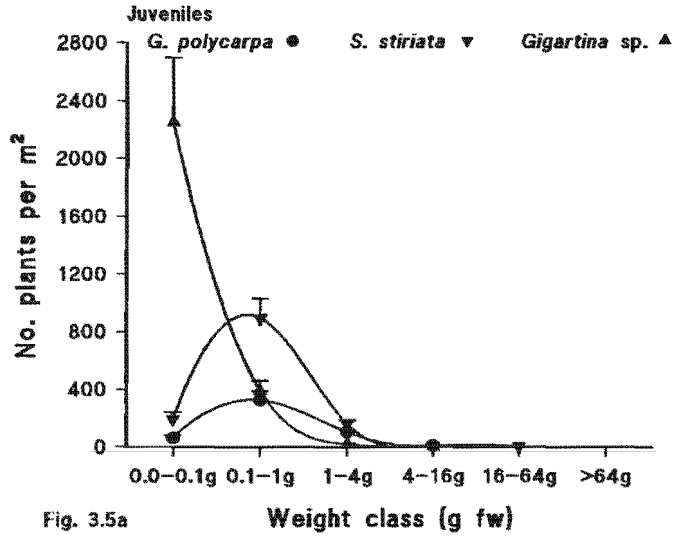


Fig. 3.5a

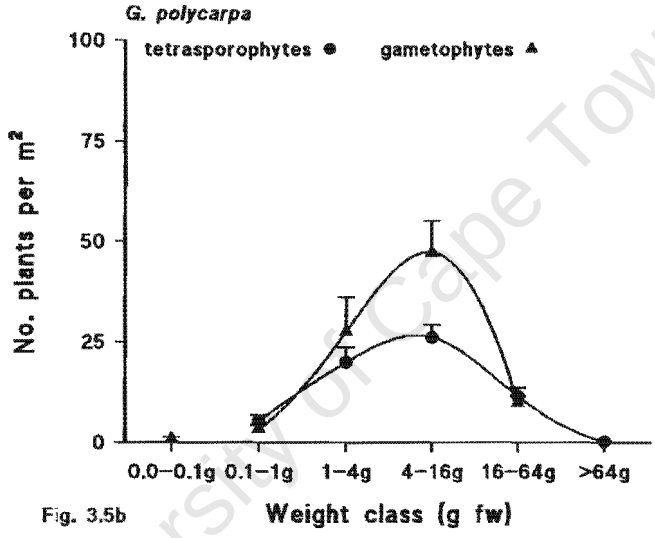


Fig. 3.5b

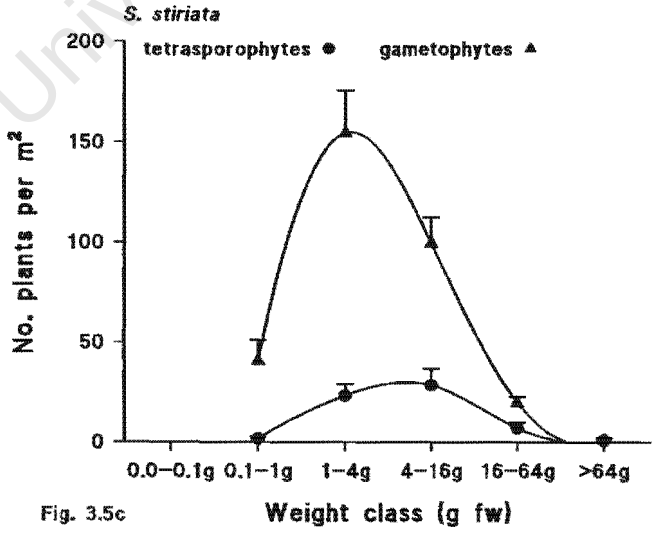


Fig. 3.5c

Figure 3.5 Mean abundance (May 1987 - May 1988) in different weight classes of juveniles, gametophytes and tetrasporophytes of *Gigartina* sp, *Gigartina polycarpa* and *Sarcothalia stiriata*: a) juveniles; b) *G. polycarpa*; c) *S. stiriata*. Standard errors indicated.

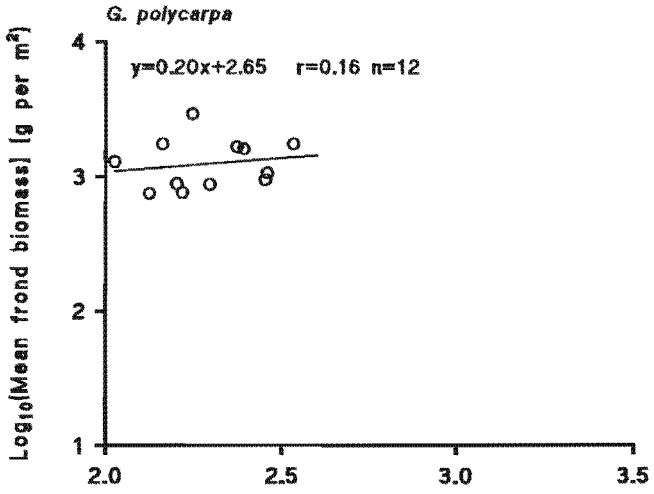


Fig. 3.6a Log_{10}(Frond density) (fronds per m^2)

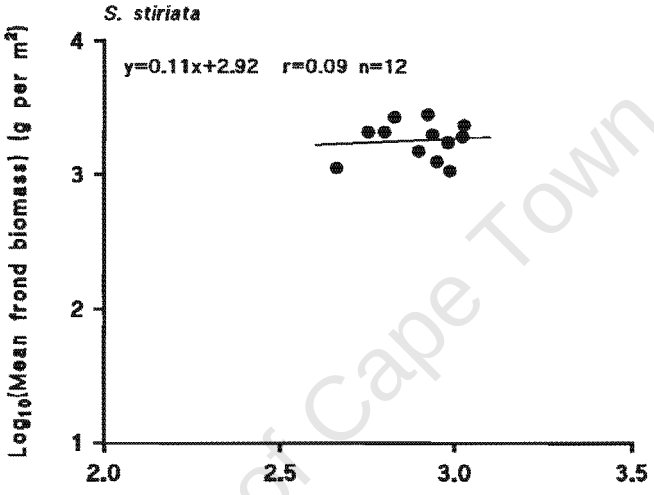


Fig. 3.6b Log_{10}(Frond density) (fronds per m^2)

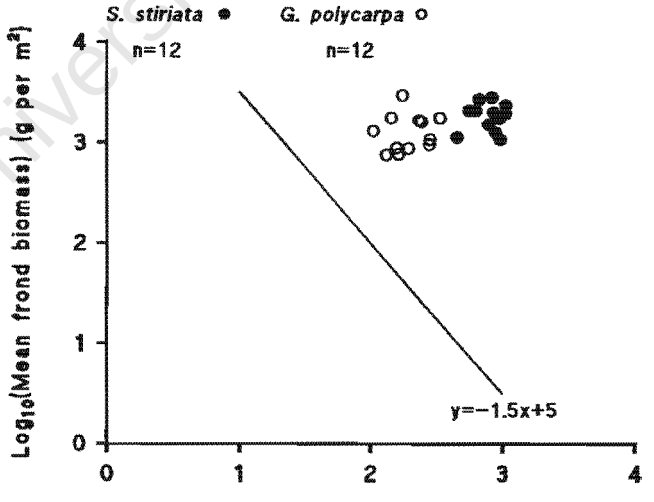


Fig. 3.6c Log_{10}(Frond density) (fronds per m^2)

Figure 3.6 Relationship between log_{10}(stand fresh biomass -g per m^2) and log_{10}(frond density per m^2) of a) *Gigartina polycarpa*; b) *Sarcothalia stiriata*; c) *G. polycarpa*, *S. stiriata* and the ultimate biomass-density line.

presence/absence of 3,6-anhydrogalactose in tissue samples heavier than 0.05g fresh weight, the presence of this polysaccharide being characteristic of the gametophyte phase, indicated by the colour change of the acetal-resorcinol from clear to pink.

Species / life-history phase	$0.0 < wt \leq 0.05g$	$0.05g < wt \leq 0.1g$	$0.1g < wt \leq 0.5g$	$0.5g < wt \leq 1.0g$
G. polycarpa tetrasporophyte	5 Clear	5 Clear	5 Clear	5 Clear
G. polycarpa gametophyte	3 Clear/ 2Pink	5 Pink	5 Pink	5 Pink
S. stiriata tetrasporophyte	5 Clear	5 Clear	5 Clear	5 Clear
S. stiriata gametophyte	5 Clear	5 Pink	5 Pink	5 Pink

Table 3.9 Colour response of acetal-resorcinol test on four fresh-weight classes of sexually mature gametophytes and tetrasporophytes of *Gigartina polycarpa* and *Sarcothalia stiriata*. Pink = anhydrogalactose present; Clear = anhydrogalactose absent (five replicates of each tested).

The proportion of indistinguishable juveniles of *Gigartina polycarpa* and *Sarcothalia stiriata* from the 10 x 10cm quadrat-size subsample are shown in fig 3.7. Although proportions of juvenile gametophytes and tetrasporophytes were variable (fig. 3.7a,b), there was no significant seasonal pattern to this variability in either life-history phase (gametophytes: $F_{0.05(2),3,8} = 1.05 < 5.42$; tetrasporophytes: $F_{0.05(2),3,8} = 1.79 < 5.42$). On average, 56.6% of the juvenile population were gametophytes and 43.4% were tetrasporophytes.

3.3.4 Fecundity

There was a significant difference between the number of cystocarps ($F_{0.05(2),1,66} = 57.02 > 5.29$) per g fresh weight of female gametophytes (fig. 3.8a) of *Gigartina polycarpa* (mean number=$\bar{t}$=140.69) and *Sarcothalia stiriata* ($\bar{t}$=55.83). There was also a significant difference between the number of tetrasporangial sori ($F_{0.05(2),1,90} = 95.18 > 5.20$) per g fresh weight of tetrasporophytes (fig. 3.8b) of *G. polycarpa* ($\bar{t}$=500.17) and *S. stiriata* ($\bar{t}$=181.00). There was no significant seasonal difference between winter and summer in the number of cystocarps present on female gametophytes of either species (*G. polycarpa* $F_{0.05(2),1,30} = 0.00 < 5.57$; *S. stiriata* $F_{0.05(2),1,34} = 2.89 < 5.57$). There was also no significant seasonal difference between winter and summer in the number of tetrasporangial sori present on tetrasporophytes of either species (*S. stiriata* $F_{0.05(2),1,30} = 3.60 < 5.57$; *G. polycarpa* $F_{0.05(2),1,58} = 4.12 < 5.34$).

Gigartina polycarpa ($\bar{t}$=1.361×10^6) possessed significantly ($F_{0.05(2),1,66} = 46.65 > 5.29$) more

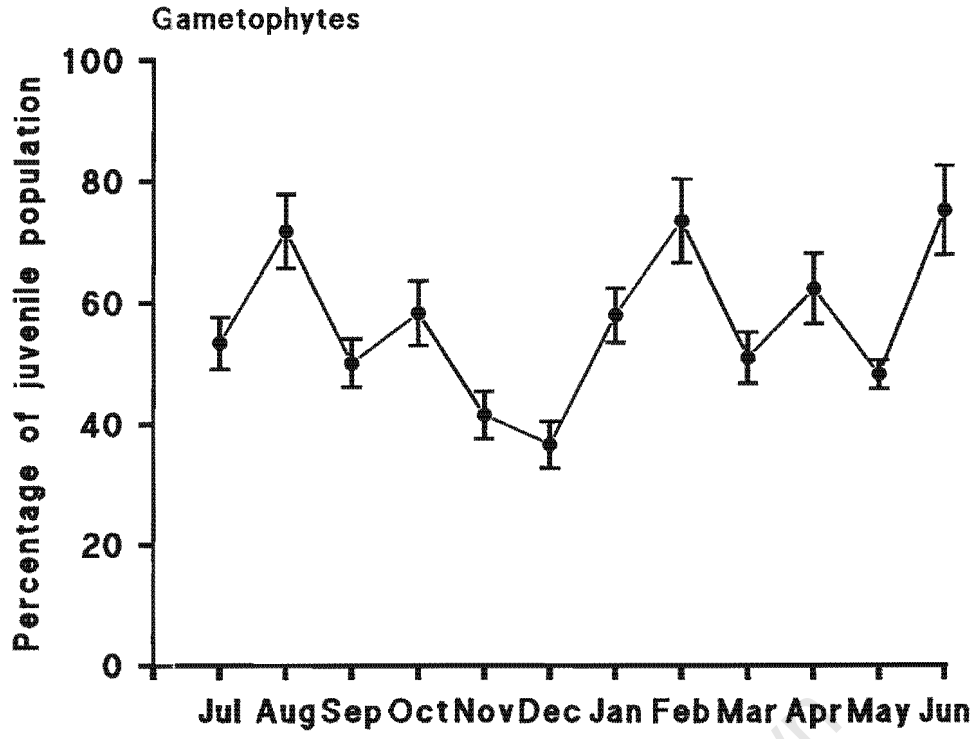


Fig. 3.7a

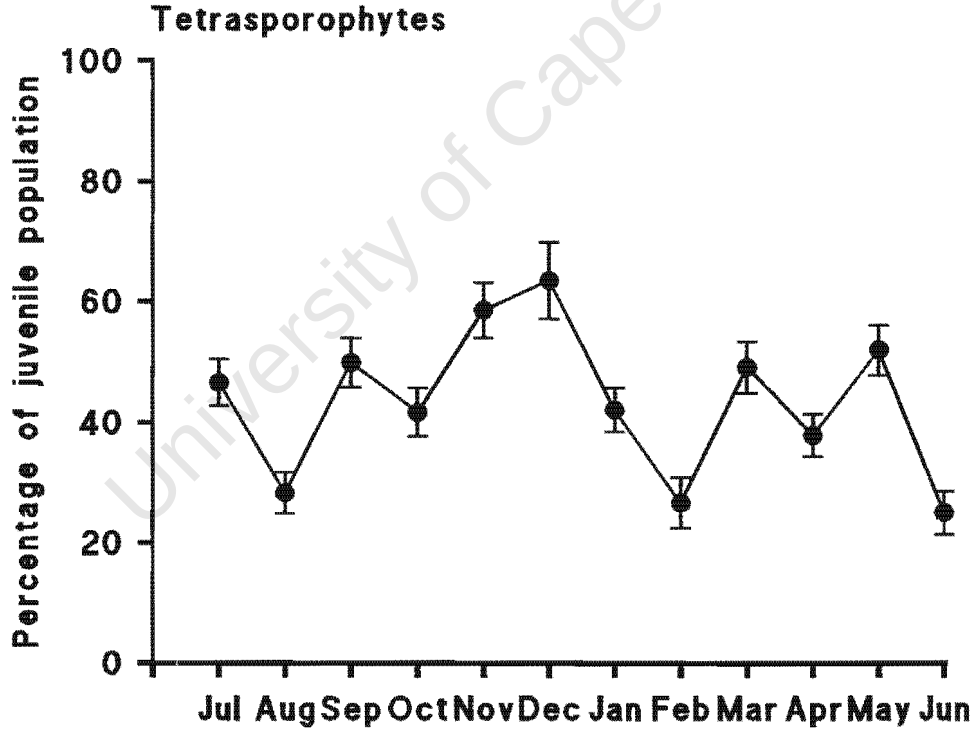


Fig. 3.7b

Figure 3.7 Seasonal (July 1991 - June 1992) composition of juvenile *Gigartina* sp. sporeling populations identified using aceto-resorcinol: a) gametophytes; b) tetrasporophytes. Standard errors indicated.

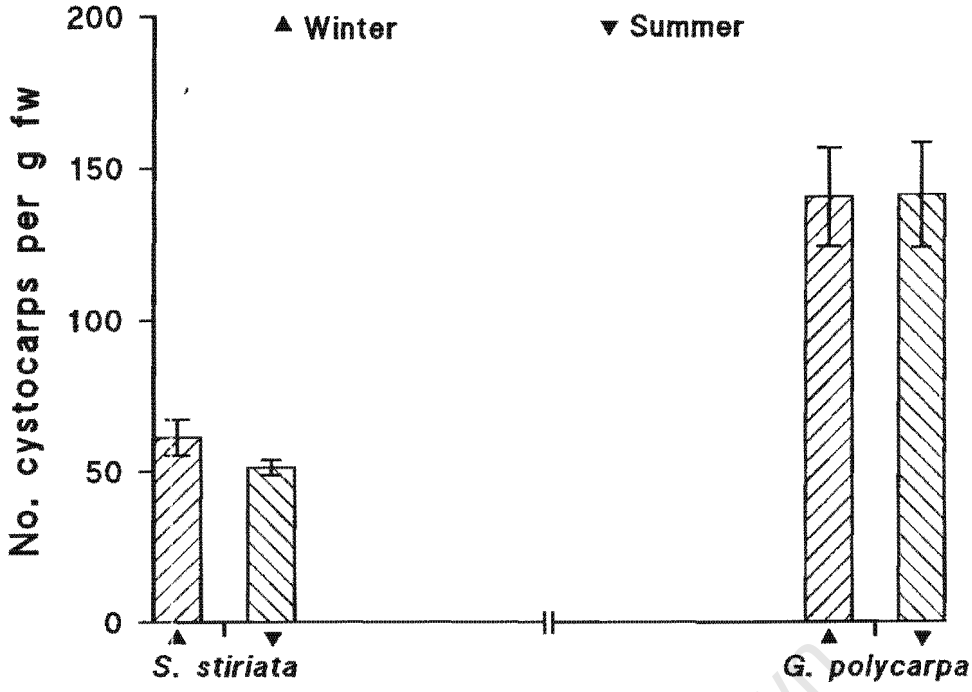


Fig. 3.8a **Winter 1992 & Summer 1992/3**

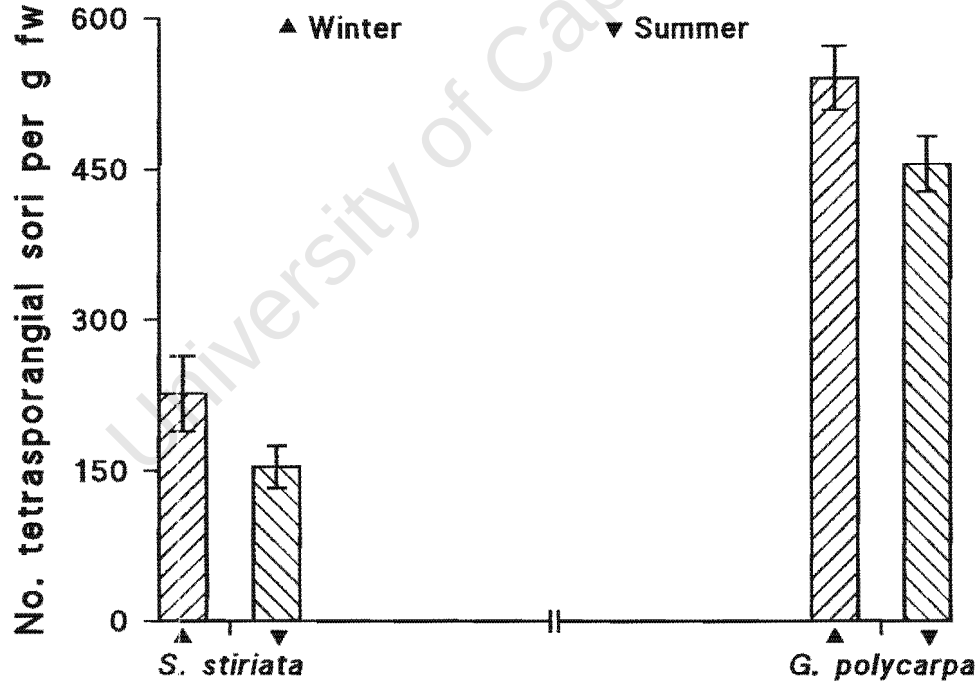


Fig. 3.8b **Winter 1992 & Summer 1992/3**

Figure 3.8 Winter (July/August 1992) and summer (December/January 1992/3) abundance of reproductive structures in individuals of *Sarcothalia stiriata* and *Gigartina polycarpa*: a) female gametophytes; b) tetrasporophytes. 95% confidence limits indicated.

carpospores per cystocarp (fig. 3.9a) than *Sarcothalia stiriata* ($\bar{t}=1.515x10^5$). The reverse was true for tetraspores per tetrasporangial sorus (fig. 3.9b), the number in *S. stiriata* ($\bar{t}=6630$) being significantly ($F_{0.05(2)\,1,90} = 27.75 > 5.20$) greater than in *G. polycarpa* ($\bar{t}=681$). There was a significant difference between winter and summer in the number of carpospores per cystocarp (fig. 3.9a) in *G. polycarpa* ($F_{0.05(2),1,30} = 9.96 > 5.57$; winter $\bar{t}=1.293x10^6$; summer $\bar{t}=1.429x10^6$) but not in *S. stiriata* ($F_{0.05(2),1,34} = 4.05 < 5.57$; winter $\bar{t}=1.439x10^5$; summer $\bar{t}=1.591x10^5$). There was no significant difference between winter and summer in the number of tetraspores per tetrasporangial sorus (fig. 3.9b) of either *G. polycarpa* ($F_{0.05(2),1,58} = 2.96 < 5.34$; winter $\bar{t}=674$; summer $\bar{t}=688$) or *S. stiriata* ($F_{0.05(2,1,30} = 4.22 < 5.57$; winter $\bar{t}=6299$; summer $\bar{t}=6962$).

Both *Gigartina polycarpa* and *Sarcothalia stiriata* produced substantially more carpospores than tetraspores both per g fw thallus and per m^2 of occupied shoreline (table 3.10). No seasonal pattern was apparent between summer and winter in the number of spores produced per g fw thallus in either carpospores or tetraspores of *G. polycarpa* or *S. stiriata*. However, *G. polycarpa* porduced an order of magnitude more carpospores per m^2 substratum in summer than in winter, reflecting the substantial increase in female biomass during this period. In *S. stiriata*, an order of magnitude more per m^2 substratum of both carpospores and tetraspores was produced in summer than in winter. In *G. polycarpa* the ratio of the mean number of carpospores to tetraspores per g fw of thallus averaged over summer and winter was 566:1, whereas in *S. stiriata*, this ratio was considerably less (6.8:1).

Species / life-history phase	Spores per g fw thallus summer	winter	Spores per m^2 substratum summer	winter
G. polycarpa carpospores	2.0159×10^8	1.8155×10^8	1.147×10^{11}	3.5039×10^{10}
G. polycarpa tetraspores	3.1296×10^5	3.6400×10^5	2.6946×10^8	1.4997×10^8
S. stiriata carpospores	8.1836×10^6	8.8356×10^6	1.0497×10^{10}	4.2764×10^9
S. stiriata tetraspores	1.0713×10^6	1.4266×10^6	4.6174×10^8	7.1332×10^7

Table 3.10 Mean no. of carpospores / tetraspores per i) g fw of total thallus and ii) m^2 of occupied shore in winter (July/August 1992) and summer (December/January 1992/3)

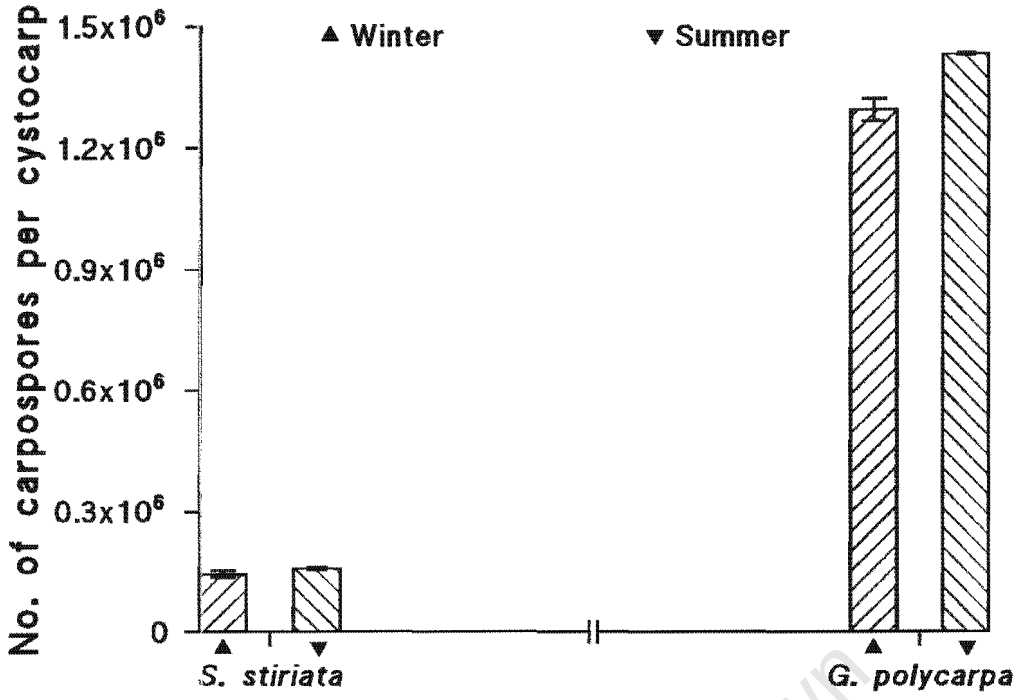


Fig. 3.9a Winter 1992 & Summer 1992/3

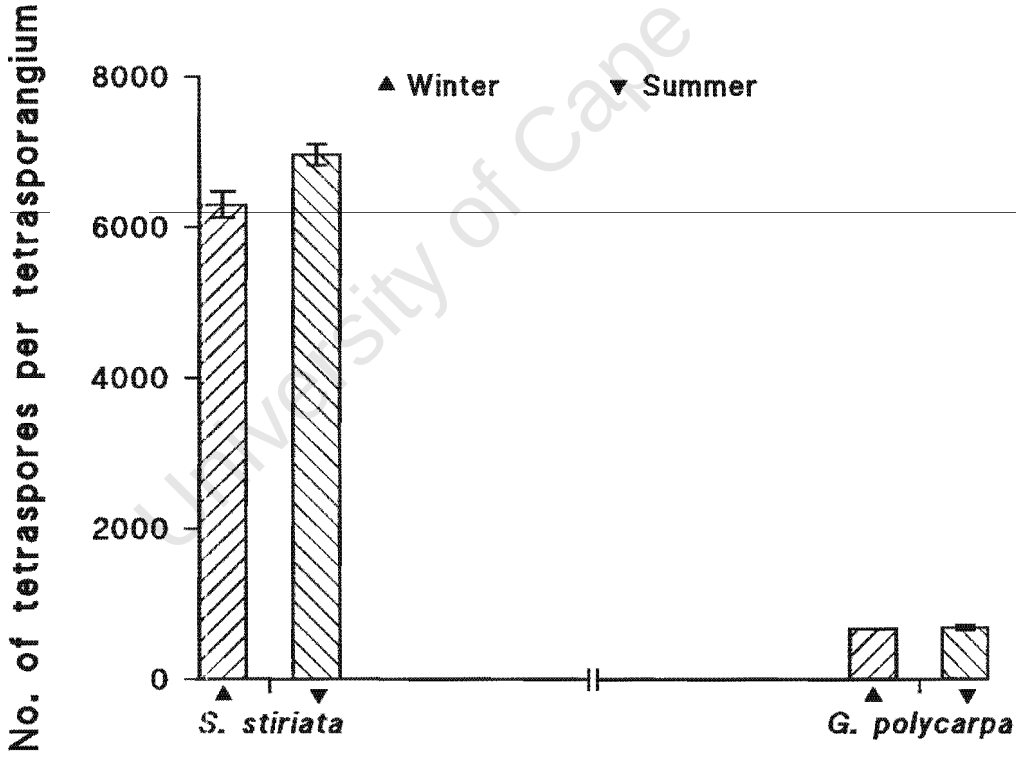


Fig. 3.9b Winter 1992 & Summer 1992/3

Figure 3.9 Winter (July/August 1992) and summer (December/January 1992/3) fecundity of individuals of *Sarcothalia stiriata* and *Gigartina polycarpa*: a) female gametophytes; b) tetrasporophytes. 95% confidence limits indicated.

3.4 DISCUSSION

It appears, from the presence of large numbers of juvenile plants, that vacant areas of substratum surrounding existing plants of *Gigartina polycarpa* and *Sarcothalia stiriata* as well as those areas which result as a consequence of plant mortality, are effectively colonized by spore settlement. However, it is also evident that the majority of sporelings do not reach maturity. Most sporelings are lost prior to growing to an identifiable size, with only a small fraction of total mortality in populations of these two species occurring in plants visible to the naked eye. Considerable mortalities in the microscopic stages are the norm in seaweed populations (Druehl and Wheeler, 1986; Schiel 1988), and *G. polycarpa* and *S. stiriata* are no exception. Whilst sporeling recruitment appears relatively constant, the fact that clear cohorts cannot be distinguished within the size classes may indicate that spore settlement is not the primary source of new plant material. May (1986) showed that regeneration from perennating holdfasts is the primary mechanism for renewing the spring blade population in a gametophyte dominated population of *Iridaea cordata*, and such a mechanism may be operating in the case of *G. polycarpa* and *S. stiriata*.

The large numbers of spores produced by the carposporophytes of *Gigartina polycarpa* and *Sarcothalia stiriata* should result in large numbers of sporophytes. This does not occur, indicating that spore recruitment and/or development of uprights from crusts or perennial holdfasts differentially favours the gametophyte. Recruitment favouring tetraspores was hypothesized as occurring in *Iridaea cordata* (May, 1986), and is highly probable in both *S. stiriata* and *G. polycarpa* given the high carpospore to tetraspore ratios observed, which supports the statement of Chapman (1986) that fecundity and fertility are not synonymous. Apomixis (female gametophytes recycling via unfertilized carpospores) is also a possibility, having been observed in heteromorphic Gigartinales (DeCew & West, 1981). However, the relatively equal proportions of male and female gametophytes of both species makes apomixis unlikely as this would increase the proportion of female gametophytes. Apomeiosis is also unlikely since the proportion of tetrasporophytes to gametophytes in both *G. polycarpa* and *S. stiriata* is not high. In a similar study, De Wreede and Green (1990) also concluded that apomeiosis is unimportant in some populations of *Mazzaella splendens*.

Alternation of generations from one dominant phase to the other was not observed in populations of either *Gigartina polycarpa* or *Sarcothalia stiriata* during the course of this

study, unlike the seasonal change observed by De Wreede and Green (1990) in *Mazzaella splendens*. Blades from plants of both phases of *G. polycarpa*, and mainly gametophytes of *S. stiriata*, are lost due to summer environmental stress, the offshore south-easterly wind prolonging the duration of low tide over the spring periods, resulting in sun and wind burn of exposed thalli. *Sarcothalia stiriata* tetrasporophytes minimize or escape such stress due to their boulder habitat providing more shelter from both the wind (the seaward side of the boulders being in the lee) and the sun (the sides of boulders providing shade). Blades are regenerated within a short period (one month) without changing the population structure. A similar phenomenon with the same lack of effect on population structure has been observed in South African *Hypnea spicifera* (van Zyl, 1993) as well as *Hypnea musciformis* (Durako and Dawes, 1980). Regeneration of plants lost due to these stress events by spores seems unlikely given the spatial domination and likely better competitive ability of regenerating plants, holdfasts limiting spore settlement (Hansen, 1977; Foster 1982) and acting as a "meristem bank" *sensu* Vadas and Wright (1986).

The lack of a negative relationship between frond biomass and frond density indicates that neither *Gigartina polycarpa* nor *Sarcothalia stiriata* undergo self-thinning, even at the highest observed densities. Scrosati and De Wreede (1997) reported that *Mazzaella cornucopiae* (Postels *et* Ruprecht) Hommersand also showed no evidence of self-thinning, a positive dynamic relationship between these two variables being noted by these authors. Similar positive dynamic relationships have been reported for *Chondrus crispus* Stackhouse and *Mastocarpus stellatus* (Pybus, 1977). Bimodal frequency distributions of plant weight would indicate that populations are density stressed (Harper, 1977), the risk of mortality increasing with density and the rate of death being proportional to the growth rate of the survivors. No significant bimodal patterns of plant weight were evident in either *G. polycarpa* or *S. stiriata*, which further indicates that self-thinning does not take place in either of these species. Consequently, there must be little or no competition for space among plants in stands of these two species.

The lack of self-thinning of populations of *Gigartina polycarpa* and *Sarcothalia stiriata* cannot be explained by the ultimate biomass-density line for terrestrial plants because the relationship is positive and not negative. Scrosati and De Wreede (1997) also noted this fact for *Mazzaella cornucopiae*. Since the biomass of ramets of *G. polycarpa* and *S. stiriata* are positive with

respect to the ultimate biomass-density, growth is not ceasing at this point. Therefore, for these species, possible constraints limiting biomass for a given frond density still have to be determined.

Coalescing holdfasts may introduce errors in identification of individual plants as well as preventing further spore settlement. Vegetative reproduction was considered by Harper (1977) to have seriously hindered the development of the science of seaweed demographic studies because of the problem of defining ramets as individuals. Furthermore, thalli of some Gigartinales arise from a prostrate perennial crust (*e.g. Mastocarpus papillatus* and *Gigartina exasperata* - Norris & Kim, 1972) and are thus better placed for rapid regrowth. This expansion of the prostrate system results in an increase in the size of the genet, a pattern typical of terrestrial species growing in unstable habitats (Abrahamson, 1980). Expansion of the genet includes a pioneering vegetative phase, a mature phase of maximum density and a degenerative phase characterized by the invasion of other genets or competitive species. In observations conducted in course of this study, the pioneering and mature phases are evident in populations of both *Gigartina polycarpa* and *Sarcothalia stiriata*. Regeneration of broken fronds occurs continuously, there being no clear indication of the degenerate phase. This lack of senescent material is further indication that the ultimate biomass-density line does not apply to these two species, since the cessation of growth and simulataneous onset of senescence are characteristic of the ultimate biomass-density line. A similar pattern was observed in South African *Hypnea spicifera* by van Zyl (1993). The inability to distinguish a cohort of sporelings once they reach a weight greater than 1g fw further supports the idea of vegetative regrowth, as such regrowth would mask sporeling growth. Mortalities also tend to support this vegetative regrowth hypothesis. High mortalities occur in very small plants (sporelings being outcompeted by larger, older plants) and in larger plants (thalli becoming too large and being damaged by wave action and sun/wind burn, or becoming overgrown by the epiphyte *Aristothamnion collabens* (Rudolphi) Papenfuss). Perennating holdfasts are ideally suited to regrow quickly following the loss of upright thalli of older plants, and thus outcompete new sporelings. Large environmental catastrophes which might cause an alternation in the dominant phase in both species due to sporeling recruitment did not occur during the study period.

Populations of both *Gigartina polycarpa* and *Sarcothalia stiriata* are perennial, mature uprights of each life history phase persisting throughout the year. Because established plants

seem to regrow vegetatively, alternation of generations in *G. polycarpa* and *S. stiriata* is much slower than if an annual population was being established by spores. When areas of substratum are completely cleared of vegetative material, the nearest sources of spores should determine the dominant re-established phase. Small catastrophes would therefore be of limited effect (see chapter 5), changes in gametophyte : sporophyte ratios resulting only from large mortalities. This appears to be the case in *S. stiriata*, with relatively constant proportions of life-history phases. *Gigartina polycarpa* however, appears to be more susceptible to small catastrophes such as the wind and sun burn of exposed thalli affecting the proportions of mature thalli. This effect can be clearly seen in the change in the proportions of gametophytes to tetrasporophytes between February 1987 and February 1988. The broad, fleshy nature of *G. polycarpa* thalli probably makes them more susceptible to sun and wind burn than the the narrower thalli of *S. stiriata*. No signs of sun or wind burn have been observed in the latter species.

The extremely high reproductive allocation in both *Gigartina polycarpa* and *Sarcothalia stiriata* (reproductive thallus weight between 50% and 70% of total thallus weight) is puzzling when the apparently low spore survival rate and apparent dominance of the vegetative prostrate system is considered. High reproductive allocations with minimal recruitment from propagules have been observed in *Ascophyllum nodosum* (L.) Le Jol (Vadas *et al.* 1990), *Hypnea spicifera* (van Zyl, 1993) and the South African fucoid *Bifurcaria brassicaeformis* (Kützing) Barton (Manuel, 1990). It appears that low recruitment success in these species, as well as in *G. polycarpa* and *S. stiriata,* is compensated by iteroparity which can be considered a viable reproductive strategy to be favoured when the chances of reproductive success are low (De Wreede and Klinger, 1988). A further advantage of a high reproductive allocation, at least for the gametophyte stages of *G. polycarpa* and *S. stiriata*, is an increase in photosynthetic production due to increased amounts of photosynthetic tissue in reproductive structures. This was also noted by Manuel (1990) in *B. brassicaeformis*. The large numbers of spores present in all life-history phases of both *G. polycarpa* and *S. stiriata* may be a means of combating the low spore survival rate, which itself may be the result of a number of biotic and abiotic factors. For example, both grazing (Chapman, 1984) and wave action (Vadas *et al.* 1990) have been shown to be major sources of seaweed spore and sporeling mortality. Also, Hay and South (1979) demonstrated in the bull-kelp *Durvillaea antarctica* (Chamisso) Hariot that the

canopy formed by adult plants reduces sporeling recruitment. Some or all of these factors may play a role in reducing the recruitment success of *G. polycarpa* and *S. stiriata*, the dominance of the mature population biomass by vegetative reproduction being the result of a combination of these and a lack of substratum availability combined with the regenerative capacity of the perennating prostrate system. The regenerative capacity of the prostrate system allows populations of *G. polycarpa* and *S. stiriata* to i) retain the primary substratum in a suitable growth locality, ii) avoid complete dependence on spore(ling) stages which are subject to high mortality, and iii) avoid competition with more opportunistic species. Dixon (1965) considered vegetative reproduction as a means of propagation in areas of environmental stress to be a major factor contributing to the long-term survival of populations. Vegetative propagation has been shown to play an important role in the population dynamics of a number of carrageenophyte genera, notably *Eucheuma* (Dawes *et al.* 1974a) and *Hypnea* (Mshigeni, 1976; Rao, 1977; van Zyl, 1993), and in accordance with the observations of Chapman and Johnson (1990), functions to prevent diversification caused by disturbance (Connell, 1978) and maintains a stable, actively growing population.

The similar phenological and demographic patterns displayed by *Sarcothalia stiriata* and *Gigartina polycarpa* are of interest since the geographical distribution of both species is similar. Gametophyte dominance in the Gigartinaceae seems remarkably common. Tetraploidy in the sporophyte generation may be means of maximizing genetic diversity and will result in large numbers of gametophytes (Santelices, 1990). Gametophyte dominance enhances the likelihood of outcrossing (heterosis) and a more heterozygous sporophyte population, but also means that there is a greater chance of deleterious genes being expressed in the dominant gametophyte phase. Failure of cytokinesis has been observed in *Gracilaria* sp. (Van der Meer, 1977), and will have a negative effect on heterosis should it occur in natural populations. The separate diploid phase therefore represents a pool of recessive alleles (Searles, 1980) and if phenotypically distinct from the gametophyte may result in the occupation of alternative ecological niches.

Because apomixis is unlikely to be occurring in *Gigartina polycarpa* and *Sarcothalia stiriata*, the greater numbers of spores in cystocarps may be a means of further maximizing heterozygosity in the sporophyte population (Searles, 1980), this being advantageous since the populations are dominated by gametophytes. It can be inferred from the observed dominance

of the gametophyte phase that sporelings of the latter have a much better chance of surviving to reproduction. Some differential factor which favours the gametophyte appears to be acting on populations of both species, with the result that heterozygosity in the sporophyte population is maximized.

The cost of sexual reproduction is usually considered in terms of a resource trade-off in that i) a certain size must be attained in order to begin reproduction, ii) the reduction or cessation of growth at the onset of reproduction is likely due to resource partioning and iii) the organism is more likely to die after releasing reproductive propagules (De Wreede and Klinger, 1988). Whilst some evidence supports the resource trade-off hypothesis (*e.g. Sargassum* spp. - McCourt, 1985), other data (*e.g. Mastocarpus stellatus* - Burns and Mathieson, 1972b; *Codium fragile* (Suringar) Hariot - Fralick and Mathieson, 1973) are not consistent with this hypothesis, maximum growth occurring simultaneously with maximum reproduction. Data from this study on *Gigartina polycarpa* and *Sarcothalia stiriata* are also not consistent with the trade-off hypothesis, reproductive weight as a percentage of total thallus weight remaining relatively constant. In further contradiction of the hypothesis, both *G. polycarpa* and *S. stiriata* continue growing after reproductive fertility is achieved, a phenomenon also noted by Hansen (1977) in *Iridaea cordata*. Theoretically, iteroparity thus helps offset the high cost of reproduction, which although reduced by the formation of reproductive structures directly on or in the vegetative blades, still necessitates the additional cost of oogonia, antheridia and sporangia. This argument assumes that organisms allocate limited resources to gametes (Vernet and Harper, 1980). However, in *G. polycarpa* and *S. stiriata*, this cost appears to be negligible. The biomass of carpospores and tetraspores represents about 0.3% of total thallus weight. This value is similar to that observed by Vernet and Harper (1980) in a number of fucoids, and supports their conclusion that the costs of gamete production, measured as biomass, are small. Similarly, Joska and Bolton (1987) estimated the biomass of zoospore production in the South African kelp *Ecklonia maxima* (Osbeck) Papenfuss at about 0.17% of total production. No seasonal measurements of spore production or release were made in this study. Seasonality of spore production is possible, having been observed in *E. maxima* (Joska and Bolton, 1987).

Why two co-occurring members of the Gigartinaceae which show such similarities in their population biology should have evolved is of interest. Differences in thallus morphology,

response to wave action (see chapter 4) and the more marked gametophyte dominance in *Sarcothalia stiriata* seem to be the only factors separating the two populations ecologically. Detailed investigations of the tolerances of both species to various environmental factors may reveal further niche separation, as well as shedding light on factors limiting their distribution (see chapter 6).

CHAPTER 4

SEASONAL GROWTH RATE AND RESPONSE TO WAVE ACTION OF *GIGARTINA POLYCARPA* AND *SARCOTHALIA STIRIATA*

4.1 INTRODUCTION

There is a limited understanding of the role that selective forces play in maintaining habitat differences among ecotypes or closely related species of seaweeds (Shaughnessy *et al.* 1996). Wave action (hydrodynamic force) is not only a direct environmental factor maintaining such habitat differences, but also operates indirectly by affecting nutrient availability, physical scouring, light penetration, temperature and salinity. Seasonal growth rates of seaweeds are particularly influenced by these environmental factors, marked seasonal fluctuations in nutrient availability and irradiance constraining growth rates being well documented (*e.g.* Hatcher *et al.* 1977; Gagné *et al.* 1982; Lyngby, 1990; Rosenberg and Ramus, 1982; Probyn and Chapman, 1983). On the South African west coast nutrient availability varies as a result of seasonally upwelled water (Andrews and Hutchings, 1980), the increase in nutrients in spring and summer being measurable within the thallus of the local kelps (Probyn and McQuaid, 1985), presumably contributing to the increased growth of kelp during the spring/summer period (Dieckmann, 1980). Growth rates of commercial South African seaweeds have been reported for the agarophytes *Gelidium pristoides* (Turner) Kützing (Carter and Anderson, 1986) and *Gracilaria gracilis* (Stackhouse) Stentoft, Irvine *et* Farnham (Anderson *et al.* 1992), the alginophytes *Ecklonia maxima* (Mann *et al.* 1979) and *Laminaria pallida* (Dieckmann, 1980), and the carrageenophyte *Hypnea spicifera* (van Zyl, 1993). Seasonal growth data are only available for *G. pristoides*, *L. pallida* and *H. spicifera*, the latter being reported as unreliable by the author. Because of this paucity of information, the initial aim of this study was to investigate the seasonal growth rates of the South African west coast carrageenophytes *Gigartina polycarpa* and *Sarcothalia stiriata*.

Hydrodynamic force, as a factor responsible for maintaining habitat diversity, operates by means of wave-induced forces controlling the rate of disturbance in species that dominate the competition for space, by influencing the course of succession and subsequent biodiversity (Paine and Levin, 1981). Hydrodynamic forces also mechanically limit the size to which wave-

swept organisms can grow (Denny *et al.* 1985). Algal morphology was shown by Carrington (1990) to effectively limit the maximum size of *Mastocarpus papillatus*, growth of this species being concentrated in the frond, the resulting increased drag limiting the size which could be retained by the stipe, which does not display a corresponding growth increment. Streamlining of the thallus of *M. papillatus* at higher water velocities was also shown by Carrington (1990) to be effective in minimizing drag created by the thallus morphology. Gaylord *et al.* (1994) proposed that even though algal thalli can become streamlined at higher velocities, substantial volumes of slower-moving water can become trapped within the thallus, increasing the plant's effective volume and consequently the accelerational force which, in turn, increases the drag on the thallus. Thallus morphology would therefore act as a size-dependent agent of mortality limiting the size of the alga.

Thus, the second aim of this study was to determine the natural responses of *Gigartina polycarpa* and *Sarcothalia stiriata* to *in situ* hydrodynamic forces by assessing their summer and winter growth rates in areas of differing wave-induced force, and to relate this to thallus morphology using empirical drag measurements.

4.2 MATERIALS AND METHODS

4.2.1 Study site

Field experiments for this study were conducted at the same site at Kommetjie (a semi-exposed ledge of Table Mountain Sandstone with a perimeter of medium-sized, immoveable boulders, (see chapter 1)) used for the demography studies (chapter 3). The ledge, which was somewhat sheltered by the boulder perimeter from the prevailing swell, was occupied by a mixed population of *Gigartina polycarpa* (all life history phases) and *Sarcothalia stiriata* (male and female gametophytes only). *Sarcothalia stiriata* tetrasporophytes occurred (together with some *S. stiriata* female gametophytes) on the surrounding exposed boulder edges, directly facing the prevailing swell.

4.2.2 Relative wave exposure

Measurement of the relative degree of exposure of the two localities (ledge and boulders) was determined in summer (December 1989) and winter (July 1990) by the use of clod cards (Doty, 1971). Cylindrical (30mm diameter, 25mm height) 90g clods were manufactured from Plaster of Paris (gypsum) and secured via a locating lug and locking screw to 90mm square

plastic mounts. These mounts were then secured to the substratum of the two experimental localities with stainless steel screws and rawl plugs. Clods were placed on open substratum in order to minimize the scouring effect of nearby plants. Twenty clods were placed during the same spring low-tide period in each locality, and recovered 24-hours later, again during the same spring low-tide period. Each clod was weighed immediately prior to deployment and after recovery. Comparative exposure of the two localities was determined by calculating the mean percentage weight loss for each group of clods over a 24-hour period. Data was analyzed by one-way ANOVA on arcsin-transformed data using the Student-Newman-Keuls multiple range test for differences between treatments ($\alpha=0.05$).

4.2.3 Seasonal growth rate

Monthly measurements of seasonal growth of female gametophytes and tetrasporophytes of *Gigartina polycarpa* and *Sarcothalia stiriata* took place *in situ* between May 1987 and April 1988. Individual plants were identified by loosely tagging them around the base of the thallus using numbered 2.5mm wide cable ties. Growth (increment in length, calculated to $mm.day^{-1}$) was recorded by measuring the length of the thallus from holdfast to the distal point of the longest blade. Five individual female gametophytes and tetrasporophytes of each species were continuously maintained throughout the experimental period by visiting the site during every spring low-tide. Where a plant was lost due to mortality or wave action, it was immediately replaced by tagging and measuring a new individual. Growth rate of male gametophytes was not measured. To test for differences between months, data were analyzed by one-way ANOVA together with the Student-Newman-Keuls multiple range test ($\alpha=0.05$).

4.2.4 Growth rate of transplanted plants

The growth rates of transplanted thalli of both *Gigartina polycarpa* and *Sarcothalia stiriata* was determined during spring/summer (October, November and December 1989) and winter (June, July and August 1990) and compared with the results obtained in the corresponding months of 1987/88 for growth rates of non-transplanted plants as determined above (section 4.2.3). Individual plants of female gametophytes and tetrasporophytes of both species were carefully removed from the substratum using a scalpel and transplanted to experimental locations as follows: Plants occurring naturally on the ledge (sheltered) were removed and relocated to the boulders (exposed) and vice versa, *i.e. G. polycarpa* gametophytes and tetrasporophytes as well as *S. stiriata* gametophytes were transplanted from sheltered to more

exposed conditions, whereas only *S. stiriata* tetrasporophytes were transplanted from an exposed to a more sheltered environment. Plants were reattached by trapping the proximal end of the thallus between the lay of polypropylene ropes. Ropes used were 30cm long with a diameter of 5mm. Five individual plants of one life-history phase were attached to each rope, four ropes being used for each species (two ropes with female gametophytes and two with tetrasporophytes). Two ropes from each species (one with female gametophytes and one with tetrasporophytes) were attached to the ledge whilst the other two were attached to the boulders. The ropes were reattached to the substratum by fastening them with cable ties to 30cm x 5cm stainless steel strips with holes for attachment and tensioning of the rope. Each strip was then attached to the substratum using stainless steel screws and rawl plugs. Growth was measured by measuring thallus length as above (section 4.3.2). Data was analyzed for differences between natural growth rate (data from section 4.4.3) and transplanted growth rate (data from section 4.4.4) in corresponding months by one-way ANOVA. The Student-Newman-Keuls multiple range test was used to check for differences between treatments ($\alpha=0.05$).

4.2.5 Determination of thallus drag at various flow rates

Thallus drag of male gametophytes, female gametophytes and tetrasporophytes of *Gigartina polycarpa* and *Sarcothalia stiriata* was determined using a specially constructed flow tube apparatus. A 15cm diameter clear perspex pipe was attached to the drain outlet of the Sea Fisheries Research Institute marine aquarium header tank (capacity 90 000ℓ), water being supplied by gravity. The flow rate was regulated by means of a commercially available PVC valve and measured (in knots) using a marine electronic log (VDO Sumlog). A 500g Pesola spring balance was rigidly suspended via a custom made metal ring inserted flush with the inside of the perspex pipe and oriented parallel to the water flow. Experimental thalli were attached to the moveable spring hook by means of nylon monofilament line. The drag reading (in g) shown by the scale for between 9 and 14 separate individuals of varying thallus size from each life history phase was recorded at steady flow rates of two, three, four and five knots. In order to analyse the data, drag and velocity observations were converted to newtons and metres per second by multiplying by constants (1kg = 9.80665 N; 1kt = 0.51445 $m.s^{-1}$). The flow rate was maintained for a period of 15 seconds to allow the scale reading to stabilize prior to each individual observation. The length, width, area and volume of each individual thallus was also noted. The drag coefficient (C_d) of each observation was calculated using the

formula:

$$C_d = 2\,F_d/(\rho A u^2) \quad \text{(Gaylord } et\ al.\ 1994\text{)}$$

where: F_d = drag N

ρ = mass density of fluid (seawater $= 1035 kg.m^{-3}$)

A = thallus area (m^2)

u = fluid velocity ($m.s^{-1}$)

In order to explore the predicted responses of thalli to heavy wave action, i.e. water velocities high enough to load plants with a maximal force ($>10m.s^{-1}$, Hoerner, 1965; Vogel, 1981; Denny *et al.* 1985; Gaylord *et al.* 1994), the C_d data obtained via the above method was extrapolated by means of linear regression of natural log transformed drag coefficient and velocity values.

In order to investigate the effect of thallus volume as a contributor to algal inertia coefficients, a linear regression of drag (F_d) versus thallus volume (cm^3) at two velocity extremes of 2 knots ($1.0m.s^{-1}$) and 5 knots ($2.6m.s^{-1}$) was fitted to the data for each life-history phase of both species. Thallus volume was obtained by measuring the volume of water displaced by immersion of the thallus.

4.3 RESULTS

4.3.1 Relative wave exposure

Figure 4.1 shows the mean percentage weight loss of the experimental clods during a 24-hour period in July (winter) and December (summer) at the ledge and boulder sites. All four experimental means were significantly different from one another: clod weight loss on the boulders was significantly greater than on the ledge in both July and December, indicating that the boulders were more exposed to hydrodynamic forces than the ledge. July clod weight losses on both boulders and ledge were significantly greater than their respective December weight losses. The magnitude of the difference between of clod weight loss on the ledge and boulders was also greater in July than in December. This indicates that hydrodynamic forces were greater in July than in December. Weight loss on the ledge during July was greater than weight loss on the boulders during December, indicating that hydrodynamic forces on the sheltered ledge during July were greater than on the more exposed boulders during the calmer December period. Weight loss due to seaweed scouring is unlikely because of the siting of the

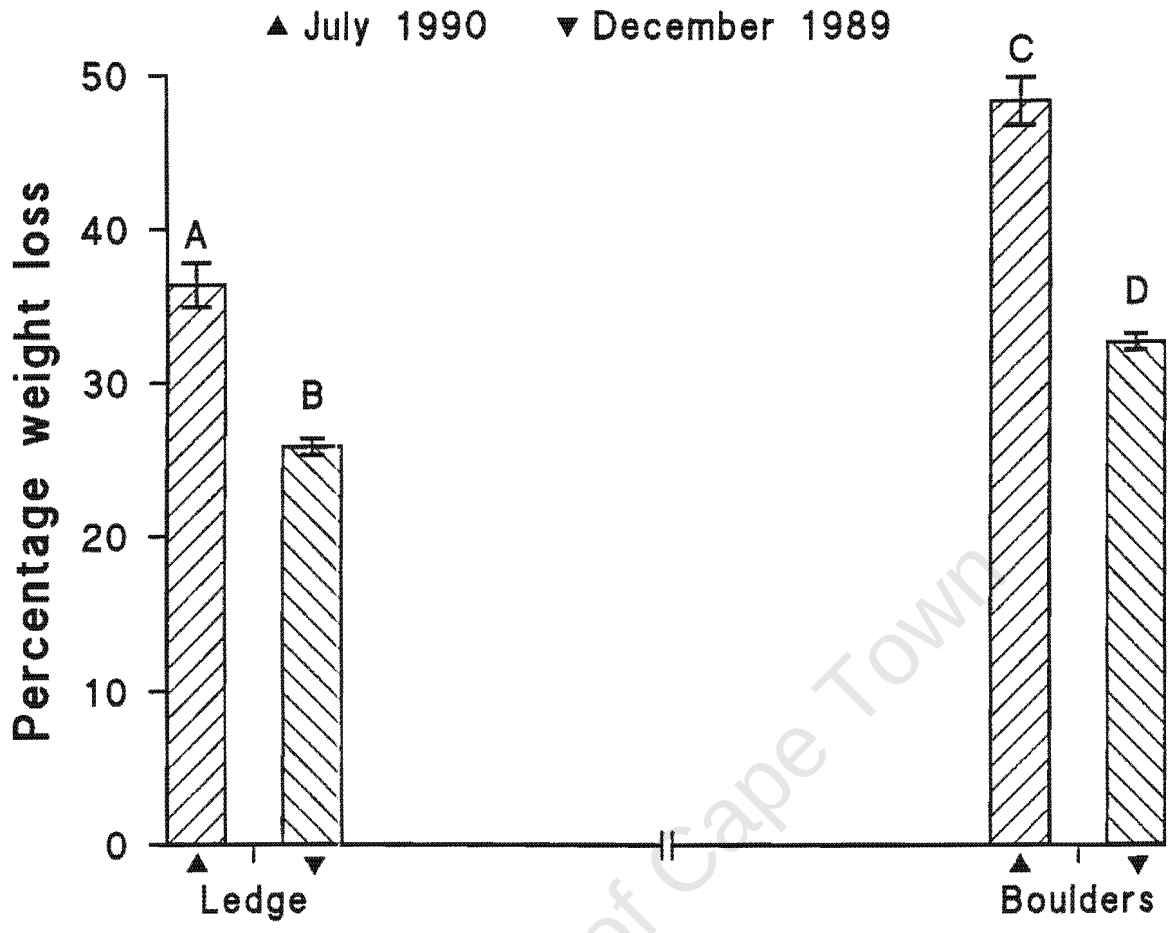


Fig. 4.1 Boulders (exposed) Ledge (sheltered)

Figure 4.1 Percentage weight loss over 24hrs of 90g clod cards located on ledge and boulders at Kommetjie during December 1989 (austral summer) and July 1990 (austral winter). Bars with the same letter are not significantly different ($F_{0.05(2),3,76} = 74.36 > 3.31$). Standard errors indicated.

clods on open substratum. Minor sand scouring by suspended particles was possible, although assumed to be minimal since the study site was located on a rocky outcrop facing away from the nearest beach.

4.3.2 Seasonal growth rate

A significant seasonal growth pattern was evident in female gametophytes and tetrasporophytes of both *Gigartina polycarpa* and *Sarcothalia stiriata*. Female gametophytes of *G. polycarpa* (fig. 4.2a) showed almost no growth during autumn (April-May, 0.06mm.day^{-1}) and early to mid-winter (June-July, 0.02mm.day^{-1}). Growth increased during late winter (August, 0.36mm.day^{-1}) and spring (September-October, 0.44mm.day^{-1}), reaching a maximum in late spring (November, 0.66mm.day^{-1}) and early to mid-summer (December-January, 0.73mm.day^{-1}), declining thereafter during late summer and early autumn (February-March, 0.22mm.day^{-1}). Tetrasporophytes of *G. polycarpa* (fig. 4.2b) grew throughtout the year, with minimum growth from early autumn to mid-winter (March-July, 0.37mm.day^{-1}), increasing during late winter and early spring (August-September, 0.67mm.day^{-1}), reaching a maximum in mid- and late spring (October-November, 1.18mm.day^{-1}), and maintaining high growth rates during early and mid-summer (December-January, 1.11mm.day^{-1}), with a rapid decline in late summer (February, 0.53mm.day^{-1}). A significant seasonal pattern of growth rate was also apparent in *S. stiriata* female gametophytes (fig. 4.3a) and tetrasporophytes (fig. 4.3b), both life-history phases displaying positive growth rates throughout the year. Female gametophytes of *S. stiriata* showed mininum growth during autumn (March-May, 0.27mm.day^{-1}) and early winter (June-July, 0.24mm.day^{-1}). Growth increased substantially during late winter and early spring (August-September, 0.49mm.day^{-1}), reaching a maximum during mid- and late spring (October-November, 0.67mm.day^{-1}). Growth rates then declined to a fairly constant level over summer (December-February, 0.53mm.day^{-1}). Tetrasporophytes of *S. stiriata* displayed a similar growth pattern to female gametophytes, growing throughout the year. Minimum growth took place from late autumn to mid-winter (May-July, 0.26mm.day^{-1}), and increased during late winter and early spring (August-September, 0.46mm.day^{-1}). Maximum growth occurred during mid- and late spring (October-November, 0.74mm.day^{-1}), declining rapidly during early summer (December, 0.43mm.day^{-1}), thereafter maintaining a constant level from mid-summer to mid-autumn (January-April, 0.32mm.day^{-1}).

Gigartina polycarpa tetrasporophytes (table 4.1) displayed a significantly greater mean annual

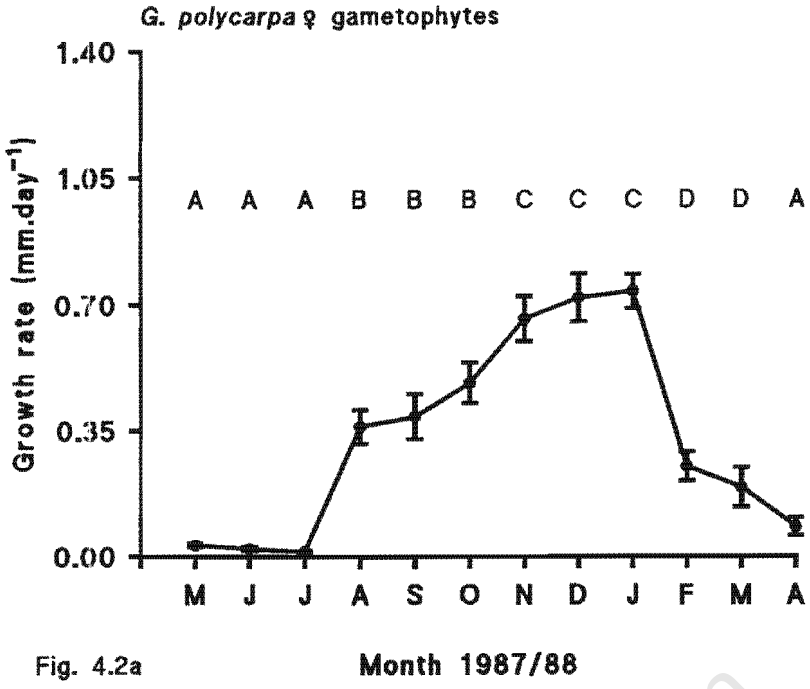


Fig. 4.2a

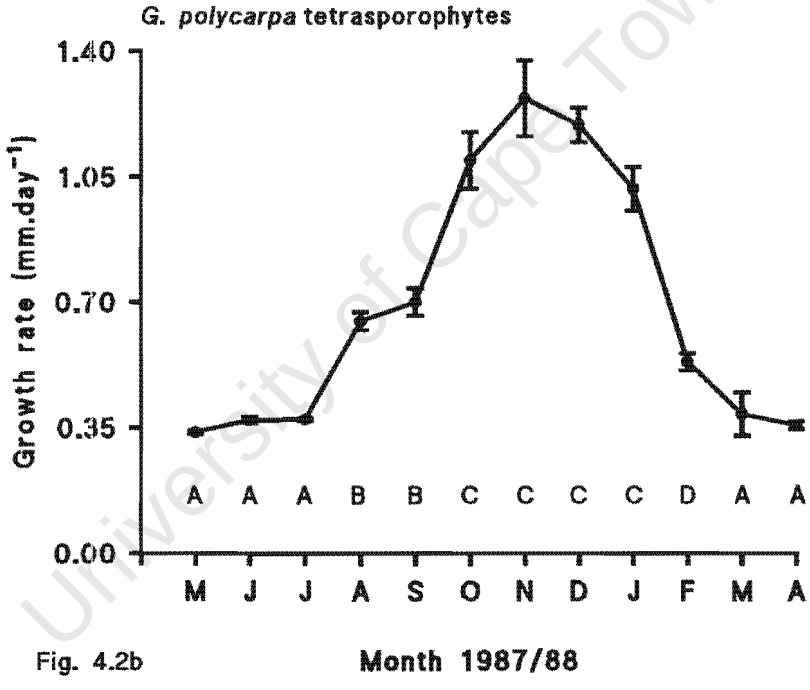


Fig. 4.2b

Figure 4.2 Mean monthly growth rate of *Gigartina polycarpa*. Rates with the same letter are not significantly different. a) female gametophytes $F_{0.05(2),11,48} = 63.53 > 2.29$; b) tetrasporophytes $F_{0.05(2),11,43} = 92.21 > 2.29$. Standard errors indicated.

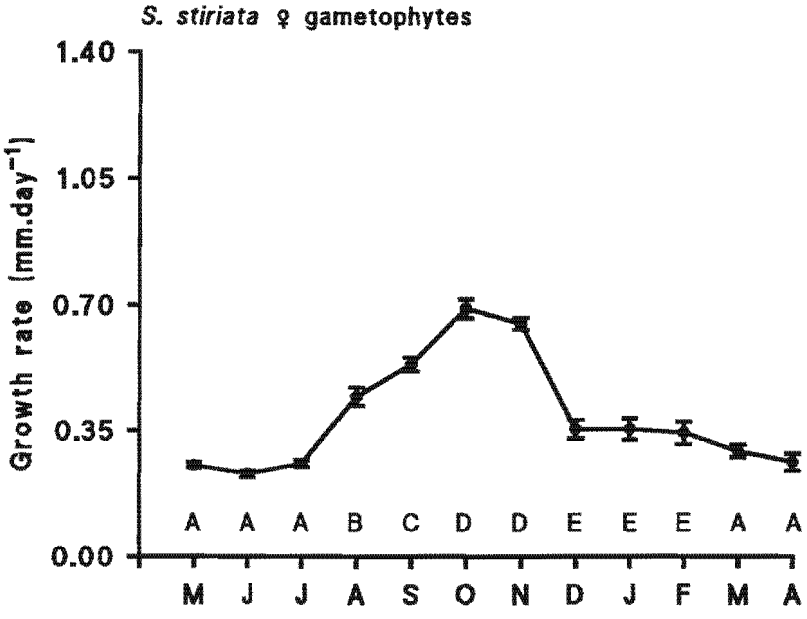


Fig. 4.3a

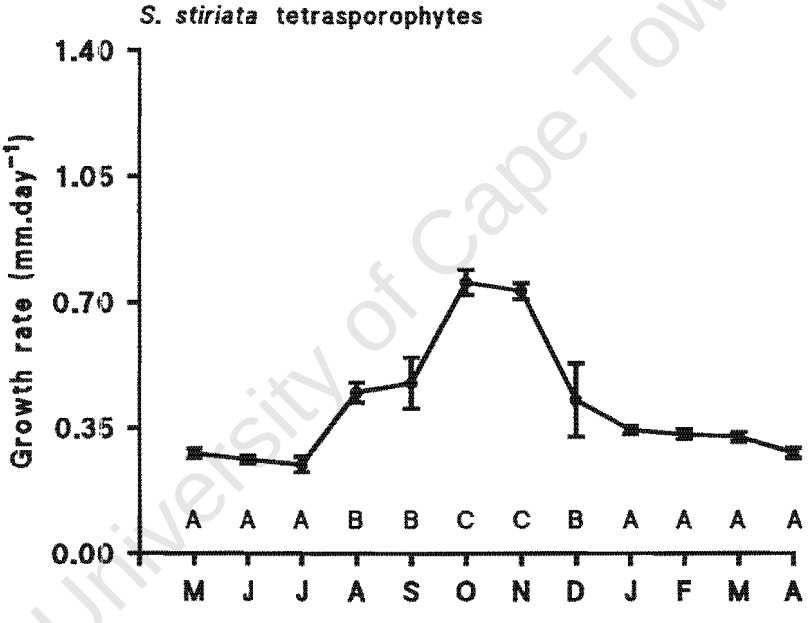


Fig. 4.3b

Figure 4.3 Mean monthly growth rate of *S. stiriata*. Rates with the same letter are not significantly different. a) female gametophytes $F_{0.05(2),11,48} = 92.13 > 2.29$; b) tetrasporophytes $F_{0.05(2),11,48} = 33.14 > 2.29$. Standard errors indicated.

growth rate than either *G. polycarpa* female gametophytes, *Sarcothalia stiriata* gametophytes or *S. stiriata* tetrasporophytes, largely because of a much greater growth rate in *G. polycarpa* tetrasporophytes during their season of maximum growth. Mean annual growth rates of the other three entities were not significantly different.

Species/life-history phase	Growth rate (mm.day^{-1})	SNK Grouping
G. polycarpa ♀ gametophyte	0.33	B
G. polycarpa tetrasporophyte	0.69	A
S. stiriata ♀ gametophyte	0.39	B
S. stiriata tetrasporophyte	0.41	B

Table 4.1 Mean annual growth rates of *Gigartina polycarpa* and *Sarcothalia stiriata* life-history phases. Student-Newman-Keuls test groups with the same letter are not significantly different ANOVA $F_{0.05(2),3,236} = 24.31 > 3.18$.

4.3.3 Growth rate of transplanted plants

The growth rates of transplanted (more exposed) plants of female gametophytes of *Gigartina polycarpa* (fig. 4.4a) during winter (June-August, 0.13mm.day^{-1}) were not significantly different from growth rates measured in non-transplanted (less exposed) individuals (0.13mm.day^{-1}). However, during late spring and early summer (October-Dec, 0.76mm.day^{-1}) growth rates of transplanted plants of female gametophytes of *G. polycarpa* (fig. 4.4a) were significantly greater than the growth rates of non-transplanted individuals (0.62mm.day^{-1}). As in female gametophytes, the growth rates of transplanted (more exposed) *G. polycarpa* tetrasporophytes (fig. 4.4b) during winter (0.46mm.day^{-1}) were also not significantly different from the growth rates measured in non-transplanted (less exposed) individuals (0.47mm.day^{-1}). However, in reverse of the situation found in female gametophytes, growth rates of transplanted *G. polycarpa* tetrasporophytes (fig. 4.4b) during late spring and summer (0.92mm.day^{-1}) were significantly less than the growth rates of non-transplanted individuals (1.19mm.day^{-1}).

As in *Gigartina polycarpa* female gametophytes, the growth rates of transplanted (more exposed) plants of *Sarcothalia stiriata* female gametophytes (fig. 4.5a) during winter (0.29mm.day^{-1}) were not significantly different from the growth rates measured in non-transplanted (less exposed) individuals (0.31mm.day^{-1}). However, in reverse of the situation

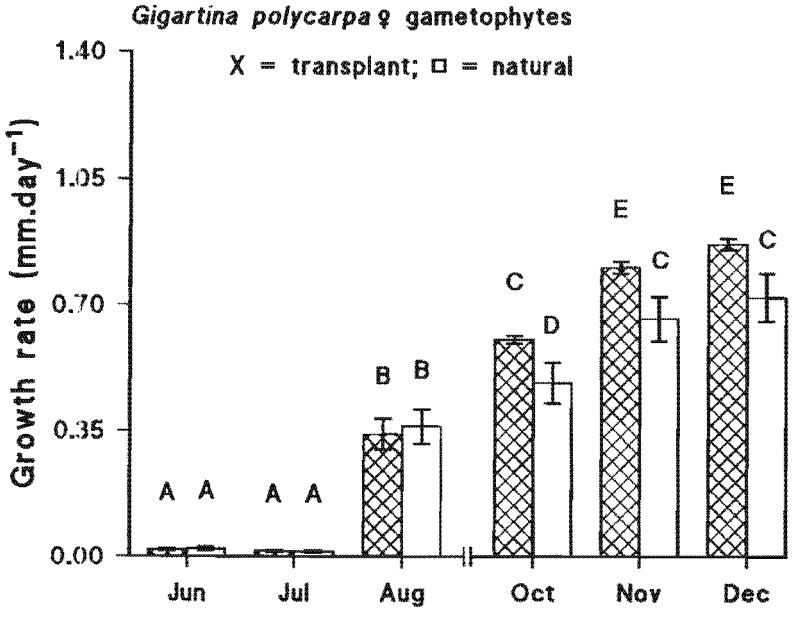


Fig. 4.4a **1987/88 natural; 1989/90 transplant**

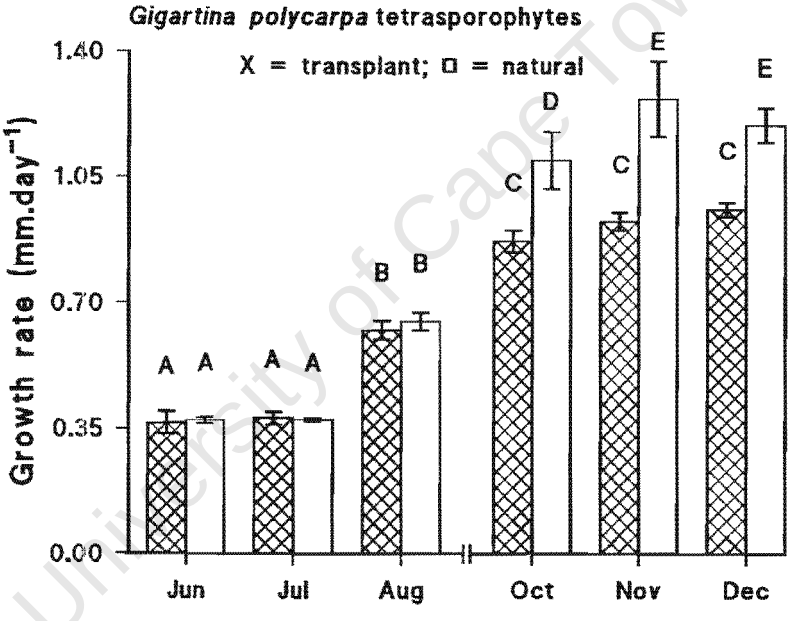


Fig. 4.4b **1987/88 natural; 1989/90 transplant**

Figure 4.4 Winter (June-August) and spring/summer (October-December) mean monthly growth rates of transplanted and non-transplanted individuals of *Gigartina polycarpa*. Bars with the same letter are not significantly different (no comparison between summer and winter statistics): a) female gametophytes - winter $F_{0.05(2),5,24} = 75.74 > 3.15$, summer $F_{0.05(2),5,24} = 16.90 > 3.15$; b) tetrasporophytes - winter $F_{0.05(2),5,24} = 78.30 > 3.15$, summer $F_{0.05(2),5,24} = 12.59 > 3.15$. Standard errors indicated.

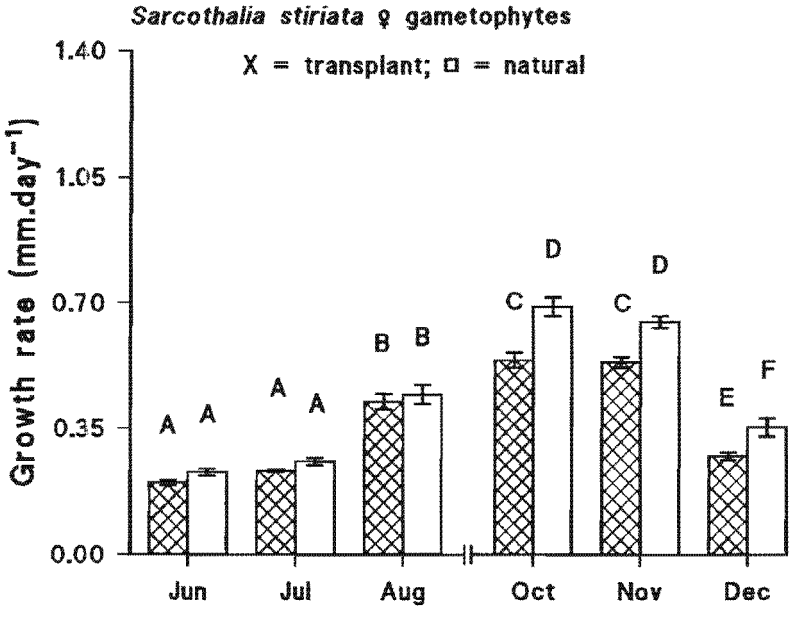


Fig. 4.5a **1987/88 natural; 1989/90 transplant**

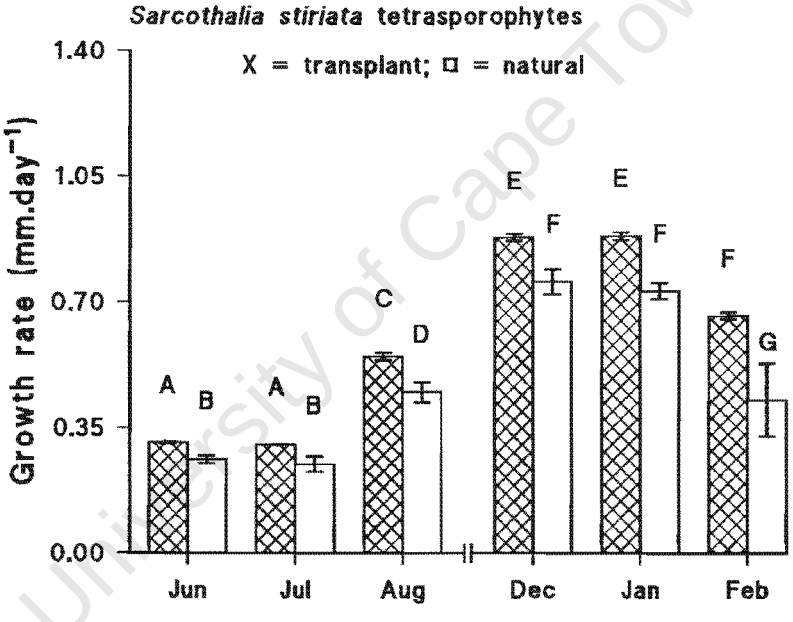


Fig. 4.5b **1987/88 natural; 1989/90 transplant**

Figure 4.5 Winter (June-August) and spring/summer (October-December) mean monthly growth rates of transplanted and non-transplanted individuals of *Sarcothalia stiriata*. Bars with the same letter are not significantly different (no comparison between summer and winter statistics): a) female gametophytes - winter $F_{0.05(2),5,24} = 96.45 > 3.15$, summer $F_{0.05(2),5,24} = 106.39 > 3.15$; b) tetrasporophytes - winter $F_{0.05(2),5,24} = 111.80 > 3.15$, summer $F_{0.05(2),5,24} = 24.67 > 3.15$. Standard errors indicated.

found in *G. polycarpa* female gametophytes, late spring and summer growth rates of transplanted female gametophytes of *S. stiriata* (fig. 4.5a) were significantly less ($0.45mm.day^{-1}$) than the growth rates of non-transplanted individuals ($0.57mm.day^{-1}$). The growth rates of transplanted (less exposed) *S. stiriata* tetrasporophytes (fig. 4.5b) during winter ($0.39mm.day^{-1}$) were significantly greater than the corresponding growth rates measured in non-transplanted (more exposed) individuals ($0.32mm.day^{-1}$). In late spring and summer growth rates of transplanted plants ($0.81mm.day^{-1}$) of *S. stiriata* tetrasporophytes (fig. 4.5b) were also significantly greater than the growth rates of non-transplanted individuals ($0.64mm.day^{-1}$).

4.3.4 Thallus drag

Measured drag coefficients in *Gigartina polycarpa* (fig. 4.6) were highest at the lowest measured water velocity ($1m.s^{-1}$, C_d=0.081-0.142) and decreased with increasing velocity ($2.6m.s^{-1}$, C_d=0.034-0.054). The drag coefficients of *G. polycarpa* tetrasporophytes measured at different water velocities (fig. 4.6c) were significantly less than the drag coefficients measured in male (fig. 4.6a) or female (fig. 4.6b) gametophytes. There was no significant difference in the drag coefficients at the same water velocities between male and female gametophytes of *G. polycarpa*.

Like *Gigartina polycarpa*, measured drag coefficients of *Sarcothalia stiriata* (fig. 4.7) were highest at the lowest measured water velocity ($1m.s^{-1}$, C_d=0.085-0.154) and decreased with increasing velocity ($2.6m.s^{-1}$, C_d=0.041-0.074). Similarly, the drag coefficients of *S. stiriata* tetrasporophytes measured at different water velocities (fig. 4.7c) were significantly less than the drag coefficients measured in male (fig. 4.7a) or female (fig. 4.7b) gametophytes. There was also no significant difference in the drag coefficients at the same water velocities between male and female gametophytes of *S. stiriata*.

There was no significant difference in the drag coefficients measured between gametophytes of the two species, nor was there any significant difference in the drag coefficients measured between tetrasporophytes of the two species.

Because of the limitation of the maximum velocity in the experimental flow tube to $2.6m.s^{-1}$, plant responses at higher velocities were explored by extrapolation. Since r^2 values of the regression were low (figs 4.8 and 4.9), the extrapolation must be regarded as tentative. At $15m.s^{-1}$, the predicted C_d of male gametophytes (fig. 4.8a) and tetrasporophytes (fig. 4.8c)

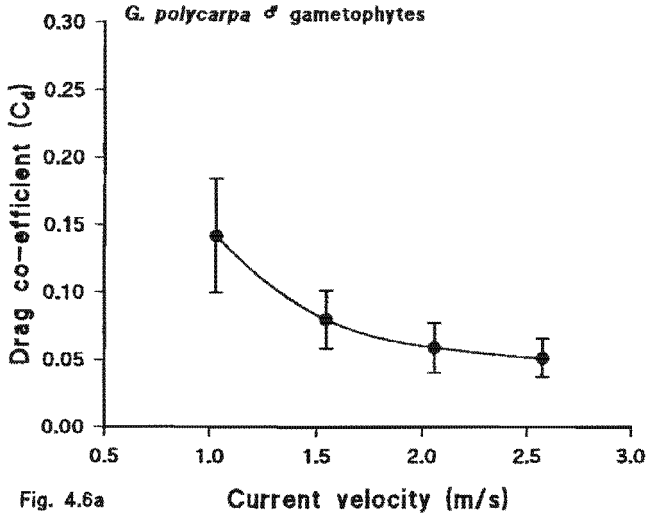


Fig. 4.6a

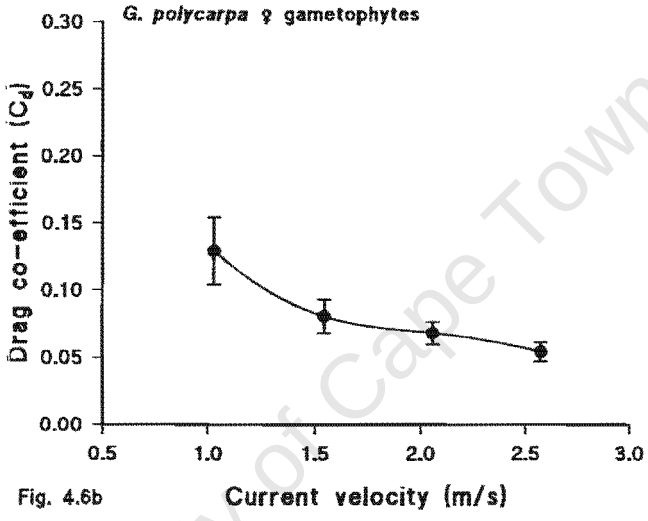


Fig. 4.6b

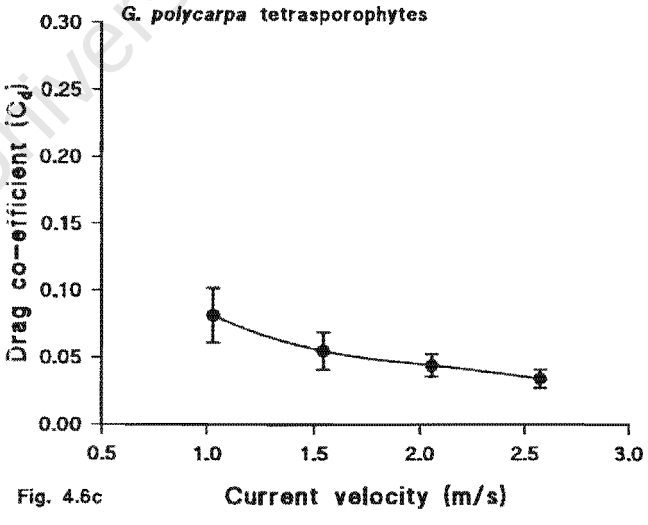


Fig. 4.6c

Figure 4.6 Measured drag coefficient versus current velocity of *Gigartina polycarpa* a) male gametophytes; b) female gametophytes; c) tetrasporophytes. 95% confidence limits indicated.

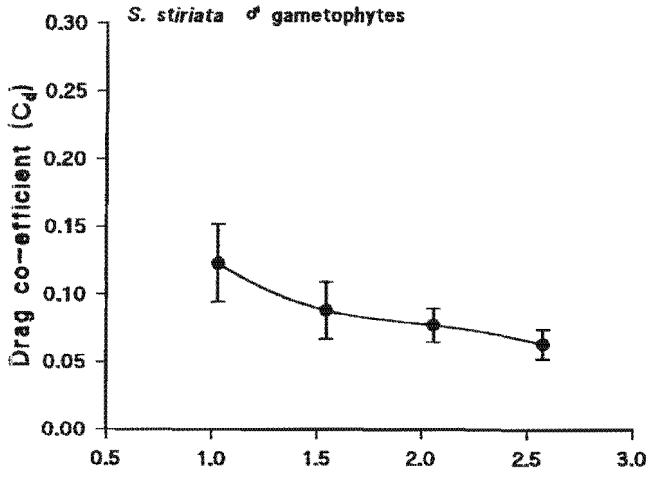


Fig. 4.7a

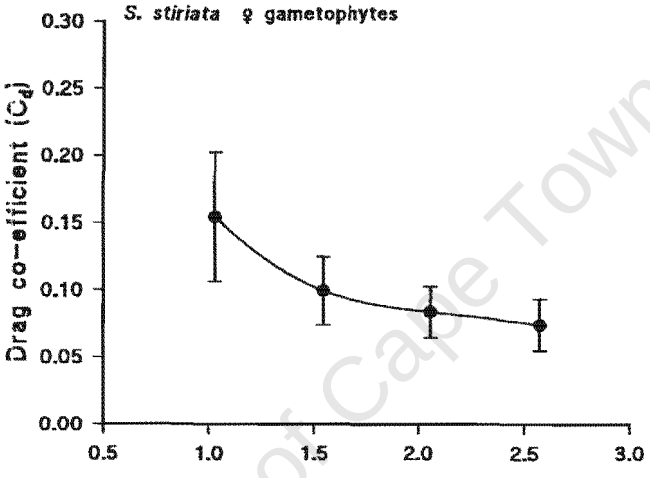


Fig. 4.7b

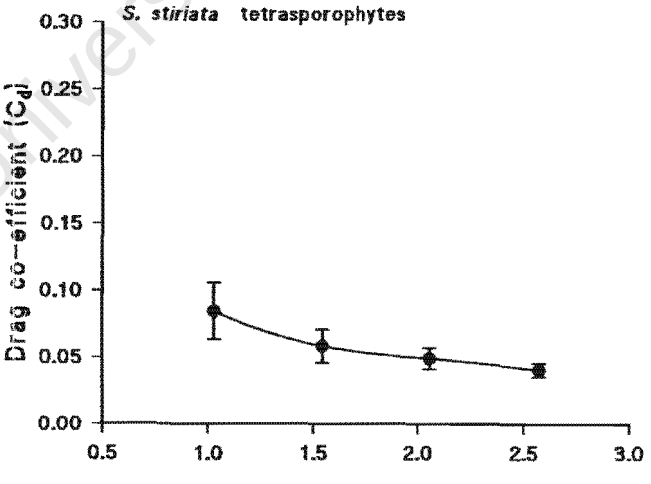


Fig. 4.7c

Figure 4.7 Measured drag coefficient versus current velocity of *Sarcothalia stiriata* a) male gametophytes; b) female gametophytes; c) tetrasporophytes. 95% confidence limits indicated.

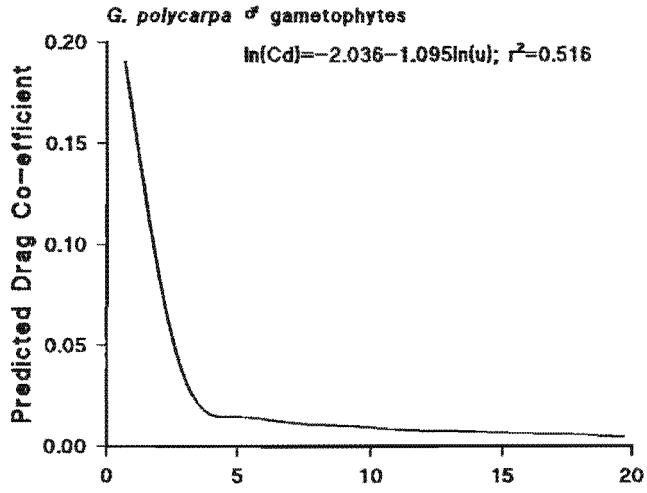


Fig. 4.8a

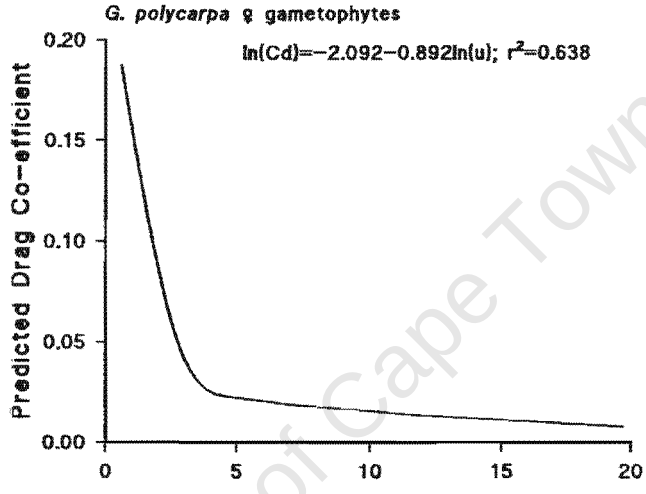


Fig. 4.8b

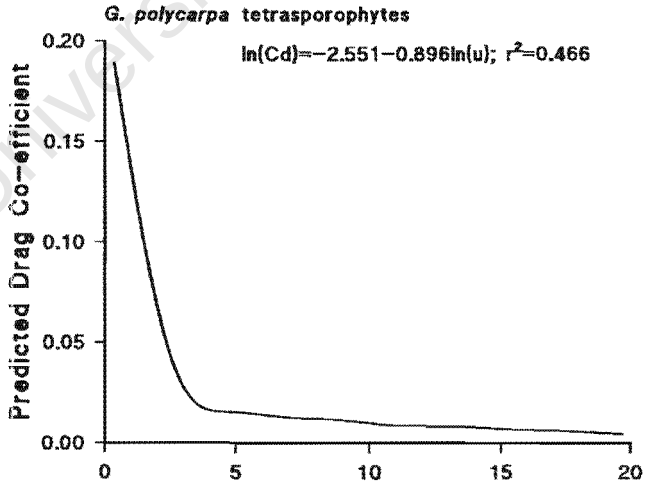


Fig. 4.8c

Figure 4.8 Predicted drag coefficient versus current velocity of *Gigartina polycarpa* a) male gametophytes; b) female gametophytes; c) tetrasporophytes.

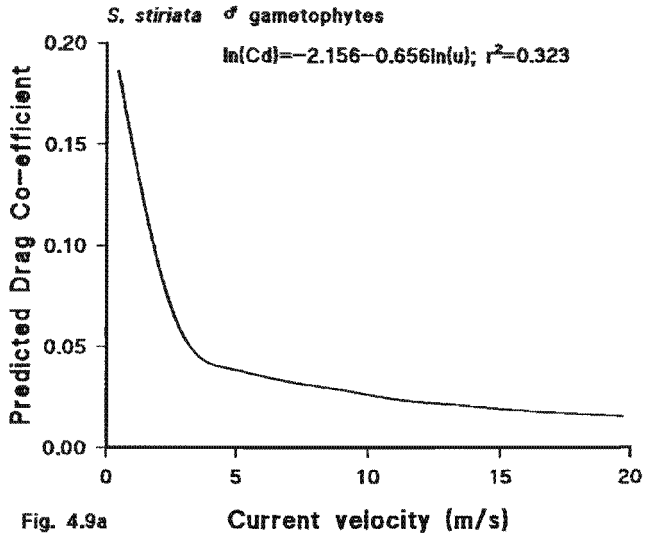


Fig. 4.9a

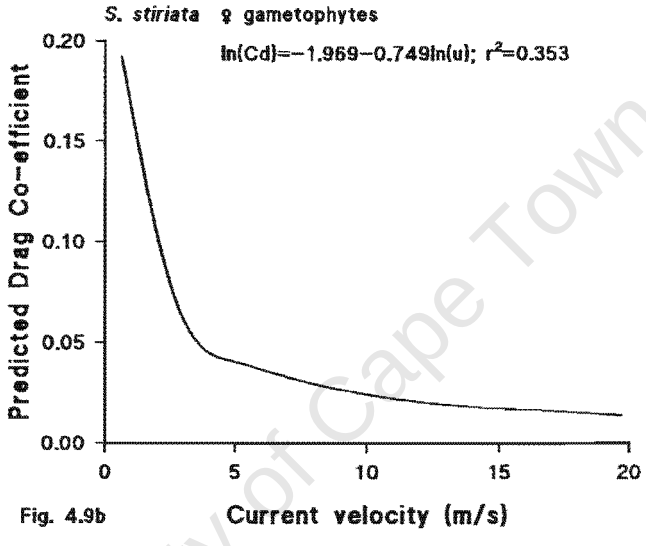


Fig. 4.9b

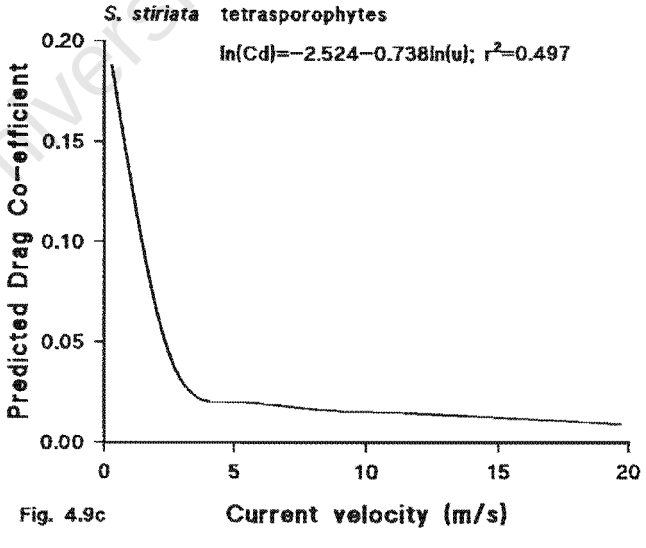


Fig. 4.9c

Figure 4.9 Predicted drag coefficient versus current velocity of *Sarcothalia stiriata* a) male gametophytes; b) female gametophytes; c) tetrasporophytes.

of *Gigartina polycarpa* declined to 0.007, whereas female gametophytes had a slightly greater predicted C_d of 0.011. At 15m.s^{-1}, the predicted C_d of gametophytes of *Sarcothalia stiriata* was greater than for *G. polycarpa*, with predicted C_d values of 0.020 and 0.018 for male and female gametophytes respectively (fig. 4.9a,b). The predicted C_d value of 0.011 for tetrasporophytes (fig. 4.9c) of *S. stiriata* at 15m.s^{-1} was also greater than that predicted for tetrasporophytes of *G. polycarpa*, and was on a par with gametophytes of the latter.

Measurements of actual thallus drag (N) showed that, at a low velocity (1.0m.s^{-1}), the drag generated by large (high volume) male and female gametophytes and tetrasporophytes of *Gigartina polycarpa* (fig. 4.10) was similar. At 2.6m.s^{-1}, the drag generated by larger plants of all three life-history phases was also similar. However, the ratio between the linear slope fitted to measured thallus drag at 1.0m.s^{-1} and the linear slope fitted to measured thallus drag at 2.6m.s^{-1} for *G. polycarpa* (table 4.2) shows that the relative increase in drag was greatest in male gametophytes and tetrasporophytes and least in female gametophytes. In *Sarcothalia stiriata*, the drag generated by large (high volume) female gametophytes was greater than that generated by male gametophytes and tetrasporophytes, which were similar (fig. 4.11).

Species/life-history phase	Thallus drag slope ratio @2.6:1.0m.s^{-1}
G. polycarpa ♂ gametophyte	2.63
G. polycarpa ♀ gametophyte	1.95
G. polycarpa tetrasporophyte	2.69
S. stiriata ♂ gametophyte	2.33
S. stiriata ♀ gametophyte	2.06
S. stiriata tetrasporophyte	2.28

Table 4.2 Ratio of the linearslope fitted to measured thallus drag at 1.0m.s^{-1} to the linear slope fitted to measured thallus drag at 2.6m.s^{-1} for life-history phases of *Gigartina polycarpa* and *Sarcothalia stiriata* (figs 4.10 and 4.11).

This pattern was repeated at 2.6m.s^{-1}. However, the ratio of the linear slope fitted to measured thallus drag at 1.0m.s^{-1} to the linear slope fitted to measured thallus drag at 2.6m.s^{-1} for *S. stiriata* (table 4.2) shows that the relative increase in drag was least in female gametophytes and similar in tetrasporophytes and male gametophytes.

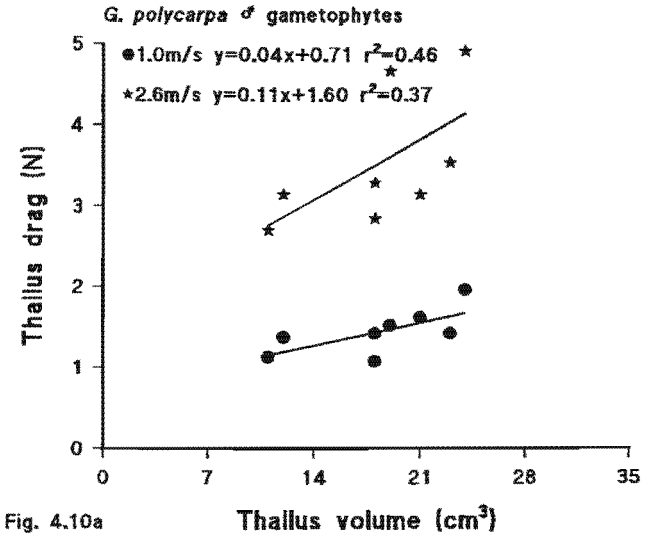


Fig. 4.10a

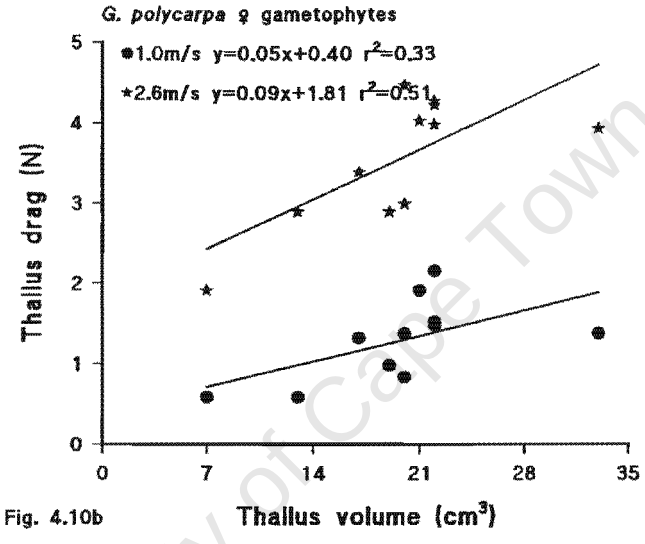


Fig. 4.10b

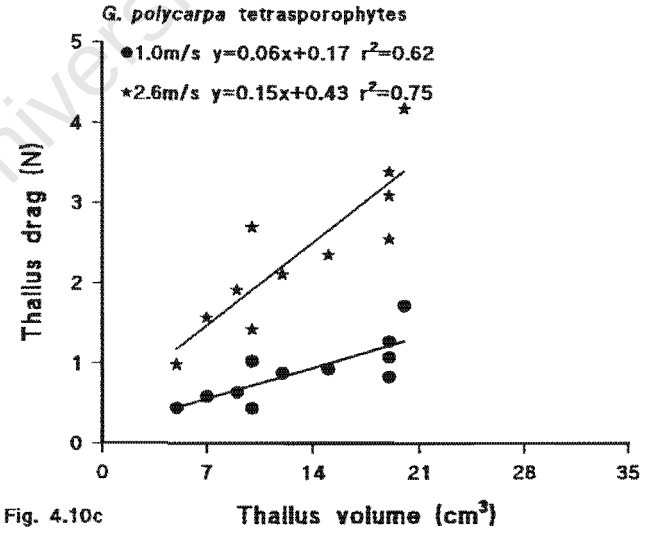


Fig. 4.10c

Figure 4.10 Measured thallus drag versus thallus volume of *Gigartina polycarpa* at current velocities of 1.0 and 2.6m.s^{-1}: a) male gametophytes; b) female gametophytes; c) tetrasporophytes. Fitted linear equation indicated.

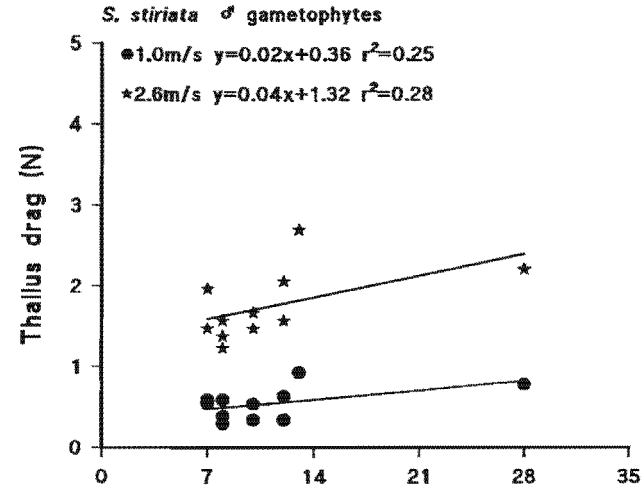


Fig. 4.11a

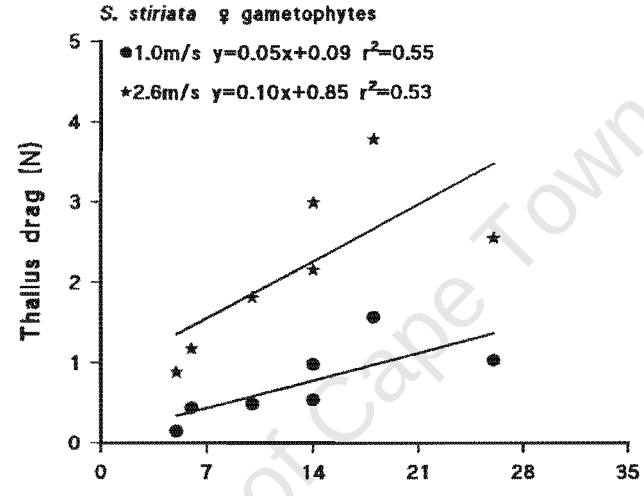


Fig. 4.11b

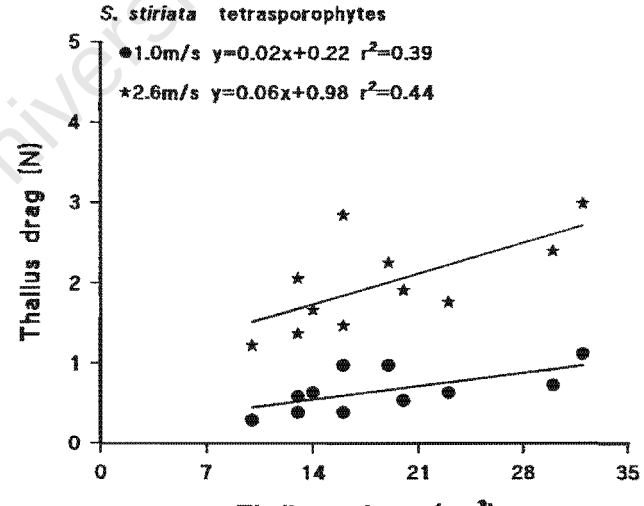


Fig. 4.11c

Figure 4.11 Measured thallus drag versus thallus volume of *Sarcothalia stiriata* at current velocities of 1.0 and 2.6m.s^{-1}: a) male gametophytes; b) female gametophytes; c) tetrasporophytes. Fitted linear equation indicated.

4.4 DISCUSSION

The mean annual growth rate of female gametophytes (0.33mm.day^{-1}) of *Gigartina polycarpa* and female gametophytes (0.39mm.day^{-1}) and tetrasporophytes (0.41mm.day^{-1}) of *Sarcothalia stiriata* were similar to that observed by Carter and Anderson (1986) in South African *Gelidium pristoides* (*ca.* 0.25mm.day^{-1}, bisporophytic and gametophytic phases). The maximal growth rate of *G. polycarpa* tetrasporophytes (1.27mm.day^{-1}) was substantially greater than that observed for *G. pristoides* (*ca.* 0.42mm.day^{-1}). The maximal rates measured in *G. polycarpa* female gametophytes (0.74mm.day^{-1}), *S. stiriata* female gametophytes (0.69mm.day^{-1}) and *S. stiriata* tetrasporophytes (0.76mm.day^{-1}) were also greater than in *G. pristoides*, but not to the same degree. Minimum growth rates of the carrageenophytic species were comparable to that observed in *G. pristoides*. Maximum growth rates in spring or summer have been recorded for many eulittoral carrageenophytes (*e.g.Hypnea musciformis* - Rao, 1970; *Mastocarpus stellatus* - Mathieson and Burns, 1971; *Chondrus crispus*- Mathieson and Burns, 1975; *Hypnea spicifera* - van Zyl, 1993). These maxima were generally forced by changes in environmental factors such as increased irradiance and nutrient availability or changes in seawater temperature, but were not predictably the same in all cases. Maximal growth in *H. spicifera* was ascribed to increasing irradiance and temperature (van Zyl, 1993). The enhanced growth rates observed in *S. stiriata* and *G. polycarpa* during spring and summer, respectively, were most likely the result of increased irradiance and day-length as well as increased nutrient availability resulting from the seasonal upwelling of nutrient-rich waters during this period. Seasonal fluctuations in growth rates of *G. polycarpa* correspond closely with seasonal changes in biomass measurements. In *S. stiriata*, seasonal biomass changes lag about one month behind seasonal fluctuations in growth rates. These seasonal growth rates may also be endogenous, a circannual rhythm synchronized by daylength being most likely, such a rhythm having been demonstrated in the kelp *Pterygophora californica* Ruprecht (Lüning, 1991).

Summer growth rates of gametophytes of *Gigartina polycarpa* were enhanced when they were transplanted to the more exposed environment of the boulders. Enhanced growth rates of transplanted individuals have been reported for *Eucheuma isiforme*, this being attributed to more favourable environmental parameters (Dawes *et al.* 1974a). Similarly, it is possible that increased growth in transplanted gametophytes of *G. polycarpa* was the result of increased

nutrient availability resulting from increased hydrodynamic force, this being sufficient to enhance nutrient availability through the reduction of the velocity boundary layer effects (Denny, 1988), but not large enough to inhibit growth through physical damage (extremely high water velocities are only rarely experienced along this coast during summer). This hypothesis is however, not supported by the reduced growth rates shown by summer transplants of tetrasporophytes, unless this can be attributed to other causes. Other causes may be that tetrasporophytes are more susceptible to wave action, or that they require more nutrients. However, given the lower C_d values obtained for tetrasporophytes compared with gametophytes, the former is an unlikely explanation. The latter explanation is also unlikely, since the thalli of gametophytes are substantially thicker than those of tetrasporophytes and are therefore more likely to require a greater nutrient concentration to achieve the same growth rate, the presence of numerous papillae on the thallus resulting in a thicker boundary layer around the plant thallus which, in turn, would decrease nutrient availability. Recent work by Hurd and Stevens (1997) has shown that the transition from a laminar to turbulent boundary layer can occur at velocities as low as 2.5cm.s^{-1} in multiple-bladed seaweeds, which makes the nutrient limitation of thalli unlikely. Similar erratic growth patterns to those noted here have been reported for transplanted individuals of *Eucheuma nudum* (Dawes *et al.* 1974a).

The similar growth rates of transplanted and non-transplanted individuals of both female gametophytes and tetrasporophytes of *Gigartina polycarpa* during winter indicates that hydrodynamic forces play a dominant role in determining growth - mechanical wave-induced forces dominating other environmental factors and resulting in physical loss of plant material from plant thalli.

Enhanced growth rates as a result of a more favourable environment is a more plausible explanation in the case of *Sarcothalia stiriata*. Summer growth responses of transplanted individuals of *S. stiriata* displayed an opposite pattern to *Gigartina polycarpa*, even though the corresponding measured drag coefficients for female gametophytes and tetrasporophyes of the two species were almost identical. Summer growth rates of female gametophytes diminished when they were transplanted to the more wave exposed environment of the boulders, possibly indicating that even a relatively small increase in hydrodynamic force was sufficient to inhibit growth. Conversely, summer growth rates of *S. stiriata* tetrasporophytes increased when transplanted to the less exposed ledge, presumably because of less wave action

and more light availability (no longer mostly in shadow). As in *G. polycarpa*, the similar growth rates of transplanted and non-transplanted individuals of female gametophytes of *S. stiriata* during winter indicates that hydrodynamic forces play the predominant role in determining growth during this period - mechanical wave-induced forces dominating other environmental factors and resulting in physical loss of plant material from plant thalli. Winter transplants of *S. stiriata* tetrasporophytes to the less exposed ledge display enhanced growth rates, which may indicate that tetrasporophytes of this species are more adaptable to changes in wave action than gametophytes of either *S. stiriata* or *G. polycarpa*, the hydroynamic forces decreasing sufficiently at the ledge when compared to the boulders to decrease mechanical damage and enhance growth.

The decreasing C_d values indicate that streamlining of the thallus (or reconfiguration of the thallus, *sensu* Gaylord *et al.* 1994) as water velocity increases is taking place in all life-history phases of both *Gigartina polycarpa* and *Sarcothalia stiriata*, tetrasporophytes of both species displaying substantially lower C_d values than gametophytes, the flexing of the plant thallus reducing the plant area presented to the water flow, resulting in greatly diminished drag force and acceleration reaction. Furthermore, as the thallus flexes, it can be bent into the slower-moving surface boundary layer where forces are further reduced (Koehl, 1986). This is especially advantageous to juvenile plants prior to their becoming more firmly attached to the substratum by the development of the holdfast. For example, streamlining was shown to be the major mechanism for reduction of drag forces in *Mastocarpus papillatus* (Carrington, 1990).

The generally linear decrease in the natural logarithm of C_d with an increase in the natural logarithm of velocity allows for a tentative extrapolation of predicted C_d at water velocities approaching maxima measured in wave stressed environments (*ca.* $15 m.s^{-1}$). These extrapolations of predicted C_d indicate that, at higher velocities, all life-history phases of both *Gigartina polycarpa* and *Sarcothalia stiriata* have drag coefficients (predicted $C_d < 0.1$; Hoerner, 1965) typical of moderately streamlined objects. The advantages of streamlining are the same for *G. polycarpa* and *S. stiriata* as for *Mastocarpus papillatus*. However, the reduction in drag coefficient for these two species is far greater than for *M. papillatus* (especially at extreme velocities; $> 10 m.s^{-1}$) and is sufficient to remove any drag-imposed practical limit to size for these two species (predicted C_d values much less than 0.1). Since the

growth rates of transplanted plants cannot be completely explained in terms of observed or predicted C_d values, it appears that drag alone is not the primary factor constraining thallus size in *G. polycarpa* and *S. stiriata*. Gaylord *et al.* (1994) showed that the inertia coefficient of the thallus was an important factor in constraining plant size in *Gigartina leptorhyncos*, the increased accelerational force imposed on the plant thallus as a result of large inertia coefficients substantially decreasing the probability of plant survival. Large inertia coefficients result from the complex foliose structure of the plant thallus, the interstices trapping water and effectively increasing the mass/volume relationship of the plant. In the absence of an effective and accurate empirical method of measuring algal inertia coefficients, a comparison of the drag/thallus volume relationships for the same individual thallus at two different flow rates will give an indication of algal inertia responses to accelerational force. In *G. polycarpa*, the ratio of the drag/volume slope at high and low velocities, as well as the slope of the drag/volume relationship itself, was smallest in female gametophytes (*cf.* male gametophytes and tetrasporophytes) and may, in conjunction with the factors previously mentioned, contribute to the enhanced summer growth response of this life-history phase when transplanted to the boulders. However, accelerational forces imposed during winter storms (*ca.* 1000-2000m.s^{-2}; Denny *et al.* 1985) are too great for small differences in algal inertia to contribute measurably to reducing the negative impact of the hydrodynamic environment, thus explaining the lack of winter differences in growth data in *G. polycarpa*.

In *Sarcothalia stiriata*, the ratio of the drag/volume slope at high and low velocities was similar for all three life history phases, indicating that the relative responses of the life history phases of this species to increased hydrodynamic forces should be similar. However, the comparative slope of the drag/volume relationship (at any velocity) shows that female gametophytes were more susceptible to accelerational forces than male gametophytes and tetrasporophytes, this conclusion being supported by their diminished growth rate after they were transplanted. In *S. stiriata*, it therefore appears that thallus morphology (expressed as the algal inertia coefficient) can play a role in determining plant responses to large fluctuations in wave exposure, this conclusion being supported by the diminished growth rate of female gametophytes and enhanced growth rate of tetrasporophytes after transplanting during winter - the former being due to increased hydrodynamic forces being greater than could be tolerated, the latter resulting from decreased accelerational forces falling within the tolerable limits of

this thallus form. The relative distribution of these two species on the shore is possibly a direct result of their differing hydrodynamic responses since the zones occupied by the two species are adjacent and to some extent intermingled, spores from either species are likely to settle in the zone most commonly occupied by the other.

The material properties of the thallus also contribute to its response to hydrodynamic stress. According to Koehl and Wainwright (1977), seaweeds have low strength, but are highly elastic. Thus, the high degree of flexibility and elasticity of macroalgae reduces the stresses of transient dynamic loads (Gaylord *et al.* 1994) and permits littoral seaweeds to survive the rapid pulses of water motion (Denny, 1987) which are characteristic of exposed rocky shores. Both *Gigartina polycarpa* and *Sarcothalia stiriata* are highly elastic, and this must contribute towards their ability to survive, albeit with reduced growth rates, the extreme accelerations experienced during winter storms. Also, *G. polycarpa* displays a wide variation in morphology, presumably as a response to suit hydrodynamic conditions. Jackelman and Bolton (1990) showed that photosynthetic rate of *G. polycarpa* is less at wave-exposed localities than semi-exposed or sheltered localities, and suggested that investment of energy in strengthening the structural components of the plant (presumably by the addition of more tissue, *i.e.* increasing cross sectional area) means that less is available for photosynthetic material. Jackelman and Bolton (1990) concluded that the response of *G. polycarpa* to varying degrees of wave exposure is manifested in its morphological, physiological and population characters. Large individuals with broadened thalli are common in sheltered bays (*e.g.* Maasbaai, see chapter 2) whilst smaller plants with extremely narrow fronds can be found on wave beaten shores (*e.g.* Smitswinkelbaai). This morphological plasticity will undoubtedly alter the critical inertia coefficient at which accelerational forces become limiting. Such morphological extremes are not found in *S. stiriata*, thus probably contributing to the narrower habitat range occupied by this species. Such plasticity of form must enhance the reproductive output of *G. polycarpa* by allowing the thallus to reach large sizes during favourable seasons when storms are uncommon, and must therefore contribute to the success (wide geographic distribution, wide range of habitats - Stegenga *et al.* 1997) of this species along the South African coast. *Sarcothalia stiriata* does not display such morphological plasticity, and this may contribute to the confining of this species to less environmentally diverse habitats. Other ecological factors may limit the distribution of *S. stiriata* (*e.g.* differential spore survival, selective herbivory,

competition and interspecific differences in holdfast attachment strength). Of these, differential spore survival after settlement is the more likely (see chapter 3), the observed dominance of the gametophyte phase in both *G. polycarpa* and *S. stiriata* indicates that although spore settlement and germination are equally successful in both phases, gametophytes have a much better chance of surviving to reproduction. Shaughnessy *et al.* (1996) also concluded that a similar selective process acting on sporelings after settlement is responsible for controlling the distribution of *Mazzaella splendens* on the wave exposed shores of British Columbia. It is likely that *G. polycarpa* and *S. stiriata* respond differently to such a selective process, and this is likely to be reflected in differences in habitat diversity. Interspecific competition and selective herbivory are unlikely explanations of wave-exposure distributions (Shaughnessy *et al.* 1996). Whilst differences in holdfast attachment were not measured, the prostrate holdfast is much more developed in gametophytes of *S. stiriata*, and may compensate for the greater coefficients of inertia produced by this life history phase. This, however, does not account for the difference in distributions of the two species as convincingly as morphological plasticity.

CHAPTER 5

EFFECT OF HARVEST METHOD AND HARVEST INTERVAL ON HARVEST YIELD AND REGENERATION AND COMMUNITY STRUCTURE OF *GIGARTINA POLYCARPA* AND *SARCOTHALIA STIRIATA*

5.1 INTRODUCTION

As a consequence of increasing commercial interest, South African seaweed resources are becoming more vulnerable to unplanned commercial harvesting. Raised expectations of artisanal fisherfolk following the award by the state of harvesting rights for marine resources to economically underprivileged communities has resulted in increasing pressure for new or underexploited resources to become commercialised. As currently underexploited resources, it can be expected that the South African carrageenophytes *Gigartina polycarpa* and *Sarcothalia stiriata* will become the subject of a harvesting application within the near future. Various authors have considered biological aspects of the most appropriate management strategies for the optimal utilization of seaweed resources (*e.g.* Carter and Simons, 1987; Nelson and Conroy, 1989; Foster and Barilotti, 1990; Santos, 1993; Vásquez and Westermeier, 1993; Avila *et al.* 1996). In order to successfully manage seaweed resources, specific information relating to the determination of a sustainable optimal harvest is required (Caddy and Fischer, 1984). Harvesting information should include specifically the rate of harvesting (optimal period between harvests) and the time of harvesting (optimal harvesting season for maximum regrowth). Ecological effects of seaweed harvesting are similar to those of natural disturbances in that they remove parts or all of a population and initiate succession (Foster and Barilotti, 1990). In comparison with anthropogenic harvesting, natural disturbances are more variable in severity and frequency. The interaction between these disturbances and the life-history strategies of affected species regulates the subsequent community structure through the process of succession (Sousa, 1984). Thus, the assessment of ecological impacts of harvesting on populations and communities would be incomplete without information regarding changes in community structure in response to disturbance. Acquistion of such information can therefore be regarded as essential in ensuring the long-term sustainable economic utilization of Western Cape carrageenophytes. At present, there are no data available

to devise and implement field harvesting practices for *G. polycarpa* and *S. stiriata*. Most studies of these species have focused on taxonomic problems (e.g Hommersand *et al.* 1993,1994), and whilst there are many studies on the nature of phycocolloid properties within the Gigartinaceae, few authors (*e.g.* Santelices and Norambuena (1987) (*Iridaea laminarioides*); Santelices *et al.* (1989) (*Gymnogongrus furcellatus* (C.Agardh) J.Agardh); van Zyl (1993) (*Hypnea spicifera*)) have considered the implications of biological information in formulating harvesting strategies for carrageenophyte species.

In light of the above, the aim of this study was to obtain relevant biological information which would permit the derivation of a management strategy for *Gigartina polycarpa* and *Sarcothalia stiriata*. The following questions were addressed in order to obtain this information for the two species:

1. What is the optimal period between harvests?
2. What is the maximum sustainable harvest yield?
3. Are there any differences between harvesting methods?
4. What effect does harvesting have on reproductive capacity?
5. Are there changes in community structure in response to disturbance, and do they persist?

5.2 MATERIALS AND METHODS

5.2.1 Study site

As in the biomass, demography and wave exposure investigations (Chapters 2-4), this study was conducted on a semi-exposed ledge of Table Mountain Sandstone at Kommetjie on the west coast of the Cape Peninsula. However, in order to avoid disturbance of other field experiments by destructive sampling, the field experiments for this study were conducted at two nearby localities. Harvesting experiments were conducted on an adjacent ledge approximately 10m to east of the site used in the biomass, demography and growth experiments, whereas disturbance (clearance) experiments were performed on a ledge approximately 120m to the north-west. Both localities were occupied by mixed populations of both *Gigartina polycarpa* and *Sarcothalia stiriata*, with all the life-history phases being present.

5.2.2 Harvesting period and yield experiments

Four harvest intervals were chosen, namely one, three, four and six months between harvests.

For each harvest interval, four permanent experimental quadrats, each 1m x 1m, were marked out by tapping a stainless steel screw into the quadrat corners. Harvesting was conducted by hand plucking, the harvesting method commonly used for the South African intertidal agarophyte *Gelidium pristoides* (Anderson *et al.* 1989), whereby a substantial remnant portion of the plant biomass (*ca.* 20% - Carter and Simons, 1987) remains after harvesting. At each harvest, the fresh weight of harvested material of *Gigartina polycarpa* and *Sarcothalia stiriata* was recorded. In order to assess any effects on reproductive capacity, the fresh weight of thallus with visible fertile frond material present was also recorded by separating fertile and vegetative material by excision and weighing. The percentage contribution of the separate life-history phases of both species to the total harvest was also noted. In order to compare harvesting methods similar data were collected in four separate 1m x 1m permanent experimental plots which were harvested at monthly intervals by cutting, all upright foliose material being removed by excision with scissors approximately 5mm above the substratum, a remnant portion comprising mainly holdfast material remaining attached to the substratum.

5.2.3 Effects of disturbance on community structure

In permanent quadrats established at the second locality using the method described above, it was decided to investigate the response of community structure (species composition and abundance) of mixed communities dominated by populations of *Gigartina polycarpa* and *Sarcothalia stiriata* to three different disturbance treatments, three 1m x 1m quadrats per treatment:

1. Removal of all plant material and molluscan grazers (CP).
2. Removal of all plant material but not molluscan grazers (CU).
3. Removal of all grazing invertebrates, but no plant material (UP).
4. Removal of neither plant material nor molluscan grazers, control (CN).

In the treatment where plant material and molluscan grazers were removed, invasion of experimental quadrats from outside by these grazers was prevented by clearing a 15cm wide barrier and painting this with copper-based marine anti-fouling paint (International Cold Plastic), this experimental treatment being described as cleared, painted (CP). This barrier was repainted at bimonthly intervals and was found to be 100% effective in preventing invasion. The territorial limpet *Patella cochlear* was the most abundant grazer, *P. oculus* and the periwinkle *Oxystele sinensis* also being recorded. Where settlement of molluscan grazers took

place in the quadrats, these grazers were removed either physically by hand, or by killing them with a hammer and nail. Quadrats were inspected for grazer invasion/settlement when repainting. Plant material was removed once only at the start of the experiment by scraping the substratum with a steel abalone lever, the broad point of the blade being ideal for removal of holdfast material.

In order to equalize disturbance effects on the experimental treatments caused by the cleared barrier, a similar barrier was cleared around all experimental treatments (including the control). In experimental quadrats where plant material was removed, but not grazers, the barrier was not painted and molluscan grazers were not killed (cleared, unpainted treatment - CU). In experimental quadrats where grazers were removed but plant material left untouched, the barrier was painted at regular intervals (uncleared, painted - UP).

Since the objective was to assess recovery, those treatments which were cleared of plant material were cleared once only at the beginning of each experiment. In order to assess whether community responses differed seasonally, the experiment was conducted twice - once with an initial clearance in winter (July 1988) and once with an initial clearance in spring (November 1988). Thereafter, species composition and abundance (percentage cover) data were collected irregularly at two or three monthly intervals (October, November 1988, March, April and June 1989 - winter clearance; March, April, June, September and October 1989 - spring clearance). In order to minimize edge effects caused by the cleared barrier, abundance data were collected only within the innermost 75x75cm of each quadrat. To allow comparison between both treatments and sampling visits, data were analyzed using indirect ordination (Detrended Correspondence Analysis) on a temporally combined data set (all sampling visits combined) for each experiment (winter or spring clearance) in order to search for group structure, i.e. one ordination on the combined data from all the winter clearance quadrats, and another on the combined summer clearance data. Although only one ordination for each experiment was performed, these data are expressed in separate graphs for clarity. The DCA was performed using the DCA component of the computer program CANOCO (Ter Braak, 1986, 1987). Using this ordination method, the similarity of the floristic composition of the quadrats was examined. The analysis is expressed in two-dimensional graphical form, each point representing an experimental quadrat. Points close together represent floristic similarity (in species composition and abundance), whilst those further apart are more dissimilar.

5.3 RESULTS

5.3.1 Harvest yield of *Gigartina polycarpa*

Monthly harvest yields (g fresh wt.m^{-2}) of *Gigartina polycarpa* varied seasonally (fig. 5.1a), with a spring maximum (October, 612g.m^{-2}) and a winter minimum (June, 90g.m^{-2}). Average harvest yield (table 5.1) was 379g.m^{-2}.$harvest^{-1}$. The proportion of harvested material bearing reproductive structures showed no seasonal pattern, although a marked drop was observed during August and September 1989. The proportion (by weight) of harvested material bearing reproductive structures averaged 51% during the study period.

Yields of *Gigartina polycarpa* harvested at three-monthly intervals averaged 871g.m^{-2}.$harvest^{-1}$ (table 5.1), with a clear seasonal pattern (fig. 5.1b) of spring maximum (November, 1678g.m^{-2}) and autumn minimum (May, 249g.m^{-2}). The proportion of harvested material bearing reproductive structures also showed a seasonal pattern, with spring/summer maxima (February/November, 78%/79%) and autumn/winter minima (May/August, 51%/54%). For material harvested at three-monthly intervals, the proportion of harvested material bearing reproductive structures averaged 63% over the entire study period.

	Gigartina polycarpa			*Sarcothalia stiriata*			Total Gigartinaceae	
Period between harvests	Annual harvest yield	Yield per harvest	Percent fertile weight	Annual harvest yield	Yield per harvest	Percent fertile weight	Annual harvest yield	Yield per harvest
1 month	4548	379	51	19217	1601	41	23760	1930
3 months	3484	871	63	6460	1615	50	9944	2486
4 months	2190	730	67	9024	3008	52	11214	3738
6 months	1002	501	48	4038	2019	50	5040	2520

Table 5.1 Comparative annual harvest yield, harvest per unit effort and percentage fertile weight of *Gigartina polycarpa* and *Sarcothalia stiriata* both individualy and combined. (Fresh weight g.m^{-2}).

For *Gigartina polycarpa* harvested at four-monthly intervals an average yield of 730g.m^{-2}.$harvest^{-1}$ was recorded (table 5.1), with a seasonal pattern (fig. 5.1c) of summer maximum (December, 1181g.m^{-2}). and winter minium (August, 196g.m^{-2}). The proportion of harvested material bearing reproductive structures also showed a seasonal pattern, with summer/autumn maxima (December/April, 73%/74%) and a winter minimum (August, 53%). The proportion

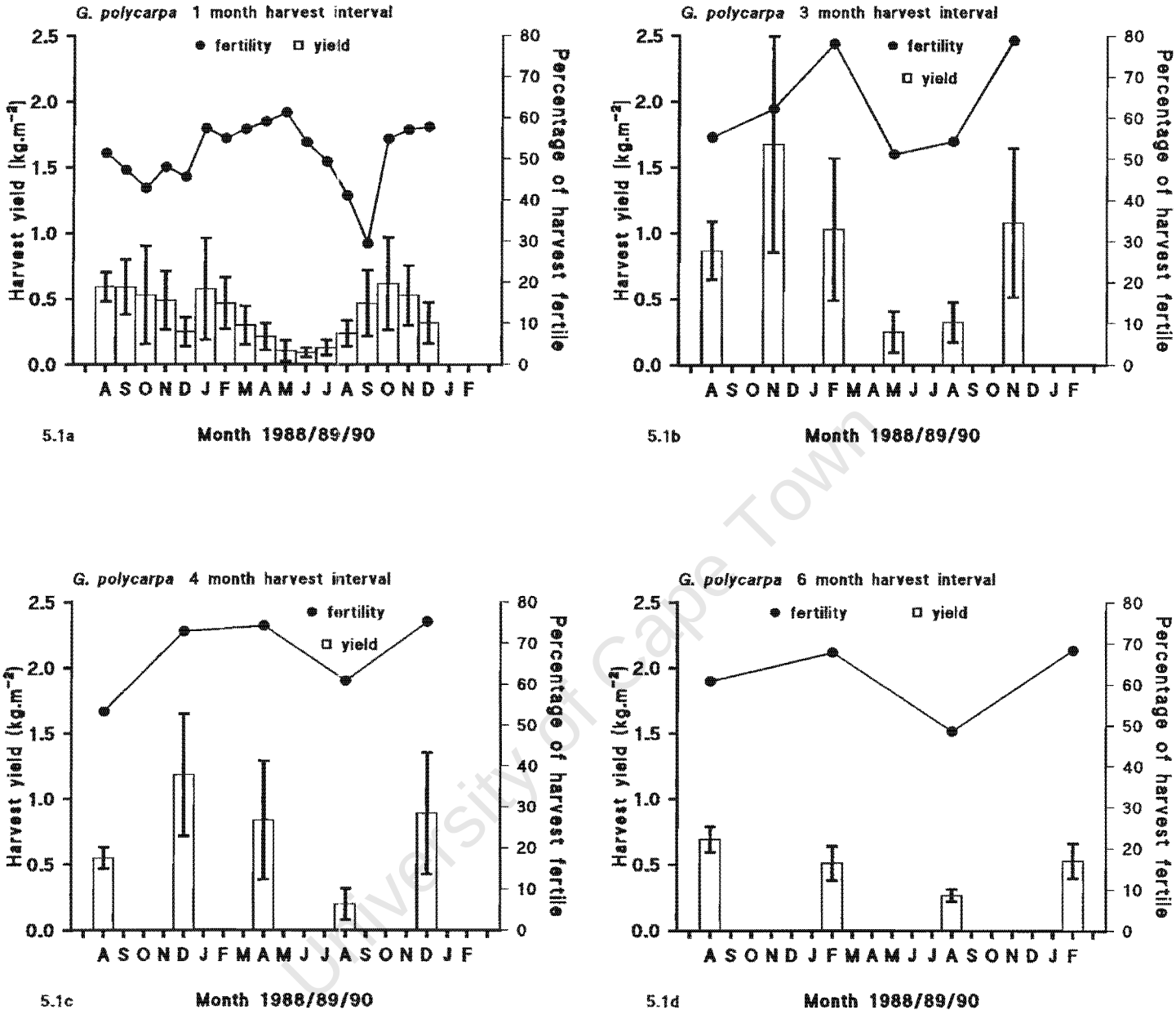


Figure 5.1 Harvest yield (fresh weight) and percentage of harvested weight bearing reproductive structures of *Gigartina polycarpa* at different harvesting intervals: a) 1 month; b) 3 months; c) 4 months; d) 6 months. Standard errors indicated.

of harvested material bearing reproductive structures averaged 67% over the entire study period for this harvesting regime.

Yields of *Gigartina polycarpa* harvested at six-monthly intervals averaged 501g.m^{-2}.$harvest^{-1}$ (table 5.1). No strong seasonal pattern of maximum harvest yield was evident (fig. 5.1d). However, a reduced winter harvest yield (August, 267g.m^{-2}) was recorded.This lack of a strong seasonal trend was also reflected in the proportion of harvested material bearing reproductive structures, the proportion of harvested material bearing reproductive structures averaged 61% over the entire study period and displayed a reduction to 48% during winter (August).

Maximum annual yield of *Gigartina polycarpa* was obtained if harvesting took place at monthly intervals (table 5.1). However, maximum harvest efficiency (yield per harvest) was achieved if harvests occurred at three-monthly intervals, whilst harvesting at four-monthly intervals had the least effect on reproductive capacity.

5.3.2 Harvest yield of *Sarcothalia stiriata*

Monthly harvest yields (g fresh wt.m^{-2}) of *Sarcothalia stiriata* showed a seasonal pattern (fig. 5.2a). Maximum harvest yield was obtained in summer (January, 2551g.m^{-2}) and the minimum in autumn/winter (May/June, 772/827g.m^{-2}), although a high biomass was also recorded in August 1988 (but not repeated the following year). Average monthly harvest yield (table 5.1) was 1601g.m^{-2}.$harvest^{-1}$. The proportion of harvested material bearing reproductive structures showed no seasonal pattern, but did show a gradual overall decline during the study period. A drop (as observed in *G. polycarpa*) was noticeable during August and September 1989, but not to the same degree. For material harvested at monthly intervals, the proportion of harvested material bearing reproductive structures averaged 41% over the entire study period.

Yields of *Sarcothalia stiriata* harvested at three-monthly intervals averaged 1615g.m^{-2}.$harvest^{-1}$ (table 5.1). No significant seasonal pattern was apparent. Maximum harvest was obtained during winter (August 1988, 2915g.m^{-2}), although this pattern was not repeated the following year (fig. 5.2b). The minimum harvest was recorded during autumn (May 1989, 736g.m^{-2}). The proportion of harvested material bearing reproductive structures showed no clear seasonal pattern (average 50% for the duration of the study), but a small autumn decline during May (45%) was evident.

For *Sarcothalia stiriata* harvested at four-monthly intervals (table 5.1), yields averaged

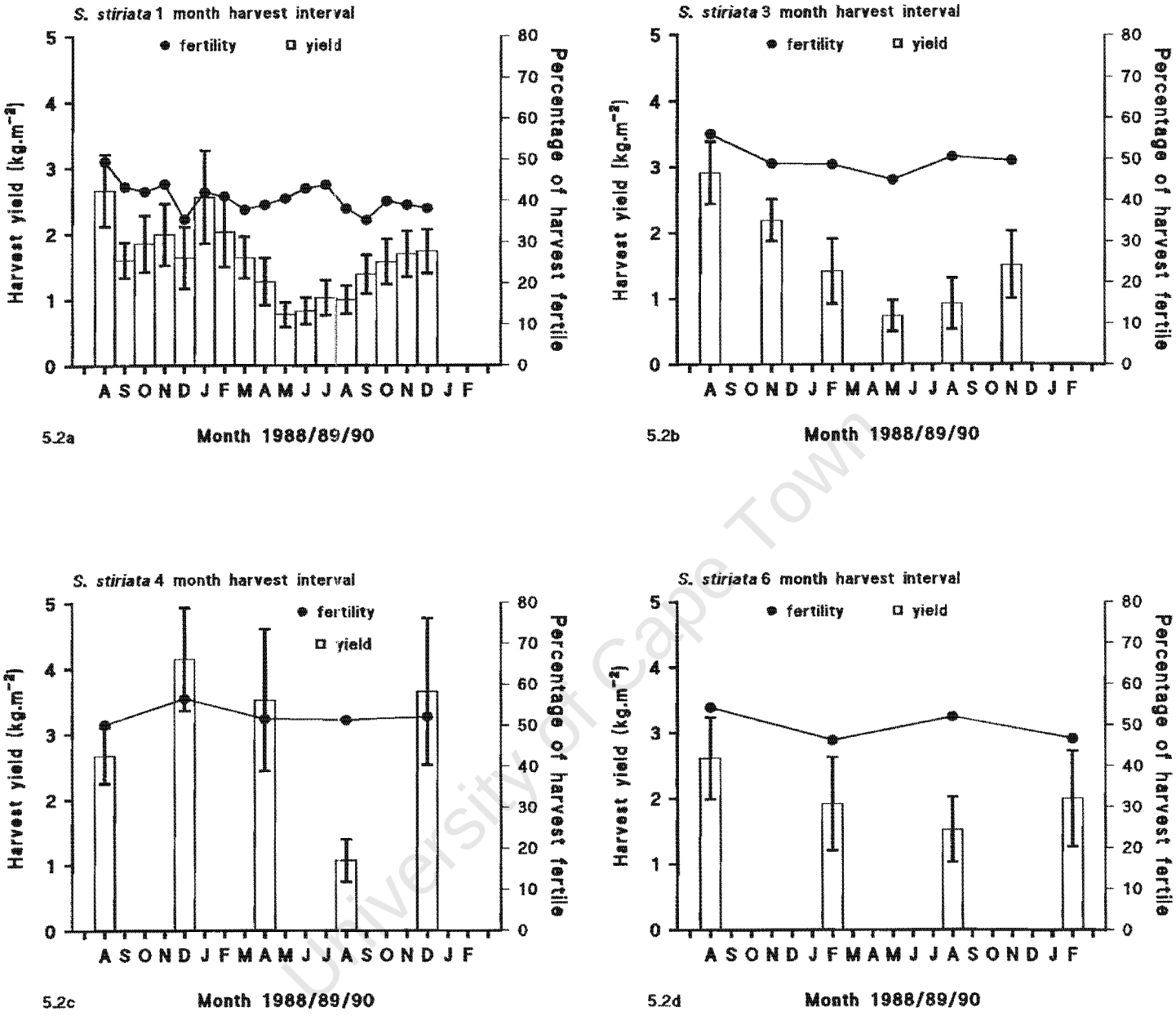


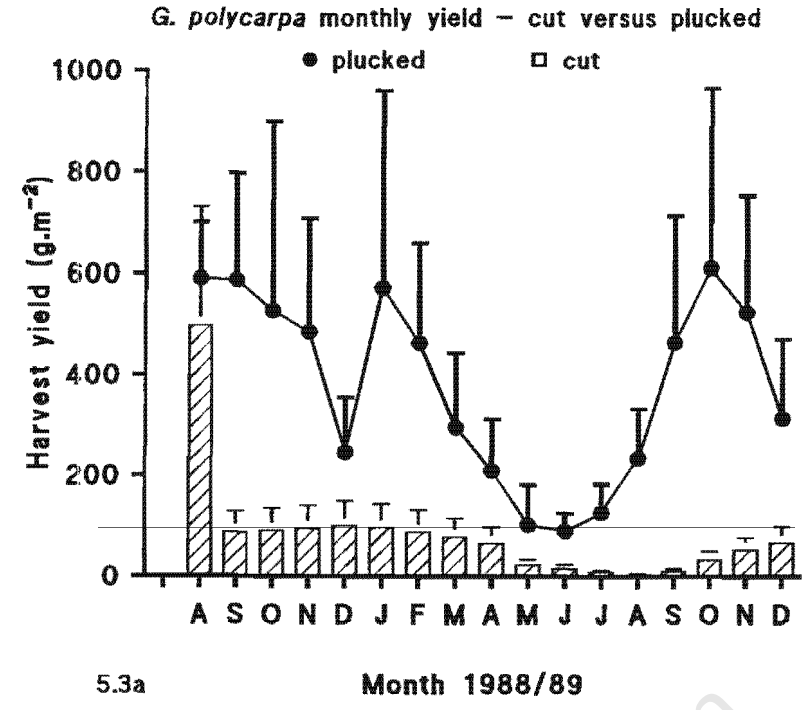
Figure 5.2 Harvest yield (fresh weight) and percentage of harvested weight bearing reproductive structures of *Sarcothalia stiriata* at different harvesting intervals: a) 1 month; b) 3 months; c) 4 months; d) 6 months. Standard errors indicated.

3008g.m^{-2} .harvest^{-1}, but with no significant seasonal pattern (fig. 5.2c). Maximum harvest was recorded during summer (December 1988 and 1989, 4143 and 3643g.m^{-2}, respectively). Lower harvests were recorded during winter (August 1988 and 1989, 1066 and 2674g.m^{-2}, respectively). No seasonal pattern was apparent in the proportion of harvested material bearing reproductive structures, with a mean proportion of 52% being recorded over the entire study period.

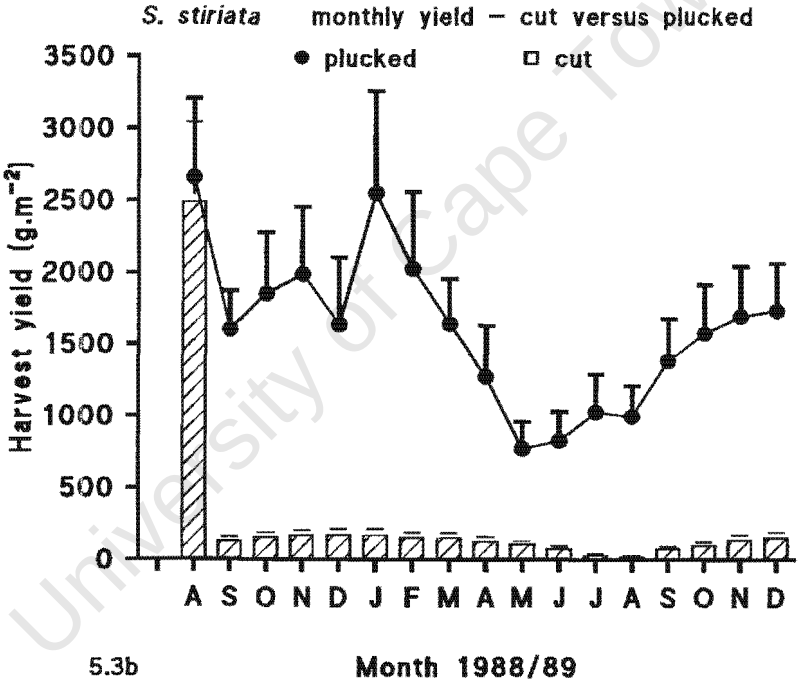
Yields of *Sarcothalia stiriata* harvested at six-monthly intervals averaged 2019g.m^{-2}.harvest^{-1} (table 5.1). No seasonal pattern in harvest yield was apparent (fig. 5.2d), these varying between 2617g.m^{-2} (August 1988) and 1529g.m^{-2} (August 1989). No seasonal trend was evident in the proportion of harvested material bearing reproductive structures, averaging 50% over the entire study period. Like *Gigartina polycarpa*, maximum annual yield of *S. stiriata* was obtained when harvesting took place at monthly intervals (table 5.1). However, maximum harvest efficiency (yield per harvest) and minimal effect on reproductive capacity were achieved when harvests occurred at four-monthly intervals.If both *Gigartina polycarpa* and *Sarcothalia stiriata* were harvested simultaneously, maximum yield was obtained when harvesting at monthly intervals (table 5.1). Maximum harvest efficiency (yield per harvest) for both species combined was achieved when harvests took place at four-monthly intervals. This coincided with the harvesting period with the minimum effect on reproductive capacity in both species.

5.3.3 Effect of harvesting method on harvest yield (plucking versus cutting)

In both *Gigartina polycarpa* (fig. 5.3a) and *Sarcothalia stiriata* (fig. 5.3b) harvesting by cutting reduced the harvest substantially. During the period of this study, the harvest yield obtained by cutting of *G. polycarpa* was 83% less than when harvested by plucking. Recorded mean harvesting yields of *G. polycarpa* were 379g.m^{-2}.harvest^{-1} when plucked and, when cut, 87g.m^{-2}.harvest^{-1}. Similarly, the harvest yield obtained by cutting of *S. stiriata* was 77% less than when harvested by plucking. Mean harvesting yields of 1601g.m^{-2}.harvest^{-1} when plucked and 267g.m^{-2}.harvest^{-1} when cut were recorded in *S. stiriata*. In both species, reduced yields are evident for both harvesting methods during mid-winter (July - August). Conversely, harvest yields of both species increase for both harvesting methods during spring and summer (October - January).



5.3a



5.3b

Figure 5.3 Monthly harvest yield obtained using different harvesting methods - cut and hand-plucked: a) *Gigartina polycarpa*; b) *Sarcothalia stiriata*. Standard errors indicated.

5.3.4 Phenological composition of the harvest

5.3.4.1 *Gigartina polycarpa* harvests

During monthly harvests of *Gigartina polycarpa*, the composition of the harvest averaged 17% male gametophytes, 30% female gametophyes, 22% tetrasporophytes and 32% sexually immature juveniles. No seasonal pattern (fig. 5.4a) was apparent in the proportions of these life-history phases, although fluctuations in the proportions of each life-history phase were apparent, especially in tetrasporophytes (12%-33% of harvest).

The harvest composition for harvests conducted at three-monthly intervals averaged 17% male gametophytes, 28% female gametophyes, 34% tetrasporophytes and 21% sexually immature juveniles. No seasonal pattern (fig. 5.4b) was apparent, the proportion of juveniles fluctuating markedly (between 6% and 32% of harvest).

For *Gigartina polycarpa* harvested at four-monthly intervals the harvest composition averaged 20% male gametophytes, 31% female gametophyes, 33% tetrasporophytes and 16% sexually immature juveniles. Over the course of this study, an increase in the proportion of tetrasporophytes was apparent under this harvesting regime, the proportions of other life-history phases fluctuating between 8% and 45% of harvest (fig. 5.4c).

Harvest composition of *Gigartina polycarpa* harvested at six-monthly intervals averaged 18% male gametophytes, 35% female gametophyes, 28% tetrasporophytes and 19% sexually immature juveniles. No seasonal variation in the various life-history phases was apparent (fig. 5.4d), the proportions of all life-history phases fluctuating between 8% and 46% of total harvest.

5.3.4.2 *Sarcothalia stiriata* harvests

During monthly harvests of *Sarcothalia stiriata*, the composition of the harvest averaged 38% male gametophytes, 28% female gametophyes, 4% tetrasporophytes and 30% sexually immature juveniles. No clear seasonal pattern (fig. 5.5a) was apparent in the proportions of these life-history phases, although fluctuations in the proportions male and female gametophytes were apparent (min. 30% and 17%, max. 48% and 41% respectively) the highest values being recorded during autumn and winter (May-August 1989).

The harvest composition for harvests of *Sarcothalia stiriata* conducted at three-monthly intervals averaged 39% male gametophytes, 30% female gametophyes, 9% tetrasporophytes and 22% sexually immature juveniles. No seasonal pattern (fig. 5.5b) was apparent in the

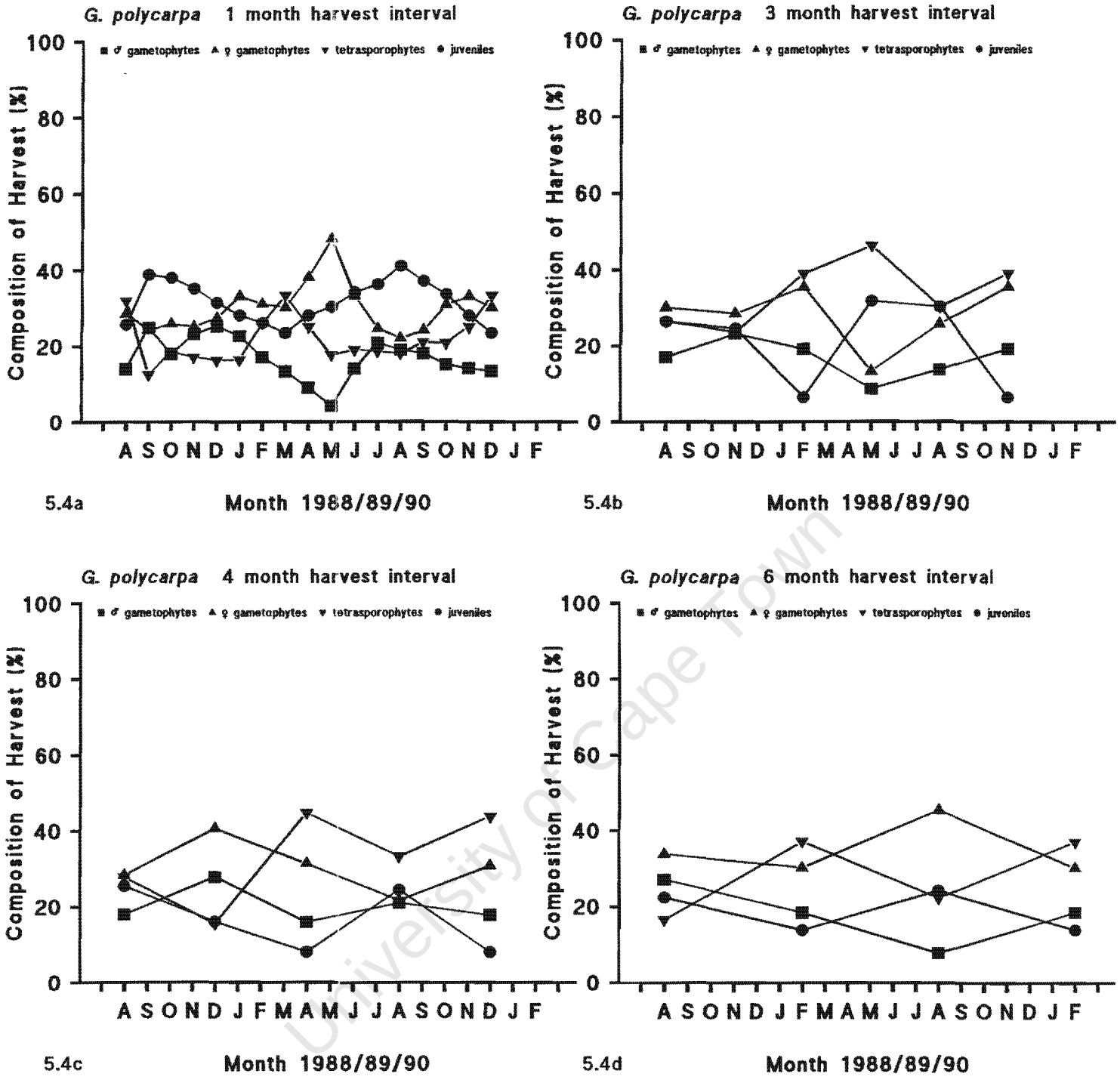


Figure 5.4 Phenological composition of *Gigartina polycarpa* harvests at different harvesting intervals: a) 1 month; b) 3 months; c) 4 months; d) 6 months.

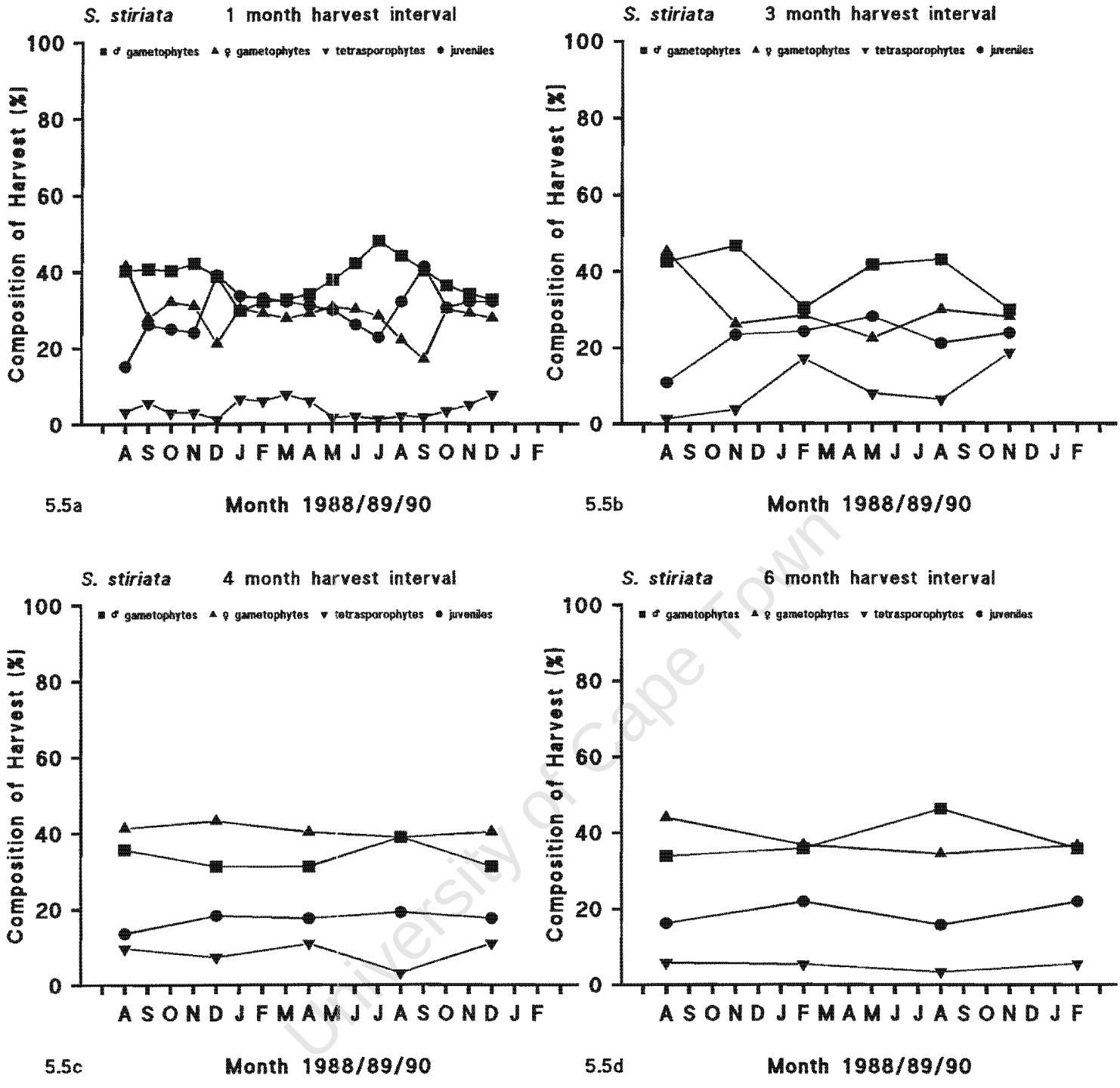


Figure 5.5 Phenological composition of *Sarcothalia stiriata* harvests at different harvesting intervals: a) 1 month; b) 3 months; c) 4 months; d) 6 months.

proportions of these life-history phases. The proportion of tetrasporophytes and juveniles increased over the course of the study (from 1% to 19% and 11% to 24%, respectively), other phases displaying less variation.

For *Sarcothalia stiriata* harvested at four-monthly intervals, the proportions of the life-history phases remained relatively constant, the average harvest comprising 34% male gametophytes, 41% female gametophyes, 8% tetrasporophytes and 17% sexually immature juveniles. No clear seasonal pattern (fig. 5.5c) was apparent in the proportions of these life-history phases. Tetrasporophytes contributed little to the phenological composition of *Sarcothalia stiriata* harvested at six-monthly intervals. The composition averaged 38% male gametophytes, 38% female gametophyes, 5% tetrasporophytes and 19% sexually immature juveniles over the course of the study. No clear seasonal variation in proportions of the various life-history phases was noted (fig. 5.5d).

5.3.5 Effects of harvesting on community structure

A total of sixteen seaweed species (table 5.2) were recorded in the disturbance experiment quadrats during the course of the study. The majority of recorded species (11 spp.) were

No	Species	No	Species
1	*Aeodes orbitosa* (Suhr) Schmitz	9	*Ceramium papenfussianum* Simons
2	*Gigartina polycarpa* (Kützing) Setchell *et* Gardner	10	*Caulacanthus ustulatus* (Turner) Kützing
3	*Sarcothalia stiriata* (Turner) Leister	11	*Gelidium pristoides* (Turner) Kützing
4	*Sarcothalia scutellata* (Hering) Leister	12	*Mazzaella capensis* (J. Ag.) Fredericq
5	*Spongites yendoii* (Foslie) Chamberlain	13	*Mazzaella convoluta* (Areschoug) Hommersand
6	*Ulva capensis* Areschoug	14	*Pterosiphonia cloiophylla* (C. Ag.) Falkenberg
7	*Hildenbrandia lecanellierii* Hariot	15	*Cladophora mirabilis* (C. Ag.) Rabenhorst
8	*Gymnogongrus glomeratus* J. Agardh	16	*Nothogenia erinacea* (Turner) Parkinson

Table 5.2 Species recorded during Kommetjie clearance experiments, 1988/89.

foliose Rhodophyceae (spp. no's: 1,2,3,4,8,9,11,12,13,14,16). Two crustose (5,7) and one turf (10) red algal species were also recorded. No member of the Phaeophyceae was present, the balance of recorded species comprising one membranous member and one filamentous member, of the Chlorophyceae (6,15).

Ordination of cover abundance data prior to clearance of plants/grazers from the experiment initiated during winter (July 1988, fig. 5.6a) showed little difference between the community structure of each treatment. These quadrats were dominated by a climax community (figs 5.7a-d) comprised mainly of *Aeodes orbitosa*, *Gigartina polycarpa*, *Sarcothalia stiriata*, *Spongites yendoii* and *Ulva capensis*. Three months after clearance of plants and grazers (October 1988), ordination showed marked differences in all experimental treatments with the exception of the control (fig. 5.6b). Quadrats in which plant material was not cleared but grazers were removed (UP) showed substantial change, with increased abundance (*cf.* July) of *G. polycarpa* and *S. stiriata* being the most notable difference (fig. 5.8b). Quadrats in which plant material was cleared and grazers were removed (CP) also showed considerable changes in the ordination, the addition of *Mazzaella capensis* and *Mazzaella convoluta* to the community and a reduction in abundance of *G. polycarpa* and *S. stiriata* being prominent (fig. 5.8c). In quadrats which were cleared of plant material but grazers not excluded (CU), differences in abundance were predominant, the percentage cover of *A. orbitosa* increasing dramatically (a likely seasonal event), whereas the cover of other species showed marked declines.

Four months after the start of the experiment (November 1988), the differences in the treatments were still extreme (fig. 5.6c). In the control quadrats (fig. 5.9a) cover of *Aeodes orbitosa* more than doubled, with a concomitant decline in the cover of *Gigartina polycarpa*. These events appear to be seasonal fluctuations. A substantial amount of *Gelidium pristoides* was also present. UP quadrats were again the most different to the control quadrats, the lower abundance of *A. orbitosa* and the presence of *Ceramium papenfussianum*, *Mazzaella capensis* and *Mazzaella convoluta* being the most notable differences (fig. 5.9b). CP quadrats were again also considerably different from the control in the ordination for the same reasons as noted for October (fig. 5.9c). CU quadrats showed little change from the October sample, with a decline in the abundance of *Spongites yendoii* and *A. orbitosa* predominating (fig. 5.9d). Seven months after the start of the experiment (March 1989), the differences between treatments were considerably less extreme (fig. 5.6d). In the control quadrats (fig. 5.10a),

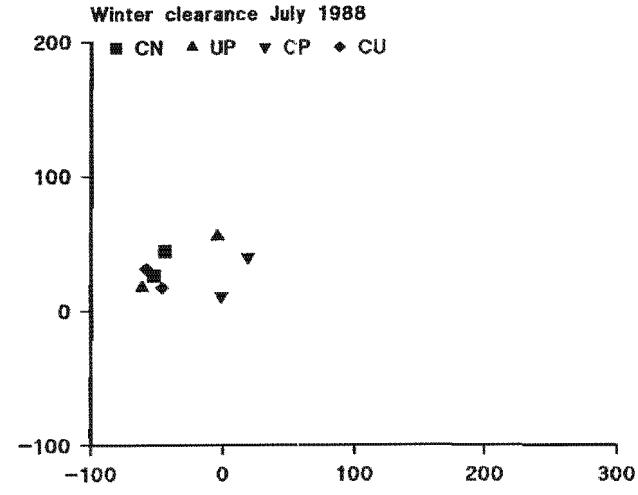


Fig. 5.6a

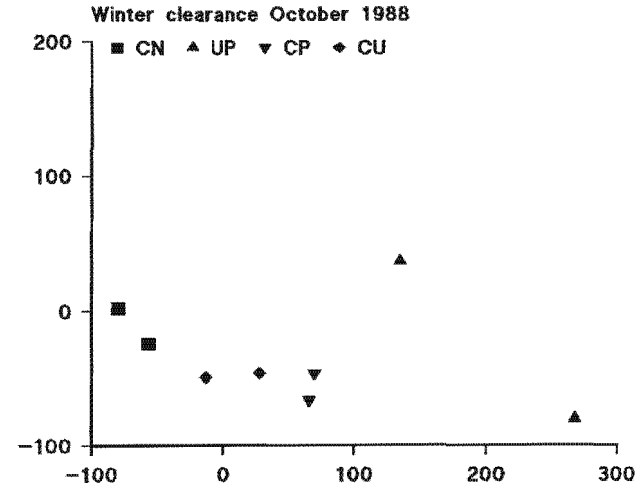


Fig. 5.6b

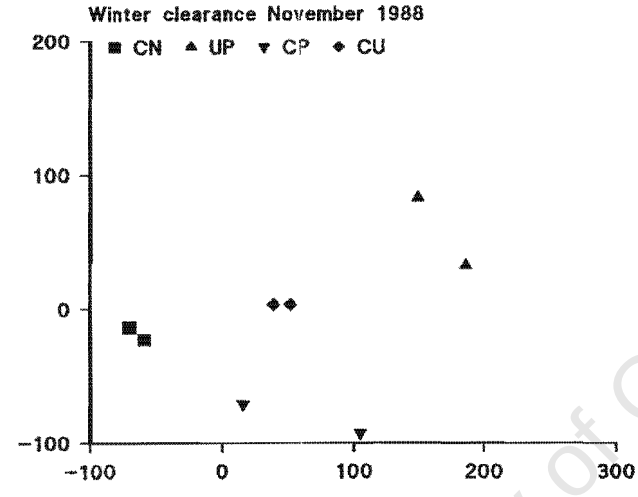


Fig. 5.6c

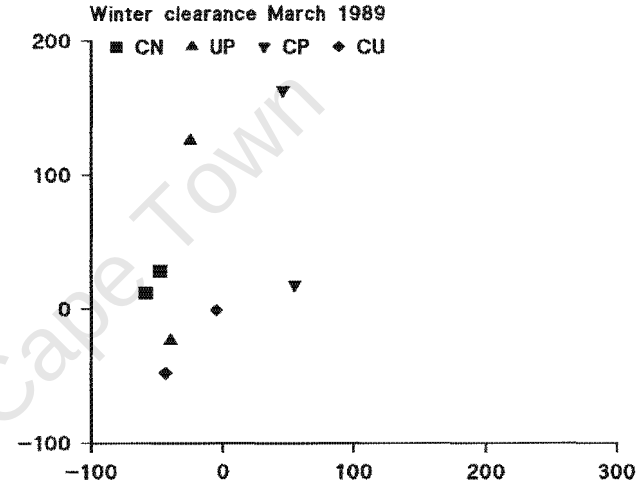


Fig. 5.6d

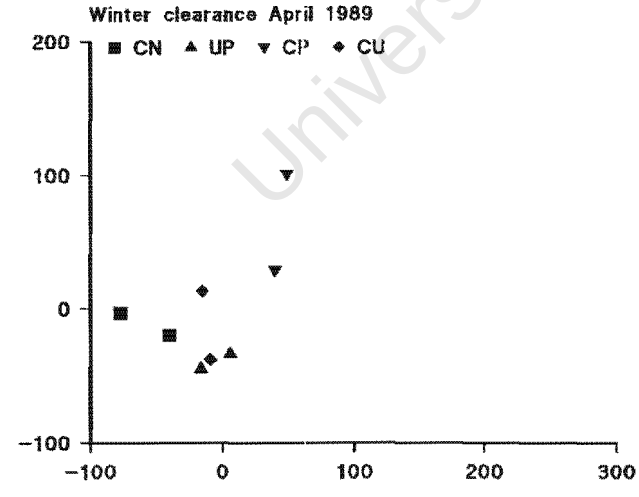


Fig. 5.6e

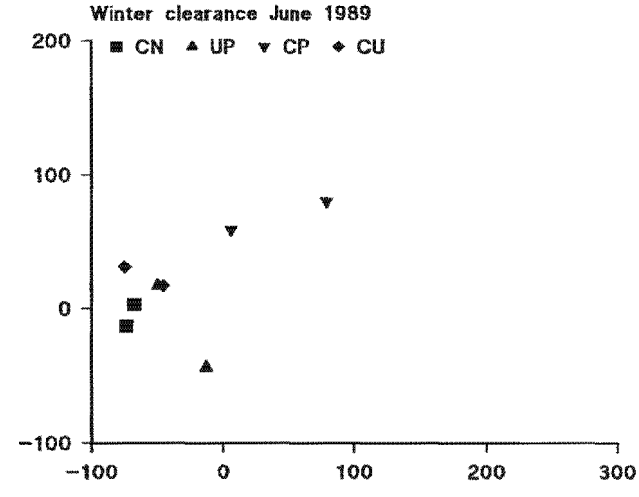


Fig. 5.6f

Figure 5.6 Combined ordination of winter-initiated disturbance quadrats sample sites: a) July 1988; b) October1988; c) November 1988; d) March 1989; e) April 1989; f) June 1989. CN=control; UP= plants presents, grazers removed; CP=plants and grazers removed; CU= plants removed, grazers present. Axes units arbitrary.

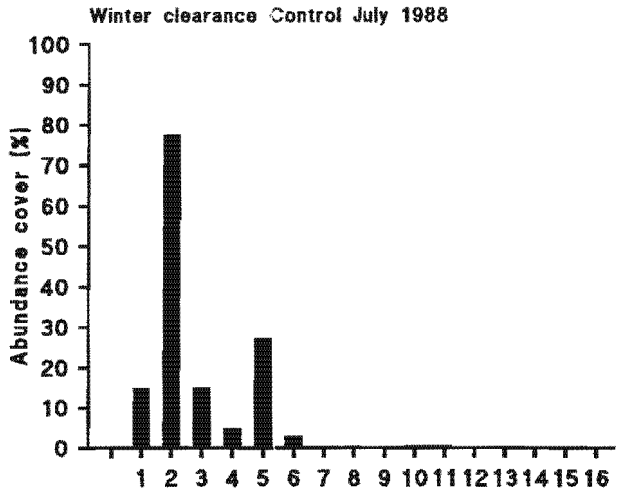


Fig. 5.7a

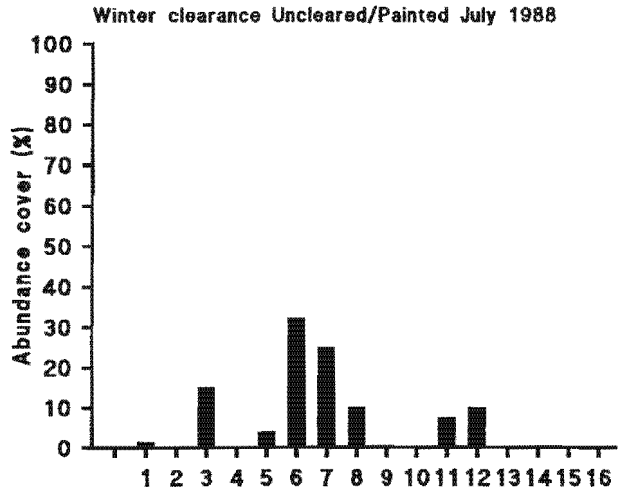


Fig. 5.7b

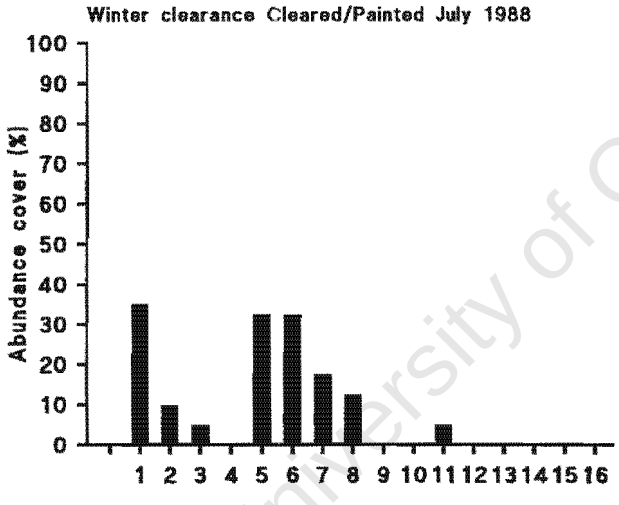


Fig. 5.7c

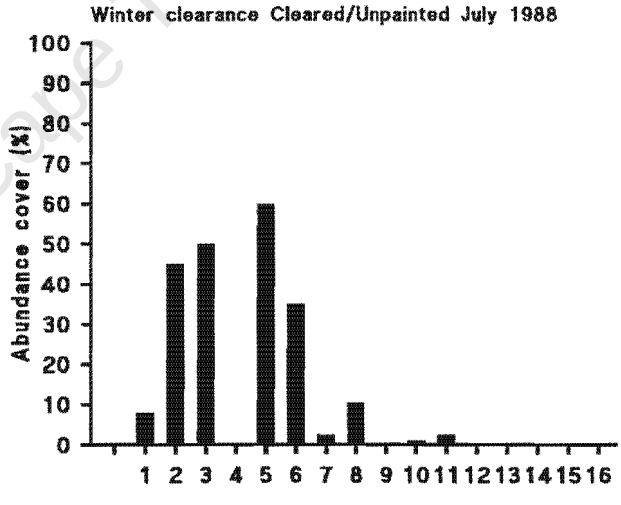


Fig. 5.7d

Figure 5.7 Species diversity and abundance cover in different treatment quadrats: winter-initiated disturbance experiment, July 1988: a) control; b) plants present, grazers removed; c) plants and grazers removed; d) plants removed, grazers present.

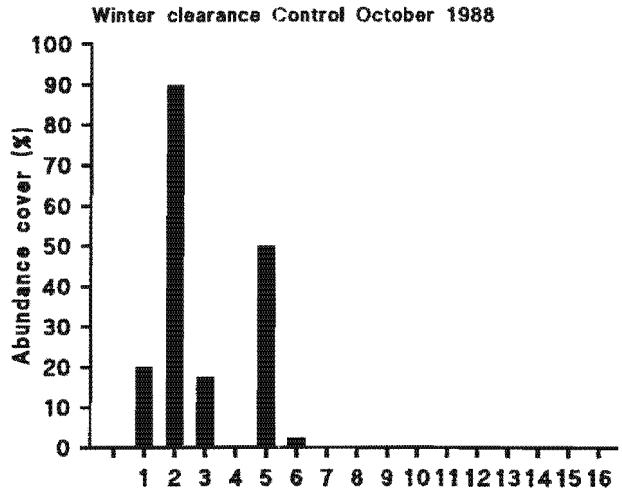


Fig. 5.8a

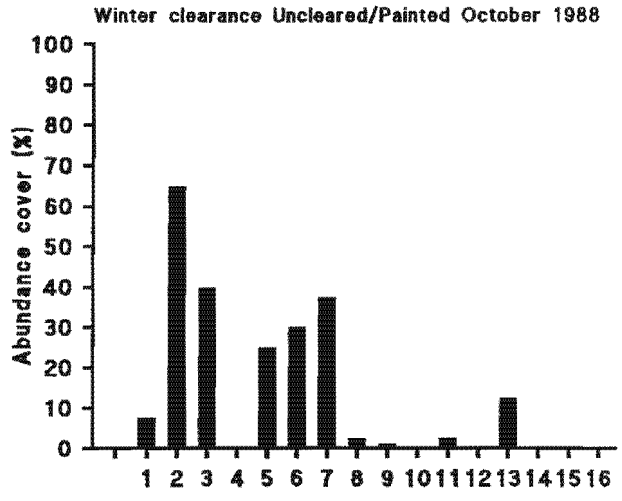


Fig. 5.8b

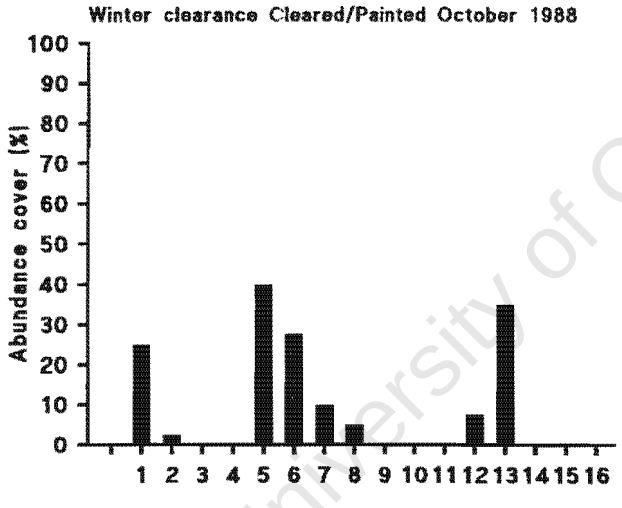


Fig. 5.8c

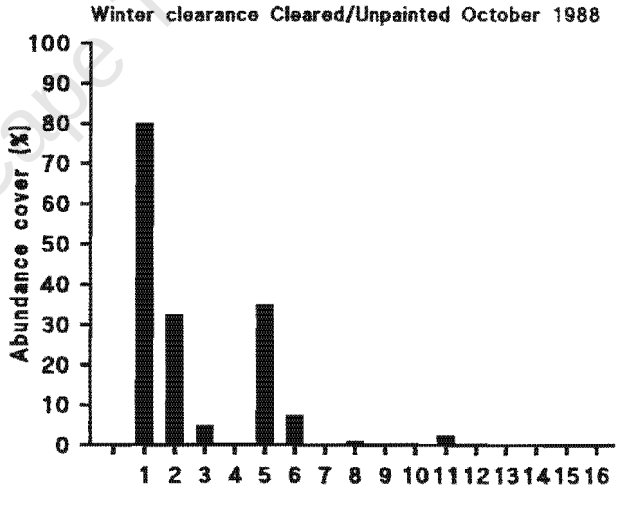


Fig. 5.8d

Figure 5.8 Species diversity and abundance cover in different treatment quadrats: winter-initiated disturbance experiment, October 1988: a) control; b) plants present, grazers removed; c) plants and grazers removed; d) plants removed, grazers present.

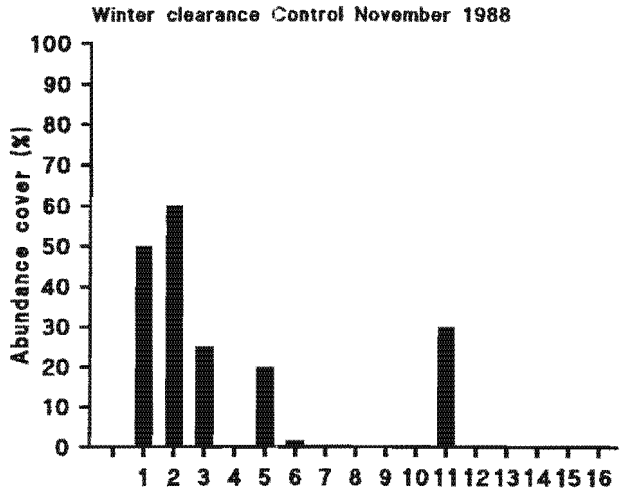


Fig. 5.9a

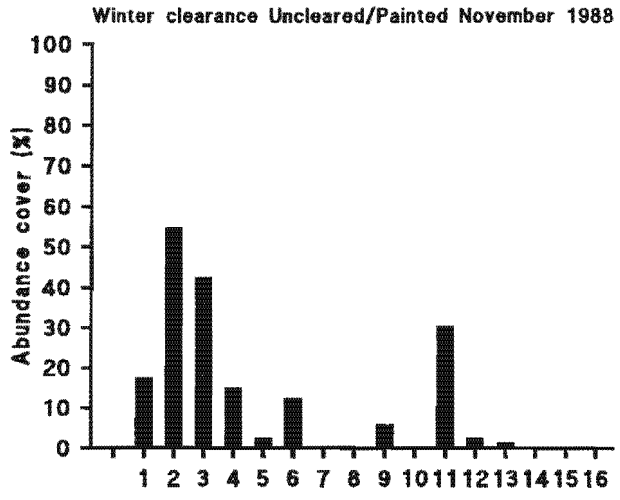


Fig. 5.9b

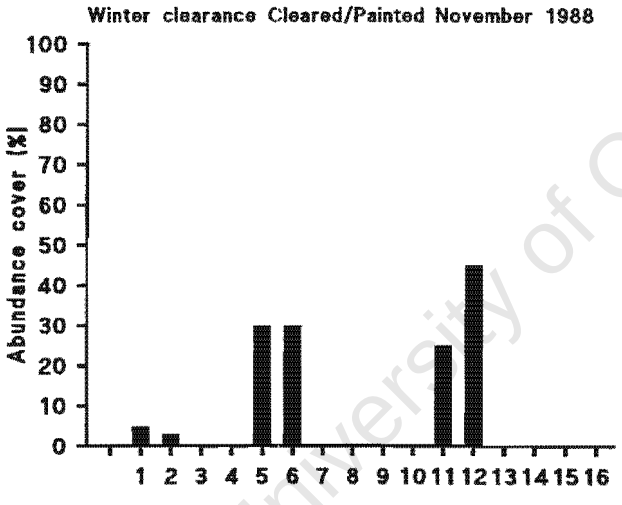


Fig. 5.9c

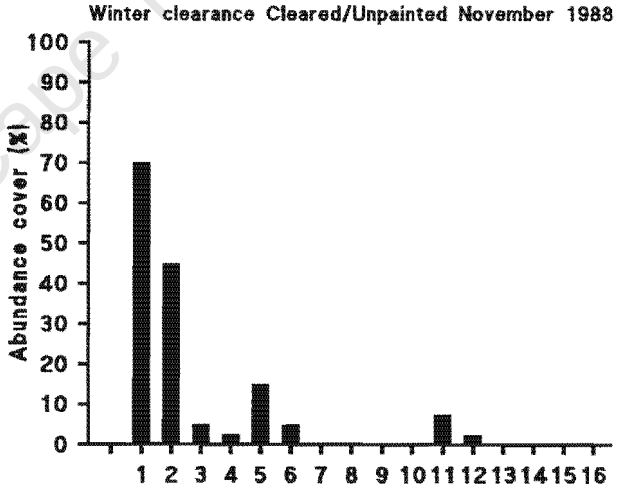


Fig. 5.9d

Figure 5.9 Species diversity and abundance cover in different treatment quadrats: winter-initiated disturbance experiment, November 1988: a) control; b) plants present, grazers removed; c) plants and grazers removed; d) plants removed, grazers present.

cover of *Aeodes orbitosa* was reduced considerably with the end of summer, as was the cover of *Gelidium pristoides,* whilst *Gigartina polycarpa* and *Sarcothalia stiriata* were dominant. UP quadrats were no longer the most different from the control (fig. 5.10b), the abundance of species not common with the control quadrats declining. CP quadrats were still considerably different from the control quadrats, *G. polycarpa* and *S. stiriata* being much less abundant than in the control as well as small amounts of other species (*Ulva capensis*, *Hildenbrandia lecanellierii*, *Mazzaella capensis* and *Mazzaella convoluta*) being additionally present (fig. 5.10c). CU quadrats were very close to the control quadrats in the ordination, the only notable differences being the absence of *A. orbitosa* and the presence of a small amount of *M. capensis* (fig. 5.10d).

One month later, eight months after the start of the experiment (April 1989), the differences between treatments were further reduced (fig. 5.6e), only CP quadrats appearing dissimilar to the initial state. In the control quadrats (fig. 5.11a) cover of *Aeodes orbitosa*, *Gigartina polycarpa* and *Sarcothalia stiriata* declined with the onset of autumn. Abundance of the dominant species in UP quadrats were less than one month before, recorded values being similar to those in the control quadrats (fig. 5.11b). *Gymnogongrus glomeratus* and *Cladophora mirabilis* were present in these quadrats, but not in sufficient quantity to make the ordination substantially different. CP quadrats were still different from the control quadrats, due to the presence of *Mazzaella capensis*, *Mazzaella convoluta* and *Nothogenia erinacea* and also because the relative abundance of the climax species (*G. polycarpa* and *S. stiriata*) were different from the control quadrats (fig. 5.11c). CU quadrats were very close to the control quadrats in the ordination, even though these quadrats were considerably more diverse, with a marked difference in abundance of the encrusting coralline, *Spongites yendoii* (fig. 5.11d). Ordination of data from the last sampling visit, ten months after the start of the experiment (June 1989), showed a further reduction in the differences between treatments (fig. 5.6f), but CP quadrats still appeared dissimilar to the initial state. In the control quadrats (fig. 5.12a) cover of the climax species, *Aeodes orbitosa*, *Gigartina polycarpa* and *Sarcothalia stiriata*, was similar to that observed at the start of the experiment. The control quadrats were more diverse than they were initially, with the addition of *Gymogongrus glomeratus*, *Caulacanthus ustulatus* and *Gelidium pristoides* (fig. 5.12a). Abundance of the dominant species in UP quadrats were greater than two months before, recorded values being similar to those in the

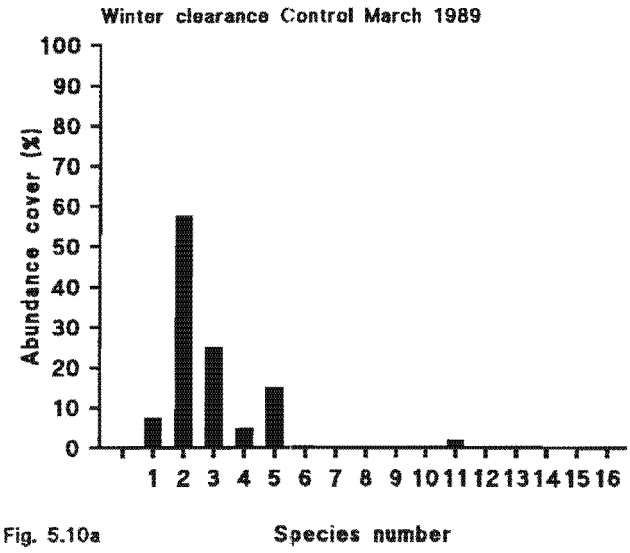


Fig. 5.10a

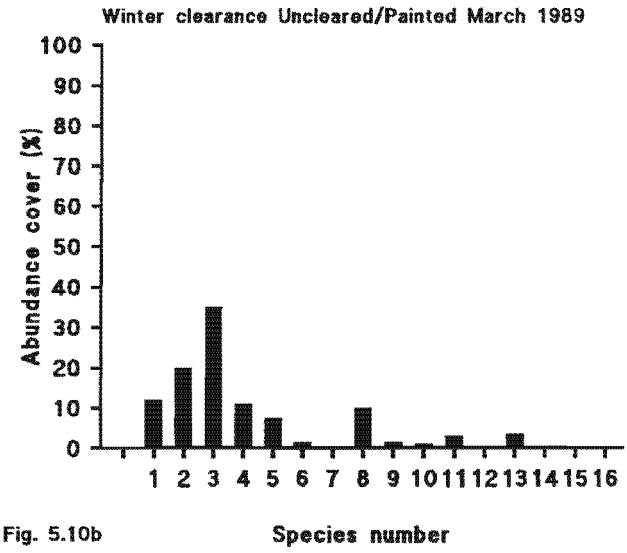


Fig. 5.10b

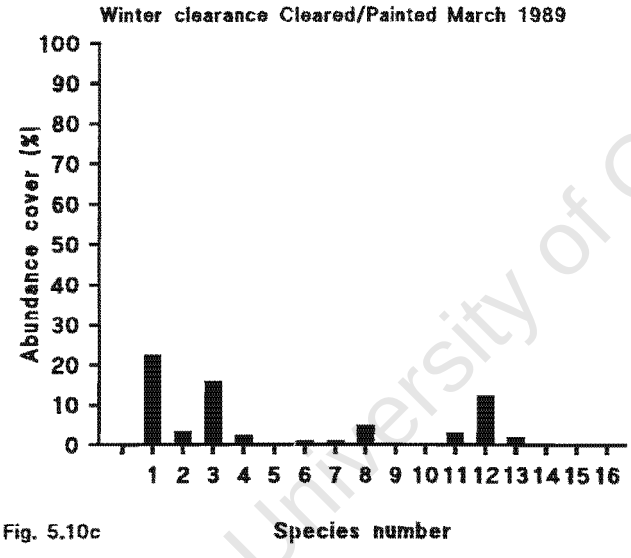


Fig. 5.10c

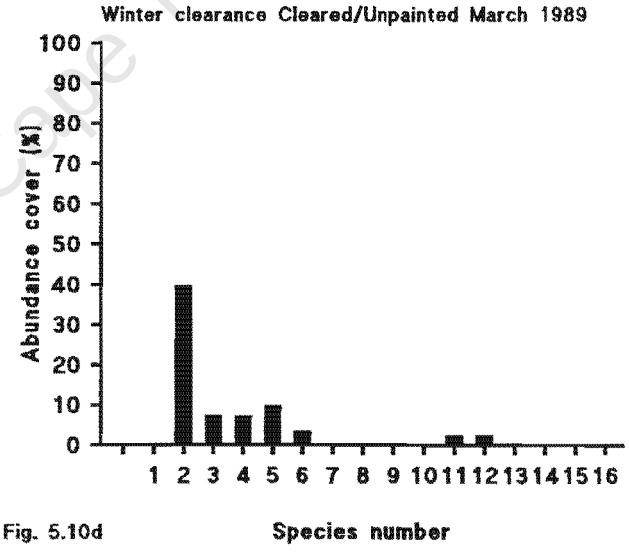


Fig. 5.10d

Figure 5.10 Species diversity and abundance cover in different treatment quadrats: winter-initiated disturbance experiment, March 1989: a) control; b) plants present, grazers removed; c) plants and grazers removed; d) plants removed, grazers present.

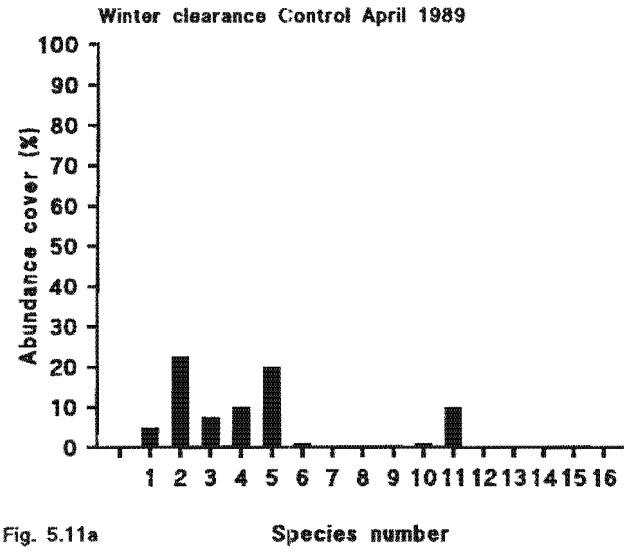


Fig. 5.11a

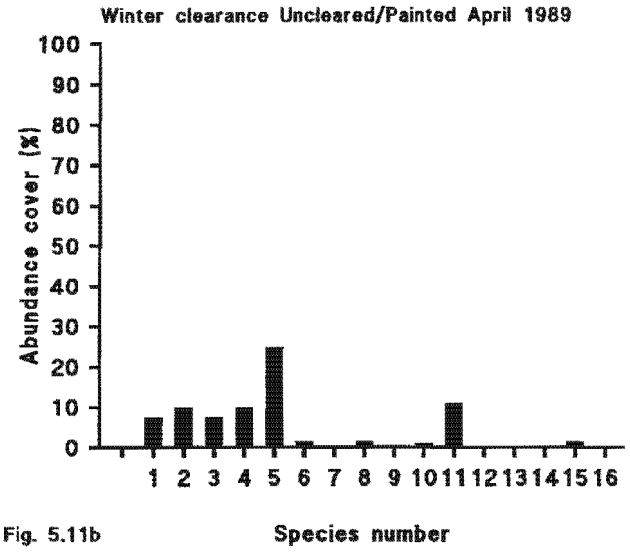


Fig. 5.11b

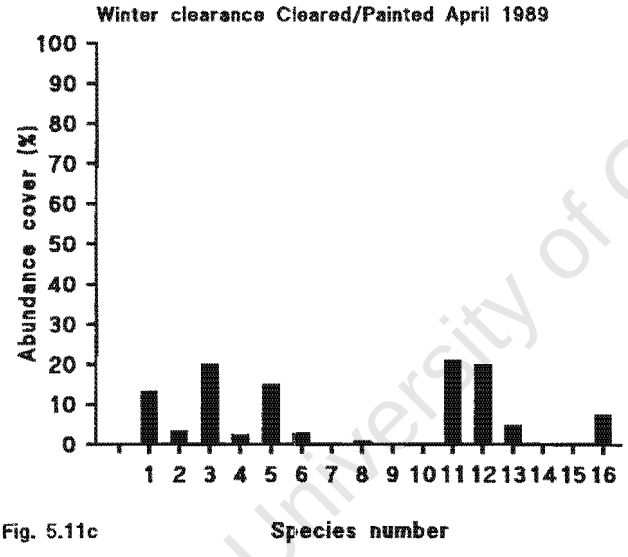


Fig. 5.11c

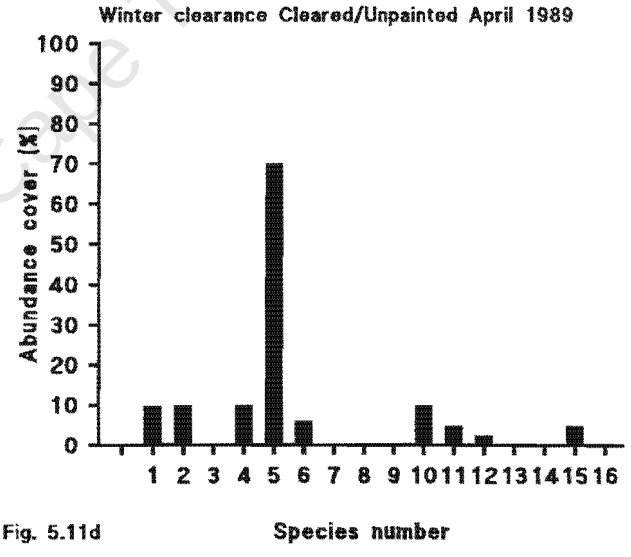


Fig. 5.11d

Figure 5.11 Species diversity and abundance cover in different treatment quadrats: winter-initiated disturbance experiment, April 1989: a) control; b) plants present, grazers removed; c) plants and grazers removed; d) plants removed, grazers present.

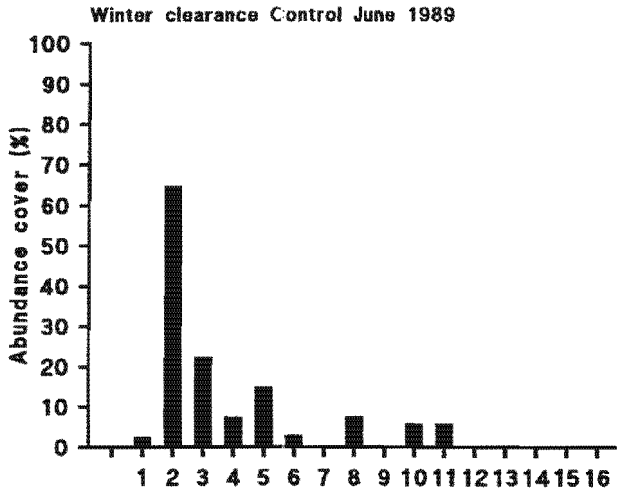


Fig. 5.12a

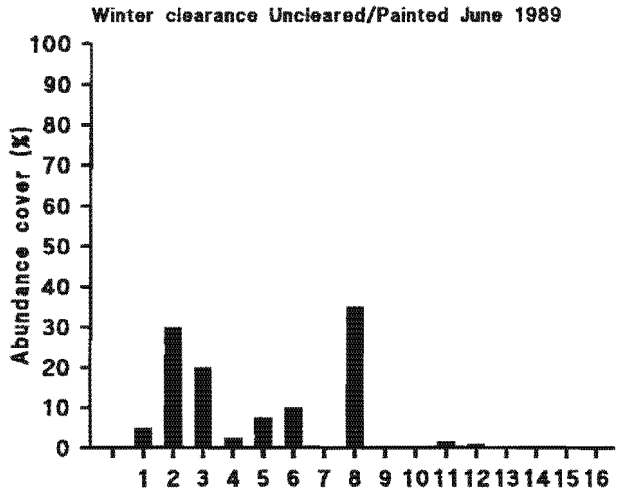


Fig. 5.12b

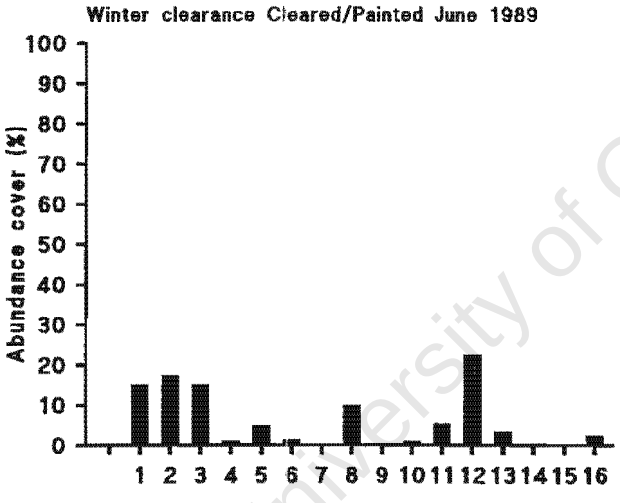


Fig. 5.12c

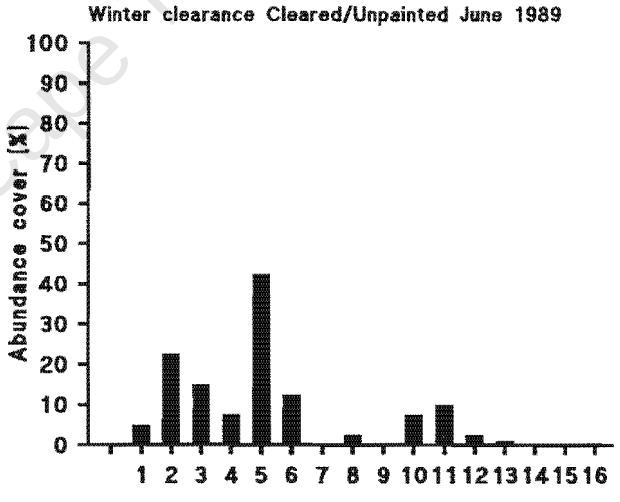


Fig. 5.12d

Figure 5.12 Species diversity and abundance cover in different treatment quadrats: winter-initiated disturbance experiment, June 1989: a) control; b) plants present, grazers removed; c) plants and grazers removed; d) plants removed, grazers present.

control quadrats (fig. 5.12b), the abundance of *G. glomeratus* increasing substantially. Species composition and abundance in CP quadrats was unchanged from the previous sample, these quadrats being still different from the control quadrats due to the presence of *Mazzaella capensis*, *Mazzaella convoluta* and *Nothogenia erinacea* (fig. 5.12c). CU quadrats were again very close to the control quadrats in the ordination. These quadrats were no longer considerably more diverse than the control quadrats, with only *M. capensis* and *M. convoluta* being additional to the species list. There was still a marked difference in abundance of the encrusting coralline, *Spongites yendoii* (fig. 5.12d).

Ordination of cover abundance data prior to clearance of plants/grazers from the experiment inititated during spring (November 1988, fig. 5.13a) showed very little difference between the community structure of each treatment. These quadrats were dominated by a climax community (figs 5.14a-d) comprised mainly of *Aeodes orbitosa*, *Gigartina polycarpa*, *Sarcothalia stiriata*, *Sarcothalia scutellata* and *Spongites yendoii*.

Marked differences in community structure as a result of clearing plants and/or grazers were visible up to seven months after the start of the experiment (March to June 1989, figs 5.13b-d). Ordination showed marked differences in all experimental treatments where grazers were removed. Four months after clearing, quadrats in which plant material was cleared and grazers were removed (CP) were most different to the control quadrats, due to the absence of the majority of the natural climax community species (*Gigartina polycarpa*, *Sarcothalia stiriata* and *Sarcothalia scutellata*), and the resulting dominance of the opportunistic *Ulva capensis* (fig. 5.15c). In uncleared plots with grazers removed (UP), *U. capensis* was not present, the main difference being increased abundance of *S. scutellata* (fig. 5.15b). In cleared, unpainted quadrats, differences were due to the change in abundance of the cleared flora, *U. capensis* being unable to dominate where grazers were present (fig. 5.15d).

Five months after clearance (April 1989), differences in the ordination were more noticeable (fig. 5.13c), differences in experimental treatments where grazers and plant material were removed were accentuated. CP quadrats were most different to the control quadrats, again as a result of the absence of *Gigartina polycarpa*, *Sarcothalia stiriata* and *Sarcothalia scutellata* and the presence of *Ulva capensis* in abundance (fig 5.16c). UP quadrats were no longer very different to the control quadrats, abundance of *S. scutellata* declining notably (fig. 5.16b). CU quadrats differed very little from the control quadrats, a small amount of *U. capensis* being

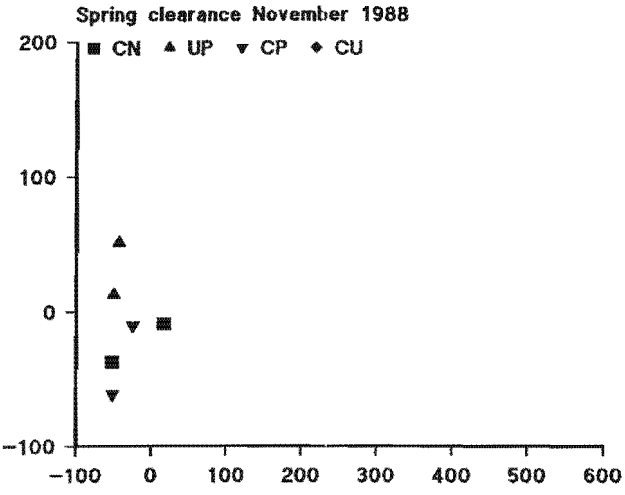


Fig. 5.13a

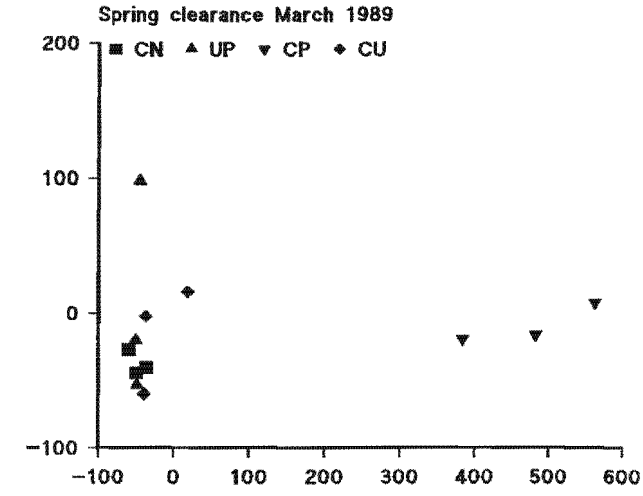


Fig. 5.13b

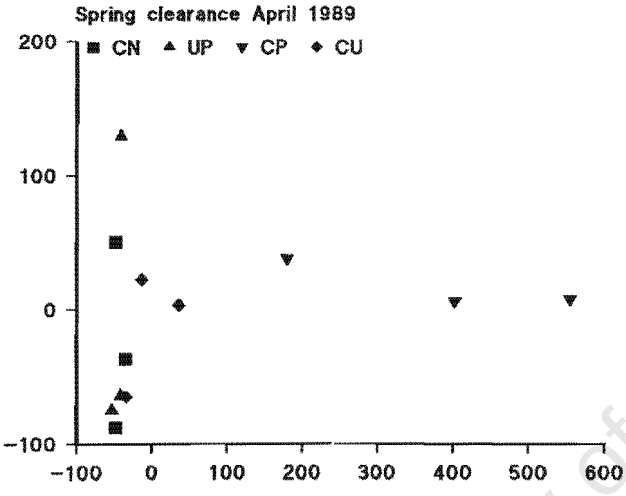


Fig. 5.13c

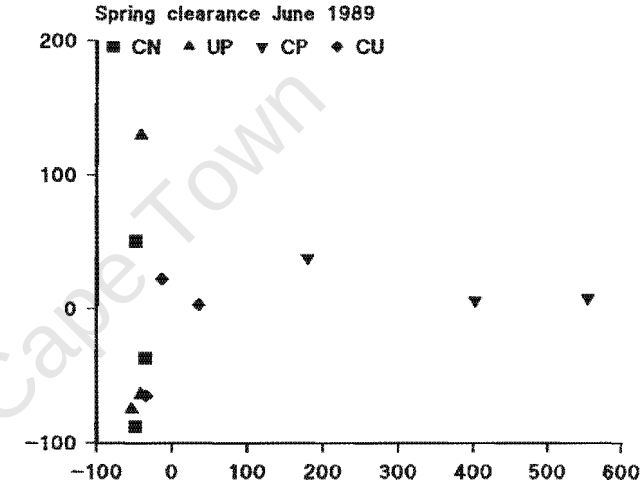


Fig. 5.13d

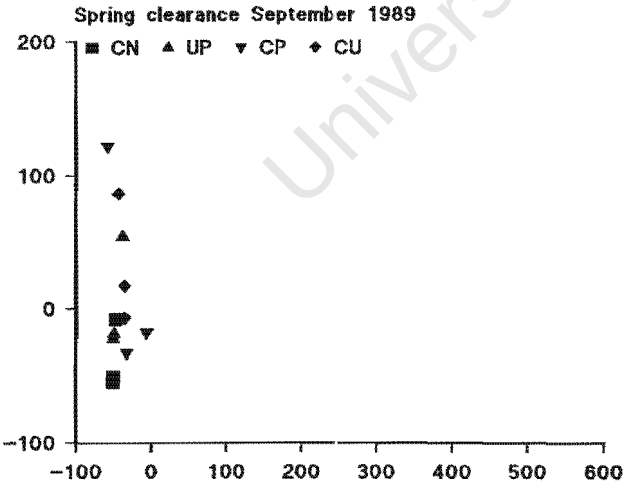


Fig. 5.13e

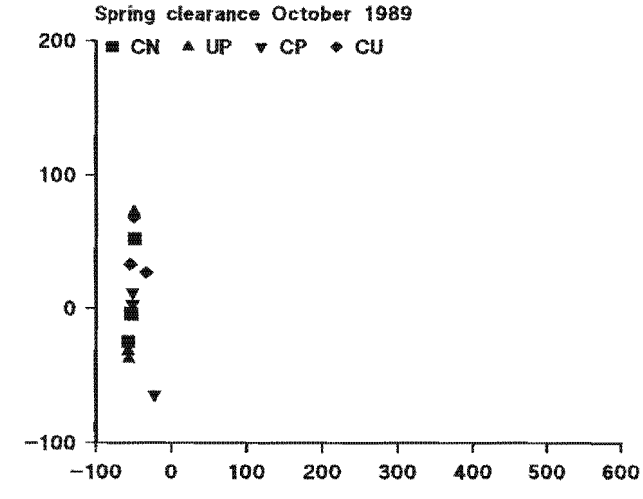


Fig. 5.13f

Figure 5.13 Combined ordination of spring-initiated disturbance quadrats sample sites: a) November 1988; b) March1989; c) April 1989; d) June 1989; e) September 1989; f) October 1989. CN=control; UP= plants presents, grazers removed; CP=plants and grazers removed; CU= plants removed, grazers present. Axes units arbitrary.

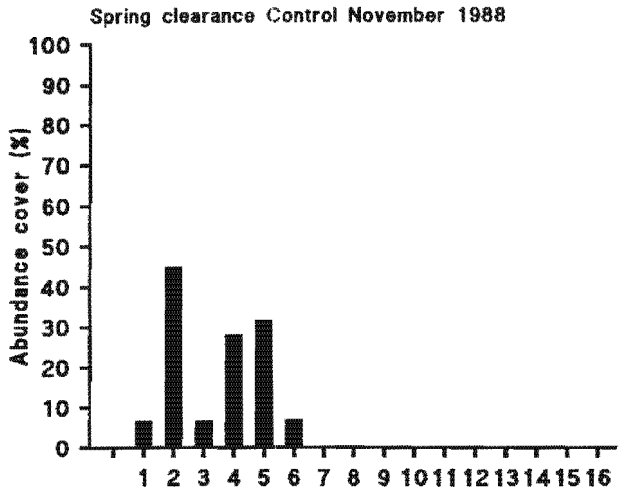


Fig. 5.14a

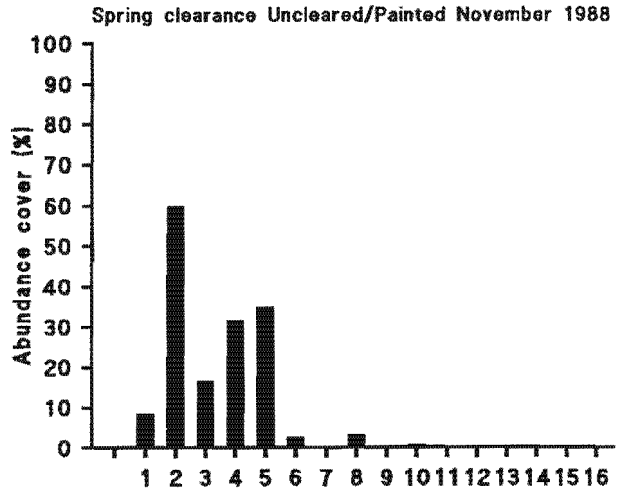


Fig. 5.14b

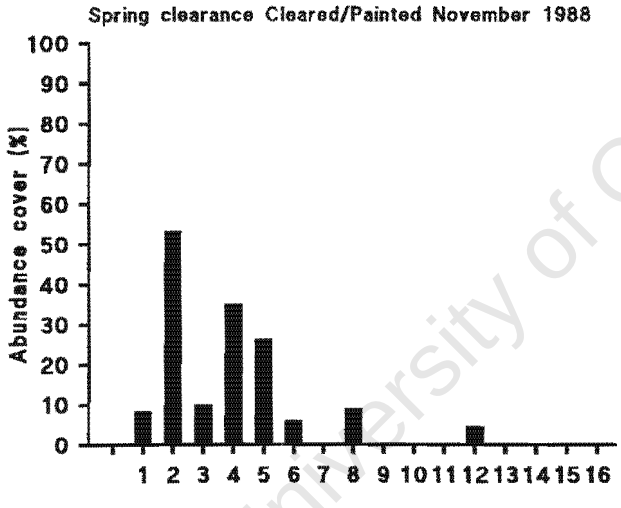


Fig. 5.14c

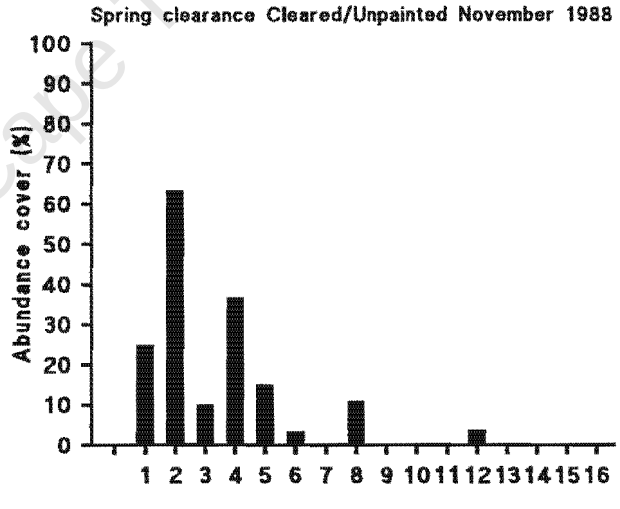


Fig. 5.14d

Figure 5.14 Species diversity and abundance cover in different treatment quadrats: spring-initiated disturbance experiment, November 1988: a) control; b) plants present, grazers removed; c) plants and grazers removed; d) plants removed, grazers present.

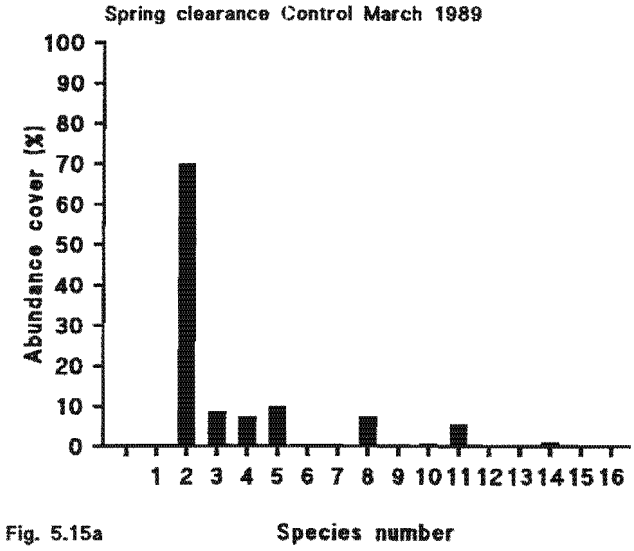


Fig. 5.15a

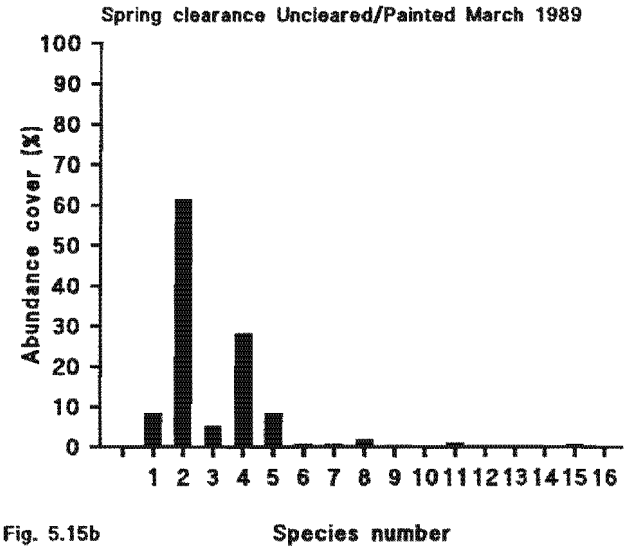


Fig. 5.15b

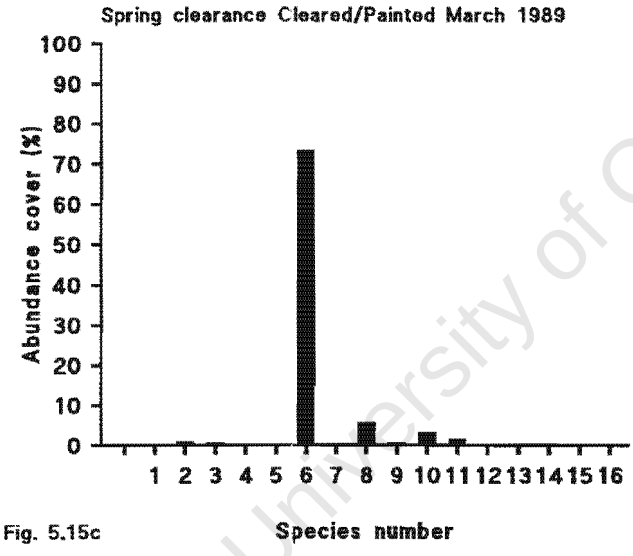


Fig. 5.15c

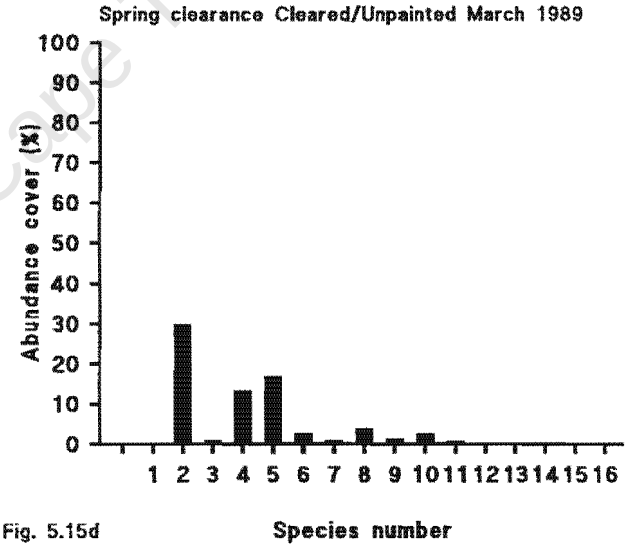


Fig. 5.15d

Figure 5.15 Species diversity and abundance cover in different treatment quadrats: spring-initiated disturbance experiment, March 1989: a) control; b) plants present, grazers removed; c) plants and grazers removed; d) plants removed, grazers present.

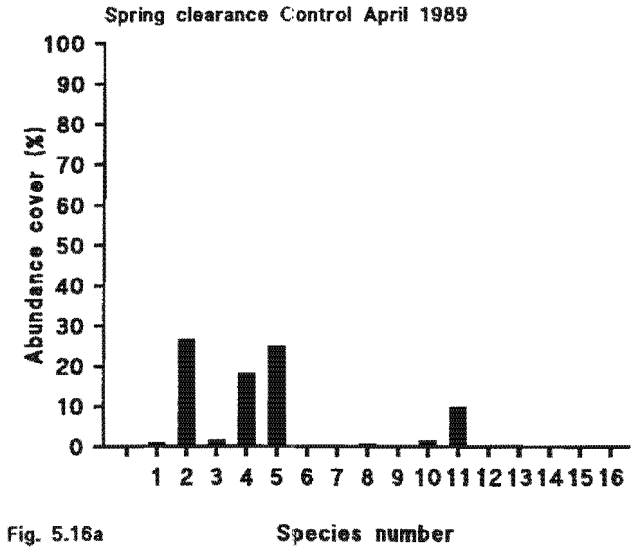


Fig. 5.16a

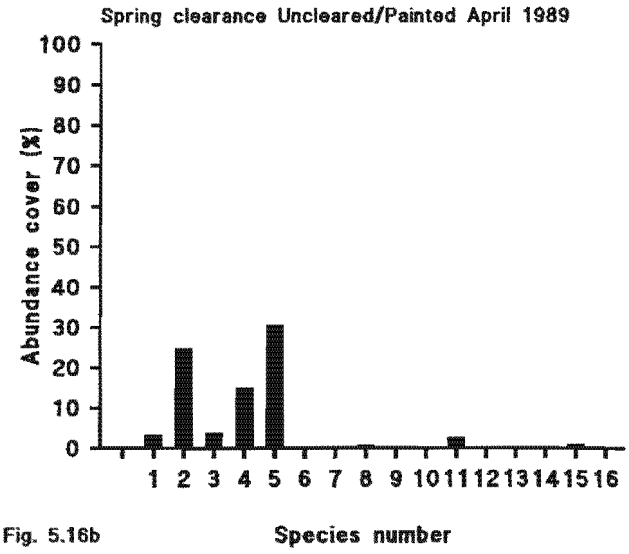


Fig. 5.16b

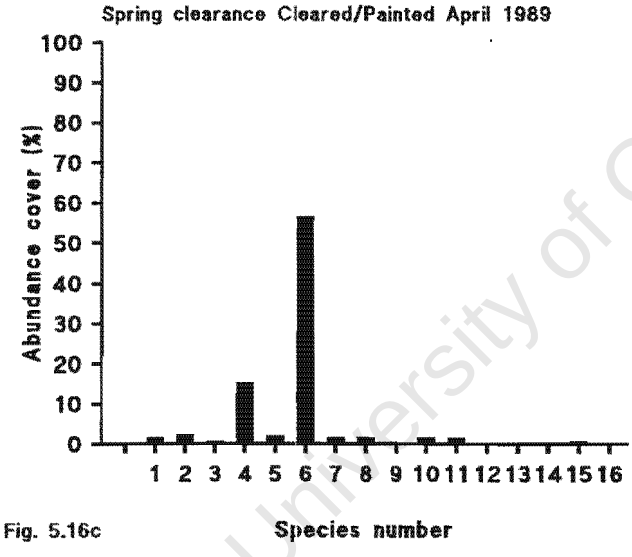


Fig. 5.16c

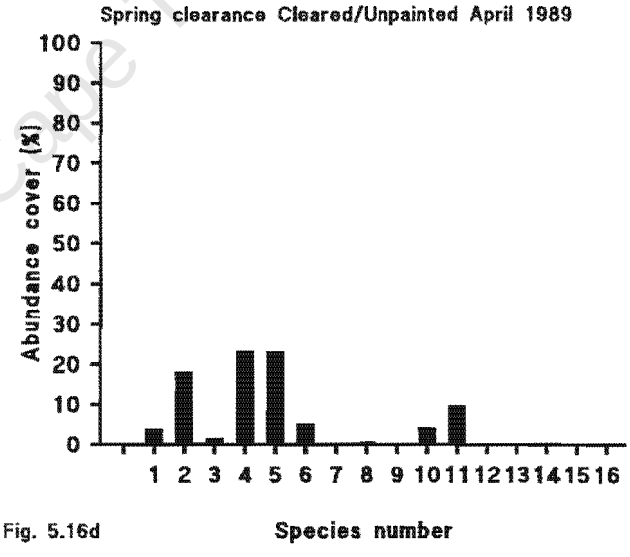


Fig. 5.16d

Figure 5.16 Species diversity and abundance cover in different treatment quadrats: spring-initiated disturbance experiment, April 1989: a) control; b) plants present, grazers removed; c) plants and grazers removed; d) plants removed, grazers present.

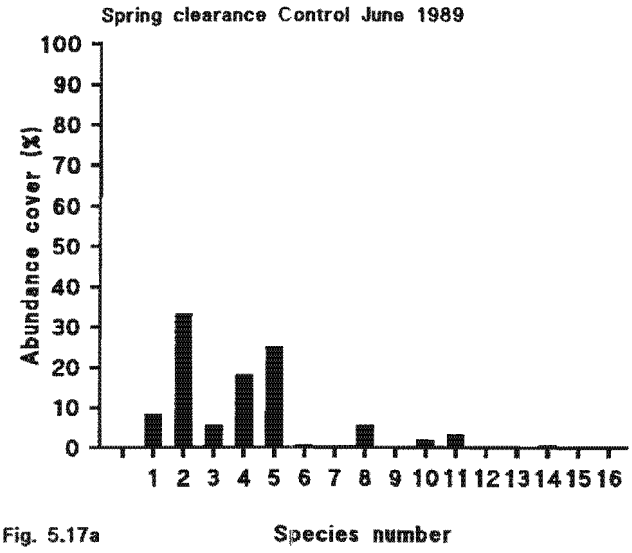


Fig. 5.17a

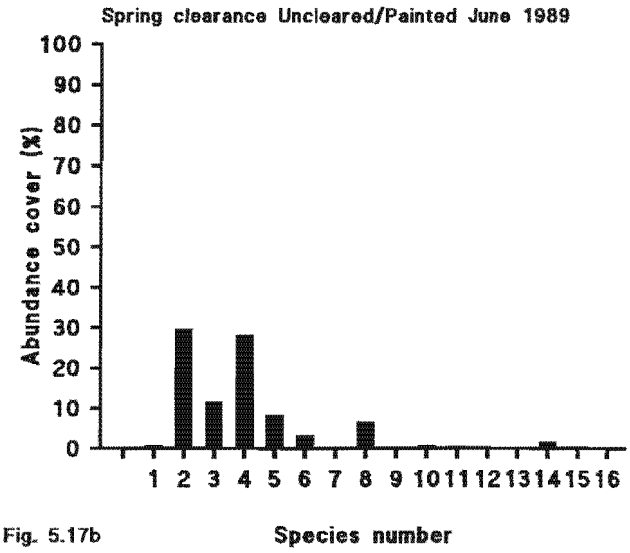


Fig. 5.17b

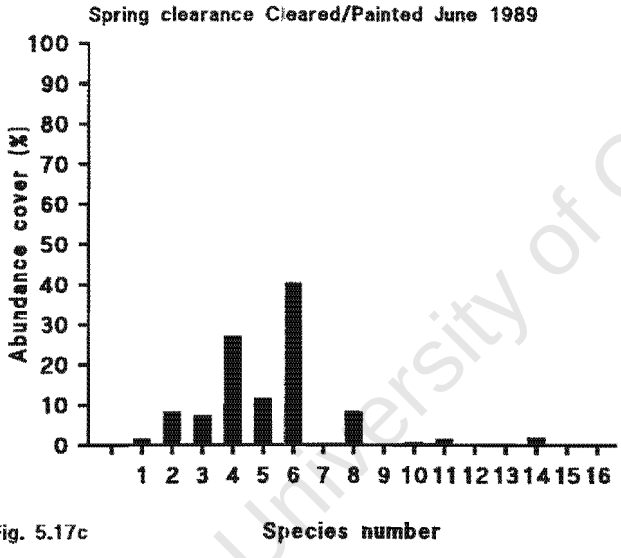


Fig. 5.17c

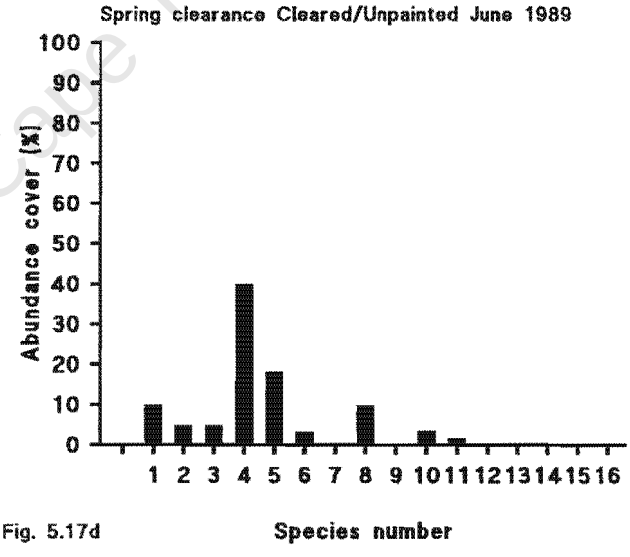


Fig. 5.17d

Figure 5.17 Species diversity and abundance cover in different treatment quadrats: spring-initiated disturbance experiment, June 1989: a) control; b) plants present, grazers removed; c) plants and grazers removed; d) plants removed, grazers present.

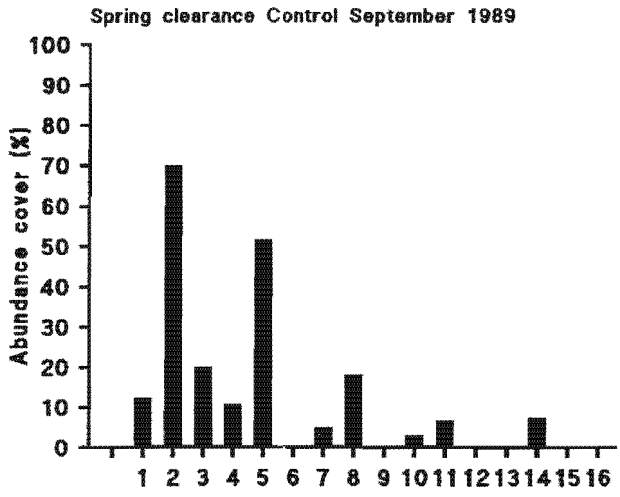


Fig. 5.18a

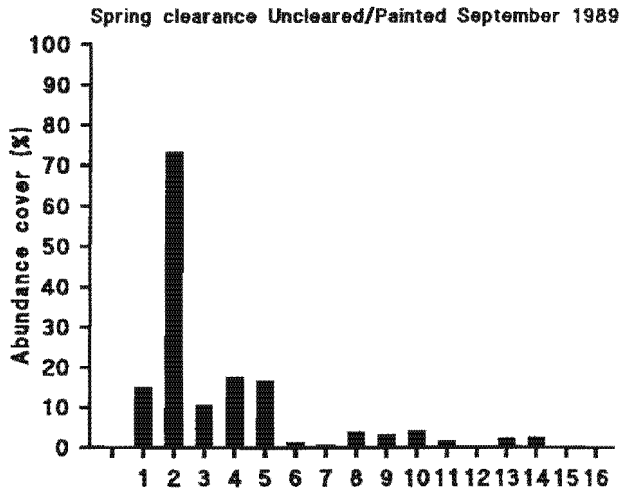


Fig. 5.18b

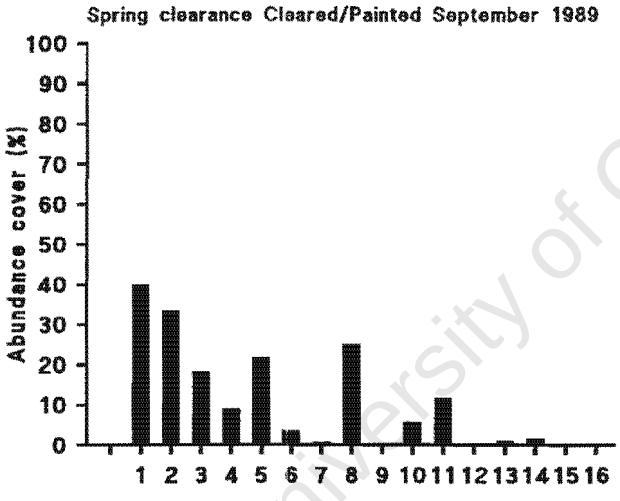


Fig. 5.18c

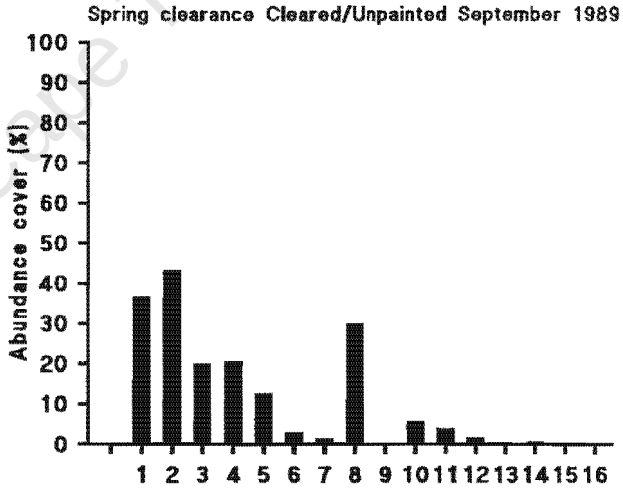


Fig. 5.18d

Figure 5.18 Species diversity and abundance cover in different treatment quadrats: spring-initiated disturbance experiment, September 1989: a) control; b) plants present, grazers removed; c) plants and grazers removed; d) plants removed, grazers present.

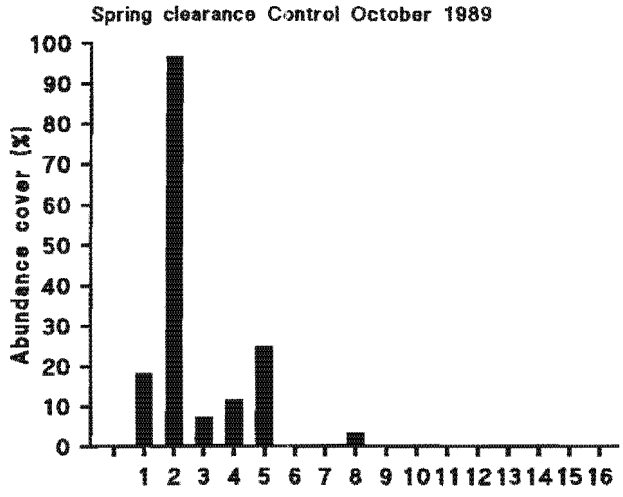


Fig. 5.19a

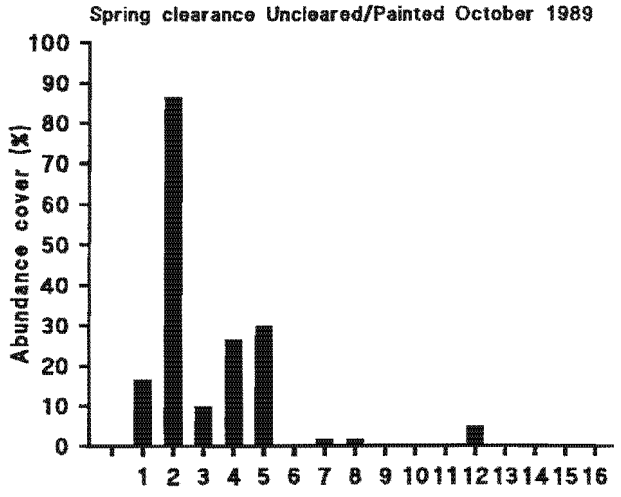


Fig. 5.19b

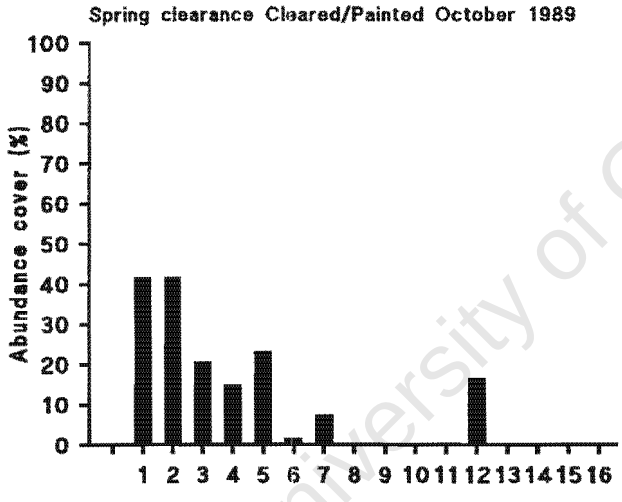


Fig. 5.19c

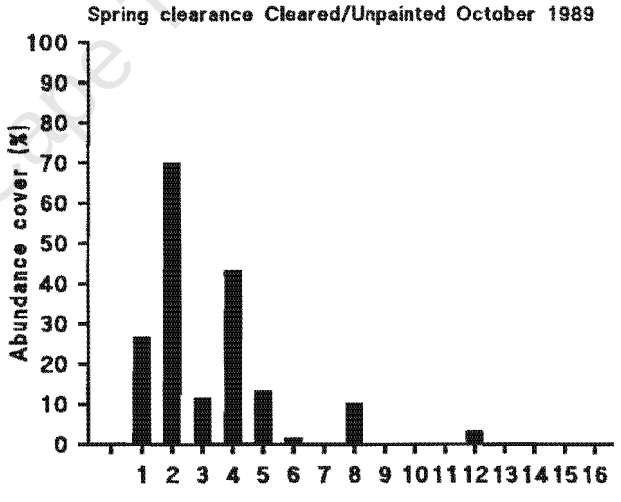


Fig. 5.19d

Figure 5.19 Species diversity and abundance cover in different treatment quadrats: spring-initiated disturbance experiment, October 1989: a) control; b) plants present, grazers removed; c) plants and grazers removed; d) plants removed, grazers present.

present (fig. 5.16d).

There was very little change in the ordination pattern (fig. 5.13d) seven months after clearance (June 1989). CP quadrats were again most different to the control quadrats, mostly as a result of the dominant presence of *Ulva capensis* (fig 5.17c), *Gigartina polycarpa*, *Sarcothalia stiriata* and *Sarcothalia scutellata* returning in small quantities. UP and CU quadrats were not very different to the control quadrats (fig. 5.17b,d), with small amounts of *U. capensis* being present.

Ten months after clearance, the ordination pattern (fig. 5.13e) was fairly similar to that at the start of the experiment, the most notable change being the decline in *Ulva capensis* in clearedquadrats. Differences appear to be the consequence of succession after the removal of plant material, rather than the effects of grazing preventing recolonization. Populations of *Gigartina polycarpa*, *Sarcothalia stiriata*, *Sarcothalia scutellata* community were equally abundant in quadrats which had been cleared of plant material (fig. 5.18c,d), whereas *Gigartina polycarpa* dominated in quadrats where plant material was left intact (fig. 5.18a,b). Eleven months after clearance, the ordination pattern (fig. 5.13f) was even more similar to that at the start of the experiment, although the effect of the experiment was still evident. The dominance of *Gigartina polycarpa* in uncleared quadrats was clear (fig. 5.19a,b), as was the more even abundance of populations of *G. polycarpa*, *Sarcothalia stiriata* and *Sarcothalia scutellata* in quadrats which had been cleared of plant material (fig. 5.19c,d).

5.4 DISCUSSION

From a commercial perspective, the simultaneous harvesting of *Gigartina polycarpa* and *Sarcothalia stiriata* makes economic sense. Whilst the maximum annual harvesting yield of both species would be attained by harvesting at monthly intervals, the negative impact on reproductive capacity gives rise to concern about the long-term viability of such a harvesting regime. Furthermore, the economic viability of monthly harvests is open to question. For simultaneous harvesting, the fact that both yield per harvest and reproductive biomass are at a maximum when harvested at four-monthly intervals, make this the recommended harvesting interval. Winter (May - August) harvests are not recommended for either species since biomass is at a minimum during this period. A harvest in April, immediately prior to the onset of the period of winter storms (May through September) appears logical, since these storms are

responsible for the natural removal of a large portion of the biomass (see chapter two). Two other harvests, one in spring (October) and another in mid-summer (January) during the growing season would also make sense, in that they would ensure maximum harvest yield and simultaneously permit regrowth without negatively impacting reproductive capacity. For example, in *Mastocarpus stellatus* (Stackhouse) Guiry recovery is related to harvesting season, recovery after summer harvests being more rapid and more extensive than after winter harvesting (Burns and Mathieson, 1972b). Before such a harvesting regime can be implemented on a broad scale, it should first be assessed over a number of growing seasons by means of an experimental pilot-scale implementation. Harvests during the middle and latter half of the growing season when plant biomass is at its greatest or plants are at their most productive have been recommended for other commercial seaweeds (eg. *Porphyra* spp., Nelson and Conroy, 1989; *Gymnogongrus furcellatus*, Santelices *et al.* 1989; *Hypnea spicifera*, van Zyl, 1993). By contrast, in *Mazzaella laminariodes,* Gomez and Westermeier (1991) observed no negative effects if harvesting took place outside the primary growth season. Under the regime recommended here, a sustainable harvest yield (fresh weight) of *ca.* $2kg.m^{-2}.yr^{-1}$ and $9kg.m^{-2}.yr^{-1}$ could be expected for *G. polycarpa* and *S. stiriata*, respectively, the mean yield per harvest under a four-monthly harvesting regime comfortably exceeding that of a monthly harvesting regime. Thus, an appropriate harvesting strategy allows regrowth and multiple harvests and has a stimulating effect on regrowth, a phenomemon which has been observed previously in various genera (*e.g. Fucus vesiculosus*, Keser *et al.* 1981; *Ascophyllum nodosum*, Sharp, 1981; *Mazzaella laminarioides*, Gomez and Westermeier, 1991). Regrowth of harvested stands of *A. nodosum* can be dependent upon the extent of the remnant portion after harvesting (Lazo and Chapman, 1996). In *Gymnogongrus furcellatus*, larger numbers of growing apices which remain in less severely harvested quadrats, promote a more rapid and more extensive recovery in biomass (Santelices *et al.* 1989). Similarly, the reduction in harvest yield for both *G. polycarpa* and *S. stiriata* by on average 80% as a consequence of harvesting by cutting (this study), ensures that harvesting by hand-plucking is the only ecologically viable harvesting method for these two species. Similar negative impacts when the majority of plant material is removed have been observed in *Porphyra* spp. (Nelson and Conroy, 1989) and *G. furcellatus* (Santelices *et al.* 1989). From these latter examples and this study, it can be concluded that recovery is good where harvesting does not impact the lower portions of the

thallus, including the attachment system, especially in species (*e.g. G. polycarpa* and *S. stiriata*) which do not have refuge in a morphologically distinct alternate life-history phase (*e.g. Porphyra* spp. - conchocelis phase). Harvesting strategies which minimize negative effects on reproductive capacity are essential management tools (Santelices *et al.* 1989) and contribute to long-term population stability. Under a four-month harvesting interval, reproductive capacity of both *G. polycarpa* and *S. stiriata* are enhanced, this interval thus serving this management objective.

In the disturbance quadrats subject to ordination analyses, the species composition of each experimental treatment at each sampling interval during both winter and summer clearances display only minor differences, implying that ecological differences in community structure are more likely the result of differences in abundance rather than species presence or absence. Within stands of *Gigartina polycarpa* and *Sarcothalia stiriata*, the disturbance provided by clearing presents an opportunity for just four additional species to become established. Dayton *et al.* (1992) concluded that large scale episodic events override biological mechanisms as community structuring processes only in the short-term, biological responses to such events being relatively rapid. Similarly, the ordination analyses presented here show relatively rapid recovery of cleared stands of *G. polycarpa* and *S. stiriata*, and contrast with the observation by Kennelly (1987), that cleared beds of the Australian kelp *Ecklonia radiata* (C. Agardh) J. Agardh are notable for their variability in species composition after recolonization. Stands of *G. polycarpa* and *S. stiriata* appear to be very resilient, persisting longer than the lifespan of individuals. This implies that small scale biological processes are more important than episodic disturbances. The fact that cleared, grazer excluded plots were colonized by the opportunistic *U. capensis* and took longer to return to a state similar to other treatments lends support to this statement, the lack of grazing pressure acting to increase abundance of the opportunist species. Paine and Vadas (1969) observed that moderate grazing pressure may increase diversity by preventing dominance by one species, this effect being apparent in cleared quadrats with grazers present, which possessed a greater species diversity than those without grazers. A similar phenomenon was observed in stands of *Gymnogongrus furcellatus* and *Mazzaella laminarioides*, where removal of patellid grazers led to a substantial increase in abundance rather than diversity (Moreno and Jaramillo, 1983), and permitted these two species to outcompete other species with a resultant change in the zonation limits of their

populations. Thus, interspecies competition is also affected by grazing pressure. Lubchenco (1978) noted that the relative dominance of *Chondrus/Enteromorpha* populations in New England was dependent upon the density of *Littorina littorina*, high densities of the latter limiting the growth rate of *Enteromorpha* sp. Similarly, Lubchenco (1980) observed that heavy limpet grazing permitted various fucoid species to outcompete the carrageenophyte *Chondrus crispus*.

The observation by Ricklefs (1987) that terrestrial community structure represents large-scale histories of dispersal and local processes such as grazing, competition and stochastic variation imposed over physical processes that influence the biota, appears to hold true for communities of *Gigartina polycarpa* and *Sarcothalia stiriata*. In contrast, the sea palm *Postelsia palmaeformis* Ruprecht is dependent upon local disturbance for its persistence (Paine, 1979). Extremely localized spore dispersal patterns (*e.g. Sargassum spinuligerum* Sonder; Kendrick and Walker, 1991) may be a causal factor in such a life-history strategy.

CHAPTER 6

LIGHT AND TEMPERATURE TOLERANCES OF *GIGARTINA POLYCARPA* AND *SARCOTHALIA STIRIATA* IN CULTURE

6.1 INTRODUCTION

Gigartina polycarpa and *Sarcothalia stiriata* are typical members of the seaweed flora of the temperate Benguela marine province of the west coast of Southern Africa, being very common between Lüderitz in Namibia and the rocky shores of the west coast of South Africa. In the south, both species are abundant between Cape Point and Cape Agulhas (Stegenga *et al.* 1997), the area presently known as the western overlap region (Bolton and Anderson, 1997). *Gigartina polycarpa* is endemic to Southern Africa, and has been recorded as far east as Three Sisters (33°35.5'S, 26°55.4'E) near Port Alfred in the Eastern Cape province (H. Stegenga, *pers. comm.*). The eastward limit of *S. stiriata* appears to be Cape Agulhas (Stegenga *et al.* 1997), this entity also having been recorded from the South Atlantic island of Tristan da Cunha (Baardseth, 1941).

Bolton (1986) related the distributions of 205 South African seaweed species to inshore seawater temperature, and found a significant discontinuity in distribution patterns at Cape Agulhas, which was proposed as the junction between the south coast (Agulhas) and west coast (Benguela) marine provinces, separated by a transition zone (the western overlap) between Cape Agulhas and Cape Point. Later studies of the distribution of various taxa (Stegenga and Bolton, 1992; Bolton and Stegenga, 1994) further strengthened the idea of a west coast transition zone.

Historically, the west coast marine province of Southern Africa has been considered cold temperate (Stephenson, 1948; Hedgpeth, 1957; Knox, 1960) and the south coast warm temperate (Stephenson, 1948). Conversely, Ekman (1953) and Briggs (1974) considered the west coast warm temperate. Bolton (1986) initially concurred with the latter, but later concluded (Bolton and Anderson, 1997) that the west coast was "cool temperate" *sensu* Emanuel *et al.* (1992), temperature conditions in this region being somewhat intermediate (minimum monthly mean 11.5°C; maximum monthly mean 14°C; annual mean 12-13°C; Bolton, 1986) between the criteria generally used to define cold and warm temperate

conditions (monthly mean temperatures: cold temperate - winter $<10°C$, summer $>10°C$; warm temperate - winter $<20°C$, summer $>15°C$). Because of the intermediate nature of seawater temperatures, observed temperate tolerances of some west coast species have been at variance with the perceived "cold" nature of the region. For example, *Ecklonia maxima* (Bolton and Levitt, 1985), *Laminaria pallida* (Branch, 1974), *Macrocystis angustifolia* (Branch, 1974) and *Suhria vittata* (Anderson and Bolton, 1985) have all shown growth optima at temperatures between 15°C and 20°C. Other studies on the temperature tolerances of South African seaweeds correlate well with their geographic distribution and the marine provinces defined by Bolton and Anderson (1997). For example, *Gelidium pristoides*, with an optimum growth range of 15-23°C (Carter, 1985) complies with the temperature criteria (Bolton, 1986) used to define the Agulhas province and the Western and Eastern overlap regions *sensu* Bolton and Anderson (1997), its geographic distribution being limited to these regions (Day, 1969). Photosynthesis-irradiance (P-I) curves have been determined for a number of South African littoral and sublittoral algae (Levitt and Bolton, 1990; Levitt, 1993), including both littoral and sublittoral populations of *Gigartina polycarpa*. Both sublittoral (Levitt and Bolton, 1990) and littoral (Levitt, 1993) populations of *G. polycarpa* are adapted to high levels of irradiance. Photosynthetic production of *G. polycarpa* is related to wave exposure, being maximal in semi-exposed localities (Jackelman and Bolton, 1990). However, photosynthetic responses of spores and sporelings can be expected to differ from adult plants because of shading of the former by the latter. No data are available regarding light-responses of *Sarcothalia stiriata*, this species being confined to the eulittoral and shallow sublittoral (<2.5m depth, Jackelman 1996).

In view of the limited potential for harvesting of natural stocks of these two species (chapter 2), their potential for mariculture should be assessed. In addition to the differences in growth rates between these two species (chapter 4), differences in light and temperature tolerances for growth would be essential in deciding which life-history phases of either or both of these species have any mariculture potential.

The aims of this study were thus twofold:

1. To determine the optimum irradiance for germination and growth of sporelings of *Gigartina polycarpa* and *Sarcothalia stiriata* and to assess the ecological implications of any differences between them.

2. To determine the temperature tolerances for germination and development of sporelings of *Gigartina polycarpa* and *Sarcothalia stiriata*, and to assess these in terms of differences in their geographic distribution and biogeographic affinities.

6.2 MATERIALS AND METHODS

Reproductively mature cystocarpic and tetrasporic material of *Gigartina polycarpa* and *Sarcothalia stiriata* was collected from Kommetjie on the west coast of the Cape Peninsula during June 1996. This material was brought to the laboratory, sorted by species and life-history phase, and kept overnight in the dark at 0°C in clear plastic bags with a small amount of seawater to provide moisture. Release of carpospores and tetraspores was stimulated in the following manner. Firstly, material relatively free of epiphytes and polychaetes was chosen for sporulation. Plant material was then vigorously cleaned using a toothbrush and a 1% povidone-iodine solution in seawater to remove epiphytic organisms. Thalli were then rinsed twice in fresh water followed immediately by a rinse in sterile seawater. Thalli of the same species and life history phase were then placed together in a clean 25ℓ bucket, covered with sterile seawater and left for six to eight hours at 15°C to allow sporulation to take place. After sporulation, the plant material was removed and the excess water poured off, leaving a volume of approximately 500ml containing a highly concentrated spore suspension. This suspension was agitated to prevent spore clumping and a 1ml suspension used to inoculate 90mm diameter crystallizing dishes containing 200ml of one-third strength enriched seawater medium (PES; Provasoli, 1968). In order to allow subsequent observation and measurement of settled sporelings, a 76x26mm microscope slide was placed in each crystallizing dish. To inhibit diatom contamination, 1ml of a saturated aqueous solution of germanium dioxide (GeO_2) was added to the medium in each dish. The medium was renewed weekly. Four replicate dishes were used for each life-history phase of both species for each experimental treatment. For light experiments, growth of sporelings was measured at five different irradiances (0.5, 5, 27, 50 and 94μmol.m^{-2}.s^{-1}) at a temperature of 15°C. Light was measured using a Licor Li-1000 datalogger connected to a Licor underwater light sensor no. UWQ3684. Incubations were conducted under banks of cool white fluorescent lamps (Osram L36W/20, 5 per bank) which could be individually switched on or off to achieve the required photon flux density, with an LD of 16:8. Temperature experiments were conducted in temperature controlled rooms at six

different temperatures, viz. 0°, 5°, 10°, 15°, 20° and 25°C, all ±1°C. Twenty five newly settled sporelings of each life-history phase of both species were measured two hours after inoculation to obtain an idea of initial spore size prior to any growth effects of experimental treatments. Sporeling development was recorded by measuring germling disc diameter of 100 individuals (25 per replicate dish) of each life-history phase of each species for each irradiance and temperature treatment at weekly intervals for 5 weeks after sporulation. After this time, coalescing germlings and the initiation of upright thalli rendered further observations of disc diameter meaningless. Measurement was by means of a calibrated eyepiece micrometer installed in a Zeiss photomicroscope.

6.3 RESULTS

6.3.1 Size of newly-settled spores

Both carpospores and tetraspores of both species are of similar size (table 6.1), there being no significant difference in size of newly-settled spores ($F_{0.05(2),3,96} = 2.89 < 3.26$). Newly settled germlings of either species are indistinguishable from one another, forming a disc 25-30 μm

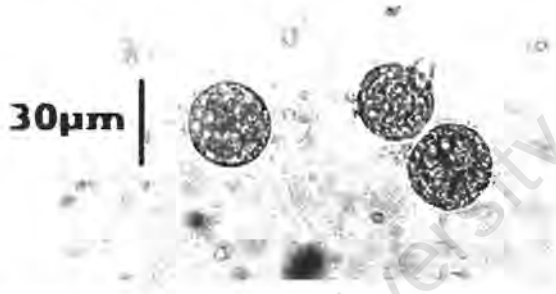


Figure 6.1 Newly released carpospores of *Gigartina polycarpa*.

Figure 6.2 One-day old carpospore germlings of *Gigartina polycarpa* undergoing mitosis.

Species	Spore diameter (μm)	S.E.
G. polycarpa carpospores	29.28	1.03
G. polycarpa tetraspores	26.79	0.59
S. stiriata carpospores	28.96	0.72
S. stiriata tetraspores	26.56	0.51

Table 6.1: Sporeling diameter of newly-settled sporelings of *Gigartina polycarpa* and *Sarcothalia stiriata*.

in diameter (fig. 6.1), which enlarges vegetatively by successive divisions (fig. 6.2) until an upright thallus is initiated after approximately five weeks at a diameter of 300-500μm

6.3.2 Growth response to light

Carpospores of *Gigartina polycarpa* (fig. 6.3a) displayed very little growth at low irradiances of 0.5 and 5μmol.m^{-2}.s^{-1}, the former reaching diameters of 45μm and 65μm, respectively, after five weeks. Significantly better growth was obtained at 27μmol.m^{-2}.s^{-1}, germling diameter reaching 111μm over the same period. Germling growth improved significantly at 50μmol.m^{-2}.s^{-1} (reaching 146μm). Germling size at 94μmol.m^{-2}.s^{-1} (149μm) was not significantly different from that at 50μmol.m^{-2}.s^{-1}.

Tetraspores of *Gigartina polycarpa* (fig. 6.3b) displayed a similar growth pattern to carpospores, reaching diameters after 5 weeks of 44μm and 64μm at 0.5μmol.m^{-2}.s^{-1} and 5μmol.m^{-2}.s^{-1}, respectively, these values not being significantly different. At 27μmol.m^{-2}.s^{-1} tetraspore growth was again similar to carpospores at the same irradiance, germling diameter reaching 110μm, which was significantly greater than growth at 5μmol.m^{-2}.s^{-1}. Tetraspore germling growth reached a maximum at an irradiance of 50μmol.m^{-2}.s^{-1} (148μm after 5 weeks), which was significantly greater than germlings at 27μmol.m^{-2}.s^{-1}. At 94μmol.m^{-2}.s^{-1}, growth of *G. polycarpa* tetraspores was almost identical (148μm) to growth at 50μmol.m^{-2}.s^{-1}, there being no significant difference between the two.

Like *Gigartina polycarpa*, carpospores of *Sarcothalia stiriata* (fig. 6.4a) displayed little growth at low irradiances, reaching diameters after five weeks of 40μm and 57μm, respectively, at 0.5 and 5μmol.m^{-2}.s^{-1}. Growth improved at 27μmol.m^{-2}.s^{-1}, germling diameter increasing significantly to 187μm over the same period. As in *G. polycarpa*, maximal growth was reached at an irradiance of 50μmol.m^{-2}.s^{-1} (222μm), growth being significantly greater than growth at 27μmol.m^{-2}.s^{-1}. Similarly, growth of carpospore germlings at 94μmol.m^{-2}.s^{-1} (227μm) was not significantly different from that at 50μmol.m^{-2}.s^{-1}.

A similar growth pattern to carpospores was shown by tetraspores of *Sarcothalia stiriata* (fig. 6.4b). At the lowest irradiance of 0.5μmol.m^{-2}.s^{-1} tetraspores grew to a diameter of 39μm after five weeks. At 5μmol.m^{-2}.s^{-1} tetraspores were marginally, but significantly, larger than at 0.5μmol.m^{-2}.s^{-1}, attaining a size (diameter 56μm) similar to that of carpospores after five weeks. Like carpospores, a significant, substantial growth increment was observed at an irradiance of 27μmol.m^{-2}.s^{-1}, (germling diameter 185μm). As in carpospores, tetraspore

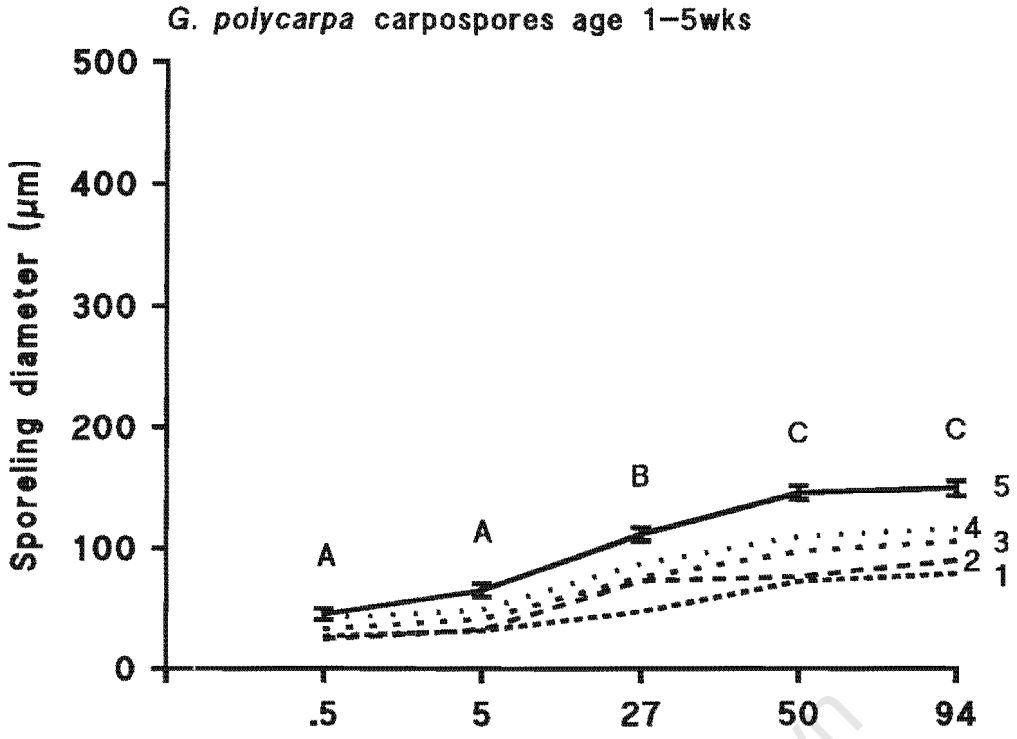


Fig. 6.3a

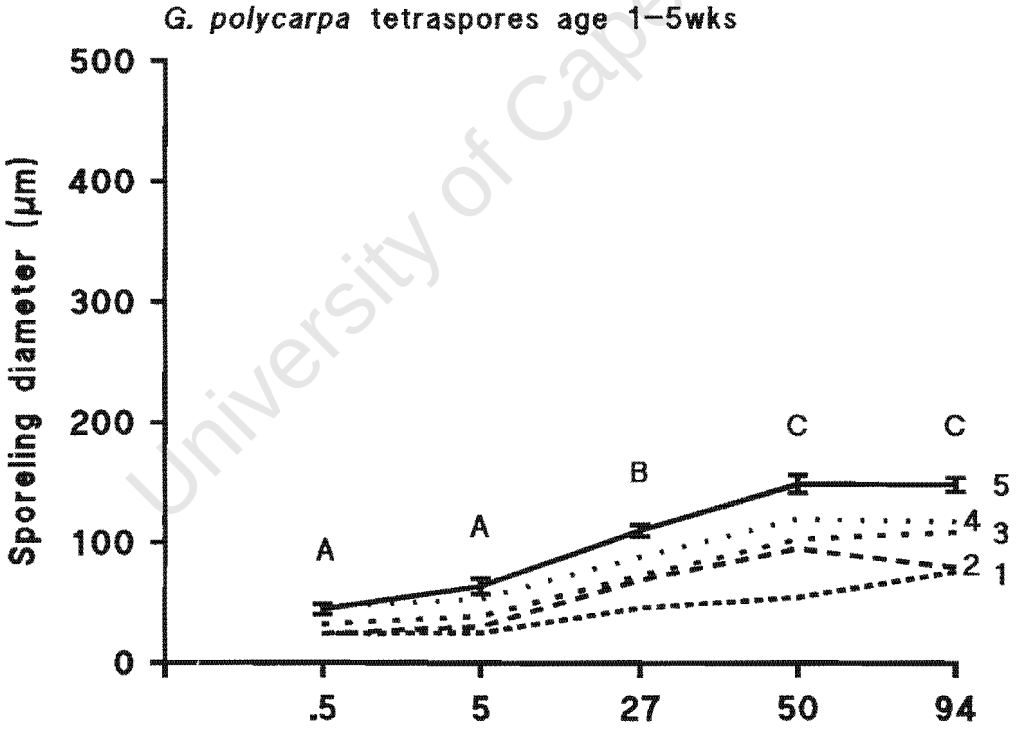


Fig. 6.3b

Figure 6.3 Growth of *G. polycarpa* germlings in culture at irradiances of 0.5, 5, 27, 50 and 94μmol.m^{-2}.s^{-1}. Treatments with the same letter (Student-Newman-Keuls test) are not significantly different. a) carpospores $F_{0.05(2),1,6} = 9.79 > 8.81$; b) tetraspores $F_{0.05(2),1,6} = 10.36 > 8.81$. 95% confidence limits indicated.

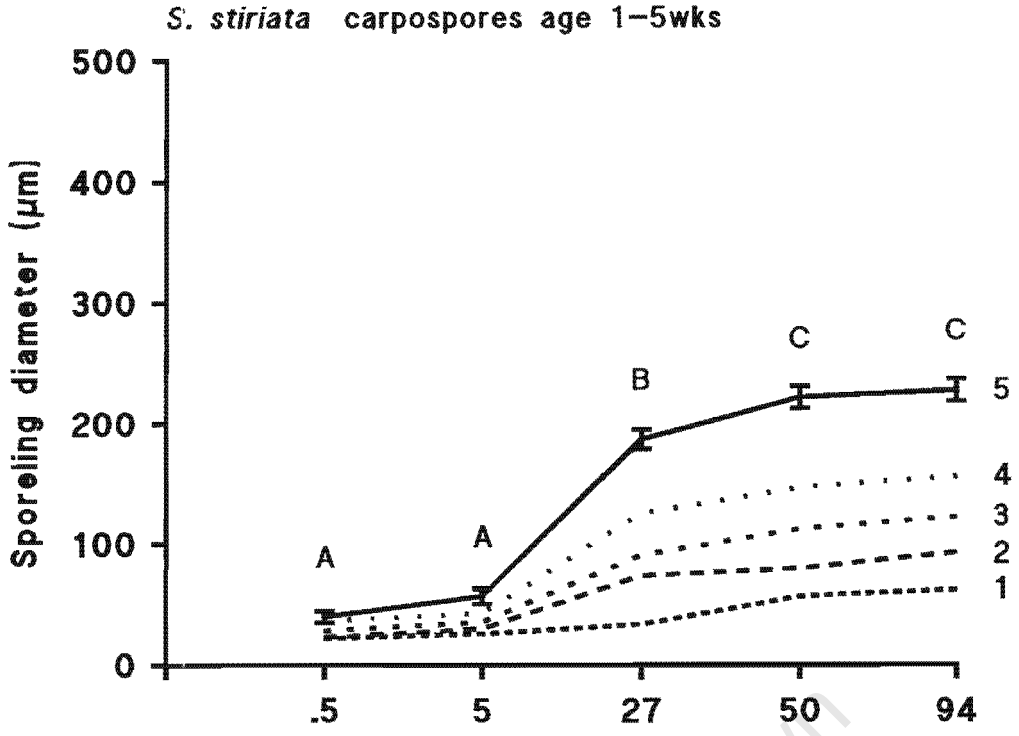


Fig. 6.4a

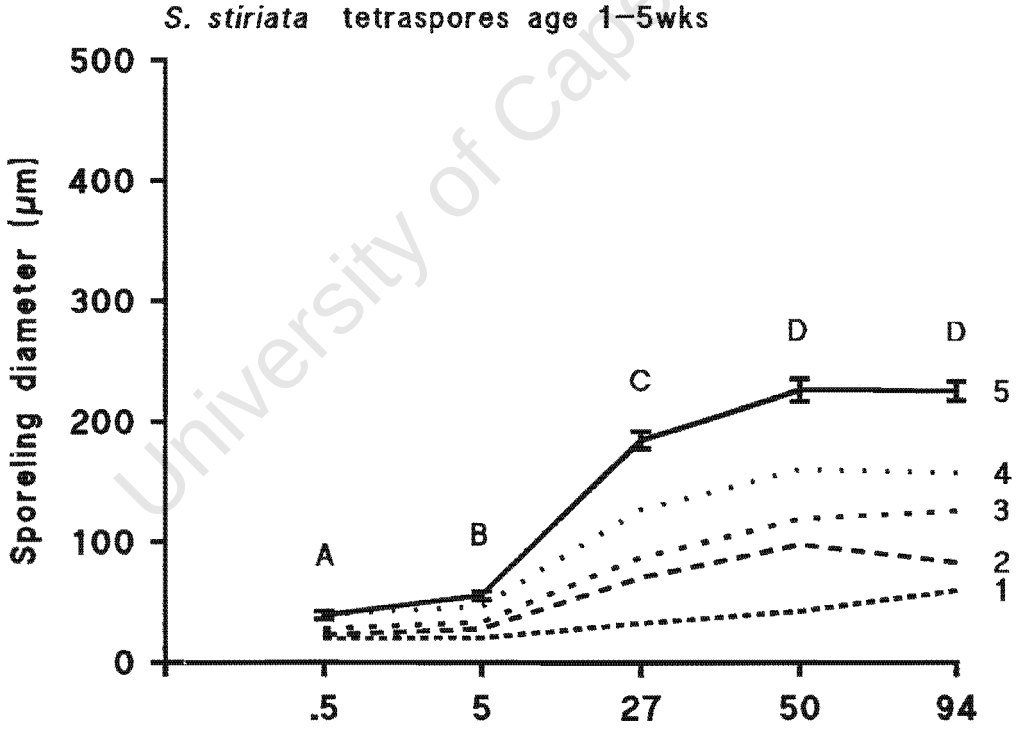


Fig. 6.4b

Figure 6.4 Growth of *S. stiriata* germlings in culture at irradiances of 0.5, 5, 27, 50 and 94μmol.m^{-2}.s^{-1}. Treatments with the same letter (Student-Newman-Keuls test) are not significantly different. a) carpospores $F_{0.05(2),1,6} = 14.62 > 8.81$; b) tetraspores $F_{0.05(2),1,6} = 13.94 > 8.81$. 95% confidence limits indicated.

germling growth was saturated at an irradiance of 50μmol.m^{-2}.s^{-1} (diameter 226μm) and was significantly greater than growth at 27μmol.m^{-2}.s^{-1}, but was not significantly different from growth at 94μmol.m^{-2}.s^{-1} (225μm) after five weeks of incubation.

6.3.3 Growth response to temperature

At 0°C, *Gigartina polycarpa* carpospores showed no growth, dying within two weeks of sporulation (fig. 6.5a). At 5°C, death did not occur, but growth was extremely slow, germling diameter increasing to only 62μm after five weeks in culture. Compared with growth at 5°C, growth of carpospores at 10°C improved significantly, germlings reaching a diameter of 153μm. Growth at 15°C was also significantly better than growth at 10°C, germlings reaching a diameter of 228μm. Growth at 20°C was not significantly different from growth at 15°C, germlings reaching a diameter of 236μm over the same period. Carpospore germlings were unable to tolerate 25°C, death resulting in less than a week.

Growth responses to temperature of *Gigartina polycarpa* tetraspores (fig. 6.5b) were similar to those observed for carpospores. At 0°C, tetraspores showed no growth and survived a little longer than carpospores, dying within three weeks of sporulation. At 5°C, growth was also slow, germling diameter increasing to 78μm after five weeks. Tetraspore germling growth was significantly greater at 10°C than at 5°C: after 5 weeks germlings reached a diameter of 154μm. At 15°C, tetraspore germling growth was significantly greater than at 10°C, germling diameter reaching 231μm. At 20°C, the maximum increase in tetraspore germling diameter was apparent, a mean diameter of 241μm being reached, but this was not significantly greater than growth at 15°C. Like carpospores, tetraspore germlings were unable to tolerate 25°C, death resulting in less than one week. Tetraspore germlings were almost identical in size to carpospore germlings of the same age at the same temperatures.

Carpospores of *Sarcothalia stiriata* survived considerably longer than carpospores of *Gigartina polycarpa* at 0°C, but also showed no growth, dying within four weeks of sporulation (fig. 6.6a). Germlings survived at 5°C, and growth was greater than either carpospores or tetraspores of *G. polycarpa* at this temperature, germling diameter increasing to 104μm after five weeks in culture. Growth of carpospores at 10°C was significantly greater than at 5°C, germling diameter increasing to 191μm, and was also slightly better than growth of *G. polycarpa* carpospores and tetraspores at this temperature. Compared with growth at 10°C, carpospore growth at 15°C showed a significant increase, germling diameter reaching 414μm.

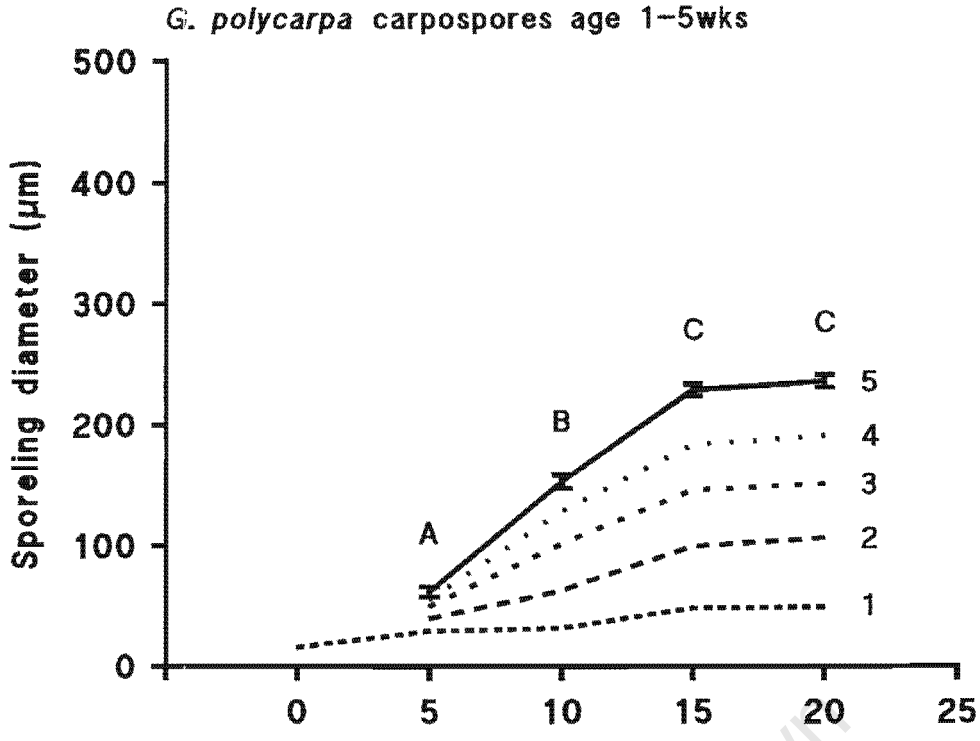


Fig. 6.5a

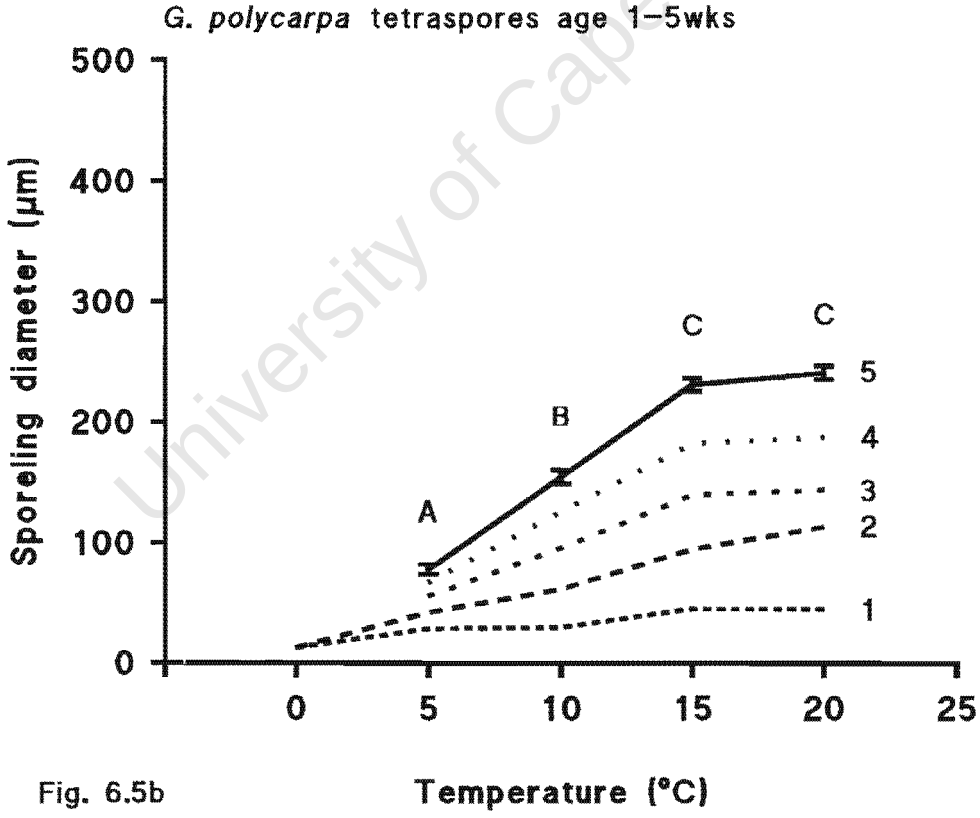


Fig. 6.5b

Figure 6.5 Growth of *G. polycarpa* germlings in culture at temperatures of 0, 5, 10, 15, 20 and 25°C. Treatments with the same letter (Student-Newman-Keuls test) are not significantly different. a) carpospores $F_{0.05(2),1,6} = 10.61 > 8.81$; b) tetraspores $F_{0.05(2),1,6} = 11.34 > 8.81$. 95% confidence limits indicated.

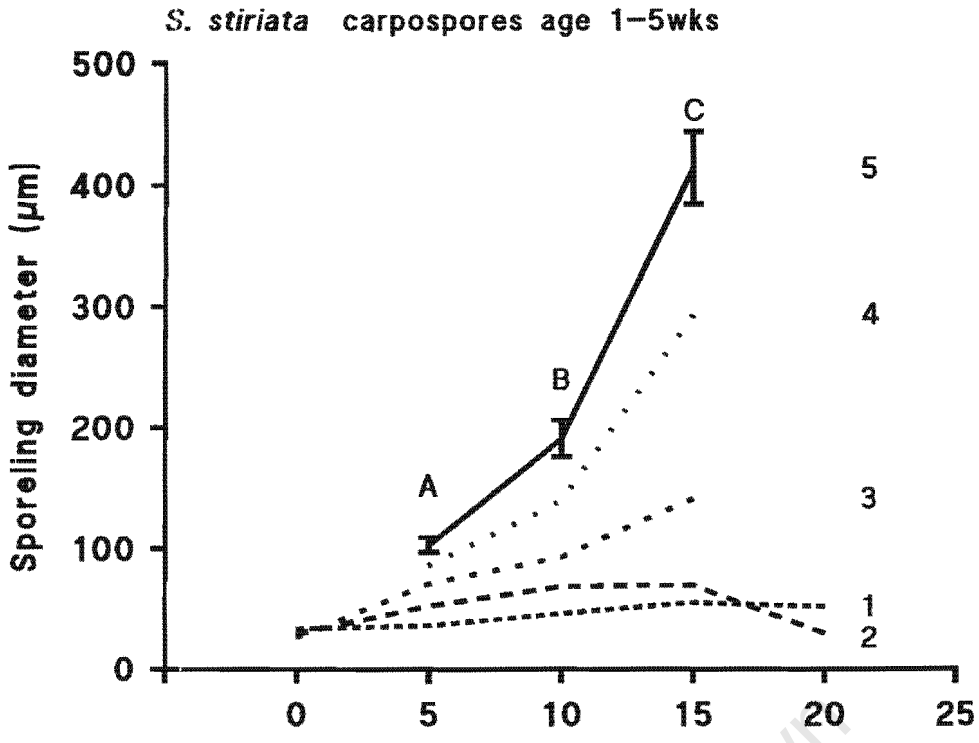


Fig. 6.6a

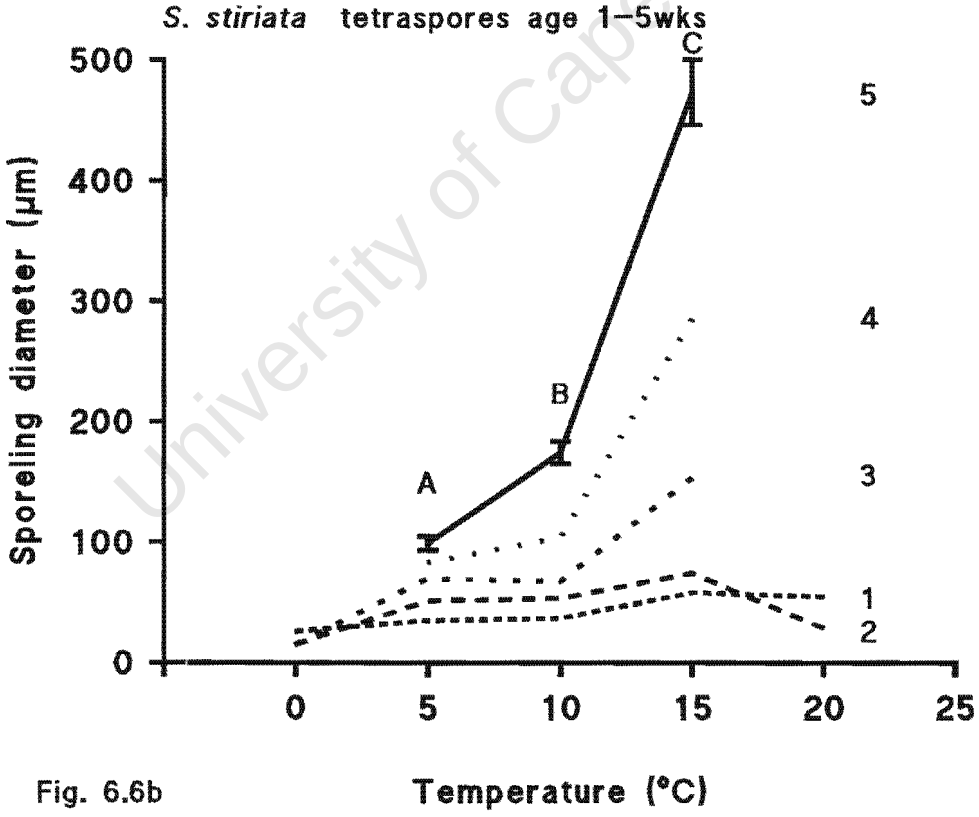


Fig. 6.6b

Figure 6.6 Growth of *S. stiriata* germlings in culture at temperatures of 0, 5, 10, 15, 20 and 25°C. Treatments with the same letter (Student-Newman-Keuls test) are not significantly different. a) carpospores $F_{0.05(2),1,6} = 9.26 > 8.81$; b) tetraspores $F_{0.05(2),1,6} = 11.75 > 8.81$. 95% confidence limits indicated.

At 20°C, survival was again negatively affected, all the germlings dying within three weeks of sporulation. At 25°C, germlings survived for less than one week after sporulation.

Growth responses to temperature of *Sarcothalia stiriata* tetraspores were similar to those observed for carpospores of this species. At 0°C, germlings survived longer than germlings of *Gigartina polycarpa* carpospores and tetraspores, but 100% mortality occurred within four weeks of sporulation. At 5°C, growth was slow, being similar to carpospores at the same temperature, germlings reaching a mean diameter of 99μm after five weeks in culture. Compared with growth at 5°C, tetraspore germling growth at 10°C was significantly enhanced (mean germling diameter 174μm), although germlings were slightly smaller than carpospore germlings at this temperature. As in carpospore germlings, a substantial and significant growth increment was evident at 15°C when compared with 10°C, tetraspore germling diameter increasing to 414μm after five weeks in culture. At 20°C, germling growth and survival were negatively affected, all germlings dying within three weeks of sporulation. As in *S. stiriata* carpospore germlings, tetraspore germlings were unable to tolerate 25°C, death resulting in less than one week.

6.4 DISCUSSION

Although carpospore and tetraspore germlings of both *Gigartina polycarpa* and *Sarcothalia stiriata* grow poorly at low irradiances ($\leq 5\mu mol.m^{-2}.s^{-1}$) the fact that they persist for at least five weeks in near darkness indicates that they are adapted for survival under sub-optimal light conditions. Presumably, this strategy facilitates rapid growth when light conditions improve. A similar strategy for optimizing survival under low-light conditions was noted by Bolton and Levitt (1985) in gametophytes of the South African kelp *Ecklonia maxima* (Osbeck) Papenfuss. The ability to survive prolonged periods of darkness is characterictic of kelp gametophytes (tom Dieck, 1993). Under ideal growth conditions kelp gametophytes are short-lived (Bolton and Levitt, 1985), reaching reproductive maturity in a matter of days. Long-term survival of near dark conditions is therefore advantageous since only a few days of ideal conditions are necessary for the sporophyte phase to be initiated. In both *G. polycarpa* and *S. stiriata*, carpospores and tetraspores give rise to perennial individuals which take a long time to reach reproductive maturity and there appears to be little advantage to a long-term germling survival strategy. The adaptation of *G. polycarpa* and *S. stiriata* to low irradiances is therefore most

likely a short-term strategy for surviving transient environmental fluctuations common in the littoral environment. The fact that germling growth of both *G. polycarpa* and *S. stiriata* improved considerably at irradiances of *ca.* 30μmol.m^{-2}.s^{-1}, and was saturated at irradiances of *ca.* 50μmol.m^{-2}.s^{-1}, supports this conclusion since daytime natural irradiances in Cape waters are commonly greater than 200μmol.m^{-2}.s^{-1} and only rarely less than 30μmol.m^{-2}.s^{-1} in water depths down to 6m (Anderson and Bolton, 1985). Thus, the necessity of surviving low irradiances for an extended period is unlikely. Mature thalli of *G. polycarpa* are sun-adapted, being photosynthetically light-saturated at an irradiance of *ca.* 200μmol.m^{-2}.s^{-1} in sub-littoral populations (Levitt and Bolton, 1990) and at *ca.* 400μmol.m^{-2}.s^{-1} in eulittoral populations (Levitt, 1993). Sun-adapted members of the Gigartinales have also been recorded elsewhere, *e.g. Chondrus crispus* and *Mastocarpus stellatus* (Burns and Mathieson, 1971,1972a). The low saturation levels displayed by germlings of *G. polycarpa* and *S. stiriata* can be interpreted as an adaptation to the low light levels experienced in the understorey of densely populated algal beds, low light-saturation levels permitting maximal growth until the thallus is large enough to outgrow shading by neighbouring plants. Maximal growth at a slightly higher saturating irradiance (80μmol.m^{-2}.s^{-1}) has been recorded in adult thalli of the South African agarophyte *Gracilaria gracilis* (Stackhouse) Steentoft, Irvine *et* Farnham (Engledow and Bolton, 1992). Values of this order are common in species occupying the lower eulittoral and shallow sublittoral (Lüning, 1990).

Gigartina polycarpa displays a broader tolerance to temperature extremes than *Sarcothalia stiriata*, carpospore and tetraspore germlings of the former surviving in the range 5-20°C. Anderson and Bolton (1985) observed a broad range of temperature tolerance (10-22.5°C) in the agarophyte *Suhria vittata* (L.) J. Ag, an epiphyte of the kelp *E. maxima*, considered a warm-temperate species by Bolton and Levitt (1985). *Gigartina polycarpa* can therefore be considered a warm temperate species. In contrast, *S. stiriata* with a survival range of 5-15°C, can be considered more a cold temperate entity. Anderson and Bolton (1989) considered the broad temperature range for growth of *Desmarestia firma* (C.Ag.) Skottsb. (8-19°C) as ideal for the west coast upwelling region. The latter conclusion however, is supported more by the fact that the sporophyte of *D. firma* shows a narrow maximum-growth peak of 15-18°C. In contrast, *G. polycarpa* shows substantial growth over a broad temperature range (10-20°C), making this entity ideal for the cool sea temperatures of the west coast as well as some regions

of the warmer south coast (minimum monthly mean 13.7°C; maximum monthly mean 21.2°C; annual mean 17.2-18.2°C; Bolton, 1986). *Sarcothalia stiriata* shows a growth pattern very similar to *D. firma*, tolerating 5-15°C, with a significant growth peak at 15°C. The fact that *S. stiriata* also grows well at 10°C, supports the conclusion that this species is adapted to the temperature regime of the South African west coast.

In both *Gigartina polycarpa* and *Sarcothalia stiriata* the light and temperature growth responses and tolerances of carpospores when compared with their respective tetraspores are almost identical. It therefore appears unlikely that gametophyte dominance in either species (see chapter 3) is the result of differential spore survival due to temperature or irradiance within "the bank of microscopic forms" *sensu* Santelices (1990). Carter (1985) observed similar growth responses in bispores and carpospores of the east coast agarophyte *Gelidium pristoides*, concluding that the imbalance in populations of that species was due to greater bispore production (as opposed to tetraspores) and a greater germination success in carpospores. No evidence to suggest any differences in germination success between carpospores and tetraspores of either *G. polycarpa* or *S. stiriata* was observed, but in both species stimulation of spore release in tetrasporophytes was much easier to achieve than in carposporophytes, and this may be a factor contributing towards gametophyte dominance in these two taxa. In the natural environment carpospore release may be facilitated by invertebrate grazing, grazers tearing open the cystocarps in a similar manner to that observed in *Mazzaella laminarioides* (Buschmann and Santelices, 1987). Nevertheless, the dominance of gametophytes suggests that mechanical methods of carpospore release do not contribute significantly to the recruitment tetrasporophytes.

Bolton and Anderson (1997) define three marine provinces on the South African coast. Of these, the Benguela and Agulhas marine provinces are relevant to this discussion. Bolton (1986) described these area in terms of temperature: the Agulhas province (south coast region, mean annual temperature 18°C); the western overlap region (mean annual temperature 15°C); and the Benguela province (south-western and namaqua sub-provinces, mean annual temperature 13°C). The wide-range of temperature tolerated by *Gigartina polycarpa* germlings place this entity well within the temperature regimes of the south coast, western overlap and the south-western and namaqua sub-provinces, which is confirmed by its geographic distribution (Bolton and Stegenga, 1990; Stegenga *et al.* 1997). The temperature tolerances

displayed by germlings of *Sarcothalia stiriata* place this entity within the western overlap and the south-western and namaqua sub-provinces, which is again confirmed by its South African geographic distribution (Stegenga *et al.* 1997). *Sarcothalia stiriata* has also been recorded from Tristan da Cunha (Baardseth, 1941), which has a mean annual sea surface temperature of 15.25°C (Chamberlain *et al.* 1985), the optimum temperature for growth of this entity.

In a study of Caribbean seaweeds, Pakker *et al.* (1995) found that the temperature tolerances of species investigated from three biogeographic groups were related to the temperatures extant during their evolution and dispersal history. In an analysis of the evolutionary biogeography of southern African Rhodophyta (Hommersand, 1986), most west coast families have an affinity with an historical region defined as the Antiboreal Pacific Ocean. These families were hypothesized to be dispersed from Antarctica into the South Atlantic during the Oligocene via cool currents emanating from the high latitude Pacific Ocean between 32 and 17Ma. The cool-temperate taxa of the west coast are considered to have mainly originated in this manner (Hommersand, 1986). The typically cold-temperate temperature tolerances observed here suggests such an origin for *Sarcothalia stiriata*. According to Bolton and Levitt (1987) upwelling of cool waters on the South African west coast has produced a seaweed flora distinct from the east coast. However, since *S. stiriata* also occurs at Tristan de Cunha, it is unlikely to have an origin as suggested by Hommersand (1986) for west coast endemic species, which are hypothesized to have originated, since the formation of the Benguela system (12Ma), from taxa of Antiboreal Pacific origin.

According to Hommersand (1986) it is possible that species which were once widely distributed in the Indian Ocean have since evolved similar morphological types in response to climatic cooling. Since South African *Gigartina polycarpa* appears to be a warm-temperate entity, it may have such an origin. Although morphologically similar (Christianson *et al.* 1981), the warm-temperate *Gigartina radula* of western Australia is considered a different entity to *G. polycarpa* (Bolton and Anderson, 1990). Womersley (1994) placed *G. radula* within the genus *Sarcothalia*, although this is not convincing since neither the carposporophyte nor the tetrasporopophyte display all the reproductive characters of the genus *Sarcothalia*. In the description of the genus *Sarcothalia*, a key character of the carposporophyte is the formation of a compact envelope which is displaced by radiating gonimoblast filaments (Hommersand *et al.* 1993), whereas in *Sarcothalia radula*, the envelope surrounding the

auxiliary cell is diffuse, and without transverse gonimoblast filaments (Womersley, 1994). Furthermore, Womersley (1994) describes the development of tetrasporangial sori within *S. radula* as being deep within the medulla, but his illustration of this shows a clear formation of the sorus at the boundary between the cortex and medulla, a characteristic of the genus *Gigartina*.

CHAPTER 7

THE TAXONOMIC POSITION OF *GIGARTINA PAXILLATA* PAPENFUSS WITHIN THE FAMILY GIGARTINACEAE

7.1 INTRODUCTION

The systematics of the Order Gigartinales has long been the subject of scientific endeavour. From early, simple species descriptions (*e.g.* Turner, 1808; Agardh, 1820,1821), developed the first classification of taxa (placed in the genus *Sphaerococcus* by C. Agardh, 1823) presently regarded as belonging within the family Gigartinaceae including, for example, *Sphaerococcus canaliculatus* Kützing (*Chondracanthus canaliculatus* (Harvey) Guiry; *Sphaerococcus radula* C. Agardh *(Gigartina polycarpa* (Kützing) Setchell *et* Gardner); *Sphaerococcus stiriatus* C. Agardh (*Sarcothalia stiriata* (Turner) Leister) and *Sphaerococcus gigartinus* C. Agardh (*Gigartina pistillata* (Gmelin) Stackhouse). Kützing (1843) further developed the classification of the Gigartinales to include some of the presently recognized genera (namely *Chondrus*, *Chondracanthus*, *Gigartina* and *Iridaea*), as well as other genera which have since undergone further taxonomic revision and are no longer placed within the Gigartinaceae (*e.g. Grateloupia, Mastocarpus, Furcellaria*). In a first revision, Kützing (1849) added the presently-recognized genus *Sarcothalia*, and renamed *Chondracanthus* as *Chondroclonium*. Shortly thereafter, J. Agardh (1851) reduced the order to four genera, namely *Gloioderma*, *Chondrus*, *Iridaea* and *Gigartina*, this being reversed by Kützing (1867) in a second revision, the changes made in the 1849 classification being reinstated insofar as they pertain to the presently accepted genera. Agardh (1879) further added the genus *Rhodoglossum* to the order. These early classifications, based largely on thallus morphology, culminated in the classification of De Toni (1903), which included extensive lists of species placed within the genera *Chondrus*, *Gigartina* and *Iridaea*. Setchell and Gardner (1933), in a review of the genus *Gigartina*, mentioned the likelihood that relationships within the group were only likely to appear when the development of the cystocarp had been determined for each species, but little further effort was made to elucidate such differences for quite some time.

A revival of interest in the taxonomy of the Gigartinaceae was stimulated by Kim's (1976)

revision which recognized only two genera within the family, *Chondrus* and *Gigartina*. This revision did not meet with general acceptance, mainly because the genera were poorly defined, with too much emphasis being placed on thallus morphology (Guiry and Garbary, 1990). A phylogenetic analysis of the Gigartinaceae by means of cladistics (Guiry and Garbary, 1990) recognized four genera within the family (*Chondrus*, *Gigartina*, *Iridaea* and *Rhodoglossum*), but emphasized the need for precise studies of carposporophyte development and the mode of formation of tetrasporangia before a final generic scheme could be proposed. In the most recent revision of the Gigartinaceae, Hommersand *et al.* (1993) addressed this issue, proposing seven genera for the family based upon a combination of observations of characters of reproductive morphology and reproductive development in both cystocarpic and tetrasporic life-history phases. The recognised genera are: *Chondrus* Stackhouse, *Mazzaella* De Toni, *Iridaea* Bory, *Sarcothalia* Kützing, *Rhodoglossum* J. Agardh, *Chondracanthus* Kützing and *Gigartina* Stackhouse. Subsequent cladistic analysis of *rbc*L gene sequences within the family generally supports this revision (Hommersand *et al.* 1994).

The genus *Gigartina* was erected by Stackhouse (1809) for *Gigartina pistillata*, based on *Fucus pistillatus* S.G. Gmelin (1768). The developmental morphology of *G. pistillata* was described by Hommersand *et al.* (1992), resulting in the first elucidation of characters used in the subsequent revision of the Gigartinaceae. Hommersand *et al.* (1993) examined five South African members of the Gigartinaceae to assess their position within the revised classification. These were *Sarcothalia stiriata*, *Sarcothalia scutellata*, *Sarcothalia lapathifolia*[1], *Gigartina clathrata* and *Mazzaella capensis*. South African material of the type species, *G. pistillata*, is morphologically similar to French material, and in the absence of the type, is presumed to be the same. Two other entities, *Gigartina polycarpa* and *Mazzaella convoluta*, were identified using *rbc*L sequence analysis (Hommersand *et al.* 1994). The taxonomic position of three other South African members of the Gigartinaceae presently located within the genus *Gigartina*, namely *G. paxillata*, *Gigartina insignis* (Endlicher *et* Diesing) Schmitz and *Gigartina minima*

[1]*Sarcothalia lapathifolia* (Kützing) Leister is a new combination published by Hommersand *et al.* (1993). This is almost certainly a misidentifcation of the entity described as *Gigartina polycarpa* in Hommersand *et al.* (1994), the type specimen held at the Rijksherbarium Leiden (L0040238) having been annotated to reflect this (Hommersand, *pers. comm.* 1997).

Kylin, was not addressed in the Hommersand *et al.* (1993) classification.

Gigartina paxillata Papenfuss (1947) was first described from material collected in 1940 from Storms River Mouth (34°01.2'S,23°54.3'E), in the Eastern Cape Province, South Africa. Gametophytes and tetrasporophytes are isomorphic, 5-20cm long, with the carposporophyte developing in one or more terminal or lateral cystocarps borne on slightly compressed papilloid to elongate superficial and marginal proliferations or branchlets (fig. 7.1). Tetrasporangial sori are borne on the marginal branchlets and also superficially on the frond (fig. 7.2). With the exception of its inclusion in a recent flora of the Indian Ocean (Silva *et al.* 1996), this species has not been the subject of further taxonomic study since it was first described. Therefore, the aim of this investigation was to determine the taxonomic position of the entity presently known as *Gigartina paxillata* Papenfuss using the characters of reproductive morphology and reproductive development used in the classification of the Gigartinaceae by Hommersand *et al.* (1993).

7.2 MATERIALS AND METHODS

Mature fertile specimens of tetrasporic and carposporic life-history phases of *Gigartina paxillata* were collected at Arniston (34°40.3'S,20°14.0'E) in the Western Cape Province, South Africa on 5 May 1997. Material was preserved immediately after collection in 5% formalin-seawater and surrounded by black plastic to prevent uncontrolled bleaching of the thallus. In the laboratory, preserved material was placed in a covered dish in formalin-seawater in full sunlight and allowed to bleach for 48 hours, even discolouration (S. Fredericq, University of Southwestern Louisiana, *pers. comm.*) being achieved by regular turning and replenishment of seawater.

Sections for microscopic examination were obtained from 24 carposporic and 21 tetrasporic individuals collected from Arniston. Additional sections were obtained from the type specimen (labelled TT10 cystocarpic, TT10a tetrasporic) which was loaned from the herbarium of the University of California, Berkeley. The type had been bleached and preserved in formalin prior to being pressed and mounted (Papenfuss, 1947). A small portion of tetrasporic and cystocarpic material was excised from the type and rehydrated in 5% formalin-seawater prior to sectioning.

All formalized material was rinsed in distilled water to remove excess salt and formalin prior

Figure 7.1 *Gigartina paxillata* female gametophyte (Bolus Herbarium I1437, G.F. Papenfuss, 9 February 1959).

Figure 7.2 *Gigartina paxillata* tetrasporophyte (Bolus Herbarium 91497, W.E. Isaac, 7 May 1951).

to sectioning. Material was embedded in freezing agent and transverse and longitudinal sections 60μm thick were made using a freezing microtome at -30°C. Sections were then stained with aceto-iron-haematoxylin-chloral hydrate (Wittman, 1965) using the method of Hommersand *et al.* (1992) and mounted in 100% Hoyer's mounting medium (Stevens, 1981). Photographs were taken with a Zeiss photomicroscope using Ilford FP4 monochrome film.

7.3 RESULTS

7.3.1 Carposporangial reproductive development in *Gigartina paxillata*

A terminal ostiole with external pericarp protecting the carposporangia is characteristic of mature cystocarps (fig. 7.3), which are borne on the adventitious branchlets of female gametophytes. Initiation of the procarp occurs between the cortex and medulla (fig. 7.4) of the adventitious branchlets. The young procarp is comprised of a supporting cell bearing a two-celled carpogonial branch (fig. 7.5). Early post-fertilization stages were not directly observed in the study material. It is therefore assumed that diploidization occurs *sensu* Hommersand *et al.* (1992), when the fertilized carpogonium fuses with the supporting cell, the supporting cell then functioning as an auxiliary cell. Cortical and medullary cells surrounding the auxiliary cell produce adventitious filaments until an envelope of secondary tissue surrounds the auxiliary cell (fig. 7.6). As the auxiliary cell enlarges, the nuclei contained within enlarge to form a central column (fig. 7.6). Diploid nuclei from within the auxiliary cell are deposited in processes which cut-off the initials of gonimoblast filaments. These gonimoblast filaments penetrate deep inside the enveloping tissue and link to it by cell fusion (fig. 7.7). Conjunctor cells which are cut off from surrounding gametophytic tissue may also fuse with the gonimoblast cells by means of secondary pit connections (fig. 7.8) to form a placenta (*sensu* Kraft, 1978; Hommersand and Fredericq, 1990). The placenta is thus heterokaryotic, and contains a mixture of haploid and diploid nuclei (fig. 7.9). Heterokaryotic placental cells may also form initials that link to other placental cells (fig. 7.10). The placenta consists of dark gonimoblast cells and lighter placental cells surrounded by enveloping tissue (fig. 7.11), the latter differentiating into a dark outer envelope and a clear inner ring of depleted cell contents (fig. 7.12). Carposporangia form in clusters (fig. 7.13) separated by the placenta. As the envelope enlarges, placental cells elongate and pit connections between the cells broaden (fig. 7.14). Carposporangia mature simultaneously (fig. 7.15) and are released through the ostiole

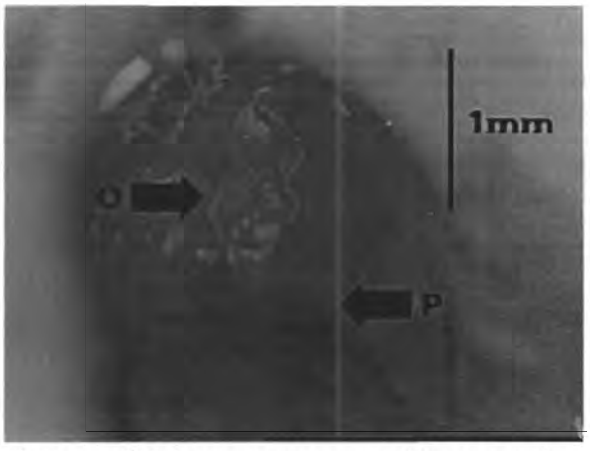


Figure 7.3 Mature cystocarp with external pericarp (P) and terminal ostiole (O); type material.

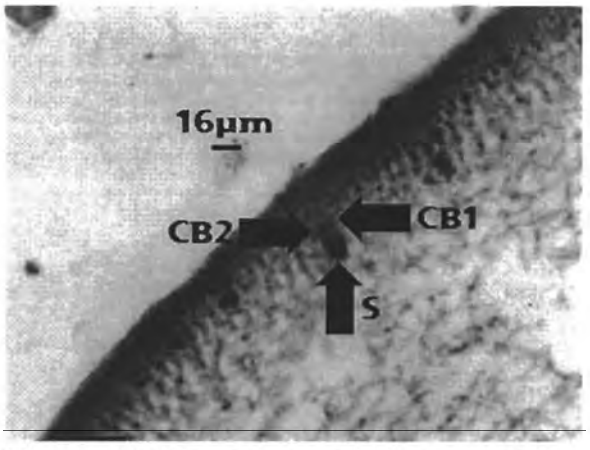


Figure 7.4 Young procarp with supporting cell (S) bearing two-celled carpogonial branch (CB1,CB2).

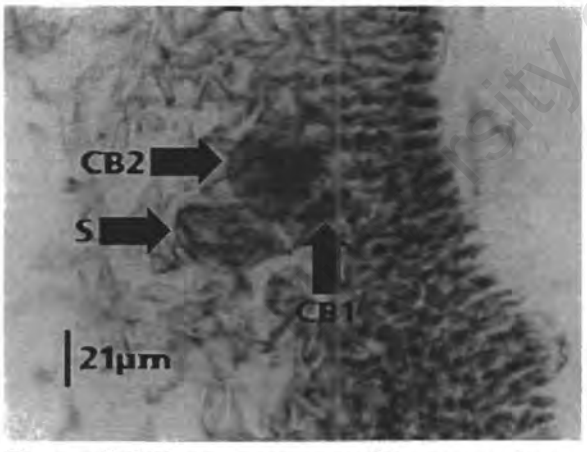


Figure 7.5 Young procarp with supporting cell (S) bearing two-celled carpogonial branch (CB1,CB2); type material.

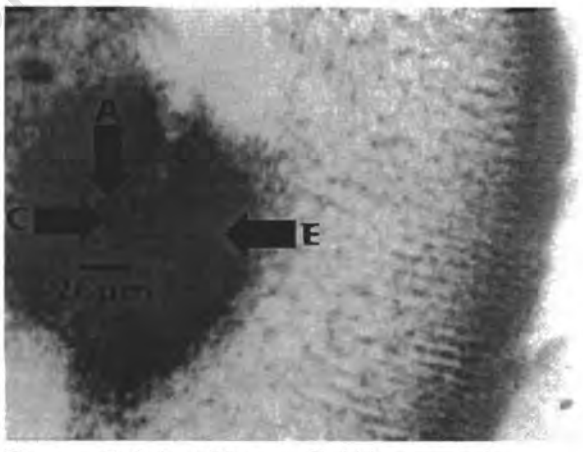


Figure 7.6 Auxiliary cell (A) containing nuclei organized in a central column (C) and surrounded by enveloping tissue (E).

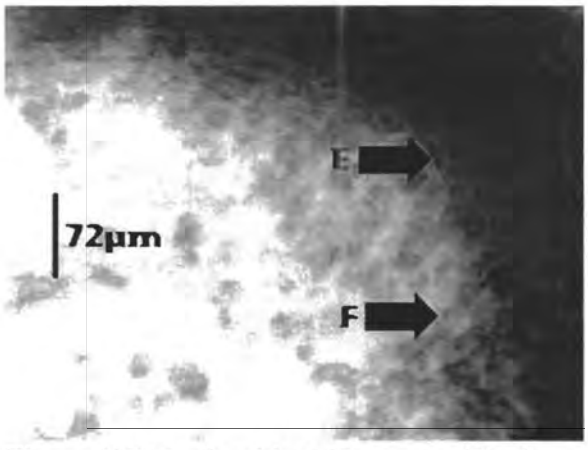


Figure 7.7 Gonimoblast filaments (F) of developing cystocarp penetrating and fusing with the surrounding envelope (E).

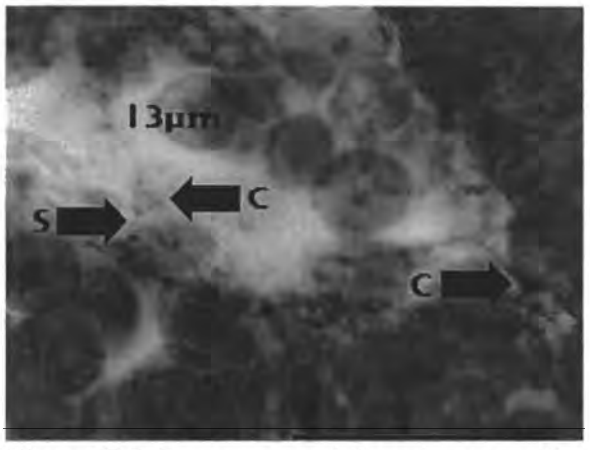


Figure 7.8 Carposporangial conjunctor cell (C) linked by a secondary pit connection (S) to a neighbouring cell.

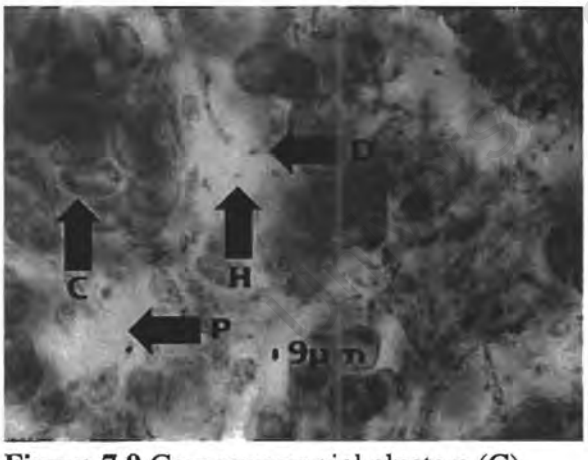


Figure 7.9 Carposporangial clusters (C), separated by placental cells (P) containing mixture of small, haploid (H) and larger, diploid (D) nuclei.

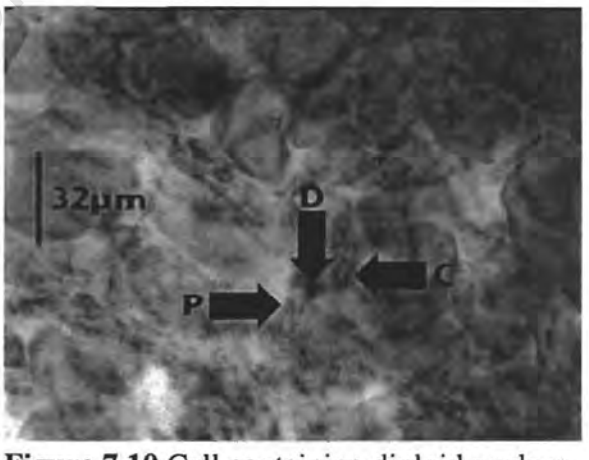


Figure 7.10 Cell containing diploid nucleus (D) linking between potential carposporangium (C) and placental cell (P).

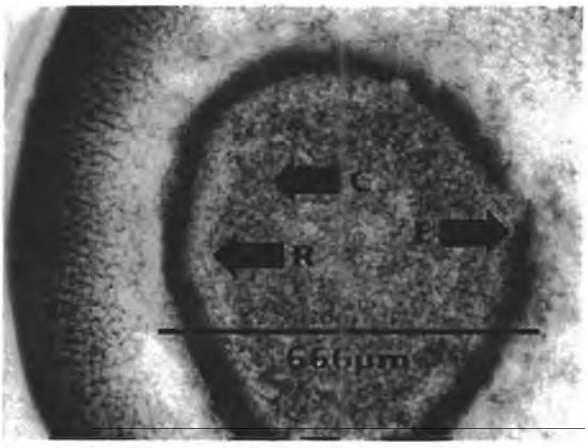


Figure 7.11 Placenta bearing young carposporangia (C) surrounded by massive enveloping tissue (E). Cells of lighter-staining inner ring (R) have depleted contents.

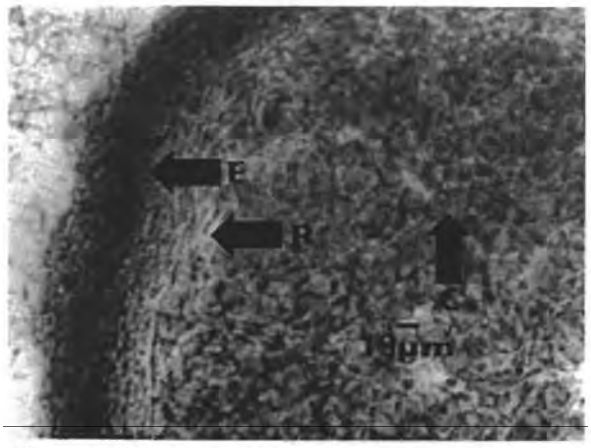


Figure 7.12 Placenta bearing young carposporangia (C) surrounded by massive enveloping tissue (E). Cells of lighter-staining inner ring (R) have depleted contents.

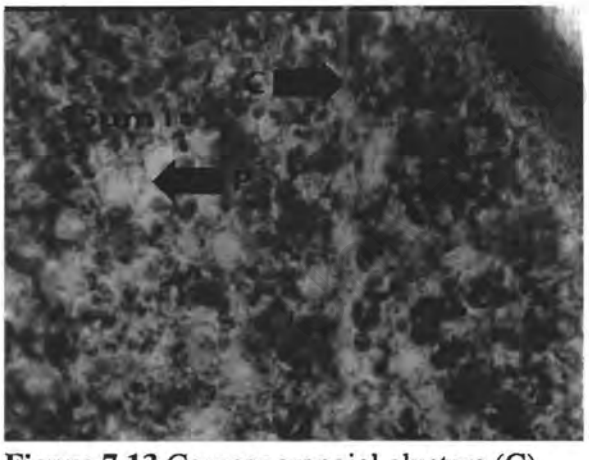


Figure 7.13 Carposporangial clusters (C), separated by placental cells (P).

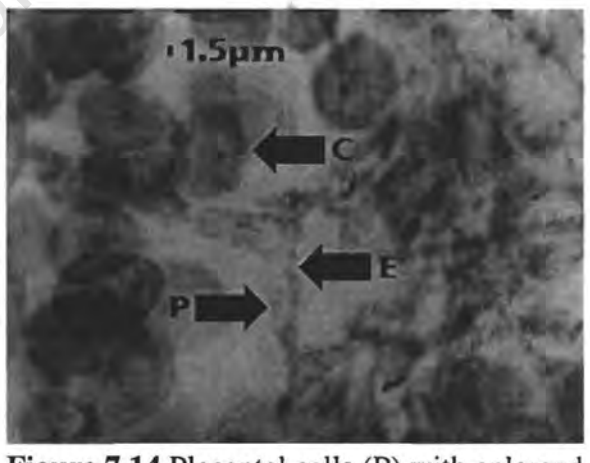


Figure 7.14 Placental cells (P) with enlarged pit connections (E) linking to each other and carposporangia (C).

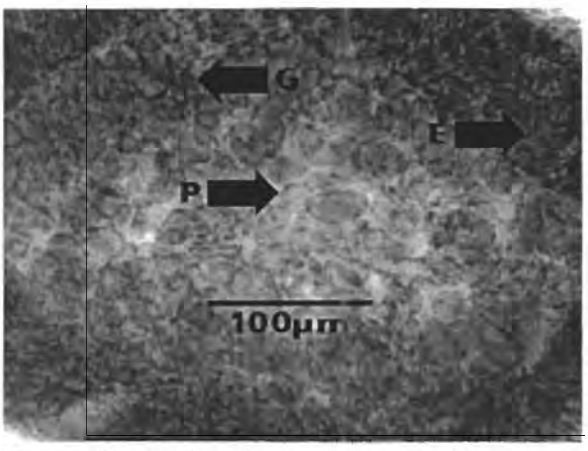


Figure 7.15 Maturing cystocarp with gonimoblast cells (G) and placental cells (P) surrounded by enveloping tissue (E).

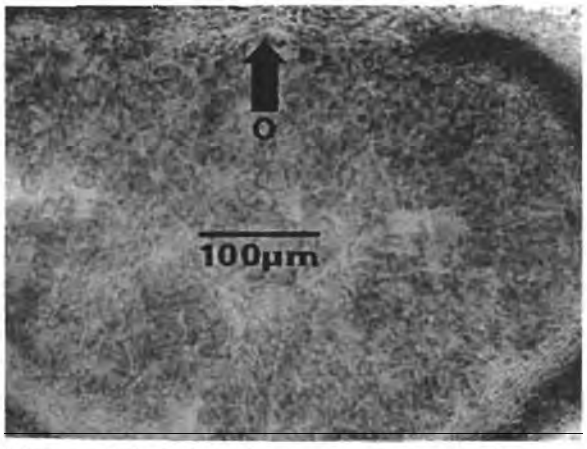


Figure 7.16 Maturing cystocarp showing differentiation of ostiole (O).

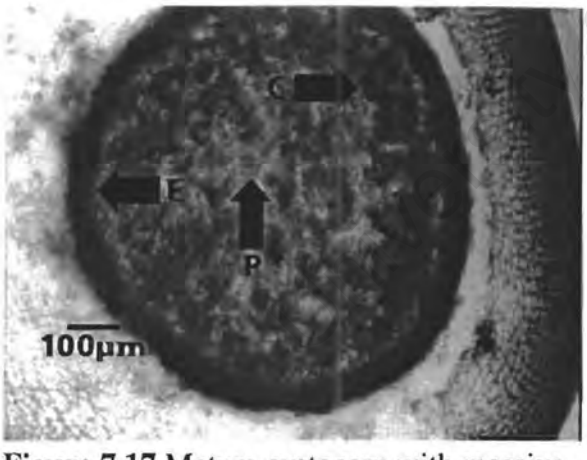


Figure 7.17 Mature cystocarp with massive enveloping tissue (E) surrounding placenta (P) with clusters of carposporangia (C).

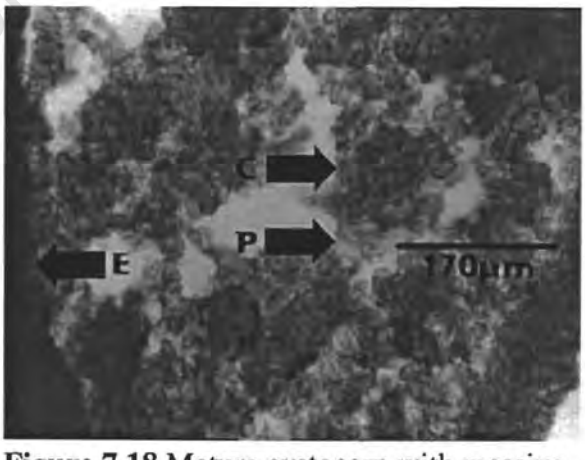


Figure 7.18 Mature cystocarp with massive enveloping tissue (E) surrounding placenta (P) with clusters of carposporangia (C); type material.

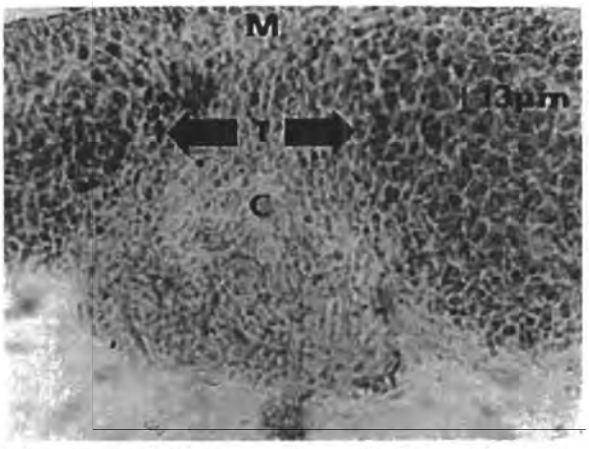


Figure 7.19 Young narrow (left) and broad (right) sorus of tetrasporocytes (T) forming between inner cortex (C) and outer medulla (M).

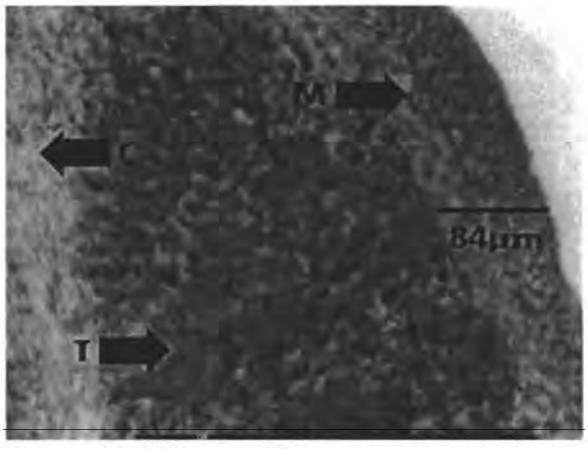


Figure 7.20 Sorus of tetrasporocytes (T) forming between inner cortex (C) and outer medulla (M); type material.

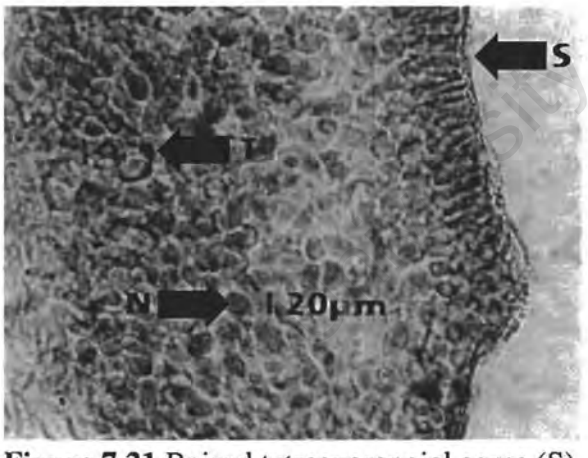


Figure 7.21 Raised tetrasporangial sorus (S) containing tetrasporocytes (T) with spherical nuclei (N).

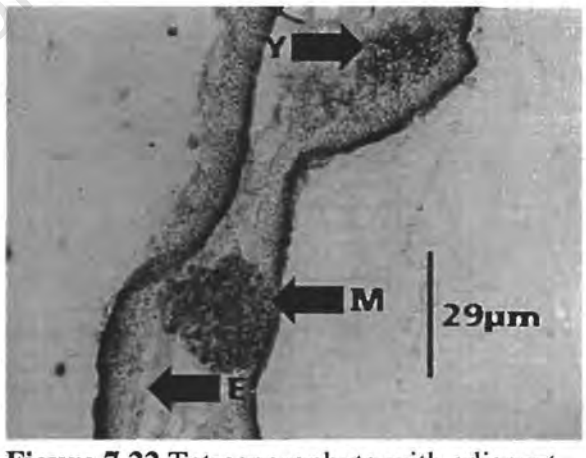


Figure 7.22 Tetrasporophyte with adjacent young tetrasporocytes (Y), mature tetrasporocytes (M) and old extruded sorus (E).

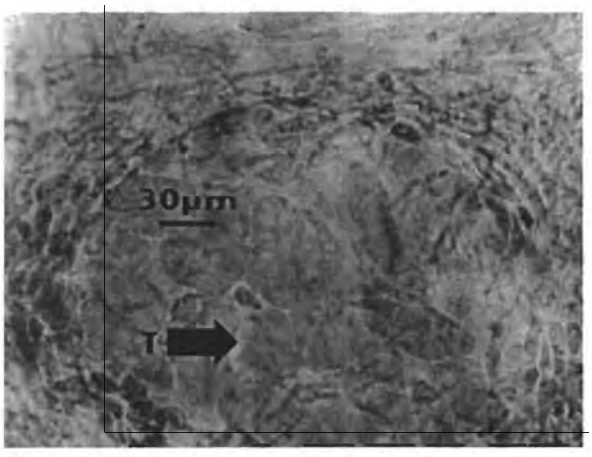


Figure 7.23 Mature tetrasporangial sorus with tetraspores (T).

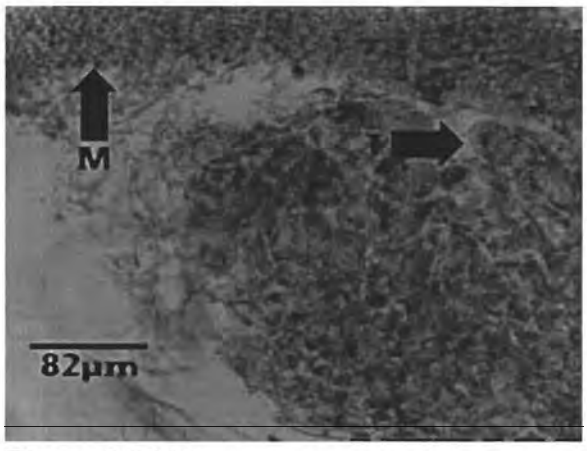


Figure 7.24 Mature tetrasporangial sorus, with tetraspores (T) and medulla (M); type material.

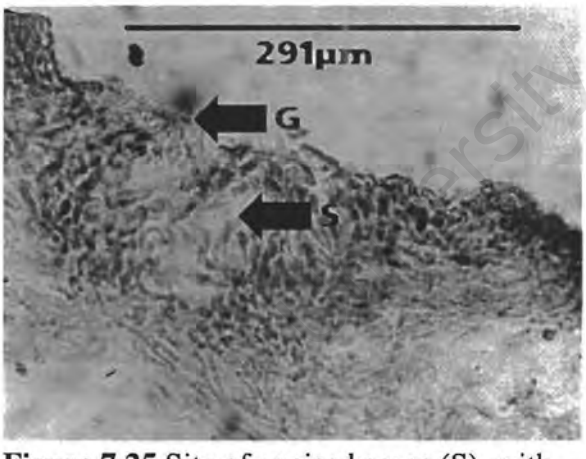


Figure 7.25 Site of excised sorus (S), with residual gelatinous material (G).

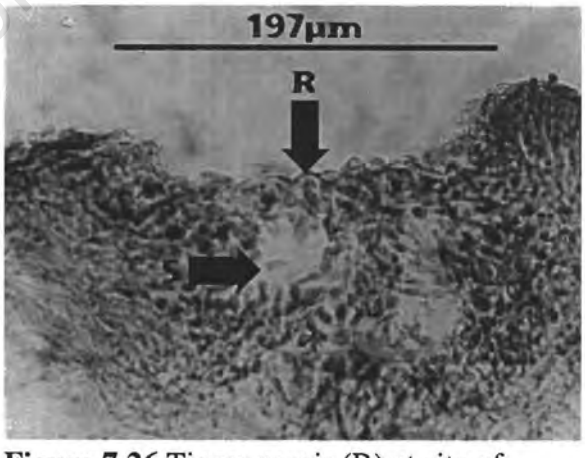


Figure 7.26 Tissue repair (R) at site of extruded sorus (S).

which is formed in the vicinity of the original supporting cell (fig. 7.16). Mature cystocarps are characterized by grape-like clusters of carposporangia surrounded by the massive enveloping tissue (figs. 7.17,7.18).

7.3.2 Tetrasporangial reproductive development in *Gigartina paxillata*

Tetrasporangia are borne in raised, lens-shaped sori which are formed at the boundary between the cortex and medulla (fig. 7.19). Sori enlarge by the formation of new tetrasporangial tissue at the cortex-medulla boundary (fig. 7.20). Potential tetrasporocytes stain more darkly than the surrounding vegetative cells, and are round in shape with a conspicuous nucleus (fig. 7.21). Mature tetraspores (fig. 7.22) are formed by tetrasporocytes cleaving to produce cruciately arranged tetraspores (fig. 7.23). Release of mature tetraspores takes place by excision and extrusion of the sorus, excision being initiated at the boundary between the sorus and the dark cells of the medulla (fig. 7.24). Spore release is via the exudation of gelatinous material at the excision site (fig. 7.25). After excision, the ruptured tissue is repaired (fig. 7.26) by the formation of a cuticle and the growth of new medullary tissue.

7.4 DISCUSSION

The derivation of procarp initials from the apical cell of cortical filaments is, according to Hommersand and Fredericq (1990), characteristic of the Gigartinaceae. The formation of enveloping tissue around the auxiliary cell is also a diagnostic feature which has been reported for some members of the Gigartinaceae (*e.g.* Mikami, 1965; Kim, 1976; Hommersand and Fredericq, 1990; Hommersand *et al.* 1992, 1993), and has been used to separate *Gigartina* from *Chondrus* (Kim, 1976), and *Gigartina* from *Chondrus* and *Mazzaella* (Hommersand *et al.* 1993). The size and density of the enveloping tissue was used by Kim (1976) to separate *Gigartina* species (in which he included *Iridaea* and *Rhodoglossum*), but this was shown by Hommersand and Fredericq (1990) to be an uncertain character due to variation in the size and thickness of the envelope tissue during the course of gonimoblast development. Subsequently, Hommersand *et al.* (1993) modified this character to one describing whether gonimoblast filaments displaced the enveloping tissue or whether they penetrated the tissue to distinguish *Rhodoglossum*, *Iridaea* and *Sarcothalia* from *Chondracanthus* and *Gigartina*. According to Hommersand *et al.* (1993), the latter two genera can be separated by the mode of carposporangial formation and tetrasporangial development. In *Chondracanthus*,

carposporangial chains are derived entirely from gonimoblast filaments separated by large, sterile cells and not forming a network. Carposporangial chains in *Gigartina* are also derived from gonimoblast filaments, but form grape-like clusters separated by a network of sterile filaments at maturity. Tetrasporangia in *Chondracanthus* are formed within the cortex, tetrasporangia being released through a pore in the wall. In *Gigartina*, tetrasporangia are formed progressively at the cortex-medulla boundary and tetraspores are released by excision of the entire sorus.

From the material examined in this study, it is apparent that *Gigartina paxillata* is correctly placed within the genus *Gigartina*. Morphologically, the flattened thallus with marginal branchlets indicates an affinity with *Gigartina* (figs 7.1 and 7.2), whilst the presence of a procarp with obvious ostiole (fig. 7.3) indicates that the genus could be *Rhodoglossum*, *Chondracanthus* or *Gigartina*. Microscopically, the derivation of the procarp initial from the cortex confirms the taxon as being a member of the Gigartinaceae (figs. 7.4 and 7.5). The formation of an envelope surrounding the auxiliary cell (fig. 7.6) excludes the entity from *Chondrus* and *Mazzaella*. Membership of *Rhodoglossum*, *Iridaea* and *Sarcothalia* can also be excluded because of the presence of heterokaryotic gonimoblast cells and gonimoblast filaments which penetrate the envelope in the material examined (fig. 7.7). *Rhodoglossum* can be further rejected because tetrasporangial sori are not formed in crypts (figs 7.19 and 7.20). The material examined therefore belongs to either *Chondracanthus* or *Gigartina*. The presence of mature carposporangia in grape-like clusters (figs 7.13 and 7.17) and broadened pit connections (fig. 7.14) within the placental tissue confirm that the carposporic material examined belongs to the genus *Gigartina*. Similarly, the tetrasporic material examined is confirmed as being of the genus *Gigartina* because of the presence of raised tetrasporangial sori (fig. 7.21) (*cf. Chondracanthus:* nemathecial sori localized in the inner cortex) and the fact that tetraspores are released by excision and gelatinous extrusion of the sorus (figs 7.25 and 7.26) (*cf. Chondracanthus*: extrusion through pores in the wall). Since the material examined included type material as well as the material from Arniston, and because the two appear to be morphologically the same, it is concluded that *G. paxillata* is correctly placed in the genus *Gigartina*.

CHAPTER 8

GENERAL DISCUSSION

It is perhaps inevitable that a diverse study such as this raises more questions than it answers concerning aspects of the biology and population ecology of Western Cape carrageenophytes. In this discussion, some of these questions are briefly examined and suggestions made as to the direction of future research.

The low standing stock (69.6 tons dry weight) of the four most abundant south Western Cape carrageenophytes (*Aeodes orbitosa*, *Gigartina polycarpa*, *Mazzaella capensis* and *Sarcothalia stiriata*) renders viable economic exploitation difficult. As a consequence of the scattered distribution and low standing stock, low levels of exploitation based upon artisanal collections by local communities appear to be the only economically viable option for the harvesting of natural populations of these resources, this being the only method whereby input costs can be minimized sufficiently. In this respect, regular harvesting of these carrageenophyte resources could provide a stable income in local communities where employment in the fishing industry is historically seasonal at best, and often non-existent due to the variable nature of fish resources. Expansion of a future carrageenophyte industry through the harvesting of additional resources is not a likely prospect, there being no other carrageenophyte species present in sufficient quantity. Only mariculture presents any prospect of substantially increasing the harvestable biomass of these resources. Because of its broader temperature tolerances and greater degree of tolerance to areas of high wave action, *G. polycarpa* appears the most suitable for mariculture since site selection would be less problematic. Furthermore, it appears that the higher natural growth rates recorded in tetrasporophytes of this species coupled with the commercial desirability of λ-carrageenan, would make this life-history phase the preferred entity for mariculture, although difficulties may be encountered in stimulating spore release. Interest in the mariculture of South African Gigartinaceae has been expressed by FMC Inc. and Copenhagen Pectin, and efforts should therefore first be concentrated upon this entity. Since the growth rate of natural populations of *G. polycarpa* is slow when compared with other local species with the potential for mariculture (*e.g. Gracilaria gracilis*, Anderson *et al.* 1996), future research should be directed toward the isolation of strains which are fast

growing, have a high carrageenan content and are resistant to disease and stress. The west coast of South Africa is subject to periodic red-tides which, upon decomposition, can produce lethal sulphurous black tides (Matthews and Pitcher, 1996), which may threaten the viability of carrageenophyte mariculture. Research into appropriate site-selection criteria as well as mariculture techniques which result in maximum yield are therefore essential.

Since the apparent lack of self-thinning among fronds of *Gigartina polycarpa* and *Sarcothalia stiriata* cannot be explained by the ultimate biomass-density line, other mechanisms controlling plant density need to be considered. Scrosati (1997) hypothesized that acclimation of small plants to the low irradiances (3-30μmol.m^{-2}.s^{-1}) experienced close to holdfasts in crowded stands could be used to explain the lack of frond self-thinning. If the light compensation point for growth is lower than these irradiance levels, growth is possible and prevents self-thinning regardless of the intensity of physiological integration of the ramets or the density dependent formation of fronds. In *G. polycarpa* and *S. stiriata* however, compensation points are in the region of 50μmol.m^{-2}.s^{-1}, which implies that the lack of self-thinning is related to density-dependent formation of fronds or to physiological integration among ramets. Regulation of frond formation limits overproduction which would result in self-thinning (De Kroon, 1993), this having been demonstrated by Scrosati (1997) in *Mazzaella cornucopiae*. Physical integration as a result of sporeling coalescence within the Gigartinaceae is also common, (*e.g. Chondrus crispus*, Tveter and Mathieson, 1976; *Mastocarpus stellatus*, Rueness, 1978), with some degree of metabolic interaction between ramets (Maggs and Cheney, 1990). Future research into the population ecology of *G. polycarpa* and *S. stiriata* should therefore be directed toward determining the degree of physiological integration between sporelings and whether frond formation is density dependent. Future culture and demographic studies of other carrageenophyte species which occur in dense stands such as *Sarcothalia scutellata* may provide additional examples of non self-thinning clonal algae.

The seasonal growth rates observed in *Gigartina polycarpa* and *Sarcothalia stiriata* are ascribed to seasonal variations in environmental parameters such as light, temperature and nutrient availability. The possible existence of an endogenous circannual rhythm has been suggested, but no data are available to support this hypothesis. Therefore, future research into the physiology of these two species should include an investigation into the possible existence of such a rhythm.

The material properties of seaweed thalli are considered important in reducing the stress of hydrodynamic forces, thalli of both *Gigartina polycarpa* and *Sarcothalia stiriata* being regarded as highly elastic. However, no empirical measurements of elasticity were made, and a comparison of such material properties from thalli of differing morphologies (specifically *G. polycarpa*) may provide a useful insight into structural variation in plants exposed to different hydrodynamic forces. A supplementary investigation comparing holdfast attachment strength between *G. polycarpa* and *S. stiriata* would be useful in determining whether the greater coefficients of inertia displayed by thalli of *S. stiriata* are compensated for by greater attachment strength of the prostrate holdfast in the latter species.

To ensure that harvesting of these carrageenophyte species is sustainable on a long-term basis, the recommended harvesting interval of four months for *Gigartina polycarpa* and *Sarcothalia stiriata* should be tested prior to its application on a broad-scale. This can be done over a number of seasons by means of an experimental pilot-scale implementation. As part of such a scheme, a comparative test of the suggested harvesting months of April, October and January with other regimes based on a four-monthly harvesting interval would be a useful supplement to the data obtained in this study.

A paucity of information ensures that discussion about the possible biogeographic origin of the west and east coast Gigartinaceae remains purely speculative. A comparative study of temperature tolerances of endemic west coast (*e.g. Sarcothalia scutellata*) and south and east coast species (*e.g. Gigartina minima, Gigartina insignis*) with more cosmopolitan entities such as *Gigartina teedii* or *Gigartina pistillata* may provide further clues as to the biogeogaphic origin of these entities within the Gigartinaceae. A more comprehensive investigation of light-temperature interactions in these species (*e.g.* P-I curves at temperature optimum, temperature survival at saturating I), may reveal significant ecological differences between them.

Finally, no amount of research is of comparative value without a clear idea of the identity of the organisms being studied. In this respect, the value of further studies in the ecology and population biology of other South African members of the Gigartinaceae will be significantly enhanced by a revision of their taxonomic position within the family. It is therefore recommended that characters of morphology and reproductive development in *Gigartina minima*, *Gigartina insignis* and South African *Gigartina pistillata* be examined to determine their position within the Hommersand *et al.* (1993) revised classification of the Gigartinaceae.

According to Lewis (1980) ecological studies must be both descriptive and dynamic. In its broad scope, this dissertation has endeavoured to satisfy both these requirements. The former by studies of standing stock and systematics, the latter by attempting to explain seasonal patterns of growth and population dynamics in terms of the physical and biological environment. By use of these approaches, it is hoped that this dissertation has contributed meaningfully toward a fuller understanding of the autecology of South African west coast carrageenophytes.

LITERATURE CITED

Abbott I.A. 1980. Some field and laboratory studies on colloid producing red algae in Central California. *Aquat. Bot., 8*:255-266.

Abrahamson, W.G. 1980 Demography and vegetative reproduction. In: *Demography and Evolution of Plant Populations*. Solbrig, O.T. (Ed.). Botanical Monographs, vol. 15. Blackwell Scientific Publications, Oxford. pp89-106.

Agardh, C.A. 1820. *Icones Algarum Ineditae*. Fasc. I. Berling, Lund. 2pp, pls 1-10.

Agardh, C.A. 1821. *Icones Algarum Ineditae*. Fasc. II. Eckstein, Stockholm. 3pp, pls 1-20.

Agardh, C.A. 1823. *Species Algarum...* Vol. 1. Mauritius, Greifswald. 531pp.

Agardh, J.G. 1851. *Species Genera et Ordines Algarum*. Vol. 2. Gleerup, Lund. xii+336pp

Agardh, J.G. 1879. *Floridеernes Morphologi*. Vol. 2. Norstedt, Stockholm.

Allsobrook, A.J.R., J.R. Nunn and H. Parolis. 1969. Some Grateloupiaceae poysaccharides. *Proc. Int. Seaweed Symp., 6*:417-420.

Anderson, N.S., Dolan, T.C.S., Penman, A., Rees, D.A., Mueller, G.P., Stancioff, D.J. and N.F. Stanley. 1968. Carrageenans. Part IV. Variations in the structure and gel properties of κ-carrageenan, and the characterisation of sulphate esters by infrared spectroscopy. *J. chem. Soc., (C)*:602-606.

Anderson, R.J. and J.J. Bolton. 1985. Suitability of the agarophyte *Suhria vittata* (L.) J.Ag (Rhodophyta: Gelidiaceae) for mariculture: geographical distribution, reproductive phenology and growth of sporelings in culture in relation to light and temperature. *S. Afr. J. mar. Sci., 3*:169-178.

Anderson, R.J. and J.J. Bolton. 1989. Growth and fertility, in relation to temperature and photoperiod, in South African *Desmarestia firma* (Phaeophyceae). *Bot. mar., 32*:149-158.

Anderson, R.J., R.H. Simons and N.G. Jarman. 1989. Commercial seaweeeds in Southern Africa: A review of utilization and research. *S. Afr. J. mar. Sci., 8*:277-299.

Anderson, R.J., G.J. Levitt, C.P. Dawes and R.H. Simons. 1992. Experimental growth of *Gracilaria* in Saldanha Bay, South Africa. In: *Proceedings of the First International Workshop on Sustainable Seaweed Resource Development, Windhoek, Namibia March 1992*. Mshigeni, K.E, J. Bolton, A. Critchley and G. Kiangi (Eds). K.E. Mshigeni,

Windhoek. pp19-36.

Anderson, R.J., G.J. Levitt and A. Share. 1996. Experimental investigations for the mariculture of *Gracilaria* in Saldanha Bay, South Africa. *J Appl. Phycol., 8*:421-430.

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

Andrews, W.R.H and D.L. Cram. 1969. Combined aerial and shipboard upwelling study in the Benguela Current. *Nature (Lond.), 224*:902-904.

Andrews, W.R.H. and L. Hutchings. 1980. Upwelling in the southern Benguela Current. *Prog. Oceanogr., 9*:1-81.

Ang, P.O. Jr and R.E. De Wreede. 1990. Matrix models for algal life history stages. *Mar. Ecol. Prog. Ser., 59*:171-181.

Avila, M., Otaíza, R., Norambuena, R. and Nuñez, M. 1996. Biological basis for the management of 'lugra negra' (*Sarcothalia crispata* Gigartinales, Rhodophyta) in southern Chile. *Hydrobiologia, 326/327*:245-252.

Baardseth, E. 1941. The marine algae of Tristan da Cunha. *Results of the Norwegian Scientific Expedition to Tristan da Cunha, 1937-1938, 9*:1-137.

Bolton, J.J. 1986. Marine phytogeography of the Benguela upwelling region on the west coast of Southern Africa: a temperature dependent approach. *Bot. mar., 29*:251-256.

Bolton, J.J. and R.J. Anderson. 1990. Correlation between intertidal seaweed community composition and sea water temperature patterns on a geographical scale. *Bot. mar., 33*:447-457.

Bolton, J.J. and R.J. Anderson. 1997. Marine vegetation. In: *Vegetation of Southern Africa*. Cowling, R.M., D.M. Richardson and S.M. Pierce (Eds). Cambridge University Press, Cambridge. pp348-370.

Bolton, J.J. and M.A.P. Joska. 1993. Population studies on a South African carrageenophyte: *Iridaea capensis* (Gigartinaceae, Rhodophyta). *Hydrobiologia, 260/261*:191-195.

Bolton, J.J. and G.J. Levitt. 1985. Light and temperature requirements for growth and reproduction in gametophytes of *Ecklonia maxima* (Alariaceae: Laminariales). *Mar. Biol., 87*:131-135.

Bolton, J.J. and G.J. Levitt. 1987. The influence of upwelling on South African west coast seaweeds. *S. Afr. J. mar. Sci., 5*:319-325.

Bolton, J.J. and G.J. Levitt. 1992. South African west coast carrageenophytes. In: *Proceedings of the First International Workshop on Sustainable Seaweed Resource Development, Windhoek, Namibia March 1992.* Mshigeni, K.E, J. Bolton, A. Critchley and G. Kiangi (Eds). K.E. Mshigeni, Windhoek. pp37-49.

Bolton, J.J. and H. Stegenga. 1990. The seaweeds of De Hoop Nature Reserve and their phytogeographical significance. *S. Afr. J. Bot., 56*:233-238.

Bolton, J.J. and H. Stegenga. 1994. Patterns of seaweed distribution in the Cape Province, South Africa, with particular reference to the Phaeophyta and Ceramiaceae (Rhodophyta) In: *Proceedings of the XIIIth Plenary Meeting AETFAT, Malawi.* Seyani, J.H. and A.C. Chikuni (Eds). *AETFAT, 2*:849-854.

Branch, M. 1974. Limiting factors for the gametophytes of three South African Laminariales. *Invest. Rep. Sea Fish. Brch. S. Afr., 104*:1-38.

Briggs, J.C. 1974. *Marine Zoogeography*. McGraw-Hill, New York. 475pp.

Burns, R.L. and A.C. Mathieson. 1971. Ecological studies of economic red algae I. Photosynthesis and respiration of *Chondrus crispus* (Stackhouse) and *Gigartina stellata* (Stackhouse) Batters. *J. exp. mar. Biol. Ecol., 7*:197-206.

Burns, R.L. and A.C. Mathieson. 1972a. Ecological studies of economic red algae II. Culture studies of *Chondrus crispus* (Stackhouse) and *Gigartina stellata* (Stackhouse) Batters. *J. exp. mar. Biol. Ecol., 8*:1-6.

Burns, R.L. and A.C. Mathieson. 1972b. Ecological studies of economic red algae III. Growth and reproduction of natural and harvested populations of *Gigartina stellata* (Stackhouse) Batters in New Hampshire. *J. exp. mar. Biol. Ecol., 9*:77-95.

Buschmann, A. and B. Santelices. 1987. Micrograzers and spore release in *Iridaea laminarioides* Bory (Rhodophyta: Gigartinales). *J. exp. mar. Biol. Ecol., 108*:171-179.

Caddy, J.F. and W.A.Fischer. 1984. FAO interests in promoting understanding of world seaweed resources, their optimal harvesting, and fishery and ecological interactions. *Hydrobiologia, 116/117*:355-362.

Carrington, E. 1990. Drag and dislodgement of an intertidal macroalga: consequences of morphological variation in *Mastocarpus papillatus* Kützing. *J. exp. mar. Biol. Ecol., 139*:185-200.

Carter, A.R. 1985. Reproductive morphology and phenology , and culture studies of *Gelidium*

pristoides (Rhodophyta) from Port Alfred in South Africa. *Bot. mar., 28*:303-311.

Carter, A.R. and R.J. Anderson. 1986. Seasonal growth and agar contents in *Gelidium pristoides* (Gelidiales, Rhodophyta) from Port Alfred, South Africa. *Bot. mar., 29*:117-123.

Carter, A.R. and R.H. Simons. 1987. Regrowth and production capacity of *Gelidium pristoides* (Gelidiales, Rhodophyta) under various harvesting regimes at Port Alfred, South Africa. *Bot. mar., 30*:227-231.

Chamberlain, Y., M.W. Holdgate and N. Wace. 1985. The littoral ecology of Gough Island, South Atlantic Ocean. *Tethys, 11*:302-319.

Chapman, A.R.O. 1984. Reproduction, recruitment and mortality in two species of *Laminaria* in southwest Nova Scotia. *J. exp. mar. Biol. Ecol., 78*:99-109.

Chapman, A.R.O. 1986. Population and community ecology of seaweeds. *Adv. Mar. Biol., 24*:1-84.

Chapman, A.R.O. and C.R. Johnson. 1990. Disturbance and organization of macroalgal assemblages in the Northwest Atlantic. *Hydrobiologia, 192*:77-121.

Chopin, T., C. Bodeau-Bellion, J.-Y. Floch, E. Guittet and J.-Y. Lallemand. 1987. Seasonal study of carrageenan structures from female gametophytes of *Chondrus crispus* Stackhouse (Rhodophyta). *Hydrobiologia, 151/152*:535-539.

Chopin, T., M.D. Hanisak, F.E. Koehn, J. Mollion and S. Moreau. 1990. Studies on carrageenans and effects of seawater phosphorus concentration on carrageenan content and growth of *Agardhiella subulata* (C. Agardh) Kraft and Wynne (Rhodophyceae, Solieriaceae). *J. Appl. Phycol., 2*:3-16.

Chopin, T., M.D. Hanisak and F.E. Koehn. 1991. Effects of seawater phosphorus concentration on floridean starch content in *Agardhiella subulata* (C. Agardh) Kraft *et* Wynne (Rhodophyceae). *Bot. mar., 34*:369-373.

Chopin, T., T. Gallant and I. Davison. 1995. Phosphorus and nitrogen nutrition in *Chondrus crispus* (Rhodophyta): Effects on total phosphorus and nitrogen content, carrageenan production, and photosynthetic pigments and metabolism. *J. Phycol., 31*:283-293.

Christianson, I.G., M.N. Clayton, B.M. Allender and B. Fuhrer. 1981. *Seaweeds of Australia*. A.H. & A.W. Reed, Sydney. 112pp.

Connell, J.H. 1978. Diversity in tropical rain forests and coral reefs. *Science, 199*:1302-1310.

Craigie J.S., and C. Leigh. 1978. Carrageenans and agars. In: *Handbook of Phycological Methods, Physiological and Biochemical Methods*. Hellebust, J.A. and J.S. Craigie (Eds). Cambridge University Press, Cambridge. pp167-201.

Dawes, C.J., A.C. Mathieson and D.P. Cheney. 1974a. Ecological studies of Floridian *Eucheuma* (Rhodophyta, Gigartinales) I. Seasonal growth and reproduction. *Bull. mar. Sci., 24*:235-273.

Dawes, C.J., N.F. Stanley and D.J. Stancioff. 1977. Seasonal and reproductive aspects of plant chemistry, and ι-carrageenan from Floridian *Eucheuma* (Rhodophyta, Gigartinales). *Bot. mar., 20*:137-147.

Dawes, C.J., J.M. Lawrence, D.P. Cheney and A.C. Mathieson. 1974b. Ecological studies of Floridian *Eucheuma* (Rhodophyta, Gigartinales). III. Seasonal variation of carrageenan, total lipid carbohydrate, protein, and lipid. *Bull. mar. Sci., 24*:286-299.

Day, J.H. 1969. *A guide to marine life on South African shores*. A.A. Balkema, Cape Town. 300pp.

Dayton, P.K., M.J. Tegner, P.E. Parnell and P.B. Edwards. 1992. Temporal and spatial patterns of disturbance and recovery in a kelp forest community. *Ecol. Monogr., 62*:421-445.

De Cew, T.C. and J.A. West. 1981. Life histories in the Phyllophoraceae (Rhodophyta, Gigartinales) from the Pacific coast of North America I. *Gymnogongrus linearis* and *G. leptophyllus*. *J. Phycol., 17*:240-250.

De Kroon, H. 1993. Competition between shoots in stands of clonal plants. *Plant Spec. Biol., 8*:85-94.

Denny, M.W. 1987. Life in the maelstrom: the biomechanics of wave-swept rocky shores. *Trends in Ecology and Evolution, 2*:61-66.

Denny, M.W. 1988. *Biology and the Mechanics of the Wave-Swept Environment*. Princeton University Press, New Jersey. 329pp.

Denny, M.W. 1991. Biology, natural selection and the prediction of maximal wave-induced forces. *S. Afr. J. mar. Sci., 10*:353-363.

Denny, M.W., T.L. Daniel and M.A.R. Koehl. 1985. Mechanical limits to size in wave-swept organisms. *Ecol. Monogr., 55*:69-102.

De Toni, J.B. 1903. *Sylloge Algarum...* Vol IV. Florideae. Sect. 3. Padua.

De Wreede, R.E. and L.G. Green. 1990. Patterns of gametophyte dominance of *Iridaea splendens* (Rhodophyta) in Vancouver Harbour, Vancouver, British Columbia, Canada. *J. Appl. Phycol,. 2*:27-34.

De Wreede, R.E. and T. Klinger. 1988. Reproductive strategies in algae. In: *Reproductive Strategies of Plants*. Lovett Doust, J. and L. Lovett Doust (Eds). Oxford University Press, Oxford. pp267-284.

Dieckmann, G.S. 1980. Aspects of the ecology of *Laminaria pallida* (Grev.) J. Ag. off the Cape Peninsula (South Africa). I. Seasonal Growth. *Bot. mar., 23*:579-585.

Dixon, P.S. 1965. Perennation, vegetative propagation and algal life histories, with special reference to *Asparagopsis* and other Rhodophyta. *Bot. Gothoburg., 3*:67-74.

Doty, M.S. 1971. Measurement of water movement in reference to benthic algal growth. *Bot. mar., 14*:32-35.

Druehl, D.L. and W.N. Wheeler. 1986. Population biology of *Macrocystis integrifolia* from British Columbia, Canada. *Mar. Biol., 90*:173-179.

Durako, M.J. and C.J. Dawes. 1980. A comparative seasonal study of two populations of *Hypnea musciformis* from the east and west coasts of Florida, USA. 2. Photosynthetic and respiratory rates. *Mar. Biol., 59*:157-162.

Dyck, L., R.E. De Wreede and W.T. Garbary. 1985. Life history phases in *Iridaea cordata* (Gigartinaceae): relative abundance and distribution from British Columbia to California. *Jap. J. Phycol. (Sôrui), 33*:225-232.

Ekman, S. 1953. *Zoogeography of the Sea*. Sidgwick and Jackson, London. 417pp.

Emanuel, B.P., R.H. Bustamante, G.M. Branch, S. Eekhout and F.J. Odendaal. 1992. A zoogeographic and functional approach to the selection of marine reserves on the west coast of South Africa. *S. Afr. J. mar. Sci., 12*:341-354.

Engledow, H.R. and J.J. Bolton. 1992. Environmental tolerances in culture and agar content of *Gracilaria verrucosa* (Hudson) Papenfuss (Rhodophyta, Gigartinales) from Saldanha Bay. *S. Afr. J. Bot., 58*:263-267.

Foster, M.S. 1982 Factors controlling the intertidal zonation of *Iridaea flaccida* (Rhodophyta). *J. Phycol., 18*:285-294.

Foster, M.S. and D.C. Barilotti. 1990. An approach to determine the ecological effects of seaweed harvesting: a summary. *Hydrobiologia, 204/205*:15-16.

Fralick, R.A. and A.C. Mathieson. 1973. Ecological studies of *Codium fragile* in New England, USA. *Mar. Biol., 19*:127-132.

Fuller, S.W. and A.C. Mathieson. 1972. Ecological studies of economic red algae. IV. Variations of carrageenan concentration and properties in *Chondrus crispus* Stackhouse. *J. exp. mar. Biol. Ecol., 10*:49-58.

Furneaux, R.H. and I.J. Miller. 1986. Isolation and ^{13}C-NMR spectral study of the water soluble polysaccharides from four South African red algae. *Bot. mar., 29*:3-10.

Gagné, J.A., K.H. Mann and A.R.O. Chapman. 1982. Seasonal patterns of growth and storage in *Laminaria longicruris* in relation to differing patterns of availability of nitrogen in the water, *Mar. Biol., 69*:91-101.

Gaylord, B., C.A. Blanchette and M.W. Denny. 1994. Mechanical consequences of size in wave-swept algae. *Ecol. Monogr., 64*:287-313.

Gmelin, S.G. 1768. *Historia Fucorum.* Academia Scientarium, St Petersburg. [8]+239+[6]pp,33pls.

Gomez, I. and R. Westermeier. 1991. Module regrowth from basal discs in *Iridaea laminarioides* (Rhodophyta, Gigartinales) at Mehuin, Southern Chile. *Mar. Ecol. Prog. Ser., 73*:83-91.

Guiry, M.D., J.A. West, D.-H. Kim and M. Masuda. 1984. Reinstatement of the genus *Mastocarpus* Kützing (Rhodophyta). *Taxon, 33*:53-63.

Guiry, M.D. and D.J. Garbary. 1990. A preliminary phylogenetic analysis of the Phyllophoraceae, Gigartinaceae and Pterocelidaceae (Rhodophyta) in the North Atlantic and North Pacific. In: *Evolutionary Biogeography of the Marine Algae of the North Atlantic*. D.J. Garbary and G.R. South (Eds). NATO Advanced Science Inst. Series G: Ecological Sc., Vol. 22, Springer-Verlag, Berlin. pp349-410.

Guiry, M.D. and J.A. West. 1984. Life history and hybridization studies on *Gigartina stellata* and *Pterocelis cruenta* (Rhodophyta) in the North Atlantic. *J. Phycol., 19*:474-494.

Hannach, G. and J.R. Waaland. 1986. Environment, distribution and production of *Iridaea*. *Aquat. Bot., 26*:51-78.

Hansen, J.E. 1977. Ecology and natural history of *Iridaea cordata* (Gigartinales, Rhodophyta) growth. *J. Phycol., 13*:395-402.

Hansen, J.E. and W.T. Doyle. 1976. Ecology and natural history of *Iridaea cordata*

(Rhodophyta; Gigartinaceae): population structure. *J. Phycol., 12*:273-278.

Harper, J.L. 1977. *Population Biology of Plants*. Academic Press, London. 892pp.

Hatcher, B.G., A.R.O. Chapman and K.H. Mann. 1977. An annual carbon budget for the kelp *Laminaria longicruris*. *Mar.Biol., 44*:85-96.

Hay, C.H. and G.R. South. 1979. Experimental ecology with particular reference to proposed commercial harvesting of *Durvillaea* (Phaeophyta, Durvilleales) in New Zealand. *Bot. mar., 22*:431-436.

Hawkes, M.W. 1990. Reproductive Strategies. In: *Biology of red algae*. Cole, K.M. and R.G. Sheath (Eds). Cambridge University Press, Cambridge. pp455-476.

Hedgpeth, J.W. 1957. Marine biogeography. In: Treatise on Marine Ecology and Paleoecology, vol. 1. Ecology. *Geol. Soc. Amer. Memoir., 67*:359-382.

Hoerner, S.F. 1965. *Fluid-dynamic drag*. Bricktown, New Jersey. Private publication.

Hommersand, M.H. 1986. The biogeography of the South African marine red algae: a model. *Bot. mar., 29*:257-270.

Hommersand, M.H. and S. Fredericq. 1990. Sexual reproduction and cystocarp development. In: *Biology of red algae*. Cole, K.M. and R.G. Sheath (Eds). Cambridge University Press, Cambridge. pp305-345.

Hommersand, M., S. Fredericq and J. Cabioch. 1992. Developmental morphology of *Gigartina pistillata* (Gigartinaceae, Rhodophyta). *Phycologia, 31*:300-325.

Hommersand, M.H., S. Fredericq and D.W. Freshwater. 1994. Phylogenetic systematics and biogeography of the Gigartinaceae (Gigartinales, Rhodophyta) based on Sequence Analysis of *rbc*L. *Bot. mar., 37*:193-203.

Hommersand, M.H., M.D. Guiry, S. Fredericq and G.L. Leister. 1993. New perspectives in the taxonomy of the Gigartinaceae (Gigartinales, Rhodophyta). *Hydrobiologia, 260/261*: 105-120.

Hurd, C.L. and C.L. Stevens. 1997. Flow visualization around single and multiple-bladed seaweeds with various morphologies. *J. Phycol., 33*:360-367.

Isaac, W.E. 1942. Seaweeds of possible economic importance in the Union of South Africa. *Jl S. Afr. Bot., 8*:225-236.

Isaac, W.E., M.H. Finlayson and M.G. Simon. 1943. Agar from South African seaweeds. *Nature, 151*:532.

Isaac, W.E. and C.J. Molteno. 1953. Seaweed resources of South Africa. *Jl S. Afr. Bot., 19*:85-92.

Istini, S., M. Ohno and H. Kusunose. 1994. Methods of analysis for agar, carrageenan and alginate in seaweed. *Bull. Mar. Sci. Fish., Kochi Univ., 14*:49-55.

Jackelman, J.J. 1996. Structure and dynamics of the algal understorey in a kelp community at Cape Hangklip, Western Cape, South Africa. M.Sc thesis, University of Cape Town, South Africa. 160pp.

Jackelman, J.J. and J.J. Bolton. 1990. Form variation and productivity of an intertidal foliose *Gigartina* species (Rhodophyta) in relation to wave exposure. *Hydrobiologia, 204/205*:57-64.

Joska, M.A.P. and J.J. Bolton. 1987. *In situ* measurement of zoospore release and seasonality of reproduction in *Ecklonia maxima* (Alariaceae, Laminariales). *Br. phycol. J., 22*:209-214.

Kendrick, G.A. and D.I. Walker. 1991. Dispersal distances for propagules of *Sargassum spinuligerum* (Sargassaceae, Phaeophyta) measured directly by vital staining and venturi suction sampling. *Mar. Ecol. Prog. Ser., 79*:133-138.

Kennelly, S.J. 1987. Physical disturbances in an Australian kelp community. II. Effects on understorey species due to differences in kelp cover. *Mar. Ecol. Prog. Ser., 40*:155-165.

Keser, M. R. Vadas and B. Larson. 1981. Regrowth of *Ascophyllum nododsum* and *Fucus vesiculosus* under various harvesting regimes in Maine, U.S.A. *Bot. mar., 24*: 29-38.

Kim, D.H. 1976. A study of the development of cystocarps and tetrasporangial sori in Gigartinaceae (Rhodophyta, Gigartinales). *Nova Hedwigia, 27*: 1-93.

Knox, G.A. 1960. Littoral ecology and biogeography of the southern oceans. *Proc. Roy. Soc. Ser. B., 152*:577-624.

Koehl, M.A.R. 1986. Seaweeds in moving water: form and mechanical function. In: *On the economy of plant form and function.* Givnish, T.J. (Ed.). Cambridge University Press, Cambridge. pp 603-634.

Koehl, M.A.R and S.A. Wainwright. 1977. Mechanical adaptations of a giant kelp. *Limnol. oceanogr., 22*:1067-1071.

Kraft, G.T. 1978. Studies of marine algae in the lesser known families of the Gigartinales

(Rhodophyta). III. The Mychodeaceae and Mychodeophyllaceae. *Austr. J. Bot.*, *26*:515-610.

Kützing, F.T. 1843. *Phycologia generalis*. Brockhaus, Leipzig, xxxii+458pp.

Kützing, F.T. 1849. *Species Algarum*. Brockhaus, Leipzig, vi+922pp.

Kützing, F.T. 1867 *Tabulae Phycologicae*, Vol. 17, 30pp, pls1-100, Nordhausen..

Lawson, C.J., D.A. Rees, D.J. Stancioff and N.F. Stanley. 1973. Carrageenans. Part VIII. Repeating structures of galactan sulphates from *Furcellaria fastigaita*, *Gigartina canaliculata*, *Gigartin chamissoi*, *Gigartina atropurpurea*, *Ahnfeltia durvillaei*, *Gymnogongrus furcellatus*, *Eucheuma cottonii*, *Eucheuma spinosum*, *Eucheuma isiforme*, *Eucheuma uncinatum*, *Agardhiella tenera*, *Pachymenia hymantophora*, and *Gloiopeltis cervicornis*. *J. Chem. Soc., Perkin Trans., I*:2177-2182.

Lazo, L. and A.R.O. Chapman. 1996. Effects of harvesting on *Ascophyllum nodosum* (L.) Le Jol. (Fucales, Phaeophyta): a demographic approach. *J. Appl. Phycol,. 8*:87-103.

Levitt, G.J. 1987. Studies on the seasonal primary production of Cape Peninsula littoral and sublittoral seaweeds. M.Sc thesis, University of Cape Town, South Africa. 196pp.

Levitt, G.J. 1993. Primary production of Cape of Good Hope littoral and sublittoral seaweeds. *Trans. Roy. Soc. S. Afr., 48*:339-350.

Levitt, G.J. and J.J.Bolton. 1990. Seasonal primary production of understory Rhodophyta in an upwelling system. *J. Phycol., 26*:214-220.

Lewis, J.R. 1980. Objectives in littoral ecology - a personal viewpoint. In: *The Shore Environment*, Vol 1, Methods. Price, J.H., D.E.G. Irvine and W.F. Farnham (Eds). Academic Press, London. pp1-18.

Lubchenco, J. 1978. Plant species diversity in a marine intertidal community: importance of herbivore food preference and algal competitive abilities. *Am. Nat., 112*:23-39.

Lubchenco, J. 1980. Algal zonation in the New England rocky intertidal community: an experimental analysis. *Ecology, 61*:333-344.

Lüning, K. 1990. *Seaweeds. Their Environment, Biogeography and Ecophysiology*. John Wiley and Sons, New York. 527pp.

Lüning, K. 1991. Circannual growth rhythm in a brown alga, *Pterygophora californica*. *Bot. Acta, 104*:157-162.

Luxoro, C. and B. Santelices. 1989. Additional evidence for ecological differences among

isomorphic reproductive phases of *Iridaea laminarioides* (Rhodophyta: Gigartinales). *J. Phycol., 25*:206-212.

Lyngby, J.E. 1990. Monitoring of nutrient availability and limitation using the marine macroalga *Ceramium rubrum* (Huds.) C.Ag. *Aquat. Bot., 38*:153-161.

Maggs, C.A. and D.P. Cheney. 1990. Competition studies of marine macroalgae in laboratory culture. *J. Phycol., 26*:18-24.

Mann, K.H., N. Jarman and G. Dieckmann. 1979. Development of a method for measuring the productivity of the kelp *Ecklonia maxima* (Osbeck) Papenf. *Trans. Roy. Soc. S.Afr., 44*:27-41.

Manuel, T.L. 1990. The biology and ecology of *Bifurcaria brassicaeformis* (Kuetz.) Barton. M.Sc thesis, University of Cape Town, South Africa. 169pp.

Martínez, E. and B. Santelices. 1992. Size hierarchy and the -3/2 "power law" relationship in a coalescent seaweed. *J. Phycol., 28*:259-264.

Mathieson, A.C. and R.L. Burns. 1971. Ecological studies of economic red algae. I. Photosynthesis of *Chondrus crispus* Stackhouse and *Gigartina stellata* (Stackhouse) Batters. *J. exp. mar. Biol. Ecol., 7*:197-206.

Mathieson, A.C. and R.L. Burns. 1975. Ecological studies of economic red algae. V. Growth and reproduction of natural and harvested populations of *Chondrus crispus* Stackhouse in New Hampshire. *J. exp. mar. Biol. Ecol., 17*:137-156.

Matthews, S.G. and G.C. Pitcher. 1996. Worst recorded marine mortality on the South African coast. In: *Harmful and toxic algal blooms*. Yasumoto, T., Y. Oshima and Y. Fukuyo (Eds). International Oceanographic Commission of UNESCO Publication. pp89-92.

May, G. 1986. Life history variations in a predominantly gametophytic population of *Iridaea cordata* (Gigartinaceae, Rhodophyta). *J. Phycol., 22*:448-455.

McCandless, E.L., J.S. Craigie and J.A. Walter. 1973. Carrageenans in gametophytic and sporophytic stages of *Chondrus crispus*. *Planta, 112*:201-212.

McCandless, E.L., J.A. West and M.D. Guiry. 1982. Carrageenan patterns in the Phyllophoraceae *Biochem. Syst. Biol., 10*:275-284.

McCandless, E.L., J.A. West and M.D. Guiry. 1983. Carrageenan patterns in the Gigartinaceae. *Biochem. Syst. Ecol., 11*:175-182.

McCourt, R.M. 1985. Reproductive biomass allocation in three *Sargassum* species. *Oecol., 67*:113-117.

Mikami, H. 1965. A systematic study of the Phyllophoraceae and Gigartinaceae from Japan and its vicinity. *Sci. Papers Inst. Algol. Res., Fac. Sci., Hokkaido Univ. 5(2)*:181-285.

Molteno, C.J., S.P. Ligthelm and M.A. Joubert. 1953. The utilization of South African seaweeds. Manuscript 25 + 9 pp.

Moreno, C. and E. Jaramillo. 1983. The role of grazers in the zonation of intertidal macroalgae of the Chilean coastline. *Oikos, 41*: 73-76.

Mshigeni, K.E. 1976. Effects of the environment on development rates of sporelings of two *Hypnea* species (Rhodophyta: Gigartinales). *Mar. Biol., 36*:99-103.

Mshigeni, K.E. and A.K. Semesi. 1977. Studies on carrageenans from the economic red algal genus *Eucheuma* in Tanzania. *Bot. mar., 20*:239-242.

Mshigeni, K.E., A.K. Semesi and T.M. Ngonyani. 1979. Studies on the phycocolloid from the red seaweed *Rhabdonia africana* Jaasund (Gigartinales, Rhabdoniaceae). *Bot. mar., 22*:447-450.

Neish, A.C., P.F. Shacklock, C.H. Fox and F.J. Simpson. 1977. The cultivation of *Chondrus crispus*. Factors affecting growth under greenhouse conditions. *Can. J.Bot., 55*:2263-2271.

Nelson, W.A. and A.M.Conroy. 1989. Effect of harvest method and timing on yield and regeneration of Karengo (*Porphyra* spp.) (Bangiales, Rhodophyta) in New Zealand. *J. Appl. Phycol., 1*:277-283.

Norris, R.E. and D.H. Kim. 1972. Development of thalli in some Gigartinaceae. In: *Contributions to the Systematics of Benthic Marine Algae of the North Pacific*. Abbott, I.A. and M. Kurogi (Eds). Japan. Soc. Phycol., Kobe. pp75-92.

Nunn, J.R. and H. Parolis. 1968. A polysaccharide from *Aeodes orbitosa*. *Carb. Res.*, 6:1-11.

Paine, R.T. 1979. Disaster, catastrophe, and local persistence of the sea palm *Postelsia palmaeformis*. *Science, 205*:685-686.

Paine, R.T. and S.A. Levin. 1981. Intertidal landscapes: disturbance and dynamics of pattern. *Ecol. Monogr., 51*:145-178.

Paine, R.T. and R.L. Vadas. 1969. The effects of grazing sea urchins, *Strongylocentrotus* spp. on benthic algal populations. *Limnol. Oceanogr., 14*:710-719.

Pakker, H., A.M. Breeman, W.F. Prud'homme van Reine and C. van den Hoek. 1995. A comparative study of temperature responses of Caribbean seaweeds from different biogeographic groups. *J. Phycol., 31*:499-507.

Papenfuss, G.F. 1947. New marine algae from South Africa: I. *Univ. Calif. Publ. Bot. 23*:1-16, pls 1-4.

Peats, S. 1981. The infrared spectra of carrageenans extracted from various algae. In: *Proceedings of the Tenth International Seaweed Symposium, Göteburg, August 1980.* Levring, T. (Ed.). Berlin; Walter de Gruyter. pp495-502.

Penman, A. and D.A. Rees. 1973. Carrageenans. Part IX. Methylation analysis of galactan sulphates from *Furcellaria fastigaita*, *Gigartina canaliculata*, *Gigartina chamissoi*, *Gigartina atropurpurea*, *Ahnfeltia durvillaei*, *Gymnogongrus furcellatus*, *Eucheuma isiforme*, *Eucheuma uncinatum*, *Agardhiella tenera*, *Pachymenia hymantophora*, and *Gloiopeltis cervicornis*. Structure of ξ-carrageenan. *J. Chem. Soc., Perkin Trans., I*:2182-2187.

Penrith, M.L. and B.F. Kensley. 1970. The constitution of the fauna of rocky intertidal shores of South West Africa. 2. Rocky Point. *Cimbebasia Ser. A, 1*:243-268.

Polanshek, A.R. and J.A. West. 1977. Culture and hybridization studies on *Gigartina papillata* (Rhodophyta). *J. Phycol., 13*:141-149.

Probyn, T.A. and A.R.O. Chapman. 1983. Summer growth of *Chordaria flagelliformis* (O.F. Muell.) C.Ag.: physiological strategies in a nutrient stressed environment. *J.Exp.Mar.Biol.Ecol., 73*:243-271.

Probyn, T.A. and C.D. McQuaid. 1985. In situ measurements of nitrogenous nutrient uptake by kelp (*Ecklonia maxima*) and phytoplankton in a nitrate-rich upwelling environment. *Mar. Biol., 88*:149-154.

Provasoli, L. 1968. Media and prospects for cultivation of marine algae. In: *Cultures and collections of algae.* Watanabe, A. and A. Hattori (Eds). Japanese Society of Plant Physiology, Tokyo. pp47-49.

Pybus, C. 1977. The ecology of *Chondrus crispus* and *Gigartina stellata* (Rhodophyta) in Galway Bay. *J. mar. biol. ass. U.K., 57*:609-628.

Rao, K.R. 1970. Studies on growth cycle and phycocolloid content in *Hypnea musciformis* (Wulf.) Lamour. *Bot. mar., 13*:163-165.

Rao, K.R. 1977. Studies on Indian Hypneaceae II. Reproductive capacity in the two species of *Hypnea* over the different seasons. *Bot. mar., 20*:33-39.

Ricklefs, R.E. 1987. Community diversity: relative roles of local and regional processes. *Science, 235*: 1009-1014.

Rosenberg, G. and J. Ramus. 1982. Ecological growth strategies in the seaweed *Gracilaria foliifera* (Rhodophyceae) and *Ulva* sp. (Chlorophyceae): soluble nitrogen and reserve carbohydrates. *Mar. Biol., 66*:251-259.

Rueness, J. 1978. A note on development and reproduction in *Gigartina stellata* (Rhodophyta, Gigartinales) from Norway. *Br. Phycol. J., 13*:87-90.

Santelices, B. 1990. Patterns of reproduction, dispersal and recruitment in seaweeds. *Oceanogr. Mar. Biol. Annu. Rev., 28*:177-276.

Santelices, B. and R. Norambuena. 1987. A harvesting strategy for *Iridaea laminarioides* in central Chile. *Hydrobiologia, 151/152*:329-333.

Santelices, B, P. Camus and A.J. Hoffman.1989. Ecological studies for harvesting and culturing *Gymnogongrus furcellatus* (Rhodophyta, Gigartinales) in central Chile. *J. Appl. Phycol,. 1*:171-181.

Santos, G.A. and M.S. Doty. 1975. IR studies on carrageenan of *Ahnfeltia concinna*, a marine red alga. *J. Pharm. Sci., 64*:1704-1706.

Santos, R. 1993 Plucking or cutting *Gelidium sesquipedale*? A demographic simulation of harvest impact using a population projection matrix model. *Hydrobiologia, 260/261*:269-276.

Schiel, D.R. 1988. Algal interactions on shallow subtidal reefs in northern New Zealand: a review. *N.Z. J. Mar. Fresh. Res., 22*:481-489.

Scrosati, R. 1996. The relationship between stand biomass and frond density in the clonal alga *Mazzaella cornucopiae* (Rhodophyta, Gigartinaceae). *Hydrobiologia, 326/327*:259-265.

Scrosati, R.A. 1997. Population Ecology of the Clonal Red Alga *Mazzaella cornucopiae* from Barkley Sound, Canada. PhD thesis, University of British Columbia, Vancouver. 189pp.

Scrosati, R. and R.E. De Wreede. 1997. Dynamics of the biomass-density relationship and frond biomass inequality for *Mazzaella cornucopiae* (Gigartinaceae, Rhodophyta): implications for the understanding of frond interactions. *Phycologia, 36*:506-516.

Seagrief, S.C. 1984. *A catalogue of South African Green, Brown and Red marine algae.* Memoirs of the Botanical Survey of South Africa 47. 72pp.

Searles, R.B. 1980. The strategy of the red algal life history. *Am. Nat., 115*:113-120.

Semesi, A.K. and K.E. Mshigeni. 1977. Contributions on the content and nature of the phycocolloid from *Halymenia venusta* Boergesen (Rhodophyta, Cryptonemiales).*Bot. mar., 20*:233-237.

Setchell, W.A. and N.L. Gardner. 1933. A preliminary survey of *Gigartina* with special reference to its Pacific North American species. *Univ. Calif. Publ. Bot. 17*:255-340, pls46-65.

Sharp, G. 1981. An assessment of *Ascophyllum nodosum* harvesting methods in Southwestern Nova Scotia. *Can. tech. Rep. Fish. aquat. Sci., 1012*:22pp.

Shaughnessy, F.J. and R.E. De Wreede. 1991. Reliability of the resorcinol method for identifying isomorphic phases in the Gigartinaceae. *J. Appl. Phycol,. 3*:121-127.

Shaughnessy, F.J., R.E. De Wreede and E.C. Bell. 1996. Consequences of morphology and tissue strength to blade survivorship of two closely related Rhodophyta species. *Mar. Ecol. Prog. Ser., 136*:257-266.

Silva, P.C., P.W. Basson and R.L. Moe. 1996. *Catalogue of the Benthic Marine Algae of the Indian Ocean*. University of California Press, Berkeley, 1259pp

Simons, R.H. and F.E. Hewitt. 1976. Marine algae from Southern Africa 2. Morphology and taxonomy of five foliaceous Florideophyceae (Rhodophyta). *Investl Rep. Sea Fish. Brch. S. Afr., 110*:1-46.

Sousa, W.P. 1984. The role of disturbance in natural communities. *Ann. Rev. Ecol. Syst., 15*:353-391.

Stackhouse, J. 1809. Tentamen marino-cryptogamicum. *Mémoires de la Société Impériale des Naturalistes de Moscou, 2*:50-97.

Stegenga, H. and J.J. Bolton. 1992. Ceramiaceae (Rhodophyta) of the Cape Province, South Africa: distribution in relation to concepts of marine provinces. *Bot. mar., 35*:99-107.

Stegenga, H., J.J. Bolton and R.J. Anderson. 1997. Seaweeds of the South African West Coast. *Contributions from the Bolus Herbarium, 18*:655pp

Stephenson, T.A. 1948. The constitution of the intertidal fauna and flora of South Africa. 3. *Ann. Natal. Mus., 11*:207-324.

Stevens, R.B. (Ed). 1981. *Mycology Guidebook*. University of Washington Press, Seattle. 712pp.

Templeton, A.R. 1982. The prophecies of parthenogenesis. In: *Evolution and Genetics of Life Histories*. Dingle, H. and J.P. Hegmann (Eds). Springer-Verlag, Berlin. pp75-101.

Ter Braak, C.J.F. 1986. Canonical correspondence analysis: a new eigen vector technique for multivariate direct gradient analysis. *Ecology, 67*:1167-1179.

Ter Braak, C.J.F. 1987. The analysis of vegetation-environment relationship by canonical correspondence analysis. *Vegetatio, 69*:69-77.

tom Dieck, I. 1993. Temperature tolerance and survival in darkness of kelp gametophytes (Laminariales, Phaeophyta): ecological and biogeographical implications. *Mar. Ecol. Prog. Ser., 100*:253-264.

Turner, D. 1808. *Fuci; or Colored Figures and Descriptions of the Plants Referred to by Botanists to the Genus Fucus*. 1. J. & A. Arch, London. 164pp.

Tveter, E. and A.C. Mathieson. 1976. Sporeling coalescence in *Chondrus crispus* (Rhodophyceae). *J. Phycol., 12*:110-118.

Vadas, R.L. 1979. Seaweeds: an overview; ecological and economic importance. *Experimentia, 35*:435-437.

Vadas, R.L. and W.A. Wright. 1986. Recruitment, growth and management of *Ascophyllum nodosum*. *Actas II Congr. Algas mar. Chil., 2*:101-113.

Vadas, R.L., W.A. Wright and S.L.Miller. 1990. Recruitment of *Ascophyllum nodosum*: wave action as a source of mortality. *Mar. Ecol. Prog. Ser., 61*:263-272.

Van der Meer, J.P. 1977. Genetics of *Gracilaria* sp. (Rhodophyceae, Gigartinales) II. The life history and genetic implications of cytokinetic failure during tetraspore formation. *Phycologia, 16*:367-371.

van Zyl, P.F.F. 1993. Ecology and management of an Eastern Cape carrageenophyte, *Hypnea spicifera* (Suhr) Harv. PhD thesis, University of Port Elizabeth, Port Elizabeth, South Africa. 203pp.

Vásquez, J.A. and R. Westermeier. 1993. Limiting factors in optimizing seaweed yield in Chile. *Hydrobiologia, 260/261*:313-320.

Vernet, P., and J.L. Harper. 1980. The costs of sex in seaweeds. *Biol. J. Lin. Soc., 13*:129-138.

Vogel, S. 1981. *Life in moving fluids*. Princeton University Press, Princeton, New Jersey.

Weller, D.E. 1989. The interspecific size-density relationship among crowded plant stands and its implications for the -3/2 power rule of self-thinning. *Am. Nat., 133*:20-41.

Wittman, W. 1965. Aceto-iron-haematoxylin-chloral hydrate for chromosome staining. *Stain Technology, 40*:161-164.

Womersley, H.B.S. 1994. *The marine benthic flora of southern Australia*. IIIA. Australian Biological Resources Study, Canberra. 508pp.

Woodward, D.L. 1988. Unbalanced gametophyte : sporophyte ratios in populations of the intertidal red alga *Endocladia muricata* in central California. PhD thesis, University of California, Los Angeles. 179pp.

Yaphe, J. 1959. The determination of κ-carrageenin as a factor in the classification of the Rhodophyceae. *Can. J. Bot., 37*:751-757.

Zar, J.H. 1984. *Biostatistical analysis (2nd ed.)*. Prentice Hall Inc., New Jersey. 718pp.

Zinoun, M., J. Cosson and E. Deslandes. 1993. Physicochemical characterization of carrageenan from *Gigartina teedii* (Rooth) Lamouroux (Gigartinales, Rhodophyta). *J. Appl. Phycol., 5*:23-28.

Zupan, J.R. and J.A. West. 1988. Geographic variation in the life history of *Mastocarpus stellatus*. *J. Phycol., 24*:223-229.

ACKNOWLEDGEMENTS

I wish to thank the Foundation for Research Development through the SANCOR coastal processes programme for financial support, Afrox Ltd for funding the helicopter survey, the University of Cape Town and the Sea Fisheries Research Institute for use of their facilities, and Chris Boothroyd, Elizabeth Bristoll, Lucia Clemente and Geoff Fridjhon for assistance with field work. Thanks also to my supervisor Prof. John Bolton for his patience and to Dr Rob Anderson of the Sea Fisheries Research Institute for his encouragement. Special thanks to the following for their assistance and support during the taxonomic part of the study: Dr Herre Stegenga, Prof. Eric Coppejans, Frederik Leliaert, Olivier De Clercq and Virginie De Munster. Special thanks to Prof. Thierry Chopin for his critical reading of the manuscript. Above all, my appreciation and thanks to my wife Marisa and children Marius and Francis for their loyal and unquestioning support.