THE BIOLOGY AND ECOLOGY OF *BIFURCARIA BRASSICAEFORMIS* (KÜTZ.) BARTON (PHAEOPHYTA, FUCALES)

by

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SUMMARY

The biology, population dynamics, and the environmental tolerances (temperature and light) in laboratory culture, of the endemic intertidal South African fucoid Bifurcaria brassicaeformis (Kütz) Barton have been investigated.

A general description is included of the morphology and anatomy, and comparisons made with that of other species in the genus. Studies on plants collected from contrasting habitats on the low-shore and from mid-shore pools revealed that while cortical thickness of vegetative uprights were similar for both habitats, medullary diameters were generally higher, corresponding to generally thicker uprights in the low-shore. Observations on the method of zygote attachment revealed that attachment of the species resembles that of the European Bifurcaria and Halidrys siliquosa which both also display delayed rhizoidal development and initially attach by means of a mucilage secretion of the zygote wall. Observations on receptacle anatomy revealed that size of conceptacles increase from the apex to the base of a receptacle.

The demography of the species was studied from February 1989 to April 1990. In the typical habitat of B. brassicaeformis in the low shore, a general seasonal pattern of summer maxima and winter minima in biomass of the upright system, branching and receptacle development, as well as conceptacle maturation was apparent. Biomass of the basal system was generally higher in winter and low in summer. Receptacles developed during spring, matured fully during summer and senesced by autumn. The seasonal patterns in

the mid-shore pools were more pronounced than for the low-shore habitats over the sampling period. Plants in the pools were thinner and stunted, with lower biomass of upright systems and much reduced reproductive development in comparison to those in low-shore habitats. These differences appeared to be due to differences in microenvironmental conditions between the two habitats at the different vertical levels on the shore, particularly elevated temperatures, and also desiccation effects in those pools which dried out in summer. In both habitats, senescence of all upright material generally occurred from late summer (February) to autumn (April), and almost complete die-back of the upright material by winter, leaving mainly the basal portions (e.g. basal system constitutes 98% in pools, 45% in the low-shore). Four different phases of growth was thus observed in the population at Clovelly: growth initiation and maximum growth in length of the upright system from late winter/ spring (August to October); reproduction in summer (December to February); senescence in autumn (by April); and stasis during winter (June - July).

Reproduction in summer implies that germlings should establish soon thereafter. However, no germlings were found at the study site. It appears that maintenance of existing populations of B. brassicaeformis at Clovelly does not rely on germlings, but occurs, perhaps almost entirely, by the perennation of uprights from the basal rhizomes. Estimates of the reproductive effort revealed that the species allocates between 66-78% of the biomass of the upright system to receptacles and 0.16-0.2% of the total biomass of an upright to eggs. The estimates for percentage biomass of the upright sytem are slightly higher than those reported for the North Atlantic fucoid *Ascophyllum nodosum*, which also has uprights arising from a rhizomatous base.

Culture experiments on the influence of temperature on growth revealed that adult thalli were relatively stenothermal (optimum 15-17.5°C), with poor growth at 12.5 and below, and 20°C and above. Germlings displayed a wider tolerance than the adult thalli, grew best between 15 and 20°C, less well at 12.5 and 22.5°C and poorly at 2.5 and 10°C. Both adult thalli and germlings died at 25°C.

Seasonal sea temperatures on the South African coast suggest that the eastern boundary for the species may be a result of high summer temperatures restricting the growth and possibly reproduction of the adult thallus, while the western limit might be set by spring temperatures being too low to ensure optimal vegetative growth necessary to facilitate later reproduction of the adult thallus.

The adult thallus and germlings were light saturated at relatively low irradiances (100 and 30 $\mu Em^{-2}s^{-1}$ respectively). Growth of adult thallus was optimal between 50-200 $\mu Em^{-2}s^{-1}$. Suboptimal irradiances caused poor growth while growth gradually declined with increasing supra-optimal irradiances. The germlings showed a linear increase in growth from 0-10 $\mu Em^{-2}s^{-1}$, which increased gradually to the optimum, and gradually declined from 40-120 $\mu Em^{-2}s^{-1}$. For both adult thalli and germlings, light saturation levels for growth are similar to those measured in low shore fucoids in the North Atlantic.

CHAPTER 1

GENERAL INTRODUCTION

1. Introduction

Bifurcaria brassicaeformis (Kütz.) Barton (1893:82) (Fucales, Cystoseiraceae) is the only South African species of the genus *Bifurcaria*. The only other currently recognised species in the genus are *B. bifurcata* Ross (1961:512) in the eastern North Atlantic and *B. galapagensis* (Piccone and Grunow) Womersley (Womersley 1964:104) which is endemic to the Galapagos Islands.

Bifurcaria brassicaeformis is ecologically important on shores of the south western Cape Province, South Africa, because it is the only South African member of the Fucales which forms extensive dense communities in the lower intertidal. In the shallow sublittoral, however, *Bifurcariopsis capensis* (Aresch.) Papenf., *Anthophycus longifolius* (Turner) Kütz. and species of *Sargassum* may be locally dominant.

The earliest studies on *B. brassicaeformis* other than taxonomic investigations were undertaken by Delf (1931, 1935). Delf studied aspects of the reproductive biology such as oogonia liberation and its ecological significance. Later, Isaac (1951) undertook a general descriptive study of the ecology of the species, investigating the systematics and morphology of the species, its distribution in relation to sea temperature, its position intertidally, and its occurrence in relation to exposure and

salinity. Other literature on the species is to be found in brief comments on the ecology of B. brassicaeformis on the South African west coast from Lamberts Bay to the Cape of Good Hope (Isaac 1937b); for the region between Rooi Els and Gansbaai on the south coast (Isaac 1949), and for St James in False Bay (Eyre 1939) (see Figure 24, page 106 for locations).
Recently, Levitt (1987) investigated the immersed primary production seasonally, and the effect of emersion on desiccation and productivity.

This study, was designed to add new information on the demography and environmental tolerances of the species in culture, as well as adding to existing information on its morphology, anatomy, ecology and reproductive biology.

2. Circumscription and geographical distribution of the Fucales

Six families are currently recognised in the Fucales (Clayton 1984); the Cystoseiraceae, Sargassaceae, Fucaceae, Seirococcaceae, Hormosiraceae and the Himanthaliaceae. They are distinguished primarily on the basis of apical cell shape and number, the pattern of thallus branching and details of the development of the oogonium (see Jensen 1974, Clayton 1984). While the first three families have a bipolar distribution, the Seirococcaceae and Hormosiraceae are found in the southern hemisphere only, being endemic to Australia and New Zealand, with the possible exception of the South African Axillariella *constricta* (J. Ag.) Silva which may be a member of the Seirococcaceae (Clayton 1984). The Himanthaliaceae is found in the northern hemisphere only.

Clayton (1984) speculates that the Fucales evolved in the temperate climate of Gondwanaland in the Miocene 90 million years ago (Raven and Axelrod 1972), with radiation from an Australian point of origin. Southern Australia is the centre of diversity of the Fucales, as all the families with the exception of the Himanthaliaceae are represented in the present day marine flora. Clayton further suggests that species of the Cystoseiraceae, a family which currently includes *Bifurcaria brassicaeformis* and *Bifurcariopsis capensis*, may have spread to South Africa some 80 million years ago when Africa was still joined to Antarctica and Australia. This was possibly how the progenitors of these South African fucoids reached South Africa. *Bifurcaria* possibly also used Southern Africa as a gateway in its migration to the North Atlantic as it is suggested was the case for many red algae (Hommersand 1986), with subsequent evolution of *Bifurcaria bifurcata* in the North Atlantic following its formation between 100 and 65 million years ago (Lüning 1985). The current geographical distribution of *B. galapagensis* in the Galapagos Islands is difficult to explain by such speculations.

The distribution of the genera of the Fucales on a worldwide basis has been reviewed by Nizamuddin (1962, 1970). Genera such as *Fucus* and *Pelvetia* are only found in the northern hemisphere, many genera such as *Bifurcariopsis* and *Hormosira* only in the southern hemisphere, being endemic to South Africa and Australia respectively, and Sargassum, Cystoseira and Bifurcaria occurring in both hemispheres.

3. Temperature and geographic distribution

Seaweed distribution can potentially be restricted by several physical and biological factors. It is generally accepted that temperature, particularly the temperature regime of the surface waters is probably the most important physical factor determining the geographic distribution of marine benthic algae. (Setchell 1920, van den Hoek 1982a,b, Lüning 1985, Bolton 1986, Breeman 1988). Specific daylength requirements for reproduction may also affect distribution in combination with temperature (Breeman 1988). Salinity caused by major intrusions from the world's large rivers (Bird and Mc Lachlan 1986) could also potentially limit distribution. Biological factors such as herbivory and competition have also been stressed (Hay 1981, Gaines and Lubchenco 1982). However, these biological factors would only allow an assessment after a detailed analysis of the physical habitat at the distribution boundaries is compared with an experimental analysis of the physiological tolerance and requirements of a species.

Much has been published on the effect of temperature on seaweed distribution, and Breeman (1988) gives a review of the topic using recent experimental and phenological evidence.

Three approaches have been adopted in determining the distribution limits of a species. The first approach was used by van den Hoek (1982a,b) for several North Atlantic distribution groups. This comprised an experimental assessment of a species' critical temperature requirements for completion of its life history, combined with a description of the annual temperature regimes at its distribution boundaries. These boundaries may then be defined as due to a growth (or reproduction) limit in the growing season and/or a lethal limit in the adverse season. However, van den Hoek's approach could be criticised in that a) experimental evidence for many species was incomplete, b) experiments were often done on a single isolate c) ocean isotherms were used to describe the annual temperature regimes at distribution boundaries, which were a rough estimate of temperatures experienced by the plants *in situ*. The second approach was used by Cambridge *et al.* (1984, 1987) for several *Cladophora* species and by other authors (Stewart 1984, van den Hoek 1982c, Mathieson and Dawes 1986) for North Atlantic seaweeds. These authors have discussed distribution patterns of seaweeds in terms of optimum growth temperatures. However, these authors all found that optimum temperatures for growth might not necessarily be related to a seaweed's southerly or northerly boundary. Futhermore, Breeman (1988) found that optimum temperature for growth and/or reproduction or lethal limits of the non-hardiest stage (often macrothalli) were irrelevant in explaining the distribution of some 60 North Atlantic seaweeds. In the third approach adopted by Breeman (1988), the author emphasises that distribution ranges of seaweeds are determined by the effect of limiting factors, restricting distributions at each boundary. Therefore, suboptimal rather than optimal or lethal temperatures should be considered in the question of a seaweed's geographic distribution, while seasonal boundaries may be set by too low summer temperatures which prevents maturation and reproduction or the increase of population size (Breeman 1988).

"Gaps" in the distribution of a species might also occur. Such gaps have been recorded for several British seaweeds (Dixon and Irvine 1977, Norton 1986) where these gaps have been attributed to the presence of sediment coasts, undersampling of rocky shores or from collections made during the wrong season (Breeman 1988).

Marine biogeography in southern Africa has a strong descriptive ecological base (Stephenson 1939, 1944, 1948, Stephenson et al. 1937, 1938, 1940, Bright 1938, Eyre 1939, Eyre et al. 1938, Isaac 1937a, 1938, 1949). The close links between biogeographical discontinuities, the patterns of oceanic circulation and the corresponding temperature regimes have also been described (Isaac 1937b, 1938).

Recently, there have been several studies, both correlative and experimental, in which temperature has been shown to be the major factor regulating geographic boundaries of southern African seaweeds (Anderson and Bolton 1985, Bolton and Levitt 1985, Bolton 1986, Bolton and Anderson 1987a,b , Bolton and Stegenga 1987, 1990, Anderson and Bolton 1989).

Stephenson (1944) divided the coast of South Africa into three major biogeographical provinces: a cold temperate west coast, warm temperate south coast, and a subtropical east coast. The south coast marine province has its western boundary at Cape Agulhas (see Chapter 5, page 106, Figure 24 for locations mentioned in text), with an overlap region between the south and west coast marine provinces form Cape Agulhas to Kommetjie on the west coast of the Cape Peninsula. In contrast to Stephenson's designation of the west coast being cold temperate, Bolton (1986) presented data on the temperature tolerances of selected west coast species to indicate that the west coast seaweed flora is best described as warm temperate in comparison with other world regions. Therefore, according to Bolton (1986), southern Africa has two warm temperate floras with the major disjunction between them in the region of Cape Agulhas.

Detailed floristic studies have been conducted for the seaweed floras of the west coast (Bolton 1986), the south coasts east of Cape St Francis (see Seagrief 1988 for a species list), a region of the Transkei (Bolton and Stegenga 1987), and a region 60km east of Cape Agulhas (Bolton and Stegenga 1990). The studies of Bolton (1986) and Bolton and Stegenga (1987, 1990) have been analysed by a compilation of the individual species present in these areas.

A study on the distribution pattern of Bifurcaria brassicaeformis using laboratory temperature tolerances would be interesting as the species is abundant only in the overlap region between the south and west coast marine provinces (sensu Bolton 1986).

4. Factors influencing the distribution and growth of seaweeds

There are a wide variety of environmental factors such as temperature, light, desiccation, water motion and nutrients which affect plant growth in the marine environment. Growth optima and tolerances may, however, vary greatly between developmental stages (e.g. Hanisak 1979, Fain and Murray 1982), and distribution limits may be dependent on the tolerances of a particular sensitive stage. While temperature has already been discussed, other factors such as light and desiccation which are particularly relevant to this study, will be discussed in more detail later. Environmental factors might also affect algal morphology thus accounting for at least part of the morphological variation observed in natural populations (Chapman 1974, Russell 1978, Mathieson _et al._ 1981). The high degree of phenotypic plasticity in morphological features considered characteristic of many algal species emphasises the importance of thallus geometry in the aquisition of resources for growth (Littler and littler 1980, Norton _et al._ 1982, Raven _et al._ 1982, Rosenberg and Ramus 1984).

There has been a large body of work on the ecology of intertidal fucoids in the Northern Hemisphere. Fucoid algal species show characteristic zonation patterns on these shores (see e.g. Schonbeck and Norton 1978, 1980). _Pelvetia canaliculata_ (L.)

Dcne et Thur. grows at the highest level on the shore, where it may be exposed to air for several days at a time. *Fucus spiralis* L. forms a second zone, followed by *Ascophyllum nodosum* (L.) Le Jol. in the third zone in the middle shore. The fourth zone also lies in the middle shore and is dominated by *Fucus vesiculosus* L., and gradually gives way to the low-shore dominant *F. serratus* L. The species higher up on the shore experience greater exposure to air, higher light levels and higher temperatures than those lower down on the shore. Subsequently, these algae react differently to these environmental factors depending on their relative position in their zone as well as their position in the intertidal. Schonbeck and Norton (1978) found that the uppermost plants of each species showed signs of tissue damage three to four weeks after plants were exposed after a time when drying conditions coincided with neap tides which exposed the plants to aerial conditions for long periods. High air temperature aggravated the damage, but neither frost nor prolonged rain had any obvious adverse effects. On spring tides, the plants were wetted every day and no damage resulted regardless of the weather. Schonbeck and Norton (1978) also carried out laboratory experiments which tested the desiccation tolerances of each species and their ability to resume photosynthesis and growth when resubmersed. Desiccation tolerance was greatest in *P. canaliculata*, the species found highest on the shore, and was progressively less in species inhabiting successively lower levels. It must be stressed that it is well documented that intertidal algae (see e.g. Johnson *et al.* 1974, Dromgoole 1980, Levitt 1987) and fucoids in particular (see e.g. Schonbeck and Norton 1979a,b,c) do photosynthesise when emersed.

4.1. Light

Although there exists a large body of literature for the relationship between irradiance and photosynthesis, our knowledge of that between irradiance and growth is poor. Most work has been done on small seaweeds and their juvenile stages growing in the eulittoral zone and sublittoral fringe (Lüning 1981).

Eulittoral species can clearly be regarded as "sun plants" and the sublittoral species as "shade plants" since their saturating light levels for growth have been found to correspond closely to that reported for sun and shade higher plants (Bohning and Burnside 1956, Boardman 1977). Lüning (1981) summarised data on light saturation for growth of adult thalli and juvenile stages of several eulittoral and sublittoral algae. Generally, the progression from high eulittoral shore species to sublittoral species correlated well with the light levels for saturation of growth. Saturation points for growth of adult thalli and juveniles gradually decreased for high shore eulittoral to low shore sublittoral species. For example, adult thalli of the eulittoral _Ascophyllum_ _nodosum_ and the sublittoral _Laminaria saccharina_ occurred at 250 and 70μEm^{-2} s^{-1} respectively, while their juvenile stages staurated at 30 and 15$\mu Em^{-2} s^{-1}$ respectively.

As this data shows, light levels for saturation of mature plants are often greater than those of juvenile stages (Lüning 1981).

Increase in length in the Fucales takes place by division of the apical cell and further elongation of the newly formed cells (Jensen 1974). Light is no doubt important in this process, providing material for photosynthesis and thereby influencing growth directly.

Very little is known about the relationship between light intensity and apical growth of adult Fucales. Strömgren (1977) determined the saturation points for growth for five intertidal fucoid species and Schonbeck and Norton (1978) determined the growth rates of several intertidal fucoids in field and culture studies. In both these studies, saturation light levels and growth rates was correlated with the vertical position of the species in the intertidal.

Much more literature exist on the relationship between irradiance and the growth of fucoid germlings (Mc Lachlan 1974, Mc Lachlan _et al._ 1971, Moss and Sheader 1972, Moss _et al._ 1973, Sheader and Moss 1975, Schonbeck and Norton 1978).

As for the adult thalli, these researchers also found that light saturation values for the germlings correlated well with the relative position of the species on the shore.

4.2. Desiccation

The factors controlling the upper and lower limits of intertidal algae have recieved much attention. Their upper limits have generally been ascribed to their susceptibility to atmospheric conditions during tidal exposure (Colman 1933, Zaneveld 1937, Lewis 1964). In a study on several European intertidal fucoids, Schonbeck and Norton (1978) have shown that the upper limits of each species is determined by its ability to tolerate prolonged exposure (desiccation). These same authors (1980) showed that the lower limits were determined largely by interspecific competition. Species found higher up on the shore tolerated desiccation better with tolerance progressively decreasing in species inhabiting successively lower levels. The high shore species could resume photosynthesis and grow under desiccating conditions while the low shore species could not. Many algae were protected from desiccation by repeated wave splash (Burrows et al. 1954, Lewis 1964), by an overlying canopy of larger algae (Menge 1975) or by inhabiting shady places or north facing slopes (Zaneveld 1937, Hatton 1938, Norton et al. 1971). In a study on three intertidal fucoids, Strömgren (1976, 1977b) found that short periods of desiccation (up to two hours) enhance growth rate while long periods (two hours and more) reduce growth rates. He concluded that considerable growth in length takes place when intertidal algae are exposed for short periods.

Desiccation tolerances of several south African intertidal algae have been studied by Levitt (1987). He found that Bifurcaria brassicaeformis, which occurred lowest down on the shore of the species tested, was least tolerant to desiccation and showed the lowest levels of carbon fixation when emersed in comparison to other algae such as Ulva rigida C. Ag., and Porphyra capensis

Kützing, *Splachnidium rugosum* (L.) Grev. and *Gigartina radula* (Esper) J. Ag. which occurred higher up.

5. Demography

The objective of a demographic study is to determine the effects of population parameters on the density or size of a single species population (Chapman 1985). The four primary parameters that affect population density are natality, mortality, immigration and emigration. Most seaweeds are attached to a surface so that immigration and emigration is of minor importance. Secondary population parameters often studied include age class distribution, fecundity and reproductive effort (Begon and Mortimer 1981, Chapman 1985). The measurement of density population parameters is central to any demographic analysis (Begon and Mortimer 1981). Density itself may be difficult to measure in seaweeds as it is often difficult to discriminate between the products of separate zygotes and spores. In these cases it is best to consider the population biology of designated areas using quadrats of the modular components (ramets) rather than genets (Harper 1977). For example, Cousens (1981a) studied the demography of upright fronds of *Ascophyllum nodosum* which has an expanded holdfast , regardless of zygotic origins. Once the measurement of density has been established, density related parameters can be assessed.

The age of a thalloid marine alga is difficult to determine from its anatomical features or its form. Exceptions to this are species of Laminaria where the sporophytes can be aged by means of stipe growth rings (Kain 1979), and Ascophyllum nodosum whose fronds can sometimes be assigned to a particular year class (Cousens 1984). In most cases the age structure of a population cannot be measured directly, although it may be possible to deduce age from the size structure (Russell 1990). Gunnill (1985) managed to measure the age of a population of Pelvetia fastigiata (J. Ag.) de Toni by examining the age-size relationship but found that this relationship can be highly variable, as some individuals grew 1-2cm in length per 30 days, some 3-4cm per 30 days, while other plants, especially longer plants became smaller during surveys. Further virtues and pitfalls of this method have been demonstrated by Grant (1989). Grant deduced that in animal populations, age composition may be safely deduced if the sizes of the individual groups exceed an absolute minimum of 50 individuals. However, Russell (1990), after analysing biomass frequencies of vegetative thalli of much larger number of algal individuals (genets) of Himanthalia elongata (L.). S.F. Gray, warns that results are often subject to misinterpretation. For example, although Russell (1988) concluded that H. elongata plants may spend up to two years in immaturity before entering the reproductive phase, additional observations (Russell 1990) suggested that some thalli may persist in the immature state for more than two years, suggesting that the conclusion on age composition was unwarranted.

While age class distribution is important from a demographic veiwpoint, the absence of juveniles in a seaweed population due to physical and biological factors (Chapman 1986) may often exclude this parameter from a study. Fecundity which is defined as the total number of eggs produced by an organism (Chapman 1985) can be measured differently depending on the seaweed's morphology. For Nereocystis leutkeana and Rhodymenia pertusa, Scagel (1961) estimated fecundity by counting eggs and spores in sporangia and oogonia before they were released. Chapman (1984) measured fecundity for two species of Laminaria by estimating the amount of spores from a known area of sorus. For a local Laminarian species, Ecklonia maxima (Osbeck) Papenf., Joska and Bolton (1987) measured fecundity by two methods; as for the two Laminarian species above, and by counting spores actually released, with season. Vernet and Harper (1980) measured fecundity of British fucoids by counting the following parameters on each plant: the number of receptacles, the number of conceptacles per receptacle and the number of oogonia and antheridia per conceptacle.

Reproductive effort, which is often confused with fecundity, is usually defined as the proportional plant weight allocated to reproductive propagules. Alternatively, reproductive effort can be defined as the total biomass of the reproductive organs in comparison to the rest of the plant.

Vernet and Harper (1980) assessed the reproductive effort of several British fucoids and found that the total biomass of

gametes was very small in comparison to the rest of the plant. Gametes only represented 0.1-0.4% of the total plant weight. Cousens (1981a) measured the reproductive effort of a fucoid Ascophyllum nodosum by the alternative method described above and found that receptacles accounted for over half (61-66%) of the biomass of the plant.
While measuring fecundity and reproductive effort might be possible, the measurement of reproductive dispersal may be a difficult task due to mortality, herbivory and the difficulty in discerning the settled juveniles (Anderson and North 1966, Dayton 1973, Deysher and Norton 1981).

A large body of literature on the demography of intertidal seaweeds has been published. These deal with survivorship and productivity (e.g. Chapman and Goudey 1983, Gunnill 1980, Cousens 1981b), seasonal growth (e.g. David 1943, Coyer and Zaug-Haglund 1982, Thom 1983, Gunnill 1985), seasonal primary production (e.g. Mann 1972, Neill 1977, Rice and Chapman 1982, Levitt 1987) and fecundity and reproductive effort (Vernet and Harper 1980, Cousens 1981a).

Among marine macroalgae, the ecology of fucoids and their population biology have been relatively well studied. Information is available on many aspects of fucoid ecology including interspecific competion (Schonbeck and Norton 1980), colonization and growth dynamics (Keser and Larson 1984, Gunnill 1985), annual production (Cousens 1981a,b , 1984, Levitt 1987), attachment strength in relation to wave exposure (Mc Eacreon and Thomas 1987), seasonal growth and reproduction (David 1943, Subramanyan 1960, 1961, Nizamuddin 1970, Edelstein and Mc Lachlan 1975, Thom 1983, Keser and Larson 1984, Gunnill 1985) and survivorship (Gunnill 1980, Cousens 1981).

No previous demographic study has been carried out on *Bifurcaria brassicaeformis*. This study will thus lead to a greater understanding of both the population biology and production ecology, elucidating factors such as growth and reproductive seasonality, development and reproductive effort and fecundity of the species.

6. Fucoid reproductive biology

Of particular importance in the life history of an alga is the efficiency of the reproductive process and the ability of the sporelings to survive through the early more vulnerable stages of attachment and germination, especially in the intertidal where there is considerable water movement. Both these processes will undoubtedly exert a major influence in determining local establishment, the maintenance of the existing population, and the local abundance and spread of the plant.

The Fucales is characterised by a diplobiontic life history (i.e. meiosis occurs at the time of gametogenises). Oogamous sexual reproduction is the rule for all species. The plants found in nature represent the diploid phase which produces haploid gametes, the egg and sperm.

Detailed studies on gamete production, fertilization and zygote development have been conducted on many fucoids in a variety of genera, such as Hormosira (Forbes and Hallam 1978), Pelvetia (Müller and Gassman 1985), Ascophyllum (Papenfuss 1951, Sundene 1973), Sargassum (Papenfuss 1951, Fletcher and Fletcher 1975a), Cystoseira (Roberts 1967) and especially Fucus (Papenfuss 1951, Pollock 1970, Brawley et al. 1976a,b, Caplin 1968 and Cook and Elvidge 1951, Novotny and Forman 1975, Quatrano 1972).

Some literature on ecological aspects of fucoid reproductive biology has been published. Fletcher and Fletcher (1975a,b) investigated the regenerative ability of Sargassum muticum (Yendo) Fernsh., and suggested that copious production of eggs coupled with the retention of fertilized eggs on receptacle surfaces, delayed rhizoid development and the ability of vegetative thalli to regenerate after becoming detached, all probably accounted for its successful dispersal and colonization abilities. Furthermore, many studies (e.g. Hoyt 1927, Delf 1935, Fletcher 1980) have shown that periodic discharge of gametes occurs in intertidal algae during and shortly after spring tides. The evolutionary success of Fucoids in the harsh marine environment may have been associated with the phenomenon of extra protection offered by the conceptacles to the gametes and the discharge of these gametes (Clayton 1984) Synchronised gamete liberation during favourable periods can thus take place with ecologically, physiologically and genetically more vulnerable haploid plants being eliminated.

In the intertidal, where alternating periods of wetting and drying occur , the above phenomenon places fucoids at an ecological and physiological advantage (Clayton 1984). As fronds of intertidal species dry out, they shrink and mature antheridia and oogonia begin to extrude from the conceptacles. The gametes are surrounded by mucilage. In contact with seawater, extrusion continues and the inner gametangial membranes dissolve (see detail later), liberating eggs and spermatozoids. Fertilization is effected rapidly (Fritch 1945, Bold and Wynne 1978). In submerged fucoids, little is known of the factors influencing gamete release (Clayton 1984) but evidence has been provided for *Sargassum muticum* that egg emission is synchronised and related to lunar periodicity (Norton 1981).

The number of eggs produced per oogonium is a taxonomically important criterion at family level and has been tabulated in Clayton (1984). All the families have one egg per oogonium except for the Hormosiraceae and Fucaceae which have four and one, two, four or eight eggs per oogonium respectively. *Bifurcariopsis* is an exception in the Cystoseiraceae in having four instead of one egg per oogonium. Eight eggs is considered primitive while one egg is thought to represent the advanced condition. Clayton further suggests that it may be of ecological and evolutionary significance that intertidal fucoids include most of the genera in which more than one egg is produced per oogonium (e.g. *Fucus* (8), *Ascophyllum* (4), *Pelvetia* (2)). Smaller eggs cost less energy to produce and therefore a greater number can be produced at the same cost (see Vernet and Harper 1980). A smaller size tends to confer a lower sinking rate and a greater dispersal and therefore colonization ability. However, larger eggs as found in the Cystoseiraceae or Himanthaliaceae may be adaptively advantageous in their ability to sink and attach rapidly.

In spite of the number of eggs produced, it is widely accepted (Moss and Sheader 1972, Moss *et al.* 1973, Mc Lachlan 1974, Sheader and Moss 1975, Clayton 1984) that the large energy stores in fucoid eggs tides them over unfavourable periods such as darkness and aids in rapid germination and initial establishment.

In the genus *Bifurcaria*, De Valera (1962) investigated the problems associated with reproduction and dispersal of the British *B. bifurcata* and compared it with other fucoids (see later) while Delf (1935) described the importance of oogonial attachment to mesochiton stalks in the reproductive process of *B.brassicaeformis* and the ecological significance thereof (see later).

6.1. Population maintenance

De Valera (1962) investigated the problems of perennation, reproduction and maintenance of existing populations of the North Atlantic *Bifurcaria bifurcata*. The author suggests that in Ireland, the maintenance of existing populations of *B. bifurcata* is less dependent on the production of new plants from fertilized eggs than is the case in other species, such as Himanthalia or Fucus. Germlings of B. bifurcata appear to be a relatively rare occurrence in nature.

Ascophyllum nodosum has a constant production of shoots from the base which Baardseth (1955, in DeValera 1962) believes to be far more important in maintaining the population than regrowth from fertilized eggs. This is because single shoots, which could be interpreted as the early initials in the develoment of an egg (De Valera 1962), have been found to be so rare, in spite of the tremendous number of eggs liberated from the fruit bodies in the spring. Although population maintenance has not yet been investigated in B. brassicaeformis, Bokenham and Stephenson (1938) have described how this species recolonize cleared patches in its community. These authors cleared patches within two communities of both animals and algae leaving nothing behind except encrusting coralline red algae and microscopic forms in May 1935. These communities were at St. James in False Bay (a 1.2 m2 patch), and at Sea Point on the western seaboard of the Cape Peninsula (a 1.3 m2 patch). Each patch was visited at least monthly until May 1936, once in August 1936, and then one final visit in February 1938. These authors reported that by August 1936, at St. James, although other algae such as Gelidium pristoides (Turn.) Kütz. and Centroceros clavatum (C. Ag.) Mont. were fairly abundant, B. brassicaeformis was beginning to "invade the patch from adjacent rocks but that the area had not regained its former appearance". At Sea Point, the species was still absent. Short growths of other algae such as Gymnogongrus glomeratus J.

Ag. and fairly abundant corallines and a few barnacles were present. By February 1938, at St. James, fairly large quantities of the species were present, so that the patch was beginning to approach its original appearance. At Sea Point, there were short growths of B. brassicaeformis, indicating that germlings had settled in the cleared patch. Bokenham and Stephenson (1938) further suggest that as at St. James, the patch would approach its original appearance eventually. Although Bokenham and Stephenson showed that recolonization and/ or colonization of cleared areas within a B. brassicaeformis community is possible, these authors failed to discover exactly the rate of inward growth of the rhizomes or when germlings first established.

In view of the importance that germlings might play in the colonization of large perennials such as Fucoids, and in the maintenance of existing populations, the nature of germling establishment will be of great importance in fucoid reproductive biology. Secure attachment of fertilized oospheres to the substratum will be of primary importance. Attachment of zygotes and embryos of several British fucoids have been investigated including Bifurcaria bifurcata (Hardy and Moss 1979).
Zygotes of Fucus (Thuret and Bonet 1878) and Ascophyllum (Moss 1975) attach first by the exudation of mucilage, then by the rapid regrowth of a primary rhizoid which adheres immediately as soon as it contacts the substratum. Species with delayed rhizoid development attach by means of a specialised mesochiton as in Pelvetia (Moss 1979), or a specialised zygote wall as in

Himanthalia (Moss, Mercer and Sheader 1973), *Halidrys* (Hardy and Moss 1978) and *Bifurcaria bifurcata* (Hardy and Moss 1979). The mechanism of zygote and germling attachment in *Bifurcaria brassicaeformis* will be investigated and compared with that of European fucoids.

6.2. Pheromones

The significance of sexual pheromones in spermatozoid release and attraction just prior to fertilization has been documented in marine brown algae (e.g. Müller 1976, 1978, Jaenike 1977, Lüning and Müller 1978) and has been known for more than a century in the Fucales (Thuret 1854).

Until recently, pheromonal attraction of sperm to eggs had only been documented in the dioecious fucoids *Fucus serratus* and *F. vesiculosus* (Müller and Seferaidis 1977, Müller and Gassman 1978), *Ascophyllum nodosum* (Müller *et al.* 1982) and *Hormosira banksii* (Turn.) Dcne. (Müller *et al.* 1984). However, in 1985, Müller and Gassman also described sperm attractants in monoecious fucoid species of the genus *Fucus* (*F. spiralis*) and Californian members of the genera *Hesperophycus*, *Pelvetia* and *Pelvetiopsis*. Müller and Gassman (1985) found that the pheromonal systems do not differ between dioecious and monoecious fucoid species. Fucoserratene is the sperm attractant in the dioecious species *Fucus serratus* and *Fucus vesiculosus* as well as in the monoecious species *F. spiralis* and in members of the Californian genus *Hesperophycus*. Likewise, the sperm attractant

finavarrene was found in the dioecoious A. nodosum and in the monoecious species of the Californian genera Pelvetia and Pelvetiopsis investigated by Müller and Gassman (1985).
The sperm attractants undecatriene and pentadene was also discovered in the species of Pelvetiopsis investigated by Müller and Gassman (1985). In Hormosira banksii the sperm attractant was described as hormosirene (Müller et al. 1984).
Therefore, to date from the literature, in the fucales, sperm attractants secreted by eggs are known for nine species from seven genera. The reason why sperm attractants were first discovered in dioecious species was due to the fact that since male and female structures are borne on separate plants, large quantities of eggs and sperm could easily be obtained for experimentation. Müller and Gassman (1985) also found that unfertilized eggs secrete the attractants for up to 24 hours. In the monoecious species, sperm attraction to eggs was more difficult to observe and detect, since eggs and sperm cannot be separated easily (Müller and Gassman 1985).

6.3. Gamete liberation and fertilization

In B. brassicaeformis, liberation of oogonia has been described by Delf (1935). As with the other members of the Fucales, oogonia contain three wall layers: exochite, mesochite and endochite which disintegrate successively upon liberation of oogonia.
When the oogonia are ripe, accumulated mucilage above it expands, pushing aside a cap of exochiton. With further expansion, the

gelatinous egg stalk straightens (the oogonia are now surrounded by endochiton and mesochiton), is withdrawn, inverted, and owing to mutual pressure, is thrust out of the ostiole.
At dehiscence, each ostiole is enveloped by a glistening drop of mucilage in which the oogonia are visible to the naked eye. About 250 oogonia (Delf 1935) each containing a single ovum are extruded from one conceptacle at any one time. Ejection of eggs seems to be periodic, although the precise timing is not known (Delf 1935). Delf suggested that secondary attachment of oogonia by mesochiton stalks in permanently submerged fucoid species with unisexual conceptacles (as is found in *Bifurcaria brassicaeformis*) is an ecologically significant adaptation because cross fertilization would be facilitated if the oogonia are held in proximity to the discharged spermatozoids. Ova would sink and chances of fertilization would be reduced. However, Delf's (1935) claims of a benefit of the mechanism described in permanently submerged fucoid species which were supported by other authors such as Dawson (1941) and Naylor (1949), were found to be at variance with the ecological facts presented by Isaac (1951). Isaac pointed out that *B. brassicaeformis* is not permanently submerged but emergent for various lengths of the tidal period. Although *B. brassicaeformis* is emergent as described by Isaac (1951), subsequent submergence followed by fertilization of eggs held by mesochiton stalks would benefit the plant as described by Delf (1935).

Certain aspects of the reproductive biology of *B. brassicaeformis* such as the purpose of the mesochiton stalks and the mucilage surrounding the oogonia before release have not yet been investigated in a Bifurcaria species.

In this study, additional information to Delf's (1935) observations on gamete liberation will be presented and a short description will be given of observations on zygote attachment and germling development in comparison with British fucoids.

CHAPTER 2

THE STUDY SITE

1. Introduction

The main study site was at Clovelly (34°08'S, 18°26.4'E) in False Bay on the Cape Peninsula, South Africa (Figure 1). The intertidal region of Clovelly (Plate 1) consists of a substratum of Table Mountain sandstone (TMS). The levels of the experimental sites were estimated in metres above Lowest Astronomical Tide (L.A.T.) by referring to readings of the tidal gauge at Simon's Town (see Figure 1) (M.T.L. = 1.06m; M.H.W.N. = 1.34m; M.H.W.S. = 1.8m; MLWS = 0.32m; L.A.T. = 0.08m (all values above chart datum).

Bifurcaria brassicaeformis occurs 0.8-1m above L.A.T. on open rock and in gulleys in the lower eulittoral bordering the sublittoral fringe and in pools in the mid-eulittoral 0.5-0.75m vertically further up the shore from the low-shore habitats (1.7m above L.A.T.).

Four open rock sites and three pools (7 microhabitats) were subjectively chosen as study areas. These not only represented different habitats lower and higher up on the shore (hereafter designated as sites and pools), but individually each represented a slightly different microhabitat which appeared to experience different environmental stresses such as wave action, light and temperature. These four sites and three pools are, in a sense, replicates with respect to sampling, but because of the variable nature of the environment, they are treated separately, initially.

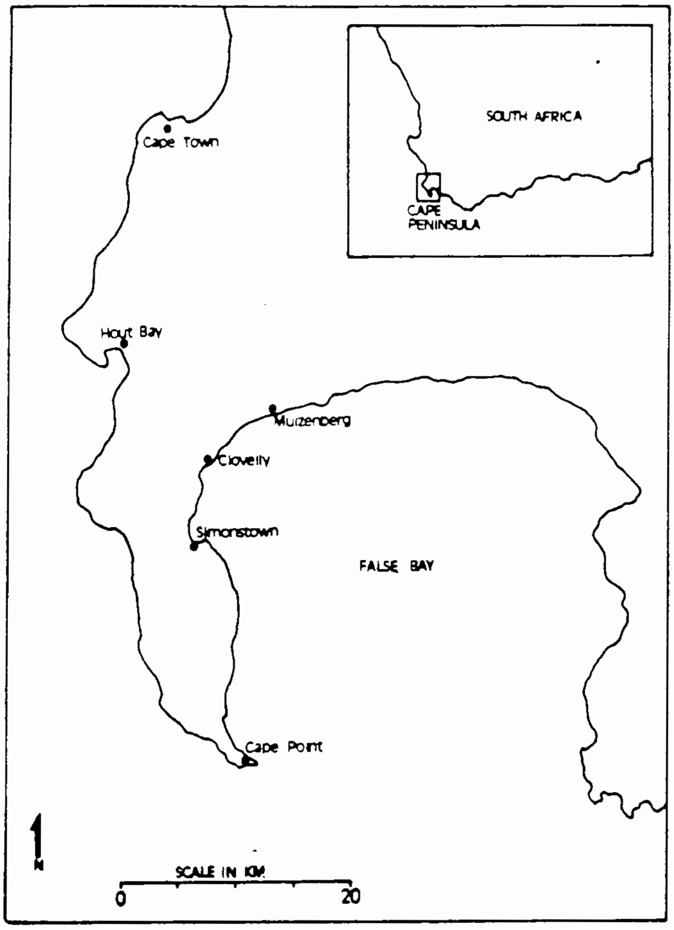


Figure 1. Location of the study site in False Bay on the Cape Peninsula. Inset: Map of South Africa.

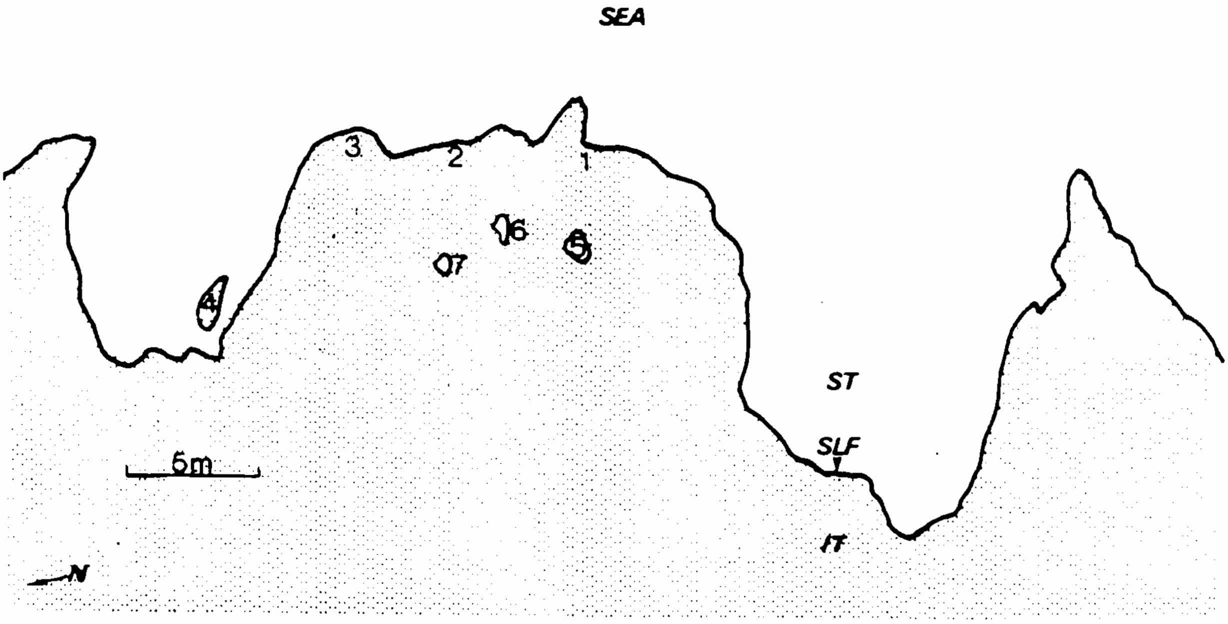


Figure 2. Diagram of the local area studied at Clovelly. Microhabitats are numbered from 1-7. (1) Rock (2) Gulley (3) Overtop (4) Triangle (5) Pool 1 (6) Pool 2 (7) Pool 3. (Note: ST = Subtidal, SLF = Sublittoral fringe, IT = Intertidal).

Plate 1. The intertidal rocky shore at Clovelly. The arrow indicates the typical habitat in the low-shore of Bifurcaria brassicaeformis (B).

The microhabitats are numbered in Figure 2 and photographically illustrated in Plates 2 - 9. All photographs were taken during December 1989.

2. Description of microhabitats

2.1. Sites

Generally, upright fronds of plants grow luxuriantly.

2.1.1. Site 1: ROCK (Plate 2)-: The species occurs on the sheltered side of a projecting rock not experiencing the impact of direct wave action although receiving moderately strong spray action during spring low tides. This keeps the plants moist.
Plants located lower on the rock are more shaded from the sun than those on top of the rock.

2.1.2. Site 2: GULLEY (Plate 3)-: Plants occur on the side of the rock in the gulley so that the tips of the upright fronds lie within the gulley pool during spring low tides and experience relatively strong wave action when the tide is in.

2.1.3. Site 3: OVERTOP (Plate 4)-: Plants occur just below the top of the rock and appear to experience moderately strong wave action when the waves wash over the top onto the plants during spring low tides.

2.1.4. Site 4: TRIANGLE (Plate 5)-: Wave exposure and moisture conditions appear similar to that of the Overtop site.

Plate 2. The Rock site.

Plate 3. The Gulley site.

Plate 4. The Overtop site.

Plate 5. The Triangle site.

2.2. Pools (Plate 6)

Generally, upright fronds of plants grow poorly.

2.2.1. Pool 1. (Plate 7)-: Upright fronds of plants are stunted, thin, often with desiccated tips and experience no direct wave action during spring low tides. Uprights are partially submerged in the little water left behind in the pool during spring low tides. This water left behind in the pool generally heats up on a sunny day. During summer, the pool does dry out completely, while in winter, the depth of the water varied between 1 and 10cm during springlow tides.

2.2.2. Pool 2. (Plate 8)-: Similar conditions to Pool 1.

2.2.3. Pool 3. (Plate 9)-: Similar conditions to Pool 1 except that drying out of the pool was never observed. Plants look slightly more robust than in Pools 1 and 2. Pool 3 is deeper than Pools 1 and 2, and shaded by a protruding rockface in contrast to Pools 1 and 2 which are completely exposed to the morning and noon sun. During summer, the depth of the pool varied between 8 - 20cm, while in winter the depth varied between 10 - 25cm at its centre during spring low tides.

Plate 6. The three pools when they were filled with water in December 1989.

Plate 7. Pool 1.

Plate 8. Pool 2.

Plate 9. Pool 3.

CHAPTER 3

TAXONOMY, MORPHOLOGY AND ANATOMY, AND REPRODUCTIVE BIOLOGY OF BIFURCARIA BRASSICAEFORMIS

1. Introduction to the genus

The genus Bifurcaria belongs to the family Cystoseiraceae of the Fucales. Jensen (1974) lists the features which serve as characteristics of the order and the family. The genus was placed into the Cystoseiraceae by Oltmanns (1889) on the basis of the configuration of the apical cell. The apical cell is three-sided in transection, as is also the case in the Sargassaceae, Himanthaliaceae and Hormosiraceae. In the Fucaceae and Seirococcaceae, the apical cell is four-sided in transection (Jensen 1974, Clayton 1981).

The Cystosieraceae differs from the Sargassaceae in its branching pattern and position of receptacles. In the Cystoseiraceae, branching is lateral and receptacles are represented by transformed terminal parts of branches, while the Sargassaceae possess axillary branching with receptacles occurring as axillary clusters. The Cystoseiraceae differs from the Himanthaliaceae in that the former has a discoid or conical basal portion giving rise to single vegetative upright thalli which gives rise to primary and secondary laterals, while the latter has a sterile basal portion and a strap —shaped receptacle that is repeatedly bifurcate (Jensen 1974).

The genus *Bifurcaria* is distinguished from other genera of the Cystoseiraceae by the possession of a distinctive rhizomatous basal portion from which arise erect branches that are terete, at least in the vegetative state. All other genera with terete vegetative branches lack rhizomes (e.g. *Cystoseira*, in part; *Bifurcariopsis*), whereas all other rhizomatous genera (i.e. *Acystis*, *Platythalia* and *Stolonophora*) have branches that are strongly compressed (Jensen 1974).

At present, the genus *Bifurcaria* comprises three species: The type species, *B. bifurcata* Ross (1961:512), which is found on the south coast of England, in Ireland, Wales, in the Channel Islands, the Atlantic coast of France, Spain, Portugal, Morocco and Libya (South and Tittley 1986). *B. brassicaeformis* (Kützing) Barton (1893:82); and *B. galapagensis* (Piccone and Grunow) Womersley (1964:104) are endemic to South Africa and the Galapagos Islands respectively (Jensen 1974).

Detailed comparative morphological studies on both the vegetative tissues and reproductive structures as well as apical and conceptacle anatomy have been carried out on these species by Jensen (1974). The only detailed anatomical study for a species in the genus *Bifurcaria* has been carried out by Rees (1933) on *B. bifurcata* on material collected from the British south coast. Little is known in detail of the anatomy of *B. brassicaeformis* and *B. galapagensis* (Jensen 1974). The only literature published on the reproductive biology of *B. brassicaeformis* deals with oogonia liberation (Delf 1935); nothing is known about the mechanism of zygote attachment although this has been described for the British B. bifurcata (Hardy and Moss 1979).

The present descriptive study not only examines past information on the taxonomy of B. brassicaeformis, but also adds new information from personal observations on the morphology, anatomy, ecological effects on morphology and anatomy, and reproductive biology of the species, over its habitat range.

2. Taxonomy

The genus Bifurcaria was first defined by Stackhouse (1809). The species dealt with in this study was first described as Pycnophycus brassicaeformis by Kützing (1860:59). Barton (1893) transferred this entity to the genus Bifurcaria. The current name therefore is Bifurcaria brassicaeformis (Kütz.) Barton.

Jensen (1974) lists the synonyms of B. brassicaeformis as:
Pycnophycus brassicaeformis Kützing (1860:9)
Pycnophycus sisymbrioides Kützing
Pycnophycus var. sisymbrioides (Kützing) Grunow, 1867:53
Bifurcaria tuberculata var sisymbrioides (Kützing) in De Toni, 1895:178.

3. Morphology

B. brassicaeformis possesses a perennial creeping rhizome which adheres to the rocky substratum by means of small discs (Figure 3). From the rhizome, erect terete branches are given off at

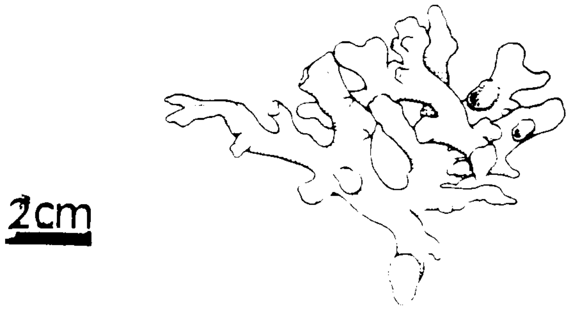


Figure 3. Rhizome of Bifurcaria brassicaeformis seen from below and showing attachment discs (From Isaacs 1951).

Figure 4. Plant of Bifurcaria brassicaeformis showing rhizomatous base, tubular upright fronds, and terete receptacles. Note- Young upright vegetative frond arising from rhizome.
(with permission of Dr. H. Stegenga)

intervals (Figure 4). Branching of the erect system is precisely bilateral and alternate to the apex. The fronds are moderately or well branched and may sometimes exceed 45cm in length. Diameters of the vegetative uprights arising directly from the base may be between 1.3 - 3.3mm depending on the microhabitat within which the plant is found in the intertidal. No vesicles are found within the frond. Growth of the terete vegetative branches proceeds from an apical cell which is three-sided in transection and biconvex in longitudinal section.

The receptacles are bilaterally flattened and terminal on the branches of the frond, are about 3 - 5mm broad and vary in length from 16 - 25cm under favourable conditions. The plant is dioecious and all receptacles of any one erect branch are either male or female.

The conceptacles are unisexual, in two rows and occur at the margins of the flattened receptacle. The conceptacle has basal groups of paraphyses and a single ostiole (Plate 10a) from which either sperm or eggs are released.

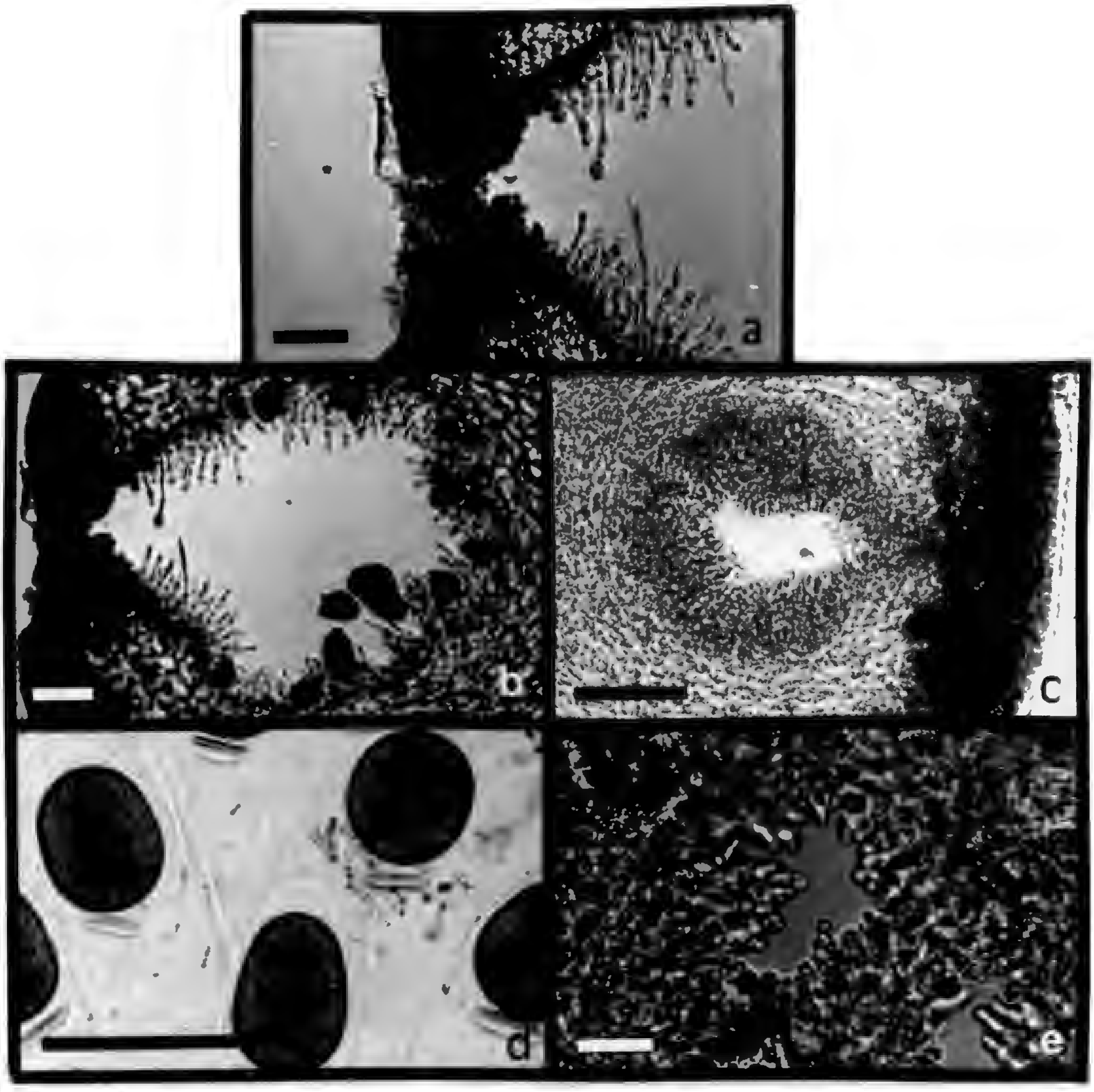
Table 1 shows that the size of the conceptacles increase from the apex to the base of the receptacle. Female conceptacles (Plate 10b) about 550 - 123μm long and 420 - 1082μm in diameter and male conceptacles (Plate 10c) vary from about 340 - 1123μm long to 340 - 1000μm in diameter. Oogonia (Plate 10d) are 120 - 160μm across and 30 - 80μm high, about 250 per conceptacle largely filling the conceptacle, and are held on stalks. The younger oogonia are partly embedded in the conceptacle wall. Antheridia (Plate 10e) are sessile on the conceptacle wall scattered between paraphyses, elongate,

Table 1. Receptacle anatomical character measurements (in µm) for different sites at Clovelly. Measurements of character at different lengths from the apex (LFA) of the receptacle. Data represents mean of the 3 readings and the range.

		SITES			
CHARACTER	LFA	TRAINGLE (female)	OVERTOP (female)	GULLEY (male)	ROCK (male)
Conceptacle diameter	apex	no conceptacles	(553.4) 556.16 (561.68) × (429.5) 432.26 (437.78)	(388.22) 396.44 (404.7) × (338.66) 344.15 (346.9)	(346) 349.06 (355.18) × (339) 346.7 (355.18)
	5mm	(669.06) 691.08 (702.1) × (660.8) 671.81 (693.84)	(982.94) 993.9 (1007.72) × (611.24) 619.5 (627.76)	(826) 949.9 (1032.5) × (578.2) 619.5 (660.8)	(925.12) 933.35 (941.64) × (503.86) 512.08 (520.38)
	20mm	(826) 850.78 (867) × (421.26) 429.51 (437.78)	(1073.8) 1076.5 (1082) × (1032.5) 1051.1 (1065.5)	(867.3) 922.36 (991.2) × (743.4) 839.7 (949.9)	(1082.06) 1090.82 (1098.58) × (842.2) 845.1 (850.78)
	base	(1073) 1103.8 (1123.3) × (826) 845.27 (867.3)	no conceptacles	(1032.5) 1073.8 (1115.1) × (495.6) 523.13 (578.2)	(1106.84) 1115.06 (1123.36) × (982.94) 991.13 (999.46)
Oogonium/ Antheridium size (length × breadth)	apex	(115.64) 123.9 (132.16) × (74.3) 82.58 (90.86)	(41.3) 44.05 (49.56) × (27.78) 30.28 (33.04)	(17.3) 20.52 (25.02) × (7.7) 8.17 (9.13)	(7.7) 8.98 (9.63) × (5.77) 7.06 (7.7)
	5mm	(156.9) 159.66 (165.2) × (82.6) 88.1 (99.12)	(66.08) 71.58 (74.34) × (49.56) 52.31 (57.82)	(25.03) 25.2 (25.52) × (5.7) 6.36 (7.7)	(17.3) 18.56 (19.2) × (17.3) 18.6 (21.18)
	20mm	(156.9) 162.4 (165.2) × (115.6) 126.64 (132.16)	(123.9) 126.65 (132.16) × (82.6) 85.35 (90.86)	(25.03) 26.91 (28.8) × (9.63) 10.26 (11.55)	(21.1) 21.77 (23.11) × (15.4) 17.94 (21.18)
	base	(115.64) 123.9 (132.16) × (74.3) 82.58 (90.84)	no oogonia	no antheridia	no antheridia

Plate 10 a-e. Reproductive morphology of <u>Bifurcaria brassicaeformis</u>.

a) Conceptacle showing paraphyses and a single ostiole. Scale bar = 100 µm
b) Female conceptacle. Scale bar = 400 µm
c) Male conceptacle. Scale bar = 400 µm
d) Oogonia held on stalks and largely filling the conceptacle. Scale bar = 100 µm
e) Antheridia sessile on conceptacle wall. Scale bar = 100 µm


a
b
c
d
e

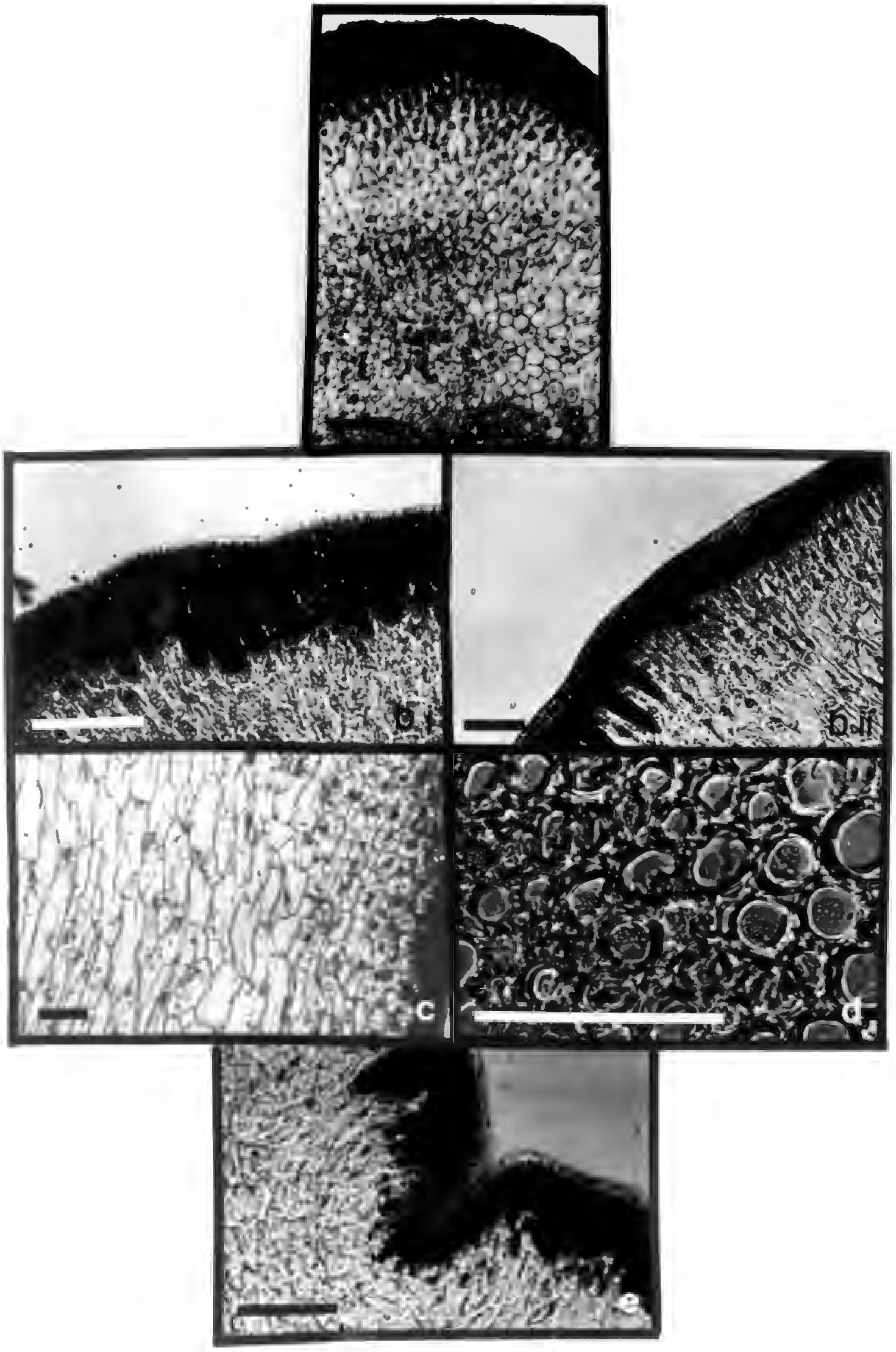
about 20 - 30µm long and 6 - 17µm in diameter. Sperm are about 5 - 7µm long and 2 - 3µm in diameter. The embryo once established usually has 4 primary rhizoids (see "Reproductive biology" later).

4. Anatomy

The anatomy of the erect fronds consists of an outer and inner cortex and a central medulla. The cortex consists of palisade-like, radially elongated cells which become more rounded with progression to the inner medulla (Plate 11a). A mucilaginous layer covers the single outer layer of assimilatory outer cortical cells (Plates 11bi,ii) while the inner 6 - 8 layers of the cortex probably also carry out a limited assimilatory function and contain abundant fucosan vesicles (Plate 11c). In cross-section, the walls of the inner cortical cells become more thickened indicating a mechanical role. The medullary cells are generally isodiametric in cross-section having thick strong walls indicating their strengthening and mechanical role (Plate 11d). In the rhizome obliquely placed cells contain abundant fucosan vesicles. Attachment discs of the rhizome are specialised to the extent that secondary strengthening hyphae occur only in the discs and not in the rest of the thallus. Young discs are composed almost exclusively of hyphae with older discs being further strengthened by the formation of branched hyphae which grow perpendicular to the original cells (Jensen 1974 and personal observations).

Plate 11 a-e . Anatomical features of the vegetative thallus of Bifurcaria brassicaeformis.
Scale bars = 100 µm

a) Outer cortex with palisade-like cells becoming more rounded towards the inner medulla.
bi) Mucilaginous layer covering the single outer layer of assimilatory outer cortical cells (Note: large ellipsoidal-shaped mucilage cells in cortex).
bii) Outer layer of assimilatory cortical cells.
c) Inner cortical cells containing abundant fucosan vesicles.
d) T/S of medullary cells showing their thick strong walls.
e) Apical pit has the form of a slit.


b i
b ii
c
d
e

5. Comparison with other species in the genus

In comparing the morphology of *Bifurcaria brassicaeformis* with that of other species in the genus, the present study confirms the impressions of Isaac (1951) and Jensen (1974) that *B. brassicaeformis* resembles *b. bifurcata* rather than *B. galapagensis* most closely. *B. brassicaeformis* and *B. bifurcata* have more, and a more highly condensed system of, tuberous branches than *B. galapagensis*. *B. brassicaeformis* differs from *B. bifurcata* in having a larger rhizome with attachment discs being more linear in arrangement, and flattened instead of terete receptacles. *B. brassicaeformis* differs both by being dioecious and having unisexual conceptacles while *B. galapagensis* (see also Taylor 1945, p112) and *B. bifurcata* are both monoecious with bisexual conceptacles.

Observations on the anatomy of *B. brassicaeformis* revealed that this species resembles *B. bifurcata* closely (see Rees 1933). In both *B. brassicaeformis* and *B. bifurcata* the tongue filament (the superficial initial cell which gives rise to the basal and apical cells during conceptacle development (Bower (1880), Oltmanns (1899), Nienberg (1913)) is considered more advanced than that of *B. galapagensis* (Jensen 1974). The tongue filament divides longitudinally in the former two species while longitudinal division does not occur in the latter.

In all three species, growth of the terete vegetative branches proceeds from the apical cell which is three-sided in transection. However, in *B. brassicaeformis* the apical pits of the tuberous branches are in the form of a slit (Plate 11e) rather than in a funnel as in *B. bifurcata*.

6. Ecological effects on morphology and anatomy

Bifurcaria is most abundant in the lower eulittoral zone, sometimes extending downwards into the lowest portion of the eulittoral zone, which on South African coasts is characterised by large numbers of the limpet *Patella cochlear* Born. (often termed the "cochlear zone" in local literature).
However in pools at about mid-tide level, *B. brassicaeformis* may also be dominant. Dense growth of the plant is achieved by covering of the substrate by the creeping rhizome. In the sublittoral fringe, *B. brassicaeformis* is infrequent or absent and *Bifurcariopsis capensis*, *Anthophycus longifolius*, and species of *Sargassum* may be locally dominant, along with considerable populations of the solitary ascidian *Pyura stolonifera* (Heller).

Macrophytic epiphytes are virtually absent from the fronds and receptacles, although species such as *Ectocarpus siliculosus*, (Dillw.) Lyngb., *Ulva capensis* and *Porphyra capensis* have been occasionally observed.
The uprights and receptacles exhibit a phenomenon of epidermal shedding when material brought from the field is placed in laboratory culture (Plates 12a,b).
Epidermis shedding has been observed in other fucoids such as

Plate 12 a-b. Epidermis shedding in apical tips of Bifurcaria brassicaeformis.
Scale bars = 2mm

a) Scanning Electron micrograph of the epidermis beginning to peel away from the thallus.
b) Light micrograph of the sloughed epidermis just before becoming completely detached from the thallus.


a
b

Ascophyllum nodosum (Filion-Myklebust and Norton 1981) and Halidrys siliquosa (L.) Lyngb.(Moss 1982). The function of this phenomenon has been proposed by these authors as an anti-fouling mechanism to rid the thallus of epiphytes.

The morphology and anatomy of the plants in the different intertidal microhabitats show differences with respect to the environmental factors experienced (see also Chapter 4).
Figure 5 shows that diameters of vegetative uprights are thicker in the gulley, followed by that on the rockfaces and are thinnest in the pools. Vegetative uprights in pool 3 were closer in diameter to the triangle and the rock site. The thinner diameters of uprights in the pools was probably due to the the raised temperatures experienced in the pools during hot summer days which lead to tissue damage and eventual growth decline. When pools 1 and 2 dried out, desiccation effects coupled with high air temperatures caused severe drying out of the uprights and damage to the apices. These findings for the effects of the environment on growth and morphology in the pools are consistent with those of Schonbeck and Norton (1978) for European fucoids situated higher up on the shore. These authors found that higher up on the shore, fucoid plants were stunted and showed severe tissue damage due to desiccation effects aggravated by higher temperatures.

ortical thickness and medullary diameters were ascertained at the apex, 5mm, 20mm from the apex and at the base of 20 vegetative uprights for each site and pool (Table 2). The cortical diameters were

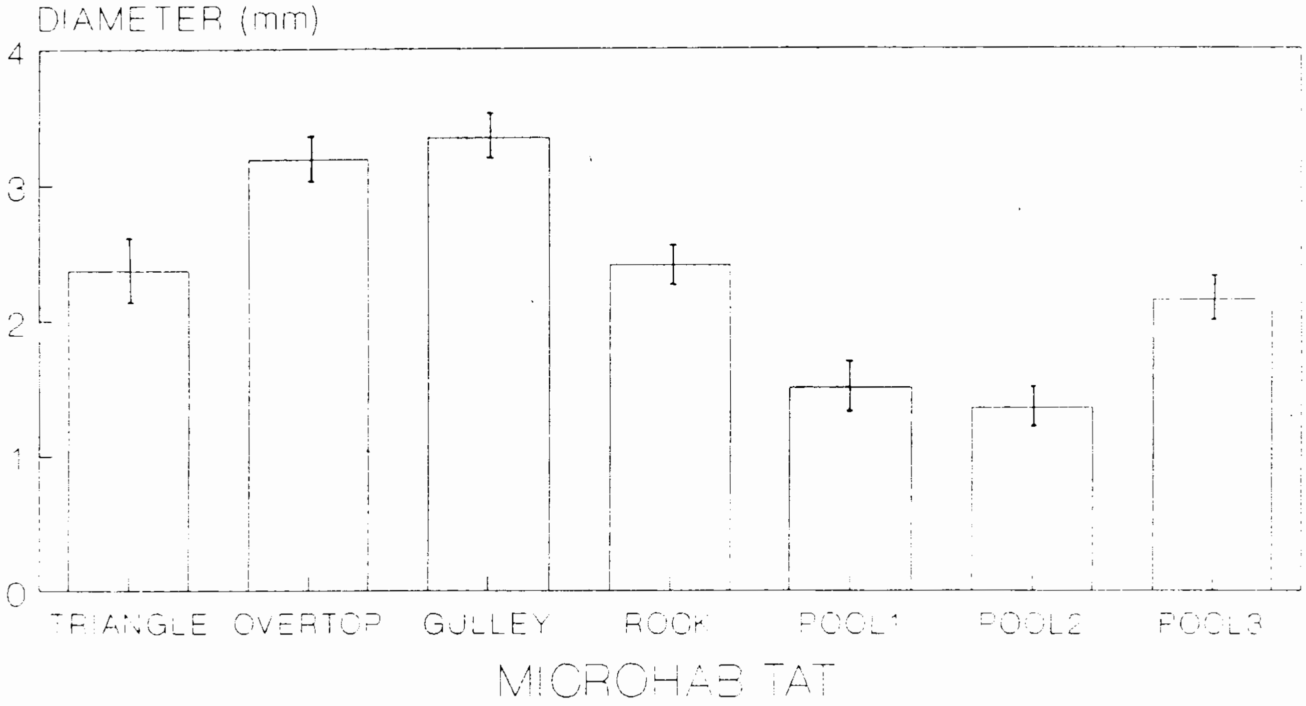


Figure 5. Diameters of vegetative uprights from the different microhabitats. n=20. 95% confidence limits indicated.

Table 2. Estimates of cortex thickness and medulla diameters (in µm) of vegetative uprights at the different sites and in the pools. Readings taken at apex,5mm,20mm and base of upright. Mean for 5 readings (±1SE) at that point.

		ENVIRONMENTS						
		SITES				POOLS		
	Point of measurement	TRAINGLE (female)	OVERTOP (female)	GULLEY (male)	ROCK (male)	POOL 1 (male)	POOL 2 (male)	POOL 3 (female)
CORTEX DIAMETER	apex	82.6(3.7)	100.77(1.65)	95.81(2.02)	84.25(3.09)	74.74(3.7)	74.34(3.7)	97.46(3.01)
	5mm	90.86(3.7)	67.73(3.09)	97.46(1.65)	85.9(3.31)	95.8(2.02)	85.9(4.52)	89.2(3.69)
	20mm	84.25(3.09)	49.56(2.61)	90.86(3.7)	66.08(2.67)	112.33(2.03)	170.12(4.49)	100.77(1.65)
	base	67.73(3.09)	46.25(4.52)	84.25(3.07)	82.6(3.7)	84.25(3.07)	133.81(3.69)	54.51(2.03)
MEDULLA DIAMETER	apex	1593.4(10.75)	1909.4(11.68)	1532.2(11.2)	1803.8(10.8)	1685.7(9.52)	1358.2(11.24)	1341.7(8.59)
	5mm	2246.6(10.32)	2137.5(11.48)	1866.6(14.1)	2163.8(13.06)	1855.8(8.26)	1799.9(10.59)	1501.8(12.96)
	20mm	2333.5(8.17)	2643.4(49.4)	2215.3(14.4)	2375.7(8.69)	1749.7(14.71)	1950.4(37.3)	1798.5(21.76)
	base	1382.2(23)	1795.8(8.14)	2793.2(19.2)	1527.2(12.03)	1390.5(11.25)	1289.6(23.43)	1350.7(10.7)

generally similar for sites and pools for sections taken at the apex and 5mm from the apex and at the base of the uprights. However, at 20mm from the apex, cortical thicknesses in pools 1 and 2 were generally higher than at the sites, although pool 3 was similar in cortical thickness
The medullary diameters were generally higher at the sites than in the pools, corresponding to generally thicker uprights.

It is interesting to note that the similar morphology (upright diameters) observed in pool 3 in comparison to the sites and the similar anatomy (medullary diameters) compared to the pools was probably indicative of the microenvironment of pool 3. As pool 3 was deeper than pools 1 and 2, and did not dry out in summer, the more stable condition probably accounted for the better growth with slightly larger upright diameters in pool 3 than in pools 1 and 2, and similar to those of the sites (Figure 5).

7. Reproductive biology

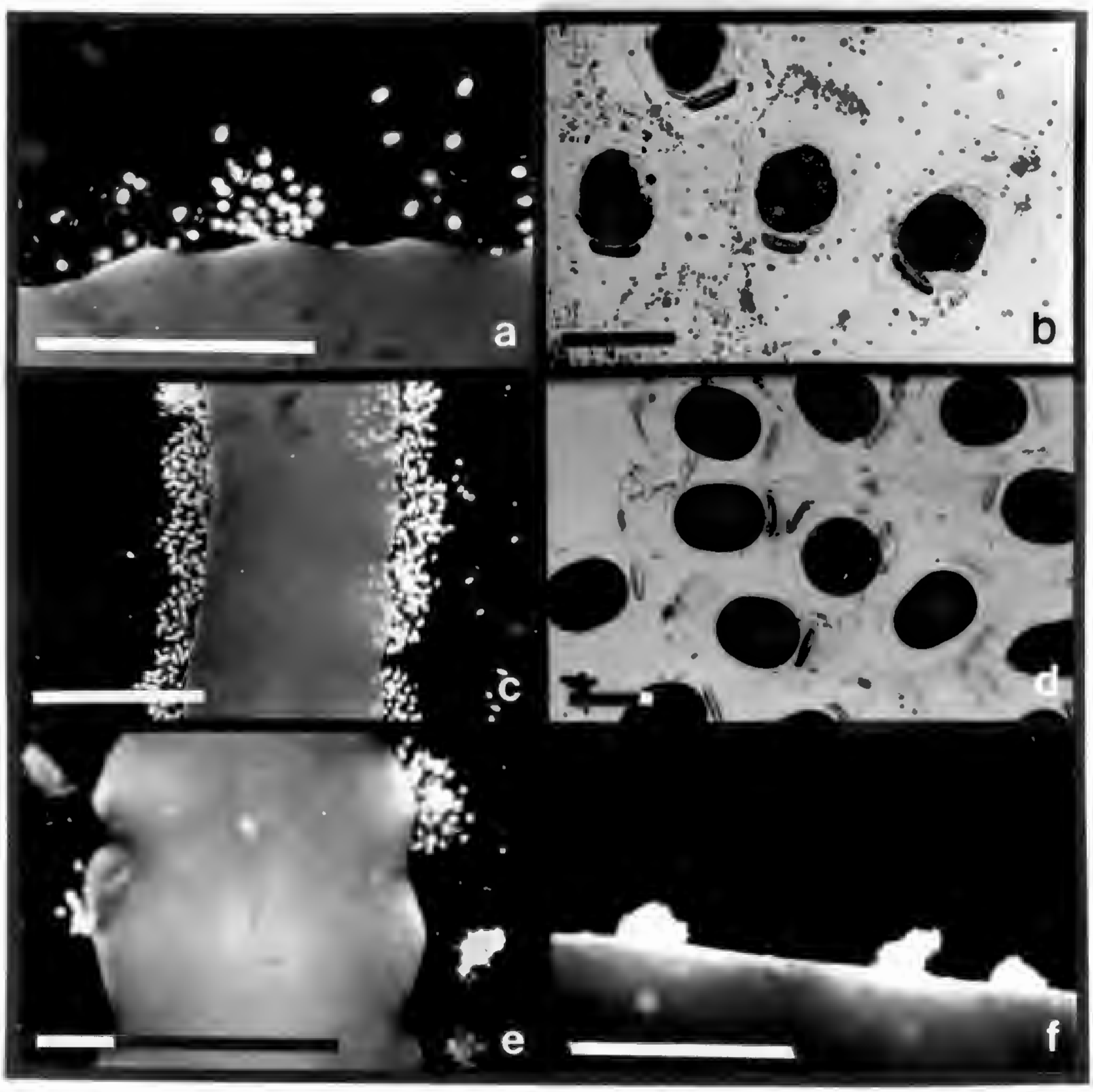
7.1 Liberation of gametes:

Delf (1935) has described liberation of oogonia in Bifurcaria brassicaeformis.

The oogonia are extruded through the conceptacle ostiole onto the receptacle surface (Plate 13a) where they are retained by their own gelatinous mesochiton stalks (Plate 13b). Usually large numbers of eggs are released onto the surface (Plate 13c), many

Plate 13 a-f . Liberation of oogonia and antheridia in Bifurcaria brassicaeformis.

a) Clusters of oogonia on receptacle surface. Scale bar = 5mm.
b) Oogonia held on gelatinous stalks. Scale bar = 80 µm.
c) Large numbers of oogonia released on receptacle surface. Scale bar = 5mm.
d) Oogonia still retained within their oogonial membranes. Scale bar = 80 µm.
e) Gelatinous mesochiton stalks having lost their oogonia. Scale bar = 5mm
f) Antheridia being discharged from the conceptacle. Scale bar = 5mm


a
b
c
d
e
f

of which are still enclosed in their oogonial membranes (Plate 13d) and held together by a blob of mucilage. The mesochiton stalks eventually lose their oogonia. (Plate 13e).

The antheridia are squeezed through the conceptacle ostiole in large numbers (Plate 13f). Unlike the oogonia they do not adhere to the receptacle surface. They are pushed well clear of the latter and were observed to enter the surrounding medium immediately. Spermatozoids are then released from the antheridia. Spermatozoids were observed to swim for up to 4 hours.

7.2 Observations on zygote attachment and germling development:

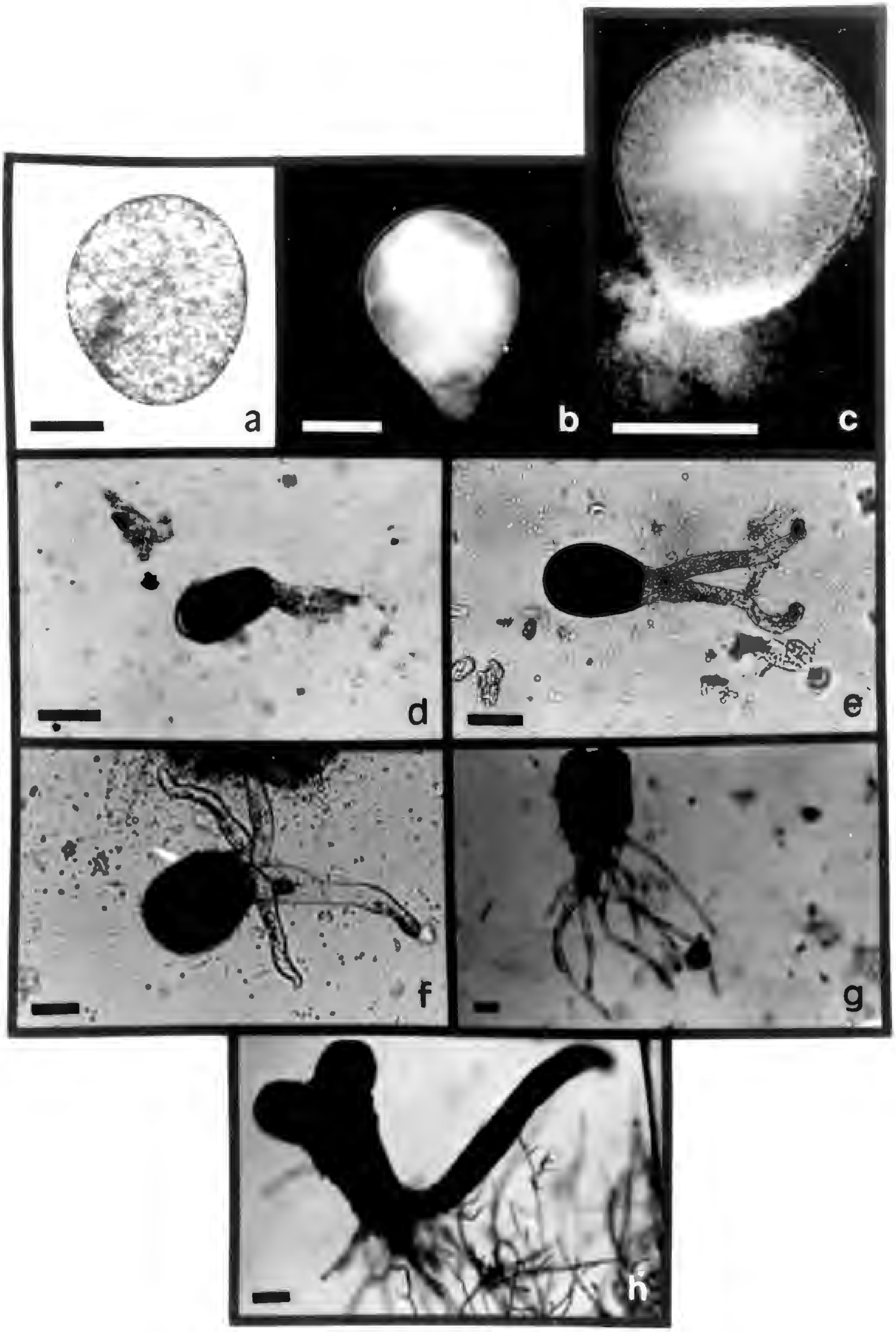
Fertile material was collected from Cape Point Nature Reserve (34°20.2′S, 18°26.8′E) on the Cape Peninsula.

Spherical oospheres are produced from the female receptacles which after fertilization (method to obtain fertilization described in chapter 5) settle onto the glass coverslip used as the substratum. Zygotes are roughly spherical (Plate 14a) with the zygote wall being 1.92 (± 0.124)µm thick 24 hours after fertilization (see Plate 14b). The zygote wall of *Bifurcaria bifurcata* measured 0.37µm 18 hours after fertilization (Hardy and Moss 1979) whereas that of *Halidrys siliquosa* measured 2.55µm 24 hours after fertilization (Hardy 1977).

The zygote wall appears to be surrounded by mucilage which may help to anchor the zygote onto the substratum, similar to that found for *Himanthalia elongata* (L.) S.F. Gray (Ramon 1972), *H siliquosa* (Hardy and Moss 1978) and *B. bifurcata* (Hardy and

Plate 14 a-h . Zygote attachment and germling development.

a) Spherical zygote 24 hours after fertilization. Scale bar = 100 µm
b) Zygote wall surrounded by mucilage 48 hours after fertilization. Scale bar = 100 µm
c) Three day-old germling with rhizoidal initiation taking place from the basal end. Scale bar = 100 µm
d) Four day-old germling showing zygote wall appearing to be shed in the form of a cap. Scale bar = 100 µm
e) Five day-old multicellular germling with 2 primary rhizoids. Scale bar = 100 µm
f) Six day-old germling with four primary rhizoids which firmly attach the germling. Scale bar = 100 µm
g) 24 day-old germling showing development of secondary rhizoids. Scale bar = 0.5mm
h) 32 day-old germling showing apical depression of the linear shoot of the germling and initiation of branching. (Note: culture contaminated by filamentous Ectocarpoid brown alga). Scale bar= 0.5mm


a
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Moss 1979).

24 hours after fertilization, the zygote divides at right angles to the substratum and 48 hours after fertilization, a second division, at right angles to the first occurs so that a four-celled germling is produced. Three days after fertilization, rhizoid initials start to push through the zygote wall (Plate 14c) although the rest of the wall still remains intact and surrounded by mucilage. The last of the zygote wall appears to be shed in the form of a cap covering the developing germling (Plate 14d).

Four days after fertilization, the first visible signs of germination is the protruberance of two primary rhizoids (Plate 14e) which eventually differentiates into four primary rhizoids (Plate 14f) from the now multicellular germling. The rhizoids appear colourless compared with the rest of the brown thallus, indicating that they contain very few plastids. The tips of the rhizoids appear slightly darker than the rest of the rhizoid. The rhizoids spread over the substratum away from the source of the incident light. It appeared that the rhizoids produce mucilage from their tips which may aid in attachment to the substratum. Once the rhizoids have been produced, the function that the mucilage surrounding the zygote wall may have had in attachment becomes obsolete as the rhizoids now anchor the germling firmly to the substratum.

The continued production of secondary rhizoids (Plate 14g) will thus result in the development of the attaching holdfast. The germling thallus gradually orientates itself vertically and enlarges to form a linearly-shaped terete shoot in which the apical depression is already visible (Plate 14h). Under certain light conditions (30-120$\mu Em^{-2}s^{-1}$), some of the upright shoots became dichotomously branched after 28 days (Plate 14h).

During germling growth experiments, ectocarpoid brown algae often contaminated the cultures from about 21 days onwards as is apparent in Plate 14h.

It is apparent that rhizoidal development was delayed till three to four days after fertilization. The adhesive mucilages secreted by the zygote wall appeared to be attaching the zygote and the very young germling to the substratum during the period several days prior to rhizoidal initiation.

The attachment mechanism thus resembles that of the British _Bifurcaria bifurcata_ and _Halidrys siliquosa_ where zygotes also initially attach by means of a mucilage secretion of the zygote wall.

CHAPTER 4

DEMOGRAPHY

INTRODUCTION

Demographic studies are central to our understanding of seaweed populations (Chapman 1986). According to Gunnill (1980) fucoids are perennial and each individual plant has the potential for living at least several years. It has been established that adult fucoid plants which occur in temperate regions in the northern hemisphere such as Ascophyllum nodosum (David 1943), Pelvetia canaliculata (Subrahmanyan 1960), Fucus serratus (Knight and Park 1950), F. vesiculosus (Knight and Park 1950, Printz 1959), Halidrys siliquosa (Moss and Lacy 1963), Himanthalia lorea L. Lyngb. (Gibb 1937) and Bifurcaria bifurcata (De Valera 1962), and also Sargassum polyceratium Mont. which occurs in subtropical Florida (Kilar et al. 1989), all show seasonal periodicity of growth and reproduction.

Nizamuddin (1970) reported that generally fucoids show spring growth of the fronds, when receptacles (branches) are initiated, maximum summer development when gametes are shed, and by autumn die back to their overwintering basal portions. However, the northern hemisphere fucoid H. siliquosa has been reported (Blacker 1956 in Nizamuddin 1970) to have gametangia throughout the year and to release gametes during winter. The subtropical Sargassum polyceratium (Kilar et al. 1989), although displaying the same growth and development phases as the above temperate fucoids, has the phases occurring in the opposite seasons, so that the species reproduces in winter (December) in the northern hemisphere.

Levitt (1987) found that B. brassicaeformis displayed no seasonal variation in primary production, although carbon content and C:N ratio of the species were highest in summer and lowest in winter.

The factor controlling periodicity of development and reproduction in fucoids has for some time eluded phycologists (Nizamuddin 1970). However, as in higher plants (Garner and Allard 1920, Vince-Prue 1975), the discovery that a genetically inherent rhythm triggered by daylength (photoperiodism) regulates the seasonal development in algae was first demonstrated in the Conchocelis-phase of Porphyra tenera (Kjellm.) (Dring 1976). The formation of fertile cell rows was promoted by short days (less than 13 hours of light per day). The first example of photoperiodism in the Phaeophyta was detected in Scytosiphon lomentaria (Lyngb.) Link (blue light effective; Dring and Lüning 1975). The species formed erect thalli only under short day conditions. Similar photoperiodism has been demonstrated in the fucoids Fucus distichus L. by Bird and Mc Lachlan (1976; effect of light break not investigated) and by Terry and Moss (1980) in Ascophyllum nodosum (L.) Le Jol. (blue and red light break effective). Both species form receptacles only in short days.

It is well known that fertilized eggs which settle and develop into germlings play an important role in the colonization and maintenance of many fucoid populations (e.g. Himanthalia elongata Moss et al. 1973; Pelvetia fastigiata (Gunnill 1980). However, environmental factors such as light and temperature have been shown to be important factors affecting early growth and development of the germlings (Moss and Sheader 1972, Moss et al. 1973, Sheader and Moss 1975). In B. brassicaeformis only scanty literature on the ecological effects of reproduction has been published (Delf 1935). Delf only counted the number of eggs per conceptacle, but did not investigate other aspects of fecundity, or the fate of the eggs after liberation and if the germlings developed.

Literature on the problems of population maintenance in fucoids has been published for Bifurcaria bifurcata (De Valera 1962) from Ireland and Ascophyllum nodosum (Baardseth 1970) from Norway. These authors found that the populations are maintained primarily from the production of new uprights from the base than from the production of germlings from settled eggs. For Bifurcaria brassicaeformis, observations made by Bokenham and Stephenson (1938) showed that patches that were cleared within a B. brassicaeformis community were recolonized either by inward growth of the rhizomes or by establishment of germlings within these patches. However, these authors did not investigate the nature of population maintenance in B. brassicaeformis in any detail.

In some respects, B. brassicaeformis is a suitable species for a demographic study. Plants are dioecious and most of the populations are exposed during spring low tides. The plant has a rhizome which produces individual upright fronds. When mature, each upright has fertile receptacles which are only of one sex. As the rhizome spreads, it becomes difficult to determine the size and extent of individual plants. Therefore, the sampling was carried out by taking a known area of the basal rhizome, with the individual uprights arising from it as the demographic units, as was done for the northern hemisphere fucoid Ascophyllum nodosum, which has uprights arising from an expanded holdfast (Cousens 1981a). This sampling method facilitates sampling throughout the year so that information could not only be gained on the total population at a study site, but also on intraspecific variation in morphology at each particular microhabitat.

As no previous demographic study has been carried out on B. brassicaeformis, the aims of this study are twofold:

1) to investigate the growth and development patterns, fecundity and reproductive effort, and the seasonal changes in the state of conceptacle maturity.

2) to make observations on the variation in growth and morphology at contrasting habitats on the shore, and population maintenance of the species.

Furthermore, the results and observations will be compared with previous literature on the species and published literature on fucoids and other brown algae.

MATERIALS AND METHODS

The location of the study site and a detailed description of the microhabitats (sites and pools) investigated is given in Chapter 2. Sampling was carried out every two months from February 1989 to April 1990 (8 collections- except that collections at the Triangle site started at April 1989). At each collection, an area of the rhizomatous base (with its upright material) of 10x10 cm (1 dm2)- a clump, was collected from each site and pool and transported back to the laboratory in plastic bags to keep the plants fresh and moist. In the laboratory, each clump was placed into a tray filled with seawater and the uprights with their receptacles excised from the rhizomatous base. The base material was then weighed. For each upright, the length and the number of branches (mature and immature receptacles) per upright were recorded. The receptacles were excised from their uprights and the receptacle weight per upright as well as the vegetative weight per upright was recorded. The two values were then later added together to obtain the total weight of each upright. The data was then further manipulated by computer so that data for the following demographic variables are presented for each individual site and pool over the 14 month period.

1) total basal biomass per clump (g/dm2)

2) total vegetative (upright minus receptacles) biomass per clump (g/dm2)

3) total receptacle biomass per clump (g/dm2)

4) total biomass (sum of the basal, vegetative and receptacle

portions) of the clump (g/dm2)

5) density (the number of uprights/dm2)

6) mean length per upright (mm)

7) mean number of branches per upright

8) mean total (vegetative and receptacle material) biomass per upright (g)

9) mean receptacle biomass per upright (g)

For fecundity estimates, twenty clumps (2x2cm each) of fertile plants were collected from Clovelly on 5 October 1989 from different microhabitats and brought to the laboratory. Fecundity of B. brassicaeformis was estimated by the method of Vernet and Harper (1980). An upright from each clump having well developed receptacles was excised from the base of the clump. Firstly, the number of receptacles per plant was counted. Then 20 receptacles were randomly chosen (1 receptacle off each upright) and each weighed. The number of conceptacles per receptacle was then estimated. Upon extrusion of oogonia, obtained by exposing the receptacles to air for about 30 minutes and then re-immersing them in sea water, the number of oogonia per conceptacle (1 conceptacle per receptacle) was estimated microscopically. Oogonia which had remained in the conceptacles were all counted by sectioning the conceptacle and counting the remaining oogonia within the conceptacle. The number of eggs per gram receptacle was then calculated for each receptacle and the number of eggs per gram upright was calculated.

The Reproductive Effort was estimated by two methods; the total receptacle weight (including gametes and sterile tissue) as a proportion of the total upright weight, for each of ten uprights from different plants (Cousens 1981a), and; the proportional biomass of oogonia of the upright weight, estimated by measuring the following characteristics for each plant (n=10) separately (Vernet and Harper 1980).

a) the total fresh weight of the upright (including receptacles).
b) the number of receptacles per upright
c) the number of conceptacles per receptacle
d) the number of oogonia per conceptacle

The number of eggs produced is the product of b), c) and d).

The mean weight per oogonium was estimated by measuring the average diameter and calculating the mean volume of oogonia. The average diameter and volume of sperm was also calculated. From these calculations it is assumed that both oogonia and sperm are spherical.

The fresh weight of oogonia was then calculated from the volume (assuming that the densities of the egg and other tissues of B. brassicaeformis is the same). The mass:volume ratio of 1cm of the cylindrical vegetative "stem" was then estimated.

The calculated weight of oogonia as a proportion of an individual upright thus gives an estimate of the total biomass involved in egg production as a fraction of other components of biomass of an upright.

The seasonal changes in the state of conceptacle maturity was ascertained by the following method. At each collection date, off each clump sampled from the seven microhabitats, 10 receptacles (each excised of a separate randomly chosen upright) were sectioned at a point medially beteen the apex and the base. The maturity status of the conceptacle and the abundance and state of the eggs within the conceptacle was ascertained using a compound microscope.

Statistics

Results for the individual components of biomass (the total basal biomass, total upright vegetative biomass, total receptacle biomass), total biomass , and density are represented as the value obtained for each microhabitat. The mean of the values at each sampling date for both sites and pools were then calculated. For each preceding parameter, each individual value for each sampling date (i.e. 4 for the sites and three for the pools at each sampling date) in a sense represent a replicate for that month. Parametric one-way ANOVA's were performed on the data by combining individual site data and individual pool data to test if these parameters differed significantly over the sampling period between the sites and pools. Furthermore, Multiple range comparisons were performed on the combined data sets to find out at which months significant differences occurred.

Results for length per upright, number of branches per upright, total weight per upright, and receptacle weight per upright are represented as the means of that parameter for each site and pool. The mean, of the initial mean values of each of the above-mentioned parameters, at each sampling date, were then calculated for the sites and pools. Non-parametric Kruskal-Wallis one-way ANOVA's were performed on the initial data for each site and pool to ascertain whether the above parameters varied significantly over the sampling period. Furthermore, the same statistical test was performed on the data for the above parameters to see if there was a significant difference between the individual sites or pools at each sampling date.

Multiple range comparisons were performed for each of the above tests to see whether any of the treatments (between months over the sampling period, between sites or pools) varied significantly from each other, and where these differences occurred (Zar 1984).

RESULTS

Results for the same demographic variables for the sites and pools will be reported on together for comparison. Seasons are designated by the following months:

early to late summer (December to February), autumn (March to May), early to late winter (June to August) and spring (September to November).

1. Biomass and density

1.1 Total basal biomass

Total basal biomass for the sites did not display a clear seasonal pattern (Figure 6), although a tendency existed for a high and low basal biomass in late winter (August) and early summer (December) respectively. (This being reflected in three of the four sites- except for the Triangle site which had low winter and high summer values). At the sites, total basal biomass did not vary over the sampling period. However, total basal biomass was twice as high in summer (February) of 1990 than in summer (February) of 1990, and three times as high in autumn (April) of 1990, than in autumn of 1989. In contrast to the sites, the pools displayed a definite seasonal pattern in basal biomass (Figure 7). Basal biomass in the pools varied significantly over the study period ($F = 3.387$, $p<0.05$), with high values in late winter (August), and decreasing markedly to low values in spring (October). Values stayed low from spring through to the end of summer (October 1989 to February 1990), rising again to similar high autumn values in 1990 as in 1989. The one-way ANOVA test

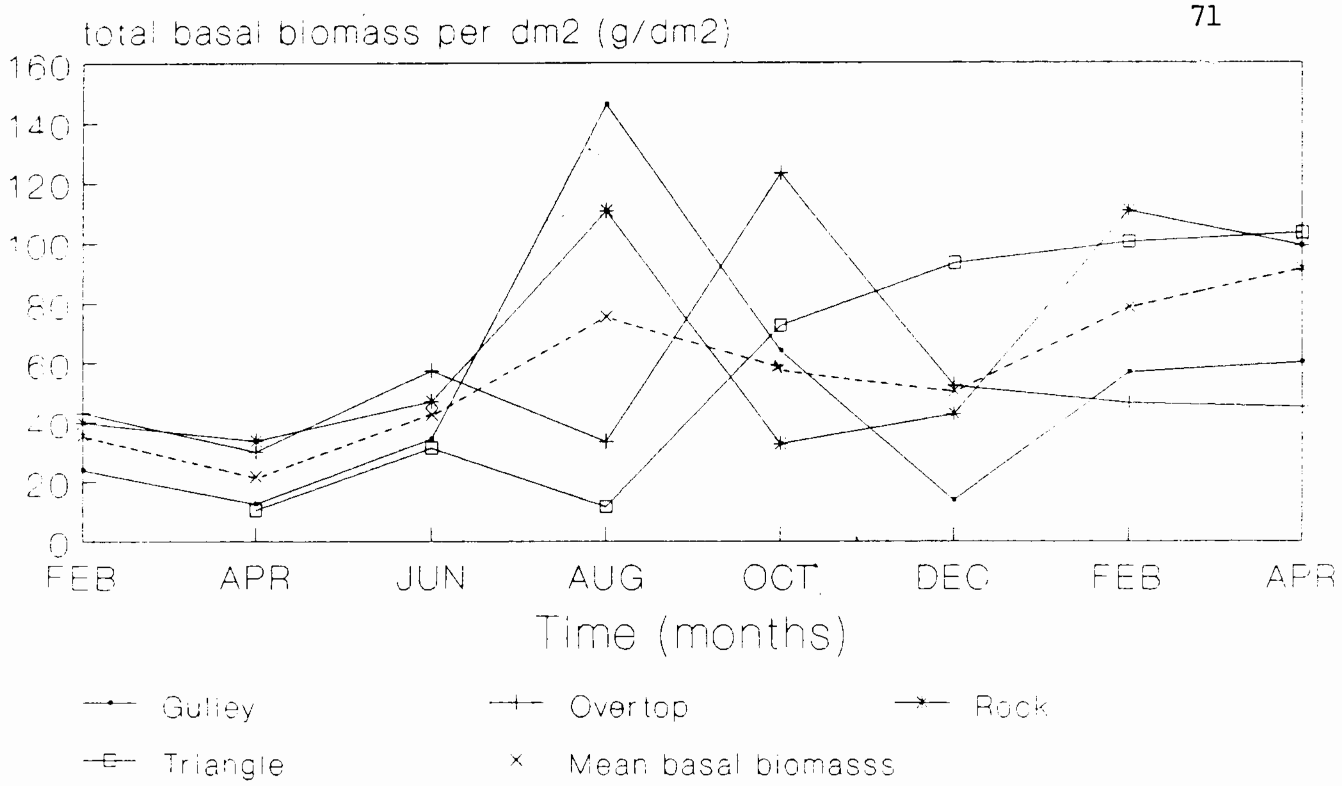

Figure 6. Total basal biomass per unit area for each of the four sites (solid lines) and mean of the four sites (dotted line) over the sampling period.

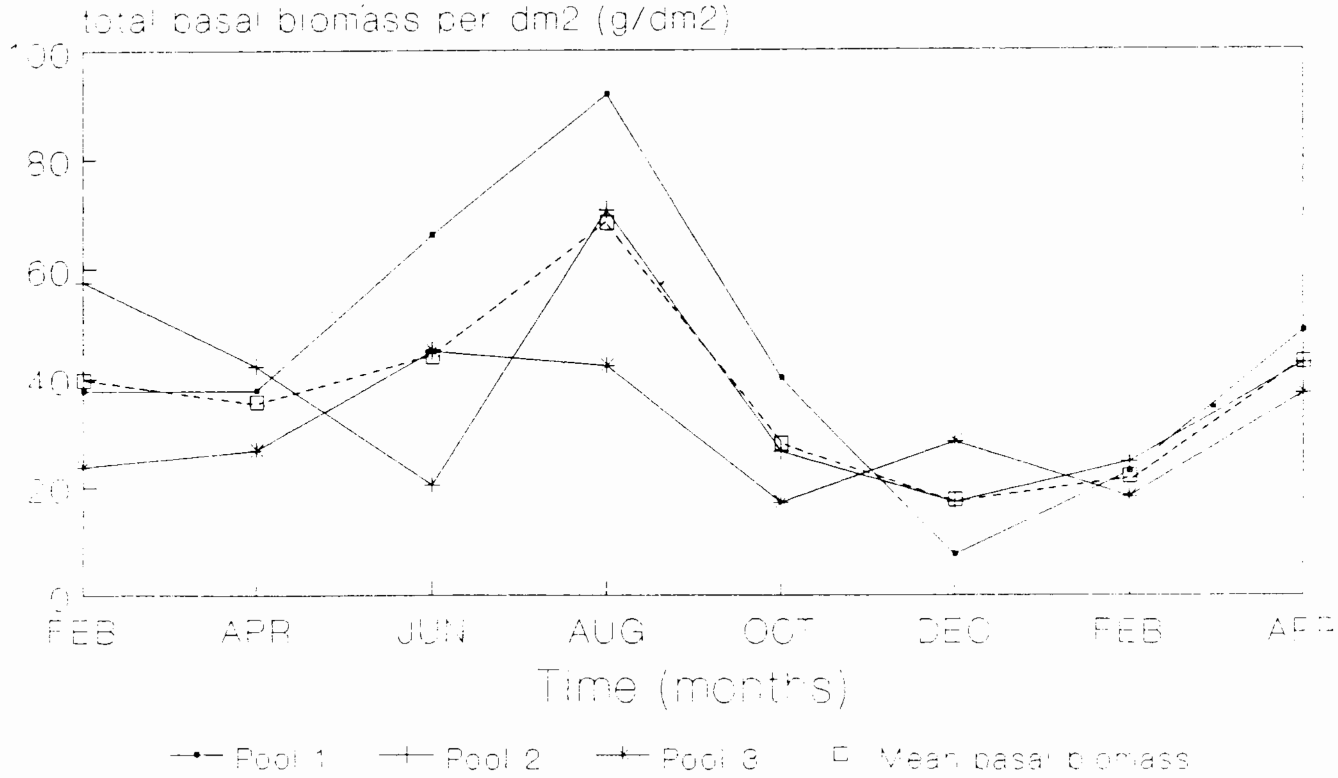

Figure 7. Total basal biomass per unit area for each of the three pools (solid lines) and mean of the three pools (dotted line) overthe sampling period.

conducted on the basal biomass between the sites and pools for each sampling date revealed that basal biomass only differed significantly during April 1990 (F=14.48, p<0.05) when the average basal biomass for the sites was twice as high than in the pools. Further comparison between the sites and pools revealed that in winter (August), plants at the sites allocate just under half (45%), while plants in the pools allocate almost all (98%) of their total biomass to their bases. In summer (February 1990) allocation of the total biomass to the base at the sites and in the pools was similar (19 and 22% respectively).

1.2 Total vegetative biomass

The data for the sites (Figure 8) reveal a weak seasonal pattern for the total vegetative biomass of the upright system but clearer than for the basal biomass (Figure 6), with minimum values in winter (June) and maximum values in summer (February) (This being reflected in three of the four sites -except for the Overtop site which had a late winter (August) minimum and an early summer (December) maximum. At the sites, total vegetative biomass did not vary significantly over the study period. On average, at the sites there is 2 1/2 times as much upright vegetative biomass in summer (February 1990) than in winter (June).

The pools exhibit a definite seasonal pattern in total vegetative biomass of the upright system (Figure 9), with low figures during the winter period (June to August) and high values throughout the following spring, summer and autumn. For the pools, total

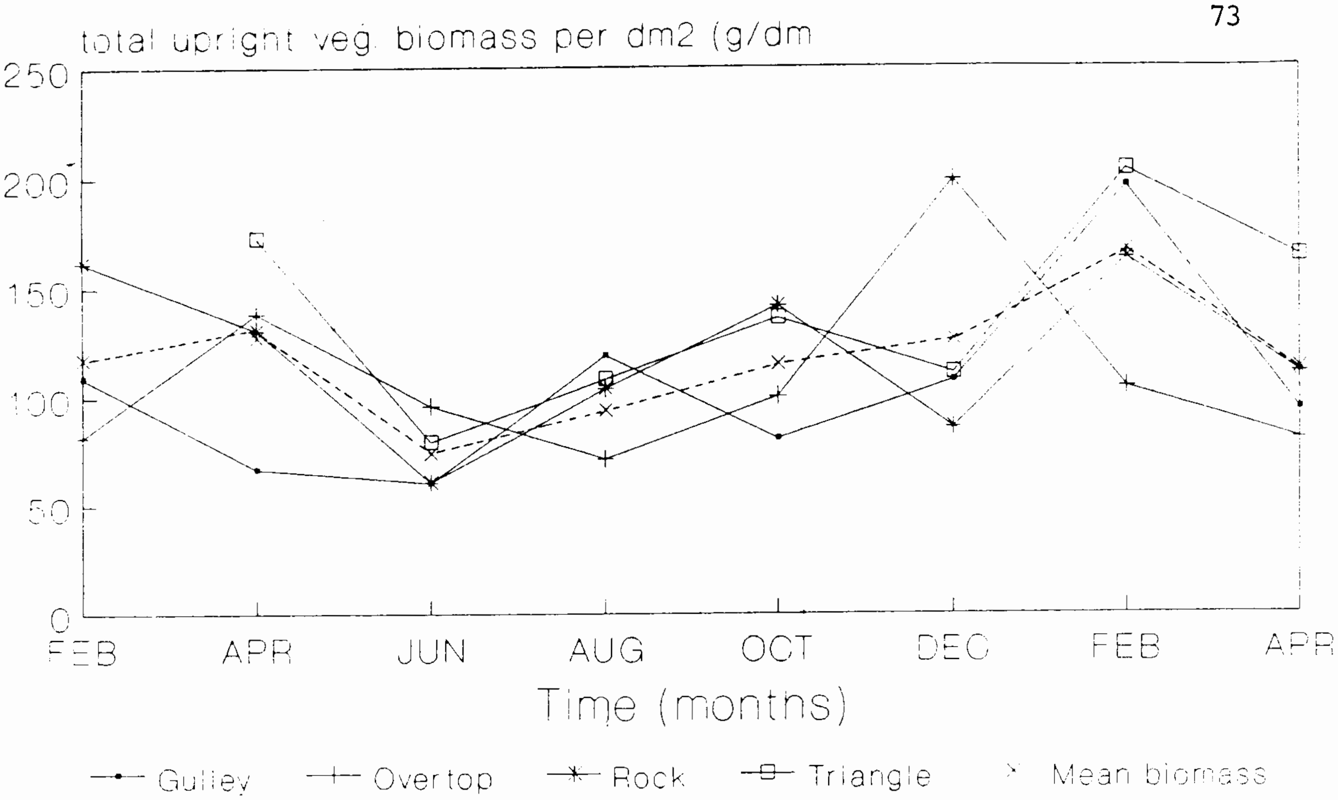

Figure 8. Total vegetative biomass of the upright system per unit area for each of the four sites (solid lines) and mean of the four sites (dotted line) over the sampling period.

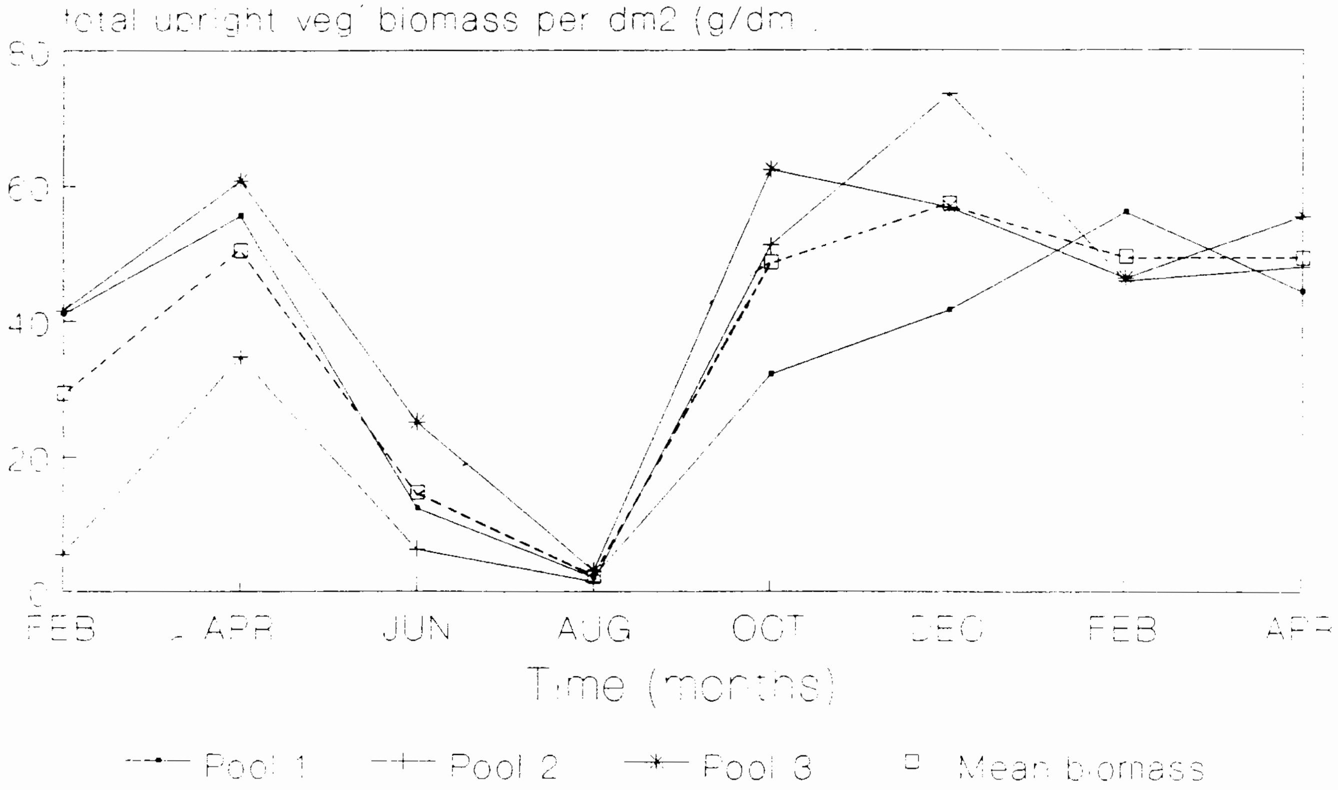

Figure 9. Total vegetative biomass of the upright system per unit area for each of the three pools (solid lines) and mean of the three pools (dotted line) over the sampling period.

vegetative biomass varied significantly over the study period ($F = 6.586$, $p<0.05$). On average, in the pools upright vegetative biomass during the summer period (December to February) is about 20 times higher than during the winter period (June to August). Summer (February) values of 1990 were about twice as high as the previous summer. In contrast to the sites where values decreased from late summer to autumn (February to April 1990), values stayed constantly high in the pools for this period. When comparing values for total upright vegetative biomass during the period of highest growth (December 1989 to Febrary 1990), values for the sites are about three times as high as that of the pools. The one-way ANOVA test conducted on the data between the sites and pools revealed that the total vegetative biomass of the upright system was significantly higher at the sites in June ($F=28.35$, $p<0.05$), August ($F=66.12$, $p<0.05$), October ($F=17.77$, $p<0.05$) and February 1990 ($F=18.98$, $p<0.05$), but did not vary at the other sampling dates.

1.3 Total receptacle biomass

For both sites (Figure 10) and pools (Figure 11), the data reveal very clear seasonal patterns in total receptacle biomass, with low winter values (June to August) rising to a peak in summer (February 1990), and decreasing again by the following autumn. Total receptacle biomass varied significantly over the sampling period for both the sites ($F=4.126$, $p<0.05$) and the pools ($F=3.304$, $p<0.05$). While total receptacle biomass increases from late winter (August) to early spring (October) at the sites,

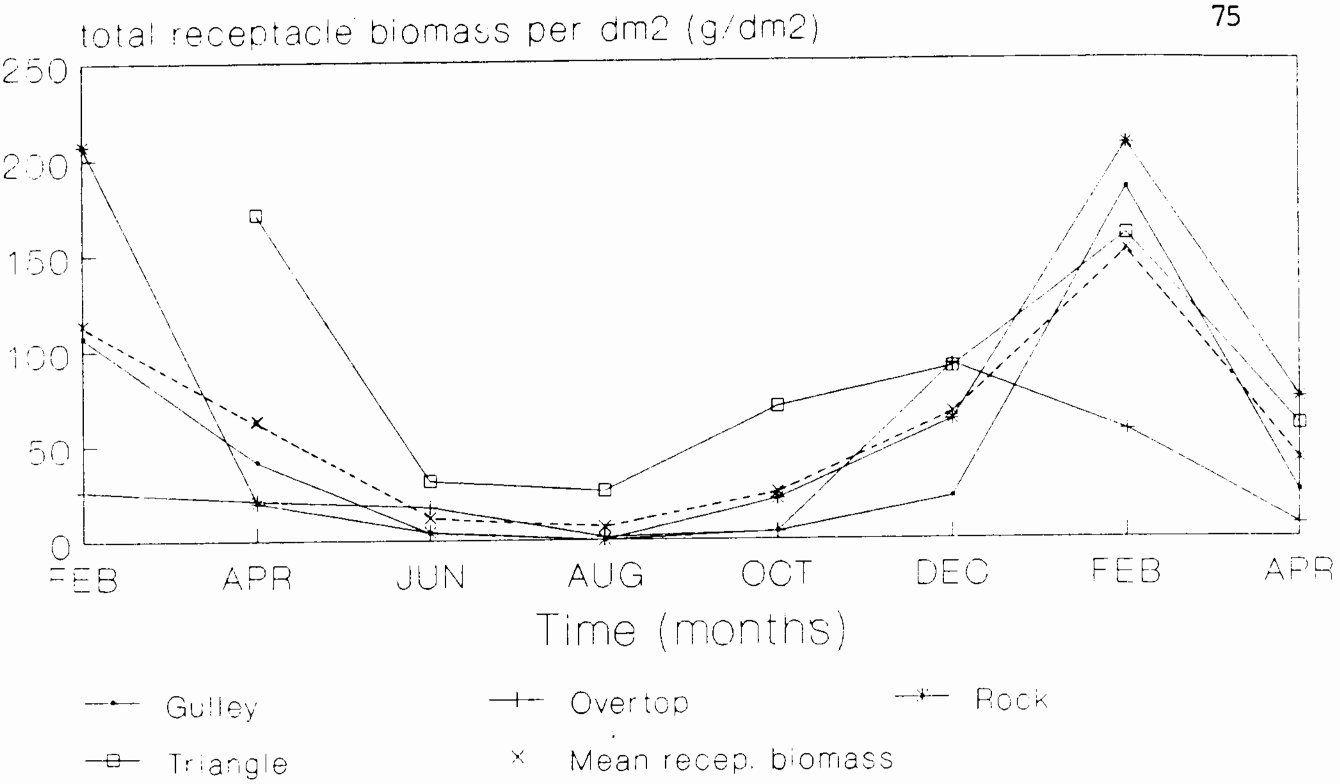

Figure 10. Total receptacle biomass per unit area for each of the four sites (solid lines) and mean of the four sites (dotted line) over the sampling period.

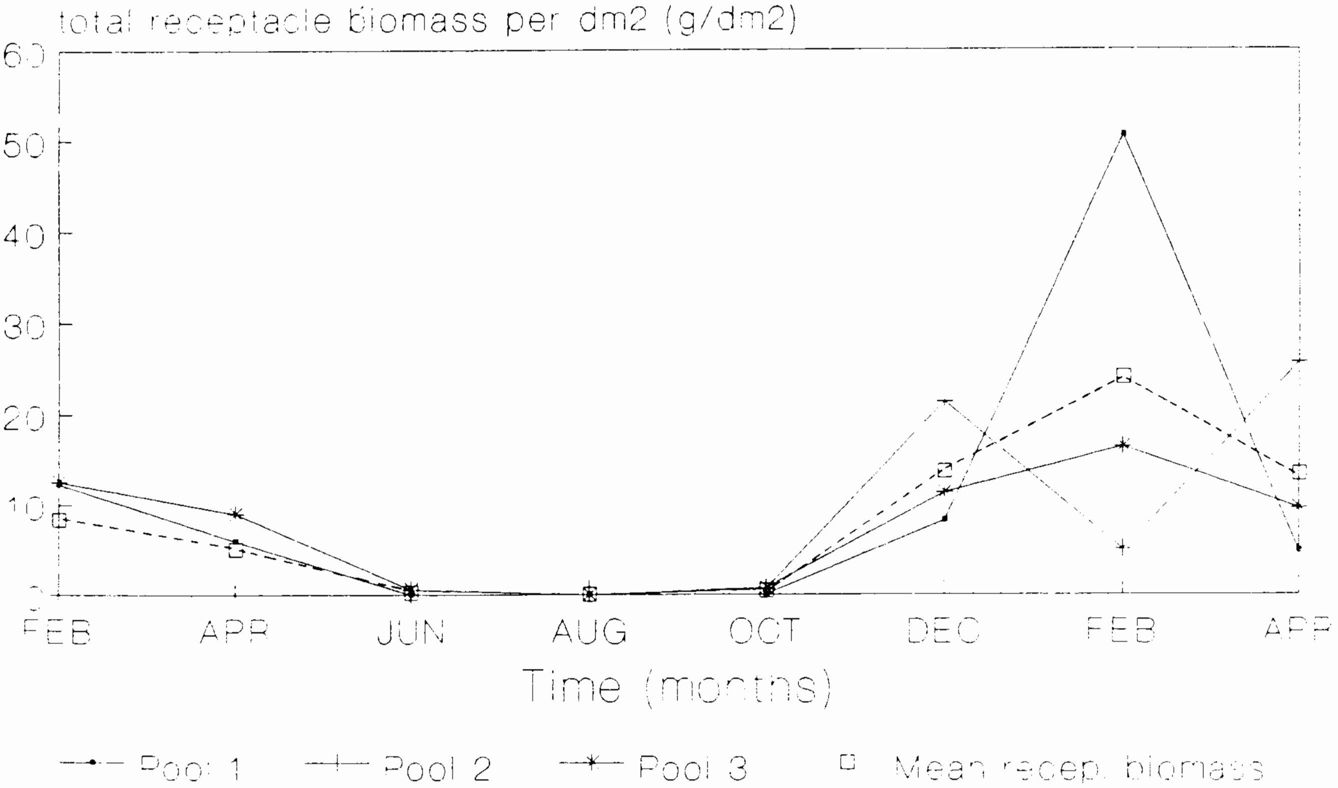

Figure 11. Total receptacle biomass per unit area for each of the three pools (solid lines) and mean of the three pools (dotted line) over the sampling period.

total receptacle biomass in the pools is still very low over this period, and only increases from spring (October) to early summer (December).

Data for the sites show that while the aforementioned pattern is evident for three of the four sites, the Triangle site differs from the others showing a peak in early summer (December) and decreasing by late summer (February 1990) when the other sites peak. Data for the pools revealed that Pool 1 has about twice the receptacle biomass than either of Pools 2 and 3 during their peak periods in December and February respectively, and about five times as much (Figure 11) in the previous summer (February 1989). Values in Pool 1 were then similar to Pool 3. Furthermore, while Pool 2 had a low biomass of receptacles in 1989, total receptacle biomass was the highest in both early summer (December) and the following autumn (April 1990).

When comparing total receptacle biomass between sites and pools during the peak reproductive period (December 1990), total receptacle biomass was about six times greater at the sites than in the pools per unit area. Furthermore, the one-way ANOVA test conducted on the data for the sites and pools for each sampling date revealed that total receptacle biomass never varied significantly between the sites and pools over the sampling period.

1.4 Total biomass

Data for the sites (Figure 12) and pools (Figure 13) reveal a definite seasonality for the total biomass at the sites and some seasonal tendency in the pools. Although values remained high throughout the summer (February) and autumn (April) of 1990, as exhibited by the site data, patterns for both sites and pools are similar to patterns of the total vegetative biomass of the upright system (Figures 8 and 9). At the sites, total biomass varied significantly over the sampling period (F=3.094, $p<0.05$), with this parameter not varying between June and August, although these two months varied from all the other months (S-N-K Test, $p < 0.05$). In the pools, total biomass did not vary significantly over the study period.

When comparing total biomass of the sites and pools, values in winter (June to August) and summer (December to February) were about 2 1/2 and 3 1/2 times higher respectively at the sites and in the pools for that periods. Furthermore, the sites had a significantly higher total biomass than the pools during October (F = 20.21, $p<0.05$) and February (F = 15.60, $p<0.05$), but did not vary during the other sampling months.

1.5 Density

Figures 14 and 15 each show the density of uprights with time for the sites and pools respectively. At the sites no seasonal pattern in density was exhibited, and density did not vary significantly over the sampling period. However, the individual sites showed some pattern. The Gulley and Rock sites both showed

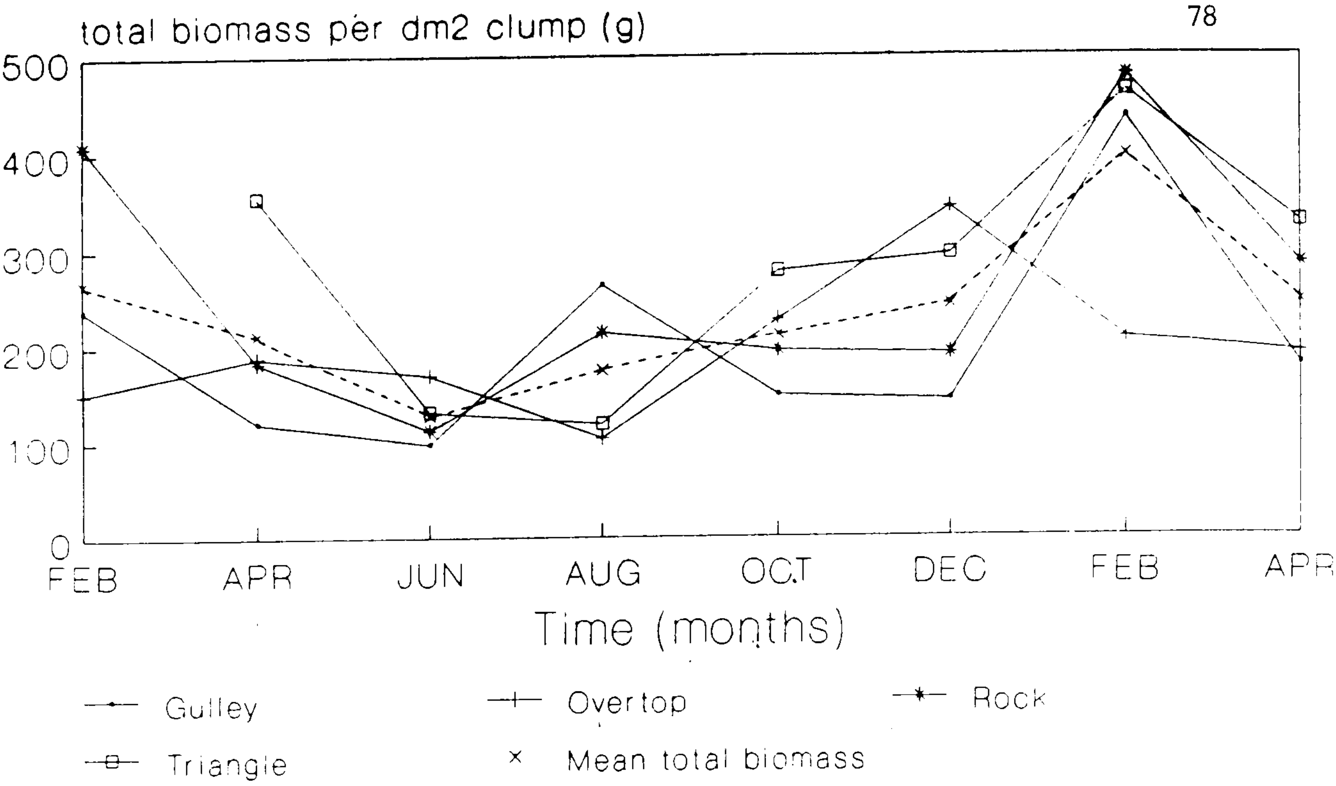

Figure 12. Total biomass of the clump per unit area for each of the four sites (solid lines) and mean of the four sites (dotted line) over the sampling period.

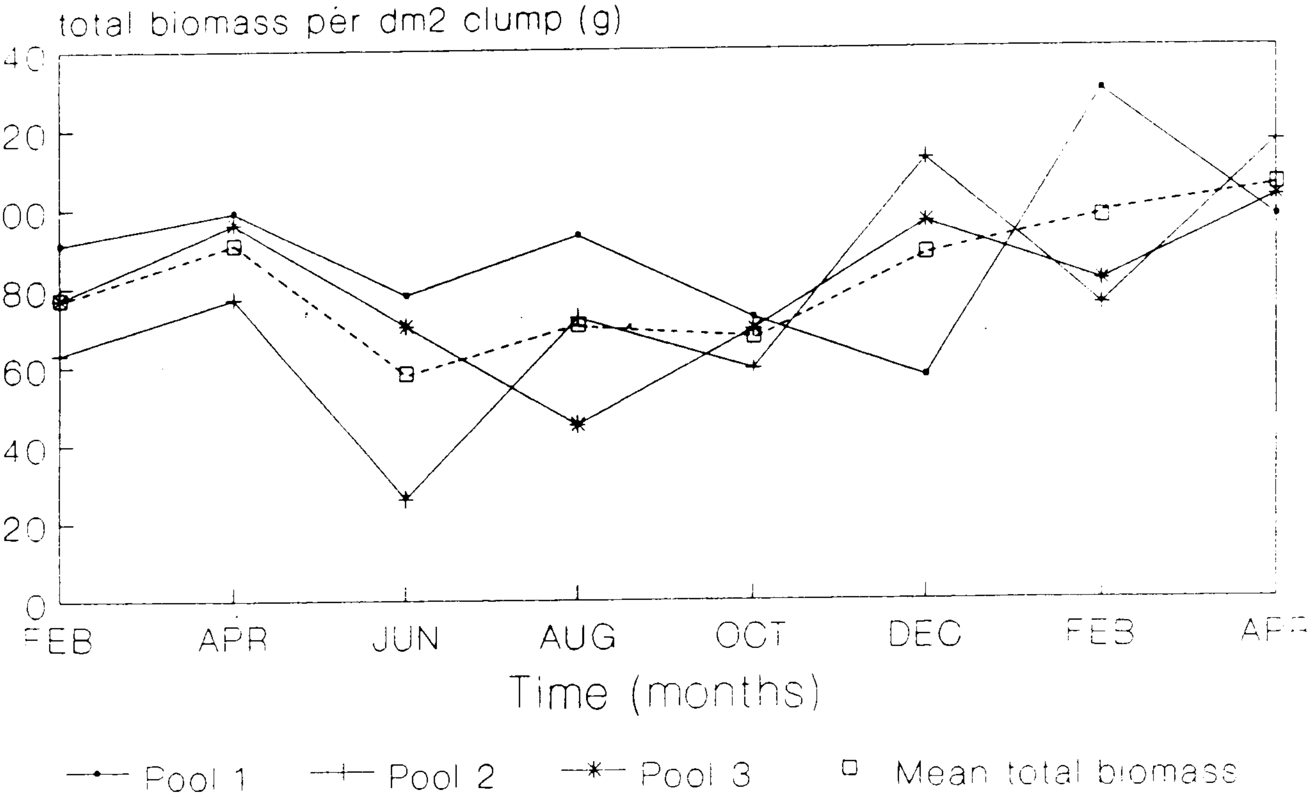

Figure 13. Total biomass of the clump per unit area for each of the three pools (solid lines) and mean of the three pools (dotted line) over the sampling period.

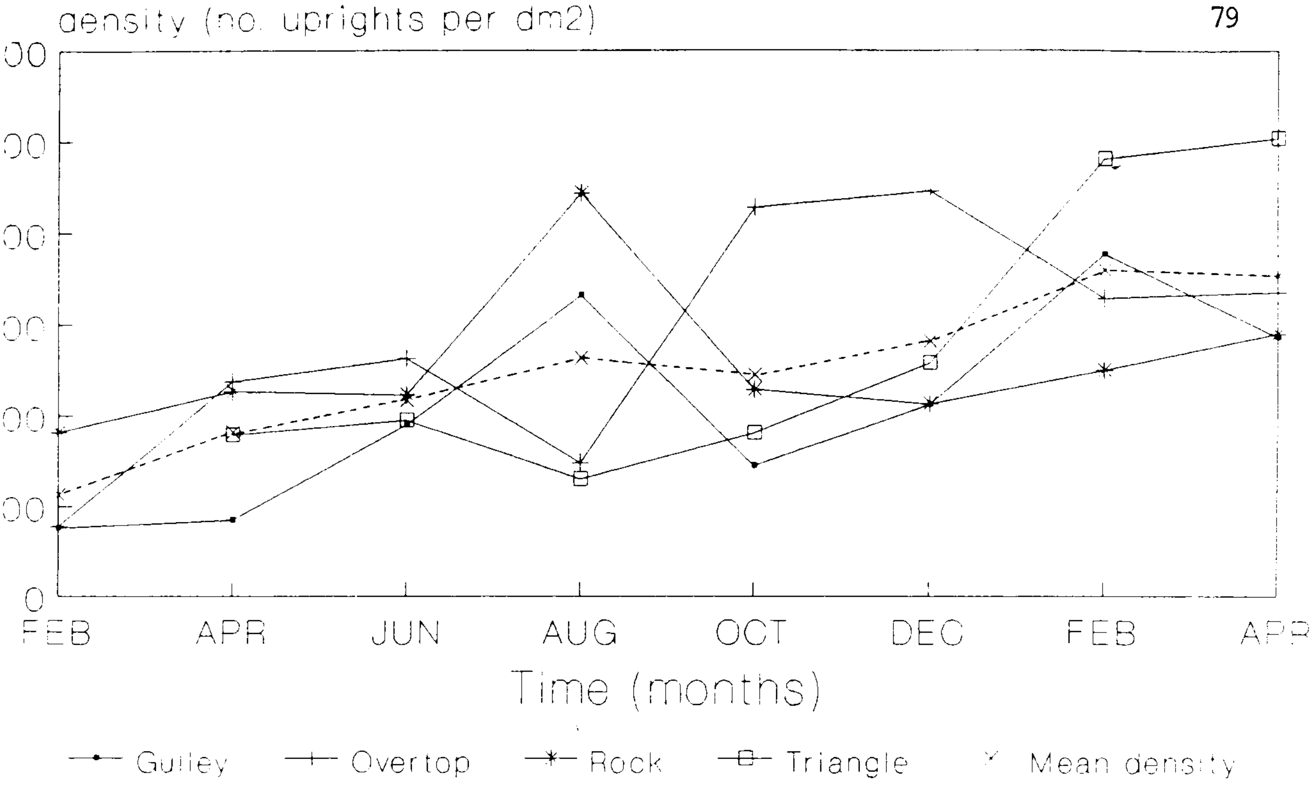

Figure 14. Density of uprights per unit area for each of the four sites (solid lines) and mean of the four sites (dotted line) over the sampling period.

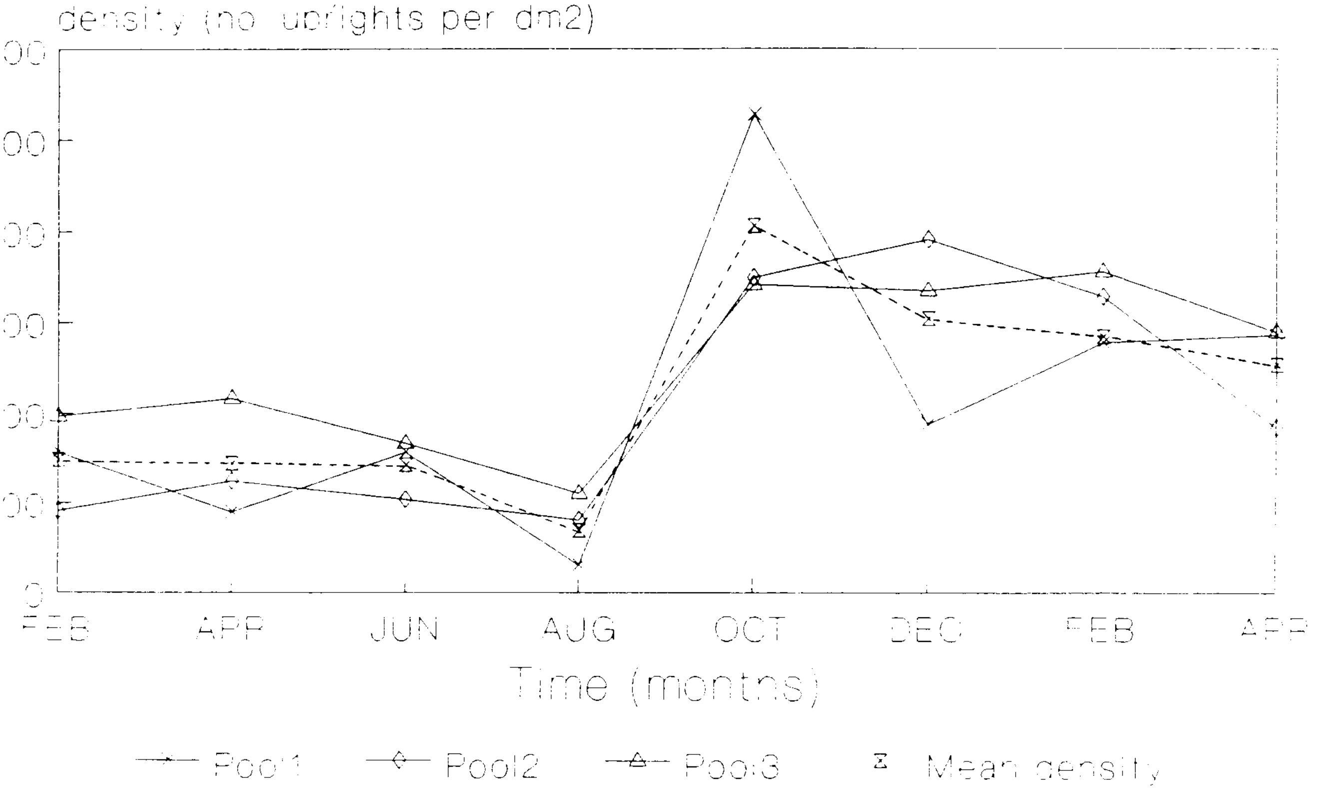

Figure 15. Density of uprights per unit area for each of the three pools (solid lines) and mean of the three pools (dotted line) over the sampling period.

a marked increase from June to peaks in August. At the Overtop site, a marked increase in density occurred from August to October, with density peaking from October to December. At the Triangle site, density only peaked in February 1990. In contrast to the lowest density figures in summer (February) of 1989, density was highest (three times as high) during the same month in 1990. Similarly, autumn (April) values of 1990 was much higher (twice as high) than those of the previous autumn. Accompanying the slight increase in density from early spring (October) to early summer (December) was a slight decrease in basal biomass (Figure 6), whereafter patterns of density and basal biomass both rose steadily to peaks in late summer (February 1990), with both remaining high until autumn (April) of 1990. In contrast to the sites, the pools displayed a definite seasonality in density. Density varied significantly over the sampling period ($F=7.847$, $p<0.05$), with a late winter (August) low and a peak in early spring (October). During late winter, a minimum in density was accompanied by a maximum in total basal biomass (Figure 7). A rapid increase in density from late winter (August) to early spring (October) was accompanied by a rapid decrease in total basal biomass over this period. The one-way ANOVA test conducted on the density between the sites and pools revealed that density did not vary significantly at each sampling date throughout the sampling period.

2. Vegetative and reproductive development

2.1 Mean length per upright

The site data for the mean length per upright (Figure 16) do not reveal a definite seasonal pattern. Although uprights were short on average during the winter period (66 and 83mm in June and August respectively), uprights were not much longer during the following summer period (91mm in December 1989, 104mm in February 1990). However, uprights were considerably longer in February 1990 (151mm) than in February 1989. The pool data (Figure 18) exhibits a strong seasonal tendency, with shorter uprights in winter and longer uprights in summer. The tendency for uprights in the pools to decrease in length from late summer (February) to autumn (April) in 1989 was in contrast to uprights remaining long over this period in 1990. For each site and pool, the length per upright varied significantly over the sampling period (Kruskal-Wallis (K-W) one-way ANOVA tests, $p < 0.05$). The site data further reveals that length per upright varied significantly at the 5% level between the sites at each sampling date except during early summer (December). Comparison of Figures 16 and 17 shows that length of uprights was more variable between the sites than between the pools. Comparison of the growth patterns between the sites and pools shows that while growth had already started by the end of winter (August) at the sites, growth only started during the period from late winter to spring (August to October) in the pools. Growth patterns of uprights in the pools show that uprights in Pool 2 remained short throughout

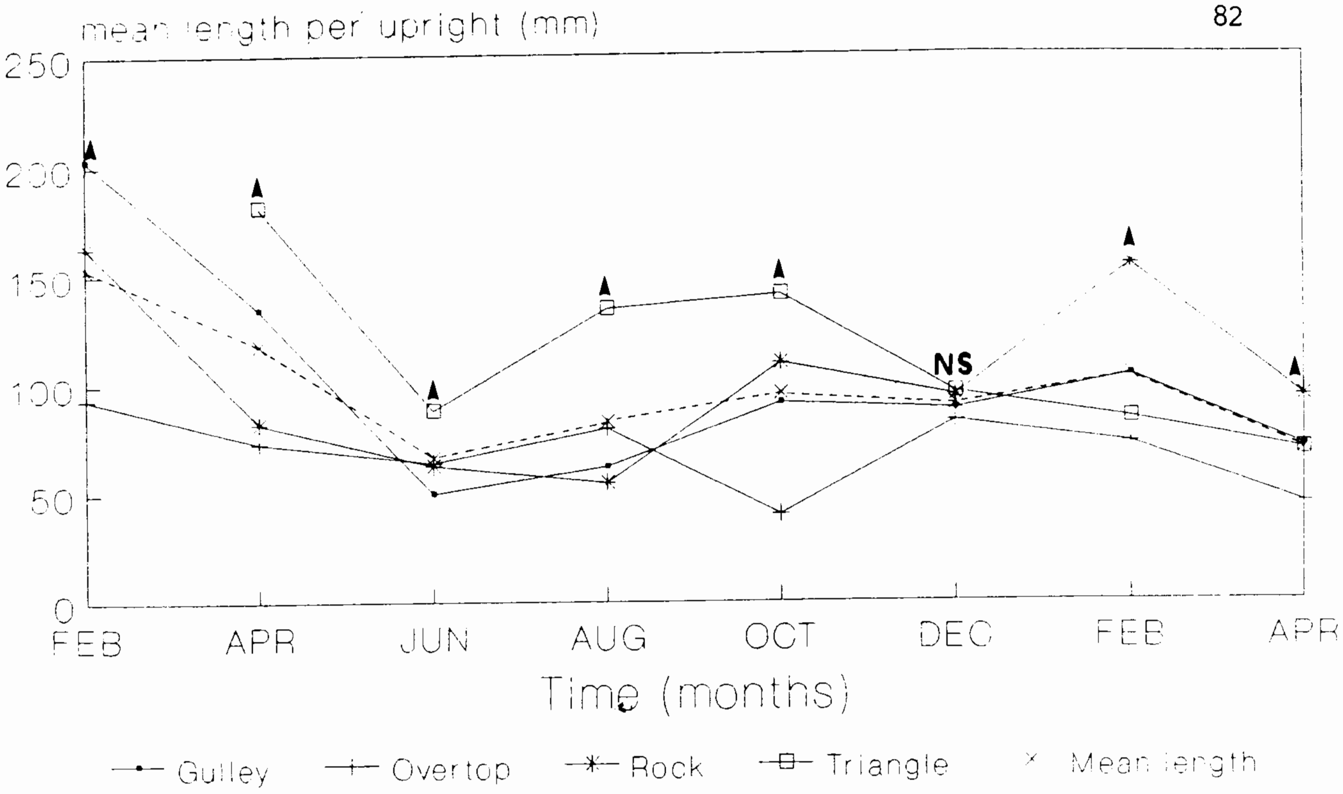

Figure 16. Mean length per upright for each of the four sites (solid lines) and mean of the four sites (dotted line) over the sampling period. ▲ = significant difference between the sites at each month by 1-way ANOVA, P < 0.05. NS = non-significant.

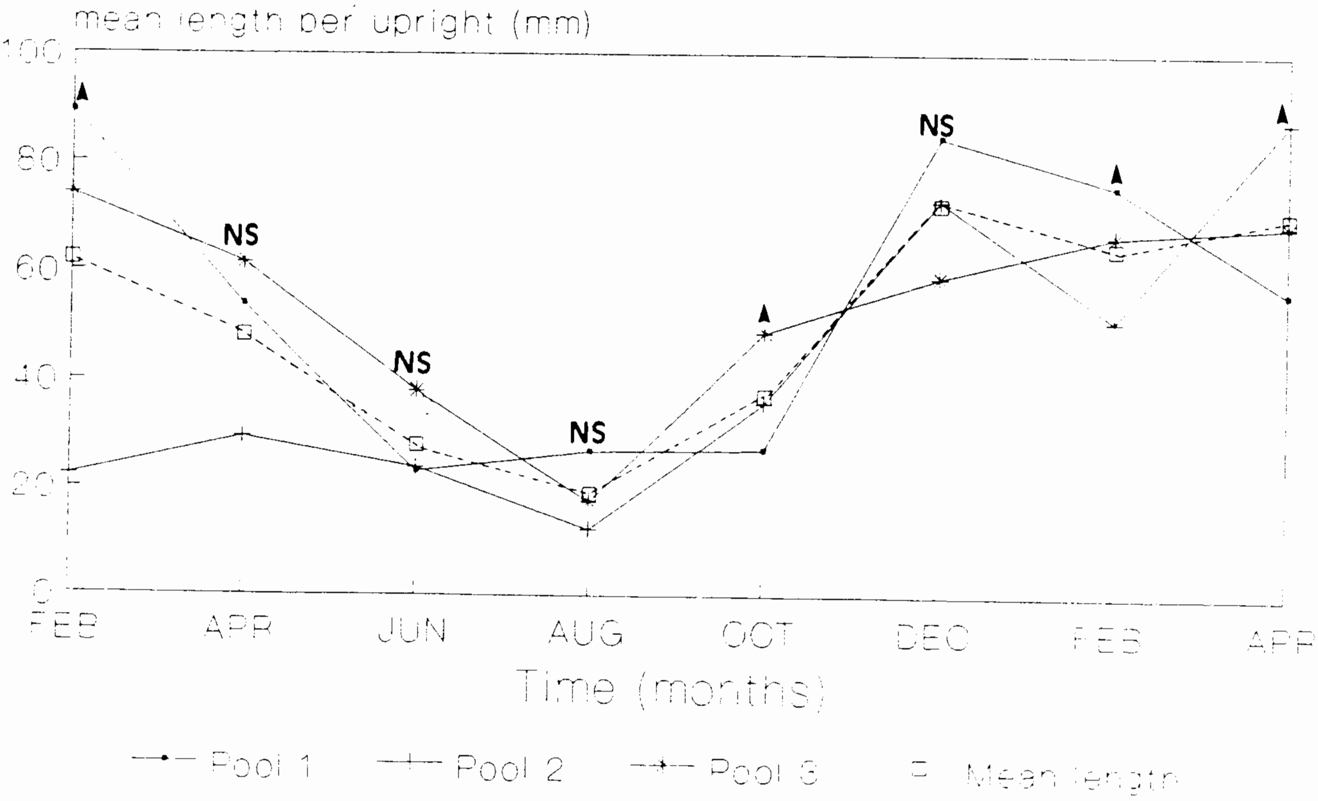

Figure 17. Mean length per upright for each of the three pools (solid lines) and mean of the three pools (dotted line) over the sampling period. ▲ = significant difference between the pools at each month by 1-way ANOVA, P < 0.05. NS = non-significant.

the first six months of the sampling period unlike those in Pools 1 and 3 which were longer. The tendency for uprights in the pools to remain long throughout summer to autumn 1990 was contrasted at the sites by uprights decreasing in length over that period. When comparing upright length between sites and pools, on average, uprights at the sites were about twice as long as in the pools in summer.

2.2 Mean number of branches per upright

The sites (Figure 18) and pools (Figure 19) both displayed strong seasonal patterns in branching with time, with low figures in winter (June to August) and peaks in early summer (December). For each site and pool, the number of branches per upright varied significantly over the sampling period (K-W one-way ANOVA Tests, $p < 0.05$). Furthermore, one-way ANOVA tests conducted at each sampling date over the sampling period between the sites revealed that the number of branches per upright only varied significantly between the sites during late winter (August) and early spring (October). The same test showed that this parameter only varied between the pools during summer (December 1989 to February 1990) and autumn (April 1990) of the following year. Although branching initiation already occurred from early to late winter (June to August) at the Triangle site, the remaining sites and the pools exhibited branch initiation from late winter (August) to early spring (October) (=the onset of the spring period). At both the sites and in the pools, rapid branching development further occurred from spring (October) to early summer (December).

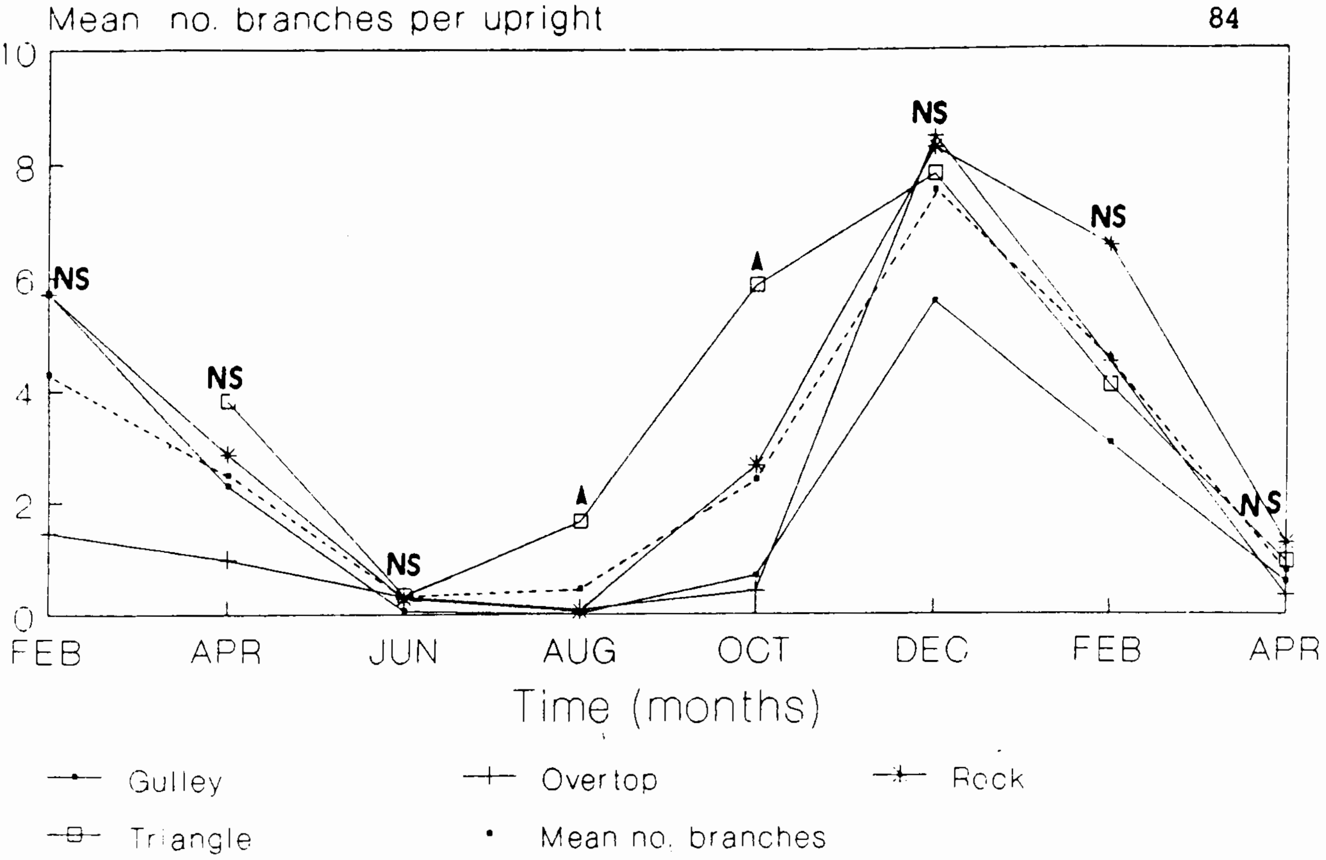

Figure 18. Mean number of branches per upright for each of the four sites (solid lines) and mean of the four sites (dotted line) over the sampling period. ▲ = significant difference between the sites at each month by 1-way ANOVA, P < 0.05. NS = non-significant.

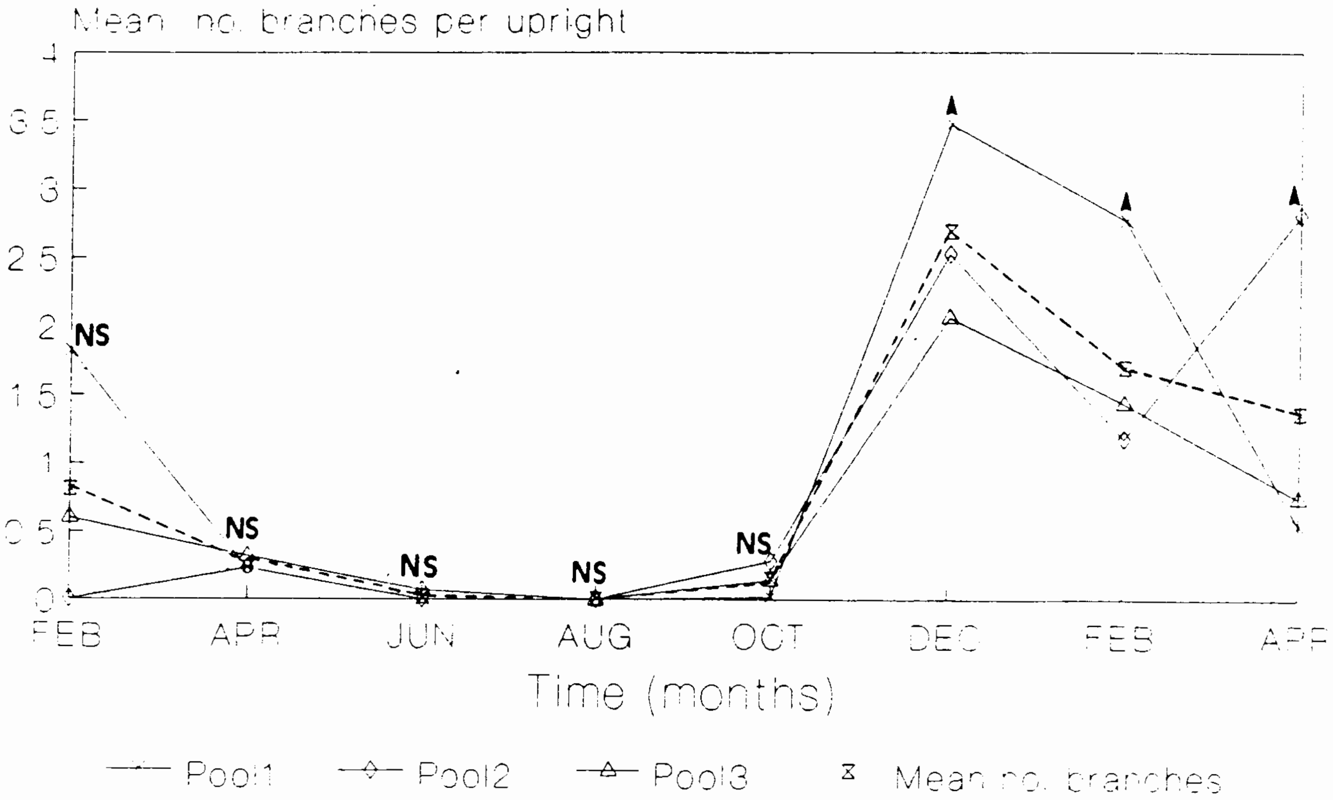

Figure 19. Mean number of branches per upright for each of the three pools (solid lines) and mean of the three pools (dotted line) over the sampling period. ▲ = significant difference between the pools at each month by 1-way ANOVA, P < 0.05. NS = non-significant.

This was followed by a rapid decline in branching at both the sites and in in the pools from summer (December) through to autumn (April) 1990. During the peak branching period in early summer (December 1989), uprights at the sites beared 2.7 times more branches than those in the pools. In the pools, there were twice as many branches per upright in February 1990 as in February 1989.

2.3 Mean total biomass per upright

Although data for the sites do not reveal a clear seasonal pattern (Figure 20), the tendency is for values to be low in winter (0.54g in June) and high in summer (1.95g in February 1989, 0.925g in February 1990). In contrast to the sites, the pool data (Figure 21) reveal a clear seasonal pattern with very low winter values (e.g. 0.08g in June) and three times higher summer values (e.g. 0.26g in February 1989). Total biomass for each upright varied significantly at the 5% level for each site and pool over the sampling period (K-W one-way ANOVA, $p < 0.05$). Total biomass per upright varied significantly between the sites at all sampling dates (K-W one-way ANOVA, $p < 0.05$), except during June, when this parameter did not vary. For the pools, total biomass per upright was only non-significant between the pools during April 1989 and differed between the pools at all the other sampling dates. As for the total vegetative biomass at the sites and in the pools respectively, high summer values continued into autumn in the pools, while values declined from summer to autumn 1990 at the sites. When comparing sites and pools, mean

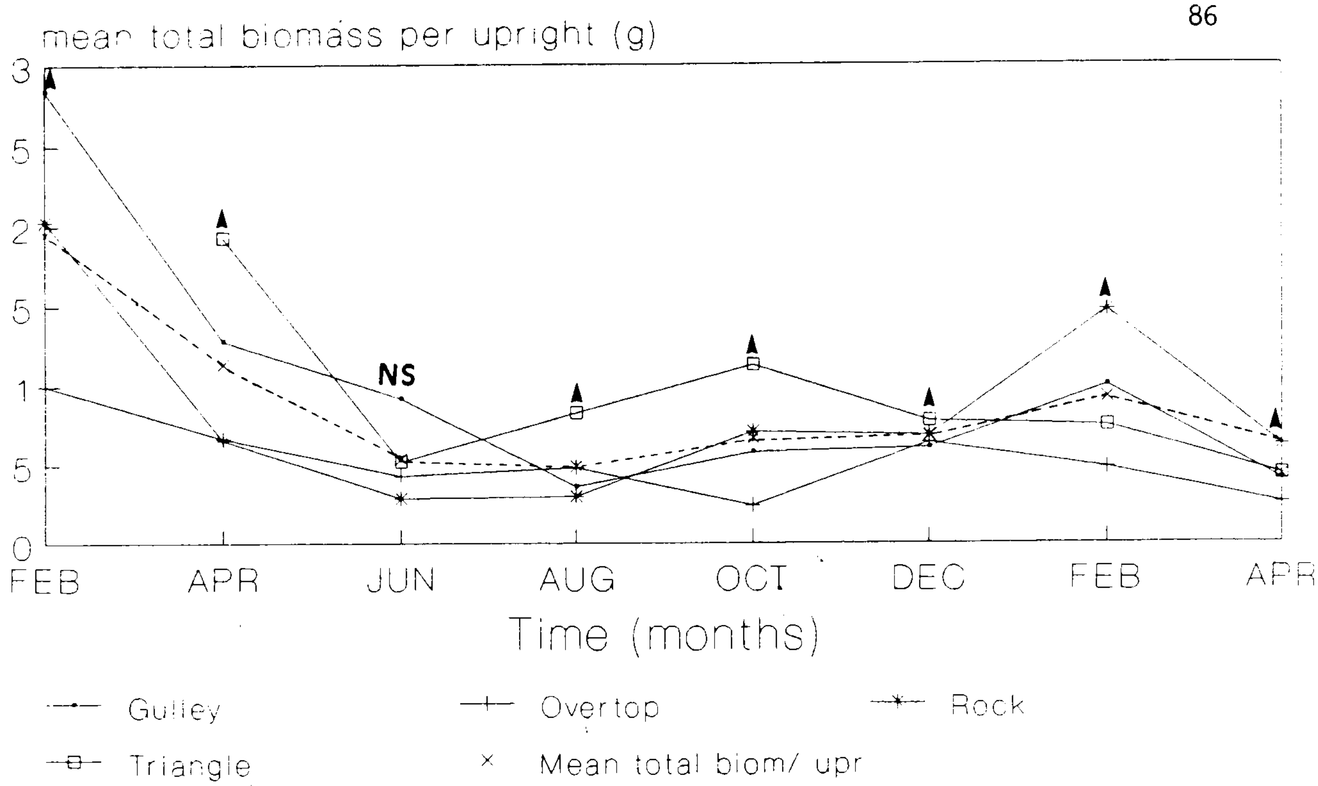

Figure 20. Mean total biomass per upright for each of the four sites (solid lines) and mean of the four sites (dotted line) over the sampling period. ▲ = significant difference between the sites at each month by 1-way ANOVA, $P < 0.05$. NS = non-significant.

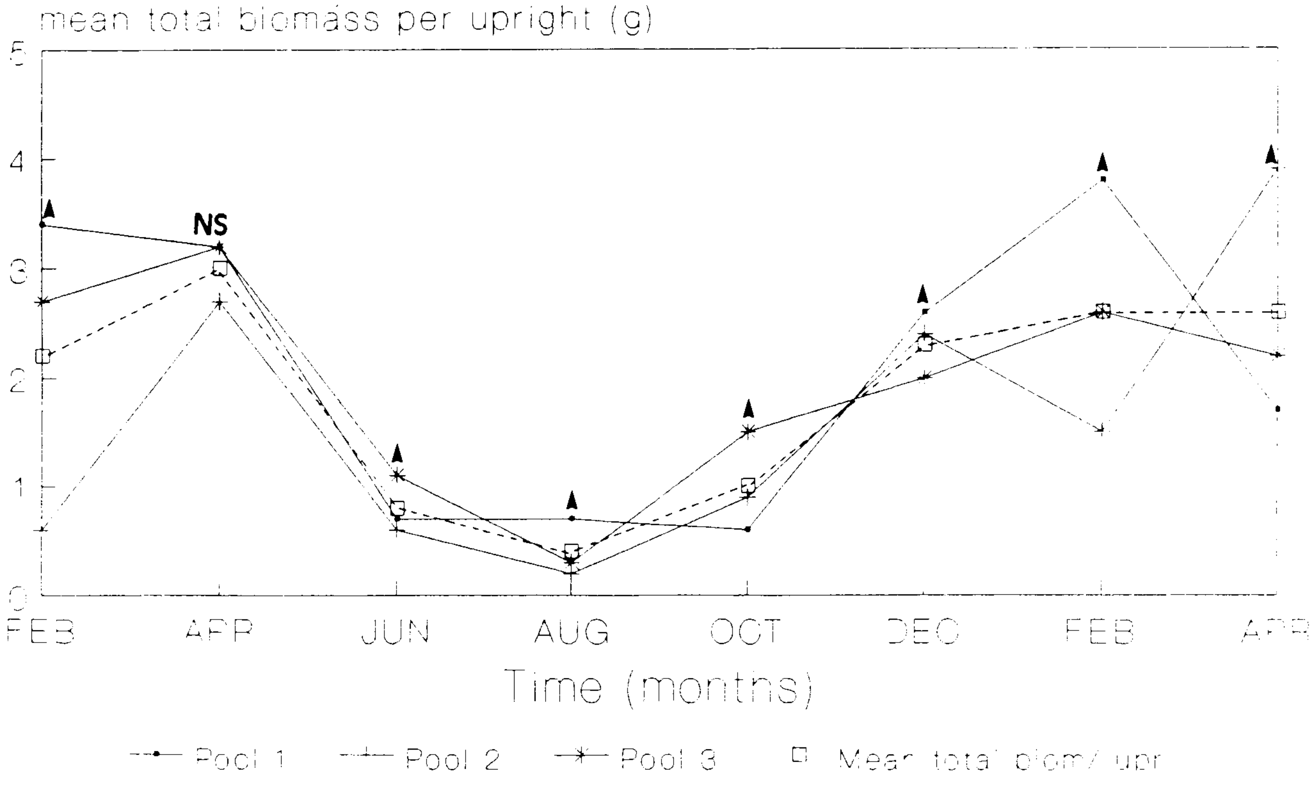

Figure 21. Mean total biomass per upright for each of the three pools (solid lines) and mean of the three pools (dotted line) over the sampling period. ▲ = significant difference between the pools at each month by 1-way ANOVA, $P < 0.05$. NS = non-significant.

total weight per upright during summer is about three times (February 1990) to eight times (February 1989) as high at the sites than in the pools. Furthermore, the mean total weight per upright is five (February 1990) to nine times (February 1989) higher during summer at the sites than in the pools.

2.4 Mean receptacle biomass per upright

The data for the mean receptacle biomass per upright for the sites (Figures 22) and pools (Figure 23) reveal strong seasonal patterns for both sites and pools, with low winter (June) and high summer (February) values. Furthermore, both sites and pools show a similar marked decline from late summer to autumn (February to April 1990). Receptacle biomass per upright varied significantly for each site and pool over the sampling period (K-W one-way ANOVA Tests, $p < 0.05$). One-way ANOVA tests conducted at each sampling date between the sites revealed that receptacle biomass per upright varied significantly at the 5% level only during the August and October sampling dates. The same tests between the pools revealed that over the sampling period, this parameter only varied during early summer (December) and the following autumn (April 1990). Post-winter patterns for mean receptacle biomass per upright for both the sites and pools were similar to patterns for the mean number of branches per upright (see Figures 18 and 19). However, while branching peaked in December 1989, mean receptacle biomass per upright peaked during February 1990 at both the sites and pools. At the sites, receptacle biomass per upright started rising from late winter to

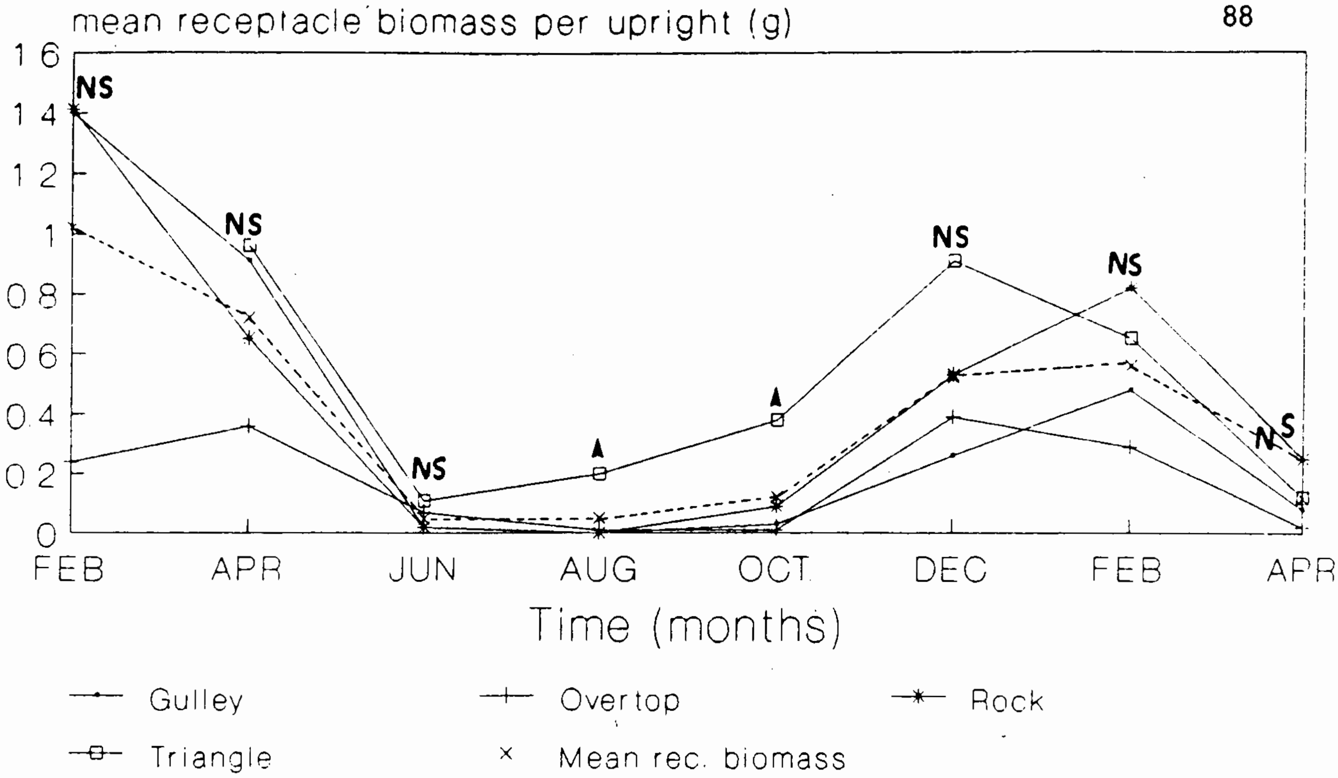

Figure 22. Mean receptacle biomass per upright for each of the four sites (solid lines) and mean of the four sites (dotted line) over the sampling period. ▲ = significant difference between the sites at each month by 1-way ANOVA, P < 0.05. NS = non-significant.

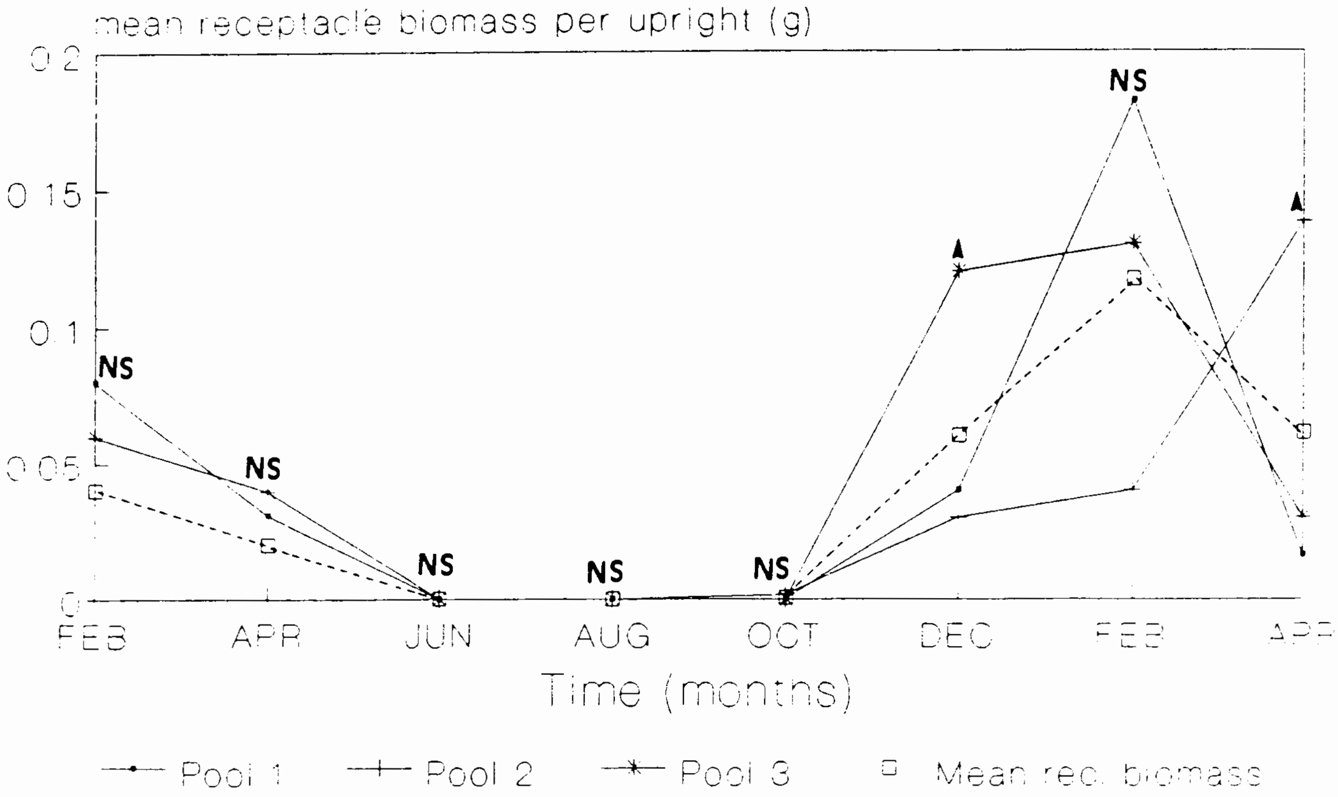

Figure 23. Mean receptacle biomass per upright for each of the three pools (solid lines) and mean of the three pools (dotted line) over the sampling period. ▲ = significant difference between the pools at each month by 1-way ANOVA, P < 0.05. NS = non-significant.

early spring, leading to early high values in early summer (December), being high throughout the summer. In the pools however, mean receptacle biomass per upright only started rising markedly from spring to early summer (October to December), values still being low in early summer, and peaking in late summer (February). Pool 2 deviated from this pattern with receptacle biomass per upright peaking in autumn (April 1990).
On average, the mean receptacle biomass per upright was about 25 (1.02g compared to 0.04g) and five times (0.56g compared to 0.117g) as high at the sites than in the pools during the peak reproductive month (February 1989 and 1990 respectively).

3. Fecundity

Table 3 shows data on the fecundity of *B. brassicaeformis*.
The species has about 38 conceptacles per receptacle, 16508 eggs per gram receptacle, about 120 000 eggs per upright and 24940 eggs per gram upright of the plant.

4. Reproductive effort

Table 4 shows data on the reproductive components of *Bifurcaria brassicaeformis*, including data on six British fucoids for comparison in the discussion. The data reveals that the species allocates between 66-78% of its upright biomass to receptacles.
Furthermore, the cost of gamete production, measured as the proportional biomass of oogonia of the frond weight is very small.
Eggs represent only 0.16 - 0.2% of the total frond weight.
The mass of a single egg is 0.8527 x 10-6 g. If we assume that

Table 3. Fecundity of *Bifurcaria brassicaeformis*. Means (±1SE) shown.

No. plants	Length of upright (mm)	Mass of upright (g)	No. receptacles/ upright	No. conceptacles/ receptacle	No. eggs/ conceptacle
10	273.14 (± 10.03)	4.83 (± 0.386)	11.52 (± 38.23)	38.23 (± 2.59)	244.6 (± 4.79)
	No. eggs/ receptacle	No. eggs/ g receptacle	No. eggs/ upright	No. eggs/ g upright	
	9352.03 (± 183.112)	16508.45 (± 323.23)	118873.3 (± 16165.34)	24940.89 (+1743.56)	

Table 4. Characteristics of the reproductive components of Bifurcaria brassicaeformis compared to data on other fucoids. Means shown. (± SE for B. brassicaeformis). (Data from Vernet and Harper 1980, except for *) Cousens 1981a. The species are listed in descending order of their respective positions in the intertidal zonation.

Species	Mass receptacle/ g upright (%)	total egg mass/ g upright	mass of an egg (g)	egg diameter (µm)	sperm diameter (µm)	egg volume (× 10^3 µm)	sperm volume (µm)
Pelvetia canaliculata						278	
Fucus spiralis						235	
F. vesiculosus						68	
Ascophyllum nodosum	61-66*					74	
F. serratus						181	
B. brassicaeformis	72.075 (± 6.29)	0.00183 (± 0.0002)	0.8527 $\times 10^{-6}$	113.12 (± 1.54)	5.597 (± 0.163)	761 (± 30.31)	92.445 (± 5.383)
Himanthalia lorea						4300	

biomass is proportional to the size (diameter) of the gametes, then the proportion of biomass allocated to eggs is about 20 times that invested in sperm. An egg is about 8000 times larger in volume than a spermatozoid.

5. Seasonal changes in the state of conceptacle maturity

Table 5 shows that the earliest stages of conceptacle initiation at both the sites and in the pools generally occurs from late winter (August) to early spring (October). At the sites, conceptacles were fully mature containing abundant gametes by early summer, while in the pools conceptacles were only mature by late summer containing few gametes. By autumn, degeneration of conceptacles and gametes left in the conceptacles generally occutrred at both sites and pools. An exception to this occurred in Pool 2 where conceptacles only matured by autumn, but contained few, albeit healthy, eggs.

Table 5. *Bifurcaria brassicaeformis* seasonal changes in the state of conceptacle maturity at the seven microhabitats. (10 receptacles per clump). Sex of receptacles in a clump did not change throughout the sampling period indicated.

COLLECTION DATE	GULLEY (male)	ROCK (male)	OVERTOP (female)	TRIANGLE (female)	POOL 1 (male)	POOL 2 (male)	POOL 3 (male)
February 1989	++	+	++	no collection	+	+	+
April 1989	(+)	(+)	(+)	(+)	(0)	(0)	(+)
June 1989							
August 1989			0	+			
October 1989	+	+	+	+		0	0
December 1989	++	++	++	++	0	+	+
February 1990	++	++	++	++	+	+	+
April 1990	(+)	(+)	(+)	(+)	(+)	++	(+)

LEGEND: ++ = healthy and abundant oogonia/ antheridia
+ = healthy but few oogonia/ antheridia
0 = oogonia/ antheridia absent
( ) = oogonia/ antheridia degenerate
empty space = no receptacles

DISCUSSION

Results obtained for the temperate fucoid *Bifurcaria brassicaeformis* clearly demonstrate that this species displays seasonal periodicity in growth of uprights, morphological development and reproduction. These findings concur with seasonal patterns of growth described for the European temperate fucoids *Ascophyllum nodosum* (David 1943), *Pelvetia canaliculata* (Subrahmanyan 1960), *Fucus vesiculosus* (Knight and Park 1950, Printz 1959), *F. spiralis* (Subrahmanyan 1961), *Halidrys siliquosa* (Moss and Lacy 1963), *F. serratus* and *Himanthalia elongata* (Nizamuddin 1970) and *F. distichus ssp. distichus* (Thom 1983). *B. brassicaeformis* showed four distinct phases in growth; no growth in winter (June to August), rapid spring growth (August to October), a period of reproduction from early to late summer (December to February), followed by senescence of upright material by the following autumn (April) to its persistent winter base. A strikingly similar growth pattern has been described for *Sargassum polyceratium* from Florida (Kilar *et al.* 1989) where periods of no growth, development, reproduction and senescence occurred at at about the same time of year, but in opposite seasons. *S. polyceratium* grows maximally and initiates receptacles in the northern hemisphere during autumn (October), reproduces in winter (December), senesces during spring (April) and displays no growth in summer (July).

During winter, only the basal rhizomes and very few stunted uprights of *B. brassicaeformis* are present. The base constitutes

almost all of the biomass (98%) of the plants in the pools, and about half (45%) at the sites.
Generally at the sites (which is the typical habitat for B. brassicaeformis), and in the pools, this period co-incides with large scale production of vegetative uprights (reflected by increasing densities, Figures 14, 15) and growth in length of uprights (Figures 16, 17) from the basal rhizomes. At one site (Triangle), growth and development even starts during the winter period.

In the pools, the rapid spring increase in density and growth in length of uprights is more pronounced. This could have been due to environmental conditions being harsher on plants in the pools during the previous summer when two of the three pools often dried out during spring low tides. These effects are reflected in the very low percentage biomass of upright material left on the bases in the pools (2%) in comparison to those at the sites (55%).

At both the sites and in the pools, small side branches (Figures 18, 19) representing receptacles which have immmature conceptacles (Table 5) also start to develop with the onset of the spring period, with branching and conceptacle development continuing into early summer at both the sites and pools.

In situ annual growth data in the literature are available for only one perennial south African west coast seaweed, Laminaria pallida (Gunn.) Fosl. (Laminariales) (Dieckmann 1980). As with B. brassicaeformis, this kelp also has a strong seasonal pattern of growth, which in *L. pallida* has been closely related with surface incident radiation. Dieckmann (1980) states that his data strongly suggests that an innate mechanism, principally regulated by the light regime, regulates growth in *L. pallida*. The onset of the rapid growth phase in late winter/ early spring coincides with increasing daylength and light intensity.

As in *L. pallida*, the northern hemisphere *Laminaria hyperborea* (Gunn.) Fosl. (Laminariales) also shows remarkably sudden growth of new fronds in spring, this having been shown to be photoperiodically mediated by short days (Lüning 1986). Critical evaluation of Dieckmann's data for the growth of *L. pallida* and seasonal light intensity data clearly shows that frond initiation occurs just before the increase in irradiance. The trigger for frond elongation therefore appears to be the shorter daylengths experienced during the previous winter. This therefore strongly suggest photoperiodic mediation of frond initiation in *L. pallida*. As the initiation of growth in length of uprights (Figures 16, 17) and branch formation (Figures 18, 19) already occurred during the winter period at some of the sites and by late winter to early spring at both some sites and in the pools, when daylengths are still short and daylengths and light levels are increasing, it strongly suggests that growth and development of *B. brassicaeformis* might, as with *L. pallida*, be photoperiodically controlled. Two fucoids in the northern hemisphere have been shown to exhibit photoperiodism. *Ascophyllum nodosum* (L.) Le Jol. initiates receptacles during the same time of year (September and October) as *B. brassicaeformis*, but in the opposite season (autumn) (Terry and Moss 1980), while *Fucus distichus* L. subsp. *distichus* also becomes fertile in autumn, and during winter in the field. In culture, the above authors have shown that these species formed receptacles in photoperiods of 8:16 and 12:12 hours light:dark. Other smaller brown algae such as *Scytosiphon lomentaria* (Dring and Lüning 1975) and *Petalonia zosterifolia* (Lüning 1980) have also been shown to exhibit photoperiodism and form erect thalli under short day conditions (less than 13 hours of light per day) in culture. In addition, the southern hemisphere bull kelp, *Durvillaea potatorum* (Labillardiere) Aresch. (Durvillaeales) has also been found to display a regular seasonal pattern of conceptacle development similar to that found for *B. brassicaeformis* (see Table 5). Conceptacle development in *D. potatorum* invariably occurs in late summer or autumn (Clayton *et al.* 1987). As the reproductive pattern was found to be consistent with a daylength reqirement of 12 hours or less (Clayton *et al.* 1987), the author suggested that conceptacle development in *D. potatorum* is under photoperiodic control.

Levitt (1987) found that the photosynthetic capacity for *B. brassicaeformis* did not display a definite seasonal pattern, but that the species exhibited a minimum in winter (June 1984, 0.82g C gdw^{-1} h^{-1}) and a maximum in spring (November 1984, 2.05 g C gdw^{-1} h^{-1}). Furthermore, photosynthetic capacity dropped to another low in late summer (February 1985, 0.9 g C gdw^{-1} h^{-1}). Light data

revealed that light was at a minimum in June and a maximum in late spring/ early summer (November/December).
Therefore, maximum growth (reflected by the high densities of uprights from the basal rhizomes) and receptacle development (branch initiation) as found in this study in the spring period (October to December) takes place when light levels (Dieckmann 1980) and photosynthetic capacity (Levitt 1987) of the species are at their maxima. Results of the increase in growth in length of uprights showed that during spring, very little increase occurred at the sites while a significant increase occurred in the pools (Figures 16, 17). As Levitt (1987) collected from the low-shore, results of the sites rather than the pools would therefore yield a good comparison. As there exists a lag-phase between photosynthesis and growth (see Dring 1982), the period of maximum photosynthesis in spring co-inciding with minimal growth in length of uprights suggests that photosynthetic material produced by these uprights during spring would be translated into structural material for the development of branches (later receptacles) in summer. Results of this study supports the above in that peaks (maxima) in the number of branches per upright and in the mean receptacle biomass per upright occurred during early (December) and late (February) summer respectively. The maxima of the upright system and of its components correspond with maximum summer carbon content found for B. brassicaeformis by Levitt (1987).

The low photosynthetic rates of the species during summer could be explained by the fact that the plant has in most cases attained maximum growth and is now reproducing. The tendency for the basal biomass material to increase (see Figures 6, 7) in winter is difficult to explain. However, this may indicate channelling of photosynthates into reserve material of the base for the oncoming winter rather than into growth as suggested for L. hyperborea by Lüning (1981). It is interesting to note that Lüning (1986) found similar senescence of fronds in L. hyperborea during autumn. He attributes this to a photoperiodic effect. Whether photoperiod influences frond senescence in B. brassicaeformis remains to be tested.

Although morphological variations of macroalgae can have a genetic basis (Chapman 1974, de Paula and de Oliviera 1982), characteristics such as stunting, bushiness (branching) and frond thickening are generally regarded as phenotypic responses to the local environment (e.g Russell 1978, Norton et al. 1982). The major physical factors include wave action and desiccation. Results of the present study showed that the different sites show variation in the length of uprights (Figure 16), degree of branching (Figure 18) and in the thickness of vegetative uprights (see Figure 5) which appeared to be related to the microhabitat conditions.

At the Rock and Triangle sites, uprights were longer, had more branches per upright but had thinner vegetative uprights than uprights at the Gulley and Overtop sites which displayed the opposite trends in these parameters Although shorter, less-branched uprights at the Overtop site may have been due to dessication effects as this site occurred vertically higher than the other sites and plants wetted least frequently during spring low tides, variation in growth, development and morphology between the sites is difficult to explain without actual data on the microhabitat conditions, and suggest that this remains to be tested.

Comparison of plant growth and development in the pools seem to indicate that plants grew longer and developed better in pool 3 than in pools 1 and 2 until October of the study period. The better growth in pool 3 compared to pools 1 and 2 certainly occurred because plants in the latter two pools experienced extreme desiccation aggravated by high air temperatures when these pools often dried out during spring tides, while plants in pool 3 only experienced high temperatures of the water with only the tips of the uprights above the water being dessicated during summer. The data also revealed that plants in pool 1 which grew poorly in 1989, grew longer (Figure 17) and showed best development in the summer of 1990 (Figures 19, 21, 23). This may have been due to the harsher conditions of the previous summer which caused extensive damage to the uprights in Pool 1. The "empty" bases therefore could facilitate more vigorous growth the following spring, this being reflected the following summer. The continuing high growth and development of uprights in Pool 2 could thus be due to a similar phenomenon.

Differences in growth and development between sites lower down on the shore and pools vertically higher up on the shore appear to be due to the differences in microenvironmental conditions at these different heights on the shore. Uprights in the pools are stunted and thin with desiccated edges while uprights at the sites are long, thick with edges rarely desiccated. Similar intraspecific variation in growth and morphology has been described for _Ascophyllum_ _nodosum_ at different heights on the shore (Dring 1982). Plants growing towards the upper limits of the intertidal zone were shorter, had smaller air bladders and thinner internodes than those at growing at the lower limits of its zone. Three species of _Fucus_ (_F._ _vesiculosus_, _F._ _vesiculosus_ _var._ _spiralis_ and _F._ _distichus_ _subsp._ _edentatus_) of Maine (USA) also had a similar growth pattern in length as _B._ _brassicaeformis_. Length was inversely proportional to the intertidal height (Keser and Larson 1984).

Indirect evidence for the aggravating effect of temperatures on plants in the pools found higher up the shore is given by Hugget and Griffiths (1986) who found that temperatures of rock pools 2.2m above LWS at Three Anchor Bay (on the Atlantic seaboard of the Cape Peninsula) reached up to 30°C during spring tides in summer. Therefore temperatures in the pools about 2.12m above LWS at Clovelly in False Bay may well reach over 30°C during spring tides in summer, and partially account for the reduced growth of plants in the pools, with desiccation being the primary factor. In contrast to the pools, more frequent wave splash at the sites will help to keep the uprights moist, thereby decreasing the temperature and preventing desiccation as described for other intertidal seaweeds (Burrows _et_ _al._ 1934, Lewis 1964).

The fecundity estimates reveal that Bifurcaria brassicaeformis has about 245 eggs per conceptacle which is very similar to that (250) found by Delf (1935). When comparing the data of the reproductive components with that of the literature (see Table 4), B. brassicaeformis allocates a slightly higher percentage of its biomass into receptacles (66-78%) as another fucoid which has an expanded holdfast, Ascophyllum nodosum from Polly Cove in Nova Scotia (61-66%, Cousens 1981a).
However, the cost of gamete production measured as biomass is very small. Eggs represent only 0.16 - 0.2% of the weight of an upright. These values are similar to that found by Vernet and Harper 1980) for the British fucoids F. spiralis, F. vesiculosus and F. serratus where the cost of gamete production for each species was found to be between 0.1 and 0.4%, and for a South African kelp Ecklonia maxima, in which annual spore production accounted for 0.17% of its biomass turnover (Joska and Bolton 1987).
When comparing the egg volume with other fucoids (see Table 4), the egg volume is three times as large as Pelvetia canaliculata and F. spiralis, four times that of F. serratus and ten and eleven times that of A. nodosum and F. vesiculosus respectively, and 5.5 times smaller than that of Himanthalia lorea (Vernet and Harper 1980). The investment in eggs compared to that in sperm on the basis of diameter is similar (20 times) to that reported for the dioecious F. vesiculosus and F. serratus (20-40 times; Vernet and Harper 1980), while these authors reported

that the investment made for this comparison amounts to 2-7000 times for the monoecious *F. spiralis*.

While large amounts of eggs are produced and fertilization occurred easily in culture when densities of eggs were low (see Chapter 5) newly settled germlings were not found at the study site throughout the study period. This indicates that large scale zygote and /or germling mortality occurs during the summer. Although no germlings were found at the study site, observations of Bokenham and Stephenson (1938) have shown that germlings do establish in *B. brassicaeformis* populations. Physical and biological factors may hamper the establishment of germlings. At the sites, germlings might not be able to establish adjacent to adult plants presumably because of whiplash abrasion, a phenomenon commonly found between adults and juveniles of the intertidal kelp *Egregia laevigata* (Black 1974) and the midtidal fucoid *Pelvetia fastigiata* (Gunnill 1980). At the sites, herbivory (particularly by limpets) might also hamper germling establishment. Herbivory hampering germling establishment has been described for the European fucoids *Fucus vesiculosus* and *F. serratus* (Knight and Park 1950), *Pelvetia canaliculata*, *F. vesiculosus*, *F. spiralis* and *F. serratus* (Schonbeck and Norton 1980). At both the sites and in the pools, germling establishment might be hampered by interspecific competion for space by the adults as found between adults and gametophytes of the kelp *Egregia laevigata* (Black 1974), although shading by adult plants which would lead to low light levels would not be likely to hamper germling establishment as germlings have been found to saturate at low irradiances ($30\mu Em^{-2}s^{-1}$, this study).

As no germlings were found in the field, the maintenance of existing populations of *B. brassicaeformis* at Clovelly would rely just about entirely on the seasonal perennation of uprights from the basal rhizomes, as found for B. *bifurcata* from Ireland (De Valera 1962) and from the expanded holdfast of *Ascophyllum nodosum* from Norway (Baardseth 1955, in De Valera 1962) which also have rhizomatous bases. Other European fucoids without rhizomatous bases such as *Himanthalia elongata* and *Fucus* species rely much more on fertilized eggs for the production of new plants (De Valera 1962). Recolonization of denuded areas within the *Bifurcaria* community most definitely takes place (Bokenham and Stephenson 1938), occurring by spreading growth of the basal rhizomes, and/or establishment of germlings, into these areas, while maintenance of existing populations occurs by perennating growth of uprights from the rhizomes.

It is well known for *B. brassicaeformis* that all receptacles on an upright are only of one sex (Isaacs 1951, this study). Furthermore, from this study it has become clear that all uprights of a 10x10cm clump are only of one sex (either male or female). As 8 clumps per habitat (totalling $0.8m^{-2}$ per habitat) were collected in close proximity to each other over the sampling period, and all "clumps" were of the same sex, it suggests that individuals grow to a very large size (up to and maybe over 1m across).

CHAPTER 5

EFFECT OF TEMPERATURE AND LIGHT ON THE GROWTH OF *BIFURCARIA BRASSICAEFORMIS*

INTRODUCTION

Bifurcaria brassicaeformis has its centre of distribution (the extent of coastline over which its distribution is substantially continuous as an ecologically important species) between Cape Town (western limit) and Cape Agulhas (eastern limit) (Isaac 1951) (Figure 24). This area corresponds with the south coast - west coast transition as described by Stephenson (1948). On the west coast, the species has been reported as far north as Paternoster (Stephenson 1948), but since then it has not been collected north of the Cape Peninsula (Bolton pers. comm.). Although its eastern limit is uncertain, the plant shows luxuriant growth as far east as Brandfontein, 20km west of Cape Agulhas, but does not occur at De Hoop and Stilbaai just 60 and 135km east of Cape Agulhas respectively (Bolton and Stegenga 1990).

It certainly occurs as far east as Cape Agulhas itself (Pocock herbarium, specimens 2675 and 8931). The species has also been recorded 300km further east in Algoa Bay (a single specimen in the British Museum, collected by Dr. Em Holub in Algoa Bay, Cape Colony; received May 1883). This specimen has branch initials, but no mature receptacles, and has much thinner fronds than typical *Bifurcaria brassicaeformis* (Bolton pers. comm.). Barton

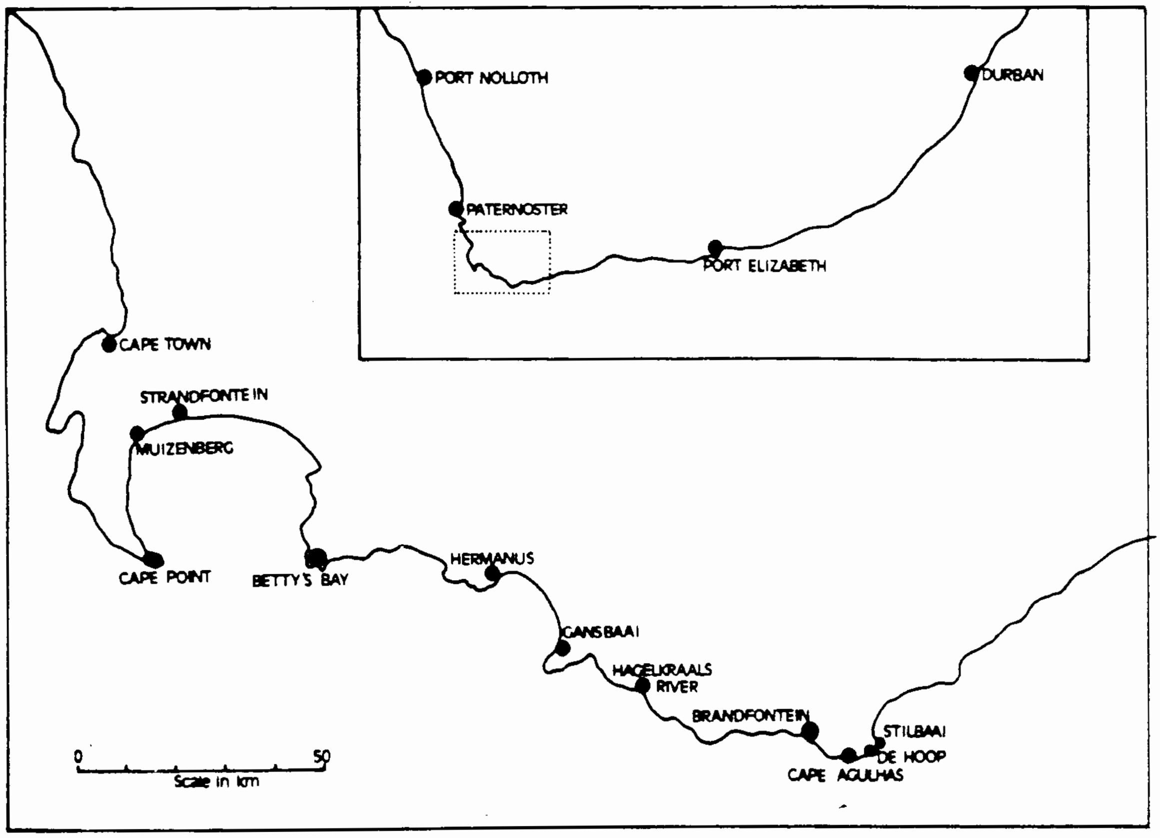

Figure 24. The region from Cape Town to Cape Agulhas. Inset : outline map of South Africa.

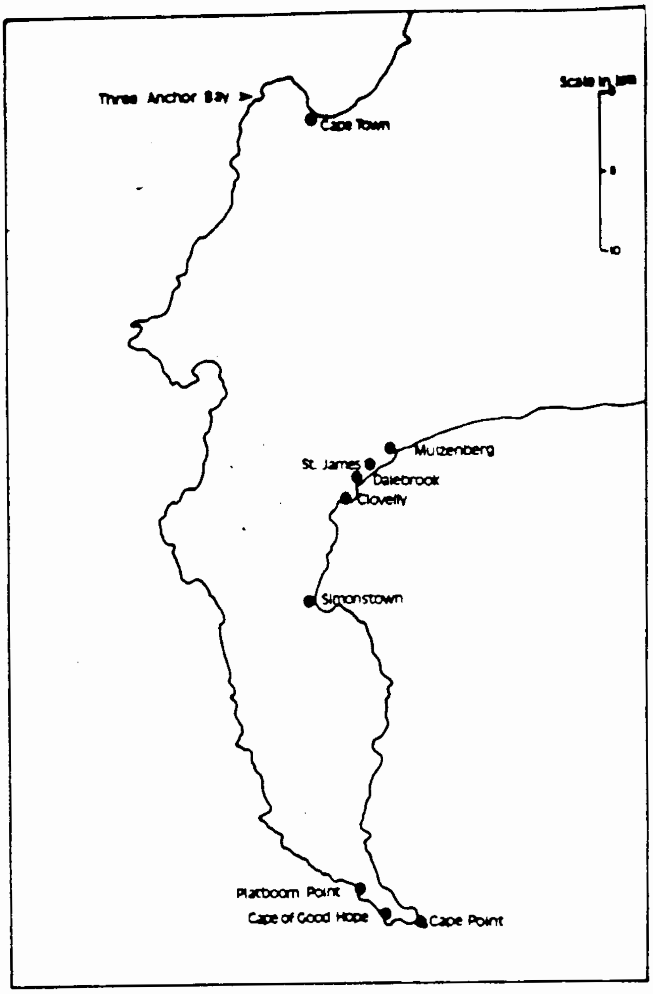

Figure 25. The Cape Peninsula. Locations mentioned in the text are indicated.

(1893) also records the species from Natal, although this seems extremely unlikely, on current information.

Isaac (1951) found that the growth of the species is not equally luxuriant throughout its distribution range, either with regard to the size of the plants, or the density and extent of the communities which it forms. On the whole, growth becomes more luxuriant in a southward direction on both eastern and western coasts of the Cape Peninsula (Figure 25).

Along the eastern coast, Bifurcaria becomes rare north of St. James (Figure 25). On the Cape Peninsula as a whole, the species reaches its peak of development on the south-west coast from Platboom Point to the Cape of Good Hope (Isaac 1951). Similar luxuriant development is seen at Gansbaai and Hagelskraal River at which localities the plant flourishes to a greater extent than at Hermanus (Figure 24).

Isaac (1951) proposed that the sea temperature conditions (see Table 6) along the north-west coast of the Cape Peninsula on the one hand, and at Muizenberg on the other, are less favourable for the growth and reproduction of B. brassicaeformis than those prevailing along the southern end of the Peninsula and at Gansbaai. Isaac (1951) suggested that annual mean temperatures between 12.8°C (Cape Town) and 16.6°C (Muizenberg) would seem most favourable for growth and reproduction of B. brassicaeformis. Although Isaac states that the species does not occur in localities where the annual mean sea water temperature exceeds 17.7°C, the

Table 6. Mean sea temperatures (°C) at sites from Port Nolloth on the west coast to Still Bay, east of Cape Agulhas. Means are for the period 1973-1982, data from South African Maritime Weather Office.

	Mean coldest month (winter)	Annual mean	Mean warmest month (summer)
Port Nolloth	11.5	12.1	13
Lamberts Bay	12.2	12.9	14
Cape Town Pier	12.3	12.8*	13.9*
Sea Point	12.4	13.1	14.5
Muizenberg	13	16.6*	19.6*
Hermanus	14.4	15.6	17.1
Gansbaai	14.1	15.3	17
Cape Agulhas	no data	17.7*	20.9*
Stillbaai	13.8	17.4	21.2

* from Isaac (1951)

Algoa record perhaps refutes this. However, it is possible that there may be localised areas of regular upwelling in this region, which cannot be verified without knowledge of the exact collection site of the specimen.

More recent inshore sea water temperature records of localities around the South African coast have been published by Bolton (1986). Isaac (1951) hypothesised that B. brassicaeformis, in relation to the temperatures of South African coastal waters, is not typical either of the "cold" waters of the west coast or the "warm" waters east of Cape Agulhas, but waters of intermediate temperatures with annual means of 12.8 to 16°C). The available information concerning the distribution of B. brassicaeformis thus suggests that on the whole, it may be a relatively stenothermal species, in comparison with other species with wider ranges on the west and/ or south coasts.

Although the study of Jensen (1974) has improved our taxonomic understanding of the taxonomic and morphological relationships in the genus Bifurcaria, very little has been reported on the controlling effects of temperature on the growth of the adult and/ or germling phases. For B bifurcata, Borel (1954, in De Valera 1962) reported a co-incidence of the northernmost distribution of the species with the 8°C isotherm, while De Valera (1962) only carried out tentative temperature experiments to test germination and germling growth in order to establish the lower temperature limit for growth of germlings of B. bifurcata.

In many studies, both correlative and experimental, temperature has been shown to be a major factor regulating the distribution of seaweed species (see e.g. Isaac 1938, Bolton 1986, Bolton and Stegenga 1987, Breeman 1988, Anderson and Bolton 1989).

There are no experimental data to correlate temperature tolerance with geographic distribution of the species.

The aim of the present study of *B. brassicaeformis* was to investigate temperatures controlling growth, and to relate experimental findings to the distribution of the species on the South African coast. By virtue of this, it can be established if temperature could be a factor limiting the seasonal growth and geographic distribution of the species, and also establish whether Isaac's hypothesis that *B. brassicaeformis* is a stenothermal species is valid. In addition, the results of the present study will be used to compare the limits for growth of *B. brassicaeformis* with the temperature regimes over the distribution range of the other two species in the genus.

Although little is known about the relationship between irradiance and apical growth of adult Fucales, much more literature exists on this relationship for the growth of fucoid germlings (see " General Introduction"). This has not yet been investigated in any South African fucoid. Schonbeck and Norton (1978) found that light tolerances for growth of adult and germling thalli of British fucoids correlated well with the position of the plants on the shore. Furthermore, Moss *et al.*

(1973) have found that siltation which blocks out light needed for zygote germination prevents initial establishment, growth and colonization of new areas by germlings.

The aim of investigating the light tolerances of B. brassicaeformis adult thalli and germlings are thus twofold for both phases:

(1) to establish the light saturation point for growth and establish whether these correlate with the species position on the shore, in comparison with literature on other fucoids.

(2) to discuss how the local distribution and seasonal growth of each phase might be affected by irradiance.

MATERIALS AND METHODS

1. General methods

All experimental plants were collected from shores on the Cape Peninsula between April 1989 and February 1990.

Material was incubated in each of two replicate 200ml crystallizing dishes containing the experimental medium. For cut apices of the adult thallus, the culture medium used was 1/3 strength Provasoli ES (PES) (Provasoli 1968), while the germlings were cultured in sterile seawater. To inhibit diatom contamination, germanium doixide (0.1ml of an aqueous solution per litre, which is slightly higher than that recommended for cultures of Phaeophyceae (Markham and Hagmeier 1982), but recommended when pieces of tissue are used) was added to the culture medium.

Experimental media for cut apices were renewed weekly, while media for germlings were renewed every four days, for the duration of each experiment. For both cut apices and germling experiments, dishes were incubated under a long day regime of L:D=16:8, with light provided using cool white flourescent tubes. For each experiment, specific growth rate (SGR) was measured as (u) doublings per day by the following formula (Friedlander and Dawes 1984).

$$u = 1/t * \log L2/L1 * 3.32$$

where t is the number of days between initial and final lengths (L1,L2). Each growth experiment continued for 28 days.

1. Collection and preparation of material

2.1 Cut apical thalli

Samples for thallus growth experiments in the laboratory were collected from Clovelly (34° 08'S, 18° 26.4'E) between 5 April and 20 July 1989.

Samples were transported back to the laboratory in black plastic bags. 5mm apical segments (10 per treatment) for the temperature and light experiments were excised from the vegetative uprights. At least four separate collections of rhizomes with uprights were used in each experiment.
Excised segments were kept overnight in sterile seawater at 15°C. The following morning, segments were washed again in sterile seawater before transference to the experimental dishes. For both temperature and light experiments, 5 apical segments were placed in each of 2 crystallizing dishes containing the experimental medium.

2.2 Germlings

Thalli bearing fertile receptacles were collected from Cape Point Nature Reserve (34°20.2'S, 18°26.8'E) on 14 November 1989 for the temperature tolerance investigation and on 29 February 1990 for the light tolerance investigation.
Material was transported back to the laboratory in a cooler bag. Germlings were prepared as for Halidrys siliquosa (Moss and

Sheader 1973) but with slight modifications. The material was Thalli were segregated by sex after sectioning. The segregated material was placed in plastic bags and kept overnight at 10'C.

The following morning, male and female receptacles were cut off and washed in sterile seawater to remove as many epiphytes as possible and also any eggs which had been extruded from the female conceptacles. Eggs which had been liberated when the thalli were out of the water always suffered physical damage and were useless for experimental purposes. Four receptacles of each sex were then placed in each of two crystallizing dishes containing sterile seawater. Each dish contained a glass slide onto which eggs could settle. The dishes were then placed in the 15°C controlled temperature room. By the following morning, a heavy crop of eggs was visible around each female receptacle. After giving female receptacles a gentle shake, eggs which had been shaken into solution settled onto the glass slide. Shaking the receptacles also ensured that settled eggs were well dispersed on the glass slide so that egg densities on the glass slide were low. Preliminary experiments indicated that lower egg densities facilitated fertilization while high densities did not. Female receptacles were then removed to ensure that there would not be more than 20 hours between the age of the first and the last eggs which were shed. Male receptacles which by now had not shown any signs of sperm extrusion, were left in the dishes.

The following morning, sperm was extruded from the male conceptacles. After four hours following the first visible signs of sperm extrusion, male receptacles were removed from the dishes. After allowing another four hours for fertilization to take place, the sterile seawater was drained from the dishes and new medium added.

To be assured of germination, cultures were left for four days as the first visible signs of germination is the protruberance of 2-4 primary rhizoids.

Two crystallizing dishes, each containing healthy five day old germlings growing on glass slides were placed into the varying temperatures and under the varying light regimes.

As the basal rhizoids lengthen, the germling grows out in the opposite direction to form the young thallus. In both temperature and light experiments, growth of the germlings was estimated by measuring the increase in length of both the thallus and rhizoids by using an eyepiece micrometer. Initial mean lengths of both thallus and rhizoids was assesessed (n=20) and final lengths were to be assessed after 28 days. In both temperature and light experiments, the mean SGR was calcualted.

3. Temperature:- tolerance and growth

For both excised apices of the adult thallus and for germlings, dishes were incubated in controlled temperature rooms at 10°, 15°, and 20°C. Additionally, the germling experiment included 25°C. Other temperatures were obtained using water baths in which the dishes were immersed to the level of the medium. A temperature range of 5 to 30°C and 2.5 to 30°C for excised adult apices and germlings respectively (in 2.5°C intervals excluding 7.5 and 27.5 - each + 1°C) was thus achieved. Dishes were incubated at an irradiance of 40$\mu Em^{-2}s^{-1}$ (± 5$\mu Em^{-2}s^{-1}$).

4. Light:- tolerance and growth

For excised apical thalli, the following light intensities were used: 0, 10, 50, 100, 150, 200, 250, 500, 750 and 1000$\mu Em^{-2}s^{-1}$. For the germlings, experimental irradiances of 0 - 80$\mu Em^{-2}s^{-1}$ (in 10$\mu Em^{-2}s^{-1}$ intervals) and 100 and 120$\mu Em^{-2}s^{-1}$ (each ± 5$\mu Em^{-2}s^{-1}$) were used. For the germlings lower irradiances were used as it is well known from the literature (Lüning 1981) that germlings of fucoids saturate at much lower irradiances than adult thalli.
Light intensities (10-250$\mu Em^{-2}s^{-1}$) were obtained using 65W cool white Crompton flourescent lamps arranged in banks. The higher light intensities were obtained by supplementing this flourescent light with a 500W Ushio Halogen lamp. Temperatures ranged from 15-16°C and 19-20°C for the adult thallus and germling experiments respectively as these temperatures proved best for growth and development during preliminary experiments. Desktop fans kept the temperature constant at 100 and 250$\mu Em^{-2}s^{-1}$.
At 500 - 1000$\mu Em^{-2}s^{-1}$, temperature was kept constant by placing the dishes in a waterbath maintained at 15°C by a water circulating cooling unit; in addition, a transparent water tray circulating water was placed between the Halogen lamps and the water bath to obtain the

correct temperature in the dishes.

The range of irradiances from 10 - 1000μEm^{-2} s^{-1} was achieved by positioning the dishes at various distances from the light banks (light was measured in quanta using a LICOR LI-188 intergrating quantum meter). 0μEm^{-2} s^{-1} was obtained by placing the dishes in a light-proof box. To test whether thalli and germlings would survive over an extended period of complete darkness and subsequently grow when placed under higher light, apices and germlings cultured at 0μEm^{-2} s^{-1} for the 28 day period were subsequently transferred to 50 and 100μEm^{-2} s^{-1}, and 30μEm^{-2} s^{-1} respectively, and further development observed.

5. Statistics

The results are graphically represented as the means of the various treatments. 95% confidence limits are indicated. One-way ANOVA's were performed on the data for each experiment to ascertain whether the differences between the treatments were significant ($p<0.05$).

RESULTS

1. Temperature:- tolerance and growth

1.1. Apices

Figure 26 shows the specific growth rates (SGR) of cut apices of the adult thallus at the nine different temperatures. Growth was poor between 5 - 12.5°C and 20 - 22.5°C. A rapid increase in growth occurred from 12.5 to a maximum at 15°C, declining rapidly to 20°C and even further to 22.5°C with death occurring at 25° and 30°C. Optimal growth rate occurred in the range 15 - 17.5°C (0.044 and 0.035 doublings per day respectively; equivalent to an increase of 6.82(±0.54) and 5.55(±0.41)mm over 28 days respectively), with no significant difference in growth rate at these temperatures. No lower temperature tolerance limit was found. The ANOVA of the S.G.R. of the apices at the various temperatures was significantly different (F= 51.53, $p<0.05$).

1.2 Germlings

Figure 27 shows the SGR of the thallus and rhizoids of the germling at the different temperature conditions. The thallus grew well between 15 and 20°C, less well at 12.5 and 22.5°C and poorly at 2.5 and 10°C. The rhizoids grew well between 12.5 and 22.5°C, less well at 10°C and poorly at 2.5 and 5°C. Both thalli and rhizoids died at 25° and 30°C although germlings still survived at 25°C after 21 days. No lower temperature tolerance limit was found for the growth of germlings. The ANOVA of the

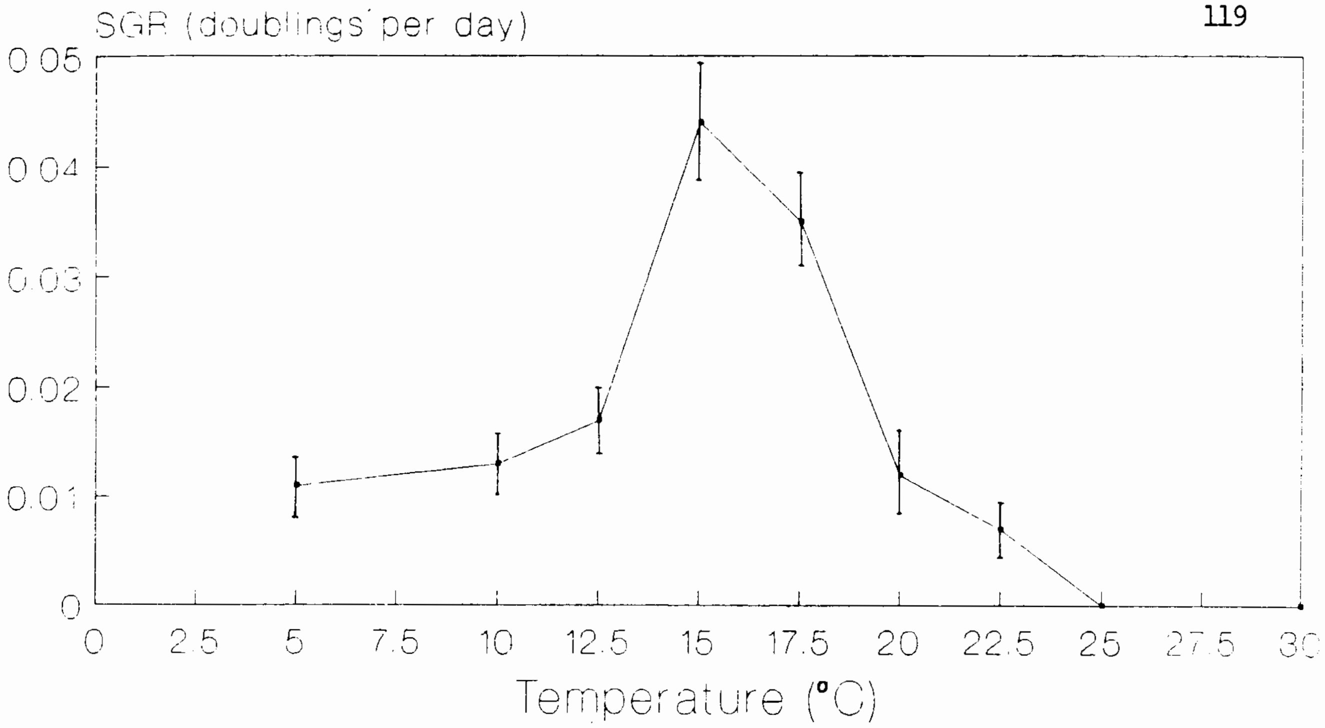

Figure 26. Effect of temperature on the specific growth rate of cut apices of the adult thallus of <u>Bifurcaria brassicaeformis</u> after 28 days growth. Bars indicate 95% confidence limits.

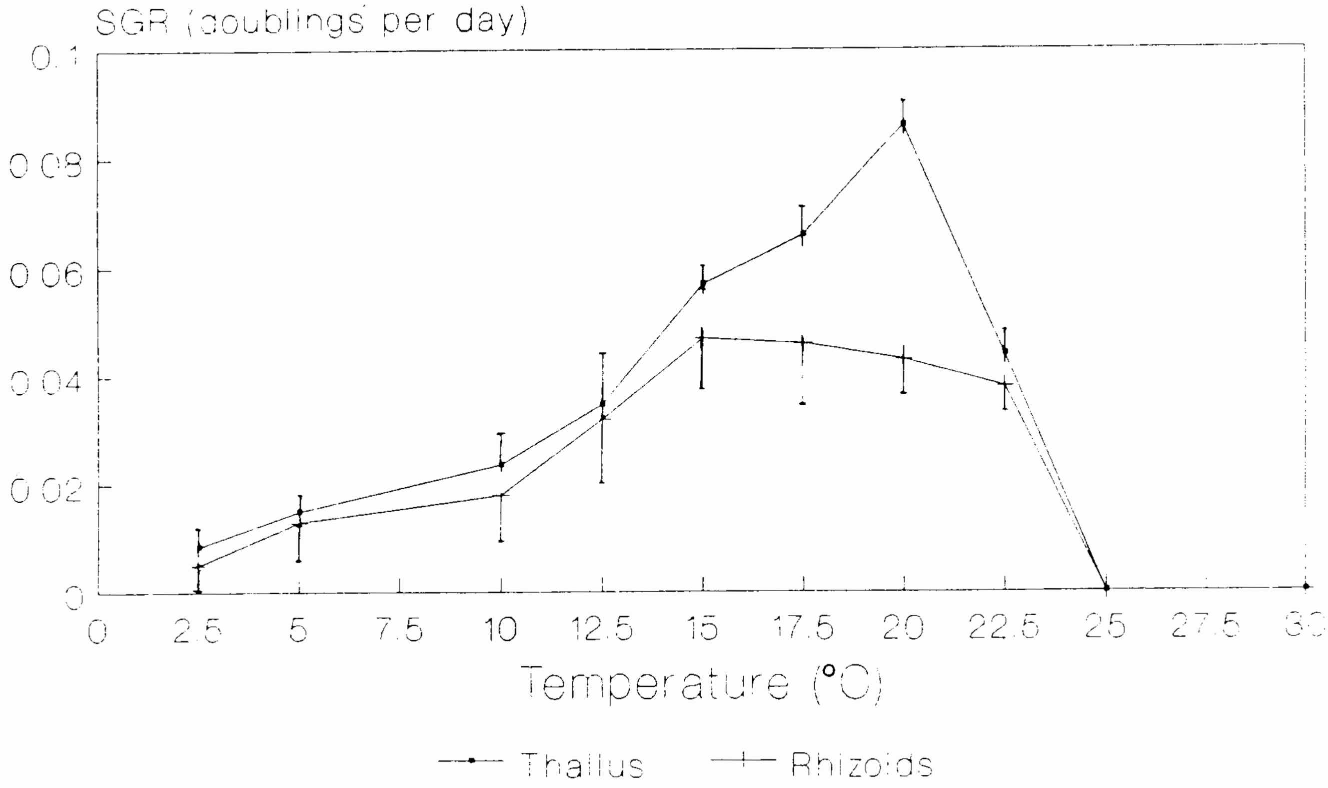

Figure 27. Effect of temperature on the specific growth rate of thalli and rhizoids of <u>Bifurcaria brassicaeformis</u> germlings after 28 days growth. Bars indicate 95% confidence limits.

S.G.R. of germling thalli at the various temperatures was highly significant (F= 371.22, $p<0.05$).

The thallus of the germling had a narrower optimum range than the rhizoids. For the germling thallus, optimal growth occurred in the range 17.7°-20°C (0.066 and 0.086 doublings per day; this being equivalent to an increase of 395(±16.58) and 619(±18.06)µm over 28 days respectively), with significantly higher growth at 20°C ($p<0.05$). Optimal growth of rhizoids occurred in the range 15°-22.5°C where growth did not differ significantly ($p>0.05$). Best growth occurred at 15°C (0.046 doublings per day; this being equivalent to an increase of 255.6(±32.02)µm over 28 days).

The ANOVA of the S.G.R. of germling rhizoids at the various temperatures was significantly different (F= 26.29, $p<0.05$).

2. Light:- tolerance and growth

2.1 Apices

Figure 28 shows the SGR of cut apices of the adult thallus at the ten light intensities investigated. Growth increased almost linearly from 0 - 100$\mu Em^{-2}s^{-1}$, declined rapidly from 100 - 150$\mu Em^{-2}s^{-1}$ whereafter growth gradually declined from 150 -750$\mu Em^{-2}s^{-1}$, with death at 1000$\mu Em^{-2}s^{-1}$. Optimal growth occurred in the range 50-200$\mu Em^{-2}s^{-1}$. Growth was significantly higher at 100$\mu Em^{-2}s^{-1}$ (0.072 doublings per day; eqivalent to an increase of 14.72(±4.91)mm in 28 days). Poor growth occurred at 10, 500, and 750$\mu Em^{-2}s^{-1}$, with significantly better growth at 500$\mu Em^{-2}s^{-1}$ and no significant difference in growth between 10 and 750$\mu Em^{-2}s^{-1}$. Six out of ten

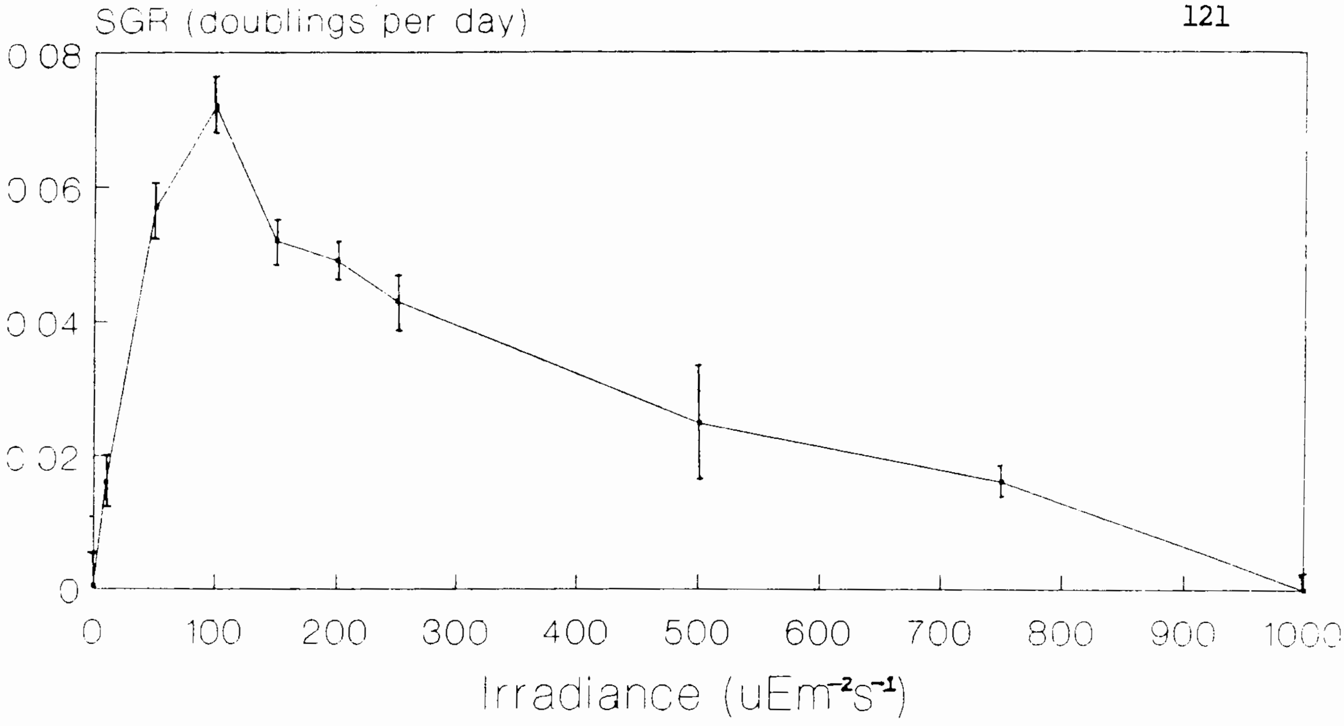

Figure 28. Effect of light intensity on the specific growth rate of cut apices of the adult thallus of <u>Bifurcaria brassicaeformis</u> after 28 days growth. Bars indicate 95% confidence limits.

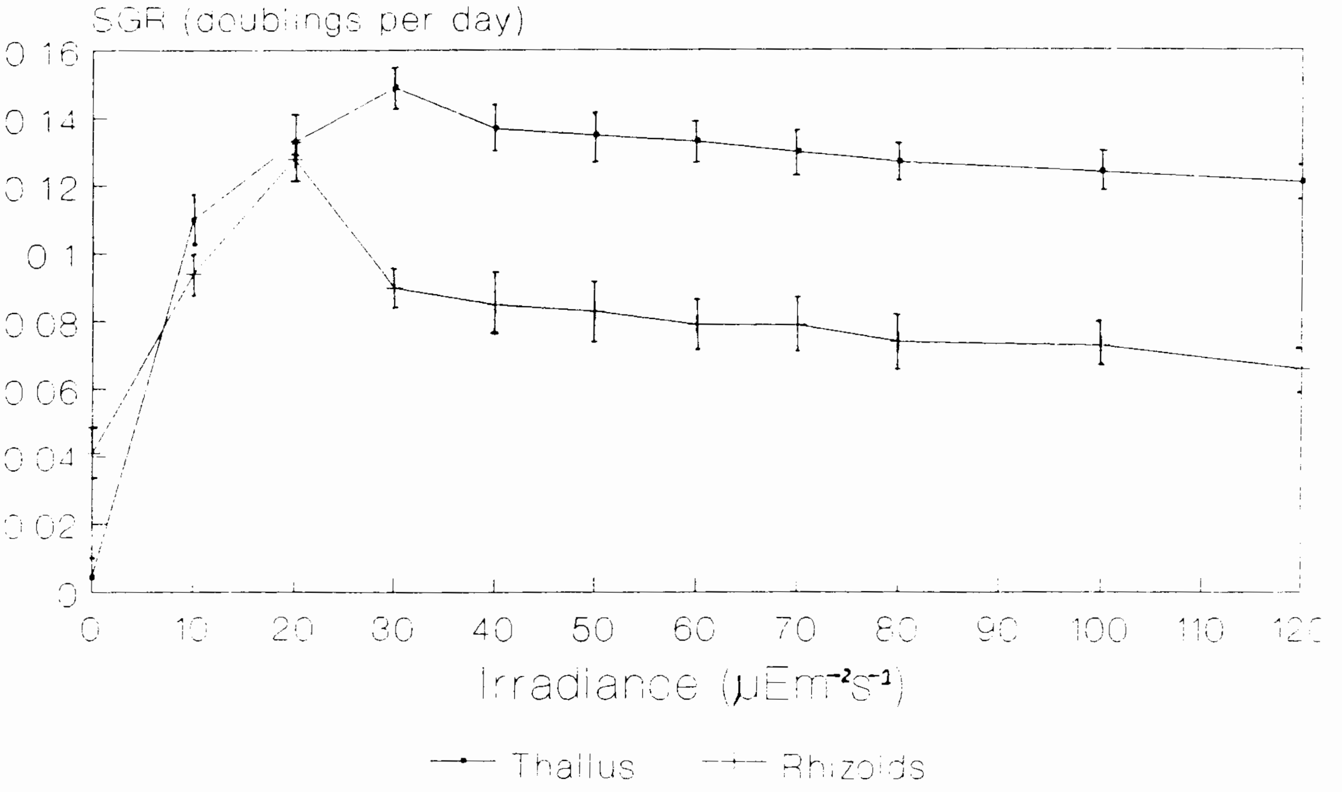

Figure 29. Effect of light intensity on the specific growth rate of thalli and rhizoids of <u>Bifurcaria brassicaeformis</u> germlings after 28 days. Bars indicate 95% confidence limits.

apices survived at 0μEm^{-2}s^{-1} after 28 days and grew normally again when three each was placed at 50 and 100μEm^{-2}s^{-1}. Bud initiation was observed on apices grown at between 50 and 150μEm^{-2}s^{-1} during the 28 day period. The ANOVA of the S.G.R. of apices at the different irradiances was highly significant (F= 210.36, $p<0.05$).

2.2 Germlings

Figure 29 shows the SGR of the thallus and rhizoids of the germling under different irradiances. Growth of the thallus was lower than rhizoids in complete darkness (0μEm^{-2}s^{-1}), similar under the lower irradiances (10-20μEm^{-2}s^{-1}) and higher between 30 - 120μEm^{-2}s^{-1}. The germling thallus and rhizoids grew well over most of the experimental irradiances (10 - 120μEm^{-2}s^{-1}) and poorly at 0μEm^{-2}s^{-1}. Light saturation for growth of the germling thallus occurred at 30μEm^{-2}s^{-1} while rhizoids saturated at 20μEm^{-2}s^{-1} (0.149 and 0.128 doublings per day; eqivalent to increases of 1005.15(±128.9μm) and 875.08(±49.19μm), for the thallus and rhizoids over 28 days respectively).

For the germling thallus, a rapid increase in growth rate occurred bewteen 0 and 10μEm^{-2}s^{-1}, whereafter growth gradually increased to a maximum at 30μEm^{-2}s^{-1} and declined gradually again from 40 - 120μEm^{-2}s^{-1}. The ANOVA for the S.G.R. of the germling thallus at the various irradiances was highly significant (F= 684.46, $p<0.05$). Above 30μEm^{-2}s^{-1} the germling thallus became dichotomously branched, but not at 20μEm^{-2}s^{-1} and below. Germlings transferred from 0μEm^{-2}s^{-1} to 30 and 40μEm^{-2}s^{-1} resumed growth immediately, and developed normally.

The rhizoids showed a linear increase from 0 - 20μEm^{-2} s^{-1} , declined rapidly from 20 - 30μEm^{-2} s^{-1} ,and displayed a gradual decline in growth rate from 30 - 120μEm^{-2} s^{-1} . The ANOVA for the S.G.R. of the rhizoids at the various irradiances was significantly different (F= 30.7, $p<0.05$).

DISCUSSION

1. Temperature

The distribution of B. brassicaeformis lies between Cape Town and Cape Agulhas which corresponds to the narrow overlap region between the south and west coast marine provinces from Cape Agulhas to Kommetjie on the west coast of the Cape Peninsula. Other South African seaweeds for which temperature tolerance data is available have much wider distributional ranges. Typically west coast seaweeds such as Desmarestia firma (C. Ag.) Skottsb. (see Anderson and Bolton 1989), Ecklonia maxima (Osbeck.) Papenf. (see Bolton and Anderson 1987a), and its epiphyte host Suhria vittata (L.) J. Ag. (see Anderson and Bolton 1985) all have their eastern limit of distribution at Cape Agulhas, and their western limits in Namibia at Lüderitz, Swakopmund and Möwe Bay respectively. The South coast seaweeds include a plumose species of Bryopsis (extending from False Bay to East London on the south coast, Manuel unpubl. 1988), Gelidium pristoides (Turn.) Kütz. (extending from Kommetjie on the western seaboard of the Cape Peninsula to Port Edward, just south of Durban, Day 1969), E. biruncinata (Bory) Papenf. (from De Hoop on the south coast to Port Edward, Bolton and Anderson 1987a), and Gracilaria verrucosa (Huds.) Papenf. (from Port Elizabeth to Lüderitz, Engeldow unpubl. 1989). The narrower distribution of B. brassicaeformis has therefore raised the question if this species is more stenothermal than the other seaweeds.

To answer this question, effective comparisons of the curves for the growth of these seaweeds to that of B. brassicaeformis must be made.

Cambridge et al. (1984) defined the lower and upper limits for growth of seaweed species as the 5°C interval in which the relative growth rate (RGR) falls below 20% of the maximum for growth. When calculations were performed on the data for the adult thallus, the range equalled 17.5°C. This was found to be a wider range than that of example, D. firma (14°C) and E. maxima (16°C, Bolton and Anderson 1987b) which have much broader distributions. However, comparing the curves for growth of the adult thallus of B. brassicaeformis to those of female gametophytes of D. firma and E. maxima revealed that the curve of B. brassicaeformis was much narrower towards the optimum 15-17.5°C) and flattened out at the suboptimum (12.5°C) and supraoptimum (20°C) temperatures. Therefore, 40% of the maximum was taken as the basis for a more reliable comparison. For B. brassicaeformis the range at 40% was only 5°C for the adult thallus and 10°C for the germling. The range for the adult thallus is therefore narrower than that of female gametophytes of west coast seaweeds (9°C for D. firma; 12°C for E. maxima, Bolton and Anderson 1987b) and south coast seaweeds (16°C for the female gametophyte of E. biruncinata, Bolton and Anderson 1987b; 15°C for the adult thallus of G. verrucosa; and 19°C for the gametophyte thallus of plumose species of Bryopsis.

The germlings of B. brassicaeformis which have the same ploidy as the adult thallus, had a wider range at 40% of the maximum for growth (10°C) than the adult thallus. Although estimates of the thermal tolerance with respect to distribution would depend more on that of the adult thallus, as it seems the more sensitive phase, comparisons of growth at 40% of the maximum of the juvenile phase with that of other species is relevant.

The range for the germling is much narrower than that of small hybrid sporophytes of E. maxima (25°C at 40% of maximum, Bolton and Anderson 1987b) and similar to those of carpo- and bisporelings of S. vittata (9 and 8°C at 40% of max. respectively). Comparisons to juveniles of south coast species also revealed a narrower range for germlings of B. brassicaeformis than for the sporophyte of the plumose Bryopsis species (15°C at 40% of max.), bi- and carposporelings of Gelidium pristoides (13°C for both, Carter 1986) and much narrower than for the small sporophytes of E. biruncinata (23°C, Bolton and Anderson 1987b) Therefore, from the above comparisons, especially those of the adult thallus of B. brassicaeformis, it appears that on the whole, B. brassicaeformis is relatively stenothermal when compared with South African species with wider distributional ranges on the west and/ or south coasts, validating the suggestion of Isaac (1951).

Before any discussion on the limiting effect of sea temperatures on the distribution of B. brassicaeformis is attempted, it must be remembered that the species displays strong seasonal patterns in growth and receptacle (reproductive) development (see Chapter

4). Therefore, limits to its distribution might be set by seasonal sea temperatures which do not ensure optimal vegetative growth of the adult thallus in order to facilitate later reproduction. In this way no new stations could be established in order to extend its distribution. Temperatures during the warmest or coldest months may also restrict the growth of the adult thallus or germlings so that no further development at a locality could take place.

The data for the adult thallus revealed that at the lower limits, growth was poor at 12.5°C and less. However, the germling still showed good growth at 12.5°C but grew poorly at 10°C. Mean winter temperatures at the reported western limit Paternoster (near Lamberts Bay) are 12.2°C, and 12.3°C at its definite limit (Cape Town). Seasonal mean monthly temperatures (Table 7) indicates that temperatures are still cold during spring, only rising to 13.9 in October at Sea Point. Here the population has been observed to develop poorly.

On the west coast, the first spring upwelling invariably occurs in August and September, causing a drop in water temperature from a winter mean of 14°C to 10-11°C by November (Shannon 1985). Furthermore, these monthly means obscure short-term fluctuations. Upwelling often causes temperature drops of 4-5°C within 12 hours, and daily mean temperatures of 9°C may persist for a week or longer. Therefore, although germlings could grow at the western limit of the species, the poor growth of the adult thallus at 12.5°C and optimum growth at 15°C strongly suggest

Table 7. Mean monthly temperatures (°C) from mid-winter to mid-summer at localities at the cold and warm end of the distribution of *Bifurcaria brassicaeformis*.

	J	A	S	O	N	D	J	F
COLD END								
LAMBERTS BAY	12.2	12.3	12.4	12.7	12.9	13.4	13	14
SEA POINT	12.4	12.7	13.3	13.9	13.8	14.3	14.5	13.9
HERMANUS	14.5	14.4	14.6	15.5	16.4	16.6	17.1	15.7
WARM END								
MUIZENBERG	13.1	13.4	14.6	16.1	18.1	19.5	19.7	19.2
HERMANUS	14.5	14.4	14.6	15.5	16.4	16.6	17.1	15.7
GANSBAAI	14.3	14.1	14.7	15.4	16	16.2	17	15.4
STILBAAI	13.8	13.7	14.8	16.5	18.5	20.2	21.2	20.9
PORT ELIZABETH	15.8	15.6	16.5	17.6	19.5	20.8	21.0	20.9

Data from Bolton (1986).

that the western limit of the species might be set by spring temperatures being too low to ensure optimal vegetative growth necessary to facilitate later reproduction of the adult thallus. The absence of B. brassicaeformis from Lambert's Bay might therefore be a result of the spring upwelling regime, although there is no direct evidence to support this suggestion.

The temperature tolerance data revealed that at the upper limit, the adult thallus grew poorly at 20°C, very poorly at 22.5°C and died at 25°C. The germlings however, still showed good growth at 22.5°C and also died at 25°C. Isaac (1951) reported that the eastern limit of the species lies at Cape Agulhas. At Cape Agulhas, the mean temperature for the warmest month is 20.9°C which is close to the upper limit for growth of the adult thallus, as well as slightly higher than 20°C at which the thallus grew poorly. However, this was close to the optimal temperature for germling growth. It appears therefore that the eastern boundary for the species may be a result of high summer temperatures restricting the growth and possibly reproduction of the adult thallus.

Although no temperature data is available for Brandfontein, 20 km west of Cape Agulhas, luxuriant growth of the plant has been observed there. Furthermore, Bolton and Stegenga (1990) carried out detailed collections at De Hoop, 60 km east of Cape Agulhas, but failed to find B. brassicaeformis. Therefore, the sharp discontinuity in the distribution of the species probably does occur at Cape Agulhas as suggested by Isaac (1951), which is the boundary for dominant west coast species such as Desmarestia firma, Ecklonia maxima, Suhria vittata and many others (Bolton 1986).

The mean temperature for the warmest month at Still Bay just east of Cape Agulhas, is 21.2°C, which is 4°C higher than at Hermanus. These are 10 year means so that at times temperatures here probably exceed the lethal limit for the growth of the adult thallus (between 22 and 26°C). Mean winter temperatures at Still Bay are low (13.8°C in the coldest month) and close to optimal for vegetative growth of the adult thallus.
The record for the species in Algoa Bay where temperatures for the warmest month are just as high as at Stilbaai (Table 7) suggests that the plant may have been collected in a locality where the temperature of the water was slightly lower, perhaps a site of localised upwelling.

Table 7 shows that the mean monthly temperatures seasonally at most of the localities within the species' natural range (e.g. spring and summer temperatures at Hermanus and Gansbaai) are favourable for maximum vegetative growth during spring, and good growth and development of germlings during summer. The temperature (Table 7) and growth data at similar temperatures (see Figure 26) of the adult thallus thus concurs with the observations of Isaac (1951) of luxuriant growth at these localities. The supraoptimal temperatures for growth of the adult thallus at Muizenberg during summer (19.7°C in the warmest month) would concur with propositions of Isaac (1951) that sea temperature conditions are less favourable for growth and reproduction at Muizenberg than at Gansbaai (17°C in warmest month).

Another site within the natural range of the species lies at Betty's Bay (see Figure 24). Field observations here have revealed that B. brassicaeformis shows good seasonal growth at this locality. Temperature data presented by Anderson and Bolton (1989) as well as hydrographic (upwelling) conditions (Boyd et al. 1985) at Betty's Bay might provide some explanation as to why the species grows well there. Hydrographic conditions differ from those of the west coast in two important aspects. First, the orientation of the coast at the former site means that summer south-easterly winds blows on-shore, often bringing warm oceanic water to the coast. Secondly, in the winter, there is no mass of cold water in-shore in this region (Boyd et al. 1985) to be brought to the surface by the localised upwelling induced by the North-West winds. Therefore, water brought to the surface in this region is not as cold as that upwelled along the Cape west coast in summer (mean of 10-11°C). In fact it seldom falls below 12°C. Therefore, while spring temperatures at Betty's Bay (August means are 14-15°C) are favourable for optimum growth of the adult thallus to facilitate later reproduction, summer warming probably does raise the temperature of the water by 2-4°C (January means are 17-18°C), so that temperatures are close to optimum for germling growth.

1.1 Worldwide distribution of the species of Bifurcaria

With data now available on the temperature tolerances of both the adult thallus and germlings of B. brassicaeformis in culture, it is possible to compare them with the temperature regimes over the distribution range of the other two species.

Earlier reports (e.g. Borel 1954, in De Valera 1962) have pointed to a co-incidence between the 8°C isotherm and the geographical limit of B. bifurcata in northern Europe. De Valera (1962) also reports on new stations of B. bifurcata in Ireland, at localities from which it was previously absent. He attributes this to germling establishment events. Experiments caried out by this same author on the effect of temperature on germination showed that cold temperatures between 4-6°C inhibited growth of germlings. He concluded that germling development could be hampered by temperatures being too low for the growth of the early stages of the germling. De Valera (1962) further reports that "in Ireland, clean vigorous receptacles are exceedingly abundant during the darker, cold winter months of the year".

Therefore, although data for the adult thallus of B. bifurcata is unavailable, it appears that the northern limit for the distribution of B. bifurcata may be set by too low winter temperatures for the development of germlings.

Taking into account that the distribution of B. brassicaeformis on the west coast might be limited by temperatures being too low to ensure optimal growth to facilitate later reproduction, the ability of B. bifurcata to reproduce during winter suggests that B. brassicaeformis is less tolerant of lower temperatures than B.

bifurcata.

The southern limit of the distribution of B. bifurcata at Morocco lies just above the 22°C summer (August) isotherm. Temperatures at the warmer southern limit of B. bifurcata are similar to temperatures in the warmest month at Still Bay (21.2°C) just east of the Cape Agulhas (the warm eastern limit of B. brassicaeformis).
Therefore, from the comparison of the temperatures at the distribution limits of the two species, it appears that B. bifurcata and B. brassicaeformis have similar upper temperature limits for distribution.

On the Galapagos Islands, B galapagensis is typically found growing in a conspicuous margin in the surf zone delimiting the intertidal from the subtidal (Robinson 1985). Its position on the shore is therefore similar to that typically found for the South African B. brassicaeformis.
As the Galapagos Islands lie roughly on the equator (between 1°S and 1°N), little seasonal variation in the temperatures of the surface waters occurs (Hayes 1985), and Hayes (1985) reports that the mean inshore sea-surface temperatures are generally around 20°C throughout the year. B. galapagensis has been collected from areas on the southern coasts of the Isla Santa Cruz as well as from the western coast of the Isla Santa Maria (see Jensen 1974). Houvanaghel (1978) reports that relatively cold waters are restricted to the western regions of the islands,

lowering temperatures to 17-19°C annually due to the influence of the upwelling Cromwell Current especially during summer. Therefore, comparing these temperatures to those at the warm end of the distribution of B. brassicaeformis (mean for warmest month at Cape Agulhas is 20.9°C) and to the temperature tolerance data of the adult thallus (grows optimally at 17.5°C) and germlings (optimal at 20°C), the comparison indicates that B. brassicaeformis could well be able to grow in localities on the Islands where upwelling is experienced and become reproductive there.

It is of interest to note that the genus Bifurcaria is temperate. The occurrence of B. galapagensis on the Galapagos Island in the tropical Pacific therefore at first seems strange. However, its occurrence in waters 17-19°C alludes to its temperate affinity. Circumstantial evidence to support its temperate affinity are reports by Robinson (1985) of many sessile invertebrates (tunicates, sponges, corals and sea pens) "which are strongly reminiscent of temperate forms occurring on the western parts of the Islands". It is of importance to note that B. galapagensis has not been encountered on the Islands (E.J. Moll pers. comm.) since the El-Nino event which occurred from 1982-1983 (Hayes 1985). No upwelling events occurred and temperatures 5°C higher than normal were experienced over this period (Robinson 1985). Surface sea water temperatures recorded were generally around 27°C, and rose to as high as 30.4°C in April 1982 (Kogelschatz et al. 1985). Robinson (1985) also reports that B.

galapagensis was only observed once during the event. During this sighting, the haptera was observed to be thinning and the species was eventually completely absent by the end of March 1983.

2. Light

The pattern of growth of apices (Figure 28) in different irradiances is similar to that found by Strömgren (1977) for apices of five intertidal fucoids from Norway. Growth increases up to the saturation point, whereafter growth gradually declines with increasing irradiances. It has been shown (Strömgren 1977, Schonbeck and Norton 1978) that the light saturation for growth correlated well with the vertical position of fucoids on British and Norwegian shores, as well as with the relative position of littoral and sublittoral algae (Lüning 1981).
The light saturation value for growth of *B. brassicaeformis* correlates well with the data from the literature for a lower eulittoral species (Table 8).

A previous study on the effect of light as a physiological process in *B. brassicaeformis* has been conducted by Levitt (1987). He investigated the light saturation values for photosynthesis and the photosynthetic rates for four other species found higher up on the shore (*Porhyra capensis*, *Ulva rigida*, *Gigartina radula*, *Splachnidium rugosum*) as well for *B. brassicaeformis* found on the low shore. *U. rigida* had the lowest light saturation value (146 $\mu Em^{-2} s^{-1}$) followed by *B. brassicaeformis* (199), *P. capensis* (239), *G. radula* (241) and *S. rugosum* (364). However, *U.*

Table 8. Light levels for saturation of growth for adult thalli and the juvenile stages of littoral and sublittoral species.

	ADULT THALLI	JUVENILE STAGE
	($uEm^{-2}s^{-1}$)	
LITTORAL SPECIES		
Pelvetia canaliculata	250[1]	
Ascophyllum nodosum	250[1]	30[3]
Fucus spiralis	150[1]	30[4]
F. vesiculosus	150[1]	30[4]
F. serratus	150[1]	30[4]
Halidrys siliquosa		30[5]
Bifurcaria brassicaeformis	100[6]	30[6]
Himanthalia elongata		15[7]
SUBLITTORAL SPECIES		
Gracilaria verrucosa	83[2]	
Laminaria saccharina	70[1]	15[8]

1) Lüning (1981)
2) Engledow (1989)
3) Sheader and Moss (1975)
4) Mc Lachlan *et al.* (1971)
5) Moss and Sheader (1972)
6) This study
7) Moss *et al.* (1973)
8) Kain (1969)

rigida was the most photosynthetically productive, fixing 4.53 mg C $gdw^{-1} h^{-1}$, followed by P. capensis (4.13), S. rugosum (2.45) G. radula (2.15) and B. brasicaeformis (1.69).

Therefore, as the light saturation curve for growth closely follows that for photosynthesis (see Dring 1982), it does not seem surprising that the lower light saturation for growth in B. brassicaeformis when compared to other European and Norwegian species found higher up the shore, is also reflected in its light saturation point for photosynthesis being very low in comparison to other species found higher up on South African shores. Furthermore, as is common for many intertidal algae (see Dring 1982), for B. brassicaeformis, the light saturation point for photosynthesis (199 $\mu Em^{-2} s^{-1}$) is higher than that found for growth (100 $\mu Em^{-2} s^{-1}$).

It is worthwhile remembering that fucoid algae frequently have a gradient of chlorophyll content down the thallus with lowest amounts at the apices (Cousens 1981a). The chlorophyll-rich proximal parts are therefore best adapted to shade conditions. The performance of 5mm shoot apices in poor light (Figure 28) should perhaps not be taken as representative of the whole thallus.

Comparisons with the literature show that the light saturation value for growth of the germling thallus is similar ($30 \mu Em^{-2} s^{-1}$) to those reported for A. nodosum which has a distribution from about mid-tide level down to the lower eulittoral (Sheader and Moss 1975), four species of Fucus distributed from the upper shore to the sublittoral fringe (Mc Lachlan et al. 1971), and for Halidrys siliquosa growing in rock pools at mid-tide level and extending down into the sublittoral (Moss and Sheader 1972). The value for

B. brassicaeformis is also twice that reported for Himanthalia elongata which occurs in the lower eulittoral (Moss et al. 1973) and early sporophytes of several Laminaria species (Kain 1969).

Seasonally, good growth at low irradiances might be advantageous for younger germlings which survive and continue growing in the first winter when photoperiod is short and light levels are generally low. The ability to survive and even grow in darkness or very low light for an extended period was also recorded for germlings of other fucoids such as Halidrys siliquosa (Moss and Sheader 1972), Himanthalia elongata (Moss et al. 1973)- although H. elongata only germinated in the light, Fucus edentatus and F. distichus (Mc Lachlan 1974) and A. nodosum (Sheader and Moss 1975). It is a feature also recorded in many brown algae inhabiting the lower part of the shore, e.g. Kain (1964) reported that gametophytes of Laminaria hyperborea survived up to 7 weeks in total darkness, while Chapman and Burrows (1970) found that the gametophytes of Desmarestia aculeata could persist for 93 days with no apparent impairment of their ability to produce new sporophytes when light conditions improved.

The feature of maximum growth of rhizoids at a relatively low irradiance ($20\mu Em^{-2} s^{-1}$) as found for B. brassicaeformis, was also recorded for rhizoids of Halidrys siliquosa, Himanthalia elongata and Ascophyllum nodosum. This feature could most probably be used by the germling as an adaptation to ensure secure attachment in low light intensities.

CHAPTER 6

GENERAL DISCUSSION

The ecology of Bifurcaria brassicaeformis is particularly interesting because this species displays perennation of uprights from, as well as the lateral vegetative spread conferred on it by, its basal rhizome. This latter feature undoubtedly places it at a competitive advantage over other low-shore intertidal species and, without it, it seems doubtful that B. brassicaeformis would be able to maintain its dominance on shores of the southwestern Cape. Although no conclusive data is available on the area over which a clone may eventually spread, it certainly appears as if individuals are very large (up to and larger than 1 m2 across) in comparison with other intertidal algae. Patches with only male or only female receptacles have been observed to be greater than 1m in diameter. The actual sizes of male and female patches, as well as the rate of rhizomatous growth need further investigation. This could be done along similar lines as in studies with Ascophyllum nodosum (see Baardseth 1970) which has a similar growth morphology. Baardseth (1970) reports that A. nodosum displays slow development with fronds living 5-15 years. The holfasts may live for several decades producing new basal shoots as the old ones are lost.

In the literature there is some evidence with respect to the dispersal of juvenile plants of large brown algae over short distances (Anderson and North 1966, Dayton 1973). Anderson and

North (1966) found that juveniles of Macrocystis pyrifera (L.) C. Ag. only managed to establish at a distance 4m from the adult plants. Although no germlings or young plants of B. brassicaeformis were found at the study site, the observations of Bokenham and Stephenson (1938) of germlings within a B. brassicaeformis community strongly suggests that the establishment of germlings at a short distance from the parent plants is possible. More detailed sampling around and within B. brassicaeformis patches therefore needs to be undertaken.

There is no evidence in the literature to support or discount long-range dispersal of juvenile or planktonic stages (spores, propagules, zygotes) of seaweeds (van den Hoek 1987). For B. brassicaeformis, the idea of long-range dispersal of a germling or zygote do not seem favourable, as their large sizes and the fact that zygotes are smooth spheres do not make them well adapted for transport over considerable distances. Very rarely however, it can be envisaged that during strong currents, fertilized eggs could be carried short distances from the parent plants.

The ability of large algae to disperse over long distances have been attributed to their floating abilities (e.g. air bladders in e.g. Fucus vesiculosus, Halidrys siliquosa) and their ability to grow on floating substrates such as wood, cork, etc, and to float on other algae (van den Hoek 1987). For example, Stegenga and Mol (1983) found drift material of the above algae in good condition, often fertile, on Netherland's shores. These algae had their

reported origin on the coasts of Normandy, Britanny or Southern England. Algae that lack floating adaptations can disperse over considerable distances (e.g in fjords see Norton and Mathieson 1983), while the lack of floating adaptations could mean that algae which possibly could have dispersed to a certain shore cannot (e.g. Borgensen (1908) attributes the absence of Fucus serratus from the Faroes Islands due to the species lack of air bladders).
In light of the above, it has been noted that for the European B. bifurcata (which has no floating mechanisms and whose morphology is almost identical to that of B. brassicaeformis), whole plants which had fertile uprights had been collected in drift material on the shores of the Netherlands, where it does not occur (Stegenga, personal observation). This material could only have been transported there by currents of the Gulf stream from "donor coasts" such as Southern England, France or the Channel Islands (Stegenga pers. comm.). Therefore, long-range dispersal of fertile "clumps" of B. brassicaeformis after becoming detached seems possible. Spreading by this means is rendered more difficult by dioecy in this species. For sexual reproduction to take place at a new locality, both male and female uprights would need to be transported.

Along the coasts of southern Africa, the colder Benguela Current travels northward up the west coast, while the warmer Agulhas Current which has strong eddies of colder water inshore, travels generally southward from Natal to Cape Agulhas (Shannon 1985).

Therefore, the record of B. brassicaeformis at Paternoster on the west coast could have been due to dispersal of a whole portion of the plant with the Benguela current.

When germlings establish locally or after being transported over a distance (e.g. to another locality further along a stretch of coastline), several environmental as well as biological factors may deter its initial establishment and development. Environmental factors experienced during late summer and early winter would be most important, as results of this study revealed that the peak of the reproductive season occurs in summer which suggested that germlings establish soon thereafter.

In light of the previous statement, at the study site, environmental conditions during late summer such as desiccation, high air temperatures and very high light levels (up to 2000 $\mu Em^{-2} s^{-1}$ throughout spring low tides) may be the factors that cause the demise of many germlings, especially if germlings do establish in the pools vertically higher up the shore. Therefore, data are needed on microhabitat climatic conditions within and around a B. brassicaeformis patch in order to assess the effect of these factors on germling growth and survival. An estimate of the average longevity of the product of a single fertilization can be obtained by placing laboratory grown germlings on sterile bricks and transferring these to the shore. The bricks with their germlings could be placed in different microclimatic conditions and cemented down to prevent loss or displacement. In this way,

data on the effect of environmental as well as biological factors affecting early growth could be obtained.
It can however, be safely said that most germlings do succumb to the above environmental conditions during late summer when populations are emersed during spring low tides. The creeping rhizome would most probably increase the chances of germling settlement by providing protection from the harsh effects of environmental factors. More detailed observations between B. brassicaeformis fronds during late summer is thus required to furnish this ecologically important information. The creeping rhizome might also impede germling establishment as it could outcompete germlings for substratum space, growing horizontally over the substratum.

An important factor not assessed in the experimental work is grazing. Other authors (Jones 1946, Newell 1948, Schonbeck and Norton 1980) noted that limpets and littorinid snails can exert a profound effect on fucoid populations by scraping algal spores and germlings off rocks, and occasionally keep an entire shore free of macroalgae (Lodge 1948, Southward 1964). However, germlings of fucoid algae have been found to escape herbivory by taking refuge beneath a canopy of other algae (e.g. Pelvetia germlings beneath a Fucus canopy, Schonbeck and Norton 1980), or growing fairly rapidly to a length at which size fucoid algae are no longer seriously damaged by grazers (e.g. in Fucus species, Knight and Parke 1950). As Pelvetia germlings have a slow early development, many succumb to grazing (Schonbeck and Norton 1980).

Therefore, although direct evidence at present is lacking, grazing by the limpet Patella cochlear in the lower eulittoral may to a large extent account for the absence of germlings.

It seems clear therefore that establishment locally of new B. brassicaeformis plants would only take place if some germlings did manage to settle in a favourable microclimate and escape herbivores during late summer. During the first winter after establishment when light levels are low and daylengths are short, germlings may well be able to survive, as this study has shown that germlings are saturated at low irradiances. Sexual reproduction at a new station could only be envisaged if basal material bearing both male and female uprights managed to land there.
The infertile specimen from Algoa Bay seems interesting and suggests that more detailed surveys in this region need to be undertaken. An indication of local environmental conditions at the collection site of the Paternoster record coupled with the time that B. brassicaeformis was first sighted there may possibly yield an indication of the conditions which prevailed at the time of establishment. As Burges (1960, p.282) points out when dealing with a perennial species " we must relate distribution not to the present conditions but to those prevailing at the time of its establishment".

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LITERATURE CITED

Anderson, R.J. and Bolton. J.J. 1985. Suitability of the agarophyte *Suhria vittata* (L.) J. Ag. 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 Bolton, J.J. 1989. Growth and fertility in relation to temperature and photoperiod in South African *Desmarestia firma* (Phaeophyceae). *Bot. Mar.* **32**:149-158.

Anderson, E.K. and North, W.J. 1966. *In situ* studies of spore production and dispersal in the giant kelp *Macrocystis*. *In* (Young, E.G. and Mc Lachlan, J.L. eds). *Proceedings of the Fifth International Seaweed Symposium*, pp 73-86. Pergamon Press, Oxford.

Baardseth, E. 1970. Synopsis of biological data on knobbed wrack *Ascophyllum nodosum* (Linneaus). Le Jolis. FAO. *Fisheries synopsis* **38**: Rev. 1.

Barton, E.S. 1893. A provisional list of marine algae of the Cape of Good Hope. *J. Bot.* **31**:82.

Begon, M. and Mortimer, M. 1981. *Population Ecology: A unified study of Plants and Animals.* Blackwell Scientific Publ., Oxford, London. 198pp.

Bird, W.L. and Mc. Lachlan, J. 1976. Control of formation of receptacles in *Fucus distichus* L. subsp. *distichus* (Phaeophyceae, Fucales). *Phycologia* **15**:79-84.

Bird, C.J. and Mc Lachlan, J. 1986. The effect of salinity on distribution of species of Gracilaria Grev. (Rhodophyta, Gigartinales). An experimental assessment. Bot. Mar. **29**:231-238.

Black, R. 1974. Some biological interactions affecting the intertidal populations of the kelp Egregia laevigata. Mar. Biol. **28**: 189-198.

Boardman, N.K. 1977. Comparative photosynthesis of sun and shade plants. Ann. Rev. Plant Physiol. **28**:355-77.

Bohning, R.H. and Burnside, C.A. 1956. The effect of light intensity on the rate of apparent photosynthesis in leaves of sun- and shade plants. Am. J. Bot. **43**:557-61.

Bokenham, N.A.H. and Stephensen, T.A. 1938. The colonization of denuded rock surfaces in the intertidal region of the Cape Peninsula. Ann. Natal Mus. **9**:47-81.

Bold, H.C. and Wynne, M.J. 1978. Introduction to the algae. Structure and reproduction. 2nd ed. Prentice-Hall. Englewood Cliffs, N.J. 706pp.

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 Anderson, R.J. 1987a. The Ecklonia species of southern Africa; variation, distribution and temperature tolerances. Br. Phycol. J. **20**:122.

Bolton, J.J. and Anderson, R.J. 1987b. Temperature tolerances of two southern African Ecklonia species (Alariaceae: Laminariales) and of hybrids between them. Mar. Biol. **96**: 293-297.

Bolton, J.J. and Levitt, G.J. 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 Stegenga, H. 1987. The marine algae of Hluleka (Transkei) and the warm temperate/sub-tropical transition on the east coast of southern Africa. *Helgoländer Meeresunters* **41**:165-183.

Bolton, J.J. and Stegenga, H. 1990. The seaweeds of De Hoop Nature Reserve and their phytogeographical significance. *S. Afr. J. Bot.* **56(2)**:233-238.

Borgesen, F. 1908. Botany of the Faeröes. 3. The algal vegetation of the Faeröese coasts, with remarks on the phytogeography - Nordiske Forl., Copenhagen 683-834.

Bower, F.O. 1880. On the development of the conceptacles in the Fucaceae. *Q. J. micr. Sci* N.S. **20**:36-49.

Boyd, A.J., Tromp, B.B.S. and D.A. Horstman. 1985. The hydrology off the South African south-western coast between Cape Point and Danger Point in 1975. *S. Afr. J. mar. Sci.* **3**:145-168.

Brawley, S.H., R. Wetherbee and R.S. Quatrano. 1976a. Fine structural studies of the gametes and embryo of *Fucus vesiculosus* (L.) (Phaeophyta) I. Fertilisation and pronuclear fusion. *J. Cell Sci.* **20**:233-254.

Brawley, S.H. R. Wetherbee and R.S. Quatrano. 1976b. Fine structural studies of the gametes and embryo of *Fucus vesiculosus* (L.) (Phaeophyta) II. The cytoplasm of the egg and young zygote. J. Cell Sci. 20:255-271.

Breeman, A.M. 1988. Relative importance of temperature and other factors in determining geographic boundaries of seaweeds: experimental and phenological evidence. Helgoländer Meeresunters **42**:199-241.

Bright, K.M.F. 1938. The South African intertidal zone and its relation to ocean currents III. An area on the northern part of of the west coast. Trans. Roy. Soc. S. Afr. **26**:67-88.

Burges, A. 1960. Time and size factors in ecology. J. Ecol. **48**:273-285.

Burrows, E.M., E. Conway, S.M. Lodge and H.T. Powell, 1954. The raising of intertidal algal zones on Fair Isle. J. Ecol. **42**: 283-288.

Cambridge, M.L., Breeman, A.M., Oosterwijk, R. van & Hoek, C. van den, 1984. Temperature responses of some North Atlantic Cladophora species (Chlorophyceae) in relation to their geographic distribution.- Helgoländer Meeresunters. **38**:349-363.

Cambridge, M.L., Breeman, A.M., Kraak, S. & Hoek, C. van den, 1987. Temperature responses of tropical to warm temperate Cladophora species in relation to their distribution in the North Atlantic Ocean. Helgoländer Meeresunters **41**:329-354.

Caplin, S.M. 1968. Fucus life cycle: time to correct the textbooks. Bioscience 18:193

Carter, A.R.O. 1986. Studies on the biology of the economic marine red alga Gelidium pristoides (Turner) Kützing (Gelidiales: Rhodophyta). PhD. Thesis, University of Cape Town, Cape Town. 190pp.

Chapman, A.R.O. 1974. The genetic basis of morphological differentiation in some Laminaria populations. Mar. Biol. **24**:85-91.

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. 1985. Demography. In Littler, M.M. and Littler, D.S. (eds.) Handbook of phycological methods: Ecological field methods: macroalgae Cambridge University Press. pp251-269.

Chapman, A.R.O. 1986. Population and community ecology of seaweeds. Adv. Mar. Biol. **23**:1-161.

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

Chapman, A.R.O. and Goudey, C.L. 1983. Demographic study of the macrothallus of Leathesia difformis (Phaeophyta) in Nova Scotia. Can. J. Bot. **61**:319-23.

Clayton, M.N. 1984. Evolution of the Phaeophyta with particular reference to the Fucales. Prog. Phycol. Res. **3**:11-46.

Clayton, M.N., Hallam, N.D. and C.M. Shankly. 1987. The seasonal pattern of conceptacle development and gamete maturation in Durvillaea potatorum (Durvillaeales, Phaeophyta). Phycologia **26**:35-45.

Colman, J. 1933. The nature of intertidal zonation of plants and animals. J. mar. biol. Ass. U.K. **18**:435-476.

Cook, A.H. and J.A. Elvidge. 1951. Fertilization in Fucaceae. Investigations on the nature of the chemotactic substances produced by the eggs of Fucus serratus and F. vesiculosus Proc. R. Soc. London B 138:97-114.

Cousens, R. 1981a. "The Population Biology of Ascophyllum nodosum (L.) Le Jolis" Ph.D. dissertation, Dalhousie University, Halifax, Nova Scotia. 273pp.

Cousens, R. 1981b. Variation in annual production by Ascophyllum nodosum with degree of exposure to wave action. Proc. Int. Seaweed Symp. **25**:253-258.

Cousens, R. 1984. Estimation of the annual production by the intertidal brown alga Ascophyllum nodosum (L.) Le Jol. Bot. Mar. **27**:217-227.

Coyer, J.A. and Zaugg-Haglund, A.C. 1982. A demographic study of the elk kelp Pelogophycus porra (Laminariales, Lessoniaceae), with notes on Pelogophycus X Macrocystis hybrids. Phycologia **21**:399-407.

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

Dawson, A.E.E. 1941. Some observations on Cystoseira foeniculacea (L.) Grev. Emend. Sauvageau. New Phytol. **40**: 316-325.

Day, J. H. 1969. A Guide to Marine life on South African shores. A. Balkema, Cape Town.

Dayton, P.K. 1973. Dispersion, dispersal, and persistence of the annual intertidal alga, Postelsia palmaeformis Ruprecht. Ecology **54**:433-438.

Delf, E.M. 1931. Release of the oogonia in the Fucaceae. Proc. Linn. Soc. London. **412**:76.

Delf, E.M. 1935. Liberation of oogonia in Bifurcaria and other members of the Fucaceae. New Phytol. **34**:245-259.

De Toni, J.B. 1895. Syllage Algarum, Vol. 3. Fucoidae. 638pp.

Wreede de, R.E. 1978. Growth in varying culture conditions of embryos of three Hawaiian species of Sargassum (Phaeophyta, Sargassaceae). Phycologia **17(1)**:23-31.

Deysher, L. and Norton, T.A. 1981. Dispersion, dispersal and persistence of an annual intertidal alga, Postelsia palmaeformis Ruprecht. Ecology **54**:433-8.

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. and Irvine, C.M. 1977. Seaweeds of the British Isles. Vol. I. Rhodophyta. Part I. Introduction, Nemaliales, Gigartinales. Brit. Mus. Lond. **1(1)**:1-252.

Dring, M.J. 1967. Effects of daylength on growth and reproduction of the Conchocelis-phase of Porphyra tenera. J. mar. biol. Ass. U.K. **47**:501-510.

Dring, M.J. 1982. The biology of Marine Plants. Edward Arnold, London. 199pp.

Dring, M.J. and Lüning, K. 1975. A photoperiodic response mediated by blue light in the brown alga Scytosiphon lomentaria Planta (Berl.) **125**:25-32.

Dromgoole, F. 1980. Desiccation resistance of intertidal and subtidal algae. Bot. Mar. **23**:149-159.

Edelstein, T. and McLachlan, J. 1975. Autecology of *Fucus distichus* ssp. *distichus* (Phaeophyceae: Fucales) in Nova Scotia, Canada. Mar. Biol. **30**:305-324.

Engledow, H.R. 1989. The effect of temperature, salinity and light intensity on the growth of *Gracilaria verrucosa* - South Africa. Honours thesis, University of Cape Town, Cape Town. 35pp.

Erye, J. 1939. The South African intertidal zone and its relation to ocean currents. VII. An area in False Bay. Ann. Natal Mus. **9**:283-306.

Erye, J., G.J. Broekhuysen and M.I. Crichton. 1938. The South African intertidal zone and its relation to ocean currents VI. The East London district. Ann. Natal Mus. **9**:83-112.

Fain, S.R. and Murray, S.N. 1982. Effects of light and temperature on net photosynthesis and dark respiration of gametophytes and embryonic sporophytes of *Macrocystis pyrifera*. J. Phycol. **18**:92-98.

Filion-Myklebust, C.and Norton, T.A. 1981. Epidermis shedding in the brown seaweed *Ascophyllum nodosum* (L.) Le Jolis, and its ecological significance. Mar. Biol. Lett. **2**:45-51.

Fletcher, R.L. 1980. Studies on the recently introduced brown alga *Sargassum muticum* (Yendo) Fenscholt. III. Periodicity in gamete release and "incubation" of early germling stages. Bot. Mar. **23**:425-432.

Fletcher, R.L. and Fletcher, S.M. 1975a. Studies on the recently introduced brown alga *Sargassum muticum* (Yendo) Fernscholt.

I. Ecology and reproduction. *Bot. Mar.* **18**:149-156.

Fletcher, R.L. and Fletcher, S.M. 1975b. Studies on the recently introduced brown alga *Sargassum muticum* (Yendo) Fernscholt. II. Regenerative ability. *Bot. Mar.* **18**:157-162.

Forbes, M.A. and Hallam, N.D. 1978. Gamete structure and fertilization in the brown alga *Hormosira banksii* (Turner) Aecaisne. *Br. Phycol. J.* 13:299-310.

Friedlander, M. and Dawes, C.J. 1984. Studies on spore release and sporeling growth from carpospores of *Gracilaria foliifera (Forskål) Boergensen var. angustissima* (Harvey) Taylor. I. Growth responses. *Aquat. Bot.* **19**:221-232.

Fritch, F.E. 1945. *The Structure and Reproduction of the Algae.* Vol. 2. Cambridge University Press, Cambridge, 939 pp.

Gaines. S.D. and Lubchencko, J. 1982. A unified approach to marine plant-herbivore interactions. II. Biography. *Ann. Rev. Ecol. Syst.* **13**:111-138.

Garner, W.W. and Allard, H.A. 1920. Effect of the relative length of day and night and other factors of the environment on growth and reproduction in plants. *J. agric. res.* **18**:553-606.

Grant, A. 1989. The use of graphical methods to estimate demographic parameters. *J. mar. biol. Ass. U.K.* **69**:367-371.

Grunow, A. 1867. Algae. *In* Reise der Oesterreichischen fregatte Novara um die Erde, in 1857-1859. *Botanischer Theil* Bd. I. Heft **1**:1-104.

Gunnill, F.C. 1980. Demography of the intertidal brown alga *Pelvetia fastigiata* in Southern California, USA. *Mar. Biol.*

59:169-179.

Gunnill, F.C. 1985. Growth, morphology and microherbivore faunas of Pelvetia fastigiata (Phaeophyceae, Fucaceae) at La Jolla, California, U.S.A. Bot. Mar. **28**:187-199.

Hanisak, M.D. 1979. Growth patterns of Codium fragile ssp. tomentosoides in response to temperature, irradiance, salinity, and nitrogen source. Mar. Biol. (Berl.) **50**:319-332.

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

Hatton, H. 1938. Essais de bionomie explicative sur quelques espees intercotidales d'algues et d'animaux. Ann. Inst. oceanogr., Monaco, **17**:241-348.

Hardy, F.G. 1977. Attachment of zygotes and germlings of the Fucales. PhD. thesis. University of Newcastle upon Tyne.

Hardy, F.G. and Moss, B.L. 1978. The attachment of zygotes and germlings of Halidrys siliquosa (L.) Lyngb. (Phaeophyceae, Fucales). Phycologia **17(1)**:69-78.

Hardy, F.G. and Moss, B.L. 1979. Notes on the attachment of zygotes and germlings of Bifurcaria bifurcata Ross. (Phaeophyceae, Fucales). Phycologia **18(2)**:164-170.

Hay, M.E. 1981. Herbivory, algal distribution, and maintenance of between habitat diversity on a tropical fringing reef. Am. Nat. **118**:520-540.

Hayes, S.P. 1985. Sea level and near surface temperature variability at the Galapagos Islands, 1979-83. In (G. Robinson, and E.M. del Pino, eds) El Nino en las Islas Galapagos: El Evento de 1982-1983. Fundacion Charles Darwin para las Islas

Galapagos, Quito, Ecuador. pp. 49-81.

Hoek, C. van den, 1982a. Phytogeographic distribution groups of benthic marine algae in the North Atlantic Ocean. A review of experimental evidence from life history studies. *Helgoländer Meeresunters* **35**:153-214.

Hoek, C. van den, 1982b. The distribution of marine benthic algae in relation to the temperature regulation of their life histories. *Biol. J. Linn. Soc.* **18**:81-144.

Hoek, C. van den, 1982c. A taxonomic revision of the American species of *Cladophora* (Chlorophyceae) in the North Atlantic Ocean and their geographic distribution. *Verh. K. Ned. Acad. Wet. (Afd. Natuurk., 2. R)* **78**:1-236.

Hoek. C. van den, 1987. The possible significance of long-range dispersal for the biogeography of seaweeds. *Helgoländer Meeresunters* **41**:261-272.

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

Houvanaghel, G.T. 1978. Oceanographic conditions in the Galapagos Archipelago and their relationships with life on the Islands., *In* (Upwelling Ecosystems, R. Boje and M. Tomczak, eds). Springer-Verlag, New York. pp. 181-200.

Hoyt, W.D. 1927. The periodic fruiting of *Dictyota* and its relation to the environment. *Am. J. Bot.* **14**:592-619.

Hugget, J. and Griffiths, C.L. 1986. Some relationships between elevation, physico-chemical variables and biota of intertidal rock pools. *Mar. Ecol. Prog. Ser.* **29**:189-197.

Isaac, W.M.E. 1937a. Studies of South African seaweed vegetation. 1. West coast from Lamberts Bay to the Cape of Good Hope. Trans. Roy. Soc. S. Afr. **25**:116-151.

Isaac, W.M.E. 1937b. South African coastal waters in relation to ocean currents. Geogr. Rev. **27**:651-664.

Isaac, W.M.E. 1938. The geographical distribution of seaweed vegetation in relation to temperature and other factors, with special reference to South Africa. Comptés rendus du Congrés international de geographie **2**:12-28.

Isaac, W.M.E. 1949. Studies of South African seaweed vegetation II. Rooi Els to Gansbaai, with special reference to Gansbaai. Trans. Roy. Soc. S. Afr. **32**:125-160.

Isaac, W.M.E. 1951. Oservations on the ecology of Bifurcaria brassicaeformis (Kutz.) Barton. J. Ecol. 39(1):94-105.

Jaenike, P.L. 1977. Sex hormones of brown algae. Naturwiss. 64:69-75.

Jensen, J.B. 1974. Morphological studies in Cystoseiraceae and Sargassaceae (Phaeophyceae). Univ. Calif. Publs. Bot., 68, i-iv, 1-61, 16 plates.

Johnson, N.S., Gigon, A., Gulmon, S.L. and H.A. Mooney. 1974. Comparative photosynthetic capacities of intertidal algae under exposed and submerged conditions. Ecology **55**:450-453.

Jones, N.S. 1946. Browsing of Patella. Nature Lond. **158**:557.

Jones, N.S. 1948. Observations and experiments on the biology of Patella vulgata at Port St. Mary, Isle of Man. Proc. Trans. Lpool. biol. Soc. **56**:60-77.

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

Kain, J. 1964. Aspects of the biology of *Laminaria hyperborea* III. Survival and growth of gametophytes. *J. mar. biol. Ass. U.K.* **44**:415-433.

Kain, J. 1969. Aspects of the biology of *Laminaria hyperborea* V. Comparison with early stages of competitors. *J. mar. biol. Ass. U.K.* **49**:455-473.

Kain, J. 1979. A view of the genus *Laminaria*. *Oceanogr. mar. Biol.* **17**:101-161.

Keser, M. and Larson, B.R. 1984. Colonization and growth dynamics of three species of *Fucus*. *Mar. Ecol. Prog. Ser.* **15**:125-134.

Kilar, J.A., Littler, M.M. and D.S. Littler. 1989. Functional-morphological relationships in *Sargassum polyceratium* (Phaeophyceae): phenotypic and ontogenetic variability in apparent photosynthesis and dark respiration. *J. phycol.* **25**:713-720.

Knight, M. and Parke, M. 1950. A biological study of *Fucus vesiculosus* L. and *Fucus serratus* L. *J. mar. biol. Ass. U.K.* **9**:445-449.

Kogelschatz, J., Solorzano, L., Barber, R. and P. Mendoza. 1985. Oceanographic conditions in the Galapagos Islands during the 1982/1983 El Nino. *In* (G. Robinson, and E.M. del Pino, eds.) *El Evento de 1982-1983*. Fundacion Charles Darwin para las Islas Galapagos, Quito, Ecuador. pp. 91-123.

Kützing, F.T. 1860. Tabulae Phycologicae, Vol. 10. Nordhausen, 39pp.

Levitt, G.J. 1987. Studies on the seasonal primary production of Cape Peninsula littoral and sublittoral seaweeds. MSc. thesis, University of Cape Town, Cape Town. 215pp.

Lewis, J.R. 1964. Ecology of Rocky shores. English Universities Press. Ltd, London, 323pp.

Littler, M.M. and Littler, D.S. 1980. The evolution of thallus form and survival strategies in benthic marine macroalgae. Field and laboratory tests of a functional form model. Am Nat. **16(1)**:25-44.

Lodge, S.M. 1948. Algal growth in the absence of Patella in an experimental strip of foreshore, Port St. Mary, Isle of Man. Proc. Trans. Lpool bot. Soc. **56**:78-85.

Lüning, K. 1980. Control of algal life history by daylength and temperature. In (J.H. Price, D.E.G. Irvine and W.F. Farnham, eds). The Shore Environment. Academic Press, New York. pp915-945.

Lüning, K. 1981. Light. In Lobban, C.S. and Wynne, M.J. (Eds.) The Biology of Seaweeds. Blackwell Scientific Publications, Oxford, pp. 326-355.

Lüning, K. 1985. Meeresbotanik. Thieme, Stuttgart, 375pp.

Lüning, K. 1986. New frond formation in Laminaria hyperborea (Phaeophyta): a Photoperiodic response. Br. Phycol. J. **21**: 269-273.

Lüning, K. and Müller, D.G. 1978. Chemical interaction in sexual reproduction of several Laminariales. (Phaeophyceae): release and attraction of spermatozoids. Z. Pflanzenphysiol. **89**:333-

341.

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

Manuel, T.L. 1988. Studies on the life history and temperature tolerances in culture of a South African plumose Bryopsis species (Bryopsidales, Chlorophyceae). Honours thesis, University of Cape Town, Cape Town. 29pp.

Markham, J.W. and Hagmeier, E. 1982. Observations on the effects of germanium dioxide on the growth of macroalgae and diatoms. Phycologia **21**:125-130.

Mathieson, A.L. and Dawes, C.J. 1986. Photosynthetic responses of Florida seaweeds to light and temperature: a physiological survey. Bull. mar. Sci. **38**:512-524.

Mathieson, A.C., Norton, T.A. and Neushul, M. 1981. The taxonomic implications of genetic and environmentally induced variations in seaweed morphology. Bot. Rev. **47**:313-347.

Menge, J.L. 1975. Effects of herbivores on community structure of the New England rocky intertidal region: distribution and diversity of algae. PhD. thesis, Harvard University, Boston, Mass.

Mc Lachlan, J. 1974. Effects of temperature and light on growth and development of embryos of Fucus edentatus and F. distichus spp. distichus. Can. J. Bot. **52**:943-951.

Mc Lachlan, J., L.C.M. Chen and T. Edelstein. 1971. The culture of four species of Fucus under laboratory conditions.

Can. J. Bot. **49**:1463-1469.

Mc Eachreon, J.C.T. and Thomas, M.L.H. 1987. Attachment strength of Ascophyllum nodosum (l.) LeJolis and exposure to wave action. Bot. Mar. **30**:217-222.

Moss, B.L. 1975. Attachment of zygotes and germlings of Ascophyllum nodosum (L.) Le Jol. (Phaeophyceae, Fucales). Phycologia **14(2)**:75-80.

Moss, B.L. 1979. Attachment and development of the zygotes of Pelvetia canaliculata (L.) Dcne et Thur. (Phaeophyta, Fucales). Phycologia **18(3)**:203-212.

Moss, B.L. 1982. The control of epiphytes of Halidrys siliquosa (L.) Lyngb. (Phaeophyta, Cystoseiraceae). Phycologia **21**: 185-191.

Moss, B.L. and Lacy, A. 1963. The development of Halidrys siliquosa (L.) Lyngb. New Phytol. **62**:67-74.

Moss, B.L. and Sheader, A. 1972. The effect of light and temperature upon the germination and growth of Halidrys siliquosa (L.) Lyngb. (Phaeophyceae, Fucales). Phycologia **12**:63-68.

Moss, B.L., Mercer, S. and Sheader, A. 1973. Factors affecting the distribution of Himanthalia elongata (L.) S.F. Gray on the north-east coast of England. Estuar. cstl. mar. Sc. **1**:233-243.

Müller, D.G. 1976. Quantitative evaluation of sexual chemotaxis in two marine brown algae. Z. Pflanzenphysiol. **80**:120-130.

Müller, D.G. 1978. Locomotive responses of male gametes to the species specific sex attractant in Fucus siliculosus (Phaeophyta)

Arch. Protistenk **120**:371-377.

Müller, D.G., Clayton, M.N., Gassman, G., Boland, W., Marner, F.J. and L. Jaenicke 1984. The sperm attractant of Hormosira banksii (Phaeophyceae, Fucales), a seaweed common to Australia and New Zealand. Experientia **40**:211-212.

Müller, D.G. and Gassman, G. 1978. Identification of the sex attractant in the marine brown alga Fucus vesiculosus Natuurwiss. **64**:389.

Müller, D.G. and G. Gassman. 1985. Sexual reproduction and the role of sperm attractants in momoecious species of the brown Algae Order Fucales (Fucus, Hesperophycus, Pelvetia and Pelvetiopsis) J. Plant Physiol. **18**:401-408.

Müller, D.G., Gassman, G. Marner, F.J., Boland, W. and L. Jaenicke. 1982. The sperm attractant of the marine brown alga Ascophyllum nodosum (Phaeophyceae). Science **28**:1119-1120.

Müller, D.G. and Sederaidis, K. 1977. Specificity of sexual chemotaxis in Fucus serratus and Fucus vesiculosus (Phaeophyceae). Z. Pflanzenphysiol. **84**:85-94.

Naylor, M. 1949. Some observations on the receptacles of Scytothalia dorycarpa, with special reference to the extrusion of oogonia. Ann. Bot. Lond. **13**:135-150.

Neill, F.X. 1977. Rocky intertidal benthic systems in temperate seas: a synthesis of their functional importance. Helgoländer Meeresunters **30**:315-333.

Newell, G.E. 1958. The behaviour of Littorina littorea (L.) under natural conditions and its relation to position on the shore.

J. mar. biol. Ass. U.K. 37:229-239.

Nienburg, W. 1913. Die konzeptakelentwicklung bei den Fucaceen. Z. Bot. 5:1-27.

Nizamuddin, M. 1962. Classification and distribution of the Fucales. Bot. mar. 4:191-203.

Nizamuddin, M. 1970. Phytogeography of the Fucales and their seasonal growth. Bot. mar. 13:131-139.

Norton, T.A. 1981. Gamete expulsion and release in Sargassum muticum. Bot. mar. 24:465-470.

Norton, T.A. 1986. Provisional Atlas of British Seaweeds. Brit. Phycol. Soc. and the Biol. Research Centre, Port Erin, 164pp.

Norton, T.A., F.J. Ebling and J.A. Kitching, 1971. Light and the distribution of organisms in a sea cave. Proc. 4th Europ. Mar. Biol. Symp,. ed. D.J. Crisp, Cambridge University Press, Cambridge, pp. 409-432.

Norton, T.A. and Mathieson, A.C. 1983. The biology of unattached seaweeds. Prog. Phycol. Res. 2:333-386.

Norton, T.A., Mathieson, A.C. and Neushul, M. 1982. A review of some aspects of form and function in seaweeds. Bot. Mar. 25:501-510.

Novotny A.M. and M. Forman, 1975. The composition and development of cell walls of Fucus embryos. Planta 122:67-78.

Oltmanns, F. 1889. Beiträge zur kenttnis der Fucaceen. Bibl. Bot. 14:1-94.

Papenfuss, G.F. 1951. The Phaeophyta. In (Smith, G.M. ed.) Manual of Phycology : An introduction to the algae and their biology. Chronica Company, Waltham, Mass., U.S.A. pp 119-150.

Pollock, E.G. 1970. Fertilization in *Fucus*. *Planta* (Berl.) **92** :85-99.

Printz, H. 1959. Phenological studies of marine algae along the Norwegian coast. III. *Fucus vesiculosus* L. Avhandl. utgitt av Det. Norske Videnskaps-Akademi i Oslo I. *Mat. Naturv. Klasse* **4**:17-28.

Provasoli, L. 1968. Media and the prospects for the cultivation of marine algae. *In* (A. Watanabe and A. Hattori, eds). *Cultures and Collections of Algae* Jap. Soc. Plant. Physiol., Tokyo. pp63-75.

Quatrano, R.S. 1972. An ultrastuctural study of the determined site of rhizoid formation in *Fucus* zygotes. *Exp. Cell Res.* **70**:1-12.

Ramon, E. 1972. Germination and attachment of zygotes of *Himanthalia elongata* (L.) S.F. Gray. *J. Phycol.* **9**: 445-449.

Raven, P.H. and Axelrod, D.I. 1972. Plate tectonics and Australasian paleobiogeography. *Science* **176**:1379-1386.

Raven, J., Beardall, J. and Griffiths, H. 1982. Inorganic C-sources for *Lemanea*, *Cladophora* and *Ranunculus* in a fast-flowing stream: measurements of gas exchange and carbon isotope ratio and their ecological implications. *Oecologia (Berl.)* **53**: 68-78.

Rees, E.M. 1933. Some observations on *Bifurcaria tuberculata* Stackh. *Ann. Bot.* **47**:101-105.

Rice, E.L. and Chapman, A.R.O. 1982. Net productivity of two cohorts of *Chordaria flagelliformis* (O.F. Müll.) C. Ag. (Phaeophyta). in Nova Scotia. *Mar. Biol.* **71(1)**:107-111.

Roberts, M. 1967. Studies on marine algae of the British Isles. 3. The genus *Cystoseira*. *Br. Phycol. Bull.* **3**:345-366.

Robinson, G. 1985. Influence of the 1982-83 El Nino on the Galapagos marine life. *In* (G. Robinson and E.M. del Pino, eds). *El Nino en las Islas Galapagos: El Evento de 1982-83*. Fundacion Charles Darwin para las Islas Galapagos, Quito, Ecuador. pp153-190.

Rosenberg, G. and Ramus, J. 1984. Uptake of inorganic nitrogen and seaweed surface area:volume ratios. *Aquat. Bot.* **19**: 65-72.

Ross, R. 1961. The type species of *Bifurcaria* Stackhouse- a correction. *J. Linn. Soc. (Bot.)* **56**:368, p512.

Russell, G. 1978. Environment and form in the discrimination of taxa in brown algae. *In* (Irvine, D.E.G. and Price, J.H. eds.) *Modern Approaches to the Taxonomy of Red and Brown Algae*. Academic Press, London and New York. pp 339-69.

Russell, G. 1988. Distribution and development of some Manx epiphyte populations. *Helgoländer Meeresunters* **42**:477-492.

Russell, G. 1990. Age and stage in seaweed populations. A cautionary tale. *Br. Phycol. J.* **25(3)**:245-249.

Scagel, R.F. 1961. Marine plant resources of British Columbia. *Bull. Fish. Res. Bd. Can.* **127**:1-39.

Schonbeck, M.W. and Norton, T.A. 1978. Factors controlling the upper limits of fucoid algae on the shore. *J. exp. mar. Biol. Ecol.* **31**:303-313.

Schonbeck, M.W. and Norton, T.A. 1979a. Drought-hardening in the upper-shore seaweeds Fucus spiralis and Pelvetia canaliculata. J. Ecol. **67**:687-696.

Schonbeck, M.W. and Norton, T.A. 1979b. An investigation of drought avoidance in intertidal fucoid algae. Bot. Mar. **22**: 133-144.

Schonbeck, M.W. and Norton, T.A. 1979c. The effect of brief periodic submergence on intertidal fucoid algae. Estuar. cstl. mar. Sci. **8**:205-211.

Schonbeck, M.W. and Norton, T.A. 1980. Factors controlling the lower limits of fucoid algae on the shore. J. exp. mar. Biol. Ecol. **43**:131-150.

Seagrief, S.C. 1988. Marine algae. In: A field guide to the eastern Cape coast, eds Lubke, R.A., Bess, F.W. and Bruton, M.N., pp. 35-72, Wildlife Society of southern Africa, Grahamstown.

Setchell, W.A. 1920. Stenothermy and zone -invasion. Amer. Nat. **54**:385.

Shannon, L.V. 1985. The Benguela ecosystem Part I. Evolution of the Benguela, physical features and processes. Oceanogr. Mar. Biol. Ann. Rev. **23**:105-182.

Sheader, A. and Moss, B.L. 1975. The effects of light and temperature on germination and growth of Ascophyllum nodosum (L.) Le Jol. Estuar. cstl. mar. Sci **3**:125-132.

South, G.R. and Tittley, I. 1986. A checklist and distributional index of the benthic marine algae of the North Atlantic Ocean.

Huntsman marine laboratory and British Museum (Natural History), St Andrews, London. 73pp.

Southward, A.J. 1964. Limpet grazing and the control of vegetation on rocky shores: In (Crisp, D.J. ed.) Grazing in terrestrial and marine environments. Blackwell, Oxford. p 265-273.

Stackhouse, J. 1809. Tentamen Marino-cryptogamicum. Mem. la Soc. Imp. Nat. Moscow **2**:50. (Quoted from Laing, E.M. 1941).

Stegenga, H. and Mol, I. 1983. Flora van de Nederlandse Zeewieren. Koninkl. Ned. Natuurhist. Ver., Hoogwoud, Netherlands, 263pp.

Stephenson, T.A. 1939. The constitution of the intertidal flora and fauna of South Africa. Part I. J. Linn. Soc. (Zool.) **40**:487-536.

Stephenson, T.A. 1944. The constitution of the intertidal flora and fauna of South Africa. Part II. Ann. Natal Mus. **10**: 261-358.

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

Stephenson, T.A., A. Stephenson and C.A. du Toit. 1937. The South African intertidal zone and its relation to ocean currents I. A temperate Indian Ocean shore. Trans. Roy. Soc. S. Afr. **24**: 341-382.

Stephenson, T.A., A. Stephenson and K.M.F. Bright. 1938. The South African intertidal zone and its relation to ocean currents IV. The Port Elizabeth district. Ann. Natal Mus. **9**:

1-20.

Stephenson, T.A., A. Stephenson and J.H. Day. 1940. The South African intertidal zone and its relation to ocean currents. VIII. Lamberts Bay and the west coast. Ann. Natal Mus. **9**: 345-380.

Stewart, J.G. 1984. Algal distributions and temperature: test of a hypothesis based on vegetative growth rates. Bull. Sth. Calif. Acad. Sci. **83**:57-68.

Strömgren, T. 1976. Length changes of growing apices of eulittoral Fucales during drying and soaking. Sarsia **61**: 47-64.

Strömgren, T. 1977. Apical growth of five intertidal Fucales in relation to irradiance. Sarsia **63**:39-47.

Strömgren, T. 1977b. Length growth rates of three species of intertidal Fucales during exposure to air. Oikos **29**: 245-249.

Subrahmanyan, R. 1960. Ecological studies on the Fucales. I. Pelvetia canaliculata Dec. et Thur. J. Indian Bot. Soc. **39**:614-630.

Subrahmanyan, R. 1961. Ecological studies on the Fucales. II. Fucus spiralis L. J. Indian Bot. Soc. **40**:335-354.

Sundene, O. 1973. Growth and reproduction in Ascophyllum nodosum (Phaeophyceae). Norwegian Journal of Botany **20**:249-255.

Taylor, W.R. 1945. Pacific marine algae of the Allan Hancock Expeditions to the Galapagos Islands. Allan Hancock Pacific Exped. **12**. University of Southern California Press, Los

Angeles.528pp.

Terry, L.A. and Moss, B.L. 1980. The effect of photoperiod on receptacle initiation in *Ascophyllum nodosum* (L.) Le Lol. *Br. Phycol. J.* **15**:291-301.

Thom, R.M. 1983. Spatial and temporal patterns of *Fucus distichus ssp. edentatus* (de la Pyl.) Pow. (Phaeophyceae: Fucales) in Central Puget Sound. *Bot. Mar.* **26**:471-486.

Thuret, G. 1854. Researches sur la fecondation des Fucacees. *Ann. des Sci. nat. Bot.* **2(4)**:197-214.

Thuret, G. and Bonet, E. 1878. *Etudes Phycologiques*. Paris.

Valera, M. De. 1962. Some aspects of the problem of the distribution of *Bifurcaria bifurcata* (Valley) Ross on the shores of Ireland, north of the Shannon Estuary. *Proc. Roy. Irish Acad.* **62(B)**:77-99.

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

Vince-Prue, D. 1975. *Photoperiodism in Plants*. Mc Graw Hill, London.

Womersley, H.B.S. 1964. The morphology and taxonomy of *Cystophora* and related genera (Phaeophyta). *Aust. J. Bot.* **12**:53-110.

Zaneveld, J.S. 1937. The littoral zonation of some Fucaceae in relation to desiccation. *J. Ecol.* **25**:431-468.

Zar, J.H. 1984. *Biostatistical Analysis*. 2nd ed. Prentice-Hall Inc., Englewood Cliffs, N.J. 07632.