LIFE HISTORY STRATEGIES OF THREE SPECIES OF *CYSTOPHORA* (PHAEOPHYTA, FUCALES) FROM A SHALLOW SUBTIDAL COMMUNITY IN SOUTH AUSTRALIA

by

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Contents

Declaration

This thesis contains no material which has been submitted or accepted for a degree or any other award in any university. To the best of my knowledge and belief the thesis also contains no material previously published or written by another person, accept where due reference is made in the text.

I consent to the thesis being made available for copying or loan if accepted for the award of the degree.

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Summary

A number of life-history traits were quantified for three species of *Cystophora* J. Agardh (Phaeophyta, Fucales) from a shallow, subtidal mixed fucoid community in South Australia. The three species studied were *C. expansa* (Areschoug)Womersley, *C. monilifera* J.Agardh and *C. subfarcinata* (Mertens)J. Agardh. The community was located in Backstairs Passage, South Australia, at an approximate depth of 4.5m (at low tide). The community was rich in algal species but the canopy was dominated by fucoids, in particular species of *Cystophora.*

The composition and dynamics of the community were monitored and related to temporal changes in the patterns of growth and reproduction of each species, and also to patterns of recruitment and early community development. These were determined using an artificial system of settlement plates.

The results showed that community structure was variable through time depending on the demographics of *Cystophora,* and in particular *C. expansa,* the community dominant. Although a number significant differences existed in the various life-history traits of each species, a general strategy for the success of *Cystophora* in the community can be proposed.

Cystophora was able to dominate the community through the maintenance of a closed canopy for most of the year and this was perpetuated through a "bank of sub-canopy juveniles" that was always present in the understorey and acted as a buffer against the removal of adults. Patterns of growth and reproduction were both seasonal and clearly linked. Increased growth occurred as the reproductive structures were developing and maximal plant size was achieved as plants became reproductively mature.

After reproduction the spent receptacles were shed and growth became minimal or even negative in *C. expansa.* Adult plants became denuded and typically dense canopy was thinned for a short period of time. This was seen to facilitate recruitment in *Cystophora* as growth conditions in the sub-canopy environment were improved and the newly settled offspring were able to achieve rapid growth.

The overall strategy for success in *Cystophora* therefore relied on the timing of the various life-history processes to promote this mechanism and enable the "bank of sub-canopy juveniles" to thrive.

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Overview and Aims

General rationale

Fucoids (Fucales, Phaeophyceae) are large brown algae, which contribute substantially to the earth's macroalgal biomass, ranging from arctic and Antarctic waters, through temperate and tropical regions (Lüning 1990). The majority of fucalean genera are found in Australasian waters where it is not uncommon to observe large, multispecies subtidal fucoid communities (Chapman 1995, Choat & Schiel 1982, Collings & Cheshire 1998, Edgar 1986, Lindauer *et al.* 1961, Shepherd & Womersley 1970, 1971, 1976). Despite this, most studies of the ecology of fucoid communities have been carried out in the northern hemisphere. A fundamental difference does however exist between the systems of the northern and southern hemispheres and this has most likely caused the imbalance in research. The fucoids of the northern hemisphere are intertidal and easily accessible whereas Australasian representatives are predominantly subtidal (with only a few exceptions including *Hormosira banksii* and *Cystophora torulosa* which are intertidal).

Mixed fucoid stands are a common feature of subtidal macroalgal systems along the southern Australian coastline and it is not unusual to find *Cystophora* J. Agardh (Fucales, Phaeophyceae) as a dominant canopy member of such communities (Collings & Cheshire 1998, Womersley 1964, Shepherd & Womersley 1970, 1971, 1981). To date however, there have been few studies on the factors which control the structure and function of these communities. This is most likely a reflection of the void in published information on the autecology of prominent species (like *Cystophora*) which is fundamental to an understanding of the processes which operate within algal communities.

The objective of this study is to provide a quantitative, temporal assessment of growth, reproduction and recruitment of three species of *Cystophora* from a shallow subtidal community in South Australia and in so doing, to provide the first insight into a number of life history strategies of this important genus.

Specific aims

In order to achieve this objective, the following aims must be addressed:-

- To quantify the dynamics of growth of *Cystophora* species within the community
- To investigate the importance of timing, and the allocation of resources to reproduction
- To monitor processes of recruitment and early community development

Thesis layout

Chapter one provides a general introduction to the biology of *Cystophora* and outlines the research rationale. Chapter two introduces the research site and the species of *Cystophora* studied. Chapter three outlines a study of the temporal changes of the community as a whole and highlights some important demographic features of the three species. Chapters four to six present information on the life history processes of growth (four), reproduction (five) and recruitment and early community development (six). Chapter seven provides a synthesis of the research by drawing together the important findings of the study. An overall picture of the community is presented and the importance of Cystophora within the community discussed.

CHAPTER ONE..General Introduction

Fucoids feature strongly in marine algal research but there is still much work to be done to improve our knowledge of their ecology (Chapman 1995, Lobban & Harrison 1994, Santelices 1990). In the northern hemisphere, fucoid research began as early as 1909 and has progressed steadily since the 1970's (Chapman 1995). In Australasia however, the research record is comparatively poor and little work has been done on the ecology of prominent species like *Cystophora.* This most likely reflects the difference between the intertidal existence of fucoids in the northern hemisphere and predominantly subtidal existence in the southern hemisphere. There is also a lack of published information on the life histories, demography and phenology of even the most prominent species, and it is this concern which is addressed in this thesis.

Cystophora is the largest fucoid genus in South Australia and is characteristically found on rocky coastlines. To date, studies have primarily concentrated on the phytochemistry (Amico 1995), taxonomy (Womersley 1964, 1987), anatomy (Fritsch 1945, Gruber 1896, Klemm & Hallam 1987, Nizamuddin 1964, Reinke 1876) and biogeography (Edgar 1986, Nizamuddin 1970, Womersley 1964) of the genus, but more recently, a few studies have addressed aspects of its ecology (Cheshire *et al.* 1996, 1999, Emmerson & Collings 1998). This information is reviewed below.

The biology of *Cystophora* J. Agardh (Fucales, Phaeophyta)

Morphology and anatomy

The order Fucales (Phaeophyceae) is classified on the basis of three major characteristics (Clayton 1988, Womersley 1964) :-

1) growth initiated from a three or four-sided apical cell found in a depression at the tip of the lateral.

2) presence of cryptostomata and conceptacles in which antheridia and oogonia are borne. Oogonia giving rise to one, two, four or eight eggs.

3) an oogamous, diplontic life history.

A study of ten species by Nizamuddin (1964) revealed that *Cystophora* underwent growth from three-sided apical cells (characteristic of the Cystoseiraceae), which were located in mucilage filled depressions at the ends of the laterals. In vegetative tissue, the meristoderm cells surrounding the apical cells remain meristematic throughout the life of the alga (Klemm 1985, Nizamuddin 1964). Examination of reproductive material showed the presence of conceptacles which were bisexual in most cases. Each antheridium gave rise to 64 antherozooids, but each oogonium produced only one egg, another feature characteristic of the family Cystoseiraceae.

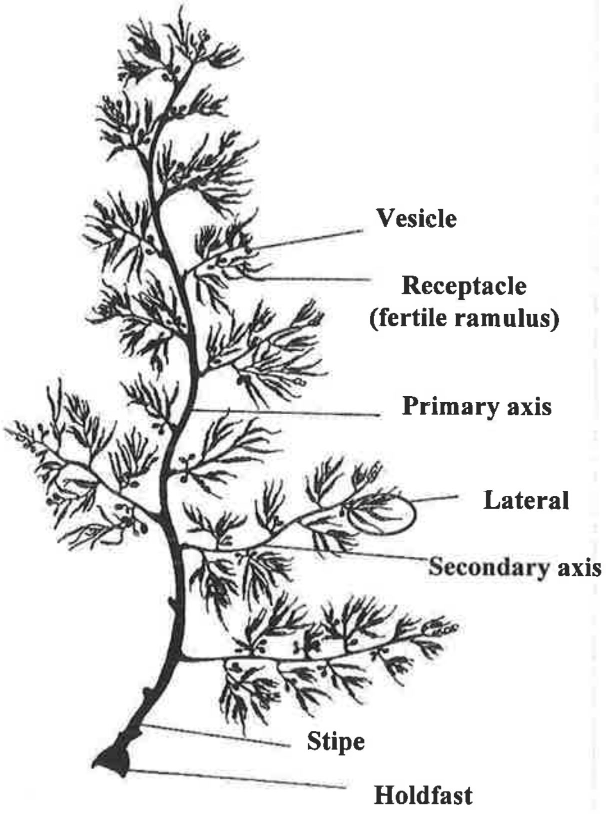


Figure 1.1. A stylised *Cystophora* thallus showing the characteristic features of the genus; a discoid holdfast for attachment, a single, flexuous primary axis which is denuded of branches in the lower (stipe) region and number of higher orders of branches which terminate in ramuli. The ultimate order of branches on which the ramuli are borne are referred to in the current study as laterals. In this case the thallus is fertile and so the ramuli have become swollen receptacles.

The algal thallus is parenchymatous and is comprised of three tissues (as with all Fucales), a pigmented outer meristoderm, which is photosynthetic, an inner cortex and central medulla. The cortex and medullary tissues, besides providing a means of support, are believed to play an important role in the transport and storage of photoassimilates.

Morphological studies have shown the genus to be characterised by the presence of a discoid holdfast, a single flexuous main axis (with the exception of *Cystophora intermedia* which has numerous primary axes) and lateral branches arising from the flattened faces or edges of the main axis (Fig. 1.1). Branching in *Cystophora* is therefore distichous as opposed to the radial branching of other members of the Cystoseiraceae. Thalli may reach lengths of several metres and may produce a number of orders of branching giving a relatively simple to bushy appearance. Vesicles are present on some species (Fig. 1.1) but their occurrence and shape vary greatly with habitat.

The genus was monographed by Womersley in 1964 and the description refined after the work of Klemm and Hallam (1987) revealed that the flexuous nature of the axes was a result of monopodial branching where the main apical cell was displaced during division to produce laterals of unequal length, and not as a result of sympodial branching as originally believed. This pattern of growth and branching is more highly organised than other Fucales and is suggested to be indicative of a more advanced genera (Klemm 1985). Womersley (1987) provides a revised description of the genus with anatomical and distributional information.

Life history

Cystophora is a perennial genus, as yet age determination is not possible but individuals are believed to live for several years (Womersley, pers. com.). Onset of reproduction in other fucoids is size rather than age specific (Creed 1995, Schiel 1985a) and in the absence of direct confirmation, it seems reasonable to assume that this is probably the case with *Cystophora*. Reproduction is sexual, oogamous and diplontic. The diploid sporophyte is the only free living phase, with the haploid phase being represented in the gametes only. The absence of an alternation of generations in the Fucales is generally accepted, however other interpretations of the situation still arise in the literature (see Clayton 1984, Jensen 1974).

The fertile *Cystophora* thallus can be identified by the presence of swollen ramuli which are termed receptacles (Figs 1.1, 1.2). The ultimate laterals are referred to as ramuli in all species except *C. xiphocarpa,* which only has secondary axes extending from the main axis with areas of these becoming fertile. Within the receptacles are conceptacles, spherical shaped pits in which the male antheridia and female oogonia develop (Fig. 1.2). The reproductive structures are protected by numerous sterile hairs or paraphyses, which develop prior to the antheridia and oogonia. The paraphyses fill the lumen of immature conceptacles and may also play a role in aiding the extrusion of the mature gametes from the conceptacle as they protrude from the ostiole (an opening in the conceptacle chamber) immediately prior to gamete release (Klemm 1985).

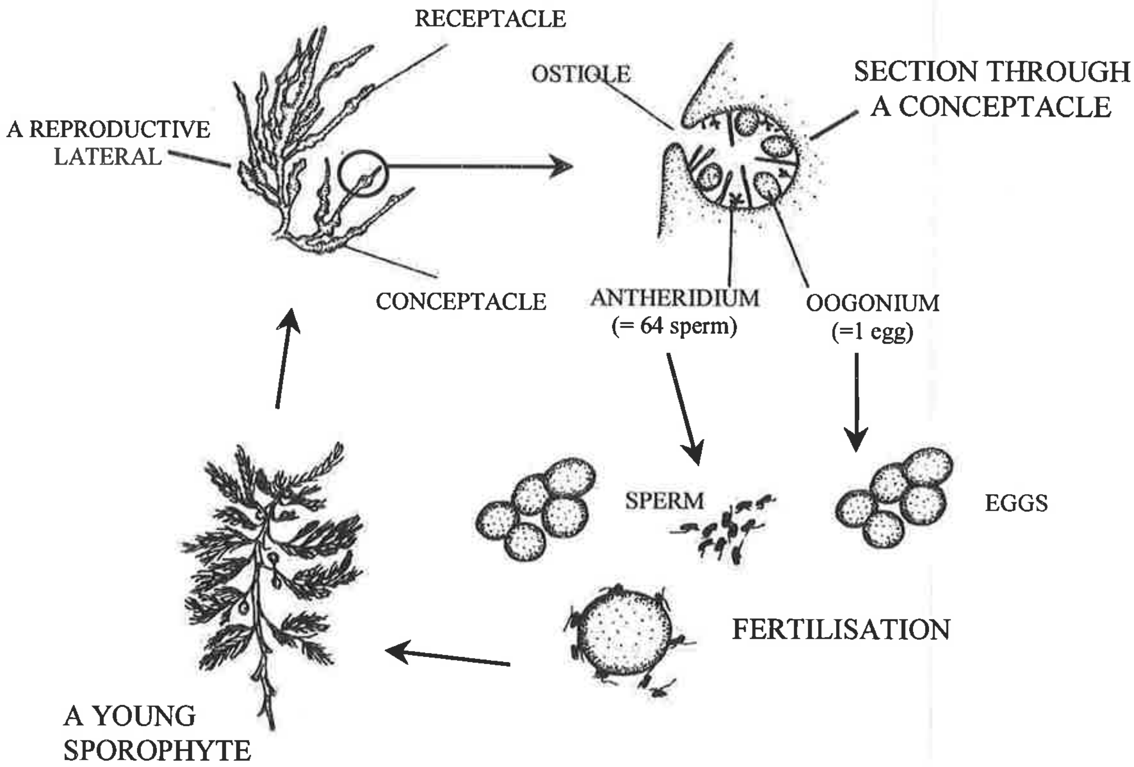


Figure 1.2. Reproduction in *Cystophora* is sexual, oogamous and diplontic. Fertile thalli can be identified by the presence of receptacles or swollen ramuli. Gametes are produced in conceptacles, which are embedded in the receptacles. Receptacles and conceptacles may be uni or bisexual. Haploid eggs and sperm are extruded via the ostiole of the conceptacles and fertilisation occurs on contact with seawater. The resulting zygote is diploid and once established, develops into the new sporophyte generation.

Some species develop conceptacles as they mature and may therefore be potentially fertile all year round; others develop fertile receptacles seasonally, which are lost after the gametes are shed (Womersley 1964). The arrangement of conceptacles, usually in rows is characteristic of the species. All species except *Cystophora siliquosa* are monoecious with numerous antheridia and oogonia contained in bisexual conceptacles. Unisexual conceptacles are common but are generally found within bisexual receptacles (Klemm 1985, Nizamuddin 1964, Womersley 1964).

Each oogonium produces a single egg and is extruded into the water column via the ostiole (Fig. 1.2). On contact with sea water the oogonium wall ruptures and releases the egg. Sixty-four antherozooids are released from each antheridium, similarly on extrusion from the ostiole and in contact with seawater (Klemm 1985, Nizamuddin 1964). Under still water laboratory conditions, eggs were observed to remain on the surface of the parent thallus once exuded and fertilisation occurred whilst there (Nizamuddin 1960). It is probable even under turbulent conditions that fertilisation occurs in close proximity to the parent thallus. Klemm (1985) found gamete production and release to be continuous through the fertile period of intertidal species of *Cystophora*, with simultaneous release of gametes from all conceptacles. Oogonia are in general released prior to antheridia; the eggs have numerous chloroplasts and are packed with vesicles containing the necessary materials for germling growth. The antherozooids are motile and possess a reduced number of chloroplasts. They have no eyespot unlike, many other algal zooids, and in the laboratory were viable for approximately one hour (Klemm 1985). After fertilization occurs, the resulting zygotes settle and develop into juvenile diploid sporophytes.

Many species of fucoids, including *Cystophora,* have cryptostomata scattered amongst the conceptacles of fertile receptacles. It is suggested that their development may be related to habitat as they have only been reported in intertidal and estuarine species (Fritsch 1945, Klemm 1985). Although observed by Klemm (1985) in intertidal species of *Cystophora,* they have not been found in any of the subtidal counterparts (Womersley, pers. com.). Cryptostomates characteristically contain dense tufts of paraphyses, intermingled with mucus producing structures and most probably play a role in reducing dehydration during periods of exposure (Fritsch 1945).

On the basis of their complex anatomical structure and the absence of an alternation of generations in their life history, the Fucales are considered by many to represent the most highly evolved order of the Phaeophyceae. Those species exhibiting bilateral branching are regarded as more primitive members from which the radially branched forms were derived (Clayton 1981, 1984, Fritsch 1945, Womersley 1964). Within the genus *Cystophora* both forms of branching are found, further comments on the possible evolutionary pathway of the various species and the relationship with other genera of Cystoseiraceae are discussed by Womersley (1964). Phytochemical studies on genera of the Cystoseiraceae by Amico (1995), suggest those species with the most complex metabolites to be more highly evolved. Those species of *Cystophora* which have been analysed in this way appear to correspond with the evolutionary scheme proposed by Womersley (1964). Jensen (1974) however, supports an alternative view and proposes the radially branched genus *Bifurcariopsis* Papenfuss (Cystoseiraceae) to approximate the fucalean progenitor, and recognises the presence of the gametophyte stage in the fucalean life history as a highly reduced endosporic form.

Biogeography

The genus *Cystophora* is endemic to southern Australasia (Womersley 1964) as are two other closely related genera *Acrocarpia* and *Caulocystis*. Of the 23 species of *Cystophora*, most are confined to southern Australia and Tasmania, with a few species extending into the temperate waters of Western Australia and New South Wales (including Lord Howe Island). Six species are found in New Zealand, two of which are found only there (Lindauer *et al.* 1961, Millar & Kraft 1994, Womersley 1964).

All species are characteristic of the upper sublittoral zone with the exception of *C. torulosa* which is frequently found in the intertidal zones of Victoria, Tasmania and New Zealand (Edgar 1984, Lindauer *et al.* 1961, Sanderson & Thomas 1987, Shepherd & Womersley 1970, 1971, 1976, 1981). *C. subfarcinata* may be found in emergent situations during low tides (Shepherd & Womersley 1971), and *C. intermedia* is characteristic of the sublittoral fringe under extreme rough water conditions (Womersley 1964). With the exception of *C. cymodoceae*, which is epiphytic on *Amphibolis antarctica*, all species are epilithic (Womersley 1987). A few species are confined to deeper waters such as *C platylobium, C. pectinata* and *C. racemosa,* but in general, species of *Cystophora* are found in most shallow, rocky subtidal environments and intertidal rockpools with the more widespread representatives being confined to pools on rough water coastlines (Womersley 1964, 1987).

On Tasmanian coastlines there is very little overlap in the distribution of *Cystophora* species, each being confined to a particular environment (Edgar 1986), but this differs from the coastlines of South Australia, Victoria and New Zealand where it is not unusual to find up to six species in close proximity (Edgar 1986, pers. obs.). In fact 18 of the 23 species of *Cystophora* are found in the Gulf Waters of South Australia (Womersley 1964). The six species found in New Zealand appear to show much overlap in their distribution with many intergrades or possible hybrids occurring (Lindauer *et al.* 1961). It is interesting to note that those species found in common with Australia are all vesiculate forms which may have been dispersed to New Zealand waters from an original Australian source (Edgar 1986).

Mixed fucoid communities in which *Cystophora* is a prominent canopy species are a common feature of rocky coastlines in both oceanic and gulf environments of South Australia (Collings & Cheshire 1998, Shepherd & Womersley 1970, 1971, 1976, 1981). These communities are generally species rich but with only a few species ever dominant at any one location. For example, a fucoid association from West Island, South Australia, was defined by Shepherd & Womersley (1970) which comprised up to 80 algal species but with only seven common canopy dominants including four species of *Cystophora.*

The surveys of Collings & Cheshire (1998) and Shepherd & Womersley (1970, 1971, 1976, 1981) showed communities dominated by *Cystophora* to generally occur on coastlines with moderate wave action. Although it was realised by these authors that many physical and biotic factors influence species distribution and community composition, a general pattern was proposed that suggested other likely canopy dominants based on depth and level of water motion.

Ecology

Despite the prominence of *Cystophora* along the southern Australian coastline, very few published accounts have dealt with the ecology of the genus (or with fucoids in general). The work of Klemm (1981, 1985) covered the growth, development and cytology of intertidal representatives of the genus, and some aspects of the ecology, but this work remains unpublished. Three important studies have been carried out in South Australia and these focused on temporal changes in primary productivity (Cheshire *et al.* 1996) and aspects of recruitment (Cheshire *et al.* 1999, Emmerson & Collings 1998).

Fucoid dominated communities, in which species of *Cystophora* formed a substantial component of the canopy, were shown to be highly productive in South Australia (Cheshire *et al.* 1996). Productivity varied on a seasonal basis and was significantly higher in summer than winter but net productivity approached 20 kg wet weight m^{-2} $year^{-1}$ (Cheshire *et al.* 1996). An average standing biomass of 3 kg wet weight m^{-2} was estimated which implied an annual rate of biomass turnover of about six times. Such communities therefore have the potential to play a major role in the maintenance of near shore food webs (Cheshire *et al.* 1996).

Growth and survival of *Cystophora* and *Sargassum* recruits were monitored in a series of different sized clearances during the first six months of their life (Emmerson & Collings 1998). The results showed that the spatial extent of disturbance and the effect of the surrounding community influenced recruit abundance and growth rate, but with evidence to suggest much variability in the interactive processes occurring within the community (Emmerson & Collings 1998).

The effect of surrounding community was also shown to influence recruitment in *Cystophora* and *Sargassum* communities on rocky reefs in South Australia (Cheshire *et al.* 1999). A number of relationships between recruit abundance and adult community composition were demonstrated. Recruitment in *Cystophora* was positively correlated with the number of *Cystophora* adults in the canopy but negatively correlated with the abundance of adult kelp (*Ecklonia*) plants. The presence of *Sargassum* in the adult community appeared to have little influence on recruitment success in *Cystophora* (Cheshire *et al.* 1999). The study was however designed to assess whether local sand dredging activities were having an impact on reef health (the results do suggest this to be likely) rather than to demonstrate the mechanisms involved in the recruitment process.

Research rationale

It is clear from the brevity of the ecology section in the above review, that there is much work to be done on the ecology of *Cystophora.* Studies such as that of Cheshire *et al.* (1999) demonstrate a need for a basic understanding of the mechanisms that drive the patterns and relationships that are observed in community research.

It is generally accepted that the structure of populations and communities at various scales is determined by temporal and spatial variation in the life history traits of organisms (Fig. 1.3) coupled with physical processes and biological interactions (Chapman 1995, Dayton

1971, Lobban & Harrison 1994, Santelices 1990, Schiel & Foster 1986). Life history traits are the phenotypic expressions of all the growth, development, and reproductive events that occur during the life of an individual (Clayton 1990) and hence comprise the life history of that individual (Begon *et al.* 1990, Clayton 1990, Schiel & Foster 1986).

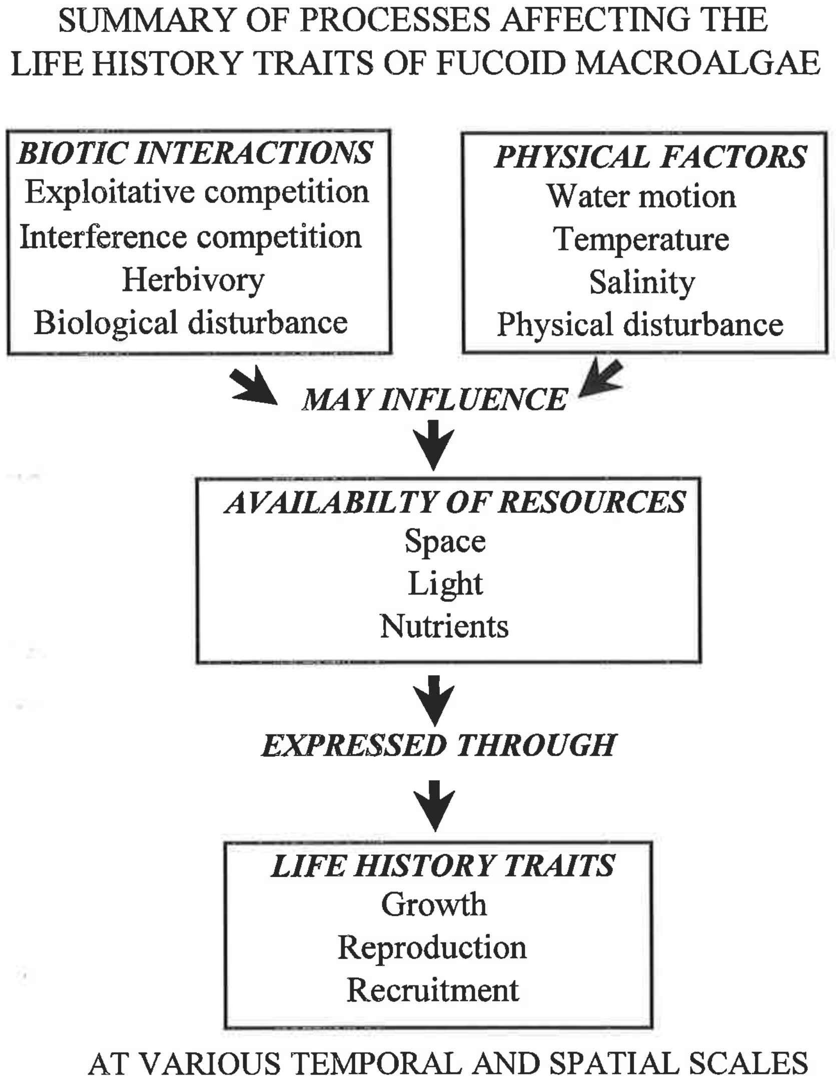


Figure 1.3. The influence of physical factors and biotic interactions on the availability of resources is ultimately expressed through the life history traits of individuals in the community. Life history traits pertaining to growth, reproduction and recruitment of individuals, are generally easy to identify and quantify which renders them ideal for monitoring patterns of change in any community, population or individual (Modified from Schiel & Foster 1986).

Some aspects of a life history are fixed by long-term evolutionary forces, and the genotype of the individual (Begon *et al.* 1990) e.g. all species of *Cystophora* produce a single egg per oogonium (Nizamuddin 1964, Womersley 1964). Most aspects do, however, vary due to the ever-changing interaction between the individual and its environment (Begon *et al.* 1990, Clayton 1990, Schiel & Foster 1986). As a result, the life history of an individual will most likely be unique as it reflects everything that has been experienced by that individual throughout its entire lifetime (Clayton 1990, Schiel 1990, Schiel & Foster 1986).

In natural communities, the biotic and physical processes operating within the system are often intricately interwoven and this makes them difficult to distinguish. Life history traits are, however, relatively easy to identify and quantify e.g. life span, growth rates, age to first reproduction and reproductive effort, and, as they reflect everything that is experienced by an individual during its lifetime (Fig. 1.3), they provide an ideal mechanism for monitoring patterns of change in any community, population or individual (Clayton 1990, Schiel & Foster 1986).

With this in mind, the objective of this research is to address a number of important phenological and demographic aspects of the life histories of three species of *Cystophora* in a mixed fucoid stand in southern Australia, and in so doing provide the first quantitative evaluation for subtidal representatives of this common genus. The work primarily concentrates on aspects of growth, reproduction and recruitment, with more specific aims being detailed in chapters four to six respectively. The research also aims to highlight any temporal changes in community structure and where possible, relate these to changes in the life histories of the three species of *Cystophora.*

It is hoped that an increased understanding of the demographics of growth, reproduction and recruitment will provide an insight into the life history strategies being employed by each species. It is also hoped that potential interactive and competitive processes that are at work within the Cape Jervis community may be highlighted and thus provide a direction for future research.

As one of the most prominent genera of subtidal communities along the southern Australian coastline, it is imperative that we improve our understanding of the biology of *Cystophora*, especially with so many of our coastal habitats under threat of degradation.

CHAPTER TWO..The Research Community and Species of *Cystophora* Studied

The community chosen for investigation was a mixed stand in which the genus *Cystophora* was a visibly dominant member of the canopy flora. This chapter provides an introduction to this community and to the species of *Cystophora* studied.

The research community

The study site was located in Backstairs Passage, about 500m east of the Cape Jervis breakwater, South Australia (Fig. 2.1). The site was approximately 60m from the shore in a depth of 4.5m (at low tide). Backstairs Passage is subjected to considerable tidal flow as it runs between the mainland and Kangaroo Island but it is protected from the majority of incoming oceanic swell by Kangaroo Island. The South Australian coastline is recognised as being cold temperate (Womersley 1984) with water temperatures in the vicinity of Backstairs Passage ranging from approximately 13°C in winter to 20°C in late summer (Tippins 1997).

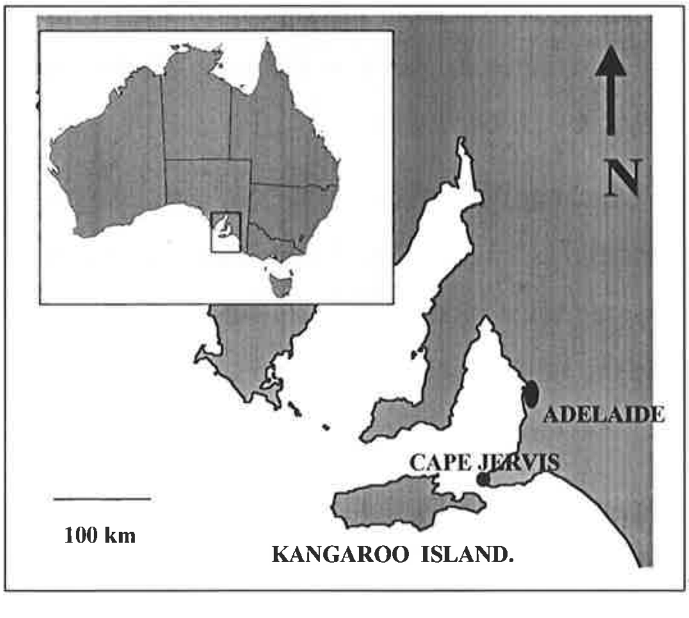


Figure 2.1. Map of Australia showing the position of the Cape Jervis study site. The site was located in 4.5m of water (at low tide) in Backstairs Passage, off the southern tip of the Fleurieu Peninsula, South Australia.

The community as a whole appeared to be rich in species (Tab. 2.1) and was structured into four levels, a stipitate canopy of predominantly *Cystophora* and other fucoid species, and a few plants of the kelp *Ecklonia radiata,* an understorey, a turfing community and encrusting coralline pavement covering the rock surface. No attempt was made to identify the species of encrusting coralline algae however they covered a substantial proportion of the substratum.

The substratum on which the fucoid community was growing mainly comprised rocky outcrops of Kanmantoo schist (S.A. Department of Mines 1954) with areas of loose rock between. Patches of sand and shingle were also intermixed and these tended to support seagrass (*Amphibolis antarctica*) communities. An interesting feature was the abundance of sponges and ascidians, which appeared to act as secondary substratum for many species of algae.

The species of *Cystophora* studied

Species of *Cystophora* appeared to dominate the fucoid community in terms of both biomass and abundance. Three of these species were studied in detail, *C. expansa*, *C. monilifera* and *C. subfarcinata.* Two other species, *C. brownii* and *C. moniliformis,* were also present and are generally referred to as "the other species of *Cystophora"* in this account. The following summaries are based on the more detailed taxonomic descriptions of each species by Womersley (1964, 1987).

Cystophora expansa (Areschoug)Womersley (Pl. 2.1a) is a common shallow water species found from Western Australia to New South Wales and Tasmania. It is typically found on shores of moderate water motion, occurring also in deeper intertidal pools. This species was dominant in the subtidal stand under study, in terms of both biomass and abundance and occurred in rockpools of the intertidal zone adjacent to the study site.

C. expansa is morphologically most similar to *C. monilifera* (Pl. 2.1a, b), but can be distinguished by its vesicles which are smaller and generally more numerous than those of *C. monilifera* and ellipsoid-ovoid in shape rather than subspherical and mutic as in *C. monilifera.* *C. expansa* is much darker in colour than *C. monilifera* and is generally very densely branched.

Table 2.1. The Cape Jervis community was rich in species with a fucoid dominated canopy. The understorey and turf component of the community was generally low in biomass despite the number of species present.

Canopy species	Understorey species	Turfing species
Acrocarpia paniculata	*Apjohnia laetrivens*	*Amphiroa anceps*
Amphibolis antarctica	*Areschougia congesta*	*Corallina officinalis.*
Caulerpa brownii	*Asparagopsis armata*	*Ectocarpus* spp.
Caulerpa flexilis	*Bellotia eriophorum*	*Haliptilon roseum*
Caulocystis cephalornithos	*Botryocladia sonderi*	*Liagora* sp.
Cystophora brownii	*Caulerpa brownii*	*Metagoniolithon stelliferum*
Cystophora monilifera	*Caulerpa flexilis*	
Cystophora moniliformis	*Caulerpa geminata*	
Cystophora polycystidea	*Caulerpa scalpelliformis*	
Cystophora subfarcinata	*Caulerpa simpliciuscula*	
Ecklonia radiata	*Chlanidophora microphylla*	
Lobospira bicuspidata	*Cirrulicarpus nanus*	
Sargassum decipiens	*Cladosiphon filum*	
Sargassum fallax	*Cladostephus spongiosis*	
Sargassum linearifolium	*Colpomenia sinuosa*	
Sargassum varians	*Dictyosphaeria sericea*	
Sargassum verruculosum	*Dilophus fastigiatus*	
Scaberia agardhii	*Erythroclonium muelleri*	
	Gloiosaccion brownii	
	Lobophora variegata	
	Lobospira bicuspidata	
	Osmundaria prolifera	
	Rhodymenia sp.	
	Sonderopelta coriacea	
	Zonaria sp.	

Cystophora monilifera J. Agardh (Pl. 2.1b) was a common member of the community under study. It is characteristically found on coasts of moderate wave action throughout the sublittoral zone. The species is widespread along the southern coast of Australia.

The secondary axes of *C. monilifera* have retroflex bases, often with broad basal wings and these usually remain as prominent residues when the axes are lost (Pl. 2.1b). This very characteristic feature of *C. monilifera* makes it easy to distinguish from the other species, in particular *C. expansa* (Pl. 2.1a).

Cystophora subfarcinata (Mertens)J. Agardh (Pl. 2.1c) is probably the commonest species on southern Australian coasts. It typically grows in areas of moderate to strong water motion to a depth of five metres. On sheltered coasts it may be vesiculate. In the subtidal community under study, *C. subfarcinata* was a common canopy constituent and was also found in the adjacent intertidal rockpools.

C. subfarcinata is easily distinguished from the other Cape Jervis species when it is fertile as the receptacles have sections of sterile tissue between the swollen conceptacles and are quite distinctive. When not fertile, the thallus characteristically has short, densely branched secondary and tertiary axes and laterals (Pl. 2.1c).

Cystophora moniliformis (Esper)Womersley & Nizamuddin (Pl. 2.1d) is a common shallow water species, widely distributed throughout southern Australia. It characteristically grows under moderate to strong water conditions but can survive in rockpools on rough water coastlines. In the subtidal community *C. moniliformis* was found frequently in the canopy.

C. moniliformis is the only species of *Cystophora* found at Cape Jervis with secondary axes arising from the edges (rather than faces) of the primary axis. The primary axis is robust and compressed with secondary axes and laterals appearing fasciculate (Pl. 2.1d). These features become obvious in the smallest of individuals making *C. moniliformis* quite distinct from the other species.

Cystophora brownii (Turner)J. Agardh (Pl. 2.1e) was found in both subtidal and intertidal communities at the study site but always at relatively low abundance. It is essentially a western species being found in Western Australia, western regions of South Australia and parts of Tasmania on coasts of moderate water motion.

The branching pattern of *C. brownii* is quite distinct even in juveniles, with laterals being alternately-distichously branched in one plane and this gives the whole thallus a rigid appearance (Pl. 2.1e). Branching of secondary and tertiary axes is similar to that of *C. monilifera,* being retroflex with broad basal wings however, *C. brownii* has very prominent rounded axils and no vesicles.

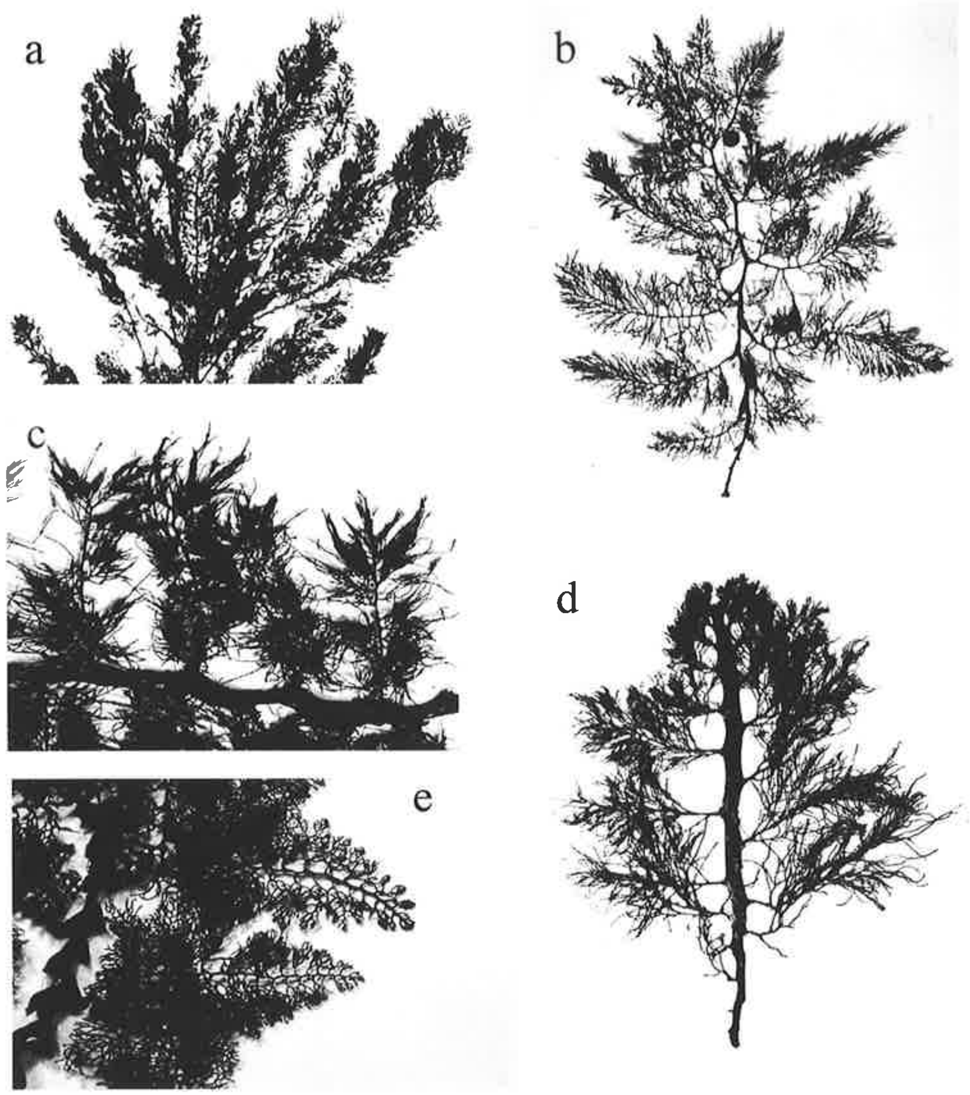


Plate 2.1. **(a).** fertile laterals of *C. expansa,* **(b).** young thallus of *C. monilifera,* **(c).** detail of fertile laterals of *C. subfarcinata,* **(d).** a juvenile thallus of *C. moniliformis* and **(e).** detail of branching in *C. brownii.* All five species of *Cystophora* from the Cape Jervis community showed similar thallus morphology however, each species was quite distinct and easily identified. The specimens shown here are part of the research herbarium lodged in the Department of Environmental Biology, University of Adelaide.

CHAPTER THREE..Temporal Patterns of Change in the Structure of the Mixed Fucoid Community

An understanding of structure and dynamics of any population or community must be based on knowledge of the quantitative descriptors of that community (Schiel 1988). This chapter outlines the results obtained from a series of surveys that were designed to monitor temporal patterns of change in three such descriptors (standing biomass, abundance and size distribution). The results show community structure to be variable through time depending on the demographics of *Cystophora,* the community dominant.

Introduction

Demographic and phenological studies provide the first step in our understanding of community organisation as they provide the quantitative data required to interpret any observed patterns of change (Chapman 1986, Schiel 1988, Schiel & Foster 1986) and as such, they are fundamental to the study of community ecology.

A comprehensive analysis of community organisation must however go beyond this to identify the functional roles of the major community components (Dayton 1971) and the mechanisms of change (Olson & Lubchenco 1990, Paine 1990). The importance of such mechanisms can only be inferred from demographic analysis and therefore once highlighted, must be rigorously tested with the use of manipulative experiments.

Algal population and community dynamics are driven by two primary demographic parameters, recruitment and mortality, at all stages in the life history (Chapman 1986). These are in turn regulated by competition, grazing and abiotic factors, over various temporal and spatial scales (Fig. 1.3). The underlying mechanisms which drive these changes are still poorly understood in many prominent algal species primarily due to the difficulty of experimentally manipulating subtidal communities (Dayton 1971, Kennelly 1983) and working with the often microscopic early life stages (Vadas *et al* 1992) .

Subtidal communities are not static due to the processes of disturbance and the complex interactions which operate within them. Change in community structure therefore, may be manifested in a number of ways. As a consequence, the quantitative descriptors used to monitor changes in the community must be chosen with care. For example, an increase in standing biomass may result from either an increase in the number of individuals present or from an increase in size of existing individuals. In either case, measures of change in both individual plant biomass and number are required to determine the likely cause of change.

A number of demographic analyses of fucoid populations are reported in the literature and the most significant of these are reviewed by Chapman (1995). None of these studies however can be considered comprehensive, with the exception of Ang's 1991 study of *Fucus distichus.* In the Australasian region a few studies have addressed aspects of the demography of *Carpophyllum* (Choat & Schiel 1982, Schiel 1985a), *Cystophora* (Emmerson & Collings 1998), *Landsburgia* (Choat & Schiel 1982, Schiel 1988) and *Sargassum* (Choat & Schiel 1982, Emmerson & Collings 1998, Kendrick 1994, Kendrick & Walker 1991, 1994, Schiel 1985a, 1988) but the only quantitative information available on the composition of mixed fucoid stands in South Australia comes from the surveys of Cheshire *et al.* (1999), Collings & Cheshire (1998) and Shepherd & Womersley (1970, 1971, 1976, 1981).

The studies of Shepherd & Womersley (1970, 1971, 1976, 1981) and Collings & Cheshire (1998) provided estimations of standing biomass for mixed fucoid communities influenced by oceanic waters and protected gulf waters respectively. Standing biomass was shown to be positively correlated with wave exposure at the gulf sites (Collings & Cheshire 1998) and these communities generally supported a lower standing biomass than those of the oceanic sites surveyed by Shepherd & Womersley (1970, 1971, 1976, 1981). Standing biomass at the gulf sites ranged from 421 to 1528 g dw m^{-2} (Collings and Cheshire 1998) whereas standing biomass at the oceanic sites was typically in excess of 1500 g dw m^{-2} (assuming a wet:dry weight ratio of 6:1, as in Collings & Cheshire 1998).

Despite the fact that seasonal patterns of growth and productivity have been recognised for many species of algae (Bacon & Vadas 1991, Brenchley *et al.* 1996, Chapman & Craigie 1977, Gagne *et al.* 1982, McCourt 1985, Prince & O'Neal 1979, Schiel 1985a, 1985b) there has been no or little consideration of temporal patterns of change in standing biomass of communities. The surveys of Collings & Cheshire (1998) essentially took place in spring although two sites were re-surveyed in autumn and reportedly showed no significant differences in the standing biomass. The surveys of Shepherd & Womersley were made at various times throughout the year and over a number of years in the case of the 1970 and 1980 studies. These authors acknowledged that changes in standing biomass occurred as a result of seasonal patterns of growth in the dominant species but did not attempt to quantify any of the changes.

A number of similar surveys have been carried out in New Zealand where *Carpophyllum, Sargassum* and *Landsburgia* are the common fucoids. Much of this work has been reviewed by Schiel (1988, 1990) who was cognisant of the importance of seasonal influences on the structure and composition of subtidal communities however, much of the research presented was more concerned with changes in community structure in terms of spatial patterns.

Other relevant studies of a demographic nature have concentrated on aspects of recruitment in *Cystophora* and *Sargassum* communities in South Australia and Western Australia (Cheshire *et al.* 1999, Emmerson & Collings 1998, Kendrick 1994, Kendrick & Walker 1991, 1994). Recruitment in mixed *Sargassum* beds in Western Australia was demonstrated as having an important role in buffering the effects of mortality in the adult population and hence contributing to the survival of the community through time (Kendrick & Walker 1994). The adult canopy however, has been shown to directly influence recruitment in both *Cystophora* and *Sargassum* communities (Cheshire *et al.* 1999, Emmerson & Collings 1998, Kendrick 1994).

A positive correlation existed between numbers of adults and recruits of both *Cystophora* and *Sargassum* on rocky reefs in South Australia (Cheshire *et al.* 1999). This suggests that the presence of an adult canopy influenced levels of recruitment in the immediate vicinity and may reflect the nature of dispersal in these species. Species of *Sargassum* from Western Australia showed limited propagule dispersal with settlement generally occurring within 1m of the parent thallus (Kendrick & Walker 1991).

Although successful recruitment in *Cystophora* may rely on the proximity of fertile adults, the presence of an adult canopy may in fact provide a physical barrier or impediment to recruitment. Fewer juveniles of both *Cystophora* and *Sargassum* were seen below the adult canopy than in adjacent areas with less or no canopy cover (Emmerson & Collings 1998, Kendrick 1994). Spatial distribution of adults and size of area available for colonisation therefore appear to influence the survival of *Cystophora* and *Sargassum* recruits but the studies of Emmerson & Collings (1998) and Kendrick (1994) also highlight the necessity to consider temporal variation in recruitment.

The current research presents information on the influence of *Cystophora,* the community dominant, on the structure of a subtidal mixed fucoid community in South Australia. The primary aims of this section of research were:-

- to quantitatively describe the structure of the mixed fucoid community
- to highlight any temporal patterns of change in this structure
- to quantify the extent to which *Cystophora* dominated the community canopy (in terms of standing biomass and abundance)
- to assess the influence of *Cystophora* dynamics on the structure of the community as a whole.

Methods

Field methodology

A quantitative description of the floristic structure of the community was obtained by destructive sampling at regular intervals from October 1991 through to March 1993. The data collected were used to monitor changes in standing biomass and abundance (number of individuals per unit area) of the community components and also changes in the size distribution of *Cystophora.*

A minimum of twenty randomly placed 30x30cm quadrats (as used by Shepherd & Womersley 1981) was collected on SCUBA at approximately six weekly intervals between October 1991 and March 1993. Sampling involved the removal of all canopy and understorey vegetation within the quadrat and as much turfing vegetation as possible without scraping. The coralline pavement was left. Particular care was taken to ensure that all fucoid juveniles were harvested. The material was collected in plastic bags, excess water was drained on reaching the surface and the bags were returned to the laboratory as quickly as possible. Only vegetation growing on rocky substratum was sampled and old sample scars were avoided.

The material harvested from each of the collections had multiple usages within the various studies. Biomass data were required for the analysis of community vegetation structure, growth rates of individual species (Chapter four) and reproductive allocation studies

(Chapter five). Tissue samples were required for the assessment of reproductive state (Chapter five).

Laboratory investigations

The harvested vegetation from each sample was divided into three categories on return to the laboratory, all species of *Cystophora,* other canopy forming species (>200mm in length), and understorey plus turfing community. The canopy was defined as any vegetation greater than 200mm in height. This criterion was set after a preliminary study of stipe length data and *in situ* measurements (distance from substratum to canopy).

Voucher specimens were taken for all species, and these are lodged in the Department of Environmental Biology, University of Adelaide.

For each *Cystophora* individual, length (mm) and dry weight (g dw) were recorded. Maximum length of the thallus was measured by extending the laterals and axes to their full. This measure was chosen in preference to length of primary axis as damage to the primary axis was not uncommon and observation of the thallus suspended in the water column showed that this method was the most realistic measure of thallus height. Each thallus was dried to constant weight and the data were used to provide estimates of standing biomass (g dw) for each species and for total *Cystophora* biomass.

The remaining canopy vegetation was scored for species presence and abundance, and a total canopy biomass (g dw) obtained per sample. Understorey (and turfing) vegetation was scored for species presence only and total understorey biomass (g dw). It was not possible to collect abundance data for many of the understorey and turfing species, as individual thalli were not clearly separated. This was also the case for several of the *Sargassum* species in the canopy. The component biomass estimations were combined to give the overall standing biomass (g dw) for each sample.

Cystophora individuals were assigned to size classes based on the following criteria:-

- recruits <50mm - individuals in this size range were usually difficult to identify beyond genus level
- juveniles 51-100mm

- sub-canopy juveniles 101-200mm - potentially in transition from juvenile to canopy status
- adult canopy 201-300mm, 301-400mm, 401-500mm and 501-600mm
- above canopy if >600mm - the lower limit of canopy height was based on preliminary studies of plant size and growth rates

The size classes chosen are comparable with the scheme proposed by Vadas *et al.* (1992) and are supported by the work of Emmerson & Collings (1998).

For the purpose of biomass determinations, species were classed as juveniles if <200mm. They were counted, measured and where possible identified, and were included in the understorey biomass component.

Analysis

Standing biomass and abundance data were analysed using univariate techniques from the JMP statistical package (SAS Institute Inc. 1995). One-way ANOVAs and post-hoc Tukey tests were used to test for significant differences in standing biomass and abundance through time. A 4th root transformation was applied to improve normality of the data. Homogeneity of variances was assessed with the Brown-Forsythe test and where these were significantly heteroscedastic a Kruskal-Wallis test was performed (Zar 1996).

Length data were organised into size classes and the % of individuals falling into each class calculated.

Results

Changes in standing biomass

General situation

A seasonal pattern of change in standing biomass was evident for the community (Fig. 3.1), which ultimately reflected the pattern of change for *Cystophora expansa*, which was the canopy dominant (Fig. 3.2a). Canopy plants comprised the majority of standing biomass (at least 73%). Understorey vegetation generally comprised less than 10% of the total biomass, and at times this dropped to negligible values (Fig. 3.1).

Standing biomass was typically low during summer (368 g dw m^{-2} in December 1992 and 404 g dw m^{-2} in December 1991) but gradually increased to peak in spring (927 g dw m^{-2} in September 1992). This pattern mirrored the change in total *Cystophora* biomass (Fig. 3.1) which comprised 47% to 84% of the total standing biomass.

The seasonal pattern of change in biomass for species of *Cystophora* and the community as a whole appeared to be an annual phenomenon (Figs 3.1, 3.2), at least within the 18 months of this study. Similar patterns of change in biomass were evident in late spring through to summer of 1991 into 1992 and 1992 into 1993 but some interannual variability existed.

The importance of *Cystophora* in the community

At any one time *Cystophora* was the dominant member of the community in terms of biomass (58% to 85%), ranging from 248 g dw m^{-2} in December 1991 to 770 g dw m^{-2} in September 1992 (Fig. 3.1).

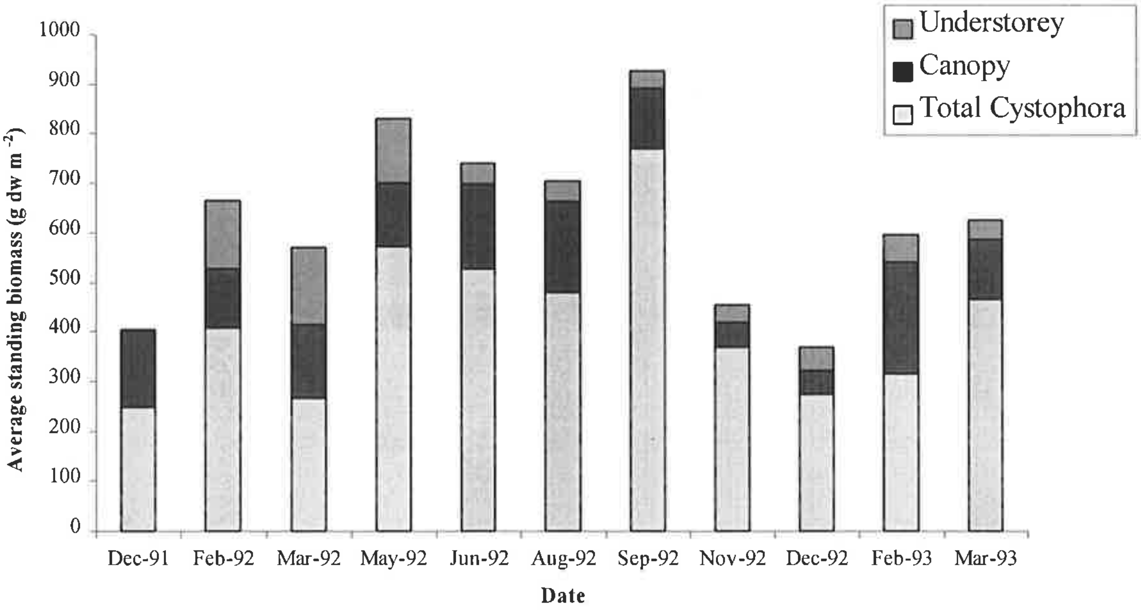
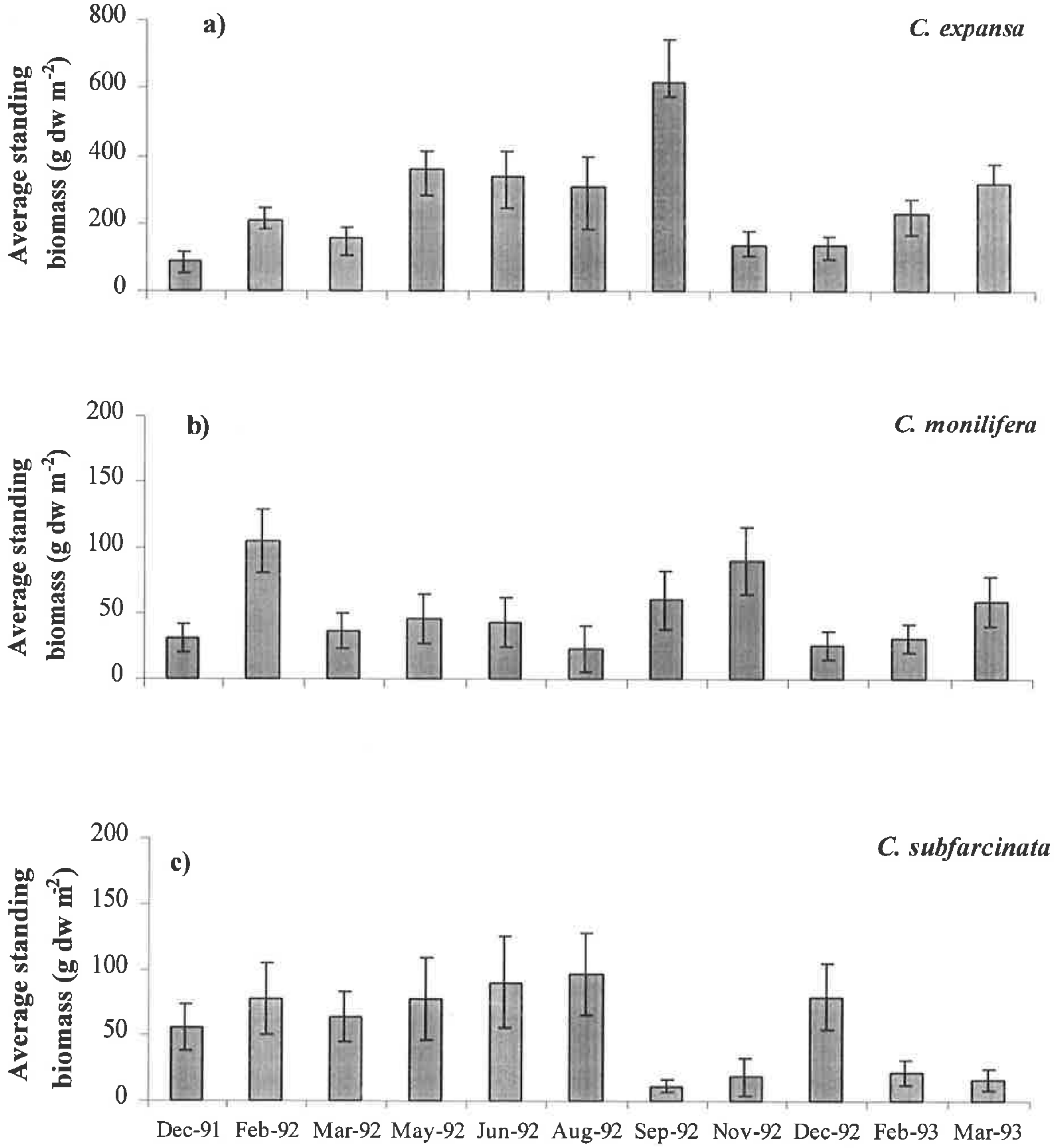


Figure 3.1. Standing biomass of the community (g dw m^{-2}) showed a temporal pattern of change and was maximal during winter and early spring. Most biomass existed in the canopy component of the community with understorey biomass being low if not negligible. At any one time, *Cystophora* comprised the majority of the canopy (and hence community) biomass. **Note** the x axis is not proportional.

The biomass of canopy species other than *Cystophora* accounted for only 49 to 226 g dw m^{-2}. The pattern of change in the biomass of these other species was generally similar to that of *Cystophora* (which may have reflected the number of other fucoid species present) but differed in showing a significant increase in late summer 1993 when *Cystophora* biomass was still low (Fig. 3.1).

C. expansa was clearly the canopy (and community) dominant at any one time (Fig. 3.2a) comprising 36% to 80% of the total *Cystophora* biomass with *C. monilifera, C. subfarcinata* and the other *Cystophora* species comprising only 5% to 26%, 1.5% to 29% and 3% to 34% respectively (Fig. 3.2b, c, d).



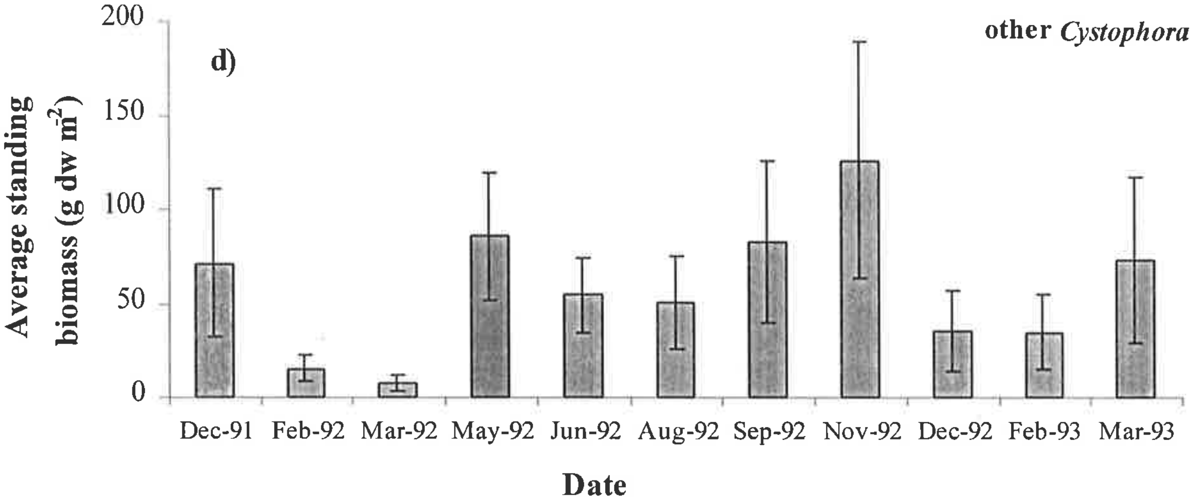


Figure 3.2a-d. A general pattern of change in standing biomass (g dw m^{-2}) was evident for all species of *Cystophora* although some specific differences were evident. Biomass was generally low in summer, increasing through autumn and reaching a maximum in late winter/early spring. The standing biomass of *C. expansa* was far greater than the other species. **Note** the x-axis is not proportional and the different scale on the y-axis for the *C. expansa* graph. Error bars = standard error.

Differences in seasonal patterns standing biomass between species of *Cystophora*

The seasonal pattern of change in biomass was similar for each species of *Cystophora* but some specific differences were evident (Fig. 3.2). Biomass was typically low during late spring/summer and gradually increased through the year to peak in late winter/spring. A distinct decrease in biomass occurred for all species subsequent to the period of maximal biomass (Fig. 3.2, Plate 3.1).

Seasonal change in biomass for *C. expansa* closely followed the general pattern, with a significant ($p<0.05$) peak in September 1992 (616 g dw m^{-2}), followed by a significant ($p<0.05$) decrease to remain low (136 to 228 g dw m^{-2}) in late spring into summer 1992/93 (Fig. 3.2a).

The pattern of change for *C. monilifera* differed in that the seasonal maximum in biomass occurred slightly later than the other species (Fig. 3.2b) in November 1992 (90 g dw m^{-2}). Great variability between replicates tended to obscure any statistical significance in the pattern of change in biomass, as highlighted by the average trends, with the exception of a significant ($p<0.05$) increase in biomass in late summer (February) 1992. This uncharacteristically high biomass value for *C. monilifera* corresponded with an apparent (although not statistically significant) increase in its abundance in the canopy (Fig. 3.3b) and most likely reflects the patchy nature of the community composition.

Plate 3.1. Denuded thalli of *Cystophora,* in particular *C. expansa,* were observed in the community during the summer months (1991) when standing biomass was typically low. Considerable thinning of the canopy occurred as a result of this decrease in standing biomass of *Cystophora.*

In *C. subfarcinata,* the seasonal maximum appeared to occur in late winter (97 g dw m^{-2}), earlier than in any other species of *Cystophora* (Fig. 3.2c). Biomass then dropped and generally remained low (less than 20 g dw m^{-2}) throughout spring 1992 into summer 1993. There were no significant changes ($p<0.05$) in biomass for *C. subfarcinata* with the exception of an increase in early summer (December) 1992. This exception to the general pattern of change in biomass again lends support to the notion of the community being patchy in its composition.

Although there was no power to test changes in biomass of other species of *Cystophora*, a pattern of change was evident but this differed slightly from the general pattern for *Cystophora* (Fig. 3.2d). Biomass was generally high during winter and spring, reaching a maximum of 126 g dw m^{-2} in November 1992, but was low during summer (less than 20 g dw m^{-2}).

Patterns of change in the standing biomass of the canopy (excluding Cystophora) and understorey

The non-*Cystophora* component of canopy biomass was variable (84 to 184 g dw m^{-2}) but appeared to gradually increase from summer 1991/92 through to spring 1992 when a significant ($p<0.05$) decrease occurred (Fig. 3.1). This decrease in biomass (to less than 50 g dw m^{-2}) coincided with the seasonal summer low in both community and *Cystophora* biomass. Biomass increased significantly ($p<0.05$) in late summer, again mirroring the pattern of change in the community as a whole (Fig. 3.1).

Understorey biomass generally accounted for less than 10% of the total community biomass (Fig. 3.1) except during late summer 1991/92 and autumn 1992 when it comprised 15.5 to 27.1%. Prior to this, biomass was negligible and therefore a relatively large increase must have occurred to produce the significant peak in late summer/autumn. This difference may have been due to the presence of *Erythroclonium muelleri,* a species of red alga which was unusually abundant in late summer/autum.

Changes in abundance of *Cystophora*

General situation

The abundance of *Cystophora* in the canopy ranged from 32 to 92 individuals m^{-2} (Fig. 3.3), increasing significantly during the course of this study due to an increase in the abundance of *C. expansa,* the most abundant species (Fig. 3.3).

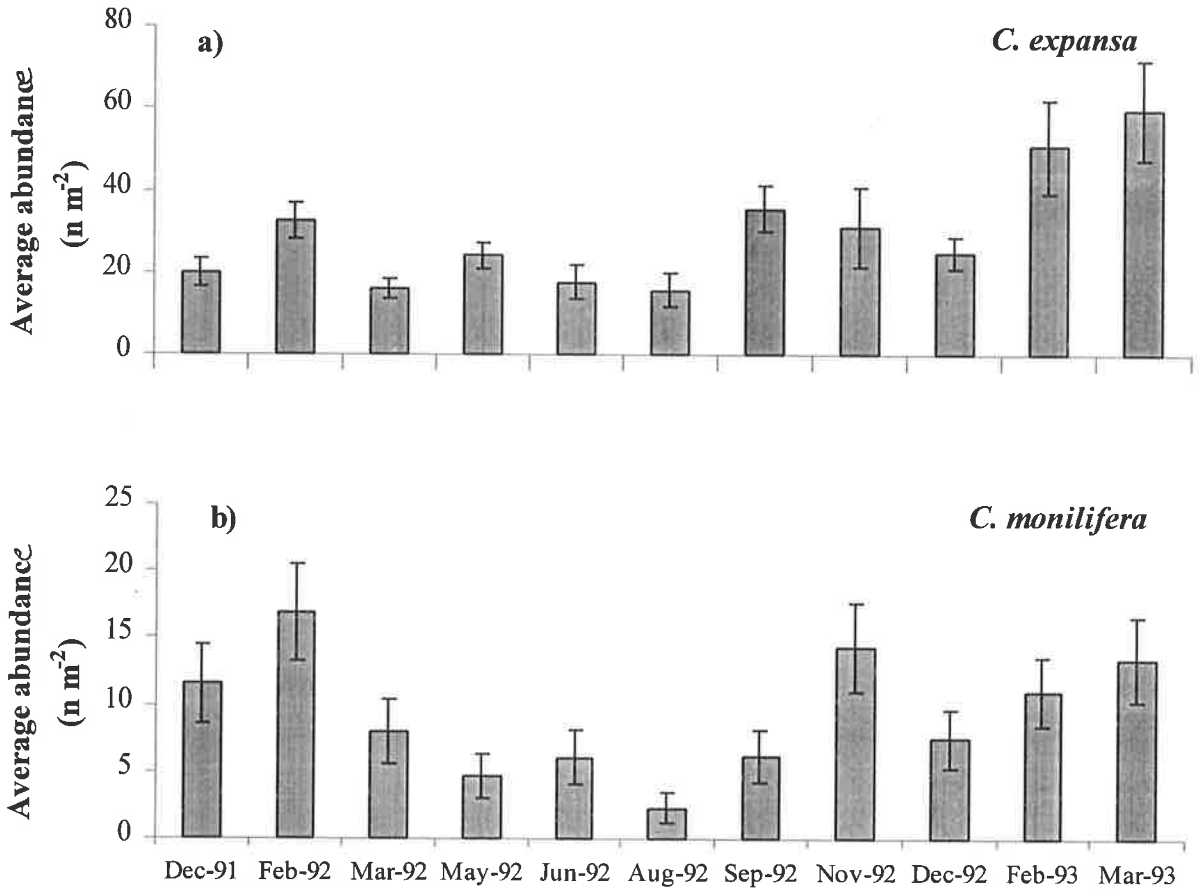
Abundance of *Cystophora* varied throughout the year (Fig. 3.3), it was generally lowest during the winter months with significant peaks ($p<0.05$) in both summer 1991/92 (81 m^{-2}) and summer 1992/93 (92 m^{-2}). This pattern essentially reflected changes in the abundance of *C. expansa,* which ranged from 16 to 60 individuals m^{-2} (Fig. 3.3).

Differences in abundance between species

C. expansa was clearly the dominant species in terms of abundance and comprised between 37% to 71% of the total number of individuals present (Fig. 3.3). At any one time there was always more *C. expansa* in the canopy than either *C. monilifera*, *C. subfarcinata* or the other species which comprised 7% to 27%, 5% to 27% and 6% to 22% respectively and in most cases *C. expansa* was more abundant than the sum of all of the other species (Fig. 3.3).

Abundance of *C. monilifera* was more variable but followed the general pattern (Fig. 3.3), being seasonally low during winter (2 to 6 m^{-2}) and significantly higher ($p<0.05$) in summer 1991/92 (17 m^{-2}) and late spring 1992/93 (14 m^{-2}). No significant changes ($p<0.05$) occurred in the abundance of *C. subfarcinata*, which fluctuated between 3 and 11 individuals m^{-2} (Fig. 3.3).

Changes in the abundance of the other species of *Cystophora* appeared to conform to the general pattern although no significant differences existed (Fig. 3.3). Abundance was high in early summer (December) 1991 (12 m^{-2}) and in the following summer/early spring in February and March 1993 (14 & 12 m^{-2}).



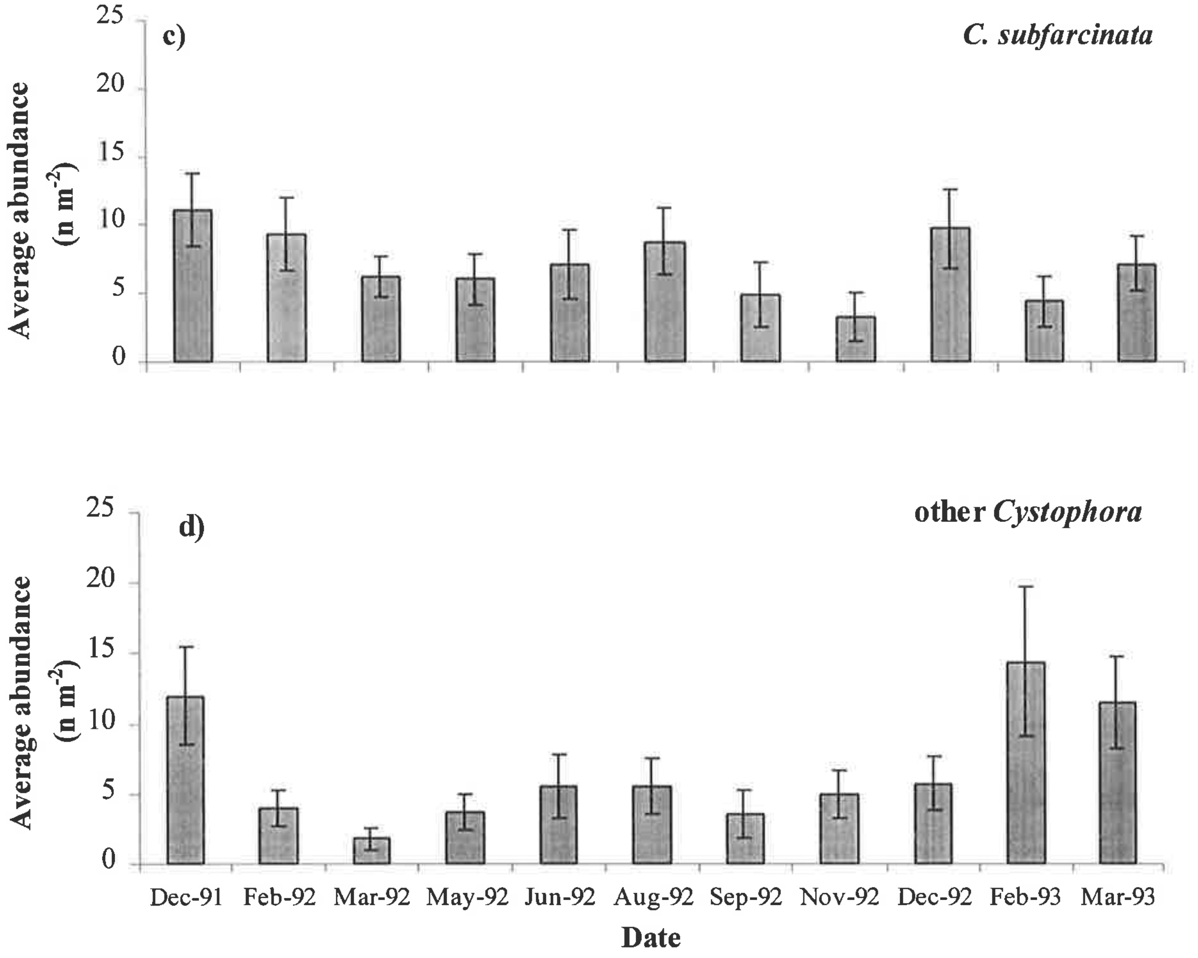


Figure 3.3a-d. The abundance (n m^{-2}) of adult *Cystophora* in the community showed a seasonal pattern of change, with low abundance occurring in autumn and winter, increasing through spring to peak in summer. *C. expansa* was by far the most abundant species in the community and was almost twice as abundant in summer 1993 than in summer 1992. **Note** the x-axis is not proportional, note also the different y-axis for the *C. expansa* graph. Error bars = standard error.

The abundance of juveniles in the community

The abundance of *Cystophora* juveniles ranged from 7 to 52 individuals m^{-2} with a maximum occurring in early autumn (March) 1992 (Fig. 3.4). The number of juveniles in the community decreased gradually from this time until early spring (September) 1992 after which they remained fairly constant (8 to 13 m^{-2}). The significant increase in abundance of juveniles between early summer (December) 1991 and early autumn (March) 1992 (Fig. 3.4) was indicative of a recruitment event at some time prior to or during summer 1991/92 but this was not observed in the subsequent year, at least before observations ceased in March 1993 (Fig. 3.4). This is not to say that recruitment did not occur in 1993, but did so outside the scope of the study, later in the season than observed in 1992 (Fig. 3.4).

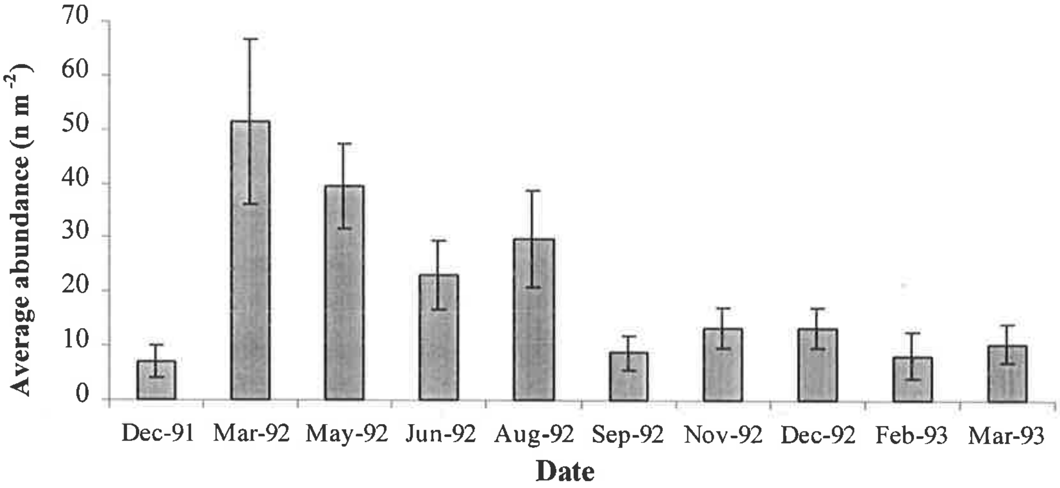


Figure 3.4. Recruits were present in the community throughout the year however they were seen in great abundance (n m^{-2}) in early autumn (March) 1992, which was indicative of a reproductive event at some time prior to that. Abundance of recruits declined gradually through the year presumably due to mortality and growth into adult status. A recruitment pulse was not observed in 1993 within the scope of the study suggesting it to have occurred slightly later in that year. **Note** the x axis is not proportional. Error bars = standard error.

Changes in the size structure of the *Cystophora* population

General situation

A progressive pattern of change in the size structure of the *Cystophora* population was evident during this period of study (Fig. 3.5) as individuals entered the system as recruits and made the transition to subsequent size classes.

The timing of recruitment and subsequent growth of individuals primarily drove seasonal patterns of change in the structure of the Cystophora population. The structure of an immediate post-recruitment population (March 1992) was typically dominated by the smaller size classes of individuals (Fig. 3.5c) but changed gradually through the year to one of more even distribution (November & December 1992) (Fig. 3.5g, h).

Important changes between different size classes

A high proportion (32%) of recruits (<50mm) were observed in the population in early autumn (March) 1992 (Figs 3.4, 3.5c) which suggested a prior reproductive event. Recruits were not observed in the community prior to March 1992 but remained in the population until the following year (March 1993) (Fig. 3.5j). The absence of recruits in the population during the first two sample periods (December 1991 and February 1992) probably resulted from them not being identified as *Cystophora* recruits at this early stage in the project. The proportion of recruits in the population declined substantially from early autumn (March) 1992 to 10% in late autumn (May) 1992 (Fig. 3.5d). This three-fold decrease did not however correspond with an equivalent increase in the number of juveniles, suggesting recruits to have been lost from the population. Numbers of recruits then decreased more gradually throughout the remainder of the study (Fig. 3.5e-j).

Juveniles (51-100mm) were always present in the population (Fig. 3.5), initially in low proportions (<5%) but they also increased substantially in early autumn (March) 1992 (Fig. 3.5c). They may have grown from very small recruits that were actually present during summer 1991/92 (Figs 3.5a & b) but not identified *in situ* (and hence not collected) or they may have resulted from a period of rapid post-recruitment growth. The proportion of juveniles in the population remained relatively constant (12% to 24%) throughout the remainder of the study.

Sub-canopy juveniles (101-200mm) were also present in the population at all times (Fig. 3.5) but contributed a larger proportion (>20%) of the population during summer/early autumn (Fig. 3.5a-d, i, j). This pattern was also observed in the 201-300mm size class of canopy plants (Fig. 3.5a-d, i, j). As both size classes represent the transition of individuals from juvenile to canopy status, this does not seem unreasonable. The strong seasonal influence suggests the summer/early autumn environment to promote the transitional phase.

Sub-canopy juveniles were highly abundant in late summer (February) 1993 (Fig. 3.5i) but their presence in the population did not correspond with any prior peak in abundance of recruits or juveniles (Fig. 3.5h) which begs the question, where did they come from? One explanation may be that damage and breakage of larger canopy plants by late summer storms could have resulted in a false representation of individuals in the sub-canopy size class. The low abundance of larger canopy plants at this time of year (Fig. 3.5i) certainly supports this theory however, during the recording of thallus length data, note was taken of any individuals that were either damaged or broken. No damaged or broken plants were recorded for February 1993.

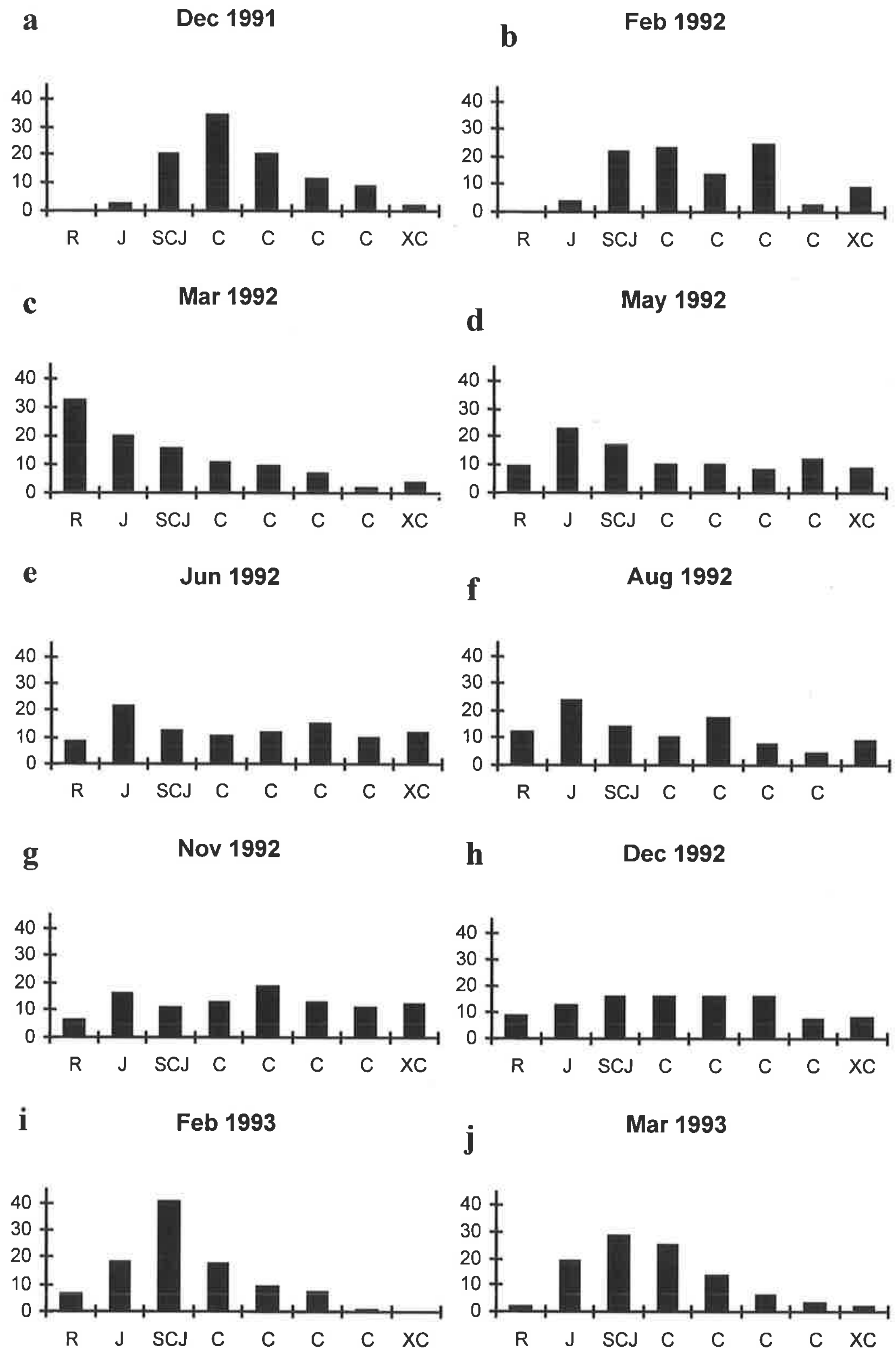


Figure 3.5. A progressive pattern of change in the size structure of the *Cystophora* population was evident as individuals entered the system as recruits and made the transition to subsequent size classes. Graphs a to j show the percentage of individuals falling into each size class at a particular time throughout the year. Codes on the x axis refer to R= recruits (<50mm), J= juveniles (51-100mm), SCJ= sub canopy juveniles (101-200mm), C=canopy plants (201-300mm, 301-400mm, 401-500mm, 501-600mm resp) and XC= large individuals (>600mm).

A more plausible explanation for the increase in sub-canopy juveniles at this time is that a patch of community was sampled in which the abundance of larger canopy plants was uncharacteristically low. Although care was taken to avoid old sample scars, destructive quadrats were chosen randomly and it is possible that the February 1993 sample was taken from an area previously disturbed. If one of the earlier sites (prior to the recruitment event) had been inadvertently re-sampled, then this could explain the size class structure of the population in February 1993 which had a lower than usual average canopy height (Fig. 3.5i).

The number of individuals falling into the other canopy size classes (201-600mm) was variable but generally showed a temporal progression of transition from one size class to the next (Fig. 3.5). Large individuals (>600mm) were generally more abundant through winter and spring (Fig. 3.5e-g).

Discussion

This research has shown community structure to be highly influenced by the temporal change in abundance of *Cystophora* and suggests dominance by this genus to be facilitated by the maintenance of a closed canopy for most of the year.

The structure of the community was typical of shallow subtidal fucoid communities found elsewhere in Australia (Collings & Cheshire 1998, Shepherd & Womersley 1970, 1971, 1976 & 1981) and New Zealand (Choat & Schiel 1982, Schiel 1985a, 1988, 1990), with a dense single layered canopy forming above a layer of understorey vegetation. Subtidal fucoid stands of the northern hemisphere generally differ in that the species are larger and form floating canopies on the sea surface, e.g. *Cystoseira osmundacea* in California (Schiel 1985b).

The seasonal range in standing biomass for the Cape Jervis community (368 to 927 g dw m^{-2}) was comparable with estimates from other southern Australian and New Zealand communities of similar depths in which large brown algae dominated. These typically ranged from 110 to 1600 g dw m^{-2} (Cheshire *et al* 1996, Collings & Cheshire 1998, Choat & Schiel 1982, Schiel 1985a, Shepherd & Womersley 1970, 1971, 1976 & 1980), with the largest biomass estimates often including the kelp *Ecklonia radiata* that was rare at the Cape Jervis site.

The abundance of *Cystophora* adults in the canopy at Cape Jervis (32 to 92 m^{-2}) was also comparable with other communities in which fucoids were dominant. Similar abundance values corresponding to the low and mid range of these estimates were found in mixed species *Sargassum* beds in Western Australia (Kendrick & Walker 1994) and mixed fucoid communities in New Zealand (Choat & Schiel 1982, Schiel 1995, 1990).

The increased abundance of *Cystophora* in the Cape Jervis canopy (to 92 m^{-2}) during summer 1992/1993 resulted from an increase in the numbers of *C. expansa* (60 m^{-2} or 75% of total *Cystophora*). These values begin to approach abundance estimates for monospecific stands of *Sargassum sinclairii* and *Carpophyllum maschalocarpum,* and single species dominated communities from New Zealand, which typically ranged from 130 to 250 m^{-2} (Choat & Schiel 1982, Schiel 1985a).

The temporal pattern of change in standing biomass for the community as a whole mirrored that of *Cystophora,* being high in spring and low in summer. Seasonal cycles of biomass change are not a new phenomenon in the fucoids and are generally linked to the production of reproductive structures (Bacon & Vadas 1991, Brenchley *et al.* 1996, McCourt 1985, Prince & O'Neal 1979, Schiel 1985b). The gradual increase in biomass at Cape Jervis through autumn and winter and substantial loss in late spring is now known to correspond with the development and post-reproductive shedding of receptacles in *Cystophora* (Chapter five). The non-*Cystophora* component of the canopy mostly comprised species of *Sargassum* with other fucoids such as *Caulocystis, Scaberia,* and *Acrocarpia.* Abundance was not estimated for the non-*Cystophora* canopy species and therefore it is not possible to determine whether the observed loss in biomass was due to the shedding of spent reproductive structures or to a loss in numbers.

Cystophora was able to maintain and even increase its dominance in the Cape Jervis community from spring 1991 through to autumn 1993. The maintenance of a closed canopy for most of the year was the strategy that enabled this. This was achieved through the coordination of reproduction, recruitment and growth processes.

For most of the year, the dense canopy mainly comprised a mix of individuals from 200mm to 600mm in length, although larger individuals did occur. As reproductive structures were produced, individuals "bulked out" and the overall density of the canopy was increased. The canopy thinned only once during the year in late spring and summer, as spent reproductive structures were lost.

Dense algal canopies have been shown to affect community composition by restricting the availability of resources and limiting recruitment of other species beneath them (Emmerson & Collings 1998, Kendrick 1994, Rapp de Eston & Bussab 1990, Schiel 1985a, 1988, 1990). Any opening of the canopy would therefore create opportunities for recruitment and improved growth in the understorey. It is probable therefore, that this was the cause of the low (and at times negligible) understorey biomass at Cape Jervis. The only significant increase in understorey biomass occurred in late summer and autumn 1992 and followed the period of canopy thinning. A significant increase in understorey biomass was not noted in the following year but may well have occurred at some time after the termination of the study as the seasonal trend in biomass change was occurring slightly later in 1992/1993.

A period of canopy thinning could be seen as the weak link in the life history of a species which dominates by the maintenance of a closed canopy, however the results of this study point to a number of advantageous outcomes. As canopy thinning resulted from the shedding of spent reproductive structures, its timing also coincided with the period of recruitment in *Cystophora.* Emmerson & Collings (1998) have shown recruitment in *Cystophora* to be higher in artificially cleared areas than under the natural canopy and attributed this, in part, to the improved growth and survival conditions experienced in the clearings.

The increase in understorey biomass subsequent to canopy thinning suggests that growth conditions may in fact be less than optimal beneath the normally dense canopy at Cape Jervis. It may be advantageous to *Cystophora* for understorey biomass to remain low, as this would facilitate recruitment of its offspring. However, the growth of recruits would presumably also be limited and an opening of the canopy would give them a boost in their early life. Recruits were not observed in the community until autumn when canopy biomass began to increase, but they were very abundant (32% of total community abundance) which must, to some extent, reflect the success of their transition through the early life stages.

As the canopy thinned, a major transition of sub-canopy juveniles to canopy status occurred, presumably as another response to improved growth conditions. This resulted in seasonal maximum levels of abundance of *Cystophora* in the canopy. Subsequent to this however, the community underwent a period of significant mortality both in the recruit/juvenile population and in the adult canopy. This study did not investigate the mechanisms of mortality in the community but the fact that high mortality followed periods of maximum abundance in both the canopy and sub-canopy environments suggests that density dependent effects may be operating.

As individuals were lost from the community, space would have become available both at the substratum level and within the canopy thus providing a number of recruitment opportunities for other species. The *Cystophora* community was well equipped to respond to such opportunities by having a constant supply of juveniles, sub-canopy juveniles and smaller canopy plants ready to take advantage and to fill the gaps.

The year round presence of recruits and juveniles in the understorey is interesting in that reproduction in *Cystophora* is now known to be seasonal with a defined period of gamete release (Chapter five) and recruitment occurring shortly afterwards (Chapter six). The presence of juveniles in the community at other times cannot therefore be a result of multiple reproductive events. Fertilized zygotes of fucoids are known to have limited viability (Hoffmann & Camus 1989, Jones & Babb 1986, Klemm 1985, Santelices 1990) but have been kept alive under laboratory conditions for several months up to a year (Ang 1991, Moss & Sheader 1973, Schonbeck & Norton 1980, Sheader & Moss 1975). Embryos of the intertidal species *Pelvetia canaliculata* have even been found *in situ* up to eight months after reproduction had occurred (Schonbeck & Norton 1980).

Recruits in the Cape Jervis community were not observed until March 1992, five to six months after gamete release (Chapter five) and this compares well with the growth rate estimates of Emmerson & Collings (1998). Growth of *Cystophora* and *Sargassum* recruits in artificially cleared areas (Emmerson & Collings 1998) was higher in the centre of clearances than at the edges and this might have been due to canopy effects. *Cystophora* recruits in the centres of clearances took 143 days (on average) to reach 50mm in length, whereas *Sargassum* recruits took 173 days (on average) but the recruits of both species from the edge of clearances did not exceed 40mm within the 173 day time frame (Emmerson & Collings 1998).

Based on these growth rates, it would take juvenile *Cystophoras* in excess of a year to make it into the sub-canopy environment and this probably explains the presence of juveniles throughout the year. Long term survival of *Cystophora* embryos cannot however be ruled out as recruits were also observed throughout the year, but it is possible that some of the individuals experienced reduced growth in the sub-canopy environment (Emmerson & Collings 1998) and hence remained in the recruit size class. Similar observations of retarded juvenile growth have been reported for other subtidal communities of *Sargassum* (Kendrick & Walker 1994), and intertidal communities of *Fucus* (Ang 1991, Creed *et al.* 1996) and *Hormosira banksii* (Norton 1998).

The aim of the research presented in this chapter was to highlight changes in a number of demographic and phenological traits of *Cystophora* and to assess the influence of these on overall community structure. The results presented obviously raise a number of questions concerning the processes which drive the dynamics of *Cystophora* (and hence the community) and the strategies employed by *Cystophora* to maintain its dominance in the community. This discussion has alluded to a number of these aspects but it is intended that they be considered more fully in Chapter seven with added information from Chapters four to six on the growth, reproduction and recruitment of *Cystophora.*

Conclusion

The fucoid community at Cape Jervis was dominated by species of *Cystophora,* in particular *C. expansa* and as a result, patterns of change in community structure essentially mirrored the dynamics of *Cystophora.*

Cystophora was able to dominate the fucoid community at Cape Jervis by maintaining a closed canopy for most of the year which enabled it to compete successfully for essential resources such as light and space (both substratum for anchorage and canopy space).

It appeared that *Cystophora* was able to perpetuate its dominance in the community canopy by means of a "bank of juveniles" that was always present in the understorey and provided a buffer against the removal of adults.

CHAPTER FOUR..The Importance of Growth Processes on the Structure of the *Cystophora* Community

The term growth generally implies an increase in the size of an individual. In the case of a highly branched species such as *Cystophora,* this may result from an increase in the length of the thallus and/or an increase in the density of branching. The importance of both were alluded to in Chapter three where seasonal patterns of biomass production and the ability of individuals to make a rapid transition from sub-canopy to canopy status were identified as likely strategies contributing to the dominance of *Cystophora* in the canopy.

The aim of this section of research was to quantify growth of canopy and sub-canopy sized individuals in terms of change in both length of thallus and thallus biomass. The results show *Cystophora* to have a clearly defined pattern of seasonal growth, which is only fully evident when both estimates of growth are considered.

Introduction

As plants in a community grow, they change in size and form, as biomass is produced and lost. Biomass production is regulated by the availability of resources and competition for these from neighbouring individuals, whereas biomass loss generally occurs through physical damage and herbivory. Any change in the growth of an individual is therefore a balance between positive processes that result in tissue production and negative ones that cause tissue loss. As a consequence, growth is typically highly variable both spatially and temporally, within and between populations (Gunhill 1985, Creed *et al.* 1996, Druehl *et al.* 1986, Mathieson *et al.* 1984).

Incremental change in thallus length (or elongation of part of the thallus) has generally been used to estimate growth, as this is the simplest, non-destructive way to measure each plant (Ang 1991, Chapman & Craigie 1977, Creed *et al.* 1998, Emmerson & Collings 1998, Gagne *et al.* 1982, Prince & O'Neal 1979, Schiel 1985a,b, Sideman & Mathieson 1983, Stengel & Dring 1997). *In situ* measurement of elongation rates in kelps has been monitored using the hole punch method (Chapman & Craigie 1977, Druehl *et al* 1986, Gagne *et al.* 1982, Gerard & Mann 1979) but this cannot be applied to fucoids as they exhibit apical rather than intercalary growth and are generally more complex in structure.

A similar method was used by Stengel & Dring (1997) to measure growth of individual fronds, rather than whole plants, of *Ascophyllum nodosum,* by threading a piece of fishing line through each frond and measuring *in situ,* the changing distance between this and the apex.

Change in thallus length however, may not necessarily be the best indicator of growth especially if a species has a complex three-dimensional structure (Creed *et al.* 1998, Gunhill 1985, Klemm 1985). With highly branched species such as *Cystophora* and *Sargassum,* each axis is divided into a number of orders of branching, each with numerous apices and hence, growing points (Fig. 1.1). Schiel's (1985b, 1990) measurement of total plant length as an estimate of the growth rate incorporates change in length of all primary and secondary branches of an individual and may therefore provide a more accurate measure of growth in such species. Unfortunately his approach appears to be unique and so his results are not directly comparable with other studies.

The results of Creed *et al.* (1998) showed no significant changes in the length of *Fucus serratus* between treatments but they attributed this to growth being expressed through bushiness of the plant rather than increase in length. Indeed the average biomass of individuals did show a seasonal increase at a time when growth rate (in terms of length) fell. Change in individual plant biomass (Andrew & Viejo 1998, Gunhill 1985, Kendrick 1994, Niemeck & Mathieson 1976), thallus volume (Gunhill 1985), thallus surface area (Haddad & Ormond 1994) and space occupation (Gunhill 1985, Keser & Larson 1984) have all been used as alternative measures to change in thallus length and all address change in growth as a function of thallus bushiness.

Mathematical models have also proved useful in estimating plant growth in terrestrial systems (Begon *et al.* 1990), based on the theory that each plant (and animal) species has a "controlled" characteristic form which can be analysed in mathematical terms (Leopold & Kriedemann 1975). Mathematical analysis of plant form relies on the demonstration (or not) of interrelationships between the growth patterns of component parts (eg. fronds, leaves, stipes, fruits, roots). It is often desirable for researchers to reduce the necessity for destructive techniques in estimating growth patterns, and this may be achieved if a relationship between biomass (destructively determined) and some thallus dimension (measured *in situ*) can be demonstrated. Many such interrelationships have been reported for marine macroalgae (Ballesteros *et al.* 1998, Brenchley *et al.* 1998, Creed 1985, Gunhill 1985, Prince & O'Neal 1979).

An important consideration when choosing an appropriate measure of growth, is that change in plant size is not always positive i.e. plants do not always get bigger. Processes of erosion and herbivory may lead to considerable negative changes in plant size. Tissue loss and erosion is a common feature in many fucoids (Ang 1991, Brenchley *et al.* 1996, Cousens 1986, Hales & Fletcher 1990, Gunhill 1985, Klemm 1985, Mathieson & Guo 1992, Schiel 1985b) and this can result in negative growth rates being observed. Fucoids annually lose their spent reproductive tissues, accounting for up to 98% of total thallus biomass (Ang 1991, Brenchley *et al.* 1996, Cousens 1986, Hales & Fletcher 1990, Mathieson & Guo 1992, Schiel 1985b) and physical damage to thalli can also cause the loss of substantial amounts of biomass. Up to 80% of some intertidal populations of *Cystophora* studied by Klemm (1985) were lost or showed serious erosion. Fortunately, changes in growth patterns due to the distribution of biomass to underground root systems and perennation organs do not complicate any estimation of growth in fucoids, unlike angiosperms.

There is an obvious need for extended research into patterns of fucoid growth and the extent of environmental control over these. Our current knowledge is not only biased with examples from the northern hemisphere intertidal species but for some species is pieced together from demographic studies with little or no consideration of seasonal patterns of change. Subtidal species feature poorly in the literature, being essentially absent from the northern hemisphere and await the attention of southern hemisphere researchers.

The first aim of this section of research was to quantify any temporal patterns of growth in adult and sub-canopy plants for each of the three species of *Cystophora.* Maintenance of a closed canopy was suggested in Chapter three to be a likely mechanism for the perpetuation of *Cystophora* dominance in the Cape Jervis community. Rapid growth of smaller plants in the understorey was also suggested as a likely mechanism for facilitating the perpetuation of the closed *Cystophora* canopy (Chapter five). Growth was measured *in situ* using incremental changes in maximum thallus length (non-destructive) and as a change in total thallus biomass through time (destructive). Growth rates of juveniles and recruits were estimated by modelling data obtained for adult and sub-canopy plants.

The second aim of the research was to relate quantified changes in growth rate with observed changes in the reproductive life history of each species, in order to assess the importance of patterns of biomass production and loss. As with other species of fucoid, reproduction is now known to be seasonal in *Cystophora,* with spent reproductive structures being shed after gamete release (Chapter five).

Methods

It must be noted that the aim of this section of research was to monitor growth in the three species of *Cystophora* for a minimum period of 15 months. The research was however terminated prematurely in mid spring (November 1992) due to health reasons that prevented the researcher from diving. After careful consideration of all options, it was decided to abandon the continuation of growth measurements beyond this point in time. Diving could not recommence until late summer (February1993) and it was felt that the quality of data obtained would be compromised if collected by another researcher.

Nevertheless, the results obtained during this nine month period provided some important information on the growth processes of the three species and are certainly worth reporting. The period of growth that was monitored is now known to correspond with that of reproductive development and maturity (Chapter five) and thus it is essential to consider the results obtained in light of this.

Field methodology

The first measure of growth employed was a non-destructive estimate of change in total thallus length. Length measurements were taken *in situ*, using SCUBA, for the three species of *Cystophora.* Growth was estimated in terms of Relative Growth Rate (RGR), using an initial and final measurement taken at approximately six weekly intervals. At each sample time, from December 1991 through to July 1992 approximately 40 canopy-sized individuals (i.e. 200mm or greater) of each species were selected, mapped and initial length measured. Two months later these individuals were relocated and remeasured to obtain their final length. At this time a different set of individuals were chosen, mapped

and measured for use in the estimation of the growth increment over the next two month interval. Plants which could not be re-located were considered to have died and were therefore used to estimate mortality rates.
Selection of individuals was largely random although some consideration was made of the "mappability" of each individual and its potential for relocation at a later date. Large clumps of similar species were avoided as potential sources of relocation error and highly damaged individuals were also disregarded. Permanent line transects were located within the mixed fucoid community but these were used as reference guides only for the relocation of four mapped areas (one on each transect). Mapped areas were chosen by generating a series of random numbers that corresponded to distances along each transect. A 60 x 60cm quadrat was placed at each mapping site to provide coordinates and a positioning guide for the individuals being measured. The quadrat was removed between measurement times to prevent damage to plants, but small metal pegs were left to mark two opposite corners of the quadrat so that a confident relocation could be made at a later date. This method of mapping proved to be very successful, with the majority of individuals being easily relocated.

Length was measured by extending the thallus to its maximum stretch, including all levels of branching, as primary axes were often damaged and were not necessarily representative of the thallus length. In some cases one or a few of the secondary axes were observed to have taken on a primary role. Length to the nearest millimetre was recorded with an ordinary plastic ruler. It is known that species of *Cystophora* can experience negative growth (Klemm 1985) and for this reason characteristics of individuals such as broken main axis, damaged tissues and general state of thallus, were noted. These comments were also useful in the relocation process, for example, a few thalli with visible tissue damage to the stipe were often found with only holdfasts and portions of stipe remaining when the second length measurement was taken.

The second method used to measure growth involved the destructive harvesting of individuals to obtain an estimate of change in total thallus biomass through time. Material harvested for the community studies (Chapter three) was used for this so as to minimise disturbance in the community. Biomass measurements (g dw) were made for all canopy-sized individuals (>200mm) for each species through time.

Analysis

ANOVA and regression analyses were carried out on untransformed data using the JMP statistical package (SAS Institute Inc. 1995). A combination of oneway and twoway crossed ANOVAs were used to test for differences in plant length, weight and Relative Growth Rate. Homogeneity of variances was assessed with the Brown-Forsythe test and where these were significantly heteroscedastic a Kruskal-Wallis test was performed (Zar 1996).

Regression analysis was used to establish relationships between initial plant size (length) and final plant size, and between initial plant size and RGR (see results section below for details of relationships). Growth rates of individuals falling outside the size range of plants from the current data set were modelled using these relationships.

Results

Growth of adult and sub-canopy plants - as a function of change in individual plant length

General Situation

The average size of individuals in the community canopy changed through time with larger individuals generally being present through winter and spring, and smaller individuals during summer (Fig. 4.1). These changes were due to seasonal patterns of growth and to mortality, which affected the size distribution of the *Cystophora* community.

Temporal Changes in the Average Length of Individuals in the Canopy

Plants in the canopy were significantly ($p<0.05$) longer on average in late autumn (May 1992) through to early summer (December 1992) than at other times of the year (Fig. 4.1). Average thallus length never exceeded 500mm (Fig. 4.1) for any species during this time but maximal lengths of 914mm, 910mm and 1070mm were recorded for *C. expansa, C. monilifera* and *C. subfarcinata* respectively. No significant differences ($p<0.05$) in average length were detected between the species (Fig. 4.1).

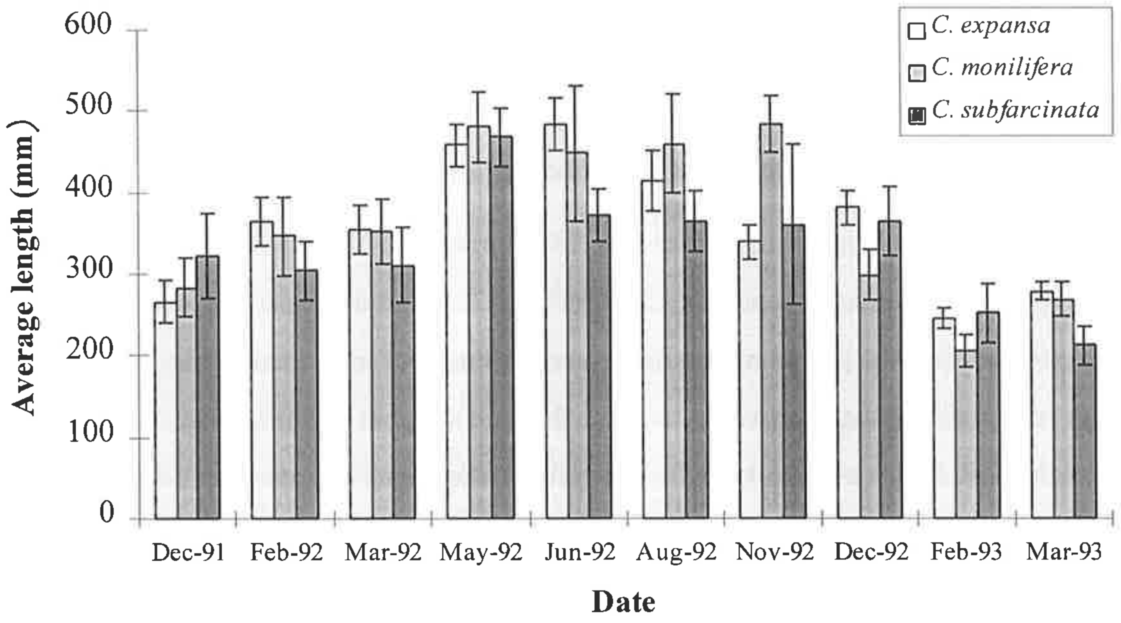


Figure 4.1. Plants in the community canopy (i.e. 200mm or greater in length) were generally longer during late autumn through to early summer, than at other times of the year. Significant changes ($p<0.05$) in length occurred in late autumn (May 1992) when plants became longer, and summer (February 1993) when they became shorter. The average length of plants did not vary significantly ($p<0.05$) between species. **Note** that the x-axis is not proportional. Error bars =standard error.

Change in average thallus length resulted from a change in the size distribution of the community and this would have been affected by a number of processes

- growth of individuals
- loss of individuals through mortality
- introduction of smaller (younger) individuals into the canopy

A progressive seasonal change in the size distribution of the *Cystophora* community was shown in Chapter three (Fig. 3.5) where it was suggested that recruitment and subsequent growth of individuals were the primary driving factors.

The importance of growth

Relative growth rate varied seasonally for all species (Fig. 4.2) with the highest rates occurring during late summer (February 1992) and autumn (March to May 1992). Maximal RGRs were 0.0044 mm/mm/day, 0.0025 mm/mm/day and 0.0022 mm/mm/day for *C. expansa, C. monilifera* and *C. subfarcinata* respectively. For all species, this period of high growth (Fig. 4.2) resulted in a significant ($p<0.05$) increase in average thallus length (Fig. 4.1).

It is unlikely that this significant change in average thallus length in the community (Fig. 4.1) was due to the canopy being composed of larger individuals at this time, as the analysis of the size class distribution of all *Cystophora* species in Chapter three (Fig. 3.5) showed the community canopy to be dominated by smaller individuals.

RGRs were much lower during winter and early spring (July to September 1992) and even negative for *C. expansa* in September 1992 (Fig. 4.2). This decrease in growth corresponded with the period of maximal average length of individuals (Fig. 4.1). Average length of individuals was shown to decrease through summer 1991/92 (Fig. 4.1) and although RGR data is not available for this period, the negative growth rate of *C. expansa* in spring (September 1992) may indicate the onset of a period of tissue loss associated with the shedding of spent reproductive tissues (see Chapter five).

No significant differences in RGR were detected between species despite the general trend suggesting *C. expansa* to have faster growth during late summer and autumn (February to May 1992) and showing very low growth in early spring (September 1992). Given the high levels of variability in the data however (Fig. 4.2), it is not surprising that statistical differences were not detected. Some of the variability may have arisen from the use of RGR as the measure of growth, as it incorporates any decrease in length due to erosion, damage or grazing and would in itself be expected to be variable.

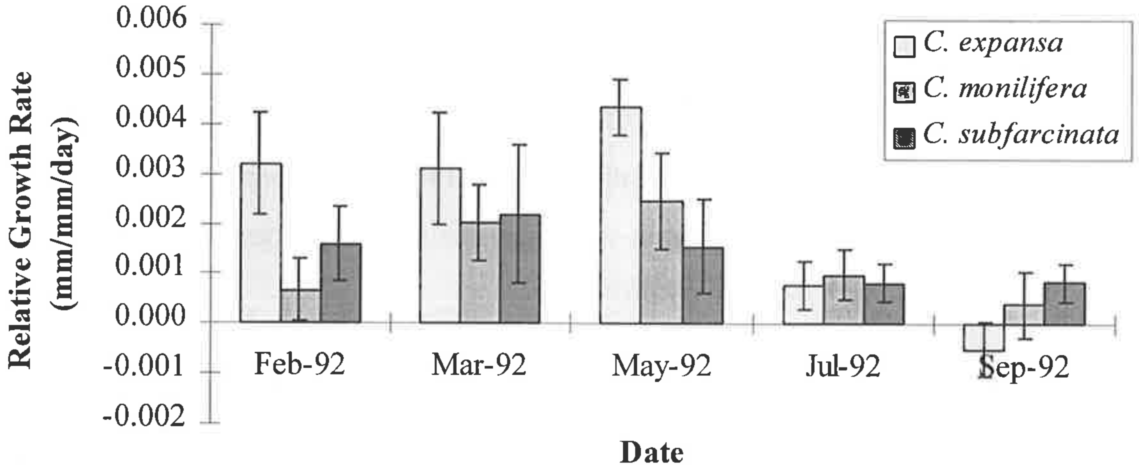


Figure 4.2. The average relative growth rate (RGR) for all species varied seasonally and was significantly ($p<0.05$) higher in late summer (February 1992) and autumn (March to May 1992). Growth slowed during winter and spring 1992 and in the case of *C. expansa,* went negative in early spring (September 1992). No significant differences existed between species although the trend suggests that *C. expansa* had a faster growth rate than the other species. These data do not account for any differences in RGR associated with size of plant, beyond the fact that all individuals were members of the canopy (i.e. 200mm or greater). **Note** that the x-axis is not proportional. Error bars = standard error.

The importance of mortality

Mortality varied seasonally (Fig. 4.3a) but was generally higher for all three species during late autumn/early winter and spring (May to September 1992). Plant loss was at all times higher for *C. monilifera* and *C. subfarcinata* (ranging from 11% to 37% and 11% to 35% respectively) than *C. expansa* (7% to 23%). Maximum losses (Fig. 4.3a) for *C. monilifera* and *C. subfarcinata* also coincided, in late autumn (May 1992) whereas most individuals of *C. expansa* were lost in mid winter (July 1992).

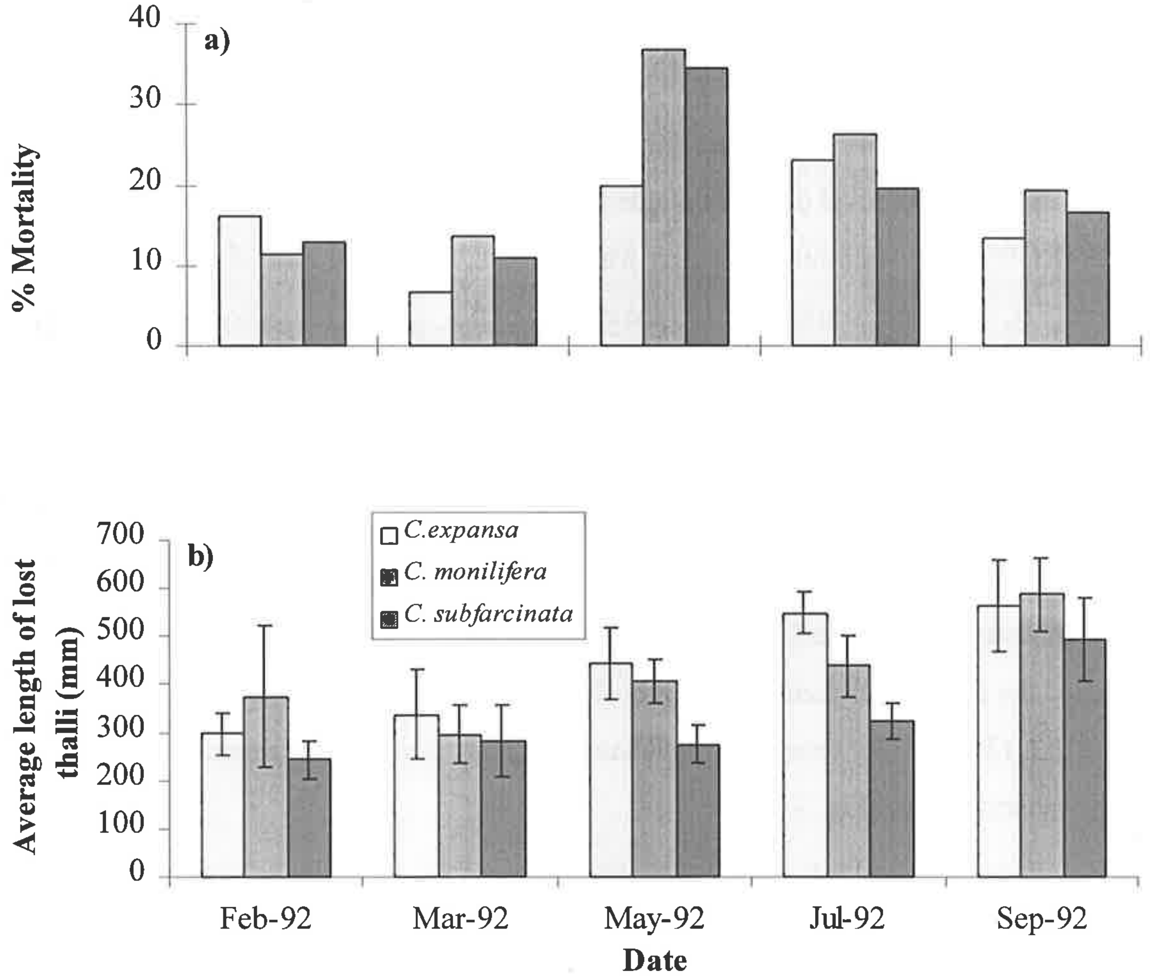


Figure 4.3. Mortality (a) was generally higher during late autumn/early winter and spring, with the average length of lost plants (b) increasing throughout this period. Plant loss (a) was particularly high for *C. monilifera* and *C. subfarcinata* in May 1992 when approximately one third of individuals were lost. Mortality of *C. expansa* was generally lower than the other species with the exception of February 1992 (a) and its highest mortality occurred in winter (July 1992). The average length of lost plants increased significantly ($p<0.05$) through winter for *C. expansa* and *C. subfarcinata* but not C. monilifera despite the obvious trend (b) with the largest individuals of all species being removed in September 1992 when plants were all greater on average than 500mm. **Note** that the x-axis is not proportional. Error bars = standard error.

The size (length) of plants lost also showed a seasonal trend (Fig. 4.3b), increasing from late summer (February 1992) through to early spring (September 1992). This change was significant ($p<0.05$) for both *C. expansa* and *C. subfarcinata* but not for *C. monilifera.* Change in plant length through time appeared to be more gradual in *C. monilifera* (Fig. 4.3b) than the other species. The plants of *C. expansa* and *C. monilifera* that were lost (Fig. 4.3b), were on average similar in length (296.7 mm to 563.4 mm and 295.5 mm to 586.7 mm respectively) but those of *C. subfarcinata* were significantly ($p<0.05$) shorter (244.0 mm to 492.5 mm).

The decrease in average thallus length of canopy plants (Fig. 4.1) in late spring (November 1992) through to summer (February 1993) probably reflected a period of decreased growth in *Cystophora,* due to loss of biomass (Fig 4.2). However, a shift in the community size structure due to the removal of larger plants in spring (Fig. 4.3b) cannot be ruled out. Growth (RGR) at the beginning of spring was minimal, and in the case of *C. expansa,* negative (Fig. 4.2), and would not have provided a buffer against mortality or the removal of tissue.

The importance of new individuals entering the canopy

The current investigation has dealt with canopy-sized individuals only, but previous analysis of community structure (Chapter three) highlighted a progressive seasonal change in the size distribution of the *Cystophora* community (Fig. 3.5). Smaller individuals dominated the post-recruitment community (Fig. 3.5 d-f) in late autumn/winter (May to August 1992) but at other times, the distribution of plant sizes in the community and canopy was more even (Fig. 3.5).

The same analysis also highlighted an unusually high occurrence of sub-canopy juveniles during February and March 1993 (Fig. 3.5i, j). It was suggested that at this time, a patch of community had been sampled in which the abundance of larger canopy plants was uncharacteristically low and this may explain the current observed decrease in average thallus length (Fig. 4.1) in summer (from December 1992 to February 1993). The influence of growth and mortality processes cannot however be ruled out.

Growth of adult and sub-canopy plants – as a function of change in individual plant biomass

General situation

The average biomass of individuals varied seasonally (Fig. 4.4), increasing gradually through summer 1991/92 and autumn 1992 to peak in early to mid spring 1992. By late spring /early summer 1992 biomass had decreased significantly ($p<0.05$) to minimum levels that were comparable with the previous year. It is now known that this pattern of biomass production and loss is associated with the production of reproductive structures (Chapter five) which mature in early spring and are shed later in the season, once exhausted (Figs 5.2, 5.3).

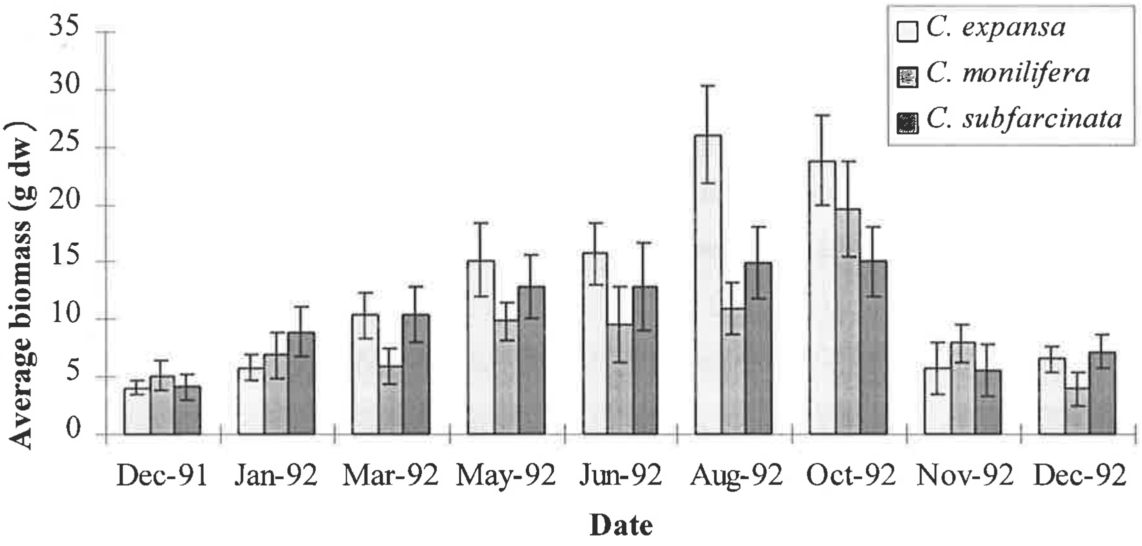


Figure 4.4. Average individual plant biomass varied seasonally for all three species, increasing through summer and winter (December 1991 to June 1992) to peak in late winter/early spring (August to October 1992). Some interspecific differences were evident in the growth pattern but a distinct decrease in biomass in late spring (November 1992) was a characteristic feature of all species. **Note** that the x-axis is not proportional. Error bars = standard error.

Interspecific differences in patterns of biomass change

All three species followed the general pattern of biomass production and loss but some differences were evident (Fig. 4.4). Maximum biomass (26 g dw) was reached slightly earlier in *C. expansa* (Fig. 4.4) in late winter (August 1992) whereas *C. monilifera* and *C. subfarcinata* achieved maximal biomass (20 g dw and 15 g dw respectively) in mid spring (October 1992). *C. subfarcinata* did not show the significant increase in biomass typical of the other two species (Fig. 4.4) but this is not to say that it did not occur. Given the substantial and rapid decrease in biomass seen in November 1992 for all species, it is possible that a peak in biomass occurred between sampling periods sometime during mid to late spring but was not picked up.

A general pattern of growth for canopy and sub-canopy sized individuals

The general pattern of growth suggests that individuals gradually increase in biomass as they get longer (Figs 4.1, 4.4) but continue to get heavier once their growth, in terms of length, slows or even ceases. Change in elongation rates were high for all species during late summer and autumn (February to May 1992) (Fig. 4.2) during which period average individual biomass increased gradually (Fig. 4.4). As change in elongation rates slowed in winter and early spring (July to September 1992) and individuals reached their maximum length (Fig. 4.1), average individual biomass almost doubled in *C. expansa* and *C. monilifera,* and continued to increase gradually in *C. subfarcinata* (Fig. 4.4).

The observation of a significant ($p<0.05$) burst in growth once maximum length had been achieved, highlights the necessity for both estimates of growth to be employed when dealing with highly branched species such as *Cystophora.* Estimates of RGR (change in length) alone would not have picked up on the almost two-fold increase in plant size (in *C. expansa* and *C.* monilifera) that occurred during late winter/early spring (Figs 4.2, 4.4).

The negative RGR of *C. expansa* in September 1992 (Fig. 4.2) was indicative of biomass loss and this is seen again in Figure 4.4 where average individual biomass of *C. expansa* began to decrease after the maximum in late winter (August 1992). Biomass continued to decrease in late spring when all three species showed a substantial and synchronous decrease in biomass (Fig. 4.4).

Predicted growth of smaller plants, juveniles and recruits

The predicted growth rates presented in this section of work were modelled on two length:growth relationships of canopy and sub-canopy individuals:-

- relationship between initial and final plant size (Fig. 4.5)
- relationship between initial plant size and RGR (Fig. 4.6)

The data set on which these relationships were based however was pooled across seasons and species, and as a consequence two assumptions have to be stated:-

- there is no seasonal influence on growth rate
- all species have similar growth rates

It is realised for canopy-sized plants that the first assumption is incorrect, as RGR is known to vary on a seasonal basis (Fig. 4.2). The second assumption is also likely to be incorrect as the general trend in RGR (Fig. 4.2) suggested some differences to exist between species. Given that the model has its limitations however, the results presented here do outline a general response for *Cystophora,* which merits further investigation.

General situation

Initial plant length affected growth (Fig. 4.5) with smaller individuals, on average, growing faster than larger ones. Sub-canopy individuals (<200 mm) showed the highest potential growth rates, with the growth of recruits (<50 mm) and juveniles (51mm to 100 mm) predicted to increase by 42% to 71% and 28% to 38% respectively over an approximately 6 week period. Although a few plants reached lengths exceeding 1000 mm, the average response was for growth to cease at about 545 mm and for growth rates to be negative beyond this (Figs 4.5, 4.6).

Change in plant growth as a function of initial length

Incremental change in plant length was affected by initial plant size (length) with smaller individuals showing a greater overall change in size than larger individuals (Fig. 4.5). For example (Fig. 4.5b), a 200mm plant increased by 14.5% (to 229 mm) during a single growth increment, whereas a 500 mm plant only increased by 1.2% (to 506 mm). A non-linear relationship between initial and final plant size existed (Fig. 4.5), with the data being best described by a power curve relationship ($y=2.3382x^{0.8652}$, $R^2 = 0.8052$). It must be recognised however, that this relationship is the average response and that much variability exists around this response.

Change in plant length was not always positive, with plants greater than 545 mm in length decreasing in size during a single growth increment (Fig. 4.5b). The larger the plant size, the greater the decrease in thallus size during a growth increment (Fig. 4.5b). A typical

600 mm plant decreased by 1.3% (to 592 mm), whereas a 1000 mm plant decreased by 7.8% (to 922 mm).

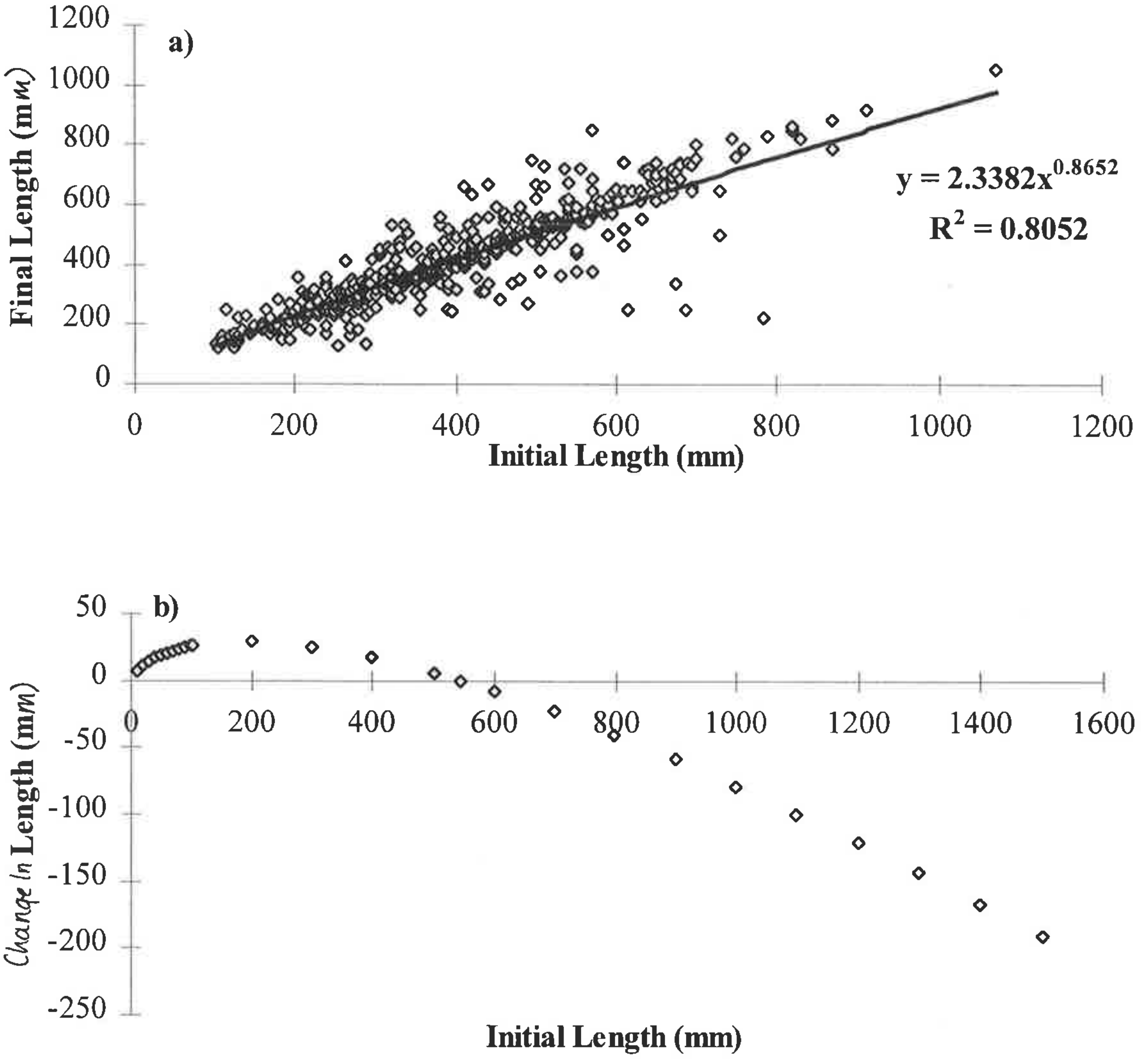


Figure 4.5. (a). A non-linear relationship existed between initial and final plant length ($y=2.3382x^{0.8652}$, $R^2 = 0.8052$) with plants <545 mm in length showing an increase in size (length) over the next period and those >545 mm in length showing a decrease in size.* (b). When these data are modelled using the above non-linear equation, changes in plant length can be estimated for individuals falling outside the size range of the current data set. Zero change in plant length occurred at 545 mm. **Note** these data provide a general response only, with no account for any influence of seasonal or species differences in change in plant length.
* The points represent measured data for all specimens across all seasons.

Sub-canopy individuals (<200 mm) showed the greatest positive change in plant length within a single growth increment, approximately six weeks (Fig. 4.5). The smallest individuals measured in this experiment were between 100mm and 110mm in length and these experienced changes of approximately 25% in length within a single growth increment (Fig. 4.5). Smaller recruits (<50 mm in length, Chapter three) and juveniles (51mm to 100 mm in length, Chapter three) would therefore be expected to show even greater changes in length. Based on the relationship demonstrated for the current data set, the following changes in length could be expected (Tab. 4.1).

Table 4.1. Predicted relative growth for smaller individuals shows the smallest recruits to have the potential for a 70% increase in length during the next growth increment (approximately six weeks). Results are based on the relationship between initial and final length of adult and sub-canopy plants, using the equation $y=2.3382x^{0.8652}$ (Fig. 4.5). **Note** these data provide a general response only, with no account for any influence of seasonal or species differences in change in plant length.

Status	Initial size (mm)	Final size (mm)	Change (%)
Recruit	10	17.14	71.4
	20	31.23	56.1
	30	44.35	47.8
	40	56.88	42.2
Juvenile	51	70.19	37.6
	60	80.79	34.6
	70	92.31	31.9
	80	103.62	29.5
	90	114.73	27.5
Sub-canopy Juvenile	101	126.77	25.5
	200	228.95	14.5

Whilst incremental change in plant length could be quite confidently predicted ($R^2=0.81$) from initial plant length, the chances of predicting RGR from initial plant length were lower ($R^2=0.11$). Nevertheless a significant ($p<0.001$) negative relationship existed. The general pattern of smaller plants growing faster and larger plants showing negative growth rates was still evident (Fig. 4.6) and the point at which growth ceased was very similar, 547 mm (Fig. 4.6) in comparison with 545 mm (Fig. 4.5). However, there was a high degree of variability around the average response (Fig. 4.6).

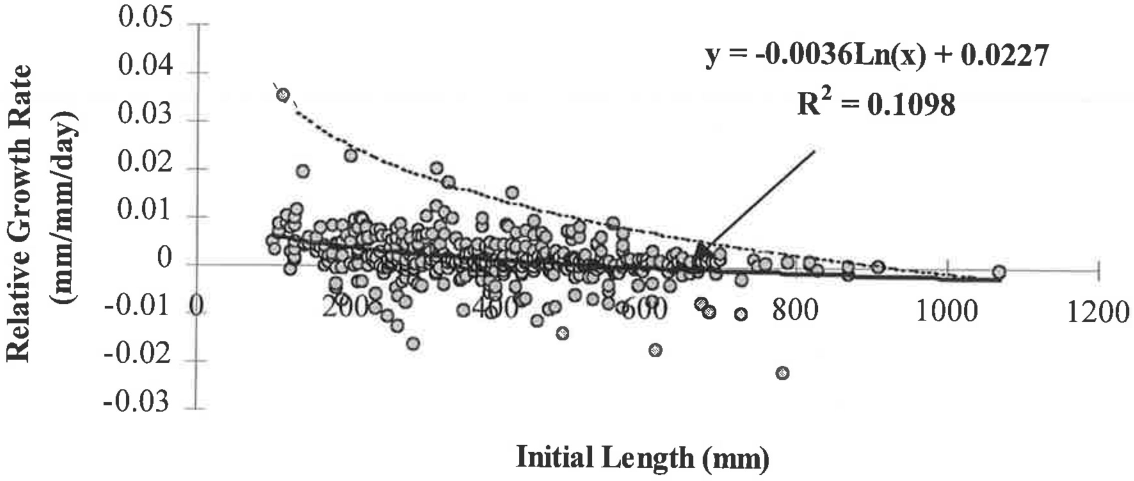


Figure 4.6. An overall negative relationship existed between RGR and plant length that was best described by a non-linear logarithmic relationship ($y=-0.0036\ln(x)+0.0227$, $R^2=0.110$). Zero growth occurred at a length of 547mm and RGR became negative for plants larger than this. A non-linear logarithmic relationship best fits these data but note that this is the average response and much variability exists. The upper boundary condition for these data is likely to represent the potential growth of plants, which experience the least amount of damage. **Note** these data provide a general response only, with no account for any influence of seasonal or species differences in change in plant length.

RGR is a measure of all changes in plant length that occur from one measurement time to the next and as such incorporates both positive changes (production of new tissues, accumulation of storage compounds) and negative ones (caused by physical damage, grazing, deterioration of tissues or shedding of spent reproductive structures). Seasonal, differences in growth rate (Fig. 4.2) would probably have also contributed to some of the variability. The RGR of each individual therefore represents the balance between all of these processes and would be expected to be variable.

In light of this balance, a number of hypotheses can be generated from the results:-

- Some individuals (of all sizes) showed much higher RGRs than others, in Figure 4.6 these are represented by the data points falling on the upper boundary of the data set. This boundary could arguably be used to define the upper limit of potential growth for any individual of *Cystophora* of a particular size as it based on individuals that have probably experienced minimal levels of damage or erosion and optimal levels of growth. With this in mind, individuals experiencing minimal damage could potentially reach lengths of approximately 950 mm before growth ceases (Fig. 4.6).

- Conversely, individuals falling at the lower boundary of the data set were most likely to have experienced much physical damage and the RGR may also have reflected changes in plant size due to shedding of spent reproductive structures (Chapter five).
- The RGR of most individuals however, approximated the general response. These individuals most likely experienced attrition of tissues and possibly minor damage inflicted by grazing rather than severe physical damage.

Discussion

This study represents the first attempt to monitor *in situ* growth rates of adult subtidal species of *Cystophora* and is one of very few studies to address the issue of growth in Australasian subtidal fucoids (Emmerson & Collings 1998, Klemm 1985, Schiel 1985b, 1990). The results showed growth in *Cystophora* to occur from late summer (February) through to late spring (November) with maximum plant size being reached in late winter/early spring (Figs 4.1, 4.4). After this, plants decreased in size, as biomass was lost (Figs 4.1, 4.4). This pattern of growth is clearly linked to the production of reproductive tissue (Chapter five) and in this respect, is similar to that of other fucoids. For *Cystophora* and these other fucoids, maximum growth coincided with the maturation of reproductive tissues, and biomass was lost with the shedding of spent receptacles (Brenchley *et al.* 1996, 1998, Gunhill 1985, Keser & Larson 1984, Klemm 1985, Niemeck & Mathieson 1976, Schiel 1985b, 1990, Sideman & Mathieson 1983).

The results also showed the growth pattern of *Cystophora* to be “bi-phasic” with an initial period of elongation (Fig. 4.2) through late summer/autumn (February to May 1992), followed by a period of bulking out (Fig. 4.4) as reproductive biomass was produced. In the case of *C. monilifera,* this period of “bulking out” accounted for a doubling in thallus biomass (Fig. 4.4). Maximum plant size, length and biomass, was reached in late winter/ early spring (Figs 4.1, 4.4) when plants were reproductively mature (Chapter five).

A similar pattern of growth does seem to be apparent in other species of fucoids, which, like *Cystophora,* have highly branched thalli, although this has not been directly reported in the literature. Elongation rates of a number of northern hemisphere intertidal species have been noted to slow as reproductive maturation was occurring (Brenchley *et al.* 1998, Gunhill 1985, Hales & Fletcher 1989a quoted in Hales & Fletcher 1989b). Unfortunately however, few studies have provided the data to test whether plants continued to bulk out after elongation had decreased or in some cases ceased. Evidence from some of these studies (Brenchley *et al.* 1996, 1998, Creed *et al.* 1998) does however suggest this to be the case. For example, *Fucus serratus* in UK elongated rapidly during late spring/early summer, i.e. March to June 1993 (Brenchley *et al.* 1998), but these rates slowed as reproductive structures were maturing (Brenchley *et al.* 1996). Biomass however, continued to increase until August 1993 as reproductive maturity was approached (Brenchley *et al.* 1996) and thus the growth period of *Fucus serratus* was actually two months longer than reported.

The situation in *Sargassum sinclairii* from New Zealand (Schiel 1988, 1990) appeared to be different from *Cystophora* and the other fucoids, with maximum elongation rates (Schiel 1990) occurring as conceptacles matured (Schiel 1988). This may however, reflect the measure of growth rate used. Elongation was measured in terms of total plant length including all primary and secondary axes and this would incorporate (to some extent) an increase in plant size due to change in bushiness as well as length. *S. sinclairii* did reach reproductive maturity at about the same time as *Cystophora.* Growth rate data are not available for canopy sized individuals of *Sargassum* in Australia, but three species in Western Australia (Kendrick & Walker 1994) showed a similar pattern of reproductive development with growth of the fertile branches initiated in autumn (April), reproductive maturity was reached in late winter/early spring (August to September) and senescence occurring during summer (December and January).

The presence of a bi-phasic growth pattern in *Cystophora,* and most likely in the other species mentioned, highlights the necessity for representative measures of growth to be used. Had either of the approaches chosen here been treated in isolation, then quite different results would have been obtained and the subsequent interpretation would also have been different.

That growth patterns of fucoids are associated with the production of reproductive tissue is inarguable, but what is still relatively unclear is how environmental variables (light, temperature and nutrients) affect the growth process. Northern hemisphere species show rapid growth during conditions of high solar irradiance and temperature (Brenchley *et al.* 1998, Mathieson *et al.* 1976, Stengel & Dring 1997) and some are most likely to be limited by low light levels in winter and spring (Stengel & Dring 1997). The onset of increased growth in these plants does occur slightly later than for *Cystophora* (Brenchley *et al.* 1998, Gunhill 1985, Keser & Larson 1984, Niemeck & Mathieson 1976, Schiel 1985b, Sideman & Mathieson 1983), with maximum rates during late spring and summer (April to August).

Strong seasonal differences in temperature and light occur in the coastal waters of South Australia (Cheshire *et al.* 1996, Tippins 1997) and these have been shown to affect the photophysiology (and hence productivity) of fucoid dominated communities (Cheshire *et al.* 1996). Productivity (net 24 hr) of these communities was highest in summer (6% of standing wet weight per day) due to longer daylength and higher maximal irradiance. Nevertheless, rates in mid-winter were still positive (3% per day) and would have provided support for active growth (Cheshire *et al.* 1996). It must be noted that whilst these communities comprise species (both plant and animal) other than fucoids, and indeed *Cystophora,* they provide the only quantitative evaluation of fucoid productivity in South Australia.

Although the estimates of productivity given by Cheshire *et al.* (1996) give an indication of the seasonal change in carbon production, they cannot provide an estimation of how the carbon is utilised within the community. Unfortunately the information is not yet available to determine what proportion of the carbon assimilated by an individual is allocated to the production of new tissues and what is used elsewhere for processes such as maintenance, defence and reproduction.

The period of maximum growth (increasing length and biomass) for *Cystophora* occurred during autumn and winter (Fig. 4.2) when daylength and irradiance were on the decline (Kildea, Ph.D. thesis, University of Adelaide, in prep.). The period of minimum growth however, occurred during summer (Fig. 4.2) when light conditions were presumably optimal. This suggests that some factor, other than the availability of light, is influencing the growth patterns of *Cystophora.*

Minimal growth occurred after spent reproductive structures had been shed (Chapter five), at this time thalli were typically denuded (Plate 3.1) and the photosynthetic surface area of the plant reduced. Low growth may have resulted from a reduction in ability of the alga to convert light to carbon however, fucoids are known to adapt their pigment systems to compensate for such changes (Ramus *et al.* 1977).

Seasonal patterns of growth and biomass production in northern hemisphere kelp systems are known to vary with seasonal fluctuations in light and temperature, however, the availability of nutrients (primarily nitrogen) and ability of individuals to accumulate internal reserves of nitrogen and carbon are also influential (Chapman & Craigie 1977, 1978, Gagne *et al.* 1982, Rosell & Srivistava 1985, Wheeler & Srivistava 1984). A general pattern of growth has been proposed for these systems, based on seasonal fluctuations in resources and temperature, and the responses of individuals to physiological requirements for growth (Chapman & Craigie 1977, 1978, Gagne *et al.* 1982, Rosell and Srivistava 1985, Wheeler & Srivistava 1984).

It appears that in environments where nitrogen is not limiting, the growth pattern reflects that of the light cycle with maximum growth occurring in early summer. Thalli do not accumulate large internal stores of carbon or nitrogen (Gagne *et al.* 1982, Buggeln 1978, Lüning 1979, Dieckmann 1980). Where nitrogen is limiting, minimal growth occurs during the summer months when nitrogen levels are low. Net photosynthetic gain is high and so surplus carbon is accumulated into internal reserves. During winter, carbon requirements for growth can generally be met by photosynthesis as water temperatures are low, respiration rates are low and photosynthetic surplus may be utilised for growth despite low light intensities. In most cases growth will be rapid as ambient nitrogen levels are high enough during this time to support growth.

Net photosynthetic gain in early winter is however, not always sufficient to support growth (Lüning 1971, Hatcher *et al.* 1977) and under such conditions, internal carbon reserves must be drawn upon to augment growth. Carbon reserves which peak in autumn fall off rapidly during the winter months due to this and also as mature tissue in which the reserves are held is eroded away. Up to 30% of the growth of new fronds in the winter can be supported by internal reserves of carbon accumulated during the previous summer (Lüning 1971).

A number of studies have looked at the accumulation of nutrients (Brenchley *et al.* 1998, Floc'h 1982, Topinka 1978) and carbohydrate reserves in fucoids (Meeuse 1962, Powell & Meeuse 1964, Pellegrini & Pellegrini 1971, but see Brenchley *et al.* 1998). The majority provide information of limited value when considering the seasonal aspects of growth and biomass production in fucoids but there are exceptions (Brenchley *et al.* 1998, Gillanders & Brown 1994a, 1994b). Internal reserves of nitrogen and carbon were shown to vary seasonally in *Fucus serratus, Himanthalia elongata* (Brenchley *et al.* 1998) and

Xiphophora gladiata (Gillanders & Brown 1994a, 1994b) and were suggested to satisfy physiological requirements for growth and the production of reproductive tissue.

It is possible that nutrient availability was low at Cape Jervis during the summer and this may have restricted the growth of *Cystophora*. A preliminary study of carbohydrate storage in the three species of *Cystophora* (not included in this thesis) showed elevated levels of mannitol (the primary carbohydrate storage compound of brown algae) in the tissues during late summer and autumn and this may be indicative of the individuals taking advantage of the good light climate to accumulate carbon reserves. It must be said that these hypotheses are purely speculative, being based on preliminary findings, but nevertheless provide a useful insight into other factors that may be affecting the growth of *Cystophora*.

The elongation rates experienced by *Cystophora* at Cape Jervis, fall within the range previously reported for other fucoids, with the exception of the September 1992 values for *C. expansa* and *C. monilifera* (Tab. 4.2). During this time, the RGR for *C. monilifera* was very low and for *C. expansa* was even negative. Overall negative growth rates have been recorded for *Pelvetia fastigiata* (Gunhill 1985) and species of *Fucus* (Ang 1991, Creed *et al.* 1998) and are attributed to the partial removal of, or damage to plants. The negative growth rate of *C. expansa* was more likely an indication of spent reproductive material being shed rather than severe physical damage occurring. Levels of mortality were relatively low for *C. expansa* during September 1992 (Fig. 4.3), which suggested physical damage to thalli was probably also low at that time.

Many studies have suggested that the erosion of spent reproductive tissue has a major influence on growth rates of fucoids (Ang 1991, Gunhill 1985, Niemeck & Mathieson 1976, Schiel 1985b) but removal of large, "reproductively heavy" plants was also noted for intertidal populations of *Fucus spiralis* (Niemeck & Mathieson 1976). Maximum levels of mortality in *Cystophora* (Fig. 4.3) occurred in late autumn and winter (May to July 1992) as thalli were reproductively maturing and bulking out. Whether this increase in thallus size made them more susceptible to physical removal is unknown but autumn storms would have increased the chances of damage and removal (mortality).

Table 4.2. For comparison, the seasonal changes in elongation rate obtained for *Cystophora (t*his study) have been converted from average RGR (mm/mm/day) to average monthly growth (mm/30 days) as this measure has been more commonly used in a number of fucoid growth studies. Growth rates for *Cystophora* generally fall within the range reported for other canopy sized fucoids, with the exception of the September 1992 values (in bold font) for *C. expansa* and *C. monilifera* which are much lower.

Species	**Growth rate (mm/30 days)**	**Source**
C. expansa	**-7.0mm** to 49.1 mm	This study
C. monilifera	**0.8mm** to 14.7	This study
C. subfarcinata	7.3mm to 15.7	This study
Fucus spp.	1mm to 78mm	Brenchley *et al.* 1998, Haddad & Ormond 1994, Mathieson *et al* 1976, Niemeck & Mathieson 1976, Sideman & Mathieson 1983
Ascophyllum nodosum	15mm to 36mm	Mathieson *et al* 1976
	8.8 to 13.33 mm (no seasonal differentiation)	Stengel & Dring 1997
Himanthalia elongata	10mm to 78mm	Brenchley *et al.* 1998
Pelvetia fastigiata	10mm to 40mm	Gunhill 1985

Grazing is also known to affect the growth of large brown algae and its effects can vary in magnitude from partial to total loss of thallus biomass (Choat & Schiel 1982, Santelices 1990). It is unlikely however, that any substantial loss of biomass due to grazing occurred in *Cystophora* as individuals typically contain very high levels of secondary metabolites which are believed to play a role in chemical defence (Steinberg 1989). These substances are generally concentrated in both vegetative and reproductive apices (Conover & Sieberth 1964, Van Alstyne 1988,1990). Although *Cystophora* is most likely to be unpalatable to a number of grazers, it may be indirectly at risk of damage from carnivorous fish that prey on resident populations of epifauna. Accidental damage to the algal host from such feeding activities has been noted (Taylor & Cole 1994).

The dominance of *Cystophora* in the Cape Jervis community is sustained through the maintenance of a closed canopy for most of the year (Chapter three) but also by the presence of a bank of sub-canopy juveniles that are able to fill any gaps that arise in the canopy. The results obtained from this study certainly suggest that small *Cystophora* plants are capable of rapid growth (Fig. 4.5, Tab. 4.1), with recruits increasing in length by up to 70% during a six-week period. These predicted growth rates are consistent with *in situ* rates obtained for *Cystophora* and *Sargassum* from South Australia (Emmerson & Collings 1998) and for other species of northern hemisphere fucoids (Ang 1991, Andrew & Viejo 1998). *Cystophora* and *Sargassum* recruits of approximately 10mm in length took 24 weeks to reach lengths of 34mm to 61mm (Emmerson & Collings 1998). Based on current estimates, a 10mm *Cystophora* recruit would have reached an average length of 58mm in the same number of weeks (Tab. 4.3).

Table 4.3. Growth trajectories for sub-canopy individuals of *Cystophora* showing the predicted time taken for transition through each size category (recruit, juvenile, sub-canopy juvenile) to canopy status. Trajectories are given for the smallest size classes within each category to show the range of potential growth for each. Trajectories are modelled from the relationship between initial and final length of adult and sub-canopy plants, using the equation $y=2.3382x^{0.8652}$. **Note** these data provide a general response only, with no account for any influence of seasonal or species differences in change in plant length.

Initial Size	**Size after 6 weeks (mm)**	**Size after 12 weeks (mm)**	**Size after 18 weeks (mm)**	**Size after 24 weeks (mm)**
recruit (10mm)	17.1	27.3	40.9	58.0
juvenile (51mm)	70.2	92.5	117.5	
Sub-canopy juvenile (101mm)	126.8	154.3	183.0	211.9

Predicted relative growth was shown to decrease with size of plant (Fig. 4.5, Tab. 4.1) and thus recruits (<50mm) showed higher growth rates than either juveniles (51mm to 100mm) or sub-canopy juveniles (101mm to 200mm). Predicted growth trajectories (Tab. 4.3) for individuals falling into each of these size classes, showed that a 10mm recruit would take, on average, about 24 weeks to reach the juvenile stage, a further 18 weeks to sub-canopy status and from here an extra 24 weeks of growth to reach the canopy (Tab. 4.3). And so, an average recruit could be expected to take its place in the canopy within about 15 months of reaching the 10mm stage.

Juveniles and sub-canopy juveniles could similarly be predicted to take up to ten months and six months respectively to enter the canopy (Tab. 4.3). And so, depending on the ambient growth conditions and the size of small plants growing beneath the canopy, any gaps caused by damage to, or the removal of adults, could take weeks, to over a year to fill. Analysis of the *Cystophora* community size structure in a previous chapter (Fig. 3.5) showed that smaller individuals (<200 mm) were present at all times. This suggests that the community should be able to maintain its closed canopy quite readily from the supply of individuals growing beneath it.

These predictions are however limited by the assumptions of the model from which they are generated, and make no account of seasonal or species variability in growth rate. This work has shown growth of canopy sized individuals to vary on a seasonal basis (Fig. 4.2) and suggests that growth rates may also vary between species (Fig. 4.2). It is not known however, whether these two factors are influential on the growth of smaller individuals or indeed what other factors may operate in the sub-canopy environment.

The presence of an adult canopy is known to affect the growth of *Cystophora* recruits (Emmerson & Collings 1998). Algal canopies are known to significantly reduce light levels and may alter localised nutrient levels (Schiel & Foster 1986). Recruits growing in artificially cleared patches achieved greater lengths at the centre of the patches than at the edges (Emmerson & Collings 1998). Growth of recruits in their natural environment would therefore expect to vary depending on the size of gap created in the canopy. The predicted growth rates from the current study are based on measurements taken *in situ* (with a canopy in place) and may not accurately reflect the growth rates of young *Cystophoras* in the Cape Jervis community. They are however directly comparable with those of *Cystophora* recruits growing in the centre of the artificially cleared patches (also at Cape Jervis) of Emmerson & Collings (1998).

The negative relationship between growth and plant length that was apparent in *Cystophora* (Figs 4.5, 4.6) has also been observed in a number of other fucoids (Ang 1991, Creed *et al.* 1998, Gunhill 1985). There are conceivably many reasons as to why such a relationship exists. A high incidence of mortality is typical of the smaller life history stages of macroalgae (Santelices 1990, Vadas *et al.* 1990) and so there is a selective advantage to grow quickly through these stages (Vadas *et al.* 1990). As small *Cystophora* plants grow however, their structure not only enlarges but also develops a complexity as tissues for other life history processes (reproduction, storage of nutrients and carbon, production of grazer deterrents) are differentiated. Thalli typically become more highly branched as individuals get larger. Energy must therefore be allocated to all of these processes, in addition to the ongoing requirement for thallus maintenance and repair (Carpenter 1990) and the process of getting bigger.

As yet we do not fully understand the physiology of *Cystophora* but there are potentially a number of trade-offs that occur between the growth process and other life history traits. In fucoids, the largest individuals become reproductive (Chapman 1995) and these typically grow more slowly than non-reproductive plants (Ang 1992, McCourt 1985, Norton 1977). This research has demonstrated the change that occurs in the growth pattern of individuals as they become reproductively mature. As individuals get larger their immediate environment changes, as does their level of interaction with other members of the community (Chapman 1995, Santelices 1990, Vadas *et al.* 1992). The effects of grazing (Choat & Schiel 1982, Gunhill 1985, Santelices 1990, Vadas *et al.* 1992), density and competition (Andrew & Viejo 1998, Carpenter 1990, Creed *et al.* 1988, Reed 1990, Schiel 1985a, Schiel & Choat 1980, Olson & Lubchenco 1990, Paine 1990, Vadas *et al.* 1992) are known to influence the growth patterns of fucoids at various stages in their life history. These important issues are beyond the scope of this study but need to be addressed in the future.

Conclusion

Growth in the three subtidal species of *Cystophora* is now known to be seasonal and was clearly linked to the reproductive cycle with maximum plant size (length and biomass) being achieved in late winter/spring as the plants became reproductively mature (Chapter five). At the end of the fertile period, spent reproductive structures were shed, at this time growth rates were minimal or even negative in the case of *C. expansa.*

The pattern of growth in *Cystophora* was bi-phasic, with an initial period of elongation followed by a period of bulking out as plants matured reproductively. This bi-phasic nature of the growth pattern highlights the necessity for appropriate measures to be used when estimating growth in highly branched fucoids such as *Cystophora.*

A negative relationship existed between plant size (length) and predicted relative growth rate with smaller individuals showing faster growth rates. Sub-canopy individuals (10mm to 200mm) had the potential to reach canopy status in as little as six months however, much variability in growth rate existed. The model on which these results were based makes no account for species and seasonal differences in growth rate and therefore represents an average response for *Cystophora* only.

CHAPTER FIVE..Aspects of the Reproductive Ecology of *Cystophora*

A generalised reproductive cycle for *Cystophora* was given in Chapter one (Fig. 1.2) but this chapter addresses further specific aspects of the reproductive phenology of *Cystophora.* In doing so, it provides information on a number of life-history characters that are important in defining an overall reproductive strategy for each of the three species. Information is presented firstly on the timing of reproduction and the development of the structures associated with this and secondly on the reproductive effort or the relative allocation of resources to reproduction.

Introduction

Many life-history characteristics have been identified as being important in defining the reproductive strategies of algae, and these have been extensively reviewed (Clayton 1990, Brawley & Johnson 1992, DeWreede & Klinger 1988, Lobban & Harrison 1994, Santelices 1990). Aspects of fucoid reproduction are well represented in such reviews, presumably because fucoids are relatively easy to study (being macroscopic with simple sexual life histories, in having large gametes, and well defined reproductive structures). Most research has however, centred on northern hemisphere intertidal communities with the exception of work on intertidal species of *Cystophora* (Klemm 1981, 1985) and *Sargassum* (Kendrick 1994, Kendrick & Walker 1991, 1994) from Australia, and several species of fucoid from New Zealand (Schiel 1985a, 1988, 1990).

Fucoids show a number of reproductive traits that are similar across species, reproduction is typically sexual with all species showing a single, free-living diploid sporophyte generation in which meiosis is gametic and reproduction oogamous (Clayton 1990, Fritsch 1945). Vegetative regeneration does occur in some genera such as *Fucus* (McCook & Chapman 1992, Moss 1964) and *Sargassum* (Kendrick 1994) but this has not been observed in *Cystophora* (Klemm 1985).

Timing of reproduction

Some fucoid species have been shown to reproduce all year round (Begum & Taylor 1991, Evans *et al.* 1982), but most show seasonal patterns of gamete development, maturation and release (Bacon & Vadas 1991, Evans *et al.* 1982, Fletcher & Fletcher 1975a, Klemm 1985, Norton 1981, 1977, Schiel 1985a, b). In Australasia, the onset of reproduction in most fucoids occurs during autumn and winter with gamete release occurring in spring (Clayton 1990, Klemm 1985, Schiel 1988). This contrasts with many northern hemisphere species, which are generally reproductive during the summer months (Brenchley *et al.* 1996, 1998, Hales & Fletcher 1990, Mathieson *et al.* 1976, Stengel & Dring 1997).

Reproductive seasonality in algae is affected by changes in environmental conditions, Brawley & Johnson (1992), Lobban & Harrison (1994) and Santelices (1990) all provide excellent reviews on this subject. It is not clear however, whether reproductive seasonality occurs in direct response to changes that satisfy the physiological requirements for reproduction or, from the use of environmental cues to coordinate reproduction with other beneficial environmental conditions.

In comparison with the wealth of information on kelp species, there has been little investigation into the effects of physical factors on reproductive seasonality in fucoids. Some evidence does however suggest that changes in ambient light climate (daylength and irradiance), temperature, salinity, and lunar cycles may be influential. Seasonal changes in any of these appear to invoke quite different responses between species (Bird & McLachlan 1976, Terry & Moss 1980) and different responses between *in situ* and laboratory cultured populations (Hales & Fletcher 1990). Variation within and between neighbouring populations also exists which suggests that combined effects may be operating (Bacon & Vadas 1991, Hales & Fletcher 1990).

Reproductive synchronisation in sexually reproducing individuals is obviously advantageous in that the number of gametes available for fertilisation is increased. The gametes of fucoids are viable for a very limited period of time once released (Deysher & Norton 1982, Hoffmann & Camus 1989, Jones & Babb 1968, Klemm 1985, Santelices 1990) and therefore any mechanism that aids their concentration, both temporally and spatially, would be of benefit.

Reproductive effort

Reproductive effort is defined as the proportion of available resources that are allocated to reproduction over a given period of time (Begon *et al.* 1990). In this study, the resource is the amount of thallus biomass that is allocated to reproduction (Chapman 1986). It provides a useful measure of relative reproductive output and may be estimated in terms of the proportion of biomass given to reproductive propagules or the reproductive structures (associated reproductive biomass) that house them. Reproductive allocation in fucoids is variable (Brenchley *et al.* 1996, DeWreede & Klinger 1988, Mathieson & Guo 1992, McCourt 1985, Schiel 1985a, b, Vernet & Harper 1980) however, much of this variability may be attributed to discrepancies in the definitions and measurements of "reproductive structure" that are used.

Identification of reproductive structures can be problematic as algal tissues can perform a multiplicity of functions and may be photosynthetic (somatic) and reproductive at the same time. Often they lack morphological differentiation and fertile structures may be embedded within vegetative tissues. Fortunately, fucoids are relatively simple in that the reproductive thallus is readily differentiated (Fig. 5.1, Pl. 5.2) but "fertile structures" can be identified at a number of levels. At the simplest level are the large gametes, which are contained within the conceptacles (Fig. 5.1). At a more complex level are the receptacles (Fig. 5.1), which although easily identified, are essentially somatic and provide the structure within which the conceptacles are borne. The somatic tissue of the receptacles is also photosynthetic (Nizamuddin 1964).

Allocation of resources to reproduction is seen as an important trait in the life-history strategy of an individual (Begon *et al.* 1990, Reekie & Bazzaz 1987). Terrestrial plants commonly invest most of their reproductive biomass either into vegetative structures or sexual structures, but not to both and the production of sexual biomass is more costly (McCourt 1985). This appears to be the case with species of *Sargassum* that can reproduce either vegetatively or sexually (McCourt 1985) with vegetative growth occurring up to five times faster than reproductive growth (Norton 1977). Reproduction in most fucoids, including *Cystophora,* is predominantly sexual and so it seems reasonable to assume that allocation of resources to reproductive structures is likely to be high.

Associated reproductive biomass as a measure of reproductive effort

Associated reproductive biomass comprises all reproductive laterals in which the gametes are borne (Fig. 5.1). Associated reproductive biomass has been used as a measure of reproductive effort in a number of species including *Ascophyllum* (Cousens 1986, Mathieson & Guo 1992), *Carpophyllum* (Schiel 1985a), *Cystoseira* (Schiel 1985b), *Fucus* (Brenchley *et al.* 1996, Mathieson & Guo 1992), *Himanthalia* (Brenchley *et al.* 1996) and

Sargassum (Prince & O'Neal 1979, Schiel 1985a); the terminology reported in these studies varies. These species produce and shed annually up to 98% of their biomass on which receptacles are borne along the entire length. Irrespective of the additional functions played by this annually produced biomass (photosynthesis, nutrient uptake), it is arguable that the primary role is reproductive, especially as shedding occurs directly after gamete release.

The production of reproductive tissue in *Cystophora* is directly linked to the production of somatic tissue, as conceptacle development is initiated when the apical cell divides and cuts off a conceptacle initial cell (Nizamuddin 1964). This cell remains inactive whilst adjacent meristoderm cells continue to divide and surround it, forming a conceptacle cavity (Jensen 1974, Nizamuddin 1964). In this sense, the vegetative ramuli, which develop into receptacles, as the conceptacles mature, may be considered as "reproductive structures" even though they also play a supportive, protective and photosynthetic role.

Total egg biomass as a measure of reproductive effort

Estimates of egg production have been carried out for a number of fucoid species including *Fucus* (Ang 1991) and *Sargassum* (Schiel 1988), but reproductive effort as a function of egg biomass has rarely been calculated (Vernet & Harper 1980).

In terrestrial plants the way reproductive material is apportioned to seeds, is found to be ecologically important, with either many small seeds or fewer large seeds being produced. The resulting seed size is considered to represent a compromise between requirements for dispersal, favouring small seeds, and establishment, favouring larger seeds (Fenner 1985). A successful seed size for dispersal will obviously depend on a number of factors such as, extent of internal reserves, avoidance of size-specific predation and the size of area available for settlement. These factors could also be seen to be important in establishment as they affect the competitive ability of the newly settled individuals (Stearns 1976). Such concepts are however, yet to be convincingly demonstrated in algal systems (DeWreede & Klinger 1988, Santelices 1990, Vernet & Harper 1980). This is not entirely surprising, given the problems experienced in accurately quantifying important phenomena such as dispersal distances, effects of grazing and allocation of internal reserves to reproductive propagules.

The reproductive life histories of fucoids are shown to be broadly similar but it is recognised that the various life history traits are phenotypic expressions of individuals, and as such, should be unique (Clayton 1990). Therefore, the primary objective of the current section of research was to investigate a number of reproductive life-history traits for three species of *Cystophora,* which coexisted in the subtidal community. In doing so, similarities or differences in reproductive strategies have been discussed in the context of each species.

The more specific aims of the research were:-

- to define the timing of reproduction in each of the species with reference to:-
- the development and maturity of eggs
- the initiation of release of eggs
- the length of the fertile period
- to quantify reproductive effort i.e. the partitioning of resources between the reproductive structures and vegetative thallus
- to make informed proposals regarding the likely reproductive strategies employed by each species

Methods

Destructive harvesting of the community at approximately monthly intervals (Chapter three) provided the algal material required for reproductive studies. For each species, the seasonal timing and cycle of development of reproductive structures was monitored, and two measures of reproductive effort were employed:-

- reproductive effort in terms of resources allocated to associated reproductive biomass
- reproductive effort in terms of egg biomass, the calculation of which included an estimation of fecundity, i.e. the total number of eggs produced (each oogonium producing a single egg).

Observations began in summer (December) 1991 and continued into December of 1992.

Seasonal timing of reproduction

Laboratory investigations

For each sample period, individual conceptacles were assessed to determine the reproductive status of each of the three species. Five states were chosen:-

- Developing or sterile conceptacles
- Developing oogonia
- Mature oogonia
- Partially released oogonia
- Exhausted conceptacles

The reproductive status of ten individuals of each species at each sample time was assessed using ten random conceptacles (per thallus) and the percentage of individuals in each fertility state calculated. Observations were made using a dissecting microscope and permanent slides were prepared so that the developmental sequence of the oogonia and conceptacles could be recorded. All three species of *Cystophora* were monoecious; all conceptacles in *C. expansa* were bisexual, *C. subfarcinata* had predominantly bisexual conceptacles and *C. monilifera* had both unisexual and bisexual conceptacles.

Empty conceptacles were observed in all species prior to egg production, whilst these structures could have been cryptostomata (sterile counterparts of conceptacles as identified by Klemm 1985), they were most likely to be developing conceptacles. Cryptostomata are known to be a feature of intertidal species (Fritsch 1945) and have not been identified in previous studies of subtidal species of *Cystophora* (Nizamuddin 1964, Womersley 1964, 1987).

Reproductive effort-associated reproductive biomass

Laboratory investigations

Associated reproductive biomass was estimated by calculating the proportion of thallus biomass (dry weight) that was allocated to the receptacles (Fig. 5.1). This was measured as the biomass of reproductive laterals (Fig. 5.1) as the separation of receptacles was very difficult. The proportion of vegetative biomass was also estimated, and this included primary and higher order axes and holdfast tissue (Fig. 5.1).

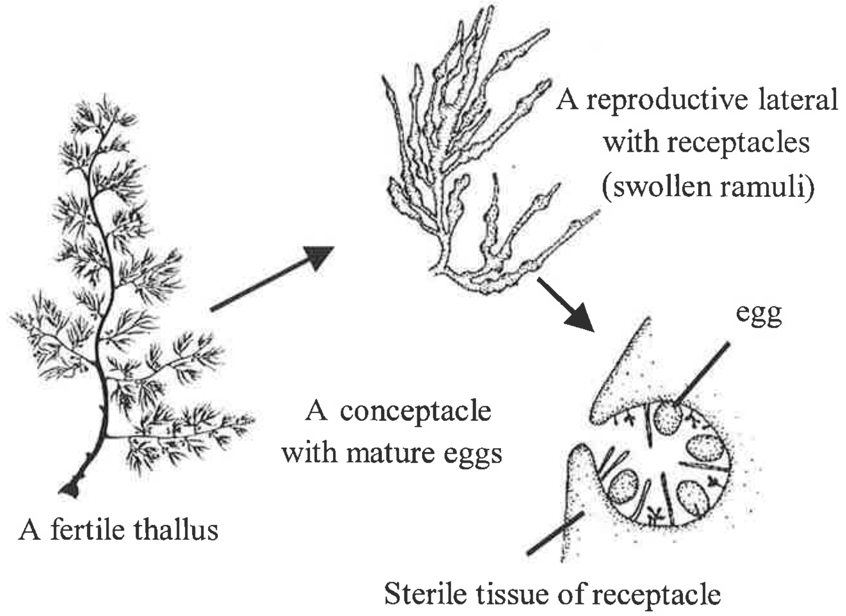


Figure 5.1. A stylised fertile *Cystophora* thallus showing the reproductive structures that were counted for the estimate of reproductive effort.

Analysis

One-way ANOVAs and post-hoc Tukey tests were used to determine any significant differences (α=0.05 unless otherwise stated) in biomass across seasons and its proportioning between thallus tissues. A 4th root transformation was carried out as this best normalised the data and the Brown-Forsythe test for homogeneity of variances was also used. Where variances were significantly heteroscedastic, a Kruskal-Wallis test was performed (Zar 1996). Individual analyses were run for each species.

Reproductive effort-biomass of eggs

Laboratory investigations

Reproductive effort as a measure of the proportion of thallus biomass allocated to the eggs was calculated using an estimate of fecundity (total number of eggs produced per individual) at reproductive maturity. The aim of the current study was to estimate the effort devoted to the production of eggs only, but a similar approach could have been used to estimate resource allocation to antheridia.

Estimation of fecundity:-

The estimation of fecundity was made for each species at peak reproductive maturity. The total number of eggs per individual was calculated as follows:-

number of receptacles per thallus x number of conceptacles per receptacle x number of eggs per conceptacle.

- The number of receptacles per thallus (Fig. 5.1) was estimated by first determining the number of receptacles per gram of dry lateral tissue. This was done using sub samples of lateral tissue (from each species) in which the number of receptacles were counted and then a dry weight obtained. The relationship between number of receptacles and dry weight was determined for each species using regression analysis (see results section below). This information was used in conjunction with the previously determined measure of the allocation of biomass to reproductive laterals (see above) to estimate the total number of receptacles on each thallus.

- The number of conceptacles per receptacle (Fig. 5.1) was also determined microscopically and was calculated as an average from five randomly chosen receptacles from each species.

- The number of eggs per conceptacle (Fig. 5.1) was calculated as an average from five randomly chosen conceptacles from each species. This was done microscopically with each conceptacle being cut in half and the number of oogonia observed in each half counted. Gentle squashing of the material dislodged the eggs so that the entire contents of each half conceptacle could be counted (Pl. 5.1). Note that in *Cystophora* eggs are produced singly unlike other fucalean genera, which produce up to 8 (Clayton 1984, Womersley 1987).

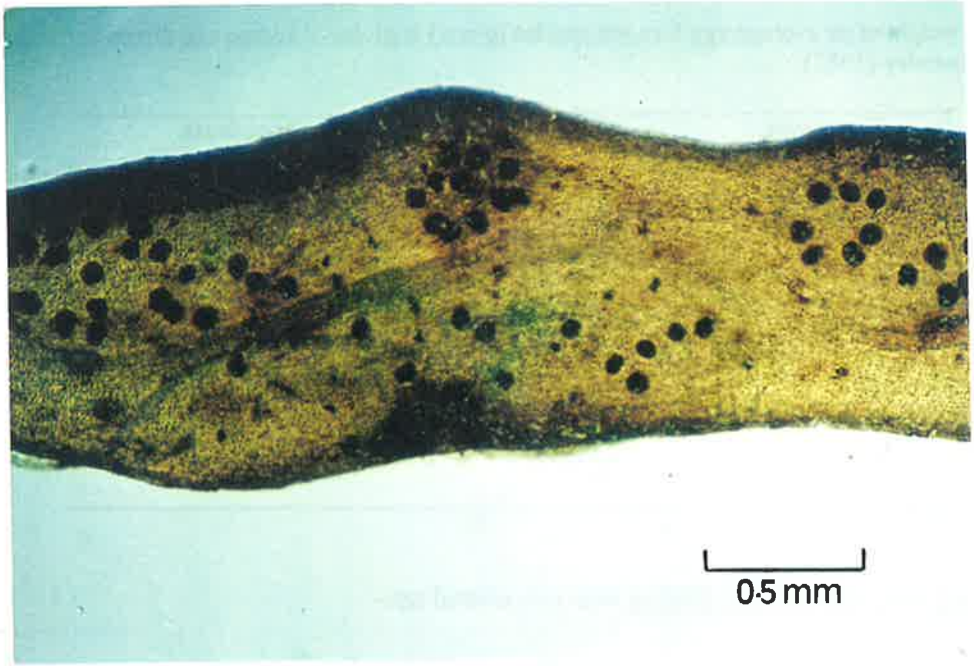


Plate 5.1. A longitudinal section through a receptacle of Cystophora subfarcinata, showing a number of half conceptacles each with developing eggs inside. Each half receptacle was assessed to determine the reproductive status of conceptacles and to estimate the average number of eggs per conceptacle.

Estimation of reproductive effort:-

- The weight (g ww) of an average egg for each species was estimated as follows:-

$$\mathbf{M=DxV} \quad \text{(Tranter 1955)}$$

Where M = mass (g ww), D = density (g.cm^{-3}), V = volume (mm^3).

A density of 1.1 was assumed (Coon *et al.* 1972).

The volume of an egg (ovoid) was calculated, using

$$\pi r^2 l+4/3\ \pi r^3 \quad \text{(Tranter 1955)}$$

Where r =radius (μm), l =length of cylindrical portion of egg, not including hemispherical ends (μm).

The estimates obtained for each species are as in Tab. 5.1.

Table 5.1. The weight of an average egg for each species (g ww) is given. Average egg dimensions were taken from Womersley (1987).

	C. expansa	*C. monilifera*	*C. subfarcinata*
r (µm)	33.5	42.5	30
l (µm)	53	15	40
V (µm^3)	373964.6	441650.7	245655
M (µg)	.037	0.44	0.25
M (g ww)	**3.79E-07**	**4.47E-07**	**2.49E-07**

- Biomass (g ww) of eggs per thallus was calculated as:-

total number of eggs per thallus x weight of an average egg

- Reproductive effort was calculated as the percentage of lateral biomass apportioned to the eggs. As biomass of eggs was estimated in grams wet weight (ww) and lateral biomass in grams dry weight (dw), lateral biomass values were converted to grams ww. A relationship between wet weight and dry weight of laterals was then established for each species at peak reproductive maturity, using regression analysis (see results section below).

Results

Seasonal timing of reproduction

General situation

A general pattern of seasonal reproduction occurred for all three species with gamete release occurring in late winter/early spring (Fig. 5.2). Some interspecific variation in the timing of gamete initiation, maturation and release was evident and this was reflected in the differing periods of potential fertility.

Conceptacles (Fig. 5.2a) developed through the summer and autumn into winter (January to June) 1992 and reappeared in late spring (November) 1992 to early summer (December) 1992.

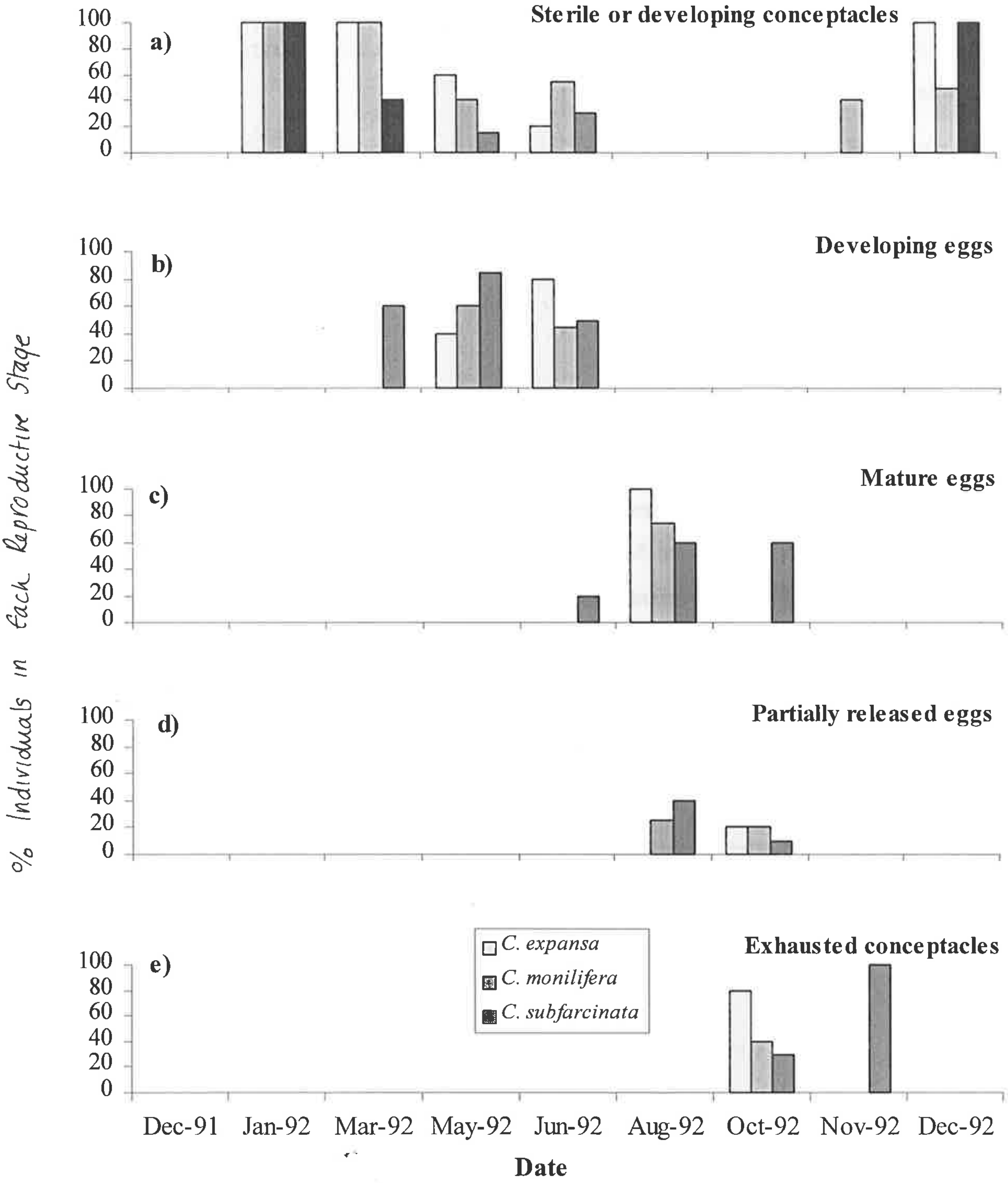


Figure 5.2a-e. A general pattern of reproductive development and maturation was evident for adult individuals of all three species although some interspecific differences were apparent. Reproductive structures developed from summer through to winter when egg release began. Spent receptacles were generally shed after egg release and new ones developed in the following year. In the case of *C. subfarcinata,* sterile ramuli were produced before conceptacle development was observed, this is indicated on graph **a)** with black bars, the subsequent observation of conceptacles is depicted with hatched bars. **Note** that the x-axis is not proportional.

Eggs (Fig. 5.2b) developed through autumn and winter (March to June) 1992. Thus, a lag phase occurred between the onset of conceptacle development and egg development of approximately two months.

Mature eggs (Fig. 5.2c) were present across winter and early spring (June to October) 1992, approximately three months after the onset of egg development.

Release of eggs (Fig. 5.2d) occurred from late winter into spring (August to October) 1992, with release being initiated approximately two months after mature eggs were first observed.

Exhausted conceptacles (Fig. 5.2e) were observed from mid spring into summer (October to November) 1992, approximately two months after egg release began.

Degeneration of conceptacles and shedding of ramular tissue occurred after gamete release (Pl. 5.2) but before new receptacles developed at the beginning of the next reproductive season. This was noted (but not quantified) in each species at the start of observations in summer (December) 1991 and again in late spring/early summer (October & November) 1992.

As the cycle repeated itself, developing conceptacles (Fig. 5.2a) were again observed in late spring/early summer (November & December) 1992.

Differences in timing between species

Within the general seasonal pattern of reproduction, some interspecific differences were evident in the timing of development of reproductive structures and the maturation and release of eggs.

Eroded or lost tissue (Pl. 5.2) was observed in all species at the beginning of the experiment summer (December) 1991. In *C. expansa & C. monilifera,* this was followed by conceptacle development (Fig. 5.2a) through mid summer into winter (January to June 1992). *C. subfarcinata* was different in that sterile ramuli (with the appearance of fertile receptacles) were produced prior to conceptacle development. Although ramuli were produced by the other species, they rapidly developed conceptacles and became receptacles. Ramuli were present in *C. subfarcinata* through summer (January) 1992 and were again observed in summer of the following year (December 1992).

Developing eggs (Fig. 5.2b) were seen for longer in *C. subfarcinata* beginning approximately two months before the other species and reaching a peak (85%) in late autumn (May) 1992. *C. monilifera* and *C. expansa* did not begin to develop eggs until mid autumn and peaked in May 1992 (60%) and June 1992 (80%) respectively. Developing eggs were not observed in any individuals after mid winter.

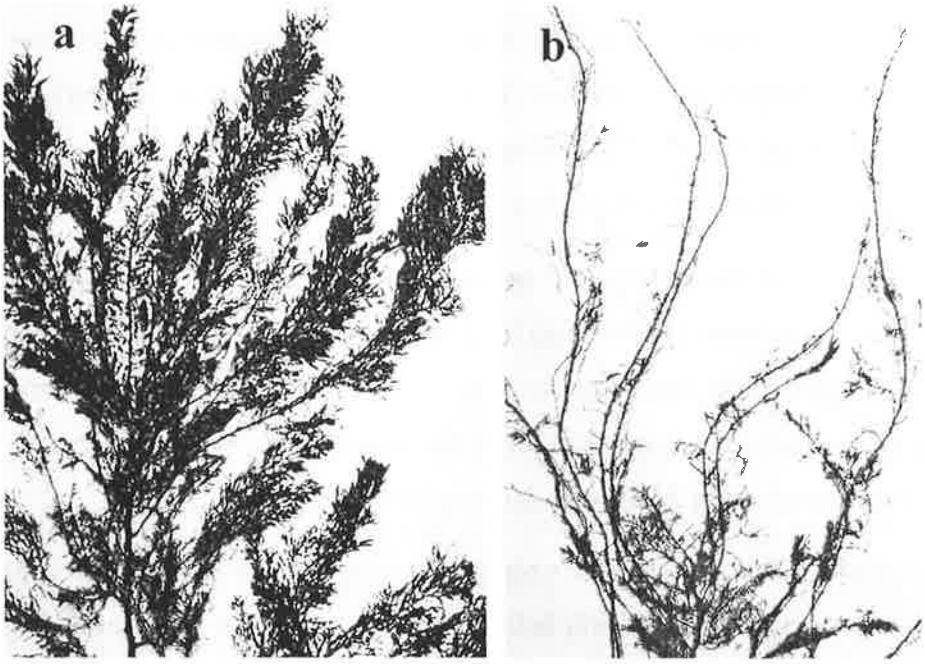


Plate 5.2a,b. Herbarium specimens of *C. expansa* from Cape Jervis, showing the difference in thallus biomass between, **a).** mid winter when thallus was reproductively mature, and **b).** early summer after spent reproductive laterals had been lost.

Mature eggs (Fig. 5.2c) were also present in *C. subfarcinata* for an extended period of time. They were first observed about two months prior to the other species and peaked in early spring (60%). *C. expansa* and *C. monilifera* had mature eggs by late winter and peaked in August (100% and 75% respectively). Mature eggs were not seen in these two species after winter (August) 1992 whereas in *C. subfarcinata* they were observed until mid spring (October) 1992.

The period of egg release (Fig. 5.2d) was shorter in *C. expansa.* Release in all species was complete by mid spring (October) but began earlier in late winter (August) in *C. subfarcinata* and *C. monilifera* than in *C. expansa.*

Exhaustion of conceptacles (Fig. 5.2e) occurred for all species at the end of the cycle in spring (October) 1992. For *C. expansa* and *C. monilifera* this coincided with a period of receptacle erosion and loss. In *C. subfarcinata* conceptacle exhaustion extended into November 1992 but no receptacle erosion or loss was observed.

New conceptacles developed at different rates in the new tissue growth of summer (December) 1992 (Fig. 5.2a). *C. monilifera* began developing new conceptacles earlier than the others and also spread this development over a longer period. New conceptacles were seen in *C. monilifera* in November (40% of individuals) and continued into December (50% of individuals) 1992, whereas *C. expansa* and *C. subfarcinata* did not develop new conceptacles until December.

The reproductive cycle for each species appeared to differ slightly between years. At the start of the study in summer (December) 1991 individuals had eroded or shed receptacles and began developing new conceptacles or ramuli (Fig. 5.2a) by January. Eroded receptacles were noted as early as October in the following years cycle and new conceptacles or ramuli (Fig. 5.2a) were forming by November/December.

From these results it is not possible to estimate the onset of reproduction for 1991, however developing and mature eggs were still being observed in October 1991 for all 3 species (pers. obs.), two to three months later in the year than in the 1992 cycle.

Implications in terms of period of potential fertility

The period of potential fertility (i.e. when mature eggs were present in the conceptacles or were being released was similar for *C. expansa* and *C. monilifera* (three months) but longer for *C. subfarcinata* (four months).

C. expansa was potentially fertile (Fig. 5.2c) from about August 1992 through to October 1992, a period of approximately three months. The reproductive cycle from the previous year was finished by December 1991 and mature eggs were being released again by October, ten months later (Fig. 5.2c). The cycle began to repeat in December 1992 (Fig. 5.2a) and so *C. expansa* was developing and maturing reproductively for approximately 85% (ten months) of the year.

Note that in making this estimation it needs to be recognised that the exact length of a reproductive cycle will not necessarily be 12 months due to interannual variability (see above).

C. monilifera was also potentially fertile for approximately three months but began releasing eggs earlier than *C. expansa.* It was therefore developing and maturing reproductively (Fig. 5.2 b, c) for approximately two thirds (eight months) of the year.

In C. subfarcinata, initial growth was invested into the production of sterile ramuli (Fig. 5.2a) and conceptacles were not observed until March 1992 (Fig. 5.2a). The period of reproductive development was therefore much shorter than in the other species (Fig. 5.2 b, c), only five months (or approximately 40%) of the year. *C. subfarcinata* was however potentially fertile for longer, from June 1992 through to October 1992, a period of five months. Sterile ramuli were observed in December 1992 at the start of the following year's cycle (Fig. 5.2a).

Allocation of resources to associated reproductive biomass

General situation

A seasonal pattern of change in total thallus biomass was clearly evident for all species (Fig. 5.3). Individual thallus biomass increased through summer and autumn, reaching a maximum in late winter/early spring, and decreased towards summer.

The seasonal pattern of change in biomass was clearly linked to the reproductive cycle of each species. Biomass gradually increased through autumn and winter as the reproductive structures developed (Figs 5.2, 5.3), and was maximal in late winter/early spring, which coincided with the period of egg maturation and release (Fig. 5.2). Sudden biomass loss for *C. expansa* (Pl. 5.2, Fig. 5.3a) and *C. monilifera* (Fig. 5.3b) resulted from the erosion and shedding of spent reproductive material in spring. This was observed in *C. subfarcinata* in summer 1991/1992 but not in the following year despite a substantial loss in biomass occurring (Fig. 5.3c). However the sequence of reproductive development in *C. subfarcinata* (Fig. 5.2) did show the presence of sterile ramuli in summer 1992/1993 which suggests that either spent receptacles were shed and new ramuli created, or that exhausted conceptacles were somehow reabsorbed into the receptacle tissue.

Patterns of total thallus biomass change - differences between species

For C. expansa (Fig. 5.3a) and C. monilifera, (Fig. 5.3b) average thallus biomass was low in December 1991 (<6.5g dw and <7g dw respectively), gradually increased throughout summer and autumn 1992 and peaked (26.1 g dw and 19.6 g dw respectively) in late winter/early spring 1992. A significant decrease followed to bring total thallus biomass again to a low in late spring/early summer 1992/1993.

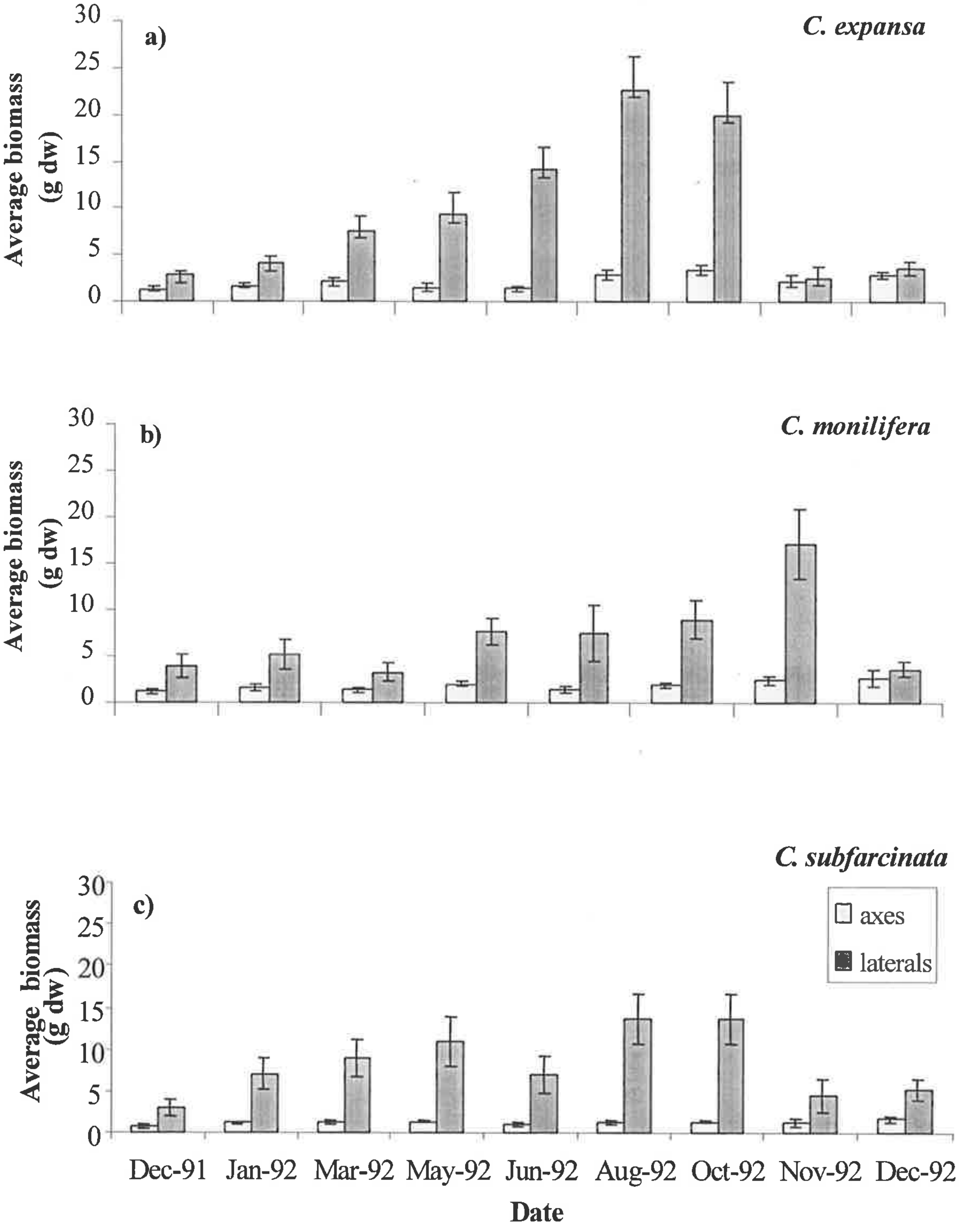


Figure 5.3a-c. A seasonal pattern of biomass production is evident for adults of all 3 species with maximum biomass occurring in late winter/early spring. This coincides with the period of peak reproductive maturity (Fig. 5.1). **Note** that the x-axis is not proportional. Error bars=standard error.

For C. subfarcinata, (Fig. 5.3c) the pattern of change was less pronounced with a gradual increase in biomass through summer to winter, followed by a decrease in spring. Biomass was lowest in December 1991 (<3.8g dw) and maximal in October 1992 (15g dw). Although more gradual, the extent of biomass increase in *C. subfarcinata* was similar to *C. expansa* (Fig. 5.2a), approximately four-fold, and higher than *C. monilifera* (Fig. 5.2b), approximately three-fold. Although not statistically significant, there appeared to be a decrease in biomass in spring 1992 (Fig. 5.3c).

Allocation of biomass to reproductive laterals- differences between species

Reproductive laterals (Fig. 5.1) comprised the majority of thallus biomass for all three species and hence seasonal fluctuations in total thallus biomass essentially reflected changes observed in the reproductive lateral biomass.

Average reproductive lateral biomass in *C. expansa* (Fig. 5.3a) and *C. subfarcinata* (Fig. 5.3c) was highest in late winter and lowest in late spring and accounted for 64% to 90% and 76% to 91% of the total biomass in each. Reproductive lateral biomass in *C. monilifera* (Fig. 5.3b) was never lower than 57% and peaked in early spring (87%), slightly later than the others.

The biomass of axes (Fig. 5.1) did not change significantly ($p<0.05$) through time for any of the species (Fig. 5.3). Additionally, total axial biomass never exceeded the total biomass of the reproductive laterals.

Reproductive effort - fecundity

The estimates of reproductive effort (fecundity) presented here and in the results section of allocation of biomass to eggs (below) were based on data obtained from linear regression analysis of the relationships between:-

- weight of laterals (g dw) **:** number of receptacles (Tab. 5.2)
- wet weight of laterals (g ww) **:** dry weight of laterals (g dw) (Tab. 5.2)

Measurements were taken for canopy-sized individuals of each species at peak reproductive maturity.

Table 5.2. Data used in the calculation of reproductive effort. Based on linear regression analysis.

	C. expansa	*C. monilifera*	*C. subfarcinata*
No. of receptacles per g (dw) laterals	1667 (r^2=0.89)	1250 (r^2=0.81)	556 (r^2=0.91)
Wet weight (g ww) of laterals equivalent to 1g (dw) of laterals	4.05 (r^2 =0.96)	3.58 (r^2 =0.99)	3.73 (r^2 = 0.93)

General situation

Mature eggs were seen in all species during winter (June to August) 1992 and in *C. subfarcinata* until mid spring (October) 1992, but peak fecundity was achieved in all by late winter (August) 1992 (Fig. 5.4c). In *C. expansa* and *C. monilifera* the reproductive structures were mostly shed by October 1992 but some eggs still remained in the conceptacles of *C. subfarcinata* beyond this time (Fig. 5.4).

Fecundity of each species reflected the structure of the fertile thallus, and *C. expansa* was clearly the more fecund species, producing a higher number of eggs, conceptacles and receptacles per individual (Fig. 5.4, Tab 5.3) than the others. *C. subfarcinata* produced the lowest numbers of receptacles and conceptacles per individual (Fig. 5.4), but the highest number of eggs per conceptacle (Fig. 5.4) and hence was more fecund than *C. monilifera.*.

Receptacle, conceptacle and egg production - differences between species

The mean <u>number of receptacles</u> produced per individual at peak reproductive maturity varied between species (Fig. 5.4a) with *C. expansa* producing the most, approximately 38000. *C. monilifera* produced about one third of this (approx. 11000) and *C. subfarcinata* only about one fifth (7550). The receptacles of *C. subfarcinata* were however, larger than the other species.

C. expansa also produced a greater mean <u>number of conceptacles</u> per individual at peak reproductive maturity (34 x 10^4), in comparison with *C. monilifera* (8 x 10^4) and *C. subfarcinata* (5 x 10^4), which produced more similar numbers (Fig. 5.4b). The higher number of conceptacles in *C. expansa* resulted not only from the much higher numbers of receptacles (Fig. 5.4a) but also from a higher (on average) number of conceptacles per receptacle (Fig. 5.4d).

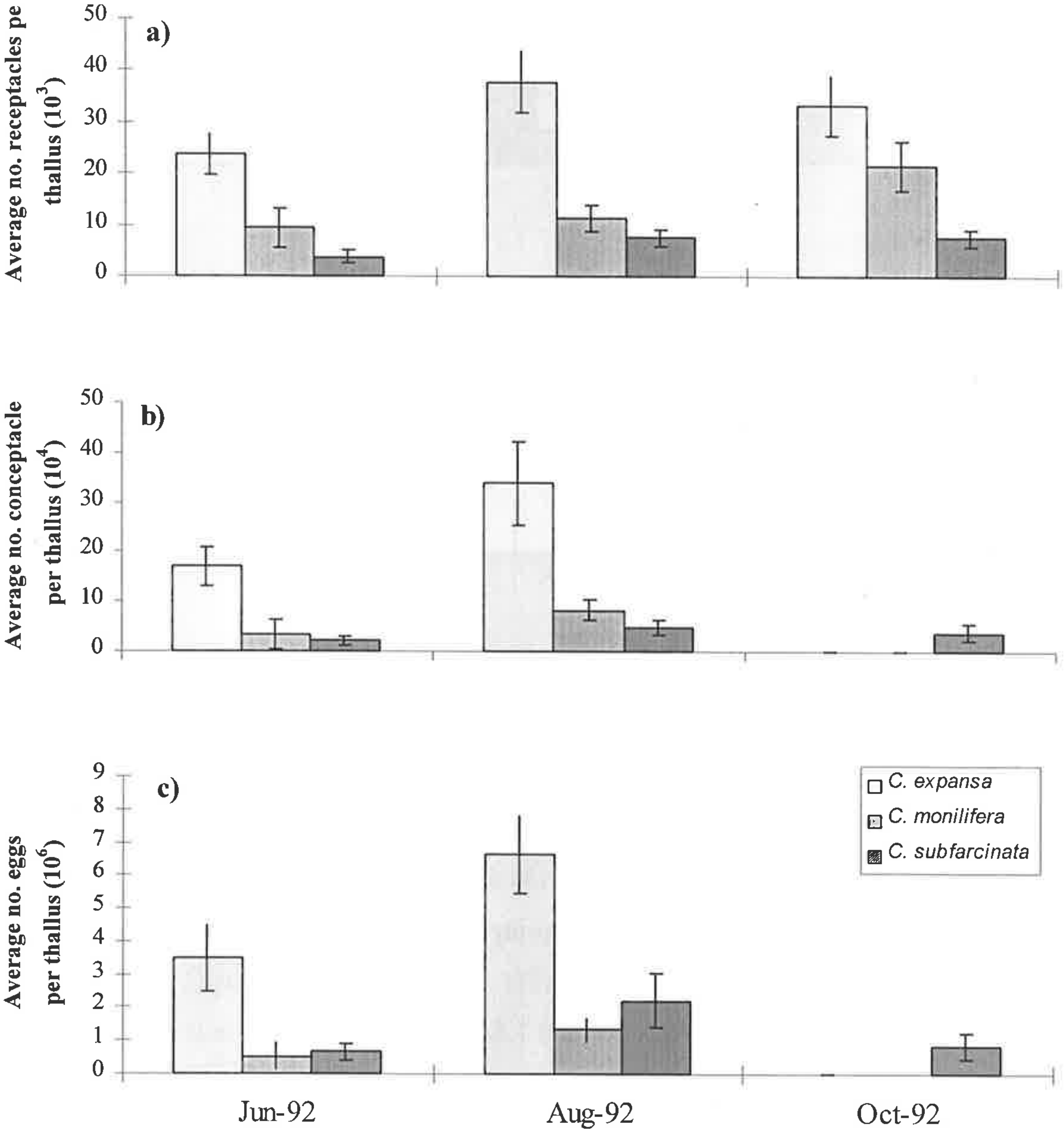
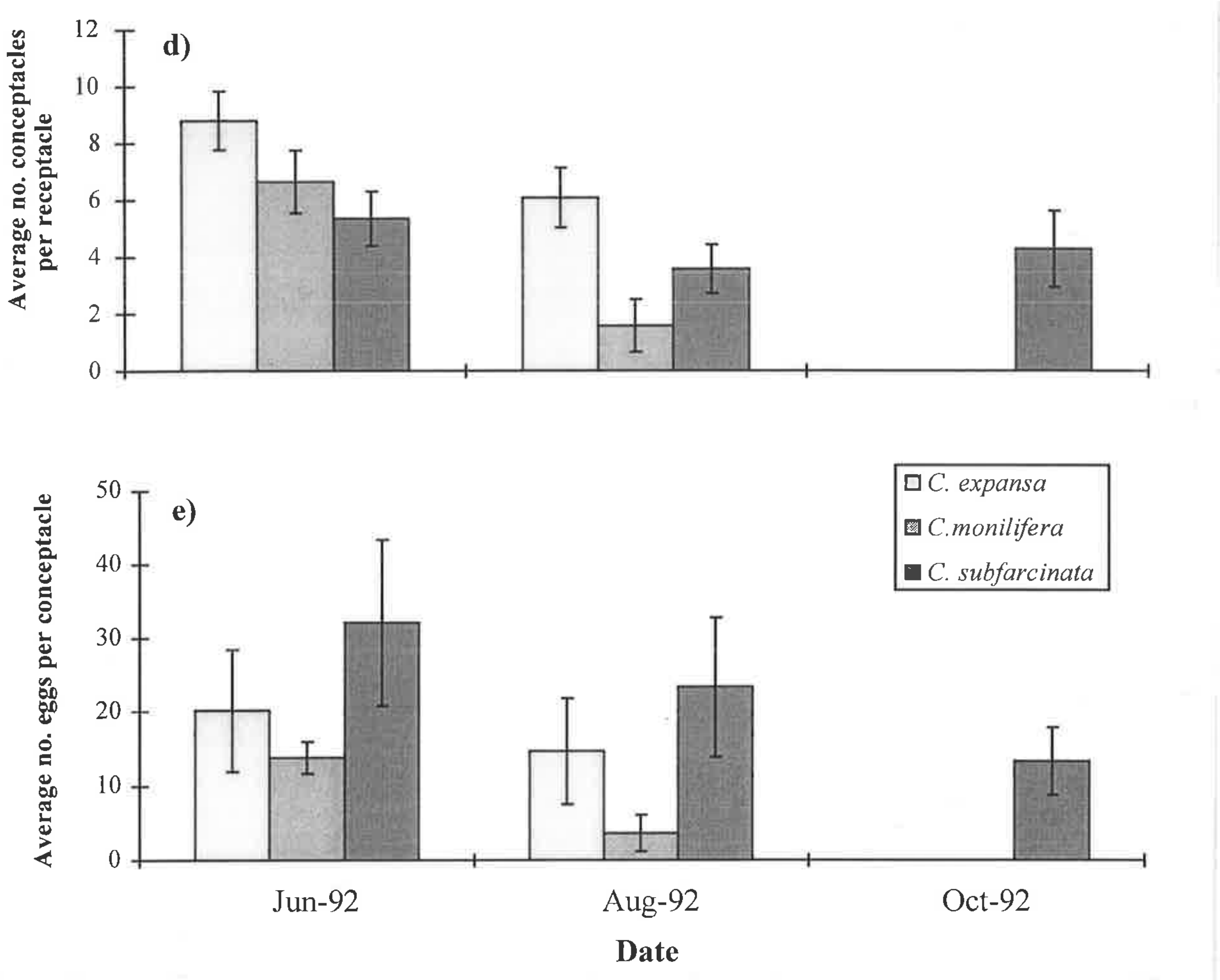


Figure 5.4a-c, d and e on following page. Mean numbers of reproductive structures per individual thallus are presented here for each species, and show peak fecundity for all to have occurred in August 1992. Mature eggs were present in the conceptacles of all species during winter (June to August) 1992 and in *C. subfarcinata* until mid spring (October) 1992. In *C. expansa* and *C. monilifera* the reproductive structures were mostly shed by October 1992 but eggs still remained in the conceptacles of *C. subfarcinata*. *C. expansa* is seen to be the most fecund species with higher numbers of receptacles, conceptacles and eggs per thallus. **Note** that the x-axis is not proportional and different scales on y-axes. Error bars = standard error.



The mean number of eggs produced per individual was clearly very different for *C. expansa* than the other species (Fig. 5.4c). During peak fecundity, individuals of *C. expansa* produced on average 6.6 x 10^6 eggs (Fig. 5.4c, Tab 5.3) whereas *C. subfarcinata* and *C. monilifera* produced only 2.2 x 10^6 and 1.3 x 10^6 eggs per individual respectively (Fig. 5.4c, Tab 5.3). Higher numbers of eggs in *C. expansa* again resulted from higher numbers of receptacles and conceptacles. *C. expansa* also produced a higher mean number of eggs per conceptacle than *C. monilifera* but not *C. subfarcinata* (Fig. 5.4e)

Although *C. monilifera* produced higher mean numbers of receptacles and conceptacles (Fig. 5.4a, b) per individual, *C. subfarcinata* produced more than twice the number of eggs per conceptacle (Fig. 5.4e) and hence was more fecund than *C. monilifera.*

Reproductive effort - allocation of biomass to eggs

General situation

Reproductive effort differed between species (Tab. 5.3) with *C. expansa* investing a greater proportion (2.7%) of lateral biomass in eggs than either *C. monilifera* (1.7%) or *C. subfarcinata* (1.1%).

Allocation of biomass to eggs did not necessarily reflect levels of fecundity due to differences in the average size of eggs between species (Tab. 5.3).

Differences between species in the allocation of resources to eggs

Greater fecundity did not necessarily result in greater allocation of resources to eggs, as egg size was also important. Although *C. expansa* was clearly the most fecund species (Tab. 5.3) and allocated the highest proportion of its resources to eggs, this relationship did not hold for other two species. *C. monilifera* was the least fecund species but showed greater reproductive allocation than *C. subfarcinata* as its eggs were much bigger (Tab. 5.3).

Table 5.3. Estimates of biomass allocation to eggs are given for each species. Estimates are based on average data at peak reproductive maturity.

	C. expansa	***C. monilifera***	***C. subfarcinata***
Eggs per thallus x 10^6	6.6	1.3	2.2
Biomass of single egg (g ww x 10^{-7})	3.79	4.47	2.49
Total biomass of eggs (g ww)	2.5	0.58	0.55
Biomass of thallus laterals (g ww)	91.6	33.6	48.7
Biomass of eggs as % of lateral biomass	2.7	1.7	1.1

Discussion

This research has provided the first quantitative reproductive data on the three species of *Cystophora* studied, and in doing so has detailed a reproductive life history, which is similar for each. Reproduction was seasonal and occurred in late winter/early spring when reproductive maturity coincided with maximal thallus biomass. The seasonal increase in thallus biomass reflected an increased allocation of biomass to reproduction, with most growth occurring in the laterals, which ultimately bore the reproductive structures. After gamete release, spent reproductive material was shed, leaving the parent thalli denuded. This pattern agrees with what is already known of the seasonal growth and reproduction of intertidal species of *Cystophora* (Klemm 1981, 1985, Womersley 1964) and of other fucoids (Brenchley *et al.* 1996, Clayton 1990, Kendrick & Walker 1994, Mathieson & Guo 1992, Norton 1977, Schiel 1985a, 1985b, 1988, Vadas & Bacon 1991).

In southern Australasia fucoids typically reproduce during late winter/early spring (Clayton 1990), which suggests this timing to be beneficial to all species. For *Cystophora* at Cape Jervis, the benefits of reproducing at this time are conceivably numerous. Autumn and winter characteristically have a high incidence of storms, which may result in physical disturbance and canopy thinning. Removal of *Fucus spiralis* (from the northern hemisphere) in this way was noted to increase when plants were reproductively heavy (Niemeck & Mathieson 1976). As a genus that appears to recruit more successfully into open areas (Emmerson & Collings 1998), *Cystophora* can only benefit from the resultant increase in available space at a time when settlement of its offspring is imminent.

Fucoids are in general, believed to have poor dispersal abilities (Anderson & North 1966, Deysher & Norton 1982, Kendrick & Walker 1991, Schiel 1988). Long distance dispersal does occur in *Sargassum* and *Ascophyllum* (Deysher & Norton 1982, John 1974, Segawa *et al.* 1962), and is believed to occur in *Cystoseira osmundacea* (Schiel 1985b) and *Sargassum* in Western Australia (Kendrick & Walker 1991). It is possible that dislodged plants or portions of fertile *Cystophora* thalli may be dispersed away from the immediate vicinity during stormy weather. Excised portions of thalli from *Sargassum muticum* continued to grow under laboratory conditions (Fletcher & Fletcher 1975b). Shedding of portions of fertile tissue has also been noted to promote sinking and settlement of reproductive propagules in other large brown algae (Amsler & Nueshul 1989).

Although environmental conditions for growth during autumn and winter in southern Australia may not be optimal (Cheshire *et al.* 1996, Kildea Ph.D. thesis, University of Adelaide, in prep.), *Cystophora* was seen to actively grow during this time (Chapter four) and produce reproductive biomass (Figs. 4.2, 4.4). As a consequence, spent reproductive material was shed during early summer when conditions for growth were good (Cheshire *et al.* 1996, Kildea, Ph.D. thesis, University of Adelaide, in prep.). It has already been established that this process facilitates recruitment in *Cystophora* (Chapter three) but the denuded parent thalli would presumably have also benefited from the good growth conditions at this time.

The seasonal nature of the reproductive cycle, and the synchronised pattern of reproductive development in Australasian fucoids, prompts questions as to the mechanisms that control the process. Very few studies however, have addressed this issue. Klemm (1985) reported that the initiation of gamete development and acceleration of gamete maturation in intertidal species of *Cystophora* occurred as daylength shortened. Gamete release in these species followed a lunar cycle and coincided with spring low water tides (Klemm 1985). Similarly, gamete release in species of *Sargassum* from Australia also coincided with lunar cycles (Kendrick & Walker 1991, May & Clayton 1991).

A number of abiotic environmental factors are believed to affect both the production and maturation of gametes, and their release, in other species of fucoids (Bacon & Vadas 1991, Begum & Taylor 1991, Bird & McLachlan 1976, Fletcher 1980, Hales & Fletcher 1990, Terry & Moss 1980). The collective evidence however, suggests that different species respond to these differently. Species of *Fucus* and *Ascophyllum nodosum* were shown to respond to a single variable either temperature (Bacon & Vadas 1991) or daylength (Bird & McLachlan 1976, Terry & Moss 1980), whereas *Sargassum muticum* responded to a combination of temperature and light climate (Hales & Fletcher 1990). *Sargassum muticum* also responded differently to these variables under laboratory conditions (Hales & Fletcher 1990) than *in situ* (Fletcher 1980). Hales & Fletcher (1990) also found the effects of the lunar cycle *in situ* to override any effects of temperature as observed in the laboratory.

The current research on *Cystophora* has primarily concentrated on the timing of reproduction in relation to patterns of change observed in the community. Further investigation is required to determine any influence of abiotic variables on the process and it is obvious from the findings of the above-mentioned research that specific studies will be required for this purpose. The results do however, show the timing of reproductive development and length of fertile period to be different between *C. subfarcinata* and the other two species (Fig. 5.2, Tab. 5.4).

C. expansa and *C. monilifera* developed new receptacles at the start of the reproductive cycle whereas conceptacles were not observed in *C. subfarcinata* until later. It is known that conceptacle initials develop as a function of receptacle growth (Nizamuddin 1964), but whether they remain inactive until the correct stimulus is received or whether they begin to develop (albeit at different rates) after their formation is unknown. The period of egg development and maturation was shorter in *C. subfarcinata* and the reproductive structures matured more quickly than the other two species (Fig. 5.2). Egg release also occurred earlier, and as a consequence, the period of potential fertility (i.e. when mature eggs were present in the conceptacles) was longer (Tab. 5.4).

Table 5.4. Important reproductive traits are summarised, based on average data at peak reproductive maturity. Although some similarities in reproductive traits were evident, each species appeared to employ a different overall reproductive strategy.

	C. expansa	*C. monilifera*	*C. subfarcinata*
Period of development to reproductive maturity	10 months	8 months	5 months
Period of potential fertility	3 months	3 months	4 months
Reproductive allocation to associated biomass(as % of total thallus)	90	91	87
Fecundity (x 10^6)	6.6	1.3	2.2
No. of eggs per receptacle	175	116	291
Biomass of single egg (g ww)	3.8E-07	4.5E-07	2.5E-07
Allocation of biomass to eggs (as % of lateral biomass)	2.7	1.7	1.1

These differences in the timing of the reproductive cycle of *C. subfarcinata* may well have resulted from the use of different environmental cues to trigger the development of conceptacles and eggs. The differences could equally have resulted from *C. subfarcinata* having a different set of physiological requirements for reproductive development, or different physiological traits in the rate of development of the reproductive structures. These hypotheses however, remain to be tested.

Although differences existed between species in the development of reproductive structures and the timing involved, the proportioning of biomass to reproductive growth was similar (Fig. 5.3). Reproductive allocation to associated biomass was high for all three species, ranging from 87% to 91% (at peak reproductive maturity) despite both *C. expansa* and *C. subfarcinata* showing a higher increase in lateral biomass during the reproductive season (Fig. 5.3). The relative proportioning of biomass between reproductive development and vegetative axes was therefore similar for all species irrespective of the amount of biomass produced. This is probably indicative of inherent mechanisms that control the way in which growth occurs in *Cystophora.*

These values of reproductive effort are comparable with those reported for other subtidal fucoids *Cystoseira osmundacea* 80% (Schiel 1985b) and *Sargassum sinclairii* 90% (Schiel 1985a) and the lower intertidal species *Himanthalia elongata* 98% (Brenchley *et al.* 1996). They are however, higher than the range of values reported for species of *Sargassum* from shallow subtidal environments 65% to 74% (McCourt 1985) and essentially intertidal species such as *Ascophyllum* and *Fucus* 13% to 70 % (Ang 1991, Cousens 1986, Hales & Fletcher 1990, Mathieson & Guo 1992). It is interesting to note that those species showing high reproductive allocation to associated biomass shed a considerable portion of this after reproduction (Brenchley *et al.* 1992, Kendrick 1994, Prince & O'Neal 1979, Schiel 1985b). Erosion and dieback of spent receptacles is however, more typical of those investing a lower reproductive effort (Ang 1991, Bacon & Vadas 1991) and these are essentially intertidal species.

The extent of reproductive allocation to associated biomass in intertidal species of *Cystophora* is unknown but interestingly, they do not shed biomass in the same way as their subtidal counterparts and undergo a process of dieback and erosion (Klemm 1985). Presumably, existence in the intertidal as a denuded thallus would render the individual vulnerable to desiccation and death, especially as spent reproductive biomass is lost during the summer months (Klemm 1985, this study). Why subtidal species appear to invest so much more reproductive effort into the vegetative structures housing gametes is unknown. The work of Brenchley *et al.* (1996) demonstrated a clear difference in reproductive allocation between *Himanthalia elongata* (a lower intertidal/shallow subtidal fucoid) and *Fucus serratus* (an intertidal fucoid) based on whether the species was semelparous or iteroparous. *H. elongata* invested 98% of its biomass into a reproductive frond but being semelparous, the whole thallus died after gamete release had occurred (Brenchley *et al.* 1996). *F. serratus* however, invested much lower amounts of biomass into receptacles but being iteroparous it reproduced the following year (Brenchley *et al.* 1996).

High allocation of resources to reproduction is a characteristic feature of a semelparous life history (DeWreede & Klinger 1988, Stearns 1976) but the subtidal fucoids in which this occurs are iteroparous and do not die after a reproductive event. By shedding this biomass at a later stage however, they exist for some time in a very denuded state (*Cystophora,* this study, *Cystoseira* Schiel 1985b) or as a holdfast (*Sargassum* Kendrick & Walker 1991, McCourt 1985). Such a strategy has been termed *pseudoperennial* (Sears & Wilce 1975). It could be conceived that the reproductive strategy of these species approaches semelparity with a phase of cessation of growth rather than death, occurring after reproduction.

An understanding of the seasonal patterns of carbon metabolism and productivity of *Cystophora* is obviously required to test such a hypothesis, as are comparisons with intertidal species of *Cystophora.* It is not known to what extent the production of so much biomass, which is lost and has to be replaced on an annual basis, affects the carbon allocation to other physiological processes. The vegetative tissue in the receptacles of fucoids is photosynthetic, but the degree to which it contributes to the cost of producing reproductive structures has only recently been addressed. Brenchley *et al.* (1996) found the carbon requirements of receptacles in *Fucus serratus* and *Himanthalia elongata* to initially exceed the levels, which they could themselves supply, but after one month, the receptacles of *F. serratus* were capable of supplying a large proportion of their own carbon requirements. In *H. elongata* a period of four months elapsed before this was achieved (Brenchley *et al.* 1996). Obviously the degree to which receptacles contribute to their own carbon demands needs to be examined in other species, but it seems probable that most fucoids, including *Cystophora,* are able to alleviate some of their reproductive expenditures in this way.

Unlike the allocation of resources to associated reproductive biomass, the allocation of biomass to eggs clearly differed between species (Tab. 5.3). Levels of allocation appeared to reflect the length of time invested in reproductive development (Tab. 5.4) with a higher proportion of biomass being allocated over a longer development period. Such a relationship is conceivable (Begon *et al.* 1990, DeWreede & Klinger 1988), however, differences in other reproductive traits of the three species make it difficult to test. Reproductive allocation to egg biomass in *Cystophora* was dependent on both the number of eggs (fecundity) and the size of eggs produced and this varied between species (Tab.

5.3). Fecundity itself varied between species as a consequence of variation in thallus structure (Fig. 5.4).

Although some aspects of thallus structure were similar for each species e.g. number of conceptacles per receptacle, the most important feature in the determination of fecundity was the number of receptacles per thallus and this varied substantially between species (Fig. 5.4). The importance of receptacle number in influencing fecundity has also been demonstrated for several intertidal species of fucoid (Vernet & Harper 1980). The highly branched nature of *C. expansa* resulted in much higher numbers of receptacles being produced. Although these were smaller than those of *C. monilifera* and *C. subfarcinata* (Womersley 1987) the arrangement of conceptacles within was more compact. *C. monilifera* and in particular *C. subfarcinata* had sections of somatic tissue separating clusters of conceptacles and often had sterile awns at the ends of the receptacles (Womersley 1987). *C. expansa* therefore, produced receptacles that had higher numbers of conceptacles (and hence eggs) and was clearly the most fecund species.

As the most fecund species, *C. expansa* allocated the highest proportion of biomass to its eggs (Tab. 5.4) but a similar relationship was not evident for *C. monilifera* and *C. subfarcinata* (Tab. 5.4). Levels of reproductive allocation to eggs in these species were also dependent on the size of eggs produced (Tab. 5.4). *C. subfarcinata* produced many small eggs whereas *C. monilifera* produced fewer larger eggs (Tab. 5.4). Such patterns of resource allocation are recognized as significant aspects of the reproductive strategies of many plants and animals (Begon *et al.* 1990, Fenner 1985, Stearns 1976) but as yet convincing evidence for their occurrence in algal species has not been demonstrated (DeWreede & Klinger 1988, Santelices 1990, Vernet & Harper 1980). Although the amount of biomass invested in eggs was slightly different between *C. monilifera* (1.7%) and *C. subfarcinata* (1.1%), these results do suggest that the two species employed opposing strategies in their partitioning of resources.

The eggs of *C. expansa* were intermediate in size to the other species but as the thallus structure of *C. expansa* was more densely branched, the sheer number of receptacles and hence eggs produced, obscured any evidence of a relationship occurring between egg size and number. If however, the average number of eggs per receptacle (at peak reproductive maturity) is considered for each species rather than the number of eggs per individual (fecundity), then *C. expansa* also adheres to the general pattern of resource allocation seen in the other two species. The allocation of biomass in *C. expansa* was to an intermediate number of eggs (175 per receptacle in comparison with 115 for *C. monilifera* and 291 for *C. subfarcinata*) of an intermediate size (Tab. 5.4).

The ecological consequences of variation in the size and number of offspring produced are numerous (Begon *et al.* 1990, Santelices 1990). In the algae, the period of life history from release to recruitment is characterised by high mortality (Santelices 1990, Vadas *et al.* 1992). Previous demographic estimates for fucoids have shown that from 0.004% to 0.08% of eggs produced make the transition to recruit status in the community (Ang 1991, Schiel 1988). The results of this study however, show these transition probabilities to be far lower in *Cystophora** with approximately 0.00005% of individuals making it to juvenile status (<100mm). Strategies that promote the survival of as many recruits as possible will therefore be of benefit to any population.

The strategy of *C. subfarcinata* appeared to be one of "strength in numbers" which relied on the probability that of the many eggs released, some would survive. That of *C. monilifera* differed in that the fewer eggs released were probably better equipped with energy reserves (Clayton 1990) to survive and grow quickly through the microscopic stages of their life. The strategy of *C. expansa* being intermediate, may well have represented a compromise in the two strategies although, the size and number of eggs produced per receptacle were closer to that of *C. monilifera* (Tab. 5.4). This suggests that the overall strategy of *C. expansa* may be combining the benefits of releasing eggs with good internal energy reserves, with that of producing great numbers of eggs. That the abundance of *C. expansa* in the community was shown to increase throughout the course of this investigation (Fig. 3.3) probably reflected a superior reproductive strategy.

Allocation of reproductive biomass to eggs appears to be higher for the three species of *Cystophora* than for other fucoids (Vernet & Harper 1980, Clayton 1990). *Ascophyllum, Fucus, Hormosira* and *Pelvetia* allocated from 0.05% to 0.4% of their reproductive biomass to gametes (eggs and sperm). It must be noted however, that these species are essentially intertidal and for reasons previously outlined, comparisons with subtidal *Cystophora* species may be inappropriate. Comparisons may also be difficult, as many

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*This estimate is approximate, and is based on estimates of the reproductive capacity of the community (Tab. 6.1) and abundance data of juveniles in the community (Fig. 3.4).

definitions have been used in the estimation of reproductive effort and the results presented in numerous forms (Chapman 1995, Clayton 1990).

When all of the reproductive traits investigated in this research are put into context, it is clear that the three species of *Cystophora* employed quite different reproductive strategies (Tab. 5.4) although the reproductive seasonality of each was similar (Fig. 5.2, Tab. 5.4). Variation in these traits between species had significant consequences for the overall strategy employed by each.

C. expansa invested much time into the reproductive development and the production of biomass. As a consequence its characteristically very densely branched thallus produced great numbers of receptacles and eggs. The period of egg release was short but the eggs were probably well supplied with internal energy reserves and far greater numbers were produced than in the other species.

C. monilifera also invested much time into reproductive development but did not produce as much reproductive biomass. Reproductive effort was directed at producing large eggs that presumably were well equipped for post-release survival. As a consequence however, fecundity of *C. monilifera* was lower than the other species. The period of egg release began earlier than *C. expansa* and was therefore slightly longer.

C. subfarcinata invested the least amount of time into reproductive development and maturation of eggs was rapid. As a consequence the period of potential fertility and egg release was the longest of all species. The rapid maturation of eggs was probably reflected in their small size.

Conclusion

Reproduction in the three species of *Cystophora* studied was seasonal and was linked to seasonal patterns of biomass production and loss. Reproductive development occurred during autumn and winter with eggs being released during spring. The benefits of such timing for subtidal species of *Cystophora* are conceivably numerous from both a physiological and ecological perspective. It is unknown whether the timing of the reproductive cycle results from the influence of environmental factors but if this is so, the species appear to respond differently.

Allocation of resources to associated reproductive biomass was similarly high for all three species irrespective of the amount of biomass produced. High allocation of reproductive biomass appears to be a feature of subtidal fucoids, as does the post-reproductive shedding of most of this biomass. It is suggested that this strategy approached that of semelparous individuals, but with a period of cessation in growth occurring after reproduction rather than death. Such a strategy would explain the high annual production of reproductive biomass as seen in subtidal fucoids but not in their intertidal counterparts which typically show a strictly iteroparous reproductive life history.

Reproductive allocation to egg biomass in *Cystophora* probably demonstrates support for terrestrial based resource allocation theories, with a clear relationship existing between the size and number of eggs produced. The total number of eggs produced (fecundity) by each species reflected the structure of the fertile thallus, and in the case of *C. expansa* was so great that it was the primary factor defining the reproductive strategy of that species. Each species clearly employed different overall reproductive strategies and these will be further discussed in Chapter seven in context with information on the other life history processes.

CHAPTER SIX..Recruitment and Early Community Development

Cystophora recruits were present in the Cape Jervis community for much of the year (Chapter three) even though reproduction and gamete release was seasonal (Chapter five). The information presented in this chapter shows the recruitment phase of *Cystophora* to be clearly defined, occurring through spring and summer (September to February).

Recruitment in a number of subtidal Australasian fucoids is influenced by the availability of free space for settlement, the supply of reproductive propagules, and the effects of the surrounding community in particular the canopy (Emmerson & Collings 1998, Kendrick 1994, Kendrick & Walker 1991, 1994, Schiel 1985, 1988, 1990). The results from this study showed temporal patterns of availability in both free space for settlement and reproductive propagules to effect recruitment in young *Cystophora* communities. Recruitment patterns however, were highly variable and spatially patchy.

Introduction

"*One of the most fundamental and precarious processes in the life history of a benthic marine alga is the colonisation of new substratum*" (Fletcher & Callow 1992). The journey from parent thallus to benthic substratum is probably one of the least understood stages in the life history of subtidal algae. There are several phases that comprise this journey and many have not been observed *in situ.* Reproductive propagules are produced and released from the parent thallus (Chapter five) and must then disperse, settle, attach and establish themselves within a community. Under controlled laboratory conditions it is often possible to isolate the various stages in this chain of events but studies *in situ* are much more limited (Kendrick & Walker 1991, Kennelly & Underwood 1984, Neushul *et al* 1972).

As a consequence, colonisation and settlement studies have generally monitored levels of recruitment. Recruitment is defined as a transitional phase of an alga's life history where newly settled individuals pass through a series of microscopic, developmental stages until they become "visible" members of the community. Thus, it is a measure that reflects both settlement and survival to an arbitrary point in time and as such, it clearly reflects the limitations of the observer (Keogh & Downes 1982).

Recruitment is characterised by huge mortality (Ang 1991, Chapman 1984, Emmerson & Collings 1998, Kendrick 1994, Kendrick & Walker 1991, 1994, Santelices 1990, Schiel 1988, 1990, Vadas *et al.* 1992), with individuals being removed from the system at every stage during their microscopic development. Those remaining are left to face a different set of environmental stresses as they grow (Amsler *et al.* 1992, Santelices 1990). Ultimately, individuals that are observed as new recruits in any population represent only a small minority of the originals (Ang 1991, Chapman 1984, Emmerson & Collings 1998, Kendrick 1994, Santelices 1990, Schiel 1988).

Estimates of the percentage of fucoid zygotes which settle into the microbenthos range from 1% to 10% and of these very few become visible recruits (Ang 1991, Schiel 1988). Although seemingly very low, these transition probabilities are believed to be higher than those of kelp species (Chapman 1984). Studies on Australasian fucoids (*Carpophyllum, Cystophora* and *Sargassum*) have found mean levels of recruits to decrease by about 50% during the first six months of life (Emmerson & Collings 1998, Kendrick 1994, Schiel 1985).

The causes of mortality are potentially numerous and relate to both the physical and biotic environment in which the propagule or recruit finds itself. The most important factors shown to affect algal recruitment appear to be biotic, a comprehensive review by Vadas *et al.* (1992) highlighted the effects of grazing, canopy, and the presence of algal turfs and animal mats to be the most influential. Although these conclusions were drawn from a relatively limited number of studies they appear to agree with observations made on fucoid communities in Australasia (Emmerson & Collings 1998, Kendrick 1994, Schiel 1985, 1988, Schiel & Choat 1980) and elsewhere (Ang 1985, Deysher & Norton 1982, Rapp de Eston & Bussab 1990).

Changes in abiotic factors such as water motion, temperature, nutrient levels, sediments and substratum properties can all affect the survival of recruits (Choat & Schiel 1982, Forbes & Hallam 1979, Foster & Schiel 1985, Harlin & Lindberg 1977, Brawley & Johnson 1991, Klemm 1985, Norton 1983, Sanderson & Thomas 1987, Santelices 1990, Vadas *et al.* 1992). Conditions must however, prove suitable not only for the dispersal, settlement and germination of the individual, but also for their subsequent growth and survival.

Inherent characteristics of individual propagules are also important in the recruitment process as they affect viability (at all stages), attachment ability, germination, and growth, all of which must be adequate to ensure survival (Clayton 1990, Deysher & Norton 1982, McLachlan & Bidwell 1978, Norton 1983). Successful individuals must also rely, to some extent, on good fortune as they are faced with the situation of dispersal to an unknown destination and with no effective means of directing this (Norton 1992).

Evidence shows there to be a continuous flux of reproductive propagules suspended in the water column through time (Amsler & Searles 1980, Deysher & Norton 1982, Hoffmann & Ugarte 1985, Hruby & Norton 1979, Zechman & Mathieson 1985) that is temporally and spatially patchy, as propagules are added to or are lost from the water column. This phenomenon has been termed a "spore cloud" (McDermid 1988). As the propagule aggregations move with the ocean flow, a variable number will precipitate out into potential habitats, this is known as "spore rain" (Hoffmann 1987). Together, the spore cloud and rain represent the potential vegetation of an area.

A common realisation of most studies therefore, is that numerous processes affect the dispersal, settlement and growth of algal propagules, and that this generally results in highly variable recruitment. It is also realised that the relative importance of factors affecting recruitment changes over various temporal and spatial scales (Emmerson & Collings 1998, Kendrick 1994, Schiel 1985, 1988, 1990).

Despite ecological research on *Cystophora* being generally limited, important work has been carried out on aspects of recruitment in subtidal species (Cheshire *et al.* 1999, Emmerson & Collings 1998). This work has concentrated on spatial patterns of recruitment and has generated a number of theories on the likely mechanisms that drive the patterns observed. The results of these studies compliment the information thus far presented in this thesis and can be used to propose a likely recruitment strategy for subtidal species of *Cystophora.*

The clearly defined seasonal nature of reproduction in *Cystophora* (Chapter five) suggests that temporal aspects of recruitment should be important in structuring the community (Santelices 1990, Schiel 1988). The aim of the current section of research therefore, was to determine the importance of seasonal differences in the availability of free space for recruitment in the *Cystophora* community. In order to achieve this aim, a number of temporal aspects of recruitment were investigated. The more specific aims of the research were:-

- to define the period of recruitment in *Cystophora*
- to relate this to patterns of reproductive seasonality in the adult community (Chapter five)
- to assess the importance of free space for settlement becoming available at different times of the year
- to assess the importance of pre-existing sub-canopy community structure on *Cystophora* recruitment
- to evaluate the importance of *Cystophora* recruitment as a structuring mechanism in young communities

By highlighting a number of temporal patterns of establishment and development of young fucoid communities it was hoped to provide an insight into some of the mechanisms structuring these communities.

Methods

Field experiment

Experimental design

Free space (new substratum) for colonisation was created at the beginning of every season, over the course of one year to monitor temporal patterns of recruitment. Five replicate experimental units were deployed haphazardly within the *Cystophora* community at the start of each season, each with four settlement plates attached (Fig. 6.1, Plate 6.1). The experiment began in summer 1990/1991 when adult *Cystophora* plants in the community were observed to be sterile.

In summer 1990/1991, the first five units (sum90) were deployed (Fig. 6.1), three months later, in autumn, the first plate from each sum90 unit was removed and a second series of units (aut91) was deployed. During winter (six months after the first deployment), the second plates from the sum90 units were removed, the first plates from aut91 units were removed and five win91 units were deployed. After nine months (spring), spr91 units were deployed and the appropriate plates from the other series removed (Fig. 6.1).

The experiment ran for 21 months and provided an array of settlement plates with different aged communities (3, 6, 9 & 12 months, for each of the four series that had been deployed at the beginning of each season throughout the year.

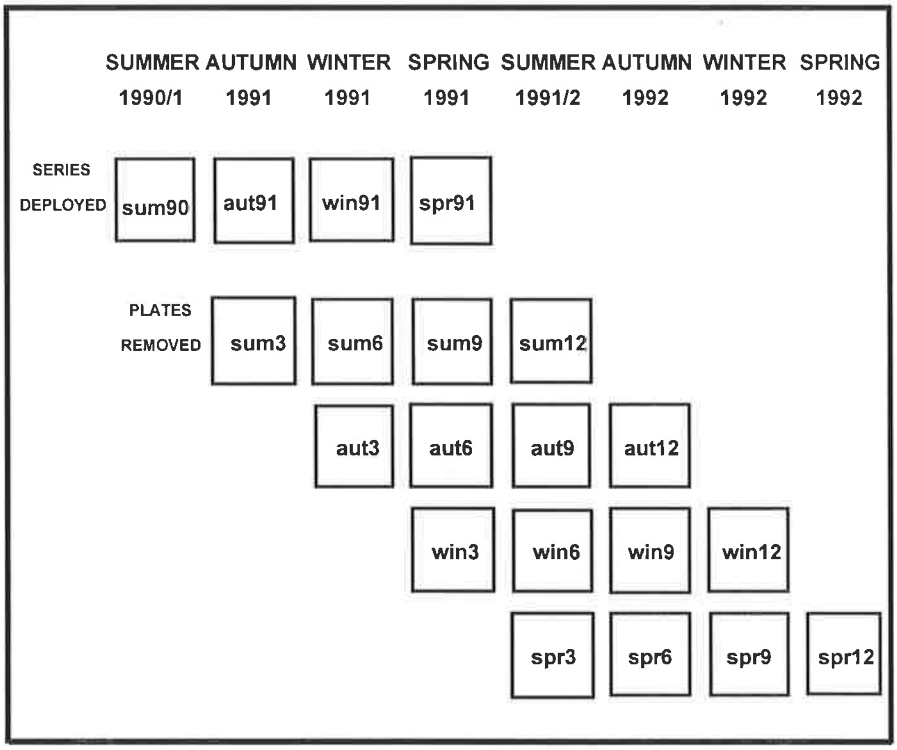

Figure 6.1. A schematic layout of the experimental design. Each box represents five replicate settlement plates that were deployed at the beginning of each season summer 1990, autumn 1991, winter 1991 and spring 1991. Settlement plates were then retrieved at three monthly intervals. Codes in boxes refer to the season of deployment and age of community at time of plate retrieval. For example, sum9 plates were deployed in summer 1990/91 and were retrieved in spring 1991 when they were 9 months old.

Experimental unit

Galvanised wire racks were used to attach the settlement plates by means of plastic electricians cable ties. The plates were cut from fibro cement sheeting to a size of 15cm x 30cm. Size of settlement plate was established from initial observations of the community taking into account both the size of rocks on which the community was growing, and areas of open space. Fibro cement was used as the artificial substratum being lightweight, tough and textured and from previous studies had proven to be durable when submerged for long periods of time. The suppliers also indicated that no anti-fungal, bacterial or algal treatments were used in the manufacture of the fibro cement. The wire racks were weighted using iron blocks, which were wired to the corners (Pl. 6.1).

Settlement plates (labelled on the underside) were positioned, one on each of the four sides of every rack with the central portion of the rack being cut away (Pl. 6.1). The positioning of racks and individual plates were mapped and coded with three different coloured acrylic tags to allow for accurate re-identification. Each rack was arbitrarily positioned as flush with the substratum as possible and secured with steel stakes and galvanised wire. All vegetation growing underneath was carefully pulled through the mesh and central cut-away area of the racks so that a natural canopy formed over the plates. Small sub-surface buoys were used to mark the position of each rack. Maintenance and plate retrieval were carried out using SCUBA or hookah.

Plate 6.1. A summer 1990/91 deployed experimental unit at the research site Cape Jervis, South Australia, several weeks after deployment. Some recruitment is apparent on the settlement plates.

Justification for the use of artificial substratum

With the primary aim of the research being to investigate temporal patterns of recruitment, it was imperative that truly replicate areas of new substratum were made available at the appropriate times. Provision of such substratum within the natural community by clearing away existing vegetation would not have been possible for a number of reasons. The clearance process itself would not have been replicable between clearances without seriously damaging, and hence altering, the natural condition of the substratum. Each natural clearance would have had a very different physical structure (i.e. substratum topography, aspect, elevation) and may or may not have been influenced by the previous vegetation (i.e. allelopathy, remnant regenerative crusts, presence of reproductive propagules), depending on the thoroughness of the clearance technique.

It was also believed to be more accurate and logistically more convenient, to be able to take the settlement plates back to the laboratory for microscopic observation and for these reasons, a model system of artificial clearances was created using settlement plates. Fibro cement was chosen as the artificial substratum for the reasons outlined in the previous section, but any number of artificial substrata could have been used (Ang 1985, Creed *et al.* 1996, Harlin & Lindbergh 1977, Kennelly 1983, Kendrick 1991, 1994).

No attempt was made to control for the use of artificial substratum in this study, as it was believed not to be possible. For the same reasons as listed above, accurate replication of a number of controls could not have been achieved. Lack of controls was not anticipated to affect the quality of information gathered as the experiment was based on a model system and not on the natural community. Given the artificial nature of the experiment, a number of limitations were anticipated:-

- species settling on the plates were most likely indicative but not representative of the local community (Lewis 1983)
- levels of recruitment were not necessarily representative of the natural community (Emmerson & Collings 1998, Kennelly 1983, Kendrick 1994)
- size of settlement plate was not necessarily typical of that of a naturally generated clearance (Emmerson & Collings 1998)
- physical and biotic factors affecting the recruitment process and post-recruitment survival of individuals were potentially different to those operating in the natural community (Kennelly 1983)

Laboratory investigations

The settlement plates removed from the racks were immediately placed into individual plastic bags and returned to the laboratory for examination. Before observation, the plates were gently rinsed with seawater to remove any loose sediment.

A transparent grid with 3cm squares was placed over each plate and each algal taxa was scored for presence/absence in each of the squares. Due to underwater erosion and damage, some of the plates were of different sizes when removed and so as to account for this, data were standardised to produce a % presence for each taxa per plate.

Identifications of specimens were taken as far as possible but the majority being juvenile or sterile, were assigned a taxonomic code (Tab. 6.1). A complete herbarium of species/taxa was created with specimens mounted on glass slides (in 80% karo solution), wet preserved (initially in 20% formalin: 80% seawater, transferred after two weeks to a solution of 70% alcohol: 25% distilled water: 5% glycerine), and dry mounted. These are lodged in the Environmental Biology Department, University of Adelaide, South Australia.

Analysis - *Cystophora* recruitment

Where required, univariate techniques were used to test for differences in *Cystophora* recruitment on the settlement plates. One-way ANOVAs and post-hoc Tukey tests were applied to determine where the differences in recruitment, if any, existed and unless otherwise stated, a αvalue of 0.05 was used. An arcsine transformation of the data was performed, as appropriate for percent presence data (Zar 1996). The Brown-Forsythe test for homogeneity of variances was used and where this demonstrated significant heteroscedasticity, a Kruskal-Wallis ANOVA by ranks was performed (Zar 1996).

Analysis - settlement plate community composition

The multivariate techniques chosen for the analysis of community composition and development on settlement plates were those available through the PRIMER software package (Version 4β Clarke & Warwick 1994). Similarity matrices were generated and the data ordinated using MDS (Non-metric Multidimensional scaling). The Bray-Curtis coefficient was applied to double square root transformed data to construct the similarity matrices. A double square root transformation was applied so as to reduce the influence of highly abundant common taxa and allow other less common and rare taxa to contribute to the definition of similarity.

Non-parametric analysis of similarity (ANOSIM) was carried out to detect any significant differences between the pre-assigned groups of settlement plates. Two treatments were defined *a priori*. The first, season (sum, aut, win or spr) depending on the season in which all replicate plates within the treatment were deployed, i.e. season when new substratum (free space) was made available. sum, aut, win and spr were deployed in summer 1990/91, autumn 1991, winter 1991 and spring 1991 respectively. The second treatment, age (3, 6, 9 or 12 months) defined the age of the community at the time of settlement plate retrieval.

The contributions of taxa to the patterns observed in the community were assessed using SIMPER (similarity percentages). Similarity percentages were calculated for all taxa in respect to their contribution to average similarity within groups of replicate plates and average dissimilarity between groups of replicate plates. The ratio of average contribution of a taxa (δ) to standard deviation (SD), SD(δ), gives a useful measure of how consistently the taxa contributes to (dis)similarity across all pairs. If the ratio is high (in this case >1) then the taxa is considered not only to contribute much to the (dis)similarity but does so consistently across all comparisons (Clarke & Warwick 1994).

A system of nomenclature is used in this section of results and in Appendix B, for the description of the 16 treatments in the experimental design (Fig. 6.1). Each treatment combines **season** (when new substratum becomes available for colonisation) with **age** (at time of plate retrieval). For example, spr6 was deployed in spring 1992 and was retrieved after 6 months (in autumn 1992). The four deployment seasons were, **sum**..summer 1991/92, **aut**..autumn 1992, **win**..winter 1992 & **spr**..spring 1992 and the age of community, **3 6 9** and **12** months. A system of nomenclature has also been used for unidentified taxa. Full names have been reported in the text where identification was possible but taxon codes have been used in figures for simplification.

Results

General situation

The time when free space became available for colonisation was important as patterns of community structure were primarily driven by seasonal patterns of recruitment. *Cystophora* recruited during spring and summer into a variety of communities of different age and structure. Mean levels of *Cystophora* recruitment were similar for all plates during the recruitment phase although recruitment was highly variable and spatially patchy. Existing community structure did not therefore significantly ($p<0.05$) affect levels of *Cystophora* recruitment. After recruitment had occurred, mean levels of *Cystophora* recruits did not change significantly ($p<0.05$) with time and as a consequence their presence in the community was an important structuring factor.

Timing of recruitment

Recruitment of *Cystophora* was first observed in spring 1991 on the summer (1990/91), autumn (1991) and winter (1991) deployed settlement plates and continued into summer 1991 when new recruits were observed on the spring (1991) deployed plates (Fig. 6.2). Recruits were not seen on any plates during autumn and winter in 1991 but settlement probably occurred during the latter part of this time. We are unable to say from these data whether recruitment continued beyond summer 1991/92 but as it did not occur during autumn and winter of the previous year (Fig. 6.2) it seems reasonable to assume that it did not.

After the recruitment phase, there were no significant changes ($p<0.05$) in the % frequency of *Cystophora* on settlement plates. *Cystophora* maintained a presence in all communities throughout the remainder of the study, although levels were highly variable (Fig. 6.2).

Influence of existing community structure on *Cystophora* recruitment

The composition of plate communities in winter 1991, when settlement of *Cystophora* presumably occurred, varied significantly ($p<0.05$) between treatments (Fig. 6.3). Of the communities present, sum6 were the most complex, comprising 11 taxa. Turfing brown algae, encrusting corallines and fucoids (other than *Cystophora*) were the important taxa characterising the communities on these plates. Aut3 communities contained only four taxa (Fig. 6.3), all of which were in common with the sum6 communities (including LITHO, CORAL and TURF) but were present at different levels. The other substratum available for colonisation was newly deployed in winter 1991 (Fig. 6.1) and hence had no pre-existing community.

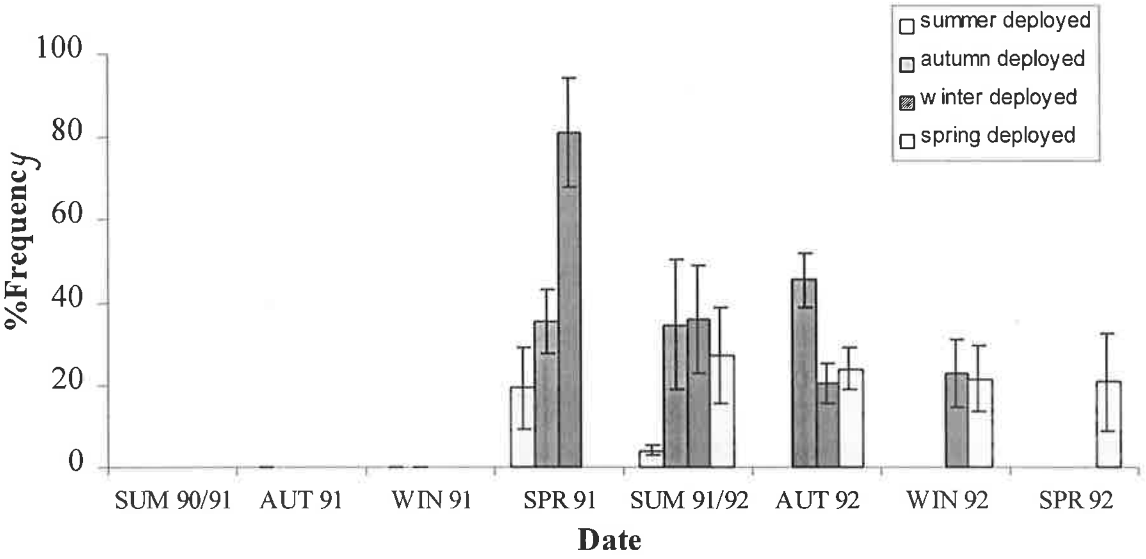

Figure 6.2. Recruitment of *Cystophora* occurred in spring 1991 on sum9, aut6 and win3 plates and in summer 1991/1992 on the spr3 plates. There were no significant differences in the levels of recruitment on plates during spring 1991 and no differences in the % presence of recruits with time after the recruitment phase. The presence of recruits was recorded for the entire surface of each settlement plate using a grid of 3cm squares and a % presence calculated for each (y axis). Error bars = standard error, n=5 with the exception of spr12 plates (n=4).

Recruitment of *Cystophora* in spring 1991 ranged from 0% to 40 % on sum9 plates, 5% to 54% on aut6 plates and 0% to 94% on win3 plates (Fig. 6.2), mean levels of *Cystophora* recruits however, did not vary significantly ($p<0.05$) between communities as recruitment was highly variable. Despite this variability, the general trend suggested that *Cystophora* recruitment was higher in the younger, less complex communities (Fig. 6.3).

Although recruitment occurred in communities of all ages during spring 1991 it did not occur on every replicate plate, and this suggested that recruitment in *Cystophora* was spatially patchy. There were no discernable patterns in the occurrence or absence of *Cystophora* recruits on particular plates during this time. Community structure was similar ($p<0.05$) for all plates within a given treatment (Fig. 6.3), and this suggests that factors other than community composition were affecting the spatial recruitment patterns of *Cystophora* (at the scale of settlement plates).

The importance of *Cystophora* recruitment in structuring young fucoid communities

The time when free space became available for colonisation was important as overall community composition was primarily driven by seasonal patterns of recruitment. A few species were more or less “ubiquitous”, being present on all or many of the plates and certainly in the majority of communities, but most, including *Cystophora* showed distinctly seasonal recruitment and peaks in abundance (Appendix B). Communities therefore, changed through time as they experienced fluctuations (usually seasonal) in the abundance of the “ubiquitous” taxa, and were exposed to different suites of seasonally recruiting taxa.

Communities that developed on plates deployed in the same season were significantly different ($p<0.05$) at 3, 6, 9 and 12 months (Fig. 6.3) but change in their composition, as they aged, did not necessarily follow a sequential successional pattern, due to the strong influence of seasonal recruitment events.

The pattern of seasonal recruitment and persistence in *Cystophora* created clear differences between pre-*Cystophora* recruitment and post-*Cystophora* recruitment communities. The presence of *Cystophora* in post-recruitment communities accounted for 8.7% to 17.1% (% contribution) of community characterisation.

Figure 6.3 on facing page. Settlement plate communities varied to such an extent between treatments that characteristic communities were identified for each treatment. Encrusting corallines (LITHO), erect corallines (CORAL) and turfing brown algae (TURF) were found in all communities but all other taxa showed seasonal patterns of occurrence or abundance. This figure is based on Fig. 6.1 with each box representing 5 replicate settlement plates. The codes in each box refer to the taxa present in each community, those in bold font were identified, using SIMPER analysis, as the primary characterising taxa, those in normal font were secondary or transient taxa (see Tab. 6.1).

summer 1990/91	autumn 1991	winter 1991	spring 1991	summer 1991/92	autumn 1992	winter 1992	spring 1992
	SCYTO **GREEN A** **BROWN A** **RED A** CHORD FUCOID GREEN B GREEN C	**LEATH** SCYTO FUCOID GREEN A CAULO	**LEATH** **CYST** SARG GRIF GREEN A SCYTO REDG BROWN D	**LEATH** SCYTO CYST CHORD FUCOID GREEN A RED B RED F			
		GREEN A	**LEATH** **CYST** **BROWN C** SCYTO GRIF RED G	**LEATH** **CHORD** CYST GRIF RED B BROWN B BROWN L	**LEATH** **BROWN B** **CYST** GRIF LAUR A RED F, RED I BROWN D		
			LEATH **SCYTO** CYST GRIF GREEN C	**LEATH** **CYST** **GRIF** **CHORD** FUCOID BROWN B RED F BROWN L	**LEATH** **CYST** **FUCOID** **LAUR A** BROWN B GRIF, SARG BROWN D RED F	**CYST** **GREEN A** **CAULO** SARG FUCOID BROWN B BROWN E LAUR B	
				LEATH **CHORD** **RED B** SCYTO CYST FUCOID	**LEATH** **CYST** **BROWN B** FUCOID LAUR A BROWN D	**CYST** **GREEN A** **CAULO** BROWN B BROWN E BROWN F SARG	**LEATH** **FUCOID** CAULO CYST BROWN B BLACK

Discussion

This research showed *Cystophora* to have a clearly defined recruitment phase during spring and summer 1991. Given that the reproductive seasonality of adult *Cystophora* in the community was shown to be clearly defined (Chapter five) it is not surprising that the recruitment phase was also well defined. Once released into the water column, fucoid gametes and zygotes have limited viability and settlement must occur quickly. Longevity of released gametes and zygotes can be as little as one hour to several weeks (Deysher & Norton 1982, Hoffmann & Camus 1989, Jones & Babb 1968, Klemm 1985, Santelices 1990). The attachment ability of *Sargassum muticum* is known to decrease with time spent in the water column due to the accumulation of dirt on the attachment surfaces, and also through a reduction in the ability of the propagule to produce the mucopolysaccharides required to make the attachment bond (Deysher & Norton 1982). It is possible that similar problems may also affect the zygotes of *Cystophora.*

Recruits were first observed on the settlement plates during spring (September to November) 1991 (Fig. 6.2) approximately five to six months earlier than when they were first identified in the natural community (Chapter three). This demonstrates the advantage of being able to return settlement plates to the laboratory for microscopic investigation. During October 1991 the adult *Cystophora* in the community still had mature eggs in their conceptacles (pers. obs.) and hence release was still occurring as the first recruits were noticed. This suggests the growth and development of tiny recruits to be substantial during the first few weeks of their life, and also lends support to the predicted growth rates presented in Chapter four. Recruitment continued into summer 1991 (Fig. 6.2) by which time the adults had shed their spent reproductive structures and were beginning to develop new receptacles (Fig. 5.2). At this time however, adult thalli were still very denuded (Pl. 3.1).

The consequences of such timing in the reproductive cycle and recruitment process in *Cystophora* have been discussed in previous chapters (three and four), and it is recognised that this strategy facilitates the growth and survival of recruits. The sub-canopy environment of a recruit in a dense algal community is likely to be less than optimal for growth where light conditions are concerned (Reed & Foster 1984) but the availability of nutrients is likely to be high (Amsler *et al.* 1992). Once the canopy thins, the growth conditions for recruits are conceivably very good.

That recruitment in *Cystophora* can occur whilst the adult thalli remain reproductively bulky illustrates that the intact canopy does not prevent the initial settlement and growth of recruits. This is also true of *Carpophyllum, Landsburgia* and *Sargassum* communities in Australia (Kendrick 1994) and New Zealand (Schiel 1990). The presence of an adult canopy however, is known to reduce the survival rate of fucoid recruits growing beneath (Emmerson & Collings 1998, Kendrick 1994, Schiel 1990).

Using artificially cleared areas to mimic disturbance events, Emmerson & Collings (1998) found that both the size of clearance and the position of recruits within the clearance affected the growth and survival of *Cystophora* and *Sargassum* recruits in South Australia. They also found that these effects changed through time. Size of clearance was initially important, with more recruits found in the larger clearances, but as recruits approached 20mm in length, position within clearance became important and more recruits were found in the centres than at the edges.

It was suggested (Emmerson & Collings 1998) that recruits settling in larger clearances and at the centre of smaller clearances were less likely to be influenced by the surrounding adult community but as they grew, would have to contend with density dependent competition from their conspecifics. Recruits in smaller clearances and at the edges of larger clearances were more likely to be affected by the adjacent canopy through limitation of resources and physical interference, and also by grazers foraging at a limited distance from the safety of the canopy. Kendrick (1994) made similar observations in his study of recruitment in mixed *Sargassum* beds in Western Australia.

Some fucoids are believed to employ mechanisms of physical interference such as sweeping and allelopathy to remove potential competitors (Ang 1985, Dayton *et al.* 1984, Rapp de Eston & Bussab 1990, Vadas *et al.* 1992, Womersley 1948). Womersley (1950) noted that adult *Cystophora* plants growing on intertidal reefs kept the immediate area clear from the juveniles of competitor species through sweeping but it is not known whether *Cystophora* removes its own offspring as a consequence. The work of Cheshire *et al.* (1999) showed that the abundance of *Cystophora* adults was negatively correlated with the presence of *Sargassum* and *Ecklonia* (kelp) recruits. This would have reflected, in part, the localised dispersal patterns of each species but could also have been indicative of *Cystophora* utilising interference mechanisms against theses species.

Although the recruitment phase of *Cystophora* was clearly defined, the levels of recruitment occurring on replicate settlement plates were highly variable, and this appears to be a characteristic of many algal systems (Ang 1991, Emmerson & Collings 1998, Kendrick 1994, Santelices 1990, Schiel 1985, 1988, 1990). When the multitude of factors affecting the recruitment of reproductive propagules is considered, this is not surprising. Levels of recruitment for any algal species essentially depend on 1) the number of viable propagules released by a population, 2) the effects of dispersal and 3) the extent of post settlement mortality, and all of these are affected by a wide range of physical and biotic processes (reviewed by Brawley & Johnson 1992, Chapman 1995, Norton 1992, Santelices 1990, Vadas *et al.* 1992).

The actual number of recruits observed in the natural community at Cape Jervis (Fig. 3.4) was approximately 0.00004% of the number of eggs produced (Tab. 6.1). This estimate is approximate as the actual number of eggs released from the parent thalli was not quantified and other fucoids do not necessarily release all of their eggs during the reproductive phase (Ang 1991). It was also based on an estimation of reproductive capacity for the community (Tab. 6.1) which did not account for the input of *C. moniliformis* and *C. brownii* and these species comprised 17% of the total number of *Cystophora* in the canopy at the time (Fig. 3.3). Being based on fecundity estimates of species at peak reproductive maturity, the estimate also does not account for any prior release of eggs. Nonetheless this result shows the transition probability of *Cystophora* during 1991/1992 to be lower than that of other fucoid species. These estimates showed that 0.004% to 0.08% of eggs produced reached recruit status (Ang 1991, Schiel 1988). Detailed survivorship studies for *Cystophora* are however required to determine the implications of these findings.

Recruitment in *Cystophora* was also shown to be spatially patchy, at the level of the settlement plate. Recruitment patterns are known to vary over smaller spatial scales (Creed 1995, Gunhill 1980, Rice 1987) and generally initially reflect the topographical nature of the substratum (Harlin & Lindbergh 1977, Norton 1983, Norton & Fetter 1981) or its suitability for successful settlement. As individuals grow however, other factors such as competition (Ang 1985, Creed 1995, Dayton *et al.* 1984, Emmerson & Collings 1998, Rapp de Eston & Bussab 1990, Kendrick 1994), grazing (Vadas *et al.* 1992) and physical disturbance (Emmerson & Collings 1998, Forbes & Hallam 1979, Norton 1983, Norton & Fetter 1981) will influence the distribution of recruits.

Table 6.1. Fecundity of individuals of each species was shown to be high, but when put into a community context, approximately 126 x 10^6 eggs m^{-2} (12600 cm^{-2}) were produced by the *Cystophora* community in August 1992. These results are based on estimates of average abundance m^{-2} (Fig. 3.3) and average fecundity (Fig. 5.4) of each species at peak reproductive maturity.

	C. expansa	***C. monilifera***	***C. subfarcinata***	**All *Cystophora* in the community**
Average abundance (m^{-2})	15.7	2.3	8.8	26.9
Average number eggs (per individual x 10^6)	6.6	1.3	2.2	10.1
Average number eggs (m^{-2} x 10^6)	104	3	19	**126**

It seems unlikely that any of the above mechanisms would have resulted in the complete absence of *Cystophora* recruits from several of the replicate settlement plates unless of course, recruitment levels on these plates were initially very low. It is possible that recruitment never occurred on the plates as a consequence of poor dispersal or some stochastic event. All of the settlement plates used in the experiment had a natural canopy above, however, the research community comprised species other than *Cystophora* and was heterogenous with respect to its structural (physical and biotic) complexity. It is therefore conceivable that some settlement plates were not colonised by *Cystophora.*

In general fucoids are considered to have limited dispersal abilities, with the majority showing a range of 10m or less (Anderson & North 1966, Deysher & Norton 1982, Kendrick & Walker 1991, Schiel 1988). For species of *Sargassum* in Western Australia, 96% of reproductive propagules settled within 25 cm of the parent thallus (Kendrick & Walker 1991). The evidence from this research suggests that limited dispersal would be favoured in *Cystophora* at least in the three species studied, as they rely on the post-reproductive period of canopy thinning to ensure a good start to life for their offspring. Such conditions would not be guaranteed for individuals dispersing outside of the immediate community. A number of kelp and fucoid species do employ mechanisms to limit the dispersal of their propagules (Amsler & Nueshul 1989, Brawley & Johnson 1992, Paine 1979).

The dispersal range for *Cystophora* has not been quantified but recruits were found in the centres of 100cm x 100cm clearances at Cape Jervis (Emmerson & Collings 1998), this suggests dispersal to have occurred over a minimum of a 50cm radius from the fertile adults at the edges of the clearances. Dispersal over longer distances must also occur in some species as isolated stands approximately 15m from their closest neighbours have been observed in South Australia (Kildea, University of Adelaide, pers. com.). Likely vectors for such dispersal are drifting portions of fertile thalli or shed reproductive biomass (Norton 1992).

Actual release of propagules from *Cystophora in situ,* was not observed during this study but released eggs and fertilised zygotes collected on the surface of receptacles under laboratory conditions (Nizamuddin 1960) and this appears characteristic of many fucoids (Fletcher & Fletcher 1975a, Kendrick & Walker 1991, Norton & Fetter 1981, Schiel 1990). Personal observation in the field found dispersal of gametes and zygotes in *Cystophora* to be likely through the sweeping action of the parent thallus in turbulent water. Thalli were observed to be constantly brushing against one another and the substratum, and it is suggested that this would enable the gametes and zygotes to be "wiped off".

One of the aims of this section of research was to investigate the effect of pre-existing sub-canopy community on the recruitment of *Cystophora.* Physical disturbance may lead to the provision of free space for colonisation at all times during the year which means that the substratum will be potentially covered with patches of community of all ages and states of development when the recruitment phase of *Cystophora* occurs. The presence of algal mats and turfs are known to hamper recruitment in some species of fucoid (Hruby & Norton 1979, Schiel 1985a, Vadas *et al.* 1992) although the presence of understorey vegetation did not affect the recruitment of *Sargassum* in Western Australia (Kendrick 1994).

Mean levels of recruitment in *Cystophora* were similar across communities of all ages, which suggests that the pre-existing community structure did not affect levels of recruitment. Recruitment of *Cystophora* on these plates however, did show a general trend with higher recruitment occurring on the youngest plates. Repetition of this work with greater numbers of replicate plates is desirable, because if this trend is real, then the consequences for recruitment in *Cystophora* could be very important. If recruitment is adversely affected by the presence of more complex sub-canopy communities then timing of disturbance events could be critical to the success of the yearly recruitment phase. Understorey vegetation was shown to be minimal or at times negligible in the Cape Jervis community, probably as a consequence of the dense *Cystophora* canopy and this would aid successful recruitment, if in fact the level of sub-canopy community was influential. Recruitment in algal systems however, is typically variable (as previously discussed) and the trend observed in this study may just be coincidental.

Although pre-existing community structure did not appear to have an effect on the recruitment of *Cystophora* within the first 12 months of development, a number of recruitment strategies were identified for the species settling on the plates (Appendix B) and these may have had more effect in slightly older, more complex communities. A number of species, mainly fucoids, showed defined seasonal recruitment but then persisted in the community, and some of these actually recruited prior to *Cystophora* (Appendix B). Other species were not restricted by seasonal recruitment and their abundance often fluctuated on a seasonal basis (Appendix B). In older communities where availability of free space may be limited, such recruitment strategies could potentially pre-empt the settling space required by *Cystophora.* The timing of disturbance events may therefore be important in the successful recruitment of *Cystophora.*

Conclusion

The recruitment phase in subtidal species of *Cystophora* was seasonal and clearly defined. Recruitment occurred during spring and summer 1991 and the first recruits were observed whilst eggs were still being released from the parent plants. This observation is important because it shows that recruitment in *Cystophora* is not prevented by the presence of an adult canopy. It also lends support to results presented in Chapter four that predicted rapid growth rates for recruits.

Recruitment of *Cystophora* on artificial settlement plates was highly variable and spatially patchy, and there was no significant ($p<0.05$) effect of pre-existing sub-canopy community on recruitment levels but a trend was evident that suggested recruitment to be higher in younger, less complex, communities. The communities that developed on the settlement plates were primarily influenced by seasonal patterns of recruitment. This could have important implications for the recruitment of *Cystophora* in the natural community depending on the timing of availability of free space for settlement and the recruitment strategies of likely competitors.

CHAPTER 7..Synthesis

Dense communities of large, perennial species of algae like *Cystophora* are generally believed to be characteristic of habitats with a low disturbance regime, and a constant or predictable seasonally variable physical environment (Clayton 1990, Littler & Littler 1980, Lobban & Harrison 1994). Competition for resources is typically high in such communities (Begon *et al.* 1990, Grime 1979) and the largest individuals, or those present in the canopy, are generally the stronger competitors (Littler & Littler 1980). Mortality is also high, particularly amongst juveniles, and therefore life history traits that promote the survivorship of individuals, are important (Begon *et al.* 1990).

The overall life history strategy for species living under these conditions has been described as *late-successional* (Littler & Littler 1980), *k-selected* (MacArthur & Wilson 1967, Pianka 1980) or *competitive* (Grime 1979). For the purpose of this discussion however, the term *late-successional* will be used, as the life-history characteristics that comprise the various strategies are essentially the same. These traits include a large thallus size, structural differentiation of thallus, long life history, slow growth rate and low net productivity per thallus, ability to store nutritive compounds, the ability to utilise chemical defences, delayed reproduction, optimally timed seasonal reproduction, low reproductive allocation, large offspring size and iteroparity (Begon *et al.* 1990, Littler & Littler 1980).

In general, the life-history traits of *Cystophora* conform to the *late-successional* strategy. *Cystophora* is a large, perennial genus (Womersley 1964) with a structurally differentiated thallus (Nizamuddin 1964). Species of *Cystophora* utilise polyphenolic compounds for grazer deterrence (Steinberg 1989) and there is some evidence that carbon reserves are accumulated (this study Chapter four). In relative terms, growth in *Cystophora* is slow (this study Chapter four c.f. Lüning 1990). The elongation rate of individuals from the Cape Jervis community decreased as they got larger (this study Chapter four), and it is suggested that processes such as grazing, erosion, increased respiration due to increased structural tissue, and the diversion of resources into thallus maintenance and repair, all acted to decrease the elongation rates of the larger individuals.

The reproductive life-history traits of *Cystophora* are also generally consistent with the *late-successional* strategy that has been proposed. Reproduction is clearly seasonally defined and individuals are strictly iteroparous (Klemm 1985, this study Chapter five).

This study did not monitor the onset of first reproduction but this appears to be size dependent in most fucoids (Chapman 1995) with only the larger individuals becoming fertile. It seems reasonable to assume that this is also the case for *Cystophora,* although this is an important demographic trait that needs verification in the future. The eggs (and hence zygotes) of *Cystophora* are large in comparison with the reproductive propagules of most marine algae (Clayton 1990, Womersley 1984, 1987, 1996, 1998) but the percentage of biomass allocated to these is low, 1.1% to 2.7% of total thallus biomass (this study Chapter five). Allocation of biomass to antheridia was not quantified in this study but these structures are much smaller than the eggs (Womersley 1987). Total reproductive allocation in *Cystophora* therefore, would probably not exceed 5% of total thallus biomass.

If however, a measure of associated reproductive biomass (reproductive laterals) is considered rather than allocation to the gametes only, then the allocation of biomass to reproduction was very high (87% to 91% of total thallus biomass) in all three species of *Cystophora* studied (this study Chapter five). This is in direct conflict with the general life history strategy that has thus far been proposed, and is more characteristic of an *opportunistic* (Littler & Littler 1980), *r-selected* (MacArthur & Wilson 1967, Pianka 1980) or *ruderal* (Grime 1979) strategy. Such a strategy would be more typical of a species inhabiting an unpredictable or ephemeral environment with a high disturbance regime (Begon *et al.* 1990), and not the community at Cape Jervis. The investment of substantial amounts of biomass into reproductive structures was also an annual phenomenon, as the spent reproductive structures were shed at the end of the reproductive cycle (this study Chapter five). This is more characteristic of a semelparous life history or one that is driven by the one-off production of offspring (Begon *et al.* 1990, DeWreede & Klinger 1988, Stearns 1976) and not of a *late-successional* individual.

The three subtidal species of *Cystophora* that were studied are not strictly semelparous because they do not die between reproductive events, but they do exist for part of the year as a denuded thallus in which growth is minimal or even negative (this study Chapter four). It is suggested therefore, that the reproductive life history of these subtidal species is in a sense pseudo-semelparous. Other species of subtidal fucoid e.g. *Sargassum* (Kendrick & Walker 1991, McCourt 1985, Schiel 1985a, Sears & Wilce 1975) and *Cystoseira* (Schiel 1985b) also show a pseudo-semelparous existence, but this has not been recorded for intertidal species.

The spent receptacles of *Cystophora* do not have the capacity for re-growth or the production of new conceptacles once the gametes have been released because their growth is apical and the apical cells disappear once reproductive maturity is reached (Nizamuddin 1964). Spent receptacles therefore, have to be shed if new ones are to be produced for reproduction during the following year. Given that this aspect of the reproductive life history of *Cystophora* is phylogenetically constrained, the strategy for dealing with this appears to differ between subtidal and intertidal species. Subtidal species of *Cystophora* shed their spent receptacles *en masse* but intertidal species have not been noted to take on the denuded appearance that is typical of their subtidal counterparts (Klemm 1985, pers. obs.). Turnover of receptacles is a more gradual process in intertidal species and this may be a response to living in an environment where the risk of desiccation is high. Not all species of fucoid grow entirely new receptacles each year, the receptacles of some develop as swollen, fertile tips of branches rather than as discrete structures (Fritsch 1945) and these are eroded away rather than shed (Ang 1991, Bacon & Vadas 1991).

Why subtidal species appear to favour a pseudo-semelparous approach and shed their spent receptacles *en masse* (this study Chapter five) is unknown, although the benefits of doing so are conceivably numerous. The annual production of reproductive structures is unlikely to be a costly process in *Cystophora* (Brenchley *et al.* 1996), as the bulk of receptacle tissue is photosynthetic (Nizamuddin 1964) but this needs to be quantified. It is conceivable however, that a pseudo-semelparous approach to receptacle production may be even less costly than a gradual turnover strategy where repair and maintenance of receptacles would require additional resources. It is interesting to note that the allocation of resources to both receptacles and gametes is lower in intertidal species that do not show this pseudo-semelparous trait (Brenchley *et al.* 1996, Vernet & Harper 1980) and this may reflect a trade off in resources between reproduction and the maintenance of the vegetative thallus (Carpenter 1990, Paine 1990).

There are other physiological advantages to shedding receptacles *en masse* during the summer in the subtidal environment. Although a denuded thallus would have a decreased photosynthetic surface area, the photophysiology of individuals would not be greatly impaired due to the high light intensities and long daylengths experienced during the summer months (Cheshire *et al* 1996). During winter months when ambient light conditions were not as good, a greater photosynthetic surface area would be required and therefore, shedding during this time would not be beneficial. Also, if nutrient availability was seasonally low during the summer (as suggested for the Cape Jervis community, Chapter four) then conditions would not be suitable for growth or for the excessive repair of a spent and eroded thallus. By existing in a denuded state with minimum growth, individuals could, in theory, take advantage of the good light conditions to accumulate excess carbon reserves. These reserves could then be utilised later in the year when nutrients were no longer limiting (Chapman & Craigie 1977, 1978, Gagne et al 1982, Rosell and Srivistava 1985, Wheeler & Srivistava 1984).

The seasonal pattern of growth (and hence reproductive development) in *Cystophora* did not reflect the seasonal change in the light climate (Cheshire *et al.* 1996, Kildea, University of Adelaide, Ph.D. thesis in prep.) and this suggests that other factors were influencing its growth. Future research needs to address aspects of the photophysiology of both intertidal and subtidal species of *Cystophora,* and seasonal patterns of nutrient availability and utilisation. Whether *Cystophora* has the ability to accumulate reserves of nutrients and excess carbon must also be addressed. Without such information it is not possible to determine the extent to which the life histories of *Cystophora* are controlled by external factors e.g. seasonal patterns of change in environmental parameters, and to what extent they are controlled by phylogeny. A number of interesting comparative studies could be made between intertidal and subtidal species, and between individuals of species such as *C. expansa* and *C. subfarcinata* that are found in both intertidal and subtidal environments (Womersley 1987).

As a consequence of shedding spent receptacles *en masse,* an otherwise dense canopy of *Cystophora* is thinned, and in the Cape Jervis community this facilitated the successful recruitment of newly released offspring (this study Chapters three and six). The thinned canopy also provided sub-canopy individuals with improved growth conditions and gave them a chance to make the transition into the canopy (this study Chapters three and four). These processes enabled *Cystophora* to dominate the mixed fucoid community through the maintenance of a dense, closed canopy for most of the year and this was perpetuated through a "bank of sub-canopy individuals" (this study Chapter three). Although the presence of an adult canopy did not prevent the recruitment of *Cystophora* (this study Chapter six), other research has shown the presence of a canopy to severely reduce levels of recruit survival (Emmerson & Collings 1998, Kendrick 1994, Schiel 1990). In a competitive environment such as the Cape Jervis community there would be limited opportunities for offspring to become established and therefore any strategies that promoted the survival of young individuals would be favoured (Begon *et al.* 1990).

Although the overall life history strategy for each species of *Cystophora* studied was broadly similar, there were a number of important differences, which when put into context, point to a superior competitive strategy for *C. expansa*. *C. expansa* was the community dominant throughout the period of observation, and actually increased in numbers by the end of the study. The overall strategy of *C. expansa* was to maintain a dense closed canopy for much of the year and hence resist sensu (Dayton *et al.* 1984) invasion by competitor species. The persistence (Dayton *et al.* 1984) of *C. expansa* was reliant on the processes of growth, reproduction and recruitment being seasonally and optimally timed in order to maintain this dense canopy. This strategy however, would not be successful in a sparse stand or one dominated by other species, and although *C. expansa* is widely distributed in southern Australia (Womersley 1987), it generally only ever occurs in dense stands (Dr A.C. Cheshire pers. com., pers. obs.).

Although *C. expansa* was the community dominant at Cape Jervis, and actually increased its abundance through the course of this study, the abundance of the other species did not change significantly. This suggests that the strategies employed by *C. monilifera* and *C. subfarcinata* enabled them to resist sensu (Dayton *et al.* 1984) a take over by *C. expansa,* but these strategies were not sufficiently competitive to exclude new *C. expansa* individuals from entering the canopy. The one life history trait that differed most between *C. expansa* and the other two species was its higher fecundity (Chapter five). As the community dominant *C. expansa* was the most influential species in the canopy thinning process and [illegible] ble to optimally time the release of its eggs coincided with the opening up of the canopy. It is suggested that *C. expansa* was able to swamp the substratum with its eggs during the most favourable time, and this provided a competitive edge over the other species. The strategy employed by *C. monilifera* was very similar to that of *C. expansa,* but it was not as abundant or as fecund, and hence did not release as many eggs into the community.

A few differences did exist between *C. monilifera* and *C. expansa,* which would have improved the chances of successful recruitment for C. monilifera. The period of reproductive development and maturation in *C. monilifera* was slightly shorter than that of *C. expansa* and as a consequence eggs were released earlier than *C. expansa* (Chapter five). Although this occurred whilst the canopy was still intact, the findings of this study have shown that successful recruitment can still occur with a dense canopy above (Chapter six). The eggs of *C. monilifera* were also the largest of all three species and it is possible that their sub-canopy growth was sustained by internal reserves (Clayton 1990) until the canopy thinned. Many of the offspring of *C. monilifera* would have settled before the recruitment phase of *C. expansa* occurred and could then take advantage of the improved growth conditions when the canopy opened.

The strategy of *C. subfarcinata* was somewhat different from the other two species with seasonal patterns of growth, reproduction and recruitment being less clearly defined. The shedding of spent receptacles was observed, as in the other species, but seasonal changes in biomass did not reflect this as clearly as in the others (Chapter five). The period of reproductive development was much shorter in *C. subfarcinata* and egg release began earlier. Egg release also continued for longer and therefore receptacles could have been exhausted and shed periodically, and this would have resulted in a more gradual turnover of receptacle biomass.

The eggs of *C. subfarcinata* were the smallest of all three species (Chapter five). They were approximately half the size of those of *C. monilifera* (2.5×10^{-7} g ww cf. 4.5×10^{-7} g ww) but approximately twice as many (2.2×10^{6} per thallus cf. 1.3×10^{6} per thallus) were produced. The eggs of *C. expansa* were intermediate in size (3.8×10^{-7} g ww) but due to the much higher number of receptacles produced by an average individual, many more eggs (6.6×10^{6} per thallus) were also produced. The high numbers of small eggs that were released by *C. subfarcinata* over a longer period of time are traits that are generally associated with an *opportunistic* (Littler & Littler 1980) or *r-selected* (MacArthur & Wilson 1967, Pianka 1980) life history. Although the life histories of species of *Cystophora* are better described as *late-successional* it is realised that these schemes are a simplification of a multiplicity of life-history traits and that intermediate strategies may exist (Begon *et al.* 1990).

By releasing large numbers of eggs into the community over an extended period of time (late autumn through to spring), *C. subfarcinata* could take combined advantage of substratum becoming available through the removal of adult plants during autumn and winter storms (Chapter four), and of openings in the canopy from the shedding of other species reproductive biomass. The smaller eggs of *C. subfarcinata* would presumably contain limited reserves to sustain their initial growth (Clayton 1990) but the high numbers released would ensure that some would survive. Such a strategy would be suited to living in a wide variety of environments where free substratum was periodically created, including those with a higher disturbance regime (resulting in higher mortality of canopy plants). *C. subfarcinata* is the most widely distributed species of *Cystophora* in southern Australia and is often found in high energy environments (Womersley 1987), unlike *C. expansa* and *C. monilifera*. In the Cape Jervis community *C. subfarcinata* persisted (Dayton *et al.* 1984) throughout the course of the study, which suggests that its reproductive strategy enabled sufficient new offspring to make it into the canopy, but it is interesting to note that many individuals were situated at the edges of the fucoid stand (pers. obs.).

This study did not focus on the ecology of the early life history stages of *Cystophora* and it is suggested that a future line of research concentrate on this. Such studies are not easy (Vadas *et al.* 1992) but are essential in the development of an understanding of the demography, and hence overall life history strategy, of a species. Comparisons between the size and number of eggs produced, and their dispersal distance, viability, and post settlement survival rates would be interesting, as the life-history strategies for the three species that are proposed above, suggest that these traits would probably differ between *C. subfarcinata* and the others from the Cape Jervis community. In terrestrial systems seed size is seen as a compromise between requirements for dispersal and establishment (Fenner 1985). The life-history strategies of *C. expansa* and *C. monilifera* would favour limited dispersal, with their offspring benefiting from the opening of the canopy. A greater dispersal shadow however, would be more suited to *C. subfarcinata,* which needs to take advantage of free substratum being created over wider temporal and spatial scales.

The conclusions and proposals presented in this thesis are based on the dynamics of the community at Cape Jervis during the period from summer (December) 1991 to autumn (March) 1993. It is realised that they may be used for comparison with studies of *Cystophora* elsewhere but may not represent the general scenario, as temporal and spatial variability in so many factors have been shown to affect the life histories of fucoids. Life history studies such as this one are useful tools for discerning patterns of change in communities, but it must be realised that they involve comparisons and not absolutes (Begon *et al.* 1990). The findings of this research have highlighted a number of areas that merit future study, and generated a series of hypotheses that require rigorous experimental testing.

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Appendix A. Authorities for species listed in the text

Table a.1. Listing of all species with authorities that are mentioned in the text of the current thesis.

Species	Authority	Species	Authority
Acrocarpia	Areschoug	*Cystoseira osmundacea*	(Turner)C. Agardh
Acrocarpia paniculata	(Turner)Areschoug	*Dictyopteris*	Lamouroux
Amphibolis antarctica	(Labillardière)Sonder & Ascherson	*Dictyosphaeria sericea*	Harvey
Amphiroa anceps	(Lamarck)Decaisne	*Dictyota*	Lamouroux
Apjohnia laetrivens	Harvey	*Dilophus fastigiatus*	(Sonder)J. Agardh
Areschougia congesta	(Turner)J. Agardh	*Ecklonia*	Hornemann
Ascophyllum nodosum	(Linnaeus.)LeJolis	*Ecklonia radiata*	(C. Agardh)J. Agardh
Asparagopsis armata	Harvey	*Ectocarpus*	Lyngbye
Bellotia eriophorum	Harvey	*Enteromorpha*	Link
Bifurcariopsis	Papenfuss	*Erythroclonium muelleri*	Sonder
Botryocladia sonderi	Silva	*Fucus distichus*	(Linnaeus)Powell
Carpophyllum maschalocarpum	(Turner)Greville	*Fucus serratus*	Linnaeus
Caulerpa brownii	(C. Agardh)Endlicher	*Fucus spiralis*	Linnaeus
Caulerpa cactoides	(Turner)C. Agardh	*Gloiosaccion brownii*	Harvey
Caulerpa flexilis	Lamouroux	*Griffithsia*	C. Agardh
Caulerpa geminata	Harvey	*Haliptilon roseum*	(Lamarck)Garbary & Johansen
Caulerpa scalpelliformis	(R. Brown)J. Agardh	*Halopteris*	Kützing
Caulerpa simpliciuscula	(Turner)C. Agardh	*Himanthalia elongata*	(Linnaeus)S.F. Gray
Caulocystis	Areschoug	*Hormosira banksii*	(Turner)Decaisne
Caulocystis cephalornithos	(Labillardière)Areschoug	*Landsburgia quercifolia*	Hooker & Harvey
Chlanidophora microphylla	Harvey(J. Agardh)	*Laurencia*	Lamouroux
Cirrulicarpus nanus	(J. Agardh)Womersley	*Liagora sp.*	Lamouroux
Cladosiphon filum	(Harvey)Kylin	*Lobophora variegata*	J. Agardh
Cladostephus spongiosis	(Hudson)C. Agardh	*Lobospira bicuspidata*	Areschoug
Codium	Stackhouse	*Metagoniolithon stelliferum*	(Lamarck)Weber-van-Bosse
Colpomenia	(Endlicher)Derbes & Solier	*Osmundaria prolifera*	Lamouroux
Colpomenia sinuosa	(Mertens)Derbes & Solier	*Pachydictyon*	J. Agardh
Corallina officinalis	Linnaeus	*Padina*	Adanson

Species	Authority	Species	Authority
Cystophora	J. Agardh	*Pelvetia canaliculata*	(Linnaeus)Decaisne & Thuret
Cystophora brownii	(Turner)J. Agardh	*Pelvetia fastigiata*	J. Agardh
Cystophora cymodoceae	Womersley & Nizamuddin	*Rhodymenia sp.*	Greville
Cystophora expansa	(Areschoug)Womersley	*Sargassum*	C. Agardh
Cystophora intermedia	J. Agardh	*Sargassum decipiens*	(R. Brown)J. Agardh
Cystophora monilifera	J. Agardh	*Sargassum fallax*	Sonder
Cystophora moniliformis	(Esper)Womersley & Nizamuddin	*Sargassum linearifolium*	(Turner)C. Agardh
Cystophora pectinata	(Greville & C. Agardh)J. Agardh	*Sargassum muticum*	(Yendo)Fensholt
Cystophora platylobium	(Mertens)J. Agardh	*Sargassum varians*	Sonder
Cystophora polycystidea	Areschoug	*Sargassum verruculosum*	(Mertens)C. Agardh
Cystophora racemosa	(Harvey)J. Agardh	*Scaberia aghardii*	Greville
Cystophora siliquosa	J. Agardh	*Scytosiphon lomentaria*	(Lyngbye)Link
Cystophora subfarcinata	(Mertens)J. Agardh	*Sonderopelta coriacea*	Womersley & Sinkora
Cystophora torulosa	(R. Brown)J. Agardh	*Xiphophora gladiata*	(Labillardière)Montagne
Cystophora xiphocarpa	Harvey	*Zonaria*	C. Agardh
Cystoseira	C. Agardh		

Appendix B..Settlement plate community composition

Introduction

The information presented in this appendix, complements that given in Chapter six on the recruitment of *Cystophora* and community development in young fucoid communities. Not all of the information gained from the analysis of settlement plate communities was considered of primary importance in addressing the aims of Chapter six but nonetheless was required to build an understanding of recruitment dynamics in the artificial system.

Information is presented here firstly, on the taxa which recruited onto settlement plates, their patterns of recruitment and persistence; and their importance as characterising or discriminating taxa in the analysis, and secondly, on patterns of change in community composition as a result of fluctuations in the taxa present.

Results

A total of 48 different taxa settled into the plate communities throughout the 21 months of study. Of these, 30 were identified by SIMPER as characteristic of particular communities (Fig. 6.3, Tab. b.1) and were therefore useful in differentiating communities. These 30 taxa were classified as either primary or secondary characterising taxa depending on the contribution made by each towards (dis)similarity. Primary taxa had a contribution ratio of >1 (see methods, Chapter six) whereas secondary taxa had a contribution ratio of <1 (Tab. b.1). Primary taxa generally occurred in a greater number of communities, were more abundant, and where seasonal in nature, showed distinct patterns of recruitment. Secondary characterising taxa generally showed seasonal recruitment but were more limited in their occurrence. The remaining 18 taxa were considered transient, showing distinctly seasonal recruitment onto 1 or a few plates of particular communities (Tab. b.1). The same system of nomenclature is used here for the description of settlement plate communities and taxa, as in Chapter six.

Primary characterising taxa

Three taxa were found in all communities throughout the year irrespective of age of community and season when the substratum became available (Fig. 6.3). They were encrusting corallines (LITHO); erect corallines (CORAL) and turfing brown algae (TURF). In the majority of cases encrusting corallines and turfing brown algae occurred at high levels although a seasonal low occurred for both during summer months. The consistently high abundance of these taxa (with the exception of summer 1991/92) accounted for much of the similarity within groups of replicate plates. Levels of abundance were less consistent for erect corallines but were generally lower in winter 1991 and summer 1991/92. Variation in the abundance of this taxa between groups of replicate plates contributed to much of the dissimilarity between them.

A fourth, LEATH (which probably belonged to the family Leathesiaceae) was also fairly ubiquitous but showed a distinct seasonal pattern in abundance. It was absent in the aut3, win12 and spr9 communities, which were present during winter (Fig. 6.3). In the only other winter community, sum6, its abundance was low. LEATH was present for most of the year, but was very abundant on most plates in summer 1991/92 and was deemed a characteristic taxa of the summer communities (Fig. 6.3). The seasonal pattern of abundance in this taxa was reflected in the level of (dis)similarity between communities.

Unidentified juvenile fucoids (FUCOID) occurred in a similar pattern to that of LEATH, being present on all but the aut3, win12 and spr9 plates (all winter occurring communities). A number of fucoid species were present in the surrounding community, including *Cystophora, Caulocystis, Sargassum, Scaberia* and *Acrocarpia,* and all but *Acrocarpia* were identified as recruits on the settlement plates at some time during the experiment. Unidentified fucoids could have been any of these with the exception of *Cystophora* as these recruits were generally distinguishable from other fucoid juveniles.

Some taxa, including *Cystophora* (CYST), showed peaks in abundance as a result of seasonal recruitment. These taxa were either present in lower levels at certain times of the year or persisted for some time after a recruitment event. *Cystophora* was one such seasonally recruiting taxa and was seen in all communities with the exception of sum3, sum6 and aut3, which existed prior to the first observation of recruits in spring 1991. *Cystophora* was more important as a discriminating taxa between communities in which it was either present or absent, than as a characterising taxa within groups of replicate plates.

Another fucoid taxa *Caulocystis* (CAULO) showed distinct seasonal recruitment in winter 1992, later than *Cystophora*, and persisted until the end of observations in spring 1992. It is, however, possible that many of the unidentified fucoids seen earlier in the year were juvenile *Caulocystis*. *Caulocystis* was characteristic of win12 and spr9 communities in 1992 (9% and 11% respectively) and was present the year before, in sum6 communities (Fig. 6.3) but it was not found in the other 1991 winter community (aut3) which suggests it to have recruited prior to autumn in 1991.

Another brown algal taxa CHORD (which probably belonged to the family Chordariaceae) also showed distinct seasonal recruitment irrespective of age of community or season of plate deployment. It was found in abundance (to a lesser degree in sum12) in communities existing through summer and was highly characteristic of them (Fig. 6.3). It was first observed in autumn 1991 on sum3 plates, which suggests its recruitment to have been slightly later in 1991. It was also found on aut6 plates in spring 1991, accounting for 11% of the characterisation of those plates and this remained constant through to summer when it was observed in all other communities.

Green A was seasonally abundant in winter 1992 and was present in all winter communities irrespective of age or season of deployment (Fig. 6.3). It was characteristic of the winter 1992 communities and was the primary discriminating taxa between these communities and others. It was present in much lower levels in 1991 and appeared to recruit earlier in autumn (sum3 plates). It did persist in all summer-deployed communities (Fig. 6.3) but at negligible levels (<0.5% presence).

Brown B also a showed seasonal recruitment, it was first observed in autumn 1991 (sum3 communities) but did not persist (Fig. 6.3). It was again seen in summer 1991/92 on the aut9 and win6 plates, it was most abundant in autumn, but some individuals persisted through to spring 1992. Brown B therefore, was seen in all communities until spring 1992. Brown B was Dictyotalean.

Griffithsia (GRIF) was first observed on spring 1991 plates of all ages and was characteristic of the win6 community where it occurred in high abundance. It persisted until autumn 1992 in the autumn and winter deployed communities but did not persist in the summer-deployed communities beyond spring (Fig. 6.3). This demise may have been due to the initially low levels of recruitment onto the sum9 plates.

Table b.1a-c. on following pages (140, 141). A total of 48 different taxa were found on the settlement plates throughout the 21 months of observation. SIMPER analysis of the data (Clarke & Warwick 1994) revealed 15 taxa that were primary characterising taxa (a) with a contribution ratio >1 (see above) and another 15 that were secondary characterising taxa (b) with a contribution ratio of <1 The remaining 18 taxa were generally transient with limited occurrence and abundance, but did contribute in a minor way to the dissimilarity between groups of replicate plates (c).

a. Primary characterising taxa	**Occurrence**	**Life history**	**References**
LITHO- encrusting coralline algae	ubiquitous, lower abundance in summer	Aseasonal perennial. Reproduction sexual or by fragmentation most likely in spring & summer	Womersley 1996
CORAL- erect coralline algae *Jania* sp., *Haliptilon roseum, Metagoniolithon radiatum*	ubiquitous, lower abundance in winter & summer	Aseasonal perennial. Reproduction by fragmentation and probably not seasonally limited. Sexual thalli observed from winter to summer.	Womersley 1996
TURF- turfing brown algae *Sphacellaria* sp. and species of Ectocarpales	ubiquitous, generally lower abundance in summer	Aseasonal annual. *Ectocarpus* more abundant in winter, fertile throughout year. *Sphacellaria* sexually reproductive in winter, asexually by means of propagules in summer.	Womersley 1987
LEATH - Leathesiaceae	ubiquitous, but absent in winter	Aseasonal annual with preferential recruitment during summer. Most species of Leathesiaceae in South Australia appear to be reproductive during summer	Womersley 1987
FUCOID- unidentifiable fucoid possibly *Sargassum, Caulocystis, Acrocarpia paniculata* or *Scaberia agardhii*	ubiquitous, generally absent in winter	Seasonal perennial. Gamete release in *Caulocystis* and *Scaberia* probably occurs in spring and early summer. *Sargassum* sexually mature in late winter/early spring.	Womersley 1987 Kendrick 1994, Kendrick & Walker 1994
CYST – *Cystophora*	recruitment in spring 1991 and persisting	Seasonal perennial with gamete release in late winter/early spring	This study
CAULO- *Caulocystis*	recruitment in winter 1991 & 1992	Seasonal perennial. Probably sexually mature in spring and summer.	Womersley 1987
CHORD - Chordariaceae	sum3, aut6 & summer 1991/92	Seasonal annual during summer but with slight interannual variability in recruitment. Several species of Chordariaceae in South Australia have only been collected during the summer months	Womersley 1987

a. Primary characterising taxa	Occurrence	Life history	References
BROWN A- brown filamentous alga	sum3 in autumn 1991 & sum9 in spring 1991	Seasonal annual	
GREEN A	seasonally abundant in autumn & winter	Seasonal perennial	
RED A	sum3 plates only in autumn	Seasonal annual	
BROWN B - Dictyotalean	recruitment in autumn & summer and persisting	Seasonal perennial	
GRIF- *Griffithsia* sp.	recruitment in spring 1991 & persisting	Aseasonal perennial. Reproduction sexual, fertile from autumn to spring.	Baldock *in* Womersley 1998 Baldock (*pers. com.*)
LAUR A- *Laurencia* sp.	autumn 1992	Probably a seasonal perennial	
RED B	summer 1991/92	Seasonal annual	

b. Secondary characterising taxa	Occurrence
GREEN B – turf-like	autumn
SARG – Sargassum sp	autumn & winter
GREEN C, BROWN D	spring & autumn
RED D	winter & spring
RED C & RED E	spring & summer
RED F	summer and autumn
BROWN E- Dictyotalean, LAUR B - Laurrencia sp, BROWN G – Dictyotalean	winter
BROWN F - Dictyotalean	summer, autumn & winter
BROWN C, BLACK, RED G	spring

c. Transient taxa	Occurrence
RED H, GREEN D - filamentous, RED I	autumn
BROWN H, BROWN I, Scaberia agardhii, BROWN M – Dictyotalean, RED L	winter
GREEN E - siphonous	winter & spring
BROWN J, RED J, BROWN K, RED K, Ecklonia radiata, RED M	spring
BROWN L, Halopteris sp., Laurencia sp.	summer

Seasonal recruitment was also observed in four other taxa, but these differed from the other seasonally abundant taxa, as they did not persist beyond the season of recruitment. Red B and *Laurencia* sp A (LAUR A) were present in a number of communities but only within a particular season. Red B only occurred in summer 1991/92 and was characteristic (16%) of the spr3 plates (Fig. 6.3) and accounted for 8.3% to 9.2% of the dissimilarity between spr3 and other spring deployed plates. *Laurencia* sp A only occurred in autumn 1992 and was characteristic (6%) of win9 communities (Fig. 6.3). Red A and Brown A were found only on sum3 plates but contributed to 18% of the characterisation of those communities.

Secondary characterising taxa

These taxa generally showed seasonal recruitment in one or a number of communities and occurred at sufficient levels on all replicates to contribute to the characterisation of the community. The majority of these taxa were unidentifiable and have been assigned taxa codes, but juvenile *Sargassum* (SARG) were identified, a second species of *Laurencia* (LAUR B) and several different Dictyotaleans species (Brown E, F, and G).

Sargassum was seen on plates in autumn and winter 1992, being characteristic of the spr9 plates (Fig. 6.3) but it was also found on the sum9 plates in spring 1991. *Sargassum* was never very abundant (<3%) and did not persist for more than 1 season after its recruitment but it is possible that some of unidentified fucoids were infact *Sargassum* and these were certainly present in all communities prior to *Sargassum* being observed.

Transient taxa

The remaining 18 taxa were classed as transient as they only occurred in low abundance in 1 or 2 communities and not necessarily on each plate within a group of replicates. They were therefore not in sufficient abundance to contribute to the characterisation of communities (Tab. b.1c) but they did make a small contribution to the dissimilarity between groups of replicate plates due to their seasonal nature.

Most of these transient taxa were assigned codes although a few were identified. Four individuals of *Ecklonia radiata* were observed on the win3 plates but did not persist. *Ecklonia radiata* was the only species of Laminariales found in the research community and only a few adult individuals were ever present. *Scaberia agardhii,* a fucoid species, occurred on win12 plates and probably represented the mature form of a proportion of unidentified fucoids.

Proposed life history strategies for recruiting taxa

Changes in community composition would have reflected the various life histories of the settling taxa and also their post-recruitment survival rates (these were not monitored in the current study). A range of life histories have been proposed for the settling taxa (Tab. b.1), based on their occurrence in the settlement plates communities:-

Aseasonal perennials- present year round and persisting after aseasonal recruitment events e.g. encrusting and erect corallines that can reproduce vegetatively by fragmentation and reproductively via propagules (Womersley 1996).

Aseasonal annuals- present year round but most likely perpetuated through rapid reproduction and turnover of individuals e.g. turfing algae. Such species are potentially reproductive year round (Womersley 1987) and characteristically show high rates of biomass specific productivity (Carpenter 1985, Clayton 1990, Westphalen & Cheshire 1997).

Seasonal perennials- showing defined seasonal recruitment and subsequent persistence. Not necessarily present throughout the year depending on post recruitment survival e.g. most species of fucoids recruited in spring and persisted throughout the remainder of the experiment. Brown B and *Griffithsia* are also likely to fall into this category.

Seasonal annuals- defined seasonal recruitment but not persisting beyond one (or two) seasons. Generally found in most communities during the recruitment phase e.g. CHORD and Green A. This strategy is potentially difficult to identify in that post-settlement mortality events can result in the removal of taxa that might normally persist and hence give them the appearance of a seasonal existence.

Transients-not persisting beyond the recruitment phase and generally only found in one or a few communities (Tab.b1c).

Seasonal patterns of change in community composition

Community structure changed on a temporal basis as seasonal fluctuations in recruitment and subsequent succession occurred. As a result, communities developing on plates deployed in the same season were significantly ($p<0.05$) different from one another as they aged, as were communities on plates of similar ages but from different seasons (Fig. 6.3).

The aut6 and aut9 communities were the only exception to this general rule and were not significantly different ($p<0.01$) in composition. Both communities were characterised by a common suite of 6 taxa (Fig. 6.3) that comprised a high percentage (98.7% and 98.8% respectively) of the similarity between replicate plates.

Change in community structure, as communities aged, did not necessarily follow a sequential pattern, due to the strong influence of seasonal recruitment events and fluctuations in ubiquitous taxa (encrusting and erect corallines, turfing brown algae and LEATH). A number of patterns of change in the levels of taxa found on the settlement plates were identified and these are outlined below:-

- Levels of encrusting corallines and turfing brown algae were typically high in all communities. Encrusting corallines ranged from 90% to 100% in most communities but were generally low in summer (average abundance 4.4 to 73.6%); levels were also low (average abundance 53.2%) on the win3 plates. This was particularly influential in the win6 community that was the only one not characterised by encrusting coralline algae (average abundance of 4.4%). Levels of turfing brown algae generally ranged from 68% to 100% (average abundance) except in summer when levels dropped to 31% to 51% (average abundance). The situation was slightly different in the spring-deployed plates, which had low occurrence of turfing brown algae in autumn 1992 (average abundance 46%) and spring 1992 (45%). The spr6 plates were the only plates in which this taxa was not a primary characterising taxa.

- Erect corallines were seasonally more abundant in autumn and spring on the summer (sum3 and sum9), autumn (aut6 and aut12) and spring (spr6) deployed plates which accounted for much dissimilarity between communities within each season of deployment. However, for those plates deployed in spring 1991, levels of erect corallines remained fairly constant and were not as important in the discriminatory process.

- The absence of LEATH, in winter occurring communities (aut3, win12, and spr9) was important and accounted for much of the dissimilarity between these and the other communities deployed at the same time. In particular, the aut3 and other (aut6, 9 and 12) autumn deployed communities.

- Seasonal recruitment and persistence of fucoid taxa, in particular *Cystophora,* created differences between pre-recruitment and post-recruitment communities.

Communities present in spring 1991 were typically rich in fucoid taxa (Fig. 6.3) having caught the recruitment phase of *Cystophora* and other fucoids (possibly *Caulocystis, Scaberia* and *Sargassum*). When present as a primary characterising taxa, *Cystophora* accounted for 8.7 to 17.1% (% contribution) of community characterisation, fucoids accounted for 6% to 31% and *Caulocystis* accounted for 9% to 11% of community characterisation.

- With the exception of aut3 plates, between 56% and 76% of taxa found in communities were considered to be seasonal recruiters. High characterisation of particular communities by these seasonally recruiting taxa was important in distinguishing them. Sum3 communities were typically high in seasonal taxa, eg. Brown A, Red A and Green A which decreased the relative importance of encrusting corallines and turfing brown algae. These ubiquitous taxa accounted for 61% to 82% of community characterisation in the sum6, 9 and 12 communities but only 33% in the sum3 communities.
- Interannual variability in the recruitment of seasonal taxa eg. *Caulocystis,* CHORD and Green A was influential in the analysis of community composition as recruitment events occurred twice within the 12 month deployment of each series of plates. For example, CHORD recruited onto sum3 and sum12 plates and was therefore common to both types of community. It was however, important in distinguishing between communities of similar age or season of deployment as its occurrence was typically seasonal.

Summary

The structure and development of communities on the settlement plates were primarily driven by seasonal patterns of recruitment. A number of patterns in taxa occurrence and abundance were identified and these reflected the reproductive life-history strategies of each. Patterns of fucoid recruitment, including *Cystophora,* were important in structuring the settlement plate communities as recruitment was clearly seasonal and individuals persisted after the event. Such strategies that enable the persistence of taxa are important in the long-term development of the community.