Simple Mathematical Models of *Semibalanus balanoides* and *Fucus vesiculosus* in a Rocky Intertidal Environment.

Kieran Hyder
(B.Sc. Marine Biology, University of Liverpool.)

Submitted for

Degree of Master of Philosophy,
Department of Statistics and Modelling Science,
University of Strathclyde.

September 1996

Acknowledgments

This research was funded by the Wellcome Trust and supported by useful discussion from the members of EUROROCK. I would like to thank my supervisors Professors Bill Gurney and Steve Hawkins for their guidance throughout my 2 years of research. I think that it has been interesting for all three of us, as close collaboration between mathematicians and biologists is difficult to organise. I only hope that I haven't exhausted my guidance for the next 2 years!

The laboratory facilities here are great as far as the computing goes. I would like to thank Ian Thurlbeck for his endless patience and support when I bust the computers on a regular basis. I would also like to thank anyone else around the department who has given me help at one time or another, especially the secretaries and other postgrads.

Port Erin Marine Laboratories, Isle of Man, have also been great and helpful in opening their doors to me. In particular, I would like to thank F. Pannacciulli, G. Cushnie, S. Jenkins and M. Johnson, who all trusted me with bits of their unpublished data.

Now to my friends. I would like to say cheers to Shahid for thrashing me at squash (regularly!) and even managing to make it look difficult on occasions. Ian, for being Ian and Andrea for being patient. Ray for laughing with/at me, as most people learn to after a while. Louise, Michail, Pauline and Gordon without whom this year would have been boring. Last but by no means least, Al for always being there (at home that is) to talk and chill when I'd had enough of work!

Finally on a more personal note I would like to say thanks to my brother, Patrick who has always been there for chat and understands about things going wrong. Lastly to my mother, Kamamla, who has supported me fully through whatever I wanted to do. You can't ask for more than that!

Abstract

A cycle has been suggested for the mid shore region of a moderately exposed rocky shore at Port St. Mary, Isle of Man (Hartnoll & Hawkins, 1985). This cycle consists of competition for space between the limpet, *Patella vulgata*, the barnacle, *Semibalanus balanoides*, and the brown alga, *Fucus vesiculosus*. This cycle is split into a number of constituent parts and modelled.

Two single species models of *S. balanoides* and *F. vesiculosus* are developed. Basic analysis, including the derivation of steady states and stability boundaries, are done on these models. The models are parameterised from the literature and the mechanisms are investigated. Four types of dynamics are found: stable underdamped; stable overdamped; point-cycles; and aperiodic solutions. The mechanism driving the model is dependent upon the ability of a cohort to increase in area over time. Thus, giving rise to a 'speed of fill mechanism' that is dependent upon the settlement rate. Seasonality is investigated and a similar mechanism is found, but only point-cycles and aperiodic solutions are observed. Settlement is the main factor that drives these models, although the length of settlement season appears to make little difference.

A two species model is created by linking the single species models and is parameterised from the literature. Steady states are derived, but are complicated making inferences difficult to draw. Thus, the investigation of this model is done by simulation. More complex dynamic are found, with stable equilibria of barnacles, stable equilibria of barnacles and fucoids, and periodic or aperiodic cycles of the two species. The sub-models are settlement driven and oscillations can be driven by one or both of the sub-models or the interaction between the two sub-models. Parameters are estimated for the Isle of Man. Within the range of parameter values individual cycle times and occupancy can be mimicked, but the total cycle time is too short. This is because the time lag between the two species is too short and requires implementation of seasonal stochastic recruitment.

Contents

List of Figures

List of Tables

Part I

Introduction

Chapter 1

An Introduction Rocky Shore Ecology

1.1 General Introduction

1.1.1 What is a Rocky Shore?

A rocky shore is found at the boundary zone between terrestrial and marine systems. They occur in areas of moderate to extreme water movement where erosion is more important than deposition. Rocky shores are good ecological systems to study since they are essentially two dimensional. The community is composed of largely sessile organisms competing for space and mobile organisms that only move relatively small distances. This makes *in situ* description of and experimentation on the rocky shore environment fairly easy (see for example, Moore, 1934; Southward, 1956; Connell, 1959, 1961a; Hawkins, 1981a&b; Lubchenco, 1983; Hawkins & Hartnoll, 1982a&b, 1983a&b; Underwood *et al*, 1983; Paine, 1984; Sousa, 1984; and Chapman, 1986a&b, 1995).

A sharp gradient of environmental conditions is found from the low to high shore. These conditions are associated with the amount of time that the area on the shore is immersed by the sea. Thus, in a relatively short horizontal distance the environment changes from essentially marine to terrestrial. However, the organisms that inhabit rocky shores are thought to have evolved largely from marine ancestors. Thus, the gradient can be thought of as uni-directional with stress increasing with increasing shore height. This is known as the vertical gradient. A horizontal gradient of conditions is also found and is associated with the degree of exposure to wave action found at the site.

1.1.2 The Vertical Gradient

The vertical gradient of environmental conditions is found between the lowest astronomical tide and the top of the wave splash zone. The largest tides, or spring tides, range between mean low water springs (MLWS) and mean high water spring (MHWS). The mean tidal level (MTL) is found at the vertical midpoint of these limits. The mid-shore of mid-tidal level covers an area on either side of MTL from about 2.5 to 3.5 meters above chart datum (see Hawkins & Jones, 1992, for a general review). The environmental gradient observed is due to the physical stress on the mainly marine organisms as they are emersed. Organisms living higher on the shore spend more time emersed and suffer greater stress from desiccation.

The unidirectional nature of the gradient of environmental conditions and biological interactions cause zonation of organisms on sheltered and exposed shores (Hawkins & Jones, 1992). Concentrating upon shores around the British Isles, sheltered shores have a seaweed dominated community (see figure 1.1). As one moves from the MHWS to MLWS distinct zones of *Pelvetia caniculata*, *Fucus spiralis*, *Ascophyllum nodosum* and *F. serratus* are found. The position of *F. vesiculosus* depends on the degree of exposure (Hawkins & Jones, 1992). On exposed shores there is a filter feeder dominated community of barnacles and mussels. Again as one moves from MHWS to MLWS distinct zones of *Porphyra*, *Chthamalus montagui*, *Semibalanus balanoides*, *Chthamalus stellatus* and *Mytilus edulis* are found.

There are a number of factors that determine the zonation of these plants and sessile animals. High on the shore, upper limits of zones are caused by physical factors (Schonbeck & Norton, 1978). However, lower on the shore the upper limit of these zones can be caused by competition (Hawkins & Hartnoll, 1985) and grazing (Southward & Southward, 1978; Underwood & Jernakoff, 1981). The lower limit of these zones are caused by competition and predation, although in a few cases physical factors are important, for example *Pelvetia* (Schonbeck & Norton 1980a).

Mobile animals also have upper and lower limits to their zones. The upper limit is set by unfavourable conditions occasionally killing an individual. Lower levels are either set by predation or by competition with seaweeds for space.

1.1.3 The Horizontal Gradient

The horizontal gradient has the most impact on the community structure (Lewis, 1964). It is not a uni-directional gradient as found with the vertical gradient. For example, with a higher degree of wave action there is a greater risk of dislodgement from the rock, but in shelter there is a greater risk of being covered in silt (see figure 1.1).

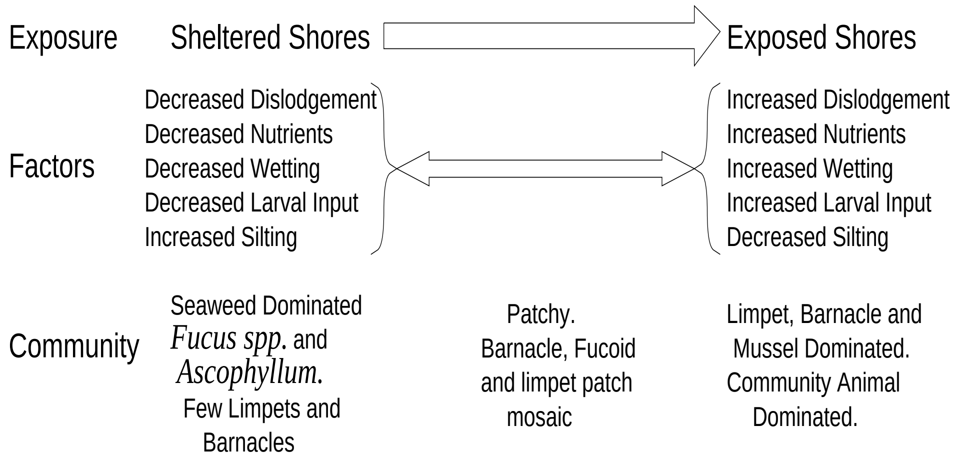

Figure 1.1: Diagram to represent the changes in stress associated with increasing exposure to wave action and the result in terms of community structure on N.E. Atlantic shores (modified from Raffaelli & Hawkins, *in press*).

The degree of exposure to wave action is difficult to assess. It can be measured using biological exposure scales. These give shores an exposure rating by looking at the community with special attention given to a number of indicator species. The two best examples of these scales were developed by Ballantine (1961) and Lewis (1964). Biological scales differ from circularity scales if they are used to study the biota themselves. Map based methods have been used to rank shores and direct physical methods are also possible.

The communities found at different degrees of exposure in the British Isles are well documented (see figure 1.1). The community structure is observed to change from an algal dominated community at sheltered places to an animal dominated shore in exposed places. At an intermediate degree of exposure the community structure appears to be a mix of these two communities with a mosaic of limpets, barnacles and seaweed. An example of a moderately exposed British rocky shore is the ledges at Kallow Point, Port St. Mary, Isle of Man. Much work has been done on this shore. The balance of the community structure was first investigated by Jones (1948) when he removed limpets from a five metre wide strip and observed a massive increase in the biomass of algae on this strip. He suggested that the balance was between the limpet, *Patella vulgata*, and algae. Burrows & Lodge (1950) noted that the presence of barnacles also had an effect on the stability of the system. Thus, the instability of the system was noted and further investigations were carried out (see for example, Southward 1956, 1964; Hawkins, 1981a&b, 1983; Hawkins & Hartnoll, 1980, 1983a&b; Hartnoll & Hawkins, 1980, 1985).

A cycle was proposed for the mid-shore region of this shore by Hartnoll & Hawkins (1985) (see figure 1.2). They suggested that both deterministic processes and stochastic events are involved in the cycle. For example, recruitment is a stochastic process and competition for space or grazing are deterministic events. Hawkins *et al* (1992) revised this theory and suggested that stochastic events initiate the cycle, for example escapes from grazing, but deterministic processes control its progression. In this cycle they propose that fluctuations in the abundances of *Semibalanus balanoides* (barnacle), *Fucus vesiculosus* (seaweed) and *Patella vulgata* (limpet) are linked to the abundances of the each other. Two other species play a minor role in this cycle. *Nucella lapillus* is a dogwhelk and preys upon adult barnacles (Connell, 1961a; Dunkin & Hughes, 1984). *Actinia equina* is a sea anemone and occupies space in shelter provided by the seaweed canopy. This cycle can be viewed as a successional sequence that never reaches a stable end point (see figure 1.2).

The Cycle

In stage one dense barnacle cover disrupts limpet grazing and barnacle settlement is enhanced by conspecifics (Lewis, 1977). Stage two shows dense adult barnacle and decreased limpet grazing because of seabird predation (Feare & Summers, 1985), storm strewn boulders (Southward, 1956) and aggregation of limpets elsewhere (Hartnoll & Hawkins, 1985). Decreased grazing pressure increases the likelihood of seaweed ‘escapes’ (Hawkins, 1981a&b). An escape occurs when a seaweed gets to a length of three to four centimeters and is then largely unaffected by *P. vulgata* grazing (Burrows & Lodge, 1950; Hawkins, 1979; Hawkins & Hartnoll, 1983a&b). Stage three has fucoid clumps growing on the barnacle matrix. Limpets tend to aggregate under these clumps and thus grazing pressure is reduced elsewhere on the shore allowing more ‘escapes’. The barnacle matrix is smothered by the fucoid algae and dies. The fucoid algae growing on the dead barnacle matrix is now insecurely attached (Proud, 1994) and plants are ripped

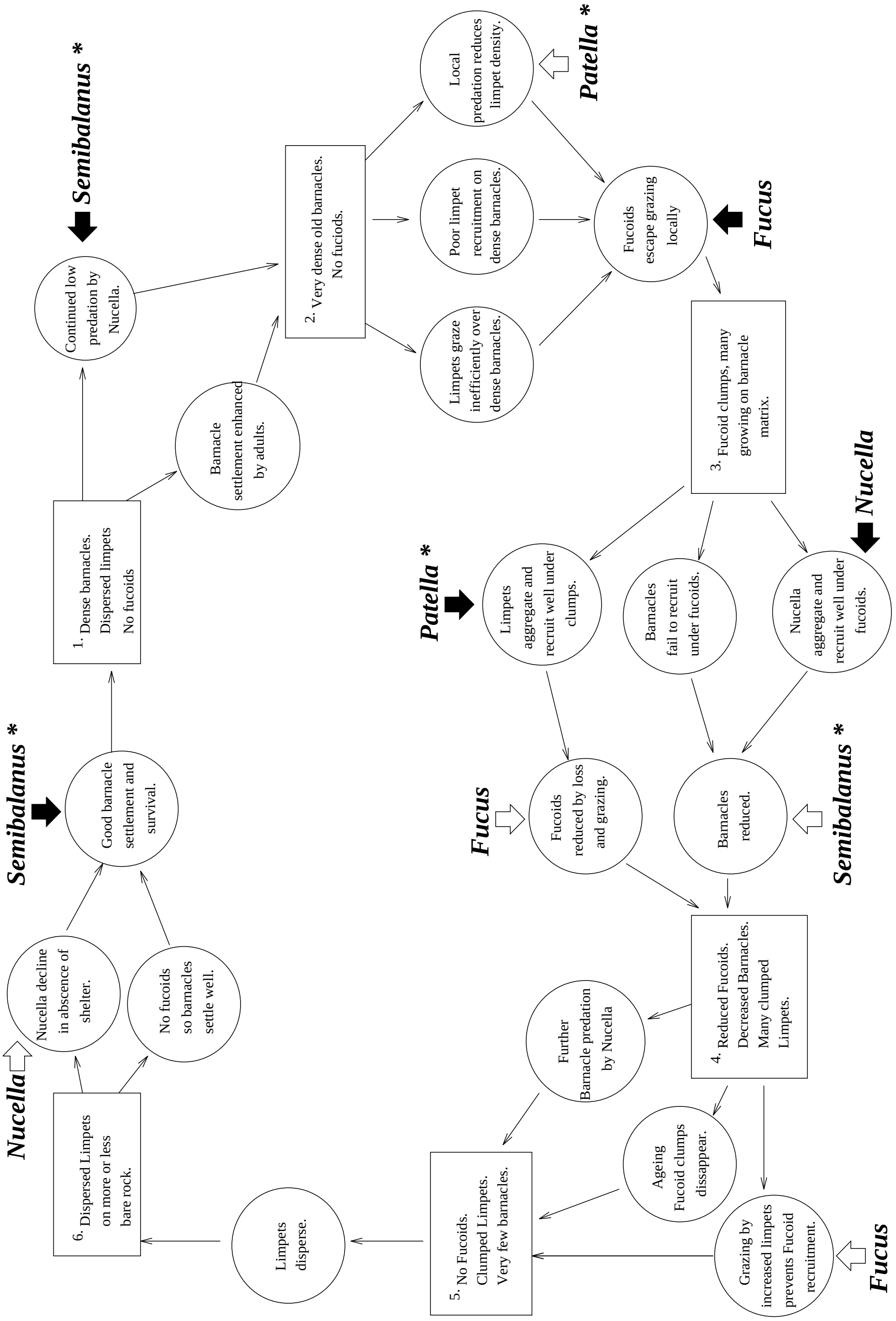

Figure 1.2: Simplified diagram to represent the cycle in the mid-tide level of a medium-exposed rocky shore in the Isle of Man. The numbered rectangles are stages in the cycle. The circles are intrinsic biological processes generating and maintaining the cycle. The heavy arrows indicate where very good settlement of named species either promotes (solid arrows) or inhibits (open arrows) the progress of the cycle. Settlement and recruitment from the planktonic phase is asterisked. Reproduced from Hartnoll & Hawkins (1985) figure 7.

off the rock in storms. Stage four shows the thinned old fucoid plants, very few barnacles as *N. lapillus* aggregate under the canopy and predate upon the remaining adult barnacles. The high densities of limpets under the canopy prevent fucoid recruitment. As there is no recruitment to the fucoid population when the old plants die there are no juveniles to replace the adults and stage five is reached. Stage five has very few barnacles, no fucoids and aggregated limpets. Gradually the limpets disperse leading to stage six in the cycle which is essentially bare rock. This cycle can be in different stages at different places on the shore and this gives the shore the appearance of a patchy mosaic of limpets, barnacle and fucoids with up to forty percent free space (Hartnoll & Hawkins, 1985).

It has been suggested that the balance of barnacles, fucoids and limpets on moderately exposed shores follow population fluctuations and the amplitude of these fluctuations is determined by the degree of exposure to wave action. Small amplitude cycles are found at both ends of the scale. Southward & Southward (1978) suggested that very sheltered and very exposed shores changed very little over time. However, moderately exposed shores exhibit large amplitude cycles with the balance shifting between the different components in the system due to biological interactions prompted by recruitment fluctuations. A conceptual model of proposed barnacle and fucoid cover at different degrees of exposure emphasises the different amplitude of the cycles (see figure 1.3) (Hartnoll & Hawkins, 1985).

Other examples of this type of interaction on moderately-exposed shores have been described both in the British Isles and worldwide. Baxter *et al*, (1985) observed a similar cycle in the Orkney Islands. On the East Coast of the United States there are no patellid limpets and the main grazer is *Littorina littorea*. Vadas & Elner (1992) noted *L. littorea* shows great variation in density over short distances and escapes occur in areas of reduced density. They also observed annual colonisation cycles of bare rock by barnacles and green ephemeral algae. Underwood *et al* (1983) looked at the dynamics of a mid-shore community in New South Wales, Australia. They found that algae prevented the recruitment of barnacles and that the arrival of barnacles has a subsequent effect upon the predators. They suggested that these effects varied in both time and space due to recruitment fluctuations. Dungan (1986) studied a three way interaction between the barnacle, *Chthamalus anisopoma*, encrusting algae, *Ralfasia*, and the limpet, *Collisella*, near Puerto Peñasco, Mexico in the Gulf of California. Carter & Anderson (1991) looked at the interaction between barnacles, limpets and *Gelidium pristoides* in the eastern Cape, South Africa. They found that the distribution

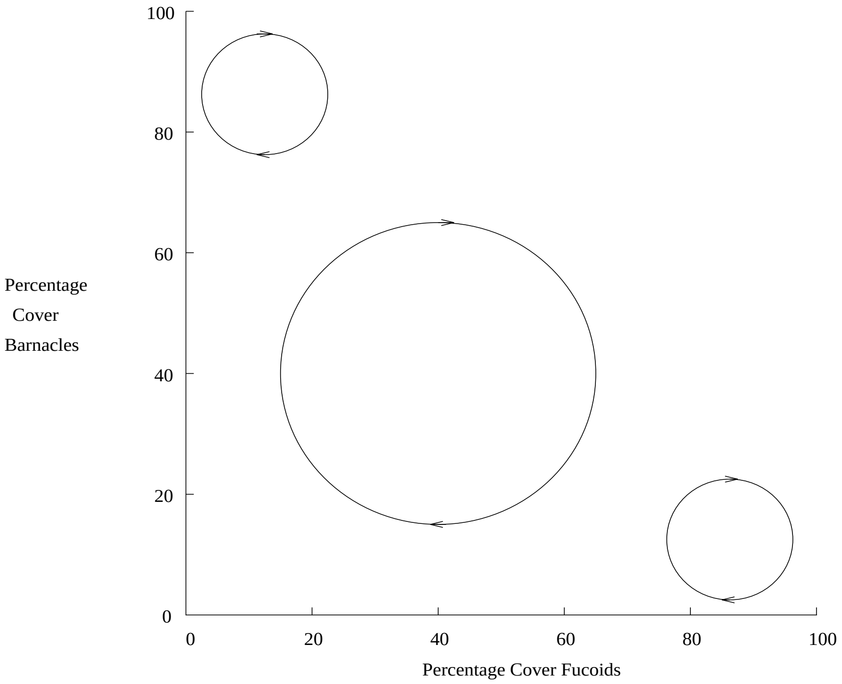

Figure 1.3: A model of barnacle cover plotted against fucoid cover in different degrees of wave exposure. Reproduced from Hartnoll & Hawkins (1985) figure 6, modified from Southward & Southward (1978).

of *G. pristoides* was dependent upon the presence of limpets and the security of attachment, *ie* whether attached to rock or barnacles.

1.2 The Barnacle

Barnacles are sessile marine invertebrates. They are members of the phylum Arthropoda, sub-phylum Crustacea and class Cirripedia. Barnacles are filter feeders using the cirral net to filter particles of suspended organic matter from the water column. They are of great economic importance as a number of common shallow water and intertidal species are responsible for fouling the hulls of ship and coastal installations worldwide. They have also been used as indicator species for global warming (Southward, 1991). For these reasons considerable research has been carried out on barnacles since the 1940s. Some of the classic work has been done by authors such as Barnes, Connell, Crisp and Southward. More work on the interaction of barnacles within the community has be done by authors such as Dayton, Hawkins, Lubchenco, Menge, Paine and Sutherland. More recently mathematical modelling of barnacle populations has been done by Bence, Iwasa, Kuang, Nisbet, Possingham, Roughgarden and So (see below). This is because barnacle populations are essentially open populations with space-limited recruitment, as they have a planktonic larval phase. Thus, new theory was required as these populations cannot be modelled using traditional Lotka-Volterra population models.

Lewis (1964) stated that barnacles were the most characteristic and dominant organisms of the eulittoral zone throughout the world. He also suggested that the barnacles were restricted in distribution by competition and adverse physical conditions. Thus, barnacles are limited to moderately-exposed shores, flat very exposed shores and vertical rocks where the competition for space is less (Connell, 1961a). On the high shore there is less predation and competition for space, but dessication stress and decreased food supply causes increased mortality and sets the upper limit. On the low shore there is intense competition for space with algae and more predation. The lower limit of the barnacle has been described as equal to the upper limit of laminarians (Lewis, 1964) or the red algal turfs (Ballantine, 1964).

In Britain there are four major species of intertidal barnacle *Chthamalus montagui*, *Chthamalus stellatus*, *Semibalanus balanoides* and *Elminius modestus*. *Balanus perforatus* can also be locally common in the south and west. All four species exhibit different distributions because of different larval dispersal, development, settlement (Burrows, 1988; O'Riordan, 1992) and juvenile mortality. The species of interest in this project is *S. balanoides*.

Much attention has recently been focused on barnacles because of their importance in structuring communities. This has been investigated experimentally in the field and more recently by modelling (Roughgarden *et al*, 1985).

1.2.1 *Semibalanus balanoides*

The strong preference of *S. balanoides* for the intertidal zone was first noted by Darwin (1854). Individuals are distributed between mean low water neap (MLWN) and mean high water neap (MHWN) (Stubbings, 1975). It is a boreo-arctic species and is distributed widely across the North Atlantic and Western Europe (Stubbings, 1975). *S. balanoides*, previously called *Balanus balanoides*, has been researched greatly. However, two problems are associated with the literature. Firstly, much of it is scattered and old so may be difficult to locate. Secondly, it is location specific, for example data for settlement, growth rates and mortality of *S. balanoides* found on the North East coast of the USA are likely to be very different to that for the West Coast of Britain.

The life history of *S. balanoides* is fairly complicated. Adults mature at the age of 2+, although a small proportion breed from the 1+ age-class (Arnold, 1977). Adults may live to as old as five on the high shore (Stubbings, 1975). *S. balanoides* is hermaphrodite and fertilisation is internal. The adults produce one brood of eggs per year (Barnes & Barnes, 1968). Each individual can produce between 400 and 8000 eggs in a single brood (Barnes and Barnes,1968). However the water temperature must drop to below twelve centigrade for several weeks to trigger fertilisation. Fertilisation takes place in autumn and then eggs are brooded internally until spring (Stubbing, 1975). Eggs hatch and larvae are released in the period from March to April (Crisp, 1964; Stubbings, 1975).

The hatched nauplii are released into the water becoming planktonic. These then develop through six feeding naupliar stages before a non-feeding cypris larva is produced (see Stubbings, 1975 for a general review). This development lasts for 18 to 30 days dependent up on the water temperature (Harms, 1984). Cyprids are the settling stage of *S. balanoides.* The larvae become photonegative and swim down through the water column. When substrate is located cyprids will only settle with the appropriate settlement cues (Knight-Jones & Stevenson, 1950; Knight-Jones, 1953; Lewis, 1977; Barnett & Crisp, 1979; Wethey, 1984), for example, arthropodin, water currents, rugotropism, light and gravity are all important cues (see Lewis, 1977, for a general review). The density in which cyprids settle is limited by the supply of larvae or the space available for settlement (Connell, 1985). Once settled the cyprids metamorphose into the adult form of the barnacle

1.2.2 Settlement

As far back as the 1950s various authors were aware of the importance of recruitment in the structure of rocky shores. This thinking was formalised and larval biology was given the name ‘Supply side ecology’ (Lewin, 1986). Underwood & Fairweather (1989) described the advent of ‘Supply side ecology’ as ‘old wine in a new bottle’. Since then there has been increasing investigation of both settlement and recruitment of barnacles, because these processes are thought to determine community structure (see, for example, Roughgarden *et al*, 1985).

Measurement of actual settlement is difficult as cyprids are only about 1 mm in length. Settlement densities are very variable and regional, local and temporal variation in density can occur (Caffey, 1985; Gaines *et al*, 1985; Wethey, 1985; Raimondi, 1990). Supply of cyprids has been correlated with strength of onshore winds (Hawkins & Hartnoll, 1982), maximum tidal range (Shanks, 1986), and increasing with increasing wave action and decreasing shore height (Bertness *et al*, 1992). This variation in settlement gives a pattern with many peaks. Various hypotheses have been put forward to explain these peaks but the process is not yet understood (Wethey, 1985).

When settlement density is high cyprid settlement density is directly correlated to the area of bare rock (Minchinton & Scheibling, 1993) and discrete cohorts are observed on the shore. However, when settlement density is low cohorts are mixed and vacant space is abundant for *Balanus glandula* (Roughgarden *et al*, 1985) and *S. balanoides* (Hawkins & Hartnoll, 1982a).

1.2.3 Growth

Growth has been widely researched. It is influenced by both abiotic factors such as water temperature, and biotic factors such as density of adults. The first studies on the growth and flow rate of *S. balanoides* were carried out by Moore (1934). In general growth rate is affected by age, season, shore level, degree of exposure (Moore 1934) and algal cover (Barnes, 1955). Most factors affect the growth rate by modifying food intake. This can be done by either reducing the water motion around the barnacle or interfering with its cirral net.

Generally younger individuals have a higher growth rate than older ones. Growth rate increases with decreasing shore height in the first year. However, in the second year growth rate on the high shore has been reported as being higher (Moore, 1934). Growth is seasonal and is higher in summer when the particulate matter in the water is high. Individuals immersed for longer tend to have a higher growth rate, but do not live as long (Barnes and Powell, 1953). Specimens can grow up to a mean of 25.8 mm in shell length (see figure 1.4) on the high shore (Barnes & Powell, 1953). Size at the end of the first season varies with height on the shore and latitude (Crisp, 1960).

1.2.4 Mortality

There are many causes of mortality both biotic and abiotic (see table 1.1). Recent studies have concentrated on predation, disturbance and competition as causative

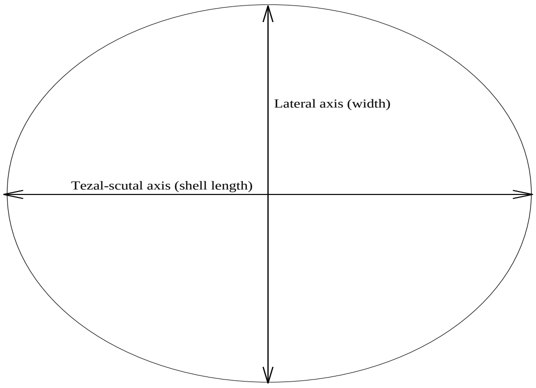

Figure 1.4: Measurements used for growth studies of barnacles

agents in distribution patterns and community structure (Connell, 1983; Sih *et al*, 1985).

Predation of *S. balanoides* is an important source of mortality. One of the main predators of *S. balanoides* is *N. lapillus*, but only eats larger individuals (Connell,1961a; Dunkin and Hughes, 1984). Overcrowding can lead to hummocks of barnacles (Barnes and Powell, 1950). This is because the limited resource on rocky shores is generally space. Thus, when little space is available hummocks are formed which are more susceptible to dislodgement (Barnes and Powell, 1950; Shanks & Wright, 1986). Mechanical damage is also an important source of mor-

Table 1.1: Causes of barnacle mortality.

Abiotic	Biotic	Anthropogenic
Dessication	Hummocks (Shanks & Wright, 1986)	Oil spill and toxic dispersants (Southward and Southward, 1978; Southward, 1979)
Increased Wave Action	Limpet bulldozing (Miller & Carefoot, 1989)	Shore trampling (Bally & Griffith 1989)
Storms	Algal overgrowth (Proud, 1994)	
Low temperature starvation (Southward, 1955)	Algal cover (Barnes, 1955)	
	Predation (Connell, 1959)	

tality. For example, tests of adult barnacle can be damaged by rocks in storms and juvenile barnacles can be dislodged by feeding limpets (Hawkins, 1983; Miller & Carefoot, 1989).

Density dependent mortality has been suggested to occur in two situations. Connell (1985) suggests mortality is density-dependent for the first two weeks after settlement if the settlement is high. Density-dependent mortality has been observed when the competition for space is high, for example hummocking mortality (Shanks & Wright, 1986).

1.3 Brown Algae

The brown algae or the phaeophyceae are found commonly in the rocky intertidal and subtidal zones world wide. The members are classified as:

Kingdom:	Plantae
Division:	Chromophycota
Class:	Phaeophyceae

Brown algal stands are often described as naturally occurring monocultures. However, Paine (1984) argues that these stands are not true monocultures because epiphytic species, especially microalgae may occupy up to 20 % of the space. Thus, Paine (1984) defines monoculture as "..at least 80 % space occupation by a single species". Monocultures are dense populations with interactions between individuals for resources. This implies that intraspecific competition within these stands can be intense and the affect on individuals can be profound.

Monocultures of brown algae lead to the formation of a canopy of adults. This affects juvenile fucoid recruitment by altering the environment (Burrows & Lodge, 1950; Dayton, 1971). This happens in a number of ways:

1. A much lower light intensity is found under an adult canopy. In fact 98% of the incident light can be absorbed by the canopy (Schonbeck & Norton, 1980a).
2. Lower nutrient levels are found under the canopy. This could either be as a direct effect of the adult plant (Dayton *et al*, 1984) or indirectly as a facet of decreased water movement under the canopy.

3. Whiplash and sweeping effects of adults cause density-independent mortality of juveniles (Dayton, 1971; Ang, 1985).
4. Sediment build up can swamp juveniles (Kennelly, 1989).
5. Scour (Ang, 1985).
6. Aggregation of grazers under the canopy (Hartnoll & Hawkins, 1985).

Harper (1967) stated that "When the carrying capacity is reached then the form or size of a plant may be modified without mortality taking place". He called this a plastic response. The brown algae have a high degree of plasticity and therefore have a vast range of potential shapes and sizes (Russell, 1986). The final size and shape of a plant is determined by genetics, form changes from juveniles to adults, reproduction and the environment. The final shape of the plant has been described as "a compromise of the range of forms and the form permitted by the environment" (Norton *et al*, 1982). Increasing plasticity is found with increasing density.

The brown algae have a very large variation in size. The average gamete is 10 to 20μm and adults range from 15 cm to 50m in length. Vadas *et al* (1992) suggested that brown algae have a change in size of about 5 orders of magnitude.

1.3.1 *Fucus vesiculosus*

F. vesiculosus is an important component of intertidal communities on British and other northern temperate shores (Knight and Parke, 1950; Keser *et al*, 1981; Chapman, 1990a). It is found predominantly in even aged monospecific stands. It is most commonly found on the mid-shore region of moderately exposed shores. The population structure of *F. vesiculosus* is positively skewed with respect to plant length. This implies a population with a few large adult plants and many juveniles (Knight & Parke, 1950; Burrows & Lodge 1951), *ie* a canopy.

The *Fucus* genus is a complex of species, subspecies, hybrids and ecads, and *F. vesiculosus* is no exception (Burrows & Lodge, 1950). The many different morphs of *F. vesiculosus* makes identification very difficult. For example, *F. vesiculosus evesiculosus* has no gas bladders and *F. vesiculosus var linearis* can only be separated from *F. spiralis* by lack of twisting and possessing no sterile margin of the fruiting bodies (Hawkins & Jones, 1992).

The life cycle of *F. vesiculosus* can be seen in figure 1.5. It has a diploid sporophyte with haploid gametes. Fertilisation is external with synchronous release of gametes (see South & Whittick, 1987, for a general review). There is a short dispersal phase in their life cycle. Dispersal distances to my knowledge have not been measured for *F. vesiculosus*, but distances have been found to be short in other fucoids, for example *F. serratus* (Arrontes, 1993).

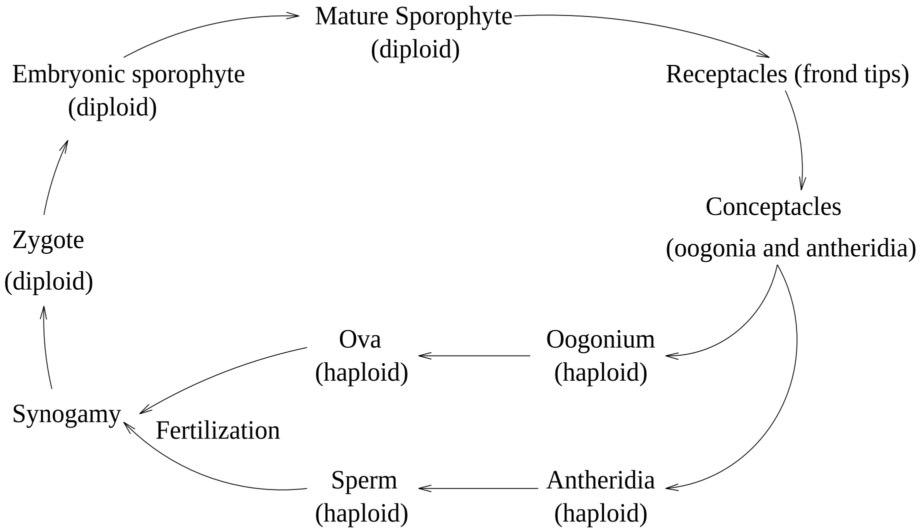

Figure 1.5: The life cycle of *F. vesiculosus*. Reproduced from South & Whittick (1987).

Various aspects of the population dynamics of *F. vesiculosus* have been studied. However, Chapman (1986b) stated “Nearly all the demographic studies of seaweed populations (single species) have been reported since 1980” and that “...little attention has been given to the ecology at an organismic level”. Although sparse, studies on observed dynamics of *F. vesiculosus* have been carried out (Knight & Parke, 1950; Keser & Larson, 1984; Creed, 1993). However, research has concentrated on population interactions with other algal species (Hawkins & Harkin, 1985; Chapman, 1990a) and population interactions in a multispecies community (Hawkins, 1981a&b; 1983). For example, Hawkins (1983) found that recruitment of *S. balanoides* under a *F. vesiculosus* canopy was much less dense than without a canopy.

The longevity of *F. vesiculosus* has only been mentioned in a few papers as algae are generally difficult to age (Cheshire & Hallam, 1989). Knight & Parke (1950) suggested individuals of *F. vesiculosus* can live for 3 to 4 years and that in Devon an area of $1m^2$ can support a biomass of 6.74 kg. Keser & Larson (1984) suggested a longevity of *F. vesiculosus* of between 2 and 4 years.

1.3.2 Settlement

Most seaweed populations reported only investigate plants of visible size allowing the possibility of seed banks (Hoffmann & Santelices, 1991). Creed (1993) states that *F. vesiculosus* on the Isle of Man has a seed bank, with a maximum of 26,000 individuals per m^2.

F. vesiculosus is a highly fecund species. Large individuals may have 1000 receptacles with maximum of 3269 eggs per receptacle. Thus there is a possibility of over three million eggs from a single large plant (Knight & Parke, 1950). Gamete release is between May and July and release is one month earlier in Devon than the Isle of Man (Knight & Parke, 1950).

If settlement is sufficiently heavy then competition for space is important. There is insufficient space to support settlement of more than 43,600 germlings per m^2 (Keser & Larson, 1984). Germlings are not visible to the naked eye until 2 weeks after settlement (Knight & Parke, 1950).

The presence of a dispersive phase in the water column in the life cycle of *F. vesiculosus* provides a similar scenario to the barnacle settlement. This dispersive phase generates temporal, seasonal and regional variation in settlement densities. However, the dispersal is not generally as far as that found for barnacles, as the gametes are immediately viable. In fact often propagules are only transported a short distance from their parents (Deysher & Norton, 1982; Arrontes, 1993).

1.3.3 Growth

Growth is characterised by large variation in rates both within and between sites. Seasonal variation is found with slow to moderate growth rates in winter and spring and rapid growth in summer and autumn (Keser & Larson, 1984). A problem is found with a number of studies of growth where authors have assumed that the oldest plants were the longest(for example, Knight & Parke, 1950). In the first year increase in length seems to be uniform regardless of time of year settled (Keser & Larson, 1984). Some experimental growths rates can be seen in table 1.2. Dring (1982) gives relative growth rates of 0.015, 0.017 and 0.024 $g.g^{-1}.d^{-1}$ for high, medium and low shore *F. vesiculosus* respectively.

Table 1.2: Growth Rates for *F. vesiculosus*. (Source Keser & Larson, 1984)

Growth Rate	Location	Source
25-33$mm.mo^{-1}$	France	Lemoine (1913)
28$mm.mo^{-1}$	Great Britain	Knight & Parke (1950)
15-21$mm.mo^{-1}$	Maine. USA	Keser & Larson (1984)
6-10$mm.mo^{-1}$	Norway	Printz (1959)
16-32$mm.mo^{-1}$	Canada	Breton-Provencher *et al*(1979)

1.3.4 Mortality

There are data available for age-specific survivorship (see table 1.3 reproduced from Knight & Parke, 1950). Mortality is especially high when individuals are less than 3cm in length due to grazing pressure. Parke (1948) showed an exponential decline in the number of *Laminaria saccharina* plant almost to zero in a 24 month period. Mortality of large plants is higher in winter due to ice damage and storms (Keser and Larson, 1984). It is possible that different curves are applicable at different stages of development (see for example Gunhill, 1980). Despite knowledge that different curves are applicable, most studies are done using tagging methods which do not work on small individuals (Creed, 1993).

Table 1.3: The composition of *Fucus* populations in year classes on the Devon and Manx coasts. Reproduced from Knight & Parke, 1950, table VIII

	Population (%)		
Station	1^{st} year	2^{nd} year	3^{rd} year
Devon			
Normal population	100	57	17.3
Experimental Population	100	33.8	5.0
Isle of Man			
Normal population	100	30.8	10.0
Experimental Population	100	31.4	9.5

There have been numerous studies of survivorship and all types of curve have been found (see for example Chapman & Goudey, 1983; Santelices & Ojeda. 1984). Creed (1993) commented on the confusion in the interpretation of the different curves and cited Chapman (1986b) as an example. This is because arithmetic and logarithmic plots have been used by authors and should be interpreted in differently (Creed, 1993). Harper (1977) constructed depletion curves and from these Chapman (1986a) suggested that age-specific survivorship schedules cannot be constructed.

Partitioning mortality into its component sources is very difficult. Generally this is not attempted and the overall mortality rate is measured (Chapman, 1986b).

Chapter 2

A General Introduction to Modelling

2.1 What is Modelling?

In the last 20 years mathematics has increasingly become an integral part of biology as it becomes more quantitative. As a result biomathematical modelling is now utilised as a research tool with powerful, well developed techniques. However, it is not the miraculous technique that many believe can prove or disprove biological theory. This is because biology does not have rigid theory and thus mathematics cannot provide a complete solution on its own. The limitations of modelling must be recognised and techniques applied accordingly. For example, even if the dynamics produced by a model are exactly the same as the data set that it is tested against, this does not necessarily imply that the mechanism that predicts these dynamics is correct.

A 'good' model has the minimum number of parameters and still produces all the dynamics exhibited by the data set that it is tested against. This allows more analytical techniques to be used. Then inferences can be drawn about the mechanisms governing the system, which can be used to construct new hypotheses for the experimental biologists to test (Murray, 1993). These experiments will support or undermine the present biological theory. Thus, any model that stimulates experiments is successful, regardless of predicting the correct mechanisms. In fact modelling can be useful if the model is formulated with an appreciation and understanding of the biological problem; a realistic mathematical representation of the biological phenomena; finds useful qualitative solutions; and, most importantly, biological insight and predictions are formed from interpretation of the mathematical results (Murray, 1993).

Nisbet and Gurney (1982) suggested that there are 3 general types of model. These are:

1. **Tactical** - a model which yields accurate short term predictions.
2. **Strategic** - simple mathematical models that aim to identify ecological principles by asking the question "Could it happen?".
3. **Testable** - models of laboratory or field data.

2.2 Structured Population Models

Structured population models (SPMs) are models where individuals are divided into classes according to their state. Individuals are able to move between states and interact with individuals in other states, as well as responding to the birth-death dynamics. A clearly defined set of rules govern the transition between the compartments describing the births, deaths, immigration, emigration and interactions. These are written as either a system of difference or differential equations.

SPMs can be discrete or continuous (see section 2.3), deterministic or stochastic (see section 2.4) and may involve time delays. However, the more biological realism incorporated the more complex the model becomes, making analytical solutions harder or impossible to find. Simple models can have exact analytical solutions, but if not, simulation allows investigation of the model. The main way of investigating the dynamics of a deterministic model is by stability analysis. This analysis can be local or global. Local stability analysis is done by investigating the behaviour of an infinitesimally small perturbation from a steady state using local linearisation. The results of this analysis give the dynamics of a model as it approaches equilibrium. For example, it is possible to predict if an equilibrium is overdamped or underdamped and the long term behaviour of a solution, *ie* whether the solution is stable or unstable (see Gurney & Nisbet (*in press*) for a review of local stability analysis). The theory of global stability analysis is far less complete. Global stability analysis examines the stability of an equilibrium to a perturbation of any size. However, the mathematics required to do global stability analysis are complicated and can only be done for very simple models. An example of global stability analysis is found in Kuang & So (1995). Nisbet &

Gurney (1982) suggested that in many cases local stability analysis is sufficient as it will hold for larger perturbations.

2.3 Discrete and Continuous Models

Discrete models use an update rule that relates the future state to the current state of the system. This is done using difference equations which forecast the systems state at equal time intervals. The validity depends on the accuracy of the update rule and the precision of the initial conditions.

Continuous models use an update rule that relates the rate at which a system is changing using differential equations. They are able to forecast the state of a system at any point in time. However, when simulated a discrete approximation has to be used where a sufficiently small time-step is chosen, such that changing it does not effect the behaviour of the model.

SPMs can be discrete or continuous. One way of structuring a model is to split the individuals into classes of different age. This is known as an age-structured model. Discrete age-structured models use a time interval that is equal to the age-class width. This is important as it allows the distribution of a cohort to move through the age-structure without changing shape. Changing the age-class width in discrete time models can effect the behaviour of the model.

The classic demographic model, the Leslie matrix model (Leslie, 1945; 1948) gives rise to discrete age-structured models. Although the matrix notation is better for analysis, it is sometimes easier to view these models as a series of equations. If $n_{a,t}$ is the number in age-class a at time t, $S_{a,t}$ is the survivorship from age-class $a \to a + \Delta a$ in the time interval $t \to t + \Delta t$, and Δa and Δt are the age-class width and time interval respectively ($\Delta a = \Delta t$), then

$$n_{a+\Delta a,t+\Delta t} = S_{a,t} n_{a,t} \qquad (a > 0).$$

If $B_{a,t}$ is the individual fecundity in the interval $a \to a + \Delta a$ at time $t \to t + \Delta t$ then the renewal equation is

$$n_{0,t+\Delta t} = \sum_{all\ a} B_{a,t} n_{a,t}.$$

There is a similar argument in the construction of continuous time age-structured models. However, there are two problems. Consider what happens as $\Delta a \rightarrow 0$, this causes the number of age-classes to tend to infinity and $n_{a,t} \rightarrow 0$. The solution to this problem is to let density per unit age vary with time and age ($f(a,t)$) rather than numbers. The other problem is that it is difficult to obtain a function in continuous time for the aging process, as all individuals must age at the same rate and suffer mortality. The solution to the second problem is to use the McKendrick von Forester equation for continuous aging. This states that, if $\delta(a,t)$ is rate of mortality of an individual of age a at time t, then

$$\frac{\delta f}{\delta t} = -\frac{\delta f}{\delta a} - \delta(a,t)f(a,t).$$

If $\beta(a,t)$ is the rate at which offspring are produced, then the renewal condition is

$$f(0,t) = \int_{all\ a} \beta(a,t)f(a,t)da.$$

Simulation of continuous time models requires a discrete approximation to the continuous process, as the age-class width must be greater than zero. The age-class width is chosen so it is sufficiently small that changing the width does not affect the behaviour of the model. Simulation of the aging process is much more complicated than for discrete time models, as it requires implementation of the McKendrick von Forester equation. This can be done using a number of techniques, for example the escalator box cart method (see De Roos, 1989).

The choice of whether to use discrete or continuous models to examine the behaviour of a system is not easy and is fairly subjective. There are times when the choice is obvious, for example the automatic choice for modelling a system with discrete generations and constant mortality is a discrete model. Usually a tradeoff is found. The computational power required to simulate a continuous time model is far greater than the analogous discrete time model. This is because of having to use an implementation of the McKendrick von Forester equation. However, this ease can only be justified if the model is easy to analyse (as analyses of discrete models is more difficult) and carefully formulated. Discrete models must be formulated carefully as it is easy to incorporate artifactual dynamics not found in the continuous model. This is especially problematic when one of the processes is not constant in continuous time. For example, density-dependent mortality is not a constant death process and could cause a discrete formulation to be non-viable. If a model is required for a system with overlapping generations of several species, then all the processes are in continuous time. At this stage the choice is a matter of convenience and personal preference. Again the formulation of these types of models in discrete and continuous time must be careful, as they must represent the same model. The discrete form of the model may not be a direct analogy to the continuous form, for example see discrete and continuous form of the logistic described in Nisbet & Gurney (1982). The forms are not analogous when there is no analytic solution to the continuous time model.

Neither the discrete nor continuous formulation of any model has been more successful in the literature. Thus, the choice of discrete or continuous time age-structured model is largely dictated by the nature of the problem and personal preference. For a full description of discrete and continuous age-structured models see Chapters 2 and 7, Gurney & Nisbet (*in press*).

2.4 Deterministic and Stochastic Models

Deterministic models produce the same dynamics when the same parameter sets are used. The phrase comes from the Greek philosophical doctrine of determinism that states "...all events including human actions and choice are fully determined by preceding events and states of affairs, so that freedom of choice is illusory".

A stochastic process is the basis of a stochastic model and is defined as "...involving a random variable successive values of which are not independent". Stochastic models are based upon probabilistic rules that make use of pseudo-random numbers. These pseudo-random numbers are used to determine events occurring at time points in the future generated by the current state of the system. A number of simulations are done to produce a sample, which is analysed statistically to give a single trajectory with limits. The use of the pseudo-random numbers is supposed to mimic the random fluctuations in nature and determine the consequences of rare events that would not be predicted by deterministic models.

Both stochastic or deterministic models must be used to gain the maximum knowledge about the system being modelled. In fact, Renshaw (1993) stated that "...slavish obedience to one technique can lead to disaster".

Deterministic models are supposed to produce the 'average' trajectory of the stochastic sample. This is not always the case. If the model has high population numbers, then deterministic models may enable sufficient knowledge to be gained about a system (Renshaw, 1993). However, if the population becomes close to extinction then stochastic analyses are essential (Renshaw, 1993).

Analysis of stochastic models is far more complicated than deterministic models. In fact, stochastic models have to be very simple for any analyses to be done. Thus, only simulation can be used to investigate many models, which makes the mechanism driving dynamics more difficult to understand. This suggests that there is a possible tradeoff between deterministic and stochastic models. If population numbers are not close to extinction then deterministic models can be used in preference. However, when the population comes close to extinction there is a tradeoff between the knowledge gained from stochastic models and lack of analysis.

2.5 Thesis Outline

There are a number of objectives of this project. The main objective is to build and understand the behaviour of sub-models of the system found on the moderately exposed shore at Port St. Mary, Isle of Man (see figure 1.2). Once the dynamics of the simple cases of the deterministic single species models are understood, then reassess the assumptions of the model and look at the behaviour of these sub-models with slightly more realistic assumptions. These sub-models will then be joined to produce a model of two interacting species.

In Chapter 3 a discrete time age-classified model of the colonisation of bare rock by the barnacle, *S. balanoides*, in a constant environment is examined. This model is a variant of the one produced by Roughgarden *et al* (1985), which assumes an open system with space-limited recruitment. The behaviour of the model with both linear and logistic growth is investigated using steady states, various stability criteria and simulation.

In Chapter 4 a similar model of the colonisation of bare rock by *F. vesiculosus* in a constant environment is constructed. However, a discrete time size-classified model is used, as seaweeds have plastic growth, and assumes an open system with space-limited recruitment. The dynamics of the model are examined using steady states, local stability and simulation. An attempt was made to parameterise the model of *F. vesiculosus* from the literature and the dynamics are re-examined.

In Chapter 5 the most advanced cases of the models produced in Chapters 3 and 4 are examined in a seasonal environment. This is done by incorporating distinct settlement periods into the models. As propagules of *F. vesiculosus* remain viable for a time after production, the presence of a seed bank is assumed, in a similar way to that found in terrestrial systems. Phase locking as a possible mechanism for the behaviour of the solutions is investigated. Different lengths of settlement period are used to look at variation in settlement strength.

In Chapter 6 the size-classified model of *F. vesiculosus* and the age-classified model of *S. balanoides* are combined to produce a two species model. This discrete time model assume that *F. vesiculosus* inhibits *S. balanoides* settlement and that *S. balanoides* enhances the settlement of *F. vesiculosus.* The model is parameterised between limits using values from the literature, in order to target simulation. The dynamics are investigated using simulation. The model is then fitted to limits suggested for the cycle at Kallow Point, Port St. Mary, Isle of Man.

In Chapter 7 the main findings of each of the models are reviewed and the biological inferences are re-examined. I also suggest additions to the model that will make the dynamics of the models produced more realistic, problems with the data sets used and where this fits into current research.

2.6 Techniques

So far in this Chapter we have considered a few of the many possible modelling techniques. In Section 2.5 the thesis outline only describes the use of one general category of model, this is a deterministic structured population model with space-limited recruitment. In this section we ask ‘Why use only this particular type of models?’. The answer to this question hinges on 2 main factors. Firstly, what these models will be used for and the training behind this M.Phil.. Secondly, the tradeoff between which models incorporating the most biological realism (and thus more complex) and the ability to understand the dynamics (De Roos, 1989).

The future of these models has to be considered before a discussion of the techniques can occur. This project has been used as a starting point for a biologist who was interested in learning modelling from the mathematicians point of view. Thus, an investigation of the basic techniques was required. May (1976) states

> "There are many situations, in many disciplines, that can be described, at least to crude first approximation, by a simple first-order difference equation. Studies of dynamics usually consist of finding constant equilibrium solutions, and then conducting a linear stability analysis to determine their stability with respect to small disturbances..."

As knowledge of some of the basic techniques of mathematical modelling was required this seemed as good a place as any to start. And anyway, as a biologist, who am I to argue with Professor May!

The second influence on my choice of model was making simple single species models, so that the mechanism driving the dynamics could be understood completely. These single species models were going to be used as sub-units in 3 species spatially explicit models, as part of my Ph.D. thesis, to model the cycle found at Port St. Mary, Isle of Man (see figure 1.2). However, to understand the mechanisms that drive these complicated models, it is necessary to understand completely the behaviour of each of the individual sub-units.

The models used in this thesis are deterministic. They are described as discrete, structured open populations models with space-limited recruitment. Therefore we have to ask whether a different approach would have been better for what is required.

2.6.1 Why Use Discrete Models?

The choice of discrete or continuous models is not simple and is often subject, *ie* due to personal preference and convenience. However, there are advantages and disadvantages of using discrete models. Discrete models require far less computational power to do simulations than continuous models. This is because continuous time models require a special function to implement structure. However, discrete models are much harder to analyse and require care when formulating. In fact if formulated incorrectly, a discrete time model can produce artifactual dynamics not found in the analogous continuous model.

In this thesis computation ease is essential. This is because the model produce in this thesis are going to be used as sub-model in a 3 species spatial model with stochastic recruitment functions. A continuous model would require a large amount of computation power to do this as a spatial and aging function would have to be used (Steele, 1993).

The models produced in this thesis are not particularly complicated. Thus, the difficultly of analysing discrete models is not a problem. This simplicity makes formulation without the addition of artifactual dynamics easy. Thus, in this case it is important to keep the computational power to a minimum by using discrete models.

Adding detail to discrete models is far more intuitive than to continuous models. This is important in this thesis as models are designed and their mechanisms are tested. Once understood, extra features are added to the model to increase the biological realism. De Roos (1989) stated that discrete models are often the obvious choice in biology as they are developed from demography. In this thesis, I investigate the demography of different species which makes discrete modelling an obvious choice.

For this thesis it appears that discrete models are the obvious choice as the models used are not too complicated. This allows formulation and analysis to be done easily and computational power to be reduced. However, the models have to be sufficiently complicated to produce a wide enough range of dynamics to mimic the system. This is not a problem even with linear discrete models. May (1976) stated:

> "First order difference equations arise in many contexts in the biological, economic and social sciences. Such equations even though simple and deterministic can exhibit a surprising array of dynamical behaviour, from stable points to a bifurcating hierarchy of stable cycles, to apparently random fluctuations. There are consequently fascinating problems, some concerned with delicate mathematical aspects of the fine structure of trajectories and some concerned with the practical implications and applications".

2.6.2 Why Use Structured Population Models?

Traditional population models use densities as their state variables. This type of model has been criticised for many different reasons. For example, unrealistic dynamics (Judson, 1994); ignoring the difference between individual organisms; and interactions between individuals only take place locally (Gross, 1986).

Structuring populations using a state variable such as age, size or stage produces a model that has less unrealistic dynamics and treats individuals in the same class as identical. This is a slightly less unrealistic from the biological point of view.

The alternative to using a structured population model is to use a physiologically structured individual based model (PSIBM). This treats all individuals within the population as different and keeps a track of each. Thus, increasing the biological realism. However, again there is a tradeoff between realism (complexity) and understanding. In this thesis there are a number of problems associated with using PSIBMs.

The time required to simulate a three species PSIBMs would become a factor when the model becomes spatially explicit. The simulations would take a long time and require large computational power.

Parameterisation of these models would not only be very difficult as the demographic rates of the species tend to be measured as an average. The standard errors associated with this model would be very large because of the large number of parameters associated with the model. The large number of parameters in the model would make the mechanism much more difficult to understand and increase the number of simulations required to investigate the parameter set. A tradeoff between realism (complexity) and understanding is sought. However, understanding is more important at this stage.

Last but by no means least the aim of this project is to produce a model that produces hypotheses for the experimentalists to test. The PSIBMs would no doubt be better predictors of the single species community, but we are interested in looking mechanistically at a moderately exposed rocky shore. Understanding the mechanism controlling the dynamics of a three species PSIBM would be very difficult as the number of parameters would be large. PSIBMs would make the production of hypotheses for the experimentalists to test very difficult. Thus we choose a structured population model.

2.6.3 Why Use Deterministic Models?

It is stated in this chapter that neither deterministic nor stochastic models should be used alone. These models should be used in unison. However, within the time scale allowed by this M.Phil. it was not possible to produce any stochastic versions of the models. So, the absence of stochastic models from this thesis is not due to choice, rather due to time limitation. However, as part of my Ph.D. thesis the effect of adding stochastic recruitment functions to the models will be investigated. From this inferences will be drawn about the relative roles of stochastic events and deterministic processes in the rocky intertidal communities.

2.6.4 Why Use Open Models with Space limited Recruitment Models?

The species that are modelled in this thesis are sessile with a pelagic eggs or larvae. The sessile adult populations have great spatial and temporal variation. Offspring are not always part of the same population as their parents (Roughgarden *et al*, 1985). Thus, Lotka-Volterra models cannot be produced for this process as the populations are not closed. Migration can be added to the Lotka-Volterra type models, but this assumes that migration is slight relative to the number of recruits. Whereas, settlement into the system from outside is the major form of settlement in systems such as these.

Open populations cannot become closed simply by enlarging the area studied. For example barnacle larvae may spend up to six weeks in the plankton before they are able to settle, during which time currents may move the juveniles long distances from their parents. The larvae can then land anywhere, they do not just migrate across the perimeter of the model, but settle anywhere in the system from the water column. If we then consider a situation where the model is spatially explicit, then the Lotka-Volterra even with migration is a useless description of this population, as individuals do not just migrate over the perimeter. Thus, we have to use a model of an open system.

Space is obviously the limiting resource in the rocky shore environment. Traditional population models do not model the nature of the resource explicitly. However, in this system the amount of space occupied dictates the number of new individuals that are able to settle. Thus, for a rocky shore environment we require a model with theory that explicitly treats the capture and release of space to attach. Roughgarden *et al* (1985) produced a model for open systems with space-limited recruitment, including the settlement of larvae being proportional to the available space, and the subsequent growth and mortality of these larvae. They suggested that the model is not meant as a literal description of a barnacle dominated shore but offers a picture of what happens when space dependent settlement, growth and mortality all occur at the same time.

As these are the major processes occurring on a rocky shore anywhere in the world this type of model appeared to be the correct choice for each of the single species models.

Part II

Single Species Models

Chapter 3

An Age Structured Model for the Colonisation of Bare Rock by the Barnacle *Semibalanus balanoides*

3.1 Introduction

3.1.1 Age-Classified Demographic Models

Classical demographic analysis is based on a system of tabulating age-specific survivorship and reproduction into a 'life table'. The original demographic analysis was done by Lotka (1924). However, matrix models for demographic analyses were not developed until the 1940s. This type of model was proposed simultaneously by Bernardelli (1941), Lewis (1942) and Leslie (1945, 1948). The most influential of these authors was Leslie. Matrix notation for demographic models was not adopted until the late 1960s by demographers and until the 1970s by ecologists (Caswell, 1989). Lefkovitch, Pennycuik, Rabenovich, Usher and Williamson were the pioneers of this technique before the 1970s.

Barnacles have a sessile adult stage and pelagic larvae. These populations cannot be modelled usefully using either the logistic or Lotka-Volterra equations of population theory (Roughgarden *et al*, 1985). Adults are sessile and live in a closed region. However, their larvae are free moving, spending up to 6 weeks in the plankton and can settle great distances from their parents. Thus, recruitment to the population is not closed and cannot, in principle, be made closed simply by enlarging the area (Roughgarden *et al*, 1985). Free space is the limiting resource and should be explicit in the model, as larvae are unable to settle without it. Settlement rates into these populations can be high resulting in large changes in population size over the lifespan of an individual. In these circumstances, construction of a reasonable model must take account of the structure of the population (see Caswell (1989) for a review of the theory). Hence, to model a barnacle population successfully we need to use an age-structured demographic model with space-limited recruitment (Roughgarden *et al*, 1985; Roughgarden & Iwasa, 1986; Bence & Nisbet, 1989; Kuang & So, 1995;).

The theory of open systems and of metapopulations of locally open systems has developed quickly in the last fifteen years. For example, Chesson and Warner (1981), Roughgarden *et al* (1984), Iwasa & Roughgarden (1985), Roughgarden *et al* (1985), Iwasa & Roughgarden (1986), Roughgarden *et al* (1987), Possingham & Roughgarden (1990) and Kuang & So (1995). Roughgarden *et al* (1985) used this theory to produce a model which is appropriate for an open, age-structured population with space-limited recruitment. Two forms of dynamics were produced by the model: a stable steady state and cyclic fluctuations. A steady state is produced when settlement is low and a stable distribution of mixed cohorts and free space is found. Cyclic fluctuations are produced when settlement is high and an unstable mosaic of cohorts and occasional free space is found. The mechanism suggested for the instability is that growth interferes with recruitment when settlement is sufficiently high. Possibly the most important mechanism of this type of model is the relationship between the growth and mortality functions. The occupied area will increase if the increase in area due to growth and settlement is greater than the loss of area due to the mortality of individuals and *vice versa*. A steady state is produced when the mortality and the growth and settlement are in balance, *ie* when the net area of the population neither increases nor decreases.

Bence & Nisbet (1989) re-examined the dynamics of simplified versions of the Roughgarden *et al* (1985) model, their most complicated models being special cases of Roughgarden's model. They noted that the model proposed by Roughgarden *et al* (1985) offers insight into any system where there is debate on whether populations are regulated by recruitment or density-dependent factors. For example, reef fish (Mapstone & Fowler, 1988) and giant kelp (Nisbet & Bence, 1989). Their conclusions were similar to Roughgarden *et al* (1985). However, as their formulation was simple, they were able to highlight the biological processes that produce the interesting dynamics and suggested that not all the inferences of Roughgarden *et al* (1985) are correct. Bence & Nisbet (1989) found the two population states, cyclic fluctuations in population density and a stable steady state.

The mechanism proposed to produced cyclic fluctuations is a time delay between settlement and recruitment to the adult population. Two types of growth are considered: determinate and indeterminate. Determinate growth is found when adults reach a maximum size and growth ceases. Indeterminate growth is destabilising (see the numerical examples presented by Roughgarden *et al* (1985)). However, when growth is determinate, there is a time delay between settlement and attaining the maximum size. Faster maturation from juveniles to adults results in a shortening of this lag allowing increases or decreases in growth to be stabilising. This result does not depend on representing the size-distribution as two discrete stages.

Kuang & So (1995) performed a global stability analysis of the delayed two stage population model proposed by Bence & Nisbet (1989). They established conditions for persistence of the system, local and global stability of the positive equilibrium. They concluded that the increasing the settlement or area occupied by an adult destabilises the model globally. However, increasing the mortality of adults or juveniles or the time delay stabilises the model globally. They inferred that the large amplitude cycles could be controlled in nature by harvesting, *ie* increasing the mortality.

Roughgarden & Iwasa (1986) extended their model to a metapopulation model with space-limited sub-populations. Larval settlement is again onto vacant space and each sub-population contributes to the common pool of larvae. The metapopulation is assumed to be closed even though each of the sub-populations is open. The metapopulation model has several simultaneous stable steady states, which lead to thresholds such that an introduced population may not become established unless the propagule size exceeds the threshold value.

Possingham & Roughgarden (1990) extended the model of Roughgarden *et al* (1985) to include spatial dimensions for both adults and larvae. This was done by integrating mesoscale features in ocean current with coastal habitat structure in an attempt to predict adult distribution.

These models described are still a massive simplification of the system described but have potential to support more detailed models of a population where space, light, rainfall or territory are limited (Kuang & So, 1995). This slow building of models has considerable potential for improving the understanding of such ecological systems (Bence & Nisbet, 1989).

3.1.2 Modelling Aims

As competition on the rocky shore is essentially for the resource of space, two dimensional models can be constructed. The aim of this chapter is to produce a general model for intertidal barnacles with space-limited recruitment. This discrete time model will be based on the concept of individuals filling up area as proposed by Roughgarden *et al* (1985).

Once the analyses of the general model are done, then linear growth will be implemented to investigate the dynamics of this model. The model will be applied to *S. balanoides* using a logistic growth function and the dynamics re-examined. This will be used to model stage six to stage two in the cycle shown in figure 1.2.

3.2 An Age-Structured Model for Intertidal Barnacles

In this section we look at a general model for intertidal barnacles space-limited recruitment.

3.2.1 The Model

The model used is developed from Roughgarden *et al* (1985) discrete time model. The model makes a number of assumptions:

1. All individuals of the same age are the same area.
2. Larvae are found in the surrounding water.
3. Larvae occupy free space, and the number landing increases as a function of free space.
4. Free space cannot be negative.
5. All recruits are the same area.
6. There is a known area at age for the barnacles.
7. The survivorship function is known and time independent.

The population is divided up into $N+1$ age-classes of equal width, Δa, and the time interval, Δt, is equal to the age-class width. In each of these age-classes individuals have the same area, a_i, measured in m^2. If $n_{i,t}$ is the number of individuals in age-class i at time t, then the total area occupied at time t, A_t, is

$$A_t = \sum_{i=0}^{N} a_i n_{i,t} \tag{3.1}$$

Free space at time t, F_t, is a function of the total available space (m^2), A, and is expressed as

$$F_t = (A - A_t)^+ \tag{3.2}$$

where the + denotes that free space cannot be negative. If the number of barnacles in age-class i at time $t + \Delta a$ is $n_{i,t+\Delta a}$, and S_{i-1} is the survivorship at age $i - 1$, then

$$n_{i,t+\Delta a} \quad = \quad S_{i-1} n_{i-1,t} \qquad i = 1, 2, \ldots, N. \tag{3.3}$$

All of the individuals of age greater than $N\Delta a$ days die. Thus, no individuals survive further than the final age-class. Age-class 0 presents a different problem. If we define I_t as the settlement function then,

$$n_{0,t+\Delta a} \quad = \quad I_t. \tag{3.4}$$

Thus, equations (3.1) - (3.4) describe the population. As we are unlikely to know the total available area, A, it is more useful to look at this problem in terms density of organisms per m^2. If equations (3.1) - (3.4) are divided by A then the population can be modelled using

$$\begin{aligned}
\hat{F}_t &= \frac{F_t}{A} = \left[1 - \sum_{i=0}^{N} \rho_{i,t} a_i\right]^+ && (3.5)\\
\rho_{i,t} &= \frac{n_{i,t}}{A} = S_{i-1}\rho_{i-1,t} \qquad i = 1, 2, \ldots, N && (3.6)\\
\rho_{0,t+\Delta a} &= \frac{I_t}{A} = \hat{I}_t && (3.7)
\end{aligned}$$

where $\rho_{i,t}$ is the density of individuals in age-class i at time t ($numbers.m^{-2}$).

The Settlement Function

Settlement per time unit cannot increase without bound. As barnacles settle in the system, they occupy space and thus reduce the space available for future settlers. If the rate at which cyprids become available to settle from the water column $m^{-2}.d^{-1}$ (κ) is low, the amount of space occupied by settlers early in the time-step is small, and thus incremental settlement $\hat{F}_t^{-1}.\Delta a^{-1}$ (σ) is unaffected. However, when κ is high, a large proportion of the space is occupied by early settlers and thus, the incremental settlement is much lower than expected from the number of cyprids available to settle. The rate of change of settlement over time can be described by a differential equation. If R is the barnacles that have already settled into the system and occupy space, then

$$\frac{dR}{dt} = \kappa\left(F(t_0) - a_0 R\right) \tag{3.8}$$

where $F(t_0)$ is the free space at time t_0 and $a_0 R$ is the area occupied by what has already settled. If equation (3.8) is solved over time (t), then,

$$R(t) = \frac{F(t_0)}{a_0}\left(1 - e^{-\kappa a_0 t}\right) \tag{3.9}$$

The discrete analogy to equation (3.9) is

$$\sigma \hat{F}_t = \frac{\hat{F}_t}{a_0}\left(1 - e^{-\kappa a_0 \Delta a}\right). \tag{3.10}$$

If κ and σ are calculated for set parameters, then an asymptotic relationship is produced (see figure 3.1). The relationship is linear at low values, but as $\kappa \rightarrow \infty$ then $\sigma \rightarrow \sigma_{max} = 1/a_0$.

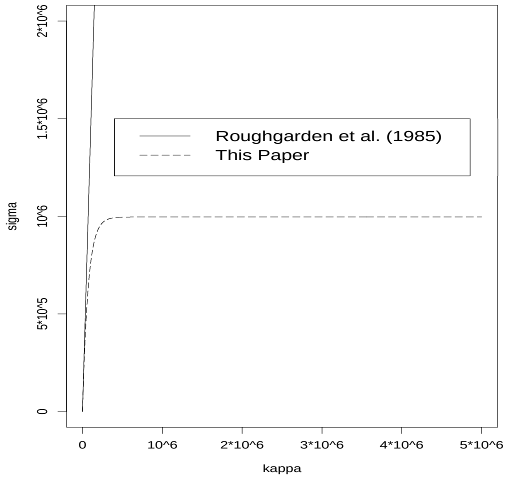

Figure 3.1: The relationship between σ and κ.

This function allows us to define the settlement function $\hat{I}_t$. As settlement is space-limited then,

$$\hat{I}_t = \sigma \hat{F}_t = \frac{\hat{F}_t}{a_0}\left(1 - e^{-\kappa a_0 \Delta a}\right). \tag{3.11}$$

Roughgarden *et al* (1985) use a different settlement function which assumes that settlement can increase without bound. This gives spurious solutions and a comparison of the two functions can be seen in figure 3.1. As can be seen at low daily instantaneous settlement rate the incremental settlements are similar. However, at high daily instantaneous settlement Roughgarden *et al* (1985) settlement function gives far greater incremental settlement than our settlement function.

3.2.2 Steady States

At equilibrium there is no variation over time. Let

$$\begin{aligned}
\rho_{i,t+\Delta a} &= \rho_{i,t} &&= \rho_i^* \\
\hat{F}_{t+\Delta a} &= \hat{F}_t &&= \hat{F}^* \\
\hat{I}_{t+\Delta a} &= \hat{I}_t &&= \hat{I}^* \\
A_{t+\Delta a} &= A_t &&= A^*
\end{aligned}$$

If these steady state variables are substituted into (3.5) - (3.7) and (3.11), with a little simple algebra the equilibrium conditions are

$$\hat{F}^* = \frac{1}{1 + \sigma \sum_{i=0}^{N} l_i a_i} \tag{3.12}$$

$$\rho_i^* = \sigma l_i \hat{F}^* \tag{3.13}$$

where the survivorship function, l_i, is defined

$$l_i = \prod_{i=0}^{i-1} S_i \qquad (\text{where } \; l_0 = 1). \tag{3.14}$$

It is useful to note that from equation (3.12) increasing either κ, a_i, or S will increase the value of A^*. Similarly increasing the area function, increases the value of $\hat{F}^*$. It is possible to look at two sets of conditions. If space filing is fast, *ie* $\kappa a_0 \Delta a \rightarrow 1$, then $\sigma \rightarrow 1/a_0$ and

$$\rho_i^* \approx \frac{l_i}{\sum_{i=0}^{N} l_i a_i}. \tag{3.15}$$

This suggests that the equilibrium age-class density varies independently of settlement and that settlement does not limit the equilibrium densities. However, if space filing is slow, *ie* $\kappa a_0 \Delta a \rightarrow 0$, then $\sigma \rightarrow 0$ and

$$\rho_i^* \approx \sigma l_i. \tag{3.16}$$

Thus, equilibrium age-class density is directly proportional to settlement and settlement limits the equilibrium densities.

3.2.3 Local Stability Analyses and the 50% Free Space Rule

Local Stability Analysis

Local stability analysis is done by examining the behaviour of a perturbation from equilibrium. If the perturbation grows then the equilibrium is unstable, if it decays then the equilibrium is locally stable. The behaviour of a perturbation is described by the roots of the characteristic equation, λ, or the eigenvalues. If all the eigenvalues lie within the unit circle, *ie* $|\lambda| < 1$, then the perturbation will decay back to the equilibrium and the equilibrium is locally stable. It is useful to note that local stability analysis assumes an infinitesimally small perturbation. However, it many cases it will hold for larger perturbations (see Nisbet & Gurney, 1982).

The first step in stability analysis is to derive the characteristic equation. This is done by defining a perturbation, $\delta_{i,t}$, from age-class i at time t and then looking at its behaviour over time. Thus,

$$\delta_{0,t+\Delta a} = \hat{I}_t - \hat{I}^* \tag{3.17}$$

$$\delta_{i,t+\Delta a} = S_{i-1}\delta_{i-1,t} \tag{3.18}$$

where,

$$\hat{I}_t - \hat{I}^* = -\sum_{i=0}^{N} \sigma a_i. \tag{3.19}$$

Equations (3.17) - (3.19) can be expressed in matrix form, where,

$$\delta_{t+\Delta a} = \mathrm{B}\delta_t$$

and

$$\mathrm{B} = \begin{bmatrix} -\sigma a_0 & -\sigma a_1 & -\sigma a_2 & \cdots & -\sigma a_N \\ S_0 & 0 & 0 & \cdots & 0 \\ 0 & S_1 & 0 & \cdots & 0 \\ \vdots & & & & \vdots \\ 0 & 0 & \cdots & S_{i-1} & 0 \end{bmatrix}, \qquad \delta_t = \begin{bmatrix} \delta_{0,t} \\ \delta_{1,t} \\ \delta_{2,t} \\ \vdots \\ \delta_{N,t} \end{bmatrix}.$$

The characteristic equation is found by considering $det(\mathrm{B} - \lambda \mathrm{I}) = 0$, where I is the identity matrix. Considering the minors gives

$$f_i(\lambda) = \det \begin{bmatrix} -\sigma a_0 - \lambda & -\sigma a_1 & -\sigma a_2 & \cdots & -\sigma a_N \\ S_0 & -\lambda & 0 & \cdots & 0 \\ 0 & S_1 & -\lambda & \cdots & 0 \\ \vdots & & & & \vdots \\ 0 & 0 & \cdots & S_{i-1} & -\lambda \end{bmatrix} \tag{3.20}$$
$$\text{(where } i = 0, 1, 2, \ldots, N)$$

Developing the last column of (3.20), we get the iterative equations

$$f_i(\lambda) = (-\lambda) f_{i-1}(\lambda) + (-1)^i (-\sigma a_i l_i) \quad \text{(where } i = 1, 2, \ldots, N) \tag{3.21}$$

and

$$f_0(\lambda) = -\sigma a_0 - \lambda. \tag{3.22}$$

From these the characteristic equation is

$$\begin{aligned} \det(\mathrm{B} - \lambda \mathrm{I}) &= f_N(\lambda) = 0 \\ &= (-1)^{N+1}\left(\lambda^{N+1} + \sigma a_0 l_0 \lambda^N + \sigma a_1 l_1 \lambda^{N-1} + \ldots + \sigma a_N l_N\right) = 0, \end{aligned} \tag{3.23}$$

or

$$\lambda^{N+1} + \sum_{i=0}^{N} \sigma a_i l_i \lambda^{N-i} = 0. \tag{3.24}$$

The 50% Free Space Rule

The net area function, $l_i a_i$, is the size of an individual after i age-classes in the system. It has an important role in the system. The area controlled by a settler cumulated throughout its life is give by

$$A_0 = \sum_{i=0}^{N} l_i a_i. \tag{3.25}$$

If there is an eigenvalue, λ_0, such that the steady state is unstable, then $|\lambda_0| \geq 1$. If equation (3.24) is divided by λ_0^{N+1}, with a little simple algebra

$$\begin{aligned} 1 &= \left|\sum_{i=0}^{N} \frac{\sigma a_i l_i}{\lambda_0^{i+1}}\right| & (3.26) \\ &\leq \sum_{i=0}^{N} \sigma a_i l_i = \sigma A_0. & (3.27) \end{aligned}$$

From equation (3.12) we know that

$$\hat{F}^* = 1/\left(1 + \sigma A_0\right). \tag{3.28}$$

From equation (3.27) we have shown that $\sigma A_0 \geq 1$. This implies that $\hat{F}^* \leq 0.5$. Therefore, if λ_0 is such that the steady state is unstable, then $|\lambda_0| \geq 1$ and $\hat{F}^* \leq 0.5$. However, if $\hat{F}^* > 0.5$ then all eigenvalues lie within the unit circle.

3.2.4 Numerical Techniques

A number of packages were used to investigate this model. The steady states were assessed using Splus (©1989, 1991 Statistical Sciences, Inc.). This package was also used for any data manipulation and curve fitting.

The characteristic equation and 50% free space rule were modelled using CONTOUR which is part of the SOLVER suite of programs (©1994, STAMS, University of Strathclyde, Glasgow, G1 1XH, Scotland). This uses the Newton-Raphson technique to follow the roots of equations. The implementation used has 125 age-classes, *ie* from age-class 0 to 124. From equation (3.24) the characteristic equation is

$$\lambda^{125} + \sum_{i=0}^{124} \sigma a_i l_i \lambda^{N-i} = 0. \tag{3.29}$$

The roots of this characteristic can be either real or complex. The boundary condition for an equilibrium to be locally stable is $|\lambda| = |x + iy| = \sqrt{x^2 + y^2} < 1$. This is to say that the eigenvalues of all the roots lie within the unit circle. Thus, the stability boundary of the model is where $\sqrt{x^2 + y^2} = 1$. If this boundary is traced it is possible to look at the stability of the model with varying S and κ.

Simulation was done using a program called ITERATOR which is also part of the SOLVER suite of programs (©1994, STAMS, University of Strathclyde, Glasgow, G1 1XH, Scotland). This is used to find the numerical solution of difference equations. We assume that the maximum age that a barnacle can reach is about 5 years. Thus, we take $\Delta a = 14$ days and $N = 124$.

3.3 Linear Growth

In this section we look at the general model of intertidal barnacles using simple indeterminate linear growth and constant survivorship to investigate the dynamics of the model.

3.3.1 The Linear Growth Function

The increase in area function is a simple linear increase with age and is described by the equation:

$$a_i = \alpha(i+1) \tag{3.30}$$

where α is the linear growth coefficient. The maximum size attained using each of the growth functions can be seen in table 3.1. The maximum area of a barnacle increases with decreasing shore height (Stubbings, 1975). The maximum diameter being about $26mm$ on submerged panels (Barnes and Powell, 1953). 'Fast', 'average' and 'slow' growth rates are examined (see table 3.1). These were calculated assuming that a circular barnacle grows linearly until reaching its maximum size in age-class 124 from an initial size of α. From these growth functions it is possible to calculate the maximum incremental settlement or σ_{max}.

Table 3.1: Linear growth functions.

Growth Function (α)	Maximum length mm	Maximum area mm^2	Shore Level	σ_{max} $(1/a_0)$
$4.2474 * 10^{-6}$	26	531	Submerged	235438
$1.6085 * 10^{-6}$	16	201	Mid	621697
$6.2832 * 10^{-7}$	10	78.5	High	1591546

3.3.2 Steady States

There is a logistic increase in the area occupied, A^*, with increasing age independent survivorship (S) and κ (see figures 3.2 and 3.3 respectively). In both cases, a higher growth rate causes increased occupancy (A^*). Intuitively this makes sense as fewer individuals are required to occupy the same space.

At both high and low instantaneous settlement rate the age-distributions are similar. The density of individuals in an age-class decreases with increasing age (see figures 3.4 and 3.5). Although the densities decrease with age the maximum space occupied is found at an age of 266 - 280 days (age-classes 19 and 20).

Figures 3.4 and 3.5 are very similar despite the difference in the settlement rate. This is because the density decreases at a constant rate from an initial value calculated from the settlement rate. The higher the settlement rate the higher the density observed. When the survivorships are equal the density curves will decrease at the same rate producing the same shape. The linear growth functions in the figures 3.4 and 3.5 are the same. The occupancy is calculated by multiplying

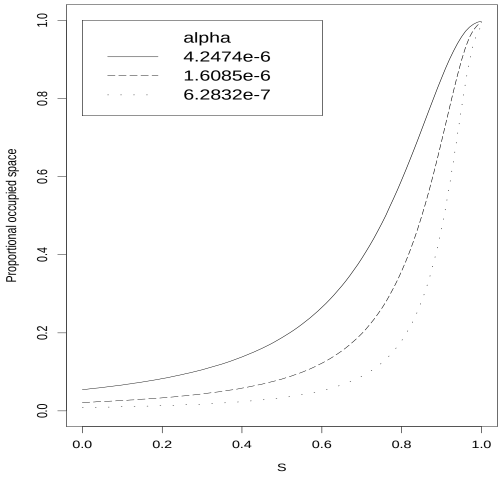

Figure 3.2: The effect on A^* of varying S with different growth functions ($\kappa = 1000$).

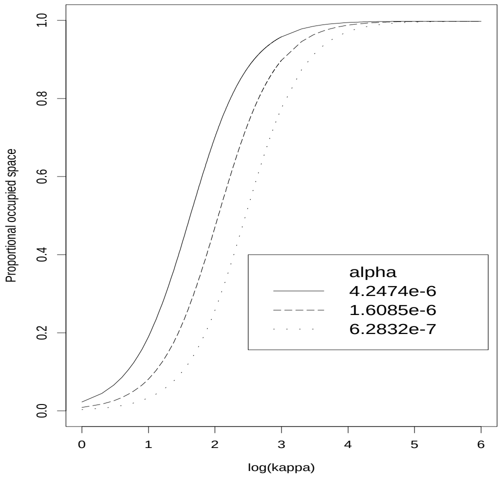

Figure 3.3: The effect on A^* of varying κ with different growth functions ($S = 0.95$).

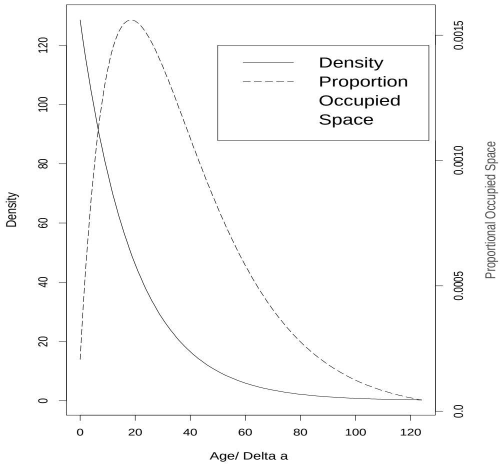

Figure 3.4: Densities and proportional occupied space for different ages ($S = 0.95$, $\kappa = 10$, $\alpha = 1.6085 * 10^{-6}$).

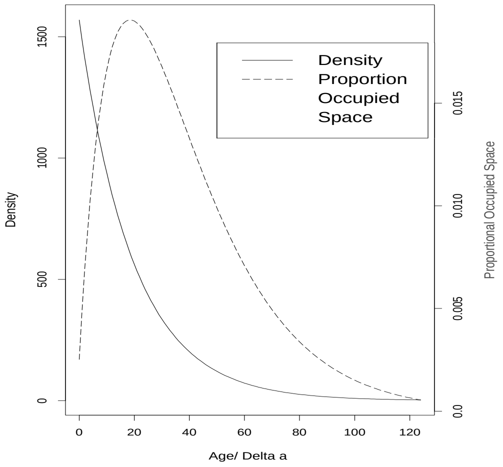

Figure 3.5: Densities and proportional occupied space for different ages ($S = 0.95$, $\kappa = 10^6$, $\alpha = 1.6085 * 10^{-6}$).

the area at age by the density. Thus, multiplying a linear function by a constantly decreasing function gives the humped curve for occupancy. As these two curve are the same shape for the parameters used, then the curve produced is the same shape. However, because the settlement rates are very different, the densities and occupancy are different.

3.3.3 Stability

The stability boundary and the 50% free space rule illustrate that increasing either S or κ is destabilising (see figures 3.6 and 3.7). Decreasing the growth rate α increases the stability of the model in both cases. This is because more individuals are required to fill up the area, and once the individuals settle space is filled at a slower speed.

The stability predicted by the 50% free space rule is far lower than that obtained by local stability analysis. This is because the 50% rule is a sufficient but not necessary condition for stability and thus is a bad approximation to the local stability analysis. The approximation becomes worse with increasing κ.

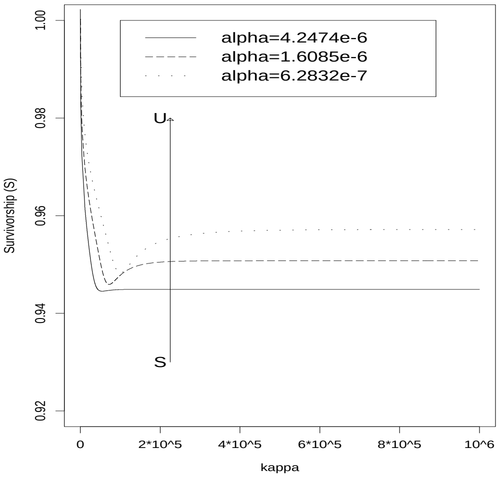

Figure 3.6: Stability boundaries for different linear growth functions where S = stable and U= unstable.

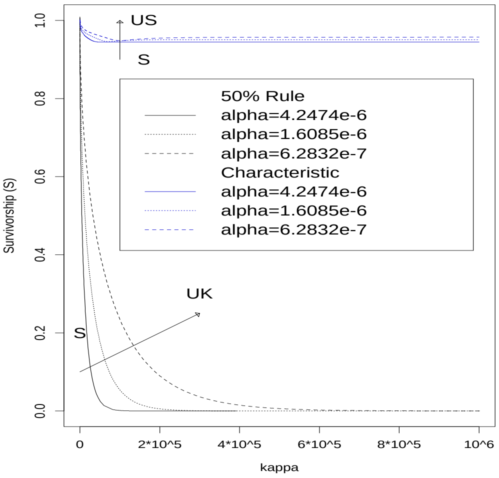

Figure 3.7: 50 % free space rule and local stability boundaries for different linear growth functions where S = stable, US=unstable and UK= unknown.

3.3.4 Simulation

Numerical simulations of the model showed that with this basic model there are a number of results. Reducing S increases the speed of reaching the steady state. Examples of stable and unstable solutions of the linear growth model are shown in figures 3.8 and 3.9 respectively.

An unstable age-distributions is shown in figure 3.10. In this case, cohorts are seen to age until they die, causing rapid freeing of space for new settlement. This

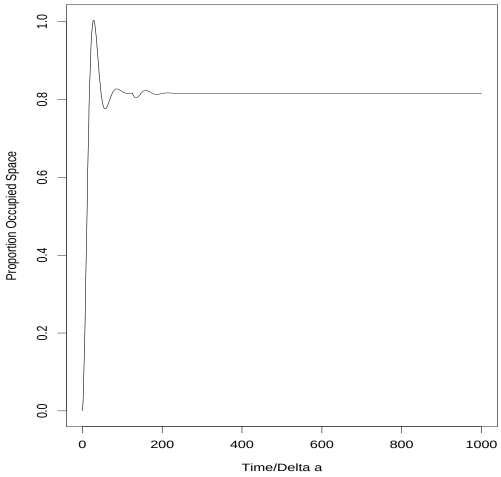

Figure 3.8: A stable underdamped equilibrium ($\kappa = 500$, $\alpha = 1.6085 * 10^{-6}$, $S = 0.95$).

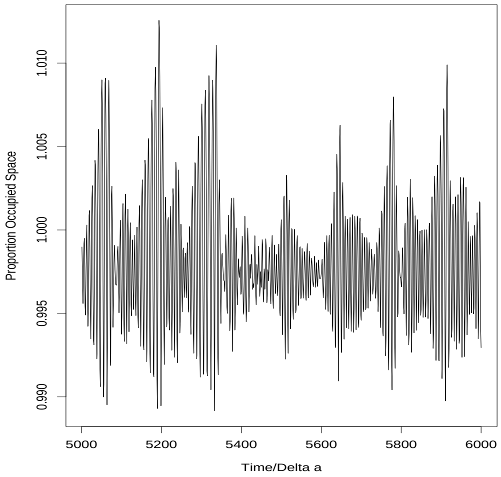

Figure 3.9: An unstable solution ($\kappa = 1.5 * 10^5$, $\alpha = 1.6085 * 10^{-6}$, $S = 0.95$).

suggests that there is a 'speed of occupancy' mechanism. When space is filled quickly, *ie* the settlement rate is high, then a lot of the area is occupied by a single cohort. This cohort will move through the age-structure until it reaches the end of the distribution. Then immediately space becomes filled by a 'pulse' of new settlers. This gives rise to the relaxation oscillation. When space is filled more slowly, *ie* the settlement rate is low, then settlement occurs of a period of time and depending on the settlement rate either underdamped or overdamped equilibria are found.

In the phase plane the unstable solution appears to be aperiodic (see figure 3.11.

3.3.5 Discussion

From this simple case increasing a_i, S or κ causes an increase in A^*. This increase in the area occupied is destabilising, which suggests that any factor contributing to the increase of A^* is also destabilising. This intuitively makes sense as increasing the area occupied will increase the 'speed of fill mechanism'. This mechanism means that the dynamics of the model are controlled by the rate of occupancy of free space. When the rate of occupancy is low, *ie* a_i, S, or κ are low, then a longer time is required to fill the same space. This gives rise to stable overdamped and underdamped solutions. However, when this rate is high, then free space is filled by short 'pulses' of settlement as soon as the space becomes available. The free

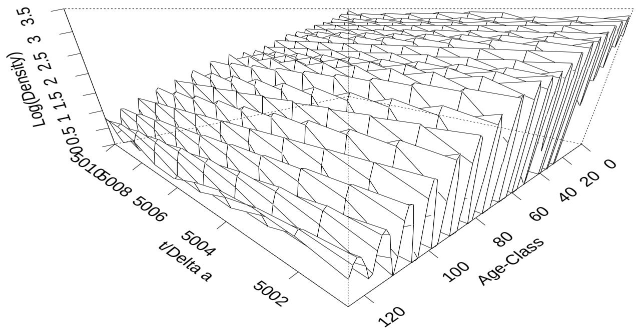

Figure 3.10: An unstable age-class distribution ($\kappa = 1.5 * 10^5$, $\alpha = 1.6085 * 10^{-6}$, $S = 0.95$).

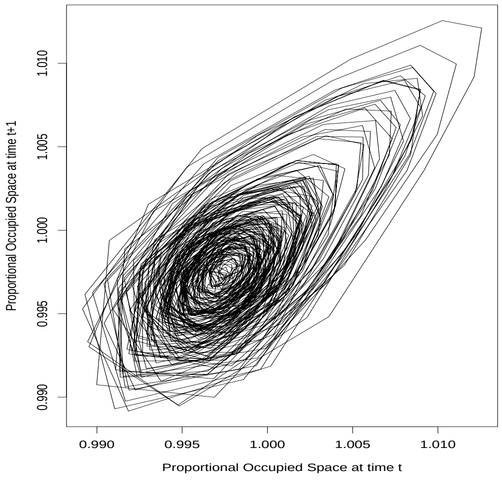

Figure 3.11: Phase plane plot for an unstable run ($\kappa = 1.5{*}10^5$, $\alpha = 1.6085{*}10^{-6}$, $S = 0.95$).

space is provided by individuals reaching the end of the age-class structure and dying, producing unstable solutions.

Investigation of the steady states shows that at both high and low values of κ young individuals occupy the most space. For example when $\alpha = 1.6085{*}10^{-6}$ the maximum occupancy is held by individuals of 266 or 280 days old. However, when the model is simulated, unstable solutions show waves of cohorts moving through the age-structure. Space is made rapidly available when all the individuals in the age-class N die, which is rapidly occupied by new settlers. This mechanism gives rise to the classic relaxation oscillations that are observed. Four types of solution were found these are stable underdamped, stable overdamped, limit cycles and aperiodic. The unstable solutions are very persistent with oscillations lasting for over 38,000 years.

The local stability boundaries and the 50% free space rule both indicate that increasing a_i, S or κ destabilises the model. This is intuitively correct for the reason stated above. However, as the 50% free space rule is only a sufficient condition for stabillity, it becomes a worse approximation to the stability boundary as κ is increased.

Understanding the mechanism that drives this model allows the derivation of a simple stability criteria. The mechanism that governs the oscillations is dependent upon the are occupied by a cohort over time (χ_t). These oscillations can either persist or decay depending upon the rate at which space is occupied. A simple heuristic stability criteria can be derived ignoring the settlement rate. If a cohort has a density of n_0 initially with area a_i, then $\chi_t = n_0 a_i$. At time $t+1$, a proportion S survive, thus $\chi_{t+1} = S n_0 a_{i+1}$. For the cohort to increase in area $\chi_{t+1} > \chi_t$, therefore $(S a_{i+1}/a_i) > 1$. The minimal condition for the area of a cohort to increase is the increase in the area between age-classes 0 and 1. As the area doubles from age-class 0 to 1, then the heuristic stability shows that oscillatory solutions exist when $S > 0.5$. The nature of these oscillations is not know, if they decay then stable underdamped solutions are produced, if not limit cycles are found. This criteria is far simpler to derive than the 50% free space rule, but it gives a much larger area of the parameter space where the behaviour of a solution is known (see figure 3.12).

3.4 An Application the Model to *S. balanoides*

In this section the general model is applied to *S. balanoides*. A logistic growth curve is fitted to data from the literature and survivorship is age-independent.

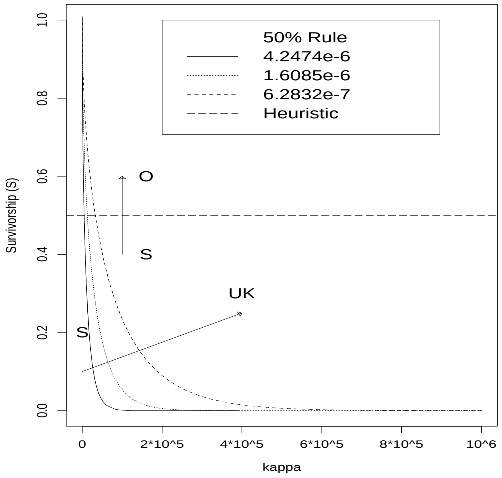

Figure 3.12: Heuristic stability and the 50% free space rule (U= unstable, UK= unknown, O= oscillatory).

3.4.1 The Logistic Growth Function

S. balanoides does not grow linearly with age. The increase in area varies with both height on the shore and age (see Barnes & Powell 1953, for a general review). Data were taken from Barnes & Powell (1953) for the mean specific growth rates of barnacles per day from 5.4 feet above chart datum. This was the closest height to the 6.2 feet of MTL. A linear regression was fitted to the change in proportional length per day against square roots of the lengths. This gave a good fit with an F statistic of $4.37 * 10^{-17}$ (see figure 3.13). Using a minimum length for the barnacle from extrapolation of the curve a growth curve was produced iteratively using the equation for the increase in length per unit length (see figure 3.14). A logistic curve fitted this data well with a residual sum of squares of 6.817496 and a residual standard error of 0.0624513. The logistic curve was of the form

$$L_i = \frac{L_\infty}{\left[1 + \left(\frac{L_\infty - L_0}{L_0}\right) e^{ib\Delta a}\right]}, \tag{3.31}$$

where $L_0 = 1.130319$, $L_\infty = 15.98195$ and $b = -0.0302853$.

It is assumed that all the barnacles are essentially circular and therefore the area at age curve is given by

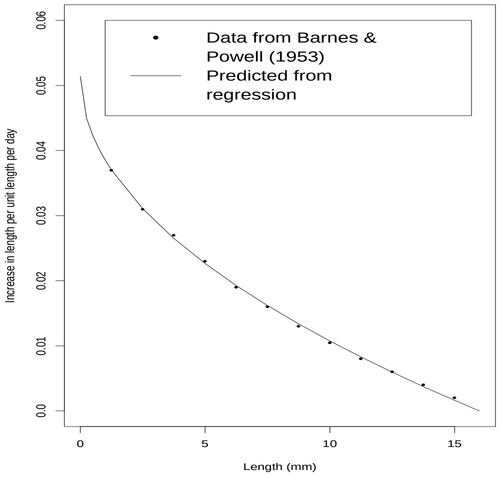

Figure 3.13: Linear regression of the proportional growth rate using a square root transform of length.

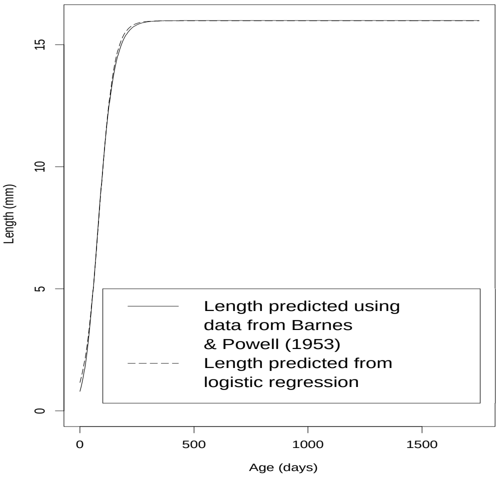

Figure 3.14: Fitting a logistic curve to the length-age relationship (Barnes & Powell, 1953).

$$a_i = \frac{\pi L_i^2}{4 * 10^6} \tag{3.32}$$

where it is necessary to use a conversion factor of $1 * 10^6$ to convert from mm^2 to m^2. The area of an individual in age-class 0, a_0, is $1.00344 * 10^{-6} m^2$, which gives $\sigma_{max} = 996571$.

3.4.2 Steady States

The steady states of the logistic growth model are very similar to the linear growth model. There is a logistic increase in the area occupied, A^*, with increasing S and κ (see figures 3.15 and 3.16 respectively). The A^* in both cases appears to be similar to the fastest growth rate in the linear growth model.

At both high and low instantaneous settlement rates the age-distributions are similar. The density of individuals in an age-class decreases with increasing age (see figures 3.17 and 3.18). Although the densities decrease with age the maximum space occupied is found at an age of 196 days (age-class 14). This is earlier than in the linear growth model. This is due to the rapid gain in area, as individuals reach their maximum size in about 1 year.

The shape of the distributions of occupancy and density are very similar. This is for exactly the same reason as the in the linear growth model (see section 3.3.2).

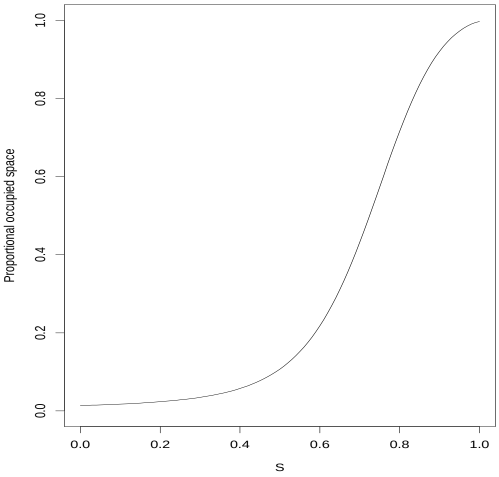

Figure 3.15: The effect on A^* of varying S with different growth functions ($\kappa = 1000$).

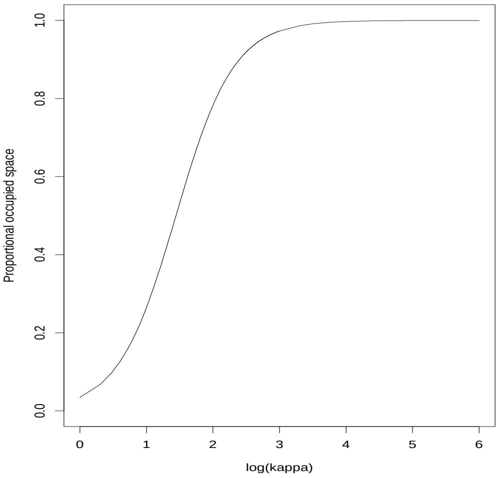

Figure 3.16: The effect on A^* of varying κ with different growth functions ($S = 0.95$).

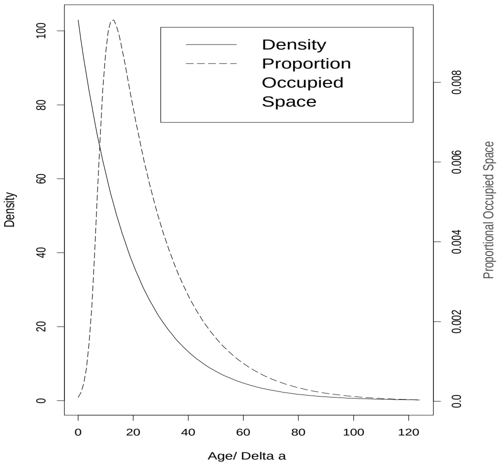

Figure 3.17: Densities and proportional occupied space for different ages ($S = 0.95$, $\kappa = 10$).

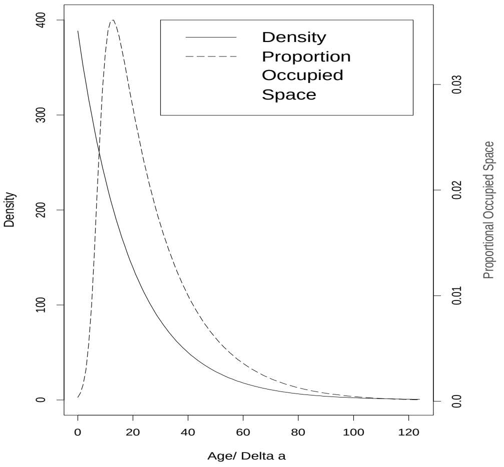

Figure 3.18: Densities and proportional occupied space for different ages ($S = 0.95$, $\kappa = 10^6$).

However, the peak occupancy is earlier than in the linear growth model. This is due to the rapid gain in area, as individuals reach their maximum size in less than 1 year.

3.4.3 Stability

Local Stability and the 50% Free Space Rule

The local stability boundary of the model can be seen in figure 3.19, the stable and unstable indicate local stability. This boundary shows that in the 125 age-class model at high S, κ is destabilising. However, at lower values of S increasing κ can be stabilising.

The 50% free space rule is also illustrated in figure 3.19. At low κ the 50% free space rule is a fairly good approximation to the local stability boundary. However, as κ is increased then the 50% free space rule become a progressively worse approximation to the local stability boundary. This is because the 50% rule is a sufficient condition for stability.

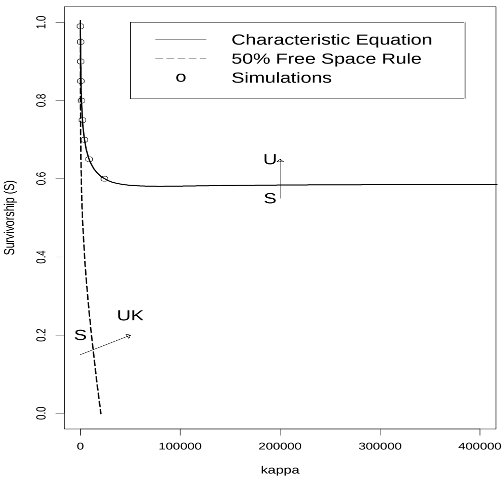

Figure 3.19: Local Stability and the 50% Free Space Rule for a model with 125 age-classes (U=Unstable, S=Stable, UK=Unknown).

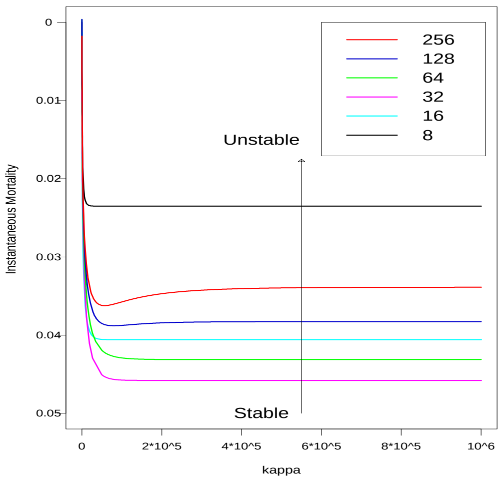

Figure 3.20: The effect of number of age-classes on local stability.

Number of Age-Classes

The number of age-classes in the model was altered in the range of 8 to 256. As the number of age-classes is varied then it is necessary to scale the age-class width, Δa, such that $N\Delta a$ is constant. The instantaneous mortality, μ, was calculated from the survivorship by

$$\mu = -ln(S)/\Delta a,$$

which allows the age-class comparison, as S is scaled to Δa, *ie* doubling age-class width is equivalent to squaring S.

The comparison of local stability for the different number of age-classes can be seen in figure 3.20. At very low κ a similar pattern is seen. However, as κ is increased, increasing the number of age-classes can be stabilising or destabilising. Increasing the number of age-classes effects the shape and position of the stability boundary. A model with 8 age-classes is most stable. However, as the number of age-classes is increased the effect is destabilising to 32 age-classes and then stabilising up to 256 age-classes (see figure 3.20). The shape of the boundary changes from almost a right angle with 8 age-classes, to a smooth curve with 256 age-classes. In the 256 and 128 age-class cases κ is first destabilising then stabilising.

3.4.4 Simulation

Increasing κ causes equilibrium to be reached more quickly. However, if κ and S are large enough then oscillations are produced. These oscillations can be periodic with stable limit cycles persisting for more than 38,000 years. When the system is unstable, decreasing κ or S causes a decreases in the periodicity and the amplitude of the oscillations (see table 3.2).

Table 3.2: Table showing the effect of changing S and κ on stability and the periodicity of unstable solutions.

Survivorship (S)	Settlement Rate (κ)	Stability	Periodicity of Solution (weeks)
0.95	10^3	Unstable	77
0.90	10^3	Unstable	56
0.85	10^3	Unstable	46
0.80	10^3	Stable	-
0.95	10^5	Unstable	120
0.95	10^4	Unstable	107
0.95	10^3	Unstable	77
0.95	10^2	Stable	-

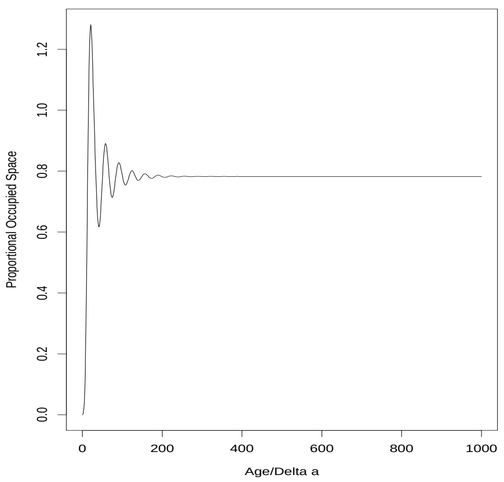

Figure 3.21: A stable solution ($\kappa = 100$, $S = 0.95$).

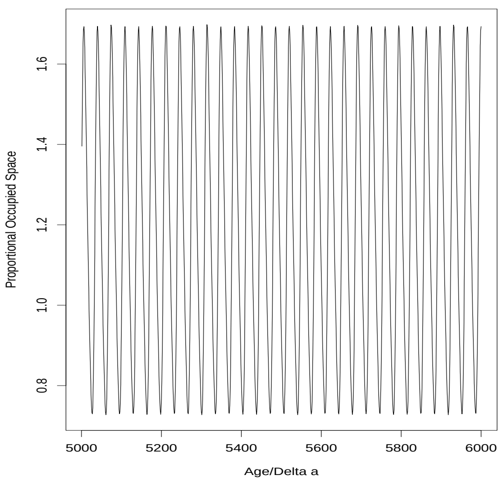

Figure 3.22: Periodic cycles ($\kappa = 500$, $S = 0.95$).

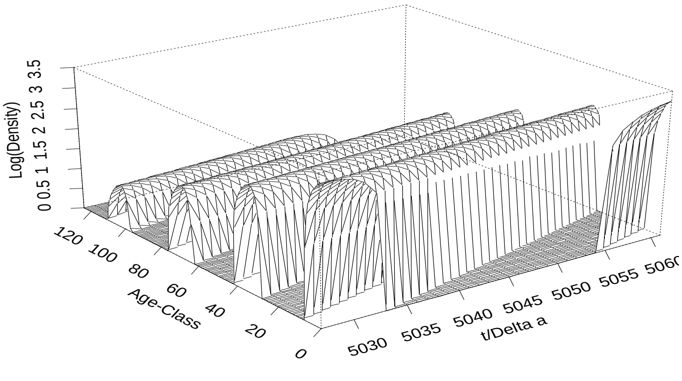

Figure 3.23: Unstable age-class distribution ($\kappa = 500$, $S = 0.9$).

When κ is small then stable solutions are observed (see figure 3.21). When κ is large then an unstable solution is obtained (see figure 3.22). It is useful to note that there are slight differences in the amplitude of each peak. This however, is a facet of discrete models as they sample at distinct points.

The pictures produced for the age-distributions are very similar to those produced by the linear growth model. For unstable solutions, waves of cohorts pass through the population (see figure 3.23). For stable solutions, a negative exponential distribution was observed, where decreasing S increases the negative gradient.

3.4.5 Discussion

The same mechanism is observed controlling dynamics in the logistic growth model as in the linear growth model. Increasing S or κ leads to an increase in the occupancy, A^*, and a decrease in the stability. This is due to the 'speed of fill' mechanism. $\alpha = 1.6085 * 10^{-6}$ is used in the linear model to compare with the logistic. This is because the maximum diameter in both cases is about $16mm$. When the steady states are compared for a similar S and κ the logistic model has a higher occupancy and is less stable than the linear growth model. This is because of the time delay inherent between the individuals settling and reaching their maximum size. In the linear growth model this process takes 5 years, but in the logistic model maximum size is reached after less than a year. This logistic growth rate is a bit high for the mid-shore, but is similar to the situation found on the low-shore or submerged panels (Hawkins, *pers. com.*).

Again four different types of dynamics are found. However, aperiodic solutions are more difficult to locate. Limit cycles are more common with persistent oscillations lasting for over 38,000 years.

The stability boundary and the 50% free space rule show similar patterns to the linear model. The same explanations for the differences can be drawn. The logistic growth model is again shown to be less stable than the linear growth model. A heuristic stability criteria can be derived in exactly the same way as shown in Section 3.3.5. In the logistic growth model $S > (L_i/L_{i+1})^2$ allows the area of a cohort to increase over time and thus, oscillations to occur (where L_i is the length of an individual in age-class i). If the minimum condition is examined then we find that $S > 0.461$ for oscillations to occur. This again provides a far larger area of the parameter space where the behaviour of solutions is know compared to the 50% free space rule (see figure 3.24) and is far simpler to derive.

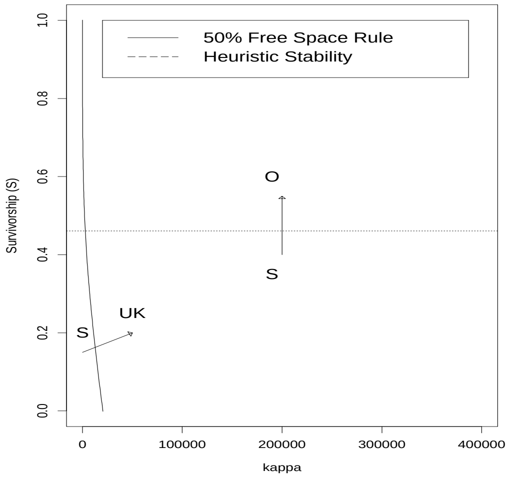

Figure 3.24: Heuristic stability and the 50% free space rule (U= unstable, UK= unknown, O= oscillatory).

Increasing the number of age-classes appears to be both stabilising and destabilising. Further work is required in order to find the exact cause. However, this investigation was not feasible within the time-scale of this project. It is important to investigate this behaviour, as the number of age-classes could require specific selection.

3.5 General Discussion

Four types of behaviour were observed in the simulations: stable overdamped, stable underdamped, limit cycles and aperiodic solutions. Roughgarden *et al* (1985) and Bence & Nisbet (1989) only observed 3 types of the 4 types of solution, as they do not categorise their stable solutions. These authors did not observe the aperiodic solutions. This is due to our survivorship being entirely density-independent. Roughgarden *et al* (1985) numerical examples use the discrete version of the model and incorporates density-dependent mortality. This is know to stabilise population fluctuations. When I added density-dependent mortality to the model, parameter values that previously gave aperiodic solutions produced two point-cycles.

The mechanism controlling the dynamics of the model is the same in both the linear and logistic growth models. Increasing a_i, S or κ causes an increase in A^*. This increase in the area occupied is destabilising, which suggests that any factor contributing to the increase of A^* is also destabilising. This intuitively makes sense as increasing the area occupied will increase the 'speed of fill mechanism'. This mechanism means that the dynamics of the model are controlled by the rate of occupancy of free space. When the rate of occupancy is low, *ie* a_i, S, or κ are low, then a longer time is required to fill the same space. This give rise to stable overdamped and underdamped solutions. However, when this rate is high, then free space is filled by short 'pulses' of settlement as soon as the space becomes available. The free space is provided by individuals reaching the end of the age-class structure and dying. This situation gives rise to unstable solutions. Although the logistic growth model has the same mechanism, it is less stable. Growth is determinant (*ie* the adults have a maximum size) and adult growth is very slow in comparison with the juveniles, which reach adult size in about a year. If a similar maximum size in the linear growth of $16mm$ is compared with logistic growth, then a higher value of proportional occupied space is found for the logistic growth model. Kuang & So (1995) stated that the best indicator of stability is the ratio of the total area occupied by juveniles to the total area occupied by adults. The higher this ratio the more stable the model is. The ratio in the linear growth model is $8 * 10^{-3}$ and in the logistic growth model is $5 * 10^{-3}$. Thus, the logistic growth model should be less stable.

The 2-cycles can be very persistent, with the cycles continuing to be stable after over 38,000 years (one million time units). The cycles shown in figure 3.22 could well be found on a exposed shore with high recruitment. Increasing growth, settlement or mortality when the fluctuations are periodic 2-cycles causes an increase in the amplitude and the period of these cycles.

The 50% free space rule and the characteristic equation suggest that increasing settlement rate or survivorship is destabilising. This reinforces the conclusions reached by Roughgarden *et al* (1985), Bence & Nisbet (1989) and Kuang & So (1995). The 50% free space rule is a good approximation to the characteristic equation at low settlement rates, but at high settlement the approximation is very bad. This is because the 50% free space rule is only a sufficient condition for stability and is dependent upon settlement. Thus, as settlement increases the approximation becomes worse.

Heuristic stability criteria were derived for both the linear and logistic growth models. This provides a greater area within the parameter set where the behaviour of the model is known and is simpler to derive. The logistic model is shown to be less stable than the linear growth model when these heuristic limits are compared. Oscillatory solutions are found where $S > 0.5$ in the linear growth and where $S > 0.461$ in the logistic growth model.

A very useful area of further work would be to investigate the effect of the number of age-classes on the stability of the model. This is because increasing the number is first stabilising then destabilising and effects the shape of the boundary. This may make the selection of number of age-classes important.

To construct this model a number of assumptions had to be made. It is now useful in the light of the present findings to review these assumptions and comment on the suitability. The assumption that larvae are found in the surrounding water is not biologically realistic. *S. balanoides* is known to have a distinct settlement period between March and August (Connell, 1961a; Hawkins & Hartnoll, 1982a). Large variation in the settlement has also been observed with peaks in settlement being correlated with shore height (Bertness *et al*, 1992), maximum tidal range (Shanks, 1986) and onshore winds (Hawkins & Hartnoll, 1982a). The mechanism that controls this process is not yet fully understood (Wethey, 1985). Thus, a discrete settlement period with peaks of settlement would be more biologically realistic.

The assumption that settlement is related to free space is under debate. However, the question of what is free space should be addressed first. Not all free space is the same. Barnacle larvae require specific settlement cues. Lewis (1977) stated that free living acorn cirripeds respond to a variety of stimuli during settlement: arthropodin (an insoluble protein found in adults); water currents; surface rugosity; light; and, gravity and hydrostatic pressure. In the absence of specific settlement cues settlement is usually delayed (Lewis, 1977). The assumption that settlement and free space are linearly related implies that settlement into areas of substratum with the same free space will reflect the supply of larvae. However, all but one of the studies of the validity of this hypothesis have found that the resident assemblage has a larger effect on settlement than the free space (Minchinton, 1995). Roughgarden & Possingham (1985) found that settlement was proportional to free space only if the patch was less than $50cm^2$ and Raimondi (1990) found no support for this relationship. This suggests that settlement is due to the cues suggested by Lewis (1977) and availability of free space. Thus, the type of free space should be taken into account and the relationship between free space and settlement should perhaps be sigmoidal (Roughgarden *et al*, 1985).

Assuming that free space cannot be negative is true, although percentage cover can be greater than 100. However, this raises the question of what is 100% occupancy? Individuals will settle on the tests (shells) of adults when settlement rates are especially high (Connell, 1961a). However, overcrowding of barnacles causes increased mortality due to hummocking (Shanks & Wright, 1986), decreased growth rates (Crisp, 1960), different growth forms (Moore, 1934) and increased mortality due to undercutting and uplifting (Connell, 1961a).

Assuming all individuals are the same area is a gross simplification of the real situation. On the shore all barnacles will have different growth rates and forms (see Stubbings (1975) for a general review). For example, when barnacles become very crowded they tend to interact in their growth form. Instead of growing diameter they become much higher and more tubular in form (Moore, 1934). Growth rate is affected on two scales, local (1 m^2) and regional (a whole shore) (Crisp, 1960). The scale that is modelled should involve all the local processes that affect growth rate. However, locally growth rate can be affected by many factors including water flow, orientation, population density and parasites (Crisp, 1960).

Circular barnacles is a reasonable assumption. Barnes & Powell (1953) show that the length-breadth ratio decreases with increasing size and tend to the circular form. For example, at about $7mm$ barnacles on all shores height have a length-breadth ratio of 1.10.

The assumption that all the recruits are the same area is reasonable. This difference is small in comparison with the area in m^2. Connell (1961a) measured newly metamorphosed barnacles at Millport, Scotland, and the mean lengths only varied between 0.7 and $1.21mm$. The assumption that there is a known area at age is again a gross simplification of the actual case. It is possible to argue that we are looking at the average of these different areas for each particular age-class. However, having a number of different growth functions would be more accurate.

To make the model more tractable we assume constant survivorship. This seems to produce a sensible survivorship curve (see Connell (1961a) figures 5, 9 & 10). However, it would be useful to look at density-dependent mortality in the first two weeks after settlement and at high occupied space (Connell, 1961a). It might also be useful to look at a differential mortality between early and late settlement, as later settlers appear to suffer increased mortality due to increased temperature (Connell, 1961a).

This model provides insight into the colonisation of rock by barnacles. However, to produced a better realisation of *S. balanoides*, it is necessary to refine the assumptions. I would suggest that a number of things are attempted in further work:

1. A sigmoidal relationship between free space and settlement.
2. A number of different growth functions with the model to simulate different growth types.
3. A realisation of the settlement cues and not treating all free space as the same.
4. Seasonal settlement.
5. Density dependent mortality and different survivorship functions.

Although these additions to the model would make it more biologically realistic, a more complex model would be produced. The mechanism driving these models would be more difficult to find, as the models have more parameters and are less tractable. This makes understanding the simple models essential before more complex variants are investigated. This is highlighted by Bence & Nisbet (1989), who investigated simple versions of Roughgarden *et al* (1985) and showed that some of the inferences that they had drawn were wrong.

Chapter 4

A Size-Structured Model for the Brown Alga *Fucus vesiculosus*

4.1 Introduction

4.1.1 General Introduction

Age-classified models assume that age-specific survival and fertility rates are sufficient to determine population dynamics (Caswell, 1989). This is not always true and organisms can be classified by a factor other than age that is a better indicator of the vital rates. This is known as the state of the stage-classified model. Formal state theory was introduced into population ecology by Caswell *et al* (1972), Boling (1973) and Metz (1977). Several circumstances combine to make other state variables more suitable than age. These include the combination of size- or stage- dependent demography with plastic growth, multiple modes of reproduction and environmental heterogeneity (Caswell, 1989).

Seaweeds have a large degree of plasticity in their growth form. Their final shape is a combination of their genetics and the environment (Norton *et al*, 1982). Individual plants can increase, decrease or remain the same size. This is due to the trade-off between growth and various different types of damage, for example, grazing and storm damage. Thus, age is not necessarily a good predictor of size (Åberg, 1992a). Generally, size is thought to be a better predictor of demographic rates than age (Chapman, 1986b; Ang, 1987, 1991b). Thus, it seems sensible to use size-class models to investigate algal demography.

Algal populations have been modelled since the 1970s. Much of this modelling has been for harvesting of subtidal algae (see for example Seip, 1980; Smith, 1986; Ang, 1987). This is because the algae are grown commercially for alginates and for consumption in the Far East. Recently models for investigation of the basic biology and ecology of algal populations have been developed. Nisbet & Bence (1989) developed a family of models depicting a simplified relationship between adult density and juvenile recruitment in *Macrocystis pyrifera.* Despite the simplification they found that they were able to mimic the real dynamics and concluded that factors affecting recruitment were very important in determining the dynamics of the population. They looked at a situation where recruitment is dependent upon the temperature and shading of light, and not directly by the adults. Burgman & Gerard (1990) developed a better model for the same species including life history stages, environmental and demographic stochasticity, and density-dependent interactions. When adults are absent, then gametophyte densities corresponding to adult densities of $0.002m^{-2}$ are used to simulate recruitment from distant kelp populations. They suggest that stochastic environmental variation and density-dependence are important in algal population models, as without these factors the models overestimate recruitment, survival and growth.

Very recently demographic modelling of intertidal algal populations has been done. Åberg (1992a) investigated two populations of *Ascophyllum nodosum* in Sweden. He assumed a closed system, divided the model into five size-classes and measured the mortality, growth and fecundity. He found that environmental ice-scour caused the population to mature earlier and decrease in numbers due to damage. If a stochastic environment is added to the model then the mean extinction time for the population is 163 years (Åberg, 1992b). Ang & De Wreede (1993) used a 9x9 matrix model based on recruit stages and plant size to investigate a population of *Fucus distichus.* They compared the dominant eigenvalues and found that population size only increased when recruitment was positive. The 'propagule' bank was very important in their model, as its absence could reduce population growth by 83% per annum. Simulations showed that 60% of populations had a negative growth rate and suggest that the populations may avoid extinction by occasional large pulses of recruitment.

Both Åberg (1992b) and Ang & De Wreede (1993) suggest that the long term dynamics of their closed demographic models is extinction. These systems are inherently closed as propagules are only transported a short distance from their parents (Deysher & Norton, 1982; Arrontes, 1993). However, both of these are systems with well established adult populations. Thus, on more exposed shores bare rock may be colonised by large infrequent recruitment events, indicating that the system is open.

4.1.2 Modelling Aims

The models discussed in this Chapter are similar to the model in Chapter 3. The construction is more akin with those produced by Roughgarden *et al* (1985), Bence & Nisbet (1989) and Kuang & So (1995).

As competition on the rocky shore is essentially for the resource of space, two dimensional models can be constructed. The aim of this chapter is to produce a general model for intertidal perennial algae based on the concept of space-limited recruitment. This is done in a similar way to the model for *S. balanoides* in Chapter 3. A strategic model will be constructed using simplifying assumptions from the general model. Steady states and local stability criteria are derived and investigated. These techniques and simulation are used to provide insight into the mechanism that controls the dynamics of the model.

Once the dynamics are understood, the model will be parameterised using values from literature for *F. vesiculosus.* Simulation, steady state and local stability will be investigated and compared to the strategic model. This model will be used as the third stage in the cycle shown in figure 1.2.

4.2 A General Size Structured Model for Intertidal Canopy Forming Algae

In this section a size-structured population model for a general intertidal algae is constructed with the minimum assumptions.

4.2.1 The Model

This model makes a number of assumptions:

1. The survivorship function is known.
2. The mean size range of sizes is known.
3. Negative free space cannot exist.
4. All individuals in the same size-class are of the same size.
5. There is a maximum canopy area that a given area of rock can support.
6. The model has $Q + 1$ size-classes.

This model assumes space-limited recruitment. Thus, the free space at time t (F_t) is a function of the total available area (A) and the area occupied by fucoids (A_t), *ie*

$$F_t = [A - A_t]^+ \tag{4.1}$$

where the + denotes that free space cannot be negative. The area occupied at time t is

$$A_t = \sum_{j=0}^{Q} a_j n_{j,t} \tag{4.2}$$

where $n_{j,t}$ is the number of individuals in size-class j at time t and a_j is the area of rock occupied by an individual in size-class j. If c_j is the canopy area of an individual in size-class j and $\Theta_j = a_j/c_j$, then

$$A_t = \sum_{j=0}^{Q} \Theta_j c_j n_{j,t}. \tag{4.3}$$

This model uses an equation relating the transition between different size-classes and adds settlement. If $n_{i,t+\Delta t}$ is the number in size-class i at time $t+\Delta t$, $S_{i,t}$ is the probability of surviving one time interval in size-class i from $t \rightarrow t+\Delta t$, then

$$n_{i,t+\Delta t} = \sum_{j=0}^{Q} P^i_{j,t} S_{j,t} n_{j,t} + I_{i,t} \tag{4.4}$$

where $P^i_{j,t}$ is the probability of being promoted or demoted from size-class j to size-class i in the interval $t \rightarrow t+\Delta t$ and $I_{i,t}$ is new settlement into size-class i at time t. Promotion occurs implicitly at the end of a time-step in the model. If $\rho_{i,t}$ is the density of fucoids in size-class i in the interval $t \rightarrow t+\Delta t$, then

$$\rho_{i,t} = \frac{n_{i,t}}{A} \tag{4.5}$$

$$\hat{F}_t = \frac{F_t}{A} \tag{4.6}$$

$$\hat{I}_t = \frac{I_t}{A}. \tag{4.7}$$

From equations (4.1) , (4.3) and (4.5) - (4.7)

$$\hat{F}_t = \left[1 - \sum_{j=0}^{Q} \Theta_j c_j \rho_{j,t}\right]^+ . \tag{4.8}$$

Expressing the model in terms of density gives

$$\rho_{i,t+\Delta t} = \sum_{j=0}^{Q} P^i_{j,t} S_{j,t} \rho_{j,t} + \hat{I}_{i,t}. \tag{4.9}$$

It is useful to note that the sum of the transition probabilities is always equal to 1, or

$$\sum_{i=0}^{Q} P^i_{j,t} = 1. \tag{4.10}$$

4.2.2 The Settlement Function

Settlement per time unit cannot increase without bound. As barnacles settle in the system, they occupy space and thus reduce the space available for future settlers. If the rate at which cyprids become available to settle from the water column $m^{-2}.d^{-1}$ (ξ) is low, the amount of space occupied by settlers early in the time-step is small, and thus incremental settlement $\hat{F}_t^{-1}.\Delta a^{-1}$ (ζ) is unaffected. However, when κ is high, a large proportion of the space is occupied by early settlers and thus, the incremental settlement is much lower than expected from the number of cyprids available to settle. The rate of change of settlement over time can be described by a differential equation. If R are the fucoids that have already settled into the system and occupy space, then

$$\frac{dR}{dt} = \zeta\left(F(t_0) - a_0 R\right) \tag{4.11}$$

where ζ is the daily instantaneous settlement rate per m^2 of rock, $F(t)$ is the free space at time t_0 and $a_0 R$ is what has already settled in the area. If equation (4.11) is solved over time (t), then,

$$R(t) = \frac{F(t_0)}{a_0}\left(1 - e^{-\zeta a_0 t}\right) \tag{4.12}$$

If $a_0 = \Theta_0 c_0$, then the discrete analogy to equation (4.12) is

$$\xi \hat{F}_t = \frac{\hat{F}_t}{\Theta_0 c_0}\left(1 - e^{-\zeta \Theta_0 c_0 \Delta t}\right). \tag{4.13}$$

If ζ and ξ are calculated for set parameters, then we find that there is an asymptotic relationship (see figure 4.1). The relationship is linear at low values, but as $\zeta \to \infty$ then $\xi \to \xi_{max} = 1/(\Theta_0 c_0)$.

This function allows us to define the settlement function $\hat{I}_{i,t}$. As settlement is proportional to free space,

$$\sum_{i=0}^{Q} \hat{I}_{i,t} = \xi \hat{F}_t = \frac{\hat{F}_t}{\Theta_0 c_0}\left(1 - e^{-\zeta \Theta_0 c_0 \Delta t}\right). \tag{4.14}$$

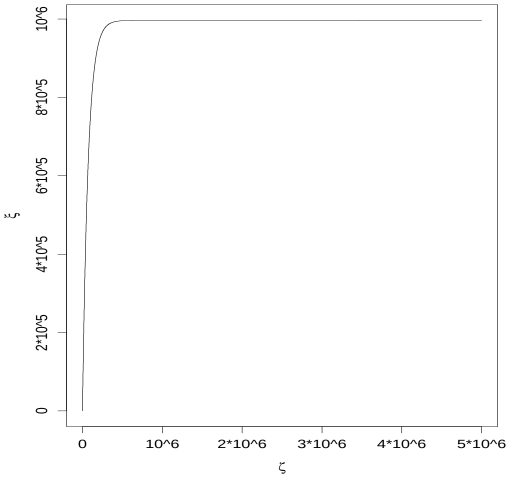

Figure 4.1: The relationship between ξ and ζ ($\Delta t = 14$, $c_0 = 5 * 10^{-6}$ and $\Theta_0 = 0.5$).

4.3 A Strategic 4 Size-Class Model

4.3.1 The Model

The general model is fairly intractable. Thus, firstly we investigate a very simplified case of the model. The assumptions made are:

1. The model has 4 size-classes.
2. All settlement is to the first size-class.
3. Survivorship (S) is constant.
4. An individual cannot be promoted more than one size-class.
5. An individual cannot be demoted to a smaller size-class.
6. An individual can only remain in the largest size-class.
7. The probability of being promoted (P) is constant.
8. The ratio of area occupied to canopy area (Θ) is constant.
9. There is a geometric increase in size as an individual is promoted.

These assumptions allow the general model to be simplified to a strategic model. This model can be simply defined using four transition equations, where from assumption 2 settlement is only into size-class 0. Thus,

$$
\begin{aligned}
\rho_{0,t+\Delta t} &= \hat{I}_t + (1-P)S\rho_{0,t} &(4.15)\\
\rho_{1,t+\Delta t} &= PS\rho_{0,t} + (1-P)S\rho_{1,t} &(4.16)\\
\rho_{2,t+\Delta t} &= PS\rho_{1,t} + (1-P)S\rho_{2,t} &(4.17)\\
\rho_{3,t+\Delta t} &= PS\rho_{2,t} + S\rho_{3,t}. &(4.18)
\end{aligned}
$$

The settlement at time t, $\hat{I}_t$, is defined as being proportional to the free space. Thus,

$$\hat{I}_t = \xi\hat{F}_t = \xi\left[1 - \sum_{i=0}^{3} a_i\rho_{i,t}\right]^+. \qquad (4.19)$$

As the ratio of are occupied by an individual (a_i) to actual canopy area (c_i) is constant, then $\Theta = a_i/c_i$. Assumption 9 implies that $c_i = \epsilon c_{i-1} = \epsilon^i c_0$. This allows equation (4.19) to be re-written as

$$\hat{I}_t = \xi\hat{F}_t = \xi\left[1 - \Theta c_0\sum_{i=0}^{3} \epsilon^i\rho_{i,t}\right]^+. \qquad (4.20)$$

The incremental settlement rate per m^2 , ξ, is related to the daily instantaneous settlement rate per m^2 , ζ using the same relationship as in the general model, *ie*

$$\xi = \frac{1-e^{-\zeta\Theta c_0\Delta t}}{\Theta c_0}. \qquad (4.21)$$

4.3.2 Steady States

Derivation

From equations (4.15)-(4.18) and (4.20) it is possible to derive the steady states of the model. If the system is at equilibrium and

$$
\begin{aligned}
\rho_{i,t+\Delta t} &= \rho_{i,t} = \rho_i^*\\
A_{t+\Delta t} &= A_t = A^*\\
\hat{F}_{t+\Delta t} &= \hat{F}_t = \hat{F}^*\\
\hat{I}_{t+\Delta t} &= \hat{I}_t = \hat{I}^*,
\end{aligned}
$$

then from equations (4.15) and (4.20) respectively

$$\begin{aligned}\rho_0^* &= \frac{\hat{I}^*}{(1-(1-P)S)} && (4.22)\\ \hat{I}^* &= \xi\left[1-\Theta c_0\sum_{i=0}^{3}\epsilon^i\rho_i^*\right]. && (4.23)\end{aligned}$$

If we let

$$\begin{aligned}\phi_1,\phi_2 &= (PS)/(1-(1-P)S) && (4.24)\\ \phi_3 &= (PS)/(1-S), && (4.25)\end{aligned}$$

then, with a little simple algebra, the equilibrium steady states are

$$\begin{aligned}\rho_0^* &= \frac{\xi}{(1-(1-P)S)+\xi\Theta c_0 A_0}\ , && (4.26)\\ \rho_1^* &= \phi_1\rho_0^*, && (4.27)\\ \rho_2^* &= \phi_1\phi_2\rho_0^*, && (4.28)\\ \rho_3^* &= \phi_1\phi_2\phi_3\rho_0^*, && (4.29)\end{aligned}$$

where,

$$A_0 = 1+\epsilon\phi_1+\epsilon^2\phi_1\phi_2+\epsilon^3\phi_1\phi_2\phi_3. \qquad (4.30)$$

The derivation of these steady states allows insight into the limiting parameters at high and low settlement densities. When $\zeta\Theta c_0\Delta t \to \infty$, then $\xi \to 1/(\Theta c_0)$ and $\rho_0^* \to 1/A_0$. This suggests that at high settlement rates the equilibrium occupied space is limited by P, S and the choice of the size-classes. However, as $\zeta\Theta c_0\Delta t \to 0$, then $\xi \to 0$ and the equilibrium occupied space is limited by ζ.

Parameter Values

A range of parameter values must be chosen such that the steady states can be investigated. Obviously both P and S must be in the interval (0,1). The strategic nature of the model allows the size-class choice to be made fairly arbitrarily. Thus, a geometric increase in area is used as an individual moves up size-classes (see table 4.1). It is assumed that the ratio of a_i to c_i is less than one as the area of rock occupied is less than the actual canopy area. Thus, for the moment we take $\Theta = 0.5$.

Table 4.1: Logarithmic size-class choice for $\Theta = 0.5$.

Size-class	Area range (mm^2)	Individual area (mm^2)	c_i (m^2)	Maximum Number.m^{-2}
0	$0 - 10$	5	$5 * 10^{-6}$	$4.0 * 10^5$
1	$10 - 10^2$	50	$5 * 10^{-5}$	$4.0 * 10^4$
2	$10^2 - 10^3$	500	$5 * 10^{-4}$	$4.0 * 10^3$
3	$10^3 - 10^4$	5000	$5 * 10^{-3}$	$4.0 * 10^2$

Investigation of the Steady States

The analytical steady states were used to investigate the effect of increasing ζ, P and S on the proportional occupied space, density of individuals and area occupied by the different size-classes.

Increasing P, S or ζ increases the proportional occupied space at equilibrium, A^* (see figures 4.2 and 4.3). Increasing S gives an exponential increase in area occupied. Increasing P or ζ gives a logistic increase in area occupied. The general increase in area is due to the mechanism controlling the model. If the area of a cohort increases with time then oscillations occur. Increasing P, S or ζ increases the potential of a size-class to increase in area. For example, increasing S causes more individuals to survive to occupy area, increasing P increases the rate at which area is gained by a cohort and increasing ζ increases the densities in a size-class and therefore the potential to gain area.

It is also possible to look at the effect of increasing P, S and ζ on the densities of individuals in and area occupied by a particular size-class. Increasing ζ gives an asymptotic increases in the density of individuals and a logistic increase in the area occupied by a size-class (see figure 4.4 and 4.6). Increasing S causes an initial increase in both densities and area occupied in size-classes 0-2. However, as S is increased further the densities and area occupied decrease (see figure 4.5 and 4.7). Size-class 3 shows a different picture with both the densities and area occupied increasing exponentially with increasing S. Increasing P gives an

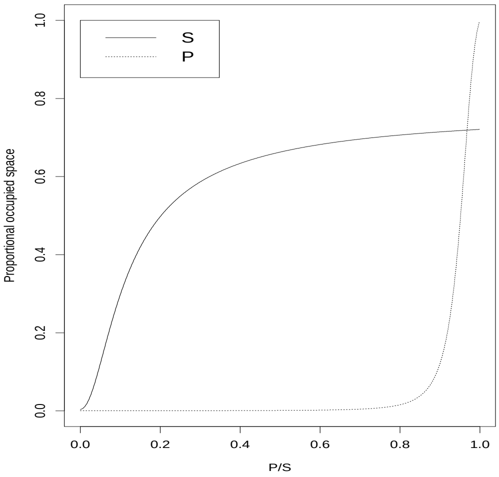

Figure 4.2: The effect of S and P on A^* for $P = 0.05$ and $S = 0.9$ respectively.

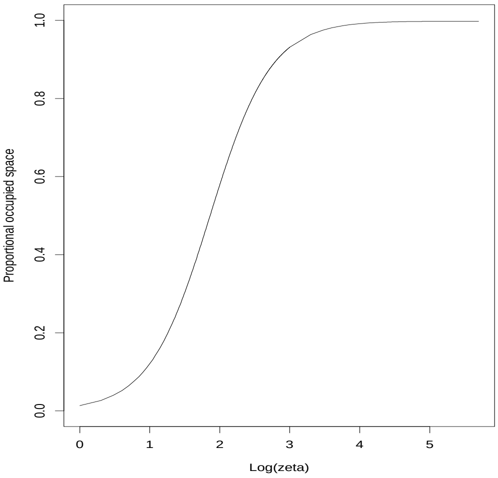

Figure 4.3: The effect of ζ on A^*.

exponential decline in the densities and area occupied in size-class 0. There is an initial increase in both densities and area occupied in size-classes 1 and 2, but after $P > 0.05$ they decline. Size-class 3 shows an asymptotic relationship for both densities and area occupied (see figure 4.8 and 4.9).

In figures 4.4 - 4.9 it is obvious that size-class 3 is the dominant size-class in terms of the total area occupied. This is similar to the situation found on sheltered shores where a few large plants dominate the area forming a canopy.

4.3.3 Stability Analyses

Local stability analysis investigates the behaviour of a small perturbation from the steady state. If the steady state is stable then the perturbation will decay and the solution will return to the same steady state value. If the perturbation is unstable then the solution will diverge away from the steady state.

The Characteristic Equation

To derive the characteristic equation for this simple model, we define a perturbation from a steady state in size-class i time t as $\delta_{0,t}$. This gives four equations for the behaviour of the perturbation

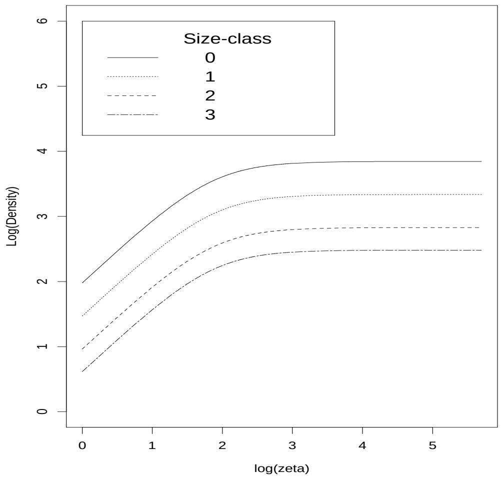

Figure 4.4: The effect of ζ on the density in each size-class ($S = 0.9$, $P = 0.05$).

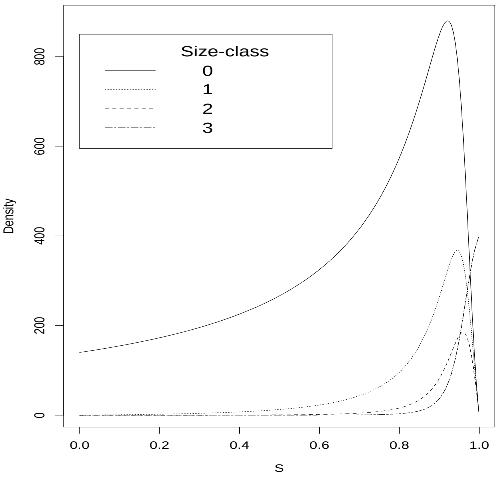

Figure 4.5: The effect of S on the density in each size-class ($P = 0.05$, $\zeta = 10$).

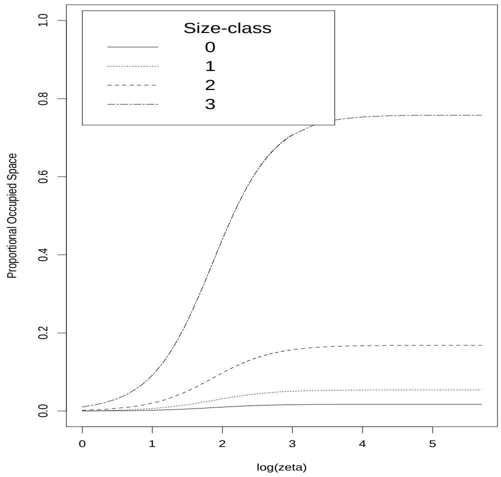

Figure 4.6: The effect of ζ on the area occupied by each size-class ($S = 0.9$, $P = 0.05$).

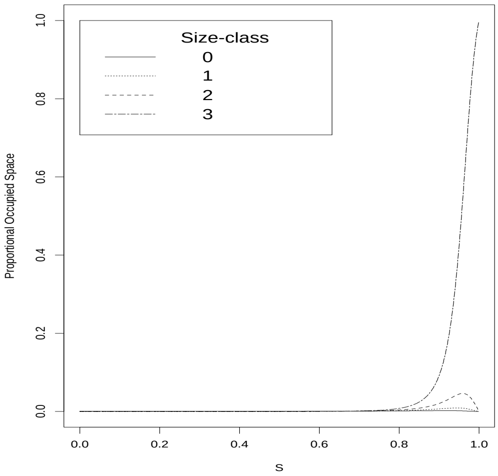

Figure 4.7: The effect of S on the area occupied by each size-class ($P = 0.05$, $\zeta = 10$).

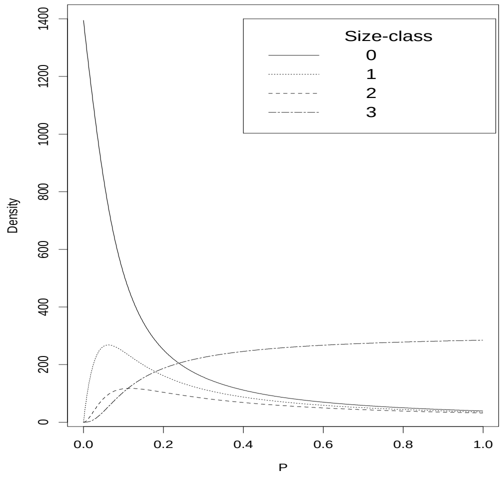

Figure 4.8: The effect of P on the density in each size-class ($S = 0.9$, $\zeta = 10$).

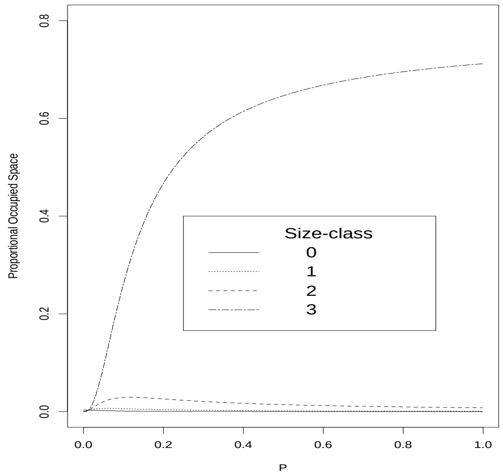

Figure 4.9: The effect of P on the size-class distribution ($S = 0.9$, $\zeta = 10$).

$$\begin{aligned}
\delta_{0,t+\Delta t} &= (\hat{I}_t - \hat{I}^*) + (1-P)S\delta_{0,t}, && (4.31)\\
\delta_{1,t+\Delta t} &= PS\delta_{0,t} + (1-P)S\delta_{1,t}, && (4.32)\\
\delta_{2,t+\Delta t} &= PS\delta_{1,t} + (1-P)S\delta_{2,t}, && (4.33)\\
\delta_{3,t+\Delta t} &= PS\delta_{2,t} + S\delta_{3,t}, && (4.34)
\end{aligned}$$

where,

$$\hat{I}_t - \hat{I}^* = -\xi\Theta c_0 \sum_{i=0}^{3} \epsilon_i \delta_{i,t}. \tag{4.35}$$

These equations for the behaviour of a perturbation can be summarised simply in matrix form.

$$\delta_{\mathbf{t+\Delta t}} = \mathrm{A}\delta_{\mathbf{t}} \tag{4.36}$$

where,

$$\mathrm{A} = \begin{bmatrix} \alpha + \gamma_0 & \gamma_1 & \gamma_2 & \gamma_3 \\ \beta & \alpha & 0 & 0 \\ 0 & \beta & \alpha & 0 \\ 0 & 0 & \beta & S \end{bmatrix}, \quad \delta_{\mathbf{t}} = \begin{bmatrix} \delta_{0,t} \\ \delta_{1,t} \\ \delta_{2,t} \\ \delta_{3,t} \end{bmatrix}$$

and,

$$\begin{aligned} \alpha &= (1-P)S \\ \beta &= PS \\ \gamma_i &= -\xi\Theta c_0 \epsilon^i. \end{aligned} \tag{4.37}$$

The characteristic equation is the determinant of the matrix $(\mathrm{A} - \lambda I)$. By looking at the minors of matrix A, the characteristic equation is

$$(S-\lambda)(\alpha-\lambda)^2(\alpha+\gamma_0-\lambda) - (S-\lambda)(\alpha-\lambda)\beta\gamma_1 + (S-\lambda)\beta^2\gamma_2 - \beta^3\gamma_3 = 0. \tag{4.38}$$

Eigenvalues (λ) are the roots of the characteristic equation, and these give information on the stability of solutions and the way in which equilibrium is approached (see Nisbet & Gurney (1982) for a general review). A solution is described as stable when all the eigenvalues are within the unit circle, *ie* $|\lambda| < 1$.

A Heuristic Mechanism for Stability

The mechanism that governs the oscillatory nature of this system is dependent upon the variation of area occupied by a cohort over time. The system is not oscillatory if this area decreases, but oscillations are produced if this area increases. These oscillations can either decay giving rise to stable underdamped solutions or can persist to produce limit cycles. The oscillations decay or persist depending on the rate at which free space is occupied, *ie* the settlement rate.

Ignoring the settlement rate allows a heuristic stability criteria to be derived. If the area occupied by a cohort at time t is defined as χ_t and start with n_0 individuals all in size-class i with area Θc_i, then,

$$\chi_t = n_0 \Theta c_i. \tag{4.39}$$

At time $t + \Delta t$, Sn_0 individuals remain P of which have been promoted to size-class $i+1$ and now occupy an area of $\Theta \epsilon c_i$. Thus the area of the cohort at time $t+1$ is

$$\chi_{t+1} = (1-P)Sn_0\Theta c_i + PSn_0\Theta\epsilon c_i. \tag{4.40}$$

Obviously for a cohort to increase in area occupied over time then $\chi_{t+1} > \chi_t$. Thus with a little simple algebra we find that

$$S > \frac{1}{1+P(\epsilon - 1)} \qquad (\epsilon > 1). \tag{4.41}$$

As we ignore the settlement rate, this solution will only be a good approximation to the stability boundary at high settlement rates. This is because at high settlement rates S, P and ϵ are the density limiting parameters. In fact the heuristic boundary should be the limit of the stability boundary as $\zeta \to \infty$.

Numerical Investigation of Stability

Equation (4.38) can easily be solved analytically with the quartic formula using a package such as MAPLE V (©1991, Waterloo Maple Software, University of Waterloo, Ontario, Canada). However, these solutions are very complicated and tell us little about the actual nature of the boundary. A far more useful implementation of the characteristic equation is to solve it numerically.

Numerical solution is done using different sets of parameter values to give an idea of the nature of the stability boundary at different values of P, S and ζ. A program called CONTOUR was used which is part of the SOLVER package (©STAMS, Livingstone Tower, 26 Richmond Street, Glasgow G1 1XH). CONTOUR is a package that uses Newton-Raphson techniques to follow the roots of equations. Initial condition for the CONTOUR code were produced using numerical solution in MAPLE V (©1991, Waterloo Maple Software, University of Waterloo, Ontario, Canada).

The roots can be real or complex conjugate pairs, with each complex boundary representing a pair of solutions. To locate the boundary we take $|\lambda| = |\mu + i\omega| = \sqrt{\mu^2 + \omega^2} = 1$. Once the stability boundary is located, setting $\sqrt{\mu^2 + \omega^2} < 1$ and $\sqrt{\mu^2 + \omega^2} > 1$ on the same plot allows the direction of stability to instability to be discerned.

The stability boundaries for different ζ can be seen in figures 4.10 - 4.13. Increasing either P, S or ζ is destabilising. From the steady state analyses we know that increasing these parameters increases the occupied space. Thus, increasing the occupied space is destabilising.

The difference between the heuristic and real stability boundary decreases as settlement rate is increased (see figures 4.10 - 4.13). As the heuristic criteria only predicts oscillations, the parameter space between these 2 curves is the region that produces stable underdamped solutions. The persistence of these oscillations depends on the rate at which the space is filled, *ie* the settlement rate. Thus, at an increased settlement rate the space is filled faster producing a smaller parameter space where the solution is stable underdamped (see figures 4.10 - 4.13). This suggests that as $\zeta \to \infty$ the space should fill infinitely fast and there should be no parameter space where stable underdamped solutions are produced. Thus, as $\zeta \to \infty$ the heuristic criteria should become a better estimate to the actual boundary.

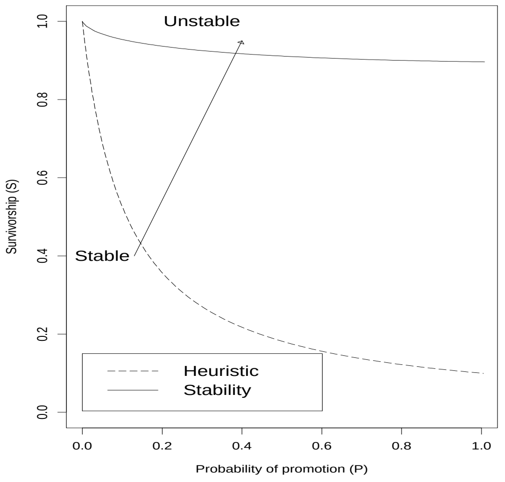

Figure 4.10: The stability boundary for $\zeta = 20$.

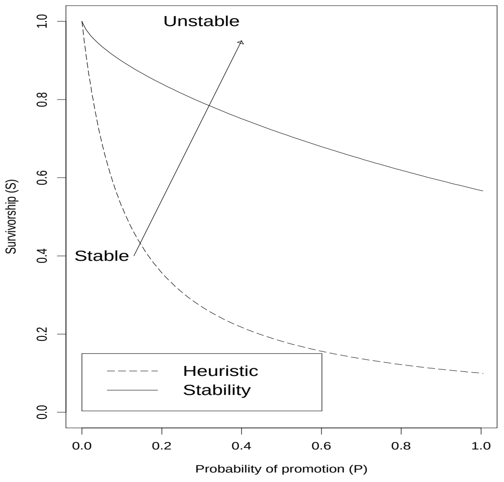

Figure 4.11: The stability boundary for $\zeta = 1 * 10^2$.

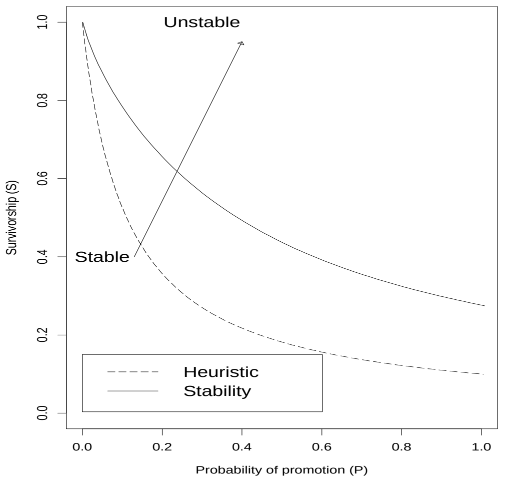

Figure 4.12: The stability boundary for $\zeta = 1 * 10^3$.

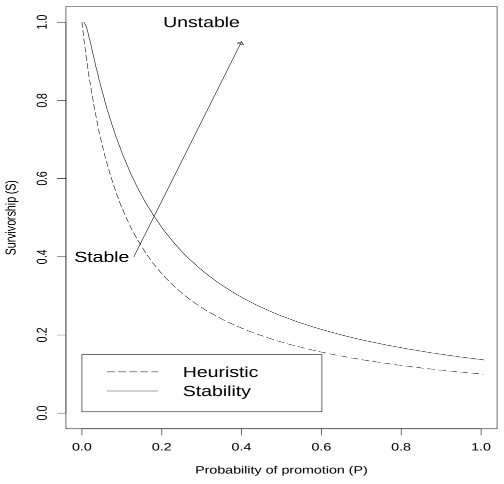

Figure 4.13: The stability boundary for $\zeta = 1 * 10^4$.

4.3.4 Simulation

A time-step must be chosen for simulation that is short in comparison to the maximum age of an individual. Thus, the vital rates are assumed not to vary within this time-step. A time-step or Δt of 14 days is used, as this value is short in comparison with the lifespan of perennial seaweeds. Also sampling on a real time scale is unlikely to happen more often than this period.

Two types of dynamics are produced by this model they are stable and periodic solutions (see figures 4.14 and 4.15 respectively). The stable solutions give stable size-class distributions (see figures 4.16). However, unstable solutions are found when waves of individuals pass through the size-classes creating an unstable size-distribution (see figure 4.17).

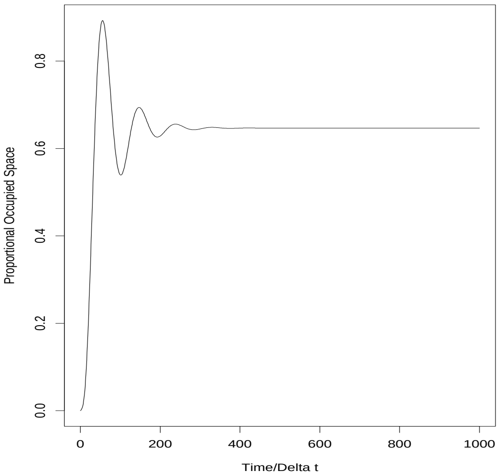

Figure 4.14: A stable solution of the model ($\zeta = 20$, $S = 0.95$ and $P = 0.05$).

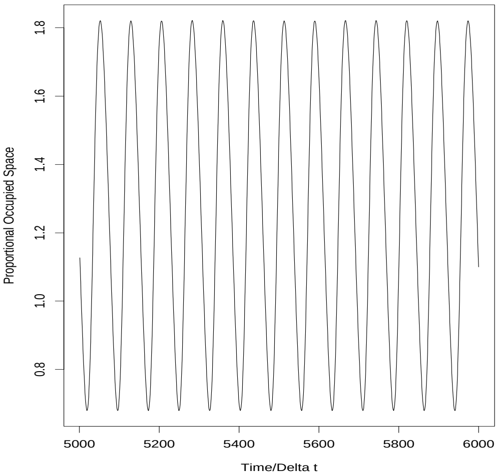

Figure 4.15: An unstable solution of the model ($\zeta = 200$, $S = 0.95$ and $P = 0.05$).

These solutions provide insight into the mechanism that controls the decay or persistence of oscillations. If the time over which free space fills is long then the size-distribution will tend to a stable distribution and the oscillations will decay (see 4.14 and 4.16). However, when the settlement rate is higher, short ‘pulses’ of settlement occur and free space is occupied quickly. In this case individuals move through to the final size-class and free space only occurs when one of the large plants dies (see figures4.17). This gives rise to the classic relaxation oscillations that are found (see figures 4.15).

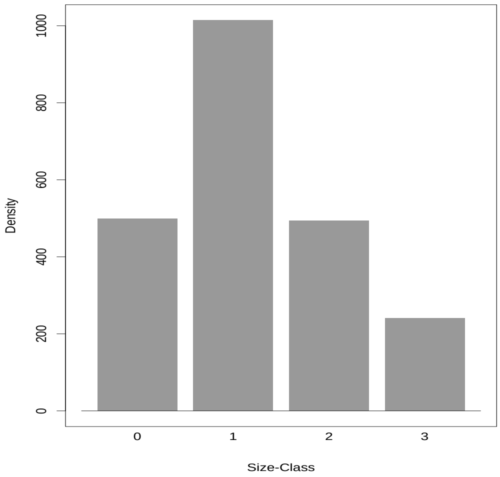

Figure 4.16: A stable size-distribution ($\zeta = 20$, $S = 0.95$ and $P = 0.05$).

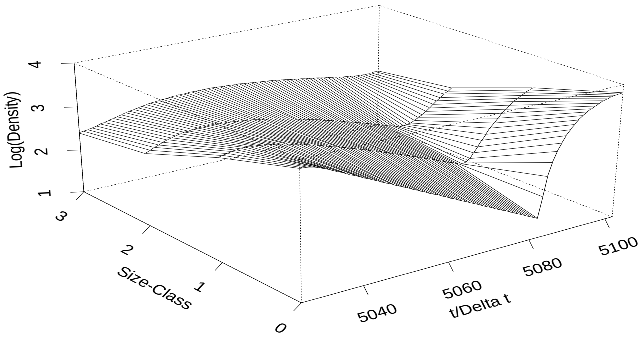

Figure 4.17: An unstable size-distribution ($\zeta = 200$, $S = 0.95$ and $P = 0.05$).

4.4 An Application of the Model to *F. vesiculosus*

In this section the strategic model is applied to *F. vesiculosus*using parameter values from the literature. The choice of size-classes, probability of promotion and size-specific survivorship are set in order to produce densities that are in the correct order of magnitude.

These new parameter values and size-specific survival will be used in the model. The results of this model will be compared with the strategic model to investigate robustness.

4.4.1 The Model

The synthesis of this model is very similar to the synthesis of the strategic model. However, in this section size-specific survivorship is assumed. Thus, the four transition equations are

$$\begin{aligned}
\rho_{0,t+\Delta t} &= \hat{I}_t + (1-P)S_0\rho_{0,t} && (4.42)\\
\rho_{1,t+\Delta t} &= PS_0\rho_{0,t} + (1-P)S_1\rho_{1,t} && (4.43)\\
\rho_{2,t+\Delta t} &= PS_1\rho_{1,t} + (1-P)S_2\rho_{2,t} && (4.44)\\
\rho_{3,t+\Delta t} &= PS_2\rho_{2,t} + S_3\rho_{3,t}, && (4.45)
\end{aligned}$$

where,

$$\hat{I}_t = \xi\hat{F}_t = \xi\left[1-\Theta\sum_{i=0}^{3} a_i\rho_{i,t}\right]^{+}. \qquad (4.46)$$

As the ratio of area occupied by an individual (a_i) to actual canopy area (c_i) is constant, then $\Theta = a_i/c_i$. This allows equation (4.19) to be re-written as

$$\hat{I}_t = \xi\hat{F}_t = \frac{1-e^{-\zeta\Theta c_0\Delta t}}{\Theta_0 c_0}\left[1-\Theta\sum_{i=0}^{3} c_i\rho_{i,t}\right]^{+}. \qquad (4.47)$$

4.4.2 Parameterisation

Choice of Size Classes

There are four size-classes in the model which are picked to represent length and average age of the plants. As the longevity of *F. vesiculosus* is about 4 years (Knight & Parke, 1950), then the size-classes will represent the 0+, 1+, 2+ and 3+ year old plants. The mid point of these size-classes is the area occupied by an individual in this class. In this case, insufficient data has been collected to fit size-classes using an algorithm (see for example Moloney, 1986) and the size-class choice had to made fairly arbitrarily.

The density of plants in each size-class is dictated by the area of bare rock occupied by an individual in size-class i, $a_i = \Theta c_i$. Thus, Θ and c_i were scaled such that reasonable densities of plants were found in the size-classes. As the area of plants is not generally measured as it is very labour intensive, reasonable lengths of plant were examined for a certain age of plant (see table 4.2). The area of rock occupied by as individual is smaller than the actual canopy area of that individual. Thus, arbitrarily we use $\Theta = 0.5$.

Keser & Larson (1984) noted that in Maine there is not enough substratum to support very high densities of germlings ($> 43,600.m^{-2}$). So if $\xi_{max} = 5 * 10^4$, then $\Theta c_0 = 1/\xi_{max} = 20mm^2$. 'Escapees' should be in the range of $0-50mm$ and are still a single frond (Hawkins, *pers. com.*). Both the area and length for size-class 0 are known and thus it is possible to derive a linear relationship between area and length. As the plants in size-class one are still single fronds, the linear length-area relationship was used to calculate the area from the lengths of these plants. Creed (1993) suggests that the density of individuals of length$\leq$ $120mm$ is around 3000 in monospecific stands. Thus the estimate produced in this scaling for a maximum density of about 8000 is in the correct order of magnitude.

After the second year the plants start to dichotomise (Knight & Parke, 1950). Thus, area is now roughly proportional to length squared. To get the densities in the final size-class in the correct order of magnitude it was necessary to scale the size-classes such that $\Theta c_i = 0.25 * length^2$. The maximum density that can be found in the final size-class is about 11.1 plants, which is within the correct order of magnitude (Hawkins, *pers. com*).

Table 4.2: Size class choice for $\Theta = 0.5$ (Hawkins, *pers. com.*).

Group	Spread of Lengths (mm)	Individual length (mm)	Area-length Trend	Θc_i (m^2)	Maximum Number.m^{-2}
$Escapees$	0-50	25	Linear	$2.000 * 10^{-5}$	$5.0 * 10^4$
$Juveniles$	50-250	150	Linear	$1.2 * 10^{-4}$	8333
$1^{st}season$	250-500	375	Quadratic	$3.516 * 10^{-2}$	28.4
$2^{nd}season$	500+	600	Quadratic	$9.900 * 10^{-2}$	11.1

Probability of Promotion

I assume that the size-classes 0 to 3 are essentially composed of plants that are 0+, 1+, 2+ and 3+ years old respectively. Thus, we are required to make the average transition time from size-class $i \rightarrow i+1$ one year. As the time interval chosen, Δt, is fourteen days, then it is assumed that 26 of these time intervals make 1 year. As promotion of the complete size-class is required in a year then the probability of promotion is 1/26.

Size-Specific Survival

A number of different conclusions have been reached on size-specific survivorship or mortality. However, most studies suggest that the probability of death remains constant with age. This is possibly due to the studies ignoring the microscopic stages. For example, Chapman (1986a) found a negative exponential relationship between age and mortality in *Laminaria saccharina*, with almost all the plants dead by 24 months. A similar relationship has been found for *Macrocystis pyrifera* (Rosenthal *et al*, 1974) and *Pelvetia fatigiata* (Gunhill, 1980). Black (1974) stated that older individuals of *Egregia laevigata* ensure a high death rate amongst individuals of the same species. Chapman (1986a) proposed that mortality is constant at a size of greater than $10cm$ in *L. saccharina*, but most mortality occurs before this stage. The maximum size that *L. saccharina* reached in this study was $4m$ in length. Creed (1993) suggested that mortality is inversely proportional to size in small *F. vesiculosus*. Thus, size specific survivorship was investigated.

This information infers that survivorship should be higher for older plants. However, the maximum longevity of the plant should still be a mean of 4 years (Knight & Parke, 1950). The size-class survivorship used is shown in table 4.3, which produces the survivorship curve shown in figure 4.18. The size-specific survivorship using $S_i = 0.9223$ was back calculated from the cumulative survivorship after

Table 4.3: Size-specific survivorship (Δt=14 days).

Group	Survivorship	Proportion Surviving
$Escapees$	0.90	$6.46 * 10^{-2}$
$Juveniles$	0.91	$5.56 * 10^{-3}$
$1^{st} season$	0.93	$8.43 * 10^{-4}$
$2^{nd} season$	0.95	$2.22 * 10^{-4}$

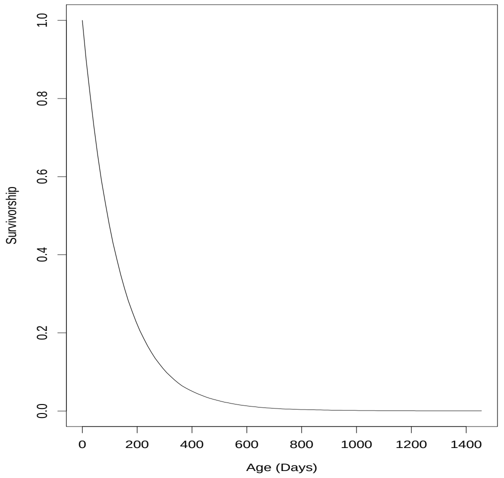

Figure 4.18: The age-specific survivorship curve ($\Delta t = 14$ days).

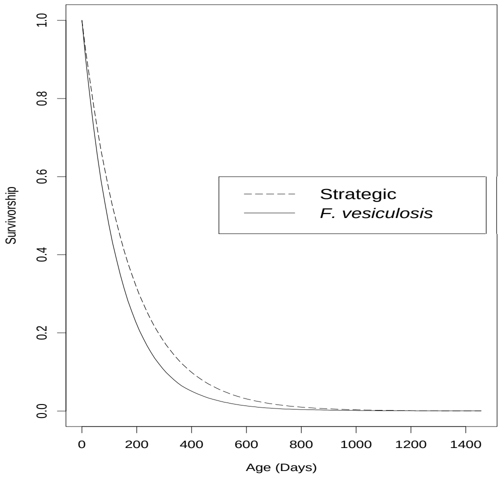

Figure 4.19: The age-specific survivorship curve of the two models ($\Delta t = 14$ days).

208 weeks. This produces a very similar curve to the survivorship curve of the strategic model (see figure 4.19). This will be used to compare the dynamics.

4.4.3 Steady States

Derivation

The derivation of the steady states is similar to that of the strategic model. If the same line of reasoning is followed and we redefine ϕ_i then steady states can be derived. If we let

$$\phi_1 = (PS_0)/(1-(1-P)S_1) \tag{4.48}$$

$$\phi_2 = (PS_1)/(1-(1-P)S_2) \tag{4.49}$$

$$\phi_2 = (PS_2)/(1-S_3) \tag{4.50}$$

then, with a little simple algebra, the equilibrium steady states are

$$\rho_0^* = \frac{\xi}{(1-(1-P)S_0)+\xi\Theta A_0} \ , \tag{4.51}$$

$$\rho_1^* = \phi_1\rho_0^*, \tag{4.52}$$

$$\begin{aligned} \rho_2^* &= \phi_1\phi_2\rho_0^*, & (4.53) \\ \rho_3^* &= \phi_1\phi_2\phi_3\rho_0^*, & (4.54) \end{aligned}$$

where,

$$A_0 = c_0 + c_1\phi_1 + c_2\phi_1\phi_2 + c_3\phi_1\phi_2\phi_3. \quad (4.55)$$

Investigation of the Steady States

The steady states give a very similar picture to the strategic model. Increasing ζ causes an increase in the area occupied at equilibrium, as it increases the potential area of a cohort and the speed at which space fills (see figure 4.20). The density of individuals and space occupied by each size-class again increase asymptotically and logistically respectively (see figure 4.21 and 4.23). The densities in each size-class are inversely proportional to the area occupied by the size-class. This is true of all perennial seaweeds. Most importantly the area of rock is dominated by a few individuals in the largest size-class. This is similar to the canopy that is found on sheltered shores.

The steady state dynamics of this model are similar to the strategic model. In all cases $P = 1/26$ and the value of ζ was varied. The different types of models used can be seen in table 4.4, where constant survivorship implies that $S = 0.9223$, and size-specific survivorship and realistic size-classes are as described in section 4.4.2. In both models increasing ζ increases the area occupied (see figure 4.22). However changing size-classes has a very large effect on the area occupied at equilibrium at low settlement rates. This is because fewer individuals are required in the *F. vesiculosus* model to fill the space quickly. When ζ becomes larger similar occupied space values are found, as even with the small size-classes space fills up relatively quickly. Changing the survivorship function make little difference to the area occupied. This is because the functions are quite similar (see figure 4.19). The trajectories produce a smaller occupied area with constant survivorship, as more individuals survive from size-classes 1 and 2 to 2 and 3 respectively. Thus the gain in area is greater as the largest increase in area is between size-class 1 and 3.

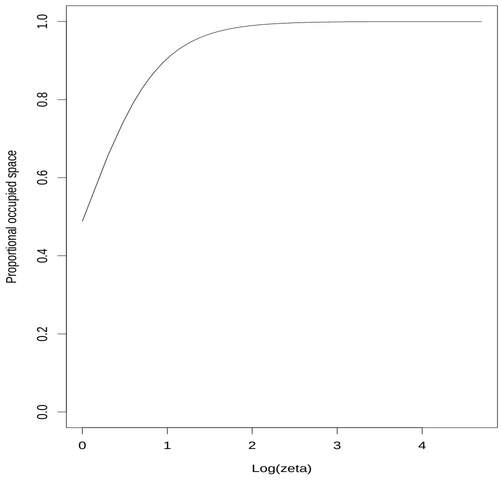

Figure 4.20: The effect of increasing ζ on the area occupied at equilibrium.

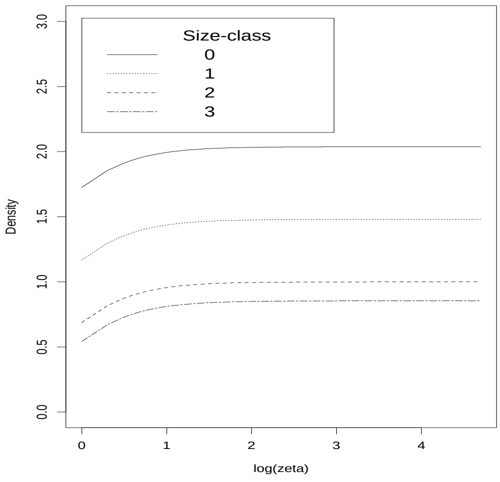

Figure 4.21: The effect of increasing ζ on the density of individuals in different size-classes at equilibrium.

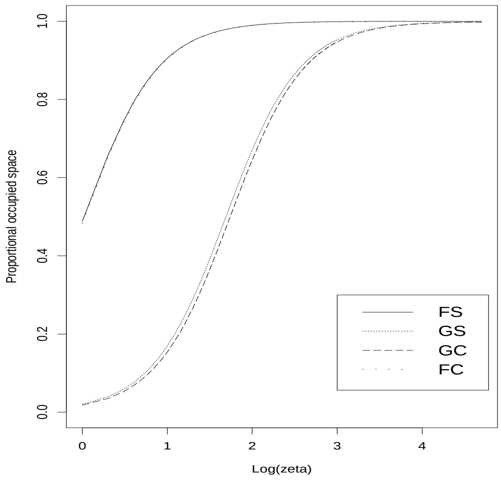

Figure 4.22: Comparison of the model for *F. vesiculosus* and the strategic model (see table 4.4).

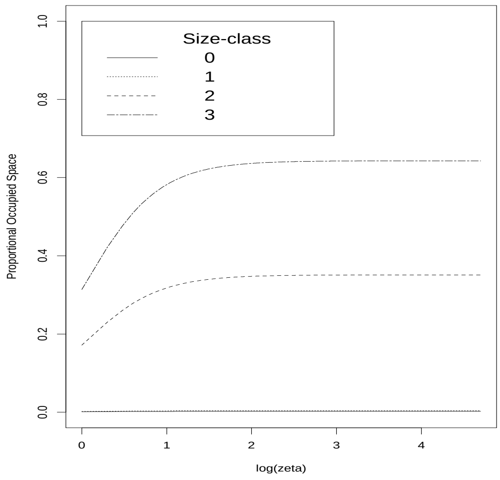

Figure 4.23: The effect of increasing ζ on the total area occupied by different size-classes at equilibrium.

Table 4.4: Model Types in figure 4.22 ($P = 1/26$).

Model	Size-class	Survivorship
FS	Realistic	Size-specific
GS	Geometric	Size-specific
GC	Geometric	Constant
FC	Realistic	Constant

4.4.4 Local Stability Analyses

In this section the characteristic equation is derived, then the behaviour of the roots of this equation is examined. This allows the investigation of a perturbation, $\delta_{i,t}$, from the steady state. The characteristic equation is found in the same way as for the strategic model. The characteristic equation is

$$\begin{aligned}(S_3 &- \lambda)(\alpha_2 - \lambda)(\alpha_1 - \lambda)(\alpha_0 + \gamma_0 - \lambda) \\ &- (S_3 - \lambda)(\alpha_2 - \lambda)\beta_0\gamma_1 + (S_3 - \lambda)\beta_0\beta_1\gamma_2 - \beta_0\beta_1\beta_2\gamma_3 = 0 \quad (4.56)\end{aligned}$$

where,

$$\begin{aligned}\alpha_i &= (1 - P)S_i \\ \beta_i &= PS_i \\ \gamma_i &= -\xi\Theta c_0\epsilon^i. \quad (4.57)\end{aligned}$$

The analytical solution to this equation is very complicated and can be solved using MAPLE V (©1991, Waterloo Maple Software, University of Waterloo, Ontario, Canada). However, the solution is uninformative and is not expressed here.

Realistic parameter values for P, S_i, and Θc_i have been described above. These values are substituted into equation (4.56) and then solved for ζ where $|\lambda| = 1$. This gives the critical value of ζ. Below this critical value of ζ the model is stable, above it the model is unstable.

The model types used are the same as described in table 4.4. If the relative stability of each of these models is investigated (see table 4.4) then it is found that the models with the highest values of A^* in figure 4.22 are the least stable.

Table 4.5: Stability of the different model types (see table 4.4).

Model type	Critical ζ $P = 0.019$	$P = 0.038$	$P = 0.077$	$P = 0.2$
FS	2.2779	7.2899	29.155	0.80746
GS	-	331.02	77.292	25.574
GC	-	317.63	78.328	26.175
FC	2.0395	5.9612	21.902	0.78030

As can clearly be seen from table 4.5 the more carefully parameterised model is much less stable than the strategic model. However, changing the size-classes has a far greater effect on the model than the instigation of size-specific survivorship.

4.4.5 Simulation

Again a time-step (Δt) of 14 days was chosen as this value is short in comparison with the maximum age of an individual and vital rates are assumed not to vary within this time.

A very similar pattern is found to the strategic model. Both stable and unstable solutions are obtained. The stable solutions have stable size-distributions. Unstable solutions have unstable size-distributions.

A similar mechanism is observed for the speed of space filling. If space is filled quickly, *ie* a high settlement rate, then persistent oscillations are found. If space fills gradually then stable underdamped solutions are found.

4.5 Discussion

The mechanisms that produce the dynamics in both of the 2 models are very similar. This is not surprising as their formulation is essentially the same. If the settlement rate, ζ, is high then the occupied space is limited by the parameters P, S, and Θ. If the settlement rate is low then the occupied space is limited by the settlement rate. Oscillations are found when the area occupied by a cohort increases over time. The decay or persistence of these oscillations depends upon the rate at which free space is filled, *ie* the settlement rate. Oscillations decay if the settlement rate is low, as free space is filled slowly, producing an underdamped solution. Oscillations persist if the settlement rate is high, as free space is filled by short 'pulses' of recruitment, producing limit cycles. This is illustrated nicely by the comparison between real and heuristic stability in the strategic model.

Increasing P, S or ζ is destabilising as it causes and increase in the area occupied at equilibrium. This is because the potential area of a cohort increases with increasing P, S or ζ.

The model for *F. vesiculosus* is much less stable than the strategic model. This is because the density of individuals required to fill the space is lower. The means that only small increases in settlement rate enhance the speed of occupation of space. Thus, smaller settlement rates are required to fill the free space and the *F. vesiculosus* model is more likely to produce oscillations.

Both models produce a size-distribution that is very similar to a canopy structure with the density of individuals decreasing with increasing size. The models also predict that a few large individual will dominate the area occupied. This is also similar to the canopy of perennial seaweeds.

The values of ζ that produce instability in the model for *F. vesiculosus* appear to be very low. However, the densities produced in the size-classes are in the correct order of magnitude.

All of the models produced for seaweeds have looked at effectively closed (see for example, Nisbet & Bence, 1989; Bergman & Gerrard, 1990). Most are systems where the density of propagules available for recruitment to the population is dependent upon the adult population (see for example, Ang, 1987, 1991b; Åberg, 1992a&b; Ang & De Wreede, 1993). These models are mainly simulation, the most similar seaweed model being Nisbet & Bence (1989). The work in this chapter is closer to the work of Roughgarden *et al* (1985), Bence & Nisbet (1989) and Kuang & So (1995). There is a similar tradeoff between increase and loss of area to that found by Roughgarden *et al* (1985) and Bence & Nisbet (1989). The stability criteria are similar, as formulation and assumptions are essentially the same. Space-limited recruitment and a deterministic system allow us to avoid the problems of extinction often experienced (Åberg, 1992b; Ang & De Wreede, 1993).

In light of the findings of this chapter it is now useful to reassess the assumptions used to formulate this model and suggest areas for further work. A difficult assumption to justify is that the system is open. As was stated in the introduction, propagules are only transported short distances from their parents (see Deysher &

Norton, 1982; Arronties, 1993). However, the specific shore that we are interested in receives sporadic settlement from outside the system (Hartnoll & Hawkins, 1985).

The assumption of constant settlement is not realistic. *F. vesiculosus* is known to have a distinct settlement period between May and July (Knight & Parke, 1950). Over this period the settlement is not constant and is effected in a similar way to barnacle settlement. This would give a series of peaks and troughs of settlement. Thus, a stochastic recruitment function would be a useful addition to the model, as without some kind of stochasticity recruitment and adult density are overestimated (Burgman & Gerard, 1990). The addition of a seed bank similar to that observed in terrestrial systems would be useful. There is great debate over the existence of the seed bank and a number of authors have suggested its existence (see for example Ang & De Wreede, 1993; Creed, 1993; Creed *et al*, 1996). Modelling it may provide some new hypotheses for the experimentalists to test.

Assuming that probability of promotion is constant across size-classes is feasible. As the assumption that the average age of an individual in each of the size-classes is 0+, 1+, 2+ and 3+ respectively, then this allows us to keep this probability constant. However, it would be useful to examine a model where the probability is not constant and it is possible to be demoted. The probability of being demoted is small. The results of Knight & Parke (1950) for the growth rate of *F. vesiculosus* at Wembery showed that only 1 of 45 plant decreased in length during their study. However, this probability will increase at sites of higher exposure, as the plants are more susceptible to wave damage.

There is little data for the estimates of S, c_i, Θ or P. This has made the model very hard to parameterise and no algorithm could be used to fit the size-classes. Thus, the assumptions that the P, S, Θ and C_i are all known is wrong. More accurate data describing all the demographic parameters would be useful in both the parameterisation of this model and the accurate prediction of densities over time. For example, Knight & Parke (1950) made one of the very few investigations into the increase in length of *F. vesiculosus* in the British Isles. They found a large variation in growth from -3 to 47.5 *cm*. However, one of the main uses of this model is to suggest where data is needed. I would suggest that a tagging study similar to Åberg (1992a) on the specific shore and species being modelled is necessary to derive accurate demographic parameters. As the longevity of *F. vesiculosus* is four years this study would have to run for at least that time period.

Density dependent survivorship would have been an interesting addition to the model. Creed (1993) suggest that *F. vesiculosus* follows the -3/2 self thinning rule which has been suggested to apply to all terrestrial plants. He also states that monospecific stands of seaweed are detrimental to the overall survivorship. Thus, at greater densities in the model the survivorship should be lower and the -3/2 self thinning law should be investigated. Another useful addition to the survivorship function would be the inhibition of smaller plants by the larger canopy plants. This occurs in a number of ways. For example, lower light intensity (Schonbeck & Norton, 1980a); lower nutrient levels (Dayton *et al*, 1984); whiplash and sweeping effects (Dayton, 1971; Ang, 1985); sediment build up (Kenelly, 1989); and aggregation of grazers (Hartnoll & Hawkins, 1985).

The problems of 'What is free space?' and 'What is 100% occupied space?' exist in this model. For a review of the arguments produced for barnacles which are essentially the same as for fucoids.

Chapter 5

Single Species Models of *F. vesiculosus* and *S. balanoides* in a Seasonal Environment

5.1 Introduction

A strong seaonality in the settlement of both *S. balanoides* and *F. vesiculosus* has been observed by many empiricists. There are small changes in timing from year to year, but general periods are found. These will be discussed separately for the two species below.

5.1.1 Seasonal settlement in *S. balanoides*

Seaonality in the settlement period of barnacles has been investigated by many authors (see for example, Connell, 1961a; Wethey, 1980; Hawkins & Hartnoll, 1982a; Caffey, 1985; Gaines & Roughgarden, 1985; Wethey, 1985; Pannacciulli, 1995). Much of the work on the settlement period has been direct, as daily densities of cyprids are measured, but many different results in both settlement period and density are observed. For example, Hawkins & Hartnoll (1982a) investigated the settlement of *S. balanoides* on the Isle of Man between 1977 and 1981. They found that cyprid settlement varied from a 40 day period in 1977 to a 90 day period in 1981. The start of settlement was found to vary between the end of April and mid-May. The end of settlement varied between June and the beginning of July. Kendall *et al* (1985) found a similar pattern for Robin Hood Bay in 1978. However, peak settlement was much later at around the beginning of June.

The settlement period of barnacles appears to be almost random, although Hawkins & Hartnoll (1982a) hypothesised that the timing is correlated with the algal bloom. Settlement patterns are not constant, peaks and troughs are observed that appear to be random. Peak settlement rates have been correlated with a number of factors including the strength of onshore winds (Hawkins & Hartnoll, 1982a); maximum tidal range (Shanks, 1986); and increasing wave action and decreasing shore height (Bertness *et al*, 1992). This temporal and spatial variation in settlement is not yet understood (Wethey, 1985).

5.1.2 Seasonal settlement in *F. vesiculosus*

Seasonal settlement has been suggested for *F. vesiculosus* (Knight & Parke, 1950; Hawkins, 1981a; Creed, 1993). The settlement period is between May and July (Knight & Parke, 1950; Creed, 1993). However, a lower background settlement has also been observed, which suggests the presence of a seed bank (Hoffman & Santilices, 1991; Ang & De Wreede, 1993; Creed, 1993; Creed *et al*, 1996).

The seed bank is supposed to operate in exactly the same way as in a terrestrial system and has been the subject of great debate. Hawkins (1981a) inadvertently found data to support the presence of a seed bank. He looked at the successional sequence of colonisation of barnacle covered rock and found that different successional sequences occur depending on the time of clearing. However, there appears to be low background settlement of *F. vesiculosus* in all treatments, although recolonisation occurs fastest during the settlement season (July's exclusion). Creed (1993) has the best evidence for *F. vesiculosus.* He suggests from extrapolation of data that there are a maximum of 26000 plants.m^{-2} available in the spore/germling bank in September, two months after settlement is supposed to cease.

5.1.3 Modelling Aims

As settlement of *S. balanoides* and *F. vesiculosus* is seasonal, the aim of this Chapter is to investigate single species models of the colonisation of bare rock by *F. vesiculosus* and *S. balanoides* in a seasonal environment. The seasonal component of the models is introduced into the most complicated models produced in Chapters 3 and 4. Phase locking is investigated as a possible mechanism for production of different solution types. The model for *F. vesiculosus* will include settlement into the system from a seed bank in the period outside the settlement season.

5.2 Modelling *S. balanoides* in a Seasonal Environment

5.2.1 The Model

In this section seaonality is added to the logistic growth model (see Chapter 3). A step function is used to model seaonality, with constant settlement during the season and none otherwise. Thus, the daily instantaneous settlement rate during the settlement season is defined as κ, then the renewal condition is written as

$$\sigma \hat{F}_t = \begin{cases} \frac{\hat{F}_t}{a_0}\left(1 - e^{-\kappa a_0 \Delta a}\right) & \text{Within the settlement season} \\ 0 & \text{Otherwise} \end{cases} \tag{5.1}$$

where σ is the incremental settlement. This is used with equations (3.5)-(3.7) and (3.11) to implement seasonal settlement in the logistic growth model.

Step functions of different lengths were used to simulate 'good' and 'bad' settlement. Settlement was assumed to be better if the period of settlement was longer. Three different periods were used to simulate 'good', 'average' and 'bad' settlement (see table 5.1).

Table 5.1: Settlement periods and strength of the years settlement for the three models.

Date of Settlement Season	Strength of Settlement	Number of Settlers
8th Apr - 12th Aug	'Good'	High
22nd Apr - 15th Jul	'Average'	Average
6th May - 17th Jun	'Bad'	Low

Fourier Transforms

Fast Fourier Transforms (FFTs) were taken to investigate the periodicity of solutions. This allows investigation into whether solutions are phase locked. A solution is phase locked when the natural period of the solution is synchronised with either the driving period or (sub-) harmonic of this period. When settlement is annual, the driving period of the model is 52 weeks or 1 year. It is necessary to look at the periodicity of the constant environment models to discern the natural period of the system. This technique was used to determine whether a solution is periodic or aperiodic.

The FFT is a technique used in Fourier Transforms to cut the time and computational power required to transform the data. The FFT algorithm requires far fewer additions and multiplications, as the number is proportional to $number * [log_2(number)]$ for FFT. For a normal Fourier algorithm the number of calculations required is $number^2$ (see Gonzalez & Woods, 1992, for a general review). The calculation of the FFT power spectra from the data was done using a program called FFT, which is part of the SOLVER suite of programs (©1994, STAMS, University of Strathclyde, Glasgow, G1 1XH, Scotland).

5.2.2 Simulation

General Results

These solutions are found when settlement occurs between the 22nd April and the 15th July. The steady state is oscillatory, as settlement only occurs during a set period of the year. Thus, all solutions are oscillatory and can be periodic (see figure 5.1) or aperiodic (see figure 5.2). Aperiodic solutions are found at the transition between the periods of oscillation, for example, when the period moves from one to two years or two to three years.

Increasing κ causes an increase in the amplitude of oscillation in the periodic

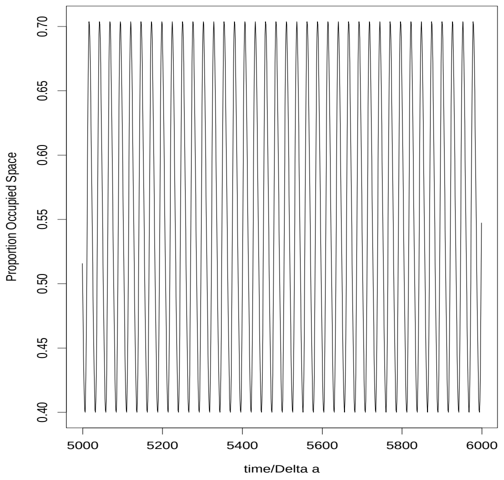

Figure 5.1: A periodic solution ($S = 0.95$, $\kappa = 10^2$).

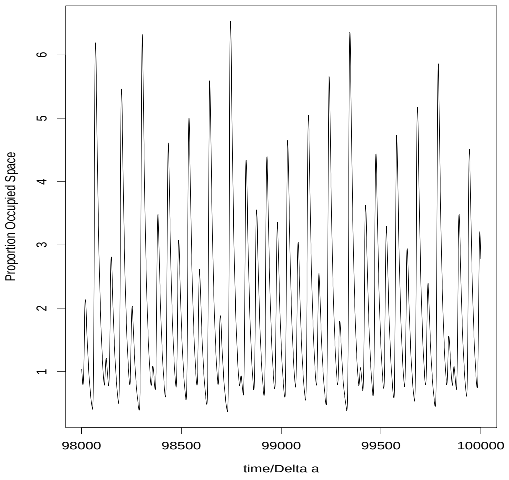

Figure 5.2: An aperiodic solution ($S = 0.95$, $\kappa = 1.5 * 10^3$).

Table 5.2: General results from the seasonal settlement model and the natural period produced using the same parameters in a constant environment, where the - indicates aperiodicity ($S = 0.95$).

Settlement Rate (κ)	Natural Period (weeks)	Period of Oscillations (weeks)	Amplitude of Oscillations	Solution Type
$1 * 10^6$	-	208	23.38	Periodic
$5 * 10^5$	-	208	23.37	Periodic
$1 * 10^5$	-	208	22.44	Periodic
$5 * 10^4$	-	208	19.79	Periodic
$2 * 10^4$	-	208	16.57	Periodic
$1 * 10^4$	106	-	-	Aperiodic
$6 * 10^3$	100	156	5.833	Periodic
$5 * 10^3$	99	156	5.514	Periodic
$2 * 10^3$	87	156	3.779	Periodic
$1.5 * 10^3$	84	-	-	Aperiodic
$1 * 10^3$	77	104	1.4303	Periodic
$5 * 10^2$	68	104	1.047	Periodic
$2.5 * 10^2$	62	52	0.230	Periodic
$1 * 10^2$	2	52	0.151	Periodic
$1 * 10^1$	2	52	0.025	Periodic

solutions. Aperiodic solutions are found at the change between annual periods (see table 5.2). The natural period shows that periodic solutions are phase locked to the next great harmonic of the driving period.

The aperiodic solutions were investigated using Fourier transforms. These solutions are produced when the natural and driving periods of oscillation are out of phase. If sums and differences of the natural and driving periods are present then the solutions are out of phase. If the natural period is not visible then the solution is phase locked.

When a periodogram of a periodic solution is calculated using FFT, a single peak and harmonics of that peak are found (see figure 5.3). As only the driving period and its harmonics are seen, the natural and driving period are in phase and the solution is phase locked. However, when the solution is aperiodic, many peaks are found with both the driving and natural periods present (see figure 5.4). Thus, the aperiodic solutions are not phase locked.

The age-class distribution given by the seasonal settlement model shows a similar picture to the unstable solutions of the logistic growth model with cohorts passing

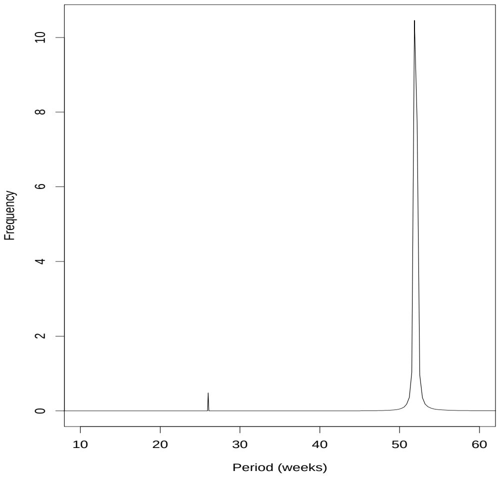

Figure 5.3: The periodogram of a periodic solution, where the natural period is 2 weeks ($S = 0.95$, $\kappa = 10^2$).

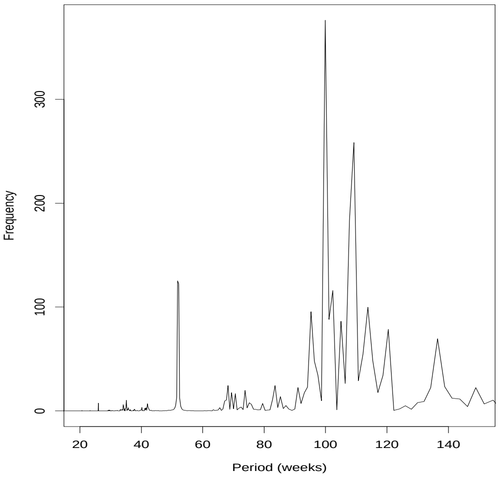

Figure 5.4: The power spectrum of an aperiodic solution, where the natural period is 84 weeks ($S = 0.95$, $\kappa = 1.5 * 10^3$).

through the age-classes.

There is a general decrease in the period and the amplitude of the oscillations of the solutions with decreasing survivorship (see table 5.3). The aperiodic solutions are again found at the changes in period of oscillations. The periodic solutions stabilise to a single amplitude more quickly as survivorship is decreased. The age-class distribution again shows cohorts moving through the age-classes, but as the survivorship is decreased the cohorts die at an earlier age and more cohorts are found.

Simulation of 'Good' and 'Bad' Settlement

There is a general increase in both amplitude and period with increasing κ (see figures 5.5 and 5.6). In the case of the amplitude the increase appears to be logistic. This logistic shape is not surprising as when κ is increased then $\sigma \to 1/a_0$. Thus, as σ reaches a limit then the period and amplitude will not increase further. The maximum period for $S = 0.95$ appears to be 208 weeks. When the period changes aperiodic solutions are found which accounts for the discontinuities in the figures. The natural period is generally less than the actual period suggesting that the solutions lock to the harmonic of the driving period that is greater that is greater than the natural period.

Table 5.3: The effect of decreasing the survivorship in the seasonal settlement model ($\kappa = 1 * 10^3$) and the natural period, where the - indicates aperiodicity.

Survivorship (S)	Natural Period (weeks)	Period of Oscillations (weeks)	Amplitude of Oscillations	Solution Type
0.99	262	260	5.579	Periodic
0.98	257	260	5.155	Periodic
0.97	93	-	-	Aperiodic
0.96	87	156	2.303	Periodic
0.955	77	-	-	Aperiodic
0.95	-	104	1.430	Periodic
0.90	2	52	0.623	Periodic
0.80	2	52	0.522	Periodic
0.70	2	52	0.219	Periodic
0.50	2	52	0.047	Periodic
0.30	2	52	0.017	Periodic
0.10	2	52	0.009	Periodic

The effect of changing the strength of settlement has little effect on the amplitude at low κ, the 'good' settlement always having a slightly larger amplitude. However, if $10^3 < \kappa < 5 * 10^4$, then 'good' settlement oscillates less than the 'average' and 'bad' settlement. This is because I could not find a solution for the 'good'

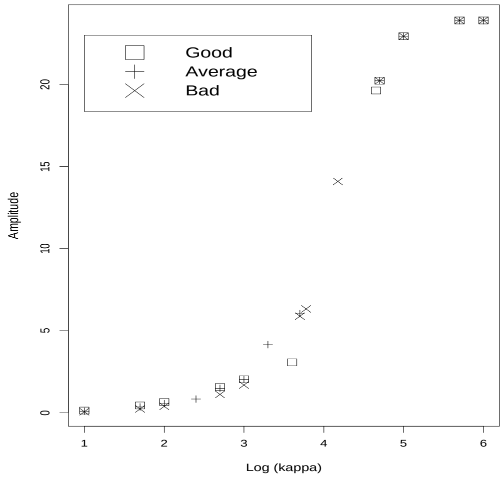

Figure 5.5: The amplitude of oscillations for models with different strengths of settlement.

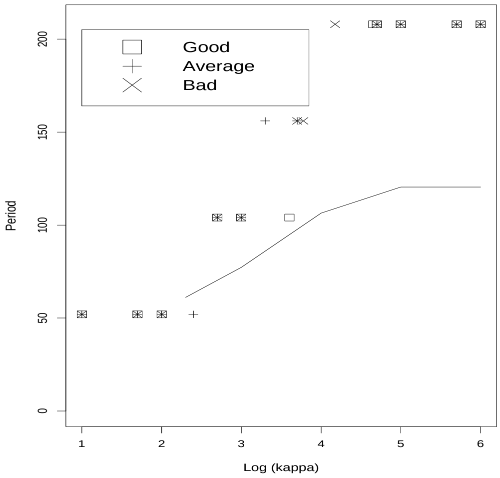

Figure 5.6: The period of oscillations for models with different strengths of settlement, where the solid line shows natural period.

settlement that was stable with a period of 156 weeks. The period of the ‘good’ settlement seems to jump straight from 104 to 208 weeks. Once $\kappa > 5 * 10^4$, the amplitudes are very similar.

5.2.3 Discussion

Two types of solution are produced when seaonality is added to the model, periodic 2-cycles and aperiodic. Although the model appears to produce 4- and 6-cycles solutions these decay to 2-cycles over after over 38,000 years ($> 10^6$ time units).

Periodic solutions are produced when the natural and driving periods of the solution are phase locked. These solutions oscillate with a period of $52n$ (where $n = 1, 2, 3, \ldots$). Aperiodic solutions are not phase locked and are found where the period is close to increasing from $52n \rightarrow 52(n + 1)$.

The mechanism that drives the model is the same as the model examined in Chapter 3. Increasing S increases the period and amplitude of the solutions. This is because increasing the survivorship increases the potential of a cohort to increase in area over time. This, as we know from Chapter 3, is a destabilising mechanism. Increasing S causes more individuals to survive to larger area and thus, the proportion of occupied space increases. This increases the amplitude of the fluctuations. As the occupied space is higher, increasing S causes the system to take longer to relax back to the state where more settlement can occur and thus the period of the solution is longer.

Increasing κ causes an increase in period and amplitude of the fluctuations. Again a similar explanation to the increase in S can be given. Increasing κ increases the density of individuals that settle, which increases the ability of the cohort to increase in area. As the cohort has a larger increase in area then the system requires longer to return to the same state, thus increasing the period of the oscillations.

The effect of ‘good’, ‘average’ and ‘bad’ settlement is not as clear. There is a general increase in amplitude and period when κ is increased in all of the settlement types. When $\kappa \leq 10^3$, the expected pattern is found with the longer settlement period having solutions with a slightly longer period and amplitude than other settlement types. This is consistent with the conclusions in Chapter 3 where we found that κ limited the area occupied at equilibrium at low values.

However, when $10^3 < \kappa \leq 10^5$ the 'bad' and 'average' solutions have larger period and amplitude than the 'good' settlement. This appears to be because this region is full of aperiodic solutions and it was hard to find any periodic solutions for these values of κ. Also this may be moving into a region where settlement is not limiting the proportional occupied space. When $\kappa \geq 10^5$ all the settlement types have very similar period and amplitude. This is because at high values of κ settlement does not limit the area occupied and thus these periods would be very similar as there is no difference in the area of an individual or survivorship.

5.3 Modelling *F. vesiculosus* in a Seasonal Environment

5.3.1 The Model

In this section seaonality is added to the parameterised model (see Chapter 4). Seasonal settlement is modelled in exactly the same way as for *S. balanoides* using a step function. The daily instantaneous settlement rate from the water column within the settlement season is defined as ζ, and 0 otherwise. In this case the settlement of fucoids is allowed outside the settlement season from a bank of propagules called the seed bank. To model the presence of the seed bank, all propagules that are not able to settle are assumed to enter the seed bank. These propagules suffer a constant mortality and can settle at a rate proportional to the available space outside the settlement season. Thus, the renewal condition is

$$\xi \hat{F}_t = \begin{cases} \hat{F}_t \left[1 - e^{\zeta \Theta c_0 \Delta t}\right] / (\Theta c_0) & \text{Within Settlement Season} \\ \Upsilon_t \hat{F}_t & \text{Otherwise} \end{cases} \tag{5.2}$$

where Υ_t is the number of propagules in the seed bank at time t. The seed bank renewal can be written as

$$\Upsilon_{t+\Delta t} = \begin{cases} \Upsilon_t \vartheta + \xi \left(1 - \hat{F}_t\right) & \text{Within Settlement Season} \\ \Upsilon_t \vartheta \left(1 - \hat{F}_t\right) & \text{Otherwise} \end{cases} \tag{5.3}$$

where ϑ is the survivorship of propagules in the seed bank from $t \rightarrow t + \Delta t$. Equations (5.2) and (5.3) are used with equations (4.15)-(4.18) and (4.20) to implement seasonal settlement in the model.

The amplitude and period of periodic solutions was investigated. If the solution was not periodic then the phase locking of the solution was investigated.

Different strengths of settlement were investigated using different lengths of step function. The longer the length of the step in the function the more propagules are available to settle. Thus, longer settlement periods mimic years with increases larval supply and *vice versa.* The period of settlement is assumed to be between the start of May and the end of July (Knight & Parke, 1950). Thus, an 'average' settlement period for *F. vesiculosus* is from the 6^{th} May - 15^{th} July in any given year. 'Good' and 'bad' settlement period are 6 weeks longer or shorter respectively (see table 5.4).

Table 5.4: Settlement periods and strength of the years settlement for the three models.

Date of Settlement Season	Strength of Settlement	Number of Settlers
22^{nd} Apr - 12^{th} Aug	'Good'	High
6^{th} May - 15^{th} Jul	'Average'	Average
20^{th} May - 17^{th} Jun	'Bad'	Low

5.3.2 Simulation

In this section, the mechanism driving the dynamics produced by the model is examined. This simulation uses runs with 'good' settlement, *ie* the settlement season is between 22^{nd} April and 12^{th} August. Investigations are done of the effect of the seed bank survivorship (ϑ) and the daily instantaneous settlement rate (ζ) on the type, period and amplitude of solutions. Different strengths of settlement will then be considered by shortening the step function.

General Results

The steady state in this model is oscillatory and thus, all the solutions are oscillatory. A wide range of behaviour is exhibited by this model, including periodic, 4-cycle, 28-cycle and aperiodic solutions (see figures 5.7 - 5.10 respectively).

The mechanism that drives this model is different to that found in the barnacle model. Settlement into this system is from 2 sources and periodic solutions can have settlement from outside and/or the seed bank in a regular order (see

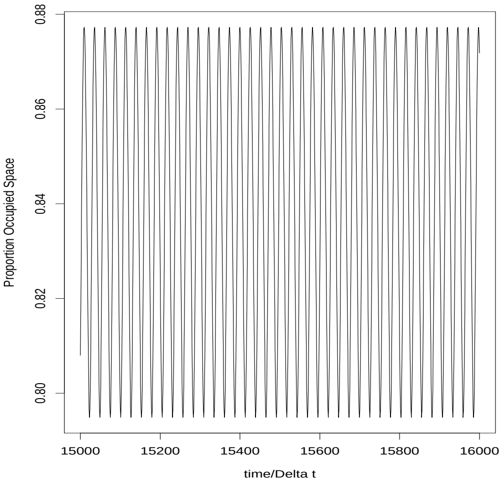

Figure 5.7: A periodic solution ($\zeta = 5$, $\vartheta = 0.9$).

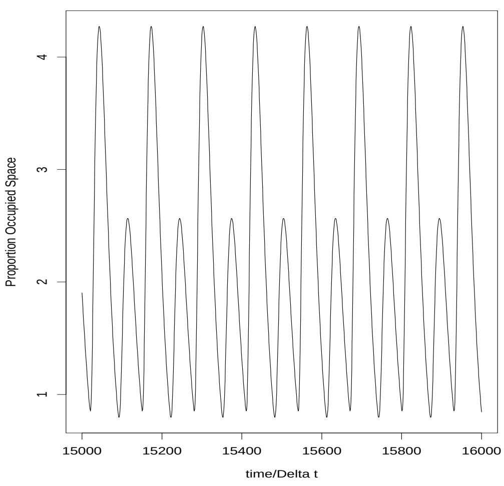

Figure 5.8: A 4-cycle solution ($\zeta = 80$, $\vartheta = 0.9$).

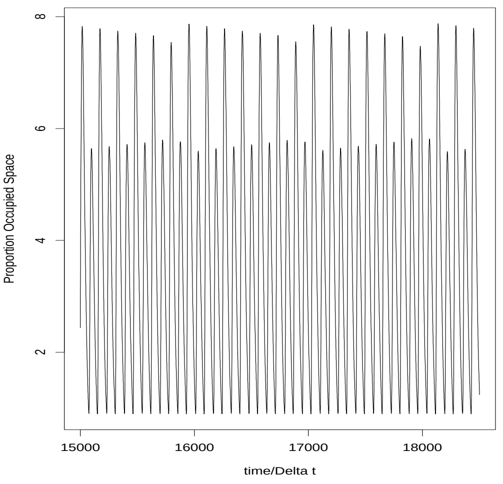

Figure 5.9: A 28-cycle solution ($\zeta = 230$, $\vartheta = 0.9$).

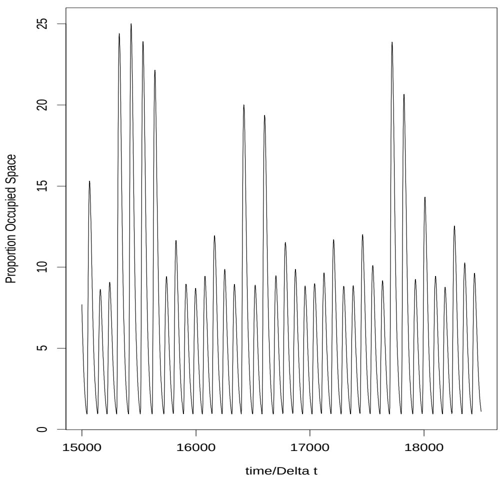

Figure 5.10: An aperiodic solution ($\zeta = 5000$, $\vartheta = 0.9$).

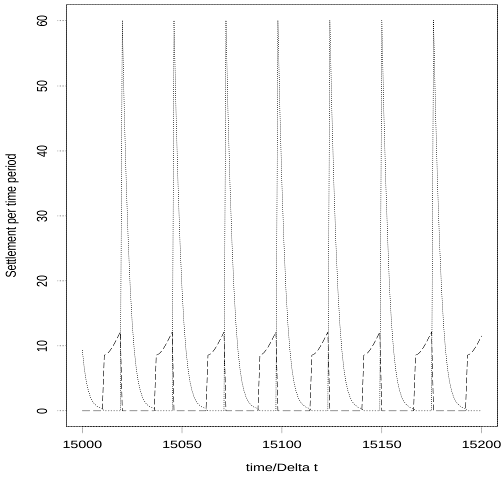

Figure 5.11: Settlement from the seed bank (dotted line) and from outside (dashed line) into a periodic solution ($\zeta = 5$, $\vartheta = 0.9$).

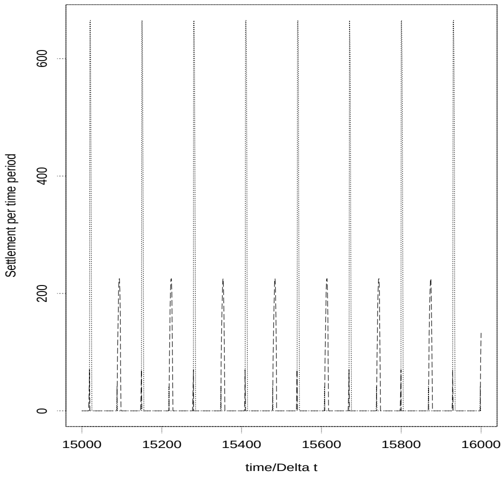

Figure 5.12: Settlement from the seed bank (dotted line) and from outside (dashed line) into a 4-cycle solution ($\zeta = 80$, $\vartheta = 0.9$).

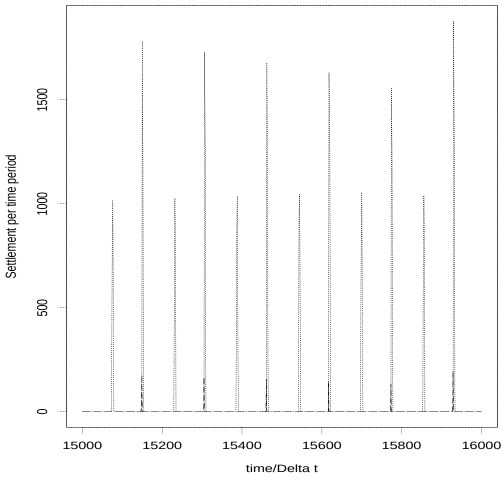

Figure 5.13: Settlement from the seed bank (dotted line) and from outside (dashed line) into a 6-cycle solution ($\zeta = 230$, $\vartheta = 0.9$).

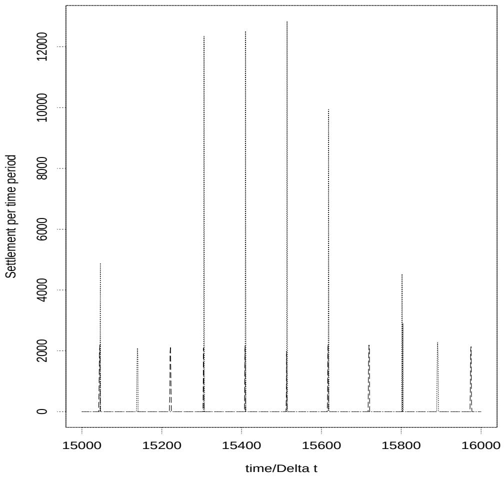

Figure 5.14: Settlement from the seed bank (dotted line) and from outside (dashed line) into an aperiodic solution ($\zeta = 5000$, $\vartheta = 0.9$).

for example figure 5.11). Thus, phase locking occurs. 4-cycle solutions have alternate settlement from the seed bank and from outside the system (see figure 5.12). These solutions are also phase locked, but are locked to one of the subharmonics of the driving period. A similar situation is found for the 28-cycle, with settlement coming from outside the system and smaller settlement coming from the seed bank (see figure 5.13). Again these solutions are phase locked to one of the sub-harmonics of the driving period. The aperiodic solutions are not phase locked, settlement can come from either source and has no pattern (see figure 5.14). It is useful to note at this stage that the majority of settlement is from the seed bank. This is not a realistic situation, on a rocky shore most of the plants come from the heavy output of propagules settling during the settlement season. This suggests that in these simulations the seed bank survivorship (ϑ) needs to be reduced.

The input into the system from a combination of two sources drives the dynamics. This can be seen by looking at the behaviour of the model as the seed bank is shut down. At high seed bank survivorship the solutions are not simple 2-cycles. As the survivorship is decreased then the solutions become stable and the amplitude and period decrease (see table 5.5). However, decreasing ϑ further cause first unstable solutions then an increase in the period and amplitude of the solutions (see table 5.5).

Table 5.5: Decreasing the survivorship in the seasonal settlement model ($\zeta = 5 * 10^2$, natural period is 147 weeks).

Seed Bank Survivorship (ϑ)	Period of Oscillations (weeks)	Amplitude of Oscillations	Solution Type
0.99	-	-	Aperiodic
0.97	-	-	4-cycle
0.95	156	2.484	Periodic
0.90	104	0.579	Periodic
0.85	-	-	Aperiodic
0.80	-	-	Aperiodic
0.70	-	-	4-cycle
0.60	156	1.527	Periodic
0.50	156	1.547	Periodic
0.30	156	1.551	Periodic
0.10	156	1.551	Periodic
0	156	0.009	Periodic

Further investigation of this shows that phase locking and the seed bank combine to produce these dynamics. When $\zeta = 5 * 10^2$, the aperiodic solution produced when $\vartheta = 0.99$ show that the natural and driving periods of the solution are not phase locked. Settlement occurs from both the seed bank and outside the system, but does not occur in an orderly pattern. Thus, creating this aperiodic solution.

4-cycles are produced by input from both these settlement sources. The natural period of the oscillations doubled, locks to the some multiple of the driving period. 2-cycles can occur by 2 different mechanisms. Settlement can be entirely from outside, for example $\zeta = 5 * 10^2$ and $\vartheta = 0$ or can be entirely from the seed bank, for example $\zeta = 5 * 10^2$ and $\vartheta = 0.9$. Settlement entirely from the seed bank causes larger oscillations as the space is filled more quickly when the seed bank survivorship is high. This is because the seed bank accumulates a higher number of propagules. As the seed bank survivorship is decreases, the period and amplitude of solutions decreases initially. This is because the settlement from the seed bank is less. However, when the seed bank survivoship is low then the period increases as more free space becomes available and a larger proportion of the settlement from outside can settle.

Finally it is useful to note increasing settlement (ζ) is generally destabilising (see table 5.6) as in the case of the barnacle model. This is hardly surprising as from Chapter 4 we know that increasing the number of propagules available to settle, increases the potential increase in area of a cohort and is therefore a destabilising mechanism.

Table 5.6: Increasing settlement in the seasonal settlement model and the natural period where the - indicates aperiodicity ($\vartheta = 0.9$).

Settlement Rate (κ)	Natural Period (weeks)	Period of Oscillations (weeks)	Amplitude of Oscillations	Solution Type
$1 * 10^5$	-	208	12.12	Periodic
$5 * 10^4$	-	208	12.12	Periodic
$1 * 10^4$	-	208	12.06	Periodic
$5 * 10^3$	-	-	-	Aperiodic
$1 * 10^3$	156	-	-	Aperiodic
$5 * 10^2$	145	-	-	Aperiodic
$1 * 10^2$	122	156	2.565	Periodic
$5 * 10^1$	112	104	0.579	Periodic
$1 * 10^1$	91	104	0.361	Periodic
$5 * 10^0$	2	52	0.041	Periodic
$1 * 10^0$	2	52	0.017	Periodic

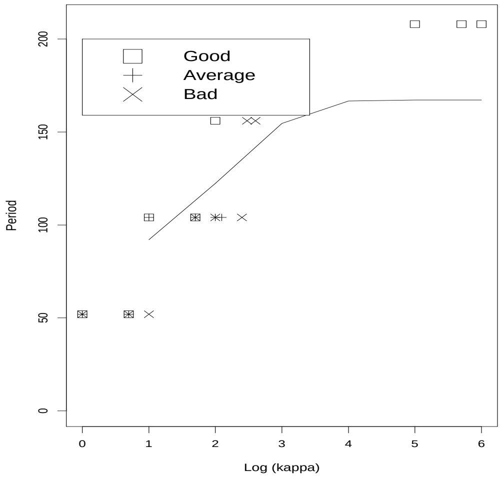

Figure 5.15: The period of oscillations for models with different strengths of settlement.

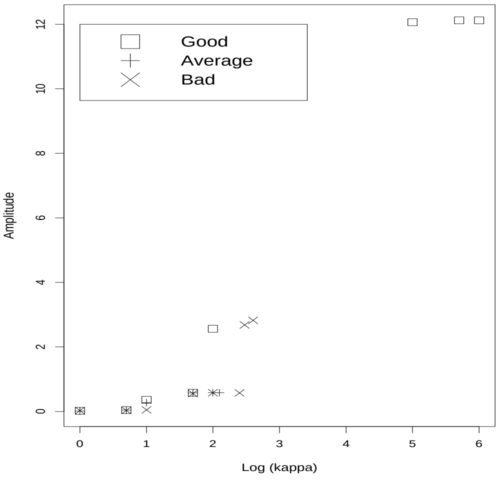

Figure 5.16: The amplitude of oscillations for models with different strengths of settlement, where the solid line indicates the natural period.

Simulation of 'Good' and 'Bad' Settlement

As can be seen from figures 5.15 and 5.16, there is a general increase in the period and amplitude of oscillations with increasing settlement. This is hardly surprising as we indicated in Chapter 4 that increasing the settlement rate was destabilising. It is very hard to find periodic solutions for the 'average' and 'bad' settlement strength above a settlement rate of about 400. However, at settlement levels below this there appears to be a generally higher period and amplitude for the higher strengths of settlement (see figures 5.15 and 5.16). It is generally the case that the natural period is lower than the solutions and thus locks to the next highest harmonic of the driving period.

5.3.3 Discussion

Adding seaonality to these models causes the steady state to be oscillatory, as settlement only occurs during a set period of the year. Thus, stable equilibria cannot be reached as the area entering the system cannot balance the area leaving the system throughout the year.

A much wider range of dynamics are produced by the model when seaonality is added. Stable periodic 2-cycle, anything from 4- to 28- cycle and aperiodic solutions are produced. This is because of the two sources of settlement in this model, the seed bank and from outside.

The mechanism that drives this model is more complicated than the seasonal barnacle model. This is because of the two separate sources of settlement. The type of solution produced is to do with the degree of phase locking between the natural and driving periods. However, the seed bank also influences the dynamics and settlement can occur at any stage from this bank. There are two ways of obtaining periodic solutions, although all of these solutions are phase locked. Firstly, the seed bank and the natural period of the solutions are phase locked to the driving period of the solution. Secondly, either the seed bank or the outside settlement is phase locked to the driving period of the solution. Point-cycles are produced when the natural period of the solution is locked to a sub-harmonic of the driving period. The lower the sub harmonic the higher the number of points. Aperiodic solutions are not phase locked and are produced when settlement can occur from either of the two source of settlement with no obvious pattern.

Increasing the settlement rate into the system increases the period and amplitude of the cycles. This is hardly surprising as we showed that increasing the settlement rate was a destabilising mechanism in Chapter 4.

Decreasing the seed bank survivorship is first stabilising then destabilising. This is because of the free space is able to drop to a lower value when there is no seed bank and thus the free space is filled with more propagules. The seed bank survival used in the simulations is probably too high as most of the settlement appears to come from the seed bank in all the runs. This suggests that if there is a seed bank on a rocky shore it would suffer large mortality and have low probabilities of escape.

Different strengths of settlement cause generally little difference in the model. Generally the ‘good’ settlement had a higher period and amplitude than the lower settlement. This is hardly surprising as again the ‘good’ settlement implies that although the rate of settlement is the same more propagules are able to settle. This is obviously destabilising as shown in Chapter 4.

5.4 Discussion

In this section we will compare the barnacle and fucoid models and then examine both of these models in a biological context. Before embarking on this it is useful to note that these models have all the biological shortcomings expressed in the discussions of Chapters 3 and 4, except of course they both have distinct discrete settlement periods.

The models of barnacle and fucoid settlement have fairly similar dynamics despite the difference in formulation. This is highlighted in the discussions of Chapter 3 and 4. When a seasonal component is added to the model the behaviour is still similar. Both models produce cyclic and aperiodic dynamics and the phase locking mechanism is similar. However, the big difference between the models is caused by the addition of a seed bank to the fucoid model. This causes a much richer spectrum of dynamics to be found in the fucoid model as there are three cyclical mechanisms that need to phase lock.

Biologically these models are still very unrealistic and require addition of many parameters (see discussion of Chapters 3 and 4). The very simple components of biological dynamics that are predicted is that the populations cycle or produce some kind of aperiodic behaviour. However, the proportional occupied space values of 23 and 12 for the barnacle and fucoids respectively (see tables 5.2 and 5.6) seem rather high. In effect, this means that on a shore this would indicate 23 layers of barnacles on top of each other or 12 times the maximum amount of canopy that an area of bare rock can support. This suggests that both of these models exhibit over-occupancy at high settlement rates. The reason that this occurs is the absence of density-dependent survivorship from these models. This would dampen the oscillations in both models.

The main settlement of fucoids is in a known period between May and July (Knight & Parke, 1950). If the survivorship of the seed bank is low, then settlement in the model is driven mainly by the seasonal settlement. However, if the seed bank survivorship is high, then settlement in the model is mainly from the seed bank and the seasonal component has little effect. As this is not the case in the real system, it is possible to hypothesise that if a seed bank exists the mortality associated with propagules in the bank is very high. However, experimental tests of this hypothesis are difficult as the is no conclusive evidence for the existence of a seed bank. This is because it is impossible to tell propagules apart on the shore, they have to be grown in the laboratory.

Part III

Two Species Models

Chapter 6

A Two Species Model for *F. vesiculosus* and *S. balanoides* in a Constant Environment

6.1 Introduction

6.1.1 General Introduction

On moderately exposed rocky shores *S. balanoides* and *F. vesiculosus* are know to compete for space. This competition results in the presence or absence of each of these species having a direct effect on the abundance of the other.

The limpet, *P. vulgata*, is a keystone predator in the system studied. It grazes upon the microalgal film, removing juvenile fucoids. Inhibition of this grazing has a marked effect on the abundance of fucoids. This has been illustrated many times, but probably the best example was when Jones (1948) removed limpets from a strip of shore $5m$ wide. He found that there was a massive increase in the biomass of algae in that strip.

The grazing pressure of limpets is decreased by the presence of *S. balanoides* (Hawkins & Hartnoll, 1982b). This is because of increased seabird predation of limpets (Feare & Summer, 1985) and aggregation of limpets elsewhere where grazing is less disrupted by a barnacle matrix or dessication stress is lower (Hartnoll & Hawkins, 1985). Once the fucoids are greater than about 3cm in length then they are too big to be grazed by limpets (Proud, 1994) and are known as 'escapes'. Thus, the presence of barnacles enhance the the ability of fucoids to settle an area of rock.

Once the fucoids have escaped grazing by *P. vulgata*, they continue to grow on the barnacle matrix. This attachment is not as secure as the bare rock, so once the plants reach a certain size many are lost (Proud, 1994). The sweeping affect of the canopy of these plants disrupts the feeding of the barnacles, by the buffeting effect and disruption of water flow (Barnes, 1955; Proud, 1994). Thus, many of the older barnacles die. Limpets tend to aggregate under the fucoid canopy as dessication stress is lower (Hartnoll & Hawkins, 1985). The sweeping effect of the canopy (Barnes, 1955; Hawkins, 1983; Jenkins, 1995) and limpet bulldozing (Miller & Carefoot, 1989) inhibits the settlement of new barnacles. Thus, the presence of fucoids inhibits the ability of barnacles to colonise an area of rock.

6.1.2 Modelling

Vast amount of time and money have been spent on modelling two species interactions in terrestrial and marine closed systems. However, very little work has been done on two species models of rocky shores.

Iwasa & Roughgarden (1986) looked at interspecific competition among metapopulations with space-limited subpopulations. Their metapopulation is not open but each of the subpopulations are, with larvae produced being contributed to a common pool. The general results are the number of species found is less than or equal to the number of distinct habitat types and where species coexist each species will have areas where their productivity relative to their larval mortality is higher than the other species. They examined the two species case. If both of the habitats are net sources of larvae, then the interspecific competition is the same as the classic Lotka-Volterra models. However, if one of these habitats is a sink then the existence of a species may require its competitor; a species that cannot invade an empty space may be able to invade if the other species is present; and one invading species may result in the extinction of both species.

Possingham & Roughgarden (1990) modelled mesoscale current features and coastal habitats in order to predict the distribution and abundance of the barnacle *Balanus glandula*. The adults on the coast are limited by recruitment, mortality and the availability of suitable habitat. They found that the persistence of a population was dependent upon the amount of suitable habitat; larval mortality; the along shore flow field; and initial conditions.

6.1.3 Modelling Aims

As competition on the rocky shore is essentially for the resource of space, two dimensional models can be constructed. The aim of this chapter is to produce a two species model of *F. vesiculosus* and *S. balanoides* in a constant environment. This discrete time model is based upon the single species models produced in Chapters 3 and 4. However, here the models are linked using generalised assumptions of interactions between the two species taken from the literature. This discrete time model represents the sixth to the second stage of the cycle shown in figure 1.2.

Investigation of this model will be mainly by simulation despite the fact that the steady states are derived. Simulation will use a set of parameters found in the literature. These will be varied by the maximum degree of error associated with the parameter. The mechanisms controlling the dynamics will be investigated using the behaviour of the sub-models.

6.2 The Model

This two species model was constructed by joining the single species models for *S. balanoides* and *F. vesiculosus* described in the previous chapters. The case of the constant environment is examined as it is a more simple case.

This model makes a number of assumptions:

1. The survivorship functions of *F. vesiculosus* (S^F) and *S. balanoides* (S^B) are known and constant with respect to time and age.
2. The mean size range of *F. vesiculosus* sizes is known.
3. The area at age function of *S. balanoides* is known.
4. Negative free space cannot exist.
5. All individuals in the same age-/size- class are of the same size.
6. There is a maximum canopy area that a given area of rock can support.
7. *S. balanoides* enhances the settlement of *F. vesiculosus* as a known function.
8. *F. vesiculosus* decreases the settlement of *S. balanoides* as a known function.
9. Settlement is constant and is only into the first age-/size- class.
10. *F. vesiculosus* can only be promoted one size-class with probability P or remain in the same class with probability $1 - P$.
11. *F. vesiculosus* in the final size-class (Q+1) cannot be promoted or demoted.
12. *S. balanoides* in the final age-class (N+1) all die at the end of that time step.

The free space at time t (F_t) is the total available area (A) minus the occupied space (A_t), *ie*

$$F_t = [A - A_t]^+$$

where the plus denotes that free space cannot be negative. The occupied space is the sum of the area occupied by fucoids at time t (C_t) and the area occupied by barnacles at time t (B_t), or

$$F_t = [A - (B_t + C_t)]^+ . \tag{6.1}$$

B_t can be expressed as the sum of the area of an individual barnacle in age-class k (a_k^B) multiplied by the number in age-class k at time t ($n_{k,t}^B$)

$$B_t = \sum_{k=0}^{N} a_k^B n_{k,t}^B. \tag{6.2}$$

In a similar way C_t can be expressed, however it is necessary to scale the area of rock that an individual occupies (a_j^F) to the actual individual canopy area (c_j) using a constant, Θ, where $\Theta = a_j^F / c_j$. Thus C_t can be expressed as

$$C_t = \sum_{j=0}^{Q} \Theta c_j n_{j,t}^F \tag{6.3}$$

where $n_{j,t}^F$ is the number of plants in size-class j at time t. The update rules for both barnacles and fucoids are easy to describe. These rules model the population for every age-/size- class apart from $j, k = 0$. The barnacles will age at a constant rate Δa which is equal to the time step Δt. If a proportion S^B survive in the interval $t \to t + \Delta t$, then

$$n_{k,t+\Delta t}^B = S^B n_{k-1,t}^B \qquad k = 1, 2, \ldots, N. \tag{6.4}$$

A similar argument is used for the fucoids. If S^F is the proportion that survive in the interval $t \to t + \Delta t$, P of which are promoted, then

$$n_{j,t+\Delta t}^F = P S^F n_{j-1,t}^F + (1 - P) S^F n_{j,t}^F \qquad j = 1, 2, \ldots, Q - 1 \tag{6.5}$$

$$n_{Q,t+\Delta t}^F = P S^F n_{Q-1,t} + S^F n_{Q,t}^F. \tag{6.6}$$

Note that as individuals cannot be promoted from size-class Q, so a different update rule is required and that promotion happens implicitly at the end of a time step.

The renewal conditions are slightly more complicated to construct and assume that settlement is proportional to free space. An assumption is made that the settlement of barnacles is inhibited by fucoids. Thus, barnacle settlement is related to the area occupied by fucoids and the incremental settlement (or settlement per proportional space per unit time, σ) *ie* $f_1(\sigma, C_t)$. A piece wise function with 2 thresholds is used to model this relationship. Below the lower barnacle threshold (α) fucoids do not affect barnacle settlement and above the upper barnacle threshold (β) no barnacles can settle. Thus, if

$$n^B_{0,t+\Delta t} = f_1(\sigma, C_t)F_t \tag{6.7}$$

where,

$$f_1(\sigma, C_t) = \begin{cases} \sigma & 0 \leq C_t < \alpha \\ \left[\frac{\alpha - C_t}{\beta - \alpha} + 1\right]\sigma & \alpha \leq C_t < \beta \\ 0 & \beta \leq C_t. \end{cases} \tag{6.8}$$

A graphical representation of equation (6.8) can be seen in figure 6.1.

A similar argument can be constructed for the renewal condition for the fucoids. If ξ is the incremental settlement (or settlement per proportional space per unit time) then the renewal condition for the fucoids can be written as

$$n^F_{0,t+\Delta t} = f_2(\xi, B_t)F_t + (1-P)S^F n^F_{0,t} \tag{6.9}$$

where,

$$f_2(\xi, B_t) = \begin{cases} 0 & 0 \leq B_t < \gamma \\ \left[\frac{B_t - \gamma}{\delta - \gamma}\right]\xi & \gamma \leq B_t < \delta \\ \xi & \delta \leq B_t \end{cases}, \tag{6.10}$$

and γ and δ are the lower and upper fucoid interaction thresholds respectively. A graphical representation of equation (6.10) can be seen in figure 6.2. It is useful to note that $0 \leq \alpha, \beta, \delta, \gamma \leq 1$, $\alpha \leq \beta$ and $\gamma \leq \delta$.

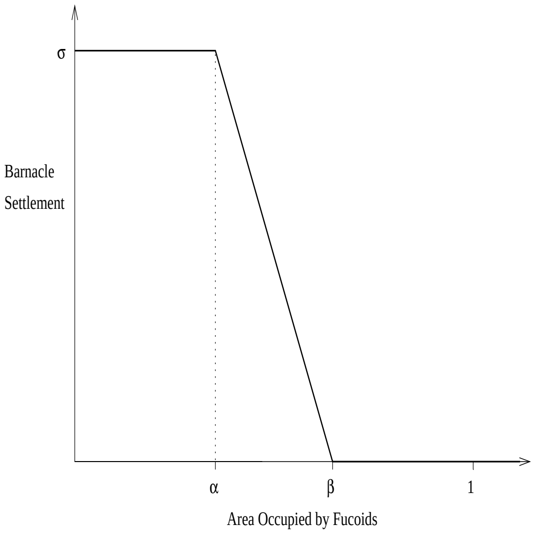

Figure 6.1: The Barnacle Settlement Function.

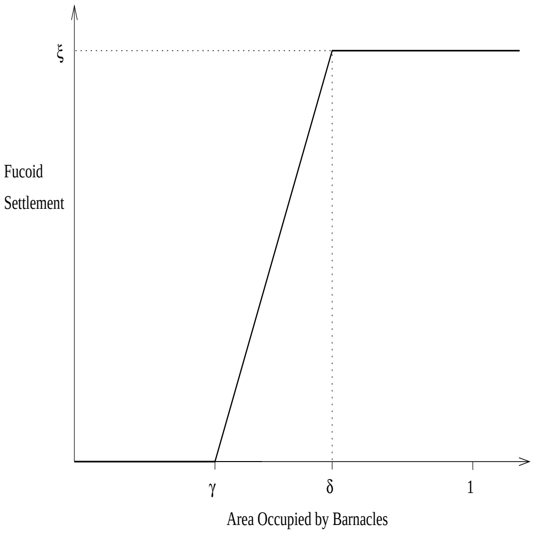

Figure 6.2: The Fucoid Settlement Function.

The total available area for occupation, A, is unlikely to be known. Thus, density and proportional space are modelled by diving by A. If the density ($numbers/m^2$) of barnacles in age-class k at time t is defined as $\rho^B_{k,t}$, the density of fucoids in size-class j at time t as $\rho^F_{j,t}$, and the $\hat{}$ denotes proportional space, then

$$\begin{aligned}
\rho^B_{k,t} &= n^B_{k,t}/A. \\
\rho^F_{j,t} &= n^F_{j,t}/A. \\
\hat{F}_t &= F_t/A. \\
\hat{B}_t &= B_t/A. \\
\hat{C}_t &= C_t/A.
\end{aligned}$$

where

$$\begin{aligned}
\hat{F}_t &= [1 - (\hat{B}_t + \hat{C}_t)]^+ && (6.11) \\
\hat{B}_t &= \sum_{k=0}^{N} a_k \rho^B_{k,t} && (6.12) \\
\hat{C}_t &= \sum_{j=0}^{Q} \Theta c_j \rho^F_{j,t}. && (6.13)
\end{aligned}$$

Combining equations (6.4) - (6.13) allows the model can be expressed as a series of 5 equations relating density, *ie*

$$
\begin{aligned}
\rho^B_{0,t+\Delta t} &= f_1(\sigma, \hat{C}_t)\hat{F}_t && && (6.14)\\
\rho^B_{k,t+\Delta t} &= S^B \rho^B_{k-1,t} && k = 1, 2, \ldots, N && (6.15)\\
\rho^F_{0,t+\Delta t} &= f_2(\xi, \hat{B}_t)\hat{F}_t + (1-P)S^F\rho^F_{0,t} && && (6.16)\\
\rho^F_{j,t+\Delta t} &= PS^F\rho^F_{j-1,t} + (1-P)S^F\rho^F_{j,t} && j = 1, 2, \ldots, Q-1 && (6.17)\\
\rho^F_{Q,t+\Delta t} &= PS^F\rho^F_{Q-1,t} + S^F\rho^F_{Q,t}. && && (6.18)
\end{aligned}
$$

where,

$$
f_1(\sigma, \hat{C}_t) = \begin{cases} \sigma & 0 \le \hat{C}_t < \alpha \\ \left[\frac{\alpha - \hat{C}_t}{\beta - \alpha} + 1\right]\sigma & \alpha \le \hat{C}_t < \beta \\ 0 & \beta \le \hat{C} \end{cases} \qquad (6.19)
$$

$$
f_2(\xi, \hat{B}_t) = \begin{cases} 0 & 0 \le \hat{B}_t < \gamma \\ \left[\frac{\hat{B}_t - \gamma}{\delta - \gamma}\right]\xi & \gamma \le \hat{B}_t < \delta \\ \xi & \delta \le \hat{B}_t. \end{cases} \qquad (6.20)
$$

6.2.1 Settlement Functions

Clearly, as in Chapters 3 and 4, the incremental settlement cannot increase without bound, as this would produce spurious stability boundaries and be biologically unrealistic. So, in this case a similar argument is used as in the single species. The relationship between incremental and daily instantaneous settlement rate is assumed to be asymptotic (see Chapters 3 and 4 for a full description).

If κ and ζ are the the rates at which cyprids/propagules become available to settle from the water column $m^{-2}.d^{-1}$ for barnacles and fucoids respectively, then we define the settlement functions as

$$
\begin{aligned}
\sigma &= \frac{1}{a_0}\left(1 - e^{-\kappa a_0 \Delta t}\right) && (6.21)\\
\xi &= \frac{1}{\Theta c_0}\left(1 - e^{-\zeta \Theta c_0 \Delta t}\right). && (6.22)
\end{aligned}
$$

6.3 Derivation of the Steady States

The steady states of this model are fairly complicated, thus inferences on the mechanisms and dynamics are difficult to draw. As a result, the steady states will be derived, although little investigation of these states will be done. The derivation is done in a similar way to the previous models. At equilibrium

$$\begin{aligned}
\hat{F}_{t+\Delta t} &= \hat{F}_t = \hat{F}^* \\
\hat{B}_{t+\Delta t} &= \hat{B}_t = \hat{B}^* \\
\hat{C}_{t+\Delta t} &= \hat{C}_t = \hat{C}^* \\
\rho^B_{k,t+\Delta t} &= \rho^B_{k,t} = \rho^{B*}_k \\
\rho^F_{j,t+\Delta t} &= \rho^F_{j,t} = \rho^{F*}_j .
\end{aligned}$$

Substitution of the steady states into equations (6.14) - (6.15) and a little simple algebra gives the steady states for the barnacles as

$$\rho_0^{B*} = f_1(\sigma, \hat{C}^*)\hat{F}^* \tag{6.23}$$

$$\rho_k^{B*} = l_k \rho_0^{B*} \qquad k = 1, 2, \ldots, N \tag{6.24}$$

where $l_k = \left(S^B\right)^k$. Similarly the steady state values of fucoids are found by substitution of state state variables into equations (6.16) - (6.18). A little simple algebra gives

$$\rho_0^{F*} = \frac{f_2(\xi, \hat{B}^*)\hat{F}^*}{\psi} \tag{6.25}$$

$$\rho_j^{F*} = \phi_j \rho_0^{F*} \qquad j = 1, 2, \ldots, Q-1 \tag{6.26}$$

$$\rho_Q^{F*} = \hat{\phi}_Q \phi_{Q-1} \rho_0^*. \tag{6.27}$$

where,

$$\begin{aligned}
\psi &= 1 - (1-P)S^F, \\
\phi_j &= \left(\frac{PS^F}{\psi}\right)^j
\end{aligned}$$

and

$$\hat{\phi}_Q = \frac{PS^F}{1-S^F}.$$

There are two piece functions in the steady states used to link area occupied by fucoids to the barnacle settlement (see equation (6.8)) and area occupied by barnacles to the fucoid settlement (see equation (6.10)). Thus, nine separate cases of the steady states must be derived (see table 6.1). When each case is derived only the calculation of ρ_0^{B*} and ρ_0^{F*} are stated as the calculation of the remaining age- or size- classes is done using equations (6.24), (6.26) and (6.27).

Table 6.1: The steady states.

	$0 \leq \hat{C}^* < \alpha$	$\alpha \leq \hat{C}^* < \beta$	$\beta \leq \hat{C}^*$
$0 \leq \hat{B}^* < \gamma$	Case 1	Case 2	Case 3
$\gamma \leq \hat{B}^* < \delta$	Case 4	Case 5	Case 6
$\delta \leq \hat{B}^*$	Case 7	Case 8	Case 9

Case 1

When $0 \leq \hat{C}^* < \alpha$ then $f_1(\sigma, \hat{C}^*) = \sigma$ and when $0 \leq \hat{B}^* < \gamma$ then $f_2(\xi, \hat{B}^*) = 0$. Let

$$\begin{aligned} A_0^B &= \sum_{k=0}^{N} a_k l_k \\ A_0^F &= \sum_{j=0}^{Q-1} \Theta c_j \phi_j + \Theta c_Q \phi_{Q-1} \hat{\phi}_Q. \end{aligned}$$

Substitution of equations (6.24) and (6.26) into (6.11) gives

$$\hat{F}^* = [1 - (\hat{B}^* + \hat{C}^*)]^+ \tag{6.28}$$

where

$$\hat{B}^* = \rho_0^{B*} A_0^B, \tag{6.29}$$

and

$$\hat{C}^* = \rho_0^{F*} A_0^F. \tag{6.30}$$

The incremental settlement is σ, and thus, from equation (6.23)

$$\begin{aligned} \rho_0^{B*} &= \sigma \left[1 - (A_0^B \rho_0^{B*} + A_0^F \rho_0^{F*})\right] \\ &= \frac{1 - A_0^F \rho_0^{F*}}{1/\sigma + A_0^B}. \end{aligned} \tag{6.31}$$

When $f_2(\xi, \hat{B}^*) = 0$ then $\rho_0^{F*} = 0$ and there are no fucoids present at the steady state. Thus, from equation (6.31)

$$\rho_0^{B*} = \frac{\sigma}{1 + \sigma A_0^B}. \tag{6.32}$$

It is useful to note that, not unsurprisingly, the equilibrium steady state found when there are no fucoid propagules is the same as the steady state found in the single species barnacle model.

Case 2

Case 2 is found when $\alpha \leq \hat{C}^* < \beta$ and $0 \leq \hat{B}^* < \gamma$. Thus, $f_1(\sigma, \hat{C}^*) = \sigma[(\beta - \hat{C}^*)/(\beta - \alpha)]$ and $f_2(\xi, \hat{B}^*) = 0$. If $f_2(\xi, \hat{B}^*) = 0$, then $\hat{C}^* = 0$ and $\rho_0^{F*} = 0$. Substitution into equation (6.23) and simplification gives

$$\rho_0^{B*} = \frac{\sigma\beta}{\beta - \alpha + \sigma\beta A_0^B} \tag{6.33}$$

Case 3

Case 3 is found when $\beta \leq \hat{C}^*$ and $0 \leq \hat{B}^* \leq \gamma$. Thus, the settlement of barnacles and fucoids are $f_1(\sigma, \hat{C}^*) = 0$ and $f_2(\xi, \hat{B}_t) = 0$ respectively. This case obviously results in the zero steady state.

Case 4

Case 4 is found when $0 \leq \hat{C}^* < \alpha$ and $\gamma \leq \hat{B}^* < \delta$. Thus, the settlement of barnacles and fucoids is $f_1(\sigma, \hat{C}^*) = \sigma$ and $f_2(\xi, \hat{B}^*) = \xi(\hat{B}^* - \gamma)(\delta - \gamma)$ respectively. Combining equations (6.25) and (6.28) - (6.30) and solving for ρ_0^{F*} gives

$$\rho_0^{F*} = \frac{\xi\left(\rho_0^{B*}A_0^B - (\rho_0^{B*}A_0^B)^2 - \gamma + \gamma\rho_0^{B*}\right)}{\psi\delta - \psi\gamma + \xi\rho_0^{B*}A_0^BA_0^F - \xi\gamma A_0^F}. \tag{6.34}$$

Similarly, combining equations (6.23) and (6.28) - (6.30) and solving for ρ_0^{F*} gives

$$\rho_0^{F*} = -\frac{\rho_0^{B*} - \sigma + \sigma\rho_0^{B*}A_0^B}{\sigma A_0^F}. \tag{6.35}$$

As equations (6.34) and (6.35) are equal, combination gives a quadratic in ρ_0^{B*}. This can be solved using the quadratic formula and the two solutions back substituted into equation (6.34) or (6.35) to give ρ_0^{F*}.

Case 5

Case 5 is found when $\alpha \leq \hat{C}^* < \beta$ and $\gamma \leq \hat{B}^* < \delta$. Thus, the barnacle and fucoid settlement is $f_1(\sigma, \hat{C}^*) = \sigma(\beta - \hat{C}^*)/(\beta - \alpha)$ and $f_2(\xi, \hat{B}_t) = \xi(\hat{B}^* - \gamma)(\delta - \gamma)$ respectively. Combining equations (6.25) and (6.28) - (6.30) and solving for ρ_0^{F*} gives

$$\rho_0^{F*} = -\frac{\xi\left(\left(\rho_0^{B*}A_0^B\right)^2 - (\gamma+1)A_0^B\rho_0^{B*} + \gamma\right)}{\xi\rho_0^{B*}A_0^BA_0^F - \xi\gamma A_0^F - \psi\gamma + \psi\delta}. \tag{6.36}$$

Similarly, combining equations (6.23) and (6.28) - (6.30) and solving for ρ_0^{B*} gives

$$\rho_0^{B*} = -\frac{\sigma\left(\left(\rho_0^{F*}A_0^F\right)^2 - (\beta+1)A_0^F\rho_0^{F*} + \beta\right)}{\sigma\rho_0^{F*}A_0^FA_0^B - \sigma\beta A_0^B - \beta + \alpha}. \tag{6.37}$$

Substitution of equation (6.37) into (6.36) gives a cubic equation in ρ_0^{F*}. This can be solved using the cubic formula and the three roots can be back substituted into equation (6.37) to get the three steady states for ρ_0^{B*}. Note that the steady state must be real and positive, thus there can be either one or three possible steady states from this case.

Case 6

When $\beta \leq \hat{C}^*$ then $f_1(\sigma, \hat{C}^*) = 0$ and $\rho_0^{B*} = 0$. When $\gamma \leq \hat{B}^* < \delta$ then $f_2(\xi, \hat{B}_t) = \xi(\hat{B}^* - \gamma)(\delta - \gamma)$. Combining equations (6.25) and (6.28) - (6.30) and solving for ρ_0^{F*} gives

$$\rho_0^{F*} = \frac{\gamma\xi}{\psi(\gamma - \delta) + \xi\gamma A_0^F}. \tag{6.38}$$

Case 7

When $\beta \leq \hat{C}^*$ then $f_1(\sigma, \hat{C}^*) = \sigma$ and when $\gamma \leq \hat{B}^* < \delta$ then $f_2(\xi, \hat{B}_t) = \xi$. Substitution of these conditions into equations (6.25) and (6.28) - (6.31) respectively, gives

$$\rho_0^{B*} = \frac{1}{A_0^B} - \left[\frac{\psi + \xi A_0^F}{\xi A_0^B}\right]\rho_0^{F*}, \tag{6.39}$$

and

$$\rho_0^{B*} = \frac{\sigma\left(1 - \rho_0^{F*} A_0^F\right)}{1 + \sigma A_0^B}. \tag{6.40}$$

Equations (6.39) and (6.40) are equal, so combining and solving for ρ_0^{F*} gives

$$\rho_0^{F*} = \frac{\xi}{\psi + \psi\sigma A_0^B + \xi A_0^F}. \tag{6.41}$$

Back substitution gives

$$\rho_0^{B*} = \frac{\psi\sigma}{\psi + \psi\sigma A_0^B + \xi A_0^F}. \tag{6.42}$$

Case 8

When $\alpha < \hat{C}^* \leq \beta$ then $f_1(\sigma, \hat{C}^*) = \sigma[(\hat{B}^* - \hat{C}^*)/(\beta - \alpha)]$ and when $\delta \leq \hat{B}^*$ then $f_2(\xi, \hat{B}_t) = \xi$. Combining equations (6.25) and (6.28) - (6.30) and solving for ρ_0^{B*} gives

$$\rho_0^{B*} = -\frac{(\xi A_0^F + \psi)\rho_0^{F*} - \xi}{\xi A_0^{B*}}. \tag{6.43}$$

Similarly, combining equations (6.23) and (6.28) - (6.30) and solving for ρ_0^{B*} gives

$$\rho_0^{B*} = -\frac{\sigma\left(\left(\rho_0^{F*}A_0^F\right)^2 - (\beta - 1)\rho_0^{F*}A_0^F + \beta\right)}{\sigma\rho_0^{F*}A_0^F A_0^B - \beta + \alpha - \sigma\beta A_0^B}. \tag{6.44}$$

Clearly equations (6.43) and (6.44) are equal. If these equations are combined a quadratic in ρ_0^{F*} is produced and may be solved using the quadratic formula. If the two solutions for ρ_0^{F*} are back substituted into equation (6.43) or (6.44) then the steady states for ρ_0^{B*} may be obtained.

Case 9

When $\beta < \hat{C}^*$, $f_1(\sigma, \hat{C}^*) = 0$ and $\rho_0^{B*} = 0$. When $\delta < \hat{B}^*$ then $f_2(\xi, \hat{B}^*) = \xi$. Combining equations (6.25) and (6.28) - (6.30) and solving for ρ_0^{B*} gives

$$\rho_0^{F*} = \frac{\xi}{\psi + \xi A_0^F}. \tag{6.45}$$

Not unsurprisingly this steady state is the same as the steady state derived for the single species fucoid model.

6.4 Parameter Estimation

Investigation of the entire parameter space of this discrete two species model would involve at least 10 values of each parameter. For 9 parameters 10^9 simulations would be required to investigate the parameter space completely. As this is not feasible in the time scale of this project, simulation has to be more targeted. The aim of this targeting is to examine the behaviour of the model using parameter sets around the observed values from literature. There will be a large degree of error associated with parameter estimates, as the methods used to acquire these parameters are quite crude. However, an upper and lower limit for the parameter will also be investigated, which, where possible, will involve variation of plus or minus an order of magnitude.

6.4.1 *S. balanoides*

In this section data are used from the literature to estimate parameter values for *S. balanoides*. Although a lot of work has been done on *S. balanoides*, much is inapplicable to this study, so only a few data sets can be used.

Settlement

The first thing that should be noted about this parameter is that there is a huge variation in the daily instantaneous settlement rates per unit area along both the temporal and spatial scales (Hawkins & Hartnoll, 1982a; Kendall *et al*, 1982; Wethey, 1984, 1985). Thus, this parameter is estimated using crude, quick and easy methods.

Hawkins & Hartnoll (1982a) measured daily settlement patterns of *S. balanoides* at Kallow Point, Port St. Mary, Isle of Man, in 1978 and 1979 (see figure 2, Hawkins & Hartnoll, 1982a). These data were scaled to produce daily instantaneous settlement per m^2. As the settlement density fluctuates, a mean of the daily settlement rate was taken. This gives estimates for the daily instantaneous settlement rate (κ) of 1206 and 977 for 1978 and 1979 respectively. The mean of these values gives an estimate of $\kappa = 1091$.

Other estimates of κ can be obtained from the data of Kendall *et al* (1982). They presented settlement data for the N.W. of Scotland and N.E. England. They measured 7 different sites at each of these locations and provided maximums, minimums and standard deviations for their data (see table 6.2). If the means for the sites in Scotland are averaged and scaled to $individuals.m^{-2}.d^{-1}$, then κ is estimated at 17,000. A similar technique for English sites gives $\kappa = 9143$.

Data of $numbers.cm^{-2}.d^{-1}$ can be estimated from figure 2, Kendall *et al* (1982) for Robin Hood Bay in 1978. They measured settlement on 5 high and 5 low

Table 6.2: Barnacle settlement rates for 2 week intervals ($numbers.cm^{-2}$).

NW Scotland

	Site						
	1	2	3	4	5	6	7
Maximum	14.8	17.4	89.0	53.6	74.0	35.0	45.9
Minimum	4.2	1.7	9.0	13.4	11.0	3.4	5.4
Mean	9.1	4.8	32.5	35.8	39.5	19.3	25.7
Sd	3.6	2.5	27.5	15.8	28.0	9.4	12.5

NE England

	Site						
	1	2	3	4	5	6	7
Maximum	20.4	23.2	39.8	40.0	19.7	14.3	14.2
Minimum	2.0	6.3	3.8	1.8	1.3	1.7	1.5
Mean	10.1	13.9	17.2	18.6	12.4	9.2	8.2
Sd	5.8	5.1	11.6	12.7	5.9	4.2	4.4

shore sites. The settlement rates can be estimated from the graph and the mean settlement rate can be derived. When scaled to $numbers.m^{-2}.d^{-1}$, then κ is estimated at 2237 and 5583 for the low and high shore sights respectively. The mid-shore is found between the high and low shore. If it is assumed that there is continuous gradient between the high and low shore, then the average of these should give an estimate of the settlement on the mid-shore (albeit very rough!). This gives an estimate of $\kappa = 3910$ $individual.m^{-2}.d^{-1}$.

The estimates for N.W. Scotland and N.E. England from Kendall *et al* (1982) are probably a bit higher than would be expected on the Isle of Man. There are two reason for this. Firstly, the estimates for N.W. Scotland will have a higher degree of exposure and thus, have a higher larval supply (Hawkins & Hartnoll, 1982a). Secondly, the Isle of Man is a locally recruiting population and thus will have lower levels of settlement than mainland sites, for example the Menai Straits, Wales (Hawkins & Hartnoll, 1982a). For this reason I will use an estimate of $\kappa = 2000$ and vary the estimate by an order of magnitude in each direction. This estimate is slightly higher than the estimate obtained from Hawkins & Hartnoll (1982a), but larval sampling is difficult and inefficient.

Survivorship

The barnacle survivorship has been estimated using data from Pannacciulli (1995). She examined the survivorship of different sub-cohorts of *S. balanoides* a Cellar Beach, North Devon using photographic time series (see figure 6.3). This is a moderately exposed shore, facing north-north-west and is fairly steep sloping. I have used her data from MTL ($3.3m$ above chart datum) and assumed that there is no difference in mortality between the sub-cohorts. This allows the assumption that all the individuals settle on the same day and gives a much larger data set.

A curve was fitted through the adjusted data set using a non-linear least squares method in Splus (©1989, 1991 Statistical Sciences, Inc.). The curve fitted was of the form

$$Survivorship \quad = \quad S^{age}$$

where S is the daily survivorship and *age* is the age of the barnacle in days. This gave a good fit with a residual sum of squares of 2.039921 and a standard error of 0.171942 (see figure 6.4). This gave an estimate that $S = 0.984477$. This is a daily survivorship and to get an estimate of S^B it is necessary to scale this value to produce a survivorship in the interval $t \rightarrow t + \Delta t$ or per two week period. This gives an estimate of $S^B = 0.8033051$.

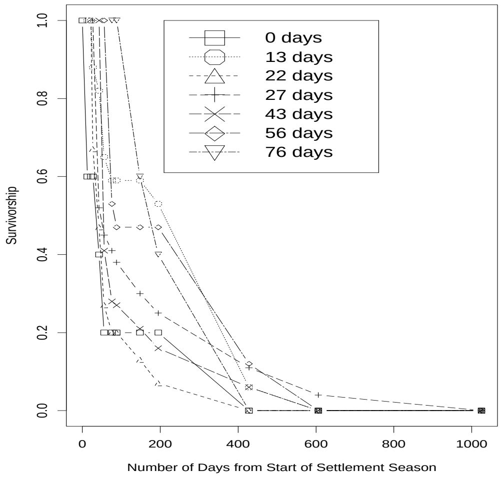

Figure 6.3: Survivorship of different sub-cohorts found at MTL on Cellar Beach (Pannacciulli, 1995).

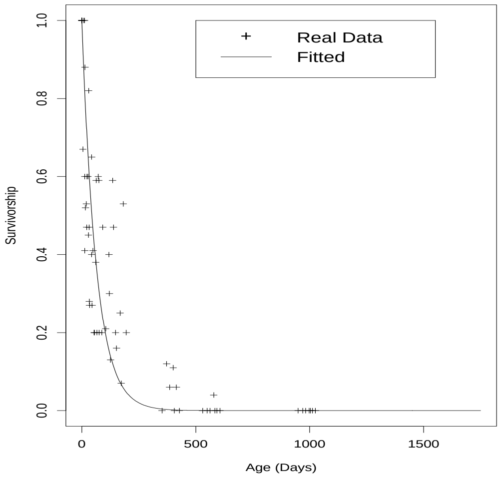

Figure 6.4: Fitting a survivorship curve to data from Pannacciulli (1995).

This estimate of survivorship seems a bit low. This is possibly because of the fact that although this beach is moderately exposed, if the tide is high and the wind is blowing in the right direction waves break directly onto the shore (Pannacciulli, 1995). This shore is also crowded (*pers. obs.*) and thus, may have a higher mortality than would be expected on the Isle of Man. For this reason, 0.8 is set as the lower limit on the parameters and use 0.875 as 'normal' estimate and 0.95 as the upper limit.

6.4.2 *F. vesiculosus*

The estimation of demographic parameters for *F. vesiculosus* is much more challenging than for *S. balanoides*. Many more tenuous assumptions (leaps of faith!) must be made in this section as this species is not as well reported.

Settlement

This parameter is probably the most difficult to estimate. This is because very little work has been done on recruitment in fucoids, as the propagules are very difficult to identify unless they are brought back to the laboratory and grown.

Knight & Parke (1950) estimated that a large plant of *F. vesiculosus* may have 1000 receptacles each containing a maximum of over 3000 eggs. Thus, each plant is capable of producing over 3 million propagules. In Section 4.4.2 I estimated that the maximum density of plants in the largest size-class was 11.1. This gives a total reproductive output $3.3 * 10^7\ propagules.m^{-2}$. Not all receptacles on the plants mature at the same time, making release of propagules gradual. If it is assumed that a 'normal' settlement season is 10 weeks, then the reproductive output is $2.36 * 10^5\ propagules.m^{-2}.d^{-1}$.

Norton (1986) suggested that dissemination by water motion and the inability of propagule to select a suitable settlement site, means that many of the propagules are deposited out of their zone. This decreases the survival of the propagules. Considering this inability to select settlement sites, it is assumed that only 10% of propagules find a suitable site. Thus, the number of settlers is $2.36 * 10^4.m^{-2}.d^{-1}$.

Even if the propagules are deposited in the right zone, 90% of the *F. vesiculosus* propagules die within the first 17 days (Bray, 1993) which is long before they reach the size allocated to size-class 0 (see Section 4.4.2). Chapman (1995) noted that only 0.4-12% of *F. distichus* settlement reach visible size. So, if it is estimated that 5% of the settlers reach visible size then the daily settlement rate (ζ) is 1179 $individuals.m^{-2}.d^{-1}$.

The number of propagules decreases exponentially with distance from the source (Deysher & Norton, 1982; Arrontes, 1993). Thus, I will use a daily instantaneous settlement of $\zeta = 1000$ as the upper limit of the settlement, assuming that there are parent plants within $1m$ of the modelled area. The 'normal' parameter estimate is obtained by assuming that parent plant are $2m$ from the modelled area. This gives a one order of magnitude drop in the number of propagules (Deysher & Norton, 1982). Thus, the normal estimate is $\zeta = 100$. The lower limit is set by assuming that parent plants are within $5m$ of the modelled area, giving an estimated further drop of 2 orders of magnitude. Thus giving a lower limit of $\zeta = 1$.

Survivorship

Many different types of survivorship curves have been found for different species of seaweed (see for example Chapman & Goudey, 1983; Santelices & Ojeda, 1984). Creed (1993) suggested that this is because the different types of curves use logarithmic and arithmetic methods and thus, should be interpreted differently. This makes estimation of this parameter difficult.

There is some data on the survivorship of *F. vesiculosus* over a number of years (see Knight & Parke, 1950). However, this data does not look at the mortality of plants of 0+ years old, as the plants examined were already established. Knight & Parke (1950) suggested that the maximum age of *F. vesiculosus* is 3 to 4 years old. This can be used in parameterising the survivorship. If it is assumed that a 'normal' survivorship means that maximum average age of the plant is 3.5 years, then we can fit a curve such that essentially zero plants survive beyond this age. This process can then be repeated assuming that 'bad' and 'good' survivorships give a maximum average age of 2.5 and 4.5 years respectively.

Gunhill (1980) used 314 individuals of *Pelvetia fastigiata* to produce a log-log regression of survivorship. From the linearity of this plot, she suggested that there were a constant proportion of the plants dying with each time interval. Thus, a curve of the form

$$Survivorship = \left(S^{F}\right)^{j}$$

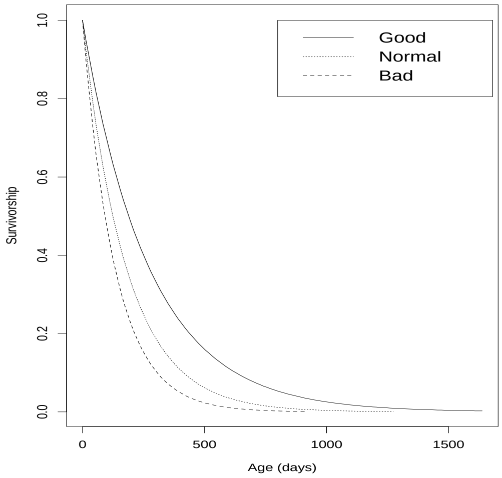

Figure 6.5: *F. vesiculosus* survivorship curves.

is used. This gave survivorship curve curves of the form shown in figure 6.5 using the values for incremental survivorship shown in table 6.3.

Probability of Promotion

The probability of promotion, P, is estimated at 1/26. This is because it is assumed for the size-class selection that individuals in each class are on average, 0+, 1+, 2+ and 3+ years old. Thus, the average time required to be promoted is 1 year (for a fuller description see Section 4.4.2). The probability of promotion will be varied by plus or minus a half of its value. Thus, the lower limit is 1/39 and the upper limit is 1/13.

6.4.3 Interaction Thresholds

These parameters are probably the most difficult to quantify. This is because there is debate over which of a number of factors is the most important and

Table 6.3: Estimates of *F. vesiculosus* survivorship.

	Maximum Age (years)	S^F	Proportion Remaining
'Good'	4.5	0.950	$2.6 * 10^{-3}$
'Normal'	3.5	0.925	$9.0 * 10^{-4}$
'Bad'	2.5	0.900	$1.2 * 10^{-3}$

because settlement itself is so difficult to quantify. In this section evidence of the interaction between the two species is examined in an attempt to quantify these interactions.

The Effect of *F. vesiculosus* on *S. balanoides* Settlement

The inhibition of *S. balanoides* by the canopy of *F. vesiculosus* is well documented (Hatton, 1938; Connell, 1961a; Hawkins, 1983; Miller & Carefoot, 1989; Proud, 1994; Jenkins, 1995). However, this effect has been attributed to a number of causes. Firstly, canopy sweeping has been suggested to reduce the recruitment of barnacles under the canopy (Hatton, 1938; Hawkins, 1983; Jenkins, 1995). Secondly, limpets aggregate under the mature canopies of *F. vesiculosus* as this reduces the stress due to dessication. This increases the incidence of limpet bulldozing, where limpets undercut juvenile barnacles (Connell, 1961a; Hawkins 1983). This effects the recruitment and mortality of juvenile barnacles. There are size and location refuges from limpet bulldozing. For example, Miller & Carefooot (1989) suggested that the size refuge is as little as $5mm^2$ basal area and that depressions in the rock or dense adult barnacles provide a refuge. Hawkins (1983) found that this effect is much less important than canopy sweeping. Finally, *Nucella* also aggregate under *F. vesiculosus* canopies and predate upon adult *S. balanoides*, reducing the density of adults under the canopy (Proud, 1994).

Jenkins (1995) tried to quantify the effect of the canopy on cyprid settlement. He found that sweeping reduced the settlement of cyprids on sheltered shores (see table 6.4). Post-settlement cyprid survival was much reduced under a canopy, for example from 92.3% to 3.4%. *F. serratus* was the best 'sweeper' on sheltered shores because of its lack of air bladders and bushy nature.

Table 6.4: Cyprid settlement onto $144cm^2$ of rock in the presence and absence of a fucoid canopy (data from Jenkins, 1995).

	22/5/93		28/5/93		2/6/93	
Species	Absent	Present	Absent	Present	Absent	Present
F. spiralis	40	7	31	3	3	2
A. nodosum	18	3	-	-	6	0
F. serratus	26	3	11	1	6	0.5

Hawkins (1983) measured the effect of canopy sweeping on moderately exposed shores. He found that *Fucus* sweeping inhibits *S. balanoides* settlement at all levels on the shore. When *Fucus* plants were transplanted to barnacle dominated ledges, after 55 days there was reduced settlement of *S. balanoides* in the presence of a canopy of *F. vesiculosus* (see table 6.5) on scraped settlement squares. This is an underestimate as the adult barnacle surrounding the settlement squares reduced the canopy sweeping effect.

Table 6.5: Number of metamorphosed barnacles in the presence/absence of a *F. vesiculosus* canopy (data from Hawkins, 1983).

Experiment	With Canopy	Without Canopy
1	37.1	100
2	10	54.3

Limpet bulldozing effects the settlement of *S. balanoides.* The density of limpets on the ledges at Port St. Mary is between 2.5 (Hartnoll & Hawkins, 1985) and 35 $individuals.m^{-2}$ (Proud, 1994). Hartnoll & Hawkins (1985) note that a density of limpet of 20 $individuals.m^{-2}$ can clear 71% of the substrate, but 7 $individuals.m^{-2}$ can only clear 25%. A normal density of limpets is $19.m^{-2}$.

To quantify this into some kind of lower and upper threshold for barnacle settlement, limpet bulldozing and canopy sweeping are quantified as the processes that act on recruitment. There are two extremes of the relationship, a full canopy and maximum limpet density completely excludes *S. balanoides* settlement; and no canopy and minimum limpet density has no effect on settlement. A density of 20 limpets allows 71% of substrate to be grazed (Hartnoll & Hawkins, 1985). Assuming that limpet density is directly proportional to canopy and that limpet grazing is directly proportional to *S. balanoides* bulldozing, then at about 50% canopy cover, 71% of the *S. balanoides* settlement is removed by bulldozing. At this level of limpets the canopy will also exclude a number of settlers, so we estimate the upper barnacle threshold (β) at 0.5. This will be varied between the limits of 0.4 and 0.7 to investigate different intensities of canopy sweeping. The lower barnacle threshold (α) is estimated in a similar way. At a density of 7, limpet can clear 25% of the substratum. At this stage we assume that the canopy has a minimal effect at 20% of the maximum, and that the encounter rate with limpets is low allowing more barnacles to reach the size refuge. Thus, the lower barnacle threshold (α) is estimated at 0.2, with a range of 0.1 to 0.35.

The Effect of *S. balanoides* on *F. vesiculosus* Settlement

Dense *S. balanoides* aids the establishment of a *F. vesiculosus* canopy. This is because *P. vulgata* grazes upon the spores of algae and is very effective at removing all of these spores from bare rock. However, when *S. balanoides* occurs it disrupts the grazing of *P. vulgata*, by making the surface topography irregular. Hawkins & Hartnoll (1982b) examined the effect of barnacle cover on number, behaviour and growth of *P. vulgata* on a vertical pier on the Isle of Man. They found that the growth rate of *P. vulgata* was inversely proportional to the percentage cover of barnacles. This suggests a lower grazing efficiency. Once *F. vesiculosus* reach about $3cm$ in length, they are too large to be grazed by *P. vulgata* (Proud, 1994). Thus, the denser the cover of barnacles, the lower the grazing efficiency of *P. vulgata* and the more likely that *F. vesiculosus* will reach the size threshold where they have 'escaped' grazing. These 'escapees' will form the canopy.

Hawkins (1981b) looked at the influence of season and barnacles on the algal colonisation of *P. vulgata* exclusion areas. He looked at the difference between *F. vesiculosus* colonisation of areas with and without barnacles. In the areas with barnacles *F. vesiculosus* settled and established a canopy much more quickly than in areas without barnacles.

The only actual value that I can find for this interaction is from Waterhouse *et al* (1986). They suggest that in Australia the grazing effects of limpets are negligible at barnacle percentage cover of greater than 67%. I think this value is an underestimate, as in *P. vulgata* are able to sustain grazing on both the 50% mosaic and the 95% cover in the Isle of Man (Hawkins & Hartnoll, 1982b). Thus, this will give us an estimate of the lower limit of the upper fucoid threshold (δ), at a proportion of 0.7. On crowded shores limpet scars maybe in the middle of dense barnacle cover and thus, I will use a upper limit of $\delta = 0.9$. The estimate will be arbitrarily set at the mid point of these values, *ie* $\delta = 0.8$.

Getting the lower fucoid threshold is more difficult. I suggest that at very low densities of barnacles there is no effect on the grazing efficiency of the limpets. However, as the cover of barnacles increases there is a rapid decrease in grazing efficiency. Hawkins & Hartnoll (1982b) show that there is a decrease in growth rate of *P. vulgata* grazing on a 50% mosaic of barnacles and therefore we assume that there is a decrease in grazing efficiency. Thus, $\gamma = 0.5$ will be used as an estimate of the lower fucoid threshold. The lower limit of the threshold will mimic a gradual decrease in grazing pressure with increased barnacle cover, so is estimated at $\gamma = 0.1$. The upper limit will be as high as possible to mimic a sharp threshold and thus is $\gamma = 0.65$.

6.5 Simulation

The parameter estimates can be seen in table 6.6. For simulation of this model, comparable models to the models found in Chapters 3 and 4 are required, as altering the number of size-/age- classes can affect the stability of the model. Thus, the fucoids will have 4 size-classes which are estimated in the same way as in Section 4.4.2. The barnacles have 125 age-classes and the model of logistic growth model is used (see Section 3.4). The same time step is used with $\Delta a = \Delta t = 14$ days.

Table 6.6: Parameter estimates.

Parameter Name	Symbol	Upper Limit	Estimate	Lower Limit
Barnacle Survivorship	S^B	0.950	0.875	0.800
Barnacle Settlement	κ	20000	2000	200
Fucoid Survivorship	S^F	0.950	0.925	0.900
Fucoid Settlement	ζ	1000	100	1
Fucoid Promotion	P	1/13	1/26	1/39
Lower Barnacle Threshold	α	0.35	0.20	0.10
Upper Barnacle Threshold	β	0.70	0.50	0.40
Lower Fucoid Threshold	γ	0.65	0.50	0.10
Upper Fucoid Threshold	δ	0.90	0.80	0.70

6.5.1 General Results

In this section the behaviour of the model is examined with different parameter sets. The effect of changing parameter on the overall dynamics is examined and oscillatory dynamics are investigated in terms of combinations of the sub-models.

Effect of changing parameters

The dynamics of this model are far more complicated than the dynamics of the single species models. However, in general, there are four types of behaviour. These are an equilibrium with only barnacles present; an equilibrium with both barnacles and fucoids present; periodic fluctuations in both the barnacles and fucoids; and aperiodic fluctuation in both of the species.

Increasing the barnacle survivorship (S^B) increases both the amplitude and the period of the oscillations of the space occupied by both fucoids (C_t) and barnacles (B_t), which increases the total space occupied (A_t). However, if the barnacle survivorship is decreased sufficiently then the space occupied by barnacles may never reach the threshold (γ) that allows the *F. vesiculosus* to settle. This results in a stable equilibrium with only barnacles present.

Increasing the daily instantaneous settlement rate of the barnacles (κ) leads to an increase in the amplitude and the period of oscillations in the space occupied by barnacles. Thus, it has a destabilising effect on the system. However, this has a variable affect on the space occupied by fucoids (C_t).

Decreasing the survivorship of fucoids (S^F) increases the the period and amplitude of oscillations of the barnacle occupancy and decreases the period and amplitude of fucoid oscillations. This is hardly surprising as, from Chapter 4, increasing survivorship increases the potential of a cohort to increase in area and thus, is destabilising. Similarly, increasing the daily instantaneous settlement rate of fucoids (ζ) is destabilising. As this also increases the potential of a cohort of fucoids to increase in area over time. Increasing this settlement rate causes an increase in the period and amplitude of both the occupancy by barnacles and fucoids. Increasing the probability of promotion of the fucoids has a destabilising effect on the model for the same reason as the survivorship and settlement.

Decreasing the lower barnacle interaction threshold (α) increases the stability of the model and decreases the amplitude of the cycles. Thus, decreasing this threshold is stabilising. Decreasing the upper barnacle interaction threshold (β) decreases the stability of the model and increases the amplitude of the cycles. Thus, decreasing this threshold is destabilising eventually giving rise to aperiodic solutions.

Increasing the lower fucoid interaction threshold (γ) increases the stability the occupancy of *S. balanoides* and decreases the occupancy of *F. vesiculosus.* This increase is therefore destabilising. Decreasing the upper fucoid interaction threshold (δ) decreases the stability of the model and increases the amplitude of the cycles. Thus, decreasing this threshold is destabilising.

How are Oscillations Produced?

Within the parameter set (see table 6.6), solutions can be found where both of the sub-models are stable and unstable. Using the same parameter sets, it is possible to see if the oscillatory dynamics in the two species model are driven by oscillations in the sub-models or by interaction between two stable sub-models. Thus, parameters are defined that cause the sub-models to be stable or unstable (see tables 6.7 and 6.8). The model will then be simulated using the sixteen combinations of the sub-model behaviour. For this the interaction threshold will be set at the estimate values, apart from the upper fucoid threshold which is set at its lower limit. This is because it is difficult to get a solution with occupancy of greater than 0.8 in the barnacle sub-model and when found, have very long transients.

Table 6.7: Stable and unstable parameter sets in the barnacle sub-model.

		Stable			Unstable
Parameter Name	Symbol	$A^* < \gamma$	$\gamma < A^* < \delta$	$\delta < A^*$	
Barnacle Survivorship	S^B	0.80	0.89	0.91	0.95
Barnacle Settlement	κ	200	200	200	200
Barnacle Occupancy	A^*	0.336	0.661	0.739	-

Table 6.8: Stable and unstable parameter sets in the fucoid sub-model.

		Stable			Unstable
Parameter Name	Symbol	$A^* < \alpha$	$\alpha < A^* < \beta$	$\beta < A^*$	
Fucoid Survivorship	S^F	0.900	0.900	0.900	0.925
Fucoid Settlement	ζ	1	3	5	10
Fucoid Promotion	P	1/39	1/26	1/26	1/26
Fucoid Occupancy	A^*	0.186	0.480	0.697	-

Initially the barnacle occupancy is important in driving the dynamics. If the barnacle occupancy is always less than the lower fucoid threshold, then a stable steady state with only barnacles is produced regardless of the fucoid parameters (see figure 6.6). This is because the fucoids are never able to settle.

When the solution of the barnacle sub-model is stable and the solution of the fucoid sub-model is less than the upper barnacle interaction threshold, then a stable steady state is produced with both barnacles and fucoids (see figure 6.7).

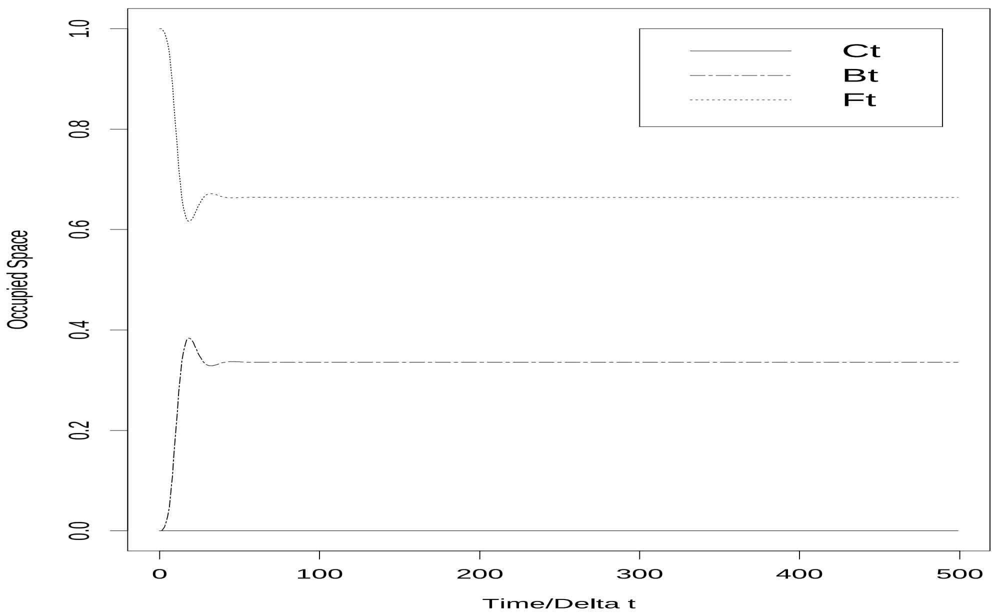

Figure 6.6: Stable steady state with only barnacles present ($S^B = 0.8$, $\kappa = 200$, $S^F = 0.9$, $\zeta = 3$, $P = 1/26$, $\alpha = 0.2$, $\beta = 0.5$, $\gamma = 0.5$ and $\delta = 0.7$).

This is because in the two species model the occupancy by barnacles is reduced and thus, settlement of barnacles and fucoids is never shut off completely. Therefore, a state can be reached where the area lost via mortality is balanced by the gain in area from settlement.

If either of the solutions to the sub-models is oscillatory, then oscillations are produced in the two species model (see figure 6.8). This is because the oscillations of one of the models causes settlement to be switched on and off and drives the oscillations of the other species. If both of the sub-models are oscillatory then oscillations are produced in the two species models (see figure 6.9). However, these oscillations interact to produce oscillations in each species with a period of greater than 2.

Oscillations in the two species model can be produced when the sub-models are both stable, *ie* by the interaction between the two sub-models. When the fucoid sub-model has an occupancy of greater than the upper barnacle interaction threshold, then oscillations occur (see figure 6.10). This is because then fucoid occupancy is sufficiently high to shut off barnacle settlement giving rise to oscillations.

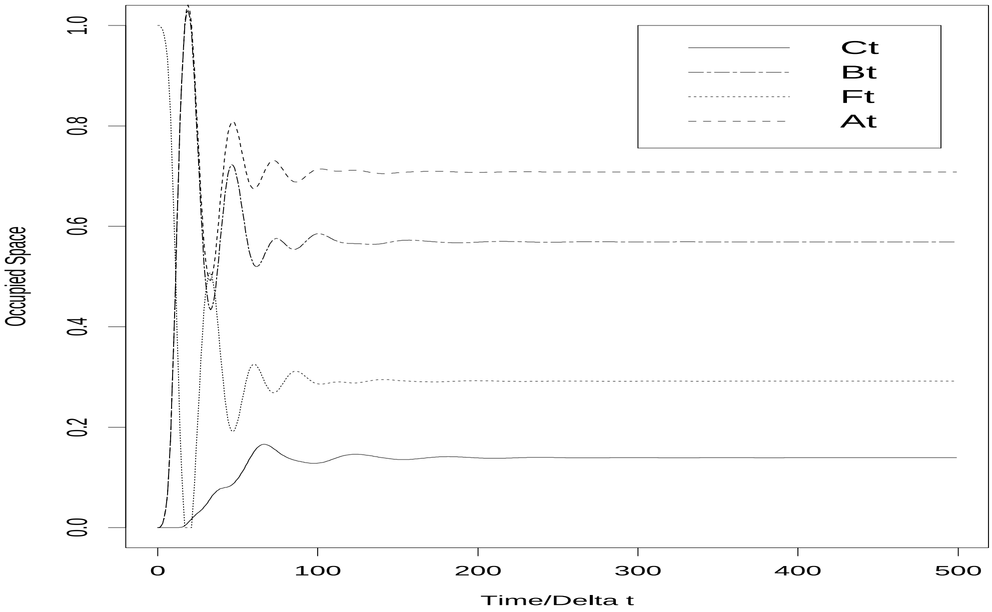

Figure 6.7: Stable steady state with both barnacles and fucoids present ($S^B = 0.89$, $\kappa = 200$, $S^F = 0.9$, $\zeta = 3$, $P = 1/26$, $\alpha = 0.2$, $\beta = 0.5$, $\gamma = 0.5$ and $\delta = 0.7$).

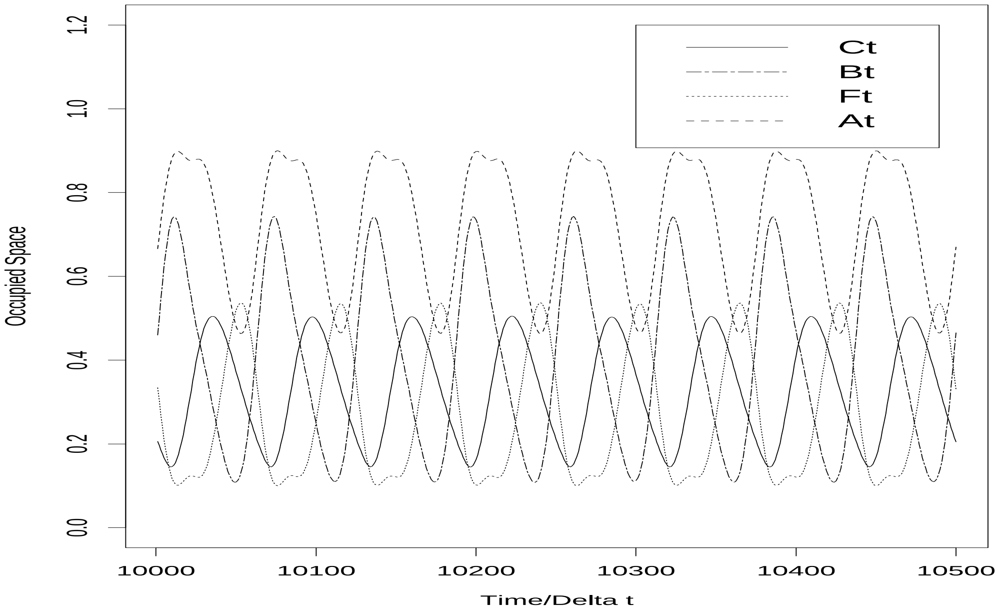

Figure 6.8: A cyclic solution of the 2 species model, where oscillations in the fucoid sub-model drive oscillations in the in the barnacle sub-model ($S^B = 0.91$, $\kappa = 200$, $S^F = 0.925$, $\zeta = 10$, $P = 1/26$, $\alpha = 0.2$, $\beta = 0.5$, $\gamma = 0.5$ and $\delta = 0.7$).

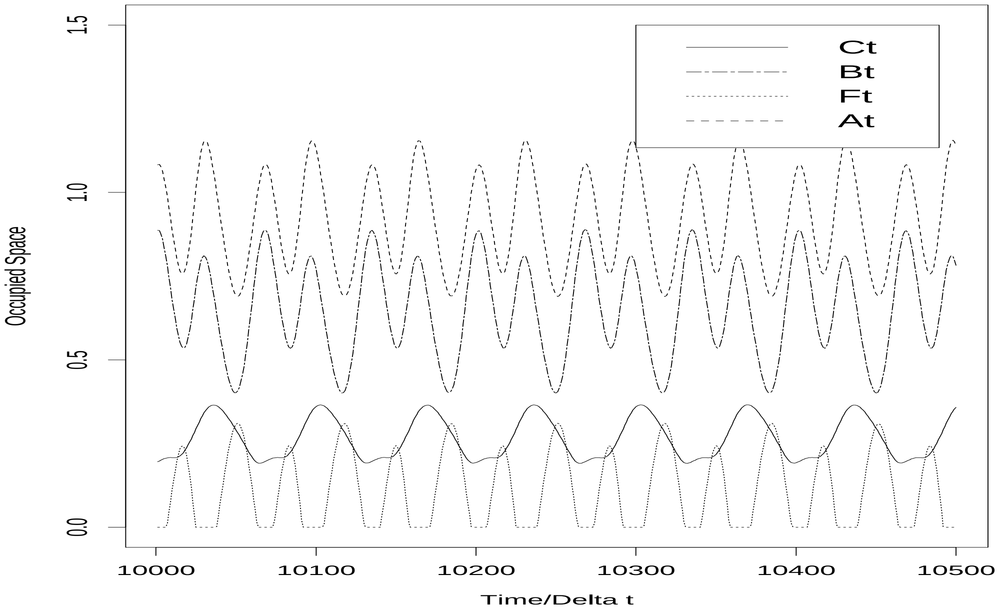

Figure 6.9: A cyclic solution of the 2 species model, where both sub-models oscillate ($S^B = 0.95$, $\kappa = 200$, $S^F = 0.925$, $\zeta = 10$, $P = 1/26$, $\alpha = 0.2$, $\beta = 0.5$, $\gamma = 0.5$ and $\delta = 0.7$).

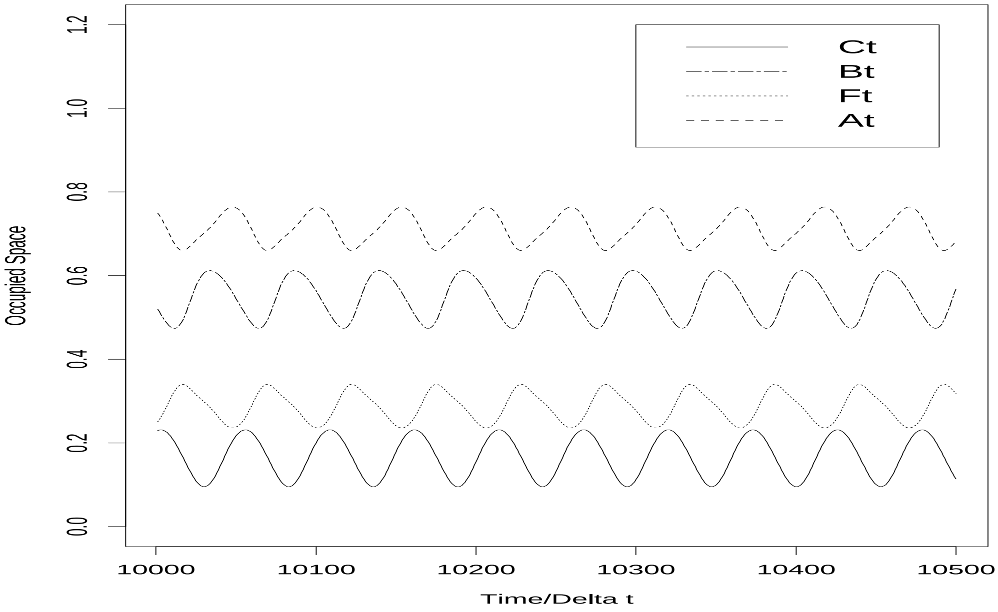

Figure 6.10: Interaction between the sub-models causing oscillatory dynamics in the two species model ($S^B = 0.89$, $\kappa = 200$, $S^F = 0.9$, $\zeta = 5$, $P = 1/26$, $\alpha = 0.2$, $\beta = 0.5$, $\gamma = 0.5$ and $\delta = 0.7$).

6.5.2 Application to the Isle of Man

In this section parameters of the model are varied to produce cycle shown in the literature (see table 6.9). This is attempted using parameter within the values suggested in the parameter estimation section.

Table 6.9: Percentage cover estimates for Kallow Point, Port St. Mary, Isle of Man (cycle is the length of the cycle in years).

	F. vesiculosus		*S. balanoides*		Bare	Total
	% cover	Cycle	% cover	Cycle	Rock	Cycle
Hartnoll & Hawkins (1985)	0 - 65	3	0 - 46	3 - 4	44 - 94	6 - 7
Proud (1994)	0 - 70	4	10 - 60	3 - 4	40 - 90	6 - 7

It soon became clear that it is difficult to obtain a correct total cycle length of about 6-7 years within the parameter set. This is possibly because the barnacles are growing too fast and thus reach the lower fucoid threshold to quickly, *ie* the time lag between barnacle and fucoid settlement is too small. So to obtain solutions with a total cycle length of 6-7 the settlement values had to be very high and the variation in percentage cover was far too great. If the actual estimated parameter set is used (see figure 6.11) then a solution is produced with an occupancy that is outside the bounds suggested. The individual cycle lengths are correct, at about 3 years for both species. However, the total cycle time is too short, at about 4 years. To obtain a longer cycle length it was necessary to use survivorships of 0.978 for both species (see figure 6.12). However, this altered the cycle time of the fucoids to around 5.6 years which is almost twice that suggested in the literature.

To produce a solution that fits nicely within the bounds suggested in the literature, it is necessary to lower the lower and upper barnacle interaction thresholds significantly (figure 6.13). However, the total cycle time of this solution is low and thus there is a problem with the time lag.

6.6 General Discussion

A number of general points about the linked model become clear with just observation. This model is non-linear and therefore will exhibit a much wider range of

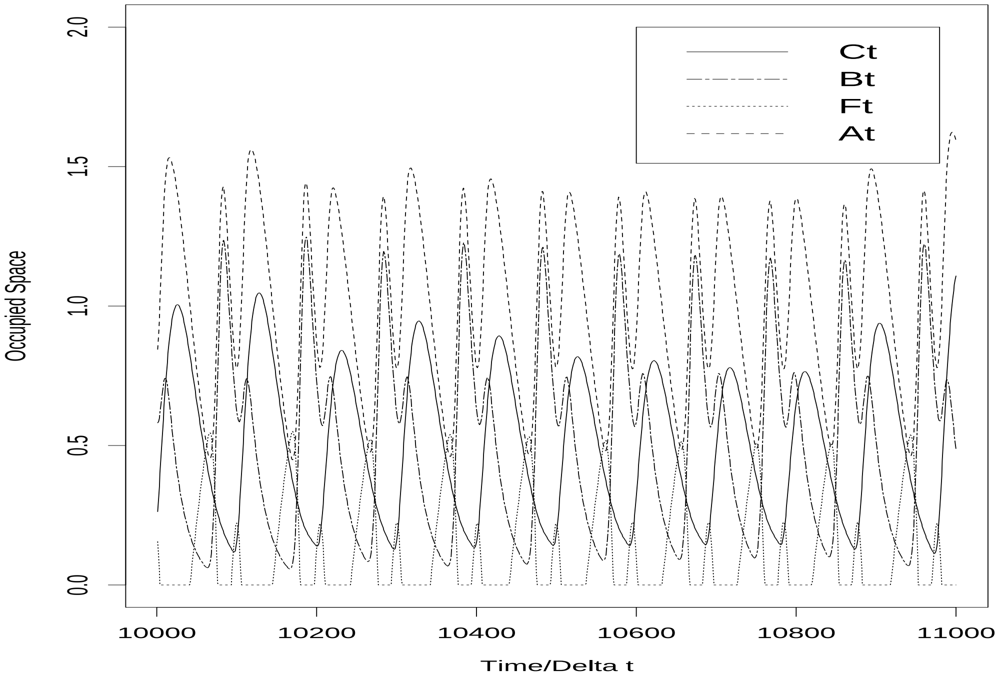

Figure 6.11: Fitting model to observed values - attempt 1 ($S^B = 0.875$, $\kappa = 2000$, $S^F = 0.925$, $\zeta = 100$, $P = 1/26$, $\alpha = 0.2$, $\beta = 0.5$, $\gamma = 0.5$ and $\delta = 0.9$).

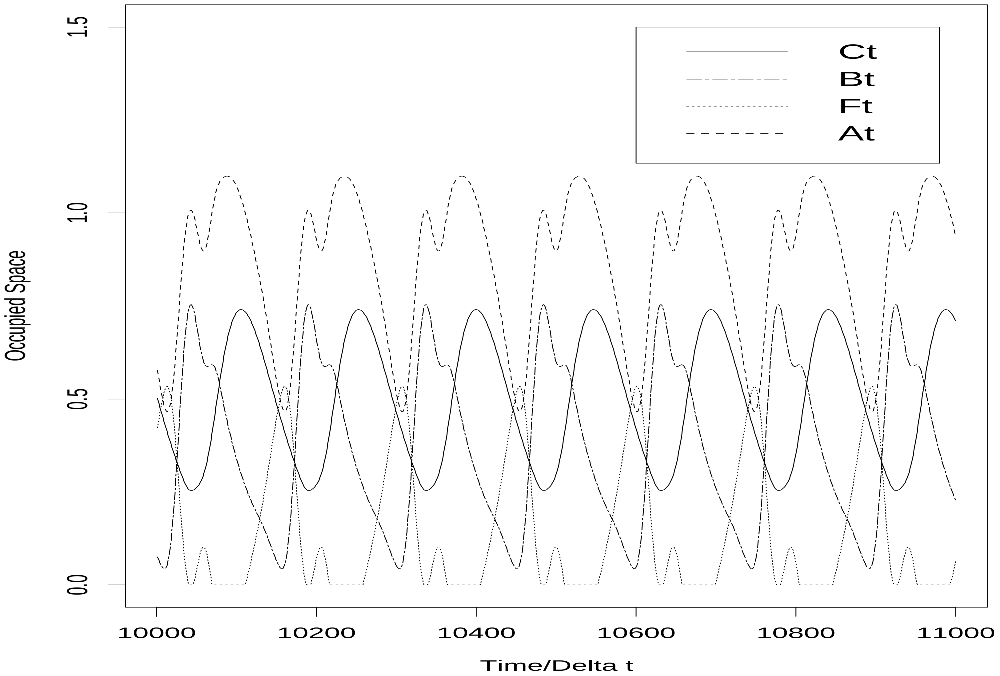

Figure 6.12: Fitting model to observed values - attempt 2 ($S^B = 0.978$, $\kappa = 100$, $S^F = 0.978$, $\zeta = 5$, $P = 1/26$, $\alpha = 0.2$, $\beta = 0.5$, $\gamma = 0.5$ and $\delta = 0.8$).

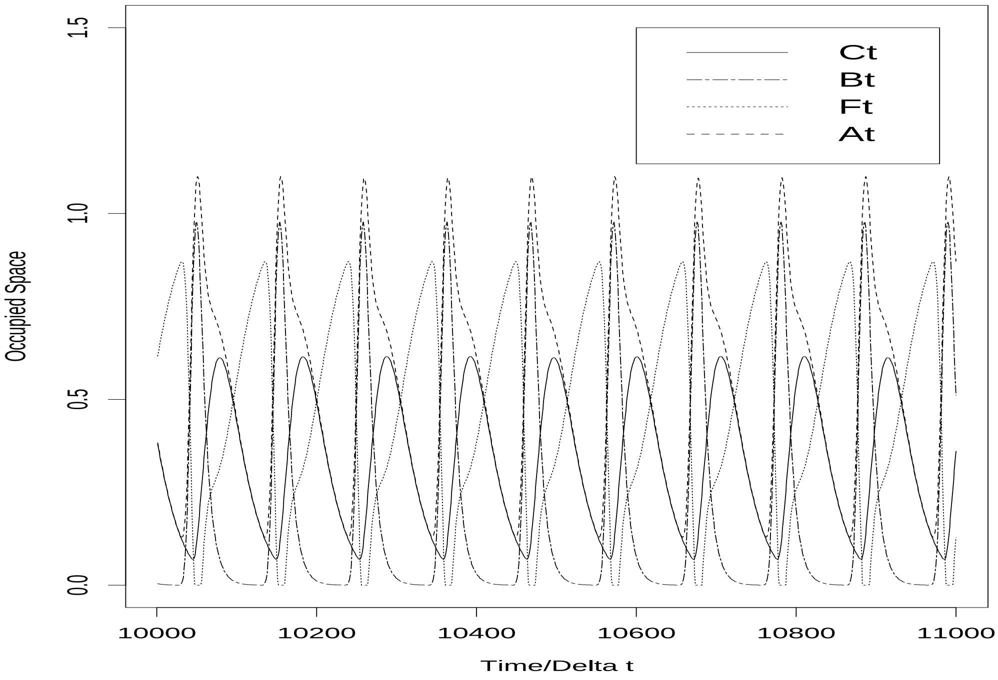

Figure 6.13: Fitting model to observed values - attempt 3 ($S^B = 0.9$, $\kappa = 200$, $S^F = 0.95$, $\zeta = 15$, $P = 1/26$, $\alpha = 0.1$, $\beta = 0.15$, $\gamma = 0.5$ and $\delta = 0.7$).

behaviour than any of the linear models described so far (May, 1976). However, the component models behave in a very similar way to the single species models described in Chapters 3 and 4. Thus, many of the observed results are the same, for example, increasing either of the survivorships or the settlement rates increases the amplitude and period of oscillations in that species. Settlement again is the main driving factor in this model.

Four types of behaviour are produced by the model. These are a stable steady state with only barnacles; a stable steady state with both barnacles and fucoids; coupled periodic oscillations; and coupled aperiodic oscillations.

The stable steady state with only barnacles is found when the barnacle occupancy is always less than the lower fucoid interaction threshold. Thus, fucoids are never able to settle. A stable steady state with both species is found when the barnacle and fucoid sub-models are stable. The barnacle sub-model has to have occupancy above the lower fucoid interaction threshold and the fucoid occupancy has to be less than the upper barnacle interaction threshold.

Oscillations are produced in two ways, either by oscillatory behaviour in one or both of the sub-models or by the interaction between stable sub-model solutions.

If one of the sub-model solutions is unstable then it will force the other sub-model dynamics to oscillate as settlement is switched on and off. If both sub-model individually have oscillatory solutions, then these oscillations interact to produce point-cycles of greater than 2. Oscillations can be produced by the interaction between stable solutions of the sub-models. When the fucoid occupancy is greater than the upper barnacle interaction threshold and the barnacle sub-model occupancy is greater than the lower fucoid interaction threshold, then oscillations are produced by interaction between the two sub-models.

The output of this model can give similar occupancy and lifespan for the individual species compared with data from Port St. Mary, Isle of Man (Hartnoll & Hawkins, 1985; Proud, 1994). However, the total cycle length is too short. Hastings (1986) stated that the key to understanding the dynamics of two species model is to look at the interaction between the time delays. In this case the time lag between the two species colonising is not sufficient. Increasing the time delay could be achieved by either stochastic recruitment functions and seasonal settlement, and implementing interaction between adults of the two species rather than just at settlement.

Before the discussion of further work required, it is necessary to again note that this two species model has all the shortcomings of the single species model in Chapter 3 and 4. It would be useful further work to implement these adjustments in the single species models singly, and then look at the overall effect on the behaviour of this two species model.

Probably the most important thing that would make this model more accurate would be a better data set to calibrate the model from. As can be seen from Section 6.4, the actual estimates of the parameters is done using bits of data from everywhere and rough crude techniques. In fact a lot of the data used is from a single $2m^2$ unreplicated quadrat. A better data set would allow a better range of parameters to be estimated, which might increase the accuracy of the model and allow the model to be more testable.

Stochastic recruitment in a seasonal environment would make a large difference to the dynamics of this model. This would give a short period where recruitment is not guaranteed, more like the situation found on the moderately exposed rocky shores where recruitment of fucoid is not a yearly occurrence and the strength of barnacle settlement is variable (Hartnoll & Hawkins, 1985).

A grazer threshold would be very useful in this model. If the fucoid settlement is very large then it would make sense to let a few plant escape even in the absence of barnacles. This is because in the field grazing is limited by the time the grazer is immersed on horizontal surfaces (see Hawkins & Jones, 1992, for a general review) and thus grazers can become saturated. Therefore, it would make biological sense for a proportion of the fucoid propagules to 'escape' at high settlement rates even in the absence of barnacles.

The interaction thresholds between the barnacle and fucoid need to be revised. Firstly a more realistic relationship between adult density and settlement would be useful. However, a large data set is required to produce this relationship, as these affects are very changeable (see for example, Jenkins, 1995). Secondly, interactions between adults of the two species is ignored in this model. For example, the fucoid canopy effects adult barnacles by canopy sweeping and increasing *Nucella* predation, and the adult barnacles provide insecure attachments for fucoids which then have higher mortality (Proud, 1994). This last statement also implies that a major problem with this model is that barnacle and fucoid occupancy is treated as the same quantity. However, fucoids are able to settle on the barnacle matrix (Proud, 1994) and thus, the free space that they are able to settle includes that area occupied by barnacles.

In summary, this chapter has been a useful first insight into the rich dynamics of two species models and the mechanisms that control it. However, although the accuracy of the individual species cycles are correct, the total cycle times are not sufficiently long. A better data sets and a few additions to the model should increase the accuracy. This model has been an interesting introduction and will provide a useful insight into the more complicated dynamics of models produced in my Ph.D.

Part IV

Overview

Chapter 7

Discussion and Conclusions

In this chapter I shall draw the major findings of this work together. The single species models (see Chapters 3 to 5) and then the two species case are examined. I will discuss in short the gaps in the data that require filling in order to parameterise the models. Finally, there will be a general summary section.

7.1 Single Species Models

7.1.1 Mechanisms

Constant Environment

In a constant environment the age-structured model of barnacle populations showed fairly simple dynamics with four types of behaviour: stable overdamped, stable underdamped, point-cycles and aperiodic solutions. Roughgarden *et al* (1985) and Bence & Nisbet (1989) did not find aperiodic solutions, as they both incorporated density-dependent survivorship in their models. This density-dependent survivorship stabilises the aperiodic behaviour of the model to point-cycles. These point-cycles can last for over 38,000 years.

The mechanism operating is controlled by the settlement rate, survivorship and the growth rate. These factors are all destabilising as they increase the area occupied at equilibrium. If the combination of these factors is sufficiently low then a stable steady state is produced with a stable age-distribution. This is not generally the case on the rocky shore where cohorts once established can occupy the space for a number of years until they die and then the area is recolonised by another heavy settlement period. However, if the combination of the settlement rate, survivorship and the growth rate is high enough then point-cycles are produced. These are produced when the space is filled by short 'pulses' of settlement and waves of cohorts pass through the age structure.

Fitting a logistic model to growth rate data (Barnes & Powell, 1953) gives an overestimate of the rate at which barnacles grow on the mid-shore. Using this function the barnacles reach their maximum size in under a year, this is more like the growth rate of *S. balanoides* at the lower limits of their range (Hawkins, *pers. com*).

Comparing a number of different stability criteria shows that in all cases increasing settlement, growth or survival is destabilising. This decrease is stability is effected by a number of factors, such as the type of criteria and the number age-classes. A simple derived criteria which assumes that there is a locally unstable eigenvalue approximates well to the local stability boundary at low settlement values, not at larger values.

The mechanism proposed to control the barnacle model in a constant environment is very similar to those that control the size-structure fucoid model, despite the difference in formulation. This is possibly because although the fucoid model is size-structured individuals cannot get smaller, with a constant probability of promotion. Thus, making increase in size with age a more constant process.

The fucoid model is slightly different to most other models developed in this field (see for example Seip, 1980; Ang, 1987; Åberg, 1992a&b). These have generally been simulation models of closed populations. The model presented here is open as the system that is modelled requires 'pulses' of recruitment from outside populations (Hartnoll & Hawkins, 1985). It also allowed me to look at seaweed models from a more mechanistic view.

The mechanisms that produce the dynamics. Increasing the probability of promotion, survivorship or size-class choice is destabilising, as it increases the potential of the area of a cohort to increase over time. If the settlement rate is high then the occupied space is limited by the probability of promotion, survivorship and the size-class selection. If the settlement rate is low then the occupied space is limited by the settlement rate. Oscillations are found when the area occupied by a cohort increases over time. The decay or persistence of these oscillations depends upon the rate at which free space is filled, *ie* the settlement rate. Oscillations decay if the settlement rate is low, as free space is filled slowly, producing an underdamped solution. Oscillations persist if the settlement rate is high, as free space is filled by short ‘pulses’ of recruitment, producing point-cycles. This is illustrated by the comparison between real and heuristic stability in the strategic model.

These models predict that a few large individuals will dominate the area occupied, which is similar to the canopy of perennial seaweeds. However, the only low settlement rates are required to produce instability which suggests that the parameterisation of the model is not correct. This is hardly surprising as the data available on *F. vesiculosus* is very sparse.

Seasonal Environment

There is a distinct discrete settlement season for both *S. balanoides* (see for example Hawkins & Hartnoll, 1982a) and *F. vesiculosus* (see for example Knight & Parke, 1950). Thus, the most logical extension of the above models is to investigate a seasonal environment.

The barnacle steady state is oscillatory as settlement is a discrete period. Thus, two type of solution are found, periodic and aperiodic. Periodic solutions are produced when the natural and driving periods of the solution are phase locked. Aperiodic solutions are not phase locked. The mechanism that drives the model is the same as in a constant environment.

Increasing the settlement or survivorship of barnacles causes and increase in the amplitude and period of the oscillations. The effect of changing the settlement period is important at low settlement rates, with ‘good’ settlement having larger oscillations than ‘average’ and ‘bad’. However, as settlement increases it no longer forces the model and there is no difference between the models. However, at intermediate settlement the results are difficult to interpret with many aperiodic solutions.

The seasonal fucoid model produces a much wider variety of dynamics, with 2 to 28 point cycles and aperiodic solutions being produced. This is because settlement is from two sources, the seed bank and from outside. The type of solution produced is to do with the degree of phase locking between the natural and driving periods. Point-cycles are phase locked, aperiodic solutions are not. The general mechanism is the same as in the constant environment model. However, the steady states are now oscillatory.

Increasing the settlement rate into the system increases the period and amplitude of the cycles. Decreasing the seed bank survivorship is first stabilising then destabilising. This is because of the free space is able to drop to a lower value when there is no seed bank and thus the free space is filled with more propagules. Different strengths of settlement cause generally little difference in the model.

The models of barnacle and fucoid settlement have fairly similar dynamics despite the difference in formulation. This is highlighted in the discussions of Chapter 3 and 4. When a seasonal component is added to the model, the behaviour is still similar. Both models produce cyclic and aperiodic dynamics. The phase locking mechanism is similar. However, the big difference between the models is caused by the introduction of a seed bank into the fucoid model. This causes a much richer spectrum of dynamics to be found in the fucoid model as there are three cyclical mechanisms that need to phase lock. Overoccupancy is a big problem in both of the models, this is due to survivorship being completely density-independent.

Biologically these models are still very unrealistic and require addition of many parameters (see discussion of Chapters 3 and 4). The very simple components of biological dynamics that are predicted is that the populations cycle or produce some kind of aperiodic behaviour. The one possibly useful biological hypothesis that has been drawn is that seed bank mortality is required to be high so that settlement generally happens within the settlement season. However, conclusive proof is needed of the actual existence of a seed bank and how to test it before this hypothesis can be tested.

7.1.2 Further Study

In this section simple extensions of the model are examined that would improve the biological realism of the models. However, the tradeoff is that with increase realism the models become more complex and less can be discerned from analyses.

These models are very simplistic. The only real biological conclusions that can be drawn are that populations cycle and settlement is the most important process in determining the structure of these populations. These simplistic conclusions reflect the construction of the models and suggest that further work needs to be done increasing biological realism.

The most important extension to the models is density-dependent survivorship, as all the models exhibit overoccupancy. Bence & Nisbet (1989) noted that open models with space-limited recruitment could provide insight into any population where there is debate on whether populations are regulated by recruitment or density dependent factors. These are essentially the processes which control both the fucoid and the barnacle populations. Density-dependent survivorship has been proposed for both *F. vesiculosus* (Creed, 1993) and *S. balanoides* (Crisp, 1960; Connell, 1961a; Shanks & Wright, 1986).

On hundred percent occupied space is difficult to define on these shores. Although all the space is occupied, individuals of *S. balanoides* will settle on the tests of adults (Connell, 1961a) and the *F. vesiculosus* will settle and join the spore/germling bank (Creed, 1993). Even when 100% occupancy does not occur not all free space is the same. For example, Lewis (1977) states that free living acorn cirripeds respond to a variety of stimuli during settlement: arthropodin (an insoluble protein found in adults); water currents; surface rugosity; light; and, gravity and hydrostatic pressure. In the absence of specific settlement cues settlement is usually delayed (Lewis, 1977). *F. vesiculosus* is also limited by the spatial aspect of free space, for example smaller plants are inhibited by the larger canopy plants. This occurs in a number of ways. For example, lower light intensity (Schonbeck & Norton, 1980a); lower nutrient levels (Dayton *et al*, 1984); whiplash and sweeping effects (Dayton, 1971; Ang, 1985); sediment build up (Kenelly, 1989); and aggregation of grazers (Hartnoll & Hawkins, 1985). To model this would require a spatial explicit model.

The inhibition of juveniles by adults would be a useful addition to the models. In both barnacles and fucoids this is an important factor. For example, juvenile *S. balanoides* suffer mortality due to undercutting (Connell, 1961a) and *F. vesiculosus* suffer shading (Schonbeck & Norton, 1980a) in overcrowded conditions. This could be implemented in the models using simple thresholds. Overcrowding also changes the growth forms of the adults with barnacles becoming more tubular (Moore, 1934) and fucoids show a general decrease in growth rate (Creed, 1993). These again could be added with simple thresholds and different growth functions.

This shows that a few simple changes would improve the realism of the models. However, there is a tradeoff between the biological realism and not just understanding of the model, but also parameterisation of the model.

7.2 Two Species Models

In this section the behaviour of the two species model is examined and further work suggested.

7.2.1 Mechanisms

In this section the dynamics and the mechanisms that produce them are examined. The behaviour of this type of non-linear model is much more diverse than the linear single species models. However, the general mechanisms that control the single species models act on the two species model. The two species model is driven primarily by settlement, but survivorship and size both influence the period and amplitude of oscillations.

The mechanism driving this model depends on the behaviour of the sub-models and the the interaction thresholds. The sub-models are driven in exactly the same way as the single species models, and can produce stable and oscillatory dynamics. If one or both of the sub-models produce oscillatory dynamics, then oscillations are driven in the other sub-model as the settlement is switched on and off. However, when the sub-models would individually be stable, interactions between the two sub-models can drive oscillations.

It is possible to fit the model to the limits suggested for the shore (Hartnoll & Hawkins, 1985; Proud, 1994). This also gives realistic cycle time for the individual species, *ie* 3-4 years for fucoids and 3 years for barnacles. However, the total cycle length is much shorter than found on the shore. Hartnoll & Hartnoll (1985) suggested that a total cycle time of about 7 years is correct. However, unless the survivorships of both species is pushed outside the bounds of the predicted parameters then the maximum cycle time is 4-5 years in the model. This suggests that the time delay between the two species is too short. Hastings (1986) stated that the key to understanding two species models is to look at interaction between the two time delays. Thus, increasing the delay between the species could be done by implementing stochastic seasonal settlement or interaction between adults of the two species rather than just at settlement.

Although this model is not very accurate, it does give a good first estimate using parameters from the literature. It will also provide a good building block to work on during the course of my Ph.D.

Further Study

Stochastic recruitment in a seasonal environment would make a large difference to the dynamics of this model. This would give a short period where recruitment is not guaranteed, more like the situation found on the moderately exposed rocky shores where recruitment of fucoid is not a yearly occurrence and the strength of barnacle settlement is variable (Hartnoll & Hawkins, 1985). This would increase the total cycle length with species able to dominate the shore for longer periods of time.

A grazer threshold would be very useful in this model. If the fucoid settlement is very large then it would make sense to let a few plant escape even in the absence of barnacles. This is because in the field grazing is limited by the time the grazer is immersed on horizontal surfaces (see Hawkins & Jones, 1992, for a general review) and thus can become saturated.

The interaction thresholds between the barnacle and fucoid need to be revised. Firstly a more realistic relationship between adult density and settlement would be useful.

7.3 Wider Implications

At this stage it is necessary to summarise how this thesis fits into the wider picture of rocky shore ecology and modelling. The implications for modelling and then rocky shore ecology will be discussed.

The theory of open models with space-limited recruitment is a recent addition to the modelling techniques (Roughgarden *et al*, 1985). These models were created to investigate systems where dispersal of juveniles can occur over long distances and in fairly large densities. Therefore traditional Lotka-Volterra systems cannot be used. However, investigation of these models does not just apply to species like barnacles. It could be used to model any system where a resource is limited, for example, light, space, territory or rainfall (Kuang & SO, 1995). These models can also provide insight into any community where there is debate over whether populations are regulated by density-dependent factors or recruitment (Bence & Nisbet, 1989). For example, reef fish (Mapstone & Fowler, 1988) and giant kelp (Nisbet & Bence, 1989). This gives a huge number of systems that can be modelled in this way. The work done in this thesis clearly demonstrates the mechanisms that control these type of models. Stability criteria have been investigated and a new type of criteria based on the mechanisms has been derived. Thus, this research could aid in the understanding of the same type of model but with a different limiting resource when applied to a different community. However, insight into the dynamics of these types of simple models is essential for the slow building of ecological models (Bence & Nisbet, 1989) and will be very useful for understanding the dynamics of these more complex models in my Ph.D.

In biology there are a number of reasons why this type of research is important. Firstly, any type of modelling aids in the formalisation of thoughts and ideas that experimental biologist have about a system and allows the testing of these ideas. Secondly, rocky shores are found all over the world, and despite their differences in species appendages, the general processes controlling these systems are very similar. The moderately exposed rocky shore is the shore that seems to have a mixture of sheltered and exposed shore characteristics, that keep the shore in a non-equilibrium state. If this research, when extended, could aid in the understanding of this particular shore, then these processes could be applied to more shores worldwide. Finally, barnacles and seaweeds are important fouling organism. They settle on the hulls of ships, causing drag and thus, increasing the fuel required. Modelling the growth of single species populations like this could give us an idea of how to reduce the population numbers naturally rather than having to use antifouling paint. This paint in many cases is toxic, for example, tributyltin from antifouling paints caused female *Nucella lapullis* in the English Channel to grow a penis (Spence *et al*, 1990). Although few biological inferences have been drawn for the experimentalist to test, in the course of my Ph.D. when the models created are more complex and thus, include more biological realism, may help to investigate these questions.

7.4 Data Problems

In this section the problem with the lack of comparable data in this field is examined. Shores tend to specific, and if a model is created for that shore then, the data set that it is parameterised from needs to be long term set and from that particular shore. In the parameter estimation sections, it has become clear that there is insufficient data on the ledges at Port St. Mary to parameterise the models, let alone test them. Although there is a relatively long biological time series for this shore (1977-1994) this is just for a single unreplicated $2 *$

$1m$ quadrat. This type of broad scale monitoring survey is useful in biology as it allows inferences about the processes occurring on the shore and is cheap. However, this quadrat may not be representative of the MTL as a whole, or even of the immediately surrounding area. The data comprises of percentage cover values only, and does not record any of the interaction coefficients. However, further replicated work has been done on the interactions and settlement on the specific shore (Creed, 1993; Proud, 1994; Jenkins, 1995).

From a number of sections (see, for example, Section 6.4) it is quite obvious that data that have been produced is generally measured using different techniques, at different time of year, in different units and by different people. Thus, most of the data are not comparable and cannot be pooled to make larger sets, as the pooling of these data would be statistically invalid. In fact, Underwood & Fairweather (1986) stated that intertidal communities do not have different ecologies, they just have different ecologists. They concluded from three examples that differences in regions are sometimes confounded with different methodology and interpretation. Gaines & Bertness (1993) suggested that field ecologists need to be able to integrate over time to produce a standard technique that works over long periods of juvenile dispersal.

I would like to state that being a biologist that I understand the difficulty with field experimentation. Underwood (1991) suggested that many modellers have spent to much time on 'easy' sciences like physics and have never had to grapple with field experimentation in complex and variable worlds. However, a standardisation in methodology, time-scales and units would provide a much better and more comparable data set for the modeller to use.

7.5 Summary

The aim of this thesis was to produced single species models that could then be linked in order to try and model the moderately exposed rocky shore, Port St. Mary, Isle of Man. The cycle was proposed by Hartnoll & Hawkins (1985).

Similar dynamics are produced by both the single species models, despite the difference in construction. Increasing settlement rate, growth and survivorship increases period and amplitude of cycles. However, further work would involve including density-dependent survivorship, spatial scales and the effect of adults on juveniles.

A two species model was producing by linking the two single species models using assumptions of the effect of barnacle on fucoids and *vice versa*. Understanding of this model was facilitated greatly by the work on the single species models. Settlement again drives the sub-models and oscillations can be caused by oscillations in one or both of the sub-models or by the interaction between the sub-models. Further work includes joining more complicated single species models, stochastic recruitment functions, a grazer saturation threshold and adult inhibition of juveniles.

These models are very simple, but it has been possible to draw a few inferences for the experimentalist to test. These are settlement is the most important factor in structuring the shore studied and that if a seed bank exists it must suffer very high mortality.

A better data set to parameterise and test these models against needs to be larger and replicated. The problem of different ecologists, methodologies and interpretation is suggested as a problem. However, the difficulty of experimentation in such a complex and variable environment is noted.

In summary I would like to say that the two main aims of this thesis have been accomplished. These were to produce simple models of *S. balanoides* and *F. vesiculosus* with understandable dynamics and to instruct the author in the techniques of mathematical modelling.

References

Åberg, P., (1990). Measuring size and choosing category size for a transition matrix study of the seaweed *Ascophyllum nodosum. Marine Ecology Progress Series*, **63**, 281-287.

Åberg, P., (1992a). A demographic study of two populations of the seaweed *Ascophyllum nodosum. Ecology*, **73**, 1473-1487.

Åberg, P., (1992b). Size based demography of the seaweed *Ascophyllum nodosum* in stochastic environments. *Ecology*, **73**, 1488-1501.

Ang, P.O., (1985). Studies on the recruitment of *Sargassum* species. (Fucales: Phaeophyta) in Balibaga, Calatagan, Philippines. *Journal of Experimental Marine Biology and Ecology*, **91**, 293-301.

Ang, P.O., (1987). Use of projection matrix models in the assessment of harvesting strategies for *Sargassum. Hydrobiologia*, **151/152**, 335-339.

Ang, P.O., (1991a). Natural dynamics of *Fucus distichus* (Phaeophyceae, Fucales) population: reproduction and recruitment. *Marine Ecology Progress Series*, **78**, 71-85.

Ang, P.O., (1991b). Age- and size- dependent growth and mortality in a population of *Fucus distichus. Marine Ecology Progress Series*, **78**, 173-189.

Ang, P.O., & De Wreede, R.E., (1992). Density dependence in a population of *Fucus distichus. Marine Ecology Progress Series*, **90**, 169-181.

Arnold, D.C., (1977). Fecundity of *Balanus balanoides* in Passamaquoddy Bay. *Journal of the Fisheries Research Board of Canada*, **34**, 273-275.

Ang, P.O., & De Wreede, R.E., (1993). Simulation and Analyses of the dynamics of a *Fucus distichus* (Phaeophyceae, Fucales) population. *Marine Ecology Progress Series*, **93**, 253-265.

Arrontes, J., (1993). The nature of the distributional boundary of *Fucus serratus* on the north shore of Spain. *Marine Ecology Progress Series*, **93**, 183-193.

Ballantine, W.J., (1961). A biologically defined exposure scale for the comparative description of rocky shores. *Field Studies*, **1**, 1-19.

Bally, R., & Griffiths, C.L., (1989). Effects of human trampling on an exposed rocky shore. *International Journal of Environmental Studies*, **34**, 115-125.

Barnes, H., (1955). The growth rate of *Balanus balanoides* (L.). *Oikos*, **6**, 109-113.

Barnes, H., & Barnes, M., (1968). Egg numbers, metabolic efficiency of egg production and fecundity: local and regional variations in a number of common barnacles. *Journal of Experimental Marine Biology and Ecology*, **2**, 135-153.

Barnes, H., & Powell, H.T., (1953). The growth of *Balanus balanoides* (L.) and *B. crenatus* (Brug.) under varying conditions of submergence. *Journal of the Marine Biological Association of the United Kingdom*, **32**, 107-128.

Barnett, B.E., & Crisp, D.J., (1979). Laboratory studies of gregarious settlement in *Balanus balanoides* and *Elminius modestus* in relation to competition between these species. *Journal of the Marine Biological Association of the United Kingdom*, **59**, 581-590.

Baxter, J.M., Jones, A.M., & Simpson, J.A., (1985). A study of the long term changes in some rocky shore communities in Orkney. *Proceedings of the Royal Society of Edinburgh*, **2**, 135-153.

Bence, J.R., & Nisbet, R.M., (1989). Space-limited recruitment in open systems: the importance of time delays. *Ecology*, **70**, 1434-1441.

Bernadelli, H., (1941). Population Waves. *Journal of the Burma Research Society*, **31**, 1-18.

Bertness, M.D., Gaines, S.D., Stephens, E.G., & Yund, P.O., (1992). Components of recruitment in populations of the acorn barnacle *Semibalanus balanoides* (*Linnaeus*). *Journal of Experimental Marine Biology and Ecology*, **156**, 199-215.

Black (1974). Some biological interactions affecting intertidal populations of the kelp *Egregia laevigata*. *Marine Biology*, **28**, 198-198.

Boling, R.H., Jr., (1973). Toward state-space models for biological populations. *Journal of Theoretical Biology*, **40**, 485-506.

Bray, A.M., (1983). Propagule production and competition in species of *Fucus*. M.Sc. Thesis, University of Glasgow.

Breton-Provencher, M., Gange, J.A., & Cardinal, A., (1979). Estimation de la production des algues benthiques mediolittorales dans l'estuaire du Saint-Laurent (Quebec). *Canadian Naturalist*, **106**, 199-209.

Burgman, M.A., & Gerard, V.A., (1990). A stage-structured stochastic population model for the giant kelp *Macrocystis pyrifera*. *Marine Biology*, **105**, 15-23.

Burrows, E.M., & Lodge, S.M., (1950). Notes on the inter-relationships of *Patella*, *Balanus* and *Fucus* on a semi-exposed coast. *Report of the Marine Biological Station at Port Erin, Isle of Man*, **62**, 30-34.

Burrows, E.M., & Lodge, S.M., (1951). Autecology and the species problem in *Fucus*. *Journal of the Marine Biological Association of the United Kingdom*, **30**, 161-176.

Burrows, M.T., (1988). The comparative biology of *Chthamalus stellatus* (Poli) and *Chthamalus motagui* (Southward). Ph.D. Thesis, University of Manchester.

Caffey, H.M., (1985). Spatial and temporal variation in settlement and recruitment of intertidal barnacles. *Ecological Monographs*, **55**, 313-332.

Carter, A.R., & Anderson, R.J., (1991). Biological and physical factors controlling the spatial distribution of the intertidal alga *Gellidium pristoides* in the Eastern Cape, South Africa. *Journal of the Marine Biological Association of the United Kingdom*, **71**, 555-568.

Caswell, H., (1989). *Matrix population models.* Sinauer Associates.

Caswell, H., Koening, H.E., Resh, J.A., & Ross, Q.E., (1972). An introduction to systems science for ecologists. In: *Systems Analysis and Simulation Ecology, Volume 2.* B.C. Patten (Ed), Academic Press, New York, pp.3-78.

Chapman, A.R.O., (1986a). Age versus stage: An analysis of age- and size- specific mortality and reproduction in a population of *Laminaria longicruris*. *Journal of Experimental Marine Biology and Ecology*, **97**, 113-122.

Chapman, A.R.O., (1986b). Population and community ecology of seaweeds. *Advances in Marine Biology*, **23**, 1-161.

Chapman, A.R.O., (1990a). Competitive interactions between *Fucus spiralis* and *Fucus vesiculosus* (Fucales, Phaeophyta). *Thirteenth International Seaweed Symposium.* Kluwer Academic Publishers, Belgium, pp205-209.

Chapman, A.R.O., (1995). Functional ecology of algae: 23 years of progress. *Phycologia*, **34**, 1-32.

Chapman, A.R.O., & Goudey, C.L., (1983). Demographic study of the macrothallus of *Leathesia difformis* (Phaeophyta) in Nova Scotia. *Canadian Journal of Botany*, **61**, 319-323.

Cheshire, A.C., & Hallam, N.D., (1989). Methods for assessing age composition of native stands of subtidal microalgae: a case study on *Durvillaea potatorum. Botanica Marina*, **32**, 199-204.

Chesson, P.L., & Warner, R.R., (1981). Environmental variability promotes coexistence in lottery competitive systems. *American Naturalist*, **32**, 199-204.

Connell, J.H., (1959). Studies of some factors affecting recruitment and mortality of natural populations of intertidal barnacles. In: *Marine Boring and Fouling Organisms.* D.L. Ray (Ed), University of Washington Press, Seattle, pp.226-233.

Connell, J.H., (1961a). The effect of competition, predation by *Thais lapillus*, and other on natural populations of the barnacle *Balanus balanoides. Ecological Monographs*, **31**, 61-104.

Connell, J.H., (1983). On the prevalence and relative importance of interspecific competition: evidence from field experiments. *American Naturalist*, **122**, 661-696.

Connell, J.H., (1985). The consequences of variation in initial settlement versus post-settlement mortality in rocky intertidal communities. *Journal of*

Experimental Marine Biology and Ecology, **93**, 11-45.

Cousens, A.C., (1981). Methods for assessing age composition of native stands of subtidal microalgae: a case study on *Durvillaea potatorum. Botanica Marina*, **32**, 199-204.

Creed, J.C., (1993). Intraspecific competition in seaweeds. Ph.D. Thesis, University of Liverpool.

Creed, J.C., Norton, T.A. & Kain, J.M. (1993). Are neighbours harmful or helpful in *Fucus vesiculosus* populations? *Marine Ecology Progress Series*, **133**, 191-201.

Crisp, D.J., (1960). The northern limits of *Elminius modestus* in Britain. *Nature*, **188**, 681.

Crisp, D.J., (1964). Radical difference between North American and European forms of *Balanus balanoides. Journal of the Marine Biological Association of the United Kingdom*, **44**, 33-45.

Darwin, C., (1854). A monograph on the sub-class Cirripedia. The Balanidae; the Verrucidae etc. *Ray Society, London.*

Dayton, P.K., (1971). Competition, disturbance, and community organisation: the provision and subsequent utilisation of space in a rocky intertidal community. *Ecological Monographs*, **41**, 351-389.

Dayton, P.K., Currie, V., Gerrodete, T., & Keller, B.D., (1984). Patch dynamics and stability of some Californian kelp communities. *Ecological Monographs*, **54**, 253-289.

De Roos, A.M, (1989). Daphnids on a train. Development and application of a new numerical method for physically structured population models. Ph.D. Thesis, Leiden University.

Deysher, L., & Norton, T.A., (1982). Dispersal and colonisation in *Sargassum muticaum* (Yendo.) Fensholt. *Journal of Experimental Marine Biology and Ecology*, **56**, 179-195.

Dring, M.J., (1982). *The biology of marine plants.* Edward Arnold, London.

Dungan, M.L., (1986). Three way interactions: barnacles, limpets and algae in a Sonoran desert rocky intertidal zone. *American Naturalist*, **127**, 292-316.

Dunkin, S., & Hughes, R.N., (1984). Behavioural components of prey selection by the dogwhelk, *Nucella lapillus* (L.), feeding on the barnacle, *Semibalanus balanoides*, in the laboratory. *Journal of Experimental Marine Biology and Ecology*, **79**, 91-103.

Feare, C.J., & Summer, R.W., (1985). Birds as predators on rocky shores. In *The Ecology of Rocky Coasts.* P.G. Moore and R. Seed (Eds), Hodder & Stoughton, London, pp.249-264.

Gaines, S., & Bertness, M., (1993). The dynamics of juvenile dispersal: why field ecologists must integrate. *Ecology*, **74**, 2430-2435.

Gaines, S., & Roughgarden, J., (1985). Larval settlement rate: a leading determinate of structure in an ecological community of marine intertidal zone. *Proceedings of the National Academy of Sciences of the United States of America*, **82**, 3707-3711.

Gaines, S., Brown, S., & Roughgarden, J., (1985). Spatial variation in larval concentrations as a cause of spatial variation in settlement for the barnacle *Balanus glandula. Oecologia*, **67**, 267-272.

Gonzalez, R.C., & Woods, R.E., (1992). *Digital Image Processing.* Addison-Wesley Publishing Company, Reading.

Gross, L.J., (1986). Ecology: An idiosyncratic view. In: *Biomathematics Volume 17. Mathematical Ecology.* T.G. Hallam & S.A. Levin (Eds) Part 1, Springer-Verlag, Berlin, pp.3-13.

Gunhill, F.C., (1980). Demography of the intertidal brown alga *Pelvetia fastigata* in Southern California, USA. *Marine Biology*, **59**, 169-179.

Gurney, W.S.C., & Nisbet, R.M., (*in press*). *Ecological Dynamics.* OUP, New York.

Hallam, T.G., (1986). Population dynamics in a homogeneous environment. In: *Biomathematics Volume 17. Mathematical Ecology.* T.G. Hallam & S.A. Levin (Eds) Part 1, Springer-Verlag, Berlin, pp.61-94.

Harms, J., (1984). Influence of water temperature on larval development of *Elminius modestus* and *Semibalanus balanoides*(Crustacia, Cirripedia). *Helgoländer Meeresuntersuchungen*, **38**, 123-134.

Harper, J.L., (1967). A Darwinian approach to plant ecology. *Journal of Ecology*,

55, 246-270.

Harper, J.L., (1977). *Population biology of plants.* Accademic press, London.

Hartnoll, R.G., & Hawkins, S.J., (1980). Monitoring rocky shore communities: a critical look at spatial and temporal variation. *Helgoländer Meeresuntersuchungen*, **33**, 484-495.

Hartnoll, R.G., & Hawkins, S.J., (1985). Patchiness and fluctuations on a moderately exposed rocky shore. *Ophelia*, **33**, 484-495.

Hastings, A., (1986). Interacting age structured populations. In: *Biomathematics volume 17: Mathematical Ecology.* T.G. Hallam & S.A. Levin (Eds), Springer-Verlag, pp.287-294.

Hatton, H., (1938). Essais de bionomie explicative sur quelques especes intercotidales d'algues et d'animaux. *Annales de l'Institute Oceanographique*, **17**, 241-348.

Hawkins, S.J., (1979). Field Studies on Manx rocky shore communities. Ph.D. Thesis, University of Liverpool.

Hawkins, S.J., (1981a). The influence of *Patella* grazing on the fucoid/barnacle mosaic on moderately exposed rocky shores. *Kieler Meeresforschungen*, **5**, 537-544.

Hawkins, S.J., (1981b). The influence of season and barnacle on algal colonisation of *Patella vulgata* (L.) exclusion areas. *Journal of the Marine Biological Association of the United Kingdom*, **61**, 1-15.

Hawkins, S.J., (1983). Interaction of *Patella* and macroalgae with settling *Semibalanus balanoides* (L.). *Journal of Experimental Marine Biology and Ecology*, **71**, 55-72.

Hawkins, S.J., & Hartnoll, R.G., (1980). Small scale relationships between species number and area on rocky shores. *Estuarine and Coastal Marine Science*, **10**, 201-214.

Hawkins, S.J., & Hartnoll, R.G., (1982a). Settlement patterns of *Balanus balanoides* (L.) in the Isle of Man. *Journal of Experimental Marine Biology and Ecology*, **62**, 271-283.

Hawkins, S.J., & Hartnoll, R.G., (1982b). The influence of barnacle cover on the numbers, growth and behaviour of *Patella vulgata* on a vertical pier.

Journal of the Marine Biological Association of the United Kingdom, **62**, 865-867.

Hawkins, S.J., & Hartnoll, R.G., (1983a). Changes in rocky shore community: and evaluation of monitoring. *Journal of Marine Environmental Research*, **9**, 131-181.

Hawkins, S.J., & Hartnoll, R.G., (1983b). Grazing of intertidal algae by marine invertebrates. *Oceanography and Marine Biology Annual Review*, **25**, 195-282.

Hawkins, S.J., & Hartnoll, R.G., (1985). Factors determining the upper limits of intertidal canopy forming algae. *Marine Ecology Progress Series*, **20**, 265-271.

Hawkins, S.J., & Jones, H.D, (1992). *Marine Field Course Guide 1. Rocky Shores.* IMMEL Publishing, London.

Hawkins, S.J., Hartnoll, R.G., Kain, J.M., & Norton, T.A., (1992). Plant animal interactions on hard substrata in the North-East Atlantic. In: *Plant Animal Interactions in the Marine Benthos.* D.M. John, S.J. Hawkins & J.H. Price (Eds), Clarendon Press, Oxford, pp.1-32.

Hoffmann, A.J., & Santelices, B., (1991). Banks of algal microscopic forms: hypotheses on their functioning in comparison with seed banks. *Marine Ecology Progress Series*, **79**, 185-194.

Iwasa, Y., & Roughgarden, J., (1985). Evolution in a metapopulation with space-limited subpopulations. *Institute of Mathematics and its Applications Journal of Mathematics Applied in Medicine and Biology*, **2**, 93-107.

Iwasa, Y., & Roughgarden, J., (1986). Interspecific competition among metapopulations with space-limited subpopulations. *Theoretical Population Biology*, **30**, 194-214.

Jenkins, S.R., (1995). The ecology of sheltered, canopy dominated shores. Ph.D. Thesis, University of Liverpool.

Jones, N.S., (1948). Observation and experiments on the biology of *Patella vulgata* at Port St. Mary, Isle of Man. *Proceedings and Transactions of the Liverpool Biological Society*, **56**, 60-77.

Judson, O.P., (1994). The rise of the individual-based model in ecology. *Trends* *in Ecology and Evolution*, **9**, 9-14.

Kendall, M.A., Bowman, R.S., Williamson, P., & Lewis, J.R., (1982). Settlement patterns, density and stability in the barnacle *Balanus balanoides. Netherlands Journal of Sea Research*, **16**, 119-126.

Kennelly, S.J., (1989). Effects of kelp canopies on understory species due to the shade and scour. *Marine Ecology Progress Series*, **50**, 215-224.

Keser, M., & Larson, B.R., (1984). Colonisation and regrowth dynamics of three species of *Fucus. Marine Ecology Progress Series*, **15**, 125-134.

Keser, M., Vadas, R.L., & Larson, B.R., (1981). Regrowth of *Ascophyllum nodosum* and *Fucus vesiculosus* under different harvesting regimes in Maine, USA. *Botanica Marina*, **24**, 29-38.

Knight, M., & Parke, M, (1953). A biological study of *Fucus vesiculosus* L. and *F. serratus* L. *Journal of the Marine Biological Association of the Uniter Kingdom*, **29**, 439-514.

Knight-Jones, E.W., (1953). Laboratory experiments on gregariousness during settlement in the barnacle *Balanus balanoides* and other settling barnacles. *Journal of Experimental Biology*, **30**, 584-598.

Knight-Jones, E.W., & Stephenson, J.P., (1950). Gregariousness during settlement in the barnacle *Elminius modestus* Darwin. *Journal of the Marine Biological Association of the United Kingdom*, **21**, 281-297.

Kuang, Y., & So, W.H., (1995). Analysis of a delayed 2 stage population model with space-limited recruitment. *Siam Journal of Applied Mathematics*, **55**, 1675-1696.

Lemoine, P., (1913). Quelques experiences sur la croissance des algues marines a Roscoff. *Bull. Inst. ocèanogr. Monaco*, **227**, 1-19.

Leslie, P., (1945). On the use of matrices in certain population mathematics. *Biometrika*, **33**, 183-212.

Leslie, P., (1948). Some further notes on the use of matrices in population mathematics. *Biometrika*, **35**, 213-245.

Lewis, C.A., (1977). A review of substratum selection in free living and symbiotic cirripeds. In: *Settlement and Metamorphosis of Marine Invertebrate Larvae.* M. Rice (Ed), Elsevier, Amsterdam.

Lewis, E.G., (1942). On the generation and growth of a population. *Sankhya: The Indian Journal of Statistics*, **6**, 93-96.

Lewis, J.R., (1964). *The Ecology of Rocky Shores.* English University Press, London.

Lewis, J.R., (1977). The role of physical and biological factors in the distribution and stability of rocky shore communities. In: *Biology of Benthic Organisms.* B.F. Keegan, P.O. Ceidigh & P.J.S. Boaden (Eds), Pergamon Press, Oxford. pp.417-424.

Lotka, A.J., (1924). *Elements of Physical Biology.* Williams & Wilkins, Baltimore. (Reprinted in 1956 by Dover Publications, New York, as *Elements of Mathematical Biology.*)

Lubchenco, J., (1983). *Littorina* and *Fucus*: the effect of herbivores, substratum heterogeneity and plant escapes during succession. *Ecology*, **64**, 1116-1123.

Mapstone, B.D., & Fowler, A.J., (1988). Recruitment and the Structure of assemblages of fish on coral reefs. *Trends in Ecology and Evolution*, **3**, 72-77.

May, R.M., (1976). Simple mathematical models with very complicated dynamics. *Nature*, **261**, 459-467.

Metz, J.A.J., (1977). State space models for animal behaviour. *Annals of Systems Research*, **6**, 65-109.

Miller, K.M., & Carefoot, T.H., (1989). The role of spatial and size refuges in the interaction between juvenile and grazing limpets. *Journal of Experimental Marine Biology and Ecology*, **134**, 157-174.

Minchinton, T.E., (1995). Demographic consequences of variations in recruitment and conspecific cover to populations of sessile marine invertebrates. Ph.D. Thesis, University of Sydney.

Minchinton, T.E., & Scheibling, R.E., (1993). Free space availability and larval substratum selection as determinants of barnacle population structure in a developing rocky intertidal community. *Marine Ecology Progress Series*, **95**, 233-244.

Moloney, K.A., (1986). A generalised algorithm for determining category size.

Oecologia, **69**, 176-180.

Moore, H.B., (1934). The biology of *Balanus balanoides.* I. Growth rate and its relation to size, season and tidal level. *Journal of the Marine Biological Association of the United Kingdom*, **19**, 851-868.

Murray, J.D., (1993). *Mathematical Biology* (Second Edition). Springer-Verlag, Berlin Heidelberg New York.

Nisbet, R.M., & Gurney, W.S.C., (1982). *Modelling Fluctuating Populations.* John Wiley & Sons, Chichester.

Norton, T.A., (1986). The ecology of macroalgae in the Firth of the Clyde. *Proceeding of the Royal Society of Edinburgh*, **90B**, 255-269.

Norton, T.A., Mathieson, A.C, & Neushaul, M., (1982). A review of some aspects of form and function in seaweeds. In: *The Biology of Seaweed* (1^{st} edition). C.S. Lobban & M.J. Wynne (Eds), Blackwell Scientific Publications, Berkley and Los Angeles, pp.421-451.

O'Riordan, R.M., (1992). Reproduction and recruitment of two intertidal Chthamalid barnacles. Ph.D. Thesis, National University of Ireland.

Paine, R.T., (1984). Ecological determinism in the competition for space. *Ecology*, **65**, 1339-1348.

Pannacciulli, F., (1995). Population ecology and genetics of European species of intertidal barnacles. Ph.D. Thesis, University of Liverpool.

Parke, M., (1948). Studies on British Laminariaceae. I. Growth in *Laminaria saccharina* (L.) Lamour. *Journal of the Marine Biological Association of the United Kingdom*, **27**, 651-709.

Possingham, H.P., & Roughgarden, J., (1990). Spatial population dynamics of a marine organism with a complex life cycle. *Ecology*, **71**, 973-985.

Printz, H., (1959). Phenological studies of marine algae along the Norwegian Coast. II. *Fucus vesiculosus* L. *Avhandl. utgitt av Det Norske Videnskaps-Akademi i Oslo. I. mat.-Naturv. Klasse.*, **4**, 17-28.

Proud, S.V., (1994). Tributyltin pollution and the bioindicator *Nucella lapillus*: population recovery and community level responses. Ph.D. Thesis, University of Liverpool.

Raimondi, P.T., (1990). Patterns, mechanisms, consequences of variability in settlement and recruitment of an intertidal barnacle. *Ecological Monographs*, **60**, 289-309.

Raffaelli, D.G., & Hawkins, S.J., (*in press*). *Intertidal Ecology.* Chapman and Hall, London.

Renshaw, E., (1993). *Modelling Biological Populations in Space and Time.* Cambridge University Press, Cambridge.

Rosenthal, R.J., Clarke, W.D., & Dayton, P.K., (1974). Ecology and natural history of a stand of giant kelp *Macrocystis perifera* off Del Mar, California. *Californian fisheries bulletin*, **72**, 670-684.

Roughgarden, J., & Iwasa, Y., (1986). Dynamics of metapopulations with space-limited sub-populations. *Theoretical population biology*, **29**, 235-261.

Roughgarden, J., Gaines, S., & Iwasa, Y., (1984). Dynamics and evolution of marine populations with pelagic larval dispersal. In: *Exploitation of Marine Communities.* R.M. May (Ed), Springer-Verlag, New York, USA, pp.111-128.

Roughgarden, J., Iwasa, Y., & Baxter, C., (1985). Demographic theory for an open marine population with space-limited recruitment. *Ecology*, **66**, 54-67.

Roughgarden, J., Gaines, S.D., & Pacala, S.W., (1987). Supply side ecology: the role of physical transport processes. In: *Organisation of Communities: Past and Present. Proceeding of the British Ecological Society Symposium, Aberystwyth, Wales (April, 1986).* P. Giller & J. Gee (Eds), Blackwell, Scientific, London.

Russell, J., (1986). Variation and natural selection in marine macroalgae. *Oceanography and Marine Biology Annual Review*, **24**, 309-377.

Santelices, B, & Ojeda, F.P., (1984). Recruitment, growth and survival of *Lessonia nigrescens* (Phaeophyta) at various tidal levels in exposed habitats of central Chile. *Journal of Experimental Marine Biology and Ecology*, **31**, 303-313.

Schonbeck, M.W., & Norton, T.A., (1978). Factors controlling the upper limits of fucoid algae on the shore. *Marine Ecology Progress Series*, **19**, 73-82.

Schonbeck, M.W., & Norton, T.A., (1980a). The effects on intertidal fucoid algae of exposure to air under various conditions. *Botanica Marina*, **23**, 141-147.

Seip, K.L., (1980). A mathematical model of competition and colonisation in a community of marine benthic algae. *Ecological modelling*, **10**, 77-104.

Shanks, A.L., (1986). Tidal periodicity in the daily settlement of intertidal barnacle larvae and an hypothesised mechanism for the cross-shelf transport of cyprids. *Biological Bulletin*, **170**, 429-440.

Shanks, A.L., & Wright, W.G, (1986). Adding teeth to wave action: the destructive effect of wave borne rocks on intertidal organisms. *Oecologia*, **69**, 420-428.

Sih, A., Crowley, P., McPeek, M., Petranka, J., & Stromeier, K., (1985). Predation, competition and prey communities: a review of field experiments. *Annual Review of Ecology and Systematics*, **16**, 269-311.

Smith, B.D., (1986). Implications of population dynamics and interspecific competition for the harvesting and management of *Laminaria. Marine Ecology Progress Series*, **33**, 7-18.

Spence, S.K., Bryan, G.W., Gibbs, P.E., Masters, D., Morns, L., & Hawkins, S.J., (1990). Effects of tributyltin on *Nucella* populations. *Functional Ecology*, **4**, 425-432.

Sousa, W.P., (1984). Intertidal mosaics: patch size, propagule availability and spatially variable patterns of succession. *Ecology*, **65**, 1918-1935.

South, G.R., & Wittick, A., (1987). *An Introduction to Phycology.* Blackwell Scientific Presss, Oxford.

Southward, A.J., (1956). The population balance between limpets and seaweeds on wave-beaten rocky shores. *Proceedings and Transactions of the Liverpool Biological Society*, **68**, 20-29.

Southward, A.J., (1964). Limpet grazing and the control of vegetation on rocky shores. In: *Grazing in Terrestrial and Marine Environments.* D.J. Crisp (Ed), Blackwell Scientific Publications, Oxford, pp.265-273.

Southward, A.J., (1979). Cyclic fluctuations in population density during 11 years recolonisation of rocky shores in West Cornwall following the Torrey

Canyon oil spill in 1967. In: *Cyclic Phenomena in Marine Plants and Animals.* E. Naylor & R.G. Hartnoll (Eds), Pergamon Press, Oxford, pp.85-92.

Southward, A.J., (1991). Forty years of change in species composition and population density of barnacles on a rocky shore near Plymouth. *Journal of the Marine Biological Association of the United Kingdom*, **71**, 495-513.

Southward, A.J., & Southward, E.C., (1978). Recolonisation of rocky shores in Cornwall after the use of toxic dispersants to clean up the Torrey Canyon oil spill. *Journal of the Fisheries Resources Board, Canada*, **35**, 682-706.

Steele, J.H., (1993). Concepts and models: an overview In: *Lecture Notes in Biomathematics 96: Patch Dynamics.* S.A. Levin, T.M. Powell, & J.M. Steele (Eds) Part 1. Springer-Verlag, Berlin, pp90-92.

Stephenson, T.A, & Stephenson, A., (1972). *Life Between the Tidemarks on Rocky Shores.* W.H. Freeman & Co., USA.

Stubbings, H.G., (1975). *Balanus balanoides.* Liverpool University Press, Liverpool.

Underwood, A.J., (1991). The logic of ecological field experiments: a case history from studies of the distribution of macro-algae on rocky intertidal shores. *Journal of the Marine Biologial Association of the United Kingdom*, **71**, 841-866.

Underwood, A.J., & Fairweather, P.G., (1986). Intertidal communities: do they have different ecologies or different ecologists. *Proceedings of the Ecological Society of Australia*, **14**, 7-16.

Underwood, A.J., & Fairweather, P.G., (1989). Supply-side ecology and benthic marine assemblages. *Trends in Ecology and Evolution*, **4**, 16-20.

Underwood, A.J., & Jernakoff, P., (1981). Effect of interactions between algae and grazing gastropods on the structure of a low-shore intertidal algal community. *Oecologia*, **48**, 221-233.

Underwood, A.J., Denley, E.J., & Moran, M.J., (1983). Experimental analyses of the dynamics of mid-shore rocky intertidal communities n New South Wales. *Oecologia*, **56**, 202-219.

Vadas, R.L., & Elner, R.W., (1992). Plant-animal interactions in the North-East Atlantic. In: *Plant Animal Interactions in the Marine Benthos.* D.M. John, S.J. Hawkins & J.H. Price (Eds), Clarendon Press, Oxford, pp.33-60.

Vadas, R.L., Johnson, S., & Norton, T.A., (1992). Recruitment and mortality of early post-settlement stages of benthic algae. *British Phycological Journal*, **27**, 331-351.

Waterhouse, J.C., Farrell, M.P., & DeAngelis, D.L., (1986). *Hierarchical Approaches to the Study of Ecological Process and Pattern.* Environmental Sciences Division Publication N° 2721.

Wethey, D.S., (1984). Spatial pattern in barnacle settlement: day to day changes during the settlement season. *Journal of the Marine Biological Association of the United Kingdom*, **64**, 687-698.

Wethey, D.S., (1985). Local and regional variation in settlement and survival in the littoral barnacle *Semibalanus balanoides* (L.): patterns and consequences. In: *The Ecology of Rocky Coasts.* P.G. Moore and R. Seed (Eds), Hodder & Stoughton, London, p. 467.