The Ecology of Sheltered, Canopy Dominated Shores

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by

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To Mum and Dad

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Ecology of sheltered, canopy dominated shores

Stuart Rees Jenkins

ABSTRACT

Sheltered rocky shores of northwest Europe are dominated by fucoid macroalgae. Limpets and barnacles, common on more exposed shores, are relatively rare. Such shores have not been extensively studied and consequently the factors structuring their communities are not well understood.

The relative importance of the fucoid canopy and *Patella vulgata* in structuring sheltered shore communities was examined using factorial field experiments in both the *Ascophyllum nodosum* and *Fucus serratus* zones. In the *Ascophyllum* zone, the canopy facilitated the presence of a red algal turf which restricts the grazing range of limpets to small patches. Removal of the *Ascophyllum* canopy resulted in degradation of this turf and a consequent expansion of the grazing range of limpets. Limpet recruitment was also enhanced. Although an *Ascophyllum* canopy did not re-establish during the three year period of this study, mixed canopies of *Fucus serratus* and *Fucus vesiculosus* rapidly developed. These canopies allowed regrowth of algal turf, which resulted in a re-stabilising of the system.

In the *Fucus serratus* zone, limpets are free to graze over a much wider area. Removal of either the canopy or limpets resulted in limited changes to the understorey community. Thus, the effect that the canopy has on community structure is dependent on the presence or absence of limpets (and vice versa). Large scale changes occurred following removal of both canopy and limpets with development of ephemeral algae and accumulation of silt. Re-establishment of the canopy following artificial disturbance was delayed but not prevented by limpet grazing. Recruitment of *Fucus serratus* juveniles was prevented on grazeable substrate, but 'escapes' occurred within patches of turf, in crevices and on the surface of the encrusting alga *Phymatolithon purpureum.*

Limpet abundance is known to decrease with increasing shelter from wave action. However, the increase in abundance of algae in shelter means the area available for grazing can be low, particularly beneath the *Ascophyllum* canopy. Density of limpets per metre square of 'grazeable substrate' was examined over a wave exposure gradient and found to remain constant. It was proposed this measure is more appropriate than simple density when considering limpet population dynamics. Populations of *Patella vulgata* beneath *Ascophyllum* were shown to be relatively stable with low levels of recruitment and mortality. Growth rate was shown to be low in comparison to a nearby exposed shore. This result is in marked contrast to previous studies The limitation of *Patella* populations on sheltered shores is discussed.

The scarcity of barnacles (*Semibalanus balanoides*) on sheltered shores was investigated by examining three factors thought to be influential: larval supply, interactions with canopy algae and post settlement predation by dogwhelks. Canopy algae may inhibit barnacle settlement in two ways, by forming a barrier to cyprid movement and by sweeping across the substratum. These two factors were examined in a factorial experiment at three shore levels. Sweeping had a negative effect on settlement at all shore levels but particularly in the *Fucus serratus* zone. Further examination of sweeping by *Fucus serratus* revealed no difference in levels of survival between settled cyprids and newly metamorphosed spat transplanted beneath a *Fucus serratus* canopy. Five day old spat showed a significant increase in survival. The importance of a barrier effect on barnacle settlement was unresolved. Measurements of cyprid supply beneath the canopy indicated no effect, but settlement data indicated the opposite. Levels of predation by dogwelks were very low on new recruits but high on transplanted adults. Dogwhelks were considered important in preventing build up of barnacle populations following chance recruitment events beneath the canopy.

CHAPTER 1

General Introduction

Rocky shores provide biologists with a readily accessible wealth of marine life that may be studied in situ with relative ease. Early work on rocky shores concentrated on the description of species and their patterns of distribution (e.g. Stephenson and Stephenson, 1949; Lewis, 1964; Stephenson and Stephenson, 1972). More recently, ecologists have attempted to explain these patterns. Many organisms on rocky shores are sessile or slow moving and space for attachment in this essentially two dimensional environment is of prime importance. Such a system is amenable to manipulation and has enabled ecologists to examine the respective roles of physical and biological factors in influencing community patterns by experimental means.

Rocky shores form a boundary zone between the land and the sea over which a sharp environmental gradient from the low to the high shore exists. Low on the shore, organisms are immersed in water for the majority of the time. With increasing height the shore will be covered with water for shorter periods. Since most shore organisms probably evolved from a marine ancestry, the environmental gradient can be considered uni-directional with increasing stress higher on the shore. The zonation of organisms over this 'vertical' gradient is a dominant feature of rocky shores and has received considerable attention (e.g. Colman, 1933; Stephenson and Stephenson, 1949; Schonbeck and Norton, 1978; Underwood, 1978; Lubchenco, 1980; Schonbeck and Norton, 1980). A second major environmental gradient is caused by different degrees of wave action. This 'horizontal' gradient has a major impact on the communities of organisms on different shores but stress associated with this gradient does not occur in a clearly defined direction. For example, at exposed sites organisms are at high risk of dislodgement from wave action, whilst in shelter deposition of silt can be detrimental, smothering both plants and animals.

This thesis examines the ecology of sheltered Manx shores and assesses the causes of distribution patterns across the wave exposure gradient. In the remainder of this introduction, studies examining the structure of shore communities at different levels of exposure are reviewed. A comparison between shores of Britain and the north east coast of North America is made. Finally, work specific to sheltered shores of Britain is examined before presenting the detailed objectives of this study.

1.1 Exposure to wave action

The degree of exposure to wave action is probably the most important factor determining the structure of shore populations and influencing their distribution

(Lewis, 1964). Wave size is primarily determined by the uninterrupted distance or 'fetch' over which the wind blows across the surface of the sea. The geographical position of a shore, relative to the prevailing winds and surrounding sea areas, will therefore have a major effect on the severity of wave action. A major complication, however, is the topography of the shore. In general the flatter and more extensive the shore the less severe the wave action. When a wave breaks against a steep shore a large proportion of the wave's energy is directed into the substratum and the attached biota. On a gently sloping shore this energy moves more parallel to the substratum. Thus organisms encounter less energetic water flows on gentle slopes (Denny, 1988). On shores of irregular profile a variety of conditions will prevail. Wave energy can be dissipated on elevated outcrops of rock ensuring that landward areas are relatively sheltered from wave action.

The quantification of exposure levels is a problem which has not been fully resolved. A number of methods have been developed which can be divided into three categories, map-based, physical and biological. Map based methods (e.g. Wright, 1981; Thomas, 1986) utilise geographical measurements which can be derived from charts or maps. The measurements vary depending on the precise method adopted but generally include some estimate of the fetch and the angle open to the sea. In addition wind data may be utilised (e.g. Thomas, 1986). Such methods may be useful in making broadscale comparisons between areas. On a small scale however, the complexity of factors involved make the ability of map based methods to predict levels of exposure doubtful. Physical methods attempt to measure wave action in the field, either directly (Jones and Demetropoulos, 1968; Denny, 1983; Palumbi, 1984) or through the effect on rates of dissolution (Doty, 1971). Such measurements may in some cases provide reasonable estimates of exposure but cannot represent the complexity of factors involved. In addition, the measurements can rarely be recorded over a long enough period to encompass the whole range of conditions likely to affect shore organisms (Hawkins and Jones, 1992). Biological methods involve the assessment of exposure by means of the abundance of certain indicator species. The most commonly cited 'biological exposure scale' is that of Ballantine (1961a) which was developed in south west Wales. This divides the exposure gradient into a linear scale with eight levels, from 'extremely exposed' (level 1) to 'extremely sheltered' (level 8).

Lewis (1964) considers that the aim of a 'detailed and widely applicable exposure scale' is unattainable. It is argued that factors such as aspect and drainage which are independent of exposure, geographical factors affecting the abundance and presence of some species and the often erratic distribution of certain dominant species can result in misinterpretation of detailed scales such as those of Ballantine (1961a). Lewis (1964) presents a less detailed exposure scale. He proposes that in the assessment of exposure, the entire character of the shore should carry more weight than the density of single species. Unfortunately, this makes assessment of exposure levels far more subjective and reliant on the experience of the researcher.

1.2 Community structure along the wave exposure gradient

1.2.1 British Isles

The broadscale changes in community structure along the wave exposure gradient in the British Isles are well documented (see Lewis, 1964). Casual observations will detect the dramatic changes from fucoid dominated shores in sheltered areas to those dominated by barnacles, mussels and limpets in exposed locations. Early explanations for the paucity of fucoids on exposed shores emphasised the direct effects of wave action. However, experimental manipulative work first carried out on the Isle of Man demonstrated the importance of grazing by *Patella vulgata* (Jones, 1948; Lodge, 1948; Burrows and Lodge, 1950; Southward, 1956; 1964).

Removal of all limpets in a 10m wide strip down a moderately exposed, sparsely vegetated shore resulted in a dense growth of fucoids within two years (Jones, 1948). The important role of limpet grazing in excluding fucoids from exposed shores was confirmed in an 11 year study of the shores of West Cornwall following the Torrey Canyon oil spill (Southward and Southward, 1978; Southward, 1979). Widespread applications of dispersants resulted in large scale mortality of limpets. This was followed by a similar successional sequence to that observed in the small scale experiments of Jones (1948), even in the most wave exposed conditions. Although the importance of limpets in excluding fucoids has been proven, wave action is also a significant factor. Individual fucoids which escape grazing are unable to survive long on very exposed shores, being eventually torn from the substratum. Wave action may also act directly on the settlement stages of fucoids. Vadas *et al.* (1990) showed that wave action is a major source of mortality to recently settled zygotes of *Ascophyllum nodosum,* preventing establishment of *Ascophyllum* on exposed shores.

Although the exclusion of fucoids from exposed shores by the combined effects of limpet grazing and wave action is well accepted, the exclusion of barnacles and limpets and the fucoid domination of sheltered shores is less clearly understood. The negative effect of a fucoid canopy on barnacle settlement has been demonstrated in a number of studies (Hatton, 1938; Dayton, 1971; Menge, 1976; Grant, 1977; Hawkins, 1983) though the means by which settlement is inhibited, whether by a barrier or sweeping effect has not been properly elucidated. In manipulations carried out on sheltered shores, Hawkins (1983) showed that high on the shore enhanced post settlement survival of juvenile barnacles under the canopy outweighs the reduction in cyprid settlement, such that post settlement numbers were higher where the canopy was left intact. In the same study, settlement of cyprids within the *Ascophyllum* zone was observed only when stones carrying live adult barnacles were transplanted beneath the canopy. Thus, although factors such as surface silting and growth of understorey algae beneath the *Ascophyllum* canopy may be important, lack of settlement stimuli from adults could be the primary factor.

The exclusion of limpets from sheltered shores is of obvious importance in explaining the domination of such shores by fucoids, since a sparse limpet population will be unable to reduce that of the algae (Jones, 1948). Lewis and Bowman (1975) consider the fucoid canopy to have a two-fold influence on limpet numbers. Limited amounts of algae reduce desiccation on the mid/upper levels of the shore and promote limpet settlement and survival, whereas a heavy perennial cover has either a screening or a dislodging effect. Rather than acting directly on limpet settlement, the fucoid canopy may act indirectly by influencing the nature of the understorey community. Limpet larvae are thought to settle preferentially in pools lined with calcified red algae (Bowman, 1981; Morse, 1991). The rarity of suitable pools and the deposition of silt and growths of understorey red alga, particularly beneath *Ascophyllum,* may limit the area of suitable substratum for larval settlement. The enhancement of *Nucella* foraging activities under a fucoid canopy (Menge, 1978a) and the possibility of a reduction in limpet larval input to sheltered shores are two areas which demand investigation.

The littoral zone on shores of intermediate exposure possesses a community structure intermediate between the two extremes of sheltered and exposed. Observations of a moderately exposed shore at Port St Mary, Isle of Man revealed a fluctuating *Fucus* population. There existed "an ecological balance not only between *Patella* and algae as suggested by Jones (1948) but a complex balance involving *Patella*, *Fucus* and barnacles" (Burrows and Lodge, 1950). Baxter *et al*. (1985) have shown a similar balance operating on moderately exposed shores of the Orkney Islands.

On such shores, reduced grazing intensity from limpets caused by sea bird predation (Feare and Summers, 1985), storm strewn boulders and pebbles (Southward, 1956), and a tendency of limpets to aggregate (Hartnoll and Hawkins, 1985) allows clumps of fucoids and ephemeral algae to develop. These "escapes" of algae are more likely to occur amongst dense clusters of barnacles (Burrows and Lodge, 1950; Hawkins, 1981a; Hawkins, 1981b) owing to a reduction in the foraging efficiency of limpets.

Barnacles seem to enhance the ability of fucoids to colonise at the expense of ephemerals such as *Ulothrix*. This may be due to the preferential grazing on green algal sporelings and diatoms by the large number of *Littorina neglecta* present within the barnacle matrix, or the feeding activities of the barnacles themselves (Hawkins, 1981b; Hawkins and Hartnoll, 1983b). Fucoids above a size of 3-4cm or so are little affected by *Patella* grazing (Burrows and Lodge, 1950; Hawkins, 1979; Hawkins and Hartnoll, 1983b). The clumps of *Fucus* that consequently develop are attractive to *Patella*, which aggregate rapidly, resulting in areas of low grazing intensity elsewhere (Hartnoll and Hawkins, 1985). Hence, the effect of *Fucus* escapes seems to be to generate more escapes. The barnacles upon which *Fucus* clumps develop are smothered and eventually die. The barnacle substratum thus becomes unstable and both *Fucus* and barnacle shells are lost, so providing bare substratum and allowing the cycle of fluctuation to continue (Burrows and Lodge, 1950; Hawkins, 1979; Hartnoll and Hawkins, 1985).

It has been suggested that the balance between barnacles, limpets and fucoid canopy cover follows cycles of fluctuations, the amplitude of which are determined by the degree of exposure (Hartnoll and Hawkins, 1985). At the extremes of exposure, cycles of very small amplitude operate, with stable systems undergoing little change (Southward and Southward, 1978). This may be seen in the stable beds of continuous *Ascophyllum* cover in extreme shelter. Under moderate exposure, cycles of large amplitude occur, with a shifting balance between the components of the system. The important biological interactions which drive the changes in community structure on moderately exposed shores have mostly been identified (see above). However, the system is not entirely deterministic; extrinsic stochastic factors influence the course and rate of change of the cycle (Hartnoll and Hawkins, 1985). Of these factors variation in recruitment is probably the most important.

There is some evidence to suggest that the balance between grazers and fucoid algae changes with latitude, with fucoids becoming increasingly important further north (Ballantine, 1961a). Limpets may be less effective in controlling fucoid colonisation at high latitudes whilst further south a more diverse assemblage of grazer species prevents algal escapes, resulting in the restriction of algae to sheltered areas (see Hawkins *et al.*, 1992).

1.2.2 North west Atlantic

A great deal of work has taken place on the rocky shores of the north west Atlantic concentrated around Nova Scotia and Maine. Changes in community structure over the wave exposure gradient have been examined by a number of authors and a number of conclusions reached regarding controlling processes. The shores of the north west Atlantic support similar assemblages of species to those of Britain and thus examination of the work on community ecology carried out there is important when considering British shores. The major difference in species composition between the two regions is the scarcity of limpets in the north west Atlantic, with species of *Patella* being entirely absent. The dominant grazer on these shores is *Littorina littorea* (Vadas and Elner, 1992).

Menge (1976) recognises three major categories of mid shore community along the wave exposure gradient of the New England rocky intertidal. Exposed sites have little or no unused primary space, being dominated by barnacles at high levels with mussels displacing them at mid-shore. Sheltered sites have large areas of unused primary space and are dominated by a fucoid canopy with an abundance of carnivores and herbivores. An intermediate community exists between these two extremes.

Manipulative experiments indicate that predation intensity of *Nucella lapillus* on barnacles and mussels increases with decreasing exposure to wave action (Menge, 1976; Menge, 1978b), although predation intensity does not necessarily correlate with predator abundance (Menge, 1978a). Intense predation pressure at sheltered sites results in exclusion of mussels and barnacles and the persistence of the canopy forming algae which are considered competitively inferior (Menge, 1976; Menge, 1978b; Chapman and Johnson, 1990). Predation intensity is low at exposed positions owing to the restriction of *Nucella* to crevices (Grant, 1977; Menge, 1978b). Here, mussels and barnacles dominate, and inter-specific competition is suggested to be the major community structuring force. This work therefore supports the predictions of models by Connell (1975) and Menge and Sutherland (1976) regarding the importance of predation and competition over the wave exposure gradient.

However, Underwood and Denley (1984), in a critique of a number of generalisations in rocky shore ecology point out the importance of topographic features such as crevices on a predators activity. They argue that since the availability of such topographic shelters is unlikely to be correlated with environmental stress, there will be no gradient of predation intensity from benign to harsh environments.

The perennial red alga *Chondrus crispus* dominates the lower shore of protected sites by out-competing and limiting fucoids to higher levels (Lubchenco, 1980). Manipulative experiments on the low shore have shown the domination by *Chondrus* to be facilitated by a similar mechanism to that operating in the fucoid zone, namely the exclusion of the superior competitor, *Mytilus*, by *Nucella* predation (Lubchenco and Menge, 1978). The abundance of *Littorina littorea*, the dominant grazer on the shores of the NW Atlantic, has been shown to increase with decreasing wave shock (Lubchenco and Menge, 1978). High densities of *Littorina littorea* on sheltered shores have little effect on the relatively unpalatable *Chondrus* (Lubchenco and Menge, 1978; Lubchenco, 1980) but by their consumption of ephemeral green algae (a superior competitor of both *Fucus* and *Chondrus* in the short term) they reinforce its dominance (Lubchenco and Menge, 1978).

Later work demonstrated no simple relationship between littorinid grazing intensity and exposure to wave action. For example, the influence of littorinid grazing is high at wave-protected sites during the summer, but low in the winter (Lubchenco, 1986). Thus, the disturbance impact of herbivory on competition between ephemeral algae and *Fucus*/*Chondrus* is variable in space and time.

It is generally assumed that grazing by *Littorina littorea* on sheltered shores reduces diversity of ephemeral algal species and promotes perennial forms (Lubchenco, 1978; Lubchenco and Menge, 1978; Lubchenco, 1983; Chapman and Johnson, 1990). Other work however indicates the opposite, that *Littorina littorea* can prevent the establishment of perennials (Keser and Larson, 1984; Petraitis, 1987). Petraitis (1987) reports that algae are rare at shores in sheltered bays. Vadas and Elner (1992) conclude that sheltered shores can be characterised on the basis of disturbance by carnivores and herbivores: "undisturbed" shores being dominated by fucoids and "disturbed" shores being controlled by consumers and containing abundant free space.

In moderately exposed locations, densities of *Littorina littorea* can vary over short distances because of differences in exposure to wave action. Consequently, escapes of algae may occur where grazing intensity is reduced, resulting in high algal diversity (Vadas and Elner, 1992). Heterogeneity and diversity of moderately exposed shores are further increased by the development of isolated patches of bare space which occur in the algal matrix of the mid and low littoral zones. These patches are colonised by ephemeral algae and barnacles each spring and recycled annually by the activities of *Littorina littorea* and *Nucella* (Vadas and Elner, 1992).

There are obvious parallels to be drawn between moderately exposed shores of the north west Atlantic and the British Isles. In both areas, the patchiness generated by escapes from grazing is a dominant feature.

Sheltered shores on both sides of the Atlantic can be dominated by fucoids, but it appears the mechanisms causing this domination differ. In the north west Atlantic, fucoid algae are considered to be competitively inferior to mussels, barnacles and ephemeral algae. Thus it has been suggested that on sheltered shores, fucoid algae can dominate only through the predation and grazing activities of *Nucella* and *Littorina* *littorea*. However, where grazing is very intense, perennial algae may be prevented from establishing altogether (see Vadas and Elner, 1992). Thus, on sheltered shores, grazing and predation are considered the dominant structuring forces. Competition between canopy algae has also been demonstrated, *Ascophyllum* outcompeting *Fucus* through its longevity (Keser and Larson, 1984). Competition is considered important on exposed shores where wave action reduces biotic disturbance allowing competitive interactions between mussels and barnacles to occur (Menge, 1976; Grant, 1977; Lubchenco and Menge, 1978). On sheltered shores of Britain, neither predation nor grazing are considered important structuring forces, although little work has investigated these factors. Instead, attention has focused on competitive interactions between canopy algae (e.g. Hawkins, 1979; Schonbeck and Norton, 1980).

1.3 Sheltered shores of Britain

On moderately exposed shores of Britain, zonation of fucoids is indistinct. High shore species such as *Fucus spiralis* can often be found alongside the low shore *Fucus serratus* (Lewis, 1964). In contrast, at sheltered sites where cover of fucoids is high, well defined belts of individual species develop, presumably owing to the increase in competitive interactions. Under sheltered conditions and a complete cover of dense fucoids, a distinct vertical sequence of *Pelvetia canaliculata, Fucus spiralis, Ascophyllum nodosum* and *Fucus serratus* may be recognised. The position of *Fucus* vesiculosus within this sequence may vary according to the degree of shelter. Lewis (1964), in describing the distribution of fucoids on 'canopy dominated shores of open coasts' states that in the mid shore a mixed population of *Ascophyllum* and *Fucus vesiculosus* often develops. In 'lochs and very sheltered bays' *Fucus* vesiculosus is excluded from the mid shore *Ascophyllum* zone and often restricted to a narrow fringe at the top of the *Ascophyllum* belt.

The ecology of sheltered canopy dominated shores of Britain is relatively under-studied, in comparison to exposed or moderately exposed shores. However, certain aspects have received considerable attention. The distinct vertical zonation of fucoids on sheltered shores has provided ideal conditions under which to examine the relative effects of physical and biological factors in determining upper and lower limits of intertidal species. Observations of tissue damage at the upper limits of a number of canopy species, following periods of hot dry weather, indicate the importance of physical factors in preventing upward extension of algae (Schonbeck and Norton, 1978; Hawkins and Hartnoll, 1985). However, some species, especially those in the low and mid shore may not reach their physiological limit. They are prevented from extending upshore by competitive interactions with more drought tolerant species above (Schonbeck and Norton, 1978; Hawkins and Harkin, 1985; Hawkins and

Hartnoll, 1985). For example, Hawkins and Hartnoll (1985) induced upward extension of *Fucus vesiculosus*, *Fucus serratus* and *Laminaria digitata* when the species zoned above was removed. The effect of competition on the upper limit of *Laminaria digitata* was confirmed by Hill (1993).

It is generally considered that with decreasing height on the shore there is a corresponding improvement in the environment as a result of increasing periods of submergence. Thus, most work on the control of lower limits of macroalgae has concentrated on the effect of biological interactions. However, in turbid conditions low shore fucoids can have lower limits controlled by irradiance levels, whilst pressure effects (Damant, 1937) or suspected increased water movement at depth (Hawkins and Hartnoll, 1985) may affect downward extension of *Ascophyllum nodosum*. Continuous submergence of the high shore alga, *Pelvetia canaliculata,* leads to its decay, although it is unlikely that this phenomenon directly controls its lower limits (Schonbeck and Norton, 1980). Lower limits of canopy algae are generally set by competition. The experimental removal of a lower zoned species and the subsequent downshore extension of the higher zoned species has been commonly used to demonstrate the influence of interspecific competition in setting lower limits of algae (Hawkins, 1979; Schonbeck and Norton, 1980; Hawkins and Harkin, 1985; Hawkins and Hartnoll, 1985). For example, zygotes of *Pelvetia canaliculata* were found to germinate readily in the lower *Fucus spiralis* zone but reached macroscopic size only when the competing species (*Fucus spiralis*) was repeatedly removed. Measurements in the field and in culture revealed the competitive superiority of *Fucus spiralis* over *Pelvetia* as being a result of its far higher growth rate (Schonbeck and Norton, 1980). This example, and those studies cited above, follow the general principle put forward by Colwell and Fuentes (1975) that a stress tolerant organism is commonly excluded from an optimal habitat by a less hardy, but competitively superior species.

In the case of *Ascophyllum nodosum*, which forms a dense monospecific stand on sheltered shores, the influence of competition on its lower limits is difficult to demonstrate since very few germlings are found on the shore (Oltmanns, 1889; David, 1943; Knight and Parke, 1950; Printz, 1956; Baardseth, 1970; Sundene, 1973; Hawkins, 1979). Colonisation of even its own zone after clearance is very slow (Burrows, 1947; Hawkins, 1979; Boaden and Dring, 1980). Hence the factors setting its lower limits are unclear.

The effect of grazing on the community structure of sheltered shores has received little attention. Investigations into the community structuring role of *Patella* have been confined to more exposed shores (e.g. Jones, 1948; Lodge, 1948; Hawkins, 1981a;

Hartnoll and Hawkins, 1985). No experimental manipulations of *Patella* have been undertaken on sheltered shores, presumably because of the perception that where canopy algae dominate, limpets can have no significant effect. The decline in importance of limpet grazing in the lower eulittoral of moderately exposed shores, where canopy and turf forming algae increase in cover, has been demonstrated in a number of studies (see Hawkins *et al.*, 1992 for review). The increase in algal cover low on the shore can be attributed to an increase in algal growth rates, allowing escape from and subsequent domination of grazers. Thus, to a certain extent the relationship between fucoids and *Patella* grazing over the vertical gradient of the shore has been established. However, this relationship has not been fully investigated across the horizontal exposure gradient.

Grazing by littorinid species on British shores does not appear to have a large impact on community structure, despite their abundance (Norton *et al.*, 1990; Hawkins *et al.*, 1992). On sheltered shores, a number of species are evident in large numbers. The flat periwinkles, *Littorina obtusata* and *Littorina mariae* live predominantly on the fronds of fucoid algae. *Littorina obtusata* occurs over the entire extent of the intertidal zone but is most abundant in the mid shore on *Fucus vesiculosus* and *Ascophyllum*. *Littorina mariae* has a more restricted distribution, being associated predominantly with *Fucus serratus* on the low shore (Watson and Norton, 1987; Williams, 1990a; Williams, 1992). Although both species live on canopy algae, only *Littorina obtusata* actually uses the alga as a food resource. In contrast, *Littorina mariae* grazes the rich epiphytic community living on the fronds of *Fucus serratus*. Williams (1990b) has suggested that by reducing epiphyte loading on *Fucus serratus*, *Littorina mariae* may have a large scale effect on community structure. Epiphytic growth on canopy algae can be sufficient to cause an increase in detachment rates (Menge, 1975: cited in Williams 1990b). Thus, grazing by *Littorina mariae* could be important in facilitating the establishment of dense algal stands. *Littorina littorea* lives on the substratum surface rather than amongst the canopy and can occur at high densities on sheltered shores (Lewis, 1964). In such areas this species may cause a local reduction in algal vegetation (Hawkins *et al.*, 1992). However, the distribution of *Littorina littorea* is highly variable in Britain, presumably because of localised differences in recruitment (Hawkins and Hiscock, 1983). At many sites *Littorina littorea* is rare or absent and it is not generally considered to have a significant impact on community structure (Norton *et al.*, 1990). This is in sharp contrast to the shores of north east America where *Littorina littorea* is the dominant grazer with a large structuring role.

1.4 Aims

This study aimed to investigate the ecology of sheltered shores. Depending on the experience and perspective of an individual observer, a number of shores across a range of exposures might be described as sheltered. Such shores could support a range of different communities. Therefore it is necessary to define more clearly the shore type investigated. Sheltered shores were selected on the basis of their biological characteristics, namely the domination of the mid shore zone by dense uninterrupted stands of *Ascophyllum nodosum*. A number of such shores occur on the Isle of Man and are characterised by a continuous cover of fucoid algae. This occurs in the vertical sequence from lower to upper shore of *Fucus serratus*, *Ascophyllum nodosum*, *Fucus vesiculosus*, *Fucus spiralis*, and *Pelvetia canaliculata*. It is notable that *Fucus vesiculosus* occurs as a distinct band between *Ascophyllum* and *Fucus spiralis* rather than interspersed with *Ascophyllum* in the mid shore. Lewis (1964) describes such shores as only occurring in lochs and very sheltered bays. It is possible that the lack of continuous swell in the semi enclosed Irish Sea results in shores with very sheltered characteristics occurring in relatively open situations.

On moderately exposed shores, grazing by *Patella vulgata* has been shown to have a major community structuring role. It is thought that on sheltered shores the fucoid canopy is important in controlling community structure but this has not been investigated thoroughly. My approach was to compare the relative structuring roles of the fucoid canopy and grazing by *Patella vulgata* in both the *Ascophyllum* (Chapter 2) and *Fucus serratus* (Chapter 3) zones. Manipulations of both canopy and grazer were carried out in factorial experiments to achieve this aim. In addition, detailed examination of the recruitment and growth of fucoids in both zones was carried out to establish how fucoid domination is maintained.

The relative scarcity of *Patella vulgata* on sheltered shores especially in the *Ascophyllum* zone may be an important factor influencing the community structure of such shores. Because of the small size of limpet larvae it is very difficult to establish the cause of this scarcity. However in Chapter 4 an attempt was made to compare levels of settlement of *Patella vulgata* across a wave exposure gradient to shed some light on this question. The population dynamics of *Patella vulgata* have received considerable attention but mainly on exposed shores. Very little research has been carried out on shores dominated by *Ascophyllum*. Therefore in Chapter 4 the effect of the *Ascophyllum* canopy on the recruitment, growth rate and mortality of *Patella vulgata* was investigated. A comparison of growth rate between sheltered and exposed shores was also carried out.

A major difference in community structure between sheltered and exposed shores is the abundance of barnacles. On the sheltered shores under study, barnacles were virtually absent from the low and mid shore. Significant populations only occurred in the *Fucus vesiculosus* and *Fucus spiralis* zones. A number of reasons for the scarcity of barnacles on sheltered shores have been suggested but not fully investigated. The abundance and large size of barnacle larvae makes assessment of patterns of supply, settlement and recruitment relatively easy. Comparative measures of supply of barnacle larvae were made between sheltered and exposed shores. Interactions between fucoid canopy algae and barnacles at settlement were investigated and levels of post settlement mortality examined.

CHAPTER 2

The respective roles of the *Ascophyllum nodosum* canopy and *Patella vulgata* in structuring the mid shore community of sheltered shores

2.1 INTRODUCTION

Ascophyllum nodosum becomes increasingly dominant over other fucoid species with increasing shelter from wave action. On sheltered shores of north west Europe it forms a near monospecific canopy covering the mid shore of the intertidal zone (Lewis, 1964; Stephenson and Stephenson, 1972). Many studies have examined the community structuring role of macroalgal canopies both in the intertidal and subtidal zones. However because of its commercial importance most work on *Ascophyllum* has concentrated on investigating its potential for regrowth or recolonisation in harvested or experimentally denuded areas (Printz, 1956; Printz, 1959; Keser *et al.*, 1981; Keser and Larson, 1984; Sharp, 1986; Vadas and Wright, 1986) and have neglected the investigation of canopy-understorey interactions (but see Burrows, 1947; Boaden and Dring, 1980).

Manipulative field experiments have examined patterns of succession in areas where fucoid canopy species were removed. In the intertidal zone, removal has generally resulted in an enhanced recruitment of the canopy species (Chapman, 1989; Chapman and Johnson, 1990; Benedetti-Cecchi and Cinelli, 1992b), ephemeral algae (Hawkins and Harkin, 1985) or both (Burrows, 1947; Lubchenco, 1986; Chapman, 1990; Hill, 1993). In the subtidal zone, similar effects have been observed, with a decrease in encrusting algae because of overgrowth first by microscopic filamentous and then macroscopic foliose algae (Kennelly, 1987c; Kennelly and Underwood, 1993). In British kelp forests removal of *Laminaria digitata* and *Laminaria hyperborea* resulted in initial colonisation of the substrate by algae which are normally restricted to an epiphytic existence on the canopy species (Hawkins, 1979; Hawkins and Harkin, 1985; Hill, 1993). In addition to complete canopy removal, partial thinning has been employed to more accurately simulate natural canopy loss. A small decrease in canopy cover has generally resulted in a similar effect to total canopy removal, both in the intertidal (McCook and Chapman, 1991) and subtidal (Kennelly, 1987c) zones. Canopy removal results in radical changes in species composition, but species diversity, when examined, has been shown to remain the same (Santelices and Ojeda, 1984; Benedetti-Cecchi and Cinelli, 1992a).

The macroalgal canopy may regulate community structure in a number of ways. A dense canopy severely limits light levels beneath it and only algal species adapted to dim light conditions will occur (Reed and Foster, 1984; Kennelly, 1989). This obligate understorey (sensu Dayton 1975) often consists of species of lower competitive abilities which die out following canopy removal, because of direct physical effects or competition from colonising fugitive species. Whiplash or sweeping of algal fronds has been shown to affect community structure by its deleterious effects on certain species (Black, 1974; Velimirov and Griffiths, 1979) although Kennelly (1989) found that the sweeping or scouring effect of kelp had little or no effect on most species but did decrease sediment accumulation. 'Positive' effects of the canopy include mechanical shelter from waves (McCook and Chapman, 1991) and shelter from physical extremes such as high temperatures, desiccation or freezing (Hawkins, 1983; Brosnan, 1990). The indirect effects of the canopy may also play an important structuring role. For example the macroalgal canopy can enhance foraging rates of grazers and predators by providing protection from desiccation (Menge, 1978a; Menge, 1978b). McCook and Chapman (1991) suggested that enhanced herbivory by littorinids beneath a *Fucus vesiculosus* canopy contributed to the inhibition of *Fucus* juveniles and ephemeral algae.

The macroalgal canopy has a significant effect on recruitment of its own juveniles. It has been suggested that the most important regulator of recruitment density in *Fucus spiralis* was the presence of a canopy of conspecific adults (Chapman, 1989; Chapman and Johnson, 1990). This has important implications for the continued recruitment of a canopy species to its own zone. Benedetti-Cecchi (1992b) showed that settlement of *Cystoseira* embryos was reduced beneath an adult canopy. Other studies however have shown a positive effect of the canopy on settlement (Hruby and Norton, 1979; Brawley and Johnson, 1991). It is likely that post settlement mortality is higher beneath a canopy (Brawley and Johnson, 1991; Benedetti-Cecchi and Cinelli, 1992b), the most probable cause of this being competition for light (Reed and Foster, 1984; Kennelly, 1989). High post settlement mortality beneath a canopy has also been attributed to the ease of dislodgement on smooth surfaces, whiplash or higher levels of herbivory (Brawley and Johnson, 1991).

Although canopy removal has been shown to enhance recruitment of juveniles of the canopy species, the simultaneous colonisation by ephemeral and epiphytic algae has been shown to inhibit zygote settlement (Hruby and Norton, 1979), restrict settlement to the edges of canopy clearances (Kennelly and Underwood, 1993) or cause a reduction in juvenile growth rate (Chapman, 1989). Conversely, however, a blanket of ephemeral algae may aid survival of juvenile fucoids in the intertidal zone by reducing desiccation (Hruby and Norton, 1979).

The important role of *Patella* grazing in regulating the recruitment of algae to moderately exposed rocky shores of Britain was first demonstrated by limpet removal experiments on the Isle of Man (Jones, 1948; Lodge, 1948; Burrows and Lodge, 1950; Southward, 1953; Southward, 1956; Southward, 1964). This was confirmed by work in west Cornwall following the Torrey Canyon oil spill (Southward and Southward, 1978; Southward, 1979). Southward and Southward (1978) suggested the successional sequence following limpet removal followed a regular pattern involving an initial transitory phase of diatoms, unicellular and filamentous algae, a green algal flush of mainly *Enteromorpha* and *Blidingia* and then *Fucus* germlings. This kind of succession shows similarities to that occurring after canopy removal, presumably since both manipulations involve the liberation of free space for colonisation. The time of year at which space becomes available has a large effect on the successional sequence. This has been demonstrated for both limpet (Hawkins, 1981b) and canopy (Dayton *et al*., 1984; Benedetti-Cecchi and Cinelli, 1993) removals, although Jernakoff (1985) rightly criticised the work of Hawkins because of lack of spatial replication.

Limpets achieve regulation of algal recruitment by grazing the epilithic microbial film, which includes the early stages of macroalgae (Hill and Hawkins, 1990). Macroalgal germlings which escape grazing by growing in cracks or pits in the rock, amongst a dense cover of barnacles or in areas of reduced grazing density (Burrows and Lodge, 1950; Menge, 1975; Hawkins, 1979; Hawkins, 1981a; Hawkins, 1981b) reach a size at which they are immune to all but the highest densities of limpet grazing (Southward and Southward, 1978; Southward, 1979).

The way in which canopy and limpets act together to regulate community structure in canopy dominated communities and the relative importance of either factor has received little attention. It is generally accepted that limpet density is reduced beneath a canopy (Burrows and Lodge, 1950; Lewis, 1964; Lewis and Bowman, 1975; Benedetti-Cecchi and Cinelli, 1992b) possibly owing to the direct effects of the canopy on limpet recruitment (Lewis and Bowman, 1975) or indirect effects such as the influence of the canopy on the understorey community. A sparse limpet population will have little effect on community structure, although Burrows and Lodge (1950) considered that even if present in large numbers, *Patella* is unable to prevent the recruitment of germlings under a thick fucoid population though no experimental evidence was put forward. Hawkins and Harkin (1985) considered canopy effects to be the dominant biological factor low on a moderately exposed shore although no manipulation of grazers was made. No simultaneous manipulation of limpets and canopy has been made on canopy dominated shores of northwest Europe (but see Benedetti-Cecchi and Cinelli, 1992b for work on *Cystoseira* canopy and limpet effects in tide pools in the Mediterranean).

A number of sheltered, canopy dominated shores with gently sloping topography occur in the south of the Isle of Man, the dominant feature of which are the extensive mid shore beds of *Ascophyllum nodosum*. The general structure of this mid shore was assessed by carrying out broad scale surveys of four sheltered shores across the vertical extent of the *Ascophyllum* zone. One of these shores was selected to carry out manipulative experimental work with the main aim of assessing the relative importance of the two factors thought to be the most important in structuring sheltered shore communities at mid shore level, the *Ascophyllum* canopy and the grazer *Patella vulgata*. A factorial approach was used in order that any interaction between the canopy and the grazer could be assessed. Initial observations had shown the understorey community to be dominated by turf forming algae, a sharp contrast to the mid shore of more exposed sites. It was therefore hoped that the way in which the canopy influenced the balance between turf forming algae and limpet grazing could be determined. In addition, special attention was paid to the way in which recruitment and growth of fucoids (both *Ascophyllum* and *Fucus* species) were affected by the canopy and *Patella*. In this way it was hoped to determine how *Ascophyllum* maintains its dominance, both spatially and temporally.

Previous work has shown the importance of the canopy in protecting understorey communities from physical extremes. Therefore, an additional experiment was carried out to determine the effect of season on canopy removal. By removing the canopy in both winter and summer it was hoped to gain more of an insight into how the *Ascophyllum* canopy regulated community structure.

2.2 METHODS

2.2.1 Study sites

Descriptive sampling of the *Ascophyllum* zone took place at four sheltered shores in the south of the Isle of Man (Figure 2.1) all of which were dominated by *Ascophyllum* at mid shore level. The substratum at the four sites consisted of Manx slate at Perwick, a sandstone conglomerate at the outer Langness site and limestone at Castletown and the inner Langness site. The inner Langness site was used for the experimental work described below.

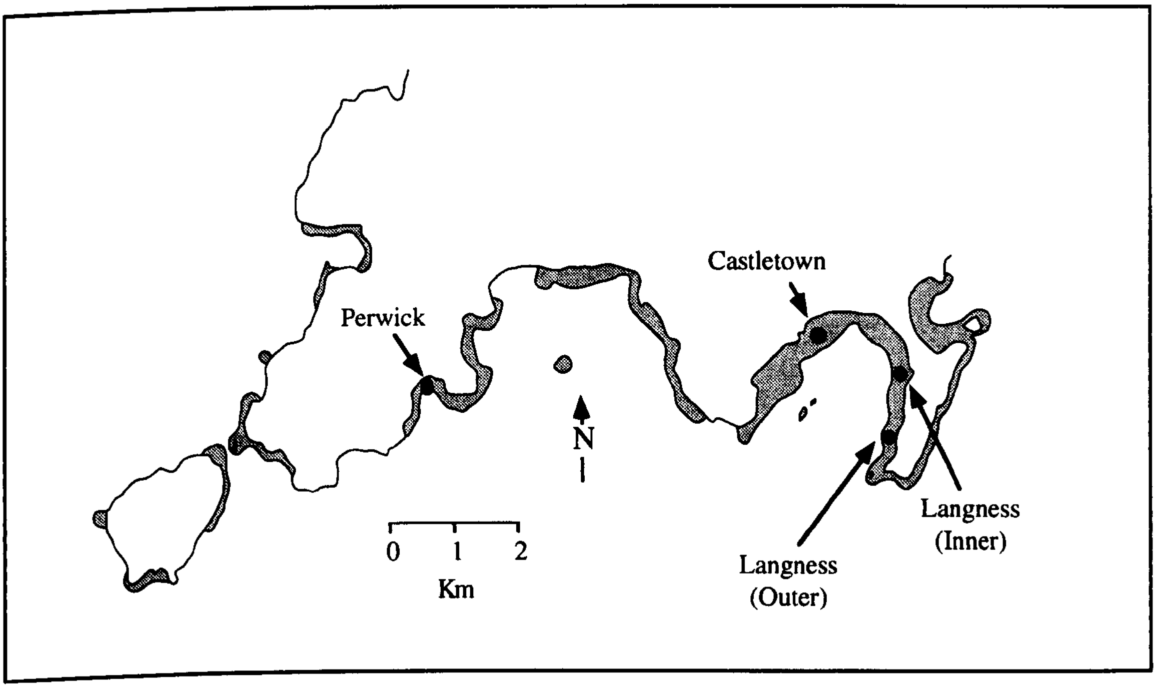


Figure 2.1 Map showing the south of the Isle of Man including the four sheltered sites which were sampled in August 1994

2.2.2 The *Ascophyllum* zone in the south of the Isle of Man: Descriptive Sampling

The abundance of the four main components of the *Ascophyllum* zone (*Ascophyllum* canopy, *Fucus serratus* canopy, red algal turf and patches of rock and 'lithothamnia') was assessed in August 1994 at the four sheltered sites described above. The patches of rock and lithothamnia were occupied by *Patella vulgata* and were therefore areas of high grazing pressure. These patches, although made up of a mosaic of bare rock and 'lithothamnia' were treated as a single functional unit and because of the absence of any erect algae, will be referred to as bare substratum.

In order to assess the abundance of these four components across the whole of the mid shore, the *Ascophyllum* zone was first divided into three parts: low, mid and high. Since all shores sampled had a relatively uniform topography, gently sloping seaward with a distinct band of *Ascophyllum*, this was relatively easy to do by eye. At each of the three shore heights a transect running parallel to the shoreline was established. Using random number tables, twenty 0.5 x 0.5m quadrats were placed at random along each transect. Thus for each of the four sites, sixty quadrats were sampled and the whole extent of the *Ascophyllum* zone was covered. The quadrat used was divided into 25 equal squares by the use of string, thus allowing the percentage cover of the four components to be more accurately estimated. Detailed investigations of the *Patella* populations of sheltered shores were also made. These will be reported on in Chapter 4. A number of other grazers occur in the *Ascophyllum* zone which were not specifically investigated. *Littorina littorea* can be abundant on sheltered shores, but was extremely rare in the mid shore of the sites studied. *Littorina obtusata* was abundant on the *Ascophyllum* canopy and qualitative observations were made on the distribution and behaviour of this species.

2.2.3 *Ascophyllum* and limpet clearance experiment (Winter)

2.2.3.1 Experimental design

A site for experimental work was selected on the west side of the Langness peninsula, the mid shore of which is dominated between 2.7m and 4.8m above C.D. by an extensive bed of *Ascophyllum nodosum*. The selected site consisted of large areas of smooth limestone rock, sloping very gently seaward. This provided a uniform area ideal for the positioning of experimental plots.

In order to examine the role of the *Ascophyllum* canopy and of the limpet *Patella vulgata* in structuring the community of the *Ascophyllum* zone, an orthogonal design experiment was used such that every combination of the two factors (limpet presence/absence and *Ascophyllum* presence/absence) was examined. The following four sets of conditions were established, each treatment or control being replicated three times:

Treatment 1	*Ascophyllum* canopy and limpets (*Patella vulgata*) removed.
Treatment 2	*Ascophyllum* canopy removed. Limpets unmanipulated.
Treatment 3	*Ascophyllum* canopy unmanipulated. Limpets removed.
Control	*Ascophyllum* canopy and limpets unmanipulated.

2.2.3.2 Establishment of experiment

The experiment was established in an area within the middle of the *Ascophyllum* zone between 3.3m and 4.3m above C.D. and covering a horizontal distance of 40 metres. In November 1991 twelve plots were chosen within the experimental area. These were all positioned in areas of smooth, gently sloping topography with a dense cover of *Ascophyllum*. Rockpools and irregularities in inclination were avoided.

The plots were spread throughout the experimental site such that a minimum of five metres separated any two plots. In this way replicates were positioned so that they were independent of each other and sufficient space was left between plots to enable a subsequent experiment to be established.

At each plot an area 2 x 2 metres square was measured. Holes were drilled into the rock at the four corners of each square using a petrol driven Ryobi hammer action drill. Plastic rawlplugs were used to enable steel ring-bolts to be securely screwed into each hole. To aid the location and identification of plots beneath the dense *Ascophyllum* canopy, a 40 cm length of orange and yellow fluorescent 'Twinglow' tape was numbered and tied to each ring-bolt.

The four treatments described above were assigned at random to the twelve plots such that each treatment was replicated three times. Before any manipulation took place, each plot was sampled (see below).

The removal of the *Ascophyllum* canopy was achieved using a wide bolster chisel. Every adult plant (including those of *Fucus serratus*) within the 2 x 2 metre area was totally removed, including as much of the holdfast material as possible. *Ascophyllum* holdfasts occupied very little of the area of each plot (<5%) and thus damage to the substratum caused by chisel scraping was minimal. Removal of holdfast material was considered important because it was hoped to assess the ability of *Ascophyllum* to recolonise through sexual means rather than through regeneration from the holdfast. Juveniles (<5 cm) of both *Ascophyllum* and of *Fucus serratus* were not removed. In order that the full 2 x 2 metre area could be considered free from the influence of the *Ascophyllum* canopy, individual plants surrounding the plot which could overhang onto its surface were cropped using a pair of garden shears. Thus, the six plots in which the *Ascophyllum* canopy was removed consisted of a central 2 x 2 metre area in which all traces of adult plants were removed, surrounded by a zone up to 1.5 metres wide in which individuals had been reduced in size.

The removal of limpets was achieved using a bolster chisel. This task was simplified because of the concentration of limpets into patches of bare substrate within the red algal turf. This turf acted as a natural barrier to limpet movement thus negating the need for the construction of artificial fences to exclude limpets from the experimental plots. In cases where a patch of bare substrate crossed the border of a 2 x 2 metre square, all limpets within that patch were removed, whether in or out of the experimental plot.

2.2.3.3 Sampling

Much of the sampling in this study involved estimation of algal percentage cover. This can be achieved in a number of ways, including visual estimates, point intercept methods (in which the presence or absence of a species is determined beneath a grid of points) or photographic methods. Photography, although having the advantage of requiring little time sampling in the field is unsuitable for use in complex multi-layered communities in which several species of similar morphology occur (Foster *et al.*, 1991; Meese and Tomich, 1992). Thus, its use in canopy dominated communities is limited.

The relative advantages of visual estimates versus point intercept methods have been debated by a number of researchers (Jones *et al.*, 1980; Dethier, 1984; Foster *et al.*, 1991; Meese and Tomich, 1992; Dethier *et al.*, 1993). Dethier *et al.* (1993) made a careful analysis of these two methodologies and concluded that 'visual estimation is a legitimate technique for estimating percent cover producing data that are accurate and repeatable'. Dethier *et al.* (1993) stressed the importance of using a subdivided quadrat. Surprisingly, the random point quadrat method using fifty points was found to be less accurate and biased toward overestimation. In addition, rare species (<5%) were often missed. Obviously the greater the number of random points used within a quadrat the greater the accuracy and sensitivity achieved, but numbers beyond 50 become very time consuming for use in the field.

Visual estimation was chosen as the sampling method on the basis that it produced relatively accurate results with the minimum effort, thus allowing the maximum number of quadrats to be used. The legitimacy of this technique has been questioned on the basis of its lack of objectivity. However, Dethier *et al.* (1993) rightly states that this is true of any technique, especially when the experimenter 'wants' a certain outcome. Point intercept methods have a subjective component in deciding whether a pin (which although representing a theoretical point, does have a finite size) actually touches a species (Greig-Smith, 1964; Dethier *et al.*, 1993). The potential for subjectivity in applying the visual estimate technique was taken into account whilst sampling.

Plots were sampled at approximately 6 week intervals using a 0.5 x 0.5m quadrat subdivided with string into 25 equal squares. This quadrat was placed at four positions within each plot, the positions being determined at each sampling date by the use of random number tables to generate co-ordinates. Percentage cover of understorey algae was then estimated. In plots where the *Ascophyllum* canopy was left intact the percentage cover of canopy alga was first estimated before gently moving it to one side to reveal the understorey. The four subsamples were used to calculate a mean value for each replicate. The use of subsamples in this way for detecting treatment effects increases precision of estimation of the properties of each experimental unit (Hurlbert, 1984).

Because of the close association of a number of similar red algal species it was only possible to monitor the percentage cover of one species of red alga, that of the more conspicuous species *Chondrus crispus*. The association of red algal species, collectively termed the turf, was treated as a single functional unit, and sampled as such. In addition, in order to monitor changes in the state of the turf an 'algal turf index' was devised so that the state of the turf could be scored on a scale from 1-5 as follows:

1) Algae severely stunted; very low levels of silt accumulation; rock visible in small patches throughout the turf.

2) Algae stunted but some growth above level of silt; low levels of silt accumulation; occasional patches of visible rock.

3) Small patches of stunted algae but majority of growth above level of silt; no rock visible.

4) Patches of luxuriant growth; thick layer of accumulated silt.

5) Luxuriant growth predominant.

In addition to this semi quantitative assessment of turf state, a purely qualitative description was made at each sampling date of the state of the red algal turf in each treatment.

Areas of bare substrate which formed obvious patches within the understorey algae were examined carefully at each sampling date and the number and size of limpets recorded. The area of each patch was estimated using the subdivided quadrat, measurements being repeated three times to ensure accuracy. In treatments where limpets were unmanipulated these measurements were felt to be a very good estimate of the true size of rock patches, since limpet grazing resulted in very obvious sharply delimited boundaries between bare substrate and turf. However, where limpets had been removed, estimates became more and more difficult as algae invaded the patches.

Since no manipulation had taken place in the control, any changes in bare substrate patch size were expected to be small. Therefore an additional method was employed to determine patch size. A sheet of clear polythene was placed over each patch and the boundary between bare substrate and turf traced onto the polythene using a permanent marker pen. The area of each patch was then determined in the laboratory by placing the polythene over a sheet of graph paper and counting the squares within the traced outline.

This not only produced an accurate measure of patch size but also a permanent record of patch shape at each sampling date. Any change in patch size or shape over time could then be followed by examining successive outlines of a single patch and thus the stability of such patches within the natural system could be assessed.

At each sampling date photographs were taken of the important successional changes and specifically of bare substrate patches, both with and without limpets.

2.2.3.4 Juvenile plant distribution

In August 1994 the distribution and density of *Ascophyllum nodosum* and *Fucus serratus* juveniles were examined in detail in the four treatments. Sampling was divided between turf and patches of bare substrate in order to establish where juveniles were recruiting to and possibly determine causal factors.

For both substrata, five 0.25 x 0.25m quadrats were thrown at random within each replicate, and the number of *Ascophyllum nodosum* and *Fucus serratus* juveniles counted. These quadrats were treated as subsamples and their mean used as a single value for each replicate.

In addition to the above, patches of bare substrate in treatment 2, where limpets had been removed but canopy left intact, were examined in detail to determine whether in the absence of grazing, juvenile density was higher on rock or lithothamnia. Results were calculated as density per metre square of each type of substrate.

2.2.4 *Ascophyllum* clearance experiment (Summer)

In order to determine how season affected the structuring role of the *Ascophyllum* canopy and sequence of succession, a summer clearance experiment was used in which only the canopy was manipulated. The following two sets of conditions were established, with the treatment and control each being replicated three times:

Treatment 1	*Ascophyllum* canopy removed. Limpets unmanipulated.
Control	*Ascophyllum* canopy and limpets unmanipulated.

2.2.4.1 Establishment of experiment

In June 1992 plots were chosen, interspersed with the winter experiment and marked out in exactly the same way as previously, using ring bolts and fluorescent marker tape. The *Ascophyllum* canopy was removed as previously described. No manipulation of limpets was attempted.

2.2.4.2 Sampling

Sampling was carried out at the same sampling dates and in exactly the same manner as the winter experiment, thus allowing results to be compared.

2.2.5 Growth rate of *Fucus serratus* juveniles

The winter clearance experiment provided the conditions required to investigate the growth rate of *Fucus serratus* juveniles in the *Ascophyllum* zone, both under the canopy and in cleared areas. In December 1991, immediately after the clearance experiment had been established, six areas measuring 0.5 x 0.5m were selected, three within plots cleared of canopy and three within plots where the canopy was left intact. Areas were chosen with a uniform algal turf and a high density of *Fucus serratus* juveniles below 6 cm in size.

The corners of each 0.5 x 0.5m area were marked by small stainless steel screws, secured in drilled holes by plastic rawlplugs. By positioning the 0.5 x 0.5m quadrat over the locator screws, the exact position of all juveniles was mapped in relation to the quadrat grid. The length of these individuals from holdfast to frond tip was then measured. Juveniles were considered to be any *Ascophyllum nodosum* or *Fucus serratus* individual not greater than 6cm in height. At approximately six weekly intervals, individuals were relocated using the mapping system and remeasured. Notes were made on their condition.

In plots from which the canopy had been cleared, the relocation of juveniles at each sampling date was hindered first by the growth of green ephemeral algae and subsequently by the large scale recruitment of *Fucus vesiculosus* juveniles. This recruitment was recorded but no attempt was made to map new recruits individually. No such large recruitment event occurred in the plots where the canopy was left intact. A very low rate of *Fucus serratus* recruitment was observed, and on July 10th 1992 these new recruits were mapped and incorporated into the sampling regime.

In June 1992 five new areas of 0.5 x 0.5m were marked out in the summer *Ascophyllum* clearances. Juveniles were mapped and monitored at six weekly intervals in the same way as above.

Increase in length of juveniles will vary according to the plants initial size. Therefore relative growth rate (Evans, 1972) was used to measure change in size over time. The relative growth rate per day for each juvenile was calculated as follows:

$$\mathrm{RGR}=\frac{\log_e l_2 - \log_e l_1}{t_2 - t_1}$$

where l_t is the total length (cm) at time t (days).

2.2.6 Silt collection

Plastic pan scourers were used to simulate the sediment trapping properties of the red algal turf. On December 17th 1991 strips of pan scourer measuring 5 cm x 11.5 cm and with a depth of 0.5 cm were screwed to areas of bare rock in three plots from which the canopy had been removed and three were located on bare rock beneath the canopy. These were removed from the shore on 15th January. The accumulated sediment was removed by washing in fresh water, dried to constant weight in an oven at 60° C and weighed.

On June 26th 1992 pan scourers were placed in the same positions and removed from the shore on August 14th 1992. The sediment content was analysed in the same way.

2.2.7 Use of Analysis of Variance (ANOVA)

The three main assumptions of analysis of variance are a) the error terms of each treatment are normally distributed; b) the variances of error terms in each treatment are equal; c) treatments are sampled independently. Violations of the assumptions of normality and of homogeneity of variance are common in biological data. It is therefore necessary to consider the effects of such violations on the outcome of analyses. Underwood (1981) considers that most types of non-normality encountered in practice should not seriously affect the outcome of the analysis and recommends that the assumption can be disregarded unless gross violations are evident in the data. On the basis of this, non normality was not tested for in this study. ANOVA is also relatively robust to departures from homogeneity of variance. However, marked heterogeneity can lead to an increase in the probability of a Type 1 error (i.e. rejecting the null hypothesis when in fact it is true). Data which are in the form of percentages, such as percentage cover data collected from quadrats often have heterogeneous variances. Because percentage data are constrained at their upper and lower limits (0 and 100%) variances will decrease in samples with a mean close to these boundaries so increasing the chances that variances of different treatments will be heterogeneous (Underwood, 1981). All data were tested for heterogeneity of variance (or heteroscedasticity) using Cochrans test (described in Winer, 1971). Data found to be heteroscedastic were transformed using either an arcsine or square root transformation and Cochrans test reapplied. Where heteroscedasticity remained, even after transformation, the ANOVA test was not applied. If possible an appropriate non parametric test was used. Unless stated otherwise, data are untransformed.

Two way ANOVA is used frequently in this study. In the interpretation of these analyses, care must be taken when a significant interaction between factors is found. Interaction occurs when the effects of the levels of one factor (A) differ when in the presence of different levels of another factor (B). Thus in the presence of a significant interaction term and a significant effect of for example factor A, broad conclusions based solely on the levels of factor A should not be made since the effects of A depend on the levels of factor B. Instead the significant interaction term should be highlighted. The way in which the interaction occurs can be clarified by examination of the data.

2.2.7.1 Multiple comparisons

Where a factor with more than two levels is found to be significant it is appropriate to test for differences between levels of that factor. Such 'multiple comparisons' may be undertaken using a variety of tests. The Tukey-Kramer test was utilised in this study. In two factor ANOVA where there is no interaction between the factors then the differences among levels of one factor are tested by comparison of the means of those levels averaged over all levels of the other factor. This would be misleading if a significant interaction between factors is present. In this case the means of the levels of one factor should be compared within each level of the other factor.

2.2.8 Statistical treatment of canopy/limpet clearance experiment

In order to determine the importance of the two manipulated factors, canopy and limpet in structuring the community of the *Ascophyllum* zone a two way ANOVA was performed. This allowed not only the two factors canopy and limpet to be assessed but also the interaction between them. The experiment ran for a period of three years and during this time sampling occurred 13 times. Thus there are 13 sampling dates at which statistical analysis could take place. Where a simple pattern of change was evident with a gradual increase or decrease in abundance over time the two way ANOVA was applied at the final sampling date. In this way the test was applied to the end result of cumulative change over time. Where a more complex pattern of change was evident, tests were applied at the peaks and troughs of abundance such that changes in significance were noted at different sampling dates.

Where only very small changes were observed over the experimental period a repeated measures ANOVA was applied to determine if this change over time was significant.

The main sampling program for this experiment finished in August 1993. However, additional sampling of fucoid canopy cover and of *Ascophyllum* juvenile density was undertaken to examine longer term trends. Statistical tests for fucoid canopy and *Ascophyllum* juveniles were made for both August 1993 and for the final sampling point in November 1994.

2.3 RESULTS

2.3.1 Descriptive sampling of the sheltered shores in the south of the Isle of Man

All four shores sampled were chosen because they represented typical sheltered shores with a dominant, near total cover of *Ascophyllum* in the mid shore. However, differences in the major components of the understorey did exist (Figures 2.3 and 2.4). A one way ANOVA revealed significant differences between sites in the percentage cover of both *Fucus serratus* and bare substrate. A Tukey-Kramer test showed that the Perwick site had significantly greater cover of *Fucus serratus* (compared to Castletown) and bare substrate (compared to Castletown and inner Langness) (Table 2.1). Subjective observations suggest that the higher levels of *Fucus serratus* and bare substrate at Perwick were due to increased exposure to wave action at this site.

Table 2.1 One way ANOVA testing for differences in *Fucus serratus* and bare substrate cover between four sheltered shore sites. Tukey Kramer test used for determining significant differences between individual shores.

	Source	df	Mean Square	F-Value	P-Value	Tukey Kramer Test*
Fucus serratus	Shore	3	3594.64	5.80	0.0008	Perwick≠Castletown
	Residual	236	619.65			
Bare substrate	Shore	3	7388.49	10.49	0.0001	Perwick≠Castletown Perwick≠Inner Langness
	Residual	236	704.49			

* ≠ indicates significant difference at 5% level between the stated shores. Experimentwise error rate (EER) = 5%.

The *Ascophyllum nodosum* zone occupied roughly similar levels on all four shores sampled (see Figure 2.2). *Ascophyllum* formed a canopy cover of approximately 100% with occasional patches of *Fucus serratus* being visible, especially toward the lower part of the zone. Detailed quantitative examination revealed cover of *Fucus serratus* ranging between 25% at Perwick to 6% at Castletown, the majority occurring as a subcanopy, obscured and overshadowed by the much larger plants of *Ascophyllum*. Thus the boundary between *Ascophyllum* and *Fucus serratus* is not as distinct as might be thought from casual observations. As expected, *Fucus serratus* was not distributed evenly throughout the zone, the vast majority occurring in the lower third. For example, at Perwick, percentage cover of *Fucus serratus* was 53.5% in the low section, decreasing to 18.5% in the mid and only 2% high in the zone

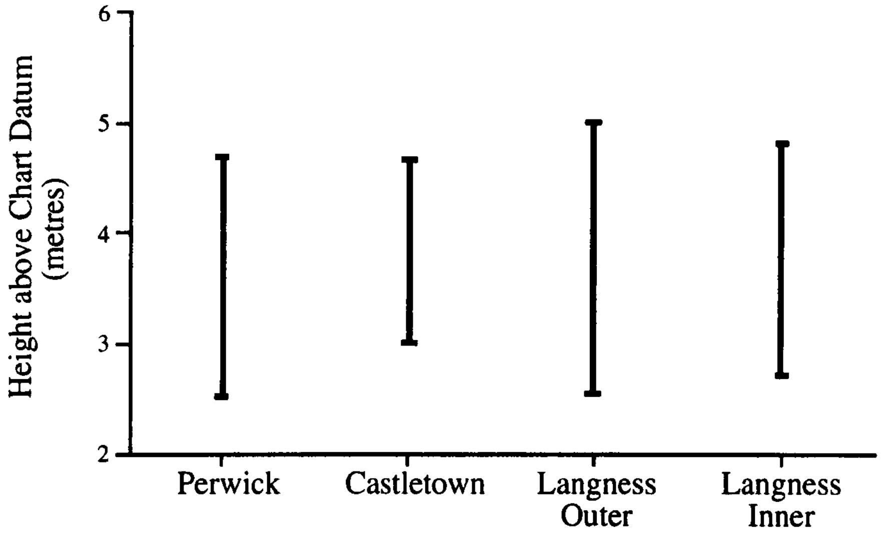


Figure 2.2 Tidal range covered by the *Ascophyllum nodosum* zone at four sheltered sites.

(Figure 2.3). Effect of shore height on cover of *Fucus serratus* was tested using a non parametric test (Kruskal Wallis) since data violated the assumption of homogeneity of variance even after transformation. At all four sites a significant difference was found between shore heights (Table 2.2).

Table 2.2 Kruskal Wallis test for effect of shore height on percentage cover of *Fucus serratus* in the *Ascophyllum* zone at four sheltered shore sites.

Site	df	H	P-Value
Perwick	2	42.61	<.001
Castletown	2	9.54	0.009
Outer Langness	2	25.42	<.001
Inner Langness	2	25.70	<.001

Red algal turf was the dominant component of the understorey at all four sites, its percentage cover ranging from 61.9% at Perwick to 86.5% at Castletown. The remainder of the substratum was a mosaic of bare rock and lithothamnia (referred to as bare substratum) grazed upon by groups of *Patella vulgata*. Calcareous encrusting algae are relatively immune to limpet grazing (Steneck, 1982) and appear able to persist in areas of high grazing pressure such as these patches.

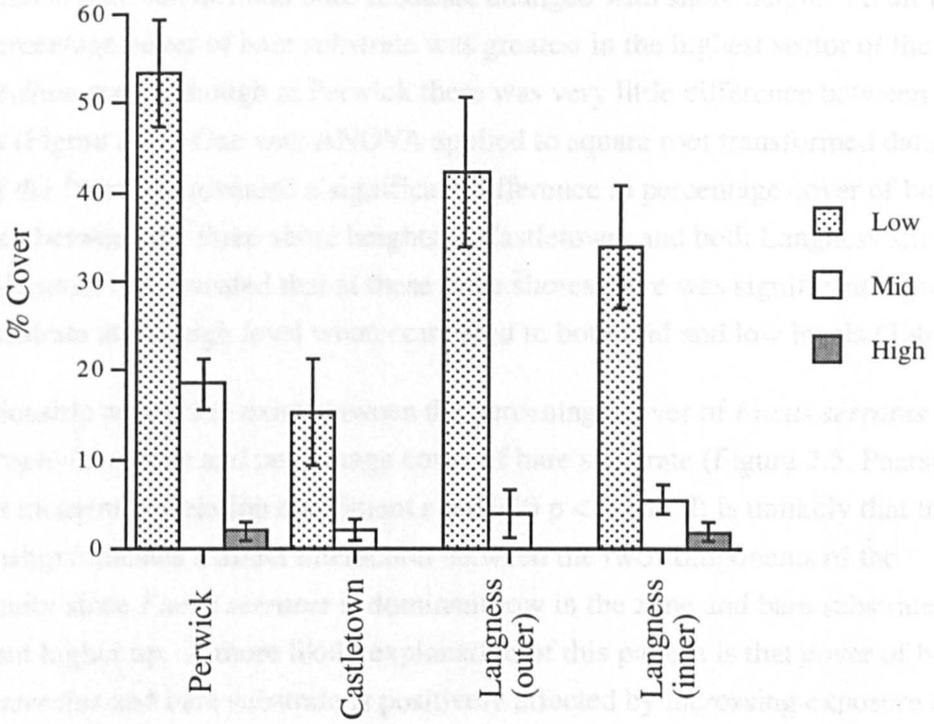


Figure 2.3 Percentage cover of *Fucus serratus* canopy at three tidal heights within the *Ascophyllum* zone at four sheltered shores in the south of the Isle of Man. Shores were sampled in August 1994. Error bars = ± 1 SE

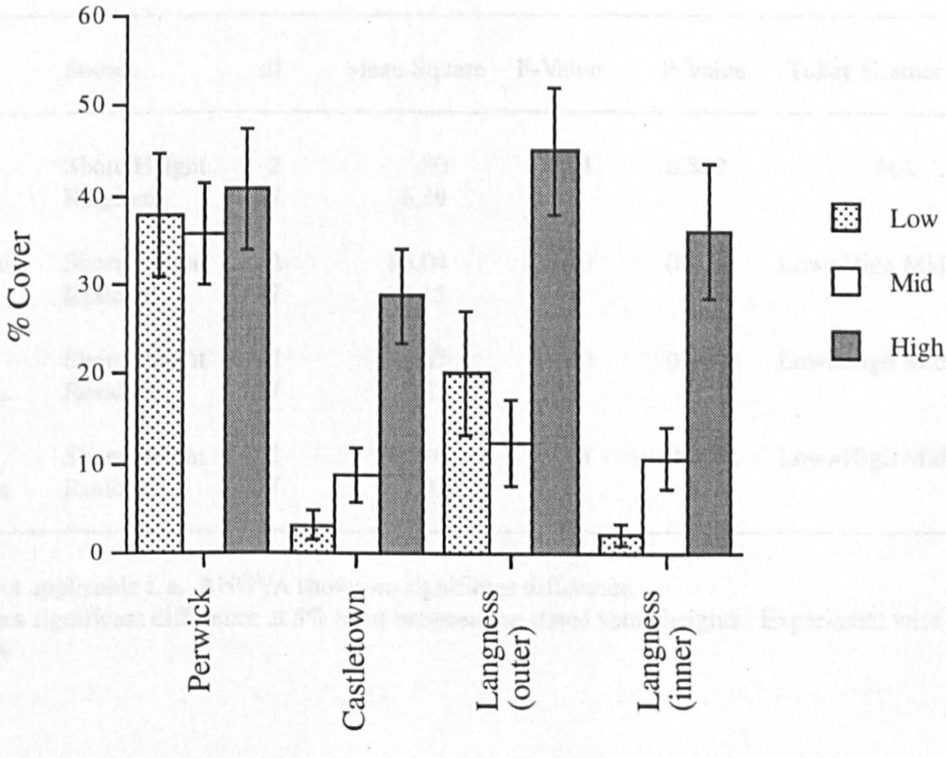


Figure 2.4 Percentage cover of bare substrate (lithothamnia and bare rock) at three tidal heights within the *Ascophyllum* zone at four sheltered shores in the south of the Isle of Man. Shores were sampled in August 1994. Error bars = ± 1 SE

The balance between turf and bare substrate changed with shore height. At all four sites percentage cover of bare substrate was greatest in the highest sector of the *Ascophyllum* zone although at Perwick there was very little difference between tidal heights (Figure 2.4). One way ANOVA applied to square root transformed data for each of the four sites revealed a significant difference in percentage cover of bare substrate between the three shore heights at Castletown, and both Langness sites. A Tukey-Kramer test revealed that at these three shores there was significantly greater bare substrate at the high level when compared to both mid and low levels (Table 2.3).

A relationship appears to exist between the percentage cover of *Fucus serratus* within the *Ascophyllum* zone and percentage cover of bare substrate (Figure 2.5, Pearson product moment correlation coefficient $r = 0.940$ $p < 0.10$). It is unlikely that this relationship indicates a direct interaction between the two components of the community since *Fucus serratus* is dominant low in the zone and bare substrate dominant higher up. A more likely explanation of this pattern is that cover of both *Fucus serratus* and bare substrate is positively affected by increasing exposure to wave action.

Table 2.3 One way ANOVA on square root transformed data testing for the effect of shore height on the percentage cover of bare substrate in the *Ascophyllum* zone at four sheltered shore sites. Where a significant ANOVA result is obtained a Tukey Kramer test was used to determine significant differences between individual shore heights.

	Source	df	Mean Square	F-Value	P-Value	Tukey Kramer Test*
Perwick	Shore Height	2	.90	0.14	0.869	NA
	Residual	57	6.39			
Castletown	Shore Height	2	83.04	20.00	0.0001	Low≠High Mid≠High
	Residual	57	4.15			
Outer Langness	Shore Height	2	93.67	10.00	0.0002	Low≠High Mid≠High
	Residual	57	9.37			
Inner Langness	Shore Height	2	105.16	17.74	0.0001	Low≠High Mid≠High
	Residual	57	5.93			

*NA - Not applicable i. e. ANOVA shows no significant difference
≠ indicates significant difference at 5% level between the stated shore heights. Experiment wise error rate = 5%

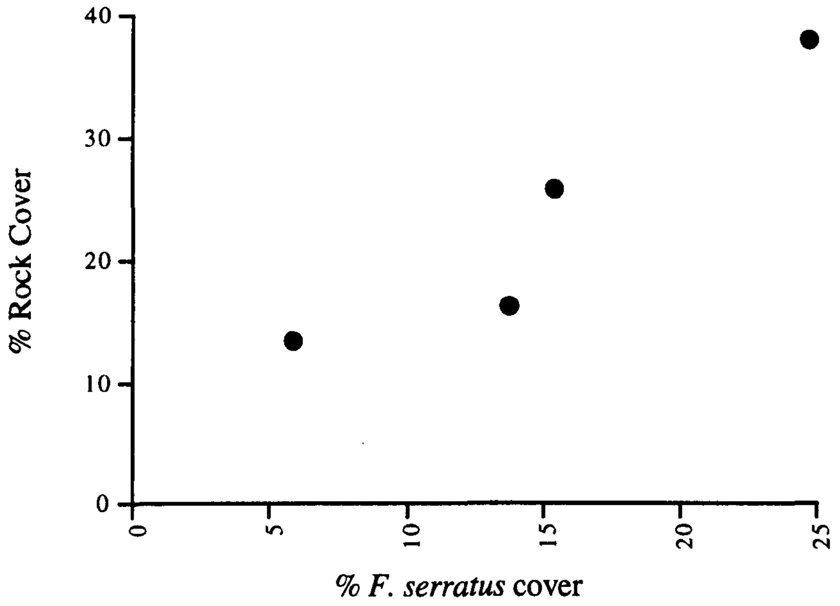


Figure 2.5 Correlation between percentage cover of *Fucus serratus* and percentage cover of bare substrate beneath the *Ascophyllum* canopy at four sheltered sites in the south of the Isle of Man. Each point represents one of the four sites sampled and is a mean of 60 quadrats.

2.3.2 Canopy and limpet manipulation experiments

The manipulation of canopy and limpets resulted in radical changes to community structure within experimental plots. Although these changes will be described in detail below, a brief overview of the successional sequence will be given here.

The most striking changes in community composition occurred as a result of canopy removal. The first visible effect was the bleaching of red algae. This occurred to a limited extent only a few weeks after the start of the experiment, and increased over the spring and summer. During the spring, increasing densities of fucoid juveniles and colonisation by ephemeral green algae transformed the appearance of the understorey. By the summer all plots where the canopy was removed had a dominant cover of green ephemeral algae of mixed species. Developing fucoids were for a brief period covered by this summer 'bloom'. During late summer and autumn the decline of ephemeral cover revealed a bleached, patchy red algal turf and high densities of rapidly growing fucoids. The development of these juveniles into canopy plants began roughly one year after the start of the experiment. This mixed canopy of *Fucus vesiculosus* and *Fucus serratus* dominated the experimental plots for the remaining period of the experiment.

2.3.2.1 Fucoid juvenile recruitment

Removal of the *Ascophyllum* canopy resulted in a dramatic change in the density of *Ascophyllum* juveniles which was first observed in September 1992, 10 months after experimental manipulation (Figure 2.6). A steady rise in density occurred in both treatments in which canopy was removed, maximum densities of 221 m^{-2} in treatment 1 (no canopy, no limpets) and 378 m^{-2} in treatment 2 (no canopy, limpets present) occurring at the final sampling date, three years after the start of the experiment. Two way ANOVA reveals a significant effect of canopy in August 1993, but not in November 1994 (Table 2.4). In addition, a significant interaction between canopy and limpets was found in August. It would be expected that removal of the canopy and limpets would result in a greater abundance of juveniles than removal of canopy alone. However, the opposite is true (Figure 2.6a). This result is difficult to explain. Consequently a more detailed study of juvenile density and distribution in all four treatments was carried out in August 1994 (see below).

Table 2.4 Two way ANOVA testing for the effect of the *Ascophyllum* canopy and the limpet *Patella vulgata* on the density of fucoid juveniles in the 'canopy and limpet manipulation experiment (Winter)'.

	Source	df	Mean Square	F-Value	P-Value
Ascophyllum juveniles t0 26.11.91	Canopy	1	0.00		
	Limpet	1	0.00		
	Canopy x Limpet	1	0.00		
	Residual	8			
Ascophyllum juveniles t10 11.8.93	Canopy	1	59502.08	8.17	0.0212
	Limpet	1	4218.75	0.58	0.4685
	Canopy x Limpet	1	39102.08	5.37	0.0492
	Residual	8	7285.42		
Ascophyllum juveniles t12 18.11.94	Canopy	1	183155.5	3.33	0.1106
	Limpet	1	5302.44	0.0965	0.7651
	Canopy x Limpet	1	33995.44	0.619	0.4573
	Residual	7	54949.19		
Fucus juveniles t0 26.11.91	Canopy	1	990.08	1.22	0.3015
	Limpet	1	0.75	0.00	0.9765
	Canopy x Limpet	1	10.08	0.01	0.9140
	Residual	8	811.50		
Fucus juveniles t4 15.5.92	Canopy	1	196352.08	12.33	0.0079
	Limpet	1	21252.08	1.34	0.2813
	Canopy x Limpet	1	37968.75	2.38	0.1611
	Residual	8	15925.00		

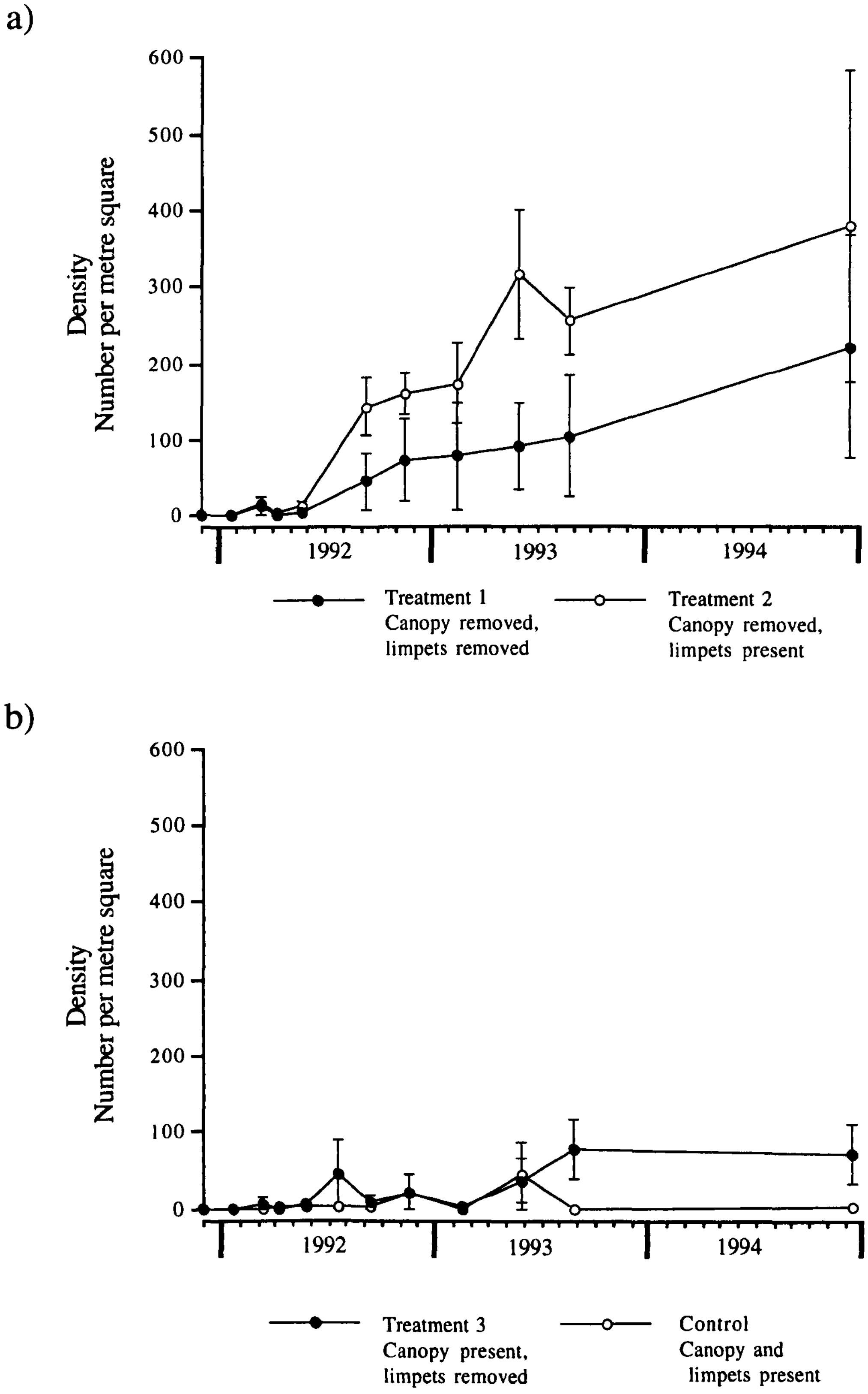


Figure 2.6 Change in density of *Ascophylllum* juveniles in the *Ascophyllum* zone following experimental manipulation in November 1991. Error bars = ± 1 SE
a) Plots cleared of canopy b) Plots where canopy is intact

Fucus juveniles also showed a sharp increase in density in areas cleared of canopy (Figure 2.7a) although in contrast to juveniles of *Ascophyllum*, this occurred immediately following experimental manipulation. Observations suggest that this difference in recruitment pattern between *Fucus* and *Ascophyllum* juveniles may be a function of differences of growth rate, rather than delayed recruitment. The *Fucus* juveniles sampled in canopy cleared areas were a mixture of *Fucus serratus* and *Fucus vesiculosus* juveniles. Unfortunately the relative densities of these two species was not determined due to difficulties in identification. In plots where the canopy was left intact, only *Fucus serratus* juveniles were present. Figure 2.7b shows a relatively constant density in the control treatment, mean densities varying between 108 and 33 m^{-2} over a two year period. In treatment 3 (canopy present, no limpets) despite large variation, a trend of increasing density is apparent. Despite this possible effect of limpet manipulation beneath the canopy, the obvious main effect is that of the canopy. In fact, densities of *Fucus* juveniles in canopy cleared areas were such that sampling was not continued beyond May 1992 due to difficulty in counting the densely packed plants. Two way ANOVA revealed a significant effect of the canopy and non significant effect of limpet grazing in May 1992 (Table 2.4).

Repeated measures ANOVA was carried out on the treatments where the canopy was unmanipulated, to establish if there had been any change in *Fucus* juvenile density over time throughout the experiment. No significant change over time for either treatment was found (Table 2.5).

Table 2.5 Repeated measures ANOVA testing for a significant change in density of *Fucus* juveniles over time in plots where the *Ascophyllum* canopy was left intact (Canopy/limpet manipulation experiment (Winter)).

Source	df	Mean Square	F-Value	P-Value	G-G	H-F
Between Subjects						
Treatment	1	52319.10	2.24	0.2313		
Subject (Group)	3	23271.54				
Within Subjects						
Time	10	12945.00	2.78	0.0148	0.1595	0.0707
Time x Treatment	10	89369.56	1.92	0.0821	0.2403	0.1664
Time x Subject	30	4659.09				

A comparison of the winter and summer experiments reveals that in general the pattern of recruitment of *Ascophyllum* and *Fucus* juveniles was not affected by the timing of canopy clearance (Figure 2.8a and 2.8b). Recruitment of *Fucus* juveniles was rapid in both experiments although in the summer experiment the density of *Fucus* juveniles after an equivalent time period was higher. However this difference was not significant (Table 2.6).

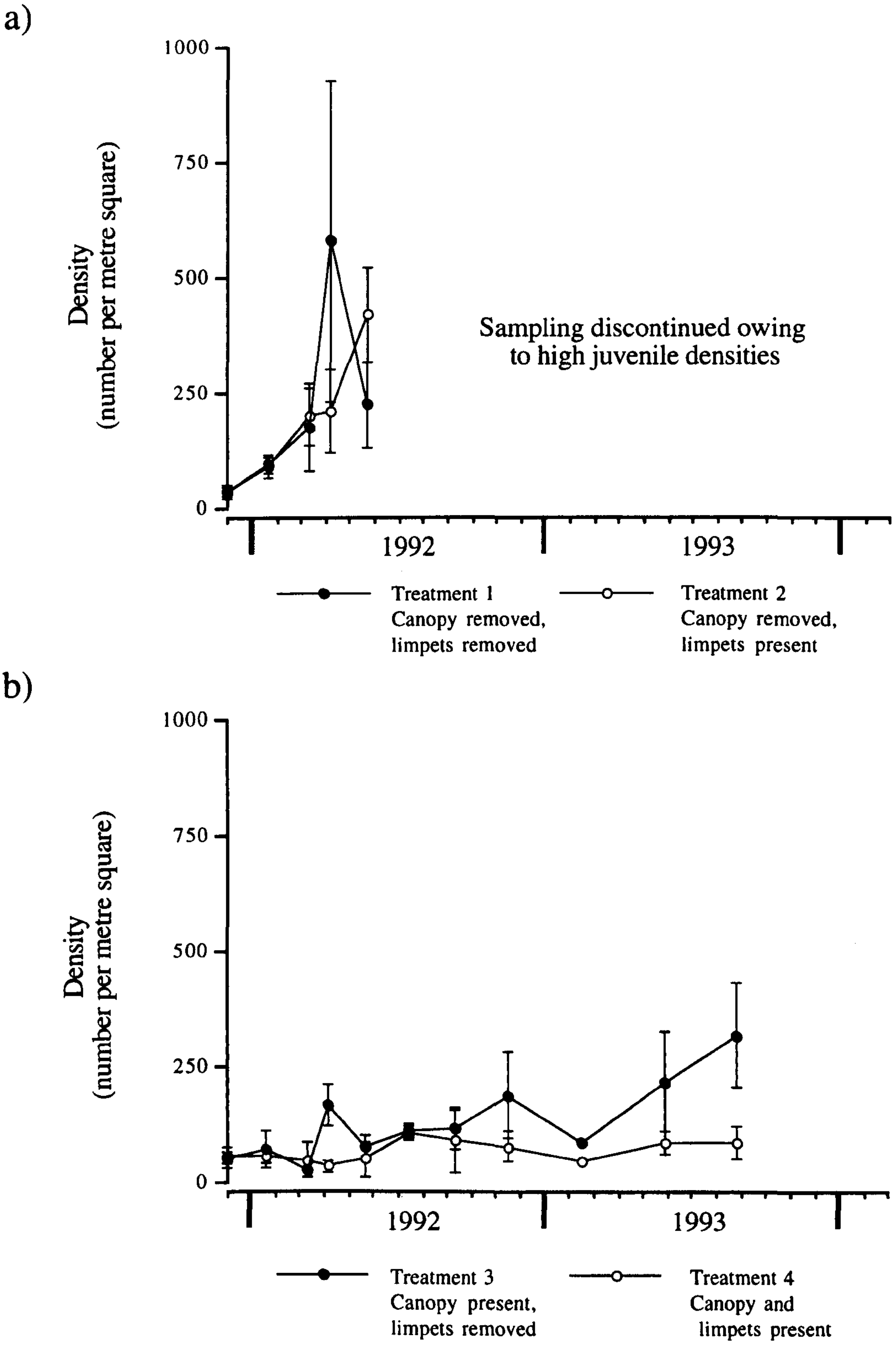


Figure 2.7 Change in density of *Fucus* species juveniles in the *Ascophyllum* zone following experimental manipulation in November 1991. Error bars = ± 1 SE
a) Plots cleared of canopy b) Plots where canopy is intact

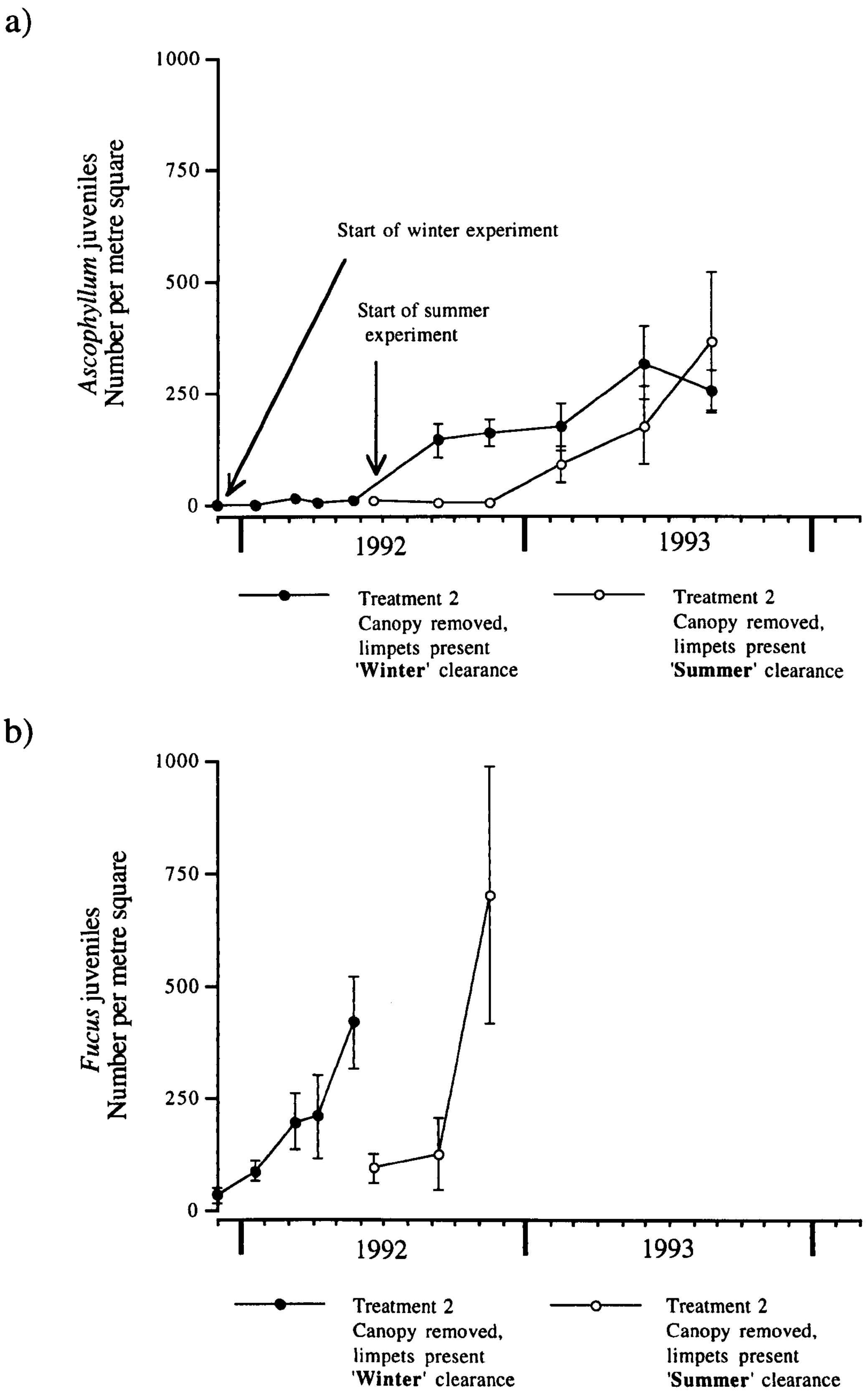


Figure 2.8 A comparison of fucoid juvenile recruitment between plots cleared of *Ascophyllum* in November (winter experiment) and in June (summer experiment). Error bars = ± 1SE
a) *Ascophylum* juveniles b) *Fucus* juveniles

Table 2.6 One way ANOVA testing for the effect of timing of canopy removal on density of *Fucus* juveniles. Test applied to data sampled five months after canopy manipulation in plots with canopy absent but limpets present.

Source	df	Mean Square	F-Value	P-Value
Season	1	119850.67	0.88	0.4022
Residual	4	547082.67		

2.3.2.2 Sampling of juvenile density and distribution in August 1994

The separate sampling of bare substrate and of algal turf revealed patterns not shown by the more general sampling program. Limpets directly affect algal recruitment to the substrate on which they graze. High densities of *Ascophyllum* juveniles occurred in patches of bare substrate when limpets were absent, irrespective of the presence or absence of the *Ascophyllum* canopy (Figure 2.9b). Two way ANOVA reveals a significant effect of limpets (Table 2.7).

In contrast, limpets had no effect on the density of *Ascophyllum* juveniles growing amongst the turf. Figure 2.9a clearly shows that high levels of Ascophyllum juveniles occurred only in plots cleared of canopy and that the presence or absence of limpets had no effect. Two way ANOVA reveals a probability value of 0.059 for the effect of canopy (Table 2.7) and although not quite significant at the 5% level, this probability value along with observations in the field suggest that the canopy does affect *Ascophyllum* juvenile density amongst the turf.

It is interesting to compare *Ascophyllum* juvenile density on the two substrata in plots in which the canopy was intact, but limpets had been removed (treatment 3). On the bare substrate juvenile density was high. However in the turf, there were very few juveniles. Thus, it seems that rock is a far better substrate for recruitment than turf. On bare substrate high densities of grazing limpets prevent juvenile recruitment; amongst the turf recruitment is low unless the *Ascophyllum* canopy is removed.

The sampling of *Fucus* juveniles at this single point, over two and a half years after the beginning of the experiment gives results which are difficult to interpret. Because of a slow growth rate, juveniles of *Ascophyllum* sampled bear a direct relationship to the original manipulations of canopy and limpets. However in *Fucus* a higher growth rate means that juveniles which recruited to plots cleared of *Ascophyllum* canopy have grown into canopy plants themselves. Therefore the *Fucus* juveniles sampled do not necessarily bear a relationship to the original experimental manipulation. This is illustrated by figure 2.9c which shows moderate densities of *Fucus* juveniles growing

Table 2.7 Two way ANOVA testing for the effect of the *Ascophyllum* canopy and the limpet *Patella vulgata* on the density of *Ascophyllum* and *Fucus* juveniles on two substrata, in August 1994.

	Source	df	Mean Square	F-Value	P-Value
Ascophyllum juveniles on turf	Canopy	1	174170.71	4.84	0.0589
	Limpet	1	94.64	0.00	0.9603
	Canopy x Limpet	1	709.94	0.02	0.8917
	Residual	6	35968.86		
Ascophyllum juveniles on bare substrate	Canopy	1	114.29	0.01	0.9405
	Limpet	1	125431.83	6.58	0.0373
	Canopy x Limpet	1	4150.84	0.22	0.655
	Residual	6	19074.35		
Fucus juveniles on turf	Canopy	1	18.75	0.00	0.9724
	Limpet	1	12096.75	0.82	0.391
	Canopy x Limpet	1	18960.75	1.29	0.2891
	Residual	6	14709.83		
Fucus juveniles on bare substrate	Canopy	1	427.45	13.49	0.0104
	Limpet	1	1509.62	47.62	0.0005
	Canopy x Limpet	1	459.22	14.49	0.0089
	Residual	6	31.70		

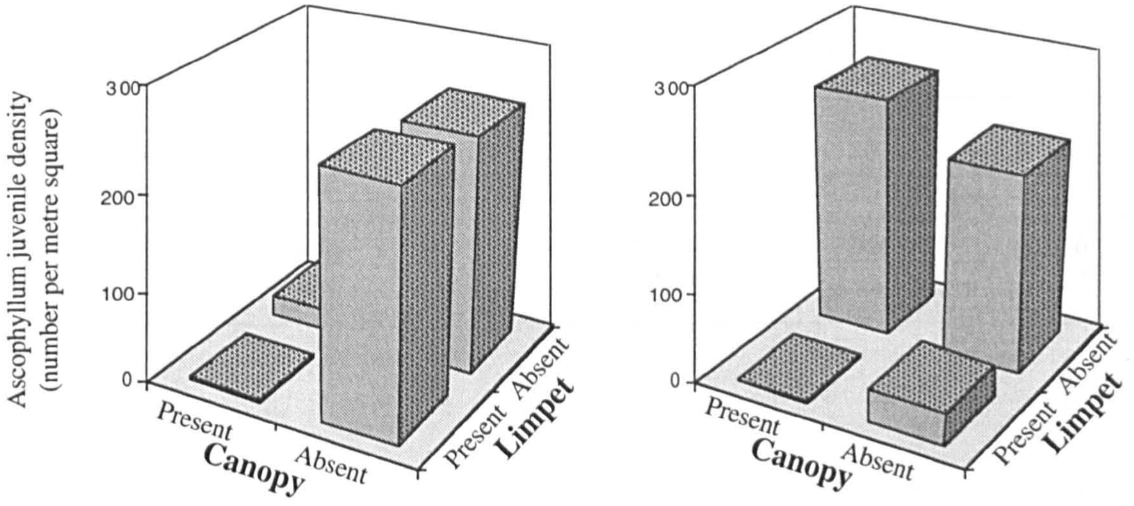
amongst the turf in all treatments. The expected effect of *Ascophyllum* canopy removal is not shown.

On patches of bare substrate, *Fucus* juvenile density was maintained at a low level by limpet grazing, in the same way as *Ascophyllum* juveniles (Figure 2.9d). However the density of *Fucus* juveniles on ungrazed bare substrate was dependent to a large extent on the presence or absence of the canopy. Surprisingly density was 12 times higher when the canopy was present. This is reflected in the significant interaction term of the two way ANOVA (Table 2.7). This result may be explained by the argument outlined above, that in the absence of an *Ascophyllum* canopy initial high densities of *Fucus* juveniles had long since progressed to form a *Fucus* canopy.

Examination of ungrazed patches of bare substrate beneath the canopy showed that for both *Ascophyllum* and *Fucus serratus*, density of juveniles was greater on lithothamnia than on bare rock (Figure 2.10). One way ANOVA on square root transformed data showed a significant difference between the two types of substrate for *Fucus* but not for *Ascophyllum*. (Table 2.8).

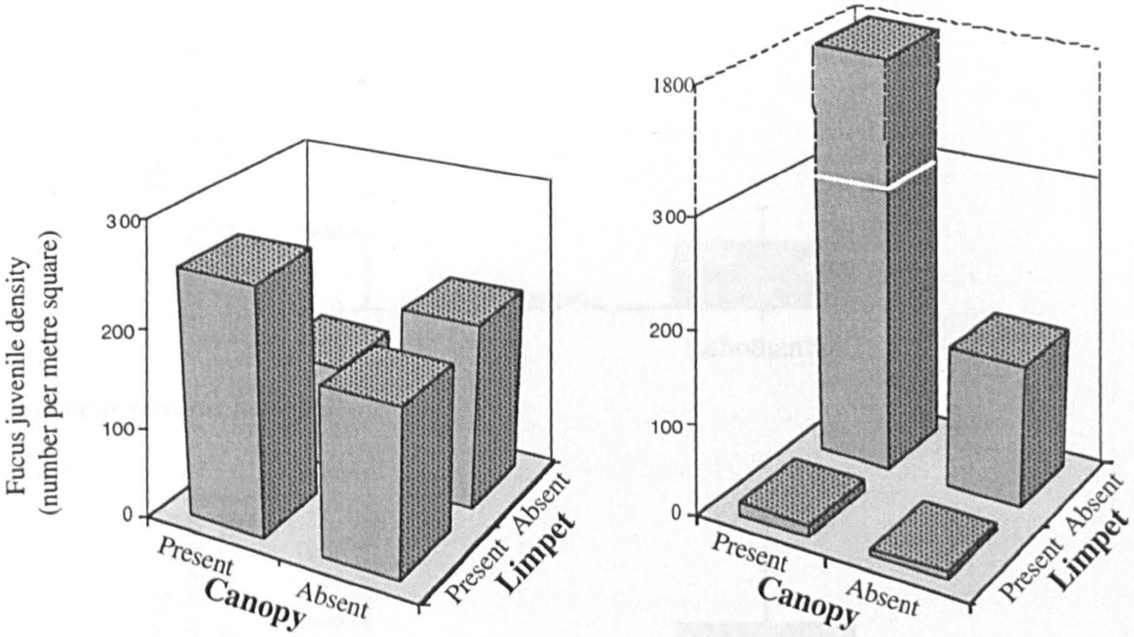
a) *Ascophyllum* juveniles amongst red algal turf

b) *Ascophyllum* juveniles on bare substrate



c) *Fucus* juveniles amongst red algal turf

d) *Fucus* juveniles on bare substate



Summary of data

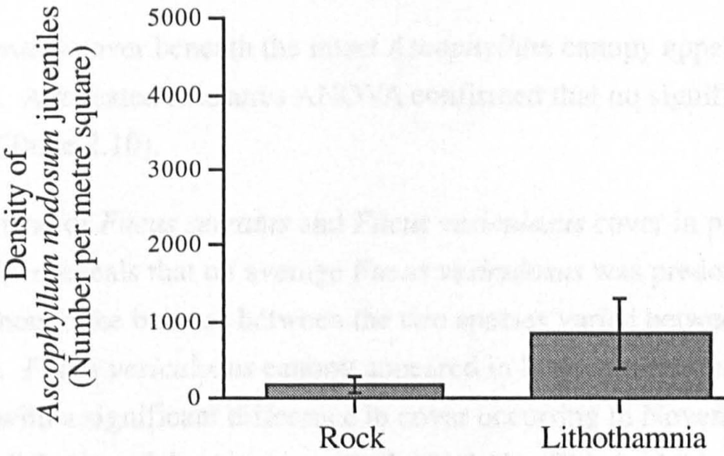
Graph	No canopy, no limpets		No canopy, limpets present		Canopy present, no limpets		Canopy present, limpets present	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE
a	248.9	177.9	258.6	125.4	23.3	23.3	2.3	2.3
b	212.0	139.2	34.6	14.2	258.0	89.2	1.7	1.7
c	193.6	29.2	177.6	18.8	116.7	84.1	259.7	106.4
d	150.6	87.9	7.45	2.9	1800.35	717.1	12.3	9.9

Figure 2.9 Density of fucoid juveniles in four experimental treatments in August 1994. Note extended Y axis in figure 2.9d

Table 2.8 One way ANOVA testing for a difference in fucoid juvenile density between rock and lithothamnia, ungrazed by limpets beneath the *Ascophyllum* canopy. (Square root transformed data)

	Source	df	Mean Squares	F-Value	P-Value
Ascophyllum juveniles	Substrate	1	315.82	1.207	0.3140
	Residual	6	261.63		
Fucus juveniles	Substrate	1	2794.17	7.066	0.0376
	Residual	6	395.44		

a) *Ascophyllum* juveniles



b) *Fucus serratus* juveniles

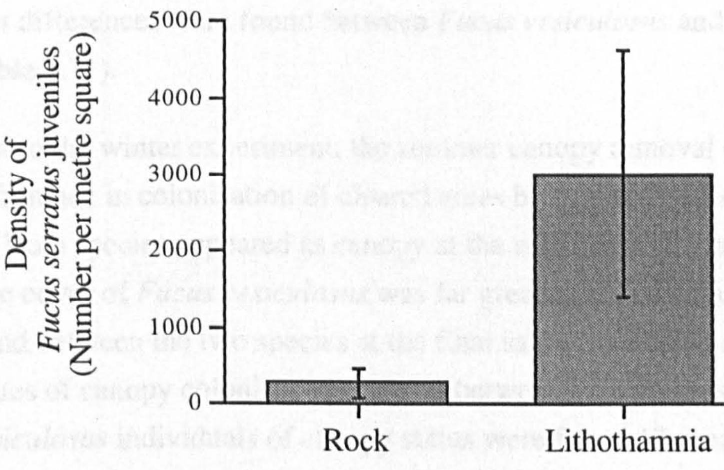


Figure 2.10 A comparison of fucoid juvenile density on ungrazed rock and lithothamnia beneath the *Ascophyllum* canopy. Sampling took place in August 1994, 30 months after experimental manipulation. Error bars = ± 1SE

a) *Ascophyllum* juveniles b) *Fucus serratus* juveniles

2.3.2.3 Fucoid canopy regrowth

As expected, regrowth of the *Ascophyllum* canopy following its removal did not occur during the experimental period of three years. However, canopies of *Fucus serratus* and *Fucus vesiculosus* did form in plots cleared of *Ascophyllum.* In contrast, in plots where the canopy was left intact *Fucus vesiculosus* was completely absent and *Fucus serratus* occurred only at a low level (Figures 2.11 and 2.12). At the final sampling dates (both August 1993 and November 1994) two way ANOVA carried out on arcsine transformed data showed a significant effect of canopy, and a non significant effect of limpets for both *Fucus vesiculosus* and *Fucus serratus* (Table 2.9a). Figures 2.11a and 2.12a suggest that the effect canopy removal had on the development of *Fucus serratus* and *Fucus vesiculosus* was at least partly determined by the presence or absence of limpets. However two way ANOVA reveals no significant interaction term in either case.

Fucus serratus cover beneath the intact *Ascophyllum* canopy appeared to change little over time. A repeated measures ANOVA confirmed that no significant change occurred (Table 2.10).

A comparison of *Fucus serratus* and *Fucus vesiculosus* cover in plots cleared of *Ascophyllum* reveals that on average *Fucus vesiculosus* was predominant (Figure 2.13a) although the balance between the two species varied between individual replicates. *Fucus vesiculosus* canopy appeared in large amounts earlier than *Fucus serratus,* with a significant difference in cover occurring in November 1992 (one year after establishment of the experiment) (Table 2.11). This initial large difference between the two species reduced with time and at the final sampling dates no significant differences were found between *Fucus vesiculosus* and *Fucus serratus* cover (Table 2.11).

In contrast to the winter experiment, the summer canopy removal experiment showed a clear difference in colonisation of cleared areas by *Fucus vesiculosus* and *Fucus serratus.* Both species appeared as canopy at the same time (Figure 2.13b), but percentage cover of *Fucus vesiculosus* was far greater, with a significant difference being found between the two species at the final sampling date in January 1994 (Table 2.12). Rates of canopy colonisation differed between the two seasonal experiments. *Fucus vesiculosus* individuals of canopy status were found 12 months after *Ascophyllum* clearance in November (winter experiment) compared to eight months after clearance in June (summer experiment).

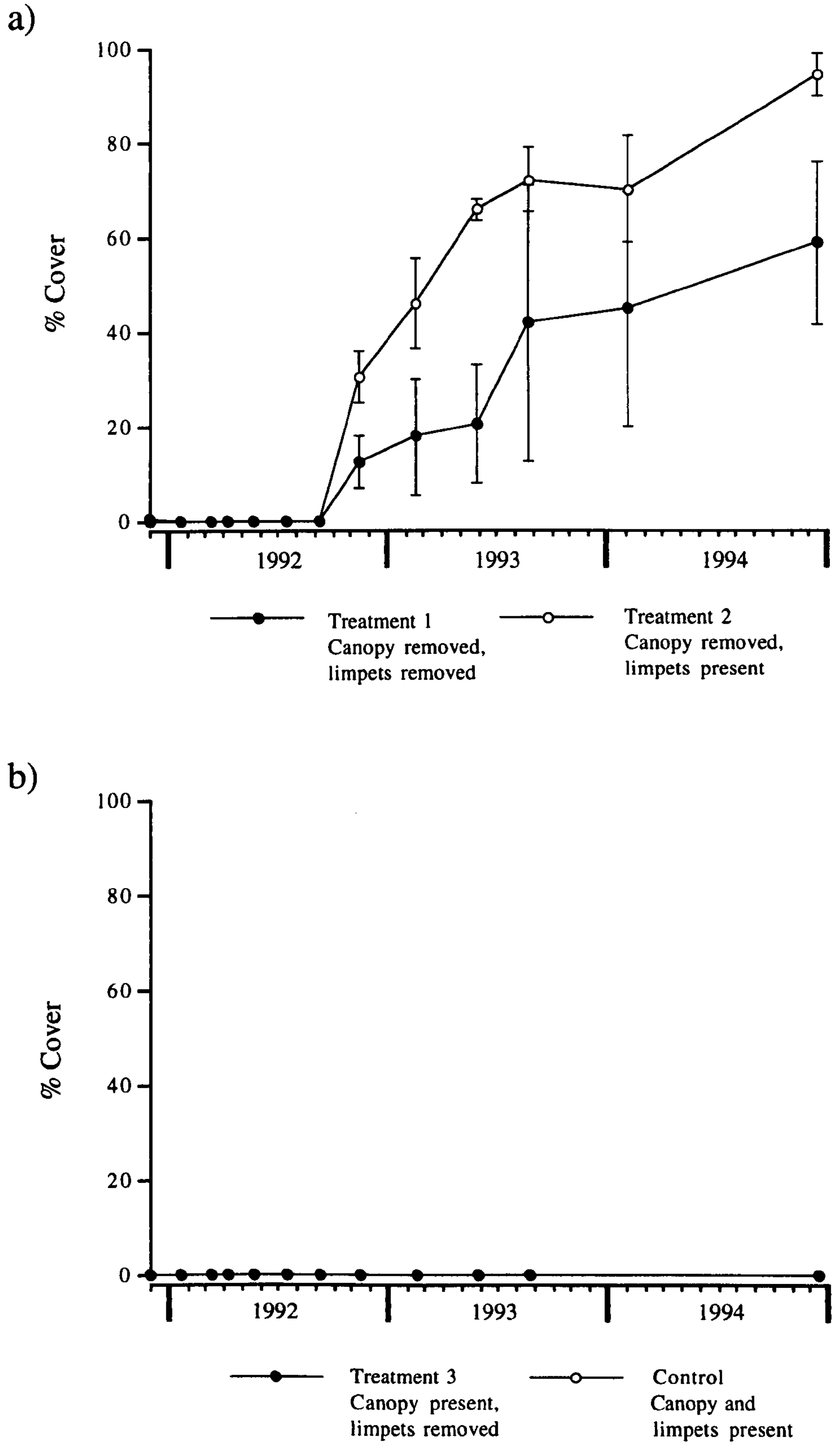


Figure 2.11 Development of *Fucus vesiculosus* canopy in the *Ascophyllum* zone following experimental manipulation in November 1991. Error bars = ± 1SE
a) Plots cleared of canopy b) Plots where the canopy is intact

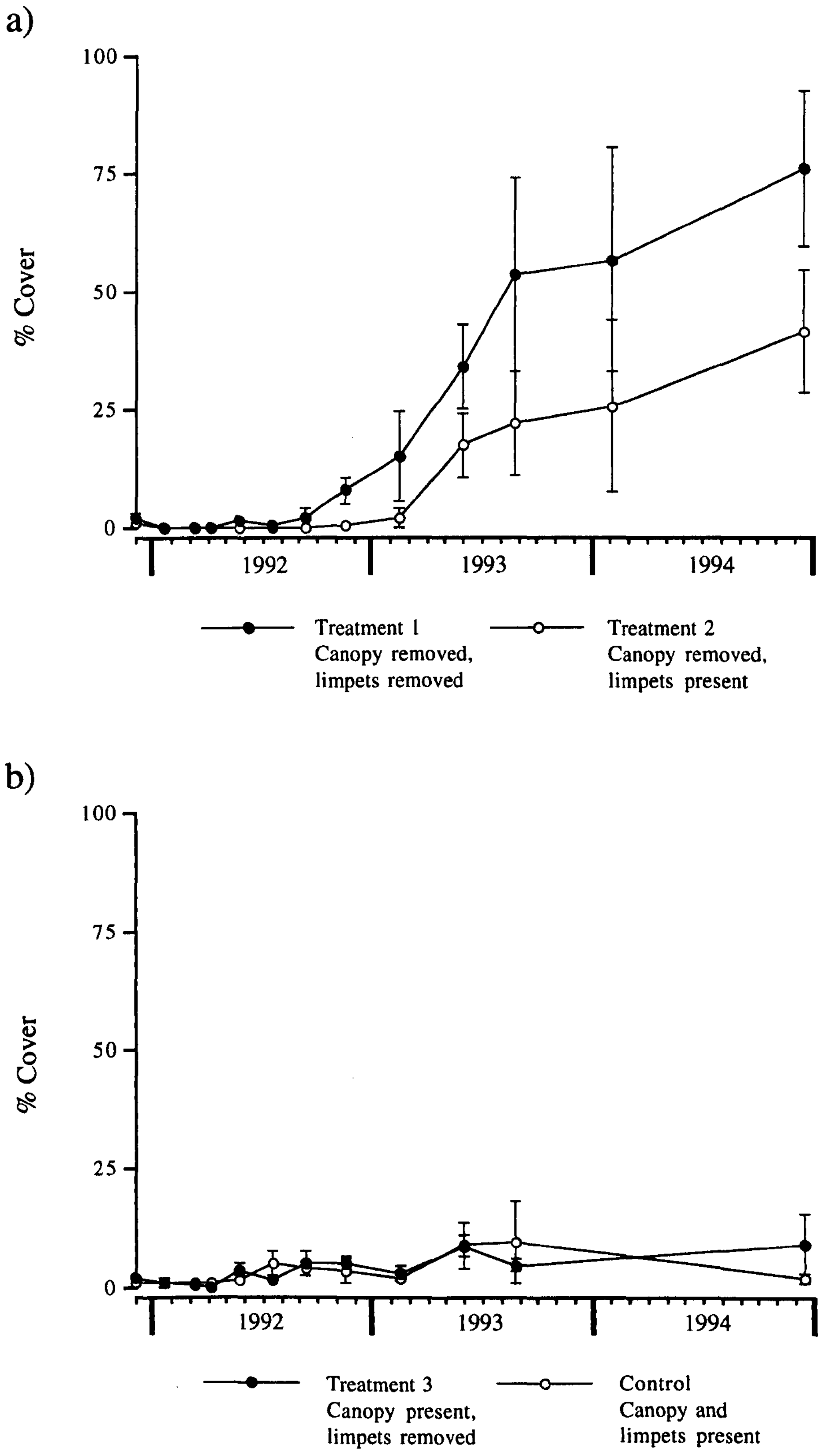


Figure 2.12 Development of *Fucus serratus* canopy in the *Ascophyllum* zone following experimental manipulation in November 1991. Error bars = ± 1SE
a) Plots cleared of canopy b) Plots where the canopy is intact

Table 2.9 Two way ANOVA on arcsine transformed data testing for the effect of the *Ascophyllum* canopy and the limpet *Patella vulgata* on the percentage cover of a number of algal species and complexes of species in the 'canopy and limpet manipulation experiment (Winter)'.

a) Fucoid canopy cover

	Source	df	Mean Square	F-value	P-value
Fucus	Canopy	1	0.60	0.03	0.8652
serratus t0	Limpet	1	2.79	0.14	0.7154
26.11.91	Canopy x Limpet	1	1.34	0.07	0.7999
	Residual	8	19.54		
Fucus	Canopy	1	1778.43	7.66	0.0244
serratus t10	Limpet	1	280.25	1.21	0.3039
11.8.93	Canopy x Limpet	1	341.55	1.47	0.2598
	Residual	8	232.23		
Fucus	Canopy	1	4700.36	19.51	0.0031
serratus t12	Limpet	1	618.59	2.57	0.1531
18.11.94	Canopy x Limpet	1	225.18	0.93	0.3659
	Residual	7	240.98		
Fucus	Canopy	1	2.75	1.00	0.3466
vesiculosus t0	Limpet	1	2.75	1.00	0.3466
26.11.91	Canopy x Limpet	1	2.75	1.00	0.3466
	Residual	8	2.75		
Fucus	Canopy	1	7819.84	18.78	0.0025
vesiculosus t10	Limpet	1	160.53	0.39	0.5519
11.8.93	Canopy x Limpet	1	160.53	0.39	0.5519
	Residual	8	416.29		
Fucus	Canopy	1	11461.15	77.46	0.0001
vesiculosus t12	Limpet	1	532.86	3.60	0.0995
18.11.94	Canopy x Limpet	1	532.86	3.60	0.0995
	Residual	7	147.96		

b) Green ephemeral species

	Source	df	Mean Square	F-value	P-value
t5	Canopy	1	12103.99	109.00	0.0001
8.7.92	Limpet	1	12.73	0.11	0.744
	Canopy x Limpet	1	131.68	1.18	0.3085
	Residual	8	111.37		
t7	Canopy	1	0.32	0.04	0.8446
5.11.92	Limpet	1	0.00	0.00	0.9896
	Canopy x Limpet	1	27.58	3.50	0.0982
	Residual	8	7.88		
t9	Canopy	1	1314.05	28.98	0.0007
17.5.93	Limpet	1	21.19	0.47	0.5136
	Canopy x Limpet	1	276.24	6.09	0.0388
	Residual	8	45.35		
t10	Canopy	1	48.00	1.82	0.2138
11.8.93	Limpet	1	0.07	0.00	0.9591
	Canopy x Limpet	1	24.94	0.95	0.3588
	Residual	8	26.32		

c) ***Cladophora* spp.**

	Source	df	Mean Square	F-value	P-value
t1 14.1.92	Canopy	1	5.44	0.58	0.467
	Limpet	1	0.01	0.00	0.9784
	Canopy x Limpet	1	8.66	0.93	0.3636
	Residual	8	9.33		
t4 15.5.92	Canopy	1	896.41	19.08	0.0024
	Limpet	1	49.85	1.06	0.3331
	Canopy x Limpet	1	77.27	1.65	0.2356
	Residual	8	46.97		
t6 1.9.92	Canopy	1	0.89	0.05	0.836
	Limpet	1	55.07	2.83	0.1309
	Canopy x Limpet	1	12.66	0.65	0.4431
	Residual	8	19.45		
t9 17.5.93	Canopy	1	689.17	26.56	0.0009
	Limpet	1	0.62	0.02	0.881
	Canopy x Limpet	1	0.95	0.04	0.8531
	Residual	8	25.95		

d) ***Chondrus crispus***

	Source	df	Mean Square	F-value	P-value
t0 26.11.91	Canopy	1	60.09	5.95	0.0406
	Limpet	1	8.94	0.89	0.3743
	Canopy x Limpet	1	46.33	4.59	0.0646
	Residual	8	10.10		
t6 1.9.92	Canopy	1	294.14	41.53	0.0002
	Limpet	1	2.18	0.31	0.5945
	Canopy x Limpet	1	0.25	0.04	0.8549
	Residual	8	7.08		
t10 11.8.93	Canopy	1	63.47	2.60	0.1455
	Limpet	1	1.49	0.06	0.8111
	Canopy x Limpet	1	33.40	1.37	0.2757
	Residual	8	24.41		

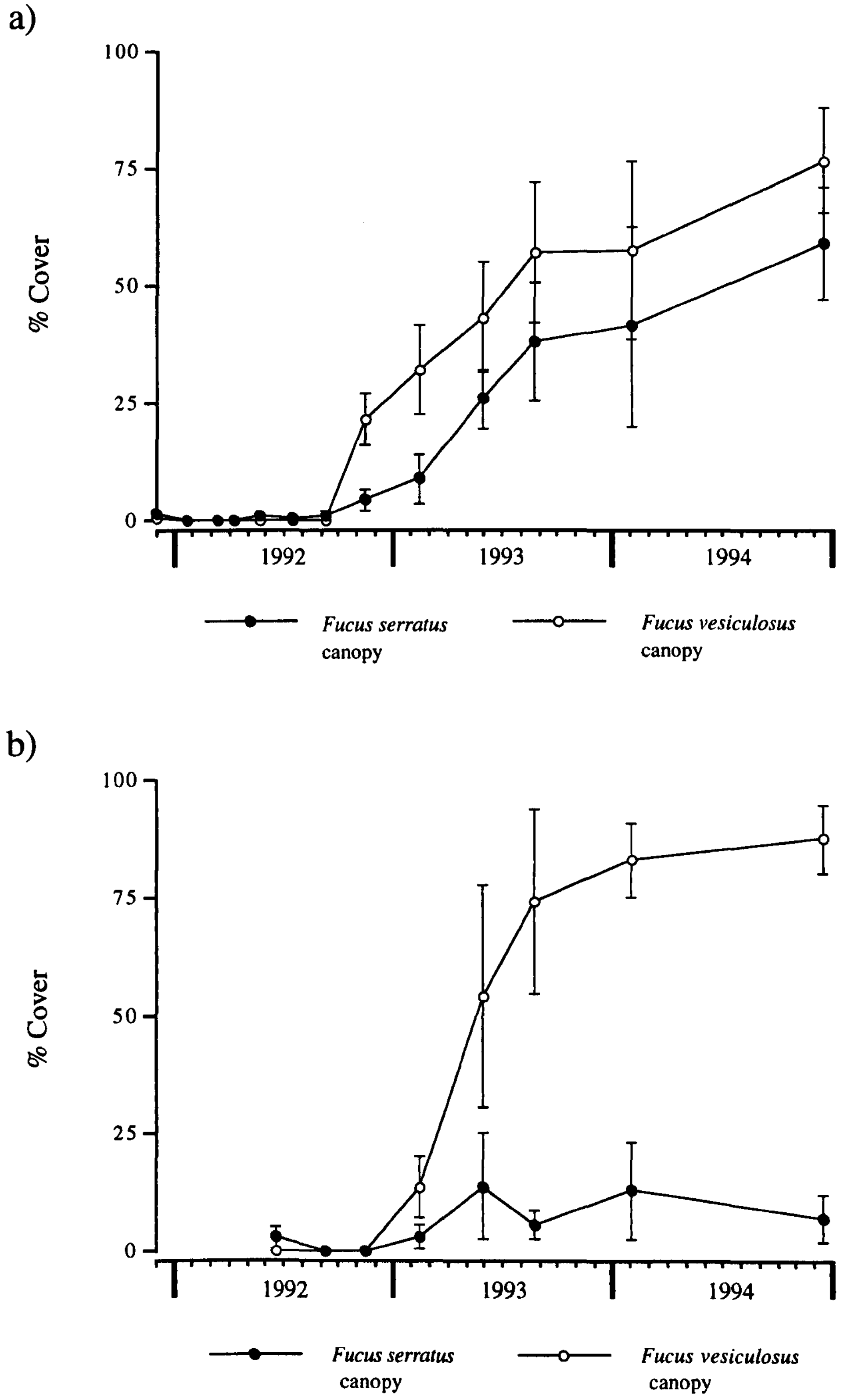


Figure 2.13 Comparison of *Fucus serratus* and *Fucus vesiculosus* canopy development in the *Ascophyllum* zone following *Ascophyllum* canopy removal. Values represent mean of all plots cleared of canopy. Error bars = ± 1 SE
a) Winter experiment b) Summer experiment

Table 2.10 Repeated measures ANOVA testing for a significant change in *Fucus serratus* canopy cover over time in plots where the *Ascophyllum* canopy was left intact (Canopy/limpet manipulation experiment (Winter)).

Source	df	Mean Square	F-Value	P-Value	G-G	H-F
Between Subjects						
Treatment	1	1.35	0.02	0.8899		
Subject(Group)	4	62.25				
Within Subjects						
Time	10	42.10	3.00	0.0064	0.1365	0.0923
Time x Treatment	10	6.75	0.48	0.8922	0.5747	0.6626
Time x Subject	40	14.03				

Table 2.11 One way ANOVA testing for a difference in percentage cover of *Fucus serratus* and *Fucus vesiculosus* canopy in plots cleared of *Ascophyllum* canopy. (Canopy/limpet manipulation experiment (Winter)).

	Source	df	Mean Square	F-Value	P-Value
November 1992 (t7)	Species	1	892.69	9.02	0.0133
	Residual	10	98.95		
August 1993 (t10)	Species	1	1083.00	0.94	0.3544
	Residual	10	1148.57		
November 1994 (t12)	Species	1	936.33	1.141	0.3106
	Residual	10	820.83		

Table 2.12 One way ANOVA testing for a significant difference in the percentage cover of *Fucus serratus* and *Fucus vesiculosus* at the final sampling date in January 1994 in plots cleared of *Ascophyllum* canopy. Canopy manipulation experiment (Summer)

Source	df	Mean Square	F-Value	P-Value
Species	1	7350.00	29.30	.0056
Residual	4	250.83		

2.3.2.4 Ephemeral algae

Percentage cover of green ephemeral algae (*Ulva* spp., *Enteromorpha* spp. and *Monostroma* spp.) was very low (<4%) throughout the experimental period in plots where the canopy was intact (Figure 2.14b). The removal of limpets beneath the canopy (treatment 3) had no overall effect on ephemeral cover, although detailed examination of rock patches in August 1994 found small amounts of *Ulva lactuca* growing on ungrazed rocks.

Removal of the canopy had a pronounced effect on ephemeral cover which directly affected other aspects of community structure (see sections on red algal turf and growth rate of *Fucus serratus* juveniles). Ephemeral algae formed blooms in the spring and summer of 1992 and 1993, with a large peak occurring in July 1992 and a second smaller peak in May 1993 (Figure 2.14a). Two way ANOVA on arcsine transformed data revealed a significant effect of canopy and no significant effect of limpets at both these sampling dates (Table 2.9b). In May 1993 the analysis revealed a significant interaction term, indicating that the effect of the canopy depended on the presence or absence of limpets. This can clearly be seen in figure 2.14a where percentage cover of ephemeral algae in treatment 2 where limpets were present was approximately half that in treatment 1 where limpets had been removed. This is consistent with field observations which showed that limpet grazing prevented recruitment of green ephemerals to bare substrate when the canopy was removed, thus restricting ephemeral algae to the turf. In plots where both canopy and limpets were removed (treatment 1) bare substrate was colonised. Examination of ephemeral species revealed no differences in species composition between the turf and ungrazed bare substrate. After each summer peak, percentage cover dropped sharply to levels similar to plots where the canopy was intact; no significant effect of canopy being found in November 1992 and August 1993 (Table 2.9b).

In the summer experiment, a peak in ephemeral abundance of 29% occurred in September, by which time cover in the winter experiment had dropped sharply to 8% in the equivalent treatment (Figure 2.15). By November, levels of ephemeral cover were still high (23%) and one way ANOVA revealed a significant effect of canopy removal (Table 2.13). There was no such effect at this time in the winter experiment. Thus, although cover of ephemeral algae had decreased to low levels in the winter experiment by September and November, levels in the summer clearance showed that ephemeral algae were still capable of colonisation given a suitable opportunity. Both winter and summer experiments showed fewer ephemerals in 1993. This can be attributed to the establishment of a new canopy of *Fucus vesiculosus* and *Fucus serratus* which causes shading to the understorey in the same way as the original *Ascophyllum* plants.

As well as the green ephemeral species described above, *Cladophora* species were ephemeral in nature, showing spring/summer blooms in both 1992 and 1993 and autumn/winter declines in plots cleared of canopy (Figure 2.16). The effect of canopy was found to be significant and limpets non significant in May 1992 and June 1993 (Table 2.9c)

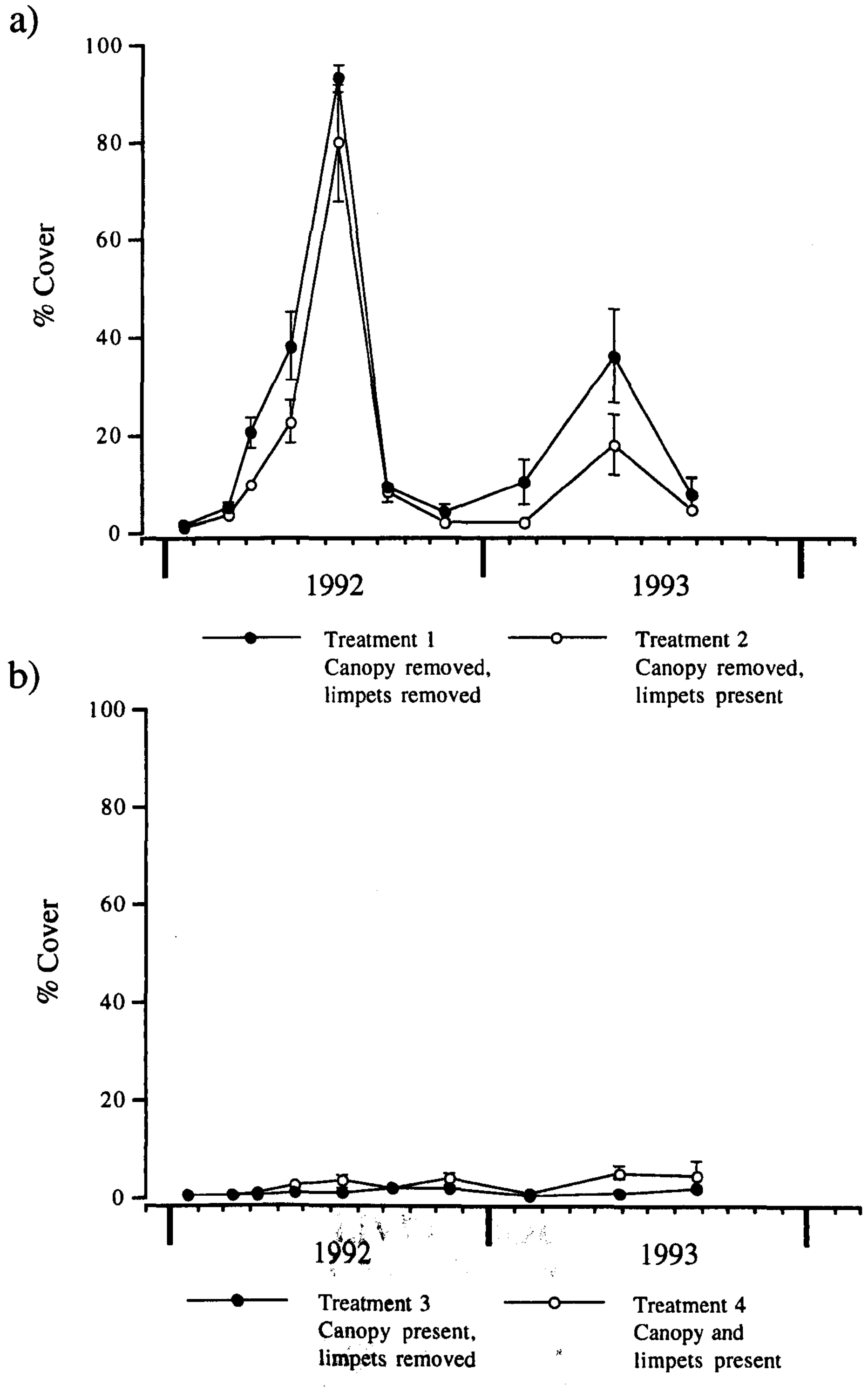


Figure 2.14 Development of green ephemeral species (*Enteromorpha* sp., *Ulva* sp., and *Monostroma* sp.) in the *Ascophyllum* zone following experimental manipulation in November 1991. Error bars = ± 1 SE
a) Plots cleared of canopy b) Plots where canopy is intact

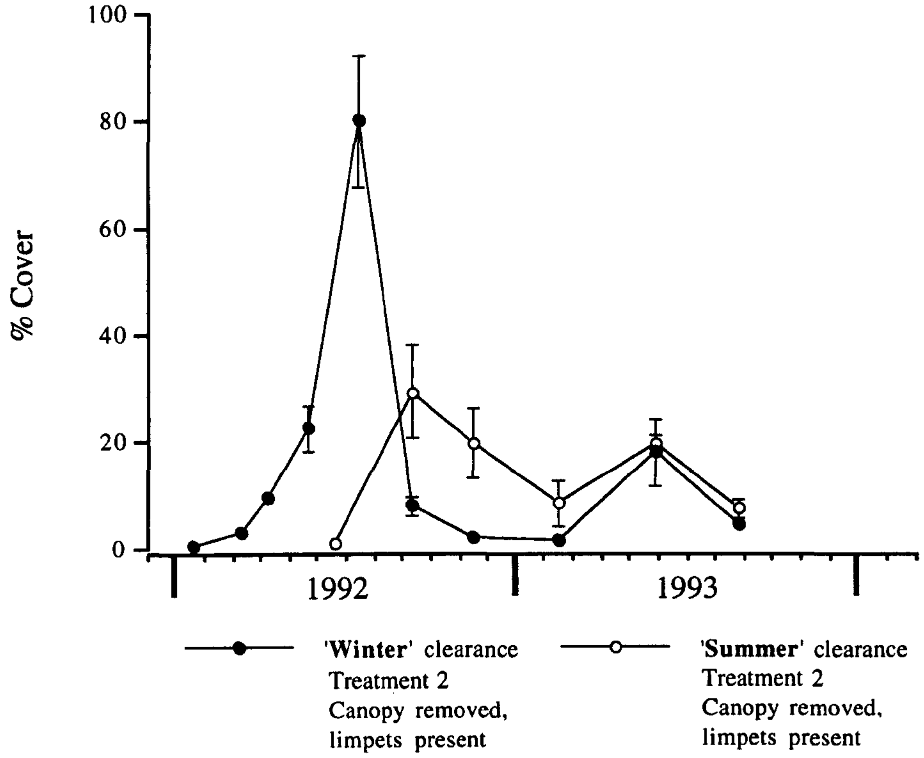


Figure 2.15 A comparison of colonisation by ephemeral algae (*Enteromorpha*, *Monostroma* and *Ulva* spp.) to plots cleared of *Ascophyllum* in November (winter experiment) and in June (summer experiment). Error bars = ± 1SE

Table 2.13 One way ANOVA testing for significant differences between plots cleared of canopy and control plots in percentage cover of green ephemeral species in November 1992. Canopy manipulation experiment (Summer).

Source	df	Mean Square	F-Value	P-Value
Treatment	1	543.23	13.56	0.0212
Residual	4	40.06		

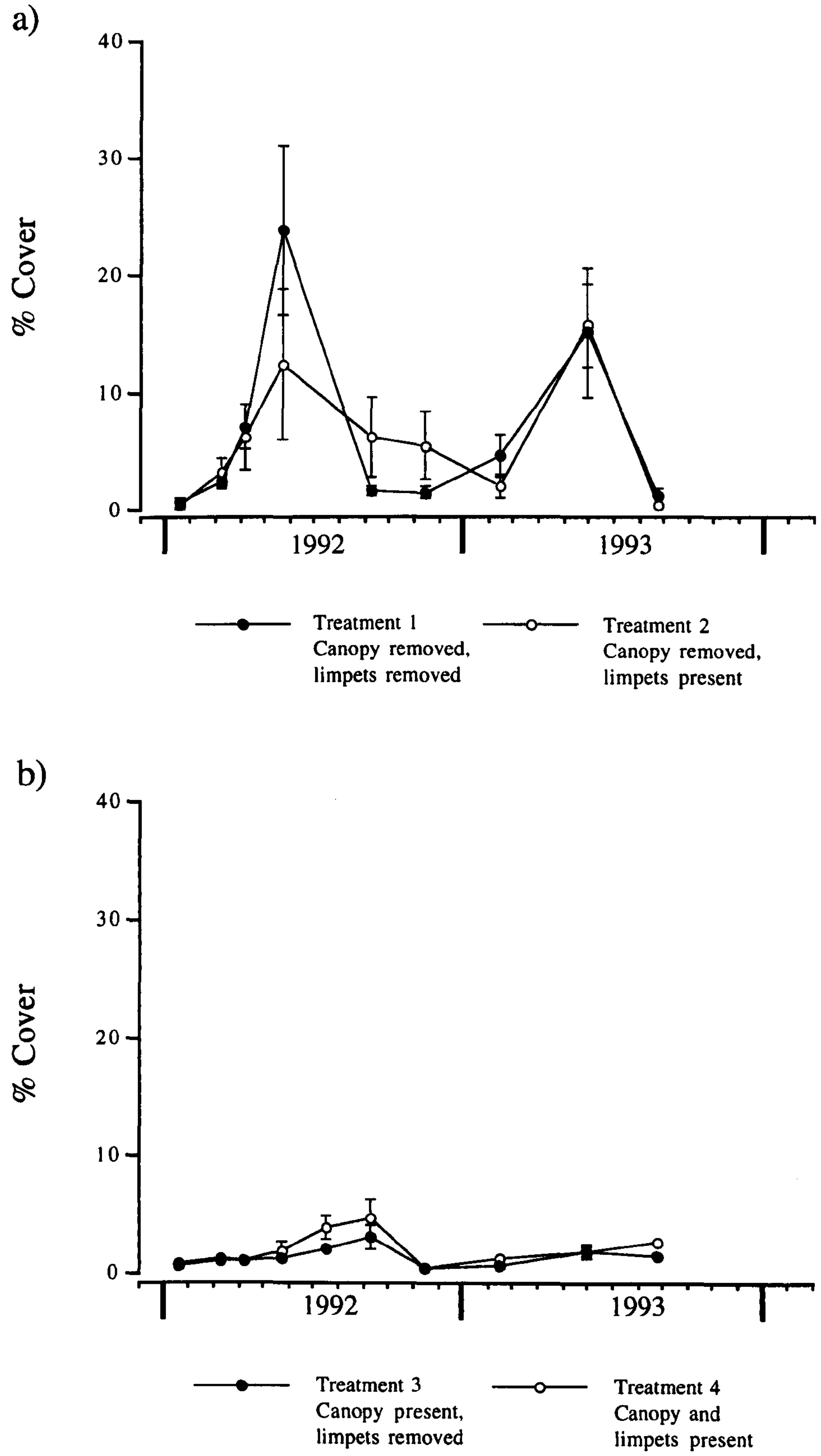


Figure 2.16 Percentage cover of *Cladophora* spp. in the *Ascophyllum* zone following experimental manipulation in November 1991. Error bars = ± 1SE
a) Plots cleared of canopy b) Plots where canopy is intact

2.3.2.5 Red algal turf

Bleaching of red algae was apparent in plots cleared of canopy as early as January with small patches of *Chondrus crispus* showing signs of yellowing. Lithothamnia crusts also showed signs of bleaching at this early stage. By April, some areas of exposed turf were highly bleached, with a distinct colour change from red to light brown especially in *Chondrus crispus*, *Gelidium* and *Laurencia* species. Bleaching led to die back of algae such that in some areas no algal material protruded beyond the level of silt. However, even over the small tidal range (<1m) of the experimental area there were distinct differences between high and low plots. For example in the lowest of the experimental cleared areas no bleaching was apparent. In plots where the canopy was intact, the turf was healthy, although some specimens of *Corallina officinalis* and *Chondrus crispus* were found to be slightly bleached. In June a dense covering of *Enteromorpha* covered plots where the canopy was removed. When the ephemeral algae were moved aside the turf appeared highly silt-dominated with very little red algae. In places, especially in damp spots, the silt/red algal mixture appeared black and anoxic. With the loss of ephemeral cover through late summer and autumn, some areas of turf which were deficient of red algae appeared to lose silt, thus opening up areas of rock. Although still predominantly stunted and brown in colour, small areas of turf began to show signs of recovery from bleaching in November. Regrowth of red algae, mainly *Gelidium,* occurred, especially beneath the new canopy of *Fucus.* This trend of recovery and regrowth continued throughout the spring and summer of 1993 where the turf was protected by new canopy. However, where canopy was absent the turf remained stunted and patchy.

The qualitative description of the red algal turf through the experimental period is reinforced by examining results from the more quantitative approaches using the algal density index and the individual sampling of *Chondrus crispus.* The algal density index shows a clear pattern of algal turf degradation in plots cleared of canopy, followed by recovery as a new fucoid canopy developed (Figure 2.17). The same pattern is shown by *Chondrus crispus.* This red alga declined in abundance through the spring and summer in plots cleared of canopy to reach its lowest level in September 1992 (Figure 2.18). Percentage cover of *Chondrus* at this time was significantly lower in plots cleared of canopy than in plots where the canopy was intact (Table 2.9d). From this point *Chondrus* recovered to original levels, no significant effect of canopy being found in August 1993.

In the summer experiment, bleaching occurred immediately following canopy clearance, so that in September all turf was stunted and pale brown in colour. No regrowth or recovery was apparent over the winter and in many areas, even beneath the developing *Fucus vesiculosus* canopy, the turf was lost completely. This can be seen clearly from results of the algal density sampling; a gradual decline in turf density is seen and in contrast to the winter experiment no recovery is apparent (Figure 2.17a). *Chondrus crispus* cover declined at a higher rate following canopy clearance in the summer and had not recovered by August 1993 (Figure 2.19). Examination of the turf in August 1994, showed that in all plots red algae were healthy, indicating recovery from bleaching. However large areas of turf were completely absent in two out of three plots.

In order to quantify this loss of turf, sampling was carried out in August 1994 on areas of the experimental plots which at the start of the experiment had been turf dominated. This revealed that the results of turf degradation due to canopy removal were still apparent (Figure 2.20). The percentage of rock visible within the turf was significantly higher in plots cleared of canopy in both the winter and summer experiments (Table 2.14). A comparison of the winter and summer experiments shows turf loss was higher in those plots cleared of canopy in the summer. (One way ANOVA p=0.062-Table 2.15). Although this could be because of a lower recovery time (26 versus 33 months), field observations and the results of the algal density index shown in figure 2.17a suggest that the intense bleaching following canopy removal in June resulted in larger scale turf loss.

Table 2.14 One way ANOVA testing for the effect of *Ascophyllum* canopy removal on the percentage of rock visible within the red algal turf (Data square root transformed).

	Source	df	Mean Square	F-Value	P-Value
Winter Experiment	Canopy	1	24.274	24.968	0.0005
	Residual	10	0.972		
Summer Experiment	Canopy	1	39.725	13.729	0.0207
	Residual	4	2.894		

Table 2.15 One way ANOVA testing for the effect of season on the state of the red algal turf in plots cleared of canopy.

Source	df	Mean Square	F-Value	P-Value
Season	1	14.021	4.914	0.0622
Residual	7	2.853		

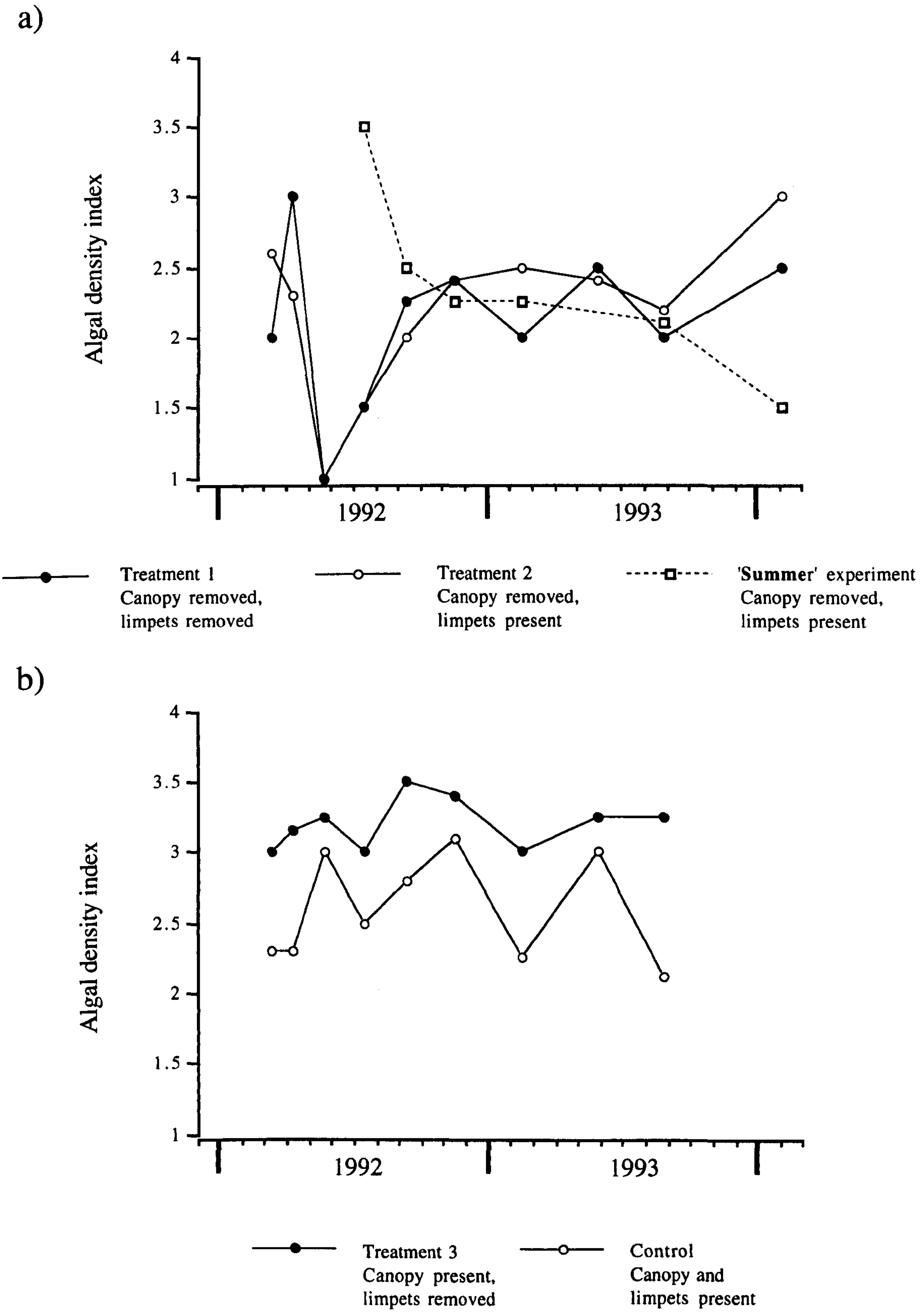


Figure 2.17 Change in algal density index in the *Ascophyllum* zone following experimental manipulation in November 1991 and in June 1992.
a) Plots cleared of canopy b) Plots where canopy is intact.
N.B. Data are not available for the 'summer' experiment control (canopy and limpets present).

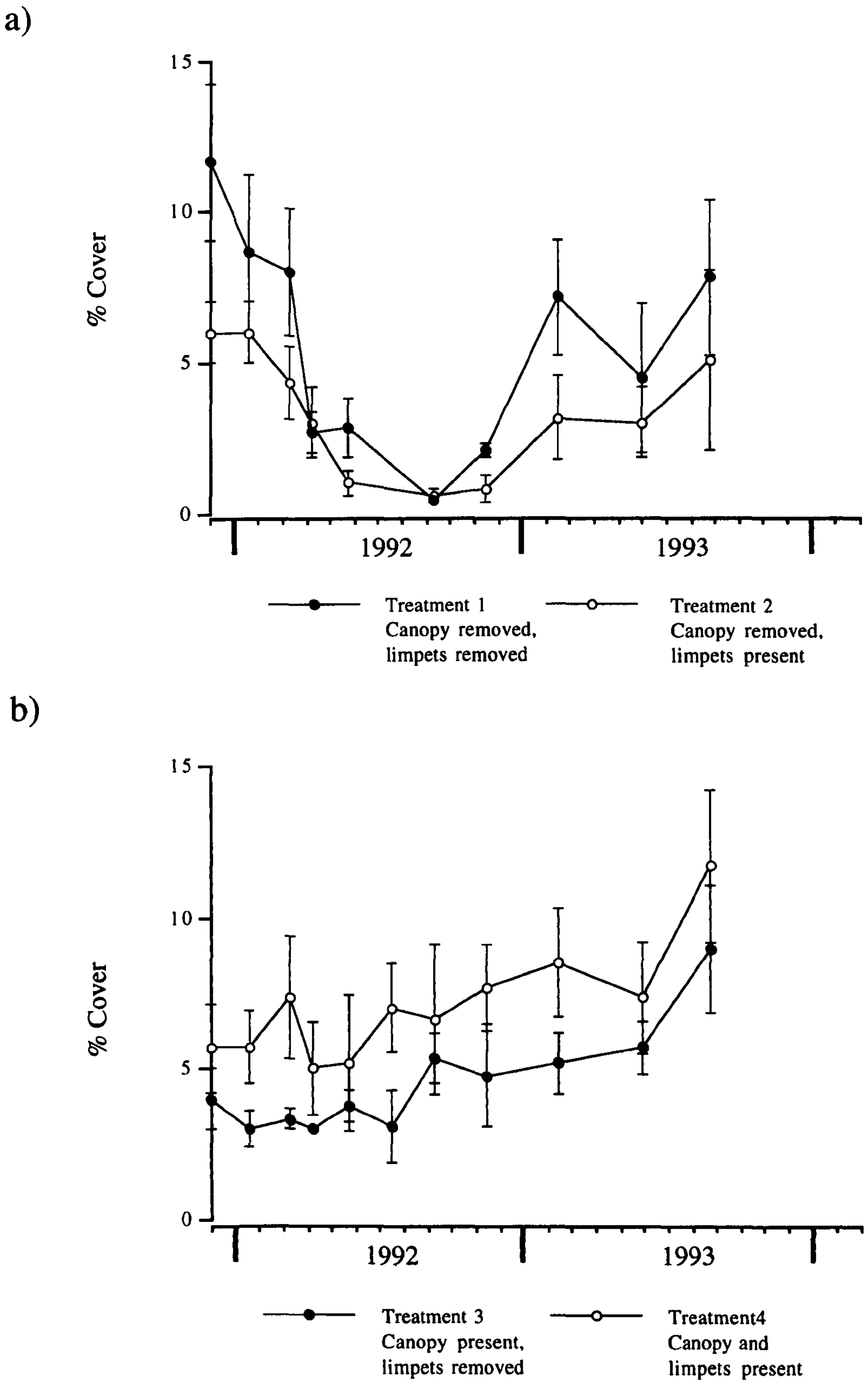


Figure 2.18 Percentage cover of *Chondrus crispus* in the *Ascophyllum* zone following experimental manipulation in November 1991. Error bars = ± 1SE
a) Plots cleared of canopy b) Plots where canopy is intact

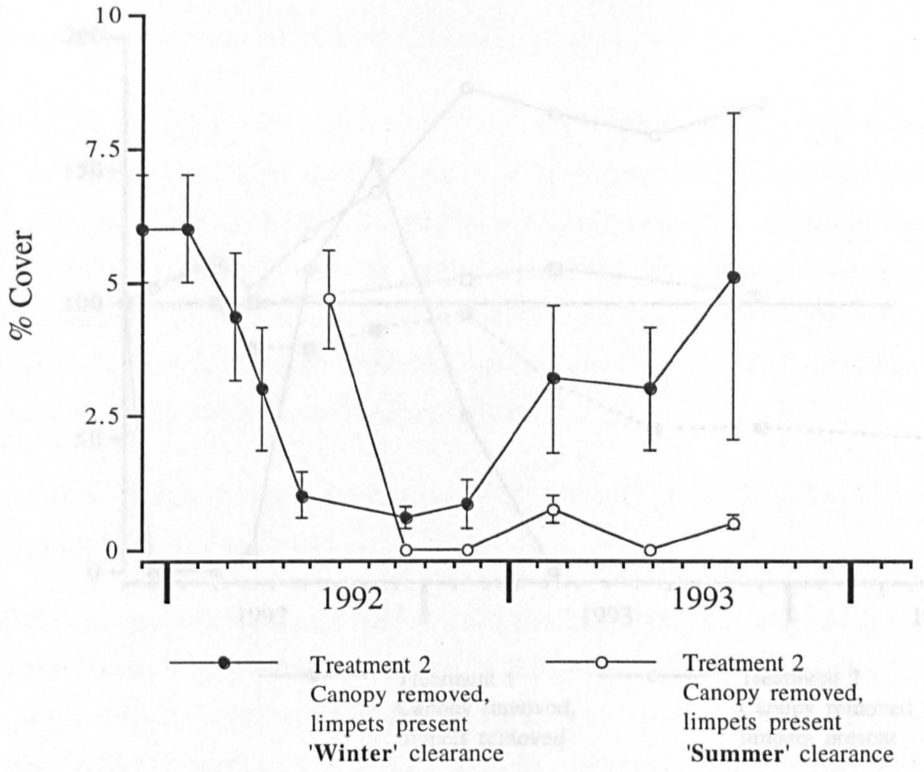


Figure 2.19 A comparison of *Chondrus crispus* colonisation in plots cleared of *Ascophyllum* in November 1991 (winter experiment) and in June 1992 (summer experiment). Error bars = ± 1SE

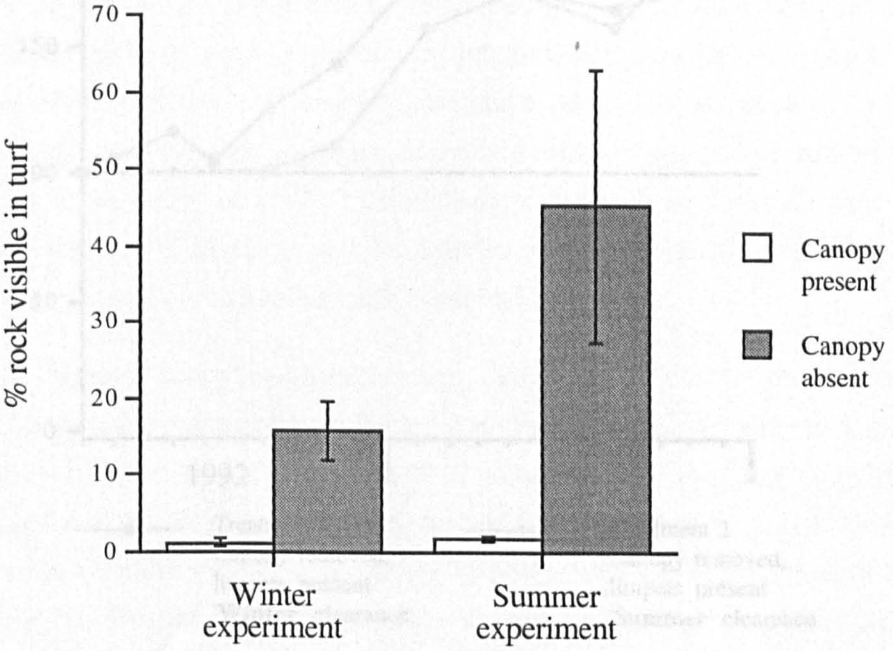


Figure 2.20 Effect of canopy removal on the state of the red algal turf in both the winter and summer experiments. Turf sampled in August 1994. Error bars = ± 1SE

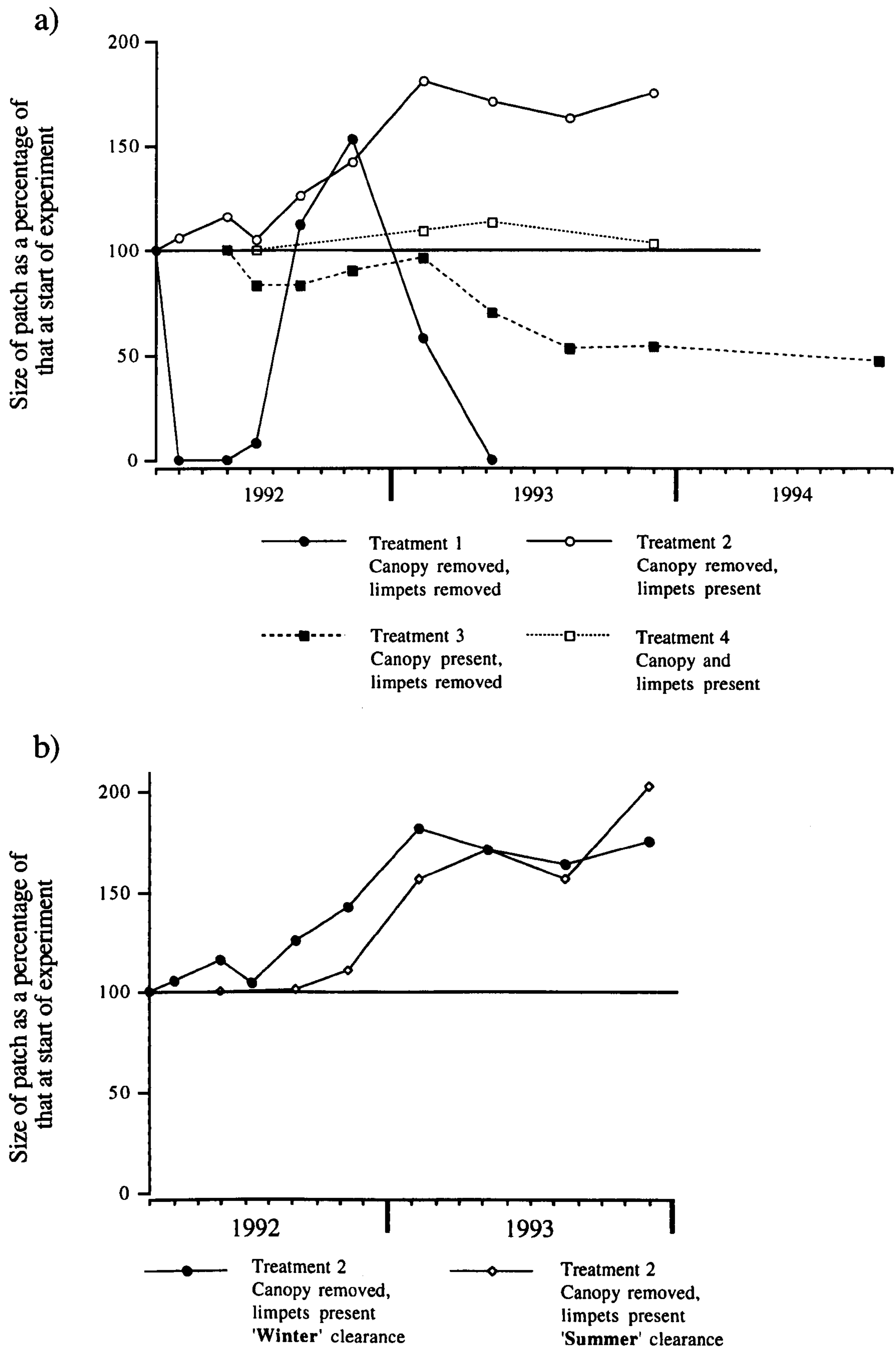


Figure 2.21 Effect of canopy and limpet manipulations on bare substrate patch sizes in the *Ascophyllum* zone. Error bars omitted for clarity

a) Winter experiment

b) Comparison of winter and summer experiments

2.3.2.6 Rock and lithothamnia (bare substrate) patch sizes

Bare substrate covered only a limited area in the *Ascophyllum* zone as demonstrated by the sampling of four sheltered mid shore sites (Figure 2.4). Consequently, even though patches of bare substrate showed large changes in size over the course of the experiment, the method of sampling involving random placement of four quadrats in each experimental plot failed to show this. However, in addition to the random sampling method, specific measurements of the size of patches of bare substrate were made in each plot at each sampling date (Figure 2.21a).

In the control treatment where no manipulation took place (treatment 4) little overall change in patch size was evident.

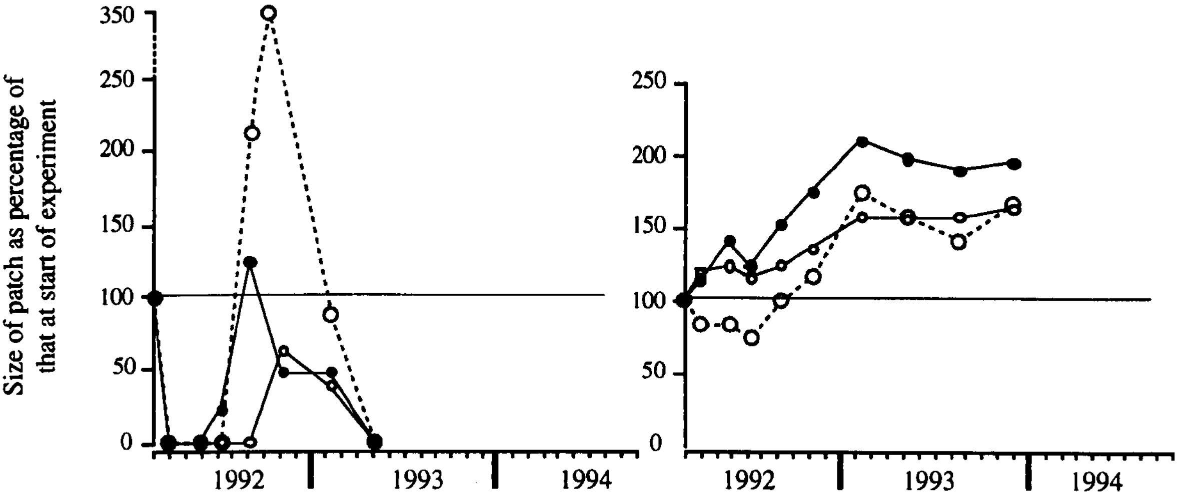
Where the canopy had been removed but limpets left in place (treatment 2), percentage cover of bare substrate showed a gradual increase over the first year, although a small decrease occurred from May to June owing to colonisation by ephemeral algae. A peak in size was reached in January 1993 when the sizes of patches were on average 1.81 times larger than at the beginning. The slight decrease following this peak can be attributed to invasion of *Fucus vesiculosus* at the edges of patches.

Where both limpet and canopy were absent as in treatment 1, percentage cover of bare substrate appeared to be governed largely by growth of ephemerals. By April 1992 all patches were completely overgrown by *Enteromorpha* spp. However as ephemeral algae died out in the autumn, cover of bare substrate increased and as a result of algal turf degradation, patches increased beyond their original size to a peak of 153% in November. A sharp decrease in bare substrate cover accompanied growth of ephemerals in the spring of 1993. Fucoid canopy regrowth, ephemeral cover and most importantly the loss of distinct patch boundaries resulting from algal turf degradation prevented further measurements in this treatment.

Removal of limpets beneath an intact canopy (treatment 3) initially resulted in little overall change since the canopy prevented growth of ephemerals and the algal turf remained healthy and intact. However, slow colonisation of ungrazed rock by *Fucus serratus* and *Ascophyllum* juveniles and species of red algae such as *Laurencia*, *Gelidium* and *Corallina* made a significant impact during the second year of the experiment. By August 1994 the patches occupied 46% of their original area.

The trends shown in Figure 2.21a are confirmed by examining change in percentage cover of bare substrate in individual plots (Figure 2.22). Although some variation exists between plots, the trends are consistent within each of the treatments in which manipulation took place (treatments 1, 2 and 3). However, in the control treatment, individual replicates, which in this case were individual rock patches, showed varying changes in size, some increasing and some decreasing slightly. The overall effect of this as shown by Figure 21a is one of little change.

Patches of bare substrate in the summer experiment where canopy had been removed but limpets were left in place showed a similar increase in size as in the equivalent winter treatment (Figure 2.21b).



a) Treatment 1 Canopy removed, limpets removed

b) Treatment 2 Canopy removed, limpets present

c) Treatment 3 Canopy present, limpets removed

d) Treatment 4 Canopy and limpets present

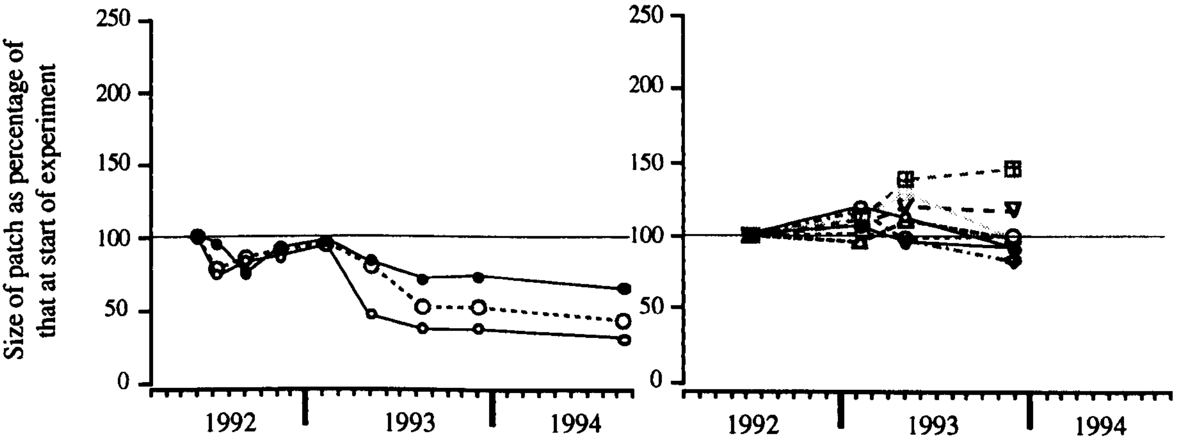


Figure 2.22 Effect of canopy and limpet manipulations on bare substrate patch sizes in the *Ascophyllum* zone. Individual replicates plotted separately.

2.3.3 Growth rate and survival of *Fucus serratus* juveniles in the *Ascophyllum* zone

The relative growth rate of *Fucus serratus* juveniles beneath the *Ascophyllum* canopy showed a distinct summer/winter cycle, with very low growth in winter rising to peaks in June 1992 and July 1993 (Figure 2.23). This simple pattern was not evident in areas cleared of canopy. A nested ANOVA showed that growth rate of juveniles in cleared areas was significantly higher than beneath the canopy during December 1991 and February 1992 (Table 2.16). However, in April, relative growth rate in cleared areas decreased sharply to a level significantly lower than that under the canopy. This decline in growth rate, coincided with the development of a dense cover of green ephemeral species in plots cleared of canopy. At the following sampling dates, July, September and December 1992 no significant difference was found in growth rates between the two treatments. However, the sharp decline in growth rate of juveniles beneath the canopy which occurred at the end of the summer, resulted in differences in September and December 1992 which were only marginally non significant at the 5% level. The results of the nested ANOVA suggest a significant difference between replicates within a treatment in February 1992 (Table 2.16).

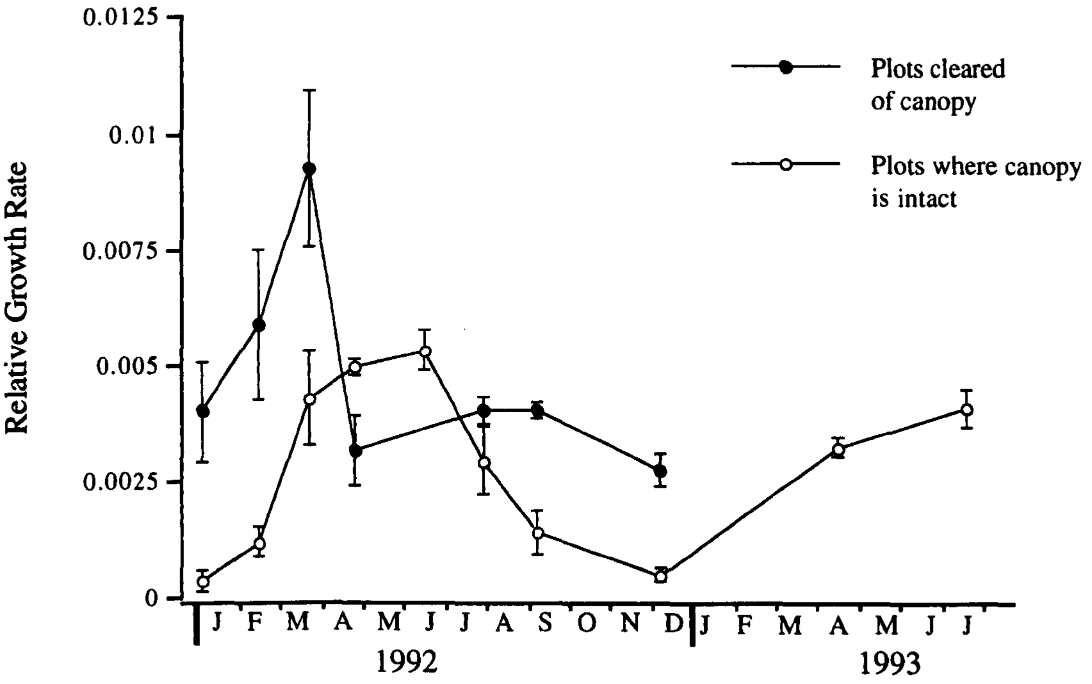


Figure 2.23 Relative growth rate of *Fucus serratus* juveniles in the *Ascophyllum* zone in plots cleared of canopy and in plots where the canopy is intact. Error bars = ± 1SE

Table 2.16 Nested ANOVA testing for the effect of *Ascophyllum* canopy removal on the relative growth rate of *Fucus serratus* juveniles in the *Ascophyllum* zone between 18th December 1991 (Day 0) and 25th September 1992 (Day 415). Underlined date indicates square root transformed data

	Source	df	Mean Square	F-value	P-value
Day 29	Canopy	1	1.950×10^{-4}	11.162	0.0288
16.1.92	Quadrat(Canopy)	4	1.747×10^{-5}	1.755	0.1515
	Residual	54	9.957×10^{-6}		
Day 82	Canopy	1	2.481×10^{-2}	12.191	0.0251
10.3.92	Quadrat(Canopy)	4	2.035×10^{-3}	2.773	0.0365
	Residual	52	7.34×10^{-4}		
Day 105	Canopy	1	3.388×10^{-4}	6.273	0.0664
2.4.92	Quadrat(Canopy)	4	5.400×10^{-5}	2.283	0.0733
	Residual	50	2.365×10^{-5}		
Day 148	Canopy	1	3.77×10^{-3}	10.036	0.0339
15.5.92	Quadrat(Canopy)	4	3.75×10^{-4}	0.41	0.8004
	Residual	41	9.25×10^{-4}		
Day 237	Canopy	1	6.039×10^{-6}	1.022	0.3864
12.8.92	Quadrat(Canopy)	3	5.906×10^{-6}	1.073	0.3710
	Residual	42	5.506×10^{-6}		
Day 281	Canopy	1	2.614×10^{-5}	8.24	0.0640
25.9.92	Quadrat(Canopy)	3	3.173×10^{-6}	1.452	0.1749
	Residual	19	2.184×10^{-6}		
Day 415	Canopy	1	2.743×10^{-3}	8.172	0.0647
5.2.93	Quadrat(Canopy)	3	3.360×10^{-4}	2.770	0.0594
	Residual	29	1.210×10^{-4}		

The survival of *Fucus serratus* juveniles in the *Ascophyllum* zone differed markedly between the two treatments of the winter experiment (Figure 2.24). Eighteen months after initiation of the experiment all of the 60 *Fucus serratus* juveniles in plots cleared of canopy had died. In plots where the canopy was left intact, over half of the juveniles were still alive. Table 2.17 shows significant regressions for both treatments. Analysis of Covariance on untransformed data revealed a significant difference in the slope of the regressions indicating a significant difference in the mortality rates (Table 2.18). Examination of the plots beneath the canopy three years after the beginning of the experiment revealed that 25% of juveniles were still alive, the largest of these being 18 cm in length. However, grazing damage caused by *Littorina obtusata* was extensive. This grazing pressure, combined with their slow growth rate probably explains why few *Fucus serratus* juveniles grow to form canopy sized plants beneath a fully intact *Ascophyllum* canopy.

Removal of the canopy in summer resulted in very high mortality, 63% of juveniles dying within 34 days of clearance. Mortality then occurred at a similar level to the winter clearance (Figure 2.25a). Examination of the five replicates of the summer experiment shows that all but one exhibited this very high initial mortality (Figure 2.25b).

Table 2.17 Regression of juvenile *Fucus serratus* survival against time

a) *Ascophyllum* canopy removed

Regression equation $Y = 90.1 - 0.192\,X$ $r^2 = 81.8\%$

(Y=% Survival X=Time)

Source	df	Mean Square	F-Value	P-Value
Regression	1	22403	100.13	<.001
Error	21	224		
Total	22			

b) *Ascophyllum* canopy intact

Regression equation $Y = 100 - 0.0931X$ $r^2 = 64.8\%$

(Y=% Survival X=Time)

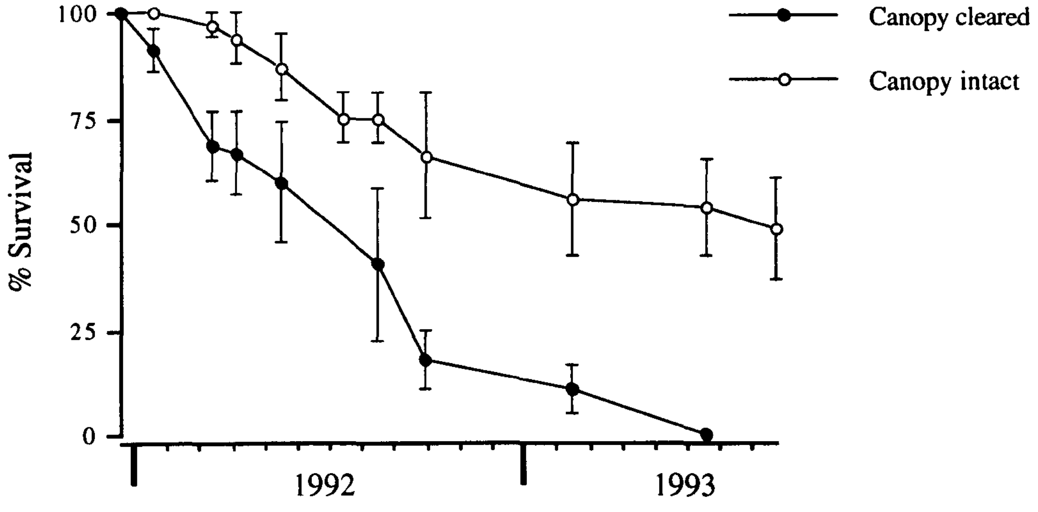
Source	df	Mean Square	F-Value	P-Value
Regression	1	10617	58.03	<.001
Error	30	183		
Total	31			

Table 2.18 Analysis of Covariance testing for a significant difference in the mortality rates of *Fucus serratus* juveniles in the *Ascophyllum* zone, in plots cleared of canopy and in plots where the canopy is intact

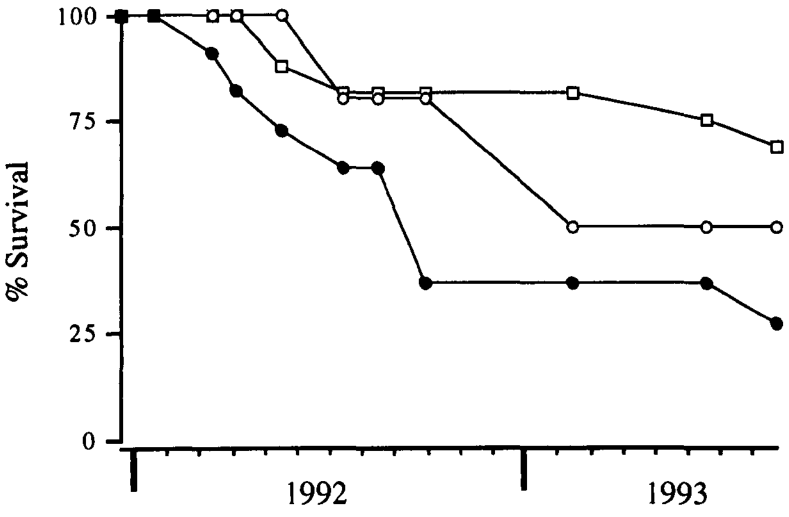
Source	df	Mean Square	F-Value	P-Value
Treatment	1	601	3.01	0.089
Time	1	33016	165.29	<0.001
Treatment x Time	1	3971	19.88	<0.001
Error	51	200		

N.B. The P-Value of <0.001 for the interaction between treatment and time indicates a significant difference in the slopes of the two regressions.

a) Mean of three replicates for each treatment. Error bars = ± 1 SE



b) Plots in which canopy is intact. Replicates shown separately.



c) Plots cleared of canopy. Replicates shown separately.

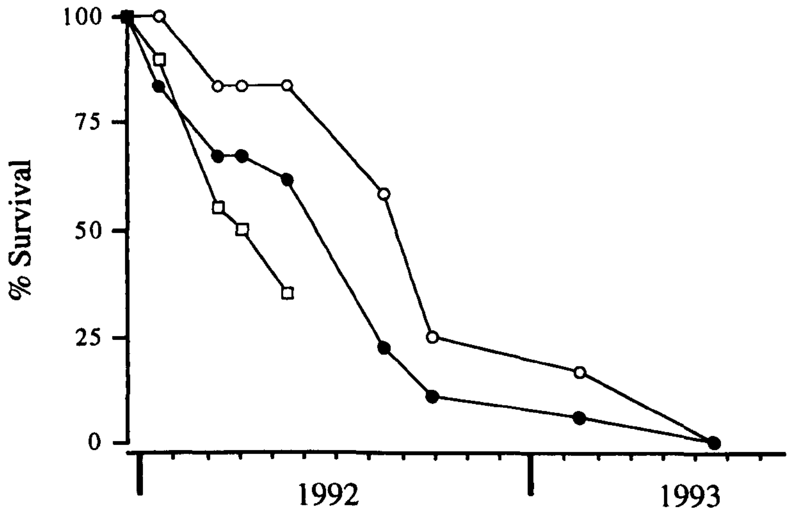
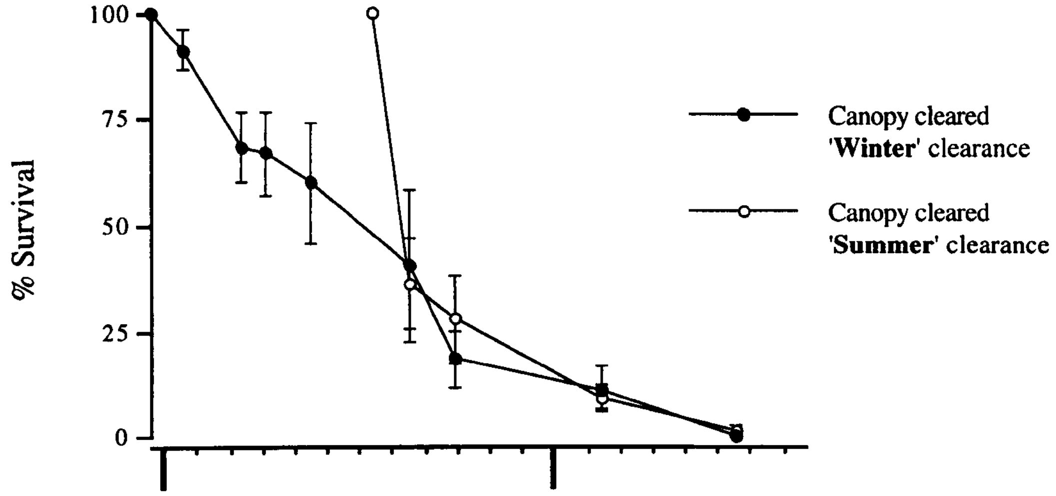


Figure 2.24 Percentage survival of *Fucus serratus* juveniles in the *Ascophyllum* zone beneath the canopy and in plots cleared of canopy (winter experiment).

a) Comparison between winter and summer clearances.



b) Individual replicates of the summer clearance

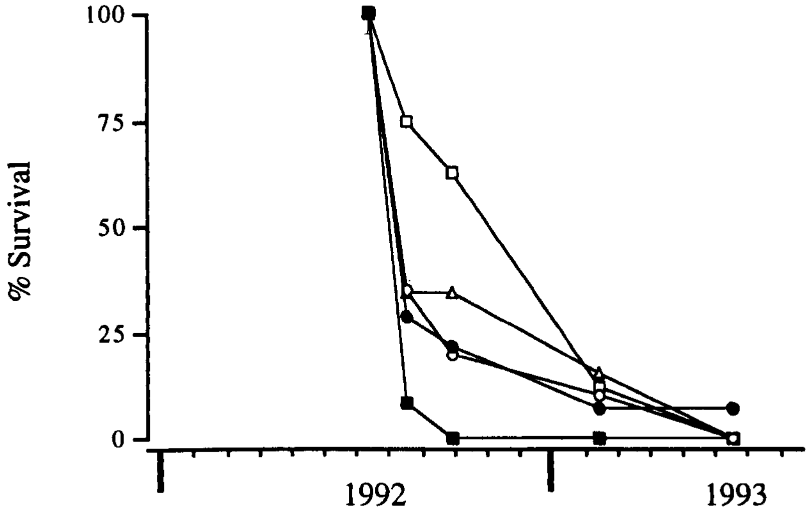


Figure 2.25 Percentage survival of *Fucus serratus* juveniles in the *Ascophyllum* zone in plots cleared of canopy. Error bars = ± 1 SE.
a) Comparison between winter and summer clearances.
b) Individual replicates of the summer clearance

2.3.4 Silt collection

The accumulation rates of sediment in artificial turf were approximately five times higher in the winter compared to the summer (Figure 2.26). However, in both seasons the presence or absence of the canopy had no effect. These observations are confirmed by two way ANOVA, with a significant effect of season, but no significant effect of canopy (Table 2.19).

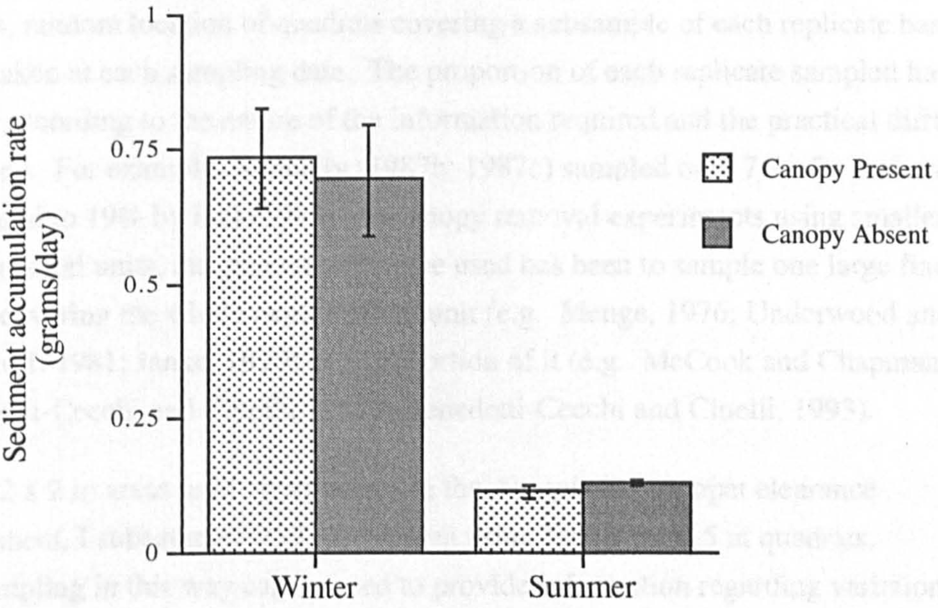


Figure 2.26 Comparison of sediment accumulation rates in artificial turf in the *Ascophyllum* zone in plots cleared of canopy and plots in which the canopy was present. Collection was made during a 29 day period in the winter of 1991/1992 and in a 49 day period in the summer of 1992. Error bars = ± 1 SE

Table 2.19 Two way ANOVA testing for the effect of season and *Ascophyllum* canopy removal on the accumulation rate of sediment in artificial turf in the *Ascophyllum* zone

Source	df	Mean Square	F-Value	P-Value
Season	1	1.054	73.33	0.0001
Canopy	1	0.0003	0.023	0.8824
Season x Canopy	1	0.0023	0.16	0.6994
Residual	8	0.0144		

2.4 DISCUSSION

2.4.1 Methodology

In studies dominated by large macroalgae, in which canopy removal experiments have taken place, experimental units or replicates are often large. Sampling of such large experimental units raises problems since it is generally impractical to accurately sample the whole area given the major constraint in intertidal studies of time. Many studies using experimental units larger than 0.5 m x 0.5 m have used subsampling as a technique to provide accurate information in the least possible time (e.g. Kennelly, 1987b; Kennelly, 1987c; Benedetti-Cecchi and Cinelli, 1992b; Hill, 1993). In such studies, random location of quadrats covering a subsample of each replicate has been undertaken at each sampling date. The proportion of each replicate sampled has varied according to the nature of the information required and the practical difficulties involved. For example, Kennelly (1987b; 1987c) sampled only 7% of a 4m^2 area compared to 19% by Hill (1993). In canopy removal experiments using smaller experimental units, the general technique used has been to sample one large fixed area either covering the whole experimental unit (e.g. Menge, 1976; Underwood and Jernakoff, 1981; Janke, 1990) or a proportion of it (e.g. McCook and Chapman, 1991; Benedetti-Cecchi and Cinelli, 1992b; Benedetti-Cecchi and Cinelli, 1993).

In the 2 x 2 m areas used as replicates in the *Ascophyllum*/limpet clearance experiment, I subsampled 25% of the area using four 0.5 x 0.5 m quadrats. Subsampling in this way can be used to provide information regarding variation within replicates, using techniques such as nested ANOVA. However, Hurlbert (1984), in considering the treatment of multiple samples from within an experimental unit, recommends that subsamples are used to generate a single datum (in this case the mean) for each replicate and that 'fancier' approaches such as nested ANOVA be ignored. This advice was followed.

Although the sampling technique employed yielded valuable information, certain improvements could be made to the way in which data was collected without spending prohibitively long periods in the field. Manipulation of limpets affected only a small proportion (<20%) of each replicate, namely the patches of bare substrate. As a consequence of this the two components of the understorey, algal turf and bare substrate reacted differently to any particular treatment. For example, removal of limpets beneath an intact canopy resulted in radical changes (albeit slowly) to the bare substrate and no change at all to the turf. Since bare substrate occupied less than 20% of the area within this treatment, subsampling of the whole area did not detect this change. Removal of the canopy alone resulted in dramatic changes to the algal turf but little change overall to the bare substrate which continued to be grazed. Thus in hindsight some form of stratified sampling in which turf and bare substrate were sampled separately would possibly have yielded more accurate and useful results.

It could be argued however that the random allocation of quadrats yielded results which gave a true reflection of the system under scrutiny since on average the different substrata will be sampled in the proportions in which they actually occur. For example, to conclude that removal of limpets beneath a canopy resulted in little overall change is in fact true since the radical changes occurring on bare substrate only occurred over a very limited area. The limitation of random sampling in lacking the subtlety to recognise and distinguish the changes occurring in bare substrate against those occurring in the turf was appreciated early in the sampling program. As a result qualitative notes regarding the different successional sequences occurring on turf and bare substrate were taken. In addition specific measurements of patch size were recorded.

2.4.2 Patterns of succession

The sequence of succession following *Ascophyllum* canopy removal followed a pattern observed in many intertidal studies, the main features of which are an increase in ephemeral algae and of juveniles of the canopy species (Burrows, 1947; Lubchenco, 1986; Chapman, 1990; Hill, 1993). The ephemeral algae which colonise canopy removal plots are opportunistic species. They commonly form blooms in the spring and summer in the intertidal zone when the inhibiting effects of canopy shading and grazing are absent. Such algae are often the first macroalgal colonisers of disturbed areas (Hatton, 1938; Rees, 1940) and although generally thought of as competitively inferior, can delay the appearance of later successional species such as *Fucus vesiculosus* (Hawkins, 1981b; Lubchenco, 1983). The bloom of green ephemerals in the spring following removal of the *Ascophyllum* canopy caused a depression of the growth rate in developing *Fucus serratus* juveniles, but failed to prevent either *Fucus vesiculosus* or *Fucus serratus* forming a canopy and outcompeting them. Hruby and Norton (1979) showed that a turf of *Enteromorpha intestinalis* reduced the settlement of *Ulothrix* spores but aided survival of those that settled by providing protection from desiccation. Although field observations showed that *Fucus* juveniles remained healthy and free from high grazing pressure beneath a blanket of green ephemerals during the summer months, no manipulations were made to examine if this temporary canopy improved *Fucus* juvenile survival

The effect of the *Fucus* canopy on ephemeral algal recruitment is clear, the spring/ summer bloom of 1993 being reduced because of shading by the new canopy.

However, it is not clear what effect the *Fucus* canopy has on recruitment and growth of *Ascophyllum* juveniles. Keser and Larson (1984a) showed that *Ascophyllum* juveniles can grow up through a *Fucus* canopy to eventually replace it. However it was not shown whether the *Fucus* canopy was necessary for successful colonisation by *Ascophyllum* as suggested by Burrows (1947) or whether colonisation would have occurred irrespective of its presence. Thus either the facilitation or tolerance model of succession of Connell and Slatyer (1977) may be applicable in this case. My work showed that *Ascophyllum* juvenile density continued to rise long after a canopy of *Fucus* had formed, emphasising that the *Fucus* canopy appears not to inhibit *Ascophyllum* colonisation. However, without experimental manipulation one cannot determine the exact effect of the *Fucus* canopy.

2.4.3 Understorey community stability: the balance between limpets and turf

Results from the manipulation of canopy and limpets suggests that limpets play a limited role in structuring the community of the *Ascophyllum* zone. This is in sharp contrast to the situation on more exposed British shores where the ability of limpets to limit algal recruitment means they are the dominant structuring organism (Southward, 1956; Hawkins, 1981a). Although limpet grazing can regulate algal recruitment (e.g. Southward, 1956; Southward, 1964; Hawkins and Hartnoll, 1983b) there are numerous examples of limpets being excluded from habitats by the growth of algae. This may occur by pre-emption of space (Dye, 1993), by the inhibition of limpet recruitment (Lewis and Bowman, 1975) or by the physical swamping of limpets by fast growing algae (Underwood and Jernakoff, 1981; Hill, 1993). Lewis and Bowman (1975) suggested that a dense fucoid canopy could physically prevent or reduce recruitment of limpets onto the shore. Attempts were made in this study to test this hypothesis (see Chapter 4) but failed owing to the relatively low supply of limpet larvae on the Isle of Man. The physical swamping of limpets by algae occurs low on the shore when a point is reached where the ability of algae to grow, exceeds the ability of limpets to graze it back. This can result in limpet exclusion since limpets require 'bare' substratum on which to move and feed. This phenomena is generally limited to the low shore since algae grow more quickly at low levels (e.g. Hatton, 1938). Pre-emption of space by turf forming algae has been shown to limit limpet densities on the low shore in southern Africa (Dye, 1993). Turf forming species of algae tend to be limited to the low shore or the subtidal zone world-wide (Stephenson and Stephenson, 1972; Kain and Norton, 1992). However, many species of algae extend further up shore when protected from desiccation by overlying large algae (Menge, 1975; Hawkins and Hartnoll, 1985). Results of the *Ascophyllum*/limpet manipulation experiment suggested that *Ascophyllum* indirectly inhibits the grazing range of limpets by facilitating the growth and spatial dominance of the red algal turf. By so doing the *Ascophyllum* canopy supports a very stable understorey community.

In the presence of the canopy, bare substrate patch size and shape remained relatively constant. Vegetative encroachment is an important means of securing space for some turf-forming species (Sousa, 1979a; Sousa *et al.*, 1981). However, a balance seemed to operate in which limpet grazing prevented vegetative expansion of red algae, but equally the red algal turf prevented limpets from expanding their grazing range. Limpets were thus limited to small gaps of highly grazed substratum. Previous work has shown that limpet invasion of established beds of space-occupying algae such as turfs is unlikely (Underwood and Jernakoff, 1981; Dye, 1993). Consequently, the role of limpets in structuring the community of the mid shore in sheltered areas is limited. Removal of the *Ascophyllum* canopy resulted in damage to and loss of silt from the red algal turf allowing limpets to rapidly expand their grazing range. This expansion stopped approximately one year after canopy removal because of regrowth of a new canopy of *Fucus serratus* and *Fucus vesiculosus.* This canopy acted in a similar way to the original *Ascophyllum* plants. By allowing regrowth of the turf and entrapment of sediment a balance between turf and limpets was renewed and the system stabilised. In the absence of recolonisation by *Ascophyllum* the growth of the *Fucus* canopy was therefore important in maintaining the stability of the system.

The facilitation of growth of the red algal turf by the *Ascophyllum* canopy not only limits the range of limpet grazing, it may also seriously affect recruitment of limpets to the shore. Limpet larvae are thought to settle preferentially in pools lined with calcified red algae (Bowman, 1981; Morse, 1991). It is highly unlikely that larvae will settle and survive on the turf and so recruitment is limited to the patches of bare substrate effectively resulting in trickle recruitment (see Chapter 4). Thus, the turf probably contributes to the overall stability of the system by limiting the available space for limpet settlement and so preventing disturbance in the form of large recruitment events.

2.4.4 Recruitment of *Ascophyllum* juveniles

It is a common observation in experimental studies that canopy algae inhibit recruitment of juveniles of the same species (Lubchenco, 1986; Chapman, 1989; Chapman, 1990; Benedetti-Cecchi and Cinelli, 1992b; Hill, 1993). However, *Ascophyllum* juveniles are especially rare. Many authors have remarked upon the surprisingly low levels of *Ascophyllum* juveniles which recruit into mature stands (Oltmanns, 1889; David, 1943; Knight and Parke, 1950; Printz, 1956; Baardseth, 1970; Sundene, 1973), especially considering the large investment placed into production of gametes (Josselyn and Mathieson, 1978; Cousens, 1986) and the ability of *Ascophyllum* zygotes to germinate and grow under a wide range of temperature and light regimes (Sheader and Moss, 1975).

Removal of the *Ascophyllum* canopy in this study, resulted in high levels of *Ascophyllum* juvenile recruitment, supporting the hypothesis that the canopy inhibits recruitment. Similar results were obtained by Keser (1981) and Keser and Larson (1984) working in Maine, North America. Whether the canopy inhibits recruitment by shading, sweeping or other means is not known. Other studies carried out in Europe found only low levels of recruitment following canopy removal (e.g. Knight and Parke, 1950).

Herbivorous molluscs play a significant role in the mortality of juvenile fucoids (Sundene, 1973; Vadas *et al.*, 1977; Lubchenco, 1980; Keser *et al.*, 1981; Lubchenco, 1986) and grazing by *Littorina littorea* has been shown to limit recruitment of *Ascophyllum* (Sundene, 1973; Keser *et al.*, 1981; Vadas *et al.*, 1982). However on Manx shores, *Littorina littorea* is only locally abundant (Norton *et al.*, 1990) and was absent from the mid shore at the study site. The role of the dominant grazer on British shores, *Patella vulgata*, in regulating *Ascophyllum* recruitment was obviously limited by its restriction to a small area of the *Ascophyllum* zone by the spatial dominance of the red algal turf. Removal of limpets resulted in high levels of *Ascophyllum* recruitment to the rock and lithothamnia patches, even in the presence of the canopy, thus showing that given a suitable substratum such as ungrazed rock or lithothamnia *Ascophyllum* juveniles can recruit successfully beneath adult plants.

Algal turfs have been shown to inhibit the recruitment of canopy algae, both in the intertidal and subtidal zones (Sousa *et al.*, 1981; Deysher and Norton, 1982; Kennelly, 1987a; Benedetti-Cecchi and Cinelli, 1992b). The means by which inhibition occurs is unclear, since initial settlement of zygotes in turfs may be higher than on surrounding bare rock (Benedetti-Cecchi and Cinelli, 1992b) owing to the ability of the turf to provide a refuge from water movement (Brawley and Johnson, 1991) or herbivory (Underwood and Jernakoff, 1981; Jernakoff, 1985). However, post settlement mortality may be high because of competition for light or possibly nutrients (Reed and Foster, 1984; Kennelly, 1987a). Thus the red algal turf may be supplementing the shading effect of the canopy. Alternatively, *Ascophyllum* zygotes may simply need a firm stable substratum on which to develop. Stewart (1982) observed that entrapped sediment within a turf can deprive spatial competitors of a firm substrate for attachment. This suggests an alternative hypothesis as to the mechanism by which canopy removal causes enhanced recruitment. Canopy removal resulted in turf degeneration and silt loss which led to the generation of a fine mosaic of algae, silt and bare rock. This may promote recruitment by allowing direct settlement of zygotes onto a suitable stable substratum. Detailed observations of the distribution of *Ascophyllum* juveniles in August 1994 did not support this hypothesis, but since turf regeneration and silt accumulation had occurred since zygote settlement, the hypothesis cannot be wholly discounted.

It appears that three factors, canopy, turf and limpet grazing are responsible for the low number of *Ascophyllum* juveniles on Manx shores. The presence of the canopy alone or the presence of turf alone is not sufficient to prevent recruitment. However, together the *Ascophyllum* canopy and red algal turf cause *Ascophyllum* recruitment to be severely inhibited. In addition, localised high densities of limpets restrict recruitment to rock and lithothamnia by grazing early stages. Since the red algal turf is dependent upon the canopy for its existence, it may be concluded that ultimately the canopy whether directly through shading or sweeping, or indirectly through promoting the algal turf, restricts recruitment of *Ascophyllum* juveniles. It should be noted that although the density of *Ascophyllum* juveniles in mature stands is low, densities increase higher in the zone closer to the boundary with *Fucus spiralis* (personal observations, Burrows, 1947; David, 1943) and in the *Fucus spiralis* zone itself (David, 1943; Burrows, 1947). In the high *Ascophyllum* zone, canopy plants are smaller, presumably allowing a higher penetration of light. In addition, percentage cover of bare rock is much greater, with a lower density of limpets. These observations thus support the conclusion that a combination of localised high densities of limpets and an unsuitable substratum of red algal turf in the understorey, together with the inhibitory effect of the *Ascophyllum* canopy limit recruitment.

Although juvenile recruitment was enhanced following canopy removal, three years after initiation of the experiment *Ascophyllum* juveniles were no more than 15 cm tall and none were observed to have produced a single vesicle. Thus, lack of canopy restoration is a function of slow growth rate rather than an inability to recruit. It is not clear from the literature whether this conclusion can be applied to other studies where a failure of *Ascophyllum* to recolonise a cleared area has occurred. Knight and Park (1950) found *Ascophyllum* germlings appeared in small numbers following removal of a mixed canopy of *Ascophyllum*, *Fucus serratus* and *Fucus vesiculosus* on the Isle of Man but disappeared shortly afterwards. It is clear that on shores which are exposed to even moderate wave action, *Ascophyllum* recruitment is very low. *Ascophyllum* zygotes appear to lack the ability to adhere quickly and firmly and it is suggested they are maladapted to water movement (Vadas *et al.*, 1990). On moderately exposed shores, germlings only survive beneath dense canopies (Vadas, Miller and Wright unpubl. cited in Vadas and Elner, 1992), the theory being that wave energy is modified by adult fucoid stands, in a similar way to the process occurring in kelp beds

(Jackson and Winant, 1983; Tegner, 1986). Where recruitment does occur, *Ascophyllum* has the ability to grow up through a *Fucus* canopy which it will eventually replace (Keser and Larson, 1984). The successful recolonisation of *Ascophyllum* observed by Keser and Larson (1984) was a result of high recruitment followed by a relatively high growth rate. Only sixteen months after canopy removal in the low intertidal, newly settled *Ascophyllum* plants had already reached a size of 15 cm. Unfortunately because of the slow growth rate exhibited by *Ascophyllum* in this study, it is impossible to predict whether *Ascophyllum* will succeed in recolonisation. However, given the continued rise of *Ascophyllum* juvenile density and the proven ability of juveniles to grow up through a *Fucus* canopy, recolonisation seems likely.

2.4.5 The balance of fucoids in the mid shore

Ascophyllum, Fucus serratus and *Fucus vesiculosus* compete for space in the mid shore of sheltered areas of Britain (David, 1943), great variability occurring in the proportions and zoning of the three species (Lewis, 1964). However in very sheltered localities the mid shore is dominated by a dense stand of *Ascophyllum*. Lewis (1964) considered that on such shores the only other canopy alga of note in the mid shore is *Fucus vesiculosus*. This contrasts with my observations on Manx shores where *Fucus serratus* is relatively common in the low and mid parts of the *Ascophyllum* zone and *Fucus vesiculosus* is restricted to the extreme upper limits.

The patterns of recruitment of both *Fucus serratus* and *Fucus vesiculosus* following *Ascophyllum* canopy removal give an insight into the causes of the distribution patterns of *Fucus* species on sheltered shores. In both winter and summer experiments *Fucus serratus* juveniles already present beneath the canopy died following canopy removal, possibly because of desiccation or competition with invading *Fucus vesiculosus*. *Fucus serratus* is fertile between November and May and *Fucus vesiculosus* between March and August on Manx shores (Creed, 1993). On the basis of these patterns of fertility and given the failure of *Fucus serratus* juveniles originally present beneath *Ascophyllum* to grow to form a canopy, one would expect *Fucus serratus* to dominate the winter experiment and *Fucus vesiculosus* the summer experiment. However *Fucus serratus* and *Fucus vesiculosus* formed a mixed canopy in the winter experiment. Knight and Parke (1950) showed at three sites in the British Isles that in their respective zones the growth rate of *Fucus serratus* was greater than that of *Fucus vesiculosus*. On Manx shores the average growth rate was 50% greater in *Fucus serratus*. In the mid shore where the two species occur together this difference in growth rate appears reversed. These results indicate that although capable of colonising the mid intertidal (see Hawkins and Hartnoll, 1985) the physiological stress associated with this zone seriously affects the competitive ability of *Fucus serratus*.

Given the apparent competitive superiority of *Fucus vesiculosus* over *Fucus serratus* at this tidal height, why does *Fucus serratus* and not *Fucus vesiculosus* occur naturally in the *Ascophyllum* zone? The scale of a disturbance event can have radical effects on the species composition of succession (Sousa, 1979a; Sousa, 1985). The presence of juveniles of *Fucus serratus* and not of *Fucus vesiculosus* beneath the natural canopy may indicate a difference in shade tolerance between the two species. Results from monitoring of growth rates of *Fucus serratus* juveniles indicate that they will not grow to form canopy plants whilst under a full canopy of *Ascophyllum*. However, the loss of one *Ascophyllum* plant, a level of disturbance appropriate to the sheltered shore under study, may allow the formation of a small patch of *Fucus serratus* canopy. The scale of disturbance required for the recruitment of *Fucus vesiculosus* is of a different magnitude, and one which may be found on slightly more exposed shores.

2.4.6 Conclusions

In conclusion, the various aspects of this study into community structuring forces in the *Ascophyllum* zone all point to the importance of the *Ascophyllum* canopy itself, either through direct effects or indirectly through the creation of conditions suitable for the growth of a red algal turf. This turf limits the density and grazing range of limpets and therefore reduces their structuring influence on very sheltered shores. The limited influence of limpets combined with low levels of disturbance through wave action and the long lived nature of *Ascophyllum* results in a very stable system.

CHAPTER 3

The respective roles of the *Fucus serratus* canopy and *Patella vulgata* in structuring the low shore community of sheltered shores.

3.1 INTRODUCTION

In the British Isles, *Fucus serratus* forms a distinct zone from sheltered through to semi exposed shores (Ballantine, 1961a). With increasing exposure canopy cover declines and is replaced by H*imanthalia elongata* and turfs of red algae (Ballantine, 1961a; Lewis, 1964). On the Isle of Man where the relatively sheltered nature of the Irish Sea means that exposed and very exposed shores as defined by Ballantine (1961a) are absent, communities dominated by a canopy of *Fucus serratus* may be found at low levels at most rocky intertidal sites.

A number of studies on the Isle of Man have investigated the structuring role of the *Fucus serratus* canopy on moderately exposed shores by performing canopy removal experiments (Hawkins, 1979; Hawkins and Harkin, 1985; Hill, 1993). A rapid increase in *Fucus serratus* juveniles and ephemeral algae was reported, followed by development of a new *Fucus serratus* canopy. In addition, the 'bloom' of understorey algae was accompanied by a decline in limpet density. Hill (1993) attributed this decline to emigration and mortality caused by swamping of the limpets and the substrate on which they feed by fast growing algae. Ballantine (1961b) recognised the possibility of limpet exclusion from the low shore, commenting on the precarious nature of *Patella* populations under the canopy and in clearings among algae.

Although the effect of *Fucus serratus* canopy removal has been investigated and some indication of the interaction between the canopy and limpets been established, the relative structuring role of both factors has not been examined. It is generally accepted that because of the increase in algal growth rates low on the shore, the structuring influence of algae is high and limpets, which can be excluded by competition for space, have little effect (Hawkins and Harkin, 1985). However, densities of limpets beneath a *Fucus serratus* canopy on sheltered shores were found to be sufficiently high to warrant investigation of their effect on the community, especially the effect on recruitment of the canopy alga. As in the *Ascophyllum* zone, it was hoped to determine how the canopy alga maintained its dominance both spatially and temporally. Given the relatively high densities of limpets found low on sheltered shores, do escapes of *Fucus serratus* occur simply as a consequence of high growth rates or is another factor involved? By using a factorial experiment similar in design to that used in the A*scophyllum* zone, it was hoped to compare community structuring forces between the two zones.

An additional aim of this experiment was to examine the effect of patch size on community succession. The removal of canopy algae creates a gap or patch in the community, freeing space for colonisation. Patch size has been shown to have a significant effect on the abundance and species composition of early colonists in a variety of intertidal communities (Sousa, 1979a; Paine and Levin, 1981; Keough, 1984; Sousa, 1984; Sousa, 1985; Farrell, 1989; Benedetti-Cecchi and Cinelli, 1993). Interactions occurring at the boundary between a disturbed and non disturbed area (the patch edge) appear to strongly influence patterns of colonisation. Small patches have a greater ratio of edge to area than large patches. Thus, any physical or biological factor associated with the patch edge will be proportionately more important in small patches. Such an argument has been applied to colonisation from both the water column and from the surrounding community.

Physical factors such as temperature and humidity (at low tide) and wave shock and water flow (at high tide) may be affected by the patch boundary. When submersed, patch edges have been shown to disrupt laminar flow of sea water. This can result in turbulent eddies (Foster, 1975) which may cause enhanced settlement of propagules and larvae along patch edges (Foster, 1975; Munteanu and Maly, 1981). This could result in a higher rate of colonisation of small patches. At low tide, the change in physical environment at patch boundaries can affect the abundance of consumer species which in turn will affect algal recruitment. Small patches in beds of mussels support higher densities of grazers than large patches (Suchanek, 1978; Suchanek, 1979; Sousa, 1984) owing to the protection from wave shock, desiccation and predation afforded by the patch perimeter. This difference in grazer density resulted in markedly different algal assemblages between large and small patches (Sousa, 1984). Small patches were colonised by grazer resistant, but seemingly competitively inferior algae in contrast to grazer vulnerable but competitively superior species in large patches. Farrell (1989) found limpet densities (*Lottia* spp.) to be higher at the edge of gaps created within a barnacle/fucoid community. Limpets moved to patch edges soon after patch creation and only moved into the patch interiors to forage at night or when submerged. This behaviour was attributed to avoidance of avian predators since limpets have been shown to be less conspicuous under algae or next to barnacles (Mercurio *et al.*, 1985). Despite higher grazer density at the patch edges, rate of algal recruitment was not higher in plot interiors, possibly because of the limited dispersal of colonising algae. Also heat stress and desiccation in plot interiors may have resulted in higher algal mortality there.

The type of organism in the undisturbed area surrounding a patch will affect how patch size influences patterns of recolonisation. Many communities in which patch recolonisation has been studied consist of species which invade by lateral movement of individuals such as mussels (Paine and Levin, 1981; Sousa, 1984) or by vegetative growth such as algal turfs (Sousa, 1979b; Sousa *et al.*, 1981). In such communities, small patches will be recolonised at a higher rate (Paine and Levin, 1981; Sousa, 1984). In some communities, competition with surrounding organisms affects patch recolonisation, for example where clearings are formed in stands of canopy macroalgae. Because of the large size of adult plants the effect of the undisturbed community on the patch will be high in all but the largest of cleared areas. In small patches, the effect of the surrounding community is exerted not only at the patch edge but on the whole area (Benedetti-Cecchi and Cinelli, 1993).

The structure of a canopy covered area is such that each individual plant occupies very little primary substratum (the area covered by an individuals holdfast), but the canopy of the plant covers a wide area. In such a situation removal of one plant may create a gap or patch in the canopy which is unrecognisable at low tide to the researcher. In this kind of patch, neighbouring plants exert a large effect by sweeping the substratum and protecting the area from high levels of desiccation and insolation during low tide. The spatial arrangement of neighbours will determine the extent to which these effects occur. In such a community it would be very difficult to create uniform conditions over a number of experimental replicates. Therefore, it was decided to create two patch sizes in which the substratum or understorey was fully exposed at low water. Neighbouring plants were removed or trimmed such that their fronds did not impinge on the experimental area at any time. In this way the aim of the experiment, to determine the effect of patch size, was not confounded by variable effects of shading and sweeping by neighbouring plants.

Thus the specific aims of this chapter were:
1) To compare the relative structuring roles of the *Fucus serratus* canopy and the limpet *Patella vulgata* on the community of the *Fucus serratus* zone.
2) To determine how the near 100% cover of canopy alga is maintained by examination of recruitment patterns and growth rates of juveniles.
3) To determine the effects of patch size on community structure.

3.2 METHODS

3.2.1 *Fucus serratus* canopy and limpet clearance experiment

3.2.1.1 Experimental design

In order to assess the relative importance of the *Fucus serratus* canopy and the dominant grazer *Patella vulgata* in structuring the low shore community, an orthogonally designed experiment was used such that every combination of the two factors (limpet presence/absence and *Fucus serratus* presence/absence) was examined. In addition, the effect of patch size on succession was examined by using two sizes of canopy clearance plots. Treatments are summarised in table 3.1.

Table 3.1 Summary of treatments for canopy/limpet manipulation experiment.

Treatment	Description	Replication
1	*Fucus serratus* canopy and limpets (*Patella vulgata*) removed. **Large** plot (1m^2)	3
2	*Fucus serratus* canopy removed. Limpets unmanipulated. **Large** plot (1m^2)	6
3	*Fucus serratus* canopy unmanipulated. Limpets removed. **Large** plot (1m^2)	3
Control	*Fucus serratus* canopy and limpets unmanipulated **Large** plot (1m^2)	3
5	*Fucus serratus* canopy and limpets (*Patella vulgata*) removed. **Small** plot (0.25m^2)	3
6	*Fucus serratus* canopy removed. Limpets unmanipulated. **Small** plot (0.25m^2)	6

Previous work low on the shore in the Isle of Man showed that canopy removal resulted in large blooms of ephemeral algae which then led to a decrease in the number of limpets in the immediate area (Hawkins, 1979; Hill, 1993). Therefore, an additional treatment was established, where the canopy was removed and limpets unmanipulated, in which it was proposed to weed out colonising ephemerals. However, large ephemeral blooms did not occur in these treatments and therefore no weeding took place. The unweeded replicates continued to be sampled and were simply used as additional replicates for treatments 2 and 6, hence the enhanced replication of these treatments shown above.

3.2.1.2 Establishment of the experiment

In December 1992 a site for experimental work was selected on the west side of Castletown Bay, approximately 500m north-east of Scarlett Point. This site is dominated in the mid shore by *Ascophyllum nodosum* and on the low shore between 1.4m and 3.0m above C.D. by *Fucus serratus*. The experiment was established in an area within the middle of the *Fucus serratus* zone between 2.0m and 2.6m above C.D. and covering a horizontal distance of 60 metres. Initial observations within the *Fucus serratus* zone revealed that *Patella* densities appeared to vary over a scale of tens of metres. Hill (1993) working on a moderately exposed shore nearby at Port St. Mary also noted this and attributed it to variations in substrate topography resulting from differences in species of encrusting algae. Since it was hoped to examine the influence of limpet grazing on the low shore community a stretch of shore was chosen which avoided areas where limpet density was noticeably low.

Eighteen plots measuring one square metre (large) and six plots measuring a quarter of a square metre (small) were chosen within the experimental area and marked using ring bolts and Twinglow tape (for method see Chapter 2). All plots were located on a smooth, gently sloping rock surface with a near 100% cover of *Fucus serratus*. The treatments described above were assigned at random to the marked plots. Before any manipulation took place, each plot was sampled (see below).

The manipulation of the canopy and of limpets was carried out in the same manner as in the *Ascophyllum* experiment. However, owing to the nature of the understorey community, which allowed much greater movement of limpets than in the *Ascophyllum* zone, fences were required to prevent the re-encroachment of limpets into plots from which they had been removed. Fences approximately 2-3 cm high were constructed from plastic coated chicken wire. These were screwed to the rock surface around the plot perimeter, so as to completely surround the 1m^2 or 0.25 m^2 plots. These fences were designed to exclude all but the smallest limpets, whilst causing a negligible impact on the community. The only noticeable impact they made on the understorey community, other than that caused by the exclusion of limpets, was to provide a substrate for *Porphyra* attachment. This algal growth was removed as soon as it appeared.

3.2.1.3 Sampling

Plots were sampled at approximately 8 week intervals. A 0.25 x 0.25 m quadrat subdivided into 25 equal squares was placed at four positions within each of the large plots, the positions being determined at each sampling date by the use of random number tables. In this way, in both the *Ascophyllum* experiment (Chapter 2) and in the large plots of the experiment described here, a random 25% of each plot was sampled. In the small plots a 0.5 x 0.5 m quadrat was used to sample the whole area. Percentage cover of canopy and understorey algae and of bare rock was estimated. The number of adult limpets (>15 mm) and juvenile limpets (<15 mm) was counted in the whole of each plot. In addition, at each sampling date photographs were taken to record important successional changes.

In each replicate of the large plots an area of 0.25 m^2 was marked using screws and Twinglow tape. At every sampling date observations were made on the levels of recruitment of new *Fucus serratus* plants. Notes were made recording the approximate number and position of juvenile plants and the substrate upon which they were growing. In this way a clear picture of recruitment processes and canopy formation was gained as well as patterns of community succession in fixed quadrats. A figure of 30 cm was selected as the size at which *Fucus serratus* individuals were recorded as forming 'canopy' plants. At this size individuals were considered to contribute significantly to shading and sweeping and thus to exert potential community structuring effects.

3.2.2. Growth rate of juveniles

Fucus serratus juveniles occur beneath the canopy in both the *Ascophyllum* and the *Fucus serratus* zones. Results from Chapter 2 showed that the low growth rate of *Fucus serratus* juveniles beneath an undisturbed *Ascophyllum* canopy, resulted in few if any juveniles attaining adult status. It was concluded that some form of disturbance was required for *Fucus serratus* to grow to form canopy plants in the *Ascophyllum* zone. It was decided to investigate whether the growth rate of juveniles beneath a *Fucus serratus* canopy was inhibited to the same extent as beneath an *Ascophyllum* canopy. It was hoped this information, combined with observations of recruitment and growth in all experimental treatments, would reveal how *Fucus serratus* recruited to and maintained its dominance on the low shore. Two sites were selected, one in the middle of the *Ascophyllum* zone, and one in the middle of the *Fucus serratus* zone.At each site, three positions were selected where the juveniles were common. Between 15 and 25 juveniles in the size range 20-50 mm were selected and individually tagged at each of the six positions. In this way the growth rate of individual plants could be monitored over time.

Tags were made from lengths of 'lacing cord' (RS Components) dipped in white enamel paint to make them more visible. Numbered micromarkers were glued onto small aluminium rings (2mm diameter) which were then passed over the two ends of a short length of lacing cord to produce a loop. The loop could then be placed over a juvenile plant and positioned just above the holdfast. The ring was then slid along the cord to shorten the loop to such an extent that the tag could slide up and down the lower portion of the plant but not slide off. The ring was crushed using a pair of pliers to hold it firmly in place.

All tagged plants were measured to the nearest millimetre and subsequently sampled approximately every 3-4 weeks. This method of tagging allowed quick and easy identification of individual plants However, unlike the mapping system used to monitor growth rates of juveniles in the previous chapter this method did not allow estimation of the mortality rate. The inability to re-locate a tagged plant could not be assumed to mean death of that plant since loss of the tag was equally as likely.

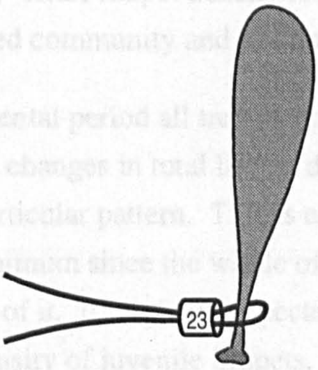


Figure 3.1 Arrangement of numbered tag on *Fucus serratus* juvenile

3.2.3 Statistical treatment of data

The main experiment in the *Fucus serratus* zone was an unbalanced design involving three factors, canopy, limpets and patch size. Although canopy and limpets were fully crossed factors, constraints of time meant that patch size was not. Thus, in analysis of this experiment a two way ANOVA was used to examine the effects of canopy and limpets. The effect of patch size was examined subsequently using two way ANOVA, patch size being crossed with limpets. As in Chapter 2, heterogeneity of variance was tested for using Cochrans test and where appropriate arcsine or square root transformations applied. Unless stated otherwise, data are untransformed.

3.3 RESULTS

3.3.1 Density and distribution of *Patella vulgata* in experimental plots

3.3.1.1 Limpet density

Initial densities of limpets in all experimental plots varied between 18 and 60/m^2. The mean values in those treatments in which limpets were unmanipulated ranged between 39 and 51/m^2. No significant difference was found between these treatments at the beginning of the experiment. Following removal of the *Fucus serratus* canopy density decreased sharply, with 33.8% and 47.6% drops in density in the large and small plots respectively (Figure 3.2a). However, limpet density in the control treatment also declined by 20.5%. Although limpet densities showed an initial sharp reduction after removal of the canopy, no further decline was observed, in fact total limpet density increased over the following six months. One way ANOVA revealed a significant effect of the canopy in determining limpet densities at only one sampling point, April 1994. Thus, limpet density remained at a level comparable to that in the natural undisturbed community and so continued to exert an effect on the community.

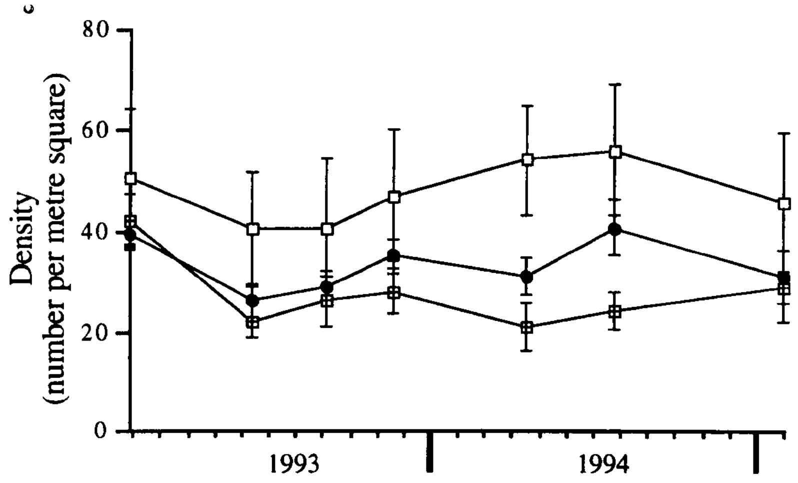
Over the experimental period all treatments (including the control) showed surprisingly large changes in total limpet density between sampling dates, without exhibiting any particular pattern. This is especially surprising given that sampling error was at a minimum since the whole of each plot was sampled for limpets rather than a proportion of it. It might be expected that these changes were a result of changes in the density of juvenile limpets. Numbers of juvenile *Patella vulgata* generally increase through the summer as recruits from the autumn move from crevices and cryptic habitats to exposed rock and reach a size at which they are recognisable (Jones, 1948; Ballantine, 1961b; Lewis and Bowman, 1975). However, no such pattern was apparent (Figure 3.2c).

It may be concluded that changes in density (especially of adults) may be ascribed to movement of individuals near plot boundaries. On some sampling dates they would be recorded inside the experimental plot and others not.

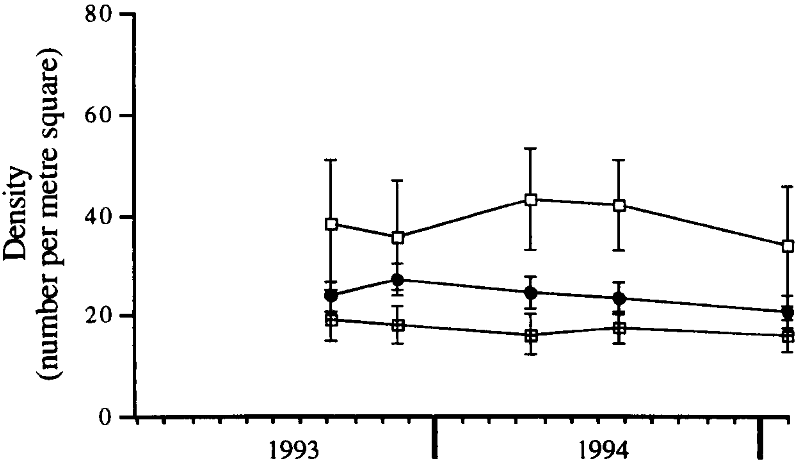
3.3.1.2 Limpet distribution

The distribution of adult and juvenile limpets between the two species of encrusting algae (*Phymatolithon purpureum and Phymatolithon lenormandii*) and bare rock is shown in Figure 3.3. A Kruskal Wallis test (used because of marked heteroscedasticity) indicated a significant difference between substrata for both adults ($H=20.41$ $p<0.001$) and juveniles ($H=6.38$ $p=0.042$). The density of juveniles and

a) Total limpet density



b) Adult limpet density



c) Juvenile limpet density

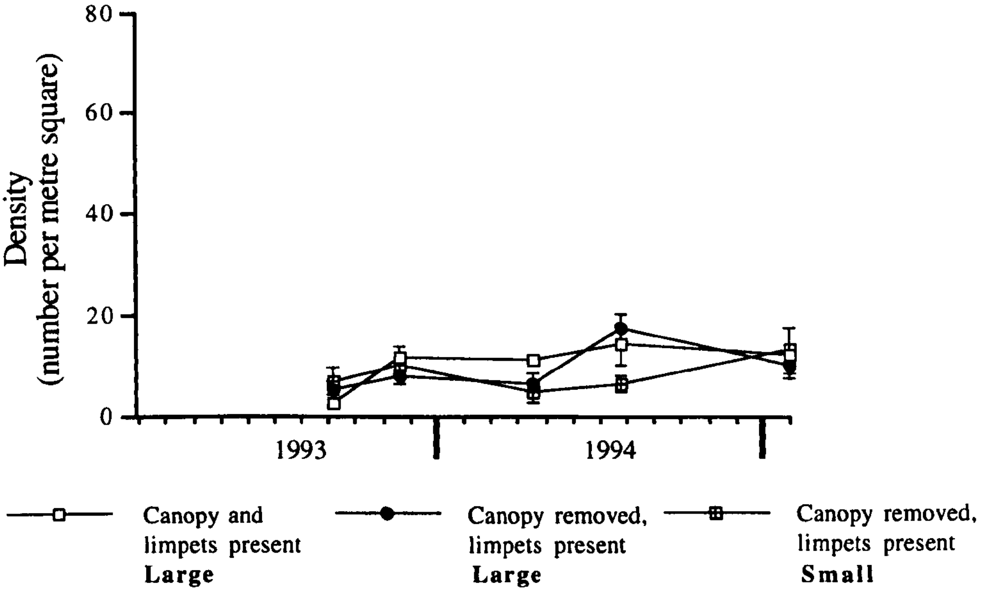


Figure 3.2 Density of *Patella vulgata* in the *Fucus serratus* zone in those treatments where limpets were unmanipulated. Error bars = ± 1 SE
a) Total limpet density b) Adult limpet density c) Juvenile limpet density

adults was highest on bare rock. In adults, this is probably simply a result of high grazing pressure around the home scar of a limpet, preventing any colonisation of the substrate by lithothamnia. The distribution of juveniles between *Phymatolithon purpureum* and *Phymatolithon lenormandii* was roughly equal, indicating no preference for either substrate. However, the density of adults on *P. purpureum* was very low. This pattern may be explained by examining the microtopography of the two crusts, *P. purpureum* having a very irregular growth form in comparison to *P. lenormandii*. It is likely adult limpets are discouraged from grazing over such a surface, much as they are over densely packed barnacles (e.g. Hawkins and Hartnoll, 1982a), whereas juveniles with small shells are not.

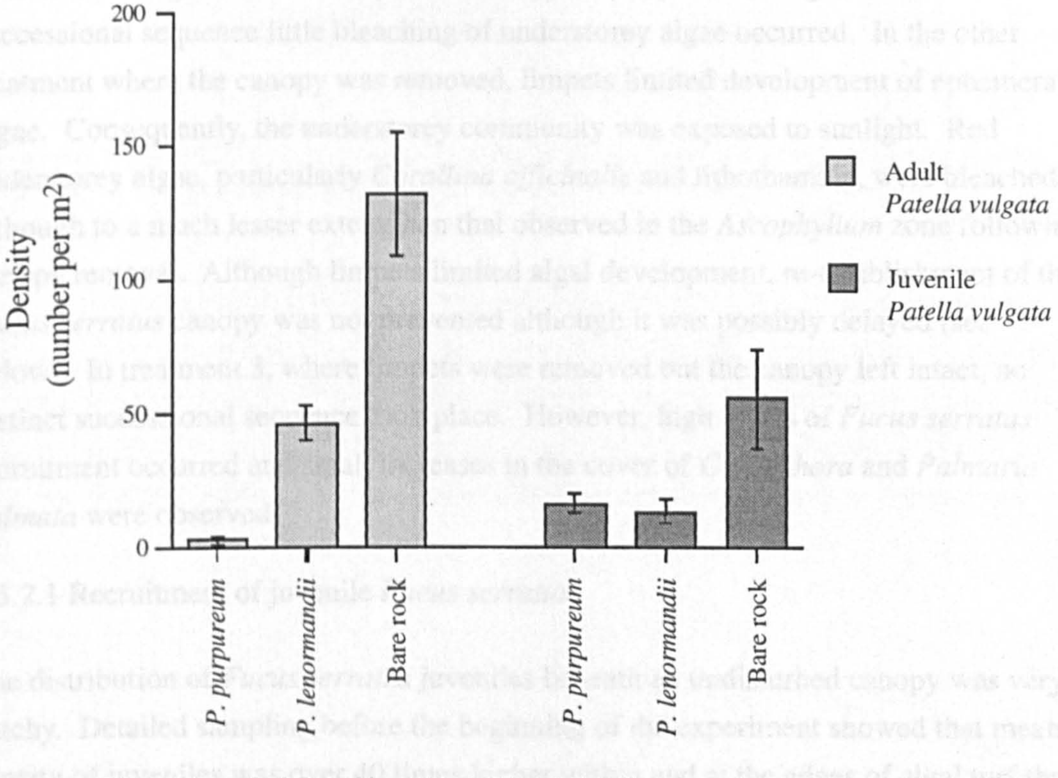


Figure 3.3 Distribution of adult and juvenile (<15mm) *Patella vulgata* between three substratum types in the *Fucus serratus* zone. Error bars = ± 1SE.

3.3.2 Changes in community structure in large experimental plots

Because of the unbalanced nature of the experimental design and the consequent inability to incorporate data from small plots in a 3 way statistical analysis, the following descriptions of community change refer only to large plots. Data from small plots are described in an analysis of the effect of patch size on community succession.

As in the previous chapter a brief overview of the successional sequence will be given before individual species and groups of species are considered in detail. The largest changes in community structure occurred in plots where both canopy and limpets were removed (treatment 1). In such plots there was an immediate colonisation of bare substrate by *Ectocarpus* species and ephemeral green algae and an associated accumulation of silt. Turfs of *Cladophora* and *Laurencia* species remained relatively free of this ephemeral growth. At the same time as ephemeral colonisation, new recruits of *Fucus serratus* were observed developing beneath this algal 'bloom'. Although *Ectocarpus* cover declined almost immediately, ephemeral green algae persisted throughout the summer but declined in the following winter. With this decline there was a large increase in cover of *Palmaria palmata* and a loss of silt from the experimental plots. *Palmaria palmata* persisted for approximately eight months before declining as the *Fucus serratus* canopy developed. Throughout this successional sequence little bleaching of understorey algae occurred. In the other treatment where the canopy was removed, limpets limited development of ephemeral algae. Consequently, the understorey community was exposed to sunlight. Red understorey algae, particularly *Corallina officinalis* and lithothamnia, were bleached although to a much lesser extent than that observed in the *Ascophyllum* zone following canopy removal. Although limpets limited algal development, re-establishment of the *Fucus serratus* canopy was not prevented although it was possibly delayed (see below). In treatment 3, where limpets were removed but the canopy left intact, no distinct successional sequence took place. However, high levels of *Fucus serratus* recruitment occurred and small increases in the cover of *Cladophora* and *Palmaria palmata* were observed.

3.3.2.1 Recruitment of juvenile *Fucus serratus*

The distribution of *Fucus serratus* juveniles beneath an undisturbed canopy was very patchy. Detailed sampling before the beginning of the experiment showed that mean density of juveniles was over 40 times higher within and at the edges of algal turf than on the remainder of the substrate which is made up of lithothamnia crust and bare rock (Figure 3.4). Observation of the control treatment over two years revealed low levels of recruitment in the natural community, with escapes occurring amongst the turf, at turf edges, on the shells of limpets, in crevices and to a certain extent on the surface of *P. purpureum*. It is interesting to note the relatively high recruitment at turf edges. This occurred at the indistinct boundary between silt-dominated turf and clean bare substrate. At this boundary a low concentration of silt and the occasional tuft of turf forming algae reduced the ability of limpets to graze whilst providing fucoid propagules access to a firm substratum.

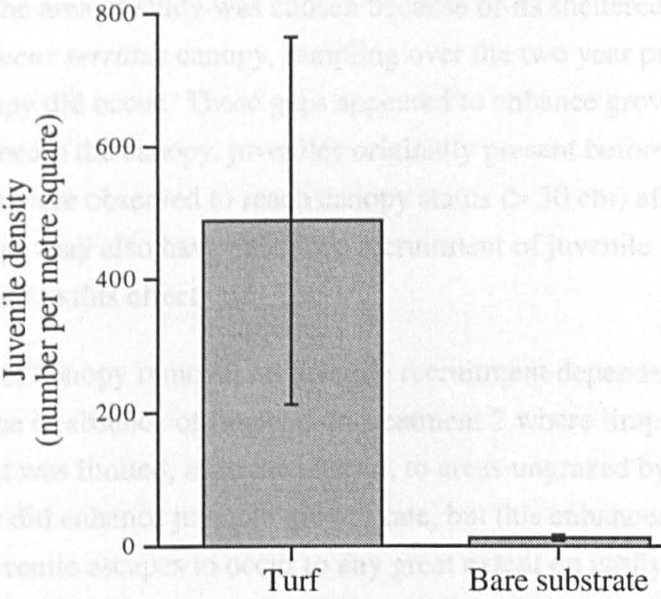


Figure 3.4 Distribution of *Fucus serratus* juveniles in all treatments at the beginning of the experiment (before any manipulation of canopy or limpets had taken place). Error bars = ± 1 SE

This pattern of juvenile distribution was radically altered by the removal of limpets beneath an intact canopy (treatment 3). Only 7 months after limpet removal, *Fucus serratus* juveniles began to appear in high numbers on the bare substrate (Figure 3.5). This recruitment did not occur uniformly across the experimental plots but in distinct patches. Recruitment to the turf remained at the same low levels as in the control.

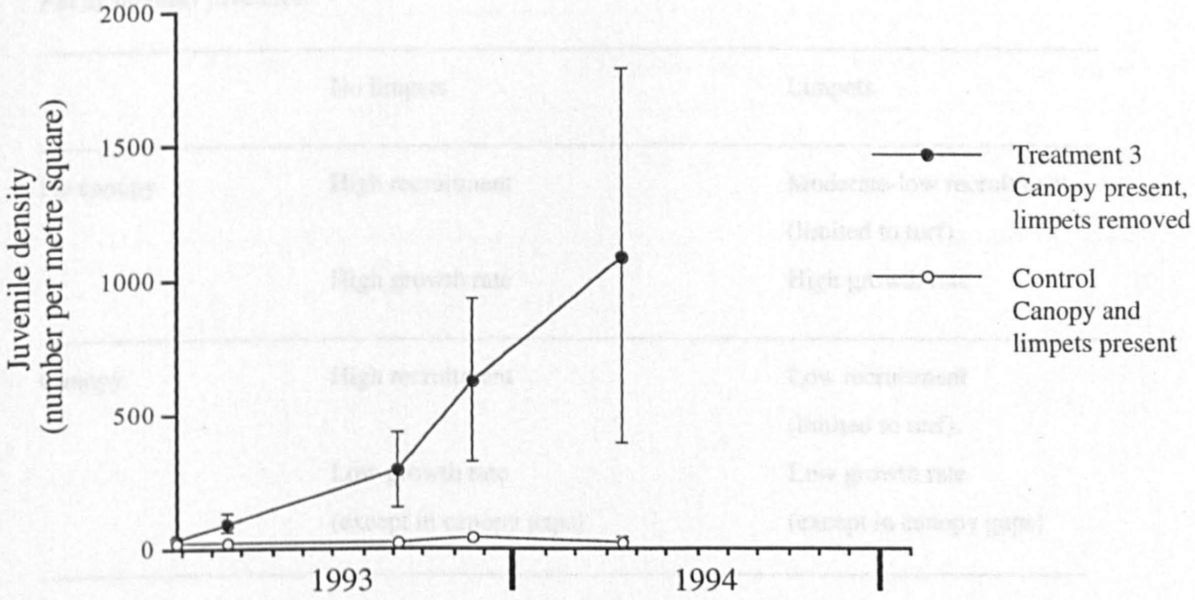


Figure 3.5 Density of juvenile *Fucus serratus* beneath an intact *Fucus serratus* canopy. Error bars = ± 1 SE

Although the area of study was chosen because of its sheltered nature and continuous cover of *Fucus serratus* canopy, sampling over the two year period revealed that gaps in the canopy did occur. These gaps appeared to enhance growth of juveniles. In one quadrat beneath the canopy, juveniles originally present before the start of the experiment were observed to reach canopy status (> 30 cm) after one and a half years. Canopy gaps may also have enhanced recruitment of juvenile plants but no evidence was gathered to this effect.

The effect of canopy removal on juvenile recruitment depended to a large extent on the presence or absence of limpets. In treatment 2 where limpets were unmanipulated recruitment was limited, as in the control, to areas ungrazed by limpets. Removal of the canopy did enhance juvenile growth rate, but this enhancement was not sufficient to allow juvenile escapes to occur to any great extent on easily grazed substrate. However, high growth rates did enable the relatively quick establishment of a new canopy. By April 1994, juveniles under observation which were originally present before the start of the experiment had reached sizes of up to 60cm.

In treatment 1 where canopy and limpets were removed, both high recruitment and high growth rate of juvenile *Fucus* occurred. High recruitment occurred on bare substrate although surprisingly no higher than in treatment 3 where the canopy was left intact. The effects of canopy and limpet manipulation on juvenile recruitment and growth are summarised in table 3.2.

Table 3.2 Summary of the effects of canopy and limpet manipulation on recruitment and growth of *Fucus serratus* juveniles.

	No limpets	Limpets
No canopy	High recruitment High growth rate	Moderate-low recruitment (limited to turf). High growth rate
Canopy	High recruitment Low growth rate (except in canopy gaps)	Low recruitment (limited to turf). Low growth rate (except in canopy gaps)

3.3.2.2 *Fucus serratus* canopy

In both treatments in which the canopy was left intact, a seasonal cycle of cover can be recognised (Figure 3.6b). As stated above, gaps occurred in the canopy due to loss of whole plants or plant fronds. This loss was greatest in the winter months resulting in a decrease in percentage cover in the winter.

In treatments 1 and 2 where the canopy was removed a new *Fucus serratus* canopy developed, although after two years a full canopy had not yet formed. The presence of limpets appeared to depress canopy recovery slightly although this was only apparent in the second year of the experiment (Figure 3.6a). In July 1994 canopy cover reached a peak of 76% in treatment 1 (limpets removed) compared to 46% in treatment 2 (limpets left in place). A one way ANOVA testing the effect of limpet grazing at this time resulted in a p value of 0.08 (Table 3.3). At the final sampling date in January 1995 canopy cover decreased, presumably as a result of winter storms. This reduction was more apparent in treatment 2 (where limpets were left in place). Data at this sampling date were heteroscedastic even after transformation and thus ANOVA could not be applied. A modified form of the t-test which assumes unequal variances was used as an alternative, and revealed a significant effect of limpet grazing (df = 3, t = 4.70, p = 0.018).

Table 3.3 One way ANOVA testing for the effect of limpets on *Fucus serratus* canopy recovery following canopy removal in the *Fucus serratus* zone.

	Source	df	Mean Square	F-Value	P-Value
18.7.94	Limpets	1	954.48	4.25	0.0782
	Residual	7	224.69		

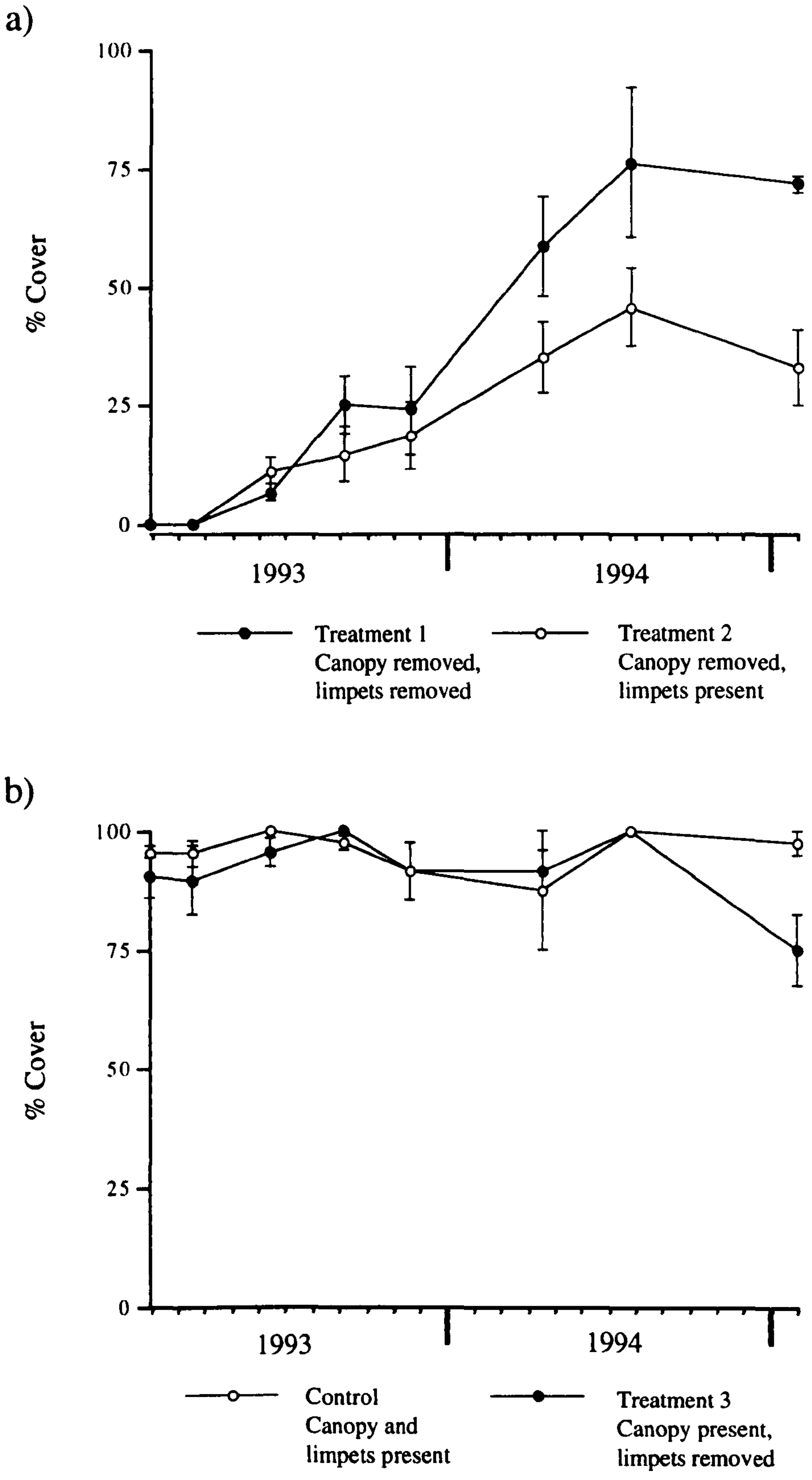


Figure 3.6 Development of *Fucus serratus* canopy in the *Fucus serratus* zone following experimental manipulation in January 1993. Large plots only. Error bars = ± 1SE.
a) Plots cleared of canopy b) Plots where the canopy is intact.

3.3.2.3 Ephemeral algae

Although a number of species of green ephemeral algae were identified (*Enteromorpha linza*, *Enteromorpha intestinalis*, *Ulva lactuca*, and *Monostroma* spp.), difficulty in making this identification quickly and accurately in the field and difficulty in assessing percentage cover of each individual species in mixed assemblages resulted in this group of algae being treated as a single functional unit. This approach can be justified on the grounds that all these species react in a similar manner to canopy and limpet removals.

Green ephemeral algae appeared at very low levels (< 1.5%) throughout the experiment in both treatments in which the canopy was unmanipulated (Figure 3.7b). The removal of limpets beneath an intact canopy (treatment 3) may have resulted in a very slight increase in these algae in the summer months.

Removal of the canopy resulted in elevated levels of ephemeral algae throughout the period of study, with a peak in June 1993 in both treatments 1 and 2 (Figure 3.7a). However, the presence or absence of limpets had a striking effect on the levels of these peaks, with treatment 1 in which limpets were removed having over 80% cover compared to only 25% in treatment 2. Thus in June 1993, 2 way ANOVA applied to arcsine transformed data revealed significant effects of both canopy and limpets in determining ephemeral cover. A significant interaction term between these two factors indicated that the effect of canopy removal on ephemeral cover was different depending on the presence or absence of limpets (Table 3.4).

Following the peak in cover in June 1993, cover of green ephemeral algae declined sharply to levels of 17% and 2.5% in November in treatments 1 and 2 respectively. However even at this time 2 way ANOVA revealed a significant effect of canopy and limpets. Over the following year levels of ephemerals declined gradually in treatment 1 (where both canopy and limpets were absent) with no apparent peak in the summer of 1994. Treatment 2 however showed a small peak in July 1994 before declining at the final sampling date.

Ectocarpus species were absent, or present at very low levels in all treatments except treatment 1 (Figure 3.7). In this treatment, where both canopy and limpets were removed, *Ectocarpus* showed a brief bloom in March 1993 the first sampling date after experimental manipulation. At this time random sampling revealed a mean percentage cover of over 30% although photographs taken at the same time indicate cover was much greater. Despite the high coverage *Ectocarpus* had almost disappeared in these plots by May.

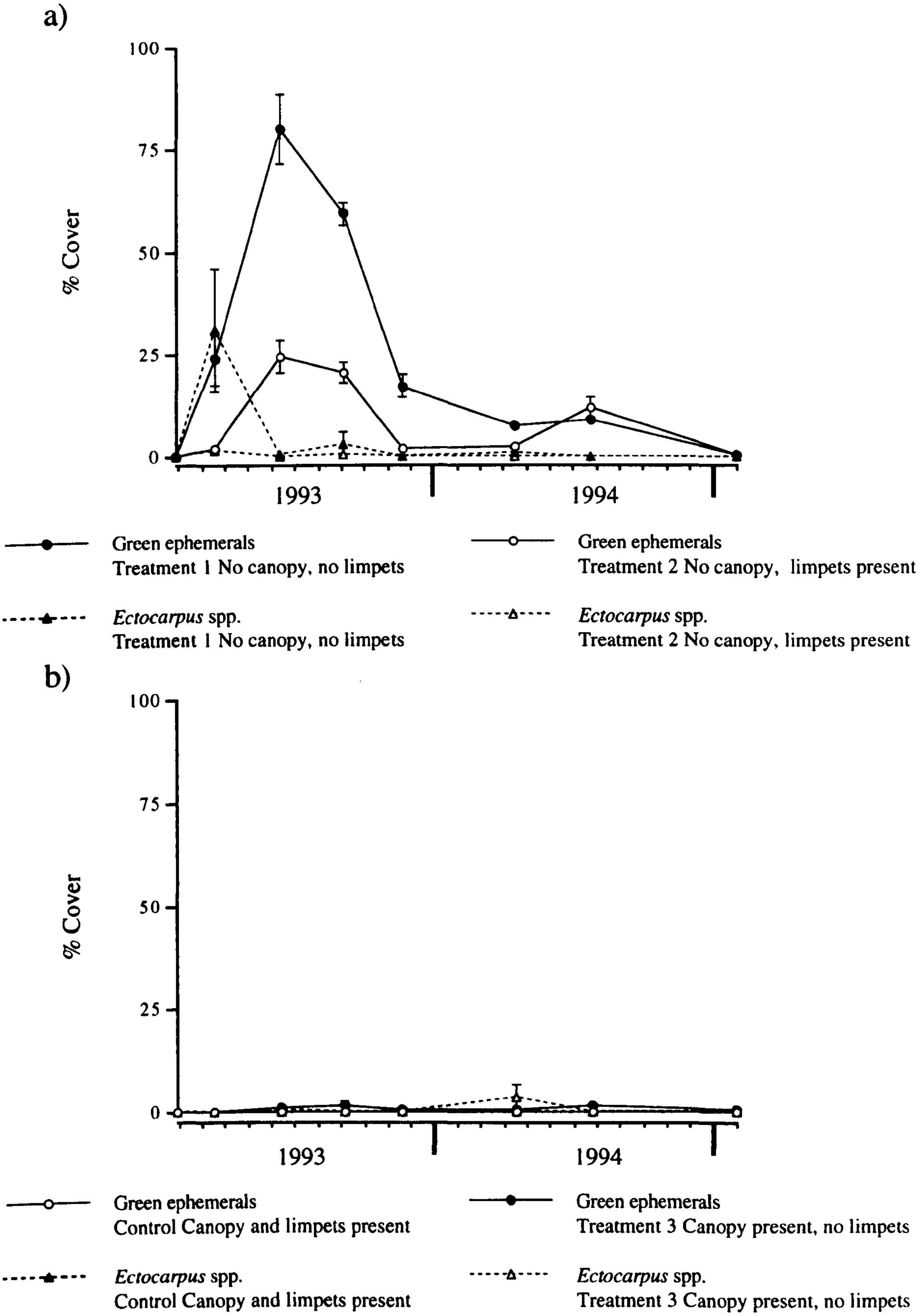


Figure 3.7 Development of green ephemeral algae and *Ectocarpus* spp. in the *Fucus serratus* zone following experimental manipulation in January 1993. Large plots only. Error bars = ± 1SE
a) Plots cleared of canopy b) Plots where the canopy is intact

Table 3.4 Two way ANOVA on arc-sine transformed data testing for the effect of the *Fucus serratus* canopy and the limpet *Patella vulgata* on green ephemeral algal cover in the *Fucus serratus* zone.

	Source	df	Mean Square	F-Value	P-Value
11.6.93	Canopy	1	6994.31	154.84	0.0001
	Limpets	1	1299.89	28.78	0.0002
	Canopy x Limpets	1	856.56	18.96	0.0011
	Residual	11	45.17		
15.11.93	Canopy	1	732.96	62.51	0.0001
	Limpets	1	331.99	28.31	0.0002
	Canopy x Limpets	1	148.24	12.64	0.0045
	Residual	11	11.72		

3.3.2.4 *Palmaria palmata*

Palmaria palmata is commonly restricted to growing epiphytically on other algae especially on the stipes of *Laminaria* (Hawkins and Harkin, 1985). It showed similar responses to manipulation of canopy and limpets as the green ephemeral alga, although *Palmaria* appeared later in the successional sequence. It was present at low levels (< 1%) in the control treatment throughout the experimental period showing no change in abundance over time. Removal of limpets beneath an intact canopy (treatment 3) resulted in a very slight increase in cover (Figure 3.8b).

The response of *Palmaria* to canopy removal differed radically depending on the presence or absence of limpets. Where both canopy and limpets were removed (treatment 1) high levels of *Palmaria* cover resulted. Unlike the ephemeral green algae *Palmaria* did not form a bloom in the summer, but reached its peak of 62% in November and declined only very slightly over the following 8 months (Figure 3.8a). During this period (November 1993- August 1994) *Palmaria* formed a dense cover over much of the area of treatment 1 plots analogous to a low canopy, before declining to 6% in January 1995. This decline was almost certainly a result of the increase in cover of *Fucus serratus* canopy. Earlier observations had shown that *Palmaria* cover was reduced where patches of *Fucus serratus* canopy were developing.

In treatment 2 where canopy was removed but limpets left undisturbed *Palmaria* showed an initial increase in cover , and remained at levels between 3% and 11% throughout the period of study. At the three sampling dates covering the period September 1993 to April 1994, two way ANOVA applied to arcsine transformed data revealed a significant effect of both canopy and limpets in determining abundance of *Palmaria*. In addition, a significant interaction between canopy and limpets was

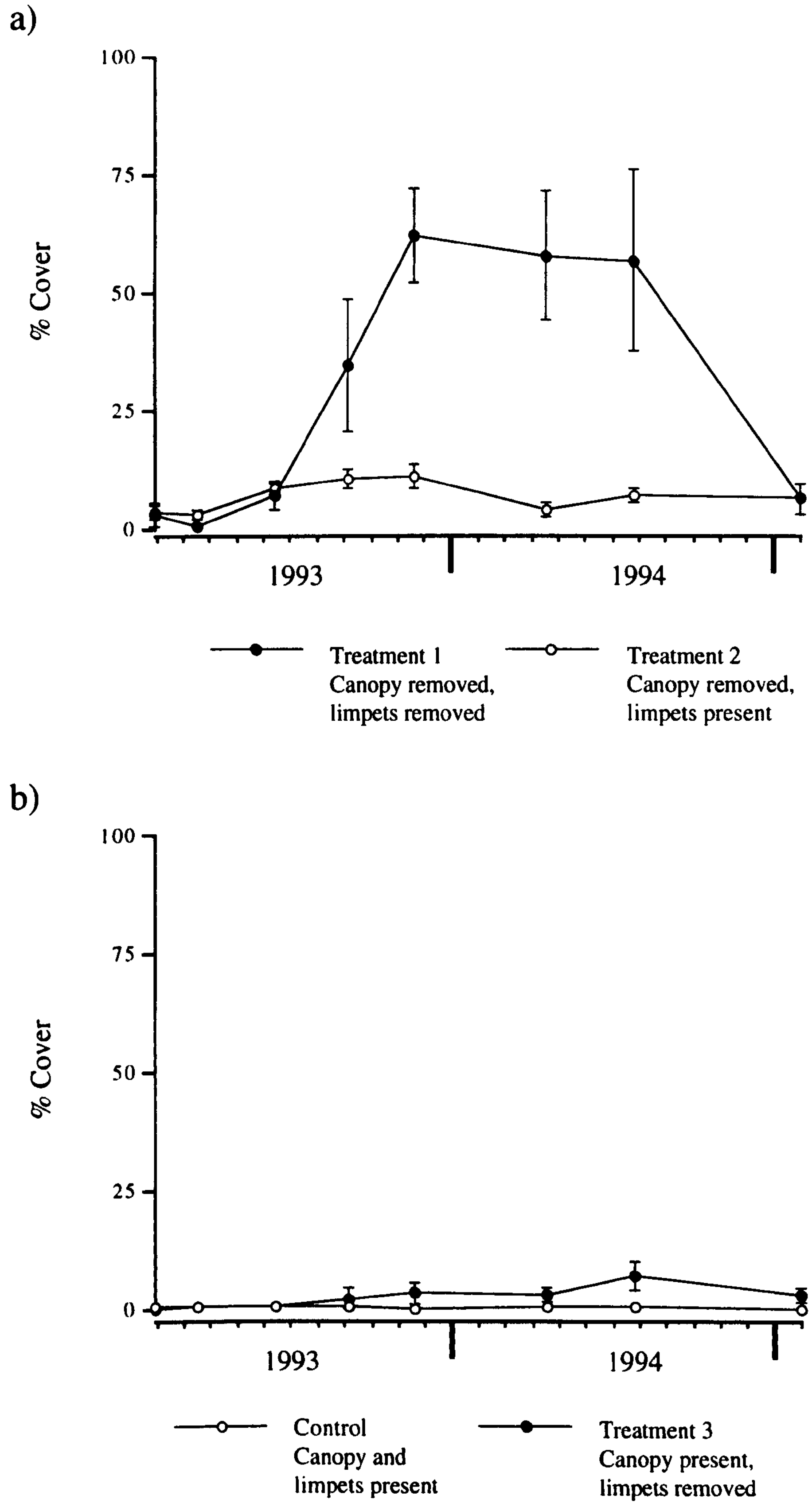


Figure 3.8 Development of *Palmaria palmata* in the *Fucus serratus* zone following experimental manipulation in January 1993. Large plots only. Error bars = ± 1SE
a) Plots cleared of canopy b) Plots where the canopy is intact

found at two of these sampling dates, in November 1993 and April 1994 (Table 3.5). Figure 3.9 illustrates the significant interaction between canopy and limpets in determining *Palmaria* cover. The effect which the presence or absence of the canopy exerts is clearly related to whether limpets are present.

The moderate levels of both *Palmaria* and ephemeral green algae in treatment 2 were a result of restriction of these algae to recruitment amongst and at the edges of turfs of *Cladophora* and *Laurencia* and on the shells of limpets. In general, despite their rapid growth, very little recruitment of these algae occurred on open readily grazeable substrate.

Table 3.5 Two way ANOVA on arc-sine transformed data testing for the effect of the *Fucus serratus* canopy and the limpet *Patella vulgata* on cover of *Palmaria palmata* in the *Fucus serratus* zone.

	Source	df	Mean Square	F-Value	P-Value
1.9.93	Canopy	1	1847.18	28.21	0.0002
	Limpets	1	329.15	5.02	0.0465
	Canopy x Limpets	1	168.69	2.57	0.1368
	Residual	11	65.49		
15.11.93	Canopy	1	3220.10	63.62	0.0001
	Limpets	1	1588.39	31.38	0.0002
	Canopy x Limpets	1	526.74	10.41	0.0081
	Residual	11	50.61		
11.4.94	Canopy	1	1704.69	26.23	0.0004
	Limpets	1	1404.70	21.61	0.0009
	Canopy x Limpets	1	911.68	14.03	0.0038
	Residual	11	64.99		

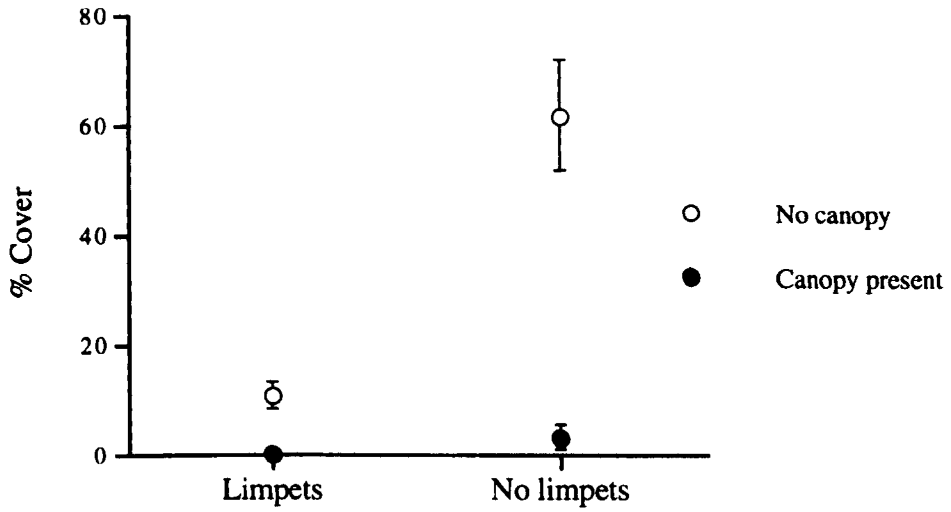


Figure 3.9 Response of *Palmaria palmata* to canopy and limpet manipulation in the *Fucus serratus* zone in November 1993. Error bars = ± 1 SE

3.3.2.5 *Cladophora rupestris*

Cladophora rupestris was the main turf forming alga present. Its ability to trap silt between its thalli enabled it to form grazer resistant turfs, upon or within which other algae recruited. No clear pattern emerged from sampling except a general increase in abundance beneath the intact canopy where limpets were removed (Figure 3.10b). This quantitative result agreed with qualitative observations of *Cladophora* recruitment over bare substrate previously grazed by limpets. Recruitment of *Cladophora* to the other treatment in which limpets were removed (treatment 1, both canopy and limpets removed) was probably prevented by the rapid colonisation by ephemeral algae succeeded by *Palmaria.*

3.3.2.6 'Bare substrate'

Removal of both the canopy and limpets (treatment 1) resulted in an immediate and very sharp decline in cover of bare substrate, from 85% in January to 6% in March (Figure 3.11). This occurred owing to the rapid colonisation of ungrazed rock and lithothamnia by *Ectocarpus* spp. The level of bare substrate cover remained very low (< 6%) between March and September owing mainly to a cover of ephemeral green algae and associated silt. During this period, two way ANOVA of arcsine transformed data revealed a significant effect of canopy and limpets and a significant interaction term (Table 3.6). The increase in bare substrate cover after September occurred as the cover of green ephemeral algae and associated silt declined. The ephemeral greens were replaced by a dense cover of *Palmaria palmata.* However this alga did not appear to induce the same levels of silt accumulation. In fact the substratum appeared relatively silt free beneath this 'dwarf' canopy.

Bare substrate, although classed as a single functional unit was in fact made up of three units, *Phymatolithon purpureum*, *Phymatolithon lenormandii* and bare rock. At the beginning of the experiment the percentage cover of these units (calculated as the average of all experimental plots) occurred in the ratio 3:6:1.Change in this ratio over time revealed patterns not clearly shown by simply plotting percentage cover of each unit. Figure 3.12a shows the proportions of *P. purpureum*, *P. lenormandii* and bare rock in treatment 2 (canopy removed, limpets unmanipulated) over the experimental period. From January to June 1993 there was a 3 fold increase in the proportion of bare rock. Almost all of this increase was accounted for by a corresponding decrease in the proportion of *P. purpureum.* From June to November 1993 the proportion of bare rock decreased and there was a corresponding increase in the proportion of *P. purpureum*. Little change was evident between November 1993 and the final sampling date in January 1995. Throughout the period of study there was little change in the proportion of *P. lenormandii*.

A very similar pattern was observed in the small plot of the same treatment with a 4 fold increase in rock cover between January and August 1993 (Figure 3.12b). This increase appeared to be a result of a decrease in the proportion of both species of crust.

In contrast to the two treatments described above, the control treatment showed very little change in the proportion of bare rock cover and consequently the proportion of lithothamnia as a whole was unchanged. Figure 3.12c however, shows that the balance between *P. purpureum* and *P. lenormandii* was not constant, although no unidirectional pattern was evident.

Table 3.6 Two way ANOVA on arc-sine transformed data testing for the effect of the *Fucus serratus* canopy and the limpet *Patella vulgata* on cover of bare substrate in the *Fucus serratus* zone.

	Source	df	Mean Square	F-Value	P-Value
18.3.93	Canopy	1	1950.69	31.01	0.0002
	Limpets	1	2008.49	31.93	0.0001
	Canopy x Limpets	1	2803.58	44.57	0.0001
	Residual	11	62.90		
11.6.93	Canopy	1	3569.32	56.64	0.0001
	Limpets	1	1967.04	31.21	0.0002
	Canopy x Limpets	1	3248.75	51.55	0.0001
	Residual	11	63.02		
1.9.93	Canopy	1	4318.81	120.9	0.0001
	Limpets	1	2075.39	58.1	0.0001
	Canopy x Limpets	1	1871.15	52.39	0.0001
	Residual	11	35.71		

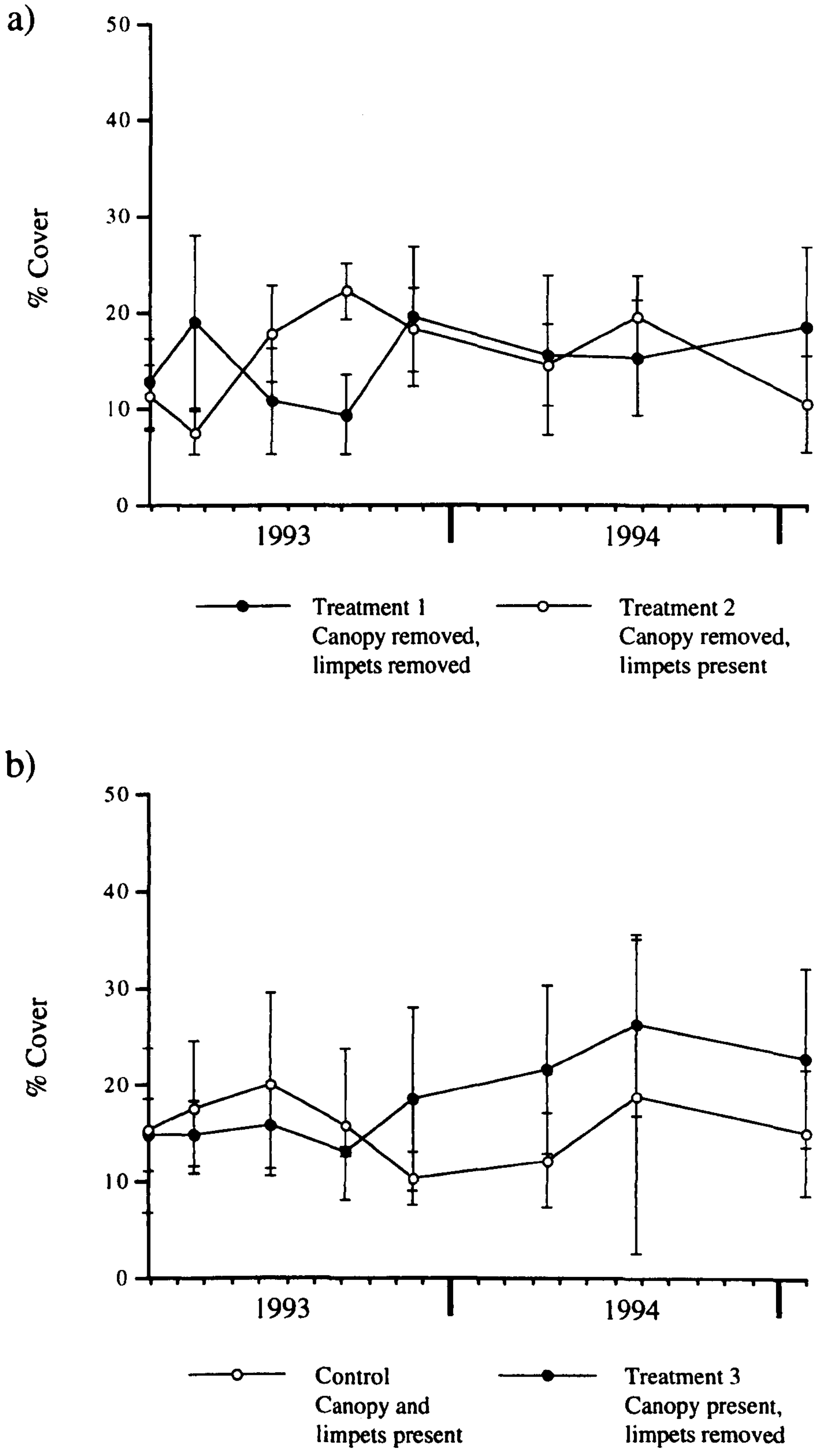


Figure 3.10 Percentage cover of *Cladophora rupestris* in the *Fucus serratus* zone following experimental manipulation in January 1993. Large plots only. Error bars = ± 1SE
a) Plots cleared of canopy b) Plots where the canopy is intact

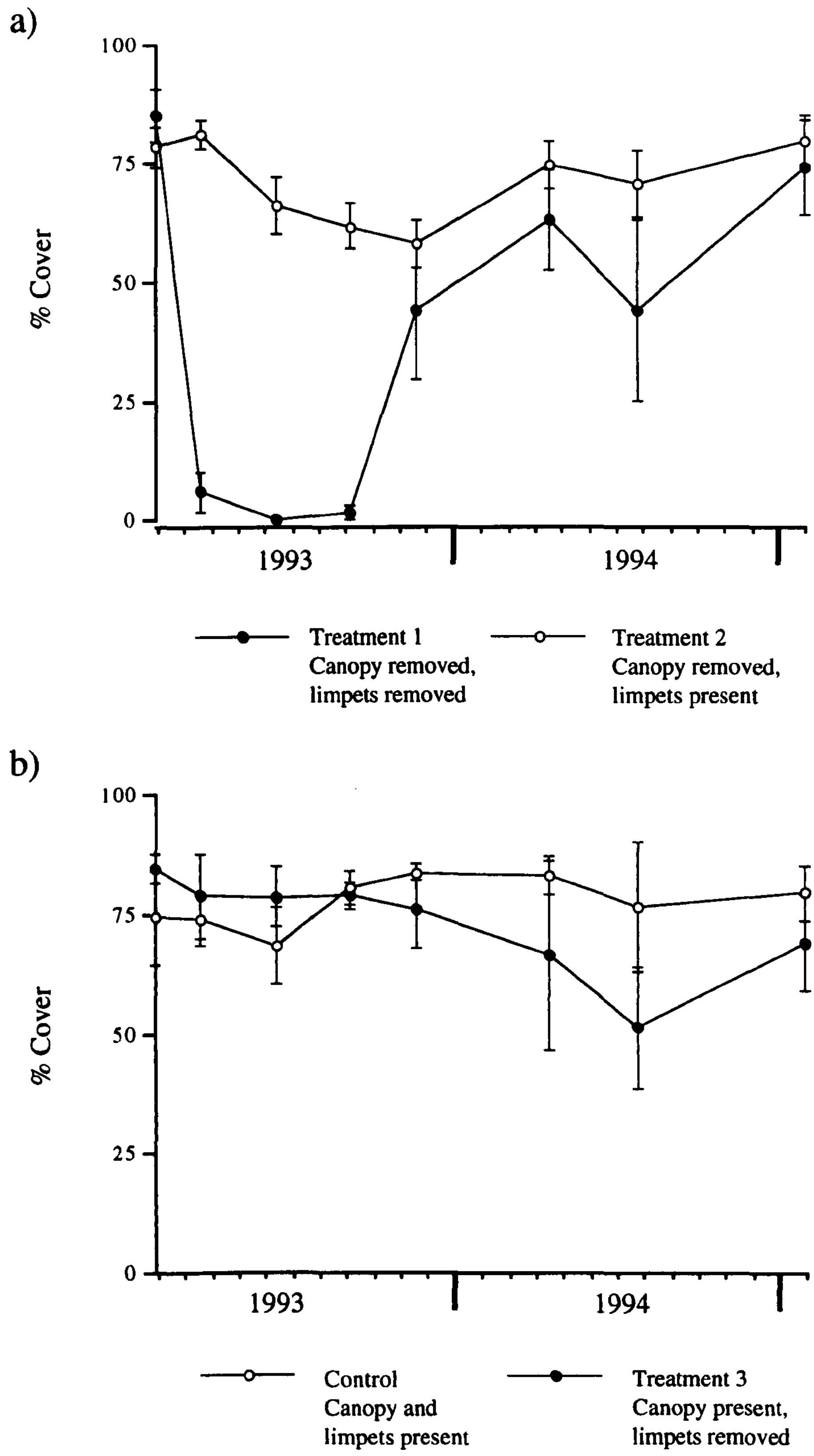


Figure 3.11 Percentage cover of 'bare substrate' in the *Fucus serratus* zone following experimental manipulation in January 1993. Large plots only. Error bars = ± 1SE
a) Plots cleared of canopy b) Plots where the canopy is intact

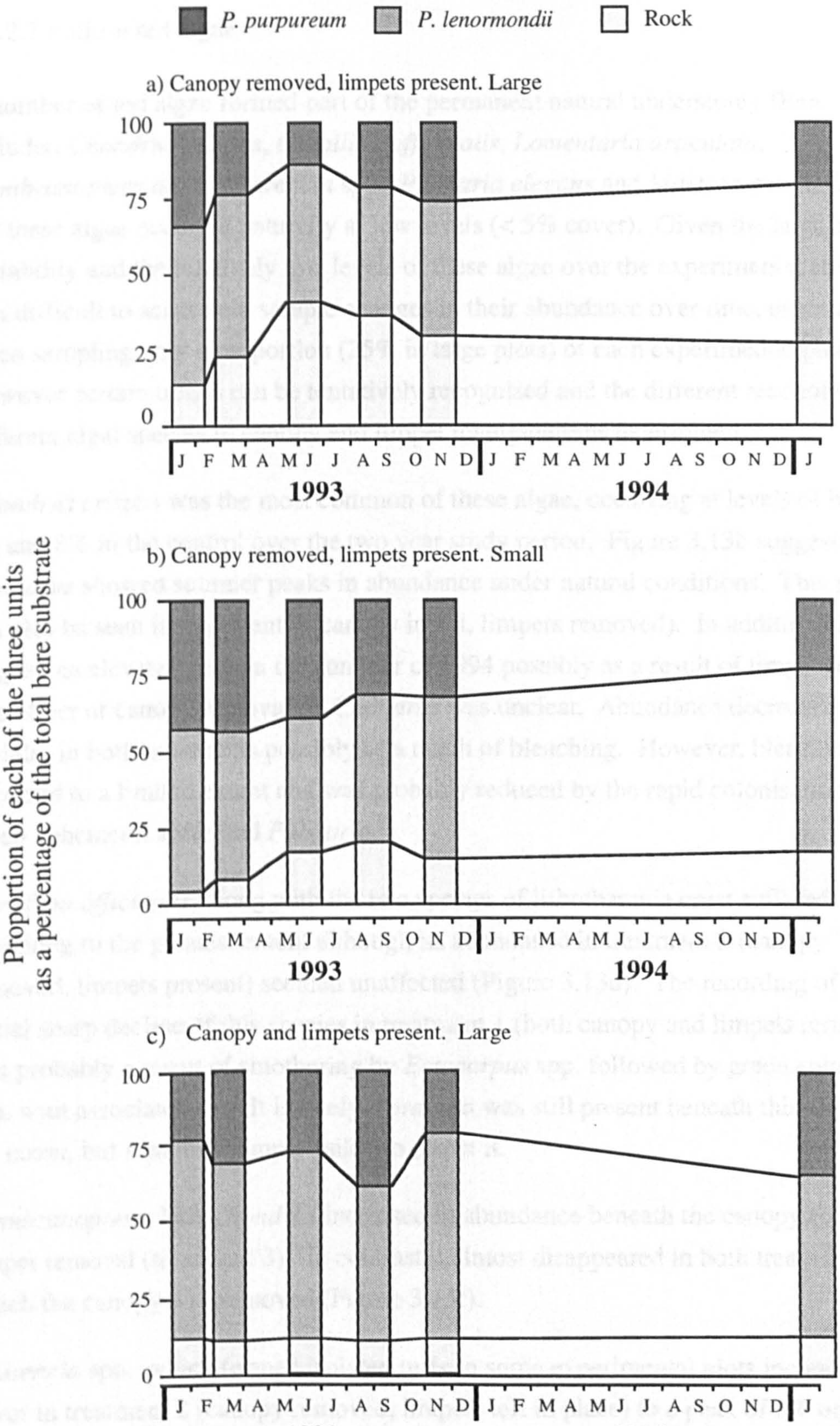


Figure 3.12 Change in proportion of the three 'units' of bare substrate over time.
a) Canopy removed, limpets present. Large.
b) Canopy removed, limpets present. Small.
c) Canopy and limpets present. Large.

3.3.2.7 Foliose red algae

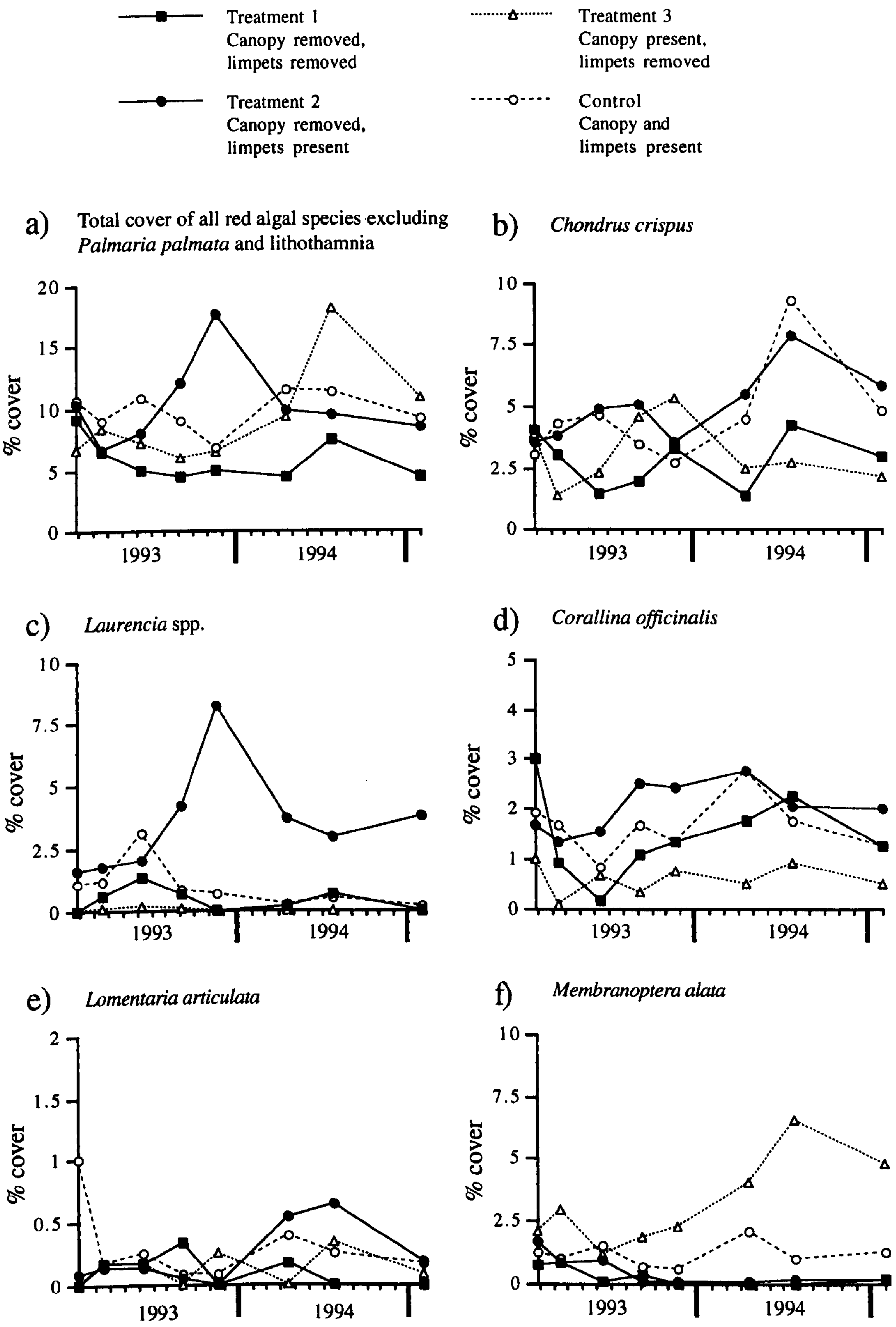
A number of red algae formed part of the permanent natural understorey flora. These included *Chondrus crispus, Corallina officinalis, Lomentaria articulata, Membranoptera alata, Laurencia* spp., *Plumaria elegans* and *Mastocarpus stellatus.* All these algae occurred naturally at low levels (< 5% cover). Given the large natural variability and the relatively low levels of these algae over the experimental area it was difficult to accurately sample changes in their abundance over time, especially when sampling only a proportion (25% in large plots) of each experimental plot. However certain trends can be tentatively recognised and the different reactions of different algal species to canopy and limpet manipulations determined.

Chondrus crispus was the most common of these algae, occurring at levels of between 3.5 and 8% in the control over the two year study period. Figure 3.13b suggests that *Chondrus* showed summer peaks in abundance under natural conditions. This pattern can also be seen in treatment 3 (canopy intact, limpets removed). In addition, the data suggest an elevated peak in the summer of 1994 possibly as a result of limpet removal. The effect of canopy removal on *Chondrus* was unclear. Abundance decreased initially in both treatments possibly as a result of bleaching. However, bleaching only occurred to a limited extent and was probably reduced by the rapid colonisation of green ephemeral algae and *Palmaria.*

Corallina officinalis, along with the two species of lithothamnia crust suffered bleaching to the greatest extent although its abundance in treatment 2 (canopy removed, limpets present) seemed unaffected (Figure 3.13d). The recording of an initial sharp decline of this species in treatment 1 (both canopy and limpets removed) was probably a result of smothering by *Ectocarpus* spp. followed by green ephemeral spp. with associated silt. It is likely *Corallina* was still present beneath this algal and silt cover, but sampling simply failed to detect it.

Membranoptera, like *Chondrus* increased in abundance beneath the canopy following limpet removal (treatment 3). In contrast it almost disappeared in both treatments in which the canopy was removed (Figure 3.13f).

Laurencia spp. which formed isolated turfs in some experimental plots increased in cover in treatment 2 (canopy removed, limpets left in place) to a peak of 8% on November 1993 before declining to near original levels. No such peak occurred in the other treatment in which the canopy was removed (Figure 3.13c).


a) Total cover of all red algal species excluding *Palmaria palmata* and lithothamnia

b) *Chondrus crispus*

c) *Laurencia* spp.

d) *Corallina officinalis*

e) *Lomentaria articulata*

f) *Membranoptera alata*

Figure 3.13 Percentage cover of red algal species in four treatments (all large plots) in the *Fucus serratus* zone. Error bars omitted for clarity. Note different Y axis scales.

3.3.3 Effect of patch size

The effect of patch size on community succession in the *Fucus serratus* zone was demonstrated by comparing equivalent treatments in small and large plots. Figure 3.14a-d shows the change in abundance of canopy, bare substrate, green ephemeral algae and *Palmaria* in the canopy removal treatments in both small and large plots. Error bars have been omitted for clarity but it is immediately obvious that the same patterns of change occurred in both plot sizes in equivalent treatments.

Two way ANOVA of arcsine transformed data, testing for the effect of patch size and presence of limpets revealed no significant effect of size at any sampling date for canopy, bare substrate and P*almaria.* For green ephemeral algae a significant effect of size was found in November 1993 and April 1994 when ephemeral algal cover was greater in small plots. Despite this it should be concluded that patch size was not an important determinant of community succession.

The addition of data from small plots allowed further analysis of the effect of limpets on community succession, in particular the effect of limpets on the re-establishment of a *Fucus serratus* canopy was re-examined. Using only large plot data a significant effect of limpets was found only at the final sampling date, and this only as a result of differential canopy loss between two treatments. Using both small and large plot data a significant effect of limpets was found at the last three sampling dates April 1994, August 1994 and January 1995, thus reinforcing the conclusion that limpets inhibited the recovery of the *Fucus serratus* canopy (Table 3.7).

Table 3.7 Two way ANOVA on arcsine transformed data testing for the effect of patch size and the limpet *Patella vulgata* on recovery of the *Fucus serratus* canopy.

	Source	df	Mean Square	F-Value	P-Value
11.4.94	Limpets	1	1345.08	4.67	0.05
	Size	1	145.30	0.50	0.49
	Limpets x Size	1	64.93	0.22	0.643
	Residual	13	288.26		
18.7.94	Limpets	1	4374.18	13.96	0.0025
	Size	1	25.00	0.07	0.782
	Limpets x Size	1	536.20	1.71	0.2134
	Residual	13	313.24		
30.1.95	Limpets	1	2927.82	13.31	0.0053
	Size	1	16.55	0.07	0.79
	Limpets x Size	1	185.45	0.84	0.383
	Residual	9	220.05		

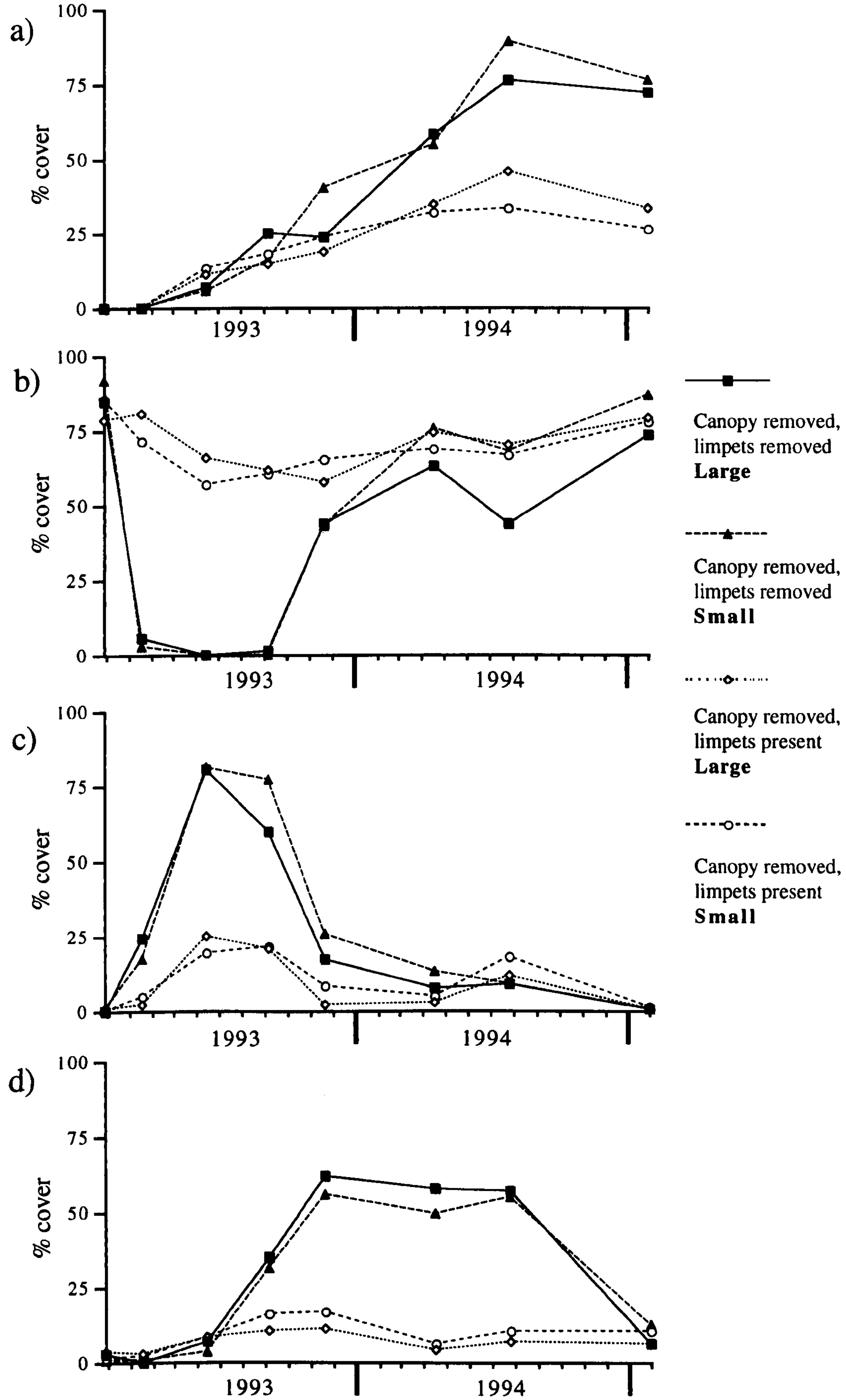


Figure 3.14 Comparison of community succession in large and small plots in two experimental treatments in the *Fucus serratus* zone. Error bars omitted for clarity.

a) *Fucus serratus* canopy b) Bare substrate

c) Green ephemeral algae d) *Palmaria palmata*

3.3.4 Relative growth rate

The experiment was designed to enable analysis of the variation in growth rate between spatially separated quadrats within a zone compared with variation in growth rate between zones. Figure 3.15a shows the mean relative growth rate of juveniles in each quadrat over four periods covering a total of just over four months. Within each quadrat, between 13 and 21 juveniles were initially marked and measured. By the end of the period of study this number had reduced owing to loss of labels and plants to between 9 and 16. Two of the quadrats in the *Fucus serratus* zone clearly showed an elevated relative growth rate over most of the study period. However, one *Fucus serratus* zone quadrat showed a mean relative growth rate similar to those found in the *Ascophyllum* zone.

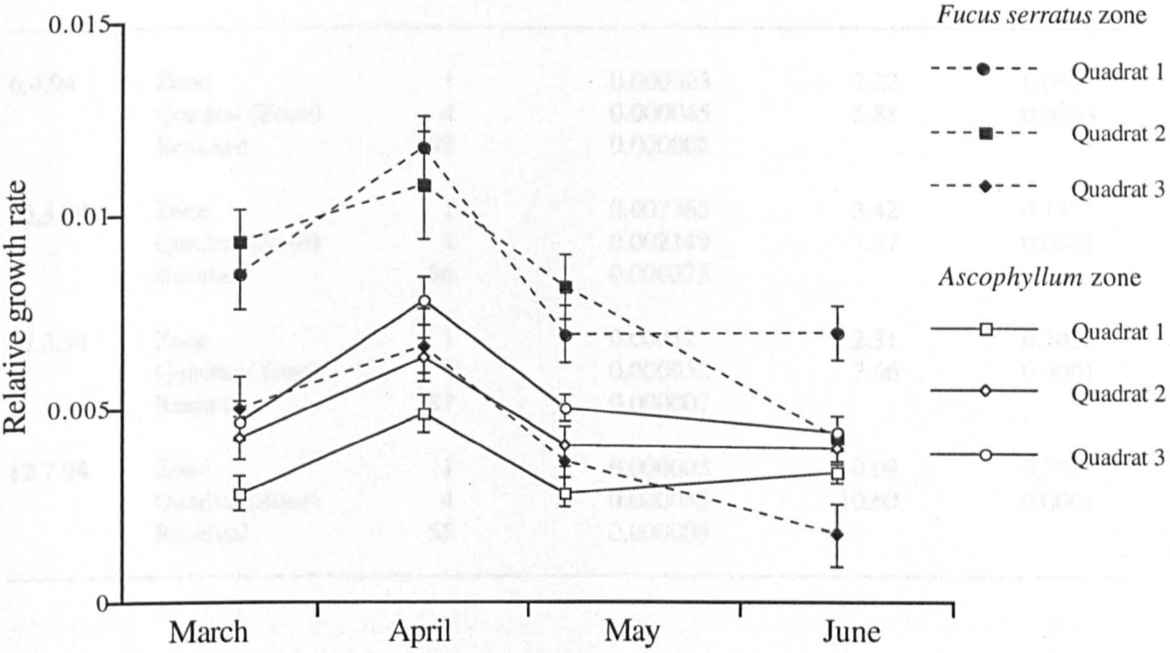
Analysis of this data using a mixed model nested ANOVA revealed no significant difference between zones at any sampling date (although at the first sampling point a p value of 0.055 was found). At all sampling dates a significant effect of the nested factor (quadrat) was found, indicating a significant difference between quadrats over the whole of the experiment (Table 3.8).

In an attempt to establish a clear pattern, the mean relative growth rate was calculated for each quadrat over the whole experimental period, rather than over four shorter periods. The results are shown in figure 3.15b which clearly shows the reduced relative growth rate in quadrat 3 of the *Fucus serratus* zone. Analysis of this data reveals the same pattern with no significant difference being found between zones (Table 3.9). Examination of the position of quadrat 3 in the *Fucus serratus* zone and the density of the overlying canopy revealed no explanation for the low relative growth rate at this position.

Although there was no apparent reason for rejecting quadrat 3 it was decided to re-analyse the data using only *Fucus serratus* quadrats 1 and 2. Nested ANOVA does not allow an unbalanced analysis. Therefore the analysis was carried out three times, each time rejecting one *Ascophyllum* quadrat (as well as *Fucus serratus* quadrat 3). Table 3.9 reveals that for these analyses a significant difference between zones was found in two out of three cases, with the third showing a p value of 0.054.

The suggested difference in potential of juveniles in the two zones was emphasised by plotting the mean size of juveniles in each quadrat over time (Figure 3.16). The final size of juveniles in the *Ascophyllum* zone was low, with little variation between quadrats, compared to an overall higher size but also higher variation in the *Fucus serratus* zone.

a) Relative growth rate calculated over each of four sampling periods



b) Relative growth rate calculated over the whole study period

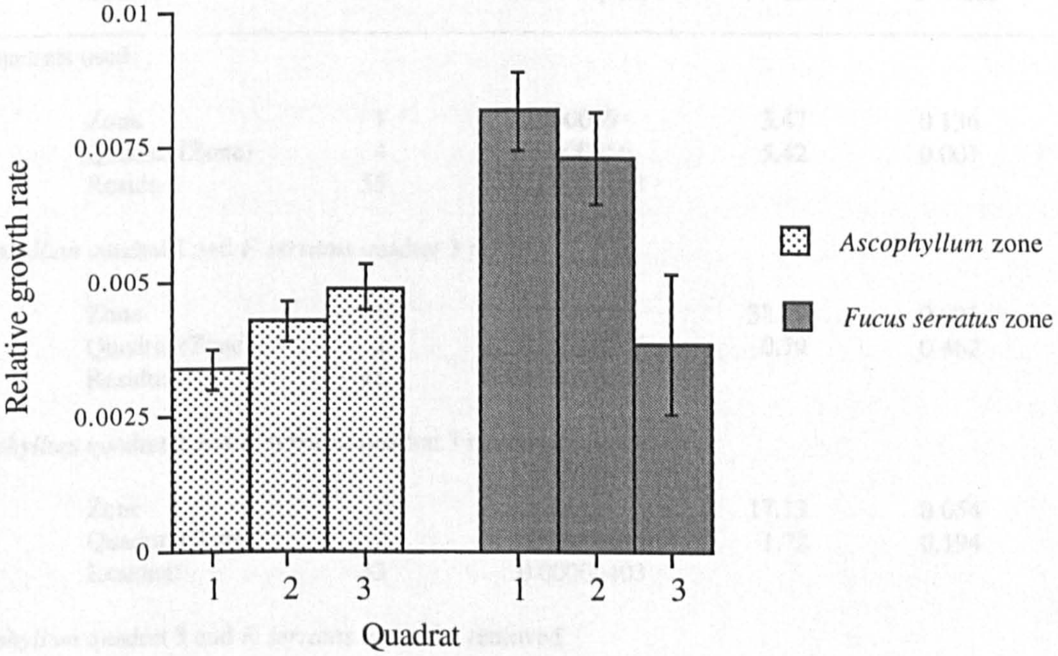


Figure 3.15 Relative growth rate of *Fucus serratus* juveniles in the *Fucus serratus* and *Ascophyllum* zones. Error bars = ± 1SE

Table 3.8 Mixed model nested ANOVA testing for a difference in relative growth rate of *Fucus serratus* juveniles between the *Ascophyllum* and *Fucus serratus* zones. Test applied to each of four sampling periods. Underlined date indicates square root transformed data.

	Source	df	Mean Square	F-Value	P-Value
6.4.94	Zone	1	0.000323	7.22	0.055
	Quadrat (Zone)	4	0.000045	5.88	0.0003
	Residual	93	0.000008		
25.4.94	Zone	1	0.007365	3.42	0.1378
	Quadrat (Zone)	4	0.002149	7.87	0.0001
	Residual	86	0.000273		
17.5.94	Zone	1	0.00012	2.31	0.2028
	Quadrat (Zone)	4	0.000052	7.66	0.0001
	Residual	87	0.000007		
12.7.94	Zone	1	0.000003	0.09	0.772
	Quadrat (Zone)	4	0.000035	10.60	0.0001
	Residual	55	0.000003		

Table 3.9 Mixed model nested ANOVA testing for a difference in relative growth rate of *Fucus serratus* juveniles between the *Ascophyllum* and *Fucus serratus* zones. Test applied to relative growth rates calculated for the whole period 3.3.94-12.7.94 using all data and subsets of the data.

Source	df	Mean Square	F-Value	P-Value
All quadrats used				
Zone	1	0.000089	3.47	0.136
Quadrat (Zone)	4	0.0000256	5.42	0.001
Residual	55	0.00000473		
Ascophyllum quadrat 1 and *F. serratus* quadrat 3 removed				
Zone	1	0.000119	38.77	0.025
Quadrat (Zone)	2	0.00000307	0.79	0.462
Residual	41	0.0000039		
Ascophyllum quadrat 2 and *F. serratus* quadrat 3 removed				
Zone	1	0.000119	17.12	0.054
Quadrat (Zone)	2	0.00000694	1.72	0.194
Residual	33	0.00000403		
Ascophyllum quadrat 3 and *F. serratus* quadrat 3 removed				
Zone	1	0.000158	37.64	0.026
Quadrat (Zone)	2	0.00000418	1.09	0.347
Residual	40	0.00000385		

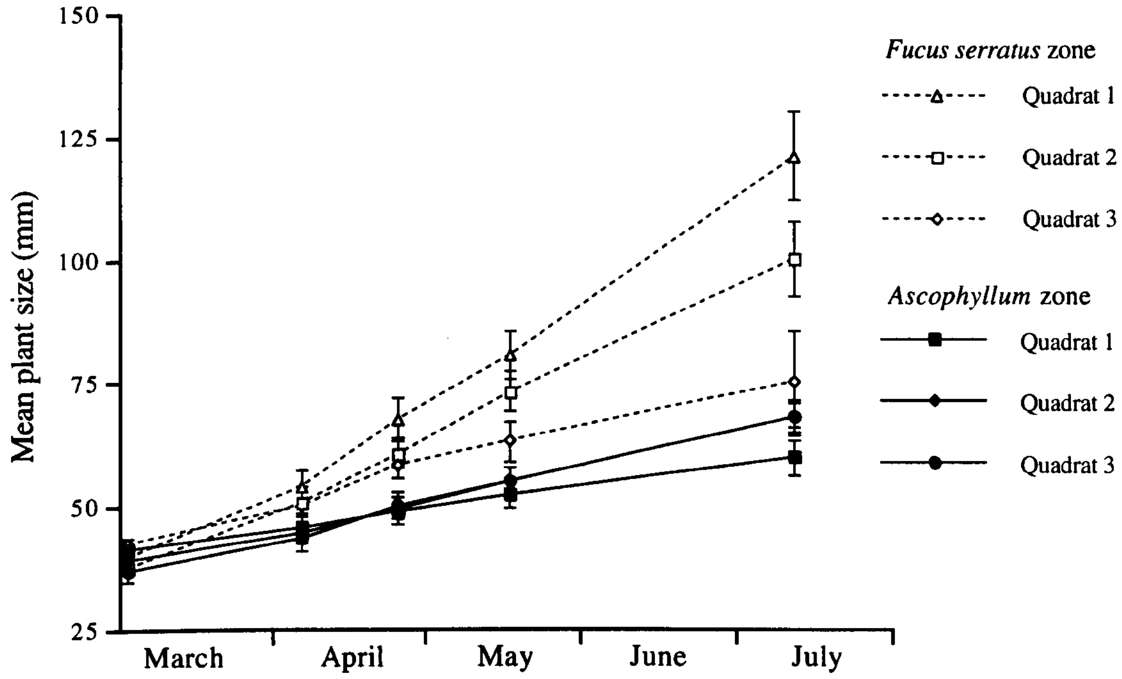


Figure 3.16 Change in mean size of *Fucus serratus* juveniles in each quadrat in the *Fucus serratus* and *Ascophyllum* zones. Error bars = ± 1SE

Observations of *Fucus serratus* juveniles showed a relatively high incidence of grazing damage in both *Ascophyllum* and *Fucus serratus* zones. Damage was higher in the *Ascophyllum* zone at all sampling dates except the last, on July 12th (Figure 3.17). However, the difference was only significant on one sampling date, March 3rd (Table 3.10). Detailed investigations into grazing damage were not made but observations suggest the main cause was *Littorina obtusata.* This species occurs over the entire extent of sheltered shores but is most abundant at mid tide levels, grazing on the *Ascophyllum* canopy (Williams, 1990a). Whether *Littorina obtusata* was present at sufficient densities in the low shore to account for the level of grazing damage was not determined. Other potential grazers of *Fucus serratus* juveniles in the low shore include *Littorina mariae* and *Gibbula* spp.. *Littorina mariae* is abundant in the *Fucus serratus* zone but is thought to be restricted to grazing on epiphytes (Williams, 1990a). *Gibbula* spp. were relatively uncommon.

In addition to grazing damage, fouling of juveniles by hydroids was recorded, this being substantially higher in the *Ascophyllum* zone.

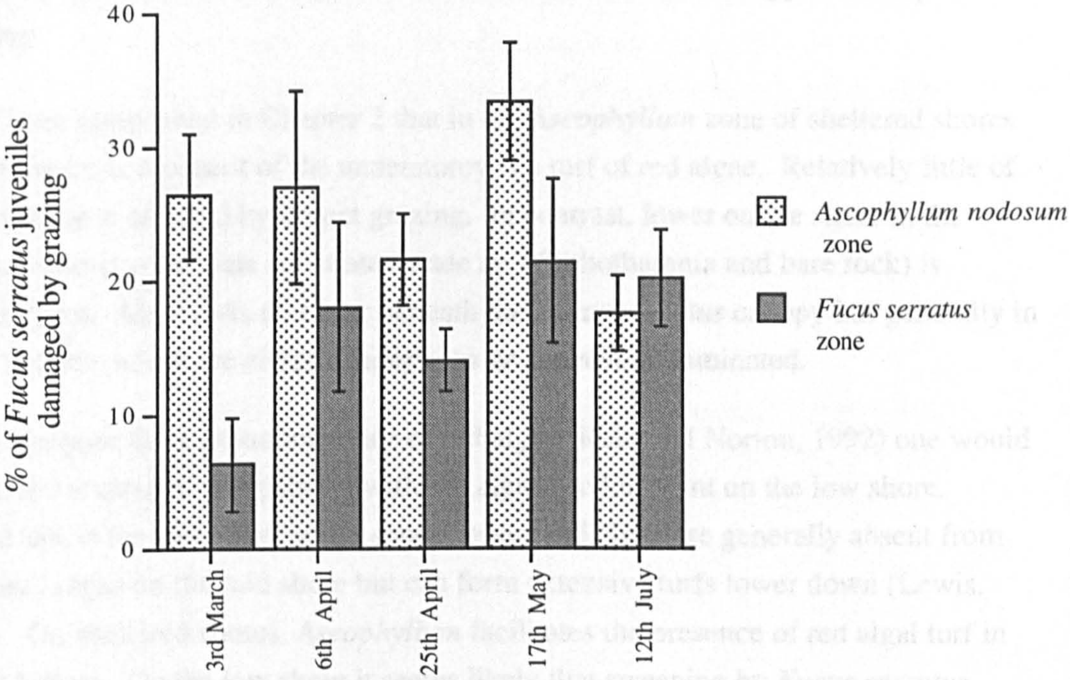


Figure 3.17 Percentage of *Fucus serratus* juveniles showing grazing damage in the *Ascophyllum* and *Fucus serratus* zones at each sampling date. Error bars = ± 1SE

Table 3.10 One way ANOVA testing for a difference between the *Ascophyllum* and *Fucus serratus* zones in the incidence of grazing damage in *Fucus serratus* juveniles .

	Source	df	Mean Square	F-Value	P-Value
3.3.94	Zone	1	603.00	12.05	0.026
	Residual	4	50.03		
6.4.94	Zone	1	117.39	0.84	0.4098
	Residual	4	138.80		
25.4.94	Zone	1	84.97	3.32	0.1422
	Residual	4	25.53		
17.5.94	Zone	1	213.36	2.53	0.187
	Residual	4	84.15		
12.7.94	Zone	1	10.48	0.33	0.5935
	Residual	4	31.24		

3.4 DISCUSSION

3.4.1 The relative structuring roles of the *Fucus serratus* canopy and limpet grazing

It has been established in Chapter 2 that in the *Ascophyllum* zone of sheltered shores the dominant component of the understorey is a turf of red algae. Relatively little of the substrate is affected by limpet grazing. In contrast, lower on the shore in the *Fucus serratus* zone, bare substrate (made up of lithothamnia and bare rock) is predominant. Algal turfs do occur beneath the *Fucus serratus* canopy but generally in small patches which are either *Cladophora* or *Laurencia* dominated.

Given the poor desiccation tolerance of red algae (Kain and Norton, 1992) one would expect the reverse of this pattern, with red algae predominant on the low shore. Indeed this is the case on exposed shores where red algae are generally absent from emergent rocks on the mid shore but can form extensive turfs lower down (Lewis, 1964). On sheltered shores, *Ascophyllum* facilitates the presence of red algal turf in the mid shore. On the low shore it seems likely that sweeping by *Fucus serratus* plants inhibits turf development. The effect of sweeping on understorey algae is discussed below. That the difference in understorey type between the two zones is a result of the different properties of the two canopy species rather than any effect of shore height is demonstrated by two observations. Firstly, patches of *Fucus serratus* within the *Ascophyllum* zone are generally associated with patches of bare substrate (see Chapter 2). Secondly, at sites where a distinct border between *Ascophyllum* and *Fucus serratus* occurs an equally distinct change in understorey type can be seen. Given the proposed inhibition of red algal turfs by *Fucus serratus* canopy one might expect expansion of turf patches following canopy removal. That this was not detected may simply be due to a slow response of red algae and a lack of sensitivity in the sampling methodology.

The difference in understorey type between the two zones affects the ability of limpets to influence community structure. The extent of limpet grazing is limited in the *Ascophyllum* zone whilst beneath a *Fucus serratus* canopy it is wide ranging. Given this fact what was the relative structuring role of the *Fucus serratus* canopy and *Patella vulgata* at the study site?

The general effect of both canopy and limpets was to cause a reduction in understorey algal cover. Removal of one factor alone resulted in subtle distinctive changes to the understorey community but large scale recruitment of algae was prevented by the unmanipulated factor. Removal of limpets alone resulted in high *Fucus* recruitment (see below) and a small increase in some understorey algal species. Interestingly, cover of *Cladophora* increased, indicating that this turf forming alga is not limited only by canopy sweeping. Removal of the canopy alone resulted in some increases in ephemeral algae but large changes were prevented by limpet grazing. In the *Ascophyllum* zone canopy removal resulted in large scale bleaching and death of red algae. At a lower level on the shore, removal of *Fucus serratus* caused limited bleaching to foliose red algae although some species showed an initial decline in cover. *Membranoptera alata* showed the greatest negative reaction to canopy removal. Hill (1993) found that permanent members of the understorey (*Chondrus crispus, Mastocarpus stellatus*, and *Corallina officinalis*) were not badly affected by canopy removal.

Both calcareous encrusting species *Phymatolithon purpureum* and *Phymatolithon lenormandii* were badly bleached in plots where the canopy was removed, with *P. purpureum* which occurs only at low levels on the shore (Figueiredo, 1993) being bleached to a greater extent. Many species of encrusting algae in the littoral zone depend on an algal covering to reduce the effects of desiccation when the tide is out (Littler, 1972; Sebens, 1986) and thus may be considered obligate understorey species (Figueiredo, 1993). Bleaching and consequent death may explain the increase in the proportion of bare rock and the simultaneous decline in encrusting algae in canopy cleared areas. In large plots this decline was almost entirely a result of the decline of *P. purpureum.* It may be significant that this species was bleached to a greater extent than *P. lenormandii.* It must be remembered however that bleaching of such species does not necessarily result in death. Figueiredo (1993) reported bleaching of crusts of *P. purpureum* and *P. lenormandii* following canopy removal in the summer but both species recovered after fouling by epiphytes. This recovery may be related to a natural ability to regenerate, but shading by epiphytes seemed to facilitate the process. An alternative explanation for the decline of the lithothamnia species is fouling by algae. Coralline crusts may decrease in cover and die following algal fouling (Paine, 1980; Steneck, 1982; Steneck, 1983). The low density of adult limpets found on *P. purpureum* may explain the greater decline of this species relative to *P. lenormandii* in large plots.

Large changes in community structure only occurred following removal of both canopy and limpets with high levels of algal colonisation being accompanied by silt accumulation. Such an effect had previously been shown to occur low on moderately exposed shores following removal of canopy alone (Ballantine, 1961b; Hawkins, 1979; Hawkins and Harkin, 1985; Hill, 1993). Hill (1993) working on a moderately exposed shore on the Isle of Man found a significant reduction in limpet numbers 20 weeks after removal of the *Fucus serratus* canopy owing to the swamping of limpets by high levels of ephemeral algae. Such results support the conclusion that low on the shore there is a dynamic balance between grazer capabilities and algal growth rate (Underwood, 1979; Branch, 1981; Underwood and Jernakoff, 1981). Hawkins and Harkin (1985) observed swamping of *Patella* by ephemeral and red algae following removal of the *Laminaria digitata* canopy. It was suggested that the usual presence of limpets in such an algal dominated area was facilitated by the reduction in understorey algae caused by canopy shading and sweeping.

Clearly the result of canopy removal on the low shore will depend on the relationship between grazer density and algal growth rate. At the site used in this study, limpet density was obviously high enough to prevent ephemeral algal blooms and the consequent swamping of limpets. Thus, in this case the *Fucus serratus* canopy did not facilitate the presence of limpets. Both Hill's study site at Port St Mary and that used in this study at Castletown were at the same tidal height. Thus algal growth rates were presumably comparable. However the mean limpet density at Port St Mary was roughly three times less than at Castletown. Observations on the sheltered shore under study revealed that such differences in grazer density occurred naturally over scales of tens of metres. Thus the balance between grazers and algae is obviously not a simple function of tidal height. The factors influencing limpet density are paramount in determining the importance of limpets in structuring communities. These factors are discussed in Chapter 4.

3.4.2 The maintenance of a *Fucus serratus* canopy

On sheltered shores, *Fucus serratus* maintains a near 100% cover over large areas. An annual cycle of *Fucus serratus* canopy cover is well documented on moderately exposed shores (Ballantine, 1961b; Hawkins, 1979; Hawkins and Hartnoll, 1983a; Hawkins and Harkin, 1985; Hill, 1993) and was observed in this study on a sheltered shore (although probably not to the same degree). The decline in winter cover of *Fucus serratus* has two possible causes. The seasonal pattern of *Fucus serratus* described by Knight and Parke (1950) involves late winter and early spring defoliation resulting from the deterioration of fertile fronds following gamete release. However Hill (1993) argues that the greater part of canopy loss on moderately exposed shores especially that occurring in autumn and early winter should be attributed to storm damage. It is likely that even on sheltered shores some loss of canopy plants occurs as a result of occasional heavy wave action. This has implications for juvenile recruitment and growth and is discussed below.

Fucus serratus has demonstrated an ability to recover following canopy loss outside its reproductive season (Hill 1993), indicating that juveniles normally present through the year under the canopy are capable of responding to canopy loss. Indeed, individual juveniles beneath an intact canopy were monitored from a few centimetres in size up to canopy status. The loss of canopy plants in winter storms may be necessary for this to occur. The high variability in growth rate at spatially separated areas beneath the canopy may indicate an important influence of canopy gaps or variable canopy cover. Hill (1993) demonstrated that the relative growth rate of juvenile *Fucus serratus* was 2-3 times higher in areas cleared of canopy.

A comparison of the density of *Fucus serratus* juveniles between the middle of the *Fucus serratus* zone and the middle of the *Ascophyllum* zone revealed very similar values (37/m^2 and 44/m^2 respectively). It is a common observation that juveniles of a species are generally more widely distributed than adults (e.g. Schonbeck and Norton, 1980) but the relatively low density of juveniles of *Fucus serratus* in its own zone is perhaps surprising. Limpet grazing and sweeping by canopy alga may both contribute to this recruitment limitation.

Unfortunately, although an attempt was made to investigate the effect of canopy sweeping this failed owing to repeated losses of the experimental set up. Sweeping has been shown to be an important factor in determining recruitment levels of canopy species both intertidally and subtidally. However its effect is far from clear. A direct negative effect of sweeping on recruitment of juveniles of the same species has been both inferred (Black, 1974; Brawley and Johnson, 1991) and proven experimentally (Vadas and Wright, 1986; Johnson, 1993). Johnson (1993) used caged settlement tiles to demonstrate that canopy sweeping had a strongly negative effect on survival of settled zygotes. However, it was also found that settlement was higher beneath canopies presumably due to a reduction in water velocities. As well as a negative effect, sweeping has been shown to positively affect recruitment levels. Velimirov and Griffiths (1979) observed that sweeping by subtidal kelp plants allowed settlement and survival of sporophytes by maintaining a herbivore free area in the immediate vicinity of the sweeping plants. Kennelly (1989) in a study to assess the relative effects of shade and scour (sweeping) by kelp plants in a subtidal community found that abundance of understorey algal species was unaffected by scour.

In this study, sweeping by the *Fucus serratus* canopy appeared to have little effect on juvenile recruitment. Removal of limpets beneath an intact canopy where sweeping obviously occurs resulted in high recruitment. This indicates the important role of limpet grazing. The data of Hill (1993) emphasise this. At a site of low limpet density (5/m^2) juveniles of *Fucus serratus* occurred at a density of over 200/m^2 compared to only 67/m^2 at a site of higher limpet density (16/m$^{2)}$.

Despite limpet grazing, escapes of *Fucus serratus* do occur. Limpets were unable to prevent the recovery of a *Fucus serratus* canopy following canopy removal (although recovery was delayed in comparison to plots where both canopy and limpets were removed). An increase in growth rate at low levels on the shore may increase the likelihood of escapes occurring although the majority occurred on ungrazeable substrate even after canopy removal. *Fucus* juveniles appeared unable to recruit to substrate which is subject to high levels of *Patella* grazing; they rely on areas of decreased grazing intensity. This may occur in areas of low *Patella* density (see Hill 1993) or in the case of this study on substratum which provides a refuge from grazing. This applies equally to other recruiting algae such as ephemeral greens or *Palmaria palmata*. At mid tide level of exposed shores, high densities of barnacles may inhibit grazing to the extent that escapes occur (Burrows and Lodge, 1950; Hawkins, 1981a; Hawkins, 1981b). On the low shore beneath the *Fucus serratus* canopy, patches of *Cladophora*- or *Laurencia*-dominated turf provide refuges from grazing. In addition, recruitment is aided by the irregular growth form of the calcareous encrusting alga P. *purpureum* (Figueiredo, 1993). Rough substrata provides a refuge from grazers other than *Patella*: for example encrusting algae provide *Fucus* germlings with the initial refuge from grazing by *Littorina littorea* (Lubchenco, 1980; Lubchenco, 1983)

Janke (1990) demonstrated that doubling the natural density of *Littorina littorea* (the dominant grazer) effectively prevented the recruitment of *Fucus serratus* and inhibited growth low on the shore in Helgoland. No such manipulations of limpets were made in my work. However it would be interesting to determine whether elevated densities could effectively prevent *Fucus serratus* recruitment. It would seem from descriptive work in the British Isles (e.g. Lewis, 1964) that low levels on rocky shores are effectively algal dominated. The ability of algae to grow rapidly at low levels on the shore means that some escapes from limpet grazing are inevitable whatever the limpet density.

3.4.3 The effects of patch size

Patch size had no discernible effect on the species composition of colonists or the rate or progress of succession. One would expect the neighbouring canopy to exert a greater influence on small patches through shading and possibly competition for nutrients. However, the design of the experiment in trimming neighbouring plants to prevent sweeping effects may have moved the surrounding community too far back from the experimental area to exert a significant influence. The lack of any patch size effect may indicate that the exposure of the whole of each plot (both small and large) at low water was of prime importance, and that greater shading in small plots when immersed was insignificant in comparison.

If the neighbouring canopy was exerting a shading effect on patches one would expect to observe a difference between the edge and the middle of patches, especially in large plots. Although not specifically examined, no difference was observed. Farrell (1989) separately sampled the edge and the centre of gaps in a high intertidal community of algae and barnacles and found no effect of position within a patch on the species composition of recruiting algae. However, density of limpets was higher at gap perimeters. Farrell (1989) considered that herbivores may avoid the interior of gaps because 'the post disturbance community has little structural complexity'. In my work in plots where the canopy was removed, limpets showed no preference for either the interior or perimeter of the patch although there was an initial decline in limpet density overall. This decline may have resulted from initial mortality or emigration from the patch. No evidence of mortality was found and it should be concluded that canopy removal stimulated some individuals to move to positions beneath the undisturbed canopy. It may be significant that the greatest decline occurred in small plots, where limpets had only a short distance to move to regain canopy shelter. The results of Hill (1993) and Hawkins and Harkin (1985) suggest that lower on the shore or in areas of lower grazing density, patch size may have an effect on community structure since limpets at the patch perimeter or in the neighbouring community may continue to exert an influence in small patches after the exclusion of limpets by algal swamping.

CHAPTER 4

Population dynamics of *Patella vulgata* on sheltered shores

4.1 INTRODUCTION

The importance of grazing by *Patella vulgata* in structuring rocky shore communities of northwest Europe has been recognised since the classic limpet removal experiment of Jones (1948). As a result, the population dynamics of this species has received considerable attention (Fischer-Piette, 1948; Jones, 1948; Ballantine, 1961b; Lewis and Bowman, 1975; Bowman and Lewis, 1977; Thompson, 1980; Baxter, 1982; Hawkins and Hartnoll, 1982a; Hawkins *et al.*, 1983; Bowman and Lewis, 1986). Most work has been carried out on exposed or moderately exposed shores and little attention has been focused on changes in population dynamics across the wave exposure gradient. Thompson (1980) made a study of *Patella vulgata* which specifically focused on the effects of exposure to wave action, although even in this study, sheltered shores, which support a dense canopy of *Ascophyllum* were relatively neglected. It is generally accepted that the density of *Patella vulgata* decreases with increasing shelter (Fischer-Piette, 1948; Jones, 1948; Southward, 1953; Ballantine, 1961b; Lewis, 1964; Thompson, 1980). Thompson (1980) recorded a sharp decline in limpet density on shores classified under Ballantine's (1961a) exposure scale as grade 7. Such shores are described as very sheltered, with a continuous cover of fucoids over most of the shore and *Ascophyllum* covering most of the midlittoral bedrock. Jones (1948) working in the south of the Isle of Man found a mean density of *Patella vulgata* of $31/m^2$ under thick *Ascophyllum* compared to $95/m^2$ on rock and barnacles. Whilst density of *Patella vulgata* populations appear to be lower on sheltered fucoid dominated shores, observations suggest that individuals can reach a greater size (Fischer-Piette, 1948; Jones, 1948; Southward, 1951). These changes in density and size distribution of *Patella vulgata* with exposure to wave action should be attributable to variation in one or more of the processes controlling population dynamics, namely recruitment, growth and mortality rates.

Recruitment levels will have a major impact on population density. Variation in recruitment over the wave exposure gradient may occur owing to variation in supply, settlement or post settlement mortality. *Patella vulgata* usually spawns in the late autumn although considerable variation in the onset and duration of the spawning period does exist (Lewis and Bowman, 1975). Bowman and Lewis (1986) report a geographical gradient in the timing of the main gametic release from August/ September in northern Scotland to November in south-west England. Little is known regarding the distribution of limpet larvae following fertilisation because of the failure to collect (or to identify) larvae in plankton trawls (Ballantine, 1961b; Bowman and Lewis, 1977). Therefore, variation in larval supply has not been investigated.

When settlement occurs, probably in autumn or early winter, limpet larvae are only 0.2mm in size (Smith 1935). This makes measurements of settlement to natural surfaces in the field impractical. Limpet spat appear to prefer to settle in shallow pools or damp situations such as crevices (Orton, 1929; Jones, 1948; Lewis and Bowman, 1975). Whether this observation is a reflection of larval choice or is simply an indication of early mortality in less favourable habitats such as dry bare rock is unclear. Whatever the reason, the distribution of suitable settling or nursery sites, especially higher on the shore, will affect recruitment success and so population density (Jones, 1948). Ballantine (1961b) reported that spat less than 6 months old or less than 2mm in length died if the surface to which they were attached dried out for more than a few minutes.

The suitability of settlement sites is not solely determined by the physical topography of the rock surface. Both barnacles (Lewis and Bowman, 1975; Branch, 1976; Hawkins and Hartnoll, 1982a) and mussels (Lewis and Bowman, 1975) have been shown to enhance recruitment of *Patella* species on exposed shores, presumably by providing cryptic habitats where humidity is higher and temperature extremes less. Areas cleared of barnacles dried out far more quickly than neighbouring barnacled rocks (Ballantine, 1961b).

Research has indicated the importance of fucoid canopy cover in determining recruitment success. However, its effect is far from clear and observations of recruitment levels under a fucoid canopy have often not been related to the level of exposure. It is apparent from experimental work that recruitment of fucoid algae to exposed shores results in increased recruitment of *Patella vulgata.* Southward (1956) reported large numbers of limpets (up to a six fold increase) amongst the *Fucus* canopy resulting from the limpet removal experiment of Jones (1948). This increase was attributed to increased recruitment rather than immigration of limpets from neighbouring areas. Similar observations were made by Southward and Southward (1978) following the widespread mortality of limpets due to dispersant spraying after the Torrey Canyon oil spill (see also Hawkins *et al.*, 1983; Hawkins and Southward, 1992). Thompson (1980) states that the establishment of fucoid cover seems to create particularly favourable conditions for limpet settlement, survival and growth and large limpet populations may result. However, in the same paper the author observes that on sheltered shores (Ballantine's grade 7) which are dominated by an almost continuous cover of fucoids, juveniles are very rare. These apparently contradictory observations may be reconciled by the conclusions of Lewis and Bowman (1975). They consider the influence of a *Fucus* canopy to be two fold, limited amounts promoting recruitment because of the reduction of desiccation, especially in the mid and upper levels, and a heavy perennial cover directly causing a reduction in recruitment either through a screening or a dislodging effect. At Robin Hoods Bay, North Yorkshire, density of *Patella vulgata* spat beneath a dense perennial cover of *Fucus* was less than 6/m^2. Fischer Piette (1948) also considered a carpet of fucoids to form a mechanical obstacle to settlement of limpet larvae.

The growth rate of *Patella* will depend on a number of factors but the amount of feeding space available per limpet is obviously important (Jones, 1948). This will depend to a large extent on the density of competing limpets and has been demonstrated experimentally by Lewis and Bowman (1975). Despite this, Lewis and Bowman (1975) consider the general contention of an inverse relationship between *Patella* density and growth or size to be an oversimplification because of the effect of other species such as barnacles and macroalgae on the amount of feeding space available. Barnacles have been shown to cause a reduction in growth rate of *Patella vulgata* (Lewis and Bowman, 1975; Thompson, 1980; Hawkins and Hartnoll, 1982a) presumably owing to the difficulty in moving and grazing over and between them and the consequent reduction in quality feeding space. A reduction in the availability of spores and sporelings caused by the filter feeding of barnacles has also been suggested as a contributory factor (Ballantine, 1961b; Branch, 1976).

Available evidence suggests that the presence of a fucoid canopy enhances the growth rate of *Patella vulgata* (Jones, 1948; Southward, 1956; Lewis and Bowman, 1975). Jones (1948) recorded *Patella vulgata* juveniles in March 1948 to have a mean length of 6.5mm under *Ascophyllum* compared to only 2.4mm amongst barnacles, whilst Southward (1956) considered the shell shape of limpets under a fucoid canopy to indicate rapid growth under favourable conditions (i.e. damp and ample food). The damp environment beneath a canopy at low water may allow limpets to increase the period over which they can forage. Within a single biological habitat growth rate is higher at low tide levels (Lewis and Bowman, 1975). This indicates that the amount of time available for feeding may be as critical as the amount of space available to feed in.

Data on the mortality rates of *Patella vulgata* are not extensive. This is probably a result of the difficulties of establishing whether limpets under observation have died or simply moved away from the study area. Predation by seabirds, mainly oystercatchers, exerts ‘an erratic and local influence’ on *Patella* populations (Lewis and Bowman, 1975). Most mortality appears to occur naturally with no known external causes, individuals possibly dying of 'old age'(Ballantine, 1961b; Lewis and Bowman, 1975; Thompson, 1980). In limpets dying of natural causes, longevity appears to be inversely related to growth rate. Again no work has directly analysed survival over the wave exposure gradient, although Thompson (1980) presents tentative survival curves for two and three year old *Patella vulgata* indicating that fucoids may increase survival.

Given the lack of research examining the population dynamics of *Patella vulgata* in very sheltered localities which support a dense canopy of *Ascophyllum*, I attempted to investigate some aspects of this at mid tide level on sheltered shores of the Isle of Man. Initially however, the population structure was investigated along a wave exposure gradient at three tidal heights. This survey aimed to establish if changes in density and number of juveniles along vertical and horizontal gradients existed. Subsequently experimental work was planned to attempt to shed some light on the observed patterns of distribution, abundance and population structure.

The *Ascophyllum* canopy was shown in Chapter 2 to have a pronounced effect on the understorey community on sheltered shores. Here its effect on the recruitment, growth rate and mortality of *Patella vulgata* was examined in a canopy removal experiment. A simultaneous investigation of *Patella vulgata* ecology on more exposed shores was carried out by B. Wilson. Use of some data from this study enabled a comparison of growth rate between sheltered and exposed shores to be made.

On sheltered shores beneath an *Ascophyllum* canopy, limpets are distributed in patches of bare substratum surrounded by red algal turf. The relationship between patch size and limpet number was examined, and an attempt was made to examine this relationship further by manipulating the density of adult and juvenile limpets. This also provided information on the effect of density on growth rate and survival beneath an *Ascophyllum* canopy.

Thus the specific aims of this chapter were:

1) To describe the density and population structure of *Patella vulgata* across vertical and horizontal gradients.
2) To determine the effect of the *Ascophyllum* canopy on levels of recruitment, growth and mortality in *Patella vulgata*.
3) To compare growth rates of *Patella vulgata* between sheltered and exposed shores.

4.2 METHODS

4.2.1 Descriptive sampling-limpet population structure across the wave exposure gradient

The stretch of rocky shore from Castletown Bay to Scarlett Point covers a gradient of exposure to wave action from sheltered in Castletown Bay to moderately exposed at Scarlett Point. The rock is consistent in its geology and the shore maintains a similar topography (gently sloping benches) along its length. It was therefore considered a suitable shore to examine the change in density and population structure of limpets with exposure to wave action.

In November 1992 three sites were chosen to represent the range of exposure along this coast; exposed at Scarlett Point, sheltered at Castletown Bay and intermediate exposure, roughly equidistant between the two extremes (Figure 4.1).

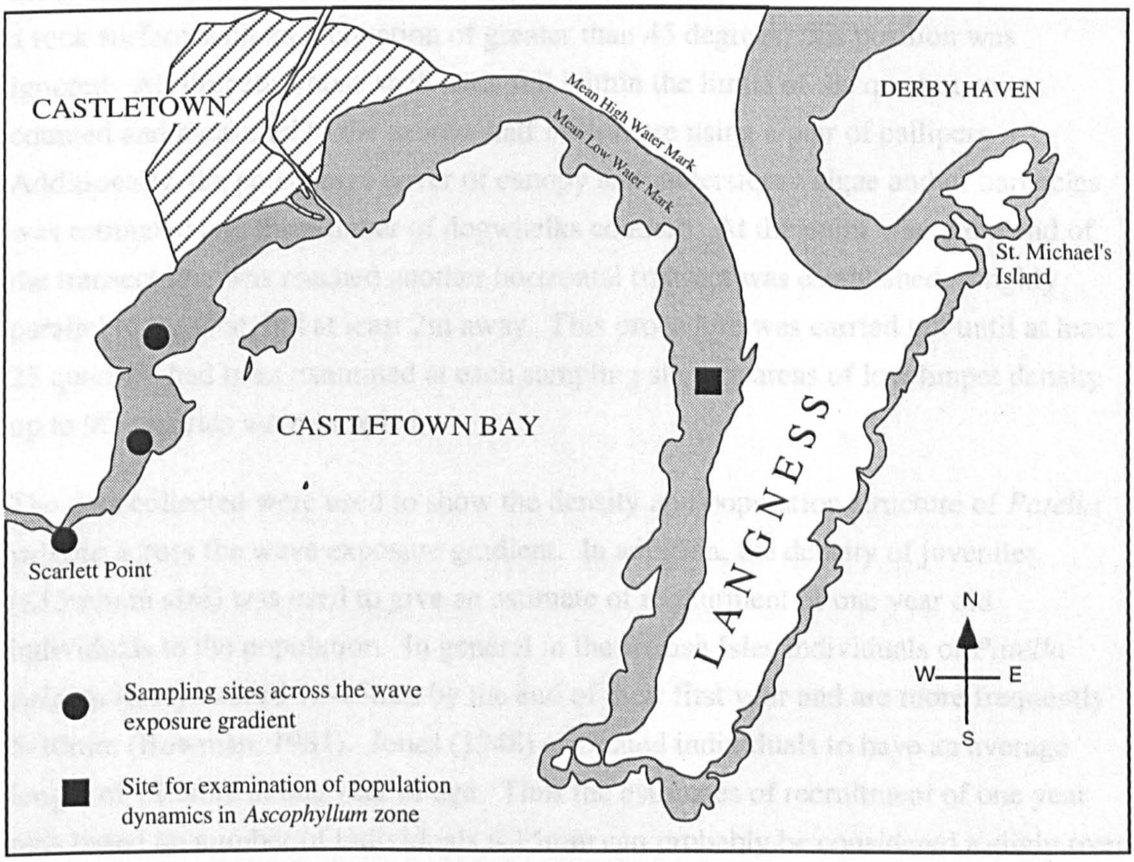


Figure 4.1 Map of Castletown Bay showing *Patella vulgata* sampling sites.

Three levels on the shore were chosen in order to examine vertical as well as horizontal variation. These levels were initially determined at the sheltered site to correspond to:

1) the upper section of the *Fucus serratus* zone (low)
2) the middle of the *Ascophyllum* zone (mid)
3) the middle of the *Fucus spiralis* zone (high).

Equivalent tidal heights at the intermediate and exposed sites were determined by noting the position of the tide when it corresponded to the designated low, mid and upper heights at the sheltered shore. The height of these three points on the shore was later measured as 2.3, 4.1 and 5.0m above C.D.

At each sampling point the following procedure was adopted to survey the limpet population and give an indication of algal and barnacle cover. A horizontal transect was established by eye and covered no more than 50m. Using a random number table, numbers were selected between 1 and 5. This list of numbers was used to determine the position of a 0.5 x 0.5m quadrat by pacing the appropriate number of steps along the transect. Whenever the quadrat or part of the quadrat fell within a rockpool or on a rock surface with an inclination of greater than 45 degrees, this position was ignored. All limpets whose shell apex fell within the limits of the quadrat were counted and measured to the nearest half millimetre using a pair of callipers. Additionally, the percentage cover of canopy and understorey algae and of barnacles was estimated and the number of dogwhelks counted. At the point where the end of the transect line was reached another horizontal transect was established, roughly parallel to the first, but at least 2m away. This procedure was carried out until at least 25 quadrats had been examined at each sampling site. In areas of low limpet density up to 90 quadrats were sampled.

The data collected were used to show the density and population structure of *Patella vulgata* across the wave exposure gradient. In addition, the density of juveniles (≤15mm in size) was used to give an estimate of recruitment of one year old individuals to the population. In general in the British Isles individuals of *Patella vulgata* rarely exceed 12-15mm by the end of their first year and are more frequently 5-10mm (Bowman, 1981). Jones (1948) estimated individuals to have an average length of 12.5mm at one year of age. Thus the estimates of recruitment of one year olds based on number of individuals ≤ 15mm can probably be considered a slight over estimate.

4.2.2 Limpet larval supply

An attempt was made in the autumn of 1992 to examine possible variation in the supply/settlement of limpet larvae across the wave exposure gradient described above (Scarlett Point to Castletown Bay). Variation in substrate type was eliminated as an influencing factor by the use of settlement tiles. Use of such tiles proved successful in analysing limpet settlement in research carried out in Robin Hoods Bay, North Yorkshire. The important feature of the tiles used in this research was the presence of grooves (c. 2mm wide and deep) in the tile surface and the location of the tiles in a permanently wet location (pers. comm. Mike Kendall).

An epoxy adhesive (Sikadur 31 Rapid) was chosen to manufacture grooved tiles which could be screwed to the rock surface on the shore. Twenty four tiles, measuring 13 x13 cm, with grooves approximately 2mm deep and 3mm wide running across the surface, were produced using a mould created from Silastic rubber. The epoxy adhesive was mixed and poured into the mould, and a synthetic roof tile cut to size placed onto the adhesive to create a stiff backing plate. The mould and filling was then placed into an oven at 60°C and left for 30 minutes. The single mould was used to create all 24 tiles. When fully hardened a single hole was drilled through the centre of each tile through which it could be screwed to the shore.

On 29th October 1992 three locations were chosen, Scarlett Point (exposed), Castletown Bay (sheltered) and a position between (intermediate). At each location 8 shallow lithothamnia covered pools were selected at mid shore level. Such pools not only provide attractive settlement sites for limpet larvae, but they also support more stable communities than open rock surfaces and thus are suitable for long term observations on limpet settlement (Bowman and Lewis, 1986). In each pool a settlement tile was screwed to the rock surface using a single screw.

The tiles were left in place over the winter and examined on the shore in February and March for the presence of juvenile limpets. On May 19th 1993 all the tiles were collected and examined under a dissecting microscope in the laboratory.

4.2.3 Growth rate, recruitment and mortality of *Patella vulgata* on sheltered shores

The effect of removing the *Ascophyllum* canopy on the recruitment, growth and mortality of *Patella vulgata* in the mid shore at Langness was investigated. As described in Chapter 2, the limpets in the *Ascophyllum* zone of the sheltered shores studied were distributed in discrete patches of grazed substrate within a red algal turf.

This provided ideal conditions for examination of the population dynamics of limpets. The problem faced by many researchers of 'losing' limpets because of migration was not encountered. Movement from their discrete patches of 'bare substrate' was prevented by the thick, sediment-filled algal turf.

Nine such patches, varying in size from 0.016 to 0.239m^{2,} were chosen beneath the *Ascophyllum* canopy Their position was marked by attaching a long length of Twinglow tape to the base of a neighbouring *Ascophyllum* plant using a cable tie. In addition, five discrete patches varying in size between 0.06 and 0.44 m^2 were chosen from within three canopy removal plots (measuring 2 x 2m) used in the experiment described in Chapter 2. All limpets measuring over 25 mm in size in the designated patches were marked. This marking and any subsequent remarking was carried out on a dry day on which the limpets shells (once uncovered by moving the canopy aside) could dry out as much as possible. Once dry, a file was used to remove a small amount of material from the shell apex to create a smooth clean patch. Onto these an individually numbered 'micromarker' was glued using Bison's hard plastic adhesive. Limpets below 25 mm were not marked in this way because of their small size and more fragile shell (see Ballantine, 1961b).

All limpets (marked and unmarked) in the designated patches were measured to the nearest half mm in November 1992. Subsequent sampling took place at approximately six month intervals over the following two years. At these sampling dates limpets were remeasured and notes made of new recruits and levels of mortality. Occasionally relabelling was required when original micromarkers were lost. Although limpets under 25 mm were not individually marked, the relatively small number of limpets within each patch meant that unmarked individuals could be recognised on the basis of size. Since all limpets could be individually recognised, and immigration and emigration were prevented by a boundary of algal turf, recruitment and mortality could be easily and accurately recorded.

4.2.4 Juvenile limpet transplant

In February/March 1994 an experiment was established at Langness to examine the survival and growth rates of juvenile limpets on sheltered shores, and to determine the effect of adult limpets on these factors. In addition, the survival of juveniles on exposed shores where the *Ascophyllum* canopy is absent was examined using artificial enclosures. The low number of juvenile limpets in the mid shore of sheltered sites necessitated transplanting juveniles from a low exposed site where they were plentiful. Transplanting enabled uniformly high densities of juveniles to be placed in the desired locations.

Ten patches of bare substrate beneath a dense *Ascophyllum* canopy were selected. All patches were between 0.09 and 0.14 m^2 in size and had a limpet density of between 74 and 165 limpets/m^2. In five of the patches all limpets were removed. The barrier effect of the algal turf was imitated on an exposed shore at Port St. Mary ledges in order to produce artificial patches from which limpets could not escape. A plastic doormat was cut into strips, and the strips screwed to the rock surface to form a square enclosure with an area of approximately 0.1 m^2. Five such enclosures were created in the mid shore zone at Port St. Mary (the same shore level as the patches at Langness). Any adult limpets present within the enclosure were removed.

Approximately 450 juvenile limpets with lengths between 10-15mm were carefully removed with a knife from the low shore at Port St. Mary ledges. These were placed in a plastic bucket and 300 transported to Langness where 30 were placed in each of the ten patches. The remaining 150 juvenile limpets were distributed between the five artificial enclosures on the mid shore at Port St. Mary. Five days after the transplant of limpets, the patches at Langness and enclosures at Port St. Mary were examined. Survival rates of the transplant were good, but in some patches up to half had died. In order to achieve equality between patches and treatments the number of juvenile limpets was reduced to 15 within each. The shell lengths were then measured.

The limpets were counted and remeasured on four occasions, 3, 6, 10 and 45 weeks after the establishment of the experiment.

4.3 RESULTS

4.3.1 Descriptive sampling: limpet population structure across the wave exposure gradient

The density of *Patella vulgata* across the wave exposure gradient followed a consistent pattern at all three tidal heights, density decreasing with increasing shelter from wave action (Figure 4.2). This was most pronounced at the mid shore level, density decreasing from 39.0 limpets/m^2 at Scarlett Point, the exposed site, to only 8.6 limpets/m^2 in Castletown Bay, the sheltered site. Cochrans test revealed data to be heteroscedastic even after transformation, so the non parametric Kruskal Wallis test, was applied. This showed a significant effect of exposure on limpet density at all three tidal heights (Table 4.1). At each exposure, densities were similar at the low and mid tidal levels, but lower on the high shore. At the sheltered site limpets were almost absent from the high tidal level with a density of only 0.9/m^2. A Kruskal Wallis test showed a significant effect of tidal height at each exposure (Table 4.2).

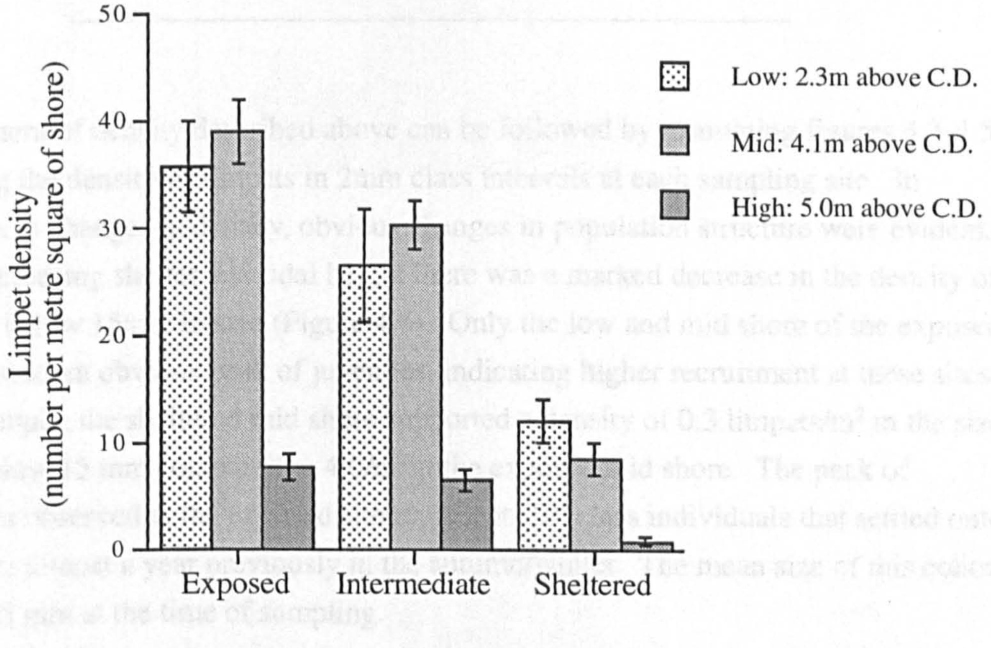


Figure 4.2 Density of *Patella vulgata* at three shore heights across the wave exposure gradient in November 1992. Error bars = ± 1SE.

Table 4.1 Kruskal Wallis test for differences in the density of *Patella vulgata* over the wave exposure gradient at three shore heights

Shore Height	df	H	P-Value
Low	2	21.61	<.001
Mid	2	73.19	<.001
High	2	36.48	<.001

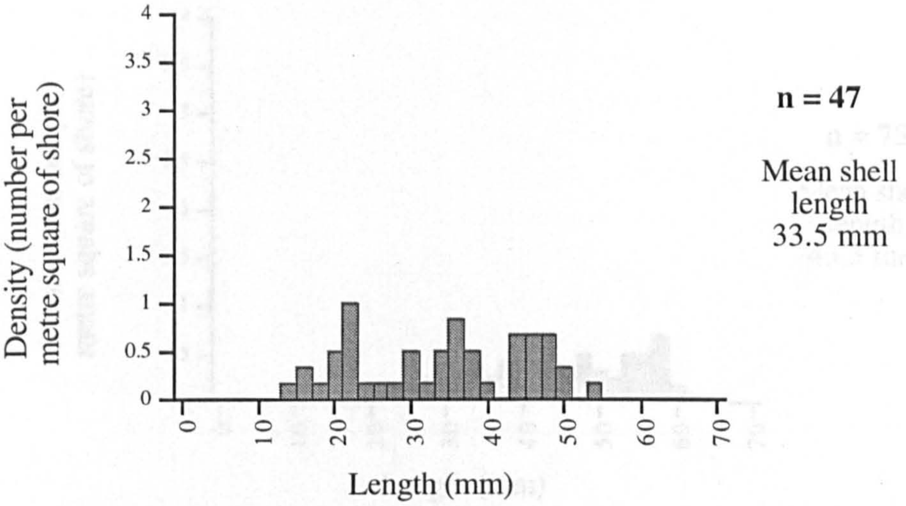
Table 4.2 Kruskal Wallis test for the effect of tidal height on the density of *Patella vulgata* at three levels of exposure

Exposure level	df	H	P-Value
Exposed	2	40.82	<.001
Intermediate	2	50.29	<.001
Sheltered	2	36.85	<.001

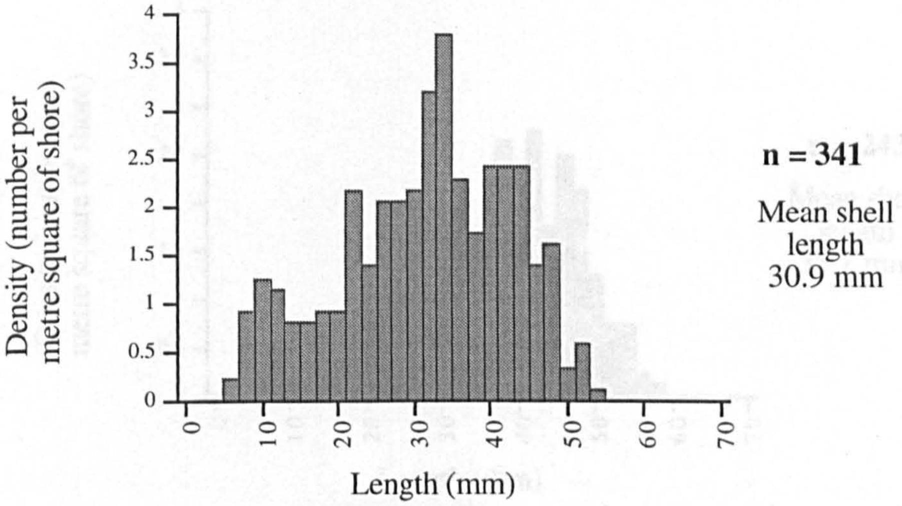
The pattern of density described above can be followed by examining figures 4.3-4.5 showing the density of limpets in 2mm class intervals at each sampling site. In addition to changes in density, obvious changes in population structure were evident. With increasing shelter and tidal height there was a marked decrease in the density of limpets below 15mm in size (Figure 4.6). Only the low and mid shore of the exposed site showed an obvious peak of juveniles, indicating higher recruitment at these sites. For example, the sheltered mid shore supported a density of 0.3 limpets/m^2 in the size class below 15 mm compared to 4.6/m^2 at the exposed mid shore. The peak of juveniles observed at the exposed site represents '0' class individuals that settled onto the shore almost a year previously in the autumn/winter. The mean size of this cohort was 10.5 mm at the time of sampling.

Mean limpet lengths at each sampling position are presented in figures 4.3-4.5. With the exception of the sheltered mid shore, mean limpet sizes appeared to reflect the increase in density of juveniles with increasing exposure. At exposed sites, where juveniles were common, the mean size was relatively low. However, this may also partly be due to a larger maximum size and a general shift in size distribution towards larger limpets in more sheltered sites. The absence of this pattern at the sheltered mid shore will be discussed later.

a) High shore



b) Mid shore



c) Low shore

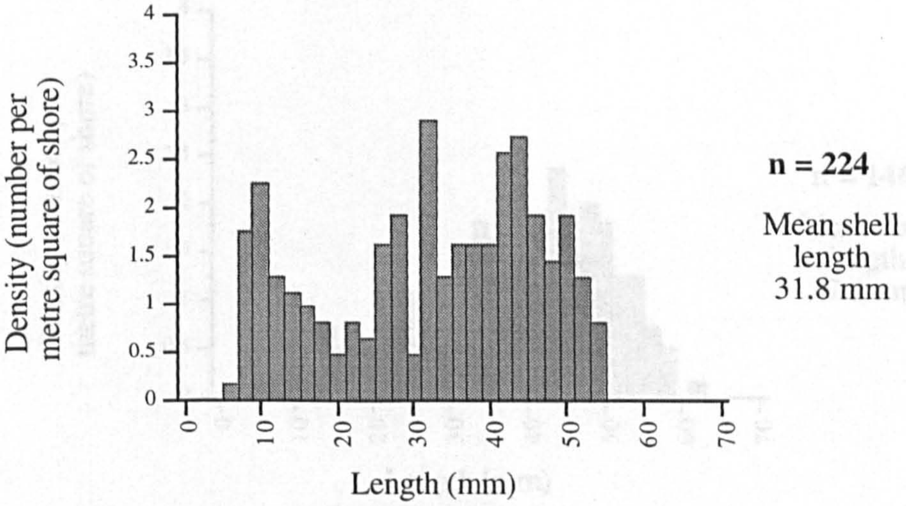
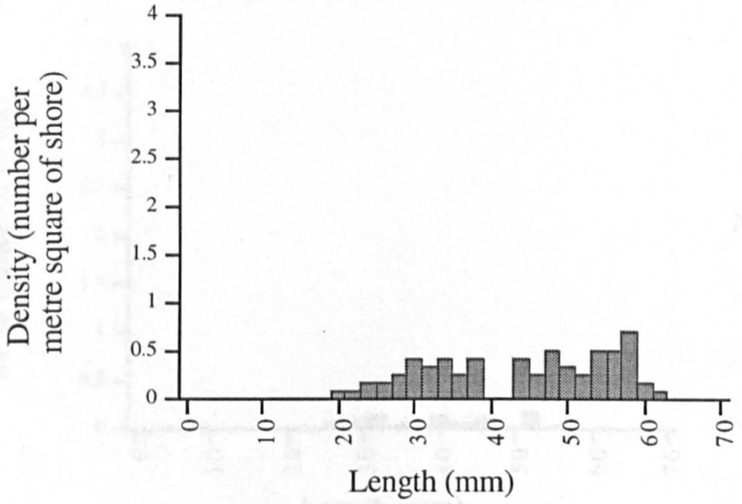


Figure 4.3 Population structure of *Patella vulgata* at an exposed site (Scarlett Point) in November 1992
a) High shore b) Mid shore c) Low shore
N.B. **n** indicates number of limpets measured

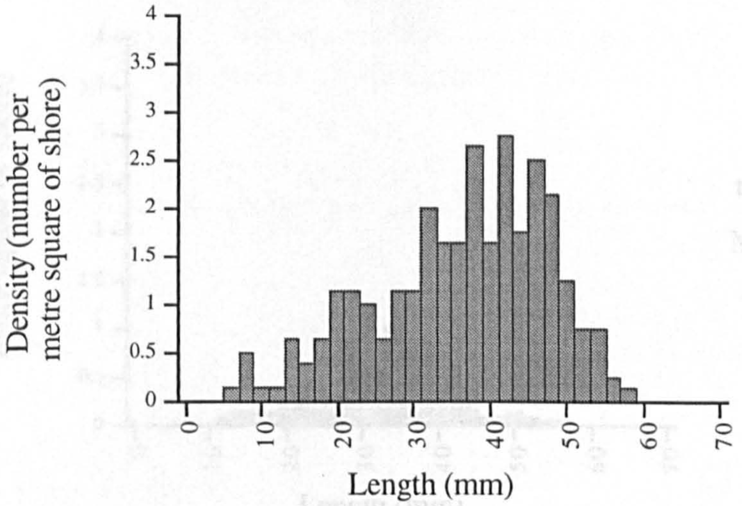
a) **High shore**



n = 75

Mean shell length 43.3 mm

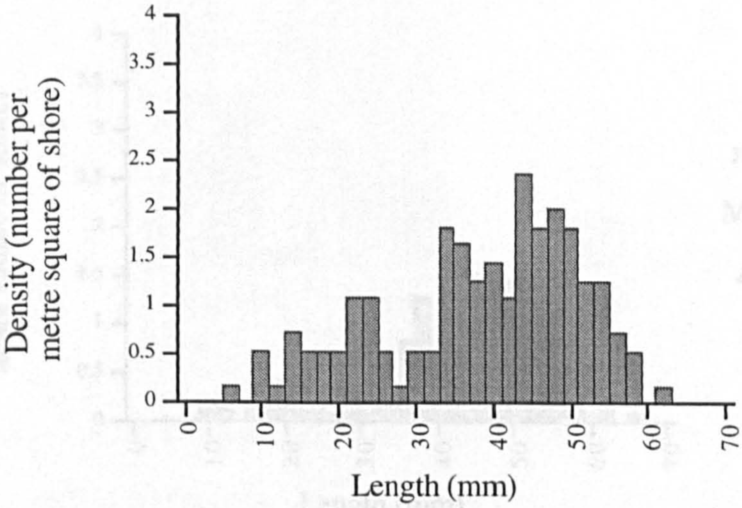
b) **Mid shore**



n = 243

Mean shell length 35.7 mm

c) **Low shore**

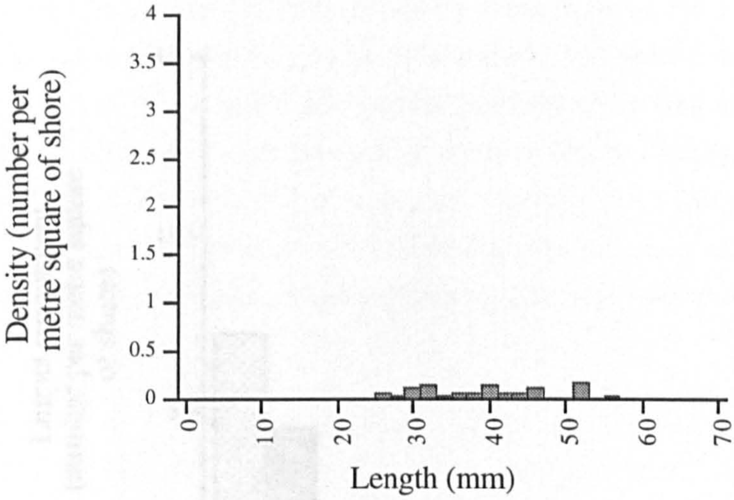


n = 146

Mean shell length 37.8 mm

Figure 4.4 Population structure of *Patella vulgata* at a site of intermediate exposure in November 1992.
a) High shore b) Mid shore c) Low shore
N. B. n indicates number of limpets measured

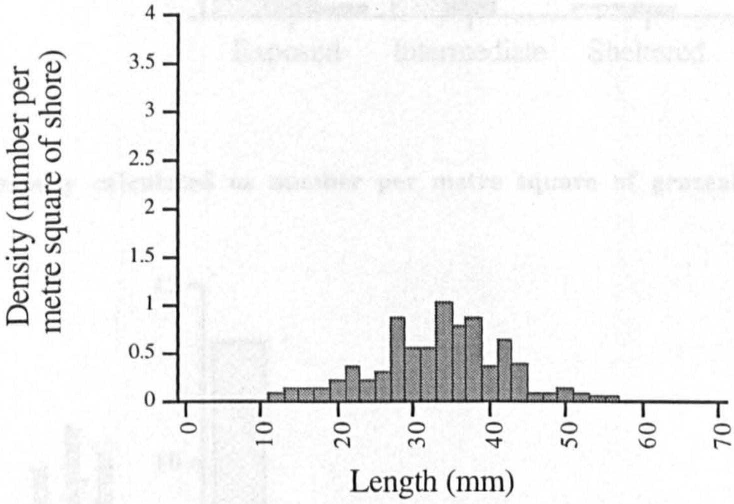
a) High shore



n = 32

Mean shell length 39 mm

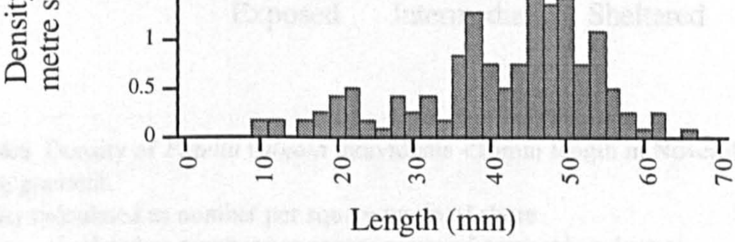
b) Mid shore



n = 187

Mean shell length 32.9 mm

c) Low shore

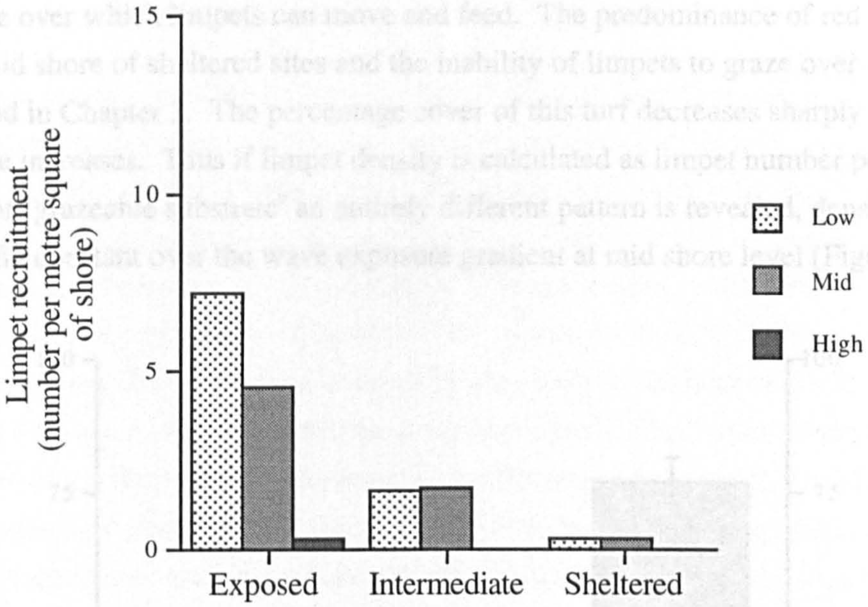


n = 174

Mean shell length 41.3mm

Figure 4.5 Population structure of *Patella vulgata* at a sheltered site (Castletown Bay) in November 1992
a) High shore b) Mid shore c) Low shore
N.B. **n** indicates number of limpets measured

a) Density calculated as number per metre square of shore



b) Density calculated as number per metre square of grazeable substrate

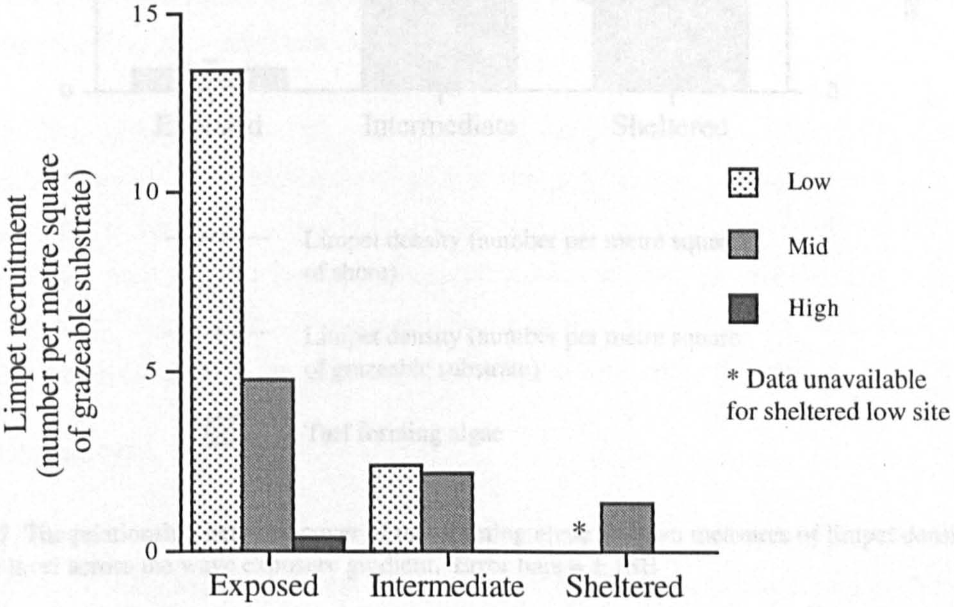


Figure 4.6 Density of *Patella vulgata* individuals <15mm length in November 1992 across a wave exposure gradient.
a) Density calculated as number per square metre of shore
b) Density calculated as number per square metre of grazeable substrate.

The decrease in density of *Patella vulgata* in the mid shore across the wave exposure gradient is described clearly above. However, this description of density does not take into account the area of substrate available to the limpet i.e. the area of grazeable substrate over which limpets can move and feed. The predominance of red algal turf in the mid shore of sheltered sites and the inability of limpets to graze over it has been described in Chapter 2. The percentage cover of this turf decreases sharply as exposure increases. Thus if limpet density is calculated as limpet number per metre square of 'grazeable substrate' an entirely different pattern is revealed, density remaining constant over the wave exposure gradient at mid shore level (Figure 4.7).

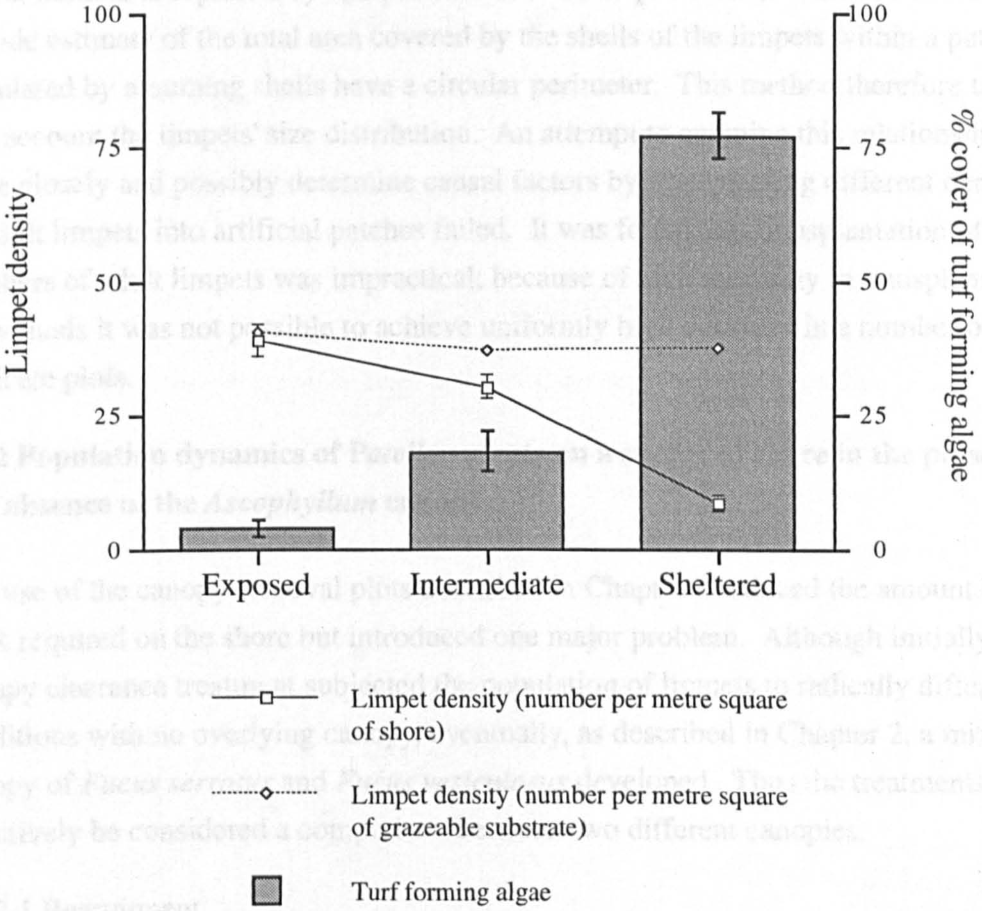


Figure 4.7 The relationship between cover of turf forming algae and two measures of limpet density at mid shore level across the wave exposure gradient. Error bars = ± 1SE

Some clarification of the method used to calculate this density measurement should be given. The initial approach taken, that of calculating density within each quadrat and then finding the mean was found to be influenced greatly by a few very high densities. These were obtained where a number of limpets were found in a relatively small area of grazeable substrate and were often simply an artefact caused by the random positioning of the quadrat. To counter this problem, the number of limpets within all quadrats was summed and divided by the total area of grazeable substrate sampled. This measure gave a true indication of density per square metre of grazeable substrate but unfortunately suffered from the lack of any error term.

A closer examination of the density and distribution of limpets at mid tide level on a sheltered shore revealed a relationship between the area of a patch of bare substrate and the number of limpets within that patch (Figure 4.8). Analysis reveals a significant correlation between the two variables (Pearson's product moment correlation coefficient $r = 0.748$ $p < 0.001$). The correlation coefficient is increased if limpet number is replaced by 'limpet area' ($r = 0.861$ $p < 0.001$). This measurement is a crude estimate of the total area covered by the shells of the limpets within a patch, calculated by assuming shells have a circular perimeter. This method therefore takes into account the limpets' size distribution. An attempt to examine this relationship more closely and possibly determine causal factors by transplanting different densities of adult limpets into artificial patches failed. It was found that transplantation of large numbers of adult limpets was impractical; because of high mortality in transplanted individuals it was not possible to achieve uniformly high densities in a number of replicate plots.

4.3.2 Population dynamics of *Patella vulgata* on a sheltered shore in the presence and absence of the *Ascophyllum* canopy

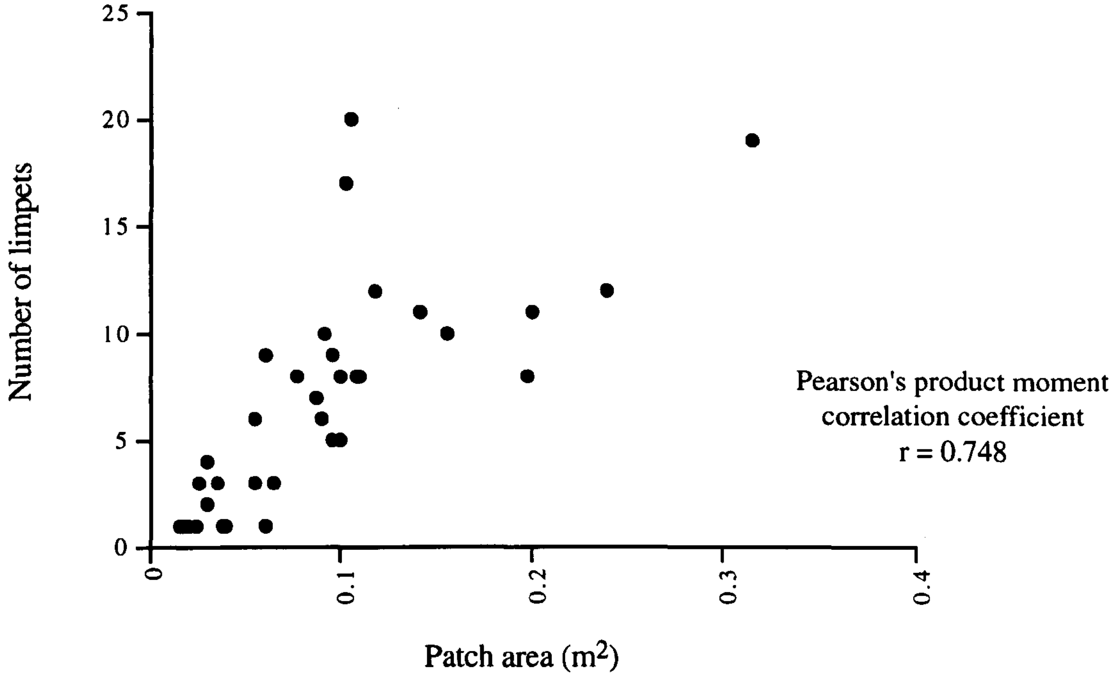
The use of the canopy removal plots described in Chapter 2 reduced the amount of work required on the shore but introduced one major problem. Although initially the canopy clearance treatment subjected the population of limpets to radically different conditions with no overlying canopy, eventually, as described in Chapter 2, a mixed canopy of *Fucus serratus* and *Fucus vesiculosus* developed. Thus the treatments may effectively be considered a comparison between two different canopies.

4.3.2.1 Recruitment

Recruitment of juvenile limpets to the two treatments, calculated as number per metre square of bare substrate, was almost identical over the period of observation. 5.56 juveniles/m^2/year recruited beneath an intact canopy compared with 5.33 to cleared plots. All except one recruit survived to one year of age.

However, recruitment, calculated as a percentage of limpet numbers present at the beginning of each year, reveals a different pattern (Figure 4.9). A higher level of recruitment was found where the canopy was cleared (One way ANOVA: Year 1 p=0.024, Year 2 p= 0.07). This apparent anomaly may be explained by examining the

a) Relationship between patch area and limpet number



b) Relationship between patch area and area covered by limpet shells

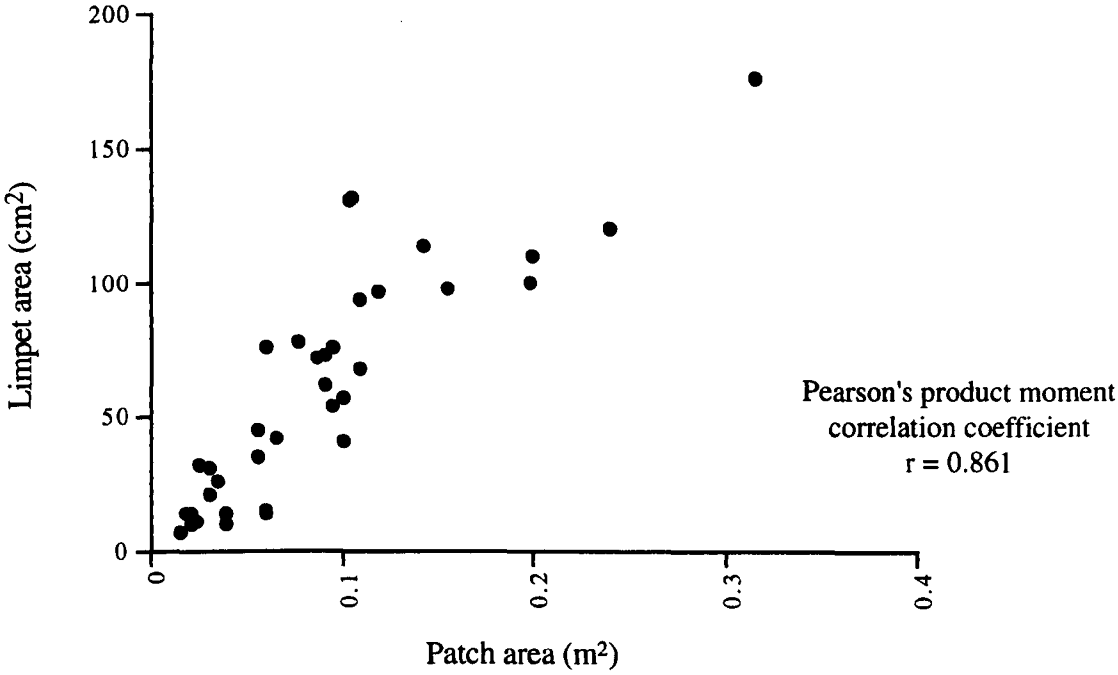


Figure 4.8 Descriptive data on patches of bare substrate occurring on the mid shore of a sheltered site at Langness beneath a dense *Ascophyllum* canopy.
a) Relationship between patch area and limpet number
b) Relationship between patch area and area covered by limpet shells.

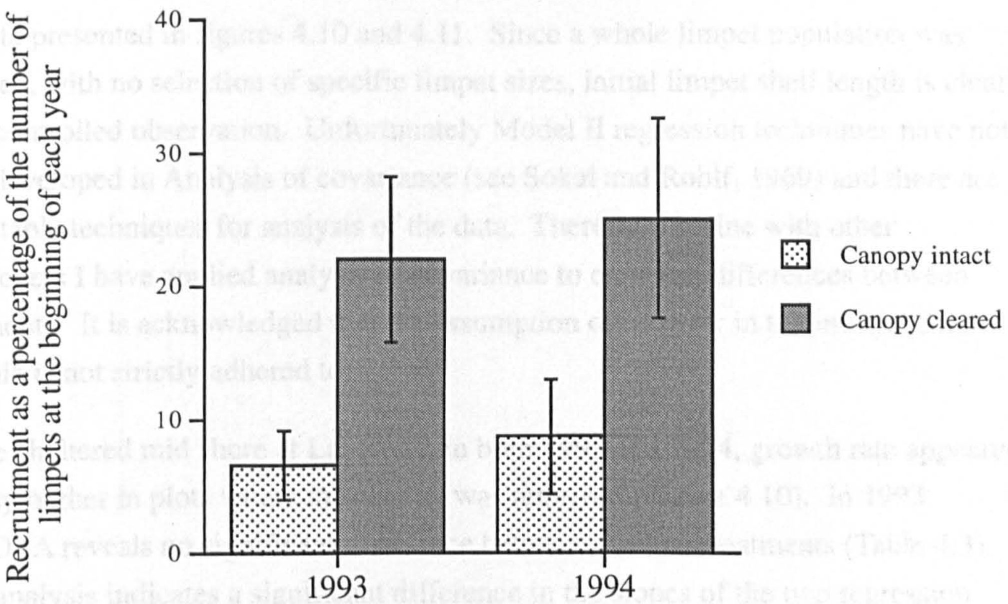


Figure 4.9 Recruitment of *Patella vulgata* on the mid shore of a sheltered site (Langness) in canopy intact and canopy cleared treatments. Error bars = ± 1SE

change in area of bare substrate under study over the period of the experiment. Initially, total area of bare substrate was approximately equal in both treatments. These areas supported similar limpet populations. The large increase in patch size (approximately two fold) in plots cleared of canopy has been described in Chapter 2. A large area for settlement of limpet larvae combined with a population size still at the level appropriate to a much smaller area resulted in high percentage recruitment levels.

4.3.2.2 Growth rate

Growth was estimated by measuring the change in length of marked individuals over one year periods. Thompson (1980) used four methods to estimate growth in *Patella vulgata* but found this technique was the only one which was entirely satisfactory. Measurement of growth across the range of sizes within populations on both sheltered and exposed shores are shown in figures 4.10 and 4.11. Model I regression lines are shown with equations and r^2 values.

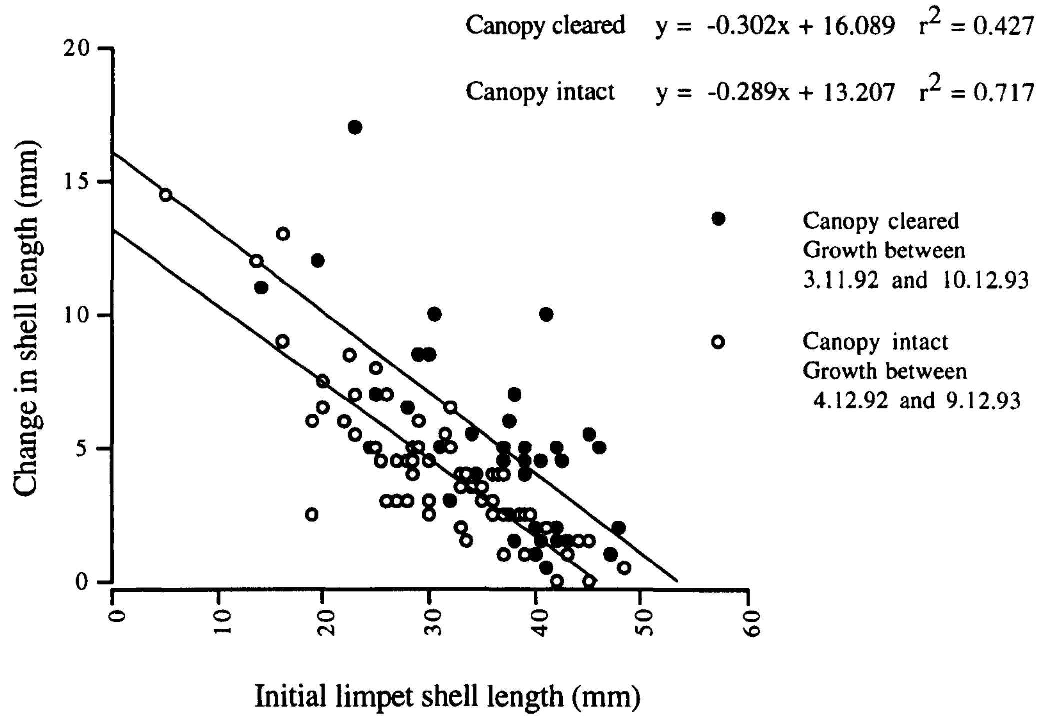
The main aim in examining limpet growth rates was to make comparisons between treatments and sites. Owing to the nature of the data certain problems arise in statistical analysis. Analysis of covariance is often utilised in the comparison of regression lines and is based on Model I regression. Model I makes certain assumptions of the data, one of which is that the independent variable is measured without error and under the control of the investigator. This is clearly not the case in the data presented in figures 4.10 and 4.11. Since a whole limpet population was sampled, with no selection of specific limpet sizes, initial limpet shell length is clearly an uncontrolled observation. Unfortunately Model II regression techniques have not been developed in Analysis of covariance (see Sokal and Rohlf, 1969) and there are no suitable techniques for analysis of the data. Therefore, in line with other researchers I have applied analysis of covariance to establish differences between treatments. It is acknowledged that the assumption of no error in the independent variable is not strictly adhered to.

On the sheltered mid shore at Langness, in both 1993 and 1994, growth rate appeared slightly higher in plots where the canopy was removed (Figure 4.10). In 1993 ANCOVA reveals no significant difference between the two treatments (Table 4.3). In 1994 analysis indicates a significant difference in the slopes of the two regression lines. However, examination of figure 4.10b shows this difference is probably simply due to a much wider spread of points in the canopy cleared treatment.

A comparison between the growth rate found on the sheltered shore at Langness, beneath an undisturbed canopy, and that measured at a moderately exposed site at Port St. Mary revealed a distinct difference. Growth rate was clearly greater at the exposed shore, Port St Mary (Figure 4.11a). This conclusion is supported by the results of ANCOVA which reveal a significant difference between the two sites (Table 4.4). In addition, the maximum size of individuals at Port St Mary was higher, with a number of limpets over 50mm in length. Using data from the canopy-cleared treatment at Langness reveals a less obvious pattern although growth rate still appears higher at the exposed site (Figure 4.11b). ANCOVA reveals a p value of 0.1 for the difference in sites.

Measurements of limpet density were made at the sites where growth rates were monitored. At Port St. Mary over the period of study (May 1993 to May 1994) density varied between 20.5 and 27.4 with a mean of 23.1/m^2 of shore. No data are available on the density per m^2 of grazeable substrate but observations at this site suggest it will not differ greatly from this value. At Langness, limpet density differed significantly between the two treatments because of the increase in area of bare substrate following canopy removal. Where the canopy was intact mean number of limpets per m^2 of grazeable substrate was 73.5/m^2, compared to only 22.9/m^2 where the canopy was cleared.

a) 1993



b) 1994

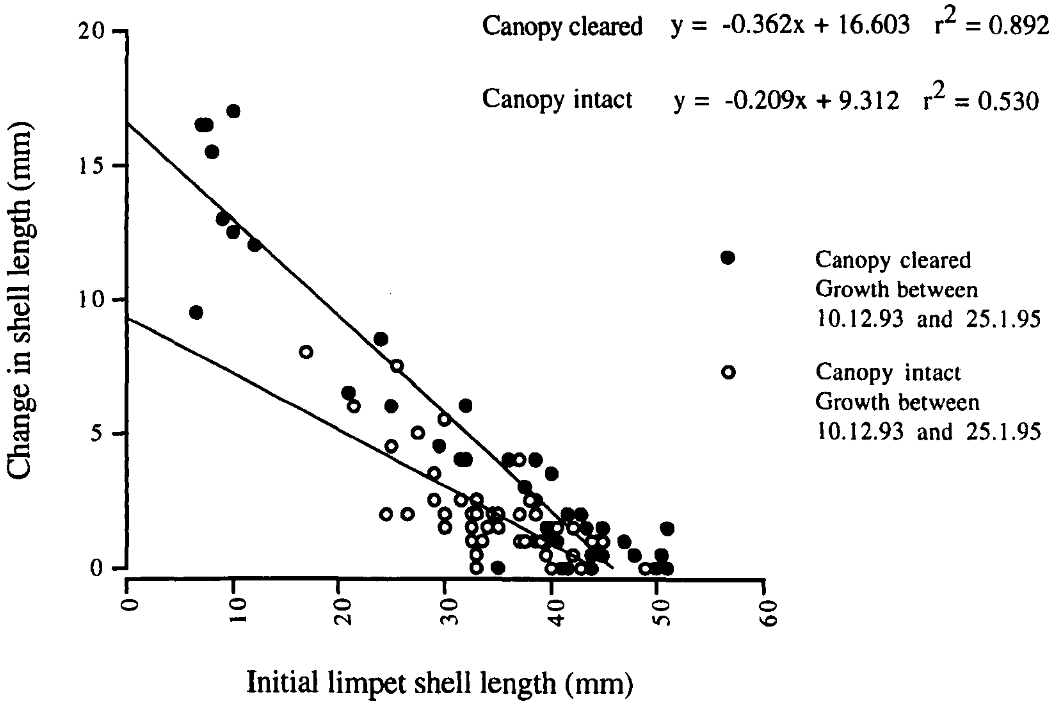
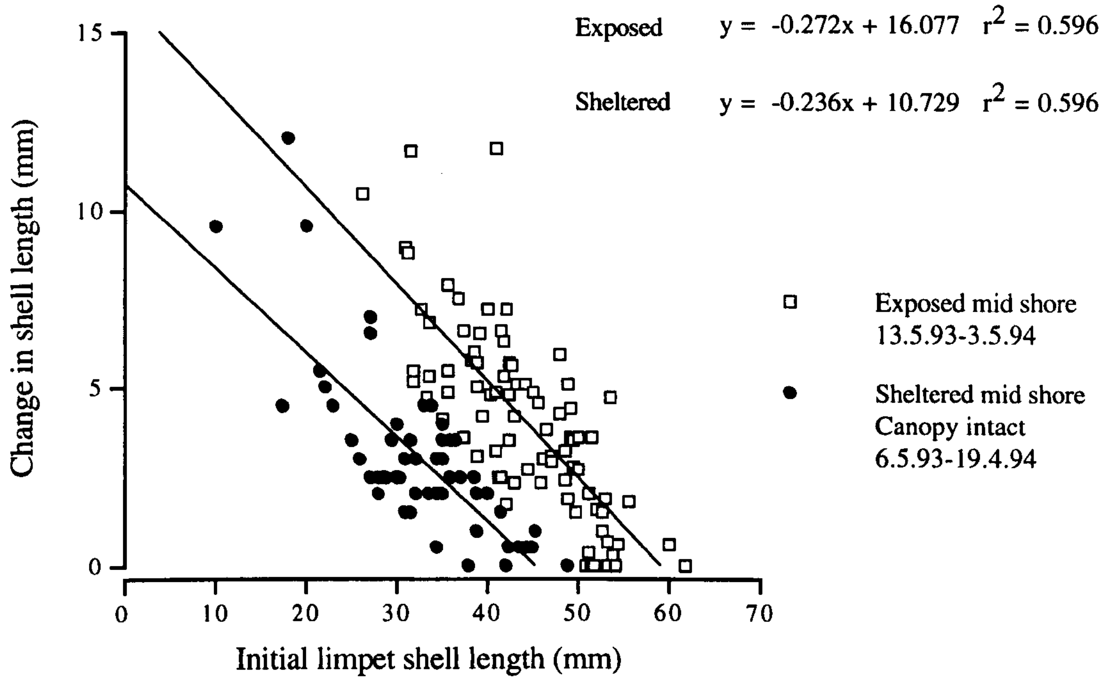


Figure 4.10 The effect of *Ascophyllum* canopy removal on the growth of *Patella vulgata* on the sheltered mid shore at Langness.
a) 1993 b) 1994

a) Intact *Ascophyllum* canopy



b) *Ascophyllum* canopy cleared

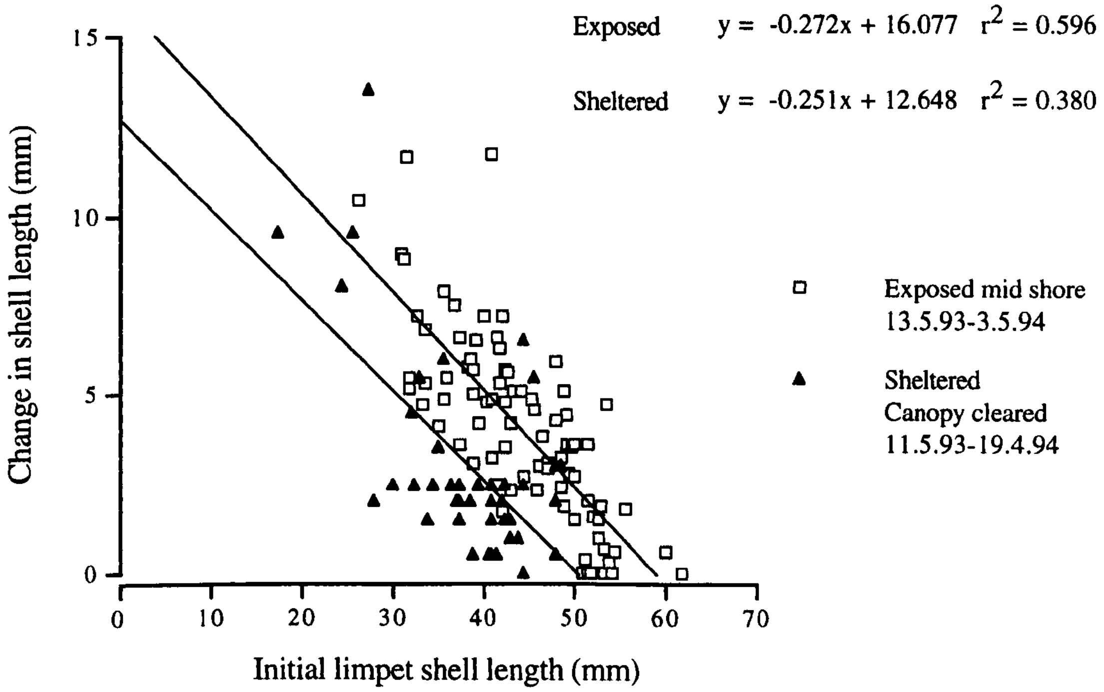


Figure 4.11 A comparison of the growth of *Patella vulgata* on an exposed (Port St Mary) and a sheltered (Langness) mid shore.
a) Comparison between a sheltered shore beneath an intact *Ascophyllum* canopy and an exposed shore.
b) Comparison between a sheltered shore in areas cleared of canopy and an exposed shore.

Table 4.3 Analysis of Covariance testing for a significant difference in growth rates of limpets in canopy cleared and canopy intact treatments on a sheltered shore.

	Source	df	Mean Square	F-Value	P-Value
a) 1993	Shell length	1	522.09	121.20	<.001
	Treatment	1	10.06	2.34	0.130
	Length x Treatment	1	0.25	0.06	0.811
	Error	98	4.31		
b) 1994	Shell length	1	491.91	205.65	<.001
	Treatment	1	64.92	27.14	<.001
	Length x Treatment	1	35.43	14.81	<.001
	Error	89	2.39		

N.B. A significant interaction term between shell length and treatment indicates a significant difference between regression slopes. A significant effect of treatment indicates a significant difference in the intercept of regression lines.

Table 4.4 Analysis of Covariance testing for a significant difference in growth rates of limpets on a moderately exposed and a sheltered shore.

Source	df	Mean Square	F-Value	P-Value
a) Intact canopy on the sheltered shore				
Shell length	1	484.83	187.58	<.001
Treatment	1	36.31	14.05	<.001
Length x Treatment	1	2.38	0.92	0.339
Error	135	2.58		
b) Canopy cleared on the sheltered shore				
Shell length	1	376.56	106.66	<.001
Treatment	1	9.77	2.77	0.099
Length x Treatment	1	0.61	0.17	0.679
Error	122	3.53		

4.3.2.3 Mortality

The mortality of limpets in the study populations, calculated over a one year period showed no significant difference between the two treatments (Figure 4.12, Table 4.5). The size distribution of the original population and of those individuals that died is presented in figure 4.13. Individuals that suffered mortality are spread across the range of sizes with only a slight bias towards mortality in older limpets.

No evidence was obtained regarding the causes of death. The shells of marked individuals which disappeared were never found and thus shell damage could not be assessed. Predation by seabirds was not observed at any sheltered shore throughout the period of study, although this activity was never specifically investigated.

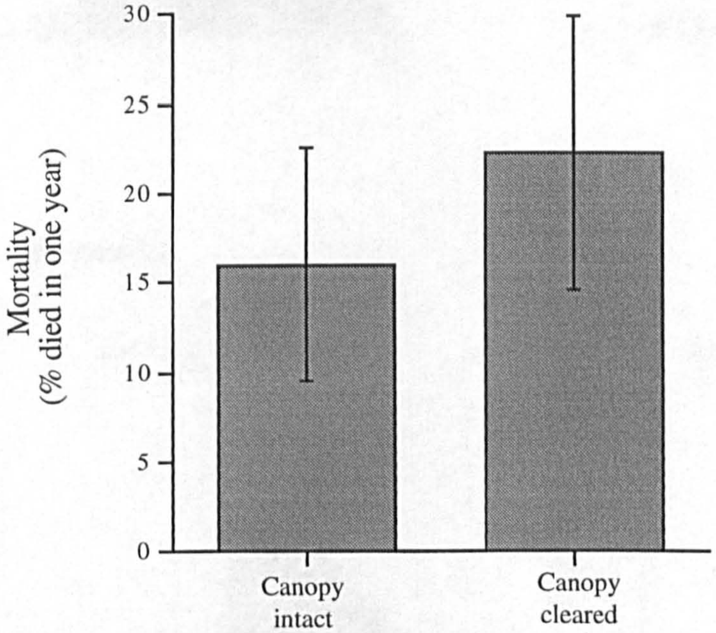
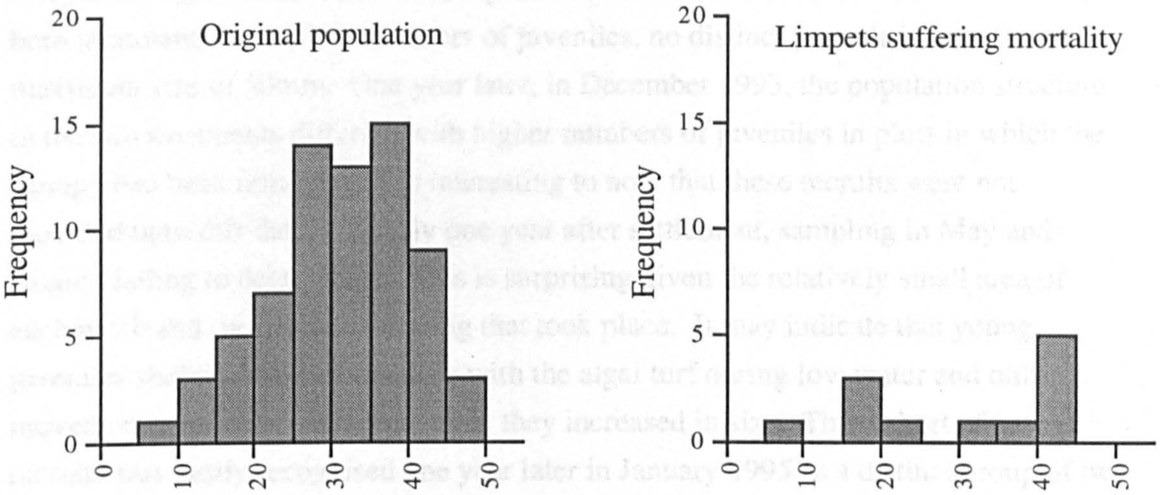


Figure 4.12 Percentage mortality of *Patella vulgata* on the mid shore of a sheltered site (Langness) between December 4th 1992 and December 9th 1993 in canopy intact and canopy cleared treatments. Error bars = ± 1SE

Table 4.5 One way ANOVA testing for the effect of *Ascophyllum* canopy clearance on the mortality of *Patella vulgata* in the mid shore of a sheltered site

Source	df	Mean Square	F-Value	P-Value
Treatment	1	104.74	0.383	0.551
Residual	9	273.57		

a) Canopy intact



b) Canopy cleared

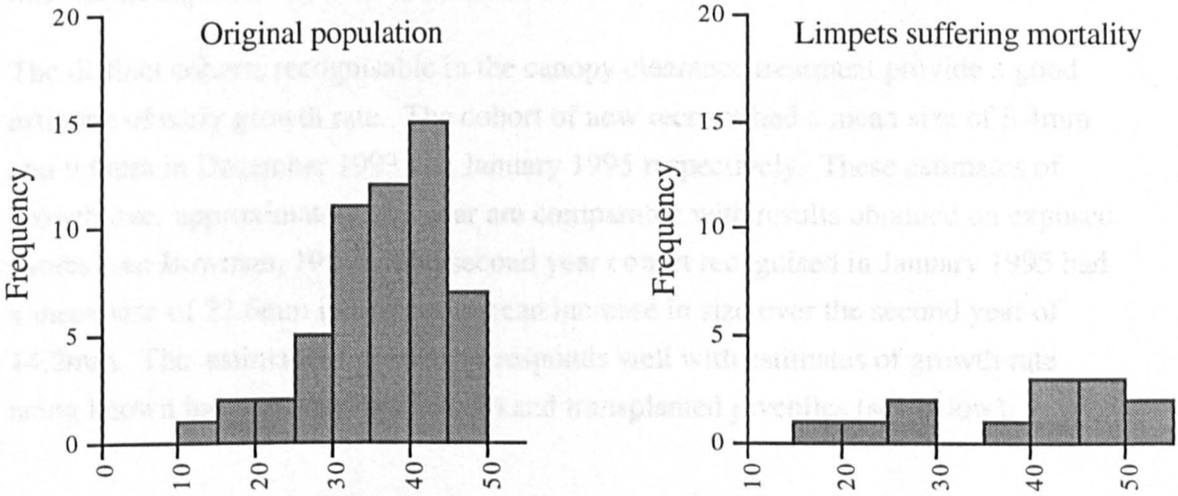


Figure 4.13 Original population structure of *Patella vulgata* in the two treatments canopy cleared and canopy intact, compared to the size distribution of limpets which died over a one year period.
a) Canopy intact b) Canopy cleared

4.3.2.4 Population structure

The frequency diagrams in figures 4.14 and 4.15 show the population structure of limpets in the two treatments over a two year period, thus reflecting the variation in recruitment, growth rate and mortality described above. The initial size distribution in both treatments shows low numbers of juveniles, no distinct year classes and a maximum size of 50mm. One year later, in December 1993, the population structure in the two treatments differed, with higher numbers of juveniles in plots in which the canopy had been removed. It is interesting to note that these recruits were not recorded until this date, probably one year after settlement, sampling in May and August failing to detect them. This is surprising given the relatively small area of each patch and the careful sampling that took place. It may indicate that young juveniles sheltered at the boundary with the algal turf during low water and only moved onto more exposed rock when they increased in size. This cohort of new recruits was easily recognised one year later in January 1995 as a distinct group of two year olds, along with a new cohort of one year old individuals. In January 1995, the population structure of limpets beneath the intact canopy contrasted sharply with that of the limpets in cleared plots, with no two year old age class evident and only a moderate recruitment of new one year old individuals. The maximum limpet size did not change significantly in either treatment.

The distinct cohorts recognisable in the canopy clearance treatment provide a good estimate of early growth rate. The cohort of new recruits had a mean size of 8.4mm and 9.9mm in December 1993 and January 1995 respectively. These estimates of growth over approximately one year are comparable with results obtained on exposed shores (see Bowman, 1981). The second year cohort recognised in January 1995 had a mean size of 22.6mm indicating a mean increase in size over the second year of 14.2mm. This estimate of growth corresponds well with estimates of growth rate using known individuals (Figure 4.10) and transplanted juveniles (see below).

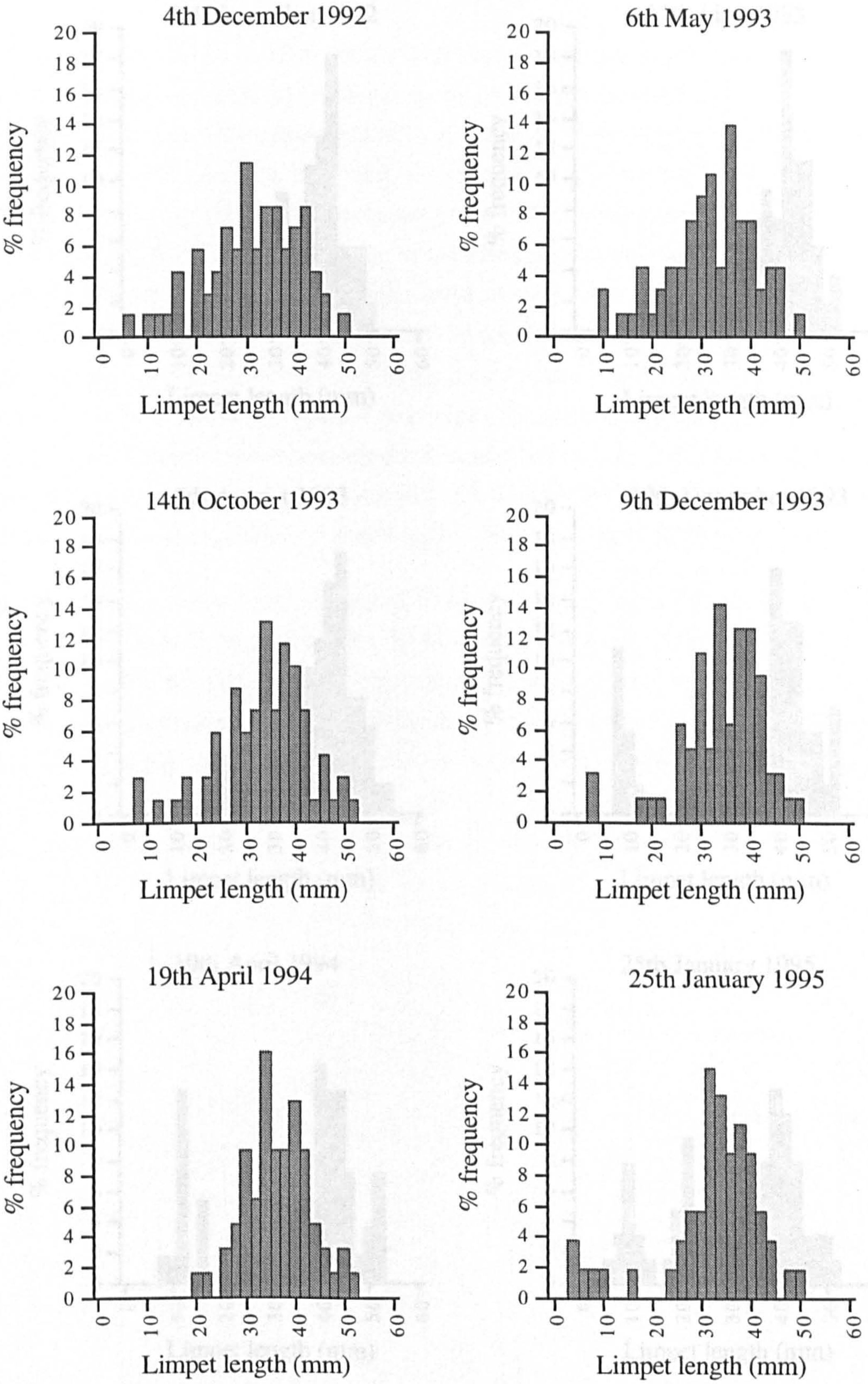


Figure 4.14 Population structure of *Patella vulgata* on the mid shore of a sheltered site (Langness) beneath a dense *Ascophyllum* canopy.

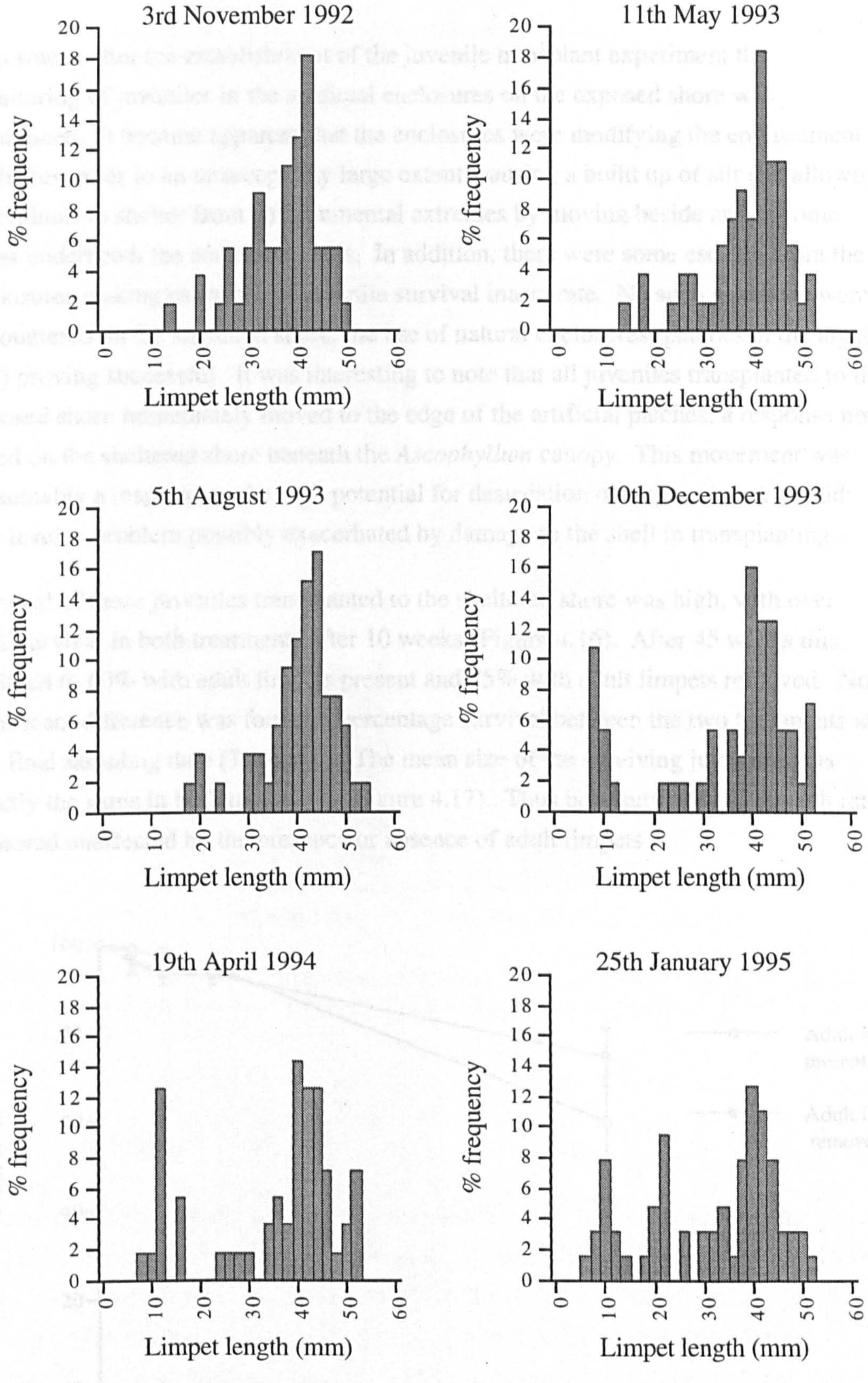


Figure 4.15 Population structure of *Patella vulgata* on the mid shore of a sheltered site (Langness) in plots cleared of the *Ascophyllum* canopy.

4.3.3 Juvenile Transplant

Two weeks after the establishment of the juvenile transplant experiment the monitoring of juveniles in the artificial enclosures on the exposed shore was abandoned. It became apparent that the enclosures were modifying the environment of the juveniles to an unacceptably large extent, causing a build up of silt and allowing individuals to shelter from environmental extremes by moving beside and in some cases underneath the enclosure walls. In addition, there were some escapes from the enclosures making estimates of juvenile survival inaccurate. No such problems were encountered on the sheltered shore, the use of natural enclosures (patches in the algal turf) proving successful. It was interesting to note that all juveniles transplanted to the exposed shore immediately moved to the edge of the artificial patches, a response not noted on the sheltered shore beneath the *Ascophyllum* canopy. This movement was presumably a response to the high potential for desiccation on exposed rock at mid tide level, a problem possibly exacerbated by damage to the shell in transplanting.

Survival of those juveniles transplanted to the sheltered shore was high, with over 90% survival in both treatments after 10 weeks (Figure 4.16). After 45 weeks this declined to 60% with adult limpets present and 75% with adult limpets removed. No significant difference was found in percentage survival between the two treatments at this final sampling date (Table 4.6). The mean size of the surviving juveniles was exactly the same in both treatments (Figure 4.17). Thus both survival and growth rate appeared unaffected by the presence or absence of adult limpets .

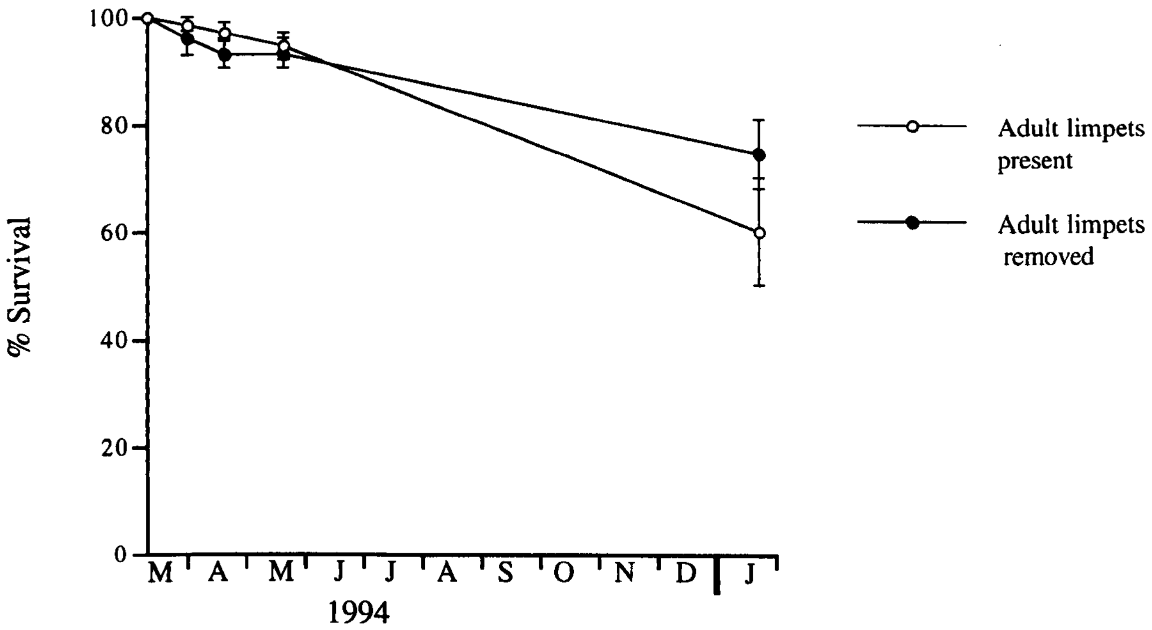


Figure 4.16 Survival of juvenile limpets transplanted beneath the *Ascophyllum* canopy. Error bars = ± 1SE

Table 4.6 One way ANOVA testing for the effect of the presence of adult *Patella vulgata* on the percentage survival of transplanted juvenile *Patella vulgata* under the *Ascophyllum* canopy.

Source	df	Mean Square	F-Value	P-Value
Treatment	1	537.78	1.49	0.256
Residual	8	360		

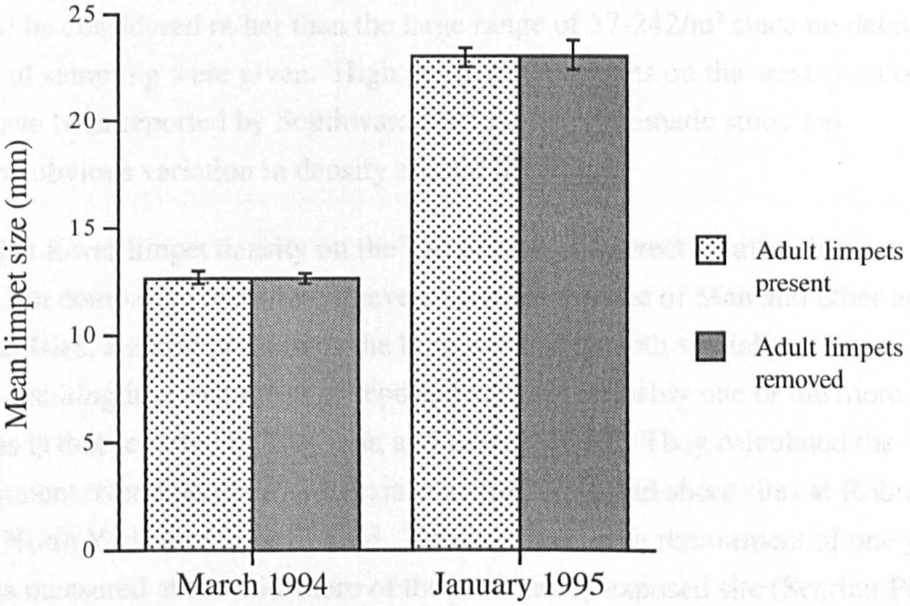


Figure 4.17 Mean size of juvenile limpets transplanted beneath the *Ascophyllum* canopy to patches of bare substrate, with and without the presence of adult limpets. Juvenile limpets transplanted in March 1994. Error bars = ± 1SE.

4.3.4 Larval Supply

Examination of the limpet settlement plates in May 1993 in the field and in the laboratory revealed no juvenile limpets on any of the 24 plates. Careful examination of the natural substrate in the pools into which the plates had been fixed showed that densities of newly settled juveniles were extremely low. Thus failure to obtain settlement on the artificial plates may simply have been a consequence of low larval supply or settlement rather than any inadequacies of the plates themselves. This type of investigation should be repeated on shores with high limpet settlement.

4.4 DISCUSSION

Limpet density on the Isle of Man especially on the south east coast where studies were carried out is low in comparison to other areas of the British Isles. Thompson (1980), working in SW Ireland at a large number of sites, found density at all sites excluding the very sheltered and very exposed to be in the range 100-800/m^2 at mid tide level. Lewis and Bowman (1975) found density of *Patella vulgata* at Robin Hoods Bay North Yorkshire varied between 87 and 385/m^2. These figures contrast with the density found in the region of Castletown Bay in this study, the highest density at any site being 39/m^2. Other work on the Isle of Man has reported a range of densities. For example Jones (1948) recorded a range of between 37 and 242/m^2 on exposed shores at Port Erin, Isle of Man (mean 90/m^2). The mean figure of 90/m^2 of Jones should be considered rather than the large range of 37-242/m^2 since no details of areal extent of sampling were given. High densities of limpets on the west coast of the island have been reported by Southward (1953). No systematic study has examined the obvious variation in density around the island.

It is likely that lower limpet density on the Isle of Man is a direct result of low recruitment. In comparing recruitment levels between the Isle of Man and other areas of the British Isles, a major problem is the high variability, both spatially and temporally, resulting in a vast range of reported values. Probably one of the more useful values is that reported by Bowman and Lewis (1986). They calculated the mean recruitment over a period of 18 years at a number of mid shore sites at Robin Hoods Bay North Yorkshire to be 314/m^2. This contrasts with recruitment of one year old juveniles measured at the mid shore of the moderately exposed site (Scarlett Point) in this study. Only 5 juveniles were found per m^2. Given the temporal variation in recruitment reported by Bowman and Lewis (1986) such a low level of recruitment may simply have been a year in which recruitment failed. However, other work in the south of the Isle of Man has revealed low levels of recruitment on exposed shores e.g. Jones (1948):mean of 20/m^2, Southward (1951): maximum of 40/m^2. Interestingly, recruitment on the west coast of the island may be much higher. For example at Niarbyl, Southward (1951) found that the density of limpets less than 10mm in size did not fall below 90/m^2 between mid tide level and low water neaps and reached a maximum of 890/m^2 at low water neaps. Thus it seems recruitment to sites of similar exposure may vary by over an order of magnitude. This recruitment variation around the Isle of Man may have a significant impact on community structure.

Low recruitment levels on shores of the Isle of Man are not confined to limpets. Hawkins and Hartnoll (1982b) recognised a lower intensity of *Semibalanus balanoides* recruitment on shores of the Isle of Man in comparison with other areas of north-west Europe. This was attributed to the 'loss of locally produced larvae by offshore dispersal and the isolation of the Isle of Man from other adult populations'. It is likely this isolation of the island is the main cause of low *Patella* recruitment.

A decrease in density of *Patella vulgata* with increased shelter, found in numerous other studies (Fischer-Piette, 1948; Jones, 1948; Southward, 1951; Ballantine, 1961b; Lewis, 1964; Thompson, 1980) was confirmed. This appears especially true when shores dominated by an *Ascophyllum* canopy are considered. For example no limpets at all occurred very far inside an *Ascophyllum* community at a sheltered site near Plymouth (Ballantine, 1961b).

The standard measure of limpet density is calculated using number of limpets per m^2 of shore. Ballantine (1961a) recognised that in some populations there was a great difference between 'available area' and 'occupied area', stating that in his low shore population the clearings occupied by limpets formed less than 30% of the total surface area in that zone. It is not clear if Ballantine's 'occupied area' is equivalent to my measurement 'area of grazeable substrate'. Using this measure resulted in a radical change in the pattern of limpet density, with number per m^2 of grazeable substrate varying little over the wave exposure gradient studied. This may have significant implications in making comparisons between sheltered and exposed shores of factors associated with density, such as growth rate and recruitment. Clearly, when considering intraspecific interactions within a limpet population, a measure of density which takes into account the area available for grazing rather than total area will be more meaningful. Lewis and Bowman (1975), in considering the relationship between P*atella vulgata* density and growth rate, concluded that the area of easily grazed surface per animal was more appropriate than simply number of limpets per unit area. However such a measure was not used in their work.

Although density per m^2 of grazeable substrate is clearly a useful measurement, it does have disadvantages. There is unfortunately no clear distinction between substrate which is grazeable and that which is not, introducing a subjective element into sampling. In addition, grazeable substrate will differ in the ease with which it can be grazed.

Differences in the density of limpets between sites may be caused by a number of factors, although in general differences are caused by variations in the 'recruitment and survival' characteristics of a particular site or habitat (Lewis and Bowman, 1975). Estimation of these factors can be problematic.

Investigation of limpet recruitment is hindered by the small size of limpet larvae. Unlike barnacles, whose larvae are extremely abundant, relatively long lived and easily recognisable in the plankton, limpet larvae have rarely been found in tow nettings (but see Smith, 1935) and most of the biology of limpet larvae is known only from artificially reared individuals (see Dodd, 1957). Ballantine (1961b) considers the failure to obtain limpet larvae from the plankton to be due either to their very low density or to their distribution near the seabed. The inability to collect limpet larvae has meant that recruitment has never been investigated in relation to larval supply. In recent years larval supply of barnacles has received considerable attention and has been shown to be a major factor in explaining variations in recruitment and distribution of adult populations (e.g. Gaines *et al.*, 1985; Minchinton and Scheibling, 1991; Bertness *et al.*, 1992; Gaines and Bertness, 1993). Unfortunately, in addition to the failure to sample limpet larvae in the plankton, it is also impractical to measure recruitment directly on the shore. Instead, it is measured over the following year as spat increase in size and move from cryptic habitats to more open rock (Ballantine, 1961b; Blackmore, 1969; Lewis and Bowman, 1975). There is thus an unknown mortality component associated with recruitment which will obviously vary depending on the time at which spat can be recognised. However, a reasonable estimate of recruitment of one year old individuals to a population may be achieved as described above. This is a useful measurement since it gives a good indication of levels of recruitment into the adult population.

Recruitment of *Patella vulgata* has been shown in a number of studies to be significantly reduced at sheltered sites where a dense fucoid canopy is prevalent (Hatton, 1938; Fischer-Piette, 1948; Jones, 1948; Lewis and Bowman, 1975; Thompson, 1980). This appears consistent with the results of this study. Estimates of recruitment of one year old individuals across the wave exposure gradient, from Scarlett Point to Castletown Bay, revealed a decrease in recruitment levels with increasing shelter at all tidal heights.

The reasons for low recruitment on sheltered shores are unclear. It has been suggested that supply of limpet larvae to sheltered shores may be low in comparison to exposed shores (Hawkins *et al.*, 1992). If, as Ballantine suggests, limpet larvae occur near the sea bed and are relatively scarce, recruitment may depend on supply of larvae from very local populations, especially in sheltered localities not subjected to tidal currents. If this were the case low limpet density on sheltered shores would supply relatively low numbers of larvae. Even given a high larval supply, successful settlement of larvae may be hindered by the communities found on sheltered shores. Fucoid canopy can inhibit barnacle settlement by sweeping (Dayton, 1971; Menge, 1976; Grant, 1977; Hawkins, 1983). However, development of a fucoid canopy on exposed shores has been shown to enhance limpet recruitment (Southward, 1956; Lewis and

Bowman, 1975; Southward and Southward, 1978), suggesting that disturbance by fucoid sweeping does not adversely affect limpet spat. It has been suggested that the dense fucoid cover which typically develops on sheltered shores acts as a barrier to limpet larvae, effectively limiting supply of larvae to the rock surface and therefore limiting settlement (Fischer-Piette, 1948; Lewis and Bowman, 1975).

The effect of the *Ascophyllum* canopy was investigated by comparing recruitment beneath an intact canopy and plots where the canopy was removed. Results from Chapter 2 showed that the *Ascophyllum* canopy can facilitate the presence of a red algal turf. Substrate type is an important determinant of recruitment success. For example, Ballantine (1961b) reported that spat only survived on relatively clean rock surfaces, in other words those not coated with mud, silt or dense growths of algae. Therefore, beneath an *Ascophyllum* canopy much of the substratum will be unavailable as a settlement surface for limpet larvae. Removal of the canopy resulted in an increase in area of bare substrate and a consequent increase in recruitment as a percentage of the adult population. Increase in recruitment was directly proportional to the increase in bare substrate area. These results suggest that the *Ascophyllum* canopy, indirectly, rather than directly, inhibits larval settlement.

If recruitment is calculated as number of recruits per m^2 of grazeable substrate, recruitment on the mid shore showed less of a decline with shelter. In fact a comparison between the mid shore at Scarlett Point and the mid shore at Langness, where detailed observations were made over two years, reveals that recruitment of one year old individuals was actually marginally higher at the sheltered site. Given this observation and the increase in recruitment with increase in area of bare substrate reported above, it would seem that recruitment and ultimately population size beneath an *Ascophyllum* canopy is limited by the availability of suitable settlement substrate.

This conclusion however cannot safely be made without knowledge of the settling behaviour of limpet larvae. Unfortunately nothing is known regarding this aspect of limpet biology. Two types of settlement behaviour may be postulated. Firstly, larvae may actively select settlement sites, rejecting unsuitable ones and moving on via the water column to find alternatives. Secondly, settlement may be passive, larvae simply settling at random out of the water column. If larval settlement were entirely passive, the observed recruitment patterns would indicate that supply at the substratum surface is similar at exposed and sheltered shores. In this case recruitment would be limited by suitable settling sites. Alternatively, if larval settlement were 'active' such that larvae would reject settlement on algal turf and eventually find a suitable settlement site on rock, then the observed recruitment pattern indicates that the supply of larvae to the substratum surface on sheltered shores is low.

The arguments outlined above do not take into account possible difference in survival of recruits between exposed and sheltered shores. The main mortality of juveniles is probably caused by desiccation stress. In southwest England spat less than six months old or less than 2mm in size died if the surface to which they were attached dried out for more than a few minutes (Ballantine, 1961b). This may explain the elevated recruitment levels amongst barnacles and mussels (Lewis and Bowman, 1975; Hawkins and Hartnoll, 1982a). Personal observations have shown that rock beneath the *Ascophyllum* canopy does not dry out at low water even at the height of summer. Thus, young spat settling beneath the canopy do not have to rely on crevices and shallow pools to avoid desiccation.

Survival of juveniles at Langness beneath a dense canopy of *Ascophyllum* was extremely high, only one juvenile failing to reach its first year. Fischer-Piette (1948) found higher juvenile mortality in exposed positions. At the end of their second year juveniles showed 57% mortality at exposed sites compared to 36% at semi sheltered sites. He considered that to a certain extent high mortality at exposed sites counteracted high recruitment levels resulting in similar adult densities. Although not specifically examined, it is likely that mortality on the mid shore of the exposed site at Scarlett Point was significantly higher than beneath the *Ascophyllum* canopy at Langness. Thus, equivalent recruitment of one year old individuals may to a certain extent be a result of higher post settlement mortality at Scarlett Point.
Although it was not possible to calculate recruitment per m^2 of grazeable substrate for the sheltered low shore, estimates show that recruitment was far lower than at the exposed site both per m^2 of shore and per m^2 of grazeable substrate. Since the community of the low shore is similar across the range of exposures investigated this evidence suggests that supply of limpet larvae does in fact decrease with shelter.

The growth rate of *Patella vulgata* is extremely variable and appears to be strongly influenced by biological habitat (Lewis and Bowman, 1975; Thompson, 1980). Lewis and Bowman (1975) consider that the influence of biological habitat on growth is so strong that changes in the community surrounding a limpet population will result in corresponding changes in the growth rate of those limpets and consequently in the population structure. However, where community composition remains unchanged growth rate has been shown to remain constant over a number of years at a particular site (Baxter, 1982).

The growth rate of limpets (and molluscs in general) are generally studied by making simple measurements of increases in shell length. Baxter (1983) considers that such measurements when used to make comparisons between populations can be misleading because of variations in shell shape (in particular shell height) between habitats (Russell, 1909; Moore, 1934; Lewis and Bowman, 1975; Baxter, 1983). Unit increase in length of 'tall' shells requires deposition of more shell material than an equivalent increase in a 'flat' shell. Unfortunately there are no published studies which have examined change in shell shape across the wave exposure gradient in Europe. However, in South Africa, Branch and Marsh (1978) found no correlation between shell height and the intensity of wave action in six *Patella* spp.

The conclusion of a number of authors of an increase in growth rate and maximum size on sheltered fucoid dominated shores (Fischer-Piette, 1948; Jones, 1948; Ballantine, 1961b) or under *Fucus* in general (Southward, 1956; Lewis and Bowman, 1975; Thompson, 1980) was not supported by this study. Comparisons of growth rates at mid shore level between a barnacle dominated moderately exposed site and an undisturbed *Ascophyllum* dominated sheltered site revealed a significantly higher growth rate on the exposed shore.

There are a number of factors to consider in analysing this result. Irrespective of the degree of exposure or algal cover, it is generally accepted that barnacle cover depresses the growth rate of limpets (Lewis and Bowman, 1975; Branch, 1976; Thompson, 1980; Hawkins and Hartnoll, 1982a). On this basis alone therefore one would expect a higher growth rate on sheltered shores where barnacles are absent. It has been proposed that algal cover itself enhances limpet growth rate by allowing extended feeding times and enhancing the microbial food supply. A fucoid canopy, by reducing desiccation stress and maintaining a damp humid environment, may increase the time available for feeding by allowing limpets to feed at low water. In addition, it has been suggested that wave shock may limit foraging times on exposed shores (Southward, 1953). This was not supported by the work of Santina *et al.* (1994), presumably because the majority of feeding in the populations studied took place during nocturnal low tides. A comparison of an exposed and sheltered site in north Wales revealed longer foraging times in limpets at the more wave exposed site. This was suggested to be a result of lower food abundance there, in comparison to the 'nutrient rich' sheltered site. Fischer-Piette (1948) considered growth rate to be enhanced under fucoids because of a higher food supply. However, he probably overestimated the extent to which limpets feed on macroalgae. Although it is a commonly stated assumption, there is no available evidence to suggest that the microalgal film on which limpets feed is any greater on rock under a dense fucoid canopy.

Considering all these factors, one might expect a higher growth rate on sheltered fucoid dominated shores. However, although all these factors may be influential, the prime factor influencing limpet growth rate is likely to be the area of easily grazed substrate per animal (Jones, 1948; Lewis and Bowman, 1975). Both Ballantine (1961b) and Lewis and Bowman (1975) found an increase in growth rate following removal of limpets, thus increasing the feeding area of each individual. Surprisingly, I found no such effect when monitoring the growth rate of juveniles transplanted into treatments with and without adults. However, the expansion of grazing area following *Ascophyllum* canopy removal appeared to result in a slight elevation in limpet growth rate, thus providing evidence to support the importance of limpet density. Obviously this result is confounded by the possibility of a direct effect of canopy removal on growth rate.

Although Lewis and Bowman (1975) showed experimentally that a reduction in density and the consequent reduction in competition between limpets could enhance growth rates, they found no correlation between density and growth rate in natural habitats. This was assumed to be due to the overriding influence of biological habitats on growth rate. Alternatively, it may simply have been because of their failure to measure density as number per m^2 of grazeable substrate.

If growth rate were purely dependent on area of easily grazed substrate per animal what pattern of growth rate across the wave exposure gradient would be expected? As stated above, most previous work has established that limpet density declines in sheltered areas (Fischer-Piette, 1948; Jones, 1948; Southward, 1953; Ballantine, 1961b; Lewis, 1964; Thompson, 1980). However, I have shown at my study sites that when density per m^2 of grazeable substrate is considered densities do not necessarily follow this pattern. At the exposure gradient from Scarlett Point to Castletown Bay, densities at mid shore level were similar at all three levels of exposure. At Langness, beneath an intact canopy, density was far higher than at either of the exposed sites examined (Port St Mary or Scarlett Point). Comparing Port St Mary and Langness it seems that the lower growth rate at the sheltered site was a direct result of a higher density. Where the *Ascophyllum* canopy was removed, densities were equivalent between the sheltered and exposed sites and growth rates were more similar. However, growth was still lower at the sheltered site. Given the factors outlined above one would expect that equivalent densities between sites of different exposure would result in lower growth rate at the exposed site. Obviously future work is required over a range of shores to establish the exact relationship between growth rate, density and exposure to wave action.

4.4.1 Conclusions

The conclusions which can be reached regarding the population dynamics of *Patella vulgata* on sheltered shores are few because of the limited nature of this investigation. The *Ascophyllum* dominated mid tide level of sheltered shores is characterised by low overall recruitment and consequently low density. Results suggest that the *Ascophyllum* canopy probably does not prevent recruitment directly but does so indirectly by facilitating the red algal turf. Populations beneath an *Ascophyllum* canopy are probably more stable than those on exposed shores as a result of low recruitment levels and a dampening of environmental extremes. Whether supply of limpet larvae is lower than at exposed sites is not clear but initial results suggest it is. Work low on the shore in the *Fucus serratus* zone may help to answer this question since differences between sheltered and exposed sites could be attributed directly to exposure rather than indirectly via the effects of differing communities.

CHAPTER 5

Investigations into the factors limiting the barnacle population of sheltered shores

5.1 INTRODUCTION

Sheltered, canopy dominated shores of north west Europe are characterised by a low abundance of barnacles (Moore, 1935; Stephenson and Stephenson, 1949; Lewis, 1964; Hawkins, 1983; Hawkins *et al.*, 1992). As one progresses from barnacle and limpet dominated shores in exposed sites to shores sheltered from wave action, the increase in fucoid canopy is accompanied by a corresponding decline in barnacle abundance. However, on vertical surfaces and steep seaward-facing slopes barnacle abundance can remain high (Lewis, 1964). At gently sloping sheltered sites, barnacles are often only abundant on the high shore (Lewis, 1964; Hawkins, 1979). Hawkins (1979), working on a sheltered shore on the Isle of Man, reported a total absence of barnacles in the *Fucus serratus* and *Ascophyllum* zones but a cover of between 10 and 20% in the *Fucus spiralis* zone. The decline of barnacles with increasing shelter on shores of north west Europe has not been fully explained. Lewis (1964) in his study of the ecology of Britain's shores considered this pattern could be a result of a number of factors including low larval supply, the destruction of juveniles by the sweeping action of algal fronds, the grazing activities of large molluscs and the lack of suitable substratum.

Variation in the supply of larvae to the shore, the factors generating this and the consequences to shore community structure have received considerable attention in recent years. By simultaneously monitoring settlement/recruitment on the shore and larval dynamics in the water column, a number of studies have established a direct correlation between larval supply and barnacle recruitment, on both large (1-30 km) (Bertness *et al.*, 1992; Gaines and Bertness, 1993) and small scales (<100m) (Grosberg, 1982; Gaines *et al.*, 1985; Minchinton and Scheibling, 1991). Thus it has been established that processes affecting larval concentration in the water column can have a significant effect on shore community structure. A comparison of supply to sheltered and exposed shores has not been attempted in Britain or elsewhere. However, the settlement rate of barnacles at shores with identical biota but differing in the degree of exposure have suggested that supply of larvae may be low in sheltered positions (Caffey, 1985; Bertness *et al.*, 1992).

Lewis (1964), in considering the scarcity or absence of many exposed shore species from sheltered shores, postulated that larvae may fail to reach sheltered sites owing to factors influencing larval transportation. He considered that the number of larvae entering narrow inlets and bays is likely to be small in comparison to exposed headlands which are subject to tidal streams and winds from many directions. However, he does accept that in sheltered bays certain wind and tide conditions can cause local accumulation of larvae. It may be significant that several 'open coast' species with planktonic larvae are least successful in shelter (e.g. barnacles, limpets. *Melaraphe neritoides*).

In order to understand larval supply, it is necessary to understand the transport processes involved. Larvae may undergo dispersal over considerable distances. Crisp (1958) estimated that larvae of *Elminius modestus* may be dispersed up to 50 miles, whilst Le Fevre and Bourget (1991) actually found cyprids and larvae of *Verruca stroemia* over 50km off shore. Such dispersal raises problems for organisms such as barnacles whose adult phase is restricted to the intertidal. Larvae must somehow return to the shore. How this is achieved is open to conjecture but some form of vertical movement in the water column to exploit onshore currents may occur (Shanks, 1986). The effect of wind speed and direction on larval transport and subsequent recruitment is not clear. Hawkins and Hartnoll (1982b) showed a positive correlation between onshore winds and settlement of *Semibalanus balanoides* in the Isle of Man. However, Bennell (1981), working during the same period and only 70 kilometres away on the North Wales coast showed a negative correlation. Shanks (1986) found daily settlement was not significantly correlated with wind speed or direction but was correlated with the maximum daily tidal range. It was suggested that cyprids may be transported onshore in slicks over tidally forced internal waves. For cyprids to utilise this mechanism they would need to remain near the surface.

The level of supply of cyprids to sheltered shores is unknown. However, even given a high supply, the physical and biological characteristics of sheltered shores may dictate that settlement and recruitment are low. The settlement behaviour of barnacles, especially *Semibalanus balanoides* has been studied intensively over a number of years (see review by Crisp, 1974). A number of factors discovered to influence settlement behaviour may have relevance when considering the pattern of *Semibalanus balanoides* distribution over the wave exposure gradient. Laboratory experiments have shown *Semibalanus balanoides* does not attach as readily to surfaces under still conditions as when exposed to some degree of water movement (Crisp, 1955). This may result in a reduction in settlement with increasing shelter from wave action and tidal flow. It is possible that such behaviour could be selected for because of the enhanced food supply in exposed conditions (Crisp, 1955). Lewis (1964) considered that slow water circulation within sheltered habitats could reduce the chance of larvae being carried near to suitable substratum.

Cyprids of a number of barnacle species tested in the laboratory settle more readily on surfaces bearing settled conspecifics or treated with extracts of conspecifics than on bare untreated controls (Knight-Jones and Stevenson, 1950; Knight Jones, 1953). This phenomenon has also been observed under natural conditions in the field (e.g. Hawkins, 1983; Raimondi, 1988). This effect, termed gregariousness, has always been interpreted as a positive attraction toward conspecifics, resulting in increased settlement on surfaces where survival is likely. An alternative view presented by Hui and Moyse (1987) is that gregariousness is an effect which 'contributes mainly to the rejection of unfavourable substrata as opposed to one which leads to increased settlement of favourable substrata'. Whichever view is taken, the 'gregarious response' of barnacles has implications for recruitment onto sheltered shores (Lewis, 1964). Hawkins (1983) showed that recruitment of *Semibalanus balanoides* into cleared areas in the *Ascophyllum* zone of a sheltered shore only occurred after stones bearing live adult barnacles were transplanted there. In contrast, much higher recruitment occurred in the *Fucus spiralis* zone where adult barnacles were common.

The lack of adult conspecifics on sheltered shores is not the only feature of the substratum which affects barnacle settlement. At mid tide level a high proportion of the substratum is already occupied by a red algal turf (see Chapter 2) effectively preventing settlement there. Thus, when considering the absence of barnacles in the mid shore it must be appreciated that this question only applies to the areas of bare substrate.

A number of studies have considered the effect of the fucoid canopy on barnacle recruitment (Hatton, 1938; Southward and Crisp, 1956; Lewis, 1964; Dayton, 1971; Menge, 1976; Grant, 1977; Hawkins, 1983). Hatton (1938) first demonstrated a negative effect of fucoids on the recruitment of *Semibalanus balanoides* and attributed this to the reduction of water circulation beneath a canopy, resulting in a limitation of larvae coming into contact with the substratum. Most work subsequent to this has considered the sweeping action of algal fronds across the substratum surface to be the main cause of recruitment limitation, settling or settled cyprids being destroyed or simply swept away. Menge (1976), working on the east coast of North America, demonstrated this experimentally; enhanced recruitment beneath a *Fucus vesiculosus* and *Ascophyllum* canopy was achieved by protecting the substratum with roofs and cages. The degree of exposure to wave action, the species of canopy algae and vertical height on the shore may influence the degree to which recruitment is affected by sweeping. Hawkins (1983) concluded that on moderately exposed shores *Fucus* sweeping inhibits settlement at all shore levels whilst at sheltered sites inhibition only occurs in the *Fucus serratus* zone 'where water movement is likely to be greater'. On the high shore Hawkins found that although the fucoid canopy (*Fucus spiralis* and *Fucus vesiculosus*) reduced cyprid settlement, this effect was less pronounced than the enhancement of post settlement survival. A similar effect was observed by Dayton (Dayton, 1971); settlement of *Balanus glandula* was not reduced under *Fucus distichus* and it was concluded that the canopy had a positive effect on recruitment owing to its reduction of desiccation.

Newly settled cyprids or small juveniles are not only at risk of dislodgement from algae but also from the grazing activities of gastropods (Connell, 1961; Menge, 1976; Denley and Underwood, 1979; Branch, 1981; Hawkins, 1983; Miller, 1989; Safriel *et al.*, 1994). This form of dislodgement has been termed bulldozing. Refuge from dislodgement may occur in depressions (Miller, 1989) or amongst dense aggregations of adult barnacles (Hawkins, 1983; Miller, 1989). Also, barnacles reach a size refuge from bulldozing relatively quickly. Miller and Carefoot (1989) found young juveniles of three barnacle species reached a size refuge from the limpet *Lottia digitalis* when their basal area was only 5mm^2. The overall significance of gastropod bulldozing is not clear. Hawkins (1983) considered that the effects of limpet grazing on the recruitment of *Semibalanus balanoides* to moderately exposed shores were much less important than the sweeping of even very small clumps of seaweed.

Newly settled and newly metamorphosed barnacles are obviously at risk of mortality from a range of sources including algal sweeping, limpet bulldozing and environmental extremes. Following this early vulnerable phase, the primary source of mortality of *Semibalanus balanoides* on British shores is from predation by *Nucella lapillus*. On moderately exposed shores this predation can not only affect barnacle abundance and population structure (Connell, 1961) but can also influence other aspects of community structure by indirectly causing a reduction in the frequency of algal escapes (Proud, 1994). The density of dogwhelks declines with increasing shelter presumably owing to a decline in prey abundance (Spence *et al.*, 1990). However, work by Menge (1976, 1978a, 1978b) in North America suggests that *Nucella* could have a significant effect on barnacle populations at sheltered sites. Menge showed that even sparse populations of *Nucella* exerted intense predation pressure on their prey at sites protected from wave action and covered with a dense canopy (Menge, 1978a). At such shores in New England, *Nucella* caused the exclusion of mussels and barnacles.

The aim of the work presented in this chapter was to determine the factors responsible for the scarcity of barnacles on sheltered shores. Three factors were identified as the main potential influences on barnacle abundance: larval supply, interactions with canopy algae and post settlement mortality from dogwhelk predation.

Comparative measures of larval supply to exposed and sheltered shores were made using two separate techniques designed to provide independent estimates of larval concentration. In addition, attempts were made to establish differences in the relationship between supply and settlement at shores differing in exposure. It was accepted that factors such as canopy algae and substratum type would radically affect this relationship at the sheltered site. Therefore these factors were removed by manipulation of algae and the provision of identical settlement substrata to both shores.

Canopy algae may interact with settling cyprids whilst still in the water column by forming a barrier to cyprid movement, and at settlement by sweeping across the substratum. The barrier effect has not been investigated in the past owing to the difficulty in separating its effect from that of sweeping. This problem was tackled in two ways. Firstly, pumping techniques were used to estimate the supply of larvae beneath the canopy. Secondly, a large scale field experiment was designed which examined the relative contribution of the canopy barrier and canopy sweeping to the inhibition of settlement and recruitment.

In the light of Menge's work in North America on *Nucella* predation intensity (Menge, 1976; Menge, 1978a; Menge, 1978b) and despite the low density of dogwhelks on sheltered shores in Britain it was felt appropriate to examine the effect of these predators on barnacle abundance. This was achieved by manipulation of dogwhelk density by simple removal rather than the use of fences or cages.

In addition to the main aim stated above, it was also hoped to explain the pattern of barnacle distribution with tidal height. With this aim in mind, experiments were established in the three main fucoid zones of *Fucus serratus*, *Ascophyllum* and *Fucus spiralis*.

The examination of barnacle settlement and recruitment rates was obviously an integral part of this study. Given the confusion in the literature caused by the imprecise use of these terms (Connell, 1985) it is necessary to define exactly what is meant by settlement and recruitment. Keough and Downes (1982) consider a barnacle larva to have settled at the moment it irreversibly attaches to the substratum, whilst a settler is considered to be a recruit once it has survived some arbitrary length of time after settlement. Since settled barnacle larvae metamorphose on average within 1.5 days (Connell, 1961) then the number of unmetamorphosed attached cyprids is a good indication of settlement. In my work I have considered settlement as the number of attached cyprids and recruitment as the accumulated number of metamorphosed recruits.

5.2 METHODS-LARVAL SUPPLY

5.2.1 Study Sites

Two adjacent study sites were selected only 600m apart but differing markedly in their degree of exposure. Scarlett Point provided moderately exposed conditions and a shore dominated by barnacles and limpets. North of Scarlett Point on the west side of Castletown Bay was a gently sloping site with a continuous cover of fucoid algae. This sheltered site will be referred to as Castletown Bay.

5.2.2 Sampling techniques

Two methods of estimating the supply of cyprid larvae to the shore were used, a petrol driven water pump and plankton net trawling.

5.2.2.1 Petrol driven water pump

A water pumping system was developed to operate from the shore and supply seawater from a given position in the littoral zone when the tide was in. The system incorporated a petrol driven water pump (Honda WB10) connected to a length of one inch diameter rigid tubing. This tubing was permanently attached to the shore, running from the point of water extraction in the mid littoral zone to a point above maximum high water. Filters with a mesh size of 1.5 cm were placed over the open tube ends to prevent entry of any large stone or algal particles into the pump.

At any time, including during bad weather, the pump could be used to sample a known volume of water from a precise location on the shore. The portable pump was attached to the tubing and used to pump water through a 100 µm plankton net. The plankton sample thus collected was immediately preserved in 5% formalin in seawater.

The pump flow rate during each pump usage was determined by recording the time taken to fill a container of volume 54 litres. In this way the number of cyprids per cubic metre of water could be quantified.

5.2.2.2 Trawling

A flat bottomed 5.5m dory the 'Corallina' powered by twin 40hp engines was used to sample plankton during the period two hours either side of high water. At this time the Corallina could be taken close inshore and sampling undertaken directly over the intertidal zone. In this way the supply of cyprids to the shore could be measured.

Initially a 100μm plankton net was used with a General Oceanics flowmeter. However, the high density of phytoplankton found during the spring and early summer was found to quickly block the fine mesh of the net, resulting in very inefficient and variable sampling. Therefore a 250μm net with 0.5m diameter mouth was used and found to be satisfactory.

The net and flowmeter were towed behind the Corallina at a depth of approximately 0.5-1m. This constancy of depth was achieved by attaching a small float to the rope towing the net as illustrated in figure 5.1.

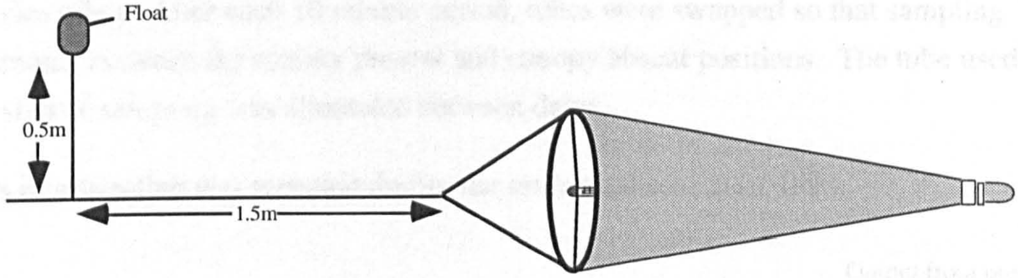


Figure 5.1 Float system used with towed plankton net.

The net was towed at a speed of approximately 1.5 knots. After the required length of tow was complete the plankton sample obtained from the'cod end' of the net was placed into a 500ml bucket and immediately preserved in formalin. A note was made of the flow meter reading, before and after the tow.

5.2.2.3 Examination of plankton samples

Preserved samples were examined in Bogorov trays using a binocular microscope. Barnacle cyprids were counted and transferred by pipette into labelled tubes. Because of the relatively low number of cyprids in the plankton, it was felt subsampling would introduce unacceptable levels of error. Therefore the whole of each sample was analysed. After counting of cyprids was complete, the length of all cyprids collected was measured as an aid to identification.

5.2.3 The effect of the *Ascophyllum* canopy on cyprid supply

Use of the pumping technique described above allowed sampling of cyprid supply beneath an *Ascophyllum* canopy. A site was found at the sheltered site in Castletown Bay where it was possible using only short lengths of tubing to sample adjacent areas where *Ascophyllum* canopy was present and absent. To achieve, this a site was found on an old quayside where a near vertical drop could be achieved from above maximum high water level to the mid littoral zone. It was important to minimise the length of tubing in order to maintain a high pump flow rate and thus sample the maximum volume of water in a given time. Long lengths of tubing reduced the pumping efficiency dramatically.

Two lengths of tubing were positioned as shown in figure 5.2. The mouths of both tubes were located at the same tidal height on the shore, 3.8m above C.D. and 30cm above the substratum. In May 1993 sampling was undertaken on six days during the barnacle settlement season. Pumping took place during the period one hour either side of high water. At each date, three 10 minute periods of pumping took place on each of the two tubes. After each 10 minute period, tubes were swapped so that sampling alternated between the canopy present and canopy absent positions. The tube used at the start of sampling was alternated between dates.

This investigation was repeated during the settlement season of 1994.

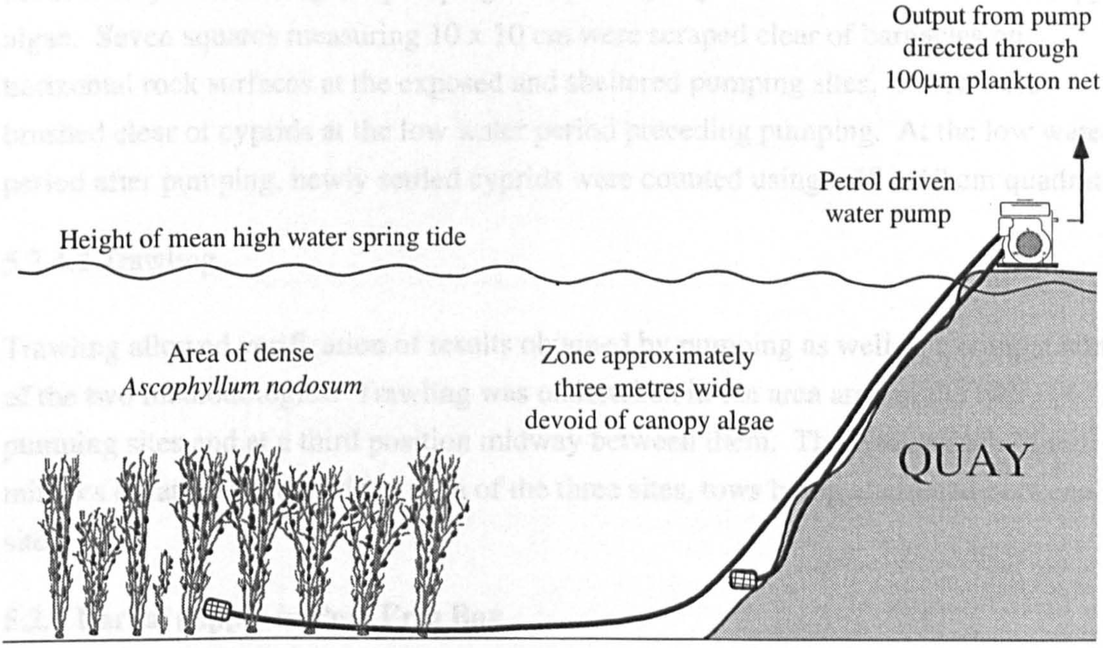


Figure 5.2 Experimental set up of pumping system designed to examine the effect of the *Ascophyllum* canopy on cyprid supply.

5.2.4 A comparison of cyprid supply to sheltered and exposed shores

In May and June 1994 a comparison of cyprid supply to the adjacent sites of Scarlett Point (exposed) and Castletown Bay (sheltered) was made using both pumping and trawling techniques. In addition an attempt was made to relate cyprid supply to settlement.

5.2.4.1 Pumping

The tube already positioned in the canopy clear area at the Castletown Bay site was used to sample for larval supply to a sheltered shore. At Scarlett Point a tube was positioned on a vertical rock face such that water was pumped from a tidal height equivalent to that at Castletown Bay. Pumping took place for three 10 minute periods at each location. Although the distance between the two sites was only approximately 600m it was impractical to alternate pumping for each 10 minute period. Therefore all three 10 minute periods were sampled at one location then the other. The site sampled first was alternated between dates.

In order to relate cyprid supply to settlement and investigate any difference in this relationship between sheltered and exposed shores, settlement squares were prepared at each site in the immediate vicinity of the tube mouths. Although barnacles are generally rare on sheltered shores they were relatively common in the area immediately surrounding the pumping site, presumably because of the lack of canopy algae. Seven squares measuring 10 x 10 cm were scraped clear of barnacles on horizontal rock surfaces at the exposed and sheltered pumping sites. These were brushed clear of cyprids at the low water period preceding pumping. At the low water period after pumping, newly settled cyprids were counted using a 10 x 10 cm quadrat.

5.2.4.2 Trawling

Trawling allowed verification of results obtained by pumping as well as a comparison of the two methodologies. Trawling was undertaken in the area around the two pumping sites and at a third position midway between them. Three tows each of ten minutes duration were made at each of the three sites, tows being alternated between sites.

5.2.5 Larval supply in Port Erin Bay

In May and June 1994 cyprid density was determined at three positions within a semi enclosed bay to determine if supply varied with increasing distance inside the bay. In addition, an attempt was made to relate cyprid supply to settlement.

Three barnacle covered vertical rock walls were selected in Port Erin bay, distributed at the bay mouth, midway inside and near the shore at the inner end. On each wall at mid tide level, ten squares measuring 10 x 10 cm were scraped clear of barnacles. At low water these settlement squares were gently brushed with a toothbrush to remove any recently settled cyprids. Trawling was undertaken at high water at transects opposite each of the three settlement sites (see Figure 5.3). Three ten minute tows were made at each transect, tows being alternated between sites. At the following low water, settlement squares were sampled for newly settled cyprids using a 10 x 10 cm quadrat.

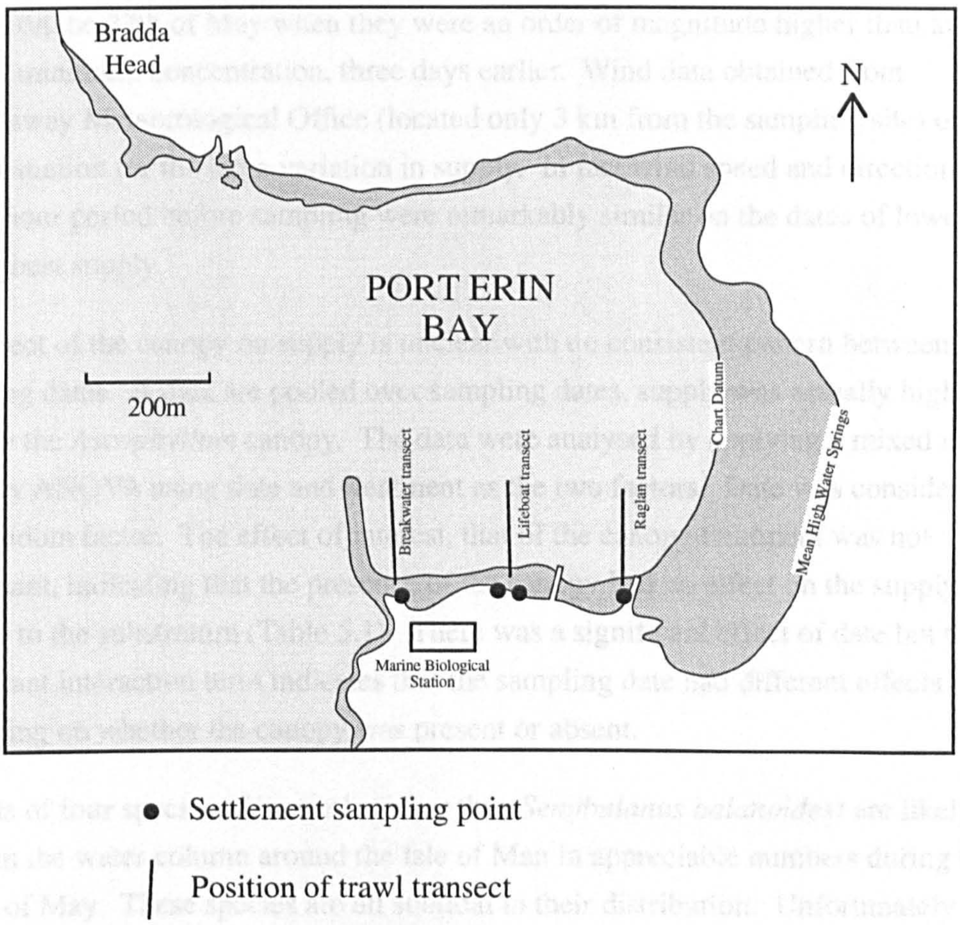


Figure 5.3 Position of trawl transects and settlement sites in Port Erin Bay

5.3 RESULTS-LARVAL SUPPLY

5.3.1 The effect of the Ascophyllum canopy on larval supply

Cyprid concentrations found at mid shore level at the Castletown Bay site differed markedly between sampling dates (Figure 5.4). Maximum concentrations were present on the 27th of May when they were an order of magnitude higher than at the time of minimum concentration, three days earlier. Wind data obtained from Ronaldsway Meteorological Office (located only 3 km from the sampling site) offered no explanation for the large variation in supply. In fact wind speed and direction for the 12 hour period before sampling were remarkably similar on the dates of lowest and highest supply.

The effect of the canopy on supply is unclear with no consistent pattern between sampling dates. If data are pooled over sampling dates, supply was actually higher beneath the *Ascophyllum* canopy. The data were analysed by applying a mixed model two way ANOVA using date and treatment as the two factors. Date was considered to be a random factor. The effect of interest, that of the canopy treatment was not significant, indicating that the presence of the canopy had no effect on the supply of cyprids to the substratum (Table 5.1). There was a significant effect of date but the significant interaction term indicates that the sampling date had different effects depending on whether the canopy was present or absent.

Cyprids of four species of barnacle (other than *Semibalanus balanoides*) are likely to occur in the water column around the Isle of Man in appreciable numbers during the month of May. These species are all subtidal in their distribution. Unfortunately cyprids have no distinguishing characteristics and so identification of species may only be achieved on the basis of size (Crisp, 1962; Salman, 1981). Mean length of cyprids collected from the intertidal in Castletown Bay was 1.052mm (Figure 5.5). However sizes ranged between 0.88 and 1.34mm. From the size data recorded by Salman (1981) for the Isle of Man and by Crisp (1962) for the Irish Sea it would appear that a proportion of the cyprids sampled were not *Semibalanus balanoides.* A number of *Balanus balanus* and possibly *Balanus crenatus* were probably sampled.

5.3.2 A comparison of cyprid supply to sheltered and exposed shores

Examination of cyprid supply to the exposed and sheltered sites was attempted during the settlement season of 1994. Unfortunately in this year the supply and settlement of *Semibalanus balanoides* to the south east coast of the Isle of Man was negligible. Although supply was higher on the west coast, no suitable sheltered shore could be found. Therefore no results were obtained.

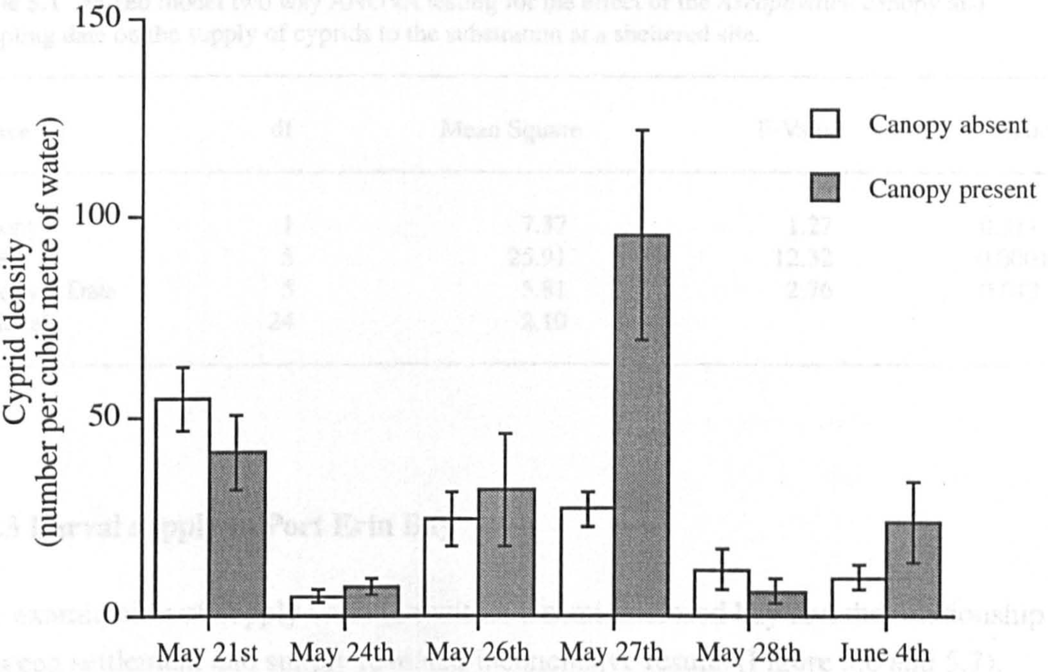


Figure 5.4 The supply of cyprids to the substratum at two adjacent areas, one with a dense monospecific canopy of *Ascophyllum nodosum* and one devoid of canopy alga. Error bars = ± 1SE

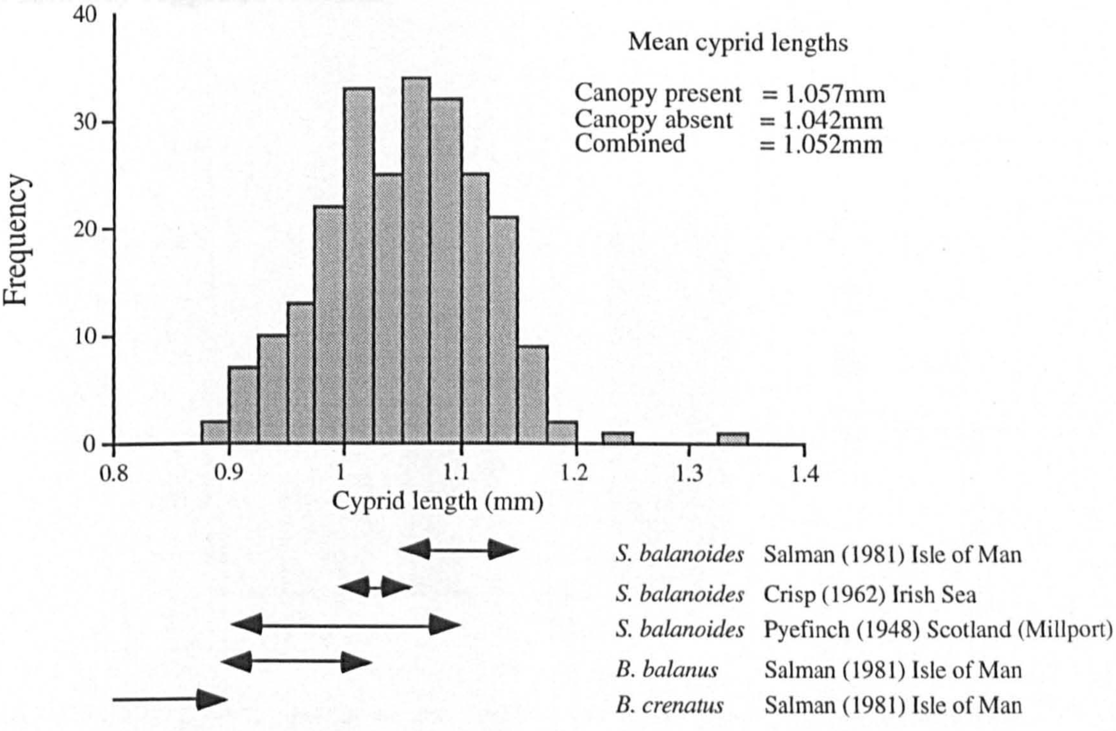


Figure 5.5 Lengths of cyprids collected by pumping from mid tide level at the Castletown Bay site. Cyprids from both treatments combined. Arrows indicate size range of cyprids of different species cited by different authors.

Table 5.1 Mixed model two way ANOVA testing for the effect of the *Ascophyllum* canopy and sampling date on the supply of cyprids to the substratum at a sheltered site.

Source	df	Mean Square	F-Value	P-Value
Canopy	1	7.37	1.27	0.311
Date	5	25.91	12.32	0.0001
Canopy x Date	5	5.81	2.76	0.042
Residual	24	2.10		

5.3.3 Larval supply in Port Erin Bay

The examination of supply variation within a semi-enclosed bay and the relationship between settlement and supply revealed inconclusive results (Figure 5.6 and 5.7). Cyprid concentrations in the water were very low in comparison to those found at the sheltered site in Castletown Bay. The contrasting high levels of settlement suggested a problem in the plankton sampling technique. Alternatively sampling was accurate but cyprids were distributed at a greater depth, or closer to the shore. Qualitative observations of cyprid levels obtained by dragging a plankton net close to the shore in Port Erin Bay suggested the latter.

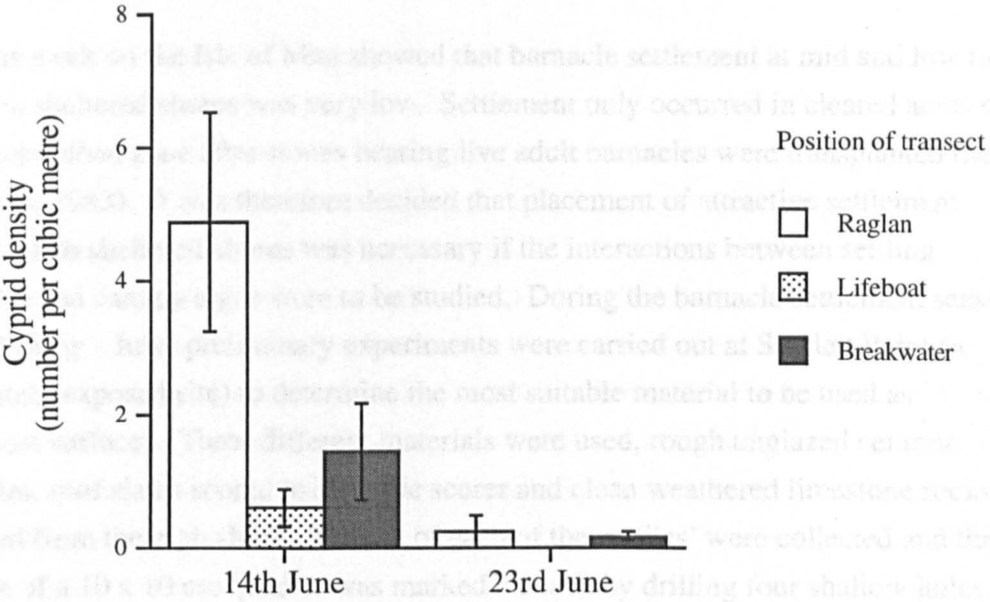


Figure 5.6 Concentration of cyprids at three transects in Port Erin Bay. Sampling undertaken by trawling a 250μm plankton net. Error bars = ± 1SE.

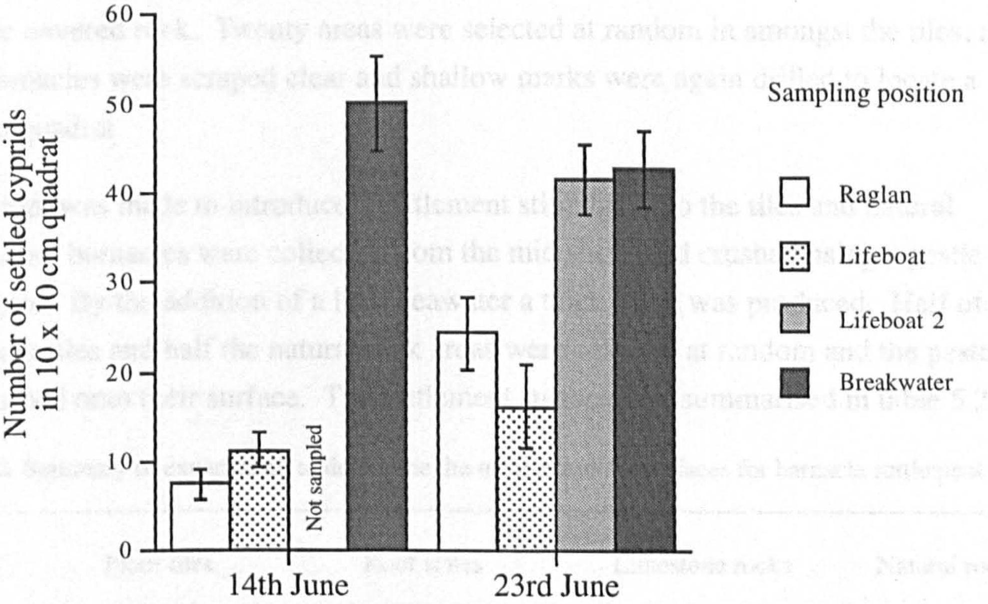


Figure 5.7 Levels of barnacle settlement onto vertical walls in Port Erin Bay during the settlement season of 1994. Error bars = ± 1SE.

5.4 METHODS-1992 SETTLEMENT SEASON

5.4.1 Preliminary experiment on different settlement surfaces.

Previous work on the Isle of Man showed that barnacle settlement at mid and low tide levels on sheltered shores was very low. Settlement only occurred in cleared areas of the *Ascophyllum* zone after stones bearing live adult barnacles were transplanted there (Hawkins, 1983). It was therefore decided that placement of attractive settlement surfaces onto sheltered shores was necessary if the interactions between settling barnacles and canopy algae were to be studied. During the barnacle settlement season of 1992 (May - July) preliminary experiments were carried out at Scarlett Point (a moderately exposed site) to determine the most suitable material to be used as settlement surfaces. Three different materials were used, rough unglazed ceramic floor tiles, roof slates scored using a tile scorer and clean weathered limestone rocks collected from the high shore. Twenty of each of these 'tiles' were collected and the position of a 10 x 10 cm quadrat was marked on each by drilling four shallow holes. All sixty "settlement tiles" were placed in sea water tanks for two weeks to enable a natural microbial film to begin to develop. After this period the tiles were positioned at random at mid tide level and attached to the rock surface using Blue Hawk Quick Set Cement.

The recruitment of barnacles onto settlement tiles was compared with that on natural barnacle covered rock. Twenty areas were selected at random in amongst the tiles, the adult barnacles were scraped clear and shallow marks were again drilled to locate a 10 x 10 cm quadrat.

An attempt was made to introduce a settlement stimulus onto the tiles and natural rock. Adult barnacles were collected from the mid shore and crushed using a pestle and mortar. By the addition of a little seawater a thick paste was produced. Half of all settlement tiles and half the natural rock areas were selected at random and the paste was brushed onto their surface. The settlement surfaces are summarised in table 5.2.

Table 5.2 Summary of experiment to determine the most attractive surfaces for barnacle settlement

Material	Floor tiles		Roof slates		Limestone rocks		Natural rock	
Stimulus	Yes	No	Yes	No	Yes	No	Yes	No
Number of replicates	10	10	10	10	10	10	10	10

Tiles and cleared areas were sampled after six days by counting the number of metamorphosed spat within a 10 x 10 cm quadrat.

5.5 RESULTS-1992 SETTLEMENT SEASON

5.5.1 Preliminary experiments on different settlement surfaces

Recruitment of *Semibalanus balanoides* over a six day period at Scarlett Point showed very obvious differences between the different substrata, with natural rock showing by far the highest levels (Figure 5.8). Floor tiles and roof slates showed negligible recruitment whilst limestone rocks only appeared effective as a settlement surface when the crushed barnacle stimulus was added. Even then, recruitment levels were in the order of 9 times less than on natural rock. Two way ANOVA indicated a highly significant effect of substrate type, but no significant effect of the added stimulus (Table 5.3). It appears however from figure 5.8 that whilst the stimulus had no effect on natural substrate, it significantly increased recruitment on limestone rocks. This is borne out by one way ANOVA carried out separately on the two different substrata (Table 5.4).

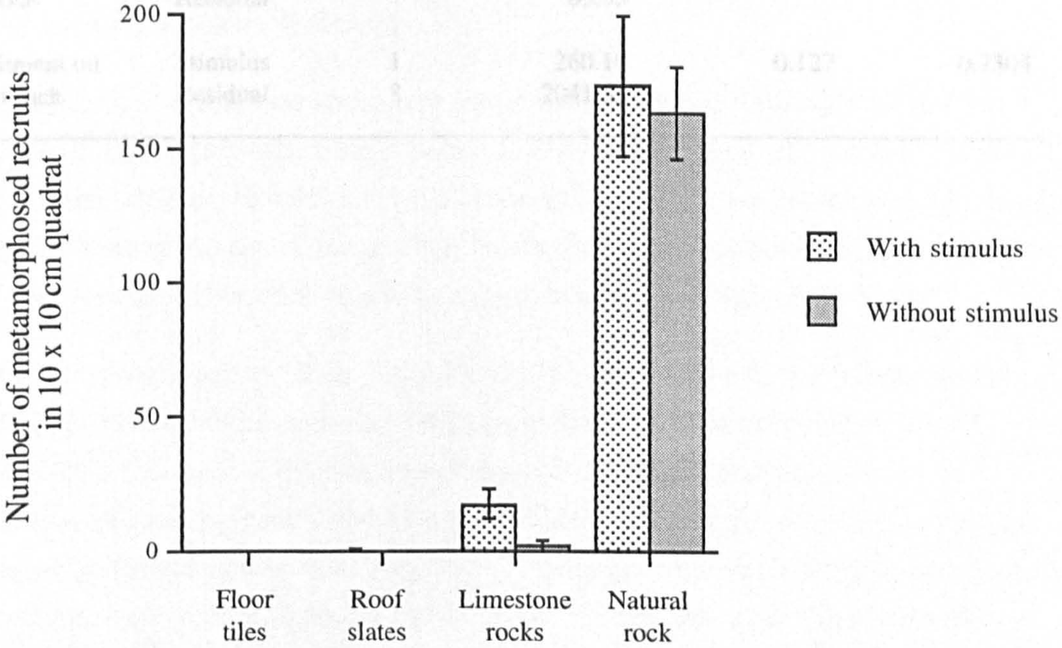


Figure 5.8 Recruitment of *Semibalanus balanoides* over a six day period (30.4.92-6.5.92) to four different substrata at Scarlett Point with and without a settlement stimulus. Error bars = ± 1 SE

Table 5.3 Two way ANOVA testing for the effect of substrate type (limestone settlement tiles or natural substrate) and the presence of artificial stimulus on recruitment of *Semibalanus balanoides* to a moderately exposed mid shore.

Source	df	Mean Square	F-Value	P-Value
Substrate	1	118259.65	105.60	0.0001
Stimulus	1	780.07	0.69	0.4169
Substrate x Stimulus	1	33.67	0.03	0.8646
Residual	15	1119.46		

Table 5.4 One way ANOVA testing for the effect of artificial stimulus on recruitment of *Semibalanus balanoides* to a moderately exposed mid shore.

	Source	df	Mean Square	F-Value	P-Value
Recruitment on limestone	Stimulus	1	537.34	8.18	0.0243
	Residual	7	65.65		
Recruitment on natural rock	Stimulus	1	260.10	0.127	0.7304
	Residual	8	2041.55		

5.6 METHODS-1993 SETTLEMENT SEASON

5.6.1 Settlement/recruitment of *Semibalanus balanoides* on sheltered fucoid dominated shores: the effect of canopy algae

5.6.1.1 Preparation of settlement slates

After obtaining very low settlement on artificial tiles and stones compared to natural rock (even when the settlement stimulus of crushed adults was used) it was decided to create experimental settlement surfaces from barnacle encrusted natural rock. This was made possible due to the presence of Manx slate on certain exposed shores on the Isle of Man. Using a lump hammer and bolster chisel it was possible to obtain fragments of rock from the mid tide level at Gansey Point where an extensive barnacle and limpet dominated area occurs. Rock fragments were selected which were between 2 and 6 cm thick with an upper surface area which accommodated a 12 x 12 cm quadrat. Although irregular in form, all pieces of rock conformed to the requirements of minimum size and a minimum of 50% adult barnacle cover. The settlement surfaces thus produced will subsequently be referred to as slates. Four shallow marks were drilled on each slate to mark the position of the 12 x 12 cm quadrat used for counting settlement.

One hundred and ninety two settlement slates were created and transported to Port Erin Marine Laboratory where they were placed in running sea water tanks. The tanks were drained between 10 a.m. and 4 p.m. each day to enable work to be carried out on the slates. During the rest of the daylight hours the tanks were covered with black polythene sheeting to provide shade, thus discouraging colonisation by algae.

During this storage period (20th - 26th April 1993) the cover of adult barnacles within the 12 x 12 cm quadrat of each slate was manipulated so as to produce a cover of between 33% and 50%. This was done in such a way as to produce a patchy distribution of adult barnacles and bare rock. One quarter of the slates were selected at random and cages constructed over them. The cages were made from plastic coated chicken wire and were designed to form a 'roof' 3-4 cm above the tile to prevent the sweeping of algal fronds over the tile surface. Previous experimentation with cage design had shown the roof to effectively prevent algal sweeping, maintaining an adequate gap between tile surface and algae for at least three months. Immediately before the slates were transplanted to the sheltered shore, all limpets were removed from the slate surface.

On 27th April, when cyprid settlement had commenced, all slates were transported to the experimental site, a sheltered, fucoid dominated shore in Castletown Bay.

5.6.1.2 Experimental design

The experiment was designed to distinguish between the two factors, barrier and sweeping, and consisted of four experimental treatments as shown in table 5.5.

Table 5.5 Design of settlement/recruitment experiment.

Treatment	Description	Barrier	Sweeping
1- 'Cleared'	Canopy removed	N	N
2- 'Sweeper'	Canopy removed. Single large plant left in place in centre of each plot	N	Y
3- 'Caged'	Canopy intact. Settlement slates caged	Y	N
4- 'Control'	Canopy intact	Y	Y

Treatments 1, 2, 3, and 4 will be described as cleared, sweeper, caged and control respectively.

The experiment was established at three shore levels; these corresponded to the middle of the *Fucus spiralis*, the *Ascophyllum nodosum* and the *Fucus serratus* zones and were at 2.8, 4.1 and 5.0m above C.D. respectively. Areas were chosen at the Castletown Bay site where a dense monospecific canopy of each species existed.

At each shore level sixteen plots were selected, within a minimum area of 400 square metres. Experimental treatments were assigned at random to these plots, such that each treatment was replicated four times at each shore level.

Canopy clearances measuring 2 x 2 metres were made in the *Fucus serratus* and *Ascophyllum* zones, whilst clearances measuring 1 x 1 metre were made in the *Fucus spiralis* zone. In the centre of each of the cleared areas, four patches of substratum were selected and cleared of algal turf using a wire brush. The same procedure was followed at each of the "non-cleared" plots. Settlement slates were distributed amongst the experimental plots and fixed to the scraped patches using Blue Hawk Quick Set Cement. In most cases slates were positioned in slight depressions, such that raising of the tile surface above the surrounding substratum was kept to a minimum.

In this way at three shore levels each of four treatments was replicated four times, with each replicate containing four sub-samples as shown in table 5.6.

Table 5.6 Replication of settlement/recruitment experiment

Shore height	Treatments	Replication of each treatment	Subsamples in each replicate
Low	1-4	4	4
Mid	1-4	4	4
High	1-4	4	4

5.6.1.3 Sampling

Sampling always took place during a single low water period. A plastic quadrat measuring 12x12 centimetres and divided into 36 equal squares was constructed. This could be located on each settlement tile in exactly the same position at each sampling date by placing its corners over the pre drilled holes.

On the first sampling date the total number of cyprids and metamorphosed individuals falling within the quadrat were counted. On subsequent dates, the quadrat was sub-sampled, 12 out of the 36 squares within the quadrat being searched. On dry days it was relatively easy to distinguish between cyprids and metamorphosed spat. However on wet days, when a film of water occurred on the tile surface, it was impossible to distinguish the two forms at the rate necessary to sample all slates in one low water period. Thus, the number of days on which sampling could be undertaken was limited.

Throughout the settlement season, it was observed that a number of cyprids were settling on the slates but failing to metamorphose. These cyprids could be recognised as being slightly darker and thinner and were rejected from the counts of cyprids. On 2nd of June counts were made of these "dead cyprids" at all shore levels.

In addition to determining levels of settlement and recruitment on settlement slates, sampling of metamorphosed spat on natural substrata in the presence and absence of the canopy was undertaken. This allowed an assessment of recruitment levels onto sheltered shores under natural conditions. These data could then be compared with recruitment onto artificial settlement slates which provided an attractive settling site.

At each plot cleared of canopy and at each experimental position under the canopy, recruitment was determined. Four 12 x 12cm quadrats were positioned at random at each plot. If the quadrat fell on an unsuitable settling surface such as algal covered rock, this position was rejected and the quadrat relocated.

After settlement of cyprids had ceased, sampling of metamorphosed recruits was undertaken on three more occasions in order to gain an insight into the effect of the canopy on post settlement mortality rates. This monitoring took place throughout the summer until it became pointless to do so because of the fouling of slates by ephemeral algae.

5.6.1.4 Comparison of recruitment between sheltered and exposed shores

Any comparison of barnacle recruitment between sheltered and exposed shores will be confounded by the difference in settlement surface between the two sites unless some form of standardised surface is used. The settlement slates described above were used to make a comparison of recruitment at Scarlett Point (exposed) and the experimental site in Castletown Bay (sheltered). Sixteen settlement slates were cemented to the mid shore at Scarlett Point, at the same tidal height as those in the *Ascophyllum* zone at the sheltered site. The slates were arranged in four spatially separated groups of four slates each. Recruitment of metamorphosed spat was determined at three dates through the settlement period.

The slates at Scarlett Point were also used to investigate the effect of adult conspecifics on recruitment. Sixteen slates were produced in exactly the way described above except they were produced from rock which bore no barnacles whatsoever. These were cemented in between the groups of rocks bearing adult conspecifics again in four groups of four. Recruitment was determined as above.

5.6.2 Dogwhelk predation

Despite fouling by green algae there was still a large number of slates remaining at the end of the summer which held a healthy, unfouled population of juvenile barnacles. These were mainly slates from beneath the canopy. In nearly all cases the original adult barnacles on the slates had been eliminated by predation from dogwhelks. This predation was not examined in detail but records of the aggregation of dogwhelks on the slates were made.

In October 1993 it was decided to use unfouled slates to investigate the effect of dogwhelk predation on the new cohort of juvenile barnacles. Sixteen suitable slates were collected from the *Ascophyllum* and *Fucus serratus* zones and the number of juvenile barnacles manipulated to between 220 and 250 individuals per tile. A numbered micromarker was glued to each tile. These slates were then positioned at random beneath the *Ascophyllum* canopy in an area covering roughly 200 m^2, and re-cemented to the rock.

Two treatments were established, with and without dogwhelks. These were assigned at random to the numbered slates. Dogwhelks were removed from an area within 1m of the 'without dogwhelk' slates and scattered at random throughout the experimental area.

For the next month dogwhelks were removed from the 'without dogwhelk' slates every few days. However it became apparent that in contrast to the summer, when dogwhelks had been observed aggregating at the introduced slates, dogwhelks in most cases now seemed to be dormant. It was therefore decided to suspend the experiment until the spring. The slates were left in place on the shore but unfortunately fouling by ephemeral algae resulted in the experiment being abandoned after a final sampling date in April.

5.7 RESULTS-1993 SETTLEMENT SEASON

5.7.1 Settlement/recruitment of *Semibalanus balanoides* on sheltered fucoid dominated shores: the effect of canopy algae

The experiment analysing the effect of fucoid canopy algae on *Semibalanus balanoides* settlement and recruitment was designed in such a way that a three way ANOVA could be performed. This analysis would partition sources of variance between three factors: shore height, the canopy barrier effect and the canopy sweeping effect. Interaction between these factors would be of particular interest. Unfortunately, it became apparent that the 'sweeper' treatment was not as effective as hoped. Observation of this treatment at all shore levels, on incoming and outgoing tides, showed that in the relatively calm waters of the sheltered site, individual sweeper plants were affecting at best only one or two out of the four replicate settlement slates. Thus this treatment could not be considered to provide an effective sweeping action. Analysis of the data as initially planned was therefore not possible. Instead, the four treatments were treated separately and analysis performed using two way ANOVA with shore height and treatment as the two factors.

5.7.1.1 Cyprid settlement

At all shore heights and sampling dates settlement was lowest in the control treatment where unprotected slates were transplanted beneath an intact canopy (Figure 5.9). The other treatment in which the canopy was left intact was the caged treatment. This showed low settlement in the *Ascophyllum* and *Fucus serratus*, but not the *Fucus spiralis* zone. Thus at mid and low shore heights settlement appeared to be lower where the *Ascophyllum* and *Fucus serratus* canopy remained intact, even when slates were protected from sweeping.

Comparison of settlement between the three shore heights shows that on the first two sampling dates settlement was highest in the *Fucus spiralis* zone (Figure 5.9). For example on May 22nd the mean number of cyprids per quadrat of all four treatments was 26.3, 12.3 and 12.6 in the *Fucus spiralis*, *Ascophyllum* and *Fucus serratus* zones respectively. On June 2nd, settlement was at its lowest level and no differences can be observed between zones.

Statistical analysis of the data appears to confirm these observations. Two way ANOVA was carried out at each sampling date to determine the effect of shore height and treatment on cyprid settlement. Data were first square root transformed in order to satisfy the assumption of homogeneity of variance. The results of the analysis are very similar on the first two sampling dates with the effects of both shore height and treatment being highly significant (Table 5.7).

To investigate these results further a Tukey-Kramer test was applied to all pairwise comparisons within the factors shore height and treatment. On May 22nd, settlement in the *Fucus spiralis* zone was significantly higher than in either the *Ascophyllum* or *Fucus serratus* zones. On May 28th, owing to constraints of time, no sampling was undertaken in the *Ascophyllum* zone. Thus the result of the two way ANOVA simply indicates a difference between the *Fucus spiralis* and the *Fucus serratus* zones.

Tukey-Kramer applied to comparisons between treatments shows significant differences between the control and all other treatments and between the caged and the cleared treatments (Table 5.7).

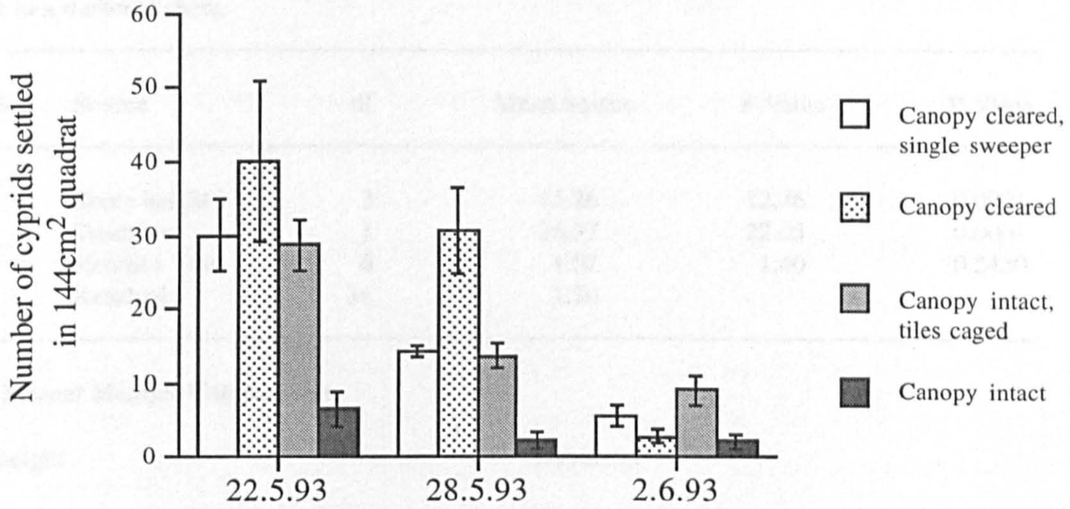
Surprisingly, the interaction term for the first two sampling dates was not significant. It appeared from the data that the effect of the treatments differed with shore height, the *Fucus spiralis* zone appearing different from the lower zones. Unfortunately, owing to lack of independence, it was not possible to add further precision to the analysis by pooling data across sampling dates.

At the final sampling date the effect of the treatments was again highly significant but shore height was not. Examination of figure 5.9 shows that settlement was very low and the effect of treatment differed between shore heights. This is reflected in the significant interaction term. Because of this significant interaction it is not valid to apply multiple comparisons (Tukey Kramer) to the treatment factor (Underwood, 1981).

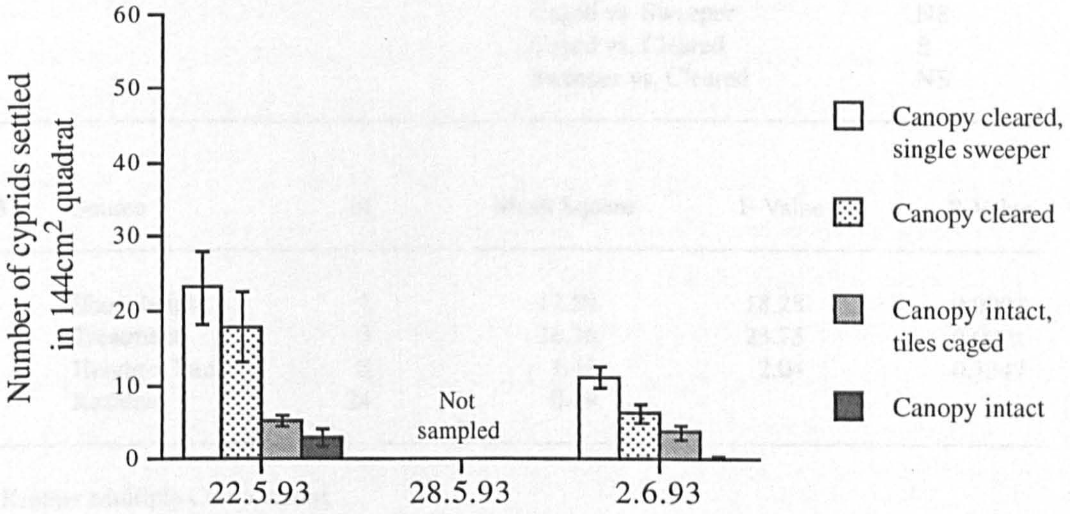
5.7.1.2 Recruitment

The number of metamorphosed recruits was monitored for a period of approximately 5 months. For the purposes of analysis this period has been separated into a phase of recruitment and a phase of post settlement mortality. This division is obviously artificial since mortality of settlers is inextricably linked with recruitment. However, the phase of recruitment, from May 22nd to June 15th is characterised by a general increase in the number of recruits, where levels of settlement obviously outweigh post settlement mortality. After June 15th very little settlement was observed and the populations of new *Semibalanus balanoides* recruits are characterised by a general decline in numbers.

a) ***Fucus spiralis* zone**



b) ***Ascophyllum* zone**



c) ***Fucus serratus* zone**

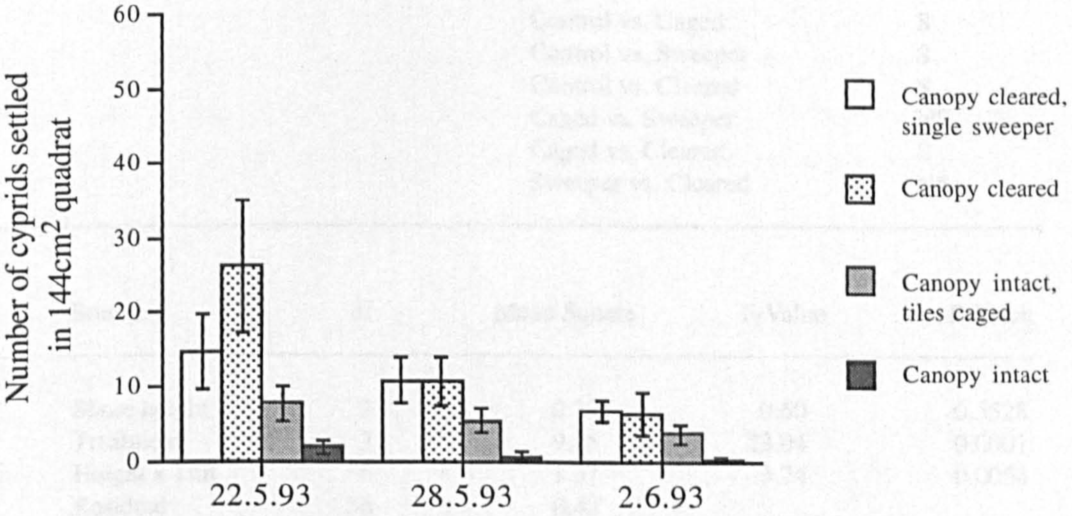


Figure 5.9 Settlement of *Semibalanus balanoides* cyprids on three sampling dates to a canopy dominated shore in Castletown Bay. Error bars = ±1SE
a) *Fucus spiralis* zone b) *Ascophyllum* zone c) *Fucus serratus* zone

Table 5.7 Two way ANOVA and Tukey Kramer multiple comparisons on square root transformed data testing for the effect of shore height and canopy treatments on settlement of *Semibalanus balanoides* cyprids to a sheltered shore.

22.5.93	Source	df	Mean Square	F-Value	P-Value
	Shore height	2	15.26	12.76	0.0001
	Treatment	3	26.37	22.05	0.0001
	Height x Tmt	6	1.67	1.40	0.2430
	Residual	36	1.20		

Tukey Kramer Multiple Comparisons

Shore height		Treatment	
Fucus spiralis vs. *Ascophyllum*	S	Control vs. Caged	S
Fucus spiralis vs. *Fucus serratus*	S	Control vs. Sweeper	S
Fucus serratus vs. *Ascophyllum*	NS	Control vs. Cleared	S
		Caged vs. Sweeper	NS
		Caged vs. Cleared	S
		Sweeper vs. Cleared	NS

28.5.93	Source	df	Mean Square	F-Value	P-Value
	Shore height	1	12.59	18.28	0.0003
	Treatment	3	16.36	23.75	0.0001
	Height x Tmt	3	1.41	2.04	0.1347
	Residual	24	0.69		

Tukey Kramer Multiple Comparisons

Shore height		Treatment	
		Control vs. Caged	S
		Control vs. Sweeper	S
		Control vs. Cleared	S
		Caged vs. Sweeper	NS
		Caged vs. Cleared	S
		Sweeper vs. Cleared	NS

2.6.93	Source	df	Mean Square	F-Value	P-Value
	Shore height	2	0.25	0.60	0.5528
	Treatment	3	9.65	23.04	0.0001
	Height x Tmt	6	1.57	3.74	0.0054
	Residual	36	0.42		

S=Significant difference. Experimentwise error rate (EER) = 5%

The recruitment of spat at all three shore heights was lowest in the control treatment thus reflecting the low settlement observed there (Figure 5.10). In the other 'canopy intact' treatment where caged slates were placed under the undisturbed canopy recruitment did not appear to reflect settlement, high levels being found in all zones. Thus, where the settlement surface was protected from canopy sweeping recruitment was high, despite the presence of an overlying canopy. In fact in the *Ascophyllum* zone recruitment to the caged treatment at the final sampling dates was higher than to canopy cleared treatments.

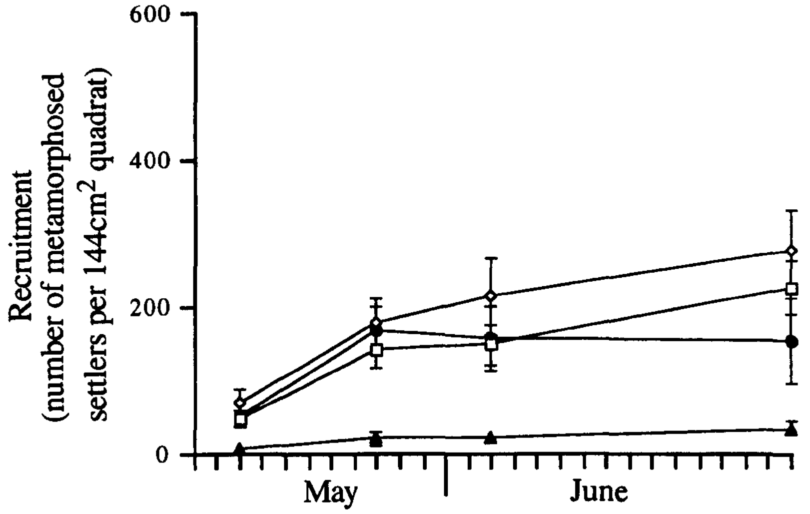
The single plant left in the centre of 'sweeper' plots was designed to provide a sweeping effect without the presence of a canopy barrier. In the *Fucus spiralis* and *Ascophyllum* zones this sweeping effect appears to have produced no depression of recruitment. However, in the *Fucus serratus* zone recruitment to the sweeper treatment is intermediate between the control and the cleared and caged treatments. It is interesting that recruitment to the *Fucus serratus* control was lower than at the other shore heights. These results suggest that sweeping by *Fucus serratus* has a more negative effect on barnacle recruitment than either *Fucus spiralis* or *Ascophyllum*.

Comparison of recruitment between zones shows that surprisingly, despite having the highest level of settlement, the *Fucus spiralis* zone showed lower levels of recruitment than the two lower shore heights. Two way ANOVA on square root transformed data supports the observations outlined above. Analysis was performed on the first three sampling dates, 22nd May, 28th May and 2nd June but not at the final date 15th June because data were heteroscedastic even after transformation. At all three sampling dates a significant effect of shore height and treatment was found (Table 5.8). Tukey-Kramer tests reveal that recruitment to the *Fucus spiralis* zone was significantly lower than to the *Ascophyllum* and *Fucus serratus* zones. Comparison of treatments using Tukey-Kramer shows the control was significantly different from all other treatments. In contrast to the settlement data the caged treatment was not found to be different from cleared treatments. The interaction term was not significant at any of the three dates indicating that the effects of the treatments were the same at each shore height.

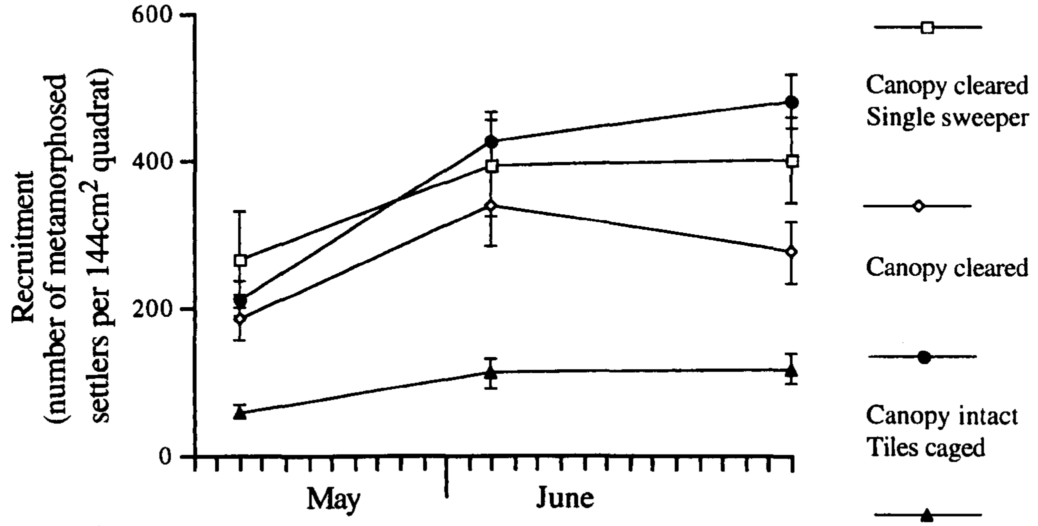
5.7.1.3 Dead cyprids

The number of 'dead' cyprids present on settlement slates was determined at only one sampling date. These were counted in all treatments in the *Fucus spiralis* zone but in only the caged and cleared plots at lower shore heights. Numbers of dead cyprids increased with increasing shore height and decreased under the canopy (Figure 5.11). Two way ANOVA was performed on square root transformed data from only the cleared and caged treatments. A highly significant effect of both shore height and fucoid canopy was found (Table 5.9). The effect of the fucoid canopy was not related to sweeping since the caged treatment was that which was considered.

a) ***Fucus spiralis* zone**



b) ***Ascophyllum* zone**



c) ***Fucus serratus* zone**

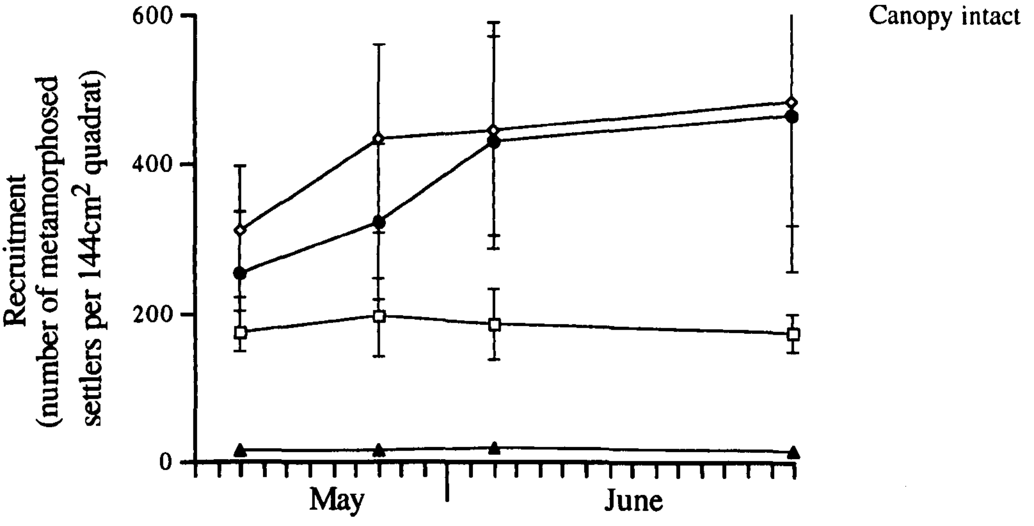


Figure 5.10 Recruitment of *Semibalanus balanoides* to a canopy dominated shore in Castletown Bay. Error bars = ± 1 SE.
a) *Fucus spiralis* zone b) *Ascophyllum* zone c) *Fucus serratus* zone

Table 5.8 Two way ANOVA and Tukey Kramer multiple comparisons on square root transformed data testing for the effect of shore height and canopy treatment on the recruitment of *Semibalanus balanoides* to a sheltered shore

22.5.93	Source	df	Mean Square	F-Value	P-Value
	Shore Height	2	212.69	25.5	0.0001
	Treatment	3	172.91	20.73	0.0001
	Height x Tmt	6	18.38	2.20	0.0651
	Residual	36	8.34		

Tukey-Kramer Multiple Comparisons

Fucus spiralis vs. *Ascophyllum*	S	Control vs. Caged	S
Fucus spiralis vs. *Fucus serratus*	S	Control vs. Sweeper	S
Fucus serratus vs. *Ascophyllum*	NS	Control vs. Cleared	S
		Caged vs. Sweeper	NS
		Caged vs. Cleared	NS
		Sweeper vs. Cleared	NS

28.5.93	Source	df	Mean Square	F-Value	P-Value
	Shore height	1	82.15	6.33	0.0189
	Treatment	3	251.01	19.35	0.0001
	Height x Tmt	3	21.31	1.64	0.2059
	Residual	24	12.97		

Tukey Kramer Multiple Comparisons

Control vs. Caged	S
Control vs. Sweeper	S
Control vs. Cleared	S
Caged vs. Sweeper	NS
Caged vs. Cleared	NS
Sweeper vs. Cleared	NS

2.6.93	Source	df	Mean Square	F-Value	P-Value
	Shore height	2	165.94	11.85	0.0001
	Treatment	3	331.26	23.65	0.0001
	Height * Tmt	6	24.44	1.74	0.1388
	Residual	36	14.01		

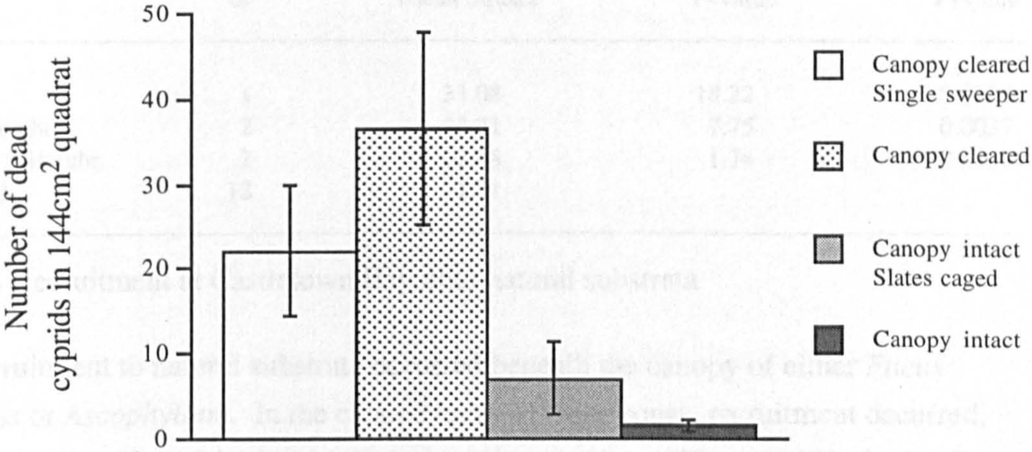
Tukey-Kramer Multiple Comparisons

Fucus spiralis vs. *Ascophyllum*	S	Control vs. Caged	S
Fucus spiralis vs. *Fucus serratus*	S	Control vs. Sweeper	S
Fucus serratus vs. *Ascophyllum*	NS	Control vs. Cleared	S
		Caged vs. Sweeper	NS
		Caged vs. Cleared	NS
		Sweeper vs. Cleared	NS

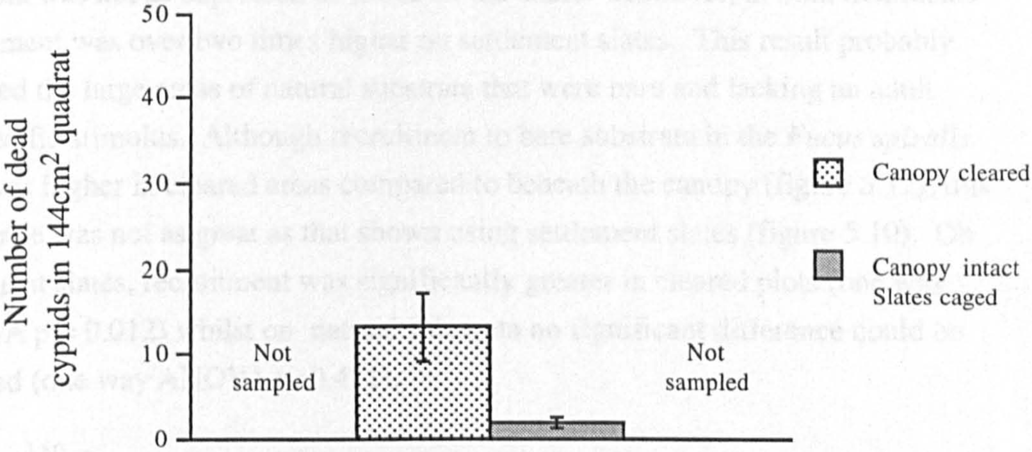
15.6.93 Analysis not performed because data was heteroscedastic even after transformation.

S=Significant difference. Experimentwise error rate (EER) = 5%

a) *Fucus spiralis* zone



b) *Ascophyllum* zone



c) *Fucus serratus* zone

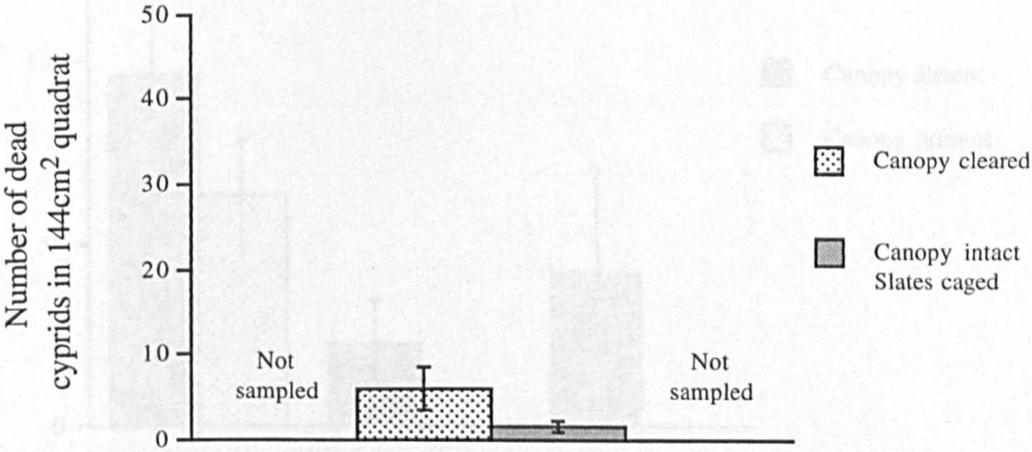


Figure 5.11 Number of 'dead' cyprids on settlement slates on June 2nd. Error bars = ± 1 SE
a) *Fucus spiralis* zone b) *Ascophyllum* zone c) *Fucus serratus* zone

Table 5.9 Two way ANOVA on square root transformed data testing for the effect of fucoid canopy and shore height on the number of 'dead' cyprids present on settlement tiles at the sheltered site.

Source	df	Mean Square	F-Value	P-Value
Canopy	1	31.08	18.22	0.0005
Shore height	2	13.21	7.75	0.0037
Canopy x Height	2	2.98	1.74	0.2030
Residual	18	1.71		

5.7.1.4 Recruitment at Castletown Bay onto natural substrata

No recruitment to natural substrata occurred beneath the canopy of either *Fucus serratus* or *Ascophyllum*. In the cleared areas of these zones, recruitment occurred, but at an order of magnitude less than on settlement slates (Figure 5.12). In the *Fucus spiralis* zone, where adult barnacles are relatively common, recruitment to natural substrata was not as depressed as lower on the shore. However, in both treatments recruitment was over two times higher on settlement slates. This result probably reflected the large areas of natural substrate that were bare and lacking an adult conspecific stimulus. Although recruitment to bare substrata in the *Fucus spiralis* zone was higher in cleared areas compared to beneath the canopy (figure 5.12), this difference was not as great as that shown using settlement slates (figure 5.10). On settlement slates, recruitment was significantly greater in cleared plots (one way ANOVA p = 0.012) whilst on natural substrata no significant difference could be detected (one way ANOVA p=0.471).

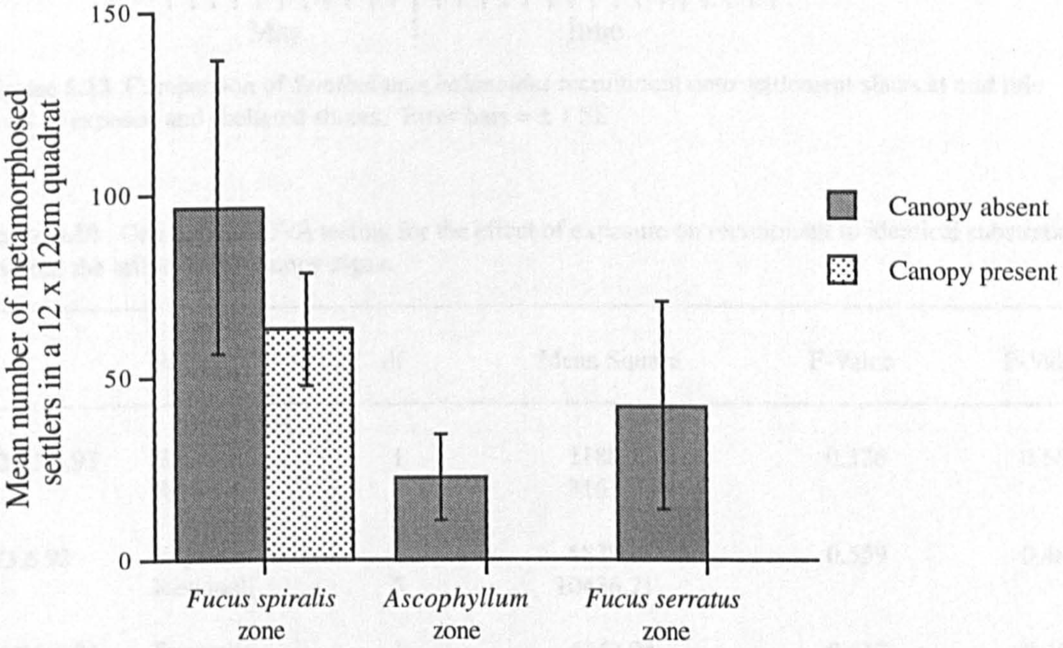


Figure 5.12 Recruitment of *Semibalanus balanoides* onto natural substrata on a sheltered shore at Castletown Bay. Sampled on June 1st 1993. Error bars = ± 1 SE.

5.7.1.5 Comparison of recruitment between exposed and sheltered shores

Recruitment of *Semibalanus balanoides* to identical settling surfaces (i.e. settlement slates) on the mid shore of an exposed and a sheltered site is shown in figure 5.13. Owing to constraints of time sampling at the two sites was not carried out on identical dates. It is clear from figure 5.13 that, given a suitable settlement surface and an area clear of fucoid canopy, recruitment to a sheltered site can be as high as that at an adjacent exposed site. In fact, on the first two sampling dates recruitment was higher to cleared areas in the *Ascophyllum* zone at the sheltered shore even though sampling was undertaken a few days later at the exposed site. One way ANOVA carried out at each sampling date revealed no significant difference in recruitment between the exposed and sheltered sites (Table 5.10).

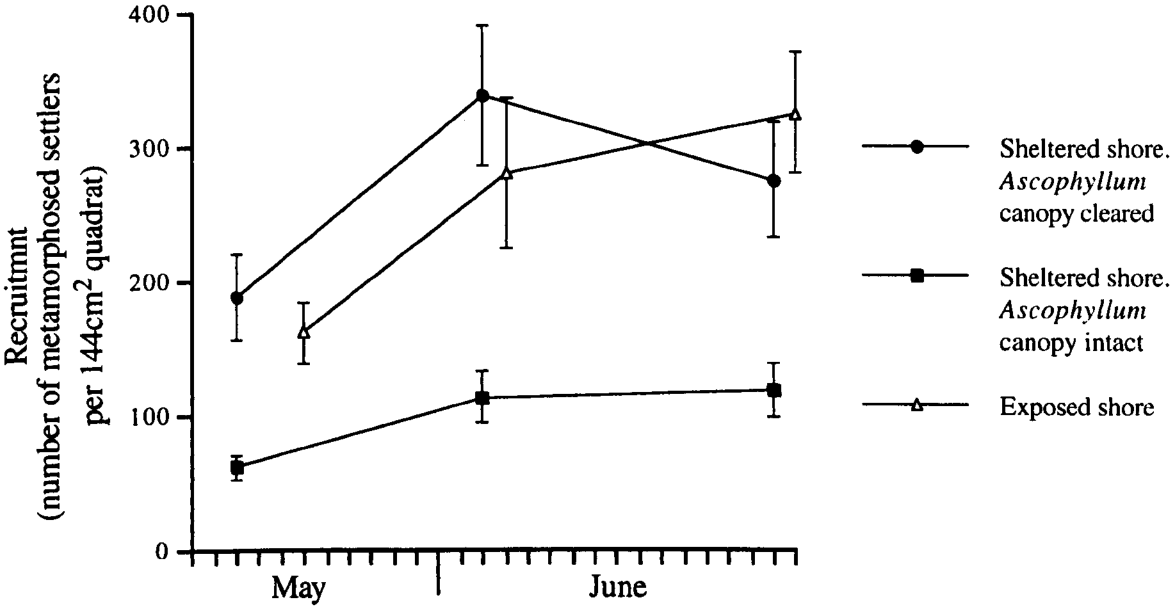


Figure 5.13 Comparison of *Semibalanus balanoides* recruitment onto settlement slates at mid tide level of exposed and sheltered shores. Error bars = ± 1 SE

Table 5.10 One way ANOVA testing for the effect of exposure on recruitment to identical substrata without the influence of canopy algae.

	Source	df	Mean Square	F-Value	P-Value
22/25.5.93	Exposure	1	1188.76	0.376	0.567
	Residual	5	3163.13		
2/3.6.93	Exposure	1	5829.17	0.559	0.488
	Residual	5	10436.71		
15/16.6.93	Exposure	1	4242.96	0.613	0.469
	Residual	5	6917.25		

The number of 'dead' cyprids at the exposed site was also determined although not on settlement slates. Thus the results are not directly comparable between the exposed and sheltered site. The same trend as at the sheltered site was identified with an increasing number of dead cyprids with increasing height on the shore (Figure 5.14).

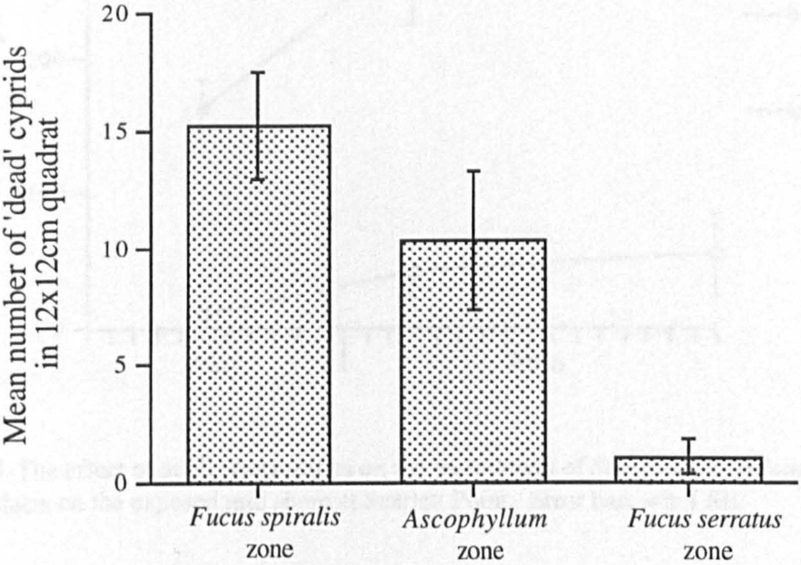


Figure 5.14 Number of 'dead' cyprids on natural substrata at an exposed site Scarlett Point.. Sampled on June 4th. Error bars = ± 1 SE.

5.7.1.6 Effect of adult conspecifics on recruitment of *Semibalanus balanoides* to an exposed shore

Examination of the effects of adult conspecifics on recruitment of *Semibalanus balanoides* revealed clear results. Using settlement surfaces of Manx slate bearing no adult barnacles resulted in very low recruitment (Figure 5.15). One way ANOVA applied at three sampling dates showed recruitment was significantly greater on slates bearing adult conspecifics (Table 5.11).

Table 5.11 One way ANOVA testing for the effect of *Semibalanus balanoides* adults on recruitment onto settlement tiles on the mid shore of a moderately exposed site.

	Source	df	Mean Square	F-Value	P-Value
25.5.93	Adult barnacles	1	39922.34	58.71	0.0006
	Residual	5	679.99		
3.6.93	Adult barnacles	1	84787.59	15.71	0.017
	Residual	4	5398.59		
16.6.93	Adult barnacles	1	109620.17	24.22	0.008
	Residual	4	4526.17		

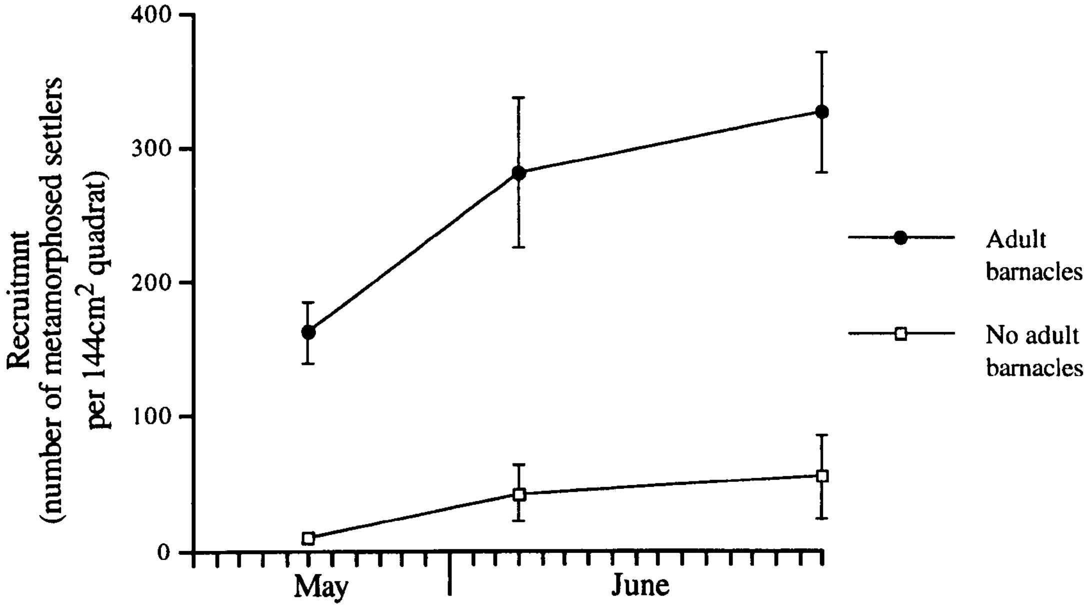


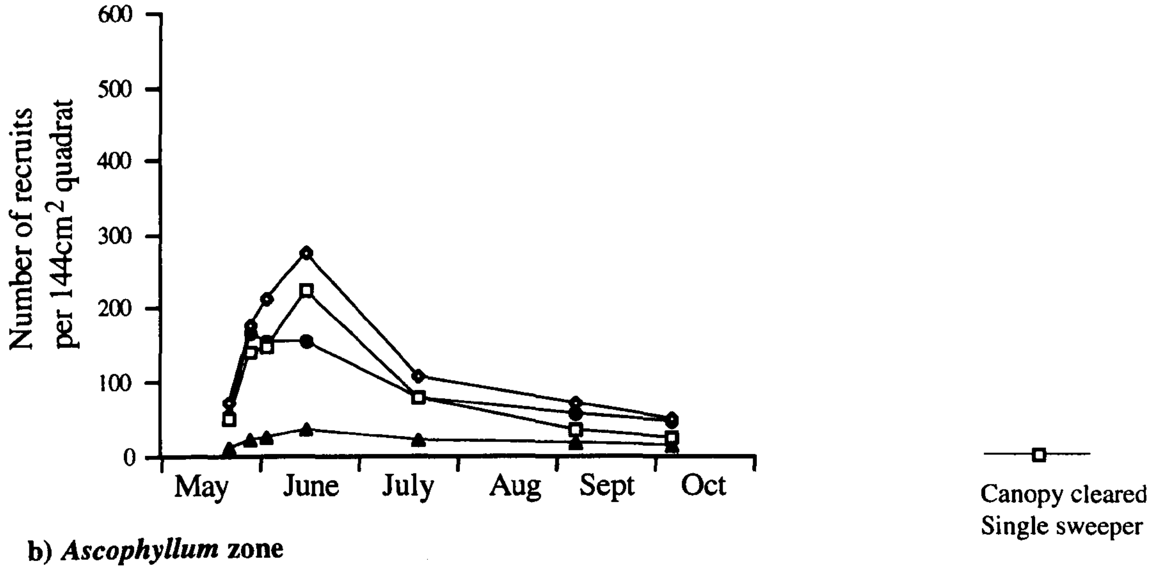
Figure 5.15 The effect of adult conspecifics on the recruitment of *Semibalanus balanoides* on settlement slates on the exposed mid shore at Scarlett Point. Error bars = ± 1 SE.

5.7.2 Post settlement mortality of *Semibalanus balanoides*

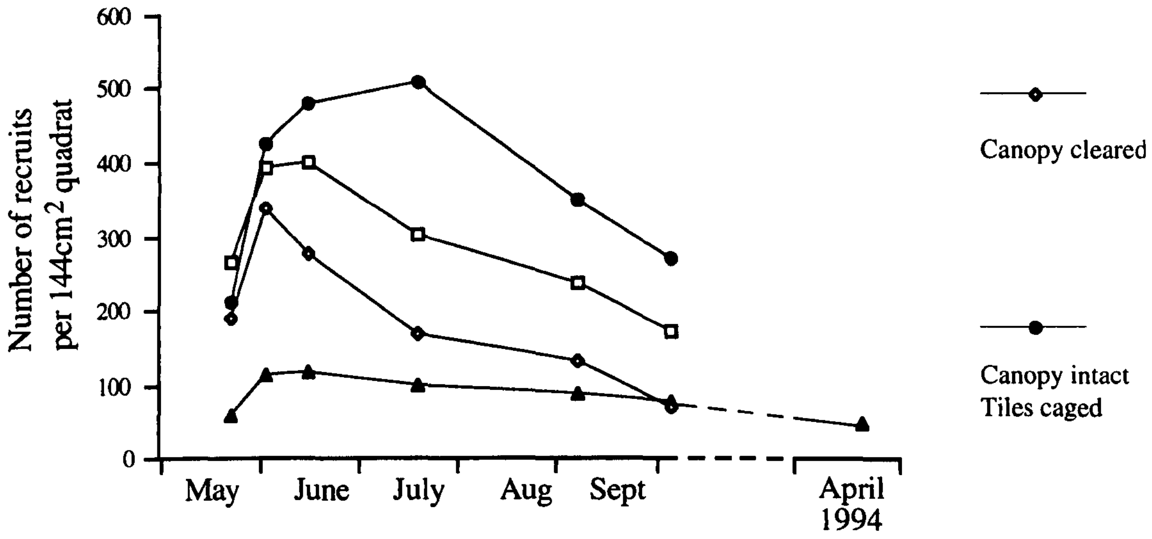
Post settlement mortality of new recruits is shown in figure 5.16. In the *Fucus serratus* zone only those treatments with an intact canopy were monitored after 15th June. At this low level on the shore settlement slates in cleared plots were heavily fouled by green algae making sampling of barnacle mortality pointless. By the end of September, cleared plots of the *Ascophyllum* zone were suffering the same problem and sampling was stopped. In the control treatment of the *Ascophyllum* zone sampling was undertaken again in April 1994 to establish whether new recruits could survive to one year of age and thus provide a settlement stimulus to new settlers. Figure 5.16 shows that indeed, individuals which settled beneath an intact canopy of *Ascophyllum* survived until the spring of the following year. Of the recruits present at the end of the settlement period (15th June), 39% survived until April 1994.

Although figure 5.16 shows the decline of new recruits in all treatments, it is not possible to compare the rate of decline because of the differences in initial numbers. In order to determine the effect of the canopy on post settlement mortality, decline was calculated as a percentage of the original number (i.e. % mortality). In both the *Ascophyllum* and the *Fucus spiralis* zones, treatments where the canopy was left intact showed lower rates of mortality than treatments where the canopy was cleared (Figure 5.17). This could not be determined for the *Fucus serratus* zone.

a) ***Fucus spiralis*** **zone**



b) ***Ascophyllum*** **zone**



c) ***Fucus serratus*** **zone**

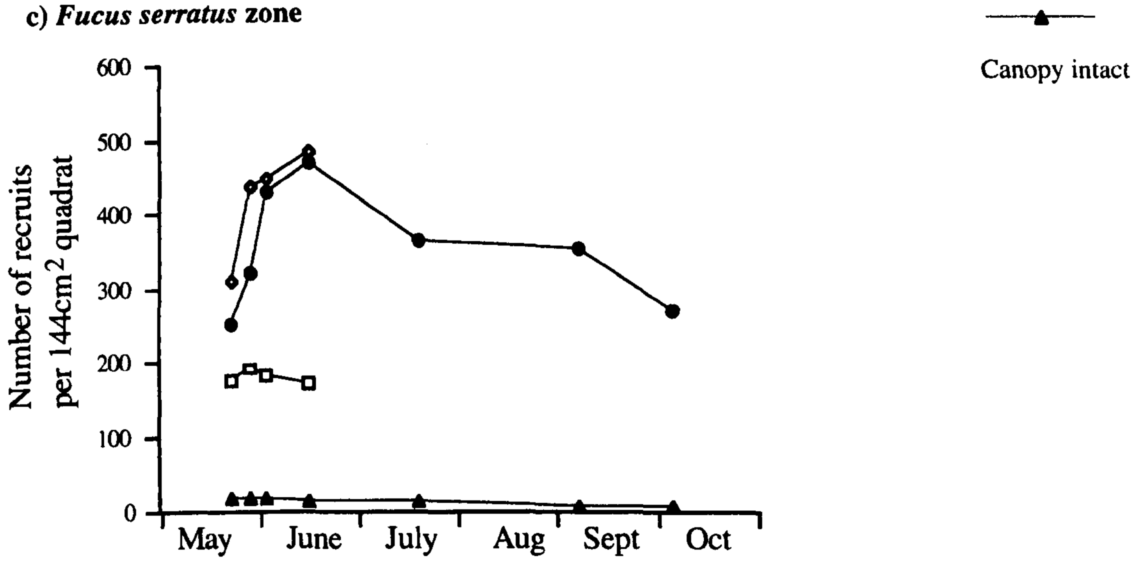
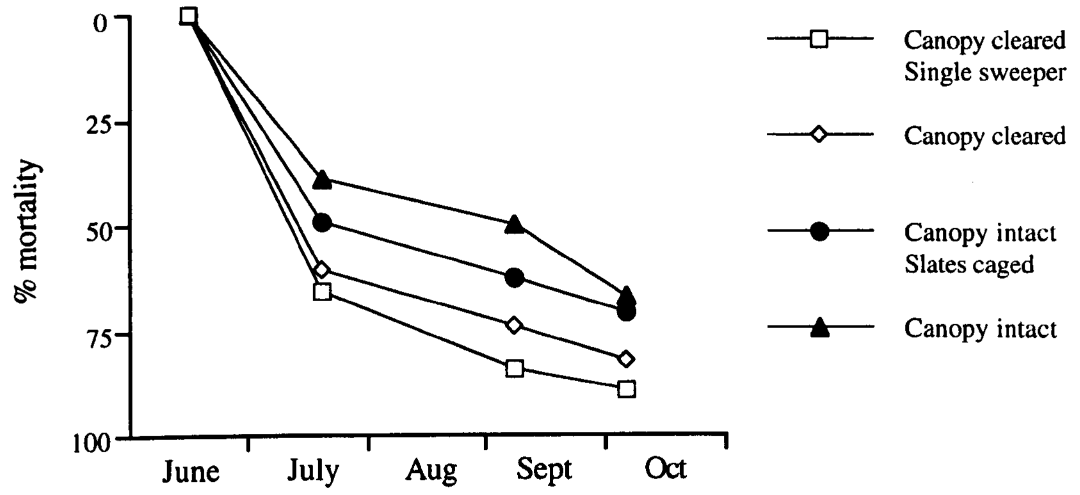
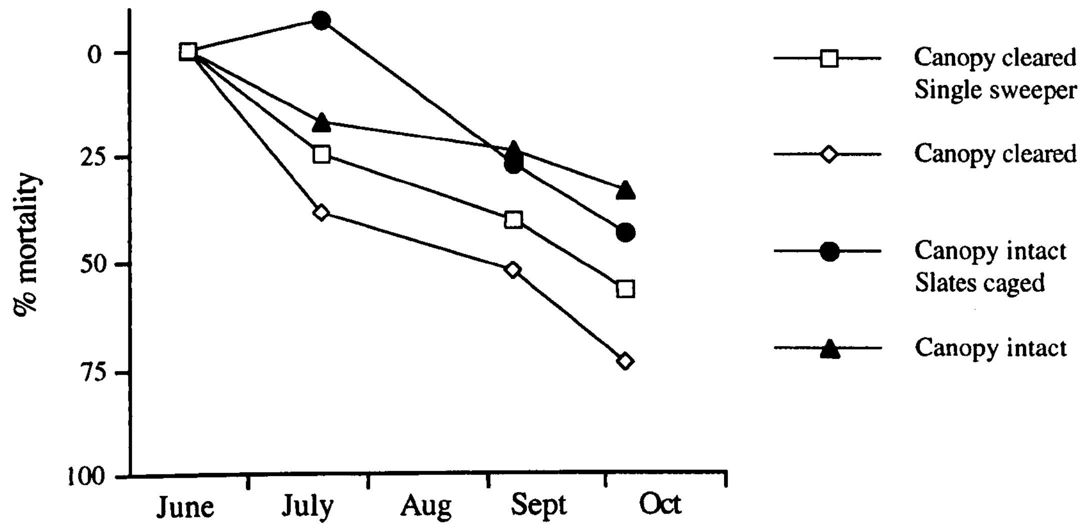


Figure 5.16 Recruitment and subsequent decline in number of *Semibalanus balanoides* in summer/ autumn 1993. Error bars omitted for clarity.
a) *Fucus spiralis* zone b) *Ascophyllum* zone c) *Fucus serratus* zone

a) ***Fucus spiralis* zone**



b) ***Ascophyllum* zone**



c) ***Fucus serratus* zone**

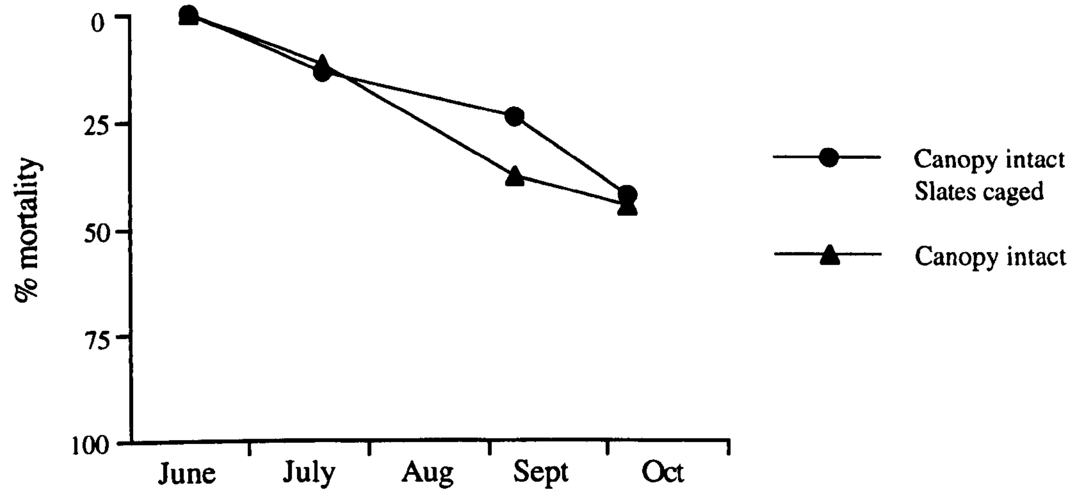


Figure 5.17 Percentage mortality of new *Semibalanus balanoides* recruits in summer/autumn 1993. Error bars omitted for clarity.
a) *Fucus spiralis* zone b) *Ascophyllum* zone c) *Fucus serratus* zone

In order to statistically compare mortality rates between treatments, regression coefficients were calculated for each individual replicate (Table 5.12). One way ANOVA was then performed to determine differences between coefficients. This analysis showed no significant difference between individual treatments at any shore level (Table 5.13). Since the point of interest was the effect of the fucoid canopy on post settlement mortality, treatments were pooled in order to compare mortality beneath the fucoid canopy with mortality in cleared areas. A two way ANOVA was performed to examine the effect of shore height and canopy on percentage mortality. A significant effect of both factors was found (Table 5.14). Percentage mortality was significantly lower beneath a fucoid canopy than in cleared areas and was significantly higher in the *Fucus spiralis* zone than at mid shore level in the *Ascophyllum* zone. The effect of the fucoid canopy was the same at both shore levels (indicated by the non significant interaction term in the two way analysis).

Table 5.12 Regression coefficients of percentage survival of new *Semibalanus balanoides* recruits between 15.6.93 and 5.10.93 in different experimental treatments.

	Treatment			
	Sweeper	Cleared	Caged	Control
Fucus spiralis zone	-0.6758	-0.7416	-0.5345	-0.5652
	-0.7184	-0.4974	-0.5797	-0.3892
	-0.7676	-0.7655	-0.7164	-0.5509
	-0.7851	-0.8021	-0.5339	-0.7396
Mean	-0.7367	-0.7016	-0.5911	-0.5612
Ascophyllum zone	-0.5462	-0.6593	-0.4081	-0.0504
	-0.1909	-0.6654	-0.5052	-0.2483
	-0.4638	-0.6671	-0.3646	-0.6768
	-0.5722	-0.4978	-0.478	-0.3109
Mean	-0.443275	-0.6224	-0.438975	-0.3216
Fucus serratus zone			-0.5655	-0.1968
			-0.4200	-0.3937
			-0.2685	-0.2887
			-0.3758	
Mean			-0.4075	-0.2931

Table 5.13 One way ANOVA testing for the effect of canopy treatment on percentage survival of *Semibalanus balanoides*. Analysis performed on regression coefficients.

	Source	df	Mean Square	F-Value	P-Value
Fucus spiralis	Treatment	3	0.0287	2.32	0.1275
	Residual	12	0.0124		
Ascophyllum	Treatment	3	0.0616	2.24	0.1358
	Residual	12	0.0274		
Fucus serratus	Treatment	1	0.0224	1.729	0.2456
	Residual	5	0.013		

Table 5.14 Two way ANOVA testing for the effect of fucoid canopy cover and shore height on the percentage survival of new *Semibalanus balanoides* recruits. Analysis performed on regression coefficients.

Source	df	Mean Square	F-Value	P-Value
Shore height	1	0.2922	14.25	0.0008
Canopy	1	0.1747	8.52	0.0069
Height x Canopy	1	0.0002	0.009	0.9256
Residual	28	0.0205		

5.7.3 Dogwhelk predation

5.7.3.1 Dogwhelk aggregation

Aggregation of dogwhelks on transplanted settlement slates was monitored throughout the settlement period. Although high numbers were found aggregating on settlement slates in the *Fucus serratus* and *Ascophyllum* zones no dogwhelks whatsoever were found on slates in the high shore *Fucus spiralis* zone. During the period of observation (22nd May - 15th June) congregating dogwhelks were observed predating only on the adult barnacles present on slates and ignoring new recruits. The first observation of dogwhelks predating on new recruits was in September. Predation pressure was such that nearly all adult barnacles transplanted to the mid and low shore zones were eaten by the end of June.

Figure 5.18 shows dogwhelk aggregation at the two shore heights in canopy cleared and canopy intact treatments. Two way ANOVA was carried out for each sampling date (Table 5.15). Although this analysis revealed some significant results the lack of any consistent pattern between the three sampling dates means no conclusions can be made regarding the distribution of dogwhelks between shore heights or treatments.

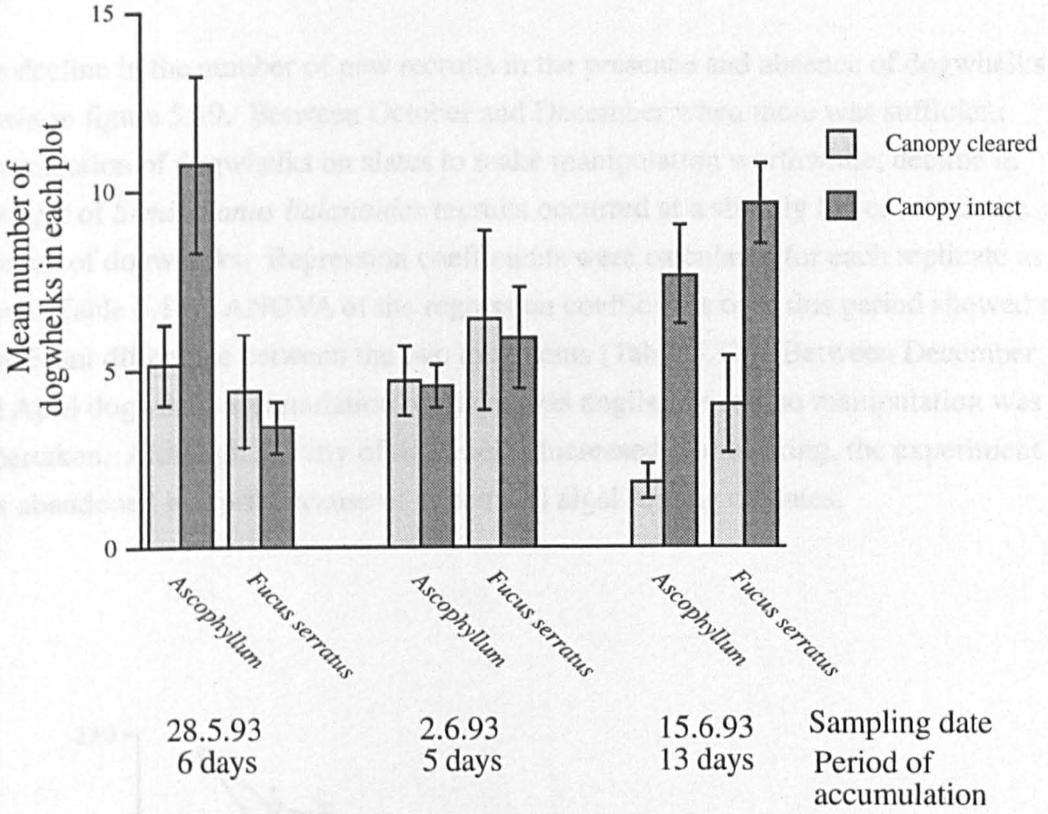


Figure 5.18 Aggregation of dogwhelks onto settlement slates. Error bars = ± 1 SE

Table 5.15 Two way ANOVA testing for the effect of shore height and fucoid canopy on the aggregation of dogwhelks on *Semibalanus balanoides* settlement tiles

	Source	df	Mean Square	F-Value	P-Value
28.5.93	Shore height	1	5.27	4.98	0.0338
	Canopy	1	1.12	1.06	0.3120
	Height x Canopy	1	1.51	1.42	0.2431
	Residual	28	1.06		
2.6.93	Shore height	1	0.243	0.368	0.549
	Canopy	1	0.0006	0.0008	0.977
	Height x Canopy	1	0.0006	0.0009	0.976
	Residual	26	0.659		
15.6.93	Shore height	1	32.04	3.12	0.0889
	Canopy	1	242.29	23.63	0.0001
	Height x Canopy	1	0.04	0.0037	0.9519
	Residual	26	10.25		

5.7.3.2 Mortality of *Semibalanus balanoides* in the presence and absence of dogwhelks

The decline in the number of new recruits in the presence and absence of dogwhelks is shown in figure 5.19. Between October and December when there was sufficient accumulation of dogwhelks on slates to make manipulation worthwhile, decline in numbers of *Semibalanus balanoides* recruits occurred at a slightly lower rate in the absence of dogwhelks. Regression coefficients were calculated for each replicate as above (Table 5.16). ANOVA of the regression coefficients over this period showed no significant difference between the two treatments (Table 5.17). Between December and April dogwhelk accumulation on slates was negligible and no manipulation was undertaken. Although activity of dogwhelks increased in the spring, the experiment was abandoned in April because of ephemeral algal fouling of slates.

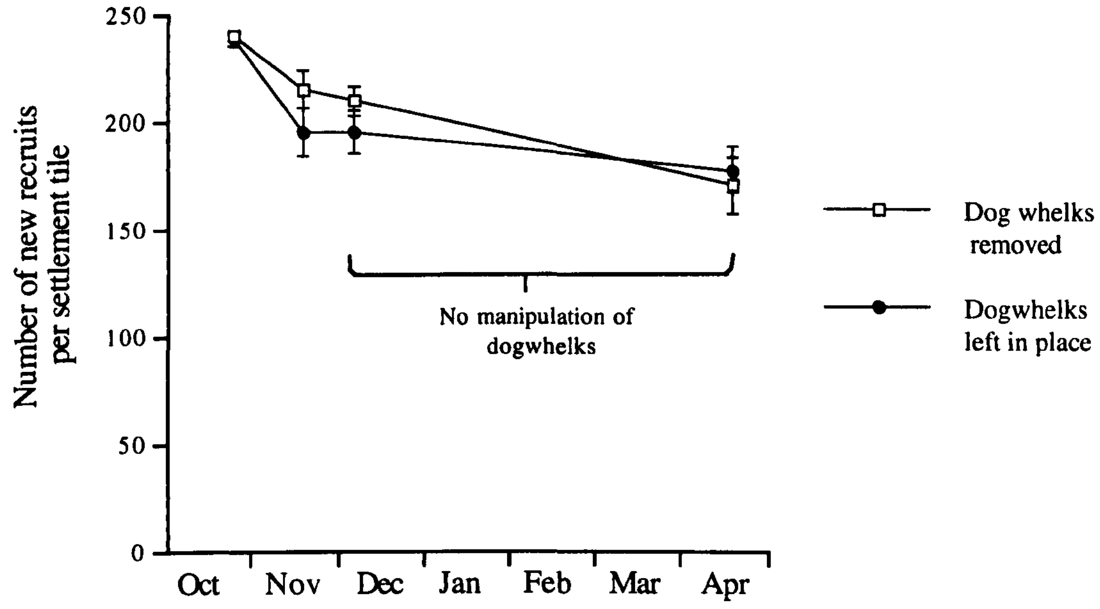


Figure 5.19 Mortality of new *Semibalanus balanoides* recruits beneath the *Ascophyllum* canopy with and without dogwhelks. Error bars = ±1 SE.

Table 5.16 Regression coefficients for decline in numbers over time of new *Semibalanus balanoides* recruits beneath an *Ascophyllum* canopy in the presence and absence of dogwhelks. Coefficients calculated for each individual replicate

Period	October-December		October-April	
Treatment	Dogwhelks removed	Dogwhelks left in place	Dogwhelks removed	Dogwhelks left in place
	-0.585	-0.495	-0.314	-0.222
	-0.201	-0.830	-0.295	-0.312
	-0.600	-0.782	-0.198	-0.234
	-0.333	-0.629	-0.144	-0.251
	-1.159	-1.692	-0.610	-0.475
	-0.929	-1.460	-0.420	
	-0.988		-0.605	
Mean	-0.685	-0.981	-0.369	-0.299

Table 5.17 One way ANOVA testing for the effect of dogwhelk presence on the mortality of new *Semibalanus balanoides* recruits beneath an *Ascophyllum* canopy. Tests carried out on regression coefficients-see table 5.16.

	Source	df	Mean Square	F-Value	P-Value
Oct-Dec	Dogwhelk	1	0.2837	1.635	0.2274
	Residual	11	0.1736		
Oct-Apr	Dogwhelk	1	0.0146	0.5896	0.4603
	Residual	10	0.0248		

5.8 METHODS-1994 SETTLEMENT SEASON

5.8.1 Sweeping induced mortality

An experiment was devised to investigate the susceptibility of newly settled barnacles to sweeping by algal fronds, and determine if the metamorphosis of cyprids to spat represented a significant change in the ability of an individual to survive a sweeping event. This involved the settling of cyprids onto specially prepared slates and the subsequent transplanting of different age classes of cyprid and spat to beneath a *Fucus serratus* canopy and to control areas.

Three age classes of juvenile barnacles were used.
a) Cyprids. This class was transplanted immediately after settlement. Thus when sweeping first took place they had been attached to the rock surface for between 6 and 12 hours.
b) Newly metamorphosed spat. Spat were transplanted immediately after metamorphosis from the cyprid stage had taken place. Thus when sweeping first took place they had been attached to the rock surface for between 30 and 36 hours
c) 'Old' spat. These spat were transplanted 6 days after metamorphosis and had thus been attached to the rock surface between 174 and 180 hours before sweeping took place.

The experiments were carried out during a period of spring tides. These occur on the Isle of Man in the early morning and evening thus ensuring that work could take place in the daylight during simultaneous low water periods.

Settlement surfaces were prepared in the following manner: thin slabs of Manx slate bearing high densities of adult barnacles and measuring at least 13 x 13 cm square were removed from the mid shore of Gansey Point. On 40 of the slates an area measuring at least 12 x 12 cm was cleared of adult barnacles. These slates will subsequently be described as 'smooth.' On 10 slates adult barnacles were removed individually to create small patches of bare substrate ($<1cm^2$ in size) within a mosaic of barnacles. These slates will subsequently be described as 'rough'. Each tile was numbered individually by attaching a micromarker to the rock using Bison hard plastic adhesive. In addition, three widely spaced marks were made on each tile using white enamel paint, to enable consistent relocation of the sampling quadrat.

A site was chosen in Port Erin Bay where cyprid settlement appeared highest. The low shore zone of this location consisted of a dense canopy of *Fucus serratus*. Seven 1 x 1 metre areas were cleared of canopy within this area.

Forty 'smooth' slates and ten 'rough' slates were cemented onto boulders at mid shore level during the morning of 9th June 1994 and brushed thoroughly using a toothbrush in order to remove any newly settled barnacles. Approximately 12 hours later after one period of high water the position of newly settled cyprids was recorded in the following manner. A piece of perspex measuring 13 x 13 cm with a thickness of 3mm was placed on the surface of a settlement tile. Looking directly from above, three marks were made on the perspex using a permanent marker pen to coincide with the three white paint marks on the tile surface. In this way the perspex 'quadrat' could be constantly relocated on the tile in exactly the same position. The position of every newly settled cyprid on the tile was then recorded on the perspex by making a small dot with the pen. This procedure was repeated using a different perspex quadrat for each settlement tile.

These individuals which settled on the 9th of June formed the basis for three experiments which examined the survival of cyprids, newly metamorphosed spat and six day old spat under a *Fucus serratus* canopy under varying weather conditions. This was achieved by taking slates from the mid shore zone where settlement had occurred and transplanting them beneath the canopy and into the cleared areas. In order that the survival beneath a canopy of different age classes could be compared simultaneously three further settlement events on new slates took place on June 10th, June 15th and June 16th. The experiments are summarised in table 5.18.

Table 5.18 Summary of experiments examining sweeping induced mortality.

Experiment	Age class of barnacle	Treatments	Number of replicates	Time of sweeping	Sea state
1	Cyprid	Beneath canopy	7	9.6.94	Rough
	Cyprid	In cleared areas	7	PM	
	Cyprid	Rough tiles beneath canopy	5		
2	Cyprid	Beneath canopy	7	10.6.94	Inter-mediate
	Cyprid	In cleared areas	5	PM	
	New spat	Beneath canopy	7		
	New spat	In cleared areas	6		
3	Cyprid	Beneath canopy	5	16.6.94	Calm
	New spat	Beneath canopy	6	PM	
	Old spat	Beneath canopy	4		

(Unless otherwise stated slates are smooth)

In all three experiments the individually recorded barnacles were subjected to one sweeping event (i.e. one high water period). They were then sampled at the following low water period using the perspex quadrats to determine mortality. Mortality was assumed by the absence of an individual.

5.8.2 Settlement and immediate post settlement survival of *Semibalanus balanoides* on sheltered fucoid dominated shores: the effect of canopy algae

The experimental site in Castletown Bay used in 1993 for the settlement/recruitment experiment was utilised again in 1994. The pattern of settlement and recruitment in caged slates under the canopy compared to caged slates in cleared areas was examined to confirm results obtained in 1993. In addition, the effect of the canopy on the survival of cyprids over the first few days after settlement was examined. The experiment was carried out at three shore heights, in the *Fucus serratus*, *Ascophyllum* and *Fucus spiralis* zones. The plots cleared of canopy in 1993 were re-used although most had become slightly overgrown with algae and so had to be re-cleared.

Settlement surfaces made from Manx slate and bearing live adult barnacles were prepared as described above. All slates were caged. In order to minimise the work required both in terms of setting up the experiment and in sampling, the use of subsamples at each replicate plot was abandoned. Previous results had shown that variation within four subsamples of a replicate was low. Thus for each of the two treatments (canopy present and canopy absent) seven replicates were used, each replicate consisting of only one settlement tile. Slates were transplanted to the shore on 25th May and cemented into positions in cleared areas or under the canopy.

5.8.2.1 Sampling

Sampling of this experiment required removal of the cages in order to provide direct access to the settlement tile surface. All cages were cut in such a way that the cage roof could be folded back. After sampling the roof could be repositioned and fixed in place using short lengths of plastic coated wire.

At low water, any newly settled cyprids were removed from the tile surfaces using a toothbrush. Approximately 12 hours later, after one period of high water, the positions of newly settled cyprids were recorded using perspex sheets in the same way as described above. All perspex sheets used had an area of 144cm^2. The cyprids marked on each sheet were counted to provide data on settlement levels. The survival of marked cyprids was examined 12, 24 and 48 hours later.

5.8.3 Settlement/recruitment and initial survival of *Semibalanus balanoides* on an exposed shore

A similar investigation into settlement/recruitment levels and survival of cyprids was carried out at the exposed site at Scarlett point. The same experimental set-up and sampling procedure was used with the exception that settlement was monitored on natural substrate rather than settlement slates. No investigation of the effect of canopy algae was made.

5.9 RESULTS -1994 SETTLEMENT SEASON

5.9.1 Mortality of *Semibalanus balanoides* as a result of canopy sweeping

Experiment 1: Sweeping effects on newly settled cyprids

Newly settled cyprids of *Semibalanus balanoides* were extremely vulnerable to sweeping by *Fucus serratus* plants. On 'smooth' slates transplanted beneath a canopy only 3.4% of cyprids originally present survived over a single high water period (Figure 5.20). In contrast 92.3% survived on slates transplanted into cleared areas. Interestingly, survival of cyprids beneath a canopy was higher when they were located in gaps of a mosaic of adult barnacles. One way ANOVA and Tukey-Kramer test revealed a significant difference between all three treatments (Table 5.19).

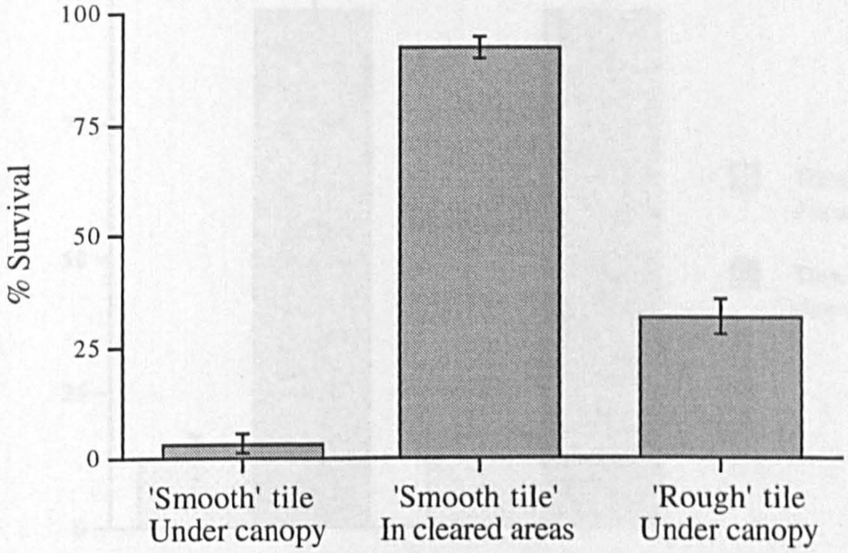


Figure 5.20 Experiment 1: Survival of *Semibalanus balanoides* cyprids over one high water period in the *Fucus serratus* zone. Sea state: Rough. Error bars = ± 1 SE

Table 5.19 One way ANOVA and Tukey Kramer multiple comparisons on the effect of *Fucus serratus* sweeping on the survival of transplanted *Semibalanus balanoides* cyprids (Experiment 1).

Source	df	Mean Square	F-Value	P-Value
Treatment	2	23901.24	276.37	0.0001
Residual	30	86.48		

Tukey Kramer Multiple comparisons

Smooth under canopy vs.Smooth in cleared areas	S
Smooth under canopy vs. Rough under canopy	S
Smooth in cleared areas vs. Rough under canopy	S

S=Significant difference. Experiment wise error rate (EER) = 5%

Experiment 2: Comparison of sweeping effects on newly settled cyprids and newly metamorphosed spat.

The survival of newly metamorphosed spat over one high water period showed very little difference with that of newly settled cyprids both beneath the canopy and in cleared areas (Figure 5.21). Survival of both these stages was under 18% beneath the canopy. Thus it appears that metamorphosis of cyprids into spat does not confer any additional resistance to the sweeping of *Fucus serratus* fronds. Two way ANOVA on arcsine transformed data shows a highly significant effect of the canopy but no effect of developmental stage on percentage survival (Table 5.20).

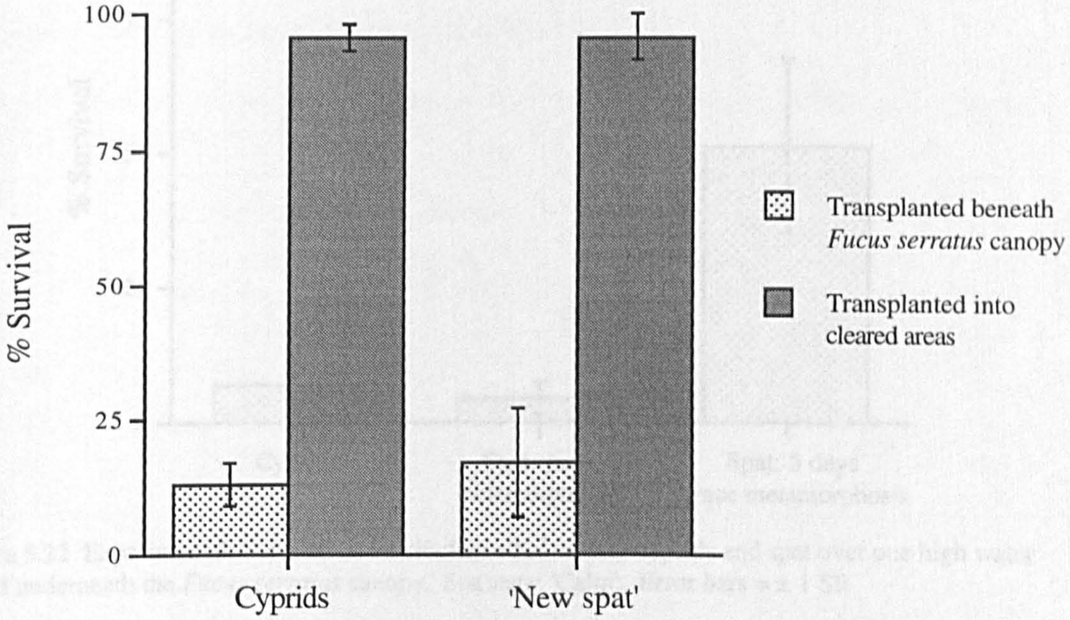


Figure 5.21 Experiment 2: Survival of *Semibalanus balanoides* cyprids and 'new spat' (just metamorphosed) over one high water period in the *Fucus serratus* zone. Sea state: Intermediate. Error bars = ± 1 SE

Table 5.20 Two way ANOVA on arcsine transformed data testing the effect of developmental stage and sweeping by *Fucus serratus* on survival of *Semibalanus balanoides*. (Experiment 2)

Source	df	Mean Square	F-Value	P-Value
Age	1	1.76	0.0078	0.9305
Presence of canopy	1	26437.47	116.9	0.0001
Age x Canopy	1	55.95	0.247	0.6241
Residual	21	226.19		

Experiment 3: Comparison of sweeping effects on newly settled cyprids, newly metamorphosed spat and five day old spat.

Although metamorphosis of cyprids to spat in itself does not increase the chances of survival an increase in age of spat appears to do so. Five day old spat showed 50.9% survival over one high water period under the *Fucus* canopy compared to only 6.7 and 4.4% in cyprids and newly metamorphosed spat respectively (Figure 5.22). One way ANOVA and Tukey-Kramer test on arcsine transformed data reveals that survival in five day old spat was significantly greater than in the earlier stages (Table 5.21).

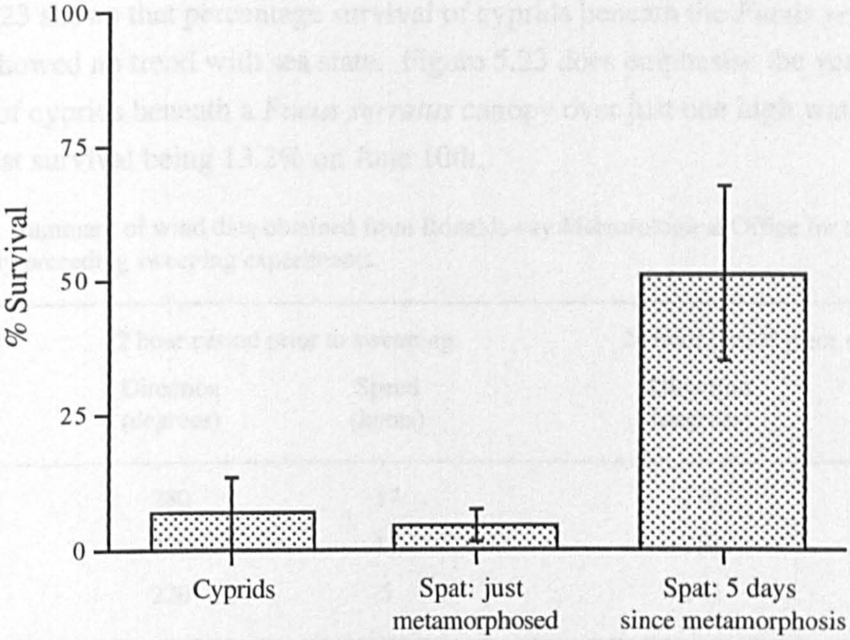


Figure 5.22 Experiment 3: Survival of *Semibalanus balanoides* cyprids and spat over one high water period underneath the *Fucus serratus* canopy. Sea state: 'Calm'. Error bars = ± 1 SE

Table 5.21 One way ANOVA and Tukey Kramer multiple comparisons on arcsine transformed data testing the effect of developmental stage/age on the ability of *Semibalanus balanoides* to survive sweeping by *Fucus serratus* (Experiment 3)

Source	df	Mean Square	F-Value	P-Value
Age	2	2136.44	8.92	0.0042
Residual	12	239.46		

Tukey Kramer multiple comparisons

Cyprids vs. New spat	NS
Cyprids vs. Old spat	S
New spat vs. Old spat	S

S = significant difference. Experiment wise error rate (EER) = 5%

Observations made at the time, and subsequent analysis of meteorological data, show that the sea state varied quite considerably between the three experiments. Wind data obtained from Ronaldsway Meteorological Office are summarised in table 5.22. Mean wind speed and direction have been calculated for the 12 hour and 24 hour periods before the time of high water at which the sweeping event of each of the three experiments took place. The experimental site in Port Erin Bay was exposed to the west and north west. From table 5.22 the predicted sea state at the experimental site was highest in experiment 1, lowest in experiment 3 and intermediate between.

Figure 5.23 shows that percentage survival of cyprids beneath the *Fucus serratus* canopy showed no trend with sea state. Figure 5.23 does emphasise the very low survival of cyprids beneath a *Fucus serratus* canopy over just one high water period, the highest survival being 13.2% on June 10th.

Table 5.22 Summary of wind data obtained from Ronaldsway Meteorological Office for the periods immediately preceding sweeping experiments.

	12 hour period prior to sweeping		24 hour period prior to sweeping	
Date	Direction (degrees)	Speed (knots)	Direction (degrees)	Speed (knots)
June 10th	280	17	270	17
June 11th	320	11	310	12
June 17th	220	5	240	10

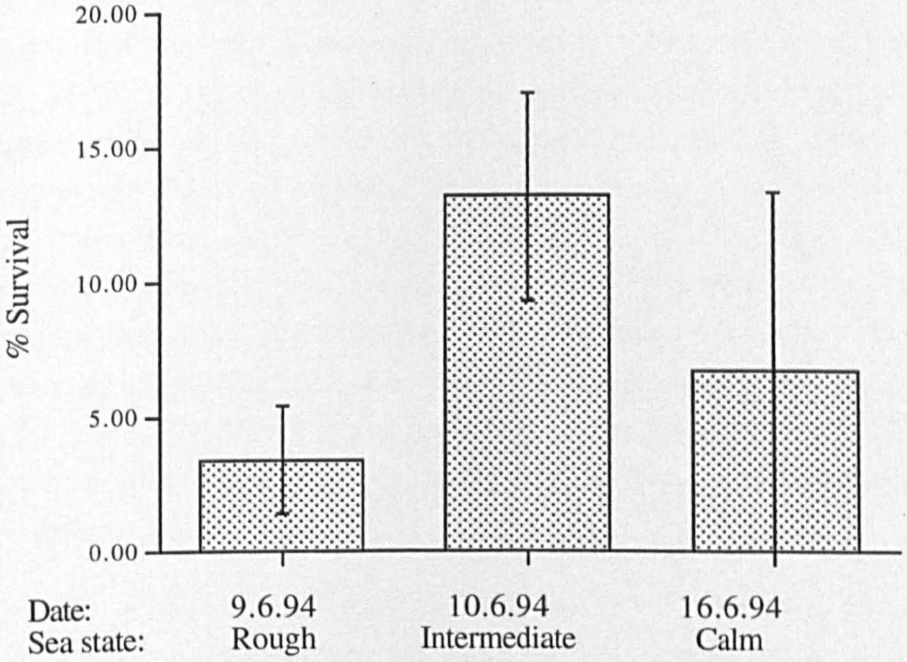


Figure 5.23 Survival of *Semibalanus balanoides* cyprids transplanted beneath a *Fucus serratus* canopy at three separate dates with different sea states. Error bars = ± 1 SE

5.9.2 Settlement/recruitment and initial survival of *Semibalanus balanoides* on an exposed and sheltered shore

No results were obtained in 1994 for the experiments established in Castletown Bay and Scarlett Point owing to the very low cyprid supply which occurred in this area during the settlement period of this year. Settlement of *Semibalanus balanoides* was very low and thus although the experiments were established on the shore and monitored throughout the settlement season no useful data could be obtained.

5.10 DISCUSSION

5.10.1 Methodology

5.10.1.1 Larval supply

Estimation of larval supply using water pumps to extract water from a position in the littoral zone or in the water column has been used in a number of studies (De Wolf, 1973; Salman, 1981; Grosberg, 1982; Salman, 1982; Gaines *et al.*, 1985; Minchinton and Scheibling, 1991). This technique provides benefits over the more traditional trawling method by sampling an easily quantifiable volume of water from a precise position. If necessary, this position can be located at the substratum surface, where, it could be argued, estimates of supply are most useful. The precision of the technique makes it suitable for analysing small scale differences in supply. In addition if the pump is located on land, sampling can take place in any weather conditions. The pumping technique provides an effective means of sampling beneath a canopy. The only disadvantage of sampling close to the substratum on sheltered shores was the amount of algal material obtained in the samples, which made examination of the plankton very laborious. This extra material was equally prevalent beneath the canopy as in the area clear of canopy.

5.10.1.2 Recruitment

The lack of adult conspecifics on the low and mid shore of sheltered sites makes examination of settlement patterns and interactions extremely difficult. The use of settlement slates was successful in providing suitable settlement surfaces onto which barnacles readily recruited. Unfortunately the production and transplanting of such slates was very labour intensive making collection of settlement data from sheltered shores far more difficult than at exposed sites where use can be made of the natural substrate. Given the levels of recruitment to slates in 1993 it may be possible to use much smaller fragments of rock in the future. This would increase the potential for experimentation and data collection because of the reduced effort needed in the production and transportation of such slates. The use of smaller slates would also reduce the extent to which settlement surfaces are raised above the surrounding substratum, an effect which could potentially alter the way in which factors such as algal sweeping act.

Unfortunately, because of time constraints imposed by the difficulty in creating settlement slates, no controls for a possible cage effect were used in the main canopy experiment. The cages used to prevent sweeping could potentially have had an unplanned effect on settlement, either causing a reduction or an increase in settlement levels. It was felt extremely unlikely that cages could increase settlement in any other manner than in preventing sweeping. However, reduction in settlement was a possibility. From the results it appears that such a reduction caused by a 'cage effect' did not occur. In order to control for possible cage effects an additional treatment in which caged slates were placed in canopy cleared areas should have been used. Settlement and recruitment to these caged slates could then have been compared to unprotected slates in cleared areas. Although it is felt unlikely that a cage effect occurred, this possibility must be borne in mind when considering the experimental results.

5.10.2 Larval supply

Owing to the very low larval supply on the south east coast of the Isle of Man in 1994, the planned investigation of supply across a wave exposure gradient and examination of the relationship between supply and settlement was not possible. Estimates made of cyprid concentration at the sheltered site alone, revealed that relatively high levels of supply can occur on sheltered shores. The mean concentration of cyprids in the absence of the *Ascophyllum* canopy was $22/m^3$ (averaged over six sampling dates). This compares with mean cyprid concentrations of $<5/m^3$ found over three seasons sampling at the mouth of Port Erin Bay (Salman, 1981). My estimates of cyprid concentration in Port Erin Bay in 1994 provided variable results but a maximum of $4.9/m^3$ was found.

Although these estimates suggest that supply to the sheltered site was not low, an additional factor to consider is the flow of water over the shore. The rate of delivery of larvae is a flux that includes both larval concentration in the water and a fluid velocity component (Bertness *et al.*, 1992). Gaines and Bertness (1993) considered ‘snapshots’ of larval concentration using either pumps or nets to be misleading, especially when comparing sites where the flow of water is expected to differ. At exposed sites, high tidal flow can result in a continuous supply of water and planktonic larvae. At sheltered sites, the influence of tidal flow will be minimal and thus supply of cyprids reduced. To overcome this problem, Gaines and Bertness (1993) proposed the use of some form of continuous sampling device such as the tube traps developed by Yund *et al.* (1991). Using these traps, a strong correlation between larval dynamics and settlement was demonstrated (Gaines and Bertness, 1993). Using pumps, the correspondence between larval concentration and shoreline settlement was low, even when the expected pattern of flow was used to create an index of larval flux.

At sheltered shores, the relationship between cyprid supply and settlement will obviously be greatly affected by factors such as the presence of conspecifics and algal sweeping (see below). When identical settling surfaces were used and the influence of algae removed, levels of recruitment at mid tide level of Scarlett Point and Castletown Bay were found to be equivalent. Given the close correlation between supply and settlement found in a number of studies (Grosberg, 1982; Gaines *et al.*, 1985; Bertness, 1989; Minchinton and Scheibling, 1991; Bertness *et al.*, 1992; Gaines and Bertness, 1993), equivalent levels of recruitment might be taken to infer equivalent levels of supply. However, the availability of suitable settling sites can radically affect the supply-settlement relationship. Bertness *et al*. (1992) found that where space was limiting (owing to high barnacle recruitment), settlement onto cleared quadrats was far higher than would be predicted from levels of supply. Although the high recruitment site of Bertness *et al.* (1992) may appear to bear no relation to sheltered shores, they are equivalent in the sense of lack of suitable settlement sites. On sheltered shores this occurs because of lack of conspecifics (see below) and on the high recruitment shores because of an overabundance of conspecifics. Thus, the high recruitment on transplanted settlement slates may simply be a result of the concentration of low larval supply onto a limited area of suitable space. Bertness *et al.* (1992) conclude that supply cannot be inferred from levels of recruitment and that sampling of the plankton must take place. Simultaneous measurements of supply and settlement at sheltered and exposed sites must be undertaken to determine the importance of supply in limiting the barnacle populations of sheltered shores.

5.10.3 Effect of adult conspecifics on settlement

Although the relative levels of supply to exposed and sheltered shores remains unresolved, it is clear that some level of supply took place at the sheltered site in Castletown Bay. High levels of recruitment took place on transplanted settlement slates at all tidal heights. However, with the exception of vertical walls, recruitment onto natural substrata outside the *Fucus spiralis* zone was very low indeed. No recruitment took place beneath the *Fucus serratus* or *Ascophyllum* canopy, whilst recruitment in cleared areas was over an order of magnitude less than on settlement slates. This difference was almost certainly a result of the absence of conspecifics on natural substrata. An alternative explanation is that the composition of the microbial film on natural substrata beneath *Ascophyllum* and *Fucus serratus* somehow inhibits settlement. Microbial films are known to influence the choice of settlement site in barnacles (e.g. Strathmann *et al.*, 1981; Hudon *et al.*, 1983; Maki *et al.*, 1988). There is no evidence however to suggest that microbial films differ beneath fucoid canopies. Hill and Hawkins (1991), working on a moderately exposed shore showed that sweeping by clumps of *Fucus* had no obvious effect on the microalgae present.

The effect of adult conspecifics on barnacle settlement are well known (Knight Jones, 1953; Crisp and Meadows, 1962; Crisp and Meadows, 1963; Larman and Gabbott, 1975; Gabbott and Larman, 1987; Chabot and Bourget, 1988; Raimondi, 1988; Dineen and Hines, 1992). This effect was demonstrated clearly in this study not only by the difference in recruitment to natural substrata and settlement slates but also by experimentation at Scarlett Point.

In order to understand the failure to settle on substrata lacking adult conspecifics it is necessary to understand certain aspects of barnacle settlement behaviour. After contact with the substratum surface, cyprids either reject it immediately and swim away, or enter an exploratory crawling phase. Whether a surface is rejected or not will depend on the attractiveness of the surface. This may be defined as the combination of its physical and chemical characteristics (see Crisp, 1974). Crisp and Meadows (1962) showed that cyprids alighting on surfaces treated with a barnacle extract were likely to begin to explore, whilst those alighting on clean untreated surfaces simply swam away. Exploration of a surface can involve a long and complicated behaviour pattern (Knight-Jones and Crisp, 1953; Crisp, 1961) during which contact with adult conspecifics (Knight Jones, 1953) or micro-topographical features such as pits or grooves (Crisp and Barnes, 1954) stimulates an increase in the frequency of halting and turning movements. Such behaviour usually occurs immediately prior to settlement.

Initial experiments by Knight-Jones (1953) showed that cyprids appear to receive the stimulus to settle (from the protein arthropodin) by direct contact with adult barnacles and their bases and not via a water soluble diffusable factor. Crisp and Meadows (1962, 1963) confirmed that settlement could only be induced when contact was made with a surface bound settlement factor. However they also showed that cyprids could detect arthropodin in solution and responded by becoming photonegative and more prone to explore inert surfaces. It is not known whether this response is of significance under natural conditions but it was considered unlikely given the low levels of arthropodin emanating from living barnacles (Crisp and Meadows, 1962; Crisp and Meadows, 1963).

Recent work has shown that larva-larva as well as larva-adult interactions may be important in influencing settlement behaviour. Cyprids of both *Semibalanus balanoides* and *Balanus amphitrite* deposit footprints of temporary proteinaceous adhesive while exploring a substratum. Laboratory experiments have shown these footprints can stimulate the attachment of conspecific cyprids (Walker and Yule, 1984; Yule and Walker, 1985; Clare *et al.*, 1994). It has been proposed that the presence of footprints, resulting from the exploratory behaviour of crawling cyprids, will increase the attractiveness of a substratum and should result in gregarious settlement, even in the absence of adult conspecifics (Yule and Walker, 1987; Clare *et al.*, 1994). Yule and Walker (1987) consider this accumulation of footprints on substrata may allow the colonisation of 'virgin' surfaces which lack adult conspecifics.

A number of studies have shown that cyprids which are prevented from settling, either through design in the laboratory (Rittschof *et al.*, 1984; Clare *et al.*, 1992) or through the absence of suitable settlement sites in the field (Knight Jones, 1953; Connell, 1961; Bertness *et al.*, 1992; Minchinton and Scheibling, 1993a), will accept unfavourable substrata. Crisp and Meadows (1963) consider that if deprived of suitable surfaces on which to settle the 'threshold of stimulation for the act of settlement would be gradually lowered'. Thus, one would expect that cyprids accumulating on sheltered shores, where there is a lower likelihood of dispersal to more favourable substrata, would eventually accept settlement on substrata lacking conspecifics.

From the above discussion a number of arguments can be put forward explaining the limited settlement of cyprids on substrata lacking adult conspecifics. The evidence put forward for the stimulatory effect of cyprid footprints on settlement (Walker and Yule, 1984; Yule and Walker, 1985; Clare *et al.*, 1994) has been based purely on laboratory experiments. Its importance in initiating settlement on bare substrata in the field is not known. If this effect does occur, then its importance in stimulating settlement on sheltered shores will probably be a function of larval supply. The level of supply will determine the incidence of cyprid footprints and consequently the level of stimulus to settle. Alternatively, cyprids may not even approach the substratum in the absence of conspecifics. The photonegative response of cyprids to arthropodin in solution was rejected by Crisp and Meadows (1963) as unlikely to occur in nature. However, to my knowledge no further research on this subject has taken place and this behavioural response remains a possibility.

Given the negligible level of settlement over large areas of sheltered shores the question arises as to what happens to cyprids transported there. The possibility exists that by rejection of unfavourable substrata or by reacting to a diffusable settlement factor most become concentrated in the *Fucus spiralis* zone or on isolated steep slopes where conspecifics are present.

5.10.4 Effect of the fucoid canopy on settlement and recruitment

The fucoid canopy at the sheltered shore site in Castletown Bay had a marked effect on the settlement, recruitment and post settlement mortality of *Semibalanus balanoides*. The possibility that the fucoid canopy could act as some form of barrier to cyprids, preventing them from making contact with the substratum was first proposed by Hatton (1938). This phenomena has also been suggested to act on limpet larvae, inhibiting their establishment on sheltered shores (Lewis and Bowman, 1975), and on seaweed propagules (Deysher and Norton, 1982). Gaines and Roughgarden (1987) showed that variation in the canopy area of a subtidal kelp forest on the coast of California was a major cause of variation in barnacle recruitment to the intertidal zone. However, this recruitment variation was thought to be a result of larval predation by juvenile rockfish living within the kelp forest, rather than any effect of canopy on water flow or larval transport.

Although a number of authors working on a variety of organisms have proposed a canopy barrier effect, no investigation has directly attempted to prove its existence, presumably because its effect is always confounded with other canopy effects such as sweeping. The effect, if present, may act in a number of ways, by forming a physical barrier to larval movement, by reducing water circulation and mixing and by creating a 'behavioural barrier'. The last effect concerns the way the canopy may influence larval behaviour. It is feasible given the complex behaviour patterns and discriminatory processes already seen in barnacle larvae that chemical or physical cues from canopy algae may discourage larvae from seeking the substratum. Whatever the mechanism, if a canopy barrier exists then the concentration of larvae at the substratum will be reduced.

The results from sampling larval concentration at the substratum in the presence and absence of an *Ascophyllum* canopy showed no effect of the canopy on supply. An attempt to repeat this investigation a year later failed due to low larval supply.

Although estimating supply appears to be the most direct way of determining if a barrier effect occurs, estimates of settlement and recruitment levels may also be used. In order to detect a barrier effect it is necessary to compare settlement or recruitment in cleared areas with that in caged areas under the canopy, where the substratum is protected from sweeping. Examination of recruitment levels to the two experimental treatments appeared to confirm that no 'barrier effect' exists. At all shore heights, recruitment to the caged treatment was equivalent to the cleared treatment, suggesting that when the sweeping effect of an algal canopy was removed, recruitment was no longer limited by any other factor associated with the canopy. However, estimation of settlement showed significantly lower numbers of cyprids in the caged treatment compared to the cleared treatment at two out of three sampling dates. Such a result would suggest that the barrier effect did in fact exist. These two conflicting results may be reconciled by considering the effect of the canopy on early post settlement mortality. Newly settled larvae suffer a high risk of mortality as a result of desiccation

(Connell, 1961; Wethey, 1985). Canopy algae, by their moderating influence on microclimate, have been shown to enhance survival of newly settled barnacles (Dayton, 1971; Hawkins, 1983). Thus, despite lower settlement on caged slates, enhanced survival beneath a canopy may result in equivalent levels of recruitment in both caged and cleared treatments. Such a hypothesis obviously needs testing by specifically examining settlement and early post settlement mortality. Unfortunately, experiments designed to do just this were abandoned owing to extremely low larval supply in 1994.

Both settlement and recruitment data show a definite inhibitory effect of sweeping at all three shore levels, demonstrated by a comparison of caged and control treatments. The conclusion of Hawkins (1983) that *Fucus serratus* exhibits the strongest sweeping effect is confirmed. Despite being at the lowest shore level and therefore expected to show the lowest levels of early post settlement mortality, recruitment to unprotected slates beneath the canopy was lowest in the *Fucus serratus* zone. However, the suggestion by Hawkins (1983) that this was probably due to higher levels of water movement low on the shore is doubtful. Experiments in Port Erin Bay examining sweeping induced mortality in more detail, showed no correlation between mortality beneath a *Fucus serratus* canopy and water movement. It is more likely that the absence of air bladders and the dense bushy nature of *Fucus serratus* plants contribute to its 'sweeping efficiency'.

The sweeping effect of *Ascophyllum*, although causing a significant reduction in settlement and recruitment was probably limited by the possession of air bladders. Recruitment to the control treatment was far higher in the *Ascophyllum* zone than in either the *Fucus spiralis* or *Fucus serratus* zones. Bennell (1981) considered that the buoyant nature of *Ascophyllum* plants caused less disturbance at the water-rock interface than other algal species.

Hawkins (1983) found that high on sheltered shores in the *Fucus spiralis* and *Fucus vesiculosus* zones the canopy caused an enhancement of recruitment levels. Cyprid settlement was reduced by sweeping but the enhancement of post settlement survival under the canopy was more pronounced and resulted in an overall increase in recruitment. A similar result was obtained by Dayton (1971). In this study, the results from settlement slates contradict those of Hawkins (1983). They indicate that the negative effect of a *Fucus spiralis* canopy on recruitment is greater than any positive one. However, on natural substrata, although recruitment was still higher in cleared areas no significant difference could be found. It is possible that the use of settlement slates may have enhanced the effect of canopy sweeping by the slight raising of the substrata. One could equally argue however, that this effect would enhance post settlement mortality in cleared areas. The reasons for the different results between my study and that of Hawkins (1983) are not clear. My work clearly shows that in the *Fucus spiralis* zone, overall the canopy has a deleterious effect on recruitment. Differences in weather conditions between years may alter the effect of the canopy at this high shore level.

The effect of tidal height on settlement and recruitment levels reveals an interesting pattern. Settlement into canopy cleared areas was highest in the *Fucus spiralis* zone at two out of three sampling dates. On the third date settlement was low overall and no pattern can be distinguished. In contrast, this zone showed the lowest level of recruitment. Low recruitment can be explained simply by high levels of mortality on the high shore (Connell, 1961; Menge, 1976; Kendall *et al.*, 1985; Wethey, 1985; Minchinton and Scheibling, 1991). The high settlement levels found in the *Fucus spiralis* zone are more difficult to explain. Minchinton and Scheibling (1991) working on an exposed shore in Canada showed that cyprids of *Semibalanus balanoides* were uniformly distributed at the water-substratum interface, and that cyprid availability at each tidal height was related to immersion time. This resulted in decreased settlement with increasing tidal height. In addition there was less settlement in the high intertidal zone and more settlement in the low zone than expected from estimates of larval availability. Minchinton and Scheibling (1991) considered this could be due to active avoidance of the high zone where chances of post settlement mortality were higher. Such behaviour could occur in response to differences in microflora between tidal heights (Strathmann *et al.*, 1981). The unexpected high levels of settlement found in the *Fucus spiralis* zone require confirmation. If verified, this result again raises interesting questions regarding the possibility of a diffusable settlement factor acting on cyprids in the water column. The *Fucus spiralis* zone is the only area of sheltered shores with a significant adult population of barnacles. Thus the possibility that stimuli from adults in this zone could act on cyprids and result in increased settlement there does exist.

A number of studies have quantified early mortality levels in barnacles on algal free surfaces. Wethey (1985) observed levels of mortality of newly settled *Semibalanus balanoides* over a five day period to be as high as 90% and 60% on the high and mid shore respectively. Connell (1961) showed that approximately 20% of attached cyprids died before they metamorphosed. Such levels are very low in comparison to the mortality of cyprids and newly metamorphosed spat beneath a canopy of *Fucus serratus*. By monitoring marked individuals, mortality levels of between 87 and 97% over just one high water period on the low shore were recorded. This illustrates the highly significant effect of algal sweeping on recruitment. As shown by Hawkins (1983), the presence of adult barnacles significantly increases the chances of survival beneath a canopy. Cyprids settled within a mosaic of adults were roughly six times more likely to survive over a high water period than those on surfaces where adults were cleared. This effect appears comparable to the protection from limpet grazing provided by adult barnacles (Hawkins, 1983; Miller, 1989). Such protection may be an additional benefit associated with gregarious settlement.

Cyprids of a number of barnacle species have been shown to settle in grooves and concavities, a behaviour thought to reduce mortality from wave action (Crisp and Barnes, 1954). This behaviour could also reduce dislodgement by sweeping. Hawkins (1983) considered that sweeping might act mainly by removing cyprids from marginal and unfavourable micro-settlement sites and that cyprids in pits and crevices would show high rates of survival. On the slate surfaces used in this study, although cyprids settled in grooves and depressions, the scale of microtopography did not appear large enough to provide any protection from sweeping.

Settled cyprids on the shore appear intrinsically fragile and prone to mechanical damage whether it be from waves, sweeping algae or gastropod grazing. Once metamorphosed, barnacles radically change their appearance and it is tempting to assume that their resistance to damage is dramatically increased. When cyprids permanently attach to the substratum (i.e. settle) a proteinaceous secretion, the cyprid cement is discharged from internal glands (Walker, 1971). It was believed that after this secretion no further means of attachment was employed until approximately 40 days after settlement when the adult cement apparatus became functional (Walker, 1973). However, Yule and Walker (1984) using staining techniques revealed an additional cement which is laid down within one day after settlement and gradually increases in area over time. This 'juvenile cement' coupled with the radical change in form could result in an increase in the resistance of newly metamorphosed individuals to sweeping.

This was shown not to be the case. No increase in levels of survival between settled cyprids and newly metamorphosed individuals occurred. Using five day old spat, a significant increase in survival was shown. These results indicate that resistance to dislodgement whether from wave action, algal sweeping or any other factor probably increases progressively as juvenile cement is laid down (Yule and Walker, 1984) and shell plates strengthen. No dramatic increase in resistance occurs with metamorphosis.

5.10.5 Effect of other algae on settlement and recruitment

Pre-emption of space by other organisms can effectively prevent settlement of barnacles. Fucoid algae do not present this problem since the amount of space occupied by holdfasts is small. Other algae which occur on sheltered shores can occupy large areas of primary substratum. The red algal turf described in Chapter 2 prevents settlement to a large proportion of the space beneath the *Ascophyllum* canopy. This effect has been demonstrated experimentally by Hawkins (1983) who showed that low on the shore of more exposed sites algal turfs can determine the lower limit of *Semibalanus balanoides.* The silt bound between the thalli of turf forming algae presents a wholly unsuitable substratum on which to settle. Whether this silt, which occurs at higher levels on sheltered shores, affects settlement on uncolonised rock is unclear. Knight Jones (1953) showed that cyprids which encounter loose particles during the exploratory phase detach and swim away. Most bare surfaces on sheltered shores appear free of silt, even those adjacent to silt bearing turfs. Despite this, the potential inhibition of settlement by silt cannot be ignored although experimental assessment of this in the field would appear difficult.

In addition to algal turfs, the crustose algae 'lithothamnia' occupies large areas of primary substratum on sheltered shores. Both these groups of algae rely on the overlying canopy to provide protection from desiccation. The effect of lithothamnia on barnacle settlement is not known but it seems likely to have a negative effect. Experimental determination of this should be relatively simple.

5.10.6 Post settlement mortality

As expected from the results of Dayton (1971) and Hawkins (1983), the canopy had a positive effect on post settlement survival. In both the *Ascophyllum* and *Fucus spiralis* zones, the canopy caused a reduction in mortality over a three month period following the settlement season. This presumably occurred because of a reduction in desiccation beneath the canopy.

Dogwhelks occur at a low density on sheltered shores (Spence *et al.*, 1990) and in the absence of barnacles predate mainly on littorinids (Hawkins, 1979; Proud, 1994). Despite the low density, isolated patches of adult barnacles introduced to mid and low tidal heights were rapidly predated by aggregating dogwhelks. The mechanism of such aggregation remains open to conjecture. Despite their significant effect on adult barnacles, dogwhelks had surprisingly little effect on new recruits. During the summer, when dogwhelks are most active (Connell, 1961), no predation of new recruits was seen. The preferential predation of larger barnacles is well known (Connell, 1961; Spence, 1989; Hughes and Burrows, 1993; Proud, 1994), but it was expected that in the absence of adults, dogwhelks would predate new recruits. Proud (1994), working on a moderately exposed shore, observed that in the absence of adult barnacles predation of six week old *Semibalanus balanoides* occurred. Dogwhelks at

Castletown Bay were not observed predating on the new cohort until September, roughly three months after settlement. It is possible that a slower growth rate of barnacles on sheltered shores (Hatton and Fischer-Piette, 1932; Moore, 1935; Bertness *et al.*, 1991) contributed to this difference. During the autumn and winter, predation did occur on the new cohort but at a very low intensity. This lack of predation, initially because of low prey size and subsequently because of low predation intensity in the autumn and winter, allowed survival of individuals until spring. This was significant given the potential importance of conspecifics in stimulating settlement.

5.10.7 Conclusions

Because of the multiplicity of factors involved, it is difficult to define precisely what excludes barnacles from the mid and low shore of sheltered sites. Given the high settlement in the *Fucus spiralis* zone, and the high density of cyprids found in the water column, it seems unlikely that larval supply prevents recruitment to sheltered shores. However, where very high levels of supply occur, large populations of barnacles can exist beneath dense *Ascophyllum* (Bennell, 1981). On shores with normal levels of supply, it appears that the sweeping and possibly barrier effects of canopy algae are the major factors preventing barnacle recruitment. From my results and those of other studies I would suggest that in the absence of a fucoid canopy, sheltered shores would have large barnacle populations. This could be tested by continuous removal of the canopy over a number of years. Initially, some settlement would have to occur in areas devoid of adult conspecifics. This would be much more likely to occur in areas of high larval supply. For example in the Menai Straits in North Wales, cyprid concentration in the water can be such that settlement can even occur on algal fronds (Hawkins, pers. comm.). On a shore of lower larval supply, initial settlement would be slow, but a positive feedback mechanism would ensure that settlement rates increased with time.

The conclusion that the fucoid canopy is the main factor preventing recruitment of barnacles to sheltered shores does not explain the abundance of barnacles in the high shore *Fucus spiralis* zone. It could be proposed that because *Fucus spiralis* plants are small they exert little or no negative effect on settlement. This is supported by the results of Hawkins (1983) study, but not mine. It seems some other factor or factors not present in the high shore may contribute to the inhibition of recruitment in the *Ascophyllum* and *Fucus serratus* zones.

The red algal turf found beneath *Ascophyllum* prevents settlement to much of the mid shore. Whether silt originating from the turf inhibits settlement in areas of bare substrate is not known. However, observations suggest that in areas of limpet grazing the rock surface is completely clear of any silt. The activities of limpets and dogwhelks may explain the distinct difference in barnacle abundance observed between high and mid/low shore. Both these species are extremely scarce in the *Fucus spiralis* zone. Bulldozing by limpets probably contributes to recruitment inhibition, but as on exposed shores its effect is not likely to be very large. Dogwhelks are likely to be effective in predating patches of barnacles which, by chance, recruit into the *Ascophyllum* and *Fucus serratus* zones. Although no recruitment was observed onto natural substrata beneath intact canopies of *Ascophyllum* or *Fucus serratus*, it seems likely that in some areas, especially in years of high supply, some recruitment will occur. If these recruits survive one would expect them to promote settlement in the following year by the provision of a settlement stimulus. Despite the low density of dogwhelks on sheltered shores it is likely, especially in the light of the aggregation behaviour observed, that predation prevents gradual build up of populations following chance recruitment to the low and mid shore.

CHAPTER 6

General discussion

Experimental field work has contributed greatly to our understanding of community organisation on rocky shores and also to general ecological theory. With the increase in importance of experimentation has come an increasing awareness of the need for adequate experimental design and replication (Underwood, 1981; Hurlbert, 1984; Underwood, 1991). Given the high spatial variation found in most biological systems and the impact of chance or stochastic events on community patterns, replication of experimental treatments at the study site is vital to gain a realistic understanding of community patterns and processes. In addition to this level of replication, experimental work should ideally be replicated between sites to establish that conclusions reached about a particular system or pattern apply generally. Unfortunately ideal levels of replication are often impractical given the time and resources available.

In replicating experiments between two or more sites one may gain a clearer understanding of how generally applicable the results are. If, when studying community structuring processes, two sites supporting similar communities are used and different results obtained, one may conclude that the communities examined may be controlled by different factors or that stochastic events play a significant role. The benefits of replication between sites are obvious but time and resources are finite. The question of whether it is better to replicate between sites and limit the depth of the investigation, or examine a community in detail on only one shore is difficult to resolve. The answer lies in considering a number of factors including the type of community under study, the current knowledge regarding such communities, and the aims of the investigation. In certain communities, such as those dominated by barnacles, experimental manipulation and sampling of organisms is relatively straightforward and unreliant on resources. In such situations replication between sites is easy. A number of recent studies on barnacle supply and recruitment have used varying levels of replication between sites. At the other extreme, experimental work in subtidal canopy communities is extremely difficult and even simple manipulative work requires large amounts of time and resources.

In many studies, replication between sites is carried out when geographical variation is specifically examined or where large variation in some aspect of community structure is suspected. Replication between sites carried out simply as a matter of experimental rigour has become more common but is still comparatively rare. My general approach was to replicate experimental treatments over a large area on a single shore. It was felt replication between sites would have necessitated a drastic reduction in the level of sampling and possibly in the overall aims of the study. In the light of previous work on such shores it was felt that a detailed examination of single sites was most appropriate.

6.1 The role of disturbance

Disturbance from both physical and biological sources can have a profound effect on community structure. The intermediate disturbance hypothesis (see Connell, 1978) predicts that in the absence of disturbance a single or very restricted number of species will dominate. With no control on their abundance, competitively dominant species will exclude others, resulting in low community diversity. At high levels of disturbance only pioneer or opportunistic species will occur and the diversity of the community will be low. At intermediate levels of disturbance, intervals between disturbance events are such that high numbers of species can invade an area but competitive exclusion is limited. On rocky shores, space for attachment and/or resources associated with open space are generally thought of as the limiting resource over which species compete. Dayton (1971) considers that on rocky shores, although there are clear competitive dominants, communities are often characterised by continuous physical and biological disturbance including the effects of carnivores and herbivores. Because of this the potentially limiting resource of space is frequently in high abundance. Consideration of physical and biological disturbance is important in analysing the contrasting communities of sheltered and exposed shores of Britain.

Sheltered shores of Britain can be considered sites of low disturbance, both from physical and biological perspectives. In contrast, at exposed sites, physical disturbance from wave action and biological disturbance from limpet grazing and dogwhelk predation constantly renews space. At the tidal heights studied and over the range of exposure experienced on the Isle of Man the effects of this gradient of disturbance appear to act differently. In the mid shore the community structure of sheltered and moderately exposed sites differs enormously. In contrast, the community structure of the low shore shows much less change over the wave exposure gradient.

In the mid shore of exposed sites, fucoid algae are either prevented from reaching macroscopic size by limpet grazing, or once at this size are detached from the substratum by wave action. *Ascophyllum* is probably affected by wave action at the zygote level and prevented even from settling (Vadas *et al.*, 1990). At sheltered sites, lack of physical disturbance by wave action is paramount in allowing the monospecific stands of *Ascophyllum* to develop and be maintained. As shown in

Chapter 2, artificial disturbance by the removal of the *Ascophyllum* canopy resulted in development of a mixed *Fucus serratus* and *Fucus vesiculosus* canopy. Observations suggested *Ascophyllum* would eventually recolonise, but only after a number of years. In the absence of canopy detachment by wave action, *Ascophyllum* will dominate because of its longevity and ability to reproduce vegetatively. With increasing exposure to wave action the dominance of *Ascophyllum* rapidly declines. A combination of loss of canopy plants because of detachment and an inability to colonise effectively means *Fucus vesiculosus* becomes more important.

The level of biological disturbance by limpet grazing on the mid shore shows a sharp contrast between exposed and sheltered sites. This can be attributed to two factors: the low density of limpets on sheltered shores and the restriction in their distribution and ability to graze by algal turfs. The reasons for the scarcity of limpets on sheltered shores have been discussed at length in Chapter 4. Although firm evidence is difficult to obtain, results suggest that limpet populations are limited by low levels of supply and a lack of suitable settlement sites. Certainly, conditions on sheltered shores appear conducive to high rates of survival of limpets once they have recruited.

Whether the low density of limpets in the mid shore enhances the ability of *Ascophyllum* to dominate is not clear. It is likely that increased densities of limpets would shift the balance between turf and limpets. Thus, a radical change in understorey community would occur and limpets would exert a more wide ranging effect. However, it is likely that increased limpet density would have little effect on *Ascophyllum* cover because of the low level of reliance on sexual reproduction to maintain the canopy.

In the low shore, a *Fucus serratus* dominated community can exist over the range of exposures experienced in the Isle of Man. It appears that unlike *Ascophyllum* this canopy species does not rely on low levels of wave action or indeed low levels of limpet grazing to be successful. It is generally accepted that with decreasing height on the shore the increase in algal growth rate results in a switch in the balance between algae and grazers (see Hawkins *et al.*, 1992 for review). High algal growth rate means that escapes from grazing occur more frequently. My results and those of a number of studies show that *Fucus serratus* has the ability to quickly recolonise its own zone after artificial or natural disturbance. Loss of *Fucus serratus* plants because of wave action or simply senescence results in an increase in the growth rate of juveniles present beneath the canopy. Rapidly growing juveniles soon form canopy plants to replace those lost. Despite high growth rates, results from Chapter 3 indicate that limpet grazing can delay development of a new canopy by excluding juveniles from grazed areas. Higher rates of canopy detachment on more exposed shores should lead to a more patchy cover which presumably persists longer because of limpet grazing. Given the variation in limpet density found both on sheltered shores (this study) and moderately exposed shores (Hill, 1993) one should predict a more patchy canopy cover in areas of higher limpet density, especially at exposed sites. At the more exposed sites of the Isle of Man, *Himanthalia elongata* and dense algal turfs increase in cover, often forming a patchy mosaic with *Fucus serratus*. Interactions affecting this assemblage of species have not been examined.

6.2 The development of monocultures on rocky shores

The dominance of the *Ascophyllum* canopy in the mid shore and the *Fucus serratus* canopy in the low shore can result in virtually monospecific stands of these canopy algae. Such 'monocultures' were examined by Paine (1984) to assess the degree of determinism in their development and determine the extent to which their formation was a result of interspecific competition. It was argued that although monocultures are usually considered the result of competitive exclusion by a single dominant species, an alternative explanation is that they simply represent aggregations of the most resistant local organisms.

The almost ubiquitous nature of the *Ascophyllum* and *Fucus serratus* communities on sheltered shores suggests their formation is deterministic i.e. that regardless of initial conditions, one can predict with certainty the community which will develop following disturbance. This has been demonstrated in a number of studies for *Fucus serratus* but not for *Ascophyllum*. Obviously it is quite possible that the mixed *Fucus serratus* and *Fucus vesiculosus* canopy which was observed in this study following *Ascophyllum* canopy removal represented an alternative stable state (see Sutherland, 1974, 1990). However, given the result of Keser and Larson (1984) in North America, and the observations made in this study, it is likely that formation of the *Ascophyllum* canopy is entirely deterministic but occurs at a very slow rate.

Competitive interactions between macroalgae were not specifically investigated in this study. However, there is no evidence against the conclusion that the monocultures of canopy algae are a result of interspecific competition. In the mid shore, removal of *Ascophyllum* results in the rapid colonisation by the competitively inferior canopy algae *Fucus serratus* and *Fucus* vesiculosus. As stated above, it is predicted *Ascophyllum* will eventually outcompete these species. Interestingly, in the low shore, removal of *Fucus serratus* did not result in colonisation by any other species of canopy algae. Disturbed areas were first colonised by ephemeral green algae and then a 'sub-canopy' of *Palmaria palmata*. *Fucus serratus* grew up through these algae and eventually outcompeted them. There is no sign of competition between *Fucus* *serratus* and the species zoned directly above, *Ascophyllum*. Results from work on vertical zonation show that competition frequently sets the lower limit of organisms. That no visible sign of this is shown at the lower limit of *Ascophyllum* probably reflects the limited ability of *Ascophyllum* zygotes to settle and germinate. *Fucus serratus* may in fact maintain a monoculture by directly preventing settlement of *Ascophyllum* zygotes through its efficient sweeping action. Alternatively, *Ascophyllum* may be prevented from settling low on the shore by higher levels of water movement there. Subjective observations at the sheltered shores under study suggested a higher degree of wave action on the low shore. On gently sloping shores at sheltered sites, any wave action is likely to be dissipated on the first shallow depths encountered, ensuring that mid and high tidal heights experience very little water movement (see Denny, 1988). Thus, increased levels of wave action on the low shore may prevent downshore extension of *Ascophyllum* and so allow the development of *Fucus serratus* monocultures.

6.3 Community Stability

It was concluded in Chapter 2 that the community of the *Ascophyllum* zone was inherently stable, showing little change over time. The community of the *Fucus serratus* zone appears slightly more dynamic but the main components of the community appear to change little and the dominance of the *Fucus serratus* canopy is maintained. This agrees with the simple model of Southward and Southward (1978) which predicts that in the absence of large scale disturbances the balance between large seaweeds and herbivores becomes stabilised or undergoes cyclic changes of 'small radius'.

Connell and Slatyer (1977) consider an assemblage of species should only be considered stable if the characteristic of interest remains relatively unchanged for at least the time required for one turnover of the population of the longest lived species. Since turnover of perennial algal populations can take many years, sampling programs or experiments to test stability may be impractical. An assemblages ability to resist change and its ability if altered to adjust to some semblance of the original state were factors considered by Sousa (1980) to indicate the likelihood of stability in a community. The *Fucus serratus* community shows a strong ability to revert to its original state following disturbance. In contrast, the ability of the *Ascophyllum* community to recover appears low, and thus it must rely on an ability to resist change in order to maintain stability. Sousa (1980) experimentally assessed the ability of boulder field communities to resist change, by applying varying levels of artificial disturbance to different successional stages and monitoring change. Since levels of disturbance on *Ascophyllum* dominated shores are low this approach would be pointless. Sousa's 'ability to resist change' should be qualified by the statement 'from disturbance levels appropriate to the environment of that community'.

The concept of stability is closely linked with that of climax communities. The question of whether succession ever comes to an end and results in a community at a point of stable equilibrium has been discussed by terrestrial ecologists for most of this century (e.g. Clements, 1916 cited in Sousa, 1980). Many ecologists argue that succession does move toward a climax but disturbance continually transforms the developing community to some earlier successional stage. This has been demonstrated in a number of intertidal studies (e.g. Sousa, 1979; Sousa, 1980; Paine and Levin, 1981; Dethier, 1984). On a broad community scale, both the *Ascophyllum* and *Fucus serratus* zones on sheltered shores appear to reach a climax community. It has been argued that any community which is said to be at its climax will actually be made up of a mosaic of 'miniature successions' (Begon *et al.*, 1986). It is probably the scale and frequency of such successions within the community which determine whether one would class the community as at a climax. The *Ascophyllum* community is possibly as close to a climax as any. Loss of canopy plants by localised disturbance and death is very low and thus the frequency of 'miniature successions' is limited.

6.4 Further research

In order to fully understand the dominant role of the fucoid canopy at sheltered sites it will be necessary to gain further insight into the causes of low limpet density on these shores. The difficulties of achieving this aim have been outlined in Chapter 4 and basically relate to the very small size of limpet larvae. Despite this, it should be possible to examine variations in limpet settlement and recruitment across wave exposure gradients. Successful use of limpet settlement plates has been made in studies at sites of high limpet recruitment in North Yorkshire. Although use of similar plates was made in this study it was felt that levels of recruitment were far too low to gain useful results. The effect of a fucoid canopy on recruitment and the prevalence of suitable settlement sites on sheltered shores are two areas which deserve attention. Whether some insight into limpet larval settlement behaviour can be made is not clear. It is possible that at sites of very high limpet settlement, detailed observations may reveal whether larval choice occurs at settlement or whether distribution of juvenile limpets simply reflects differential larval mortality in different habitats.

The results presented in Chapter 5 extend our knowledge of factors influencing the pattern of barnacle distribution across the wave exposure gradient. However, owing to low levels of supply to experimental sites in 1994 a number of questions were left unresolved. These were outlined in Chapter 5 but most importantly include examination of supply across the wave exposure gradient and re-examination of the potential 'barrier' effect of canopy algae. Of additional interest is the relationship between supply and settlement at sites of contrasting exposure. The way in which settlement behaviour may affect recruitment to a limited number of suitable settlement sites was discussed in Chapter 5. It is possible that low levels of supply to sheltered shores are 'concentrated' onto the few attractive settlement sites available at mid and low tide levels, and to the attractive sites in the *Fucus spiralis* zone. Simultaneous measurements of supply and settlement at exposed and sheltered shores may provide an insight into settlement behaviour under natural conditions.

In Chapter 2, the balance of fucoid species in the mid shore of sheltered sites was briefly addressed. On the shores studied, *Ascophyllum* was dominant, but experimental manipulation showed that both *Fucus serratus* and *Fucus vesiculosus* were capable of colonisation. Lewis (1964) observed that on shores which support a full fucoid cover, great variability can occur in the proportions and zonation of the three species, *Ascophyllum nodosum*, *Fucus serratus* and *Fucus vesiculosus*. In Chapter 2 I speculated that varying levels of disturbance from wave action might influence the distribution patterns of *Fucus vesiculosus* and *Fucus serratus* relative to *Ascophyllum*, which was considered to be the competitive dominant. Most work on sheltered shores, especially that examining factors influencing upper and lower limits of macroalgae has taken place where there are simple, clearly defined patterns of zonation. This situation however is clearly not always the case. Deviation from simple patterns of zonation may simply be a result of increasing disturbance opening up free space and allowing competitively inferior species to invade. However, the patterns observed by Lewis (1964) point to other factors such as slope, aspect and nature of the substratum being important. The way in which physical factors such as these, plus exposure to wave action affect the biological interaction between the three species of macroalgae is of interest. Examination of these interactions may also provide insight into the factors affecting the lower limit of *Ascophyllum*.

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