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The Role of Topographic Complexity in the Structure and Dynamics of Rocky Shore Communities

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ABSTRACT

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THE ROLE OF TOPOGRAPHIC COMPLEXITY IN THE STRUCTURE AND DYNAMICS OF ROCKY SHORE COMMUNITIES

by Natalie Jane Frost

The overall aim of this work was to assess the importance of topographic complexity in structuring rocky shore communities. In order to achieve this the distributions of intertidal species were related to physically and biologically generated features of the habitat. In addition manipulative experiments were used to gain a more complete understanding of the processes in operation.

Initially a review of the methods and indices used to measure habitat complexity was made. Three methods were compared using field trials: stereophotography, profile gauges and lengths of chain contoured over the substratum. Chains were the most efficient method to use, followed by stereophotography and profile gauges respectively. The results derived from the chain method and profile gauges were directly related, but stereophotography results were not comparable. Stereophotography, however, offered the additional benefit of allowing direct correlations between topographic features and the distribution of the overlying biota. This led to the development of an automated technique that directly linked these parameters. The strongest correlations between topographic features and biological distributions were typically observed for algal species. The influence of complexity, however, varied across a number of scales depending on the species examined.

Both physical and biological complexity was demonstrated to have an important role in structuring rocky shore communities. Details of the recruitment of algae and sessile invertebrates to substrata of varying complexity were first examined. In order to achieve this the topography of the substratum was manipulated by the use of concrete blocks cast with differing surface features. The succession of intertidal communities was also observed on mussel beds. The recruitment of algae did not appear to be related to the complexity of the physical substratum, but was affected by biologically generated complexity. In contrast the settlement of barnacles was influenced by both habitat types.

The distribution of mobile invertebrates in relation to topographic structures was highly variable; crevices therefore represented temporary habitats and refuges for these organisms. The shelter provided by both mussel beds and the physical properties of macroalgal canopy also influenced the distribution of such species. Results regarding species number and diversity on the concrete blocks were not consistent with the commonly held view that increased habitat complexity leads to increased richness and diversity.

The movement patterns of intertidal predators were examined via the use of underwater camera technology. Biologically generated complexity was investigated in mussel beds in North Cornwall. Factorial manipulations of grazers and mussels were studied to examine their respective roles within a community. Predation and grazing pressure were influenced by both physical and biological structures. As a consequence the distribution of prey species were in part determined by the complexity of the habitat. Spatial and temporal scales of the structure and dynamics of mussel mosaics was also investigated.

Habitat complexity was observed to have an impact on a number of community structuring processes. The generalities of these results and the requirements for future research are discussed throughout the thesis.

CONTENTS

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1. General Introduction

(1.) INTRODUCTION

Community ecology deals with the structure, composition and dynamics of groups of species and the interactions between them and with their environment. The physical and chemical environment ultimately determines which species can occur in a particular habitat. Organisms within a shared environment interact via competition, facilitation, predation and herbivory - processes that shape community patterns. Ecologists may therefore use knowledge of the interactions between organisms in an attempt to explain the behaviour and structure of a whole community. Processes that shape communities, however, may occur at a number of spatial and temporal scales. Until recently the effects of small scale topographic variation have been largely ignored. Such features not only serve to modify the physical environment but they also influence the outcomes of biological interactions.

The overall aim of this thesis was to assess the importance of spatial heterogeneity and topographic complexity in the structuring and dynamics of rocky shore communities. In order to achieve this a review of the techniques currently used to measure habitat complexity was required. A novel method was then developed to establish the predictive relationship between topographic features and species distributions. The importance of both physically and biologically generated complexity in determining the colonisation and succession of intertidal communities was assessed. The source of biological complexity investigated was that of mussel beds. Implications of topography for the behaviour of intertidal predators was explored through underwater video analysis. Spatial patterns of mussel mosaics were defined and used as guidance for designing manipulative experiments to establish the roles of mussels in providing a refuge for algal species from limpet grazing pressure.

(1.1.) Spatial Heterogeneity

Spatial heterogeneity is an obvious feature of the natural world, affecting a complex suite of environmental factors which interact to form a complex pattern of species distributions in time and space (Kolasa & Pikett, 1991; Kostylev, 1996). While nature is clearly heterogeneous, the scale at which spatial heterogeneity manifests itself varies widely: from micro to macro scales, in freshwater, brackish and marine environments (see Wiens, 1989; Hunt & Schneider, 1987; Pinckney & Sandulli, 1990). The scale of investigation thus determines the range of patterns and processes that can be detected. Our ability to predict ecological phenomena depends on the relationships between spatial and temporal scales of variation (Delcourt *et al.,* 1983; Butler & Chesson, 1990; Underwood & Chapman, 1996; Huston, 1999). Moreover, identifying spatial patterns is important in improving the design and interpretation of surveys and experimental studies through relating sampling programmes to natural scales of variation (Livingston, 1987; Kotliar & Wiens, 1990; Russell *et al.,* 1992; Keeling *et al.*, 1997; Underwood *et al.*, 2000).

Extent is the overall area encompassed by a study, grain is the size of the individual unit of observations and these units define the upper and lower limits of resolution of a study (Wiens, 1989). Investigators addressing the same questions have often conducted their studies on quite different scales which has resulted in discrepancies between results (see Simberloff, 1988). Physical factors can be more important on one scale and biological factors on another. Local biological interactions have the effect of decoupling systems from direct physical determination of patterns, by introducing temporal or spatial lags in system dynamics, or creating webs of indirect effects (Menge, 1995). However, at broader scales, physical processes may dominate or dissipate these biological effects (Levin, 1992). Shifts of scale may create homogeneity out of heterogeneity, and vice versa, and the information contained at one level of resolution may look like noise at another (Dutilleul, 1993).

(1.2.) Topographic Complexity

Topographic complexity refers to the structural components of a habitat at a particular location observed at a defined scale; this complexity can be both physically determined or biologically generated. The substratum upon which organisms live and move can vary considerably in complexity from place to place.

It may vary in non-biological characteristics, such as slope, aspect and relief, or in biological characteristics, such as the presence or absence of sessile organisms. The effects of complexity on the distribution of organisms can be well studied in rocky shore habitats. Such systems are accessible, comparatively easy to observe and manipulate, and the animals and plants are relatively numerous (Lewis, 1964; Connell, 1972; Paine, 1977; Hughes, 1985). Traditionally rocky shore ecologists have circumvented the problem of topographically generated small-scale environmental differences by choosing areas of uniform horizontal or gently sloping rock. More recently, however, studies have explicitly tried to measure heterogeneity (e.g. McCormick, 1994; Beck, 1998, 2000) and have attempted experimental manipulations in the field to assess its importance (e.g. Bourget *et al.*, 1994; Jacobi & Langevin, 1996; Jones & Boulding, 1999; La Pointe & Bourget, 1999).

(1.3.) Rocky Shore Ecology

Depending on local geology rocky shorelines can range from steep overhanging cliffs to wide, gently shelving platforms, from smooth uniform slopes to highly dissected, irregular masses or even extensive boulder beaches (Lewis, 1977). Many open coasts are continuously exposed to oceanic swell and extreme wave action, whilst deeply indented coastlines may be largely calm.

Biologically the intertidal zone is essentially a marine province: it is inhabited principally by marine organisms and a few terrestrial species tolerant of short periods of tidal submersion (Southward, 1958; Lewis, 1964; Connell, 1972; Raffaelli & Hawkins, 1996). Consequently the vertical dimension of the shore is generally regarded as a unidirectional stress gradient associated with the degree of submersion caused by the twice daily ebb and flood of the tide (Connell, 1972). It can therefore be concluded that higher on the shore there is a greater variability and hence unpredictability in physical factors such as salinity, oxygen, humidity, temperature, light penetration and availability of food and nutrients (Hawkins & Jones, 1992; Raffaelli & Hawkins, 1996).

The existing gradient of differing wave exposure also influences the species present at a particular location. Further factors such as topography, nature of the substratum and aspect affect distribution patterns of the observed species. On a broader scale there are the gentle but overriding gradients associated with lattitude and climate. The composition of shore communities is therefore determined by a suite of both physical and biological interactions (Lewis, 1964).

For rocky intertidal systems, there have been studies focused on the influence of scales of patchiness of intertidal assemblages (e.g. De Vogelaere, 1993; Petraitis & Latham, 1999) and on spatial scales of diversity of species (e.g. Hawkins & Hartnoll, 1980; Armachault & Bourget, 1996; Underwood & Chapman, 1996; 1998). For most intertidal species, which disperse via a planktonic larval stage, but which have limited adult mobility, variations in recruitment and mortality will lead to variations in abundances from one shore to another (Hawkins & Hartnoll, 1982; Underwood & Denley, 1984; Kendall *et al.*, 1985; Lindegrath *et al.*, 1995; Jenkins *et al.*, 2000).

Within a single shore, mobile animals can show considerable small scale (less than metres to tens of metres) variability in abundance which is primarily determined by behavioural response to the habitat (Fairweather, 1988; Underwood & Chapman, 1989, 1996; Jones & Boulding, 1999). Behaviour of mobile predators may not only determine small-scale patterns of abundance of prey, but may itself be altered by these patterns of abundance (Fairweather, 1988; Moran, 1995; Johnson *et al.*, 1998; Burrows *et al.*, 1999). At intermediate scales of tens or hundreds of metres upshore or alongshore, patterns of abundance may be determined by differences in recruitment (e.g. Connell, 1985; Underwood & Fairweather, 1989; Caceras-Martinez & Figueras, 1997; McQuaid & Phillips, 2000), in mortality due to the physical environment (e.g. Underwood & Chapman, 1996; Hunt & Scheibling, 1997), and biological interactions such as competition (e.g. Connell, 1961; Lubchenco, 1984; Hawkins & Hartnoll, 1985), grazing (e.g. Underwood, 1980; Hawkins & Hartnoll, 1983b; Jenkins *et al.*, 1999a, b) and predation (Underwood *et al.*, 1983; Fairweather & Underwood, 1991; Noda, 1999). Disturbance, however, can operate across all spatial scales (e.g. Dayton, 1971; Dethier, 1984; Pickett & White; 1985; Carroll & Highsmith, 1996; Airoldi, 2000).

(1.4.) Statistical Considerations

In descriptions of observed patterns, heterogeneity can be evaluated either at a continuous scale (e.g. autocorrelation techniques; Sokal & Oden, 1978; Sokal *et al.*, 1999), or within a hierarchical framework (e.g. nested analysis of variance; Underwood & Chapman, 1996; Miller & Ambrose, 2000). In benthic soft bottom ecology serial data and spatial autocorrelation techniques have been used to define the patch structure within a specified area (e.g. Sokal & Oden, 1978; Thrush *et al.*, 1989; Sokal *et al.*, 1999). Others have adopted the approach of hierarchical analyses of variance, using either a regular or a randomised sampling design (Morrisey *et al.*, 1992; Lindegrath *et al.*, 1995).

It is commonly held that samples closer together in space should be more similar to each other than those farther apart because of responses of organisms to patchy habitats or other organisms (e.g. Palmer, 1988, 1992; Carlile *et al*, 1989), although Bell *et al.*, (1993) indicated that terrestrial habitats may be very variable at small spatial scales. Similarly, samples taken at short intervals would be expected to have a smaller variance than those at larger intervals because of serial autocorrelation (Pielou, 1974) and temporal changes in abundances (e.g. Connell & Sousa, 1983).

A further method of identifying the size of the patches (when they exist), initiated by Greig-Smith (1952) in point-pattern analysis, is to use a square grid of continuous quadrats and to combine neighbouring quadrats to study how the variation among quadrats varies as a function of grid size (Dutilleul, 1993). Ver Hoef & Glenn-Levin (1992), among others, have proposed a refined method for detecting pattern at several spatial scales (see also Kotliar & Wiens, 1990; Johnson *et al.*, 1997). In surface pattern analysis, variograms combined with mapping (Legendre, 1993) may also help to detect patches.

(1.5.) Measuring Complexity

(1.5.1.) Measurement Techniques

Despite the potential importance of topographical complexity in structuring rocky shore communities, a true understanding of the interacting components is hindered by the inherent problems of its measurement (McCoy *et al.*, 1991). To date a standard assessment of the varying techniques at a variety of spatial scales is lacking (McCormick, 1994). Where possible, subjective terms such as 'heterogeneous' and 'homogenous' (Levings & Garrity, 1984) or 'simple' and 'complex' (Underwood & Chapman, 1989) should be avoided. Complexity encompasses variation in habitat structure attributable to the abundance of individual structural components (Beck, 2000). Structural components are distinct physical elements of the habitat such as boulders, crevices and pits (McCoy & Bell, 1991; Downes *et al.*, 1998). Heterogeneity encompasses variation in habitat structure attributable to variation in the relative abundance of different structural components (Beck, 2000).

Investigations to date have used a wide variety of techniques to measure complexity which have led to quite different statistical properties and indices, which are described briefly here and reviewed fully in Chapter 2. Three methods were selected for detailed comparison, these were stereophotography, profile gauges and lengths of chain contoured over the substratum.

Profile gauges of varying design have been used by a number of investigators at a range of spatial scales (e.g. Yule & Walker, 1984; Le Tourneux & Bourget, 1988; Underwood & Chapman, 1989; Young, 1992; Beck, 1998, 2000). McCormick (1994) for example, measured the complexity of topography in quadrats via a series of equal length needles dropped vertically onto the substratum. Data from such profiles are processed in a variety of ways resulting in some form of statistical index (Kostylev, 1996). In addition the ratio of the length of a chain contoured over a surface to the linear distance between the chains end points has been used as a simple index of surface complexity (e.g. Luckhurst & Luckhurst, 1978). Variations on this theme, developed by Dahl (1973), include using different link lengths to examine the effects of scale or to make measurements at different resolutions.

Photographic techniques have also been used to derive measures of complexity. Stereophotography, for example, allows the calculation of three dimensional co-ordinates of any specified point (Van Sciver, 1972). This technique has been used successfully in both marine (e.g. Fryer, 1984; Svane, 1988; Van Rooji & Videler, 1996; Evans & Norris, 1997) and terrestrial situations (e.g. Grayson *et al.*, 1988). It is this method that has been developed further in order to allow correlations of topographic features with species distributions (Chapter 3). Alternatively texture analysis which uses grey scale images to produce profile lines of a specified area has been used (Haralick *et al.*, 1973; Parsley, 1989; Sanson *et al.*, 1995). More recently Guichard *et al.*, (2000) have used a balloon based remote sensing technique to examine surface complexity in the rocky intertidal. On a larger scale, biologically generated habitat complexity scores of Eucalypt forests have also been derived from video analysis (Coops & Caitling, 1997).

In a few instances surface attributes such as crevice dimensions and frequency have been directly measured in relation to the focus of the respective study (Raffaelli & Hughes, 1978; Bergeron & Bourget, 1986; Roberts & Ormond, 1987; Levin, 1991). In addition substratum manipulations have also been carried out in the intertidal zone (e.g. Bourget *et al.*, 1994; Downes *et al.*, 1995, 1998; Jones & Boulding, 1999; LaPointe & Bourget, 1999; Beck, 2000).

(1.5.2.) Measurement Indices

Numerous indices have been developed to define complexity by a single numerical figure (reviewed fully in Chapter 2). These are typically based on differences in height between adjacent points along a profile and trigonometric relationships between these parameters (Zar, 1984; Carelton & Sammarco, 1987; McCormick, 1994). Such methods have been reviewed using both field trials and computer simulations (Underwood & Chapman, 1989; McCormick, 1994). Indices have been defined and correlated with biological characteristics (Levin, 1991; Kostylev, 1996) and habitats to determine which index best identified features of the habitat that appeared to be related to density (e.g Stoner & Lewis, 1985; Underwood & Chapman, 1989; McCormick, 1994; Hills & Thomason, 1996; Jacobi & Langevin, 1996; Beck 1998, 2000).

Comparisons of the use of profile gauges, lengths of chain and stereophotography on deriving four such indices are covered in Chapter 2. The indices incorporated were the consecutive substratum height difference, which represents a summation of the squared differences between the consecutive needles of a profile gauge (McCormick, 1994; Beck, 1998, 2000). Secondly, the angular standard deviation of vectors normal to the line joining two consecutive needle heights along a profile was used (Carleton & Sammarco, 1987). The widely used chain method of Dahl (1973) was also utilised and finally the fractal dimension (*D*).

A fractal is a complex geometrical shape, constructed of smaller copies of itself (Mandelbrot, 1989). Completely self similar shapes are rarely found in nature, therefore the calculation of the fractal dimension of natural patterns and shapes is based on statistical self- similarity and is executed over a range of scales. The fractal dimension increases with an increase in complexity of a natural object, providing ecologists with a numerical descriptor of heterogeneity (Kostylev, 1996). Roughness and fractal dimension, however, are not synonymous (Cox & Wang, 1993).

Fractals have been successfully used in marine biology to describe shapes of marine snow (e.g. Logan & Wilkinson, 1991), describing and modelling growth (Kaandorp, 1991; Mistri & Ceccherelli, 1993), quantifying movement patterns (Bundy *et al.,* 1993; Kostylev, 1997), spatial patterns (Davenport *et al*., 1996, 1999; Kostylev, 1996; Hills *et al*., 1999) and description of habitat complexity (Bradbury *et al.,* 1984; Le Tourneux & Bourget, 1988; Gee & Warwick, 1994a, b; Avosky *et al*., 2000). Reservations, however, have been expressed regarding the usage of fractals in describing habitat features (see Williamson & Lawton, 1991; Hills *et al*., 1999). A full review of various possible applications of fractals in ecology is given by Frontier (1987).

(1.6.) Physical Complexity

The concept that the structure of a community is related to the complexity of its habitat, first formulated by MacArthur & MacArthur (1961), is now firmly established in terrestrial (e.g. Pianka, 1969) and aquatic ecosystems (Heck & Wetstone, 1977; Stoner & Lewis, 1985). On intertidal rocky shores the physical complexity of a habitat is important in protecting animals from exposure to excess light, adverse temperatures and hence desiccation stress. Complex rock structures also decrease the influence of wave action, humidity and increase the relative sedimentation; thus increasing the range of microhabitats with different micro-climates (Sebens, 1991). Disturbance regimes will also be modified by the complexity of the substratum (e.g. McGuinness & Underwood, 1986). These factors by themselves, play an important role, in altering competition, predation and dispersion rates in different species (Kareiva, 1990) with subsequent consequences on overall diversity (Kostylev, 1996).

(1.6.1.) Species Distributions

Habitat structure has effects on species diversity (e.g. Archambault & Bourget, 1996; Downes *et al.*, 2000), population abundances (e.g. Bergeron & Bourget, 1984, 1986; Underwood & Chapman, 1996) and body sizes of resident organisms (Williamson & Lawton, 1991). Experimental studies as well as theoretical considerations show that architectural complexity by itself, when surface area is held constant, increases species richness in aquatic communities (O'Connor, 1991; Douglas & Lake, 1994; Downes *et al.*, 1995). Contrasting results, however, suggest that complexity has no effects on either abundance nor diversity (Heck & Wetstone, 1977; Downes & Jordan, 1993; Bourget *et al.*, 1994). Blanchard & Bourget (1999), however, highlight the importance of scale when correlating complexity with community characteristics.

The physical structure of the habitat, specifically the fractal nature of the habitats, has also been regarded as one of the main factors structuring animal size distributions (Morse *et al.,* 1985; Williamson & Lawton, 1991; Gee & Warwick, 1994a, b). Surfaces of high fractal dimension create an unequal share of available space for animals of different size; an increase in the fractal dimension of a surface leads to growing differences in space availability, with a disproportionate bias towards small animals (Morse *et al.,* 1985). Evidence from this and other studies seems to suggest that resource partitioning in a community is not in accordance with Damuths (1981) energetic equivalence rule but that small species appear to take a disproportionately small share of community resources (Pagel *et al.,* 1991).

(1.6.2.) Recruitment

Marked settlement preferences related to surface complexity have been recorded for invertebrate groups such as sponges (Russ, 1980), scleractinian corals (Carleton & Sammarco, 1987), barnacles (Crisp, 1974; Bergeron & Bourget, 1986; Bernston *et al.*, 2000) and mussels (Seed, 1976; Petraitis, 1990; Suchanek, 1992 ; Hunt & Scheibling, 1996; Chiba & Noda, 2000). Many barnacle species, for example, settle more abundantly in crevices close to their size (Crisp, 1974; Wethey, 1986; Chabot & Bourget, 1988) or the size of their settling organs (LeTourneux & Bourget, 1988), and bryozoan species settle in pits of a preferred diameter (e.g. Crisp, 1974). Indeed, Caddy & Stamatopaulos (1990) recorded that fractal surfaces enhance recruitment and survivorship in crevice dwelling organisms.

Hydrodynamic forces, when interacting with topographic features can also determine settlement patterns. Eckman (1990), for example developed a one dimensional, advection-diffusion model that predicts rates of settlement by larvae onto substrata of differing roughness. The model predicts that rates of settlement should increase monotonically with the complexity of the substratum. In addition Gregoire *et al.*, (1996) also investigated the density of adhering particles to panels of differing roughness.

(1.6.3.) Movement Patterns

Changes in abundance or age distribution of local populations of mobile animals may be brought about by differential recruitment and survival or by movement. Movements may cause animals to be limited to certain areas or to be directed to particular areas. The movements of intertidal gastropods have been shown to be affected by non biological features of the substratum, such as rock pools

(Underwood, 1977), crevices or depressions (Levings & Garrity, 1983; Underwood & Chapman, 1985; Davies & Williams, 1995; Kostylev, 1997; Chapman, 2000), slope (Petraitis, 1990) and the type of shore (i.e. boulder fields or basalt shores: McCormack, 1982). The movements of larger species such as crabs and blennies are also influenced by structural complexity (Burrows *et al.*, 1999). Movement pathways are strongly influenced by environmental structure and they may reflect differences in how organisms perceive habitat heterogeneity on a given range of scales.

(1.6.4.) Herbivory and Predation

General observations suggest that substratum heterogeneity is important for algal settlement, since holdfasts of newly established *Fucus* are often in small crevices or between tightly packed barnacles (Lubchenco, 1983). Experiments where grazer densities have been manipulated support this notion (e.g. Williams *et al.*, 2000). In general, only if all gastropod herbivores are excluded, does *Fucus,* become established on smooth rock (Hawkins, 1981). The size of the crevices is also important; if they are small most invertebrate grazers cannot effectively graze within them. In contrast, slightly larger crevices provide refuge for such species and may represent areas which are grazed intensively (Raffaelli & Hughes, 1978). Indeed, in tropical areas invertebrate consumer pressure appears to be strong inside crevices, while both fish and invertebrate predation is intense on open surfaces between holes (Menge & Lubchenco, 1981). Grazing in and outside of such topographic features is therefore qualitatively very different.

Habitat complexity also considerably affects the foraging success of predators, thus altering the selective pressure on prey species (Cowder & Cooper, 1982). Prey densities of the whelk *Nucella lapillus*, for example, when observed by Gosselin & Bourget (1989) were not significantly different between substratum types. However, the prey size and the prey yield index were both more favourable to the predator on irregular surfaces. Heterogeneous surfaces also allow dog whelks to forage on surfaces otherwise too exposed to wave action creating predation haloes around the edges of crevices (Moran, 1985; Underwood, 1985; Burrows & Hughes, 1989; Johnson *et al.*, 1998). Surface heterogeneity might equally act to expand the range of *Nucella* upward (Menge, 1978b), providing a greater access to prey species. The observed consistent selection by *Nucella* of heterogeneous over uniform surfaces shows it can, and suggests it actually does, take advantage of small-scale structural heterogeneity (Jones & Boulding, 1999).

Foraging pathways of large mobile predators are also influenced by topographic features (Menge & Lubchenco, 1981; Burrows *et al.*, 1999). When consumers have been excluded from sections of tropical shores, many sessile species have increased greatly in abundance and occupied different microhabitats (Menge & Lubchenco, 1981). These have included species from across all taxonomic groups (e.g. macroalgae, solitary sessile invertebrates and colonial sessile invertebrates). Species found previously almost exclusively in holes and crevices settled, survived and grew abundantly on homogenous surfaces formerly dominated by crustose alga species. These experiments suggest that early stages of succession in holes are a function of the local grazing regime. Thus, the successional state of a particular hole is probably determined by variations in consumer pressure.

(1.6.5.) Refuges

The importance of crevices as refuges from physical disturbance such as ice scouring (Bergeron & Bourget, 1986), extreme environmental conditions including wave action and desiccation stress (Dayton, 1971; Underwood, 1980; Garrity & Levings, 1984; Vadas *et al.*, 1992; Johnson & Brawley, 1998) and intense consumer pressure (Menge *et al.*, 1983, 1985) have all been identified in both invertebrate and algal species. Littorinids, for example, retire into crevices when they are not foraging to avoid adverse conditions (Emson & Faller-Fritsch, 1976; Raffaelli & Hughes, 1978; Atkinson & Newbury, 1984). The close relationship between local density of dogwhelks and crevices has also been extensively documented (Moran, 1985; Fairweather, 1988; Burrows & Hughes, 1989; Johnson *et al.*, 1998).

(1.7.) Biological Complexity

Settled organisms, such as macroalgae, barnacles and mussel populations, provide a biogenic structure for co-existing species (Seed, 1976; Jernakoff, 1985; Suchanek, 1986; Chapman & Johnson, 1990; Tokeshi & Romero, 1995). Not unlike the physical features of a location the architectural complexity of such secondary habitat decreases the influence of wave action, temperature and sunlight while increasing relative humidity and sedimentation (Seed, 1996; Thompson *et al.*, 1996). Thus, the community structure is altered by the changing effects of competition, predation and physical stress imposed on marine animals (e.g. Underwood & Denley, 1984).

(1.7.1.) Species Distributions

Mussels are major space occupiers across a number of rocky coasts throughout the world (Stephenson & Stephenson, 1972; Paine & Levin, 1981; Suchanek, 1986; Petraitis, 1995, 1998). While the dominance of mussels on rocks may be to the detriment of diversity on rock, it certainly plays a much different role in the community, when its use as a secondary space is considered (Dayton, 1971; Paine & Levin, 1981; Sousa, 1985; Tsuchiya & Nishihira, 1985; Seed, 1996). The surface of *M. edulis* shells and shell fragments serve as a substrate for detritus, bacteria, micro-algae and small animals which may also support animals in the patches. Many epibiotic individuals are also capable of reproducing on this secondary substratum (Sousa, 1984; Lohse, 1993a, b). Indeed their structure is an important habitat to an entire range of organisms, many of them being restricted to this habitat on exposed rocky shores (Tokeshi & Romero, 1995).

Barnacles may provide sites for protection, similar to those provided by pits or crevices and, thus act by altering the complexity of the substratum (Jernakoff, 1985; Boulding & Harper, 1998). Alternatively they may have indirect effects, by occupying space and therefore, reducing the amount of food available (Underwood *et al.*, 1983). The density of the barnacle *Tesseropora rosea*, for example, is known to influence the distribution and abundance of several species of algae

(Jernakoff, 1985), of two species of limpets (Underwood *et al.,* 1983) and littorinids (Underwood & McFadyen, 1983; Underwood & Chapman, 1985).

Sessile macroflora also provide an additional biogenic structure on rocky intertidal shores. The physical properties of a canopy can provide shelter for herbivores and cause an accumulation in species number (e.g. Lubchenco, 1986; Chapman, 1989; McCook & Chapman, 1991). Indeed, plants with higher fractal dimensions have been associated with a greater diversity of animal communities (Gee & Warwick, 1994a, b; Davenport *et al.*, 1996, 1999).

(1.7.2.) Recruitment

Flora and fauna of the rocky intertidal zone settle on both physically and biologically generated habitats. Recruitment of algal species on secondary habitats such as barnacles and mussels, for example, is well documented (Burrows & Lodge, 1950; Lubchenco, 1986; Chapman & Johnson, 1990). Mussels are also known to settle on all kinds of substrates including those provided by adult mussel beds and filamentous algae (Seed, 1976; Peterson, 1984; Caceras-Martinez *et al.,* 1994; Harris *et al.*, 1998; Chiba & Noda, 2000). In contrast natural aggregations of barnacles receive poor recruitment of mussels relative to resin castings of barnacles (Petraitis, 1990). It is possible that barnacles ingest settling mussel larvae or that mussels avoid settling in the presence of barnacles, which are potentially competitors for food. Barnacles and other sessile filter feeders are known to ingest pelagic larvae (Young & Gotelli, 1988) including those of conspecifics (Navarrete & Wieters, 2000).

In general, it may be more risky for larvae to settle on mussels because adult filter feeders, like mussels, can filter out planktonic larvae (Young & Gotelli 1988). Lohse (1993a), however, found no difference in recruitment on feeding and non-feeding mussels. Since increased surface structure enhances settlement (Eckman, 1990), settlement may be higher within the mussel bed because its outer surface is more irregular (i.e. has more surface structure) than a given expanse of rock. Previous studies have found that limpet recruitment is enhanced by both mussels

(Lewis & Bowman, 1975) and barnacles (Lewis & Bowman, 1975; Hawkins & Hartnoll, 1982).

The presence of macroalgae can also serve to inhibit the settlement and recruitment of intertidal species. *Fucus* plants, for example are capable of reducing barnacle settlement by a sweeping action of the fronds which can cause cyprid dislodgement (e.g. Menge, 1976; Hawkins, 1983; Jenkins *et al.*, 1999c; Leonard, 1999). Lubchenco (1984) also found inhibition of ephemeral and fucoid species under canopy which can occur even in the absence of herbivores (Jenkins *et al.*, 1999b).

(1.7.3.) Herbivory and Predation

The movements of intertidal grazers are potentially limited over biogenic structures such as mussels and barnacles (Little *et al.*, 1988; Kostylev, 1997). It is thought that grazing largely occurs around the edge of the mussel matrix (Suchanek, 1986). Algal species may therefore take refuge in such locations to increase their rates of survival (Jenakoff, 1983; Lubchenco, 1986; Chapman & Johnson, 1990). Grazing marks have, however, been observed directly on mussel shells (Lohse, 1993b). In addition where grazers have been removed from mussel beds, fouling is observed (Witman, 1987; Robles & Robb, 1993; Albrecht & Reise, 1994). Holdfasts of adult kelp also provide refuges from grazing for recruitment of juvenile algae (Anderson *et al.*, 1997).

Species such as mussels may also use the secondary structure provided by sessile species as a means of predator avoidance. The settlement of mytilids on filamentous algae, above the substratum could provide a means of escaping whelk predation (McGrath *et al.,* 1988; Moreno, 1995). Only when they are somewhat larger do juvenile mussels then establish themselves on the primary substratum (Bayne, 1964). Organisms living within the mussel matrix, within barnacle casts or under algal canopy may also be less detectable by predators (McCook & Chapman, 1991; Moreno, 1995; Seed, 1996; Hedvall *et al.*, 1998).

(1.7.4.) Refuges

The architectural complexity of the secondary substratum provides refuge from both harsh environmental conditions (Vadas *et al.*, 1992; Boulding & Harper, 1998; Johnson & Brawley, 1998) and mortality via predation or grazing (Lubchenco, 1986; Chapman & Johnson, 1990; Moksnes *et al.*, 1998). *Fucus* canopy, for example, provides shelter for predatory whelks, littorinids and alters the competitive relationships between such species (McCook & Chapman, 1993). The physical structure of the canopy may be important as mechanical shelter from waves, especially for mobile species, as shelter from high temperatures, desiccation, or freezing, or as shade to other plants (McCook & Chapman, 1991).

(1.8.) Terms, Definitions and Nomenclature

A number of terms used throughout this thesis can be interpreted differently depending on the context in which they are used. Specific terms therefore require definition prior to the start of experimental work to avoid confusion and lack of consistency. Spatial heterogeneity encompasses both physically and biologically generated spatial variation in environmental conditions at a defined scale. Topographic complexity refers to specific structural elements of a habitat such as crevices or ridges and biological features such as mussel beds. Patch structure is also discussed in detail and in this context refers to a habitat type, such as mussel beds, with a definable boundary at a set scale. In this context it does not refer to the open space between groups of mussels. Disturbance relates to a relatively discrete event that removes organisms and opens up space which can be colonised by individuals of the same or different species. Finally, the species names used throughout this thesis are in accordance with the Joint Nature Conservancy Council species directory.

(1.9.) Overall Aims

My intention was to investigate the influence of topographic complexity and spatial heterogeneity on the structure and dynamics of rocky shore communities. Two main systems were used: firstly mid shore *Fucus*, barnacle, limpet areas on rocks of different topographic complexity and secondly the biologically generated complexity of mussel beds.

In Chapter 2 the methods and indices currently used to measure habitat complexity were reviewed and then compared through field trials. The aim of the work was to standardise the techniques used by different investigators across distinct habitat types. The overall aim of Chapter 3 was to develop a predictive model of species distribution in relation to physically generated topographic features. As a first step the methodology involved in recreating and correlating surface features with species distributions was fully developed.

Chapters 4 and 5 addressed the influences of physically generated complexity on the recruitment, succession and behavioural patterns of intertidal species. Specifically, the affect of topography on the movement patterns of intertidal predators and the implications for prey structure was investigated for Chapter 4. The importance of habitat architecture in structuring communities was assessed using artificial substrata of varying complexities (Chapter 5).

A spatial and temporal description of intertidal mussel mosaics is presented for three shores in North Cornwall (Chapter 6). In Chapter 7 the importance of mussels as a source of refuge from limpet grazing and the interactions between these species was investigated.

The general discussion (Chapter 8) synthesises the results and issues addressed throughout the thesis. Conclusions were drawn from throughout the work and the importance of complexity in structuring and modifying community dynamics was discussed.

2. A Comparison of Three Techniques Used to Derive Complexity Indices in the Rocky Intertidal

(2.1.) INTRODUCTION

Previously much emphasis in ecological research has been laid on the analysis of relationships between the number, abundance and size of species in natural communities. More recently parameters such as these have been correlated with varying aspects of habitat architecture and complexity (e.g. Bourget *et al.*, 1994; Jacobi & Langevin, 1996; Blanchard & Bourget, 1999). Theoretical and empirical work has shown that spatial heterogeneity affects the dynamics of populations, the structure of communities and the functioning of ecosystems (Pacala, 1987; Hastings, 1990; Kareiva, 1990, 1994; Turner & Gardner, 1991; Levin, 1992; Palmer, 1992; Tilman, 1994). On rocky shores there has been considerable recent attention to the influence of surface topography and complexity (e.g. Bergeron & Bouget, 1986; Arachmabault & Bourget, 1996; Underwood & Chapman, 1996; Beck, 2000).

Despite the potential importance of habitat complexity in structuring rocky shore communities, a true understanding of the interacting components is hindered by the problems of its measurement (McCoy *et al.,* 1991). There has been little consistency in the definition or measurement of habitat structure between different studies or habitats. Each method also suffers from a series of limitations, for example, none of the techniques can uniquely identify all possible combinations of corrugation frequency and amplitude. Moreover the techniques are limited in their ability to quantify specific surface features of particular interest, such as the size and density of holes or the presence of overhangs (Evans & Norris, 1997). These problems make it difficult to compare methods and results between studies, limiting the understanding of the effects of habitat structure on the diversity and abundance of species (McCoy *et al.*, 1991; Beck, 1998, 2000).

(2.1.1.) Aims and Objectives

In this chapter I have undertaken a detailed review of three methods (profile gauges, stereophotography and chains of different link lengths) used to derive complexity indices. Field trials were carried out on two shores along the South coast of Britain; Port Wrinkle in Cornwall and Heyboork Bay in Devon. This allowed the testing of the null hypothesis that the three techniques would not produce a comparable index, or a similar ranking of complexity for the 30 quadrats. If the resulting indices were positively correlated then a comparison between locations would be feasible regardless of the technique used and the simplest least time consuming method could be used.

To test the hypothesis that indices derived from the same technique would be correlated four indices (vector dispersion (VD), consecutive height difference (CHD), contoured versus linear length of a chain (chain ratio) and the fractal (*D*)) were calculated from the profile gauge data. It was possible that one or more of these indices would be most suitable for describing these particular rocky shore locations. Calculating fractal dimensions at different scales of resolution allowed the testing of whether these habitats were truly fractal in nature. Average fractals of quadrats were also calculated based on a different number of profiles to assess the variability associated with such measures.

Despite the difficulties surrounding the measurement of complexity numerous investigators have attempted to assess its impact in structuring rocky shore communities (e.g. Underwood & Chapman, 1989; Beck, 1988, 2000). This study attempts to standardise comparisons between both methods and indices used to define different locations. A review of the various techniques and indices was therefore required.

(2.1.2.) Techniques That Have Been Used

Investigations to date have used a wide variety of techniques to measure complexity which have led to quite different statistical properties and indices. A standard assessment of these procedures at a variety of spatial scales is currently lacking (McCormick, 1994). Methods include the use of profile gauges, photographic and video analysis systems, as well as direct observations and manipulations of heterogeneity.

Profile gauges have been the most frequently used tool; with varying designs used by a number of investigators (e.g. Gore, 1978; Slatzner, 1981). Underwood &

Chapman (1989), for example, measured the complexity of topography in quadrats via a series of equal length needles dropped vertically onto the substratum. On a finer scale microheterogeneity has been measured using a TALYSURF-4 profilometer (Le Tourneux & Bourget, 1988). Typically profiles have been digitally scanned into an image analysis system and the resulting line plots used to determine an appropriate statistical index (Kostylev, 1996).

Luckhurst & Luckhurst (1978), among others, used the ratio of a length of chain contoured over the surface to the linear distance between the chains end points as a measure of surface complexity. Variations on this theme, developed by Dahl (1973), have included using different link lengths.

Small-scale stereophotography, similar to the two-dimensional photography used by Gee (1978), has also been used to define habitat complexity (e.g. Evans & Norris, 1997). Stereophotography, allowing three-dimensional measures, has been used successfully in terrestrial situations (Grayson *et al.,* 1988) and for marine applications (Klimley & Brown, 1983; Fryer, 1984; Svane, 1988); there seems to be no reason why it should not also be useful on the rocky shore. Three dimensional co-ordinates of any point within a stereopair of photographs can be calculated via a series of trigonometric equations. Van Sciver (1972) described the geometrical relationships on which this technique is based.

Other photographic methods currently available for characterising surface features are either hard to interpret in a biologically useful way, are qualitative, or are habitat specific (Loehle, 1991; McCoy *et al.,* 1991). Texture analysis, for example, using grey scale images produced by modern video image-enhancement systems, is an established method (Haralick *et al.*, 1973). The data for texture analysis is primarily obtained by the use of a profile gauge, where the resulting profile is photographed in the field. For more detailed work a latex-rubber peel of the surface has been painted and placed under a video camera (Parsley, 1989; Sanson *et al.*, 1995). Stereo-photography also offers an alternative to the shadow method which again calculates heights of surface features (Partridge, 1982). On a larger scale, biologically generated habitat complexity scores have been derived from video analysis (Coops & Catling, 1997). More recently Guichard *et al.*, (2000) have used a low cost balloon-based high resolution remote sensing technique to acquire environmental and biological variables over intertidal landscapes.

In a few instances surface attributes such as hole size, slope and height have been directly measured in relation to the focus of the respective study (Roberts & Ormond, 1987; Levin, 1991). The physical parameters determined on the substratum, in a study conducted by Bergeron & Bourget (1986), were the linear distance along the surface (as described by Dahl, 1973), the vertical height of each crevice and the number of crevices. The shape of each crevice was described in terms of its size, slope and orientation. Raffaelli & Hughes (1978) also recorded the presence or absence of a crevice at 5mm intervals along a rock section. In addition surface manipulations have also been carried out in the intertidal (Raffaelli & Hughes, 1978; Menge *et al.*, 1983; Wethey, 1986).

Despite their differences, these methodologies have all been used to derive similar indices. A comparison of the methods used to derive complexity indices is currently lacking. Evans & Norris (1997) compared heights derived from stereo-photography with those obtained from a profile gauge. Similarity in height measurements between the photogrammetric and substratum pin profiler methods were poor despite the expectation of exact matching. Until now it has been assumed that indices derived from such techniques will be correlated; so different areas would be ranked similarly in terms of their complexity, regardless of the method used. It was the intention of this study to determine the degree of association between measures derived by stereophotography, profile gauges and lengths of chain in defining habitat complexity.

(2.1.3.) Indices

All these techniques generally lead to a single index, the effect of each method on deriving a complexity measure is therefore important. Numerous such indices exist and these have been used in a number of different habitats and locations. In some instances a single index has been defined and correlated with biological characteristics (Levin, 1991; Kostylev, 1996). Luckhurst & Luckhurst (1978), for example, found that the chain method was useful in assessing the influence of spatial heterogeneity in terms of species richness and diversity. Different indices have also been compared within habitats, to determine which index best identified features of the habitat that appeared to be related to the density of a species (e.g Stoner & Lewis, 1985; Underwood & Chapman, 1989; McCormick, 1994; Hills & Thomason, 1996; Jacobi & Langevin, 1996; Beck 1998, 2000).

McCormick (1994) reviewed six such indices, with measures derived from the use of a profile gauge. These were the consecutive substratum height difference, the angular standard deviation of vectors, angular standard deviation, contour versus linear length and finally the standard deviation of regularly measured substratum heights and the coefficient of variation of the regularly measured substratum height. All the techniques gave similar results and could differentiate between surfaces differing in number and height of corrugation, with the exception of the co-efficients of variation. The consecutive height difference index, however, had by far the highest number of significant correlations with fish species (McCormick, 1994).

Underwood & Chapman (1989) also utilised computer simulated substrata of varying complexity to distinguish between the various indices of topographic complexity. The heights of the gauge needles were used to estimate topographic complexity using standard geomorphological estimates of relief (Hobson, 1972). They decided to use the circular variance of vectors normal to triangular planes as an index in subsequent work. Carelton & Sammarco (1987) compared six indices of structural complexity (vector dispersion (VD), vector strength, average surface angle and three measures related to deviations from a plane): all were correlated with the density and diversity of coral spat at settlement.

Other methods include the mathematical characterisation of two dimensional profiles of a surface. The joined x and y co-ordinates of a surface profile can represent a complex wave form, the signature of which can be characterised by a Fourier analysis using a Fast Fourier Transformation (Ehrlich *et al.*, 1987). However, the signature obtained is not easy to compare with other signatures or easy to interpret.

An important consideration is the interval or scale of measurement (McCoy *et al.*, 1991). The results of all topography measures are dependent on scale and there is a definite requirement to examine the scale of interest. This is particularly important when comparing such indices with biological features of the habitat. Different organisms perceive their environment at a variety of spatial scales thus influencing the use of such techniques. Recently, Gee & Warwick (1994), for example, have indicated that for marine plants the measures of complexity used by previous workers (e.g. Russo, 1990) are unsatisfactory in describing fine scale heterogeneity. The use of the fractal dimension *D* was proposed as a more suitable alternative.

Fractals by definition, are structures that are heterogeneous at all spatial scales, with a scale dependent self similarity (Mandelbrot, 1983). The fractal dimension increases with an increase in complexity of a natural object, providing ecologists with a numerical descriptor of heterogeneity (Kostylev, 1996). For a linear fractal function, the dimension *D* may vary between one (completely differentiable) and two (so rough and irregular that it effectively takes up the whole of a two dimensional topological space). For surfaces, the corresponding range for *D* lies between two (absolutely smooth) and three (infinitely crumpled) (Burrough, 1981).

Most applications of fractal ecology have been concerned with the links between plant complexity and the associated faunal community structure (e.g Morse *et al.*, 1985; Lawton, 1986; Gunnarsson, 1992; Gee & Warwick, 1994a,b; Davenport *et al.*, 1996, 1999). Such studies have revealed an association between high fractal dimensions of vegetation and greater diversity, numbers and biomass of animal communities. The use of fractals in the intertidal has also been suggested to have the best correlations with biological characteristics (e.g. Kostylev *et al.*, 1997; Beck, 1998, 2000). In the rocky intertidal habitat, the density of gastropods has been significantly and positively correlated with four indices (vector dispersion, chain and tape, consecutive height substratum height difference, fractal) of complexity; *D*, however, had the highest correlations with density (Beck, 1998).

One of the suggested advantages of *D* is that it includes assessment of structural complexity across a range of intervals that may be relevant to the organism in question (Morse *et al.*, 1985; Williamson & Lawton, 1991; Kostylev *et al.*, 1997).

Fractal geometry can be applied across a number of spatial scales ranging from very small (Kampichler & Hauser, 1993) to kilometres (Milne, 1988; Azovsky *et al.*, 2000). Most other indices do not account for the potential size specific effects of structural complexity on species. Even for specific size classes within species, the effects of structural complexity are likely to be important at more than just one scale (e.g. Bourget *et al.*, 1994; Lemire & Bourget, 1996). It is, however, possible to calculate most indices at several intervals to examine the size specific effects of structural complexity (e.g. Carleton & Sammarco, 1987; Sanson *et al.*, 1995; Beck 1997).

The fractal dimension *D*, like other indices, is a general descriptor of the complexity of a surface; it does not provide a description of the numbers and sizes of refuges available to organisms. Additionally, there is yet little evidence that habitats are generally 'self similar', i.e. that the value of *D* remains constant over different spatial scales of measurement. If *D* is not constant it becomes more difficult to use (Williamson & Lawton, 1991). It has also been argued that the use of *D*, however, does not imply that surfaces are fractal or self similar; it only implies that *D* can usefully describe some features of the habitat (e.g. Avnir *et al.*, 1998). It seems unlikely that any one index will be best in most habitats, or for most species, as different locations vary across a whole range of spectra.

Surfaces do not display a unique complexity value; *D*, for example, seems to be greatly dependent on the method of measurement and may differ even within a single measurement technique (Cox and Wang,1993; Corbit & Gabary, 1995). A lack of consistency between such indices is likely to result in conflicting results with regard to the importance of structural features. Assumptions regarding complexity and biological characteristics are limited by such problems. The use of different methods to produce such indices therefore needs to be assessed.

(2.2.) METHODS

(2.2.1) Study Sites

Two shores along the South coast of Britain were studied: Heybrook Bay in Devon and Port Wrinkle in Cornwall (Figure 2.1). Data was collected from two sites for the ease of collection only and was combined for the further analyses. The underlying geology in each area was a sedimentary rock type and both sites were moderately exposed. The fauna on each shore was predominantly barnacle dominated, with patches of barnacles interspersed with largely unoccupied rock surfaces. *Fucus* and other large algal species were sparsely distributed throughout the shore. Encrusting algae were also relatively rare. Invertebrate animals typically found on such shores were also observed in abundance (Lewis, 1964; Hawkins & Jones 1992; Raffaelli & Hawkins, 1996).

A total of 30 (0.25x0.25m) quadrats were examined in the mid intertidal zone on both shores. Quadrats were selected at random; if the area encompassed greater than 50% of standing water (a rockpool) it was discarded. Within each quadrat a stereopair of photographs were taken, as well as three profiles using a gauge and three profiles using chains of different link lengths.

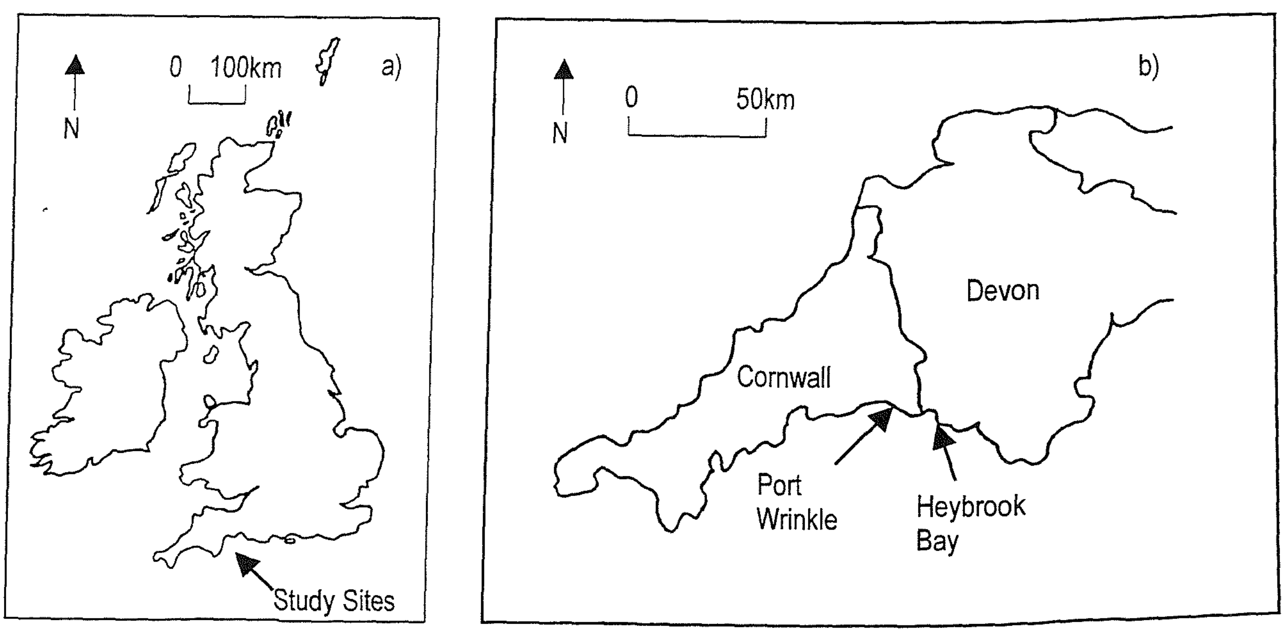


Figure (2.1): a) A map of the UK to place the sites in a wide geographical context. b) A map of the location of the two study sites (Port Wrinkle in Cornwall and Heybrook Bay in Devon).

(2.2.2.) Profile Gauges

Three profiles were taken from each quadrat; two across the diagonals of the quadrat and the third between two adjacent corners. The profiler used here had 300 pins which were packed closely together. Each pin was 1mm in width and 50mm in height equating to a total profile length of 300mm. The profile gauge was pushed in to the rock surface so that the pins were moulded into the rock surface. The resulting profile was then traced on to a sheet of paper. In order to ensure that the heights were relative to each other the paper was premarked at set heights on the sheet. The two ends of the profile gauge were then aligned with the marked heights. Where the crevices were too deep for the profile gauge a note was made of the change in vertical height. This was then corrected for, with the additional height measures calculated using trigonometry and added to the respective points.

The resulting profiles were scanned into a personal computer where they could be analysed further. A specifically designed programme (Techdig; Jones, 1997) was used to digitise each of the lines. Co-ordinates were digitised at every point along the profile where there was a change in the vertical dimension. To obtain equidistant measures, at 1mm intervals, these co-ordinates were interpolated via a programme which traced the existing line and used linear interpolation to define each point (specifically designed analysis programme: T. Carter, 2000).

Four indices (Fractal dimension (*D*), Vector dispersion (VD), Consecutive Height Difference (CHD) and the contoured versus linear length of a chain held against the rock surface (chain ratio)) were later compared from these profiles.

(2.2.3.) Lengths of Chain

Chains of three different link lengths (10mm, 20mm, 45mm) were laid directly over the substratum and were made to conform as closely as possible to all contours and crevices. A measure of the actual surface distance relative to linear distance (chain ratio) was then obtained for the same three profiles as used with the profile gauge. The higher the ratio obtained the more complex a profile is said to be.

The ratios produced by the chains were ranked for each quadrat; with the highest complexity score receiving a rank of one and the lowest a rank of three. The average rank of each link length was then calculated. If the chains produced a successive rank with the largest link length attaining the smallest ratio and vice versa then it is possible to calculate a fractal dimension from these values.

(2.2.4.) Stereophotography

Stereophotography allows the calculation of the three dimensional co-ordinates of any photographed point, based on the relative position of that point, on both exposures of a stereo-pair. All that is required is that the distance between the two cameras is known, and secondly the optical axes of the cameras are parallel (Van Sciver, 1972). The three dimensional co-ordinates of each specified point shared by the images can be calculated based on a series of mathematical equations (vanRooij & Videler, 1996).

Figure (2.2) represents a diagrammatic representation of stereo-photography. The positioning of the two cameras is aligned so that they are parallel to the underlying subject (showed by •). There is a region of overlap between the resulting images in which three dimensional co-ordinates can be calculated. On examination of the image from the left camera the point of interest (•) would be displaced to the left in relation to the image from the right hand camera. The relative displacement of any particular point between two images is dependent on its vertical distance from the camera. It is therefore possible through a series of trigonometric equations, based on the ratios between similar triangles, to calculate these vertical distances and hence three dimensional co-ordinates for any point in this region of overlap.

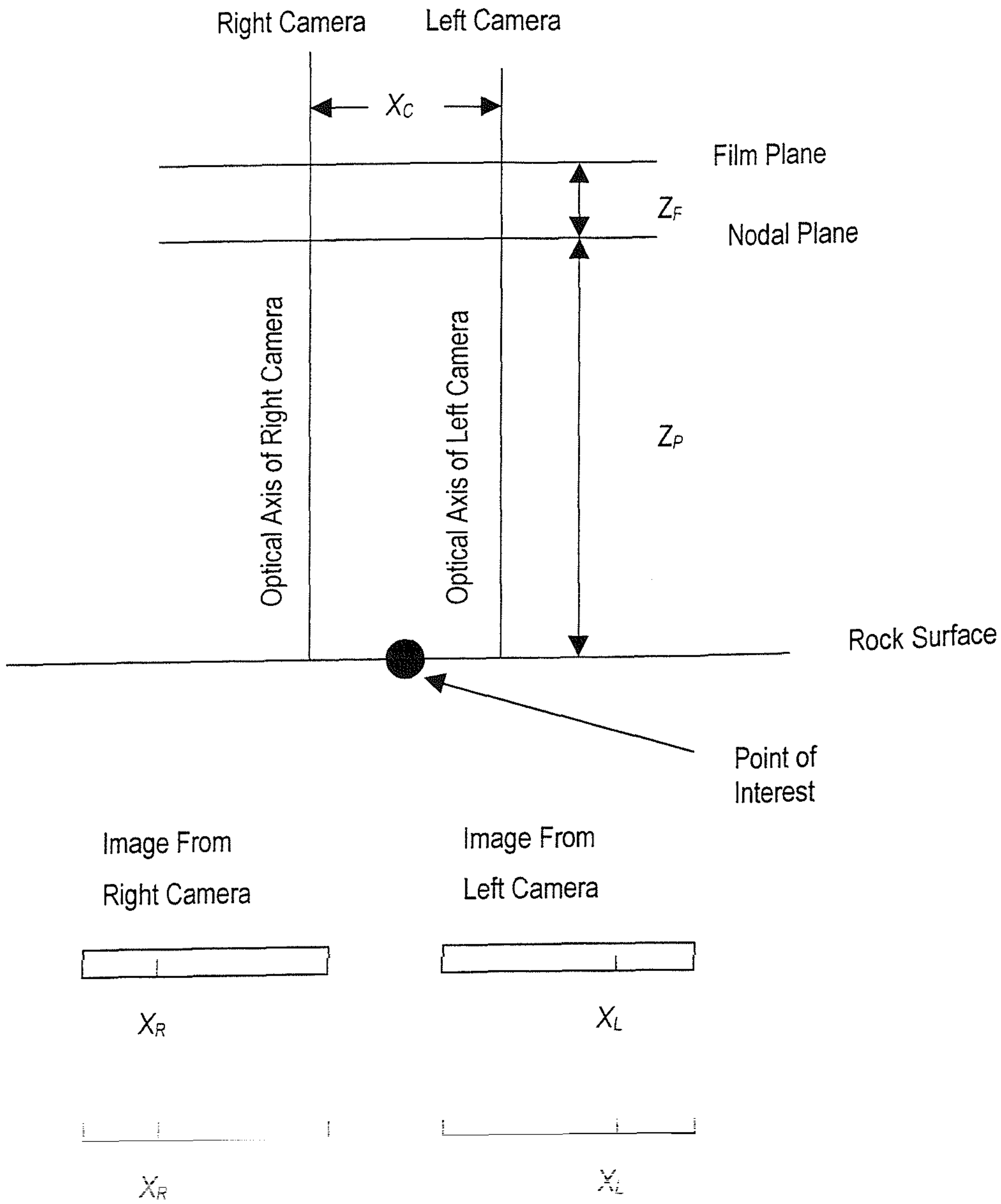


Figure [illegible] A diagrammatic representation of stereophotography. Where X_C represents the distance between the two cameras. Z_F is the focal length of the camera. Z_P represents the distance between a point and the camera (i.e. the height dimension). X_R and X_L represent the difference between the x co-ordinate of the optical axis and that of the point (•) for the left and right camera respectively.

30

The vertical distance of a set point from the plane of the cameras (Z_p, cm) can be defined as:

Equation (1):

$$Z_P = \frac{Z_F . X_C}{X_L - X_R}$$

Where Z_F is equivalent to the distance from the camera lens to the film plane (38mm) and X_C was the separation distance between the two camera lenses (14cm). While (X_L. Y_L) and (X_R, Y_R) were the co-ordinates of the same feature in the left hand and right hand images respectively.

Similarly the *x* and *y* co-ordinates along the plane of the cameras (X_P, Y_P, cm) can be calculated:

Equation (2):

$$X_P = \frac{X_L . Z_P}{Z_F}$$

Equation (3):

$$Y_P = \frac{Y_L . Z_P}{Z_F}$$

(2.2.4.1.) Survey Technique and Image Analysis

The stereo-photographic measurements required the use of two aligned Ricoh RDC300 digital cameras attached to a portable frame. A tripod was adapted to allow the attachment of the two cameras, each held horizontal to the plane of the rock surface. The adjustable legs of the frame were utilised to ensure the cameras were held level. The distance between the two cameras was held constant at

140mm. Once positioned the images were taken simultaneously and were downloaded to a PC for viewing.

Each stereo-pair encompassed an overlapping region of 25cm by 25cm. A specifically designed programme was employed which enabled the overlaying of the corresponding area within the stereo-pair of photographs (specifically designed analysis programme: M.T. Burrows, 1999). For the analysis each of these quadrats was further subdivided into 506 grid cells. Each grid cell was equivalent to 1.2cm by 1.2cm. Within each grid cell an identifiable feature, such as an irregularity of the rock was digitised in both of the corresponding images from the pair of stereo-photographs.

Once the point in the left hand image was digitised the programme automatically switched to the same point on the right hand image; this minimised errors and facilitated the collection of data points. The three dimensional co-ordinates of each point were subsequently calculated from equations 1 to 3. The bias of the dominant slope was removed from the data within each quadrat via regression. The z co-ordinates were regressed against the x and y to produce a set of predicted z values lying on a plane. Subtraction of predicted from observed z values yielded residual z values. Interpolation between these residuals gave an equidistant grid that could be used to calculate fractal dimensions.

(2.2.5.) Calculation of Statistical Indices

The four indices calculated from the profile gauge data were *D*, VD, CHD and the Chain ratio (Figure 2.3). The calculation of all statistical indices from the profile gauge were based on a minimum resolution of 5mm. The fractal dimension, however, was also calculated based on a separation distance of 1mm.

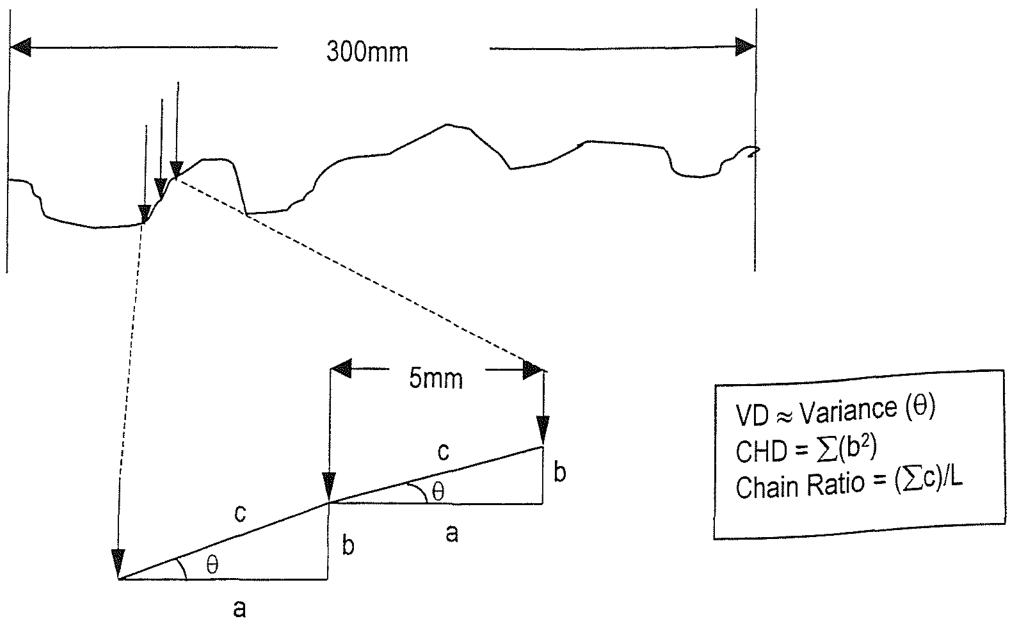


Figure (2.3): A diagrammatic representation of the calculation of 4 statistical indices (Vector Dispersion (VD), Consecutive Height Difference (CHD), Fractal (*D*), and the ratio of a contoured chain over a rock surface versus the linear length of the chain (Chain ratio). (adapted from Beck, 2000).

VD is a measure of the angular variance and was calculated with a two dimensional modification of the formula in Carelton & Sammarco (1987).

Equation (4):

$$VD = \frac{\{n - [\sum_{1}^{n} (a/c)]\}}{(n-1)}$$

Where n denotes the separate triangles along the transect, a represents length of the adjacent and c is equivalent to the length of the hypotenuse.

The consecutive height difference was calculated as the sum of the squared differences in height from one point to the next (Values were square root transformed to linearise the index) (McCormick, 1994).

Equation (5):

$$\sum dh^2 = \sum(b^2)$$

Where b represents the difference in height between two adjacent points and dh is the overall consecutive height difference.

The chain index was the ratio of a profile length moulded to the surface to the linear distance between its start and end point (Dahl, 1973; Luckhurst & Luckhurst, 1978).

Equation (6):

$$\text{Chain} = (\sum c)/L$$

Fractals were calculated using the divider method (Sugihara & May, 1990; Cox & Wang, 1993). This involved taking length measurements of the profiles at different step lengths (Figure 2.4). The log of the profile length versus the log of the step length was then plotted; if the data when plotted give a straight line the profile has fractal geometry as demonstrated by line two in the Figure (2.4). In contrast lines one and three represent profiles that would not be classified as self similar and hence fractal. These profiles represent transects that contain greater variability in length at one scale than another. Where profiles were considered fractal the slope of the line which best fitted the data was used to calculate *D*: equivalent to one minus the value of the slope. This was done for each profile and the average fractal was calculated per quadrat for the various techniques employed. The fractal of a line ranges between 1 and 2, with 1 being the least complex and 2 being the most.

D was calculated with the finest scale of resolution set at both 1mm and 5mm intervals. The step lengths increased by a factor of two in both instances (i.e. 1mm, 2mm 4mm 8mm- until the end of the line was reached and 5mm 10mm 20mm 40mm etc.). The use of different scales allowed the testing of self similarity and provided evidence that these rock surfaces were indeed fractal. A matched pair t-test was used to compare the average fractal derived from the 30 quadrats at the two resolutions (Fowler & Cohen, 1994). If there was no significant difference between the mean values of the two data sets then the same fractal was obtained regardless of step length. As a consequence of this property the fractal dimension of a surface was predictable at different spatial scales and hence demonstrated self similarity.

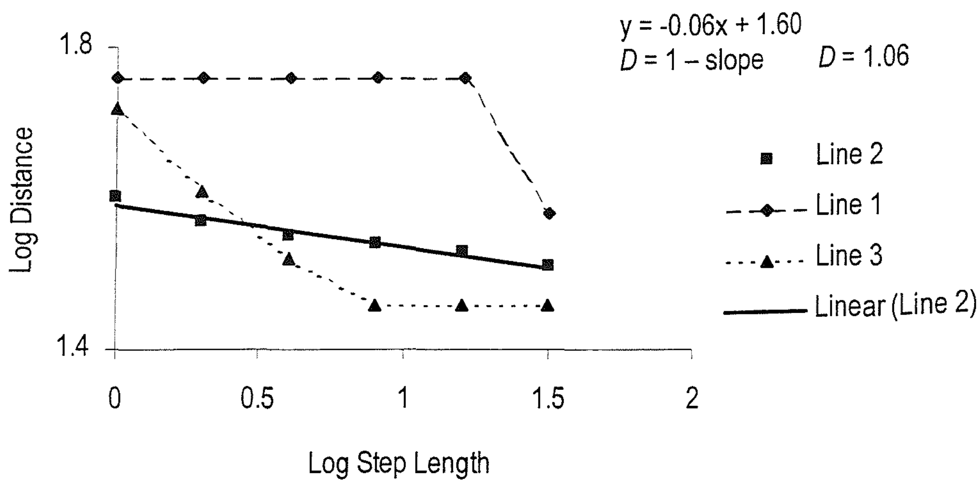


Figure (2.4): The calculation of a fractal dimension (*D*). The data from the example profile of line 2 fitted a straight line and hence the fractal dimension was calculated as one minus the slope.

The same method was applied to the stereo photo data. The finest scale of resolution was based on the average distance between two adjacent digitised points (approximately 2cm). A total of 80 interpolated lines were used to calculate fractals; profiles were taken in both a horizontal and vertical direction. The average fractal per quadrat was therefore based on 80 lines.

Fractals were also calculated based on the chain data. The link lengths were equivalent to the different step lengths and similarly the contour versus linear ratios were equivalent to the distance component. A fractal was therefore calculated for each of the three profiles through each quadrat. Again the average fractal was then calculated.

Complexity within a single quadrat may be highly variable; some profiles may be totally flat while others may be highly convoluted. Conversely there may be no variability within a quadrat; with all lines either smooth or irregular. The variability surrounding the average fractal per quadrat therefore reflects the variability of complexity within a single quadrat. The average fractal for each quadrat from the different methods was based on a different number of individual profiles (or fractals), the effect of this was therefore investigated.

The relationship between the variance and the average fractal per quadrat was calculated. The natural log of the average fractal for each quadrat was plotted against the natural log of the variance surrounding the average fractal value. This was done for the stereophotograph fractal, using three lines, and the 1mm fractal from the profile data. For an additional comparison the average fractal and variance from the entire stereophoto data were compared with that obtained from three randomly selected lines. If there was a strong positive correlation between these values, regardless of the number of lines taken it would mean that fewer replicate profiles would be adequate in order to rank complexity.

The accuracy obtained when using three profiles per quadrat in either sterophotography or from a profile gauge was calculated from equation 7 (Bakus, 1990). This was done across a range of complexity values namely fractal dimensions between 1 and 1.1 at 0.05 intervals. The variance associated with each fractal was predicted from the equation that represented the best relationship between these two variables (calculated above).

Equation (7):

$$L = \sqrt{\frac{\sigma^2 (Z.05)^2}{N}}$$

Where L represents the error from the true mean, σ is the standard deviation, N is the number of profiles (in this case 3) and Z is a function of the distance from the mean in standard deviation units.

It was also possible to rearrange this equation in order to calculate the number of profiles required to attain a set level of accuracy (the mean fractal ± 0.01) surrounding the mean D per quadrat. Again this was done across a range of complexity values ranging from 1 to 1.1 at 0.05 intervals. The variance associated with each fractal was predicted from the equation that represented the best relationship between these two variables.

Equation (8):

$$N = \frac{\sigma^2 Z.05^2}{L^2}$$

Where N is the number of profiles required to achieve a set accuracy, L is equivalent to the allowable error (±) from the true mean level (in this case ±0.01), σ is the standard deviation, and Z is a function of the distance from the mean in standard deviation units.

A correlation matrix using Pearsons' product moment correlation coefficient was used to compare all the indices derived from the three techniques. The significance of these relationships were also calculated. Pearsons' product moment correlation coefficient (r) reflects the linear extent of the relationship between two data sets. The R-squared value can be interpreted as the proportion of the variance in y attributable to the variance in x (Fowler & Cohen, 1994) when a regression line is calculated.

(2.3.) RESULTS

(2.3.1.) Profile Data

In terms of the first null hypothesis the indices derived from all the methods were not comparable. The results of all complexity indices obtained from the three methods, however, were positively correlated with the exception of the fractal derived from stereophotography (Table 2.1). The different indices obtained from a single technique were examined before more generalised comparisons could be made.

Four indices of complexity were derived from the profile gauge data, with a minimum scale of resolution set at 5mm. The degree of correlation between these indices varied depending on the comparison being made (Figure 2.5). The most significant positive correlation was between the vector dispersion index and the fractal dimension. The positive relationship between the chain index and *D*; and the chain index and VD were also highly significant. Out of the four indices the consecutive height difference was the least correlated with the other three measures. One exception, however, was displayed between this measure and the chain index, which was again highly significant. The three quadrats with substratum features larger than the profile pins (where additional height measures were required) consistently presented outlying points in the correlation plots (Figure 2.5). This was particularly pronounced when comparing the consecutive height difference with the alternative indices. The three outlying points were excluded from the lines of best fit as they distort the relationship displayed by the majority of quadrats.

Table (2.1): The correlation between the complexity indices derived from stereophotography, chains and a profile gauge.
(*** denotes significance p<0.05; ** p<0.01**).

	Contoured Vs Linear Chain Ratio			Chain Data	Stereo-Photography Data	Profile Gauge Data				
	10mm Chain	**20mm Chain**	**45mm Chain**	**Fractal Chains**	**Fractal SP**	**Fractal Profile (1mm)**	**Fractal Profile (5mm)**	**Vector Dispersion**	**Consecutive Height**	**Chain Ratio**
Chain 10mm	-									
Chain 20mm	**0.96****	-								
Chain 45mm	**0.86****	**0.93****	-							
Fractal Chains	**0.64****	**0.47****	0.18	-						
Fractal SP	-0.12	-0.13	-0.20	0.05	-					
Fractal Profile (1mm)	**0.59****	**0.47****	0.41	**0.51****	-0.13	-				
Fractal Profile (5mm)	**0.64****	**0.54****	**0.46***	**0.51****	-0.04	**0.89****	-			
Vector Dispersion	**0.55****	**0.42***	0.30	**0.56****	-0.08	**0.86****	**0.93****	-		
Consecutive Ht Diff	**0.46****	**0.47****	**0.45***	0.22	0.06	0.33	**0.37***	**0.36***	-	
Chain Ratio	**0.69****	**0.65****	**0.58****	**0.46***	-0.03	**0.77****	**0.85****	**0.81****	**0.76****	-

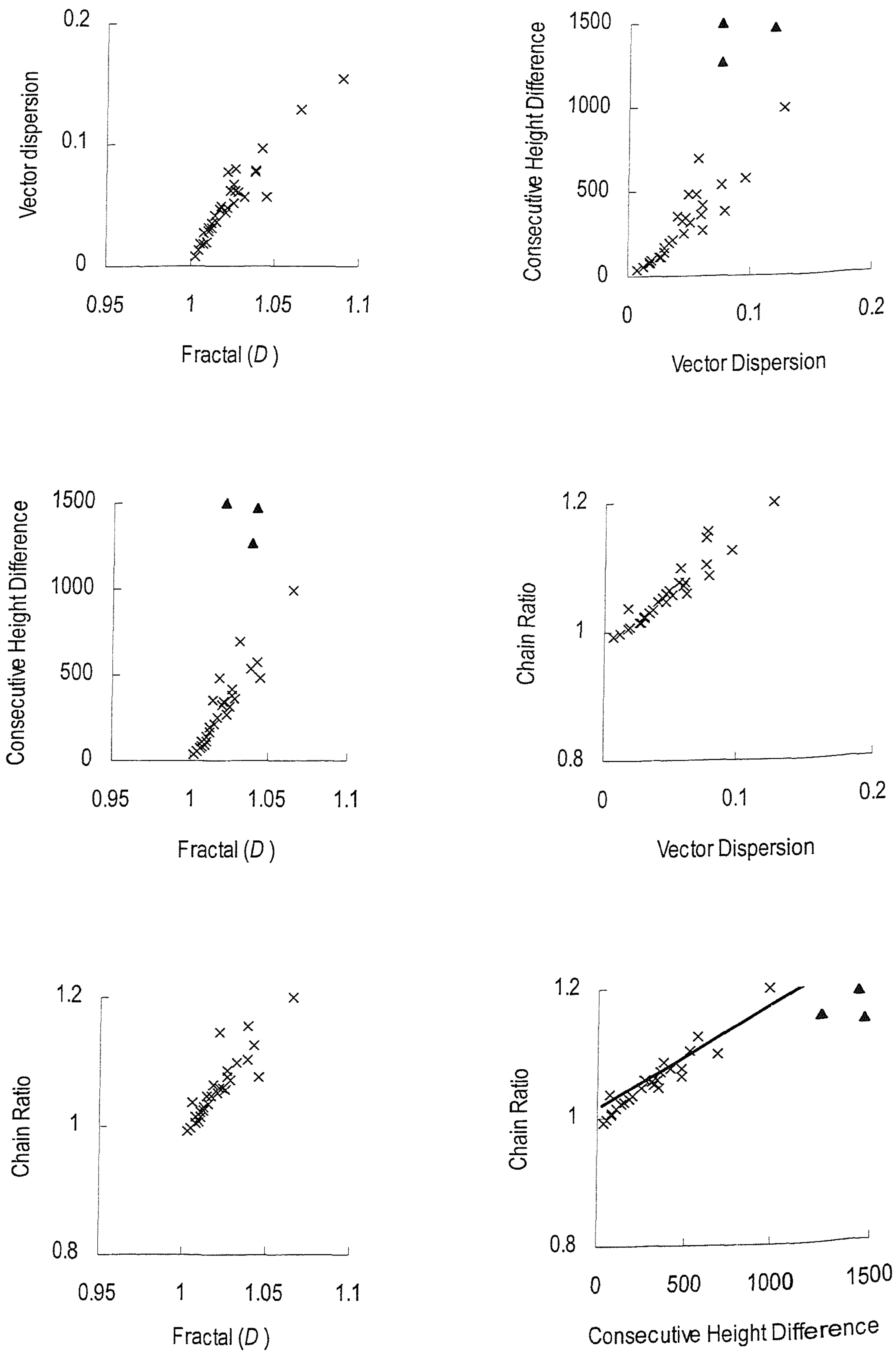


Figure (2.5): A comparison of all indices derived from the profile gauge data (n=30 quadrats). The three outlying points excluded from the lines of best fit (▲)represent quadrats with features larger than the profile pins. Fractal dimensions were based on 5mm resolution.

Fractals from the profile gauge data were determined with a minimum resolution set at both 5mm and 1mm. The scale of resolution did marginally affect the fractal obtained per quadrat. At the scale of 1mm the fractal was larger than at a scale of 5mm in 64% of cases. The average fractal, however, remained the same with 1.02 at 1mm intervals and 1.02 at 5mm intervals. By increasing the resolution this also served to slightly decrease the range of fractals obtained. A matched pairs t-test between the fractals derived at 1mm and 5mm intervals demonstrated no significant difference between the two means ($t=0.28$, d.f.=29, $p=0.78$). The same ranking of complexity and fractal dimension was obtained regardless of the minimum resolution of step lengths. The fractal of a quadrat was therefore predictable across different spatial scales and hence the profiles were considered to be fractal in nature.

(2.3.2.) Chain Based Methods

The ratio of the contoured length versus linear length varied depending on the link size of the chain. As the link size increased in size the chain ratio decreased signifying a reduced level of complexity (Figure 2.6). The level of surface detail incorporated by the smaller link lengths was therefore greater than the larger chains. This was highlighted by the average rank of each chain ratio within a quadrat. The ratios obtained were ranked within each quadrat; with the highest complexity score receiving a rank of 1 and the lowest a value of 3. A rank of 1.17, 2.03 and 2.8 was obtained for the 10mm, 20mm and 45mm chain respectively. As the line length increased while the step size decreased it was possible to calculate a fractal dimension from this data.

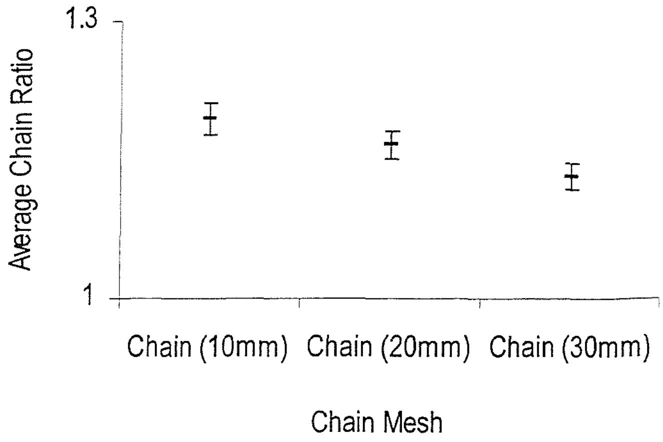


Figure (2.6): The average contoured versus linear profile length when using chains of three different link lengths. (Error bars =S.E., n=30).

The ratios obtained from the three different chains were significantly correlated with each other. Ratios from chains with the closest link lengths were, however, most strongly correlated with each other (Table 2.1). The ratios obtained from the different link lengths correlated with the alternative indices from the profile gauges to varying degrees. The chain with the smallest link length was significantly and positively correlated with all the indices derived from the profile gauge data. This was particularly true for the correlation with the equivalent chain index. The ratio, like all indices from the profile gauge, was least correlated with the consecutive height difference. The same was also true for the 20mm chain, although the significance values were all slightly lower than with the 10mm chain. This ratio was least correlated with the VD index. The ratio obtained from the third chain incorporated not only the least surface detail but was also least correlated with all other indices. The relationship between this ratio and the VD index was not significantly correlated at all.

The fractals obtained from the chains were significantly correlated with the ratios derived from the first and second chain. These fractals were also correlated with the vector and chain indices as well as the 1mm and 5mm profile data. The consecutive height difference was again the least correlated with this chain fractal.

(2.3.3.) Stereophotography

The relationship between the stereophotography fractal and all indices derived from the profile gauge were negative with the exception of the consecutive height difference (Table 2.1). The fractal derived from the stereophotography was also positively correlated with *D* derived from the chains, although this relationship was not significant.

(2.3.4.) Comparison of Fractals

The relationship between the fractals derived from the different techniques was explored in greater detail (Figure 2.7). There was no significant correlation between *D* from the stereophotography and profile gauge methods: in fact a negative correlation was apparent between these two techniques. While there was no relationship between the stereophotography and profile gauge data the chains fractal was positively and significantly correlated with the profile fractal. Fractals obtained from the stereo- photographs were also consistently higher than those obtained from profile gauges. The corresponding averages were 1.06 and 1.02 respectively. The range in fractals was also greater for the stereophotographs than from the profiles (0.10 and 0.07). The chain fractals were between these two extremes in terms of both the average and range of *D*.

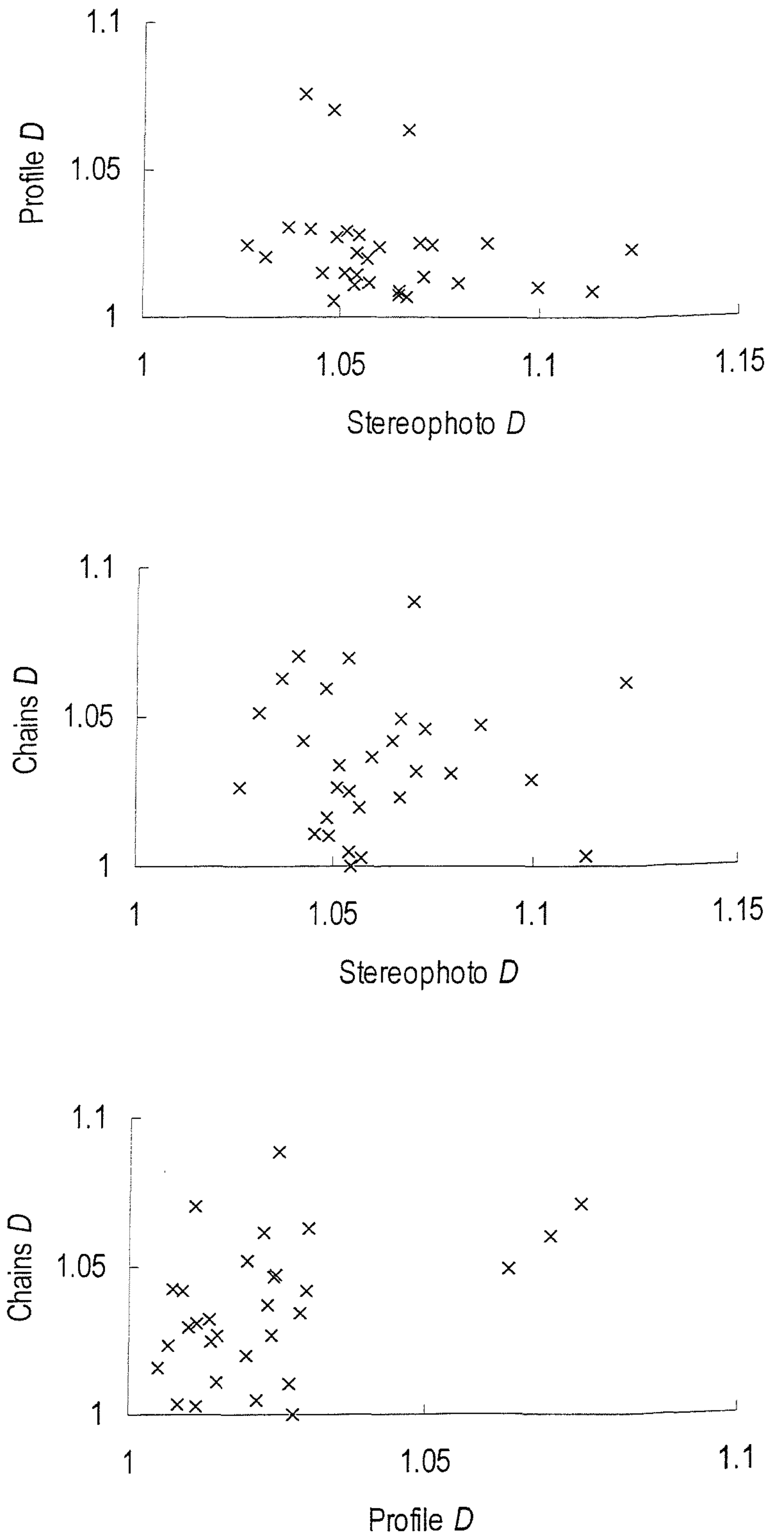


Figure (2.7): The relationship between fractals derived from stereophotography, a profile gauge and chains (n=30).

The fractal that was calculated for an individual quadrat was based on a different number of profiles. Each profile line has its own fractal dimension – the overall quadrat fractal is therefore the average derived from the individual profiles. The calculation of the fractal for the stereo-photo and profile gauge therefore took into account a very different number of individual fractals. In order to assess the effect of taking a different number of profiles a fractal was also calculated based on the average of three random lines from the stereophotography data. A correlation plot between the fractal derived from the 3 and 80 lines was significantly correlated (R^2=0.63). The variance surrounding the average fractal from 80 lines was similarly correlated with that of 3 lines (Figure 2.8). The difference in magnitude and rank between the profile gauge and stereophotography fractals was therefore not attributable to the number of sampled profiles.

When using either stereophotography, the profile gauge or the chains, the variance surrounding the average fractal per quadrat also varied within a technique. Those demonstrating the least variance would have had all profiles with a similar level of complexity. In contrast those with a high variance represent quadrats where the selected profiles were very different in terms of their complexity.

The lowest fractal obtained from the profile gauge data was considerably less than that of the stereophotography (Figure 2.9). The correlation between the log photo fractal and variance was a much shallower relationship than the equivalent profile data. The stereophoto *D* was also more variable at lower levels of complexity than the profile measures. With regard to the image data, after a fractal of 1.06, the variance surrounding each fractal reached a plateau; where no further increase in variance was observed with an increasing complexity. In contrast the variance surrounding the profile data continued to increase throughout all values of *D*. This shift in variance made it impossible to determine a required number of profiles per quadrat for assessing complexity. The number of profiles required to incorporate all topographic variation would vary depending on the particular quadrat examined.

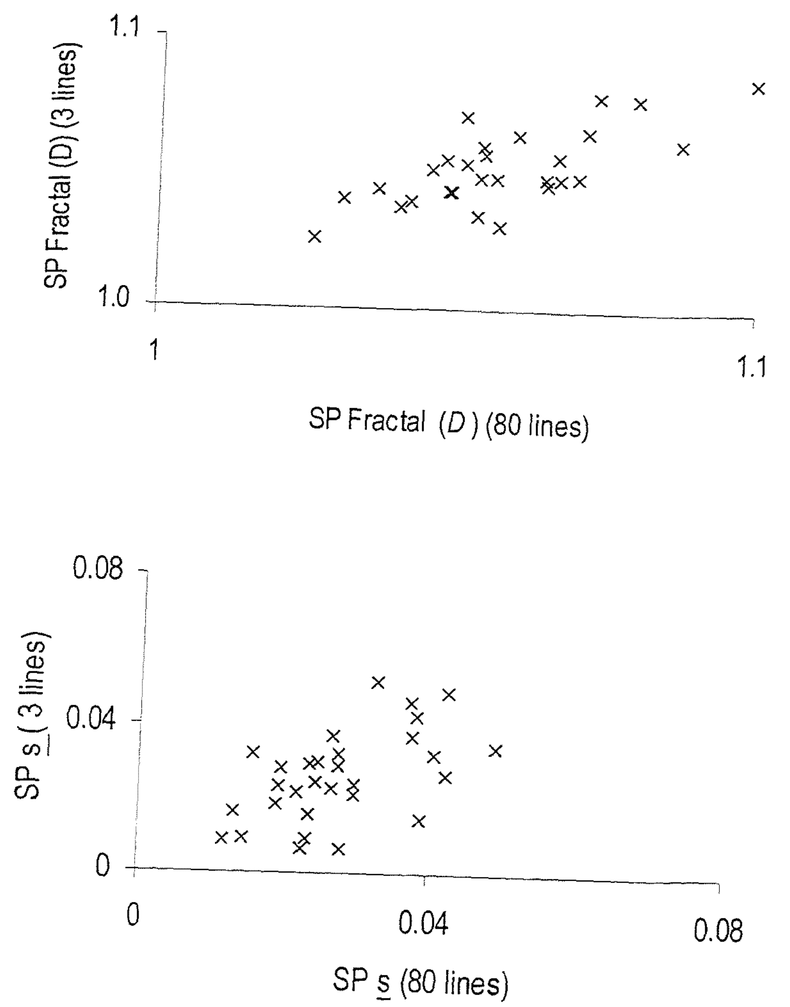


Figure (2.8): The relationship between D and the variance associated with fractals derived from 3 and 80 lines from the stereophotography (SP) data from each of the 30 quadrats.

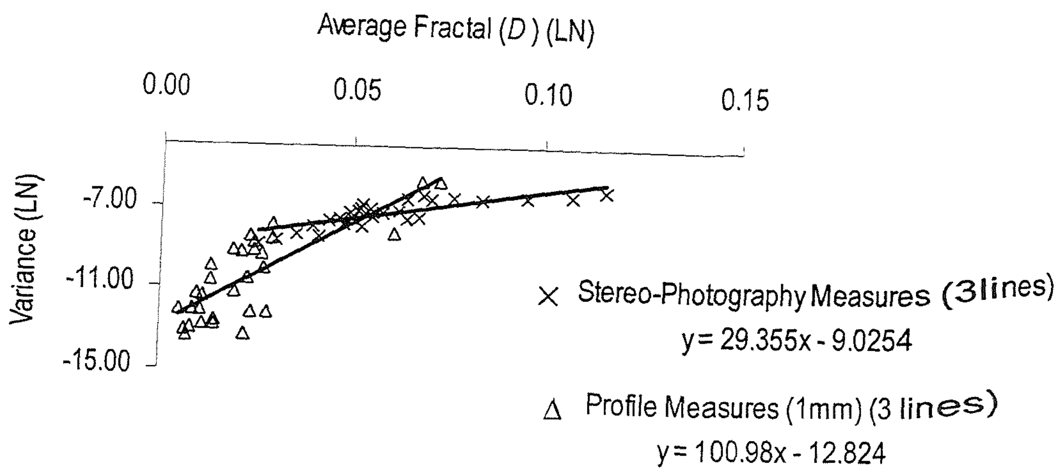
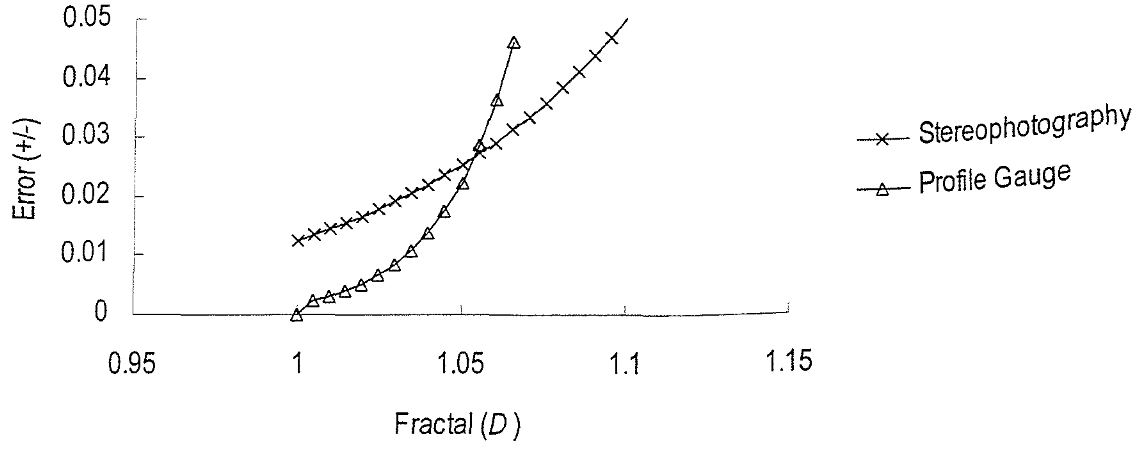


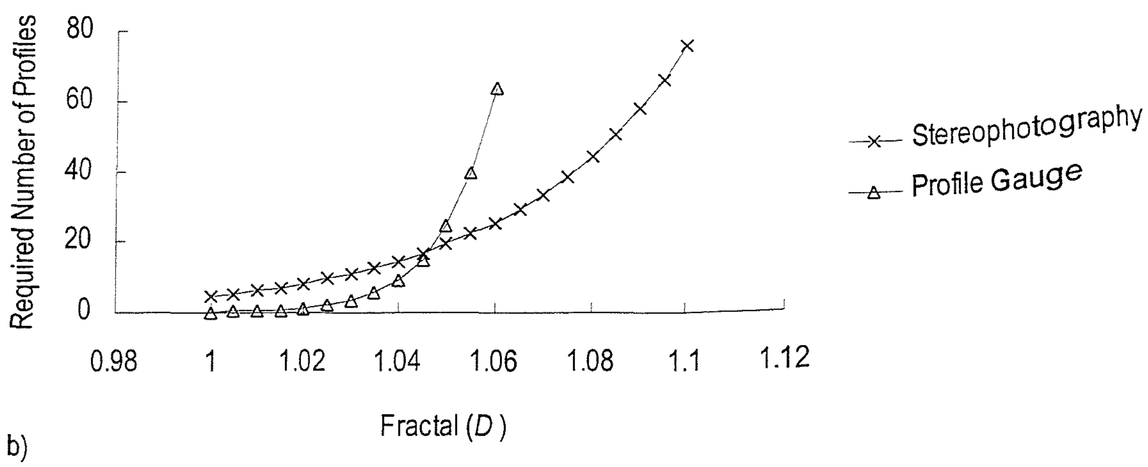
Figure (2.9): The log of the average D versus the log variance for each of the 30 quadrats from the stereophotography and profile gauge data.

The level of accuracy in calculating a fractal based on three profiles per quadrat varied depending on the overall complexity of the quadrat (Figure 2.10a). When using both the profile gauge and the stereophotography the accuracy surrounding the mean fractal per quadrat decreased with an increase in complexity. It was evident on smoother surfaces that the level of accuracy attained from a profile gauge was much higher than that from stereophotography. In contrast once a *D* value of 1.05 was obtained the reverse was true with values of the mean ±0.03 and ±0.02 for profile gauge data and stereophotography respectively.

Likewise if a set level of accuracy was determined, in this case the average fractal ± 0.01, the number of profiles required to attain this value varied with the overall average complexity of the quadrat (Figure 2.10b). Again at lower levels of complexity fewer replicate profiles were required with the profile gauge than stereophotography to attain this degree of accuracy. The converse was true after an average fractal of 1.05, where at this point 19 profiles would be required for stereophotography and 24 for profile gauges to achieve an accuracy of ±0.01.



a)



b)

Figure (2.10): a) The accuracy obtained when using 3 profiles per quadrat using both stereophotography and profile gauge data.
b) The required number of profiles to attain an average fractal ±0.01 using both stereophotography and a profile gauge.

(2.4.) DISCUSSION

(2.4.1.) Comparison of the Techniques

Hobson (1972) in a discussion of spatial analysis in geomorphology, noted that for a measure of surface complexity to be useful it must have three characteristics: be conceptually descriptive, easily measured in the field, and capable of being measured and compared on a number of scales. The technique also needs to be economical and analysis should be not too time consuming so as to allow sufficient replication.

The three methods: stereophotography, profile gauges and chains, compared here each presented a number of advantages and disadvantages with regard to measuring habitat complexity. The easiest and quickest method to use in the field was the lengths of chain with different link lengths. No specialised equipment was required for the technique and further analysis was also the least time consuming. The use of a profile gauge again required a single low cost instrument. The tracing of the profiles under field conditions was the most time consuming part of the exercise. The use of stereophotography required a camera, although this was not a limiting factor as no specialised photographic equipment was required. Once the tripod was adapted, it was quick and easy to ensure the cameras were a set distance apart and held parallel to the rock surface. In terms of further analysis the profile gauge data was equally as time consuming as the stereophotography.

The indices derived from the three techniques differed in both magnitude and scale. The indices obtained from both the chain data and the profile gauge data, however, ranked the 30 quadrats in a similar order of complexity. If a ranking of complexity was all that was required, data from a profile gauge or chains could be legitimately compared. The differences that arise via the use of stereophotography isolate this technique in terms of comparing the values obtained with alternative methods.

Evans & Norris (1997) while not comparing an actual index, but exact height measures, found a similar result. They used correlation analysis to determine whether profile gauge and stereophotography transect heights varied in the same direction. Similarity in height measurements between the two techniques were poor since they should have matched almost exactly. Only 30 of 110 pairs of height transects measured by the profile gauge and stereo photographs were significantly correlated. Unfortunately, it was not determined whether dissimilarities in transect heights occurred because of variability in profile gauge errors or in stereo photograph interpretation. If these height values had been converted to an index the discrepancies between these two techniques would have been magnified; with all the uncorrelated measures accumulated into a single figure.

The reasons for the differences between stereophotography and the alternative techniques in ranking complexity are numerous. Firstly the level of resolution obtainable by the different methods varied depending on a number of factors. When using a profile mapping method, the distance between the vertical measurements and their number, govern the scale at which heterogeneity will be quantified. Likewise for the chain method it is the length of the chain and size of the linkages that will govern the index value. Stereophotography would be limited by the accuracy of the equipment, the amount of digitised points from a stereopair and the resolution of the images.

The accuracy level of the techniques was also different. The most accurate technique for obtaining small scale relative changes in height were from the profile gauge. Inaccuracies were introduced, however, where the profile gauge did not fit the rock surface. The inaccuracies of the chain increased with an increase in link size, where they were no longer able to fit to surface irregularities. It has also been reported that stereophotography can be more accurate than a surface profiler in a number of instances (Grayson *et al.*, 1988). The accuracy of this technique could be affected by a number of factors including light levels, the reflective properties of the surface and the standard of photographic equipment. Stereophotography, however, can still be a very powerful tool; Van Rooji & Videler (1996), for example, obtained an accuracy level as high as high as ±0.3 to 3.5% of measured distances. The accuracy obtained in the current study was approximately the true height value ± 1cm. The method used in a particular investigation would therefore depend on the level of precision required.

The contrast between the stereophotography and profile gauge fractal was not attributable to the difference in the number of profiles taken. The inaccuracies introduced by using stereophotography in determining heights must therefore have played a key role in generating differences in fractal values. Stereophotography had a greater degree of variability surrounding smooth surfaces than the equivalent profile measure. This was because where an area was smooth inaccuracies introduced through the image processing technique distorted height measurements and hence increased the value of D. The fact that the photo fractals were generally much larger than the profile values also supports this notion. In general the variance surrounding the average fractal per quadrat increased with an increase in complexity. With regard to the stereophotographs, where a plateau was reached and no further variation was added with an increasing complexity, this point could represent the maximum level of noise added to the analysis via random inaccuracies. Stereophotography is therefore likely to over estimate complexity where an area is smooth. Conversely when using profile gauges, confidence in the derived fractal drops sharply as complexity increases because it becomes possible to sample and miss certain features.

(2.4.2.) Comparison of Indices

The greatest potential benefit of statistical indices to compare habitat complexity is that they enable direct comparisons between different studies and habitats. The importance of complexity in shaping and determining community patterns in a number of different locations and habitat types can be assessed. The indices derived here (VD, CHD, D and chain ratio) represent examples that have been useful in such investigations (e.g. McCoy & Bell, 1991, Gee & Warwick, 1994a; Sanson *et al.*, 1995). Beck (1998) for example demonstrated that structural complexity was more important in affecting the distribution of gastropods in rocky shore habitats than mangroves. Although, it should be remembered that other factors, such as wave action or desiccation, can all shape intertidal patterns and it is an interaction of these factors that result in the observed community assemblages. It has also been argued that condensing complexity into a single measure may lead to a great loss of information (Simberloff *et al.*, 1987) .

All indices from the profile gauge data set were correlated; this was as to be expected as they were all calculated from an identical data set. Such similarities between indices has been identified by previous investigators (Carelton & Sammarco, 1987; Underwood & Chapman, 1989; McCormick, 1994; Beck, 1998; 2000). The least correlated value in all instances was the CHD. Where additional heights were required (i.e. where profile depths were greater than 5mm) the CHD was most susceptible to these relatively large scale changes in substratum height. The three outlying quadrats particularly associated with CHD correlations represented points where this correction was necessary. The CHD index was therefore more sensitive to changes in height than the other indices.

When relating species distributions to biological characteristics each organism of interest is likely to be correlated with a specific physical or biological factor. The index required for a particular investigation should therefore be capable of reflecting any small scale changes in this parameter. McCormick (1994), for example found that the CHD index was most suited to describe the abundance of damselfish. In contrast Underwood & Chapman (1989) used the VD index to relate topography with littorinid populations.

(2.4.3.) Chain Based Methods

With regard to the chain ratios, as expected an increase in link length caused the relative length of the profile to decrease (Luckhurst & Luckhurst, 1978). The smaller link lengths therefore incorporated a greater amount of surface detail than the larger chains. The size of the smallest link length (10mm) was most similar to the resolution of the profile data explaining why this ratio was the best correlated with the gauge indices. The method best suited to a particular investigation would therefore depend on the scale of interest. If a ranking of complexity was required for a set of quadrats, the ratio from a chain with a set link length would provide as much information as a detailed profile analysis set at the same resolution.

(2.4.4.) Fractals

It has been argued that fractal geometry is useless for ecology because ecological patterns are not fractals (Williamson & Lawton, 1991). Alternative arguments suggest that a self-similar object is a geometrical abstraction that exhibits precisely the same pattern on all spatial scales (Avnir *et al.*, 1998). The average fractals obtained from the profile gauge data, with a minimum resolution of 1mm and 5mm, were not significantly different. The same fractal was therefore obtained regardless of step length. As a consequence of this property the fractal dimension of a surface was predictable at different spatial scales and hence demonstrated self similarity. This was taken as evidence that the use of fractals was valid in this investigation. Indeed there is growing recognition that many natural objects have a graininess or nested irregularity to them, which places them within the realm of fractal geometry (Azovsky *et al.*, 2000).

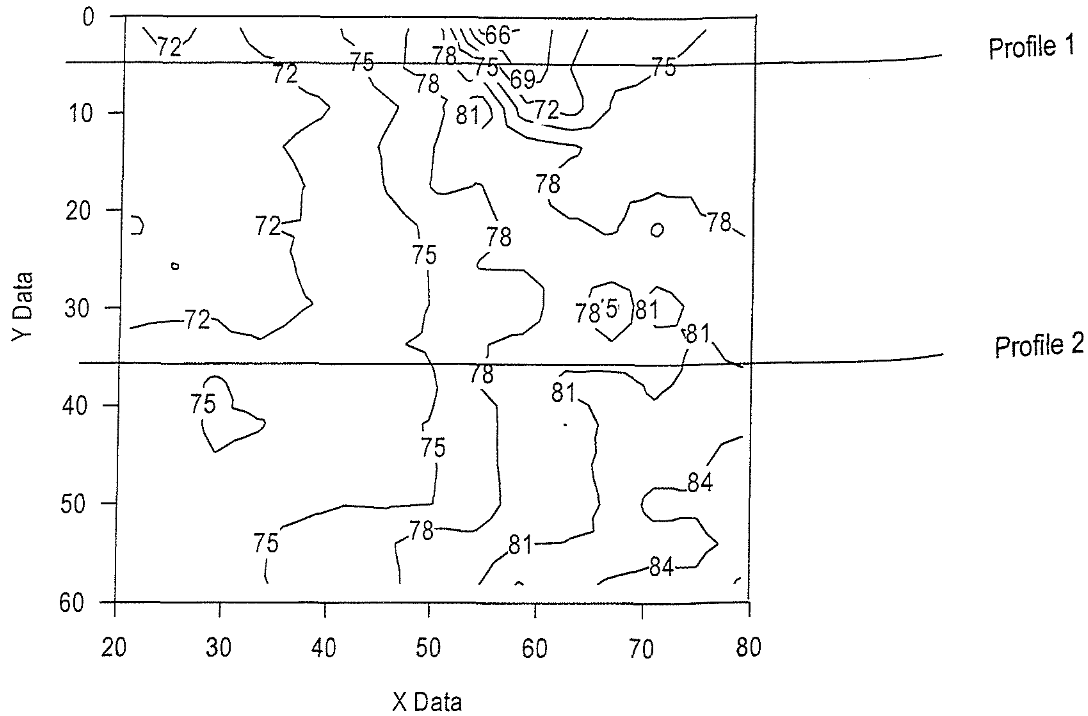
Different observational scales capture different aspects of structure, and these transitions are signalled by shifts in the apparent dimension of the object. This latter fact suggests an interesting application of fractals as a method for distinguishing hierarchical size scales in nature (Sugihara & May, 1990; Bradbury *et al.*, 1984). D is also useful because it is calculated across different intervals of measurement, which forces consideration of the concordance in scale between measures of complexity and the size of the species in question (Gee & Warwick, 1994a, b; Kostylev, 1997; Beck, 1998).

Practically speaking, scale dependent variations in D can be introduced while creating the digital images used for deriving estimates. Studies of plant and algal architecture have demonstrated that the thickness of the lines within digitised images can have a large and significant impact on the estimated D (Bernston, 1994; Corbit & Garbary, 1995). This demonstrates that current methods of deriving D are sensitive to both the overall space filling properties of a given structure, as well as the smaller scale features. Secondly, when digitising real world structures the resolution of acquired images needs to be carefully considered. This decision has the effect of delimiting the minimum spatial scale that can be examined (Bernstoll & Stoll, 1997). A calibration of methods is therefore required in order to make these results comparable and ultimately more useful in determining the importance of habitat complexity.

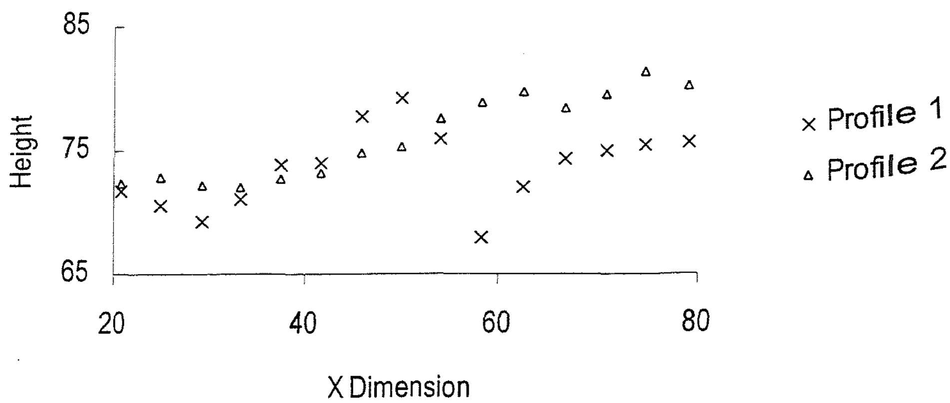
(2.4.5.) Sampling Effort

The accuracy obtained when using the average D of three profiles per quadrat varied depending on complexity. As the complexity of a quadrat increased so did the amount of error surrounding the average D value. In order to attain a set level of accuracy surrounding the average fractal a different number of profiles would be required depending on both the complexity of the area and the technique used. At lower levels of complexity (D =1.00-1.04) more profiles per quadrat would be required for stereophotography than with a gauge and the converse was true at higher levels. The number of profiles sampled therefore needs to be a compromise between accuracy and sampling effort. In a study such as this where three replicate profiles were taken for thirty quadrats an additional profile per quadrat would be equivalent to approximately an extra seven hours of analysis. When using stereophotography, however, once the images were digitised it was possible to take at least 80 profiles through a quadrat without any extra processing.

The shift in accuracy accompanying the changes in complexity made it impossible to determine a number of profiles for a future sampling strategy. The number of profiles required to incorporate all topographic variation within a quadrat varies depending on the overall complexity of that area. A set number of profiles therefore needs to be pre-decided prior to any investigation. It should be remembered, however, that on examination of only a couple of profiles it would be possible to completely miss a deep narrow crevice running parallel to the measured line. This is highlighted in the example below where the examination of two randomly selected transects results in two very different profiles and hence complexity values (Figure 2.11).



a)



b)

Figure (2.11): The result of selecting two different profiles from a randomly selected quadrat. (a): Contour Plot. (b): Resulting Profiles.

(2.4.6.) Practicality of the Techniques

All three techniques, when used on the rocky shore, allowed a non destructive sampling technique. Previous studies, however, have reported that profile gauges shift bottom sediments altering the shape of profiles (Young, 1993). The habitat which is being examined may therefore alter the accuracy of the techniques. Gauges only give an indication of rock heights and their basic spatial extent; they cannot show how long a rock is, if there are spaces between the rocks, or if there is sand or debris present. Stereophotography, despite not viewing beneath the surface, can provide a more complete description of the substratum *in situ*. It also has the advantage of placing substrate elements in a relevant spatial context and is less limited in terms of the number of variables that can be measured (Klimley & Brown, 1983). The size, density, and spatial dispersion of individuals can be established without disturbing them or removing them from the study population.

Using stereophotography also allows the construction of three dimensional representations of a particular area. The biota within that area can then be directly correlated with surface features (see Chapter 3). This would not be feasible with the other two techniques. Firstly, realigning the profiles to recreate the surface would introduce a considerable amount of inaccuracy. Secondly any biota recorded in a quadrat would not be directly linked to specific topographic regions.

Photographic methods can also provide actual numbers and sizes of crevices as well as quantify roughness at different spatial scales. Methods using indices of complexity, such as those obtained from profile gauges, supply single values for surfaces, which themselves provide no specific information on actual gap sizes. Additionally it is possible for surfaces with differing numbers and sizes of refuges to attain the same value of the index (Sanson *et al.*, 1995). Difficulties can arise, however, if crevices or other complex features are larger than the area incorporated by an image. As with any method of measurement several profiles of a surface are required and the technique is also limited by the interpretation of the relevant features (Evans & Norris, 1997).

(2.4.7.) Conclusions, Limitations and Future Work

The lack of clear definitions and adequate measurement techniques has, so far, hindered the development of our understanding of complexity on community patterns and processes (Beck, 2000). The hypothesis that all techniques would lead to a similar ranking of complexity has been disproved. The rock surfaces were described as fractal, although the values of D, from the various techniques were not correlated for all methods. The indices derived from either chains or profile gauges were ranked in a similar order and could therefore be compared across studies and environments. The differences that arise via the use of stereophotography, however isolate this technique in terms of comparing the values obtained from the alternative methods. If a ranking of complexity was required then a ratio derived from a chain would provide as much detail as the more sophisticated and time consuming analyses.

All indices derived from a single data set, however, were correlated and a complexity ranking based on such values could therefore be compared. Each index is likely to be best suited to describe a particular relationship and this needs to be investigated for each individual case.

All the indices derived via the three methods were limited by the inaccuracies of the techniques. To counteract this, comparisons could be made in a controlled environment, although field conditions are usually quite different in terms of the limitations that arise. The minimum resolution of the indices were also constrained by the measurement and analysis procedures. Now that it has been established that the techniques incorporate different aspects of surface complexity it would be useful to correlate such indices with associated biological features. Habitats with different underlying substratum could be compared to assess the generality of these results. The importance of complexity in shaping communities requires further quantification. The development of methods used to define such surface features therefore plays a key role in advancing our understanding of these interactions.

3. The Use of Stereophotography in Predicting the Location of Species in Relation to the Topography of the Substratum

(3.1.) INTRODUCTION

(3.1.1.) Complexity and Scale

Two fundamental and interconnected themes in ecology are the development and maintenance of spatial and temporal patterns of abundance, and the consequences of those patterns for the dynamics of populations, communities and ecosystems (Levin, 1992). Spatial variability is a fundamental characteristic of animal and plant populations and community structure as well as of the environment in which the organisms live (Lindegrath *et al.*, 1995). Such variability is known to influence abiotic and biotic properties in ecosystems over a wide range of spatial scales from kilometres (Wolanski and Hammer, 1988; Boose *et al.*, 1994; Johnson & Hanson, 1995) down to less than a millimetre (Le Tourneux & Bourget, 1988; Carpenter & Williams, 1993; Bell *et al.*, 1993; Archambault & Bourget, 1996; Thompson *et al.*, 1996). In intertidal marine habitats, topographic heterogeneity under the scale of 1m scale has also been shown to influence both hydrodynamics and benthic community structure (Cusson & Bourget, 1997; Guichard & Bourget, 1998).

Physical complexity serves to increase the range of microhabitats, with different micro-climates available to intertidal species (Kolasa & Pikett, 1991; Sebens, 1991). Complex rock structures can provide shelter from adverse environmental conditions such as wave action, temperature extremes and desiccation stress whilst influencing humidity levels and relative sedimentation rates (e.g. Fairweather, 1988; Hughes, 1995; Jones & Boulding, 1999).

High heterogeneity can also affect biological parameters such as competition (Walters & Wethey, 1986; Palmer, 1992) and consequently is thought to affect species diversity and abundance patterns (Pringle, 1990; Bourget *et al.*, 1994; Lindegrath *et al.*, 1995; Downes *et al.*, 1995, 1998; LaPointe & Bourget, 1999). Environmental variability influences the impact of predation (Gilinsky, 1984; Bologna & Heck, 1999) and of parasitism (Nachman, 1981), increases population stability (Lodge *et al.*, 1988), and helps maintain intraspecific genetic polymorphism (Lechwicz & Bell, 1991). Recruitment patterns are also influenced by the degree of topographic complexity (Lively *et al.,* 1993; Hunt & Scheibling, 1996; Chiba & Noda, 2000).

Each individual and populations of each species experiences the environment on a unique range of scales. Thus responses to variability can be very different, making the characterisation of spatial patterns more complicated (Kotliar & Wiens, 1990). The role of topographic complexity may therefore change with scale. As a consequence research efforts need to relate to the appropriate scale at which a particular process is operating (Wiens, 1989; Russell *et al.,* 1992: Keeling *et al.*, 1997).

(3.1.2.) Predicting Species Distributions From Topographical Features

Surface topography has two components: firstly the frequency and amplitude of corrugation, and secondly the degree of angulation (Hobson, 1972). Together these give an overall summary of the three dimensionality of the surface. Investigations to date have used a wide variety of techniques to measure such complexity which have led to quite different statistical properties and indices (see Chapter 2).

Many of the methods commonly used to measure the substratum at the microscale: profilers, lengths of chain and direct rock measurements (e.g. Le Tourneux & Bourget, 1988; Underwood & Chapman, 1989; Kostylev, 1996) have limitations. These include their intrusive nature, an inability to measure the spaces between substrate elements, limitations on the number of variables that can be measured and a lack of information on the spatial context of elements in a sampling site (Evans & Norris, 1997). In contrast, image analysis can provide biologically meaningful measurements of habitat structure and complexity. These measurements permit ecologists to estimate the space potentially available to organisms of particular sizes and to quantify the heterogeneity of a surface so that it may be compared with other workers (Sanson *et al.*, 1995).

Small-scale stereophotography, in particular, provides the advantage of allowing three dimensional measures which can be used to reconstruct a surface map of a particular area. The biota within that area can then be directly correlated with surface features. In fact no other method is both non-destructive and capable of yielding so many variables to which organisms may respond. The photographs of each quadrat also provide a permanent record. This can be stored for future reference and used in correlating abundance with topographic or other environmental features including elements of the biota.

Stereophotography has been used successfully in terrestrial and marine systems (Gee, 1978; Fryer, 1984; Grayson *et al.*, 1988) and has also proved more accurate than a surface profiler (Grayson *et al.*, 1988). More recently, Guichard *et al.*, (2000) have used a balloon-based high resolution remote sensing technique to acquire high resolution data of environmental (topographic) and biological (algal biomass) variables over intertidal landscapes. They performed stereo analysis on digitised images over an 18m by 18m area to reconstruct topographic maps to be correlated with algal biomass.

Observations of both organism distributions and values of environmental variables provide some of the most complete information on spatial distributions of organisms and factors that affect them (Evans & Norris, 1997; Guichard & Bourget, 1998; Zacharias *et al.*, 1999). The description of pattern is a necessary precursor to experimentally manipulative analyses of ecology and provide a logical starting point from which to propose explanations or theories (Underwood *et al.*, 2000). Maps, in particular, can depict categorical or numerical data. The numbers, proportions, and dominance of different patch types, as well as the spatial arrangement of patches, patch sizes and shapes, contrast between neighbouring patches and connectivity among patches can be estimated from categorical maps (Li & Reynolds, 1994, 1995). Densities of organisms along a transect can also be recorded and, with a knowledge of species size-mass relationships the biomass over an area can be determined. Furthermore, the dispersion of animals can be characterised as either random, uniform or clumped (Klimley & Brown, 1983).

Previous studies have correlated the occurrence of species with specific topographic features but have rarely considered the community as a whole. Barnacles and mytilids for example are known to preferentially settle in crevices as opposed to open rock surfaces (Crisp, 1961; Bergeron & Bourget, 1986; Chiba &

Noda, 2000). Crevices and / or pools have been reported to affect the distribution of numerous intertidal gastropods including littorinids, dog whelks and limpets (e.g. Underwood, 1977; Levings & Garrity, 1984; Hughes, 1995; Jones & Boulding, 1999). Algal species are also commonly associated with such features (Norton & Fretter, 1981; Jernakoff, 1983; Bergeron & Bourget, 1986; Sutherland & Ortega, 1986). If the relationship between benthic species and their habitat is deterministic it should be possible to predict macroinvertebrate and algal distributions on the shore. Such relationships are not likely to be univariate; the distribution of species is more likely to depend on several habitat features as well as other organisms (Evans & Norris, 1997; Underwood *et al.*, 2000). It was the intention of this study to predict the distribution of a number of species on rocky shores in relation to topographic heights of the substratum.

(3.1.3.) Aims and Objectives

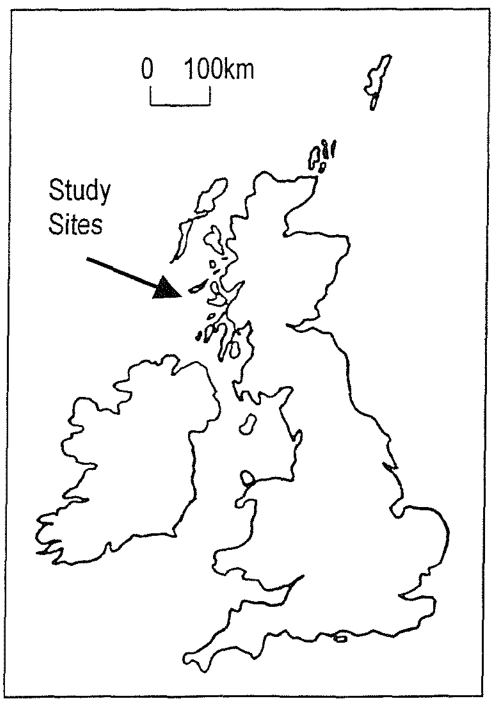
The overall aim of this chapter was to develop a predictive model of species distribution in relation to the topography of the substratum. If refuges provide a preferable habitat to that of a flat surface, it would be predicted that where possible species would be associated with such features. The null hypothesis was therefore that there would be no relationship between the distribution of each species and a set topographic height, either above or below the average height of an area. The likelihood of each species locating within their preferred habitat type, if space became available, was also estimated based on the strengths of their relationship with topography. If topography did not influence the location of each species then all taxa would be equally likely to colonise any surface feature.

Initially the methodology involved in recreating and correlating surface features with species distributions was fully developed. In order to demonstrate the potential of this technique photographic images were taken at two shores along the coastline of Northwest Scotland. A total of ten quadrats were analysed from three tidal heights along two transects on each shore. The consistency and the predictability of the relationship between the occurrence of a species and a topographical feature was assessed via logistic regression.

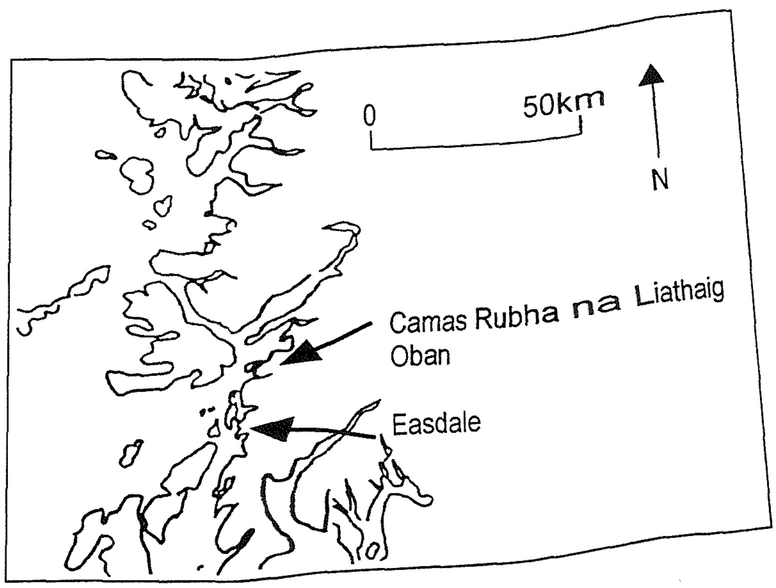
(3.2.) METHODS

(3.2.1.) Study Sites

Two sites were studied along the Argyll coastline, Northwest Scotland during the spring of 1998. The first shore, Easdale (Figure 3.1b) is a moderately exposed intertidal environment with an extensive wave cut platform of smooth hard bedrock. The site is primarily dominated by a typical barnacle based community (Lewis, 1964; Raffaelli & Hawkins, 1996) with species displaying evidence of moderate exposure throughout the shore. The topography of the shore is characterised by a series of crevices and raised areas of varying dimensions. In contrast the transects on the second shore, Camas Rubha na Liathaig (Figure 3.1b), were located within a sheltered bay. The rock type is far more irregular than at Easdale and has volcanic origins; the surface is characterised by numerous interspersed cobbles embedded in the metamorphic rock, creating circular crevices. The biota is typical of that predicted for a sheltered shore (Lewis, 1964; Hawkins & Jones, 1992; Raffaelli & Hawkins, 1996), being largely *Fucus* dominated.



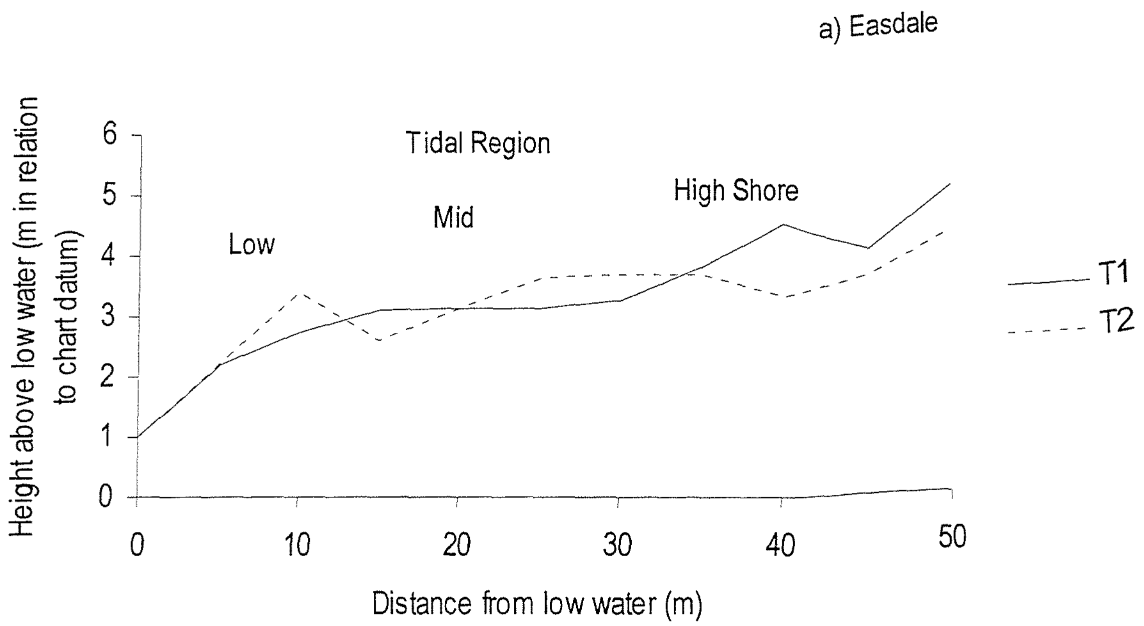
a)



b)

Figure (3.1a): A map of the UK to place the sites in a wide geographical context.
Figure (3.1b): The exact locations of the two study sites, Camas Rubha na Liathaig and Easdale.

These sites were further subdivided, at random, into two transects which ran perpendicular to the shore line. Once profiled these areas were further segregated into low, mid and high shore based on their location in relation to chart datum (Figure 3.2). A total of ten (30cm x 30cm) quadrats were subsequently analysed at each tidal height on each transect.



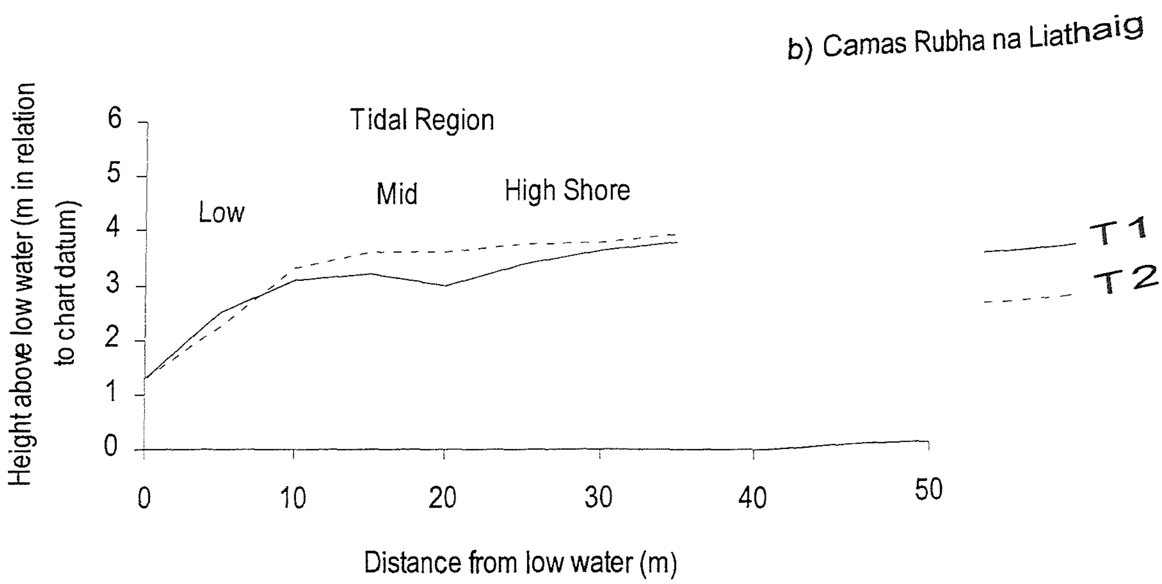


Figure (3.2): Profiles of the two transects sampled at each shore, a) Easdale and b) Camas Rubha na Liathaig.

(3.2.2.) Survey Technique

Correlations of surface topography with the overlying biota were conducted via the use of stereophotography, a procedure already described in detail in Chapter 2. Each stereo-pair encompassed an overlapping region of 30cm by 30cm. A specifically designed programme (M.T. Burrows, 1999) was employed to obtain both the three dimensional co-ordinates and biological components of each quadrat. The corresponding area within each stereo-pair of photographs was directly overlaid and a grid was superimposed on this region. The grid served to divide each quadrat into 506 grid cells: each equivalent to 1.4cm by 1.4cm. Within each grid cell an identifiable feature was digitised in both of the corresponding images from the pair of stereo-photographs. The three dimensional co-ordinates of each point were subsequently calculated (via a series of mathematical equations (vanRooij & Videler, 1996; see Chapter 2)). Simultaneously the biota of each cell was recorded in the form of a code that was later correlated with surface topography.

(3.2.3.) Data Processing

In order to eliminate the bias of the dominant slope within each quadrat a regression of the z co-ordinates against the x and y co-ordinates was undertaken. This produced a series of predicted z values lying on a plane, which were subsequently subtracted from the observed z values in order to produce a set of residual z co-ordinates. As demonstrated in Figure 3.3 without removing the effect of the dominant slope point one would be considered to be in a crevice, whereas in reality it is higher than the immediate surrounding area. In contrast point two would be considered to be in a raised area where it is actually within a crevice. The replacement of the original height measurements with the corresponding residuals served to standardise each point so that all co-ordinates were relative to a horizontal plane (Figure 3.3).

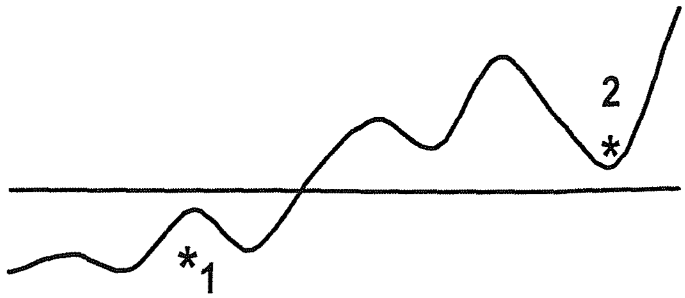
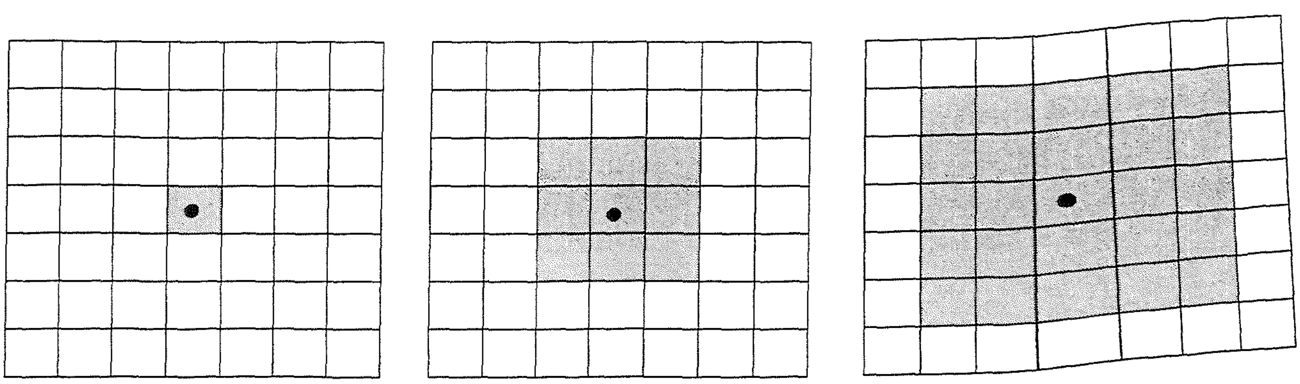


Figure (3.3): A two- dimensional representation of the relative effect of a dominant slope within a quadrat.

The distribution of species in relation to topography over a range of scales within the 30cm quadrat was quantified by the use of a local averaging technique. The residual height of each point was related to surrounding points in all directions at a range of distances (equivalent to 0cm – 30cm apart, at 3cm intervals). The first local average is equivalent to the original residual of any particular point (• in Figure 3.4). The second local average, incorporating a slightly larger scale, is the average of the residual height of that point and all the cells at a distance of one cell away (Figure 3.4b). Each progressive local average represents a larger scale of observation; with the average taken from an increasing number of surrounding cells (Figure 3.4c). The largest local average calculated incorporated the average height of a point and all cells up to and including a distance of 15 cells. The distance of any cell was determined by euclidian moves (Durret & Levin, 1994), with the resulting values rounded to the nearest cell.



(a.): Local Average 1 (b.): Local Average 2 (c.): Local Average 3

Figure (3.4): The number of cells incorporated into the calculation of a local average.

The surface can be decomposed into a number of spatial scales or components. The first component represents the smallest scale of topographic variation; with each progressive component representing a slightly larger scale until the last component consists solely of the largest scale features. An example of the effect of each component is displayed in Figure 3.5. The original line is a two dimensional representation of differing height measurements along a transect. Component one represents all the small scale features of the original line and therefore follows a similar pattern to that of line one. The mid component (c5) only identifies features that are of an intermediate scale and the final component (c10) only detects large scale differences in topography.

Each component is calculated by the subtraction of local average (n+1) from local average (n). The first component, for example, is equivalent to the first local average subtract the second local average. In Figure 3.4, the second component for the specified point shown, would be calculated from the subtraction of the average height of the highlighted cells in Figure 3.4c from the equivalent cells in 3.4b.

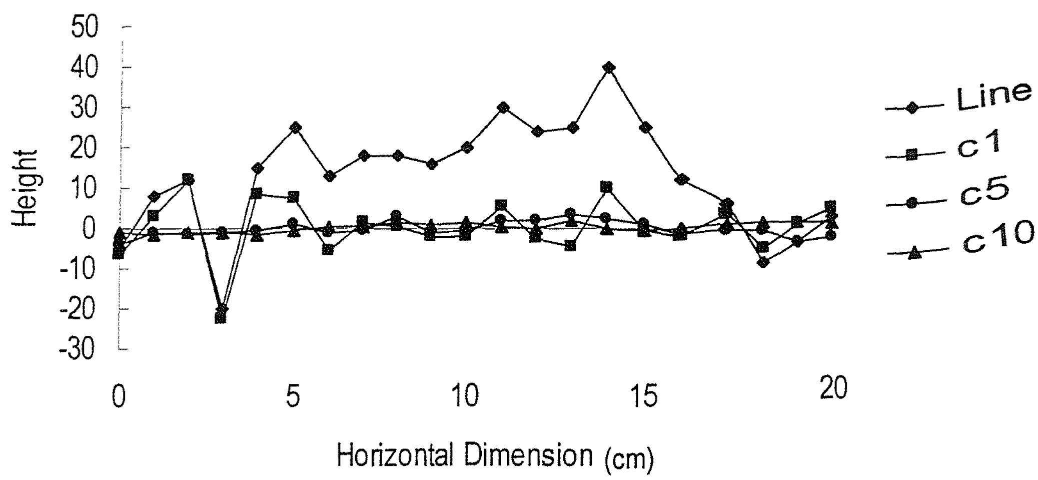


Figure (3.5): An example of a two dimensional topographic plot and the effect of decomposing the surface at a number of spatial scales. (c= component, where c1 represents small scale topographic features and c10 represents solely the largest scale features)

These components, as a consequence of their progressive subtraction, differ in their order of magnitude: with values at component ten being substantially lower than at component one. This large range in numbers has the effect of altering where a species will be predicted to occur regardless of true topographical differences. Each component was therefore weighted to alleviate the effect of the decreasing values throughout the ascending scales. All components were therefore divided by their respective standard deviations in order to give standardised components. Following standardisation the difference between the heights of each component were reduced (Figure 3.6).

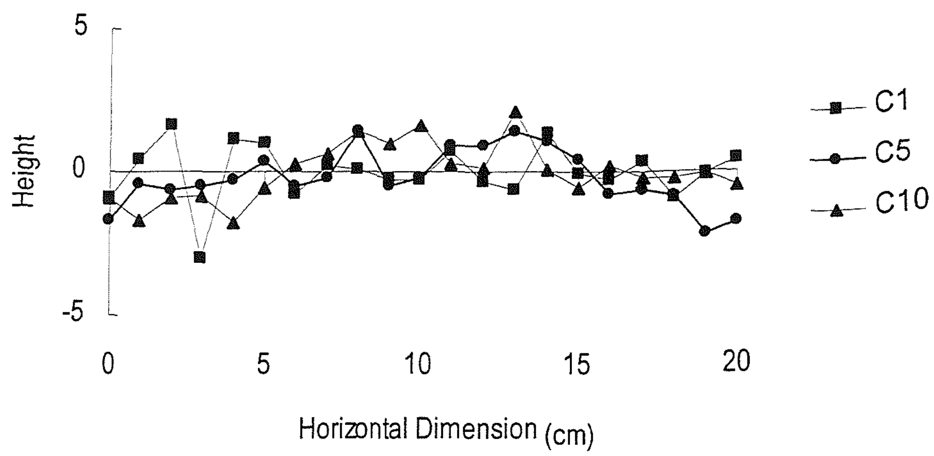


Figure (3.6): An example of a two dimensional topographic plot of the effect of standardising the components (c) into which a surface has been decomposed. (Where c1 represents small scale topographic features and c10 represents solely the largest scale features). (Original Line is the same as Figure 3.5).

As previously stated the sum of the components is equivalent to the original residual for each point. A cumulative plot of the increasing sum of the components therefore provides a level at which no larger scale of variation is being described. Once a plateau has been reached, such as at component ten in Figure 3.7, no further information is gained by examining components beyond this level. The components incorporated into any further analysis therefore ranged from one to ten.

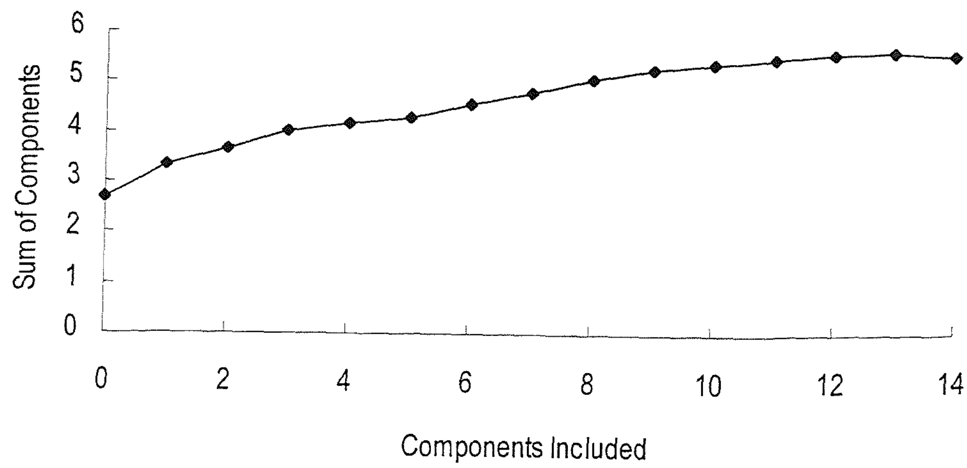


Figure (3.7): A progressive sum of each of the components taken from an example residual point.

Each of the derived components, however, were not necessarily independent of each other. A correlation matrix between the components of different spatial scales, based on Pearson's product moment correlation co-efficients, allowed the determination of the scale at which independence was reached. All possible pairs of components were compared and the correlation statistic (r) was based on the average of these values. The example provided in Figure 3.8 suggests that the components were not independent until they were a minimum distance of five components apart (r= 0.2). In terms of further analysis, only the residual and components one, five and ten were incorporated.

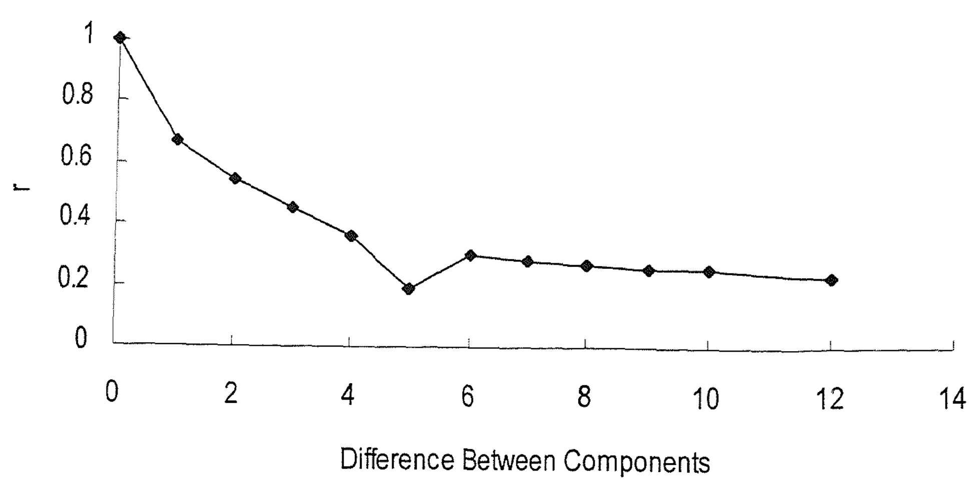


Figure (3.8): Correlation r between components of different spatial scales.

(3.2.4.) Statistical Analysis

Data in which the distribution of a dichotomous dependent variable (in this case presence or absence of a species) depends on an independent variable (in this case residual substratum height), is properly analysed using a logistic procedure (Hosmer & Lemeshow, 1989; Dobson, 1990). A logistic regression was therefore carried out for all the species present in each photograph to assess the relationship between species occurrence and the topography of each quadrat.

Logistic regression relates the proportions of a dependent variable to an independent variable *X* according to the following equation (1):

Equation (1):

$$\hat{p} = \frac{e^{a+bx}}{1+e^{a+bx}}$$

Where $\hat{p}$ is the probability parameter, x represent the values of the independent variable (residual substratum height) and a and b are the parameters to be estimated.

Equivalently equation one can be written as equation two, which is often referred to as the logit of p.

Equation (2):

$$\ln\left(\frac{\hat{p}}{1-\hat{p}}\right) = a + bx$$

Since the dependent variable is binomially rather than normally distributed, the maximum likelihood method is used to fit a regression line to the logit transformed data. The maximum likelihood method will result in the values for the parameters (a and b) that make the observed values in the data set seem most probable (Dobson, 1990). Associated with each parameter estimate is a standard error that may be used to construct confidence intervals or tests of significance of individual regression coefficients. The consistency of species occurrence in relation to surface height can therefore be established. An estimate of parameter b (called estimate from here on) with a value less than zero signifies the presence of that species on a lowered surface i.e. in a crevice, conversely a value above zero indicates a greater presence on raised regions. The intercept value (parameter a) provides a measure of the background or average abundance of organisms overall; the more negative the value the fewer organisms of a taxa encountered and vice versa.

The number of instances where the presence or absence of a species was predicted correctly in relation to topographic height was also calculated. The maximum likelihood approach produces a statistic called concordance, which is useful for testing the fit of the model, and to compare different models (Flury & Levri, 1999). In fact concordance is a measure of fit based on the comparison of the likelihood values of the model under consideration and a "saturated model" ; that is a model that fits the data perfectly by using as many parameters as observations (Dobson, 1990).

To assess the significance of the effect of the smallest scale, tidal height, transect and shore, an ANOVA was conducted for each individual species, on both the estimate and concordance values (Sokal & Rohlf, 1995). Where no significant differences were recorded the information was pooled across the appropriate levels of the design to increase the level of replication for each species. Where significant differences were apparent the consistency and predictability of the relationship between topography and species distribution was examined at the required spatial scales.

A *t*-test was performed on the subsequent means and standard errors of both the estimates and concordance values (Fowler & Cohen, 1994). If replicate numbers exceeded 30, however, hypotheses were tested against the normal distribution (z test). In terms of estimate the significance of each species was tested against a level of zero, and for concordance a value of 50% was used.

The overall ability of a species to locate within a defined topographical feature was also assessed; a model that could ultimately be used to predict where species would occur if uncolonised rock surface became available. It should be noted that the model assumes that all factors other than topography are equal and are therefore not limiting the distribution of each species. It solely represents where each species will be found based on the strength of the relationship between topographic height and distribution patterns. The maximum likelihood values for the parameters in equation two were averaged across all spatial scales of the analysis for each species. The relationship between topographic height and the distribution of each species was therefore represented by a single equation. The significance of the estimates and concordance values were again tested by a Z or t test. Where both of these values were significant the species were included in the analysis. A quadrat was then selected at random and the residual heights of each grid cell were entered into the equation for each species. The resulting values for each species were then regressed against each other and the slope of the best fit line was entered into a matrix. Where the slope between the two species was greater than one the taxa were potentially occupying the same habitat space, and the species on the y dimension of the matrix had a greater affinity for this feature. If, however, the slope was between zero and one the species along the x axis of the matrix had the greatest affinity for space. A value of one would mean that the species would match each other and conversely a value of minus one or less would indicate the species are associated with different topographical features.

(3.3.) RESULTS

With the use of stereophotography it was possible to reconstruct the three dimensional rock surface of a particular quadrat and correlate major topographical features with the occurrence of the overlying biota. The three dimensional maps derived from the use of stereo-photography were accurate to ±2cm in the x, y and z dimensions. An example of a stereo-pair of photographs from which a surface plot has been derived is displayed below (Plates 3.1 & 3.2). The three dimensional co-ordinates derived from the stereophotography analysis were interpolated to form the associated surface plot (Figure 3.9).

Plate (3.1): (Left): An example quadrat taken from Easdale: an area approximately 30cm by 30cm is depicted by the orange dots.
Plate (3.2) (Right): The second view represents the same quadrat area as the left hand image but all points are displaced to the left relative to plate 3.1.

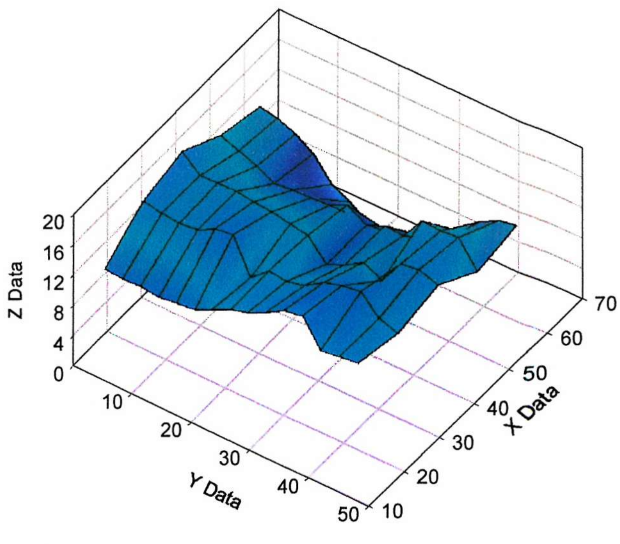


Figure (3.9): A surface plot of the marked quadrat area.

Once a surface topographic plot had been constructed it was possible to overlay a corresponding image of the overlying biota: correlations were then established between these two components as described in the methods (Plate 3.3).

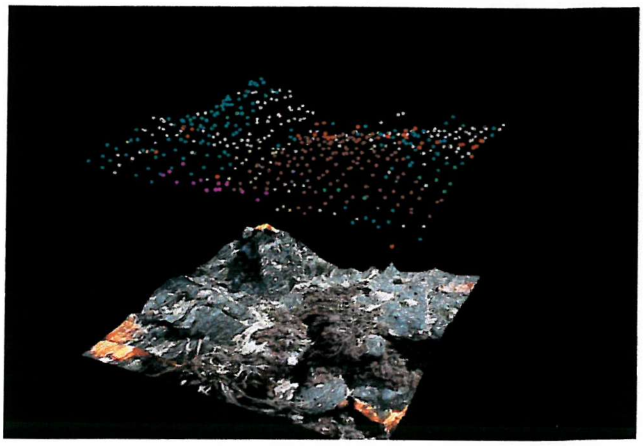


Plate (3.3): A three dimensional image of the marked quadrat. The raised colour points denote the occurrence of the identified species.

A total of thirteen different taxa (not all organisms recorded were identified to species) were observed in varying frequencies across the tidal heights, transects and shores (Table 3.1). The occurrence of bare rock was also recorded. For a number of species, particularly those encountered at higher frequencies the location of a species could be predicted in relation to the topographical features of an area.

Table (3.1): The number of quadrats in which a species was found at each tidal height on the two shores (Maximum Occurrence =10) . (C= Camas Rubha na Liathaig, E= Easdale).

Taxa	**C1 Low**	**C1 Mid**	**C1 High**	**C2 Low**	**C2 Mid**	**C2 High**	**E1 Low**	**E1 Mid**	**E1 High**	**E2 Low**	**E2 Mid**	**E2 High**
Corallina	10	0	0	10	0	0	10	3	0	10	3	0
Fucus	10	9	0	7	10	0	5	0	0	3	5	0
Laurencia	1	1	0	4	0	0	9	0	0	6	1	0
Porphyra	1	0	0	3	0	0	0	0	0	3	0	0
Enteromorpha	3	3	0	5	2	0	3	0	0	9	3	0
Pelvetia	0	0	7	0	0	6	0	0	8	0	0	5
Ulothrix	0	0	1	0	1	0	0	0	1	0	0	0
Xanthoria	0	0	8	0	0	10	0	0	3	0	0	4
Patella	9	6	2	10	7	0	10	10	0	10	10	2
Barnacle	2	10	3	4	10	0	10	10	3	9	10	3
Nucella	1	0	0	0	0	0	6	4	0	2	3	0
Actinia	0	1	0	1	1	0	0	1	0	0	0	0
Littorina	0	0	3	0	0	8	0	0	8	0	0	10
Rock	10	10	10	10	10	10	10	10	10	10	10	10

(3.3.1.) Relationship Between Topographic Height and Species Distributions

The consistency and predictability of the relationship between topography and the distribution of the overlying biota varied across the observed classifications. Where the frequencies of a particular organism were low it was necessary to pool the data across all spatial scales of the analysis. Similarly where no significant differences (assessed by SNK tests; Underwood, 1997) were apparent between the sampled levels (either site, tidal height, or component scale), all data were pooled to give an overall predictability of the species distributions (Tables 3.2 & 3.3). Where significant differences were apparent the consistency and predictability of the relationship was examined at the required spatial scales.

For a number of species the relationship between distribution patterns and topographic heights was significantly consistent. *Enteromorpha* spp., *Laurencia* sp. and *Actinia equina* were consistently found in areas below the average substratum height across all spatial scales of the analysis (Table 3.4; Figure 3.10). *A. equina*, however was found at very low abundance levels and all data was combined for this species. A single exception occurred to this pattern at the smallest scale of observation; the consistency of the relationship between species distribution and topographic height component was significantly smaller at this scale. The smallest component (1.4cm scale) was therefore excluded from the summary equations for these species. The relationship between topography and distribution was also considered predictable where these species could be predicted to occur in surface indentations in over 50% of cases (Table 3.5; Figure 3.10).

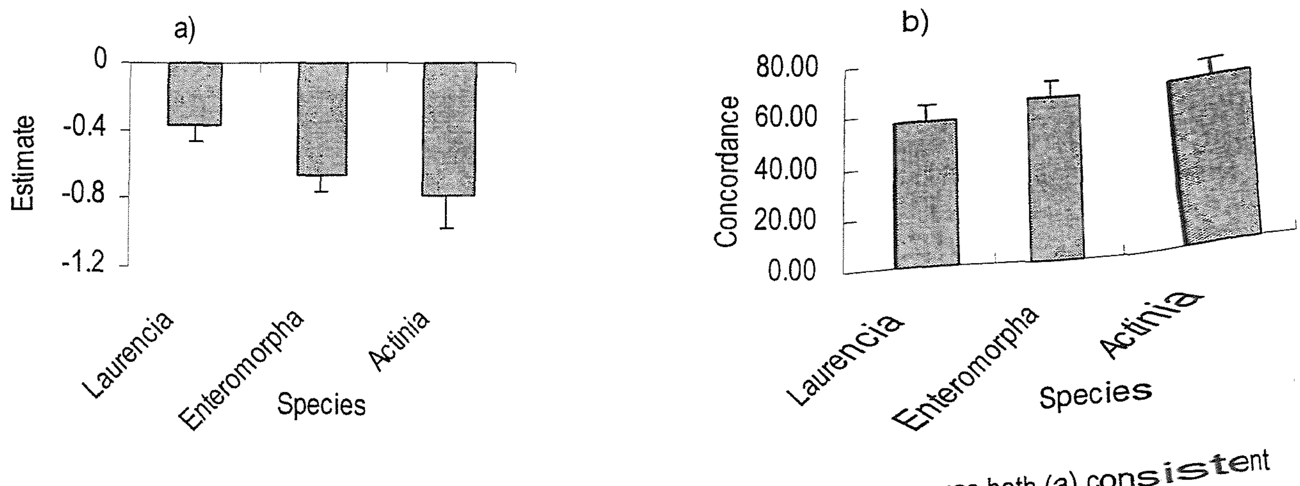


Figure (3.10): Species whose distribution in relation to topographic features was both (a) consistent and (b) predictable across all spatial scales of the analysis. (Error bars = S.E.).

Corallina officinalis also demonstrated a significantly predictable relationship with topography (Table 3.5). The consistency with which this species was associated with a topographic height, however, varied depending on the particular shore being examined. At Camas Rubha na Liathaig *C. officinalis* was consistently found in crevices (Table 3.4). The same relationship was also displayed at Easdale although the species was only significantly associated with surface indentations on one of the two transects. Again, the smallest scale of topographic variation was excluded from the summary equations for this species.

In contrast *Patella vulgata* was typically associated with crevices at both Camas Rubha na Liathaig and Easdale (Table 3.4). The predictive nature of this relationship however, varied between the shores. At Camas Rubha na Liathaig and on a single transect at Easdale limpets were correctly predicted to occur in crevices significantly greater than 50% of the time (Table 3.5). On the second transect at Easdale this predictive relationship was not significant.

The association of the different classifications with topographical features also varied between shores. *Fucus*, for example, was associated with raised areas at Camas Rubha na Liathaig and crevices on a single transect at Easdale (Table 3.4; Figure 3.11). The relationship was not significant on the second transect at Easdale. On both shores these associations were predictable in greater than 50% of their occurrences (Table 3.5).

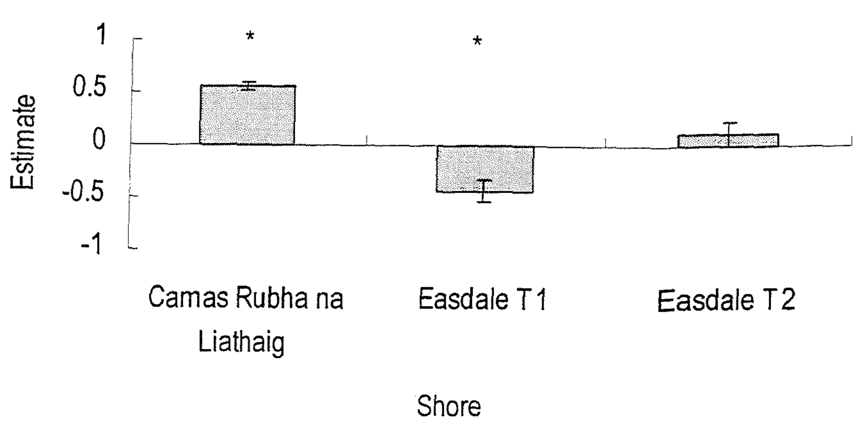


Figure (3.11): The relationship between topographic height and the distribution of *Fucus* at the two sites. (T= Transect; Error bars = S.E.) (* denotes significance p<0.05).

The converse pattern was observed for barnacles, where this taxa was consistently associated with crevices at Camas Rubha na Liathaig and raised areas at Easdale (Table 3.4; Figure 3.12). The relationship at Camas Rubha na Liathaig, however, was only predictable at mid tidal levels. In contrast at Easdale, barnacles would be predicted to occur in raised regions significantly greater than 50% of the time (Table 3.5).

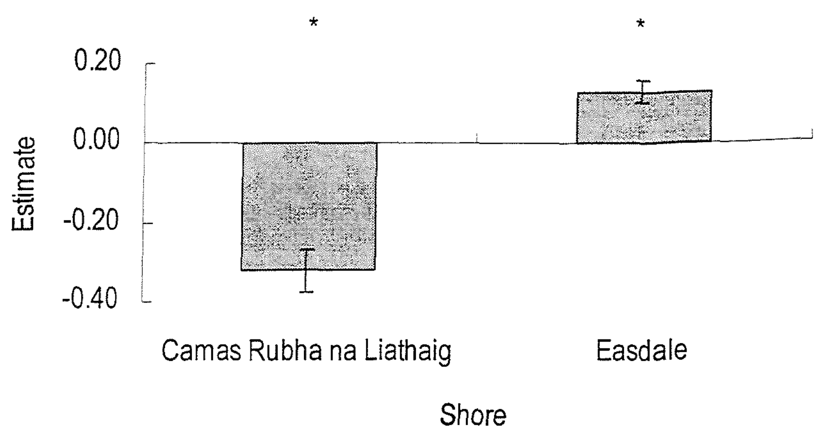


Figure (3.12): The relationship between topographic height and the distribution of barnacles at the two sites. (Error bars = S.E.) (* denotes significane p<0.05)

Pelvetia canaliculata and littorinids (*Littorina saxatilis*) only demonstrated a significant association with a topographical feature on a single transect at Easdale (Table 3.4). On this particular transect, the estimate for each species was significantly below zero, and therefore they were consistently associated with areas below the average substratum height. The relationship was, however, predictable at both sites with concordance values significantly exceeding 50% on both shores (Table 3.5).

In the case of *Xanthoria parietina*, whilst sharing the same level of consistency as *Pelvetia* and littorinids the relationship displayed was exactly the converse to these species (Table 3.4). On a single transect at Easdale this lichen was found to be significantly associated with raised areas. Again the observed patterns were found to be significantly predictable (Table 3.5).

No significant relationship between the distribution of organisms and topographic features was observed for three of the observed taxa. The green alga, *Ulothrix flacca*, for example, displayed no significant association with any surface height. The dog whelk, *Nucella lapillus*, was significantly associated with surface indentations, however, this relationship was in no way predictable. The same was also true for *Porphyra*, although this species was significantly associated with raised areas (Tables 3.4 & 3.5).

The relationship between bare rock and topographic height was complex and only general patterns could be depicted. At Camas Rubha na Liathaig crevices tended to be bare and the reverse was true at Easdale, where bare rock occurred in raised regions. This relationship was, however, predictable with the exception of the smallest spatial scales considered at component level one (Table 3.5).

Table (3.2): Summary of ANOVA statistics used to detect differences in the consistency of the relationship (estimate values) between species distributions and topographic height at the different spatial scales of the analysis. (**Significance: *= p<0.05; ** = p<0.01; *** = p<0.001**).
(Sh= Shore, Tr = Transect, He= Tidal Height, Sc= Component Level, ' = Random Factor).

a) Where species were found at all scales at each tidal height, transect and shore.

	Patella			Barnacle			Rock		
Source	**d.f.**	**MS**	**F**	**d.f.**	**MS**	**F**	**d.f.**	**MS**	**F**
Shore'	1	9.58	**19.14***	1	4.01	9.77	1	3.90	3.25
Transect' (Sh)	2	0.50	1.20	2	0.41	2.57	2	1.20	**7.79*****
Height	1	1.31	3.83	1	3.72	5.73	2	0.09	0.09
Scale	3	1.59	1.47	3	0.23	0.70	3	0.13	0.66
Sh x He	1	0.34	1.27	1	0.65	2.81	2	1.08	0.43
Sh x Sc	3	1.08	3.56	3	0.33	**6.00***	3	0.20	**5.99***
He x Tr (Sh)	2	0.27	0.64	2	0.23	1.44	4	2.52	**16.32*****
Sc x Tr (Sh)	6	0.30	0.73	6	0.05	0.34	6	0.03	0.22
He x Sc	3	0.10	0.33	3	0.18	2.91	6	0.03	0.29
Sh x He x Sc	3	0.31	2.64	3	0.06	0.48	6	0.13	0.87
Sc x He x Tr (Sh)	6	0.12	0.28	6	0.13	0.80	12	0.15	0.99
Residual	160	0.42		32	0.16		432	0.15	

b) Where species were found at all scales at one tidal height, on each transect and shore.

		Enteromorpha		*Laurencia*		*Corallina*		*Fucus*	
Source	**d.f.**	**MS**	**F**	**MS**	**F**	**MS**	**F**	**MS**	**F**
Shore'	1	0.25	1.22	0.39	0.59	0.22	0.31	4.88	1.85
Tr' (Sh)	2	0.20	0.59	0.66	1.39	0.73	**5.66****	2.63	**11.69*****
Sc	3	1.50	14.02	0.38	**10.82 ***	0.29	**13.87***	0.35	0.62
Sh x Sc	6	0.10	0.63	0.03	0.10	0.02	0.40	0.58	2.64
SC x Tr (Sh)	6	0.17	0.49	0.36	0.76	0.05	0.39	0.22	0.96
Residual (d.f.)	32	0.35		0.48 (16)		0.13 (144)		0.23 (32)	

b cont.) Where species were found at all scales at one tidal height, on each transect and shore.

		Pelvetia		Littorinids		*Xanthoria*	
Source	**d.f.**	**MS**	**F**	**MS**	**F**	**MS**	**F**
Shore'	1	6.42	2.73	2.00	1.44	0.84	0.37
Tr' (Sh)	2	2.35	**8.80*****	1.39	**6.92****	2.28	**3.55***
Sc	3	0.05	0.10	0.36	0.75	0.32	2.41
Sh x Sc	6	0.54	3.44	0.48	1.16	0.14	0.13
SC x Tr (Sh)	6	0.16	0.58	0.42	2.07	1.04	1.62
Residual (d.f.)	64	0.27		0.20 (32)		0.64 (32)	

c) Where species were found at all scales at one tidal height, on both transects at one shore.

	Porphyra		
Source	**d.f.**	**MS**	**F**
Transect'	1	0.91	**5.04***
Scale	3	0.02	0.54
Tr x Sc	3	0.04	0.24
Residual	16	0.18	

d) Where species were found at all scales at each tidal height, on both transects at one shore.

	Nucella		
Source	**d.f.**	**MS**	**F**
Transect'	1	0.85	3.14
Height	1	0.82	0.41
Scale	3	0.61	0.33
Tr x He	1	0.46	0.21
Tr x Sc	3	0.35	0.31
He x Sc	3	0.30	0.47
Tr x He x Sc	3	0.27	0.42
Residual	16	0.27	

Table (3.3): Summary of ANOVA statistics used to detect differences in the predictability of the relationship (concordance values) between species distributions and topographic height at the different spatial scales of the analysis. (**Significance: *= p<0.05; ** = p<0.01; *** = p<0.001**).
(Sh= Shore, Tr = Transect, He= Tidal Height, Sc= Component Level, ' = Random Factor).

a) Where species were found at all scales at each tidal height, transect and shore.

	Patella			Barnacle			Rock		
Source	**d.f.**	**MS**	**F**	**d.f.**	**MS**	**F**	**d.f.**	**MS**	**F**
Shore'	1	4351.97	4.50	1	466.56	2.49	1	48.45	0.22
Transect' (Sh)	2	967.90	**3.33***	2	187.63	0.81	2	220.31	1.93
Height	1	6.49	0.12	1	258.41	0.13	2	334.41	2.64
Scale	3	2297.03	2.08	3	252.82	2.15	3	23757.32	**12.72***
Sh x He	1	454.29	0.13	1	2004.80	**30.13***	2	126.46	0.65
Sh x Sc	3	1105.21	1.60	3	117.75	1.48	3	216.77	2.17
He x Tr (Sh)	2	405.14	1.39	2	66.53	0.29	4	194.26	1.70
Sc x Tr (Sh)	6	689.79	**2.37***	6	79.68	0.35	6	100.07	0.88
He x Sc	3	50.99	0.32	3	12.90	0.05	6	136.68	1.97
Sh x He x Sc	3	158.66	0.96	3	242.58	1.75	6	69.27	0.43
Sc x He x Tr (Sh)	6	165.48	0.57	6	138.68	0.60	12	161.04	1.41
Residual	160	290.49		32	230.80		432	114.07	

b) Where species were found at all scales at one tidal height, on each transect and shore.

	Enteromorpha			*Laurencia*		*Corallina*		*Fucus*	
Source	**d.f.**	**MS**	**F**	**MS**	**F**	**MS**	**F**	**MS**	**F**
Shore'	1	7.13	0.02	436.60	13.70	14.28	0.06	40.89	0.32
Tr' (Sh)	2	2254.07	0.71	31.87	0.15	251.59	2.91	128.24	0.75
Sc	3	169.89	**13.27***	1071.61	3.57	954.82	**69.83****	660.11	**17.74***
Sh x Sc	6	352.88	0.48	299.83	0.99	13.67	1.28	37.22	0.27
SC x Tr (Sh)	6	462.93	0.76	302.63	1.46	10.65	1.12	139.71	0.82
Residual (d.f.)	32	462.93		206.60 (16)		86.43 (144)		170.59 (32)	

b cont.) Where species were found at all scales at one tidal height, on each transect and shore.

		Pelvetia		*Littorinids*		*Xanthoria*	
Source	**d.f.**	**MS**	**F**	**MS**	**F**	**MS**	**F**
Shore'	1	1384.45	18.06	6.02	0.02	1952.03	**22.85***
Tr' (Sh)	2	76.65	0.36	307.44	1.36	85.43	0.71
Sc	3	483.90	**10.48***	302.61	2.09	736.66	6.08
Sh x Sc	6	46.15	0.49	144.94	0.68	121.16	1.23
SC x Tr (Sh)	6	94.25	0.45	213.22	0.95	98.90	0.82
Residual (d.f.)	64	211.58		225.61 (32)		120.34 (32)	

c) Where species were found at all scales at one tidal height, on both transects at one shore.

	Porphyra		
Source	**d.f.**	**MS**	**F**
Transect'	1	0.57	0.00
Scale	3	815.36	8.45
Tr x Sc	3	96.48	0.34
Residual	16	282.09	

d) Where species were found at all scales at each tidal height, on both transects at one shore.

	Nucella		
Source	**d.f.**	**MS**	**F**
Transect'	1	2289.95	**5.77***
Height	1	2465.78	1.40
Scale	3	578.45	4.07
Tr x He	1	1756.76	4.43
Tr x Sc	3	142.25	0.36
He x Sc	3	1096.77	4.91
Tr x He x Sc	3	223.56	0.56
Residual	16	396.57	

Table (3.4): Summary of Z /T- test statistics used to determine whether each taxa was significantly associated with a topographic height (estimate values). For convenience the relationship was summarised for each tidal height on each shore. (- = significant association with crevice, p<0.05; + = significant association with raised area, p<0.05; n.s. = not significant, distributed at random).

Species	**Camas 1**	**Camas 2**	**Easdale 1**	**Easdale 2**	**Factors excluded from analysis**
Enteromorpha	-	-	-	-	Component one
Laurencia	-	-	-	-	Component one
Actinia	-	-	-	-	
Corralina	-	-	-	n.s.	Component one
Patella	-	-	-	-	
Fucus	+	+	-	n.s.	
Barnacle	-	-	+	+	Camas - Residual
Pelvetia	n.s.	n.s.	-	n.s.	
Littorinid	n.s.	n.s.	n.s.	-	
Xanthoria	n.s.	n.s.	n.s.	+	
Ulothrix	n.s.	n.s.	n.s.	n.s.	
Nucella	-	-	-	-	
Porphyra	+	+	n.s.	n.s.	
Rock	n.s.	n.s.	n.s.	n.s.	

Table (3.5): Summary of Z /T- test statistics used to determine whether the relationship between topography and species distribution was significantly predictable (concordance values). For convenience the relationship was summarised for each tidal height on each shore. (+ = significantly predictable, p<0.05; n.s. = not significant).

Species	**Camas 1**	**Camas 2**	**Easdale 1**	**Easdale 2**	**Factors excluded from analysis**
Enteromorpha	+	+	+	+	Component one
Laurencia	+	+	+	+	
Actinia	+	+	+	+	
Corralina	+	+	+	+	Component one
Patella	+	+	+	n.s.	Camas -Component one
Fucus	+	+	+	+	Component one
Barnacle	+ (Mid tidal level only)	+ (Mid tidal level only)	+	+	
Pelvetia	+	+	+	+	Camas -Component one
Littorinid	+	+	+	+	
Xanthoria	+	+	+	+	
Ulothrix	n.s.	n.s.	n.s.	n.s.	
Nucella	n.s.	n.s.	+	N/A	
Porphyra	n.s.	n.s.	n.s.	n.s.	
Rock	+	+	+	+	(not c1)

(3.3.2.) Affinity for Space

The affinity of each taxa for a preferred topographic feature on a section of bare rock was assessed by a summary equation. The average equation relating topographic height with either presence or absence was calculated for each individual taxa. This gave an indication of the overall trend of species occurrence in relation to topographic height. Variation displayed at the levels of shore, transect, tidal height and smaller spatial scales was therefore masked. Of all the species examined only *Fucus* was found associated with raised areas. The estimates of all other species were negative highlighting the trend towards their occurrence in crevices (Table 3.6).

Table (3.6): The average equation for each taxa based on their occurrence as a whole across the different spatial scales of the analysis. Where Y (Logit p)=ax +b: a = estimate, x = residual height and b = overall incidence of the species.

Species	Equation	Topographic location
Laurencia	Y = -0.34x - 3.28	crevice
Barnacle	Y = -0.04 x – 1.88	crevice
Corallina	Y = -0.29x – 1.29	crevice
Actinia	Y= -1.18x – 6.09	crevice
Fucus	Y = 0.52x – 0.52	Raised area
Enteromorpha	Y = -0.61x – 4.01	crevice
Patella	Y = -0.39x – 4.12	crevice
Pelvetia	Y = -0.10x – 2.03	crevice
Littorinids	Y = -0.36x – 4.37	crevice

Residual heights were entered into the average equation for each taxa, and their relative affinity for a topographic height was compared (Table 3.7). *A. equina* was the species most likely to be found in a crevice (Table 3.7). In contrast with an equation based on all occurrences over the different tidal heights, transects and shores barnacles had the weakest affinity for any topographic residual height. As *Fucus* was the only species predicted to occur on raised areas it was not co-existing with any other taxa. The three algal species *Laurencia, Pelvetia* and *Corallina* all demonstrated a relatively weak affinity for association with set topographic heights. The two animal species *Patella* and littorinids, however, were quite likely to occur in crevices if the required space was available.

Table (3.7): A matrix of the slope of the line of best fit between the resulting values of the different taxa after the residuals of an example quadrat were entered into each equation.

X Dimension

Y Dimension	*Lauren.*	Barn.	*Cor.*	*Actinia*	*Fucus*	*Enter.*	*Patella*	*Pelvetia*	Litt.
Laurencia	-								
Barnacle	8.50	-							
Corallina	1.17	0.14	-						
Actinia	0.29	0.03	0.25	-					
Fucus	-0.67	-0.08	-0.57	-2.31	-				
Enteromorpha	0.55	0.07	0.47	1.92	-0.83	-			
Patella	0.88	0.10	0.75	3.05	-1.32	1.59	-		
Pelvetia	3.48	0.41	2.97	12.08	-5.22	6.30	3.97	-	
Littorinid	0.94	0.11	0.81	3.28	-1.42	1.71	1.08	0.27	-

(3.4.) DISCUSSION

At the start of this investigation it was predicted that physical topography would be correlated with the distribution of species observed in the rocky intertidal. Indeed, topography was found to play a key role in determining the distribution of the majority of species encountered via the use of the stereo-photographic sampling technique. The importance of topography, however, varied across a number of spatial scales depending on the species examined.

Where a species was consistently located with a particular topographic residual height it could now be predicted that this relationship would be found across all spatial scales, at least at these two sites. Species demonstrating such a relationship with crevices included *Enteromorpha* spp., *Laurencia* spp. and *A. equina*. Specific requirements of these species provide reasons for this occurrence. *A. equina* for example is commonly found in pools, under canopies and in crevices (Hawkins & Hartnoll, 1983a; Hawkins & Jones, 1992). This is consistent with other species of anemone such as *Actinia tenebrosa* and *Anthopleura elgantissima* whose distribution are apparently influenced by desiccation (Dayton, 1971; Ottaway, 1973).

The consistency of the relationship between *Enteromorpha* spp., *Laurencia* spp. and *A. equina* and topographic features was, however, considerably less at the smallest scale (1.4cm) than with all larger components (7cm and 14cm). It is possible therefore that the small scale features of topography were not providing the same resources as larger cracks and grooves. It is also possible that noise added to the topography by measurement error in the use of stereophotography distorted the effect of these small scale characteristics. Component one, however, was not always significantly different from the other components which suggests that this latter explanation is unlikely.

The three algal species *Enteromorpha*, *Laurencia* and *Corralina* were consistently associated with crevices. *Pelvetia* was also significantly associated with crevices but this was only demonstrated on a single transect at Easdale. In general, crevices may accumulate more algal propagules than flatter surfaces (Norton & Fretter,

1981) and allow more species to recruit by providing the propagules with a refuge against desiccation and / or grazing by molluscs (Burrows & Lodge, 1950; Lewis & Bowman, 1975; Choat, 1977; Lubchenco, 1980; Hawkins, 1981; Jernakoff, 1983; Sutherland & Ortega, 1986). *C. officinalis*, for example, is typically correlated with damp areas and is therefore likely to inhabit surface indentations, such as crevices, wherever possible (Hawkins & Jones, 1992). The ephemeral algae *Enteromorpha* is also commonly observed in crevices due to its high susceptibility to grazing pressure (Lubchenco, 1978; Jenkins *et al.*, 1999a; Lotze *et al.*, 2000).

Temporal and spatial variability in propagule supply caused by variations in reproductive output, dispersal, settlement and survival are important structuring factors in marine plant assemblages (Reed *et al.*, 1988; Reed, 1990; Santelices, 1990; Vadas *et al.*, 1992; Worm & Chapman, 1998). Grazers, in particular, may affect the distribution and abundance of algae by their grazing preferences or rates (e.g. Jones, 1948; Southward, 1964; Lubchenco & Gaines, 1981; Hawkins & Hartnoll, 1983b; Jenkins *et al.*, 1999a, b). Grazers preferentially move and forage across smooth rather than complex surfaces thereby creating refuges from such pressures (Burrows & Lodge, 1950; Hawkins & Hartnoll, 1982; Lubchenco, 1986; Little *et* al., 1988; Erlandsson *et al.*, 1999). In contrast, herbivores may also seek refuge in crevices from adverse physical and biological parameters making these areas of particularly intense grazing (Raffaelli & Hughes, 1978; Atkinson & Newbury, 1984; Kostylev *et al.*, 1997). Indeed in this study limpets were located in crevices at both Easdale and Camas Rubha na Liathaig. The size and scale of topographic features is therefore important in influencing the distribution patterns of intertidal species.

In contrast to all the other algal species observed the encrusting lichen *Xanthoria parietina* was only predicted to occur on raised areas. This species typically occurs between the terrestrial margins of the shore down to the upper limits of the littoral fringe. Its location on raised surfaces may be due to a high degree of tolerance to desiccation; as it capable of withstanding, and may indeed prefer extended periods without tidal inundation (Hawkins & Jones, 1992). Grazers at this tidal height are also less abundant than at the other tidal levels: refuge from grazing pressure is therefore less vital to plant survival and development (Raffaelli & Hawkins, 1996).

In addition this encrusting lichen is also likely to be more resistant to grazing than other algal forms (Underwood, 1980; Dethier, 1994).

The association between the occurrence of *Fucus* with either convex or concave surface features differed between the two shores; with lower regions at Easdale and raised surfaces at Camas Rubha na Liathaig. There are several reasons that may explain such differences. Firstly, it is important to note that the overall abundance of *Fucus* was greater at Camas Rubha na Liathaig than at Easdale, probably due to differences in the wave exposure at each site (pers. obs., 1998). The difference in algal cover may also be influenced by the recruitment pattern of some algal species. The dispersal distances of macroalgae are typically very low and occur in close proximity to adult plants (Sundane, 1962; Anderson & North, 1966; Koehl *et al.*, 1987; Norton, 1992; Johnson & Brawley, 1998). The number of settling propagules are therefore likely to be much more numerous at Camas Rubha na Liathaig than at Easdale. As a consequence food resources for grazing herbivores are likely to be much less readily available at Easdale and escapes from such pressures may therefore be restricted to small scale crevices at this site. In contrast the larger number of propagules at Camas Rubha na Liathaig would increase the chance of algal escapes and the role of crevices for plant survival would be less vital.

The presence of large *Fucus* plants at Camas Rubha na Liathaig may also have allowed settlement of new plants on open surfaces by providing the required shelter that is typically provided by crevices in more exposed locations (Norton, 1983; Farrell, 1991; Brawley & Johnson, 1991). Previous work has shown that the zygotes and embryos of fucoid species are extremely vulnerable to post settlement stresses associated with the period of low water and they therefore require protection from some structural feature at this time (Brawley & Johnson, 1991; Davison *et al.*, 1993; Johnson & Brawley, 1998). Crevices also provide algal species with protection from wave dislodgement (Vadas *et al.*, 1990, 1992). It should be remembered, however, in the case of *Fucus* all fronds of the species were digitised, not just the holdfasts; observed distributions may therefore not reflect the initial settlement pattern.

The converse pattern was observed for both barnacles and rock, where both were associated with the open rock surface at Easdale and with crevices at Camas Rubha na Liathaig. There are a number of factors that potentially affect the recruitment of sessile epibenthic invertebrates that need to be considered to explain such patterns including: free space for settlement (e.g Bergeron & Bourget, 1986; Minchinton & Scheibling, 1993), induction chemical cues from conspecifics (e.g. Chabot & Bourget, 1988; Raimondi, 1988), larval supply (e.g. Gaines & Bertness, 1992, 1993; Noda *et al.,* 1998) and topography (Bergeron & Bourget 1986; Chabot & Bourget, 1988; Chiba & Noda, 2000).

Barnacle larvae, in particular, show strong preferences in their choice of settlement surfaces. Physical cues like surface contour (Barnes, 1956; Crisp, 1961) are used to choose pits and grooves in a surface. This would therefore be consistent with the settlement of barnacles in crevices at Camas Rubha na Liathaig. Although in contrast Berntsson *et al*., (2000) found that *Balanus improvisus* preferred smooth surfaces which was consistent with the distribution pattern observed at Easdale. It should be noted, however, that barnacles use settlement cues smaller than that of the minimum resolution of the stereophotography technique (e.g. Crisp, 1974; Wethey, 1986; Chabot & Bourget, 1988). Indeed, factors in operation at such small scales could potentially affect any of the species that were observed in this study.

Barnacle settlement in crevices at Camas Rubha na Liathaig may also reflect the availability of free space at this site (Dayton, 1971); which on the open rock surface was largely occupied by *Fucus*. Dayton (1971) has demonstrated that in the rocky intertidal substrate space is potentially the most important limiting resource, with its use controlled by a combination of physical and biological disturbances. In addition *Fucus* fronds inhibit barnacle recruitment via mechanical abrasion of the substrate which can cause cyprid dislodgement (Lewis, 1964; Menge, 1976; Grant, 1977; Hawkins, 1983; Leonard, 1999; Jenkins *et al*., 1999c). The reverse would therefore be true at Easdale where *Fucus* largely occupied crevices, and barnacles were more apparent on the open, raised surfaces. In marine systems large canopy forming vegetation influences both environmental conditions (e.g. light, temperature, water motion; Fonseca *et al*., 1982; Lobban & Harrison, 1994) and can also physically interfere with recruiting and established organisms (Grant, 1977; Duggins *et al.*, 1990; Grizzle *et al.*, 1996; Jenkins *et al.*, 1999a, c) and indirectly alter predator densities and per capita predation rates (Menge, 1978a).

Differences in wave exposure and geological conditions between the two sites will also affect the distribution patterns of the observed species. Different geological rock types, for example, result in different characteristic shore topographies (Fuller *et al.*, 1991). Indeed, the rock type at the two sites is different; with fractured slate at Easdale with generally larger and fewer crevices than the metamorphic rock at Camas Rubha na Liathaig. The dimensions of crevices within a shore can also range depending on the tidal height at which they occur. A common feature of wave exposed shores is that the mean crevice width decreases downshore as a result of the scouring action of waves which smooths out crevices soon after they are formed at low levels (Raffaelli & Hughes, 1978). Such parameters will affect the settlement of larvae from the water column onto a chosen substratum (LeTourneux & Bourget, 1988; Eckman, 1990; Gregoire *et al.*, 1996).

In contrast tidal height seemed not to affect the consistency of occurrence of any of the biota observed. Conditions on the rocky shore become less favourable to intertidal organisms along the gradient of low to high tide (Raffaelli & Hawkins, 1996). It would therefore be expected that the importance of refuges provided by crevices would increase along the same dimension. The results obtained here, however, could be explained by the relatively low tidal range at these two sites. Alternatively crevices at the two sites may have demonstrated equal resource value across the tidal heights. It should also be noted that not all species were observed at all tidal levels of the analysis.

Variability is natural and important in understanding population dynamics and in developing general ecological understanding (Horne & Schneider, 1995; Underwood *et al.*, 2000). The availability and quality of habitat may vary from place to place at scale from centimetres to hundreds of kilometres (Bell *et al.*, 1993; Archambault & Bourget, 1996; Thompson *et al.*, 1996). This can affect the distribution of organisms directly by only providing appropriate habitat in some places (e.g. Chapman, 1994), or indirectly by modifying biological interactions among different species (Menge *et al.*, 1985; Fairweather, 1988; Underwood & Chapman, 1996; Chapman, 1998).

Where no significant relationship was found between topography and the distribution of a species a number of alternative explanations exist. Typically, a lack of significance was associated with species that were observed in low frequencies, *Ulothrix flacca*, *Porphyra* spp. and *N. lapillus*; a correlation between these two factors would therefore be difficult to establish. The distribution of mobile invertebrates, such as *N. lapillus* is also likely to vary with conditions such as the weather and the degree of wave exposure (Menge *et al.*, 1985; Burrows & Hughes, 1989; Gosselin & Bourget, 1989; Jones & Boulding, 1999). Littorinids are also well documented for occupying crevices in order to gain some degree of protection from dislodgement by wave action, moving stones, predation, or desiccation (e.g. Dayton, 1971; Raffaelli & Hughes, 1978; Underwood, 1980; Moran, 1985). It is also possible that these species are opportunistic and do not have the competitive ability to maintain a characteristic habitat throughout the intertidal zone.

Where an average equation was used to assess the affinity of each taxa for topographic heights this served to mask variation displayed at the smaller spatial scales of the analysis. In general, however, where the overall predictive relationship between distribution and topographic height was examined species were associated with the same surface feature as when they were examined individually. In contrast, the relatively low affinity for space of barnacles reflected the fact that this taxa was associated with converse topographic features at the two sites. The predominance of *Fucus* on raised areas at Camas Rubha na Liathaig resulted in this species being associated with raised features overall. Where there was no co-occurrence between taxa at set topographic heights then these species would not be directly interacting. Previous interactions, including predation and competition, between these species may therefore have lead to the observed distribution patterns.

Typically the affinity of a particular species for a set topographic height is influenced by a number of variables that can vary not only in time but space. Parameters such as exposure, rock type and the availability of crevices may differ sufficiently at different sites to alter the competitive edge of a particular species (Sebens, 1991). This therefore highlights the importance of examining the correct scale when examining the distribution of species. Data requires careful analysis prior to pooling of results or before generalisations can be made.

(3.4.1.) Conclusions, Limitations and Future Work

Stereo-photography provides a very useful tool for assessing habitat complexity and there is no reason why it could not be applied to different habitats. The key advantage of the technique is that three dimensional aspects of the surface can be readily evaluated and correlated with biological characteristics. The topography of the substratum was an important indicator of the location of certain intertidal species. The importance of topography, however, varied across a number of spatial scales depending on the species examined. Tidal height, however, seemed not to affect the consistency of occurrence of any biota and rarely affected the predictability of this relationship. It is important to remember that both physical and biological parameters, in addition to the substratum, are important in determining the distribution of intertidal species.

The advantages and disadvantages, including the potential inaccuracies of using stereophotography, have already been discussed in Chapter 2 but some additional points are raised here. While the non-destructive nature of the sampling technique has the benefit of *in situ* measurements, in some instances it can distort a true measure of a topographic dimension. By digitising the top of a limpet shell, for example, this could potentially add a further two centimetres to the height of a particular point. The fronds of large plants may also have masked some of the true topographical features within an area. Such inaccuracies were avoided where possible by the digitising of actual rock surfaces but this was not always feasible. This probably also relates to the prediction of the distribution of algae, where during the image analysis it was not possible to locate individual holdfasts of the larger plant species. The observed distribution of such species may, therefore, not represent the initial settlement patterns. These limitations were only present in the minority of quadrats.

Now that a method for such a sampling technique has been fully developed it would be possible to extend the survey both temporally and spatially. This would then incorporate a greater range of species and habitats. The results could also be supported by a thorough field investigation examining the true location of holdfasts and other such features. A survey of this nature could also investigate the densities of grazers and predators to gain a greater understanding of biological interactions that could potentially be shaping distribution patterns. In addition manipulations of the substratum would allow the exact settlement and distribution patterns of intertidal species to be established in relation to topographic features.

4. The Effects of Surface Topography on Foraging in Intertidal Predators

(4.1.) INTRODUCTION

Rocky shores have a wide range of microhabitats that affect species distributions. The substratum that shore organisms live and move on can vary considerably in complexity from place to place. It may vary with regard to a whole range of both abiotic and biotic parameters. These factors play an important role in altering community patterns and processes (Kareiva, 1990) with subsequent consequences on overall diversity (Kostylev, 1996). Most importantly in this study, physical features of the substrate such as the topography, or the roughness of the rock surface also influence movement patterns of predators and the intensity of predation.

(4.1.1.) Predation

The role of predation has been strongly emphasised in marine rocky intertidal communities (e.g. Connell, 1961; Paine, 1966). Indeed the marine intertidal system appears to stand out as showing stronger effects of predation than any other system (Sih *et al.*, 1985); causing a large amount of variability in the distribution, abundance, size structure, composition and/or diversity of species (Paine, 1966, 1974; Dayton, 1971; Castilla & Paine, 1987; Menge *et al.*, 1994; Navarrete, 1996). Predation can also indirectly, mediate interactions such as competition amongst prey (Fairweather, 1988).

The impact of predation, however, is variable in both space and time (Fairweather & Underwood, 1991; Lively *et al.*, 1993; Menge *et al.*, 1994), where in some cases it has a strong influence on community structure, whilst in others it does not. This intensity is a function of both physical and biotic characteristics of the environment. It should also be noted that all predators are different, both within and between species, and this will in turn affect predator-prey models.

Work on intertidal invertebrates has provided some early graphic examples of the influence of predation on the distribution of species (Fischer-Piette, 1935; Connell, 1961; Kitching & Ebling, 1967; Paine, 1969, 1971). Predators, for example, are capable of determining lower limits of zonation and reducing the overall abundance levels of their prey. In the high intertidal of the North American Pacific coast, for example, predation by the whelk *Nucella lamellosa* was discovered to be largely responsible for preventing *Semibalanus glandula* from occupying lower shore levels (Connell, 1970). Paine (1971) cleared the large starfish *Pisaster ochraceus* from below the zone of the mussel *Mytilus californianus* and achieved a downward extension of *Mytilus* in excess of 1m. These are examples of keystone predators whose removal causes marked shifts in relative species abundance at lower trophic levels (Paine, 1966, 1969, 1974, 1980; Fairweather *et al.*, 1984). More recently, however, the usefulness and generality of this concept has been questioned (e.g. Foster & Schiel, 1988; Elner & Vadas, 1990; Strong, 1992; Mills *et al.*, 1993; Menge *et al.*, 1994).

The combined effect of several predator species, which is termed "diffuse" predation, is also capable of altering community structure (e.g. Menge & Lubchenco, 1981; Menge *et al.*, 1986). Whether interactive or not, diffuse predation differs from keystone predation because the removal of any one predator produces comparatively small changes in the abundance of the dominant prey and associated species (e.g. Menge & Lubchenco, 1981).

(4.1.2.) Spatial Complexity

Predators and grazers must move around in order to exploit their prey. These movement pathways are strongly influenced by habitat structure and may reflect differences in how organisms perceive habitat heterogeneity on a given range of scales (Kostylev, 1996). Different features of the substratum have been shown to affect populations and the patterns of movement of several intertidal animals. The movements of intertidal gastropods, for example, have been shown to be affected by non biological features of the substratum, such as rockpools (Underwood, 1977), crevices or depressions (Levings & Garrity, 1983; Underwood & Chapman, 1985), slope (Petraitis, 1982, 1983) and the type of shore (i.e. boulder fields or basalt shores: McCormack, 1982). Movement of transient predators such as *Lipophrys pholis* and *Carcinus maenas* have also been observed to be affected by topography (Burrows *et al.*, 1999).

The degree of sinuosity in an animal movement may maximise the likelihood of an encounter with a food patch, with directional paths preferred if food is distributed regularly (Dusenbury, 1989) or more complex paths if the food is clumped (Duvall *et al.*, 1994). Movements may cause animals to be limited to certain areas or to be directed to particular areas. The impact on prey by mobile predators is therefore likely to vary depending on habitat structure.

Gotceitas & Colgan (1989) highlight that numerous studies have demonstrated a negative relationship between increasing habitat complexity and predator foraging success. Structural heterogeneity can provide spatial refuges thereby reducing predator efficiency and should therefore generally reduce the overall effect of predators on prey (Russ, 1980). Even in the absence of actual spatial refuges structural heterogeneity can influence the predator prey interaction by creating transient refuges. Menge & Lubchenco (1981) demonstrated that 88% of the macroinvertebrate and plant species in a tropical intertidal environment depend on habitat irregularities for their persistence in the community. Field experiments indicated that the mechanism restricting these species to holes and crevices was primarily feeding by fishes, crabs, and slower moving invertebrate herbivores and predators.

The scale of substratum heterogeneity is again important; if crevices are small the movement of predators may be restricted and in larger crevices the refuge provided may not be as effective. It has also been proposed that homogenous surfaces experience uniformly intense consumer pressure but that grazing in holes varies more in space and time (Menge *et al.*, 1983). Spatial variation between temperate and tropical systems can also exist; refuges such as pits and crevices are thought to be far more important as refuges from predators in tropical than temperate areas (Menge & Lubchenco, 1981).

Predators also make use of habitat heterogeneity: mobile predators are repeatedly reported to retreat to crevices, as a refuge in which to shelter from waves, high temperatures, desiccation, or freezing (e.g. Burrows & Hughes, 1989; McCook & Chapman, 1991). Consequently, haloes of bare space, where prey have been removed, may appear around refuges used by predatory gastropods (Fairweather, 1988; Hughes & Burrows, 1993). In fact Johnson *et al*., (1998) demonstrated the presence of spatial gradients in prey sizes, in this case barnacles, around crevices. Such results suggest that topographic complexity can affect predator prey dynamics in a number of different ways.

(4.1.3.) Role of Mobile Predators

The complete predator fauna of temperate shores is a diverse assemblage of species displaying varied foraging adaptations (Robles, 1987). The species involved include not only invertebrates such as whelks, starfishes and crustaceans but also numerous species of teleost and elasmobranch fishes. Birds and mammals also remove large numbers of prey items from the shore (Goss-Custard *et al*., 1982; Bahomondes & Castilla, 1986; Wooton, 1992; Ens & Alting, 1996; Burrows *et al*., 1999). In the current investigation barnacles, *Semibalanus balanoides*, were the main source of sessile prey identified in the mid intertidal of Camas Rubha na Liathaig.

It was previously thought that dog whelks are the main predator affecting barnacle populations (Menge, 1976, 1978b). Newman (1960), however, demonstrated higher balanoid stocks in parts of the Indo-Pacific reefs in situations where fish predation was minimised. Paine (1981) also acknowledged the importance of predation by fish in shaping barnacle communities. Edwards *et al*., (1982) however, were the first to highlight that *Nucella lapillus* may not be the only significant predator of mid-intertidal rocky shores in New England. Robles (1987) made observations on temperate shore at high tides using scuba and revealed that resident populations of whelks were joined by an assemblage of transient predators, including fishes and spiny lobsters. Fish are now recognised as being capable of affecting community structure in numerous locations (e.g. Cancino & Castilla, 1988). Firstly fish are capable of removing primary space occupiers such as barnacles and secondly they may consume mobile benthic species such as limpets, dog whelks, limpets and littorinids, which in turn are important grazers and predators shaping community patterns.

The three mobile predators interacting with the rock surface in Camas Rubha na Liathaig during June 1998 were the blenny *Lipophrys pholis*, crab *Carcinus maenas* and corkwing wrasse *Crenilabrus melops*. All three of these species are typically restricted to specific zones on the shore, *L. pholis*, for example, occurs in tide pools and rocky walls, and this is related to its differential feeding habits (Hartley, 1949). *C. maenas* inhabits a wide variety of estuarine and open shores around the British Isles, from near high water mark down to at least 10m below low water mark of spring tides (Yonge, 1949; Green, 1968). Corkwing wrasse are also usually associated with rocky shores, commonly in areas of high algal cover (Sayer & Treasurer, 1996).

More importantly barnacles, either adults or cirri, form part of the diet of all three species. The diet of *L. pholis* varies with age (Dunne, 1977; Milton, 1983); the smallest fishes concentrate on cypris larvae and cirri of upper shore barnacles, and as they get larger they also take adult barnacles. The diet of *C. maenas* does include barnacles although molluscs form its major food source (Elner, 1981). While gastropod molluscs are the main food source for the wrasse *C. melops*, barnacle cirri have also been found within the guts of this species (Deady & Fives, 1995; Sayer *et al.*, 1996).

(4.1.4.) Aims and Objectives

As suggested by Moran (1985) a knowledge of the patterns of foraging activity and rates of feeding of the major predators is crucial to any understanding of the functioning of rocky intertidal communities. This study was designed to test the hypothesis that surface topography has a strong influence on foraging behaviour. It was predicted that the movement patterns of mobile intertidal predators would be affected by varying topographic features such as crevices and convexities. The investigation was further designed to predict the consequences for prey patchiness via spatial variation in predator impacts. It was proposed that the patchy distribution of prey on the rocky shore would be as a result of topographically determined movement pathways of predators. In addition it was hoped to assess whether the ecological role of larger transient predators has been largely underestimated in terms of shaping barnacles populations.

In order to address these hypotheses a section of rock in the intertidal zone of Camas Rubha na Liathaig (Northwest Scotland) was filmed continuously for a two week time period at times of both high and low water. Trajectories of *Lipohprys pholis*, *Carcinus maenas* and *Crenilabrus melops* were analysed in relation to topographical features contained within the section of rock (60cm x 80cm). The implications of these patterns in terms of prey species distributions were examined. Generalisations could also be made in terms of movement patterns in relation to both diel and tidal cycles. Detailed analyses, such as those permitted by 24 hour video recordings are therefore very useful in determining our knowledge of predator-prey relations in shaping community structure.

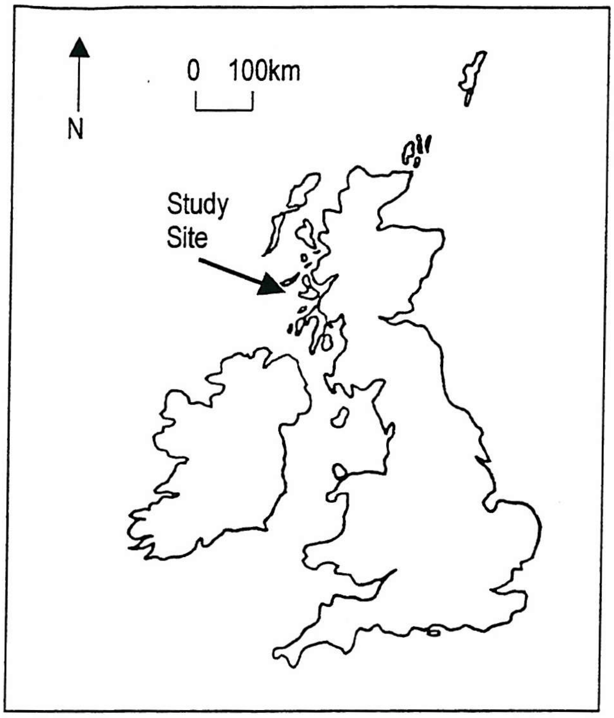
(4.2.) METHOD

(4.2.1.) Study Sites

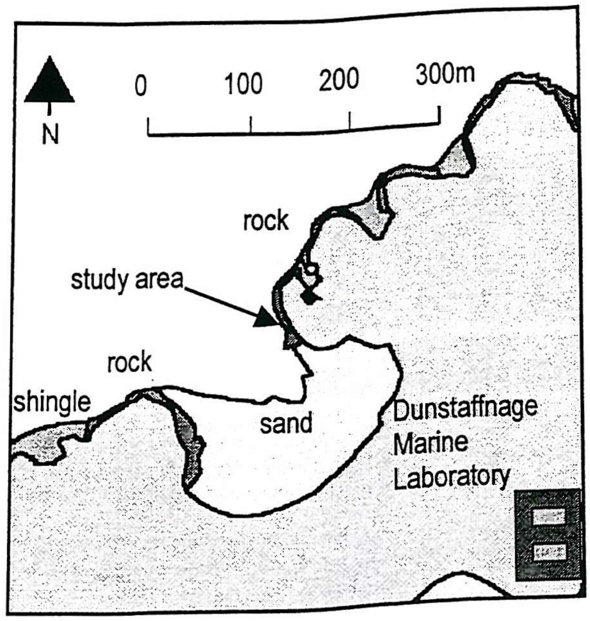
The rock surface selected for surveillance was less than 0.5 km from the Dunstaffnage Marine Laboratory on the West Coast of Scotland (Figure 4.1). The site is relatively sheltered from wave action and is characterised by a rocky cliff surrounding a sheltered bay (Camas Rubha na Liathaig (5°27'5''W, 56°26'50''N)). The biological features of the rocky shore are consistent with those associated with moderately sheltered shores (Lewis, 1964; Hawkins & Jones, 1992; Raffaelii & Hawkins, 1996), being largely *Fucus* dominated except for the barnacle, *Semibalanus balanoides*, which dominated steeply sloping rocks at mid to high tidal levels.

A section of rock with the video frame encompassing an area of approximately 0.6 by 0.8m (Plate 4.1) was selected from within a small cove. The frame was positioned in order to orientate the camera towards the vertical rock surface, at a tidal height of between low water springs (0.7m) and the mid tidal level for the region (2.4m above chart datum). The height of the camera was sufficiently above the level of *Fucus* to prevent any obscuring of the view by algal fronds at times of high water. The underlying substratum within the cove consisted of a number of cobbles of varying dimensions. The surrounding region provided areas that were likely to serve both as refuges and movement pathways for intertidal predators.

Plate (4.1): Rock surface encompassed by the camera.



a)



b)

Figure (4.1a): A map of the UK to place the site in a wide geographical context.
Figure (4.1b): The location of the study site near to Dunstaffnage Marine Laboratory. (Adapted from Burrows *et al.*, 1999).

(4.2.2.) Underwater Camera Set Up

An underwater camera (OE1390, Simrad Osprey Ltd.) was assembled on a trapezoidal frame measuring 1.15m along the base and 1.05 from base to apex (Plate 4.2). Sand bags, filled with cobbles, were used as a ballast to ensure a fixed horizontal view of the rock surface from the camera. Filming was continuous for a two week period during June 1998, with the exception of low tide periods in darkness. Whilst submerged during periods of darkness the rock surface was illuminated by two 300-W underwater lights (Osprey OE1132) fitted with infra red filters.

Video recordings were made with a time lapse of 5.56 frames/s (Panasonic AG6024). A time code signal was subsequently added to each recording (IMP Electronics time code generator V9000A) to enable further analysis to be quantifiable both spatially and temporally.

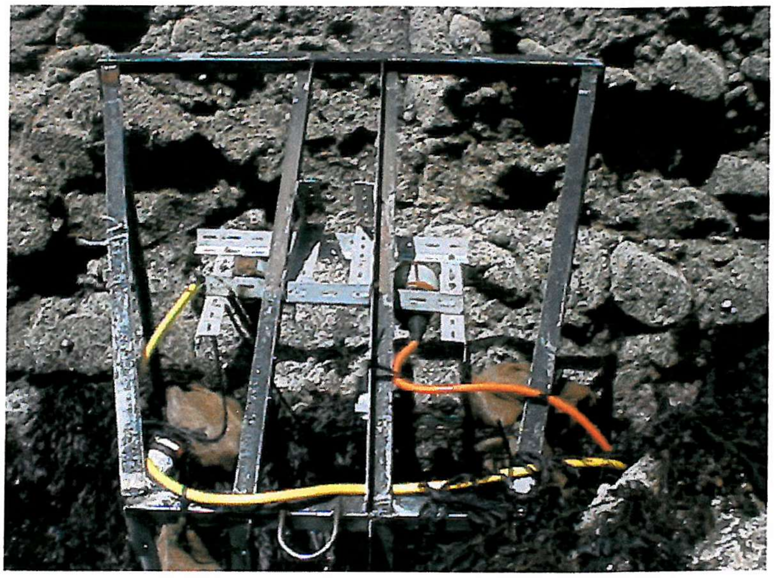


Plate (4.2): Underwater camera set up. The camera pointed horizontally forward toward the vertical rock surface.

(4.2.3.) Measurement of Movement Patterns

The tracking of species which interacted with the rock surface was carried out by digitising the movement pathways of each relevant organism that entered the field of view. The location of the animal was recorded at the beginning of each individual move and this continued until the animal departed from view. The sum total of the moves, from the time of entry to the time of departure from the area of rock, was called a sequence. Coordinates were recorded using a pointer on the screen overlying the TV image. The time at each location was also recorded via the same programme using a time code reader linked to the computer (VMR V9, IMP Electronics Ltd.).

Species observed included: corkwing wrasse (*Crenilabrus melops*), blenny (*Lipophrys pholis*), dogwhelk (*Nucella lapillus)*, limpet (*Patella vulgata*), crab (*Carcinus maenas*), two-spot goby *Gobiusculus flavescens* and butterfish (*Pholis* spp.). Out of all of these species, movement patterns were only recorded for the wrasse, blennies and crabs as these were the only large mobile intertidal predators observed to directly interact with the rock surface.

The frequencies of sequences and summary measures of behaviour were calculated for the three species. Median durations, distances and speeds of both individual sequences and moves were calculated. The convolution of each sequence pathway was obtained from the ratio of the total distance moved to the straight line distance, from the point of entry to the point of exit from the field of view. These statistics were then compared among the species using the Kruskal Wallis test (Sokal & Rohlf, 1995). Observations were also made with regard to movement pathways in relation to both tidal and diurnal cycles.

Correlation analysis was made between the patterns of behaviour and the underlying topography of the rock surface. The trajectories of each species were mapped on to a still frame of the video image. This was done for the entire duration of the study. The time series was also divided into a number of time periods to examine any changes that might have occurred during the investigation. The selected dates included periods of four, four, and three days for blennies and crabs. In contrast wrasse were too numerous for these particular periods to be imposed. Pathways were therefore examined for two dates at the start, middle and end of the experiment.

The video image was also subdivided into a number of grid cells of 5cm by 5cm, which coincided with the grid size used to determine the relative heights of each cell in relation to each other (see below). The edge cells were ignored leaving a total of 194 grid cells. Frequencies of occurrence and the number of movements were then compared among the different regions of the video image. The number of visits to each cell by the different species were then correlated with the height of each cell. A Spearmans Rank Correlation Coefficient was calculated to test the significance of any relationship demonstrated (Sokal & Rohlf, 1995).

The spatial structure of the patterns of visits was demonstrated by the use of standardised variograms. A variogram models the average degree of similarity between values as a function of their separation distance. Generally variogram models tend to level off at a sill which is equal to the variance of the variable. The distance at which the variance levels off is known as the range; beyond that distance the sampling units are not spatially correlated i.e. they are independent (Legendre & Legendre, 1998).

Constant variogram values mean that, on average, the variance between values does not change with distance. Small variogram values at short lags correspond to data that are all closer together and more alike or more spatially continuous. Conversely, large variogram values reflect data that are farther apart and more dissimilar or spatially discontinuous (Rossi *et al.*, 1992). In order to standardise these measures each variogram value is divided by the overall sample variance. Standardising variograms allows meaningful spatial dependence comparisons to be made between data with disparate measurement units and/or levels of spatial variability (Rossi *et al.*, 1992).

In order to highlight the usage of the different grid cells the data was analysed with a Poisson frequency distribution. The purpose of fitting a Poisson distribution was to test whether the visits to cells occurred independently of each other. If the observed visits follow those predicted by the Poisson distribution then the visits are considered to be distributed at random and independent of each other. If, however, the visit to a cell enhances the probability of a second visit to that cell a clumped or contagious distribution is obtained. In contrast if a visit to a cell discourages a return visit to that cell a repulsed, spatially or temporally distribution is obtained (Sokal & Rohlf, 1995).

The observed and expected numbers of visits to cells were further compared with a *G*-test which tests for goodness of fit of frequencies arranged in a one-way classification (Fowler & Cohen, 1994).

Following the examination of the distribution of predator movements barnacle counts were made to try and establish a direct link with predation. Barnacles were collected from the rock surface in 15, 5cm by 5cm grid cells. Five of these areas coincided with frequently visited cells, five were visited infrequently and five were at an intermediate level. The total number of barnacles were counted within each cell and the presence or absence of cirri was also recorded. A one way ANOVA was used to determine whether the counts in the different regions were significantly different.

(4.2.4.) Topography of the Study Area

In order to quantify certain behavioural patterns, measurements of the rock surface needed to incorporate scale. It was possible to reconstruct a three dimensional image of the area under surveillance through the use of stereophotography.

Stereophotography allows the calculation of the three dimensional co-ordinates of any photographed point, based on the relative position of that point, on both exposures of a stereo-pair. The three dimensional co-ordinates of each specified point shared by the images can be calculated based on a series of mathematical equations (vanRooij & Videler, 1996) (see Chapters 2 & 3 for details).

A stereo-pair of photographs were therefore taken of the rock surface and used to reconstruct a three dimensional contour plot (Figure 4.2). The bias of the dominant slope was removed from the data within the rock surface via regression. The z co-ordinates were regressed against the x and y to produce a set of predicted z values lying on a plane. Subtraction of predicted from observed z values yielded residual z values. A residual plot allows the small scale difference in topography to be depicted (Figure 4.2).

In order for these depth measurements and scaled x, y co-ordinates to be related to the corresponding TV image the left-hand stereo-image and the TV image were digitised simultaneously. The TV image was then rescaled to produce measures of the distance of the camera from a large number of points within the field of view of the TV camera. To estimate the distance from the camera of any object in the camera view, the relationship between measured distance and position within the image was determined by stepwise polynomial regression. Parameters from the best-fit model were used to predict distances from the camera for all digitised positions of predators. These predicted distances were then used to predict co-ordinates along the x and y plane of the camera all scaled to cm in dimensions.

The use of this technique also provided a means to ensure that the camera image was not rotated in any direction. Any rotation or differing distances of the rock surface from the frame could bias the estimation of distances and speeds travelled. A regression of the y co-ordinates on the x co-ordinates gave an indication of the angle at which the cameras were rotated in relation to a horizontal plane. Water levels were also digitised at ten minute intervals for a period of one hour to ensure a horizontal water line. It was concluded that no correction was necessary.

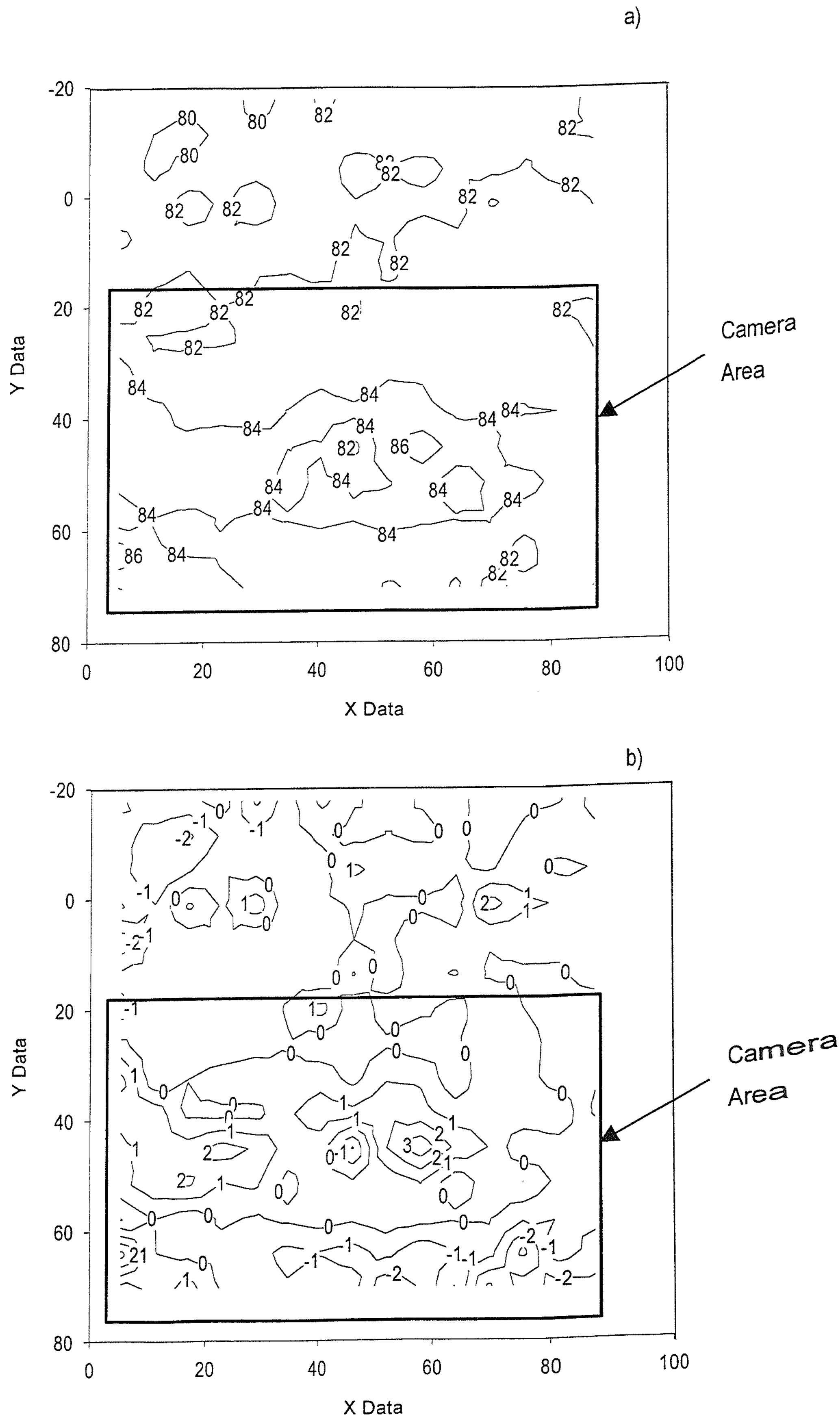


Figure (4.2): a) A contour plot of estimated distances of the rock surface from the camera. b) Residual surface plot to give an indication of small scale topographical features.

(4.3.) RESULTS

(4.3.1.) General Observations

Three mobile intertidal predators were recorded throughout the two week time series: the wrasse *Crenilabrus melops*, the blenny *Lipophrys pholis* and the crab *Carcinus maenas* (Figure 4.3). The frequency of occurrence of these species varied greatly, with seven times as many wrasse viewed as blennies. A sequence incorporated all digitised moves by a particular organism from when it entered the field of view to when it left the field of view. Sequences of movements were recorded across the rock surface; more specific behavioural acts such as feeding could not be reliably quantified. Whilst interacting with the rock surface wrasse did, however, appear to be removing barnacle cirri from the area. The same was also true for *L. pholis* where a rapid movement across the surface was followed by a sharp twisting of the body, possibly representing attacks on barnacles. A single blenny was also seen to remove a dog whelk from the rock surface.

Differences in the frequencies of movements were observed in relation to both tidal and diurnal cycles. Crabs were much more typically observed during periods of darkness than during daylight. This was in direct contrast to the other two species which were almost exclusively viewed during periods of daylight. The number of instances of fish movement was also particularly reduced during periods of direct sunlight. The activity for all three species was greatest during periods of high water. In fact there were no recorded movements at times of low water and the number of observed sequences substantially dropped off towards this time.

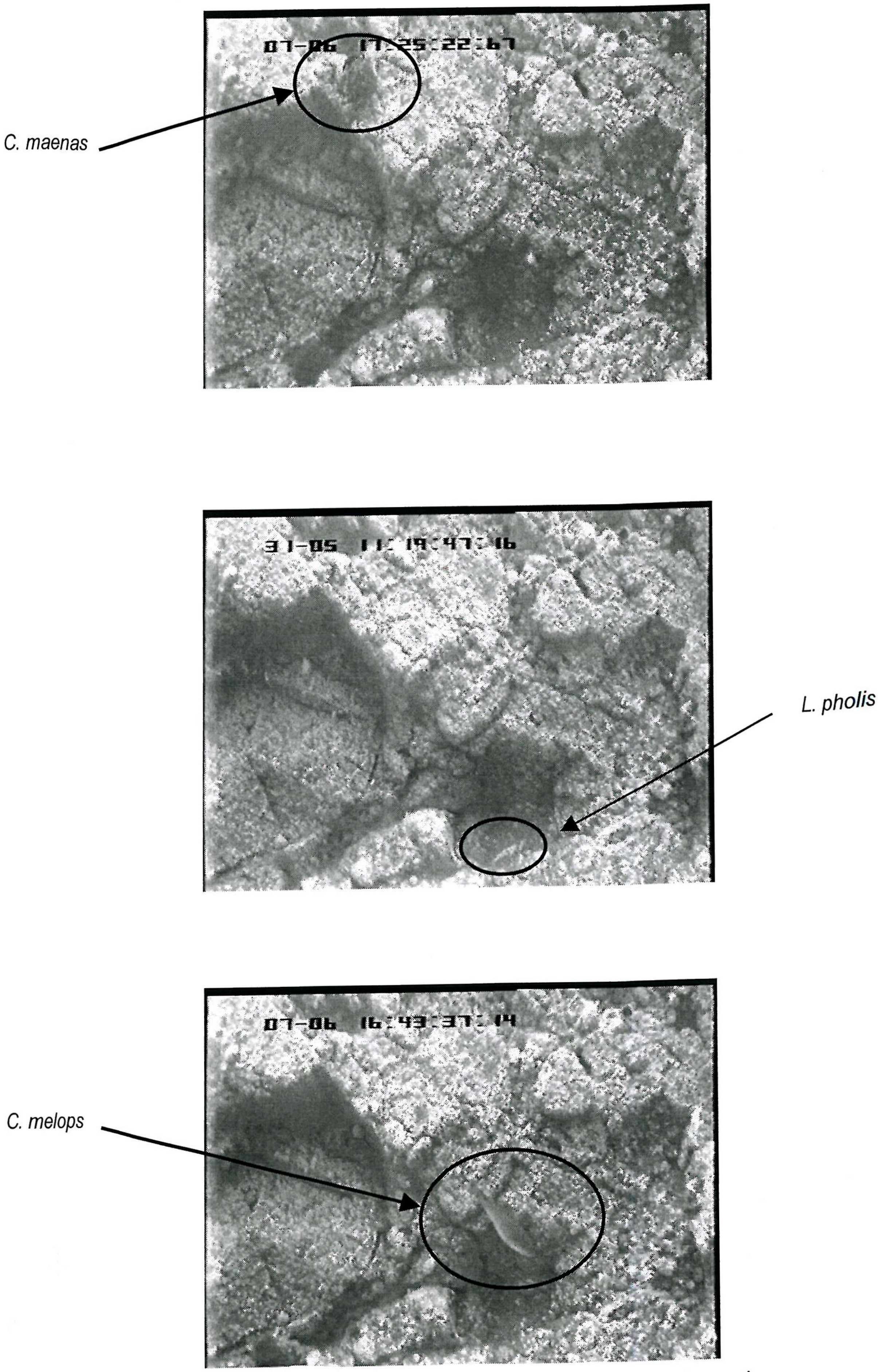


Figure (4.3): The three intertidal predators for which movement patterns were observed.

(4.3.2.) Patterns of Movement

The median number of moves per sequence ranged from between 8.5 for *L .pholis* and 12 for *C. melops*. The properties of these moves were highly variable both within and between species. The greatest distances per move were typically made by *C. melops* with the furthest distance being recorded reaching 32cm and an average of 6cm per move. In contrast the shortest average distance was by the crab *C. maenas* (4.8cm). The frequency distributions (Figure 4.4) highlight the relatively fewer moves at larger distances as opposed to shorter distances for all three species.

The average duration per move for *C. melops*, *L. pholis* and *C. maenas* was 2.1, 3.2 and 7.0 seconds respectively. The frequency distributions for the duration of moves demonstrates the restricted number of longer moves by *C. melops* as compared to the other two species (Figure 4.4). As a consequence of these distance and duration patterns the typical speeds per move were lowest for *C. maenas* and highest for *C. melops* (Figure 4.4), with averages of 1.8 and 3.4 cm/second respectively.

At the level of entire sequences, the greatest distances were travelled by *C. melops*, with a maximum length of 170cm. In contrast to the individual moves, however, the shortest median distances were moved by *L. pholis* (45.7cm). Both duration and speed for the sequences followed the same distribution as individual moves (Figure 4.5). The median duration of a sequence was longest for the crab and relatively similar for the other two species (Table 4.1). The differences in these measures varied greatly both within and between species. All statistics calculated to compare these parameters showed significant differences between the species in terms of duration, distance travelled and speeds obtained (Table 4.1). The only exception was the convolution of movement pathways where there was no significant difference between the species.

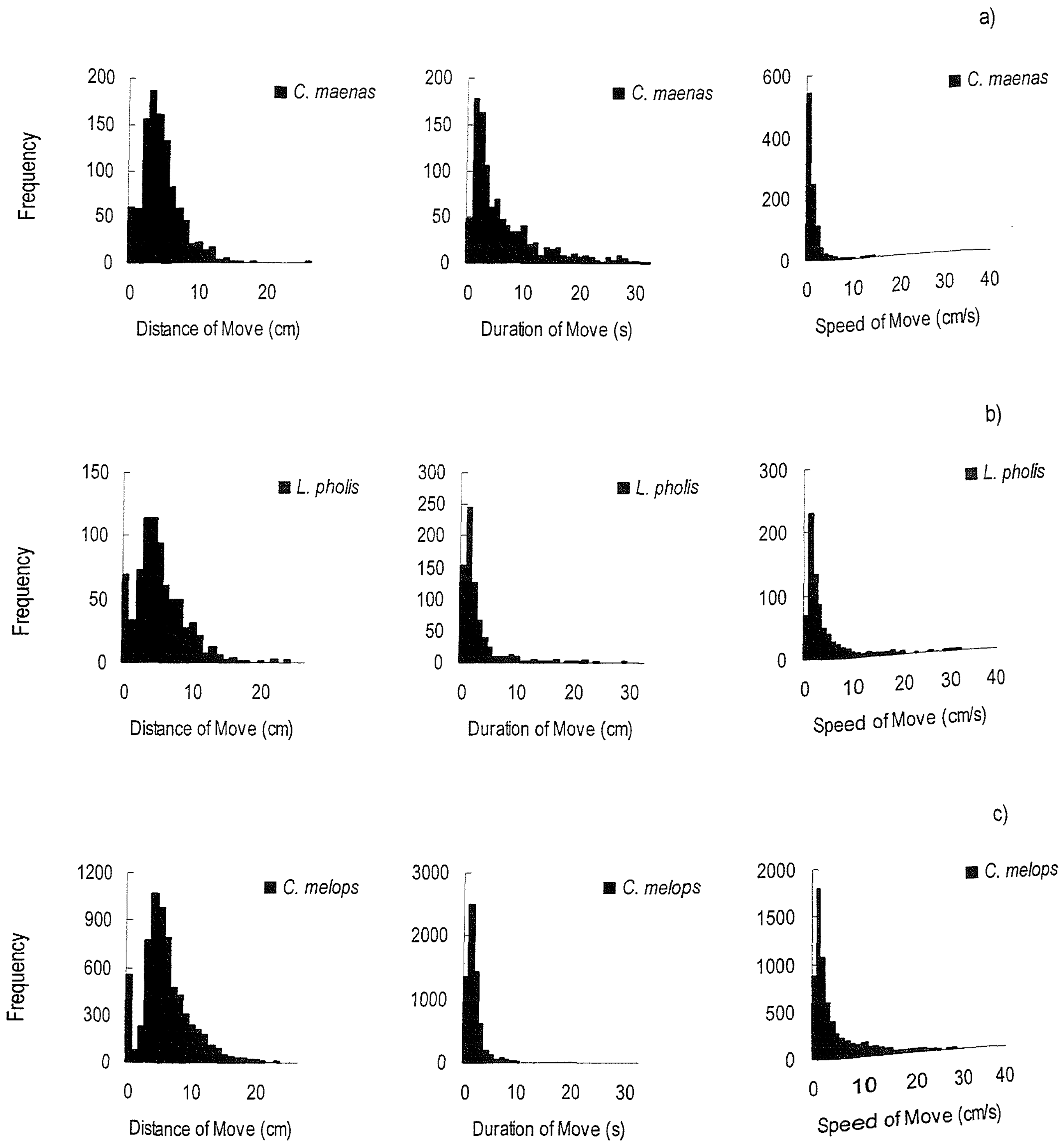


Figure (4.4): Frequency distributions of moves in terms of distance, duration and speed for a) *C. maenas*, N= 75 b) *L. pholis*, N=71 and c) *C. melops*, N=565. N= number of animals from which data was derived.

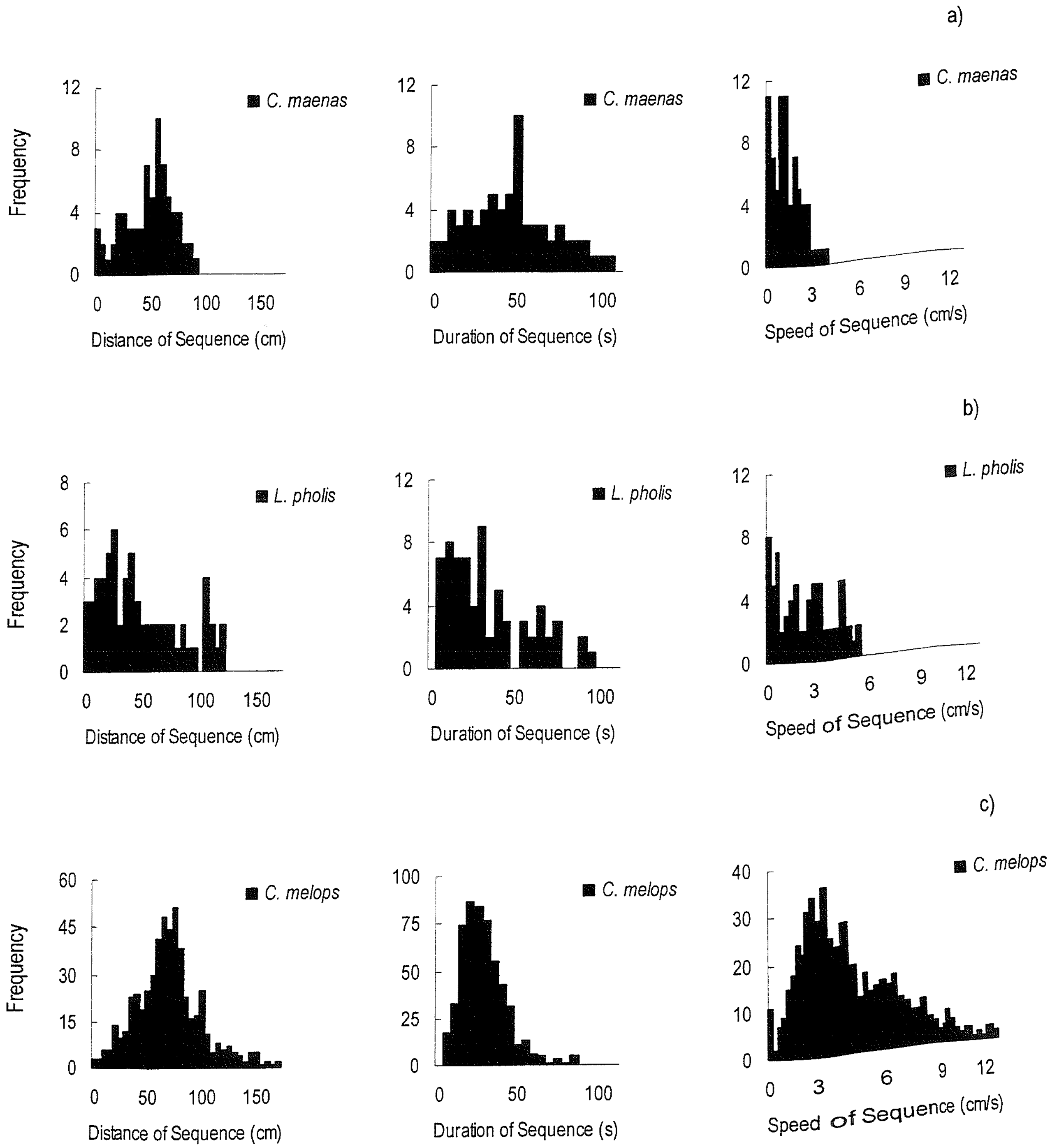


Figure (4.5): Frequency distributions of sequences in terms of distance, duration and speed for a) *C. maenas*, N= 75 b) *L. pholis*, N=71 and c) *C. melops*, N=565. N= number of animals from which data was derived.

Table (4.1): Summary of the properties of behavioural sequences for three mobile intertidal predators.

	n	Median Number of Moves	Median Duration (s)	Median Distance Travelled (cm)	Median Speed (cm/s)	Median Convolution of Path
Crenilabrus melops	565	12	24.3	71.0cm	2.8cm/s	1.3
Carcinus maenas	75	11	71.1	62.3cm	0.8cm/s	1.3
Lipophrys pholis	71	8.5	31.3	45.7cm	1.4cm/s	1.5
Kruskall-Wallis Chi-square	df=2	26.1	48.6	22.6	162.3	2.4
p		<0.001	<0.001	<0.001	<0.001	0.300

(4.3.3.) Movement in Relation to Topography

Each species appears to have its own distinctive pattern with regard to movement across the topography (Figure 4.6). Crabs for example appear to follow the lines of crevices and other surface indentations. This is particularly clear along the central concavity running across the bottom of the image, and along the ridge presented up the right hand side of the field of view (Figure 4.6). While movement pathways were concentrated along these surface features other pathways were also taken across the surface.

A similar distribution was also observed for the movement patterns of blennies, where again the most concentrated regions of movement were along the crevices. There was also a strong correlation between occurrence and the lower part of the image. The lower frequencies at which this species was recorded cause the pattern to appear less concentrated than for the crabs (Figure 4.6).

C. melops were commonly seen swimming throughout the entire field of view along all the open rock surfaces. In contrast to the two previous species the movement patterns of wrasse did not appear to follow crevices but the surrounding convexities. A representative sample of trajectories obtained from the wrasse is displayed in Figure 4.6; if all points were included the image would be totally obscured masking any affects generated by topography.

The corresponding trajectory plots over the different dates of the study demonstrated no shift in movement patterns over time (Figures 4.7-4.9). The concentration of crab movement focuses on the same areas throughout all three time frames. One difference that does become apparent is that the number of blenny pathways increased throughout the two week period. The pathways of *L. pholis* appeared to be slightly more focused towards the central bottom region on date two as compared to the remainder of the filmed period. Despite being considerably more numerous, again the wrasse demonstrated no obvious differences in the trajectories that were typically followed. Spearmans rank correlation coefficients highlight these similarities of movements to grid cells across the three time periods (Table 4.2).

Table (4.2): Spearmans Rank Correlation Coefficients between movements to different grid cells over separate dates of the analysis for each of the three species. (**Significance: * = p<0.05; ** = p<0.01**)

(a) *C.meanas*

	Date 1 (27/5/98-30/5/98)	Date 2 (31/5/98-3/6/98)	Date 3 (4/6/98-8/6/98)
Date1	-		
Date 2	**0.46****	-	
Date 3	**0.24****	**0.28****	-

(b) *L. pholis*

	Date 1 (27/5/98-30/5/98)	Date 2 (31/5/98-3/6/98)	Date 3 (4/6/98-8/6/98)
Date1	-		
Date 2	0.14	-	
Date 3	0.09	**0.22****	-

(c) *C. melops*

	Date 1 (27/5/98-30/5/98)	Date 2 (31/5/98-3/6/98)	Date 3 (4/6/98-8/6/98)
Date1	-		
Date 2	**0.71****	-	
Date 3	**0.65****	**0.68****	-

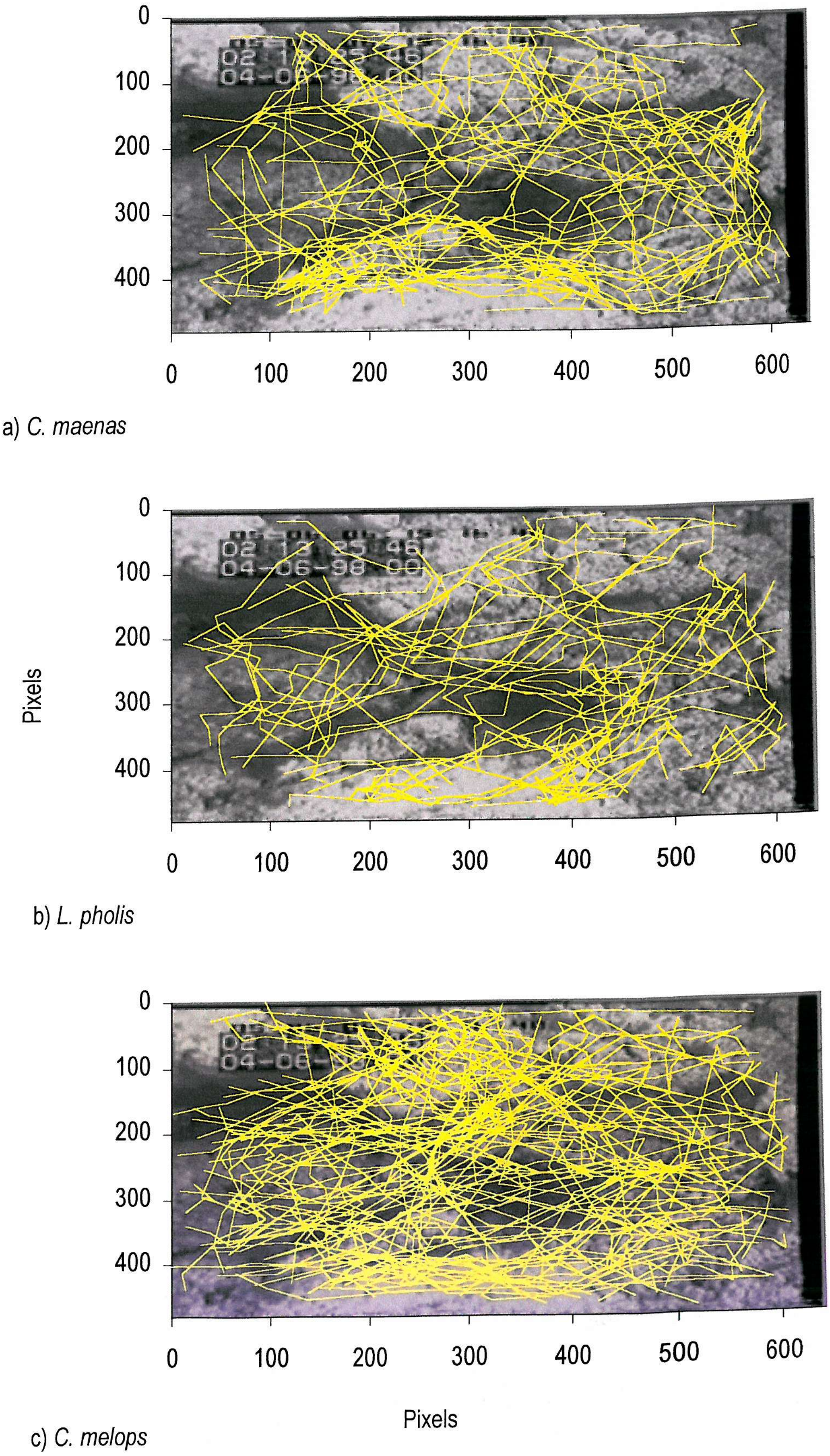
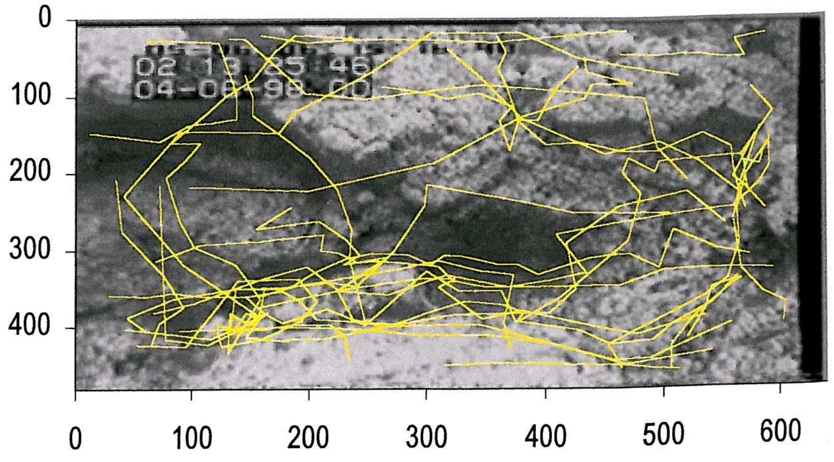
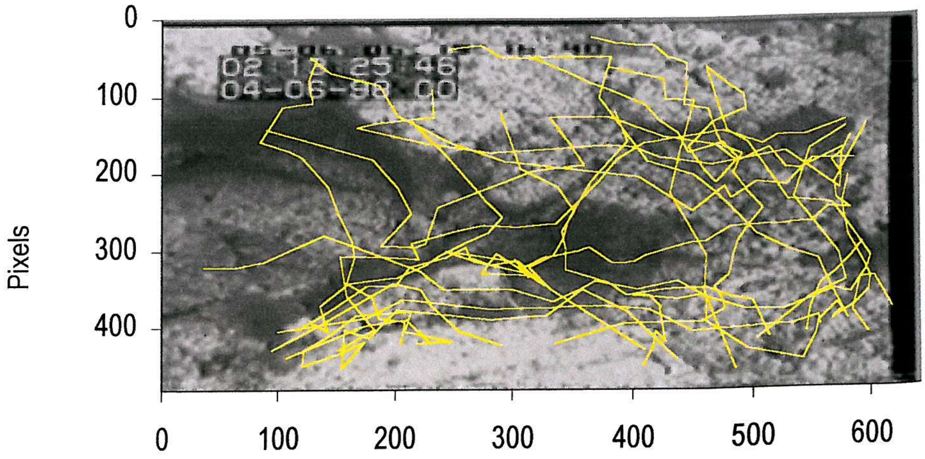


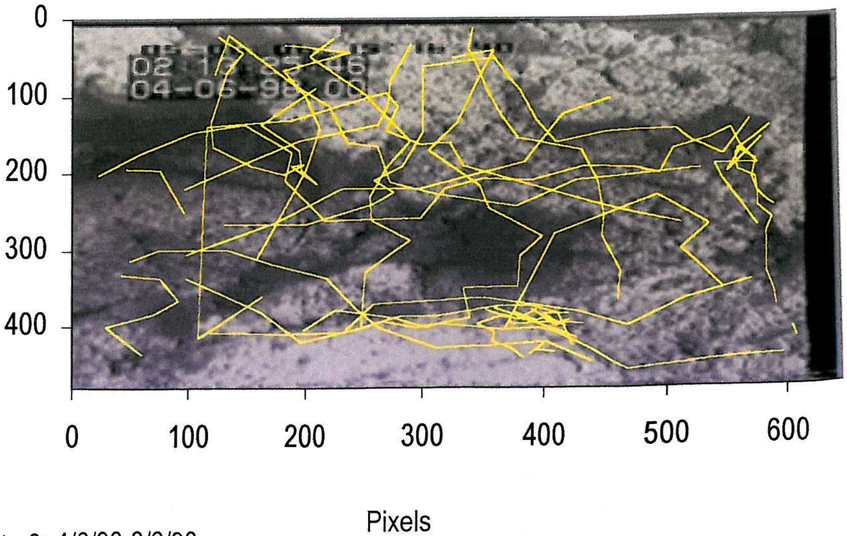
Figure (4.6): Total observed movement pathways across the rock surface during the two week period a) *C, maenas*, b) *L. pholis* and c) *C. melops*.



(a) Date 1: 27/5/98-30/5/98.

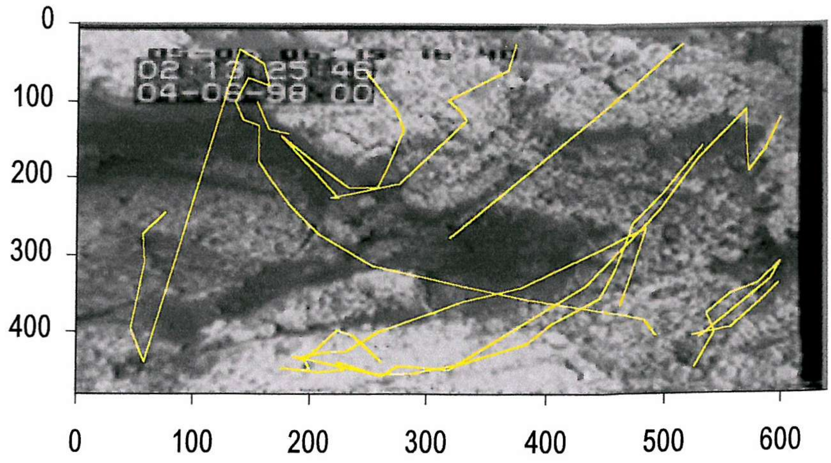


(b) Date 2: 31/5/98-3/6/98.

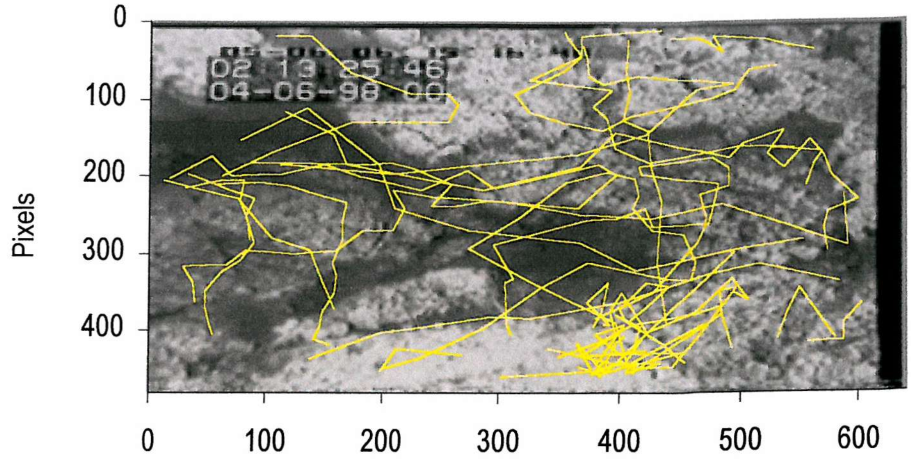


(c) Date 3: 4/6/98-8/6/98.

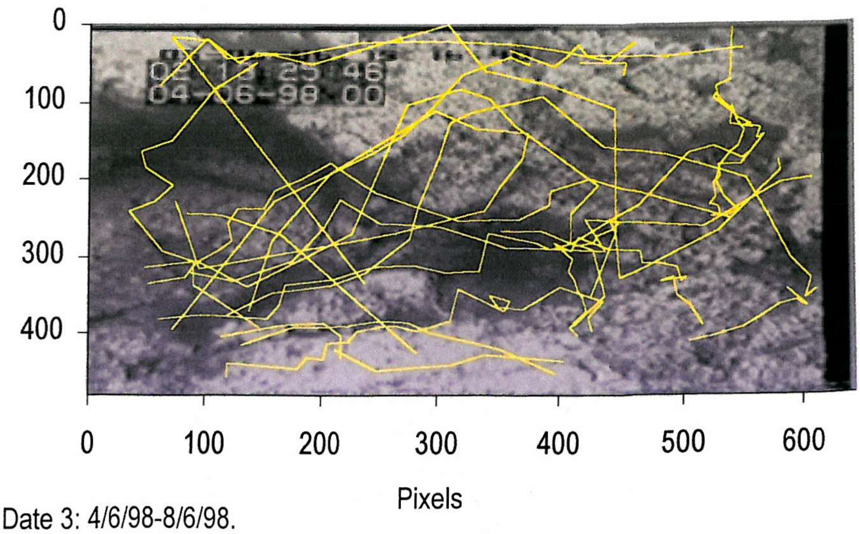
Figure (4.7): Movement pathways of *C. maenas* over different dates during the two week sampling period.



(a) Date 1: 27/5/98-30/5/98.

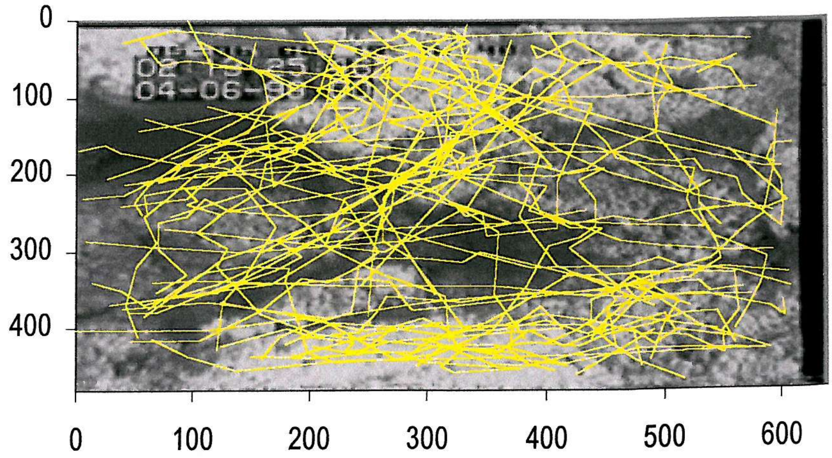


(b) Date 2: 31/5/98-3/6/98.

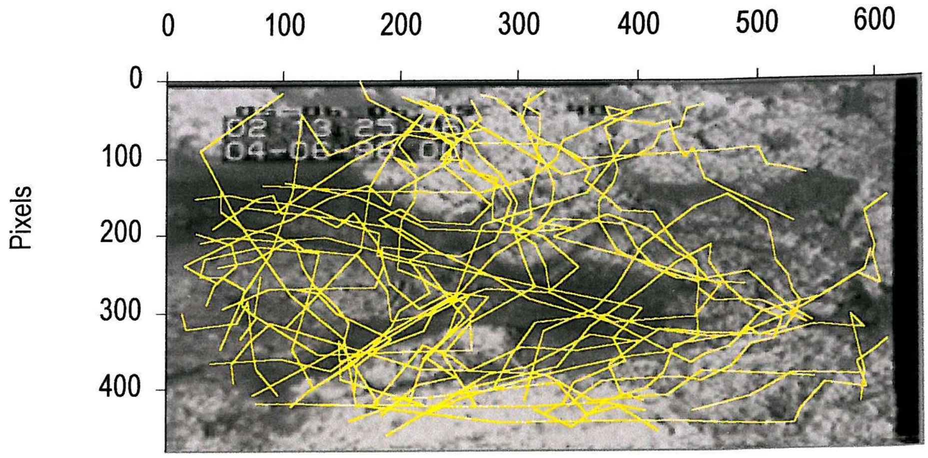


(c) Date 3: 4/6/98-8/6/98.

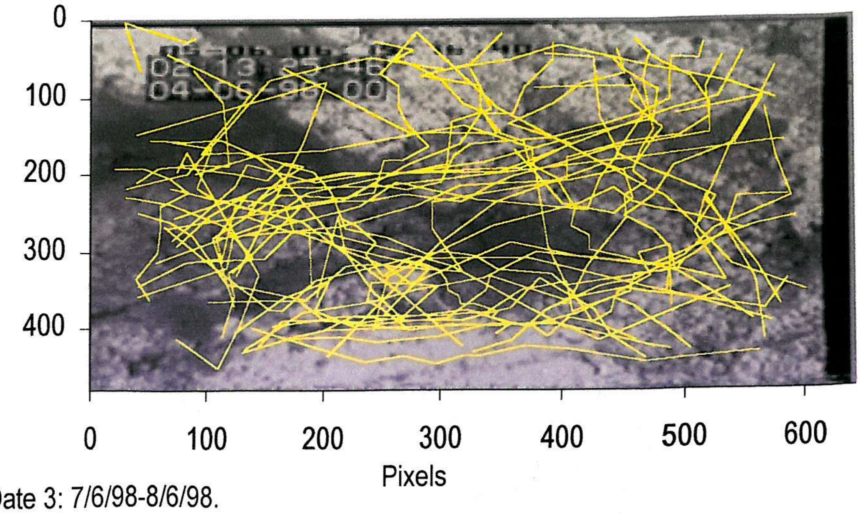
Figure (4.8): Movement pathways of *L. pholis* over different dates during the two week sampling period.



(a) Date 1: 27/5/98-28/5/98.



(b) Date 2: 1/6/98-2/6/98.



(c) Date 3: 7/6/98-8/6/98.

Figure (4.9): Movement pathways of *C. melops* over different dates during the two week sampling period.

(4.3.4.) Spatial Analysis

A grid was superimposed on to these areas in order to examine the concentration of moves made by the three species. All three species demonstrated a degree of dependency with regard to visiting neighbouring cells. Semivariance counts for the crab *C. maenas* approached the average variance for cells separated by 10cm (Figure 4.10). This means that cells close to each other are more likely to be visited in a sequence than those further apart up to a distance of 10cm. The remaining two species demonstrated a greater degree of dependency, with spatial independence not reached until a distance of 27cm for *L. pholis* and 30cm for *C. melops*. Movement patterns for all three species were therefore highly clumped with large areas visited often and other areas relatively ignored.

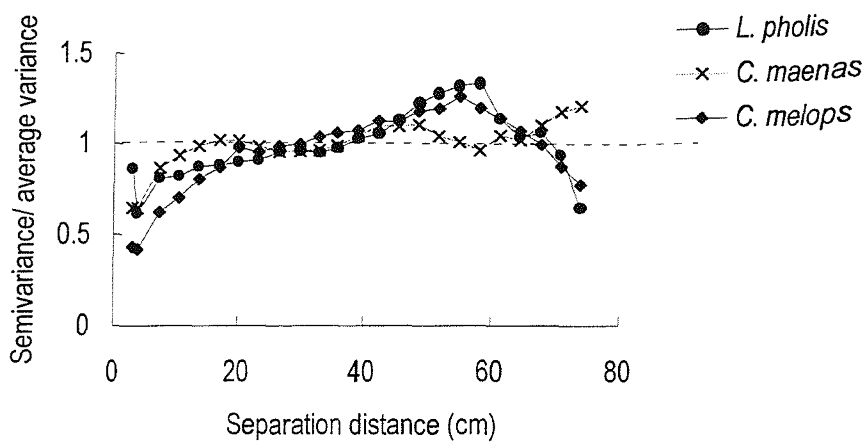


Figure (4.10): Semivariograms of numbers of visits to 25cm^2 areas for *C. maenas*, *L. pholis* and *C. melops*.

A poisson distribution was not displayed for the frequency of visits to grid cells by any of the three species; demonstrating non random behaviour (Figure 4.11). In fact the observed and expected number of visits to grid cells were significantly different for all species (G=0.11,0.08,0.31; d.f=14,10,40; $p<0.01$ for *C. maenas*, *L. pholis* and *C. melops* respectively). For all three species it became apparent that there was a large number of cells that were never visited as well as a large number of cells that were visited far more frequently than would be expected at random. With *L. pholis*, for example a total of 31% of the total possible grid cells were never visited. The moves of *C. maenas* were similarly concentrated in small regions of the grid, although a higher proportion of cells were visited relatively more frequently than for *L. pholis*, with only 26% of cells never visited. In terms of *C. melops* relatively high densities were recorded throughout the grid with the exception of the extremities, with only 5% of cells never visited. The maximum number of visits to any one grid cell was 40. The movement patterns for these three species were therefore clumped, at least during this two week time period.

The physical structure of the habitat did appear to affect the movement patterns of the three species. A positive correlation existed between the number of times a grid cell was visited and the depth of the respective grid cell. A similar relationship was displayed by all three species, with the deepest cells being visited more frequently in all cases (Figure 4.12). Spearmans Rank correlation coefficients of 0.39, 0.31, 0.32 were obtained for *C. maenas*, *L. pholis* and *C. melops* respectively. These values were all highly significant ($p<0.001$, $n=194$) even with adjustments made for the lack of spatial dependence which involved removing cells less than 10cm apart from the analysis.

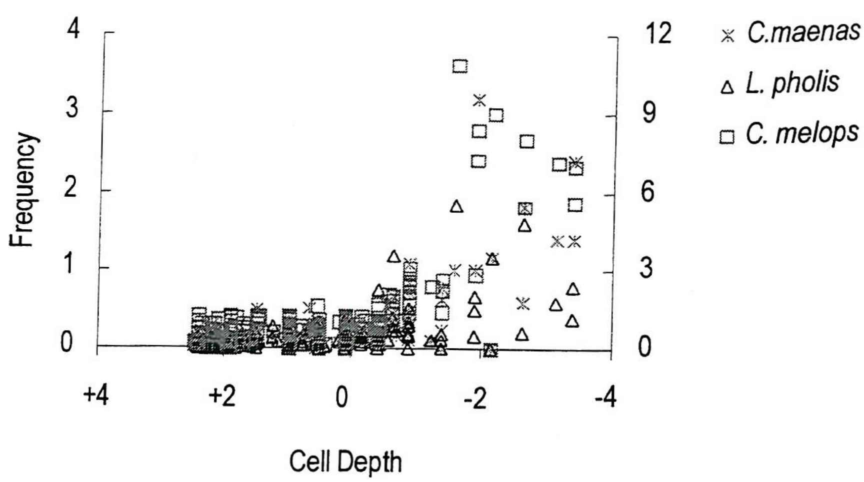


Figure (4.12): A correlation between the number of moves per 25cm^2 cell and the estimated depth of each cell in relation to the average depth within the rock surface (0cm). (Right hand axis relates to *C. melops*).

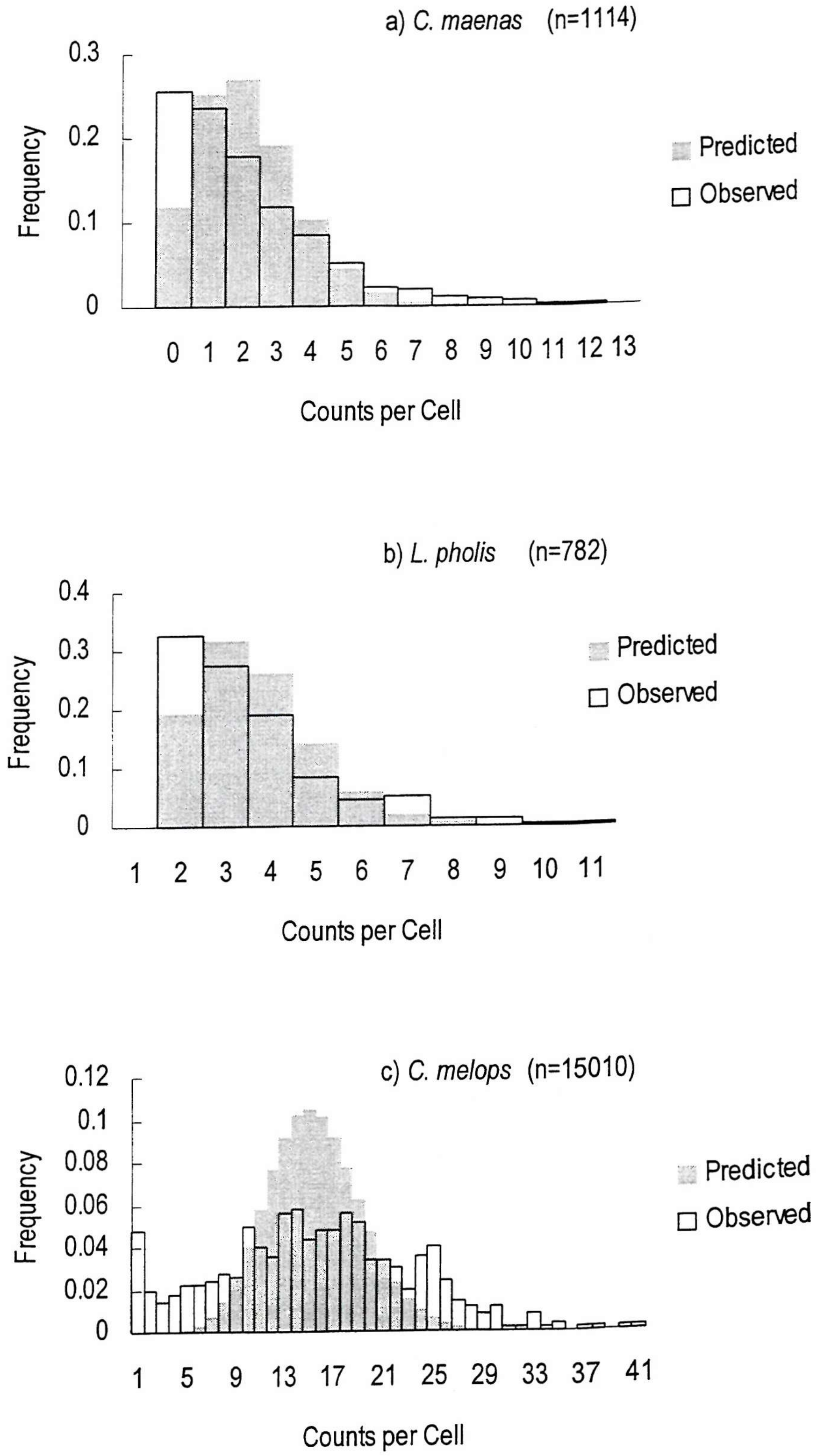


Figure (4.11): Observed and expected visits per 25cm^2 cell as compared to the Poisson distribution, a) *C. maenas*, b) *L. pholis* and c) *C. melops*.

(4.3.5.) Direct Links to Predation

There was no apparent damage to any of the cirri of the barnacles that were removed from the quadrats within the rock section. This was true in terms of both the presence of cirri and the overall length of these appendages. There were, however differences in the overall numbers of barnacles present in the differentially visited zones. The average numbers of barnacles present in the highly, mid and infrequently visited areas were 40.2, 65.4 and 82.8 per $25cm^2$ respectively. The numbers recorded in these different zones were found to be significantly different (Table 4.3).

Table (4.3): A one-way ANOVA to demonstrate the different numbers of barnacles in differentially visited areas.

Source	DF	SS	MS	F	P
Counts	2	4587.60	2293.80	19.03	<0.001
Residual	12	1446.80	120.57		
Total	14	6034.40			

(4.4.) DISCUSSION

(4.4.1.) Underwater Camera Observations

Most observations of rocky shore predators have been made during periods of low water; since large mobile predators are not seen at this time their ecological role may have been largely underestimated. In fact it has been suggested that in the temperate zone transient crabs and fishes are uncommon and ineffectual above the lowest shore levels (Bertness *et al.*, 1981; Menge & Lubchenco, 1981). The results presented here are in direct contrast to this notion; with large numbers of *C. melops*, *L. pholis* and *C. maenas* recorded within the two week time frame. Burrows *et al.*, (1999) also recorded high numbers of such predators at these latitudes.

Predation pressure may vary on diurnally, tidally and annually rhythmic schedules; factors that may have been misinterpreted with conventional sampling designs (Edwards *et al.*, 1982). The underwater camera technology employed here offered a number of advantages in observing predator activity as compared to more traditional techniques. Previous methods include experimental manipulations (e.g Menge & Lubchenco, 1981; Sala, 1997; Ojeda & Munoz, 1999) or experiments with tethered prey (Behrens Yamada & Boulding, 1996); however these techniques may serve to modify behaviour patterns. Predators have also been observed by direct observations (e.g. Wells, 1980; Parry, 1982; Lowell, 1986; Iwasaki, 1993) and their attack activities recorded with artificial prey (Thompson *et al.*, 2000). The main disadvantages of these recorded results is that they are not continuous measurements and they only provide direct observations for short periods.

Crabs have been examined with SCUBA; but such methods are limited by dive time and sea conditions (Warman *et al.*, 1993). Earlier video analysis was also limited to periods of daylight (Dare & Edwards, 1981). The camera deployed in this study was held in a fixed position for a two week period and therefore incorporated a spring neap tidal cycle. The system had the additional advantage of incorporating 24 hour continuous recordings; incorporating both tidal and diurnal cycles. The equipment is, however, expensive and would be unsuitable for highly wave exposed areas or where human interference was likely to present a problem.

(4.4.2.) Patterns of Behaviour

While direct observations of actual feeding could not be clearly identified the overall number of sequences recorded highlight the activity levels of these predators. It was also unknown how many of the sequences were made by the same or different individuals. In certain instances a single animal was, however, known to be accountable for more than one sequence. Despite this fact these species collectively appeared to exert a considerable amount of predation pressure during this two week time period.

The speed of movements across the rock surface varied for each species. The total duration of time visible was longest for the crab. This is possibly due to the fact that it appears to have a much less concentrated foraging effort than *C. melops* or *L. pholis*. The feeding efforts of both *C. melops* and *L. pholis* appeared much more concentrated, with a distinct action, assumed to be associated with the removal of barnacle cirri, noted on each foraging attack. The fastest speeds, recorded for *C. melops,* may be associated with the fact that this species does not directly swim along the rock surface. The patterns of movements and behavioural acts for *C. maenas* and *L. pholis* were in the same order of magnitude as previous observations in this region (Burrows *et al*., 1999).

L. pholis and *C. maenas* have both been shown to have endogenously controlled rhythms of circatidal periodicity in their patterns of behaviour and physiology (Naylor, 1958; Gibson, 1967; Northcott *et al*., 1990). In fact there is good evidence that many coastal marine animals when kept in the laboratory away from the influence of tides and natural light changes demonstrate such rhythms (Naylor, 1985).

The times predicted for the concentration of foraging activity of crabs varies within the literature. In the present study movements of the crabs were concentrated in periods of darkness; findings that are consistent with other authors (Kitching *et al*., 1959; Burrows *et al*., 1994; 1999). In contrast Hunter & Naylor (1993) used a trapping technique and found no difference in the extent of migrations between night and day. Thompson *et al.*, (2000) also observed similar distributions of movements throughout all parts of the diel cycle.

The nocturnal tide in behaviour of the crabs may demonstrate predator avoidance. Foraging birds, for example, are less active during periods of darkness than during the day (Wooton, 1992). The magnitude of intertidal movements may also be expected to vary with such factors as time of year, locality, food supply and with the spring-neap tidal cycles.

Warman *et al.* (1993), using diver surveys and Dare & Edwards (1981), using TV monitoring, observed crab migrations up and down the shore with the rise and fall of the tide. In both cases these movements were associated with feeding migrations. Crabs in Camas Rubha na Liathaig could only be seen at times of high water and there was no direct evidence of vertical migration up or down the rock surface. This may be because the observed surface was almost vertical and represented only a small section of the intertidal zone. Pathways where food was not limited would not necessarily be in a vertical straight line. In fact most of the moves observed were horizontal in direction and appeared to be influenced by the localised topography.

In contrast to *C. maenas* the two predatory fish observed were most active during periods of daylight. It has long been recognised that *L. pholis* displays a diurnal pattern of behaviour with activity ceasing at night (Gibson, 1967). It is thought that they rely on the light for feeding and protection from predators. *C. melops* is also strictly diurnal with activity levels highest during the day (Darwall *et al.*, 1992). Movements, were however, rarely recorded during periods of extreme direct sunlight and it is therefore possible that in certain light intensities some fish may become more vulnerable to predation. The activity of the goldsinny wrasse *Ctenolabrus rupestris* also tends to be reduced at mid-day, perhaps to avoid predation; the generality of this pattern throughout other wrasse species is unknown (Darwall *et al.*, 1992).

Gibson (1965, 1967) reported that activity peaks for intertidal fish were generally phased about high tide in constant conditions and suggested that this corresponded to feeding migrations. The main food source of *L. pholis* is barnacles and these would therefore only become accessible during periods of submergence. Major food groups for *C. melops* also demonstrate the same patterns of availability.

(4.4.3.) Topographic Complexity and Movement Patterns

The movement patterns of *L. pholis* and *C. maenas* during the two week video sequence were consistent with those observed in previous works (Burrows *et al.*, 1999). As predicted in the initial hypothesis the trajectories of *C. maenas*, *L. pholis* and *C. melops* were all affected by structural heterogeneity. Topography is also known to affect the movement of a number of different intertidal species. The movements of *Littorina unifasciata* for example are generally less directional on more complex surfaces and more directional on simple substrates (Underwood & Chapman, 1989). At present the potential causal factors underlying the local distributions of mobile benthic marine fishes (e.g. Ogden & Enrlich, 1977; Leum & Choat, 1980; Bray, 1981; Kingett & Choat, 1981) has been much less investigated.

Intertidal blennies have been reported to follow the pathways of surface indentations in a number of studies (Almada *et al.*, 1992; Dodd, 1998; Burrows *et al.*, 1999). In fact the agonistic behaviour of tide pool fishes is strongly related to the priority of access to holes and crevices (Faria & Almada, 1999); an action that is likely to play a role in predator avoidance. For a fish living in turbulent conditions, the risk of being dislodged by water movements and even wounded is likely to be high they therefore minimise time spent without contact with the surface (Almada & Santos, 1995). Observed behaviour patterns of the species, including courtship and agonisitic displays are designed to minimise the loss of contact with the substrate (Goncalves & Almada, 1998). Direct damage or mortality caused by waves and turbulence is also difficult to estimate, although Nursall (1977) noted that *Ophioblennius atlanticus* frequently bore minor abrasions on the body.

The morphology of *L. pholis* is well adapted for movement across such concavities, for example, the ventral surface of each fish is covered by a thick cuticle (Whitear, 1970). The pectoral fins also allow the animals to hold on to the rock and prevent dislodgement during times of susceptibility to shear wave action (Gibson, 1982). Apart from the cost of physical damage (Nursall, 1977), displaced animals may be at greater risk and be less able to exploit areas for which they have no spatial memory (Hughes *et al.*, 1992). It is also possible this species is capable of exploiting populations of dogwhelks and other such species that reside in crevices.

L. pholis is also reported to be capable of learning pathways in mazes provided in tanks (Dodd, 1998); it is therefore possible that the main track pathways of the blennies represented learned pathways. Fishes introduced into novel areas show exploratory behaviour before developing stereotypical routes between topographic features (Almada *et al.*, 1992). Learning about the habitat is important in terms of homing behaviour, territoriality, refuging and foraging (Hughes *et al.*, 1992). Spatial and temporal changes in habitat are likely to occur, making learning advantageous throughout the life of the fish. This is particularly true with regard to foraging behaviour since food supplies vary so much in type and productivity.

The movement of crabs in relation to small scale topographical features is much less documented. Crabs have been recorded in the intertidal environment via the use of underwater cameras (Dare & Edwards, 1981; Burrows *et al.*, 1994) but data collected was in relation to migration up and down the shore. Again the following of crevices by this species may provide a means of avoiding predators and exploiting the available food resources. The degree of wave action would be less in crevices facilitating movement pathways in general.

In contrast *C. melops* did not directly interact with the rock surface; movement pathways were more common along the convexities surrounding the surface indentations. Following the line of crevices may offer no advantage to this species as it is not adapted to cling to the rock surface. Remaining in close proximity to such topographic features may, however, offer some advantage in terms of predator avoidance and shelter. Juveniles of the wrasse *Pseudolabrus celidotus*, for example, are largely associated with features of shelter and therefore display patchy distribution patterns (Jones, 1984). Goldsinny wrasse are also almost always observed in or close to refuge holes (Sayer *et al.*, 1993; Sayer, 1999).

C. melops has the scope for improving its foraging efficiency, by learning the distribution and status of food sources. With the use of a radial maze it was demonstrated that wrasse can use endogenous rules and visual cues to avoid food sources that are already depleted (Hughes & Blight, 1999). Wrasse can also associate visual cues with the status of potential food sources and use the memorised information to guide foraging behaviour (Hughes & Blight, 1999, 2000).

(4.4.4.) Impacts of Large Mobile Predators

In terms of the second hypothesis, it appears that foraging pathways of large mobile predators do play some role in structuring the community patterns observed on rocky shores. All three species examined here were affected by relatively small scale topographical features. The feeding activity of the species must therefore be concentrated in restricted areas of the rock surface. This result is not atypical, in similar systems the foraging activities of mobile consumers leads to fine scale heterogeneity in otherwise homogenous environments (Wilson *et al.*, 1999).

There are numerous factors that may shape the distribution patterns of intertidal barnacles including tolerance to the physical environment (Connell, 1961), space limitation and competition (Dayton, 1973; Grant, 1977; Lubchenco & Menge, 1978). As highlighted in this study, predation also plays a key role (Menge, 1978a, b). All three species examined appeared to feed on the resident *S. balanoides* population. It is already established that barnacles form the major food source of *L. pholis* (Quasim, 1957; Milton, 1983) and have also been found to be part of the diet of *C. maenas* (Elner, 1981). Barnacle cirri and shells have also been found in the gut of *C. melops* (Sayer *et al.*, 1996). Wrasse, blennies and crabs are all known to be actively feeding during the month of June (Gibson 1965, Deady & Fives, 1995).

The clumped distribution of foraging activity will affect the distribution of *S. balanoides*. As compared to a random distribution of moves a large proportion of the filmed area was over visited. The predation intensity in such areas must therefore be higher than in regions that were under visited. At the extreme, where no visits at all were made to an area, there can have been no influence of predation during the two week period. The non random distribution of predators must therefore create a patchy distribution of the barnacle species or vice versa.

The overall counts of barnacles in frequently and infrequently visited cells were significantly different: with lower numbers recorded in the most visited areas and vice versa. The areas most frequently visited were those with greater depths in relation to the entire substratum under view; highlighted by the positive correlation between the number of visits to certain areas and the depth of the corresponding regions. Differential counts of barnacles in relation to topographical features have been previously attributed to predation from slow moving gastropods (Fairweather, 1988). The large numbers of mobile predators observed here and in other studies (Robles, 1987; Burrows *et al.*, 1999) question this pattern and suggest that prey distribution is more likely to be a consequence of a combination of these factors. Barnacles are also known to be capable of regenerating their cirri after they have been removed (Spiers, 1999). The impact of such regrowth remains uninvestigated. While the cirri are capable of regrowing they are generally shorter in length than in unattacked barnacles. The impact of predation on cirri could therefore be examined by the direct observation of barnacles in these zones. The cirri of all barnacles examined in this study appeared to be intact. While predation intensity overall appeared high, subsampling the barnacle population generated a low probability that an attacked barnacle would be examined.

As a whole the effects of intertidal fishes as predators on the fauna and flora of rocky shores are virtually unknown. The few studies of fish grazing on epifaunal communities on hard substrata in the subtidal region (Day, 1977 in the tropics; Sutherland, 1974a, b, and Foster, 1975 at temperate sites) suggest that selective removal of competitively dominant epifaunal species by fishes may prevent their monopolising space and result in a high level of local diversity. Herbivorous fishes have also been described as important components of littoral fish assemblages in temperate waters; affecting algal biomass & diversity (Choat & Clements, 1992; Barry & Ehret, 1993; Horn & Ojeda, 1999; Ojeda & Munoz, 1999). A specific example relating to *L. pholis* demonstrated that the species may be responsible for maintaining colour polymorphism in populations of the gastropod *Littorina mariae* (Reimchen, 1979). In a wider geographical context Menge and Lubchenco (1981) highlight that rock surfaces in tropical areas are regularly grazed by fishes, crabs and slower invertebrate consumers, and it is a combination of these species that affect distribution patterns.

(4.4.5.) Conclusions, Limitations & Future Work

It is important that the effects of mobile predators, only apparent during times of tidal inundation, are not forgotten when examining distribution patterns on temperate rocky shores. Indeed much of the spatial structure of local communities depends on spatial and temporal escapes from predators and herbivores (e.g. Menge, 1976, 1978a, b; Lubchenco, 1978, 1980; Lubchenco & Menge, 1978; Lubchenco & Cubit, 1980).

The frequent occurrences of large mobile predators, particularly of *C. melops*, indicated a high degree of predation pressure in this area. The major source of prey in this mid tidal zone was *S. balanoides* and predation from such predators is therefore likely to have consequences on its distribution. Small scale topographical features did influence the movement patterns of all three species. The clumped distribution of moves may therefore have resulted in the differential barnacle counts in the frequently and infrequently visited areas. The patchy nature of barnacle distribution will therefore be the result of a combination of both physical and biological processes.

The generality of these movement patterns both spatially and temporally could be assessed by repeated measurements of this type. However, a major limitation of the technique is that the analysis is time consuming and replication is therefore difficult. The placement of the equipment is also restricted in terms of access to suitable sites. To establish a more direct link between movement patterns and prey distributions it would be beneficial to examine the gut contents of these predators at the time of the study. Within the intertidal zone there is an entire suite of different predators from a number of different taxonomic backgrounds. Research which serves to examine the individual roles of such species and the interactions between them will help to describe the processes shaping rocky shore communities.

5. Habitat Complexity and Its Effects on the Succession of Rocky Intertidal Communities

(5.1.) INTRODUCTION

Some habitats are physically complex and provide qualitatively different living space to that available in physically simple habitats. Cracks, crevices and holes greatly enhance the complexity of the microtopography. In the rocky intertidal zone, substratum topography influences diversity (Kohn & Levetin, 1976; Russ, 1980; Menge *et al.,* 1985; McGuiness & Underwood, 1986), abundance (Emson & Faller-Fritsch, 1976; Kohn & Levetin, 1976; Bergeron & Bourget, 1984, 1986), larval settlement (Russ, 1980; Chabot & Bourget, 1988; LeTourneux & Bourget, 1988), size structure of populations (Emson & Faller-Fritsch, 1976) and the general persistence of distribution patterns (Menge *et al.*, 1983; Bergeron & Bourget, 1986). Further, irregular substrata have been shown to provide refuges from temperature extremes, desiccation (Garrity, 1984) and wave action (Menge, 1978a). The use of artificial substrata cast with differing surface features therefore provides a system in which to assess the importance of habitat structure in the recruitment and succession of communities.

(5.1.1.) Species Diversity

The role of habitat complexity in increasing species diversity is a well documented phenomenon (reviewed in Dean & Connell, 1978b; Bell *et al.*, 1991). Even small increases in surface complexity have resulted in considerable increases in species richness, even with surface area held constant (O' Connor, 1991; Douglas & Lake, 1994; Downes *et al.*, 1995; 2000). In contrast microhabitat manipulations have also resulted in no effects of complexity on either abundance or diversity (Molles, 1978; Downes & Jordan, 1993; Bourget *et al.*, 1994). Numerous studies investigating this subject, however, have been confounded by not taking into account the surface area of the substratum (e.g. Hart, 1978; Trush, 1979; Gillinsky, 1984).

Increasing habitat complexity may provide more of the resources already present within a habitat; any accompanying rise in species richness could therefore be as a result of an increase in sample size alone. This idea of Dean and Connell (1987a, b) was termed the sampling phenomenon hypothesis by O'Connor (1991).

Alternatively if changes in habitat complexity generate new resources and microhabitats then new species may arrive to use such resources and more species may be able to co-exist (Williams, 1943; Connor & McCoy, 1979; McGuiness, 1984; Douglas & Lake, 1994). O'Connor (1991) called this the resource availability hypothesis, which was derived from Dean and Connell's (1987a, b) niche availability hypothesis.

The importance of scale in determining species assemblages also requires consideration. Small scale substratum heterogeneity plays a major role in determining the biomass and diversity of subarctic benthic communities (Archambault & Bourget, 1996; Blanchard & Bourget, 1999), with little evidence for large scale influences (km, coastal contour). Underwood & Chapman (1996), however, have pointed out the importance of small (cm or 1 to 2m) and large scale processes (hundreds of metres) in explaining the variability in abundance of many species in New South Wales, Australia. Thus the questions of whether topographical heterogeneity and complexity influence initial settlement and subsequent community developments, and if so which scales are significant and central to benthic community ecology (LaPointe & Bourget, 1999).

(5.1.2.) Colonisation and Succession

(5.1.2.1.) Larval Settlement

Substratum heterogeneity has long been known to influence larval settlement of marine epibenthic invertebrates (Crisp & Barnes, 1954; Barnes, 1956; Crisp, 1974; Bergeron & Bourget, 1986; Chabot & Bougert, 1988). Geometric complexity of the substratum can enhance colonisation rates by protecting organisms from the environment and by increasing the area available for settlement (e.g. Connell, 1961; Keough & Downes, 1982; Lubchenco, 1983; LeTourneux & Bourget, 1988; Walters 1992). As a result on topographically complex surfaces, the distribution of settled larvae is rarely random (e.g. Dean, 1981; LeTourneux & Bourget, 1988; Walters & Wethey, 1991). This can be as a result of both larval behaviour and/or hydrodynamic conditions. Either can result in preferential settlement in pits and crevices.

Eckman (1990) developed a hydrodynamic model to predict rates of settlement of larvae onto bottoms of differing roughness. The model predicted that rates of settlement should increase with the density of roughness features. Heights of the structural components also affected the distribution of particles. Gregoire *et al.*, (1996), with an experimental setup, also investigated the density of adhering particles to panels of differing roughness.

The potential importance of microhabitat selection of larvae in structuring the developing community has also been investigated (Keough & Downes, 1982; Walters, 1992; Underwood & Chapman, 1996; Hills & Thomason, 1998; LaPointe & Bourget, 1999). Many barnacle species, for example, settle more abundantly in crevices close to their size (Crisp, 1974; Bourget, 1988; Chabot & Bourget, 1988) or the size of their settling organs (LeTournex & Bourget, 1988), and bryozoans settle in pits of a preferred diameter (for other examples see Crisp, 1974; Keough & Downes, 1982; Walters & Wethey, 1996).

(5.1.2.2.) Algal Succession

A number of authors have investigated the recolonisation of algae on intertidal substrata after clearing, or the initial colonisation of new surfaces (e.g. Pyefinch, 1943; Moore, 1939; Rees, 1940; Dayton, 1971; Benedetti-Cecchi, 2000). The general pattern of colonisation appears to be diatoms, followed by opportunistic ephemeral algae such as *Ulva*, *Enteromorpha* and *Porphyra*. In northern temperate waters, fucoid algae appear later, and they or other foliose species can dominate the algal community (Underwood, 1980). Early arrivals may create favourable environmental conditions for later colonists (see Hruby & Norton, 1979) indicating that succession may be occurring according to the Facilitation model of Connell and Slatyer (1977). The development of the algal community, however, may also depend on the rates and times of dispersal of the component species (Connell, 1972). In some systems, for example, grazers need to remove ephemerals so that the successional sequence can progress (Lubchenco, 1978; Sousa, 1985; Farrell, 1991; Benedetti-Cecchi, 2000).

The persistence of algae is also dependent on both substratum complexity and grazer abundance (Lubchenco, 1983). The holdfasts of newly established *Fucus* plants are often located in small crevices or between tightly packed barnacles (Norton & Fretter, 1981; Reed & Foster, 1984; Lubchenco, 1986; Chapman & Johnson, 1990). Only if all gastropod herbivores are excluded does *Fucus* become established on smooth rock. Heterogeneity is only important for *Fucus* colonisation where grazers are present (Lubchenco, 1983). The scale of the heterogeneity is again important. If crevices are small, most snails cannot effectively graze within them. However, slightly larger crevices or holes provide refuges for such herbivores and may therefore represent areas of extreme grazing (Raffaelli & Hughes, 1978; Atkinson & Newbury, 1984; Kostylev *et al.*, 1997).

(5.1.2.3.) Habitat Modification

Frequently it is the pioneer sessile organisms themselves that provide the extra shelter by adding to the complexity of the habitat (Dean, 1981; Thistle *et al.*, 1984), thus facilitating colonisation by later settlers. Species by their very presence alter the complexity of an area; this can be in the form of both autogenic or allogenic ecosystem engineers (Lawton *et al.*, 1994; Jones *et al.*, 1994, 1997). The results of the presence of such species can vary depending on the exact nature of the environment examined (Jones *et al.*, 1997). They can provide refuge from harsh environmental conditions, such as wave action or temperature extremes and biological parameters such as predation (McCook & Chapman, 1991; Moreno, 1995; Seed, 1996). The physical properties of a macroalgal canopy for example provides shelter for herbivores and can cause an accumulation in species number (e.g. Reed & Foster, 1984; Lubchenco, 1986; Chapman, 1989; Chapman & Johnson, 1990).

(5.1.2.4.) Habitat Selection

Habitat selection can be defined as selection of one habitat from a variety of potential habitats encountered (Rosenzweig, 1981; Krebs & Davies, 1991; Manly *et al.*, 1993). Microhabitat selection by an individual can be altered by the presence of other individuals using the same resources. Competition within and among species forces the use of a wide variety of habitats besides the preferred ones and, as densities increase, the better quality habitats are chosen first (Fretwell & Lucas, 1970; Rosenzweig & Abransky, 1985; Rosenzweig, 1991). Microhabitat selection can also be state dependent: Jones & Boulding (1999) found that *Littorina sitkana* showed stronger preferences for more protective microhabitats on days when thermal and desiccation stresses were higher. Dynamic models have also been used and these predicted similar patterns of behaviour (Burrows & Hughes, 1991).

On topographically complex hard substrata, pits and crevices are predicted to provide refuge for sessile invertebrates from predators and physical disturbances (Barry & Dayton, 1991), while topographic high spots may provide refuge for poor spatial competitors (Connell & Keough, 1985). Previous studies (Menge & Lubchenco, 1981) demonstrated that 88% of the macroinvertebrate and plant species on the shores of Panama depend on these irregularities for their persistence in communities. When consumers were excluded from portions of the shore, many sessile species increased greatly in abundance and occupied different microhabitats (Menge & Lubchenco, 1985).

Some species of intertidal gastropod remain in protective microhabitats, such as crevices, when immersed during high tide to avoid risk of dislodgement by waves (Levetin & Kohn, 1980; Burrows & Hughes, 1989; Behrens Yamada, 1992; Hughes, 1995) and/or when emersed during low tide to avoid predation pressure (Bertness *et al.*, 1981; Garrity & Levings, 1984) and thermal stress (Garrity, 1984; Garrity & Levings, 1984; Moran, 1985; Fairweather, 1988). Dogwhelks, for example, are better protected from wave action (Dayton, 1971; Feare, 1971; Moran, 1985; Burrows & Hughes, 1989; Gosselin & Bourget, 1989; Johnson *et al.*, 1998), desiccation (Yamada, 1977; Menge 1978b) and temperature (Garrity, 1984; Menge *et al.*, 1985) on heterogeneous than homogenous substrata. The observed consistent selection by *Nucella* of heterogeneous over uniform surfaces shows it can take advantage of small-scale structural heterogeneity (Gosselin & Bourget, 1989).

In contrast the increased diversity of microhabitats could potentially increase the effect of grazers and predators by providing them with refuge from physical stress (Menge, 1976, 1983; Fairweather *et al.*, 1984), rather than providing a refuge for prey species (Keough & Downes, 1982; Gosselin & Bourget, 1989). Garrity & Levings (1981), for example, documented how increased habitat complexity enhanced the effects of the predatory gastropod *Purpursa pansa*, by protecting it from desiccation and its own predators. Marinelli & Coull (1987) also found that predation by juvenile fish on meiobenthos was greater in complex than smooth areas.

(5.1.3.) Surface Manipulations

Most studies of complexity have measured living space in a subjective manner, are only applicable to one habitat or result in numbers that cannot be compared with any other measure (McCoy & Bell, 1981). In contrast surface manipulations and artificial substrata have been used to directly assess settlement patterns and community assemblages in relation to habitat complexity. Artificial substrata serve to simplify replication and allows the sizes of topographic features to be quantified and held constant.

In a few instances surface attributes have been directly manipulated; where holes have been drilled into native rock surfaces to observe distribution patterns (Raffaeli & Hughes, 1978; Menge *et al.*, 1983). The importance of succession and the seasonality of larval recruitment, on the species composition of epifaunal assemblages has also been assessed on perspex panels (e.g. LeTourneux & Bourget, 1988; Turner & Todd, 1993; Bourget *et al.*, 1994; Jacobi & Langevin, 1996; Lapointe & Bourget, 1999; Beck, 2000). McGuiness & Underwood (1986) increased habitat diversity on experimental concrete blocks by the addition of pits and grooves in the surface of the blocks. Concrete blocks have also been placed into river systems to assess the impact of differing complexities (e.g. Downes & Jordan, 1993; Downes *et al.*, 1995, 1998, 2000).

Artificial surfaces have also been created to mimic structures naturally found on the rocky shore. Jones & Boulding (1999) used both natural conditions and artificial plates to form an artificial substrate with barnacle shaped, algae shaped, crevice and flat microhabitat types. Wethey (1986) investigated the consistency of responses of barnacle larvae to plastic models of surfaces complete with adult barnacles, cyprids and bare rock.

(5.1.4.) Aims and Objectives

Complexity of the substratum serves to modify environmental conditions and consequently influences species interactions. The overall aim of this work was to assess the importance of habitat structure in determining and developing communities over a range of quantifiable scales. Twenty concrete blocks, five each of four designs, were placed into the intertidal zone at two sites within Camas Rubha na Liathaig, on the West coast of Scotland.

It was firstly predicted that species number and diversity would increase with the increased complexity of the block type. The null hypothesis was therefore that species number and diversity would remain constant regardless of increased habitat complexity. The community assemblages and the distribution patterns of key algal and faunal species were compared between the different block types. It was predicted that community patterns observed on each of the block types would differ in relation to the differing surface complexities. In particular it was expected that the numbers of gastropods, such as littorinids and dogwhelks, would increase as the complexity of the block increased. In turn it was expected that the distribution of these grazers and predators would affect the abundance of algal and prey species on the different block types. Finally within block variation was examined for the location of species within the separate structural components; either surface, side or crevices, of the blocks. If species were distributed at random they would be found equally on all types of components. The development of the community on each block was followed for a period of one year and the importance of complexity assessed.

(5.2.) METHODS

(5.2.1.) Study Site

Concrete blocks of four increasingly complex designs were constructed and placed in the intertidal zone, less than 0.5 km from the Dunstaffnage Marine Laboratory on the West Coast of Scotland. The shore (Camas Rubha na Liathaig (5°27'5''W, 56°26'50''N)) is relatively sheltered from wave action; facing Northwest across the Firth of Lome. The location is characterised by a rocky cliff surrounding a sheltered bay. The biological features of the rocky shore are consistent with those associated with sheltered shores (Lewis, 1964; Hawkins & Jones, 1992), being *Fucus* dominated in the eulittoral and with a predominance of *Semibalanus balanoides* in the mid to high tidal levels.

The blocks were placed on the seabed at low water at a height of approximately 0.9m above chart datum. The substratum is characterised by a mixture of coarse sand and gravel. There are also numerous boulders and cobbles surrounding the area. These stones are typically covered by species such as *Fucus* spp., barnacles (*Semibalanus balanoides* and *Elminius modestus*), *Patella vulgata*, *Nucella lapillus* and littorinids (mainly *Littorina littorea*).

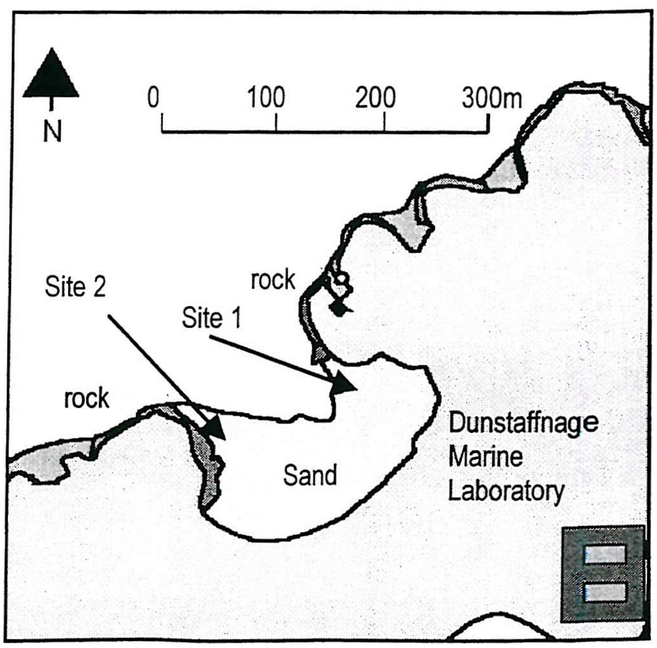


Figure (5.1): Study sites within Camas Rubha na Liathaig near Dunstaffnage on the West coast of Scotland.

(5.2.2.) Block Design and Construction

A total of 40 concrete blocks were constructed: ten of each design (Figure 5.2) for placement in the intertidal zone (Plate 5.1). The blocks were constructed from rapid set concrete (mastercrete, Blue Circle) at a ratio of three parts sand to one part cement. A wooden mould was used to shape each block. Between each phase the mould was coated in Febstrike (Feb Limited), a releasing agent used to ensure a consistent finish to each surface, with no additional small scale crevices. Once set, the blocks were allowed to harden for a period of one week, during which time two coats of Febond (Feb Limited) were applied to all surfaces to prevent surface erosion.

The simplest design was smooth and served as a control against the blocks with increased complexity (Block A). The surface area of the top of each block was $900cm^2$ and each side of the block had a depth of 10cm and a surface area of $300cm^2$. The next level of complexity had a single large crevice running centrally from the top to the bottom and left to right across the top surface, segregating the surface into four smaller units (Block B). The largest width of the crevice, at the top surface, was 6cm and it formed an isosceles triangle descending to a depth of 3cm. The number of crevices on each block then continued to increase throughout blocks C and D. All crevice dimensions were kept relative to the initial ratio between the surface length and crevice width of block B. In block type C each of the four top surfaces present on block B were divided by a cross shaped crevice (3.5cm wide, 2cm deep; again in the form of an isosceles triangle). This created sixteen areas of flat surface, which were further split on block D by a crevice, 0.6cm wide and 0.5cm wide.

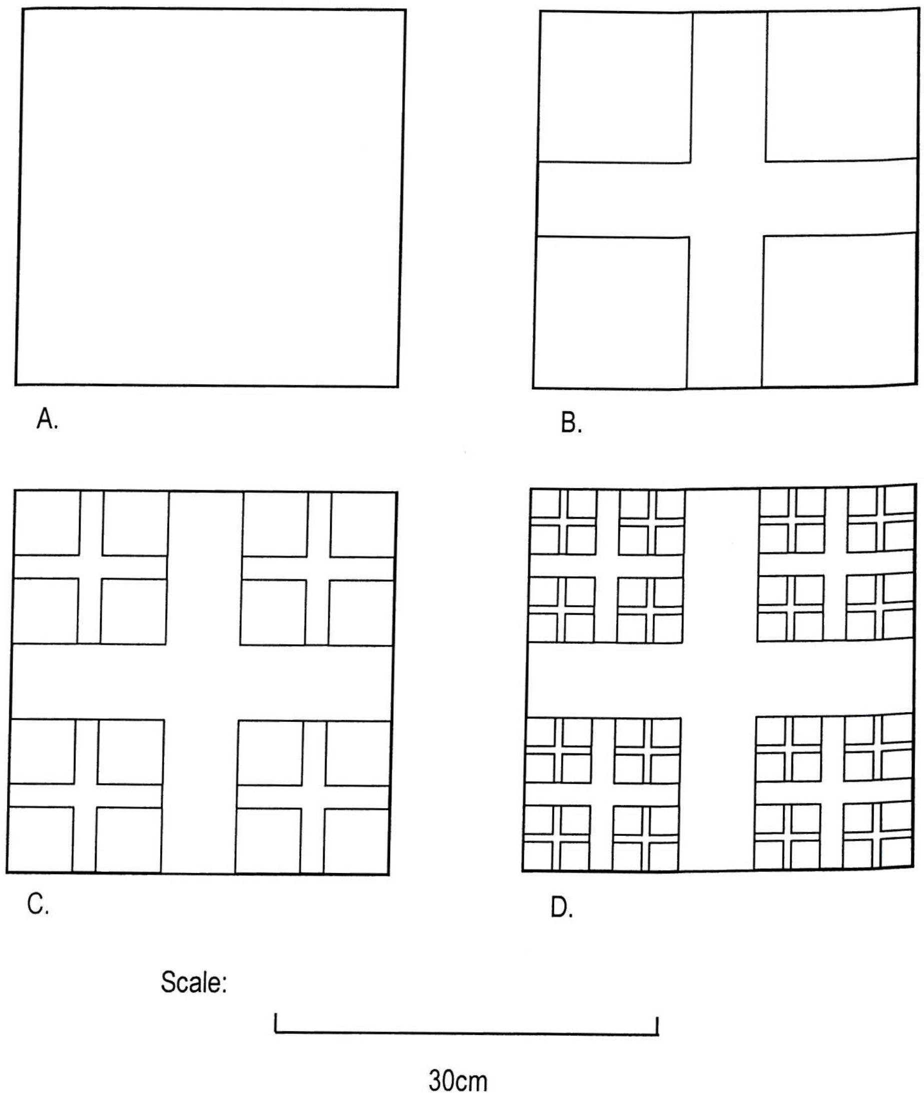


Figure (5.2): The four block types of varying complexity placed in Camas Rubha na Liathaig. Each block was 10cm deep and crevices were in the form of isosceles triangles.

Plate (5.1): Each of the four block types placed into the intertidal zone of Camas Rubha na Liathaig.

(5.2.3.) Block Deployment and Sampling

Two experimental areas were used at Camas Rubha na Liathaig: one at the extreme left and one at the extreme right of the bay (Figure 5.1). A total of 20 blocks were placed at each site, located in a randomised block design with five groups of four blocks, each group containing one of each type of block (Plate 5.1). The blocks were buried to a depth of 3cm reducing the total surface area of the sides to $840cm^2$.

Once positioned the blocks were monitored at approximately six week intervals. Each block was firstly divided into a series of regions corresponding to the different surface types on block C. A code was allocated to each area and the percentage cover of major space occupiers was estimated for each region (Figure 5.3.). Counts were also made of less numerous organisms. The code system allowed a distinction to be made between the different structural components of the blocks. Corrections for difference in surface area could also be applied to these coded regions.

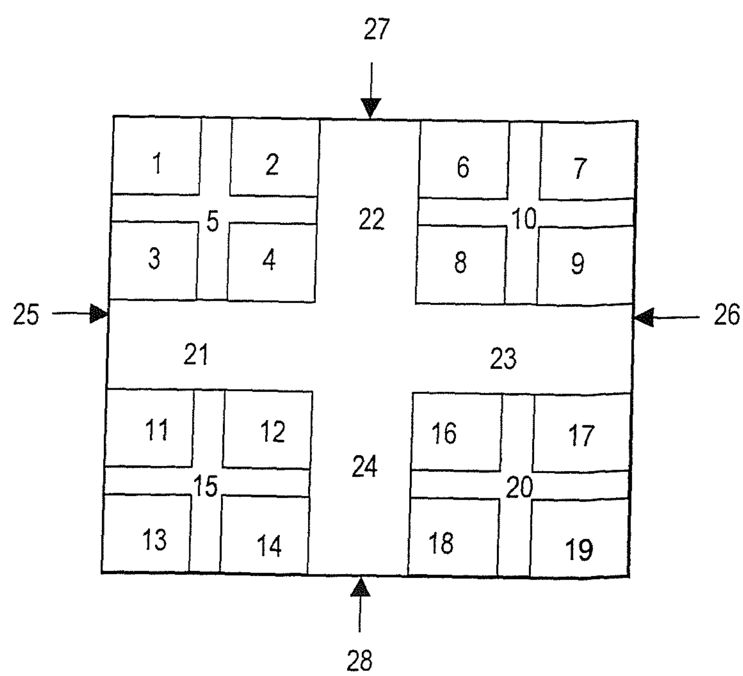


Figure (5.3): The coded regions of a block used to determine percentage cover and species number counts.

(5.2.4.) Analysis

Analyses of species number and diversity were based on faunal organisms that were located on either the surfaces or the crevices of each block. The sides were a constant feature of all blocks and of no real interest to the current study. In order to test the first hypothesis the Shannon Weiner Index (*H*) was calculated for each individual block. This is calculated by determining for each species, the proportion of individuals or biomass that it contributes to the total sample using equation 1.

Equation (1):

$$H = -\sum_{i=1}^{S} Pi \ln Pi$$

Where *S* is the species richness and *Pi* represents the proportion of total individuals in the *i*th species.

An analysis of variance (ANOVA) was used to test for differences in both species number and diversity associated with the blocks of differing complexity.

In order to assess differences in population density of major species associated with the different block types ANOVA was again used. Numbers of littorinids, *Gibbula*, limpets and dog whelks were compared across the different block types. Prior to analysis the numbers were log transformed (Log(x+1)) to homogenise the variances between treatments. Similarly the percentage cover of *Fucus* and *Ralfsia* were compared across the different treatments. In this case the numbers were logit transformed (Log(x/(100-x))) to homogenise the variances (Sokal & Rohlf, 1995). The total percentage cover per block was calculated based on the percentage cover and the surface area of each structural component. Firstly the percentage cover on each topographic feature was multiplied by the surface area of that particular feature. This was done for all the coded regions on a block and the resulting values were summed to give an overall figure. The derived value was then divided by the total surface area of all the combined topographic features to give the percentage cover on each block as a whole.

Within block variation in relation to counts on the different structural components of a block were analysed using the chi-squared test (X^2). The chi-squared test is a goodness of fit test and compares the observed and expected frequencies in a study on the basis of a null hypothesis (Fowler & Cohen, 1994). The expected values for each component were calculated by multiplying the total number of a species observed by the proportion of the total surface area occupied by each particular feature. In order to increase sample size the numbers of each species, *Littorina littorea*, *Nucella lapillus*, *Gibbula umbilicalis* and limpets, were combined for each block type at the two sites. The two sites were analysed separately. Three dates: August 1999, November 1999 and June 2000 were selected for this more specific analysis.

Each block type was considered individually; on block B species number were compared between the surfaces and the large crevice (crevice 1), on Blocks C and D numbers were compared between the surfaces, crevice 1 and the smaller crevices (crevice 2). If the observed numbers were significantly different from those expected then the organisms were not distributed at random and were associated with a certain structural component. When analysing block type B there was only one degree of freedom; the Yates correction for continuity was therefore applied to the data to reduce the value of the test statistic (Fowler & Cohen, 1994).

When comparing percentage cover between the different structural components of the blocks an ANOVA was conducted. This was done for the occurrence of both *Ralfsia* and *Fucus*.

(5.3.) RESULTS

(5.3.1.) General Observations

The blocks placed into the intertidal zone at Camas Rubha na Liathaig remained in position over the twelve month period of the study. Within the first two weeks of initial placement, however, the blocks at site two were repositioned due to human interference. The original arrangement was reinstalled within seven days of the disturbance.

Following the placement of the blocks in the intertidal zone at Camas rubha na Liathaig a number of species settled upon them. The first species to be observed were littorinids including *Littorina littorea*, *L. obtusata* and *L. mariae.* For the remainder of the analysis these species were pooled in order to prevent inaccuracies in identification when sampling conditions were not optimal. These were closely followed by *Fucus vesiculosus* germlings and *Ralfsia* spp. Ephemeral species such as *Enteromorpha*, *Ulva* and *Porphyra* soon became established. As time progressed more species became apparent on the blocks. Algal species present included *Laurencia hybrida*, *Lithothamnium* spp. and *Scytosiphon lomentaria*. Both mobile and sessile faunal species were also recorded: dog whelks *Nucella lapillus*, barnacles *Elminius modestus* and *Semibalanus balanoides*, limpets *Patella vulgata*, *Tectura tessulata* and *Acmaea virginea,* anenome *Actinia equina* and the chiton *Lepidochitona cinerea*. Large mobile predators such as the crab, *Carcinus maenas*, were observed both in close proximity to and actually on the blocks. The species observed were typical of those observed on neighbouring natural boulders. The high occurrence of *Ralfsia* on the artificial substrata was, however, not typical of the adjacent natural substrata.

(5.3.2.) Comparisons Between Block Types

(5.3.2.1.) Species Numbers

Following the initial deployment of the blocks in June 1999 there was no substantial increase in species number until September of the same year. After this date there was a continual increase in the average species number per block during the full twelve months of the study (Figure 5.4.). The rise in the number of species was, however, more accelerated at site one than site two. While a large number of organisms were located on the sides of the blocks, they were all typically represented on the top surface and hence included in the species counts. A maximum of ten different species were recorded on any one block throughout the year. The only species to be lost throughout the sampling period were the ephemeral algae which were only observed during the summer months of 1999.

In both June and August 1999, and January and June 2000, there was a significant difference in species number per block between the two sites. Typically there were more species per block at site one than site two. There were, however, no significant differences between the species numbers on the different block types. This was true at both sites and on all the dates sampled. In April 2000 the ranking of species numbers on the different complexity types varied between the two sites. The number of species counted per block, however, was highly variable both within and between block types.

Table (5.1): Summary of ANOVA statistics used to assess the differences in species number between the blocks of differing complexity. (**Significance: *= p<0.05; ** = p<0.01; *** = p<0.001**).

	Jun-99		Aug-99		Sep-99		Nov-99		Jan-00		Apr-00		Jun-00	
Source (d.f.)	**MS**	**F**	**MS**	**F**	**MS**	**F**	**MS**	**F**	**MS**	**F**	**MS**	**F**	**MS**	**F**
Site (1)	0.03	**6.40** *	0.25	**9.30** *	0.00	0.82	0.01	0.50	0.05	6.34	0.06	3.78	0.06	**15.21** *
Block (Site) (8)	0.01	0.35	0.03	2.19	0.00	0.77	0.01	0.96	0.01	0.81	0.02	1.97	0.00	0.94
Topography (3)	0.02	2.00	0.06	5.43	0.01	2.04	0.01	2.71	0.03	2.56	0.00	0.11	0.01	0.97
Site x Top (3)	0.01	0.74	0.01	0.85	0.01	0.96	0.00	0.21	0.01	1.13	0.03	**4.00** *	0.01	2.29
Residual (24)	0.02		0.01		0.01		0.01		0.01		0.01		0.00	

(5.3.2.2.) Species Diversity

The number of animal species on the block types was too low during the first ten months of the experiment to assess species diversity. The numbers present in June were slightly higher so indices were calculated for this time period. It was found that there were no significant differences between the index values derived from the different block types (Table 5.2). Significant differences were, however, apparent between the two sites.

Table (5.2): ANOVA used to assess the differences in species diversity between the blocks of differing complexity.

Source	DF	SS	MS	F	P
Topography	3	0.96	0.32	2.16	0.27
Site	1	1.12	1.12	14.06	**0.01**
Block (Site)	8	0.63	0.08	0.77	0.64
Topography * Site	3	0.45	0.15	1.44	0.26
Residual	24	2.49	0.10		
Total	39	5.65			

(5.3.2.3.) Predominant Species

Species present in sufficiently large numbers to assess densities on the different block types were littorinids, *Fucus* and *Ralfsia*. The numbers of *Gibbula* and *Nucella* on the different treatments could only be assessed later in the time series.

On the first sampling date, two weeks after initial deployment, the only species present in sufficient numbers to assess density was *Littorina littorea*. While there were much fewer of this species at site two than at site one the abundance of the organism at the two sites was too low to analyse statistically. By the second sampling date the overall number of littorinids had increased at both sites; from 29 to 56 at site one and 7 to 11 at site two. The differences in number between the two sites were statistically different (Table 5.3). There were, however, no significant differences between the numbers present on the blocks of differing complexity.

The general pattern for littorinid numbers was an increase in numbers on the blocks over the year until a peak was reached at site one in January 2000. In contrast, at site two numbers continued to increase throughout the entire year of the study. The average number per block, regardless of complexity type, was consistently higher at site one than site two, particularly in the first six months after initial placement (Figure 5.5). These differences were significant in August 1999, November 1999 and January 2000 (Table 5.3).

Typically there were less littorinids on smooth blocks as compared to those with crevices (Figure 5.5). Blocks which demonstrated at least some complexity had similar numbers regardless of the number of crevices. There were only significant differences between the complexity types, however, in September 1999 and January 2000 (Table 5.3). In April 2000 at site two, in contrast to site one, there were less littorinids on the blocks of intermediate complexity level (block B) as compared to those with completely smooth surfaces.

Table (5.3): Summary of ANOVA statistics used to assess the differences in littorinid numbers between the blocks of differing complexity. (**Significance: *= p<0.05; ** = p<0.01; *** = p<0.001**).

	Aug-99		Sep-99		Nov-99		Jan-00		Apr-00		Jun-00	
Source (d.f.)	**MS**	**F**	**MS**	**F**	**MS**	**F**	**MS**	**F**	**MS**	**F**	**MS**	**F**
Site (1)	0.60	**8.25***	0.04	0.43	2.18	**18.72****	3.03	**17.64****	0.13	1.04	0.03	0.29
Block (Site) (8)	0.07	**2.58***	0.09	1.55	0.12	**2.41***	0.17	**4.31****	0.13	**9.08*****	0.09	**2.84***
Topography (3)	0.19	1.01	0.25	**10.96***	0.42	6.97	0.10	**58.41****	0.08	0.81	0.04	6.24
Site x Top (3)	0.19	**6.72****	0.02	0.40	0.06	1.25	0.00	0.04	0.10	**7.42*****	0.01	0.19
Residual (24)	0.03		0.06		0.05		0.04		0.01		0.03	

By the third sampling date, four months after deployment, there was a wider range of species found at greater abundance levels. The most noticeable change was the development of algal cover in terms of both *Ralfsia* spp. and *Fucus* germlings.

The percentage cover of *Fucus vesiculosus* was not affected by the complexity of the surface (Figure 5.6; Table 5.4). The ranking of abundance levels on the different block types varied throughout time. After the initial settlement of the germlings in the Autumn 1999 the algal cover on the blocks increased dramatically in the following spring. The rate of increase was more accelerated at site two than site one particularly between January and April 2000. Significant differences were apparent between the two sites in April and June 2000. At the end of the twelve month period all blocks at both sites had almost one hundred percent cover.

Table (5.4): Summary of ANOVA statistics used to assess the differences in the percentage cover of *Fucus* between the blocks of differing complexity. (Significance: *= p<0.05; ** = p<0.01; *** = p<0.001).

	Sep-99		Nov-99		Jan-00		Apr-00		Jun-00	
Source (d.f.)	**MS**	**F**	**MS**	**F**	**MS**	**F**	**MS**	**F**	**MS**	**F**
Site (1)	0.23	4.52	2.62	4.13	1.46	4.32	29.22	**14.82****	2.02	**9.35***
Block (Site) (8)	0.05	0.81	0.63	**4.11****	0.34	1.63	1.98	**3.01***	0.22	**3.43****
Topography (3)	0.13	0.93	0.27	2.64	0.30	1.78	0.71	0.72	0.44	8.36
Site x Top (3)	0.14	2.27	0.10	0.67	0.17	0.80	0.98	1.50	0.05	0.84
Residual (24)	0.06		0.15		0.21		0.65		0.06	

The percentage cover of *Ralfsia* was again not significantly different across the blocks of differing complexity on any sampling date (Table 5.5). In contrast to *Fucus*, *Ralfsia* increased in abundance at a greater rate at site one than site two. In fact abundance levels remained relatively low and constant at site two throughout the entire period (Figure 5.7).

Table (5.5): Summary of ANOVA statistics used to assess the differences in the percentage cover of *Ralfsia* between the blocks of differing complexity. (Significance: *= p<0.05; ** = p<0.01; *** = p<0.001).

	Sep-99		Nov-99		Jan-00		Apr-00		Jun-00	
Source (d.f.)	**MS**	**F**	**MS**	**F**	**MS**	**F**	**MS**	**F**	**MS**	**F**
Site (1)	0.49	0.49	1.25	0.85	5.43	3.23	8.10	**7.50***	10.26	11.54
Block (Site) (8)	1.00	**4.57****	1.47	**7.50*****	1.68	**8.13*****	1.10	**7.15*****	0.89	7.79
Topography (3)	0.17	0.35	0.18	0.54	0.28	8.29	0.96	2.91	0.48	3.60
Site x Top (3)	0.50	2.28	0.34	1.72	0.03	0.16	0.33	2.19	0.13	1.16
Residual (24)	0.22		0.20		0.21		0.15		0.11	

Barnacle settlement occurred in late spring and was concentrated predominantly on the sides of blocks and covered as much as 70% in some instances. Limpets were again primarily located on the sides of blocks and were not present in sufficient densities on the block surfaces to analyse. Algal species such as *Lithothamnium* and *Laurencia* were only observed on a couple of blocks and hence the results were too variable to be tested.

Nucella lapillus and *Gibbula umbilicalis* were observed at sufficient densities to permit further analysis in the latter months of the experiment. There was no main effect of topographic complexity in determining the counts of these species. There were however, differences in number between the two sites in April 2000, for *G. umbilicalis* and June 2000 for *N. lapillus* (Table 5.6).

Table (5.6): Summary of ANOVA statistics used to assess the differences in *Gibbula* and *Nucella* numbers between the blocks of differing complexity. (Significance: *= p<0.05; ** = p<0.01; *** = p<0.001).

	Gibbula		***Gibbula***		***Nucella***	
	Apr-00		**Jun-00**		**Jun-00**	
Source (d.f.)	**MS**	**F**	**MS**	**F**	**MS**	**F**
Site (1)	0.67	**52.61*** **	0.09	0.62	0.53	**10.35***
Block (Site) (8)	0.01	0.17	0.15	**3.66****	0.05	0.58
Topography (3)	0.19	6.77	0.08	0.57	0.05	0.97
Site x Top (3)	0.03	0.37	0.15	**3.50***	0.05	0.58
Residual (24)	0.07		0.04		0.09	

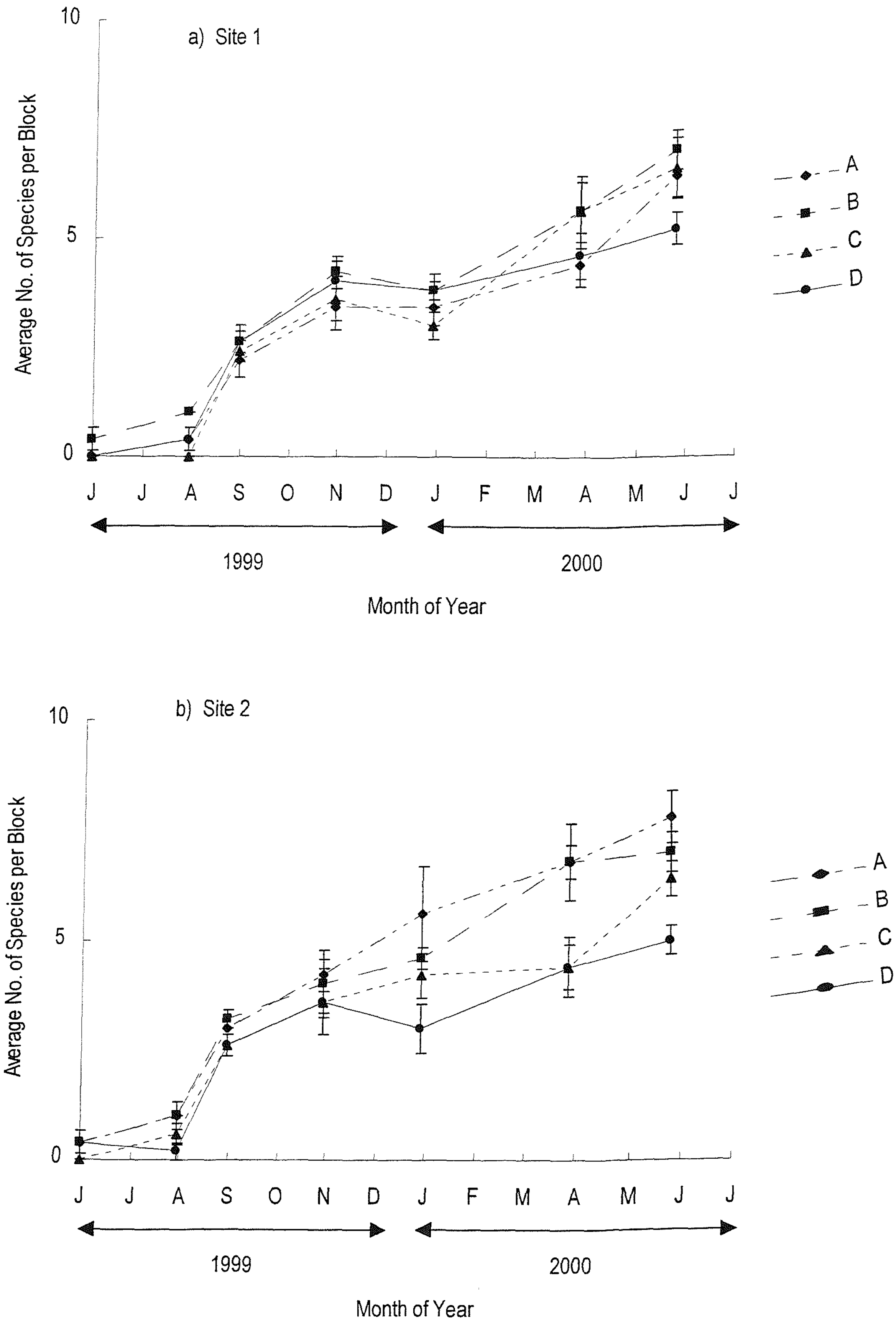


Figure (5.4): The average number of species per block through the time series of the experiment. (± S.E., N=5). (A= smooth, B-D= progressive in complexity).

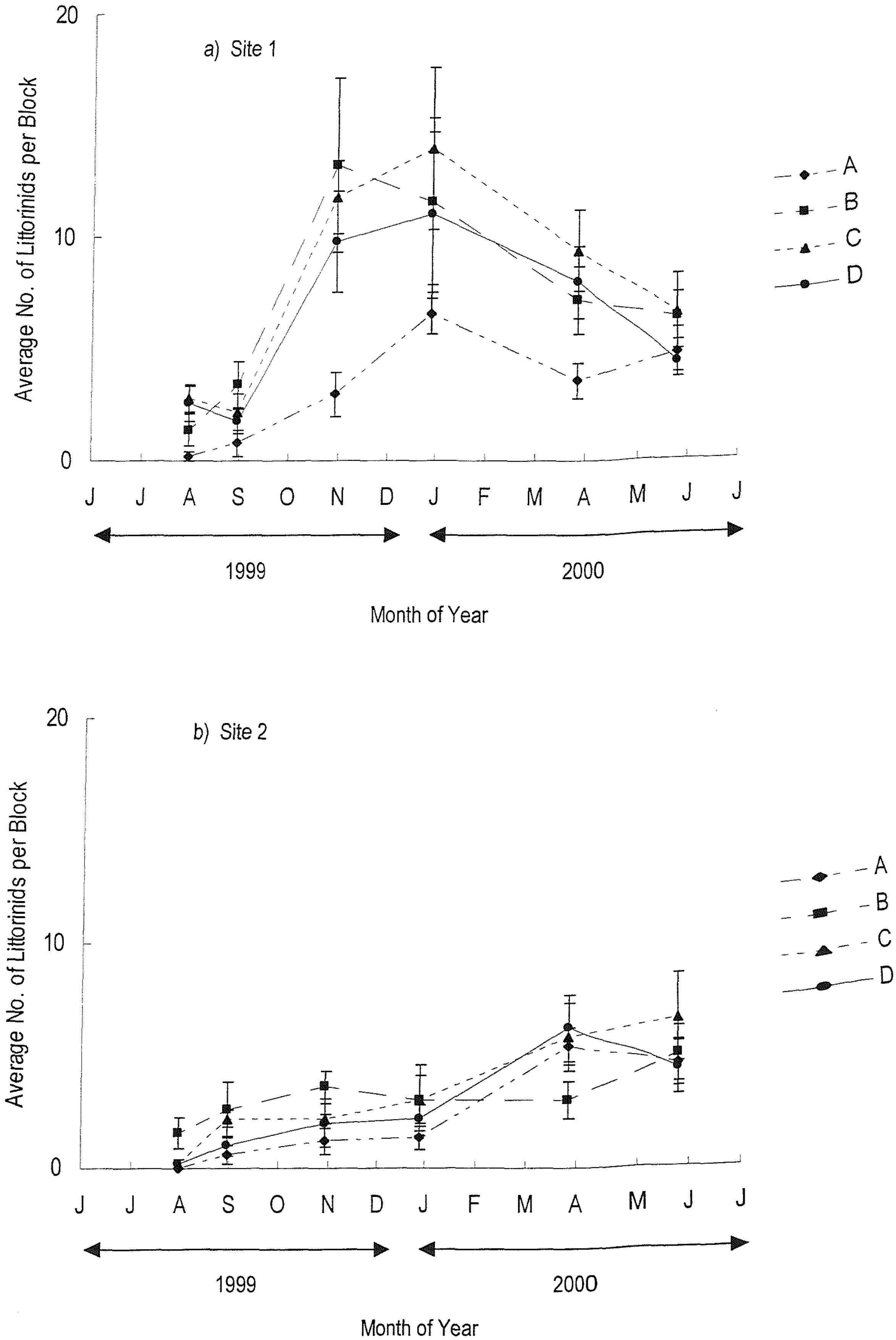


Figure (5.5): The average number of littorinids per block through the time series of the experiment. (± S.E., N=5). (A= smooth, B-D= progressive in complexity).

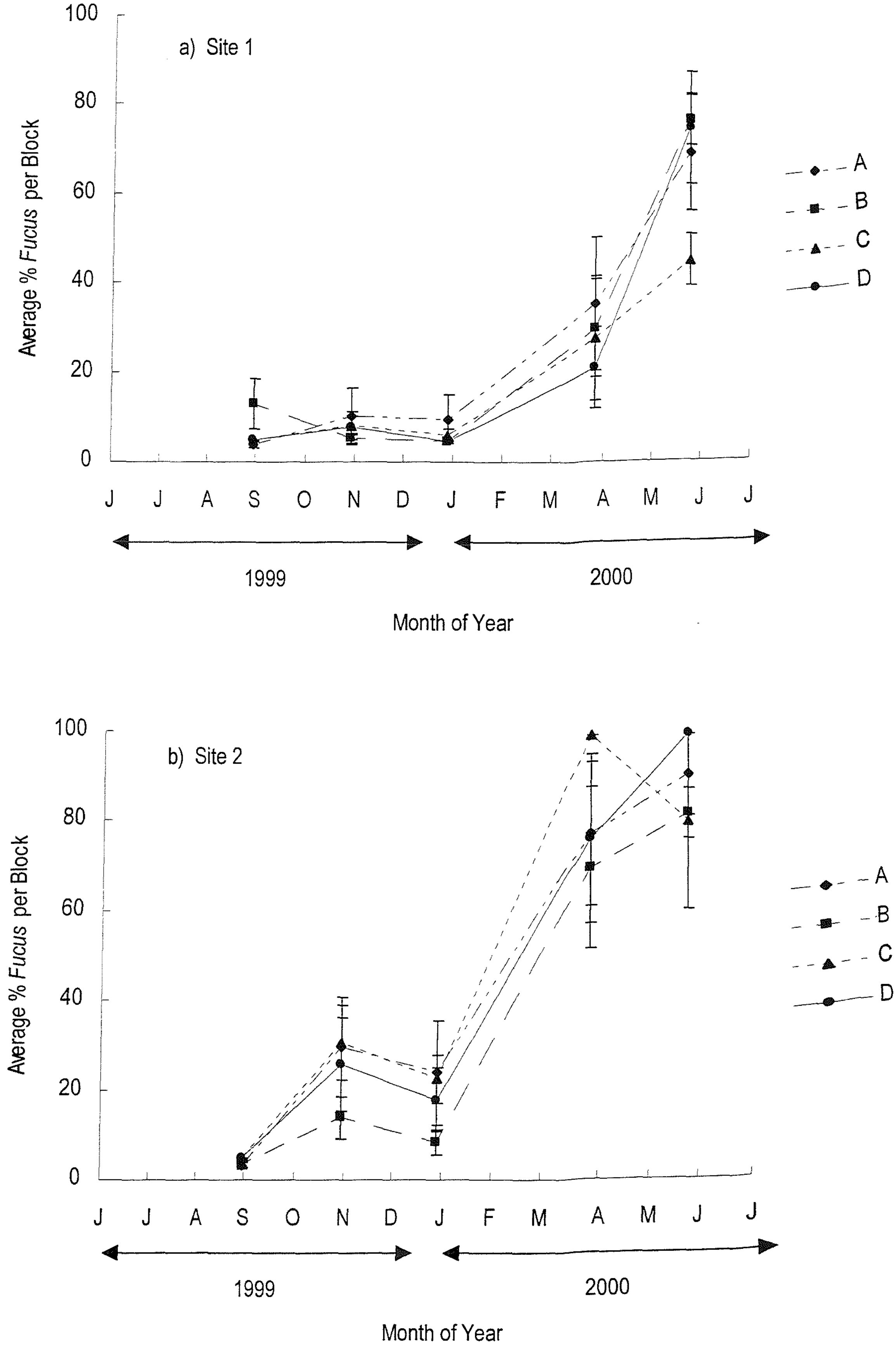


Figure (5.6): The average percentage cover of *Fucus* per block through the time series of the experiment. (± S.E., N=5). (A= smooth, B-D= progressive in complexity).

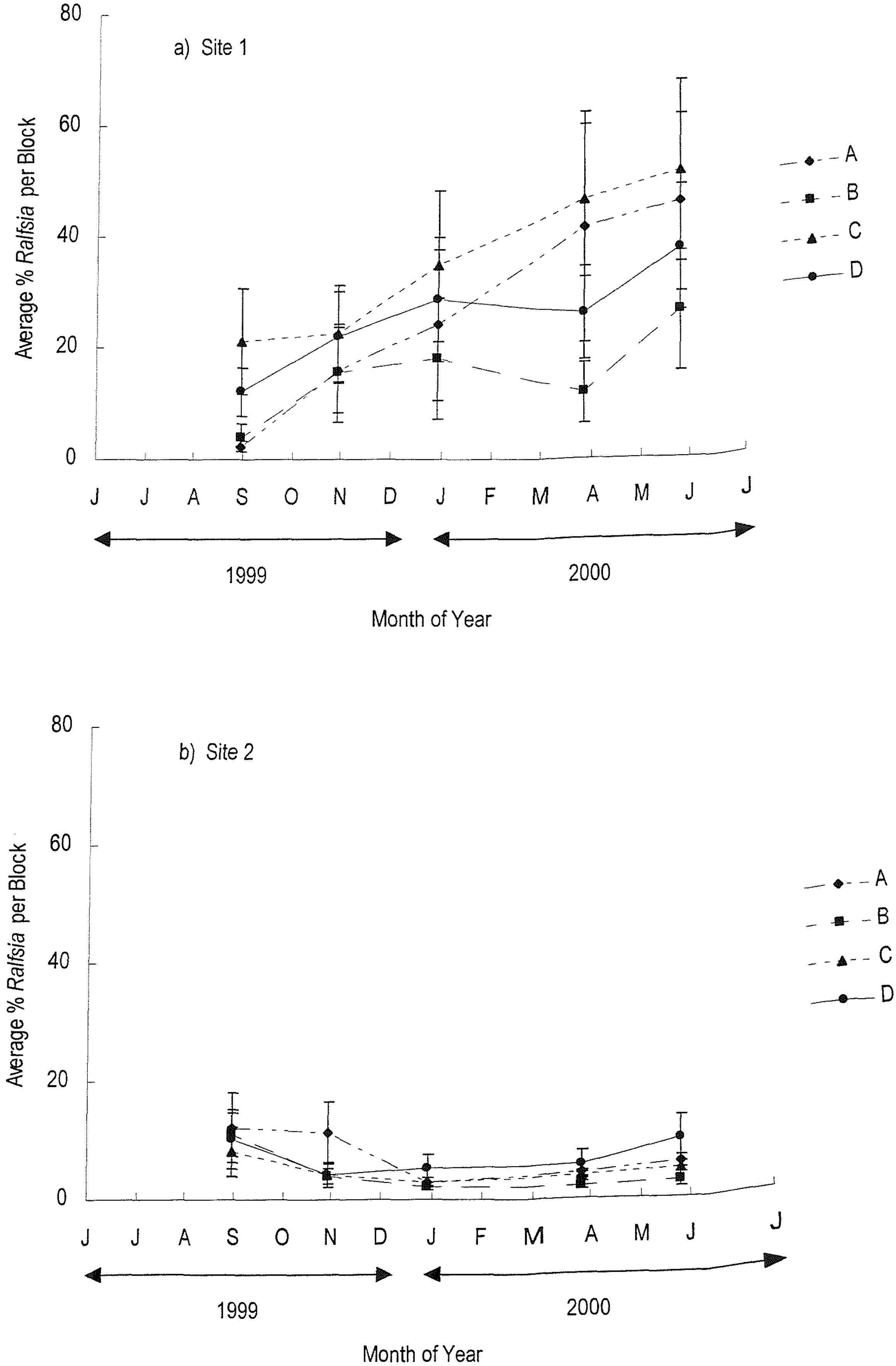


Figure (5.7): The average percentage cover of *Ralfsia* per block through the time series of the experiment. (± S.E., N=5). (A= smooth, B-D= progressive in complexity).

(5.3.3.) Comparisons Between Structural Components

The distribution of species on different topographic features within a block type was also analysed. This could only be conducted for taxa with sufficiently high abundance levels which included littorinids, *G. umbilicalis* and *N. lapillus*. Three dates were selected for this more detailed analysis: August 1999, November 1999 and June 2000. The majority of the animals recorded were located on the sides of the blocks, regardless of its complexity type but these numbers were not included in the analysis. The locations of species with low abundance levels throughout the entire experiment were too variable to draw any general conclusions.

On block type B littorinids were observed in the large central crevice more frequently than would be expected at random both in August and November 1999 (Table 5.7). Numbers on the open flat surfaces at this time were particularly low, with numbers ranging from 62 in the crevices to four on the surface at site one in November 1999. In June 2000, however, there was no significant difference between the observed and expected values on the surfaces or in the crevices. There was no differences in the patterns observed at the two sites on any of these dates.

In August 1999 littorinids were not sufficiently abundant on the more complex block types (C and D) at site two to perform an analysis. At site one at this time, where overall numbers were still low, there was no significant differences between observed and expected values (Tables 5.8 & 5.9). In November 1999 at site one in particular, there were significantly more littorinids in crevices, especially the narrower crevices than expected at random; there were only three littorinids on the surfaces and 28 in each type of crevice. At site two the animals were distributed at random with no preference demonstrated for any particular topographic feature except in block type D. In June 2000 the reverse was true on block type C with significantly more snails in the narrower crevices than would be expected at random at site two and no differences at site one. In June 2000 the littorinids observed on type D were distributed at random across the block features at both sites.

The exact location of *N. lapillus* was analysed at site one as densities were too low at site two. In June 2000, on block type B there were significantly more in crevices than would be expected if the species was randomly distributed. In contrast limpets in June 2000 demonstrated a preference for the open surfaces. The distribution of *Gibbula* in June 2000 was biased towards crevices at site one but no differences were apparent at site two (Table 5.7).

On the more complex blocks (C and D) dogwhelks and limpets only occurred at very low densities. In one instance *Gibbula* were located more frequently in the large central crevice than expected, but otherwise no preferences were apparent (Tables 5.8 & 5.9).

In order to test for differences in percentage cover between the different structural components of a block; the cover on treatments B, C, and D were divided into either surface or crevice. Corrections were made in relation to surface area to make this a realistic comparison between the different block types. On block types B, C and D there were no differences between the percentage cover of *Fucus* and *Ralfsia* in either the crevices or surfaces of a block (Table 5.10a & b). Generally there were no differences between sites, except for *Ralfsia* in June 2000, where percentage cover was typically less at site one than site two.

Table (5.7): Summary of X^2 statistics for comparing the occurrence of species on different structural components of block type B.

	Site 1				Site 2			
Type B	**O**	**E**	X^2	**p**	**O**	**E**	X^2	**p**
Littorinids								
August 1999								
Surface	1	4	4.08	n.s.	0	4.7	9.20	P<0.01
Crevice 1	6	3			8	3.3		
November 1999								
Surface	4	39	74.30	P<0.01	2	11	15.14	P<0.01
Crevice 1	62	27			16	7		
June 2000								
Surface	21	17.1	1.64	n.s.	16	14.2	0.31	n.s.
Crevice 1	8	11.9			8	9.8		
Dogwhelk								
June 2000								
Surface	3	7.1	4.41	P<0.05		Insufficient Data		
Crevice 1	9	4.9						
Limpet								
June 2000								
Surface	13	8.3	5.31	P<0.05		Insufficient Data		
Crevice 1	1	5.7						
Gibbula								
June2000								
Surface	2	7.7	8.50	P<0.01	6	6.5	3.76×10^{-5}	n.s.
Crevice 1	11	5.3			5	4.5		

Table (5.8): Summary of X^2 statistics for comparing the occurrence of species on different structural components of block type C.

	Site 1				Site 2			
Type C	O	E	X^2	p	O	E	X^2	p
August 1999								
Surface	0	3	4.88	n.s.	0	0.25	1.5	n.s.
Crevice 1	5	4.8			1	0.4		
Crevice 2	7	4.2			0	0.35		
November 1999								
Surface	3	15	12.80	P<0.01	1	2.75	4.95	n.s.
Crevice 1	28	24			8	4.4		
Crevice 2	28	21			2	3.85		
June 2000								
Surface	11	8.5	5.35	n.s.	8	8.25	8.74	P<0.05
Crevice 1	7	13.6			6	13.2		
Crevice 2	16	11.9			19	11.55		
Dogwhelk June 2000								
Surface	4	2.3	1.88	n.s.		Insufficient Data		
Crevice 1	3	3.6						
Crevice 2	2	3.2						
Gibbula June2000								
Surface	0	1.5	2.57	n.s.	0	2.5	7.14	P<0.05
Crevice 1	4	2.4			8	4		
Crevice 2	2	2.1			2	3.5		

Table (5.9): Summary of X^2 statistics for comparing the occurrence of species on different structural components of block type D.

	Site 1				Site 2			
Type D	O	E	X^2	p	O	E	X^2	p
Littorinids August 1999								
Surface	3	3	0.02	n.s.			Insufficient Data	
Crevice 1	5	4.8						
Crevice 2	4	4.2						
November 1999								
Surface	2	12	23.49	P<0.01	0	2.5	6.25	P<0.05
Crevice 1	14	19.2			3	4		
Crevice 2	32	16.8			7	3.5		
June 2000								
Surface	5	5	1.07	n.s.	7	5	1.07	n.s.
Crevice 1	6	8			7	6.8		
Crevice 2	9	7			6	7		

Table (5.10a): Summary of ANOVA statistics used to assess the differences in the percentage cover of *Fucus* on either the surfaces or crevices of each block.
(Si= Site, Bl= Block, To = Topographic complexity, SC= Structural component.)
(Significance: *= p<0.05; ** = p<0.01; *** = p<0.001).

	Sept-99		Nov-99		June-00	
Source (d.f.)	**MS**	**F**	**MS**	**F**	**MS**	**F**
Site (1)	0.58	2.49	3.55	3.06	9.64	2.82
Block (Site) (8)	0.23	**2.22***	1.16	**10.91*****	3.42	**4.48****
Topography (2)	0.00	0.01	0.67	1.70	1.22	2.72
Structural Comp. (1)	0.47	1.16	1.62	6.57	0.00	3.73
To X SC (2)	0.17	2.65	0.37	16.09	0.00	1.25
Site x To (2)	0.24	2.24	0.40	**3.72***	0.45	0.59
Site x SC (1)	0.40	3.79	0.25	2.32	0.00	0.00
Site x To X SC (2)	0.60	0.60	0.02	0.22	0.00	0.00
Residual (40)	0.11		0.11		0.76	

Table (5.10b): Summary of ANOVA statistics used to assess the differences in the percentage cover of *Ralfsia* on either the surfaces or crevices of each block.
(Si= Site, Bl= Block, To = Topographic complexity, SC= Structural component.)
(Significance: *= p<0.05; ** = p<0.01; *** = p<0.001).

	Sept-99		Nov-99		June-00	
Source (d.f.)	**MS**	**F**	**MS**	**F**	**MS**	**F**
Site (1)	0.11	0.09	4.82	2.31	13.74	**8.52***
Block (Site) (8)	1.24	**6.88*****	2.10	**15.65*****	1.61	**15.08*****
Topography (2)	0.78	1.10	0.28	1.08	1.40	3.93
Structural Comp. (1)	2.16	46.58	1.23	20.17	1.01	1.00
To X SC (2)	1.30	**68.32***	0.11	0.85	0.04	1.00
Site x To (2)	0.71	**3.94***	0.26	1.95	0.36	**3.35***
Site x SC (1)	0.05	0.26	0.06	0.46	1.01	**9.48****
Site x To X SC (2)	0.02	0.11	0.13	0.97	0.04	0.34
Residual (40)	0.18		0.14		0.11	

(5.4.) DISCUSSION

(5.4.1.) The Use of Artificial Surfaces

The use of artificial substrata to assess the effects of complexity offers a number of advantages over direct field measurements. Firstly replication is simplified and the spatial scales under investigation can be readily quantified. Additionally the advantage of repeated non destructive sampling allows detailed studies of both short and long term changes during community development. It is important, however, that artificial substrata are realistic and representative of naturally occurring habitats so as not to confound the understanding of the effects of habitat structure on species distributions (Beck, 2000).

The blocks constructed in this study where kept relatively simple and were designed to represent topographical features occurring on natural surfaces. Sanson *et al.*, (1995) showed that their blocks were within the natural range of texture shown by stream stones. In contrast some experiments have designed structural components that bear little or no relationship to those naturally observed (e.g. Bourget *et al.*, 1994; Jacobi & Langevin, 1996; Lemire & Bourget, 1996). Artificial components are often assumed to resemble natural components, but this assumption is rarely tested (e.g. Hart, 1978; Russ, 1980; Gilinsky, 1984; Bell *et al.*, 1987; Gunnarsson, 1992; Caley & St. John, 1996).

The species observed on the blocks in this study were typical of those observed on adjacent natural boulders; a result consistent with previous investigations. Caffey (1982), for example, demonstrated no differences in recruitment of an abundant local barnacle or numerous mobile species to many different rock types. McGuiness & Underwood (1986) concluded that the artificial blocks placed on to a boulder shore typically reflected the natural community. Bricks placed into streams have also been colonised at similar rates to natural stones (Downes & Lake, 1991; Douglas & Lake, 1994; Downes *et al.*, 1998). In contrast Jacobi & Langevin (1996) found that the amphipod community on artificial substrata did not reflect the distribution on nearby natural substrata.

Abundance levels, with the exception of *Ralfsia* were also typical of the surrounding area. The high percentage occurrence of *Ralfsia* as compared to the adjacent natural boulders has been observed previously. McGuiness & Underwood (1986) found that the algae *Ulva* and *Ralfsia* were more abundant on concrete than natural boulders, probably because the porous concrete reduced stresses associated with emersion and thus favoured the growth of these species.

(5.4.2.) Colonisation Sequence

The species first to occur on the blocks were mobile taxa present on the nearby substratum. The following changes in patterns of species composition appeared to be as a consequence of both the mobility of faunal species and the seasonal variations in the abundance of larvae. This pattern was also observed by Turner & Todd (1993) in the development of a community on artificial surfaces.

The timing of the placement of the blocks is also likely to have influenced the development of community patterns. Ephemeral species and *Fucus vesiculosus* germlings were observed at times consistent with those expected in natural assemblages (Hawkins, 1981; Hawkins *et al.*, 1992). In a typical successional sequence *Fucus* plants typically occur after ephemeral species have been removed, either by grazers or environmental disturbance (Lubchenco, 1983). In this instance the date on which the blocks were placed in the field was after the date of the typical peak in ephemeral abundance (Moore, 1939; PyeFinch, 1943; Hawkins 1981). *Fucus* plants could therefore establish themselves directly on the block surfaces (Hawkins *et al.*, 1992).

The distribution of barnacle settlement, which largely occurred on the sides of the blocks, can also be explained by the timing of placement. *S. balanoides* settled during the spring 2000, at a time when *Fucus* plants were already large and covering the top surfaces of the blocks. These large plants may have hindered settlement by both competition for space and by the sweeping action of the fronds (Lewis, 1964; Dayton, 1971; Menge, 1976; Hawkins, 1983; Hawkins & Hartnoll, 1983; Jenkins *et al.*, 1999a; Leonard, 1999). Some barnacles *Tesseropora rosea*, for example, do not settle at all amongst algae (Denley & Underwood, 1979).

Results regarding species number and diversity were not consistent with the commonly held view that increased habitat complexity leads to increased richness and diversity (O'Connor, 1991; Douglas & Lake, 1994; Downes *et al.*, 1995, 1998; LaPointe & Bourget, 1999). This is typically explained by the fact that surface modifications are likely to have produced new microhabitats. LaPointe & Bourget (1999), for example, noted that the V-shape in artificial panels may have provided a refuge against predation and adverse physical conditions; a factor increasing diversity on the panels.

There are several reasons that could explain the lack of differences in diversity between block types. Firstly the overall abundance levels of organisms on the blocks was low and this may have prevented any differences being detected between the block types. The results obtained here may also be explained by the highly variable nature of the data obtained from both within and between block types. Turner & Todd (1993) and Bourget *et al.*, (1994) found that recruitment of all species was variable both temporally and spatially. Other physical and biological parameters would also be operating in the environment and affecting the overall pattern of species distributions. McGuiness & Underwood (1986) found that the effects of habitat structure interacted with, and were dependent upon the intensity of a variety of other biotic and abiotic factors. Such factors could vary from place to place and lead to inaccurate estimates of the importance of the effects of habitat structure on community patterns.

The results were, however, in agreement with Bourget *et al.*, (1994) where both substratum heterogeneity and complexity had little influence on diversity and abundance during the early phases of community development. LaPointe & Bourget (1999) described time as the most important factor affecting abundance. Similarly Downes *et al.*, (1995, 1998, 2000) found that species richness and numbers of individuals were higher on rough stones than on smooth, but appeared unrelated to the numbers of large pits and crevices present. McGuiness & Underwood (1986) also found that there were significant effects of pits and grooves but that these did not usually result in the blocks with the greatest surface complexity having most species.

Differences in diversity between the sites could be explained by the proximity of the blocks to the nearest cliff; a potentially large source of mobile fauna. The blocks at site one were positioned closer to the cliff edge than the blocks at site two and hence would be more accessible to a potentially large reservoir of species; analogous to the theory of island biogeography (MacArthur & Wilson, 1967; Fridriksson, 1975; Willaimson, 1981). The substratum at site two was also more sandy and less stony at site two than site one making it potentially harder for animals to move across this substratum. The differences detected between the two sites in the very early stages of the analysis could have been accentuated by the human interference that occurred at site two.

(5.4.3.) Differences Between Block Types

Littorinids were the first and only grazing taxa to become abundant on the blocks throughout the year. This may be a reflection of high densities of these taxa in the surrounding area (pers. obs., 2000). These snails are also highly mobile and capable of moving across complex surfaces and sediments (Underwood & Chapman, 1989; Kostylev, 1996). The lack of difference in the overall numbers on the different block types during the first two months of the experiment was probably as a result of the very low abundance levels at this time. The effect of topography on species distributions may therefore interact with the supply of individuals.

Differences in total littorinid numbers between each of the block types became apparent in September 1999 and remained until the following spring. Numbers were always least on the smooth blocks, but there were no differences in snail densities between the three complexity types. Indeed, when examining numbers of littorinids within the separate structural components snails were typically found in crevices during this same time period. Some variability between dates may also have been introduced by factors such as climate and wave action (Dayton, 1971; Underwood, 1980; Garrity & Levings, 1984; Moran, 1985).

The association of littorinids with crevices can be explained by the protection provided by these structures. Crevices provide protection from physical factors such as wave action and temperature stress (e.g. Underwood, 1980; Levetin & Kohn , 1980; Garrity & Levings, 1984; Behrens Yamada, 1992; Hughes, 1995). Habitat complexity can also modify biological interactions by providing a refuge from predation and altering competition (Bertness *et.*, 1981; Garrity & Levings, 1984; Walters & Wethey, 1986). Crevice size and availability are thus likely factors causing variations in the population structure of crevice dwelling snails (Raffaelli & Hughes, 1978). This is not the case for all species, however, as distributions of *Littorina unifasciata* could not be explained by topographic features (Underwood & Chapman, 1989).

Differences in littorinid number between each block type were no longer apparent by April 2000. Littorinids were also less associated with crevices at this latter time period as compared to earlier in the time series. This was probably due to the large increase in percentage cover of *F. vesiculosus* during the spring months of the year. The large plants would have provided a secondary structure under which snails could take refuge from adverse conditions.

Previous studies have highlighted the importance of the physical properties of macroalgal canopy in providing shelter for herbivores (e.g. Reed & Foster, 1984; Lubchenco, 1986; Chapman, 1989; Chapman & Johnson, 1990). Stones with an algal covering have also been shown to have greater species richness and different faunal compositions to bare stones (Downes *et al.*, 1995). Jacobi & Langevin (1996) found that the effect of the original substratum complexity seemed to be restricted to the early stages of colonisation, since after twelve weeks of immersion the original geometry was greatly modified by fouling organisms. Furthermore the importance of biologically generated habitat provision in enhancing biodiversity has been well documented (e.g. Suchanek, 1979; Tsuchiya & Nishihira, 1985; Thompson *et al.*, 1996; Downes *et al.*, 1998, 2000).

There was no difference in the percentage cover of *Fucus* and *Ralfsia* on the different block types. This was despite the numbers of grazers being different on each treatment. One possible explanation, relating specifically to *Fucus*, is that any effects generated by topography may have been masked by measuring percentage cover rather than exact counts of holdfasts. Secondly at the start of the experiment the blocks were essentially free of grazers. Until such species became abundant they are unlikely to have had an impact on algal density (Jones, 1948; Southward, 1964; Hawkins & Hartnoll, 1983; Liu, 1994). Plants therefore had a couple of months in which to get established and cover all regions of the blocks. Once plants attain a certain size they are also less susceptible to damage from grazers (Lubchenco, 1983). There were however, sufficient differences in grazer density between the two sites to affect growth and abundance levels of *Fucus* plants.

In previous studies substratum complexity has been shown to affect algal abundance (e.g. Dudley & Antonio, 1991; Sanson *et al.*, 1995). In particular, grooves have acted as sediment traps and possibly sites for higher growth rates of algae (Douglas & Lake, 1994). In contrast Downes *et al.*, (1998) found that algae was less abundant on blocks with large crevices than those without. McGuiness & Underwood (1986) also found fewer algal species where there were pits on the blocks.

In contrast to *Fucus, Ralfsia* was more abundant at site one than site two and this may represent a difference in grazing resistance between the two species. Gaines (1982), for example, found *Ralfsia* to be relatively resistant to grazing. Menge & Lubchenco (1981) also found that *Ralfsia*, being a crustose algae, was capable of growing in the presence of grazers. In accordance with Menge *et al.*, (1983) this experiment suggested that early stages of succession on a substratum may reflect the local grazing regime of an area.

The reduction in *Ralfsia* at site two as compared to site one may also be as a result of the large *Fucus* cover at this site. *Fucus* cover may outcompete the encrusting species for limiting factors such as light and space. Indeed overgrowth is considered to be an important mechanism in the competition for space (Schoener, 1983; Denley & Dayton, 1985; Sebens, 1986; Airoldi, 2000). Encrusting algae are widely considered as subordinate to algae of other morphologies in their ability to compete for space (Littler & Littler, 1980; Breitburg, 1984; Dethier, 1994; Steneck & Dethier, 1994). *Fucus*, not unlike mussels beds, could also act as a sediment trap which again causes changes to the microhabitat (e.g Sebens, 1991).

Other species observed such as limpets, dog whelks and top shells were not recorded in sufficient densities to detect any differences between block types. In the one instance where the data was analysed (June 2000) the results would again have been affected by the large abundances of *Fucus*. Crevices have also been reported to affect the distribution of the chiton *Sypharochiton pelliserpentis* (Boyle, 1970) but again frequencies were too low to detect any patterns here.

(5.4.4.) Small Scale Patterns – Within Blocks

The refuge provided by crevices for littorinids has already been discussed; preferences for the size of crevices will now be addressed. On the more complex block types (C and D) there were occasional preferences for the narrower rather than wider crevices. Snails will achieve maximum protection from harsh environmental conditions by wedging themselves tightly into crevices. In the case of large V shaped crevice, a small snail must crawl a greater distance down into the crevice before it becomes wedged than in a narrower structure. The use of smaller crevices may therefore be a much more energy efficient method of protection (Raffaelli & Hughes, 1978). Littorinids also move randomly when foraging so this will affect the crevices that are occupied during periods of emersion (Underwood, 1977).

Dogwhelks also seek refuge in crevices from harsh environmental conditions (Dayton, 1971; Yamada, 1977; Menge *et al.*, 1985; Moran, 1985; Gosselin & Bourget, 1989; Jones & Boulding, 1999). In this case dogwhelks were largely found on the sides of the blocks. This may be a direct result of the location of their main prey species, barnacles (see Menge, 1976). The lack of effects demonstrated by dogwhelks may also be due to insufficient temporal sampling. The variation in numbers between crevices and open rock surfaces can occur over a matter of days depending on the weather and tide (Moran, 1985; Burrows & Hughes, 1989; Hughes *et al.*, 1992). Limpets were also present on the sides of the blocks, with large flat areas possibly easier to graze than complex surfaces (Burrows & Lodge, 1950; Little *et al.*, 1988; Erlandsson *et al.*, 1999).

It was expected that algal species such as *Fucus* and *Ralfsia* would be less abundant in crevices due to the sheltering of herbivores; this, however, was not the case. With regard to *Fucus*, again, any pattern generated by differences in topography may have been masked by the fact analyses were based on percentage cover rather actual plant numbers.

A clear gradient in percentage cover of *Ralfsia* was, however, detected in crevices, where the species was least abundant at the greatest depths. Menge *et al.*, (1983) observed a similar gradient pattern in holes on tropical shores and attributed the differences to differential grazing. Grazing depends on size and scale of both the crevices and the consumers (Choat, 1977: Hawkins, 1981; Lubchenco, 1983, Menge, 1983). It is suggested that homogenous surfaces tend to be experience uniformly intense grazer pressure but grazing in holes is more variable in space and time. As a consequence the biotic composition of holes varies tremendously (Menge *et al.*, 1983).

(5.4.5.) Conclusions, Limitations and Future Work

The numbers of species observed on the blocks was highly variable both within and between block types. There were no significant differences in either species number or diversity between the different block types. Littorinids were typically associated with crevices in the early stages of succession. After this time *Fucus* plants had reached a size that provided an equivalent refuge to that of crevices; snails were therefore observed on all structural components. Despite differences in grazer abundance on the different block types algal abundance was not significantly different across the treatments. Sufficient differences in grazer density, however, existed between the two sites to cause differences in algal abundance.

Habitat complexity played an important role in determining the distribution of faunal species in the early stages of community development. The resulting communities after a twelve month period were not significantly affected by the original habitat configuration of each treatment.

The study could be furthered by the destructive sampling of the blocks. The exact locations of hold fasts could be established and this may provide a more complete description of the impact of grazers and topography on algal biomass. Blocks of similar designs could also be placed into locations experiencing different environmental conditions such as wave exposures and tidal heights. To assess the affect of the proximity of the blocks to a potential reservoir of species, each treatment could also be placed at different distances to cliff edges. In addition the supply of individuals to the blocks of differing complexity could be manipulated to test for an interaction between these two factors. This would also serve to remove the effect of a grazer exclusion zone at the start of the experiment. The complexity of a habitat may interact with other environmental parameters to produce the observed community patterns; considerations therefore need to relate to both of these factors in order to gain a true understanding of the importance of topographic features in shaping intertidal assemblages.

6. Mussel Patch Dynamics on Exposed Shores of the North East Atlantic Coast

(6.1.) INTRODUCTION

Community structure can be described in terms of patterns in space and time of species abundances and distributions. Spatial distributions can be considered at many scales of resolution. The smallest is the scale occupied by a single organism or in which a mobile organism spends its life, a patch is occupied by many individuals and a region includes more than one patch or population linked by dispersal. Finally there is a biogeographic scale of resolution (Wiens *et al.*, 1986). On rocky shores, patch structure in particular has received a considerable amount of attention (Lewis, 1964; Stephenson & Stephenson, 1972; Paine & Levin, 1981; Sousa, 1985; Hartnoll & Hawkins, 1985; Sgrott Sauer Machado *et al.*, 1992). The generation and filling of space on the rocky substratum leads to a constantly changing mosaic of patches varying in both physical dimensions and biological characteristics (Paine & Levin, 1981; Sousa, 1984).

Information on the patchiness of species and resources is used in many ecological models and in generating ecological theory over a number of spatial scales (Pickett & White; 1985; Kolasa & Pickett, 1991). Moreover, identifying spatial patterns is important in improving the design and interpretation of surveys and experimental studies through relating sampling programmes to natural scales of variation (Levin, 1992; Legendre *et al.*, 1997; Petraitis & Latham, 1999; Underwood *et al.*, 2000). Mussel beds are one of the most conspicuous examples of patch formation occurring epibenthically on both hard and soft substrata (Stepehenson & Stephenson, 1972; Suchanek, 1986; Svane & Ompi, 1993; Petraitis, 1998). As they biologically generate topographic complexity they were selected to be described and examined in the current study. Knowledge of mussel bed spatial patterns may be particularly useful because growth, survivorship and recruitment for several mussel species have been shown to be dependent on the spatial position of individuals (Archambault & Bourget, 1996; Hunt & Scheibling, 1996; Reusch & Chapman, 1997).

Mussels settle densely and grow quickly to reproductive size, often occupying 75 to 80% of the substratum soon after settlement (Suchanek, 1978). These characteristics, combined with their relative mobility compared to other space occupying intertidal species, lead to the competitive superiority of the mussels (Paine, 1966; Menge, 1976; Seed, 1976; Lubchenco & Menge, 1978; Paine, 1994), often resulting in extensive mussel beds on many rocky shorelines worldwide (Lewis, 1964; Stephenson & Stephenson, 1972; Paine & Levin, 1981; Suchanek, 1986; Petraitis, 1995, 1998). The upper limits of these zones appear to be controlled by physical factors such as temperature (heat or freezing) and/ or desiccation (e.g. Seed, 1969b; Suchanek, 1981). Lower limits seem to be more under the control of intra- or interspecific competition or predation by a wide variety of taxa, both invertebrate and vertebrate (e.g. Paine, 1966, 1971, 1974).

The factors maintaining mosaics in mussel populations requires the consideration of three distinct phases: patch creation, patch colonisation, and the patch dynamics of established mosaics (Paine & Levin, 1981; Sousa, 1985). Gaps or patches in general are created by spatial variation in processes such as physical disturbance (Paine & Levin, 1981; Sousa, 1985), settlement and recruitment (Gaines & Roughgarden, 1985; Vadas *et al.*, 1992), grazing (Hawkins & Hartnoll, 1983; Jernakoff, 1983; Johnson *et al.*, 1997), predation (Fairweather, 1988; Hunt & Scheibling, 1998) and competition (Dayton *et al.*, 1984).

Complete monopolisation of space by *Mytilus californianus* has been shown to be prevented by localised disturbances (Sousa, 1984). Disturbances are events, either abiotic or biotic in origin, that destroy biomass, affecting from one organism to entire communities (Denny *et al.*, 1985). The role of disturbance in structuring communities has been viewed in a number of ways: (1) as a "negative" force that destroys climax assemblages, causing deterioration of the ecosystem to an unstable state (Clements, 1936), (2) as a "positive" force preventing competitive exclusion by dominants and thus allowing increased diversity (Paine, 1966; Lubchenco, 1978; Huston, 1979), or (3) as a "necessary" portion of community dynamics and the means by which regional steady states are maintained (Watt, 1947; Sprugel, 1976; Woodin, 1978; Reiners & Lang, 1979).

Physical disturbance by storm generated waves is an important structuring force for intertidal mussels on rocks (Dayton, 1971; Paine & Levin, 1981; Witman & Suchanek, 1984; Witman, 1987; Reusch & Chapman, 1995). Denny (1987) has calculated that fluid dynamic lift forces generated by breaking waves can be large enough to remove mussels from beds on emergent substrata, initiating gap formation. Mussels, however, are more susceptible to dislodgement by waves if they 'hummock' to form a mat several individuals thick, since the mussels in the centre of the hummock lose contact with the substratum (Seed, 1969b, Dayton, 1971). The growth of algae on mussels can also serve to increase drag and lead to patch initiation (Dayton, 1973; Witman & Suchanek, 1984; McCook & Chapman, 1991). Alternative physical factors include localised battering by logs (Dayton, 1971), scouring (Shanks & Wright, 1986) and larger scale stochastic events such as massive mussel losses when a severe freeze coincided with a spring low tide (Carroll & Highsmith, 1996).

Biological causes of patch formation include both competition and predation. Intraspecific competition can cause mortality as a result of overcrowding which results in either diminished food intake or subsequent instability of the mussel matrix and detachment by strong wave action (Seed, 1969b; Suchanek, 1986; Seed & Suchanek, 1992). Self thinning is the reduction in population density caused by competitively induced losses within a cohort of mussels. Individual growth cohorts of mussels is accompanied by density dependent disappearance (self-thinning), with the result that, over the course of time, mean individual mass, is related to population density by an exponent of approximately $-^{3}/_{2}$ (Hughes & Griffiths, 1988).

Predation on mussels can also have dramatic effects on intertidal community structure on temperate rocky shores (Paine, 1966, 1974; Menge, 1976; Lubchenco & Menge, 1978; Robles, 1987; Robles & Robb, 1993; Carroll & Highsmith, 1996; Hunt & Scheibling, 1998; Smith & Jennings, 2000). Predators include shorebirds, fishes, asteroids, decapod crusataceans and whelks (Kitching *et al.*, 1959; Paine, 1966, 1974; Menge, 1978; Suchanek, 1978; Meire & Ervnyck, 1986; Ojeda & Dearborn, 1991; Dolmer, 1998). It is important to remember, however, that the relative importance of physical and biological parameters may vary depending on the location examined. Noda (1999), for example, observed that the spatial pattern of mussel mortality was defined by the density of *Nucella canaliculata*, but not related to mortality by wave dislodgement.

Patch recovery has also been recognised and documented (Paine & Levin, 1981; Suchanek, 1986). The closure or recovery process of gaps can occur in a number of ways: recruitment, growth and immigration (Paine & Levin, 1981; Tokeshi & Romero, 1995). Mussel recovery rates may vary with several factors including patch size, season, height on the shore, angle of the substratum, thickness of mussel bed and larval recruitment (Paine & Levin, 1981; Suchanek, 1981, 1986; Paine, 1984; Seed & Suchanek, 1992). Although rates of recovery from disturbance in mussel beds vary, the process is thought to be deterministic (Suchanek, 1986), with mussels predictably returning to dominance. However, this is not always the case; minimal post disturbance recovery of mussel populations as a result of *Nucella lima* predation has been observed (Carroll & Highsmith, 1996).

In small disturbance patches 'healing' may be achieved by mussels leaning over, especially when adjacent mussel beds are relatively thick (Paine & Levin, 1981; Suchanek, 1986). Subsequent recovery of the patch can occur by inward movement of the perimeter mussels (Paine & Levin, 1981). Although apparently sessile, adult mytilids retain a degree of mobility via their foot and byssus retractor muscles: mussels have been observed 'rolling and re-attaching' to patches of clear rocky substratum (Suchanek, 1986) and reforming mussel banks following their destruction by storms (Seed, 1976). Patches of mussels facing high mortality may also show no change in substrate cover as long as growth by the remaining survivors can fill the vacant space (Petraitis, 1995).

Larger gaps are more likely to require successful invasion by planktonic propagules (Paine & Levin, 1981). Initially the dispersal of larvae will affect the observed recruitment patterns and this can be predicted from hydrographic data (McQuaid & Phillips, 2000). The maximum effective dispersal of mussel larvae in South Africa was shown to be relatively limited (<100km), with the great majority of successful recruits appearing within less than 5km of the parent population (McQuaid & Phillips, 2000). Generally there is also an increase in larval supply with increased water flux (Hunt & Scheibling, 1996).

Recruitment, however, may act in one of three ways: firstly it may enhance mosaic structures as larvae settle in amongst adults, alternatively it may fill gaps between existing mussel beds or finally a combination of these processes may be in operation. The patchy distribution of mussels within some shores, for example, is likely to be enhanced by what appears to be preferential settlement of larvae in adult clumps (e.g. McGroty *et al.*, 1990; Hunt & Scheibling, 1996; Harris *et al.*, 1998; Chiba & Noda, 2000). Nevertheless, Petraitis (1991), in a study of recruitment at six localities on the coast of Maine, showed that recruitment was not correlated with cover of adult mussels nor with availability of bare space. Suchanek (1986) also observed that recolonisation of artificially induced $0.10m^2$ disturbance patches in *M. californianus* beds was predominantly through primary and secondary settlement.

It is generally considered that the settlement of mussel larvae is a two stage process (Bayne, 1964). In the first instance mussels are usually associated with filamentous substrata or small crevices and depressions in the rock surface (Seed, 1976; Seed & Suchanek, 1992; Caceras-Martinez *et al.*, 1994; Davis & Moreno, 1995; Pulfrich, 1996). It is not fully agreed, however, whether the settlement process is passive (Harvey *et al.*, 1995) or whether it involves active larval choice (Bourget *et al.*, 1994). Subsequent studies have shown that movement of post larval mussels, whether by drifting in the water column on threads of mucus (Sigurdssin *et al.*, 1976; Lane *et al.*, 1985) or by crawling along the substratum (Seed & Suchanek, 1992; Caceras-Martinez *et al.*, 1994), may be important in determining the distribution pattern of recruits. However, settlement behaviour of *Mytilus* appears to vary considerably among populations (e.g. *M. edulis* & *M. trossulus*; Hunt & Scheibling, 1996). The rate of colonisation also varies with patch size and position. This pattern may be explained by the hydrographic environment of a patch edge created by the flowing tides (Svane & Ompi, 1993). In addition, the settlement of *Mytilus edulis* larvae is strongly influenced by light (Crisp, 1976); the shaded conditions along edges of patches may therefore facilitate settlement.

The processes involved in the generation and closure of gaps lead to a dynamic system reflected in the cover of major space occupying species. The phrase 'patch dynamics' embraces disturbance external to an organism assemblage (community) as well as internal processes of change and variation occurring at many scales of observation (Pickett & White, 1985). Indeed patch dynamic models have been developed to describe processes occurring within patches and successional mechanisms of species replacement and patch closure (Paine & Levin, 1981; Petraitis, 1981). A complete understanding of mussel dominated communities therefore requires the characterisation of the scales, patterns and processes that are in operation in such environments.

(6.1.1.) Aims and Objectives

The overall aim of this work was to assess both temporal and spatial variability in mussel patches. Firstly, a nested analysis of variance was employed to measure heterogeneity in mussel patches at a range of temporal and spatial scales. In addition spatial autocorrelation was used to quantify more specific patch dimensions. To follow the dynamics of individual patches over the period of one year marked quadrats were set up and photographed at regular intervals. This allowed the testing of specific hypotheses relating to the turnover of individual mussel patches. The first null hypothesis tested was that the loss or gain of mussels would not be density dependent and the relationship would not vary with the scale examined. Secondly it was proposed that the sequence of transitions, in terms of either mussel loss or gain would not be dependent on the previous state of occupancy at a particular location. All surveys were conducted on three shores along the North Cornwall coastline, Polzeath, Harlyn Bay and Constantine Bay, which are all characterised by large mussel populations.

(6.2.) METHODS

(6.2.1.) Study Sites

The three shores were selected at random, from those potentially available within a 25km section of the North Cornwall coastline (Figure 6.2.1). Shore 1, Polzeath, was the first area to be selected. Shore 2, Harlyn Bay, lies 10km west of Shore 1, and Shore 3, Constantine Bay is a further 5km in the same direction.

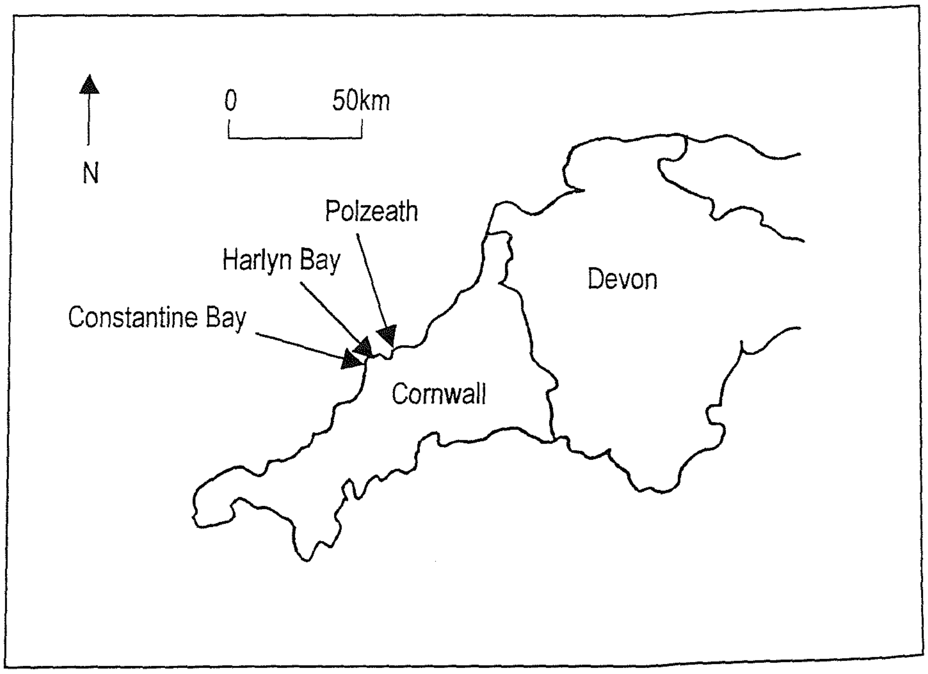


Figure (6.1): The locations of the study sites along the North Cornwall coast. For U.K. placement see Figure 2.1.

The shore at Polzeath consists mostly of gently sloping, slate bedrock, platforms with only a few boulders and loose rocks. Despite the exposed position of this site, the shallow gradient causes a reduction in the waves energy as it breaks over the rocky shore, with much of the force absorbed. This enables a relatively large diversity of organisms to survive, many present in a form typical of an exposed shore (Lewis, 1964; Raffaelli & Hawkins, 1996). Harlyn Bay has a similar bed rock to that of Polzeath, with a higher degree of wave exposure on the rocky outcrops. Constantine Bay again directly faces the Atlantic swell, the gradient of the topography, however, is much shallower than that of the other two shores.

Consequently the species present at this site are more characteristic of a moderately exposed shore (Lewis, 1964; Hawkins & Jones, 1992; Raffaelli & Hawkins, 1996). A large proportion of the intertidal zone of each shore is dominated by mussel patches interspersed with *Fucus* and barnacle mosaics.

(6.2.2.) Analysis

(6.2.2.1.) A Nested Design

In order to measure spatial and temporal heterogeneity in mussel patches, at a variety of scales, a nested design of sampling was employed (Underwood & Chapman, 1996). The issue of temporal variation was addressed by the selection of three random dates in both summer (1998) and winter (1997). On each shore, on each sampling date, three sites (100m x 100m) were selected at random. Within each site, three areas of midshore (25m x 25m) were selected and from those five quadrats (0.5 x 0.5m) were sampled.

Recordings from individual quadrats included percentage cover (derived from counts under 49 equidistant intersection points) of major space occupying species including; *Fucus*, barnacles and mussels. Counts of mobile species and those at lower abundance levels were made throughout the entire quadrat.

The relative importance of different scales to the overall variabilty in mussel cover was calculated using a nested analysis of variance (Underwood, 1997). There were five levels to the analysis; the highest level was that of season the remaining components: date, shore, site and area (stated in descending order) were all nested within all higher levels of the analysis.

(6.2.2.2.) Autocorrelation

In order to quantify the scale of spatial heterogeneity in the observed mussel patches a series of contiguous quadrat transects were used on each of the three shores. Each of the three replicate transects consisted of 62 (0.5m x0.5m) quadrats, equivalent to a total length of 32m each. One replicate was therefore a series of quadrats deployed along a mid shore section; recordings from quadrats were as above. Observations were conducted within a narrow time period (April 1998) and therefore incorporated no temporal variation.

Spatial autocorrelation analysis tests whether the observed value of a nominal, ordinal of interval variable at one locality is independent of values of the value at neighbouring localities (Sokal & Oden, 1978). Spatial autocorrelation may be defined as the property of random variables taking values, at pairs of locations a certain distance apart, that are more similar (positive autocorrelation) or less similar (negative autocorrelation) than expected for randomly associated pairs of observations (Sokal & Oden, 1978; Sokal *et al.*, 1999). Autocorrelation is a very general property of ecological variables and indeed, of all variables observed along time series (temporal autocorrelation) or across geographic space (spatial autocorrelation).

Moran's *I* was used as the index of autocorelation (equation 1) (Sokal & Oden, 1978; Cliff & Ord, 1981). It is a measure of correlation between all pairs of quadrats separated at different spatial distances. In this instance spatial autocorrelations were calculated for separation distances of between 1 and 32 quadrats (i.e. half the length of the transect). Distances greater than half of the length of the transect were not included in these analyses because they were not adequately replicated along the length of the transect (Rossi *et al.*, 1992).

Equation (1):

$$I = \frac{\left[\dfrac{\sum_{t=1}^{N-k}(xt-\bar{x})(x_{t+k}-\bar{x})}{(N-k)}\right]}{s^2}$$

Where *I* is Moran's Index of autocorrelation, *k* represents the step length, *N-k* is the number of possible pairings at that step value and s^2 is the variance.

The significance of each of the statistics was calculated by the comparison with a distribution generated by 999 random permutations of the data, a total of 1000 times including the original data set (Edington, 1987; see Crowe, 1996 for details of computation).

(6.2.2.3.) Monitored Quadrats

To follow the dynamics of individual mussel patches, fixed quadrats were assessed in terms of total patch cover, new spatial occupation, and space lost by the patch, for a series of consecutive sampling dates. The study covered a period of twelve months with a periodicity of three months, equivalent to four consecutive photographs per replicate.

A total of 32 fixed (1m x 1m) quadrats were set up and photographed within the mussel zones of each of the three shores. Each shore was segregated into four sites (25m x 25m), and eight quadrats were sampled from each of these sites. The quadrats (1m x1m) were subdivided into four smaller areas (0.5 x 0.5m) for the purposes of photography. Each photograph was scanned into a PC for further analysis. A specifically designed programme loaded each photograph in turn, each corner of the quadrat was then digitised to form the outer perimeter of the square (M.T. Burrows, 1998). A grid across the entire area was automatically formed, in which each outer edge of the quadrat was divided into ten equidistant points and were joined horizontally and vertically respectively. This served to correct for any differences in orientation whilst taking the photographs through time. The presence or absence of mussels in each cell was then recorded and compared throughout time.

Firstly each date was assessed for the percentage cover of mussels within each quadrat. This was then analysed with an ANOVA for each of the sampling dates to assess differences between the different spatial scales. Subsequently the number of cells that underwent a transition either from unoccupied to occupied or vice versa between each sampling date was analysed. ANOVA, was again used to analyse the number of each transition type between each date across the different shores.

(6.2.2.3.1.) Patch Structure

In order to compare the small scale definition of patches between the different shores a univariate measure of patch structure was required. The first lag derived from spatial autocorrelation analysis gives a good indication of how strongly defined patches are (Hendry & McGlade, 1995) and was therefore used in the current investigation. In contrast to the autocorrelation statistic conducted along the contiguous transects, this analysis incorporated cells within a grid.

The number of times that neighbouring cells were recorded in the same state, either unoccupied or occupied by mussels, was used to characterise spatial autocorrelation (join counts; Upton & Fingelton, 1985). The neighbourhood for each cell included all orthogonal and diagonal connections at a specific distance (Johnson *et al.*, 1997). If mussel patches existed at a scale above 25cm^2 (one grid cell) then there would be positive spatial autocorrelation and higher than expected numbers of joins between cells. Deviations from the average level of join to counts in the absence of spatial autocorrelation were assessed using z, the standardised normal deviate (Sokal, & Oden, 1978; Upton & Fingelton, 1985). The magnitude of individual z scores can also be interpreted as a measure of how well defined patches are; if these values are above 1.96 they are significantly autocorrelated at the scale of 10cm (neighbouring cells). The z scores between directly adjacent cells (lag 1) were used in an ANOVA to assess the definition of small scale patch structure between the three shores on each individual sampling date.

An example of the data derived from a single autocorrelation plot is displayed in Figure (6.2). The z score on the first lag is considerably higher than between cells at greater distances apart; indicative of strongly defined patch structure between adjacent cells. As stated previously the z score of the first lag is also considered to be representative of autocorrelation values throughout the grid.

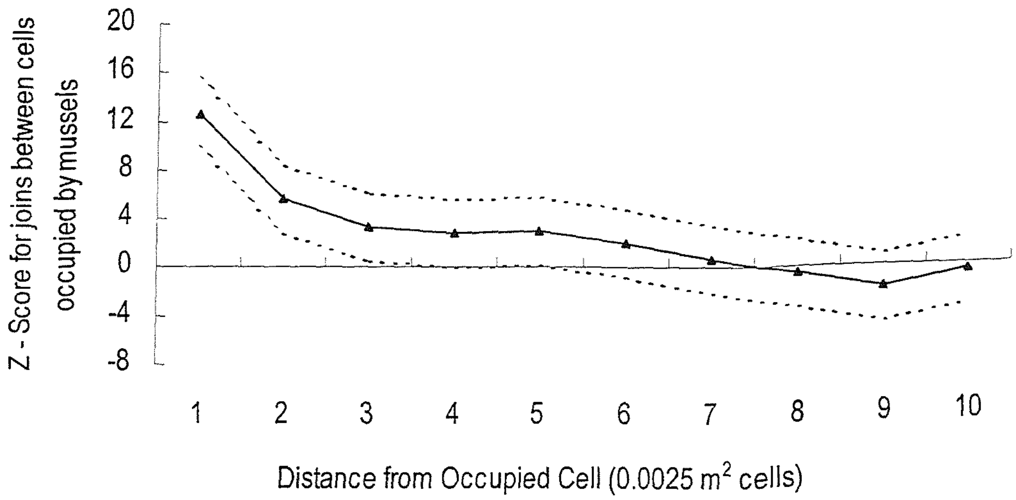


Figure (6.2): An example of spatial autocorrelations for cells containing mussels. (± a two tailed bonferoni correction for multiple scales = ± 2.81)

(6.2.2.3.2.) Mussel Turnover – Density Dependence

The probability of mussel loss or gain in a particular cell was also assessed in relation to the occupancy state of neighbouring cells at different densities. As previously described each quadrat was subdivided into a series of four hundred 0.05m x 0.05m grid cells. In order to examine mussel turnover at a range of spatial scales each grid was divided into a series of one hundred 2x2 grids, twenty five 4x4 grids, four 8x8 grids, one 16x16 grid and one 20x20 grid. Initially the number of occupied and unoccupied cells within each grid, at each scale, were counted for each date. Within the smallest grid, for example, there were four cells which could have been either unoccupied or occupied by mussels. The number of transitions within each grid from occupied to unoccupied cells between adjacent sampling dates was then established. Similarly the number of cells within each grid that changed from having no mussels present to having mussels present was also recorded between each date. In order to calculate the probability of a particular transition depending on the density of surrounding mussels the number of cells that had changed from occupied to unoccupied were divided by the number of occupied cells at the start of the transition. Likewise the number of cells that had changed from unoccupied to occupied was divided by the number of unoccupied cells at the start of the transition. The number of cells which had the same starting density was also recorded so that the average probability of transitions, depending on the condition of cells within a particular grid size, could be weighted according to the number of grids that had a particular number of either occupied or unoccupied cells.

(6.2.2.3.3.) Overall Transitions

There were sixteen possible routes that any one cell could have followed through time (Figure 6.3). This was further reduced to eight possible options given that the cell started as either occupied or unoccupied by mussels. Expected transition rates were therefore calculated for each of the sixteen pathways based on the average turnover across all cells and dates. The number of cells that remained either occupied or unoccupied and those which gained or lost mussels between each date were counted. The proportions of cells that were initially occupied and then lost mussels and those that remained the same were then calculated. Likewise the probability of cells that were initially unoccupied remaining in the same condition or gaining mussels was established. Each possible transition through time therefore had an associated probability. The expected probabilities were multiplied along the sixteen possible sequences of transitions. The end result for each sequence was then multiplied by the average number of cells (derived from the original quadrat data) that were originally unoccupied or occupied depending on the starting point of each sequence. This then resulted in an expected number of cells that would follow each of the sixteen pathways. The expected values were then compared with the average number of observed cells that followed the same sequence of events using a chi-squared test (Sokal & Rohlf, 1995).

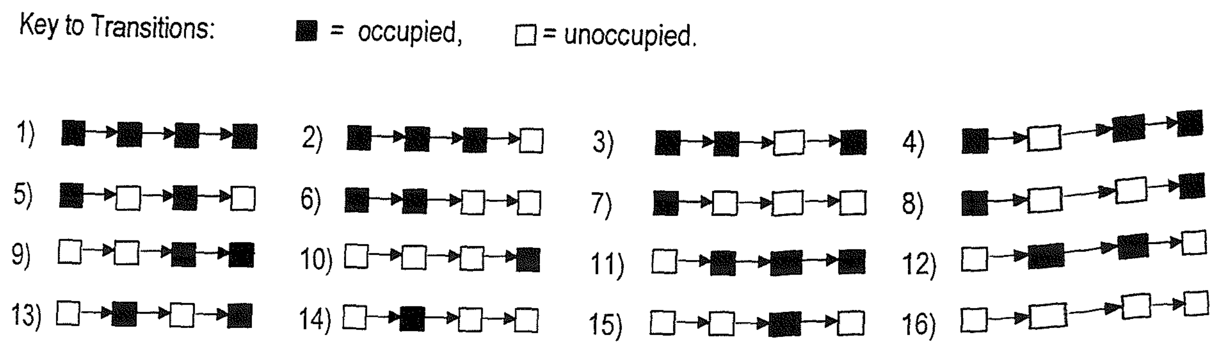


Figure (6.3): Diagrammatic representation of the sixteen possible pathways that any one cell could have potentially followed during the year of sampling.

(6.3.) RESULTS

(6.3.1.) Spatial and Temporal Heterogeneity in Mussel Patches

There was a high degree of variability with regard to the percentage cover of mussels in any one 0.5m x 0.5m quadrat. The overall range in percentage cover of mussels recorded in a quadrat was from 5% to 95%. There was, however, some evidence that the cover of mussels was influenced at a number of both temporal and spatial scales.

Differences in the percentage cover of mussels between seasons were not testable using the ANOVA design due to the large number of random factors within the analysis (Underwood, 1997). From examination of the raw data, however, there does not appear to have been a seasonal trend in the amount of space occupied by mussels. The overall average cover per quadrat ranged from 61% in the winter to 54% in the spring. On examination of Figure 6.4, where dates one to three were winter and dates four to six were spring, it was possible to identify this limited variability across the sampling period. Variation did exist, however, between dates within the winter months (Table 6.1; Figure 6.4).

At the largest scale of the investigation, at the level of shore (km), there was no differences with regard to the percentage cover of mussels per quadrat (Table 6.1). When descending through the spatial scales of the analysis, however, the degree of variability between both sites (100m) and areas (25m) was significant.

Table (6.1): ANOVA used to detect differences in percentage cover of mussels across three shores and two seasons (' = random Factor).

Source	DF	SS	MS	F	P
Season	1	657.90	657.90	0	No Test
Date' (Season)	4	10552.47	2638.12	4.42	0.04
Shore'	2	1416.85	708.43	1.19	0.35
Site' (Season x Date x Shore)	36	26245.56	729.04	1.70	0.02
Area' (Season x Date x Shore x Site)	108	46236.67	428.12	1.51	0.001
Season x Shore	2	26.73	13.36	0.02	0.98
Shore x Date (Season)	8	4773.83	569.73	0.82	0.59
Residual	648	183380	282.99		
Total	809	273290			

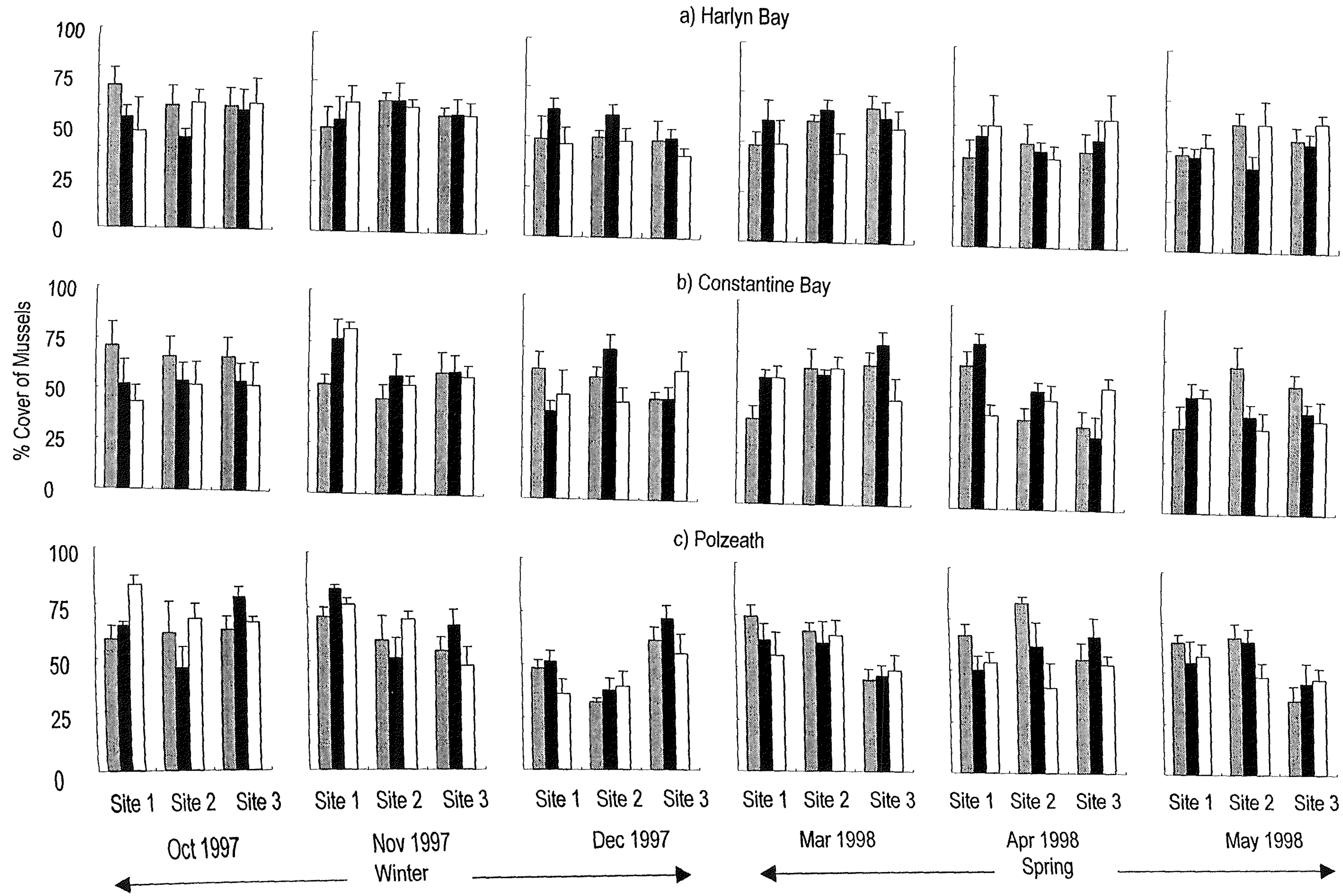


Figure (6.4): The average percentage cover (± S.E.) of mussels per quadrat in each patch on each shore (a) Harlyn Bay, (b) Constantine Bay and (c) Polzeath. (n=5).

Area 1 Area 2 Area 3

(6.3.2.) Spatial Autocorrelation

The trends demonstrated by the transects varied quite considerably regardless of the shore on which they were located. This suggests that there is a number of processes acting at different spatial scales serving to maintain the spatial patterns observed at each location. Patch structure was not observed to occur at a single spatial scale but at a number of intervals. With the exception of a single transect at Polzeath and Harlyn all the sampled transects demonstrated positive autocorrelation between adjacent quadrats (Figure 6.5-6.7). Mussel patches were therefore typically larger than a single quadrat (0.5m) and within the scale of up to 1m.

On a number of transects significant spatial autocorrelation values were also present at a distance of four to five quadrats (2-3m). This was true for two transects at Polzeath and a single transect at both Harlyn and Constantine. In some instances patches were also evident at considerably larger scales. At Polzeath in particular patches seemed to be present at a scale of up to 17 quadrats, equivalent to a distance of 8m to 9m (Figure 6.7). This pattern was also observed at a single transect at Constantine Bay (Figure 6.6d). Patches running the entire lengths of the transects (32 quadrats; 16m) occurred on two transects at both Constantine Bay and Polzeath. Typically there were more significant spatial autocorrelation values at Polzeath than the other two shores, suggesting that this shore was more spatially structured than either Harlyn or Constantine Bay (Figures 6.5-6.7).

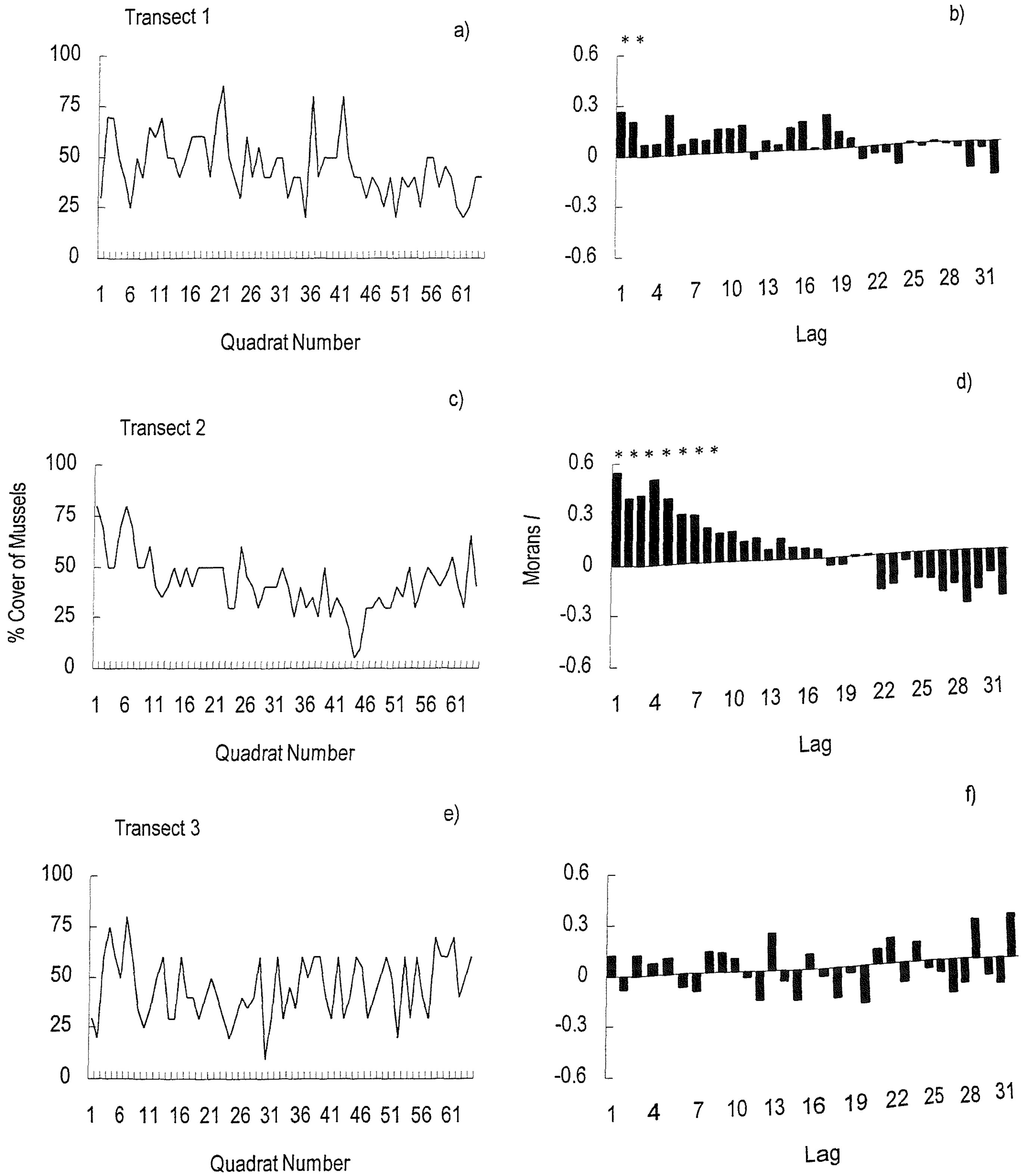


Figure (6.5 a, c & e): Percentage cover of mussels per quadrat in 64 consecutive ($0.25m^2$) quadrats along a transect at Harlyn Bay.
Figure (6.5 b, d & f): Spatial autocorrelation of mussel cover at Harlyn bay (* denotes significance).

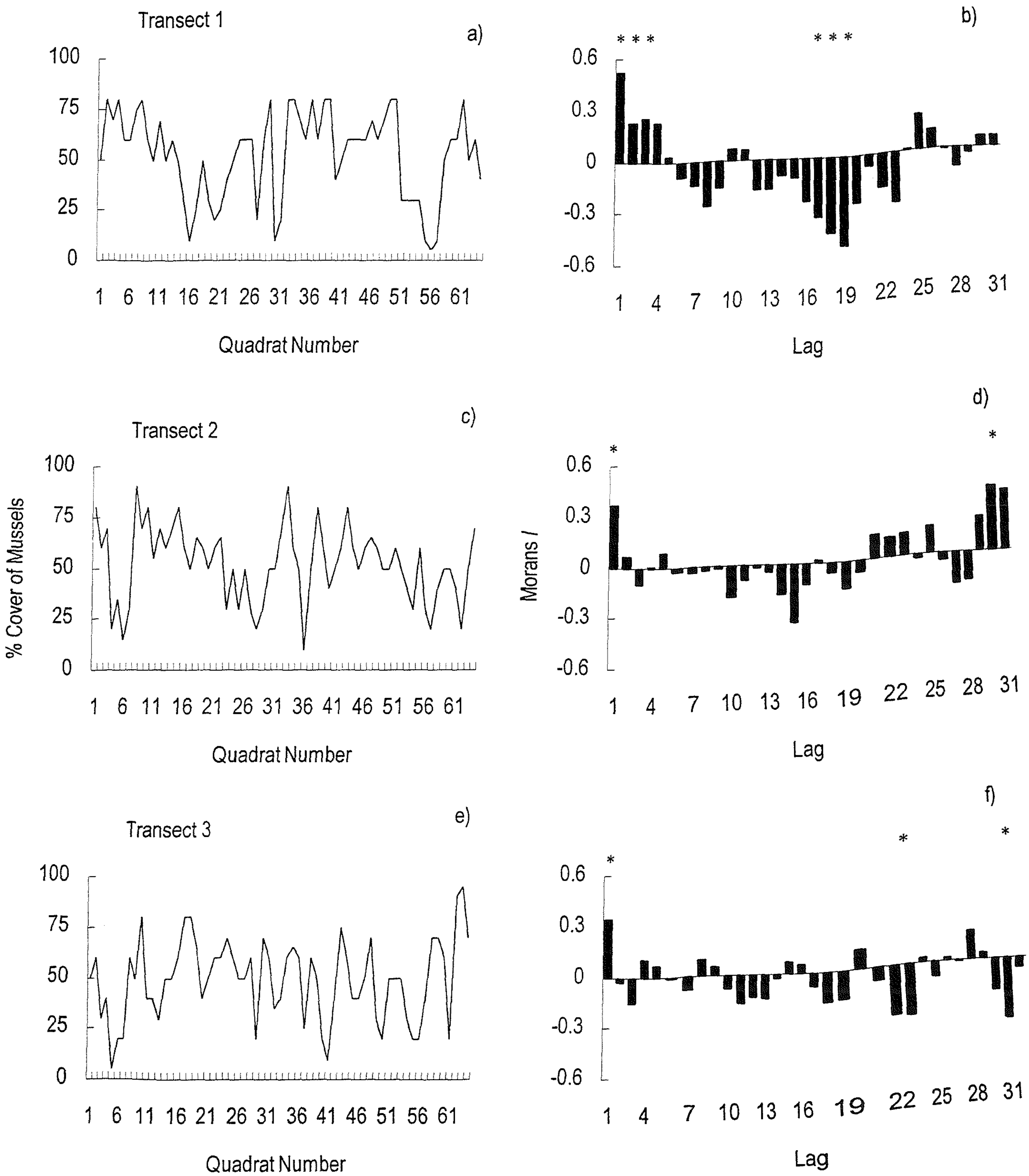


Figure (6.6 a, c & e): Percentage cover of mussels per quadrat in 64 consecutive ($0.25m^2$) quadrats along a transect at Constantine Bay.
Figure (6.6 b, d & f): Spatial autocorrelation of mussel cover at Constantine bay (* denotes significance).

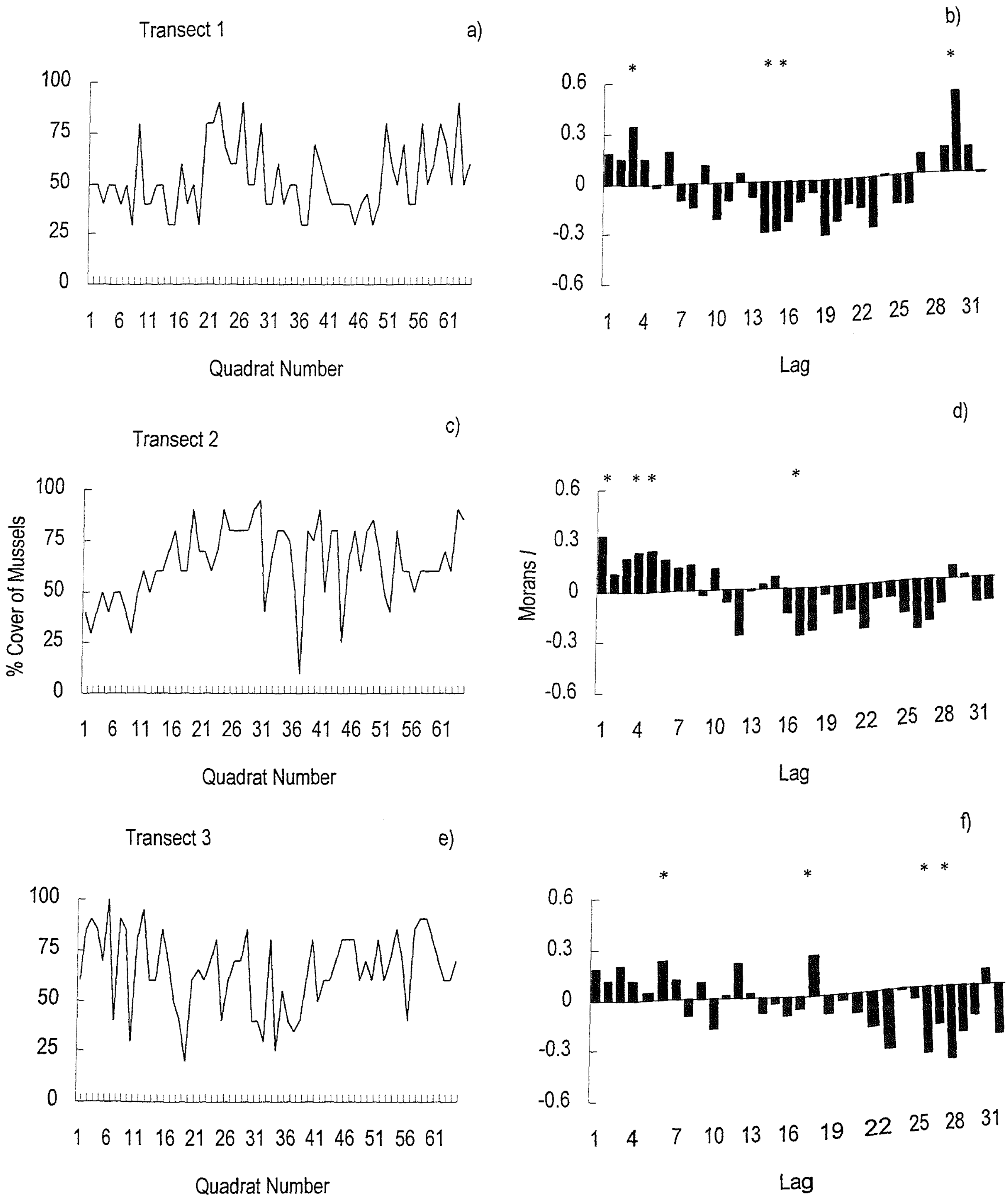


Figure (6.7 a, c & e): Percentage cover of mussels per quadrat in 64 consecutive ($0.25m^2$) quadrats along a transect at Polzeath.
Figure (6.7 b, d & f): Spatial autocorrelation of mussel cover at Polzeath (* denotes significance).

(6.3.3.) Patch Dynamics

(6.3.3.1.) Overall Cover and Turnover

On all four dates where photos were taken there was no significant difference in the percentage cover of mussels between the three shores (Table 6.2). In contrast there were significant differences in cover between sites within both Polzeath and Harlyn. Indeed, when looking at the partitioning of the variance, variation in percentage cover was least at the level of the shore (Table 6.5).

The overall rate of turnover from mussel occupied to mussel unoccupied cells was the same across all three shores (Table 6.3) on all three sampling occasions. Sites within shores also demonstrated limited variability in turnover with significant differences only observed between sites at Polzeath between August 1998 and November 1998 (Table 6.3). Likewise the turnover from mussel unoccupied cells to occupied cells did not significantly vary between shores (Table 6.4). When the variance was partitioned, there was very little variability displayed at this level (Table 6.5). The majority of the variance in the turnover of mussels was found within each of the sites.

Table (6.2): ANOVA summary statistics for percentage cover of mussels per quadrat at Polzeath, Harlyn and Constantine Bay on four sampling dates (' = Random Factor). (**Significance: *= p<0.05, **=p<0.01, ***=p<0.001**).

		Aug 98		Nov 98		Feb 99		Jul 99	
	d.f.	MS	F	MS	F	MS	F	MS	F
Shore'	2	4652.28	2.38	2744.19	1.18	724.96	0.28	1606.29	0.73
Site' (Shore)	9	1953.79	**9.17*****	2323.84	**9.13*****	2622.17	**3.87*****	2214.37	**11.59*****
Residual	84	212.97		254.41		678.15		191.06	
Average cover									
Polzeath		42%		37%		37%		30%	
Constantine		22%		24%		31%		20%	
Harlyn		44%		42%		39%		33%	

Table (6.3): ANOVA summary statistics for turnover of mussels (occupied to unoccupied cells) at Polzeath, Harlyn and Constantine Bay between four sampling dates (' = Random Factor). (**Significance: *= p<0.05, **=p<0.01, ***=p<0.001**).

		Transition 1 Aug 98- Nov 98		Transition 2 Nov 98- Feb 99		Transition 3 Feb 99- Apr 99	
	d.f.	MS	F	MS	F	MS	F
Shore'	2	4384.20	4.24	2696.57	2.83	896.64	0.86
Site' (Shore)	9	1035.08	**2.11***	951.25	1.74	1036.65	1.39
Residual	84	490.92		548.24		748.03	

Table (6.4): ANOVA summary statistics for turnover of mussels (unoccupied to occupied cells) at Polzeath, Harlyn and Constantine Bay between four sampling dates (' = Random Factor). (**Significance: *= p<0.05, **=p<0.01, ***=p<0.001**).

		Transition 1 Aug 98- Nov 98		Transition 2 Nov 98- Feb 99		Transition 3 Feb 99- Apr 99	
	d.f.	MS	F	MS	F	MS	F
Shore'	2	818.82	0.93	413.28	0.60	0.58	0.56
Site' (Shore)	9	879.00	1.63	684.98	1.53	1.04	**4.83***
Residual	84	539.13		447.78		0.22	

Table (6.5): Variance partitioned among the three different levels of analysis (Shore, Site and Patch) for the percentage cover and turnover of mussels at Polzeath, Harlyn and Constantine Bay on four sampling dates.

	Among Shores	Among Sites within Shores	Within Sites
Aug-98 %cover	16.38	42.26	41.36
Nov-98 %cover	2.50	49.16	48.35
Feb-99 %cover	0	26.38	73.62
Jul-99 %cover	0	56.99	40.03
Occupied to Unoccupied Transition 1	15.77	10.25	73.98
Occupied to Unoccupied Transition 2	8.35	7.71	83.94
Occupied to Unoccupied Transition 3	0	4.60	95.40
Unoccupied to Occupied Transition 1	0	7.34	92.69
Unoccupied to Occupied Transition 2	0	6.21	93.79
Unoccupied to Occupied Transition 3	0	31.78	68.20

(6.3.3.2.) Patch Structure

The grid cells into which each quadrat was divided (5cm x 5cm) demonstrated significant positive autocorrelation between adjacent cells. This was true for all quadrats sampled at the three shores and on all four sampling dates. Small scale patches were therefore structured at a scale of between 5cm and 10cm. The shores had a similar definition of patch structure at all times of the year with the exception of February 1999 (Table 6.6). At this time Constantine Bay demonstrated higher significance levels than Polzeath; suggesting that patch structure was more defined at Constantine Bay at this time. Sites within shores were also significantly different on all four sampling dates (Table 6.6).

Table (6.6): ANOVA summary statistics used to determine differences in the definition of patch structure at Polzeath, Harlyn and Constantine Bay on four sampling dates (' = Random Factor). **(Significance: *= p<0.05, **=p<0.01, ***=p<0.001).**

		Aug 98		Nov 98		Feb 99		Jul 99	
	d.f.	MS	F	MS	F	MS	F	MS	F
Shore'	2	114.50	4.09	131.17	2.48	203.92	**4.51***	163.17	2.46
Site' (Shore)	9	27.97	**3.99*** **	52.97	**6.44*** **	45.20	**5.76*** **	66.21	**10.01*** **
Residual	84	7.01		8.23		7.85		6.62	

(6.3.3.3.) Mussel Turnover – Density Dependence

The effect of density dependence on patch turnover was assessed at a number of spatial scales. The smallest scale was that of four grid cells where it was evident that mussel loss was indeed affected by density. A single mussel occupied cell was more likely to become unoccupied than where a number of adjacent cells were occupied by mussels (Figure 6.8). As a consequence larger patches of mussels were less likely to be removed from the rock surface than smaller patches. This pattern was also consistent when observing subdivisions of each quadrat at 16, 64, 256 and 600 cells (Figure 6.8). Likewise cells were more likely to change from unoccupied to occupied where the number of occupied surrounding cells was highest (Figure 6.9). This was again observed across all the scales examined. These factors operating together would therefore result in strongly defined patch structure on the three shores.

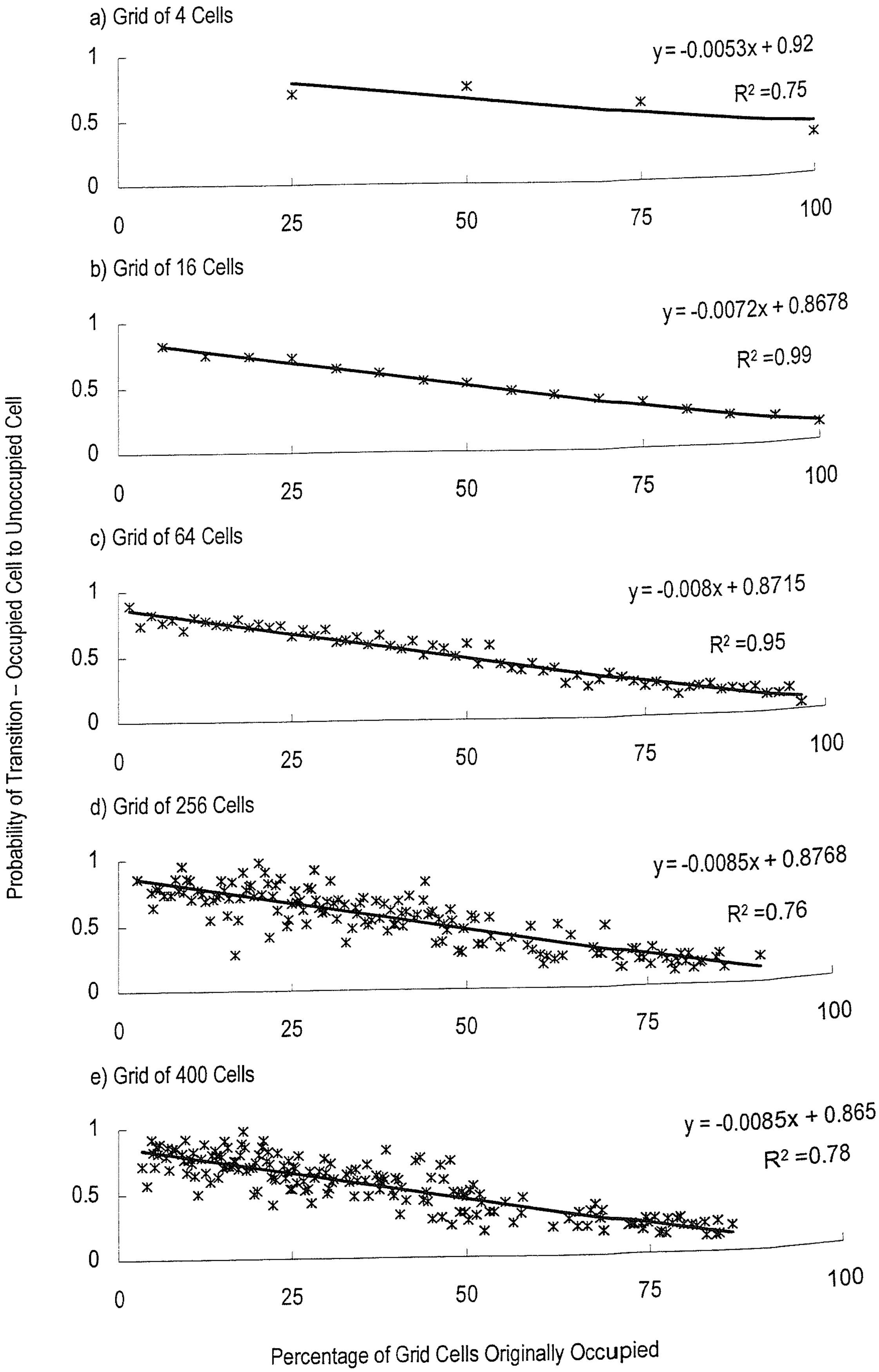


Figure (6.8): The effect of the number of occupied grid cells on the probability of transition from mussel occupied to mussel unoccupied cells over a range of spatial scales. Average Probability of Transition = 0.54.

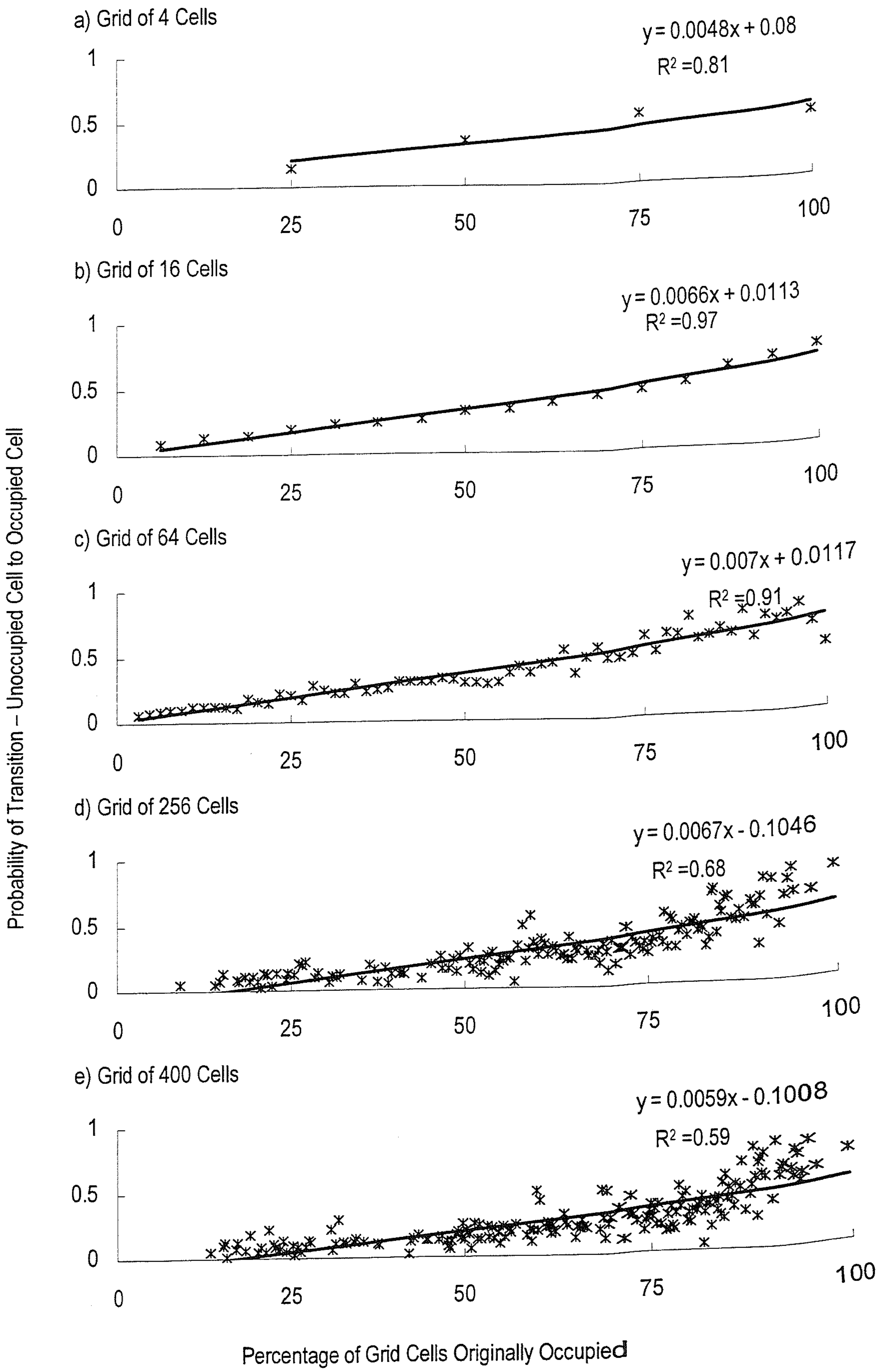


Figure (6.9): The affect of the number of occupied grid cells on the probability of transition from mussel unoccupied to mussel occupied cells over a range of spatial scales. Average Probability of Transition = 0.46.

(6.3.3.4.) Overall Transitions

Throughout the time series there were sixteen possible transitions that any one cell could have passed through. Observed values for each transition were compared with those derived from average transition rates (Figure 6.10). There was a significant difference between these observed and expected values ($X^2 = 67.04$, d.f = 15, $p<0.01$). In particular there were more cells that remained either occupied or unoccupied throughout the time series than would be expected at random (Figure 6.8). In addition cells that were unoccupied for the first two or three sampling dates were unlikely to gain mussels later. In contrast cells which actually lost or gained mussels sporadically through time were in similar proportions to those expected.

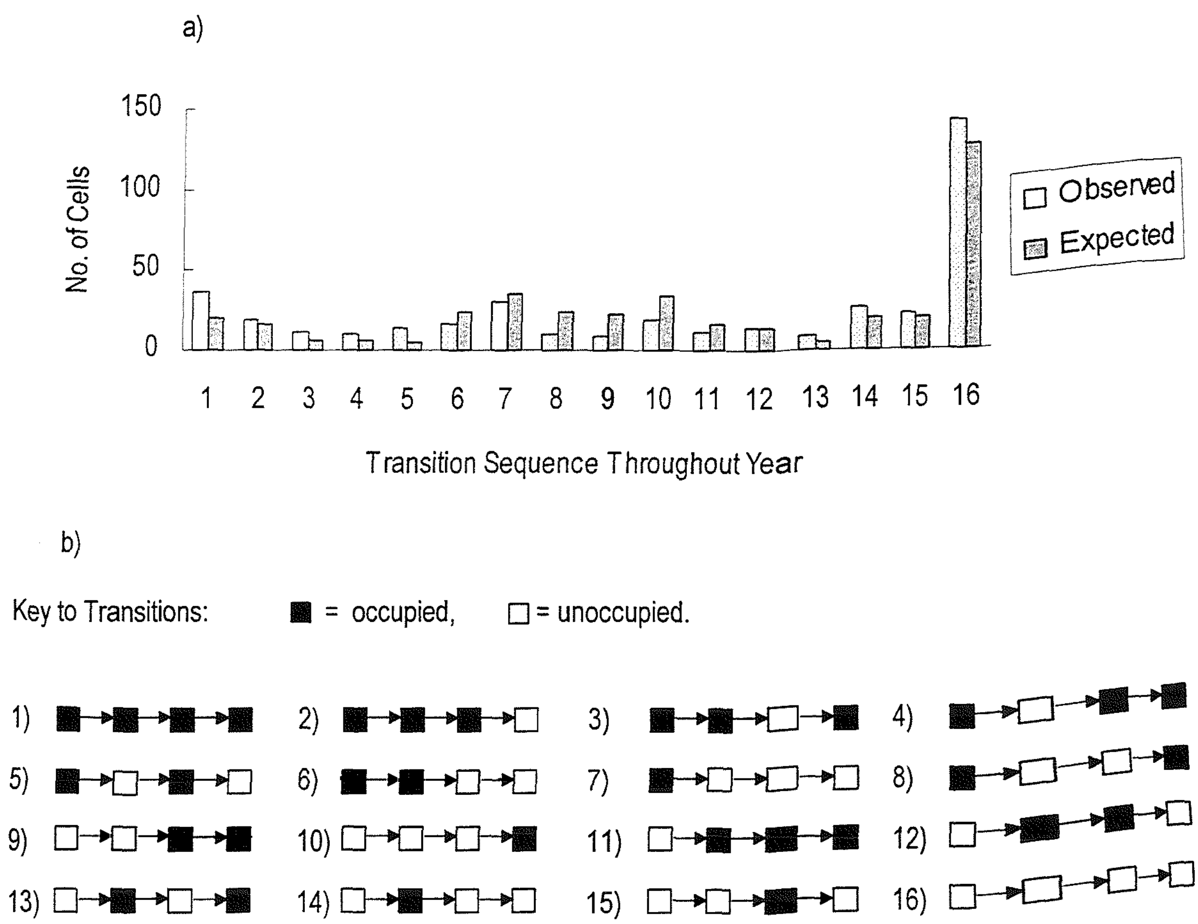


Figure (6.10): a) Observed and expected transitions in mussel cover that could have potentially occurred in each cell (depending on its original occupancy) throughout the year of sampling.
b) Reminder of possible transitions that any one cell could follow.

(6.4.) DISCUSSION

(6.4.1.) Spatial Patterns

The percentage cover of mussels on the three shores was both temporally and spatially variable. This heterogeneity was observed using both a hierarchical framework (nested analysis of variance) and at a continuous scale of measurement (autocorrelation techniques). Kostylev (1996) also found that these two analysis techniques along with fractals gave complementary knowledge about the spatial variation in mussel populations. Such high levels of variation are not atypical when describing abundance patterns of organisms (Lindegrath *et al.*, 1995; Legendre *et al.*, 1997; Syms & Jones, 1999; Vanderklift & Lavery, 2000). Indeed over the last couple of decades considerable attention has focused on ecological heterogeneity and patch dynamics over different scales (Paine & Levin, 1981; Pickett & White, 1985; Kolasa & Pickett, 1991; Lively *et al.*, 1993; Wu & Levin, 1994; Vidono *et al.*, 1997; Petraitis & Latham, 1999).

Variation in mussel cover did not occur between shores, but significant variability was present within each location. Patch structure, however, was defined on all three shores at a scale of $1m^2$ and at a smaller scale of $0.001m^2$. Patches were also apparent at intermediate scales along the contiguous transects at approximately 2 to 3m, 8 to 9m and at 16m but these were not observed consistently. The lack of consistency in the size of patches in some instances is not an uncommon finding; patches within mosaics may differ in size, age and community composition (e.g. Dayton, *et al.*, 1984; Dethier, 1984; Sousa, 1984). Hierarchies of spatial pattern such as this reflect the operation of different processes at different scales (O' Neill *et al.*, 1991; Farnsworth & Ellison, 1996). It therefore seems likely that processes affecting the overall abundance of mussels in this study were operating at a scale smaller than shore. The hydrodynamic conditions of each shore, for example, were potentially very similar as they were all located along the same coastline. As a consequence larval supply and wave action were likely to be of a similar magnitude across the three shores.

In contrast variation within a shore may be as a result of a number of more localised processes. Previously, within shore differences have been examined in terms of tidal heights, and high levels of variation in both mortality and settlement have been observed (Seed, 1969a, b; Caceras- Martinez & Figueras, 1997; Petraitis, 1998). Processes that are likely to lead to differences at the scale of metres may include variations in habitat availability, predation, local hydrodynamic flows, restricted dispersal of propagules and the influence of established assemblages on potential recruitment (Lindegrath *et al.*, 1995; Vanderklift & Lavery, 2000).

In the case of mussels it is highly likely that localised settlement patterns will have influenced the within site variability. Currents and waves have been demonstrated to be important in determining settlement patterns (Gaines *et al.*, 1985; Underwood & Fairweather, 1989; Seed & Suchanek, 1992; Caceras- Martinez & Figueras, 1997; McQuaid & Phillips, 2000). This can act at two levels: firstly larval supply to the shore may be locally patchy, and/ or settlement preferences of recruits may be sensitive to subtle small scale differences in adult density within mussel clumps (Harris *et al.*, 1998). Biological parameters such as predation and competition may also influence patch structure (e.g. Svane & Ompi, 1993; Petraitis, 1998). Differential predation by whelks, for example, can cause both between and within patch variability of mortality of *Mytilus trossulus* (Noda, 1999).

The well defined patch structure at smaller scales may again be the result of a number of combined physical and biological parameters. In the current study recruitment of mussels was largely associated with adult mussels. The more of the rock substratum that was occupied by mussels the more likely the neighbouring substratum would gain mussels, demonstrating a degree of inverse density dependence and disproving the first hypothesis. This pattern was observed across all the spatial scales examined, ranging from $0.001 m^2$ up to $1 m^2$. It should be remembered, however, that this could have been the result of a single or multiple processes acting at each of the different scales. As the current study was purely observational it was not possible to define causal mechanisms of patch structure, however, testable hypotheses could now be proposed. Factors leading to the increase in mussel cover where adults were already established could have included settlement patterns, growth rates, habitat selection and/ or differential predation.

The recruitment of larvae onto adult beds of *Mytilus* has been frequently detailed (McGrath *et al.*, 1988; King *et al.*, 1990; Lasiak & Barnard, 1995). The patchy distribution of mussels within these three shores in Cornwall is therefore likely to be enhanced by such preferential settlement (McGroty *et al.*, 1990; Hunt & Scheibling, 1996; Harris *et al.*, 1998; Chiba & Noda, 2000). In contrast previous investigators have found recruitment not to be correlated with adult density (e.g. Petraitis, 1991). Svane & Ompi (1993) also found that small isolated groups were more likely to receive recruits than larger patches.

Growth around the edges of patches will result in previously unoccupied rock appearing occupied by mussels on consecutive sampling dates. Patches of mussels facing high mortality may show no change in percentage cover as long as growth of the remaining survivors can fill the vacant space. Indeed Petraitis (1995) developed a model to highlight that this process was feasible. Factors such as height on the shore may also affect growth rates of mussels and as a result patch recovery (Suchanek, 1986). Closing rate by perimeter encroachment is variable over time and depends on such conditions as patch shape, and orientation, the depth of the surrounding mussel bed, slope, and exposure (Paine & Levin, 1981). Small scale disturbances will therefore have a smaller impact than larger ones (Petraitis & Latham, 1999).

The higher than expected number of cells that were unoccupied throughout the entire year would also lead to strongly defined patch structure. This may reflect that some areas were unsuitable for mussel colonisation. Such substrata may not have provided the necessary protection against the currents, wave action, competition and predation for mussel post-larvae to become established. Similarly some areas remained occupied during the entire study. The reasons for such within patch stability are complex and likely to be a combination of all processes acting to determine patch structure. For instance variation in mussel bed stability may reflect historical factors, microtopographic protection and chance (Paine & Levin, 1981). It was therefore concluded that transitions of sections of rock from unoccupied to occupied by mussels or vice versa were dependent on the local environment and the previous state of the area.

The density of mussels on a section of rock also affected the likelihood of loss from a patch. Mussels in isolated cells were more likely to be lost than where they were present in groups. Again this pattern was observed for a grid of $0.001m^2$ up to $1m^2$. From the data obtained it was impossible to determine whether this was the result of a single process acting across all scales, or whether a series of different processes were in operation. Such inverse density dependence in mussel loss has been recorded elsewhere (Bertness & Grosholz, 1985; Denny *et al.*, 1985; Denny, 1987).

A general ecological question is whether patch or group formation has an adaptive value (e.g. Buss, 1981; Wrona & Dixon, 1991; Bologna & Heck, 1999). Substratum stability is a likely ecological benefit for mussels to form aggregations or beds (Young, 1983) and a likely cost is decreased food and space availability (Frechette *et al.,* 1989; Asmus & Asmus, 1991). This is consistent with the inverse density dependence of mussel loss observed in the current study, where large patches of mussels were less likely to be lost from the substratum than smaller groups of individuals. Physical interference in mussel beds by crowding is likely to affect growth and cause intraspecific competition (Peterson, 1982; Bertness & Grosholz, 1985; Sebens, 1987). These costs and benefits are also unlikely to be shared evenly among individuals in a mussel bed (Svane & Ompi, 1993).

Susceptibility to storm damage is inversely related to mussel density (Bertness & Grosholz, 1985) and depends on the position in the clump, the individuals at the perimeter being the most susceptible (Tsuchiya & Nishihira, 1985). Each mussel in the bed shields its down stream neighbour from the prevailing flow and thereby from the hydrodynamic forces acting along the direction of the flow (e.g. Denny *et al.*, 1985; Denny, 1987). In contrast, larger mussels are usually found along the edge of a patch and are favoured by abundant oxygen and food supply compared to mussels within the patch (Okamura, 1986; Svane & Ompi, 1993). Selective predation is also a likely factor influencing the size distribution patterns within a mussel bed (Edwards *et al.,* 1982; Goss-Custard *et al.*, 1982; Durrell & Goss-Custard, 1984; Okamura, 1986). Indeed Okamura (1986) and Bertness & Grosholz (1985) concluded that overall group living was disadvantageous.

(6.4.2.) Temporal Variability

The percentage cover of mussels on each shore was similar across all seasons. Similarly there were no differences in patch turnover; either mussel loss or gain demonstrated throughout the period of a year. Factors affecting the increase in mussel cover (recruitment, immigration, growth) and the loss of mussels (wave action, predation and other sources of mortality) must therefore have operated at similar rates. Previous studies have also found that individual *Mytilus* patches were dynamic, but there were no significant differences in patch area recorded between time intervals (McGroty *et al.*, 1990; Hunt & Scheibling, 1995). In contrast Lubchenco & Menge (1978) and Paine & Levin (1981) noted that mussel beds on exposed shores undergo a cycle of winter removal and summer recovery. The time scale of each study and the different conditions at each location may have resulted in the observed discrepancies.

The main factor thought to reduce mussel cover in winter months is loss through storms, although such clearings are less frequent than disturbances produced by waves of lesser magnitude in any other season (Paine & Levin, 1981). In addition there is also evidence of year to year variation in mussel loss (Paine & Levin, 1981). In the current study it was possible that storm clearings were not of sufficient density to produce large scale losses. If the observations had been extended for a longer time period it is possible that large scale losses from such damage may have been observed. The density of mussels within a particular location could also result in such differences between results. Mussels may have been hummocked, for example, which results in a less firm attachment to the substratum and a greater probability of loss by wave action (Seed, 1969b; Dayton, 1971). On the three shores in Cornwall hummocking was rarely observed (pers. obs., 1999).

The seasonality of mortality resulting from predation may differ depending on both the predator involved and the location examined (Seed & Suchanek, 1992). In the current study rates of predation were not assessed at any point; no evidence therefore exists to whether this pressure was constant or variable throughout the year. The feeding of *N. lapillus*, however is affected by wave action, temperature, tidal height, canopy cover and snail phenotype (Menge, 1978a, b; Burrows & Hughes, 1989). Different patches will therefore experience different predation rates both spatially and temporally. Crabs tend to focus on juveniles at the edge of patches (Elner, 1978), this may therefore occur throughout the year. Oystercatchers, *Haematopus ostralegus*, also remove large numbers of mussels (Heppleston, 1971; Goss-Custard & Durrell, 1987). These birds over-winter around the shores of Great Britain, predation pressure from this species is therefore concentrated at this time (Heppleston, 1971; Goss-Custard & Durrell, 1987; Goss-Custard *et al.*, 1998; Durrell *et al.*, 2000).

Newly settled mussels were observed throughout the year, although the highest numbers were recorded during the winter and early spring. These data support the observations of Seed (1976) that mussel settlement density is sporadic over space and time. The settlement of other mussel species have also been reported to occur throughout the year with more concentrated periods apparent (e.g. Seed, 1969a; Wilson & Seed, 1974; King *et al.*, 1989, 1990; Snodden & Roberts, 1997). In Spain, for example, *Mytilus galloprovincialis*, settlement is continuous throughout the year but peaks during the spring and summer months (Caceras-Martinez *et al.*, 1994). Mussel recruitment in Santa Catalina and other Channel Islands is greatest from winter to early spring (Robles, 1997).

The growth rate of mussels may also have affected the cover of mussels present in each season for a number of reasons. Firstly, mussels generally show reduced growth rate in winter, primarily due to low temperature and low food levels (Seed & Suchanek, 1992). In addition the space provided by the removal of mussels may alleviate the effects of intraspecific competition allowing neighbouring mussels to grow at an increased rate. Juvenile mussels from within the matrix may also be able to become established on the rock surface (Kautsky, 1982). The absence of a temporal trend in patch size may reflect the protracted period of mussel recruitment, variation in growth rate and the lack of any clear seasonal trend in overall mortality.

(6.4.3.) Conclusions, Limitations and Future Work

A high degree of variability existed in the abundance of mussels within the three shores. There were, however, no differences in the overall cover of mussels between the three locations. Processes operating to define patch structure must therefore have been operating at smaller spatial scales than the level of shore. Despite such high variability, patches of mussels were well defined at the scales of $1m^2$ and $0.01m^2$. There was no temporal variability in either the percentage cover or turnover of mussels. Processes acting to remove mussels must therefore have operated at a similar rate to those which increase their numbers. Inverse density dependence existed in terms of both the loss and gain of mussels. The loss of mussels was more likely to occur where mussels were in small rather than large patches. Similarly mussels were more likely to be gained where larger patches of adult mussels were present compared to largely uncolonised areas. A comparison between expected and observed transitions of each particular rock section revealed that some areas remain largely uninhabited while others provide a stable location.

The major limitation incorporated in this study was the use of image analysis software to characterise the location of mussels. In the presence of a large canopy forming algae it was not possible to determine whether mussels formed part of the understorey community. It was therefore possible that not all mussels were identified on all dates. The use of the grid overlaying the image will also have reduced the resolution at which the analysis could be performed. A balance was required between the level of accuracy and the number of replicate quadrats that could be processed. A large number of the tags used to mark the continuously monitored quadrats were also lost throughout the year, making a continuation of this investigation impossible. It is also possible that a number of processes acting to define patch structure operate on a larger time and spatial scale than was observed here.

This observational study has identified a number of spatial and temporal patterns in mussel mosaics. It has also been possible to discuss possible processes that may have determined such patterns. It would now be beneficial to use manipulative experiments to test the ideas put for forward in this discussion. Modelling of processes at different scales could also be a useful approach to adopt. In addition it would be possible to extend the survey over a longer time period and a wider geographical range to examine the generality of the conclusions established here.

7. The Roles of Mussels and Limpets in Structuring Intertidal Communities

(7.1.) INTRODUCTION

Ecologists have often argued that some species in an assemblage, particularly consumers, are more important than others, and as such some communities are controlled by keystone predators (Paine, 1969; 1974). Recently, however, both the usefulness and the generality of this concept have been questioned (e.g. Strong, 1992; Mills *et al.*, 1993). The majority of criticism derives from the ambiguity in definition leading to either very broad or narrow usage of the term. A keystone species is recognised by the consequences of its removal, which results in marked shifts in relative abundance and distributions at lower trophic levels, including the replacement of dominant species and the alterations of size class and diversity (Paine, 1966, 1969, 1974, 1980; Menge & Lubchenco, 1981; Lubchenco *et al.*, 1984; Menge *et al.*, 1986). Mathematical modelling has also been used to quantify what species transitions are important in controlling the dynamic behaviour of species assemblages (Tanner & Hughes, 1994). The strength of interactions and the impact of keystone organisms may, however, vary in different habitats and locations (Menge *et al.*, 1994).

Many organisms modify their environment and make conditions more suitable for themselves and other organisms simply through their presence or as a by-product of their activities (Lawton, 1994; Jones *et al.*, 1994, 1997). Such organisms have been termed "ecosystem engineers" and they directly or indirectly modulate the availability of resources (other than themselves) to other species, by causing physical state changes in abiotic or biotic materials (e.g. Bertness, 1984; Naiman, 1988; Facelli & Pickett, 1991; Thompson *et al.*, 1993; Bruno, 2000). In this way these species modify, maintain and /or create habitats. Autogenic engineers such as mussels, change the environment via their own physical structures', that is their living and dead tissues (Jones *et al.*, 1994). Alternatively allogenic engineers (e.g. rabbits digging burrows) change the environment by transforming living or non-living materials from one physical state to another (Jones *et al.*, 1994). The effects of ecosystem engineers can range in magnitude quite considerably and can include the creation of a completely new habitat upon which a whole community is based (Jones *et al.*, 1997).

Exposed rocky shores in Southwest England support dense and patchy beds of mussels as well as large numbers of grazing limpets. Both limpets (Southward, 1964; Branch, 1981; Hawkins & Hartnoll, 1983b; Jenkins *et al.*, 1999b) and mussels (Paine, 1966; Seed 1969a, b, 1976; Dayton, 1971; Suchanek, 1978, 1981; Castilla & Paine, 1987) are thought to play a key role in structuring intertidal communities and the relative importance of their respective roles is yet to be established, especially on Northeast Atlantic shores (Hawkins *et al.*, 1992). It is the intention of this study to examine the relative effects of limpet grazing in controlling the abundance of algal density as opposed to the role of mussels in providing a refuge from such pressures.

(7.1.1.) The Role of Limpets

Limpets and other molluscan grazers have a profound ecological impact on the rocky shore through their herbivory (Southward, 1964; Branch, 1981; Lubchenco & Gaines, 1981; Gaines & Lubchenco, 1982; Hawkins & Hartnoll, 1983b; Liu, 1994). In the mid-intertidal zone of Northwest Europe, *Patella* is the dominant grazer, and on all but the most sheltered shores it has an extremely important community structuring role (Jones, 1948; Southward, 1964; Southward & Southward, 1978; Hawkins & Hartnoll, 1983b and see Hawkins *et al.*, 1992 for review) and has been proposed as a keystone species (Raffaelli & Hawkins, 1996).

Limpets regulate algal recruitment by grazing the early stages of macroalgae, contained within the epilithic microbial film (Hill & Hawkins, 1991). They are capable of removing all algal germlings and preventing any further development of settled germlings (Jones, 1948; Southward, 1964; Branch, 1981; Hawkins & Hartnoll, 1983b; Johnson *et al.*, 1997). This has been demonstrated by the establishment of opportunistic species of algae, and an increase in abundance of fucoids where limpets have been removed from areas of the shore (Jones, 1948; Lodge, 1948; Southward, 1964; Hawkins, 1981; Jenkins *et al.*, 1999b). The upper limit of some lower algal beds also depends on the grazing of algal propagules by gastropods (Jernakoff, 1983). Only in the absence of grazers do physical factors become important in determining the upper limits of low shore macroalgae (Underwood, 1980).

Where grazing species have been excluded the growth of the biofilm in general has been reported to increase (Cubit, 1984; Dye & White, 1991; Mak & Williams, 1999). Studies of the interaction between primary production and herbivory have revealed that seasonal and spatial variation in primary production influences the abundance of grazers (Underwood & Jernakoff, 1981). It is therefore possible that grazers, other than those excluded from an area, may take advantage of the increase in food availability in these areas.

The effect of herbivory on primary producer diversity is still controversial (Olff & Ritchie, 1998). High grazing pressure seems to reduce plant diversity while moderate grazing pressure seems to increase it (Paine & Vadas, 1969; Lubchenco, 1978). However, there is also circumstantial evidence that spatial heterogeneity and variance of the grazing pressure may be more important for the maintenance of plant diversity than the overall mean intensity of grazing (Olff & Ritchie, 1988; Benedetti-Cecchi, 2000; Sommer, 2000).

Grazer abundance has also proved to be the key factor in determining the extent and type of algal recolonisation in cleared areas (Suchanek 1978; Underwood, 1980, 1981; Paine & Levin, 1981; Sousa, 1984, Dye, 1993). Grazers may affect the distribution and abundance of algae by their grazing preferences or rates (e.g. Jones, 1948; Southward, 1964; Paine & Vadas, 1969; Lubchenco, 1978, Raffaelli, 1979; Underwood, 1980; Underwood & Jernakoff, 1981). Lubchenco (1983) determined that during succession *Fucus*, following the removal of ephemerals by grazers, becomes the most abundant species in a climax state. In the absence of grazers, however, ephemeral algae remains unhindered and these species can outcompete *Fucus* (Hawkins *et al.*, 1992). It is more likely that herbivores accelerate succession than cause the species replacement (Lubchenco, 1983).

(7.1.2.) The Role of Mussels

Mussels are members of one of the most important functional groups of intertidal communities (Paine, 1966; Seed 1969a, b, 1976; Dayton, 1971; Suchanek, 1978, 1981; Castilla & Paine, 1987). Mussel aggregations both occupy space and change the surface of rocky shore habitats considerably. The habitats thus become an inhabitable volume instead of a surface (Kostylev, 1996). A mussel bed community consists of three major components: the mussel matrix, a diverse assemblage of associated organisms, and accumulated detritus at the base of the mussel bed. The mussel matrix is structurally more complex than the surrounding substratum, which, as in many other biologically generated systems (e.g. freshwater, marine and terrestrial) leads to increased species richness (e.g. MacArthur, 1964; Kohn & Leviten, 1976; Tsuchiya & Nishihira, 1985).

Intertidal mussel populations therefore provide a biogenic structure for co-existing species including polychaetes, crustacea and nemerteans. The surface of *Mytilus edulis* shells and shell fragments also serve as a substrate for bacteria, micro-algae and small animals which in turn support animals within the patches (Tsuchiya & Nishihira, 1985). The architectural complexity of the secondary habitat decreases the influence of wave action, temperature and sunlight while increasing relative humidity and sedimentation (Sebens, 1991). Thus the community structure is altered by the changing effects of physical stress, competition, grazing and predation imposed on marine animals (e.g. Underwood & Denley, 1984; Witman, 1985; Sebens, 1991; Gosselin & Chia, 1995). The effects caused by biological activities of living mussels, such as filter feeding and biodeposition also affect macrofaunal patterns (Crooks & Khim, 1999).

(7.1.3.) Mussel - Grazer -Algae Interactions

The post settlement survival of macroalgae is generally poor and this is accountable for by a number of physical and biological factors. Wave action (Vadas *et*., 1990) and heat and desiccation stress (Hruby & Norton, 1979) dramatically reduce the survival rate of recent settlers. After secure attachment, grazing is an important source of mortality in seaweeds (Vadas *et al.,* 1992; Lazo *et al*., 1994; Vejo *et al*., 1999). Furthermore, the presence of dense adult canopies generally limits the survival of recruits by reducing the irradiance that reaches the bottom or by the continuous sweeping action of adult fronds (e.g. Dean *et al*., 1989).

In the intertidal zone, however, the positive effects of biogenic structures may outweigh the negative effects, enhancing germling survival (Brawley & Johnson, 1991). The mussel matrix may provide a refuge against grazing for settling algae. The added protection gained from architectural features has been clearly demonstrated where the presence of barnacles and large canopy plants have enhanced algal survival (e.g. Reed & Foster, 1984; Lubchenco, 1986; Chapman, 1989; Chapman & Johnson, 1990). Burrows & Lodge (1950) stated that although *Patella vulgata* could graze over barnacles, its movements were restricted, and these workers suggested that crevices could be an important refuge for algal propagules from grazing. Crevices may accumulate more propagules than flatter surfaces (Norton & Fretter, 1981) and allow more species to recruit by providing the propagules with a refuge against desiccation and/or grazing by molluscs (Burrows & Lodge, 1950; Lewis & Bowman, 1975; Choat, 1977; Lubchenco, 1980; Hawkins, 1981; Sutherland & Ortega, 1986; Jernakoff, 1983). The same principle therefore applies to the additional structures and crevices provided by mussel beds (Lohse, 1993b).

While the movements of large grazers, such as patellid limpets, may be restricted over mussel beds, such foraging can also be important. One mechanism that protects mussels from fouling and subsequent mortality is the constant action of mobile grazers such as small limpets, chitons and/or sea urchins within the mussel matrix (Suchanek, 1979; Witman, 1987; Robles & Robb, 1993). In fact large areas of mussel beds in the Wadden Sea often remain largely uncolonised by macroalgae, with the exception of *Fucus vesiculosus*. When the grazers *Littorina littorea* were removed from the mussel beds ephemeral algae grew highlighting the fact that grazers were having an impact on community structure (Albrecht, 1998). The mussel matrix provides increased protection for these mobile grazers from predation and/or desiccation.

It has also been suggested that rough mussel patches may act as barriers for dispersal of littorinids rather than as refuges (Kostylev, 1996). Mobile grazers found on mussels at low tide, may therefore require open space on the rock to forage during high tide. The presence of browsing haloes around some mussel beds (Suchanek, 1978) lends support to this idea. However, it is possible that these haloes are caused, in whole or in part, by individuals living on rock under the edge of the mussel beds. Furthermore, even if some epibiotic individuals do forage on rock, grazing marks found on mussels imply at least some grazing does occur on this substratum (Lohse, 1993b). This therefore suggests that open space on rock is not necessary for the survival of all mobile grazers. Furthermore, the limpet *Collisella heroldi* lives both within and around mussel patches and it moves relatively freely between patches and the surrounding area (Tsuchiya & Nishihira, 1985).

The scale of the substratum complexity is also important. If crevices are small, most snails cannot effectively graze in them. However, slightly larger crevices or holes provide havens for the herbivores and probably represent areas of particularly intense grazing (Raffaelli & Hughes, 1978). In some studies (e.g. Southward, 1964; Choat, 1977; Hawkins, 1981) the size of barnacles and/or grazers have been shown to interact and alter the efficiency of the herbivores in finding and consuming propagules. Heterogeneity is only important for *Fucus* colonisation where grazers are present (Lubchenco, 1983). The growth and development of algae may not be dependent on the presence or absence of limpets (grazers) or mussels (habitat structure) but on an interaction between these components.

It has been suggested that on the rocky shores of Northwest Atlantic that where there was no physical or biotic disturbance fucoids were competitively inferior to the mussels *Mytilus edulis* (Menge, 1975, 1976; Menge & Sutherland, 1976; Petraitis, 1987; Chapman & Johnson, 1990). It was thought that where mussels did not dominate the *Fucus* this was due to whelk predation reducing mussel cover. Experiments done in several areas indicated that in the absence of *Nucella*, *Mytilus* pulls *Fucus* in to the matrix of the mussel bed, eventually either smothering it or tearing it loose when the mussels are washed off the shore during storms. In this system large patellid limpets are missing from mid shore mussel beds. Petraitis (1987), however, clearly demonstrated that at very sheltered shores *Fucus* and mussels were limited or affected by herbivory, and that dominance by mussels was not controlled by whelk predation. In these conditions mussels were not competitively dominant to *Fucus* and perhaps the opposite was true (McCook & Chapman, 1991).

(7.1.4.) Aims and Objectives

On rocky shores in Southwest England community structure is thought to be affected by a keystone grazer and an ecosystem engineer: limpets and mussels respectively. Interactions between such species play a key role in structuring rocky shore assemblages. The strengths and directions of such interactions may vary in intensity depending on the particular location under investigation. It was the aim of this project to assess the relative importance of mussels and limpets in structuring algal communities observed on the rocky shore in the Northeast Atlantic. The importance of these species has been examined on an individual basis (e.g. Hawkins *et al.*, 1992; Lohse, 1993a, b) but the potential for interactive effects has until now been largely ignored.

A factorial experiment incorporating the removal of mussels and limpets was set up in the intertidal zone of two shores in North Cornwall. The removal of species both individually and in combination allowed the testing of specific hypotheses. Firstly it was predicted that where limpets were removed there would be an increase in food availability that alternative grazers would exploit. Secondly the impact of limpet and mussel removals on algal abundance was assessed. The hypotheses tested were that either mussels, limpets or a combination of both taxa would affect algal abundance. Finally the impact of the manipulations on community as a whole were identified under the following hypotheses: (1) It is the presence of mussels that dictates the composition of the observed rocky shore assemblage regardless of the presence of limpets. (2) It is the presence of limpets that causes the composition of the observed rocky shore assemblage regardless of the presence of mussels. (3) It is the combination of mussels and limpets that dictates the assemblage. The manipulation plots were monitored for a period of one year to assess changes in community structure associated with each treatment. The relative importance of a keystone species, an ecosystem engineer and the strengths of the interactions between these two taxa were then assessed.

(7.2.) METHOD

(7.2.1.) Study Sites

The work was carried out at Polzeath and Harlyn Bay, on the North Cornwall coast. For a more complete site description see Chapter 6. Sites were chosen to be representative of those on the North coast of Cornwall and have similar cover of mussels and numbers of limpets. Prior to the start of the manipulations a preliminary survey was made of the two sites in order to characterise the communities present. Non-metric Multidimensional Scaling (MDS) analysis was also used to ensure that there were no differences between plots prior to the manipulations (see section 7.2.3)

(7.2.2.) Experimental Manipulations

A factorial design was employed in order to assess the relative importance of the roles of both limpets and mussels in structuring the associated communities. At each of the sites a set of thirty four 0.5m x0.5m plots were marked. A minimum distance of 1m was maintained between each plot to ensure independence and to allow for limpet movement. Each of the plots was randomly assigned a treatment. The following manipulations were performed: limpets and mussels were removed from eight plots; limpets alone were removed from nine plots, with one serving as a spare in case mussels were lost (e.g. by storm action); mussels alone were removed from a further eight plots; nine plots served as a control, with both mussels and limpets left in place. Again one of these acted as a spare in case of mussel loss.

Mussels were scraped from the substratum and limpets were removed by hand using chisels. Where limpets were removed, a further band of 0.25m was cleared around the edge of the plot to serve as a buffer zone against limpets moving in to the area. Limpet exclusion plots were cleared at monthly intervals for the duration of the experiment.

The experimental plots at both sites were monitored monthly for the first three months of the study, subsequent counts were made at quarterly intervals. Plots were monitored using a quadrat with 49 equidistant intersection points, enabling estimates of percentage cover. Recordings from individual plots were taken in a four stage process. Initially the percentage cover of *Fucus* was estimated by counting the number of intersection points which overlaid such species. Secondly the primary space occupiers of the rock surface were established and categorised into two general sub-headings: mussel covered or non mussel covered (the latter also incorporated sessile species such as barnacles; and is termed rock from here onwards). Thirdly a record was made of each sessile species found under each of the 49 intersection points and it was noted whether these species were present on either rock or mussels. Finally counts of mobile species were made throughout the entire quadrat. Any species that were present but not under an intersection point were noted.

To ensure a constant standard of observation a set of guidelines were introduced. If the shell of a motile species was within 0.5cm of mussels it was classified as being on mussels, as opposed to rock. The location of littorinids present on algae was classified based on the point of attachment of the algae. *Fucus* germlings were counted as fronds less than 2cm in length. Similarly juvenile limpets were classified as less than 1.5 cm in length. Species too numerous to count were ranked on an abundance scale (Hawkins & Jones, 1992).

(7.2.3.) Analysis

Firstly the number of grazers, other than limpets, found in the different treatments and controls were analysed. The percentage cover of mussels per plot was first scaled to convert the figure to a percentage per metre squared; numbers of grazers were therefore expressed in terms of this unit. A series of univariate ANOVAs were used to test the first hypothesis over a number of dates. The count data were Ln (x+1) transformed prior to analysis.

The changes in algal and macrofaunal abundances in the four treatments were first examined throughout the duration of the experiment. Time series plots were constructed for the major algal groupings in each of the treatments and controls. The species assemblages associated with the different treatments were examined in detail for three time points namely December 1998, May 1999 and September 1999. These times corresponded to samples before, during and after a marked summer peak in abundance (Figure 7.1).

At these times, a series of univariate ANOVAs were used to test specific hypotheses. The total cover of algae, *Fucus*, and ephemerals were tested. The percentage cover of barnacles and *Porphyra* spp. per quadrat were also tested on these dates. All percentage data were arcsine transformed and all count data were Ln (x+1) transformed prior to analysis. Where significant differences between means are stated in the results section this is based on statistics derived from the Student Newman Keuls test (SNK) in which $p<0.05$ (Underwood, 1997).

For comparisons of community composition, three multivariate procedures from the PRIMER software package (Plymouth Marine Laboratory) were used (Clarke & Warwick, 1994). SIMPER (Similarity Percentage Procedure) allows the examination of the contribution each species makes to the average similarity within a treatment and dissimilarity between treatments. The average contribution of a particular species is defined by taking the average over all pairs of quadrats within a treatment. The more abundant a species is within a treatment the more it will tend to contribute to the intra-group similarities. It typifies that treatment if it is found at a consistent abundance throughout so the standard deviation of its contribution is low, and the ratio between the average and the standard deviation of the species is high (Clarke, 1993).

Non-metric Multidimensional scaling (MDS) was used to assess the impact of each treatment on the overall change in community patterns. MDS is an ordination technique that provides a two dimensional representation of the Bray-Curtis similarities of the communities in each plot relative to other plots.

Once this graphical representation of the data had been established ANOSIM (analysis of similarities) a re-sampling technique, was used to test the hypotheses about difference in community structure. ANOSIM is a non parametric permutation procedure, applied to the rank similarity matrix underlying the ordination or classification of samples (Clarke & Warrick, 1994).

The multivariate analyses used to compare community patterns were done on non standardised, square-root transformed data.

(7.3.) RESULTS

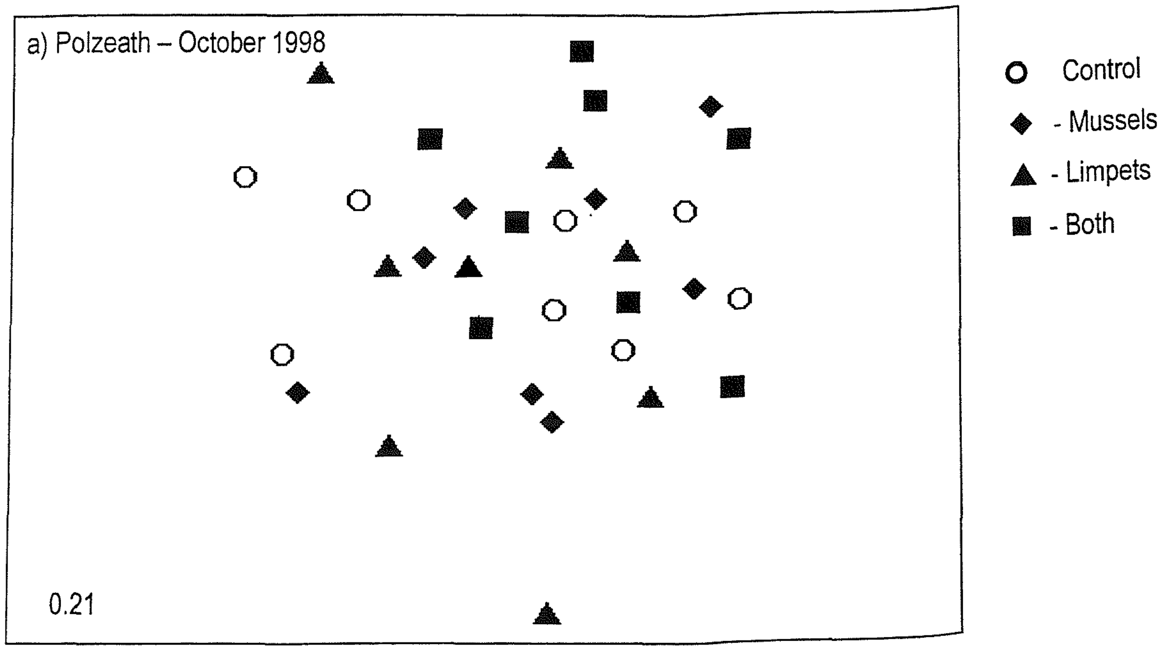
(7.3.1.) Site Characterisation

The midshore at both sites was largely dominated by a mosaic of mussels *Fucus*, and barnacles. The average percentage cover of mussels per plot at the two sites was 79% and 64% at Polzeath and Harlyn respectively. The algal species observed at the two sites were also generally similar but varied in their relative proportions. They included *Fucus vesiculosus*, *Fucus serratus*, *Porphyra* spp., *Ulva*, *Enteromorpha* spp. and small amounts of encrusting algae such as *Corallina officinalis* and lithothamnia. The most notable difference between the two sites, however, was the overall abundance of algae. The abundance of algae was considerably higher at Harlyn than Polzeath (Figure 7.3) with an average percentage cover of *Fucus* at 30% and 4% respectively. In contrast, grazers including limpets, a number of littorinids, *G. umbilicalis* and occasional *Osilinus lineata* were present in similar densities at the two shores. Typical numbers of *Patella* and *Gibbula*, for example, included 64 ± 5 and 14 ± 3 per m^2 respectively at Polzeath and 41 ± 5 and 13 ± 2 per m^2 at Harlyn.

Prior to the start of the experiment care was taken that that there were no differences between the plots selected for manipulations; any effects observed could therefore be attributed to the treatments. The MDS analysis constructed for each shore demonstrated a random assortment of plots assigned to each treatment (Figure 7.1). Communities observed within each plot therefore had similar characteristics prior to the start of the manipulations.

(7.3.2.) Effectiveness of Treatments

Manual removals of limpets were successful in reducing their abundance in the relevant plots. In December 1998, for example, on revisiting each site the average number of limpets in the quadrats where this taxa had been removed was 3.5 per m^2; much lower than those where the organism had been left in place (21 per m^2).



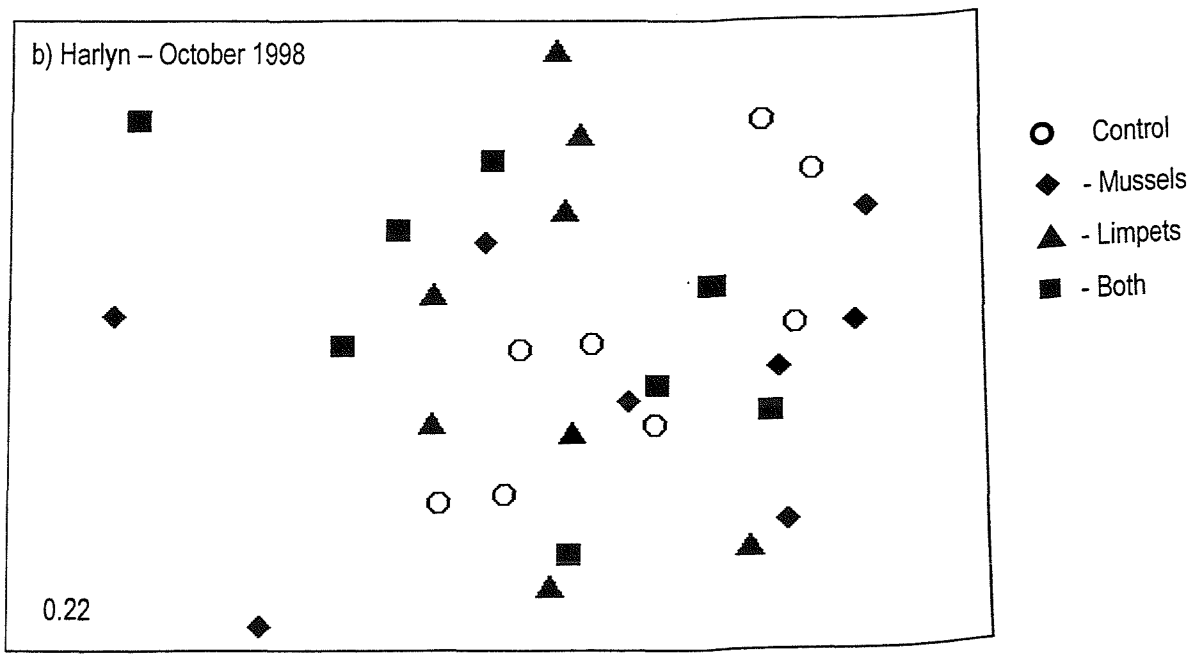


Figure (7.1): Non metric multi-dimensional scaling (MDS) of average community compositions in the three experimental treatments and the control plots at the start of the experiment (N=8). (Stress Value = Bottom Left).

(7.3.3.) Abundance of Grazers Other Than Limpets

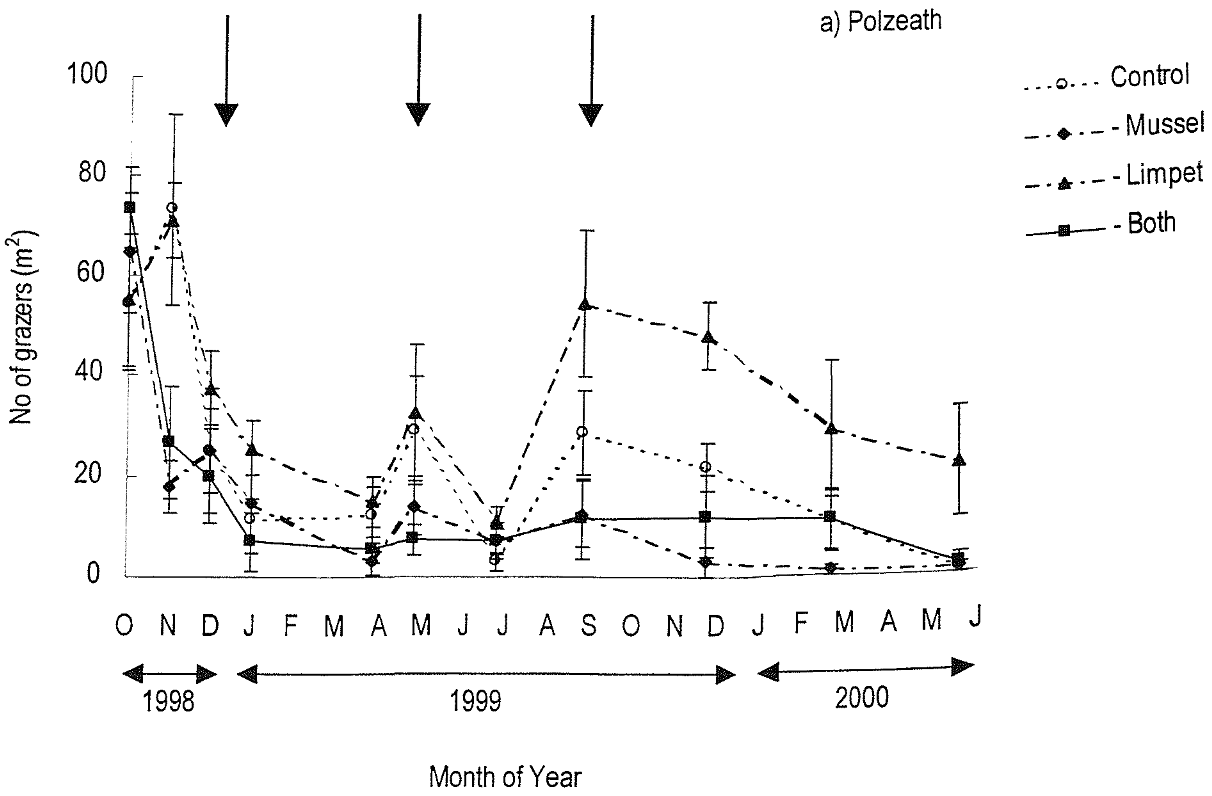
The average number of grazers, other than limpets, observed per quadrat varied considerably through time and may have been affected by short term variation in detectability (see discussion). There were, however, always significantly more grazers associated with the presence of mussels than without (Figure, 7.2; Table 7.1). The absence of limpets within a plot significantly increased the total number of grazers, in both the presence and absence of mussels on only one occasion, July 1999 (Table 7.1). In contrast the number of grazers located on mussels were significantly affected by the presence or absence of limpets in both January 1999 and July 1999 (Table 7.2). Where limpets had been removed the numbers of grazers, other than limpets, present on mussels was significantly higher than where limpets were left in place (Figure 7.2).

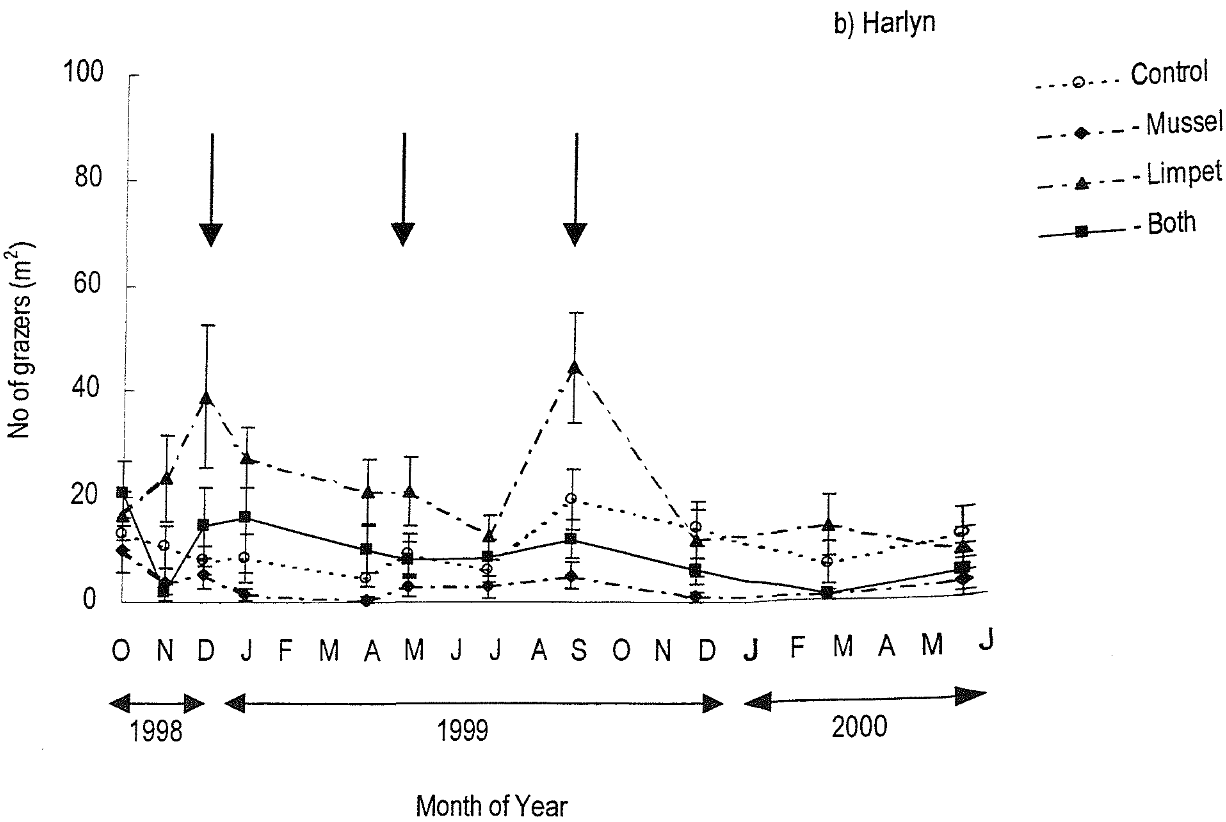
Table (7.1): Summary of ANOVA to examine the effects of limpet removal on the number of other grazers in the presence or absence of mussels. (d.f.=1; **Significance: * = p<0.05, ** = p<0.01, *** = p<0.001**) (' = Random Factor, Si = Site, Li = Limpet, Mu = Mussel)

	Dec-98		Jan-99		Apr-99		May-99		Jul-99		Sep-99	
Source	MS	F	MS	F	MS	F	MS	F	MS	F	MS	F
Site'	5.14	6.12*	0.35	0.44	0.00	0.00	2.47	3.17	0.10	0.20	0.32	0.35
Limpet	3.12	3.72	4.51	2.64	5.04	3.47	0.62	0.30	1.27	**637.78***	1.56	**1.70**
Mussel	6.70	**8.18****	9.39	**11.82****	6.58	**12.14*****	7.19	**9.24****	0.41	**203.19***	16.94	**18.42*****
SixLi	0.62	0.74	1.71	2.15	1.45	2.68	2.10	2.7	0.00	0.00	0.59	0.64
SixMu	0.04	0.05	0.00	0.00	0.02	0.04	0.00	0.00	0.00	0.00	0.29	0.31
LixMu	1.66	1.98	2.66	3.34	0.00	0.00	0.36	0.46	0.93	0.87	0.25	0.28
SixLixMu	0.03	0.04	0.45	0.56	0.03	0.05	0.01	0.02	1.07	2.09	0.44	0.48
Residual	0.87		0.81		0.56		0.81		0.15		0.95	

Table (7.2): Summary of ANOVA to examine the effects of limpet exclusions on the number of other grazers on mussels. (d.f.= 1; **Significance: * = p<0.05, ** = p<0.01, *** = p<0.001**)

	Dec 98		Jan 99		Apr 99		July 99		Sept 99	
Source	MS	F	MS	F	MS	F	MS	F	MS	F
Site'	7.72	3.81	476.55	0.86	0.18	0.08	155.14	1.04	208.28	0.25
Limpet	8.94	5.50	4748.98	**8.59****	1.82	0.77	633.94	**4.44***	2936.46	3.47
Si x Li	1.62	0.80	233.12	0.42	0.04	0.02	27.94	0.19	293.06	0.35
Residual	2.03		563.94		2.44		27.94		866.75	





(Figure 7.2): The average number of grazers (other than limpets) in the control and treatment plots throughout the experiment (a) Polzeath and (b) Harlyn. (Error bars = standard error; n=8). (↓ denotes occasions on which formal statistical treatment was undertaken).

(7.3.4.) Impact on Major Space Occupiers

When examining the control plots an underlying seasonal trend in algal abundance became apparent. Ephemeral and total algal levels at both sites reached a peak during the summer months. In contrast *Fucus* only showed this pattern at Harlyn with percentage cover remaining relatively constant at Polzeath (Figure 7.3). It is also clear from these plots that ephemeral species represented a large proportion of total algal cover throughout the year at both sites.

In terms of total algal cover the treatment plots at Harlyn and Polzeath followed the same temporal pattern as controls, except where just mussels had been removed (Figure 7.4). Where mussels had been removed algal cover remained relatively low and constant for the entire duration of the study. In contrast the overall abundance of algae was greatest where solely limpets had been removed. This relationship was significant in December 1998 where there was more algae with reduced limpet grazing in both the presence and absence of mussels (Table 7.3a). In May and September 1999, however, the difference in algal cover between plots with and without limpets was greater at Harlyn than at Polzeath (Figure, 7.4; Table 7.3b & c). This was probably attributable to the overall difference in algal abundance between these two sites (Figure, 7.3; Table 7.3b & c). There was also more algae where mussels remained in place in both the presence and absence of limpets (Figure 7.4). Again this relationship was significant in both May and September 1999 (Table 7.3b & c).

In December 1998 there was a significant interaction between the effects of mussels and limpets on the total cover of algae on rock and barnacles (excluding *Fucus*) (Table 7.3a). In plots where mussels were present, the removal of limpets made no difference to the algal cover on the rock and barnacle covered surfaces. In contrast, where mussels were absent there was more algae in plots which contained reduced limpet numbers relative to those where limpets were left in place. In May 1999 limpets were important in determining the total amount of algae on rock (excluding *Fucus*) irrespective of the of the presence of mussels. If limpets were absent, however, then algal abundance on rock was greater in the absence rather than the presence of mussels (Table 7.3b). In September 1999 the only significant difference between algal cover on the rock was between the two sites (Table 7.3c); no differences were apparent between the two treatments (Figure 7.4).

Ephemeral cover followed the same temporal pattern as total algae in both the control and treatment plots (Figure 7.5). In December 1998 there was no significant difference in ephemeral cover as a result of any treatment or site (Table 7.3a). In May 1999, seven months after the start of the experiment the only significant difference in ephemeral cover was between sites (Table 7.3b). There was, however, significantly more *Porphyra* in the absence, rather than presence of limpets, at both sites in May 1999 (Table 7.3b). By the September of the same year there was no significant difference in total ephemeral cover between the two sites. Although plots with higher limpet densities did demonstrate significantly reduced cover of such species (Table 7.3c). When observing the example of *Porphyra*, this species was more abundant on mussels at Polzeath than Harlyn at this time. In the absence of mussels, however, there was no differences between the two sites. At Polzeath there was also more *Porphyra* on mussels than on rock surfaces, this was in contrast to Harlyn where there was no difference with regard to the cover on the different substrata (Figure 7.5; Table 7.3c).

At Harlyn the peak in *Fucus* abundance was much less pronounced than the other algal categories and also occurred later in the year (Figure 7.6). Again *Fucus* cover was greatest in the presence of mussels and the absence of limpets; it was least where mussels were absent and limpets were present. At Polzeath the pattern was far less pronounced with very low abundance levels throughout the experiment in all treatments. In addition to the overall differences between sites in the *Fucus* abundance, in December 1998 there was significantly more *Fucus* on mussels than rock at both sites (Table 7.3a). In May and September the effects of mussels and limpets varied from site to site (Table 7.3b & c). At Polzeath the presence or absence of either species made no difference to the amount of *Fucus*, which was extremely small in all treatments. At Harlyn there was significantly more *Fucus* in the absence of limpets relative to where they were present. Likewise, *Fucus* abundance was greatest at this site in the presence rather than absence of mussels.

Another major space occupier, barnacles, also responded differently to the three treatments. Initially the percentage cover of barnacles was similar across all treatments (Figure 7.7). There were, however, significantly more barnacles at Harlyn than Polzeath in December 1998 (Table 7.4). There was also significantly greater cover in the presence of mussels at this time. In May and September 1999 there was a significant interaction between site and mussels. At Polzeath there were more barnacles in the absence rather than presence of mussels: a trend not apparent at Harlyn. There was also more barnacles associated with the presence of limpets at both sites (Figure 7.7; Table 7.4).

Table (7.3a): Summary of ANOVA to examine the effects of limpets and mussels on algal cover in the treatment and control plots in December 1998.
(d.f. =1; **Significance: * = p<0.05, ** = p<0.01, *** = p<0.001**) (' = Random Factor, Si = Site, Li = Limpet, Mu = Mussel, nf = not *Fucus*)

	Total Algae		Total Algae nf		Total ephemerals		Total *Porphyra*		Total *Fucus*	
Source	**MS**	**F**	**MS**	**F**	**MS**	**F**	**MS**	**F**	**MS**	**F**
Site'	7347.28	**29.11***	1477.15	**17.34*****	266.45	2.52	0.84	0.03	4974.42	**65.83 *****
Limpet	515.57	0.94	524.72	7.49	485.06	14.20	49.35	1.68	19.46	2.27
Mussel	3716.88	**14.73 *****	1.45	0.56	191.08	7.58	20.23	0.21	1725.47	**265.51***
Si x Li	551.02	2.18	70.02	0.82	34.16	0.32	29.45	1.07	8.56	0.11
Si x Mu	21.06	0.08	2.62	0.03	25.22	0.24	95.84	3.49	6.50	0.09
Li x Mu	182.82	**706.36***	457.27	**5.37***	285.87	3.65	3.41	0.29	3.43	25.5
Si x Li X Mu	0.26	0.00	7.87	0.09	78.36	0.74	11.87	0.43	0.13	0.00
Residual	256.52		86.59		105.78		27.46		75.57	

Table (7.3b): Summary of ANOVA to examine the effects of limpets and mussels on algal cover in the treatment and control plots in May 1999.
(d.f.= 1; **Significance: * = p<0.05, ** = p<0.01, *** = p<0.001**) (' = Random Factor, Si = Site, Li = Limpet, Mu = Mussel, nf = not *Fucus*)

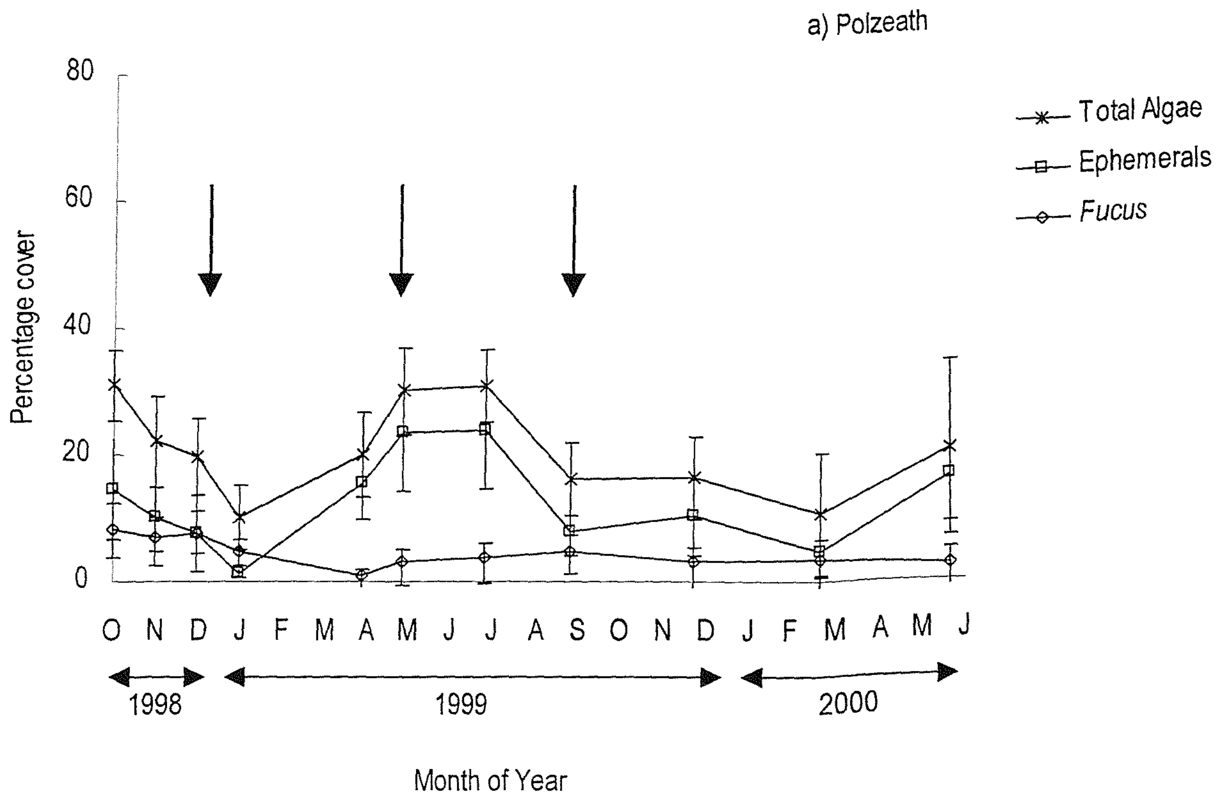
	Total Algae		Total Algae nf		Total Ephemerals		Total *Porphyra*		Total *Fucus*	
Source	**MS**	**F**	**MS**	**F**	**MS**	**F**	**MS**	**F**	**MS**	**F**
Site'	39492.62	**51.6 *****	10668.82	**23.54 *****	3113.92	**8.99 ****	14.32	0.08	11108.64	**128.55 *****
Limpet	31888.14	3.62	22676.60	3.13	13206.35	10.73	1880.32	**10.88 ****	663.05	1.41
Mussel	14374.21	**18.78 *****	494.28	2.80	3437.46	6.80	2526.45	3.71	1657.64	4.06
Si x Li	8812.05	**11.51 ****	7237.76	15.97	1230.47	3.55	13.05	0.08	468.67	**5.42***
Si x Mu	150.00	0.20	176.62	0.39	505.53	1.46	681.01	3.94	408.19	**4.72***
Li x Mu	1016.81	1.33	1896.82	**4.19***	1533.99	1.26	62.50	0.18	1.82	0.02
Si x Li X Mu	690.24	0.90	432.43	0.95	1218.67	3.52	349.63	2.02	0.09	0.00
Residual	777.76		453.57		346.39		175.69		87.95	

Table (7.3c): Summary of ANOVA to examine the effects of limpets and mussels on algal cover in the treatment and control plots in September 1999.
(d.f. =1; **Significance: * = p<0.05, ** = p<0.01, *** = p<0.001**) (' = Random Factor, Si = Site, Li = Limpet, Mu = Mussel, nf = not *Fucus*)

	Total Algae		Total Algae nf		Total Ephemerals		Total *Porphyra*		Total *Fucus*	
Source	**MS**	**F**	**MS**	**F**	**MS**	**F**	**MS**	**F**	**MS**	**F**
Site'	6875.61	**38.91 *****	1173.97	**15.77 *****	0.25	0.00	2.58	2.79	8387.20	**56.83 *****
Limpet	6803.30	4.42	1187.63	18.76	1148.69	**12.24 ****	8.39	36.69	3008.19	1.14
Mussel	3586.10	**20.30 *****	2.58	0.06	1207.20	4.25	11.06	1.59	1563.48	2.55
Si x Li	1538.47	**8.71****	63.30	0.85	60.28	0.64	0.21	0.23	2629.18	**17.81 *****
Si x Mu	52.09	0.29	40.89	0.55	284.15	3.03	6.95	**7.52****	612.31	**4.15***
Li x Mu	3.56	0.35	113.84	0.94	7.99	0.03	0.43	0.19	5.27	0.22
Si x Li X Mu	10.23	0.06	120.69	1.62	317.04	3.38	2.22	2.40	23.49	0.16
Residual	176.69		74.44		93.88		0.92		147.59	

Table (7.4): Summary of ANOVA to examine the effects of limpets and mussels on barnacle cover in the treatment and control plots on three dates.
(d.f. =1; **Significance: * = p<0.05, ** = p<0.01, *** = p<0.001**) (' = Random Factor, Si = Site, Li = Limpet, Mu = Mussel)

	December 98		May 99		Sept 99	
Source	**MS**	F	**MS**	F	**MS**	F
Site'	218.32	**6.66***	34.59	0.49	90.21	1.81
Limpet	13.29	0.15	401.39	**5.67***	506.80	**10.16****
Mussel	178.95	**5.46***	189.07	0.40	195.89	0.58
Si x Li	88.53	2.70	11.08	0.16	19.17	0.38
Si x Mu	1.18	0.04	476.58	**6.74***	338.64	**6.79***
Li x Mu	1.26	0.04	2.36	0.03	11.38	0.60
Si x Li X Mu	32.34	0.99	81.55	1.15	19.02	0.38
Residual	33.37		71.83		49.88	



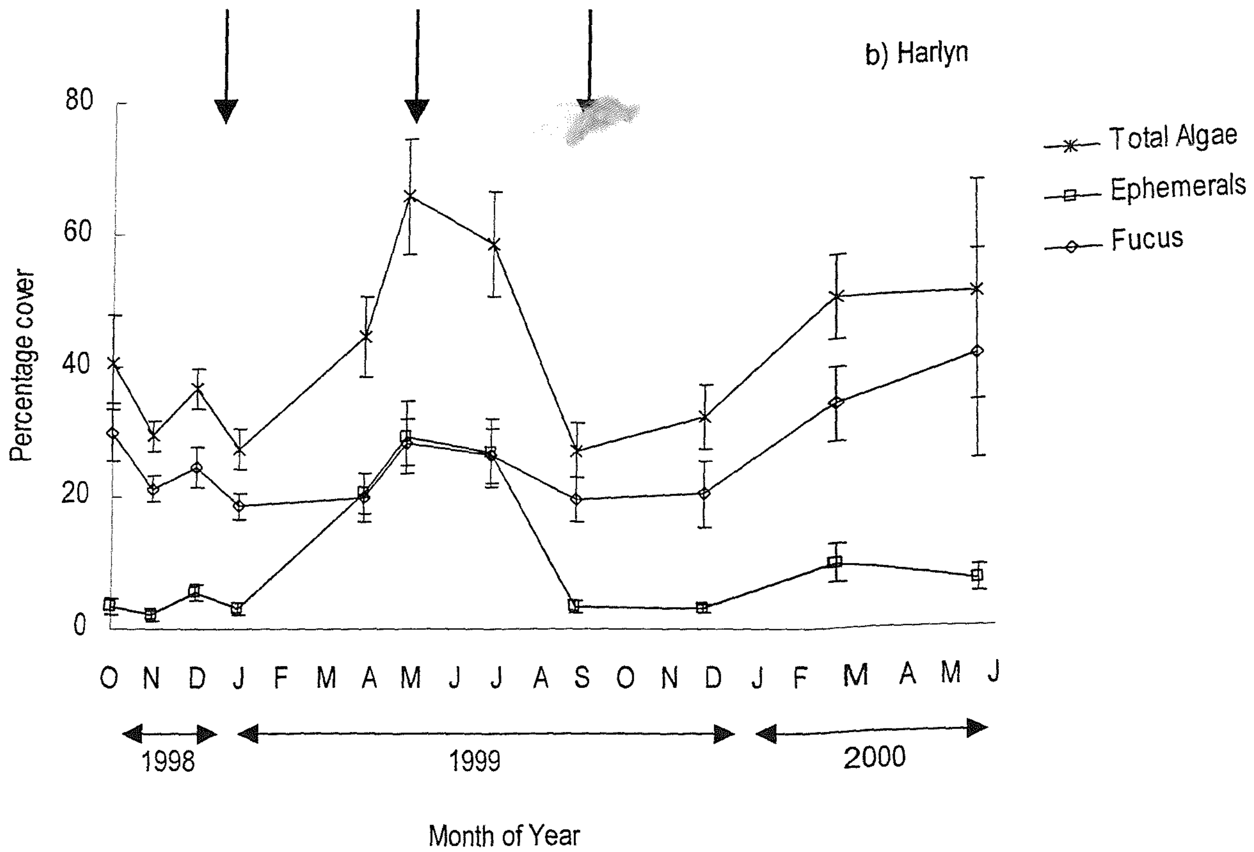


Figure (7.3): The average percentage cover of *Fucus*, ephemerals and total algal cover in control plots throughout the experiment (a) Polzeath and (b) Harlyn. (Error bars = standard error; n=8). (↓ denotes occasions on which formal statistical treatment was undertaken).

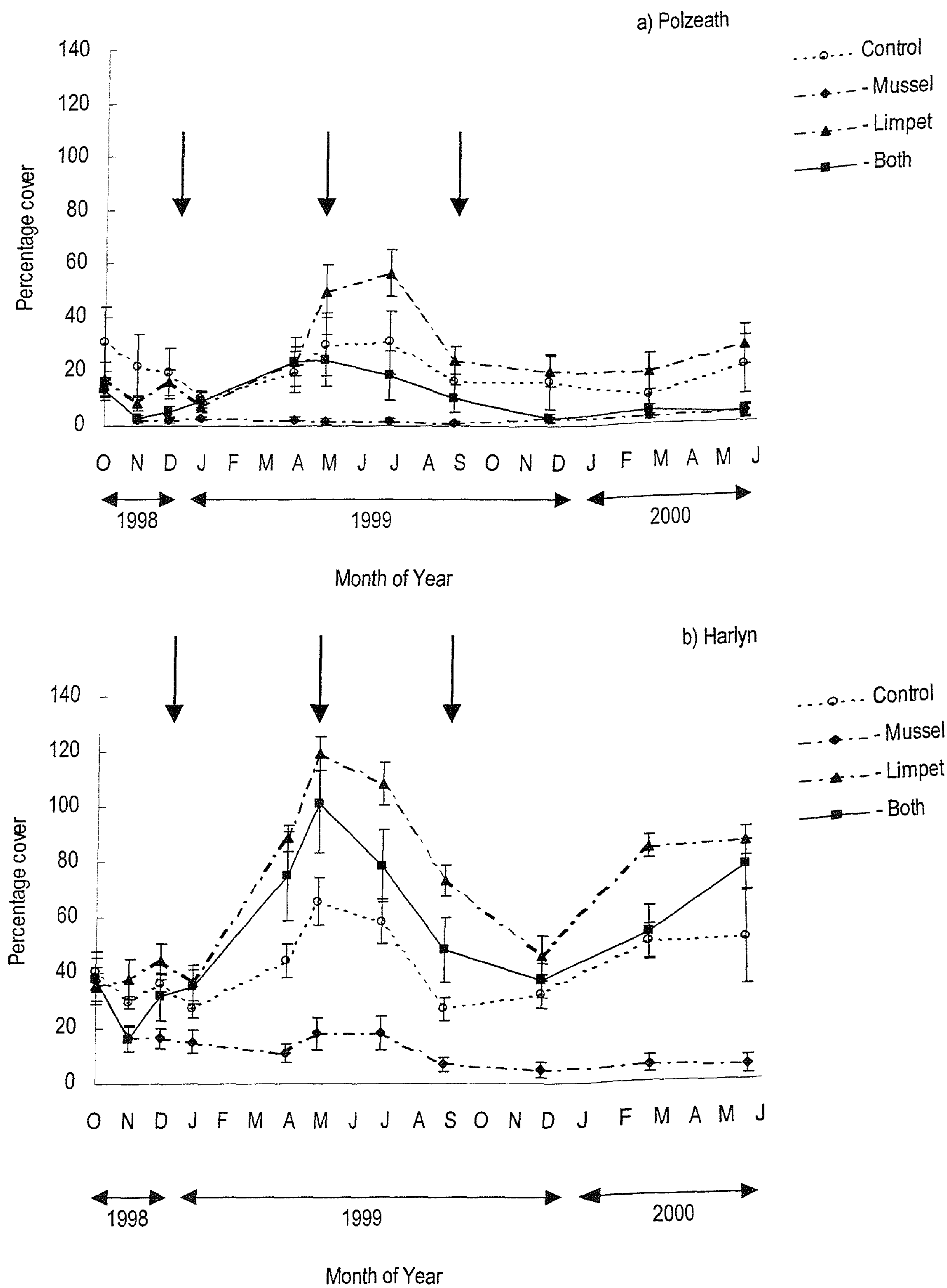
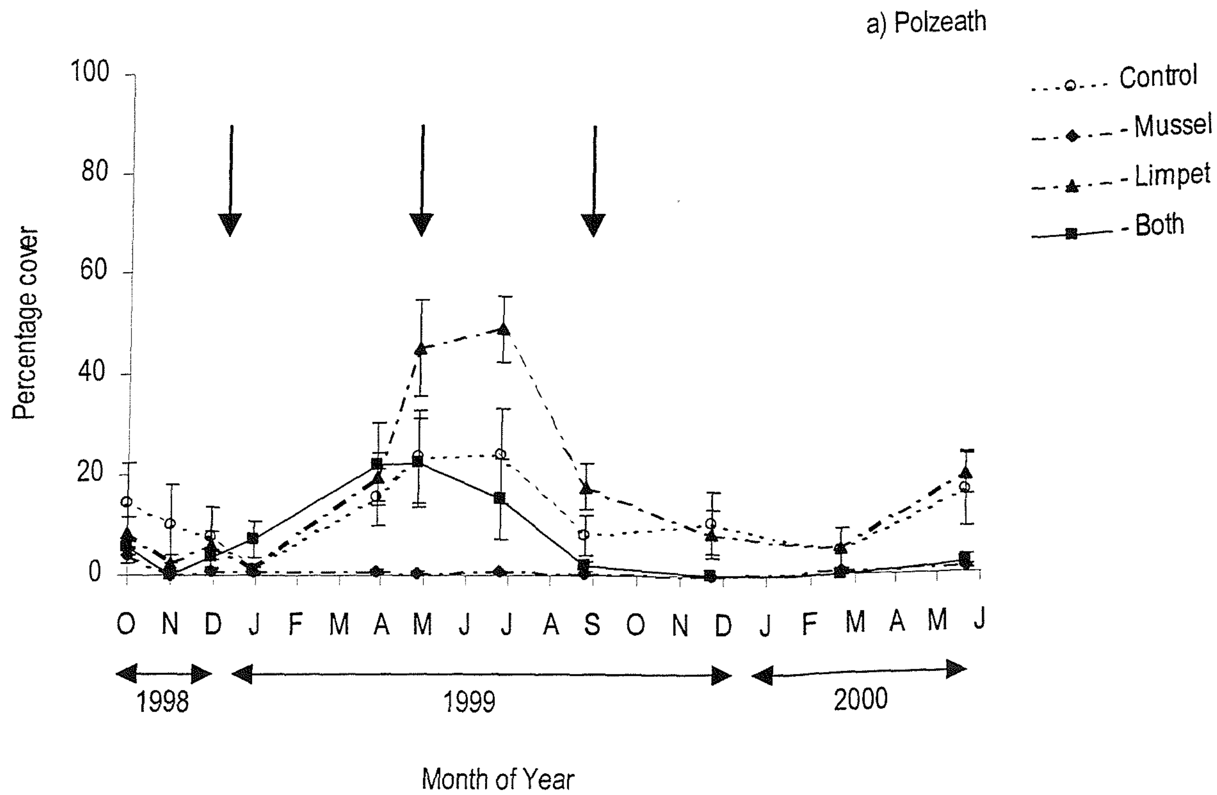


Figure (7.4): The average percentage total algal cover in the control and treatment plots throughout the experiment (a) Polzeath and (b) Harlyn. (Error bars = standard error; n=8). (↓denotes occasions on which formal statistical treatment was undertaken).



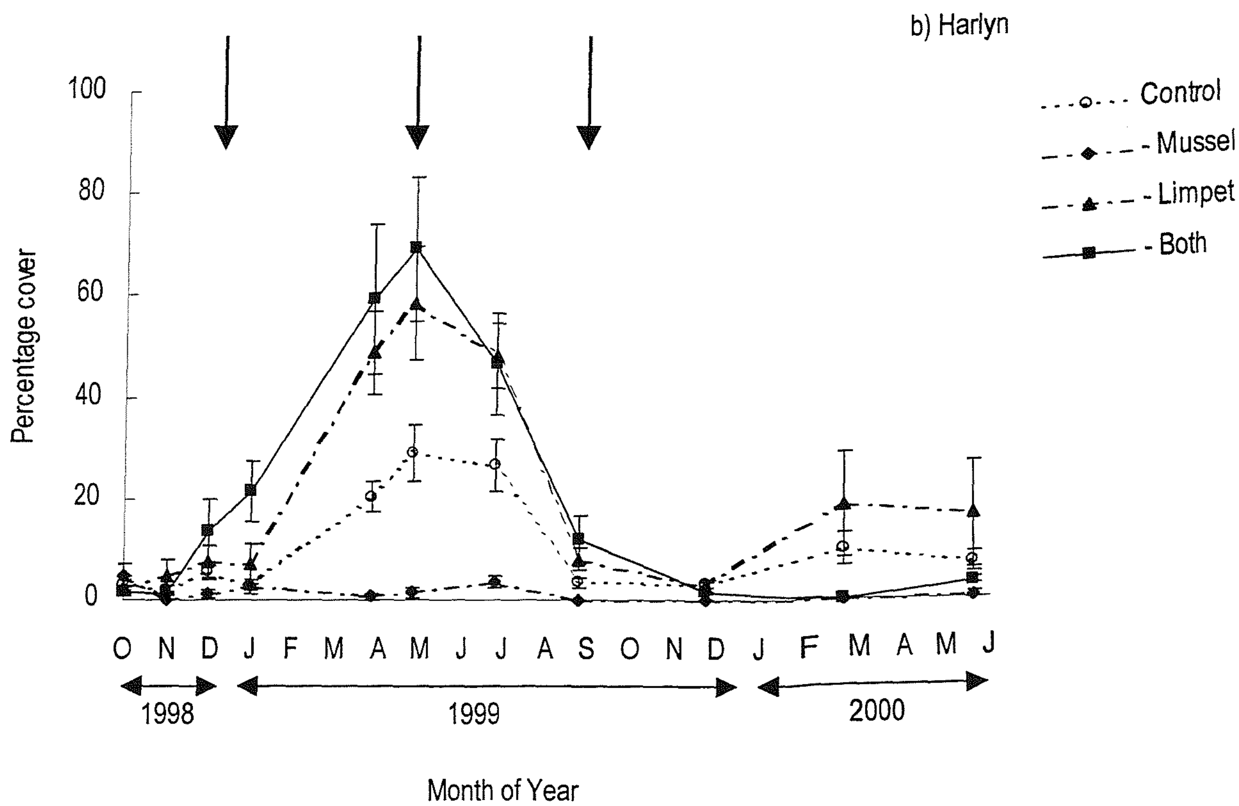


Figure (7.5): The average percentage ephemeral algae cover in the control and treatment plots throughout the experiment (a) Polzeath and (b) Harlyn. (Error bars = standard error; n=8). (↓ denotes occasions on which formal statistical treatment was undertaken).

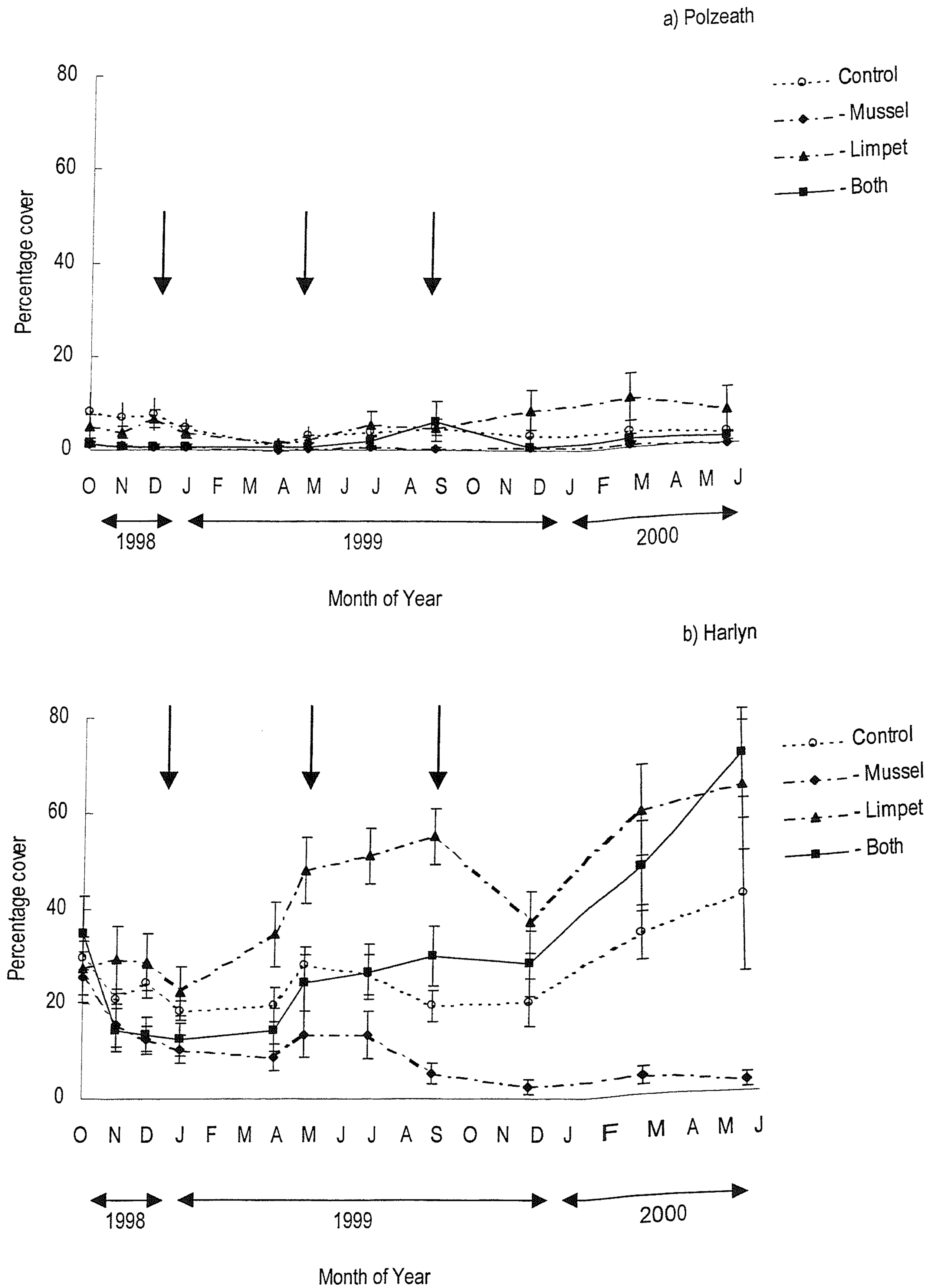
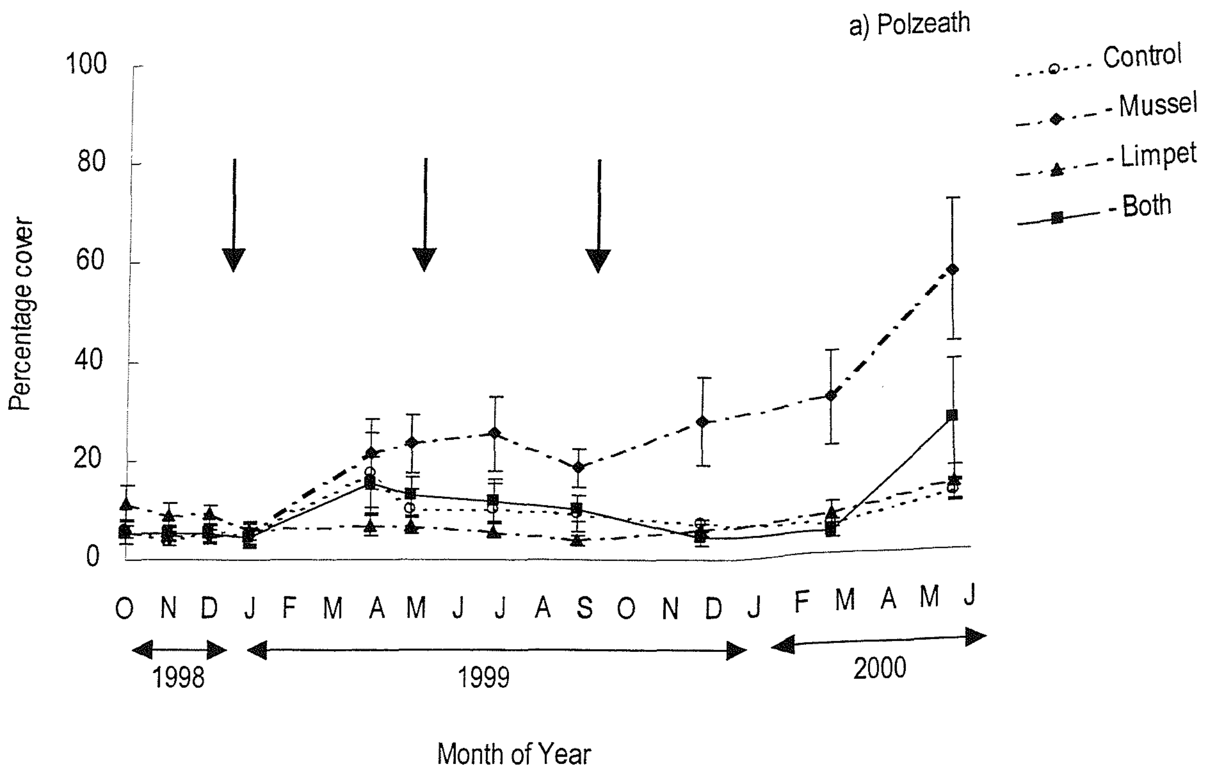


Figure (7.6): The average percentage *Fucus* cover in the control and treatment plots throughout the experiment at (a) Polzeath and (b) Harlyn. (Error bars = standard error; $n=8$). (↓denotes occasions on which formal statistical treatment was undertaken).



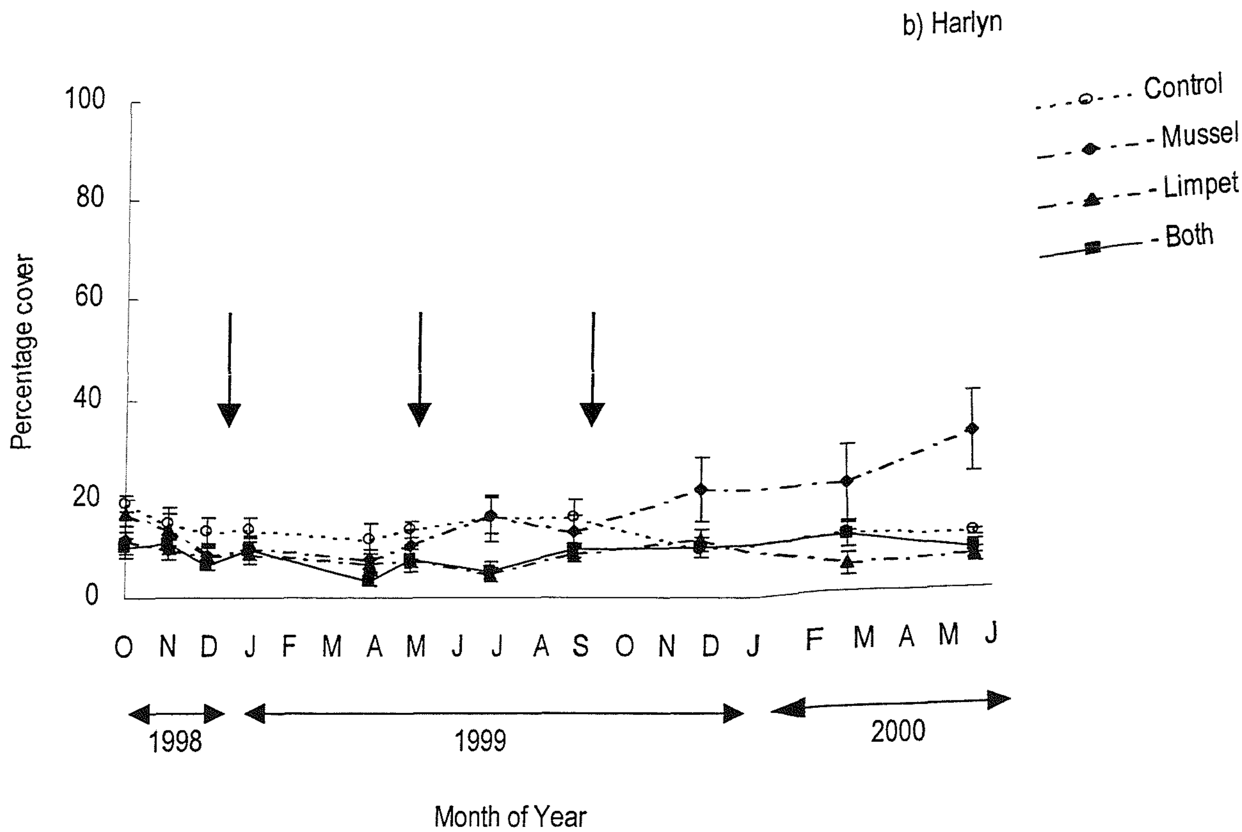


Figure (7.7): The average percentage cover of barnacles in the control and treatment plots throughout the experiment at (a) Polzeath and (b) Harlyn. (Error bars = standard error; *n*=8). (↓ denotes occasions on which formal statistical treatment was undertaken).

(7.3.5.) Community Level Changes

On the same three dates as the univariate analyses (December 1998, May 1999, September 1999), SIMPER was used to determine key community characteristics within each treatment at both sites. The species observed and their typical abundance levels prior to the manipulations have already been described (section 7.3.1). Throughout the course of the experiment control plots at Polzeath were characterised by the percentage cover of barnacles, *Fucus* spp. and counts of *Gibbula umbilicalis*. In contrast at Harlyn ephemeral algae species were ranked higher in importance. Where mussels had been removed the quadrats at Polzeath were again characterised by a higher percentage cover of barnacles and lower counts of *G. umbilicalis*. At Harlyn the predominance and importance of algae, in this case *Fucus* was highlighted. In the absence of limpets algal species, both macroalgae and ephemerals, characterised the plots at both sites. Where both species were removed again similar trends were apparent between the two shores. Barnacles and ephemeral green algae represented a key characteristic of this treatment. In addition high numbers of *G. umbilicalis* at Polzeath and a high percentage cover of *Fucus* at Harlyn were typical of these exclusions.

Two months after the start of the experiment at Polzeath, no differences were detected between the various treatments, except where either mussels or limpets were removed (Figure 7.8a; Table 7.5a). Once algal abundance was at its peak (May 1999) significant differences became apparent. In the absence of mussels a higher proportion of barnacles had settled in the quadrats as compared to the controls. There was also considerably more *Porphyra* and *G. umbilicalis* in control plots as compared to the mussel removals. At this time where limpets were absent and mussels were present there was more *Porphyra*, an undifferentiated ephemeral green alga and *G. umbilcalis* and fewer barnacles than where limpets were present and mussels were removed. From Figure 7.8b it would appear that control plots were most similar in their community composition to plots where limpets were excluded, and least like those where mussels were removed.

In September 1999 these differences were still apparent with a shift towards fewer algal species in the absence of mussels and presence of limpets (Table 7.5a). In terms of algal abundance, in particular ephemerals, the presence of mussels had a higher impact than that of limpets; mussels made the biggest difference to community composition regardless of limpets. *Porphyra*, for example, was more abundant where limpets were in place and mussels were removed compared to quadrats where both species were absent. The role of mussels was highlighted in Figure 7.8c where the symbols for plots without limpets and plots without both taxa were separated along the *x* axis. In general where mussels were present there was a greater percentage cover of *Porphyra*, larger numbers of *G. umbilicalis* and fewer barnacles as compared to where they were lacking.

At Harlyn, in contrast to Polzeath, significant differences between treatments were already apparent by December 1998 (Figure 7.9a; Table 7.5b). Control plots contained significantly more *Fucus* and barnacles than those in which both taxa were removed. The same was also true between control and mussel removal plots for *Fucus*, barnacles and ephemeral green algae. Plots in which either mussels or limpets had been removed were also significantly different, with more *Fucus* and *Gibbula* in the presence of mussels than without.

At Harlyn, in May 1999, there was considerably more algae, both macroalgae and ephemerals, present in the control plots as compared to the removal of just mussels (Table 7.5b). Algal abundance was also greater in control plots than in the limpet removal or the limpet and mussel removal plots. In the absence of mussels there were more algae without limpets than where they were present. Plots without limpets and plots with both taxa removed, however, were not significantly different. If there were no limpets, the presence or absence of mussels made no difference to the overall community structure. In contrast to Polzeath the limpet removals and the plots with limpets and mussels removed were the most similar treatments (Figure 7.9b).

The differences between the treatments increased throughout the time series. In September 1999 there was more *Fucus*, barnacles and *G. umbilicalis* in controls than quadrats where mussels had been left in place and limpets were removed (Table 7.5b). Where limpets were present and mussels were excluded there was considerably more algae, particularly *Fucus*, than where mussels were left in place and limpets were removed. The removal of limpets therefore made a difference to community structure regardless of the presence of mussels. Where mussels were removed and limpets left in place there was considerably less algae than where mussels and limpets were removed. In contrast to Polzeath, mussels and limpets had an interactive role in shaping community structure (Figure 7.9c).

Table (7.5): ANOSIM statistics to assess community level differences between the different treatments. (Where C= Control, -M = -Mussel, -L= -Limpet, -B= -Both.) (Significance levels: * = p<0.05, **=p<0.01, ***=p<0.001).

(a) Polzeath:

	December 1998	**May 1999**	**September 1999**
Treatment	Statistic Value	Statistic Value	Statistic Value
C , -M	0.14	**0.43****	**0.34****
C , -L	-0.06	-0.03	0.10
C , -B	0.06	0.04	0.13
-M , -L	**0.31****	**0.75*****	**0.84*****
-M , -B	0.06	0.07	0.12
-L , -B	0.21	0.16	**0.46****

(b) Harlyn:

	December 1998	**May 1999**	**September 1999**
Treatment	Statistic Value	Statistic Value	Statistic Value
C , -M	**0.36*****	**0.50*****	**0.33*****
C , -L	0.06	**0.32****	**0.26****
C , -B	**0.30*****	**0.18***	0.16
-M , -L	**0.44*****	**0.60*****	**0.73*****
-M , -B	**0.16***	**0.40*****	**0.45*****
-L , -B	**0.24***	0.04	0.06

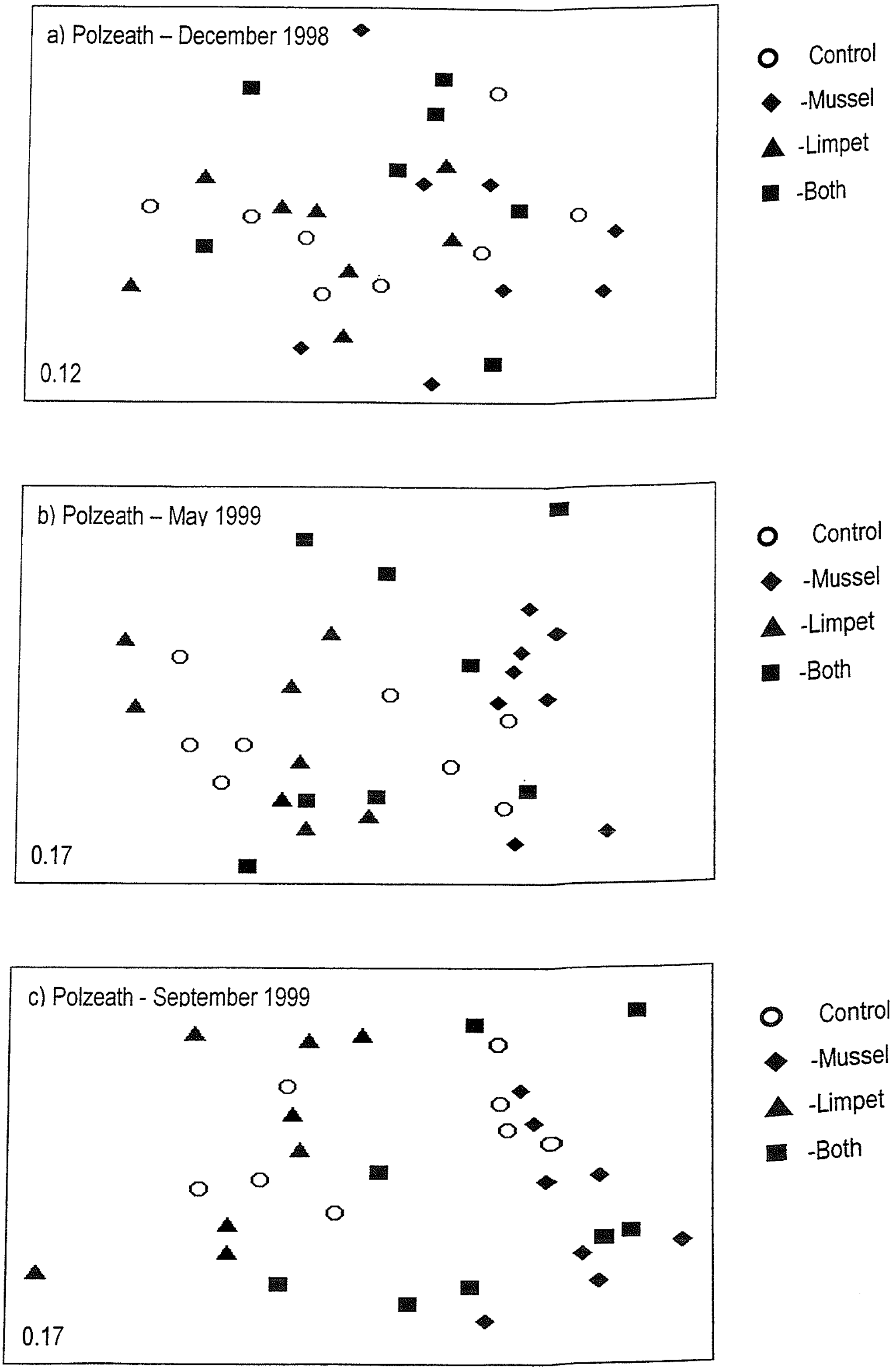


Figure (7.8): Non metric multi-dimensional scaling (MDS) of average community compositions in the three experimental treatments and the control plots (N=8). (Stress Value = Bottom Left).

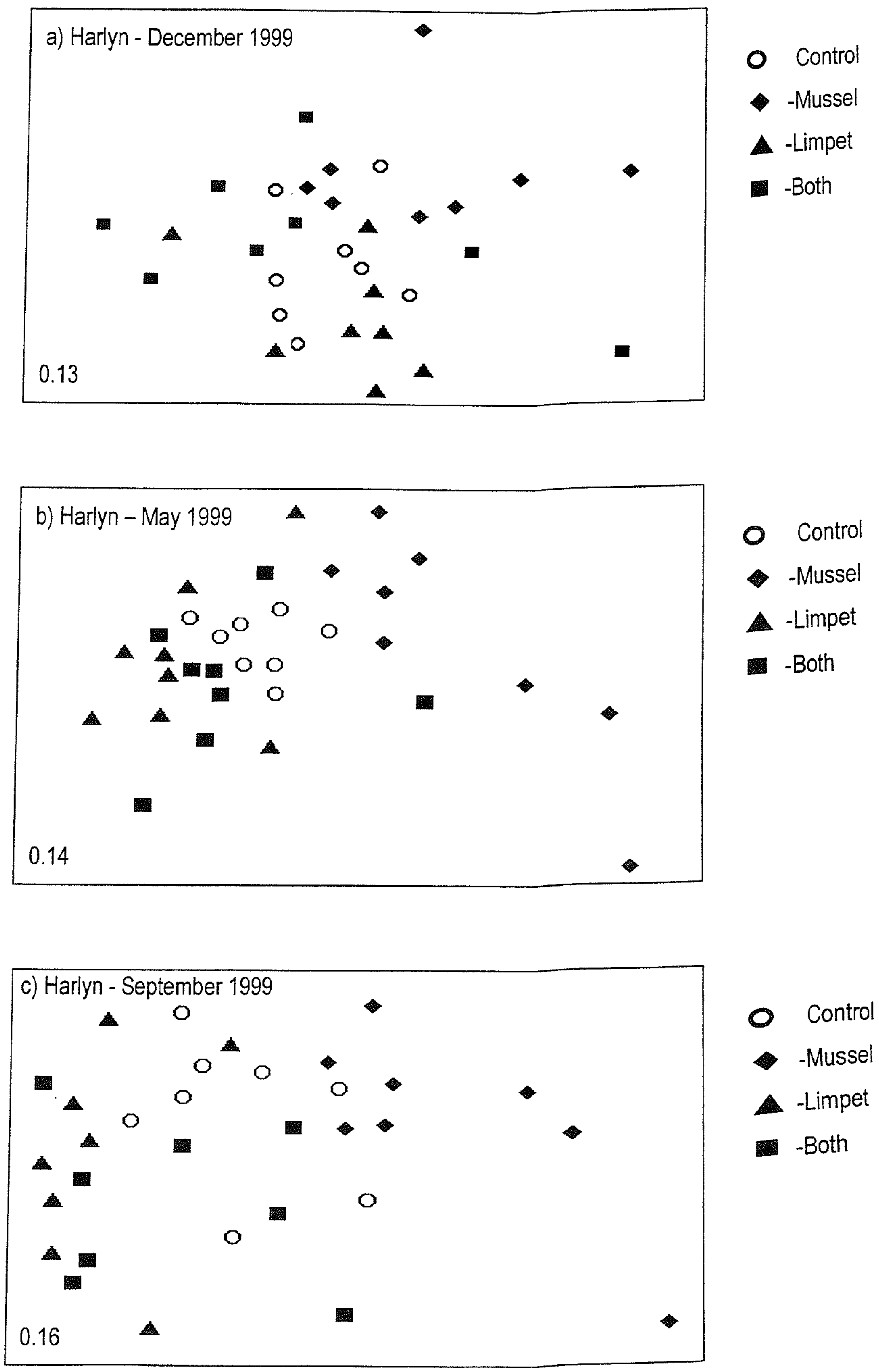


Figure (7.9): Non metric multi-dimensional scaling (MDS) of average community compositions in the three experimental treatments and the control plots (N=8). (Stress Value = Bottom Left).

(7.4.) DISCUSSION

(7.4.1.) Experimental Procedures

Previous studies have used exclusion cages to reduce the number of limpets in a quadrat (e.g Underwood, 1980; Hawkins, 1981; Underwood & Jernakoff, 1981). Where limpets have been excluded an increase in algal biomass, relative to the associated controls, has been apparent; a result consistent with the current study. Such experiments have highlighted the importance of removing all grazers, or the effects are not nearly as pronounced (e.g. Raffaelli, 1979). This experiment demonstrated that the removal of limpets from within an extended boundary of the observed quadrat is equally as effective at reducing limpet densities. There were also marked advantages in not using cages as controls were not required for caging artefacts (e.g. Underwood, 1980). The removal frequency of one month was also found to be appropriate. It is important to remember that unlike previous investigations, that used cages, the only grazers excluded in this study were limpets. The direct effect of limpets in shaping community patterns could therefore be examined.

(7.4.2.) Algal Colonisation

The two sites were largely similar with respect to their community composition with the exception of overall algal abundance. The large difference in total algal cover between the two sites is likely to be associated with differential recruitment between the two locations. Hydrodynamic conditions in an area are capable of affecting larval supply and mortality of newly settled larvae and juveniles of a number of species (Emerson & Grant, 1991; Lindegrath *et al.*, 1995). Dispersal of macroalgae can also occur in close proximity to adult plants; where *Fucus* is in short supply it is therefore likely to remain this way and vice versa (see Norton, 1992 for review). Such plants are adapted to release zygotes close to the rock surface and this reduces dispersal distances considerably (Sundene, 1962; Anderson & North, 1966; Koehl *et al.*, 1987). Settlement distances of *Pelvetia compressa*, for example, have been demonstrated to be higher inside patches of adults than a mere 25cm away (Johnson & Brawley, 1998).

The seasonal pattern in algal abundance at both sites was largely driven by ephemerals. Species such as *Porphyra* spp., *Enteromorpha* spp. and *Ulva lactucata* all reached a peak during the spring and summer months. Such features are typical on Northeast Atlantic shores where the composition and sequence of algae which colonise lightly grazed areas varies with season (Hawkins, 1981; Hawkins *et al.*, 1992). On barnacle covered rock, diatoms may be initial colonisers in autumn to late spring, followed by various ephemeral algae such as *Enteromorpha*, *Blidingia* and *Porphyra*, which are eventually outgrown by fucoids (Pyefinch, 1943; Moore, 1939; Rees, 1940; Dayton, 1971; Underwood, 1980).

The peak in fucoids later in the year was also consistent with previous observations. In the summer, fucoids can directly colonise barnacles without any preliminary stages (Hawkins, 1981; Hawkins & Hartnoll, unpublished data; Hawkins *et al.*, 1992). Physical factors vary throughout the year and can be associated with such algal changes (Williams, 1993). Grazer activity levels also vary with season and this may affect successional patterns. Limpets, for example, are thought to be more active during the summer months (Thompson *et al.*, in press; Jenkins *et al.*, in press).

(7.4.3.) The Role of Limpets in Determining Algal Abundance

At both sites where limpets were removed there was an increase in algae as compared to the controls. This is consistent with previous findings where limpets have been described as the keystone grazers (Southward, 1964; Southward & Southward, 1978; Hawkins & Hartnoll, 1983b; Farrell, 1988; Mak & Williams, 1999). Even with the replacement by other grazers the loss of limpets had a comparatively large effect on algal abundance highlighting the fact that other herbivores do not have such important effects as limpets. In some instances the presence of limpets appears to facilitate the activity of other primary space grazers which, on their own, would be unable to maintain bare rock. Species such as *Oxystele tabularis,* may be favoured by the presence of limpets provided that microalgal productivity is high enough (Dye & White, 1991).

During the first couple of months of the experiment there was also more algae in the presence of mussels regardless of limpet density. It seems unlikely therefore that mussels were being grazed effectively; limpets within a plot were not reducing the algal cover on mussels as compared to having no limpets in a plot. Previous studies have also suggested that limpets and other intertidal gastropods are restricted in their ability to graze such complex surfaces (see Kostlyev, 1996).

Field observations suggest that *Cellana grata*, for example, does not move directly over barnacles or other complex irregular objects on the rocky shore, perhaps because feeding is more difficult in such microhabitats (Kostylev, 1996). A similar behaviour has been observed for *Patella vulgata* in Southwest Ireland where limpets avoided moving in areas of high barnacle density (Little *et al.*, 1988). Grazing marks have, however, been found on mussels implying that at least some grazing does occurs on this substratum (Lohse, 1993b). The overgrowth of mussels by algae is also largely prevented by such activity (Suchanek, 1979; Witman, 1987; Robles & Robb, 1993).

In December 1998 there were no significant differences in ephemeral cover between the two sites or the different treatments. This can be explained by the fact that such species are typically not established at this time of year (Hawkins *et al.*, 1992). Likewise in September 1999 these species had died back considerably and contributed less to the system and overall community patterns. In the specific example of *Porphyra*, this species was much more abundant in the absence of limpets in May 1999. The reduction in grazing pressure may have resulted in the increased survival of algal propagules. Field observations have shown that limpet grazing can prevent recruitment of ephemerals to bare substrate, thereby restricting colonisation of the surface (Jenkins *et al.*, 1999b).

The percentage cover of *Fucus* was a reflection of the area of each plot covered with fronds; the number of holdfasts were not counted. Trends apparent at each site could therefore reflect an increase in size of a single plant rather than an increase in the total number of plants. *Fucus* levels at Polzeath were too low to detect any treatment effects. The patterns of *Fucus* abundance at Harlyn were typical of those described for the total algal cover.

(7.4.4.) Keystone Grazers Versus Ecosystem Engineers

The difference in magnitude in the importance of the mussels and limpets at the two sites became particularly apparent when examining *Porphyra* in September 1999. At Polzeath mussels were essential to the recruitment and survival of this ephemeral species. In contrast at Harlyn there was no difference in the cover of *Porphyra* with or without mussels. Even without limpets algae, in particular ephemerals, needed mussels to establish themselves at Polzeath. In the absence of algae there is nothing for limpets to remove; in effect limpets become redundant at Polzeath. At Harlyn if there were no limpets the presence or absence of mussels made no difference to the total algal cover; abundance was the same on barnacles and bare rock as on mussels. It was therefore an interaction between grazing pressure and the provision of secondary habitat at this site that had the greatest effect on community patterns.

Supporting evidence was that communities in control plots were far more similar to the plots where limpets were removed and least similar to the those where mussels were excluded at Polzeath (Figure 7.8). In contrast at Harlyn control communities were mid way between plots where either mussels or limpets were removed, suggesting that both species were important in shaping the natural communities (Figure 7.9).

The importance of limpets at Harlyn and not Polzeath, may again reflect the difference in algal cover and recruitment potential between the two sites. At Harlyn the larger number of propagules would increase the chance of algal escapes on both the rock and mussel substratum. The provision of refuge from grazing and other environmental parameters is therefore more important in such conditions. Such a situation would enhance an interaction between grazers and refuge provision.

The importance of mussels in the absence of limpets highlights the role that biogenic structures play in offering a refuge from additional environmental stresses. Irregular surface features can potentially enhance recruitment in several ways (Vadas *et al.*, 1992). Firstly they could act as a propagule trap by providing protection against hydrodynamic or mechanical dislodgement (Benedetti-Cecchi & Cinelli, 1992). Indeed mussel patches act as sediment traps and are therefore capable of trapping such particles (Suchanek, 1979). Previous work has also shown that the zygotes and embryos of fucoid species are extremely vulnerable to post settlement stresses associated with the period of low water (Brawley & Johnson, 1991; Davison *et al.*, 1993; Johnson & Brawley, 1998). Algal turf, mussels and barnacles are all capable of creating a more physically benign environment during low tide (Norton, 1983; Farrell, 1991; Brawley & Johnson, 1991, 1993; Sebens, 1991). Even structurally simple cyanobacterial mats have been shown to enhance the recruitment of fucoids (McCook & Chapman, 1993).

It is not unusual to attain differences in interaction strength between species at different locations. Such discrepancies are a reflection of the differing abiotic and biotic conditions and the relative species abundances at each site (e.g. Farrell, 1991; Kim, 1997). In different habitats grazers may have different effects (Lubchenco, 1983). Results presented by Johnson *et al.*, (1997) showed that limpets had an impact at some sites on the Isle of Man but not all. Where they had an impact, however, limpets generally reduced the probability of local algal recruitment. Manipulations of grazer density and *Ascophyllum* on sheltered shores in the Isle of Man provide a further example where the effects of limpets were not significant (Jenkins *et al.*, 1999b). The work suggested that limpets played a very limited role in structuring the mid-shore community of sheltered shores. This is in sharp contrast to the situation on more exposed barnacle dominated shores of Northwest Europe, where the ability of limpets to limit algal recruitment means they are the dominant structuring organism (Southward, 1964; Southward & Southward, 1978; Hawkins, 1981; Hawkins *et al.*, 1992).

While the interaction examined here was the role of limpet grazing and mussel refuges in determining algal abundance; on other coastlines different interactions between these taxa are apparent. On Northwest Atlantic coasts, in the absence of biotic or physical disturbance, mussels are thought to competitively exclude *Fucus* from mid shore assemblages. (Menge, 1975, 1976; Menge & Sutherland, 1976; Petraitis, 1987; Chapman & Johnson, 1990). Menge (1976) suggested that where this did not occur, this was due to whelk carnivory on the mussels. In contrast

McCook and Chapman (1991) found the opposite result where *Fucus* was dominant to mussels and that factors other than whelk predation were having an impact. The impact of grazing intensity on the fucoids at the different locations may have caused the differences in these results.

(7.4.5.) Associated Changes in the Community

The patterns of grazer movements (other than limpets) into areas where limpets had been removed were variable through time. Typically the spatial distribution of microalgae can be very patchy on rocky shores (Underwood, 1984; MacLulich, 1987; Hill & Hawkins, 1991; Williams, 1993) and this may have consequences for the behavioural patterns of mobile grazers. Where limpets have been removed there may be patches of increased food availability exploitable by other grazers (Cubit, 1984; Dye & White, 1991; Mak & Williams, 1999). This may therefore explain why in some instances where limpets had been removed from quadrats there was an influx of other grazers. The overall abundance of algae is greater at Harlyn Bay than at Polzeath; it would therefore be assumed that food was more of a limiting resource at Polzeath. This was, however, not reflected in the numbers of grazers moving into the limpet removal plots at each site.

The variable pattern through time may be explained by the different environmental conditions on each sampling date. Intertidal gastropods are known to seek refuge in crevices to avoid desiccation and thermal stress (Garrity, 1984; Garrity & Levings, 1984; Moran, 1985; Fairweather, 1988). During periods of strong wave action such species may also remain in refuges (Dayton, 1971; Feare, 1971; Moran, 1985; Gosselin & Bourget, 1989). This means there is a trade-off between time spent foraging or grazing and time spent in microhabitat refuges (Burrows & Hughes, 1991; Jones & Boulding, 1999; Burrows *et al.*, 2000). While these species were located in crevices or deep within the mussel matrix they would not have been visible to count.

These factors may also explain the reduction in the number of grazers other than limpets in the absence of mussels. The association of *G. umbilicalis* with mussels, for example, was particularly pronounced and this was at least partly explained by the refuge provided by the mussel beds. The biogenic structure serves to reduce the effect of wave action, temperature and sunlight while increasing relative humidity and sedimentation (Suchanek, 1979; Sebens, 1991). Such conditions are favourable to numerous intertidal gastropods and as such may cause an accumulation of these species (Tsuchiya & Nishihira; 1985; Moran, 1985; Fairweather, 1988; Jones & Boulding, 1999). Sousa (1984) also demonstrated that small patches of bare rock within mussel beds, supported higher densities of grazers than larger ones. As a consequence, the assemblage of algae which developed within small patches consisted of grazer resistant but competitively inferior species.

Another major change in community structure was displayed by barnacles (mainly *Chthalamus* spp.) where each treatment resulted in different abundance levels of this functional group. These differences were not apparent immediately after the initial experimental set up because there was a delay until the start of the settlement seasons of the barnacles. After this time there were more barnacles in the absence of mussels than in their presence, particularly at Polzeath. It is highly likely that mussels, which act as major space occupiers, reduce the amount of substratum available for barnacle settlement. Despite the risk of ingestion of barnacles larvae by mussels (Goodbody, 1961; Woodin, 1976; Young & Gotelli, 1988) cyprids of some species are capable of settling on this secondary substratum (Lohse, 1993a). In fact Lohse (1993a) found that there was no difference between barnacle settlement on rock surfaces and mussel shells. In the current study, however, barnacles, typically *Chthamalus*, were rarely observed settled on mussel shells.

At Harlyn mussels must also reduce the space available to barnacles but the greater amount of algae may moderate this effect. *Fucus* plants, for example, are capable of reducing barnacle settlement by a sweeping action of the fronds which can cause cyprid dislodgement (e.g. Lewis, 1964; Dayton, 1971; Menge, 1976; Hawkins, 1983; Jenkins *et al.*, 1999; Leonard, 1999). In fact the barnacle *Tesseropora rosea* does not settle amongst algae (Denley & Underwood, 1979). Hawkins (1983) suggested that *Fucus* acts mainly by removing cyprids from marginal or unfavourable micro-settlement sites. Cyprids in grooves, pits and crevices will survive irrespective of whether they are swept or not. Miller & Carefoot (1989), however, found that close proximity to adult barnacles was a more effective survival strategy.

At both sites there were also more barnacles in the presence of limpets. It has been found that *Patella* grazing permits *Semibalanus balanoides* settlement by not only stopping the growth of fucoids (Branch, 1981; Hawkins & Hartnoll, 1983b), but by removing growths of green algae. Patches of green algae are abundant during spring on moderately exposed shores, occurring in "escapes" from grazing (see Hawkins & Hartnoll, 1983b for review). These algae are probably the main competitor with settling *S. balanoides* recruitment, particularly as dense swards can suppress settlement on adjacent clear areas. In contrast, dislodgement of barnacle cyprids by grazing gastropods has been found in many previous investigations (e.g. Lewis, 1954; Connell, 1961; Menge, 1976; Denley & Underwood, 1979; Branch, 1981 for review). The importance of indirect effects in rocky shore habitats was recently assessed by Menge (1995), who concluded that such effects accounted for approximately 40% of the change in community structure resulting from experimental manipulation.

(7.4.6.) Conclusions, Limitations and Future Work

Limpets were effectively removed from the required treatments. The replacement of limpets with alternative grazers was variable through time: probably as a reflection of different environmental conditions between the sampling dates. In functional terms, the relative importance of limpets and mussels in structuring rocky shore communities was spatially variable. At Polzeath mussels were more important in determining algal abundance than limpets. In contrast at Harlyn interactions between both mussels and limpets were important. A key difference between these sites was the overall level of algal abundance. The specific importance of ecosystem engineers and keystone grazers may therefore depend on the particular location and assemblage under investigation.

The study was potentially limited by the fact that there was no control for disturbances to quadrats when limpets were being removed at monthly intervals. However, it was felt that such disturbance would be minimal compared to the uncontrollable variation in disturbance caused by environmental factors and human trampling. While the removal of limpets was largely successful, more frequent removals during the summer months would have further eliminated the possibility of re-invasion.

The influence of these treatments on species that could not be observed in the field, including cryptic grazers, remains uninvestigated. Destructive sampling to establish the species assemblages located within the mussel matrices and algal fronds will be conducted as part of another study. This will allow an investigation into the effects of these manipulations on biodiversity. The exact movement patterns and the relative impact of alternative grazers on community patterns could also be investigated in greater detail. The impact of allowing limpets to re-invade plots where they had previously been excluded would also help to examine the interaction between this keystone grazer and an ecosystem engineer.

8. General Discussion

(8.) GENERAL DISCUSSION

The main aim of this work was to assess the importance of spatial heterogeneity and topographic complexity in the structure and dynamics of rocky shore communities. Despite the increasing awareness of the importance of such factors (e.g. McCoy & Bell, 1991; Bourget *et al.*, 1994; Jacobi & Langevin, 1996; Petraitis & Latham, 1999; Chiba & Noda, 2000) a standardised measurement technique is not currently available (McCormick, 1994; Beck, 2000). This study therefore aimed to replace subjective terms with more objective definitions and make results between locations and investigators comparable. The importance of both physically and biologically generated complexity in determining recruitment and distribution patterns, stages of succession and behavioural activities were then assessed. As the results of this work have been discussed in detail at the end of the respective chapters this general discussion will address limitations and generality of this study. Three themes are explored: the measurement of complexity including the use of image analysis, scales and patterns of variability and the respective roles of physically and biologically generated complexity. The requirements for further work to enhance our understanding of the complex relationship between habitat complexity and both species distributions and interactions are then outlined before drawing conclusions.

(8.1.) Measuring Complexity

(8.1.1.) Measurement Techniques

Each of the techniques (stereophotography, chains and profile gauges) used to measure habitat complexity had advantages and limitations (Table 8.1). These were primarily associated with the resolution at which they were focused (see Chapter 2). The most precise and accurate technique for obtaining small scale relative changes in height were from the profile gauge. Inaccuracies were introduced, however, where the profile gauge did not fit the rock surface. The resolution of the chain decreased with an increase in link size, where they were no longer able to fit to surface irregularities. The precision and accuracy of stereophotography could be affected by a number of factors including light levels, the reflective properties of the surface, the standard of photographic equipment and the level of resolution of the image analysis (Evans & Norris, 1997). The practicalities of using the methods in terms of both in the field and further analysis were also very different. Chains were the most efficient method to use, followed by stereophotography and profile gauges respectively.

Table (8.1): A Summary of the Advantages and Disadvantages of the Three Measurement Techniques (Stereophotography, profile gauges and lengths of chain). Observations are in relation to each other.

	Stereophotography	Profile Gauge	Chains
Equipment Required	Camera – Tripod Most Specialised	Profile gauge	Lengths of Chain Least Specialised
Ease of Use in The Field	Simple - Following Initial Set Up	Tracing of Profiles Most Time Consuming	Very Easy Least Time Consuming
Analysis	Image Analysis Time Consuming	Digitising of Profiles Time Consuming	Very Easy Least Time Consuming
Small Scale Resolution	Least Resolution	Highest Resolution	Decreased with an Increased Link Size
Accuracy and Precision	Least Accurate and Precise	Most Accurate and Precise	Dependent on Link Size of Chains
Identification of Surface Features	Most Useful – Can View Entire Surface	Only Identifies Features Along Sampled Profiles	Only Identifies Features Along Sampled Profiles
Relation to Biota	Surface Features Can be Easily Correlated with Biota	Difficult to Relate Topographic Features with Biota	Difficult to Relate Topographic Features with Biota

Despite inaccuracies introduced by each of the three measurement techniques it was possible to compare and standardise these methods. The indices derived from either chains or profile gauges were ranked in a similar order of complexity and could therefore be compared across studies and environments. The differences that arose via the use of stereophotography, however, isolate this technique in terms of comparing the values obtained from the alternative methods. Evans & Norris (1997) while not comparing an actual index, but exact height measures, also found a similar result, showing there were discrepancies between stereophotography and profile gauge measures. It has also been reported that stereophotography can be more accurate than a surface profiler in a number of instances (Grayson *et al.*, 1988). If a ranking of complexity was required then a ratio derived from a chain would provide as much detail and information as the more sophisticated and more time consuming analyses. The method used in a particular investigation would therefore depend on the level of precision required.

Each method generally leads to a single index or figure designed to represent the complexity of a surface (Kostylev, 1996; Beck, 1998). Surfaces with different numbers and sizes of refuges could therefore result in the same index value which can lead to a great loss of information (Simberloff *et al.*, 1987). They do, however, enable comparisons between different studies and habitats. The importance of complexity in shaping and determining community patterns in a number of different locations and habitat types can be assessed (e.g. McCoy & Bell, 1991, Gee & Warwick, 1994a; Sanson *et al.*, 1995). All indices from the profile gauge data set obtained in this thesis (vector dispersion (VD), consecutive height difference (CHD), fractal (*D*) and the chain ratio) were correlated; this was as to be expected as they were all calculated from an identical data set. Such similarities between indices has been identified by previous investigators (Carelton & Sammarco, 1987; Underwood & Chapman, 1989; McCormick, 1994; Beck, 1998; 2000).

When relating species distributions to biological characteristics each organism of interest is likely to be correlated with a specific physical or biological factor. The index required for a particular investigation should therefore be capable of reflecting any small scale changes in this parameter. McCormick (1994), for example, found that the CHD index was most suited to describe the abundance of damselfish. In contrast Underwood & Chapman (1989) used the VD index to relate topography with littorinid populations. In addition Beck (1998) found that the distribution of gastropods was correlated with all four indices of complexity (VD, CHD, *D* and chain ratio), the fractal dimension, however had the highest correlation with density. The development of methods and indices used to define topographic complexity therefore plays a key role in advancing our understanding of the processes shaping intertidal communities.

(8.1.2.) Image Analysis

A considerable number of the techniques used in this thesis incorporated image analysis. The benefits of using such methodologies include a non-destructive sampling technique, creating *in situ* measurements and a permanent record of each location. Image analysis software can also provide biologically meaningful measurements of habitat structure and complexity (Sanson *et al.*, 1995; Evans & Norris, 1997). When examining the distribution of algae, however, it was not possible to locate individual holdfasts. The observed distribution of species may therefore not represent the initial settlement patterns. In the presence of a large algal canopy or mussel cover it was also not possible to view understorey species. The distributions of such species therefore went un-recorded. The use of image analysis software also affects the level of resolution at which the analysis can be performed. A balance is therefore required between the level of accuracy and the number of replicates that can be processed.

Stereophotography in particular had additional limitations that required consideration. While the non destructive nature of the sampling technique had the benefit of *in situ* measurements, in some instances it could distort a true measure of a topographic dimension. By digitising the top of a limpet shell, for example, this could potentially add a further two centimetres to the height of a particular point. The fronds of large plants may also have masked some of the true topographical features within an area. Such inaccuracies were avoided where possible by the digitising of actual rock surfaces. Stereophotography, however, can still be a very powerful tool; Van Rooji & Videler (1996), for example, obtained an accuracy level as high as high as ±0.3 to 3.5% of measured distances.

Despite the noise added to topographic surfaces using stereophotography it was possible to develop a method to correlate surface topography with the distribution of some intertidal species (Chapter 3). The processes involved in establishing the strength of the relationship between topographic features and the distribution of the biota is now automated and the technique could be applied elsewhere. The generality of the observed patterns could be assessed on shores of different topographies, exposure gradients and geographical locations. The use of stereophotography is also transferable across habitat types.

(8.1.3.) Stereophotography and Species Distributions

The strongest correlations between topographic features and biological distributions were typically observed for algal species. Algal species such as *Enteromorpha*, *Pelvetia*, *Laurencia* and *Corallina*, for example, were consistently associated with crevices. In general, crevices may accumulate more algal propagules than flatter surfaces (Norton & Fretter, 1981) and allow more species to recruit by providing the propagules with a refuge against physical parameters and/ or grazing by molluscs (e.g. Burrows & Lodge, 1950; Lubchenco, 1980; Hawkins, 1981; Sutherland & Ortega, 1986; Jenkins *et al.*, 1999a, b; Lotze *et al.*, 2000).

The importance of topography, however, varied across a number of spatial scales depending on the species examined. *Fucus* and barnacles, for example, were associated with raised areas of rock on one shore and with crevices on another. Variability in the patterns of species abundance across different scales is not an uncommon finding (Morrisey *et al.*, 1992; Underwood & Chapman, 1996; Underwood *et al.*, 2000). The lack of patterns in the distribution of species is probably due to the presence of microhabitats created by topographic features. This thesis therefore contributes to the explanation of high levels of observed variability across a number of habitats. Differences in environmental parameters such as wave exposure and the geology of the substratum also result in such patterns (Gaines *et al.*, 1985; Chapman, 1994; Caceras-Martinez & Figueras, 1997; McQuaid & Phillips, 2000). In addition differences in life history characteristics and strengths of competitive and consumer interactions between species may vary between locations (Fairweather, 1988; Menge, 1995). Indeed, all of these processes are potentially modified by the topographic features of the substratum.

(8.2.) Scales and Patterns of Variability

The variability demonstrated by species in their association with topographic features across different scales highlights the importance of this issue for any ecological investigation (see also Wiens, 1989; Russell *et al.*, 1992; Keeling *et al.*, 1997). Indeed each chapter within this thesis required the consideration of scale. In Chapter 2, for example, the importance of scale was highlighted by the minimum resolution of each method. The three techniques were also restricted in the area that could be effectively sampled at comparable levels. The size and scaling of the crevices incorporated on the concrete blocks placed into the intertidal zone (Chapter 5) also had the potential to affect patterns of recruitment and succession on their surfaces. The size of crevices, for example, may affect the type of refuge provided from environmental conditions (Raffaelli & Hughes, 1978; Burrows & Hughes, 1989; Jones & Boulding, 1999) as well as biological factors such as consumer pressure and competition (Garrity & Levings, 1981; Menge & Lubchenco, 1981; Marinelli & Coull, 1987; Johnson *et al.*, 1998).

Temporal variability was also apparent throughout the entire course of the work for this thesis. All the stereophotographs analysed in Chapter 3 were taken within a relatively short time period therefore inferences regarding the distribution of species was limited to the same time frame. The distribution of mobile species such as dog whelks and littorinds, however, can change over short periods of time depending on localised exposure and climatic conditions (Garrity & Levings, 1984; Moran, 1985; Burrows & Hughes, 1989; Hughes *et al.*, 1992). Ephemeral species of algae also vary in abundance in a cyclical nature, which may again affect the observed distribution patterns (Hawkins, 1981; Hawkins *et al.*, 1992). Analysis of this type therefore, requires careful interpretation and replication over a number of time intervals (Underwood *et al.*, 2000). The advantage of long term studies such as those used in Chapters 5, 6, and 7 is that analyses were calculated throughout at least an annual cycle. It is still important, however, to construct sampling strategies based on appropriate time scales.

The consideration of a range of both temporal and spatial scales in determining patterns of species distributions and abundance was used to examine mussel mosaics in North Cornwall (Chapter 6). The structure and turnover of mussel mosaics is particularly important because they provide a secondary habitat for the co-existence of species (Seed, 1976; Suchanek, 1986). The aggregated occurrence of various mussel species therefore affects not only the mussel population as such

(Bertness & Grosholz, 1985; Okamura, 1986), but also the associated flora and fauna (Chapter 7). Diversity within mussel beds, for example, is thought to be affected by patch structure at a variety of spatial scales (Tsuchiya & Nishihira, 1985; Seed & Suchanek, 1992; Svane & Setyobudiandi, 1996). In marine benthic habitats, the formation of gaps is also of considerable significance to sessile organisms which require open space. Various attributes of a newly created gap (i.e. its size, shape, location and time of creation) can affect subsequent patch colonisation and ensuing biological interactions (Sousa, 1985).

Indeed, information on the patchiness of species and resources is used in many ecological models and in generating ecological theory over a number of spatial scales (Pickett & White; 1985; Kolasa & Pickett, 1991). Identifying spatial patterns is important in improving the design and interpretation of surveys and experimental studies through relating sampling programmes to natural scales of variation (Levin, 1992; Legendre *et al.*, 1997; Guichard & Bourget, 1998; Zacharias *et al.*, 1999; Underwood *et al.*, 2000).

In the case of mussels examined in North Cornwall processes operating to define patch structure were operating at a number of spatial scales smaller than the level of shore (Chapter 6). Currents, waves and larval preferences have been demonstrated to be important in determining settlement patterns (Gaines *et al.*, 1985; Underwood & Fairweather, 1989; Seed & Suchanek, 1992; Caceras- Martinez & Figueras, 1997; Harris *et al.*, 1998; McQuaid & Phillips, 2000). Biological parameters such as predation and competition may also influence variability in patch structure (e.g. Svane & Ompi, 1993; Petraitis, 1998; Noda, 1999). In addition, there was no temporal variability in either the percentage cover or turnover of mussels. Processes acting to remove mussels must therefore have operated at a similar rate to those which increase their numbers (see also McGroty *et al.*, 1990; Hunt & Scheibling, 1995). Such variability in the size and structure of patches is a common finding across a number of habitats (e.g. Dayton *et al.*, 1984; Sousa, 1984; Wu & Levin, 1994; Vidono *et al.*, 1997; Ramage & Schiel, 1999).

(8.3.) Physical and Biological Complexity

Both physical and biological complexity was demonstrated to have an important role in structuring rocky shore communities. Example systems examined here were the recruitment of algae and sessile invertebrates to substrata of varying complexity (Chapters 5 & 7). Secondly, the distribution patterns and overall diversity of species in relation to topography was assessed (Chapters 3 & 5). The effects of predators and grazers were also studied in relation to rock features and mussel beds (Chapters 4 & 7).

(8.3.1.) Recruitment and Succession

The recruitment and succession of algal species in both Cornwall and on the West coast of Scotland was typical of that previously recorded. In a typical successional sequence on barnacle dominated rock, diatoms may be initial colonisers followed by various ephemeral algae such as *Enteromorpha*, *Blidingia*, and *Porphyra*, which are eventually outgrown by fucoids (Dayton, 1971; Underwood, 1980; Hawkins *et al*., 1992). In the current study the recruitment of algae did not appear to be related to the complexity of the physical substratum (Chapter 5), but was affected by biologically generated complexity (Chapter 7).

Fucus and *Ralfsia* were the most common species observed on the blocks placed into the intertidal at Camas Rubha na Liathaig (Chapter 5). The different physical structures on each block type, however, did not affect the degree of algal covering throughout the year. This is in contrast to Chapter 3 where when using stereophotography a number of algal species (e.g. *Enteromopha*, *Corralina* and *Xanthoria*) were correlated with set topographic features. In previous studies substratum complexity has been shown to affect algal abundance (e.g. Dudley & Antonio, 1991; Sanson *et al*., 1995). In particular, grooves have acted as sediment traps and possibly sites for higher growth rates of algae (Douglas & Lake, 1994). In contrast Downes *et al*., (1998) found that algae was less abundant on blocks with large crevices than those without. McGuiness & Underwood (1986) also found fewer algal species where there were pits on the blocks.

Sources of biological complexity positively affected the growth and survival of algae; abundance levels were greater on mussel beds than on adjacent rock surfaces (Chapter 7). This was true in both the presence and absence of limpets; considered to be the most important grazer on Northeast Atlantic shores (Hawkins *et al.*, 1992). The importance of mussels in the absence of limpets highlights the role that biogenic structures play in providing a refuge from additional environmental stresses. Irregular surface features can potentially enhance recruitment in several ways (Vadas *et al.*, 1992). Firstly they could act as a propagule trap by providing protection against hydrodynamic or mechanical dislodgement (Benedetti-Cecchi & Cinelli, 1992). Secondly, algal turf, mussels and barnacles are all capable of creating a more physically benign environment during low tide (Norton, 1983; Farrell, 1991; Brawley & Johnson, 1991, 1993; Sebens, 1991) - a period when zygotes and embryos of algal species are extremely vulnerable (Brawley & Johnson, 1991; Davison *et al.*, 1993; Johnson & Brawley, 1998).

Physical and biological complexity also affected the recruitment of barnacles. While barnacles were correlated with crevices at Camas Rubha na Liathaig and raised areas at Easdale the scales of complexity examined did not truly reflect those thought to influence barnacle settlement (Chapter 3). Where limpets and mussels were removed from quadrats, however, barnacles were more abundant in plots where mussels had been removed (Chapter 7). This pattern was likely to be as a result of the lack of availability of space in the presence of mussels. Despite the risk of ingestion of barnacles larvae by mussels (Woodin, 1976; Young & Gotelli, 1988) cyprids of some species are capable of settling on this secondary substratum (Lohse, 1993a). *Fucus* plants are also capable of inhibiting settlement by a sweeping action of the fronds which can cause cyprid dislodgement (Menge, 1976; Hawkins, 1983; Jenkins *et al.*, 1999c; Leornard, 1999).

(8.3.2.) Distribution and Diversity of Species

Results which observed the distribution of intertidal gastropods in relation to topographic complexity were variable in all instances (Chapters 3, 5 & 7). Dogwhelks, for example, were not correlated with any topographic feature on either the blocks or in the stereophotographs (Chapters 5 & 3). Similarly there was no consistent pattern in the distribution of *G. umbilicalis* on mussel beds and rock surfaces in North Cornwall (Chapter 7). Crevices, mussel beds and barnacles casts serve as a refuge from harsh environmental conditions such as wave exposure and desiccation (Underwood, 1980; Garrity & Levings, 1984; Moran, 1985; Burrows & Hughes, 1989; Jones & Boulding, 1999). Such structures therefore represent temporary habitats for mobile invertebrates, as a consequence distribution patterns may simply reflect localised conditions over a short time period.

Although the distribution of littorinids was variable through time, they were typically associated with refuges provided by both physical and biological structures. Following the initial positioning of the concrete blocks of differing complexity littorinid numbers were least on the smooth blocks (Chapter 5). Indeed these snails were typically associated with crevices for the first eight months of the analysis. Differences in littorinid number between each block type, however, were no longer apparent by April 2000. This was probably due to the large increase in percentage cover of *Fucus* during the spring months of the year. Previous studies have highlighted the importance of the physical properties of macroalgal canopy in providing shelter for herbivores (e.g. Reed & Foster, 1984; Lubchenco, 1986; Chapman, 1989; Chapman & Johnson, 1990; Jacobi & Langevin, 1996).

Results regarding species number and diversity on the concrete blocks were not consistent with the commonly held view that increased habitat complexity leads to increased richness and diversity (O'Connor, 1991; Douglas & Lake, 1992, 1994; Downes *et al.*, 1995, 1998, 2000; LaPointe & Bourget, 1999). The results were, however, in agreement with Bourget *et al.*, (1994) where both substratum heterogeneity and complexity had little influence on diversity and abundance during the early phases of community development. Similarly Downes *et al.*, (1995, 1998, 2000) found that species richness and numbers of individuals were higher on rough stones than on smooth, but appeared unrelated to the numbers of large pits and crevices present. McGuiness & Underwood (1986) also found that there were significant effects of pits and grooves but that these did not usually result in the blocks with the greatest surface complexity having most species.

(8.3.3.) *Consumers*

The use of underwater camera technology provided several benefits in that the measurements were continuous and incorporated both tidal and diurnal observations of predator behaviour. This is in contrast to previous investigations that have used direct observations (e.g. Parry, 1982; Lowell, 1986; Iwaski, 1993), experimental manipulations (e.g. Sala, 1977; Menge & Lubchenco, 1981; Ojeda & Munoz, 1999), experiments with tethered prey (Behrens Yamada & Boulding, 1996) and attack activities recorded with artificial prey (Thompson *et al.*, 2000). The equipment used, however, is expensive and would not be suitable for highly wave exposed areas or where human interference was likely to present a problem. The examination of the generality of the results across a number of locations is therefore limited.

The movement patterns of three intertidal predators, *L. pholis*, *C. maenas* and *C. melops*, were affected by the physical complexity of rock surfaces (Chapter 4). This has been demonstrated previously for both *C. maenas* and *L. pholis*, which typically follow the pathways of surface features such as crevices (Almada *et al.*, 1983; Dodd 1998; Burrows *et al.*, 1999). In contrast *C. melops* did not directly interact with the rock surface; movement pathways were more common along the convexities surrounding the surface indentations (Chapter 4). In contrast juveniles of the wrasse *Pseudolabrus celidotus* are largely associated with features of shelter and therefore display patchy distribution patterns (Jones, 1984). Goldsinny wrasse are also almost always observed in or close to refuge holes (Sayer *et al.*, 1993; Sayer, 1999).

At present the potential causal factors underlying the local distributions of mobile benthic marine fishes (e.g. Ogden & Enrlich, 1977; Leum & Choat, 1980; Bray, 1981; Kingett & Choat, 1981) has been largely uninvestigated. The work in this thesis provided an extension to the study of Burrows *et al.*, (1999) incorporating both an additional fish species and season. The generality of the movement pathways first examined for these species (Burrows *et al.*, 1999) was also assessed in a different location and found to be very similar.

It appeared that the foraging pathways of these large mobile predators does play some role in structuring the community patterns observed on rocky shores. All three species examined here were affected by relatively small scale topographic features. The feeding activity of the species must therefore be concentrated in restricted areas of the rock surface creating a patchy distribution of the prey species, in this case barnacles. Differential counts of barnacles in relation to topographic features have been previously attributed to predation from slow moving gastropods (Fairweather, 1988). The large numbers of mobile predators observed here and in other studies (Robles, 1987; Burrows *et al.*, 1999), however, highlight the potential importance of these species in shaping prey distribution patterns. Herbivorous fishes have also been described as important components of littoral fish assemblages in temperate waters; affecting algal biomass & diversity (Choat & Clements, 1992; Barry & Ehret, 1993; Horn & Ojeda, 1999; Ojeda & Munoz, 1999). In a wider geographical context, Menge & Lubchenco (1981) highlight that rock surfaces in tropical areas are regularly grazed by fishes, crabs and slower invertebrate consumers, and it is a combination of these species that affect distribution patterns.

The impact of grazers on the distribution of algae on primary and secondary habitats was also assessed (Chapter 7). During the first couple of months of the experiment the abundance of algae was generally higher in the presence rather than absence of mussels regardless of limpet density. It seems unlikely therefore that mussels were being grazed effectively; limpets within a plot were not reducing the algal cover on mussels as compared to areas having no limpets. Previous studies have also suggested that limpets and other intertidal gastropods are restricted in their ability to graze such complex surfaces (Little *et al.*, 1988; Kostlyev, 1996). Grazing marks have, however, been found on mussels implying that at least some grazing does occurs on this substratum (Lohse, 1993b). The overgrowth of mussels by algae is also largely prevented by such activity (Suchanek, 1979; Witman, 1987; Robles & Robb, 1993). Indeed the potential interactions between species where mussels or barnacles are used as refuge from grazers and harsh environmental conditions are numerous (Figure 8.1).

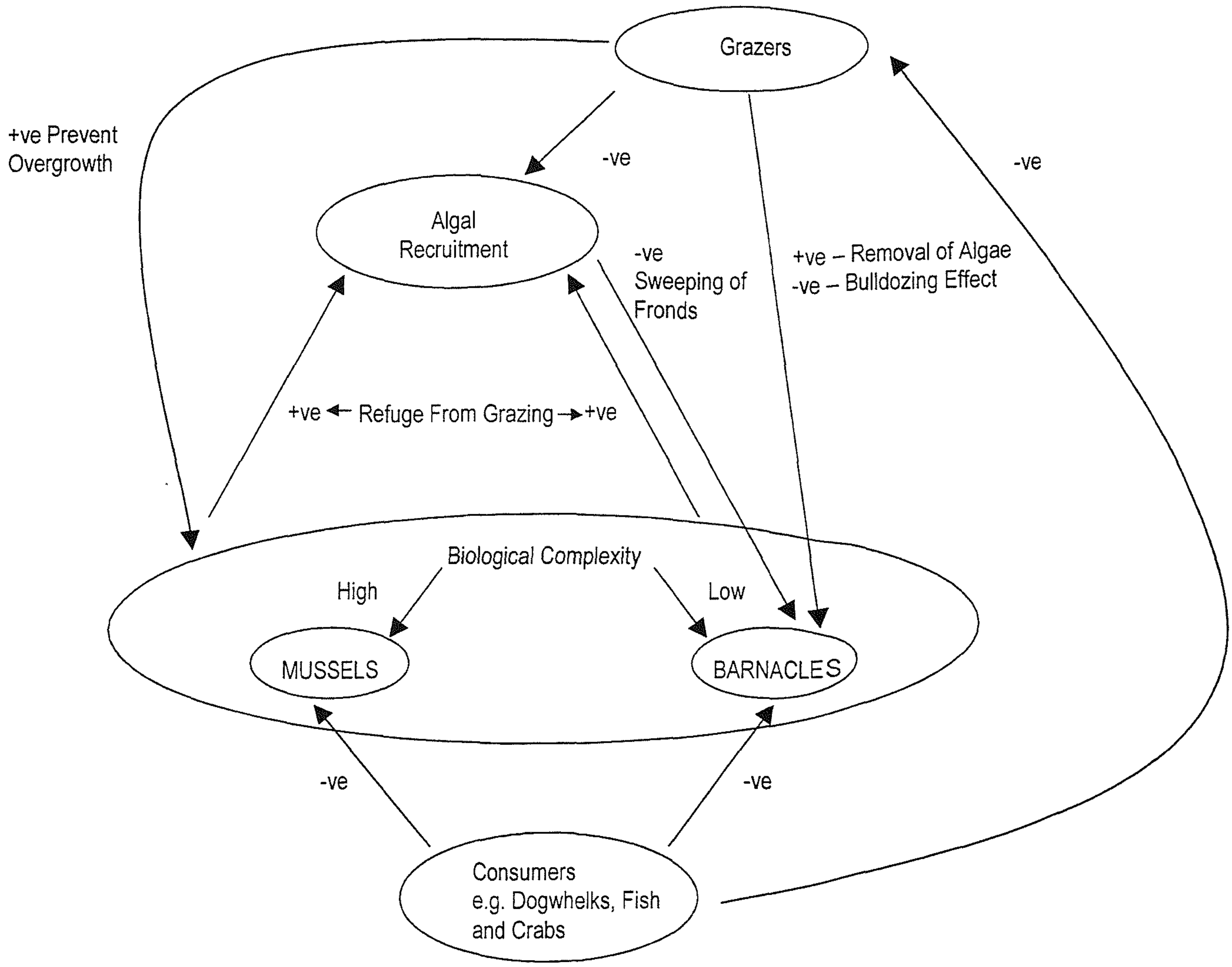


Figure (8.1): Web of putative direct interactions among species affected by a biological source of complexity – in this case mussels and / or barnacles. + / - indicates positive and negative effects respectively.

The provision of secondary habitats, such as mussel beds therefore plays an important role in structuring intertidal communities. There was, however, a difference in magnitude in the importance of mussels and limpets at the two sites. This was particularly apparent when examining the distribution and abundance of *Porphyra* in September 1999. At Polzeath mussels were essential to the recruitment and survival of this ephemeral species regardless of limpet density; in effect limpets were redundant at Polzeath. In contrast at Harlyn there was no difference in the cover of *Porphyra* with or without mussels but the limpets did affect algal abundance levels. It was therefore an interaction between grazing pressure and refuge provision at this site that caused community patterns. It is not unusual to attain differences in interaction strength between species at different locations. In different habitats grazers may have different effects (Lubchenco, 1983; Johnson *et al.*, 1997). Such discrepancies are a reflection of the differing abiotic and biotic conditions and the relative species abundances at each site (e.g. Farrell, 1991; Kim, 1997).

(8.3.4.) Summary

Spatial heterogeneity and topographic complexity play an important role in structuring rocky shore communities. Settlement processes of benthic organisms, for example, have been extensively studied because of their implications for basic ecological questions. Where complexity affects settlement and recruitment patterns this has further implications for the succession of a community. The strengths of interactions between species may also be affected depending on the exact habitat and location examined. In addition the distribution of mobile species may be altered by the complexity of the substratum which can again affect competitive and consumer relationships. Predation and grazing pressure in particular are influenced by both physical and biological structures. As a consequence the distribution of prey species are in part determined by the complexity of a habitat. The scales at which each of these processes are examined, however, influences the conclusions that can be drawn from any particular study.

(8.4.) Future Work

The importance of habitat complexity in structuring rocky shore communities has now become widely accepted. This has been supported by advances in the methodologies and indices used to define topographic complexity. Despite such advances more work is required to ensure both systems and results are comparable between authors and habitats. The work in this thesis concentrated on the use of different techniques. It would now be beneficial to correlate the derived indices with biological features. The most appropriate index could then be defined for the quantification of species distribution patterns and interactions.

In particular the method of stereophotography has the potential for development over a greater number of scales. The use of derived maps to assess species distributions could be extended to incorporate a wider range of locations and habitats. In addition temporal variation in abundance could be examined by the use of repeated sampling throughout the year. Once patterns of distribution have been depicted this provides a better framework on which to base manipulative experiments and understand processes shaping communities. The description of patch structure in mussel mosaics and the relationships demonstrated by the stereophotography analysis, for example, generated a number of testable hypotheses. Modelling and field trials could be employed to answer questions generated from such observations.

The importance of physical and biologically generated complexity on the recruitment and succession of species requires further attention. In terms of the current thesis greater detail regarding settlement patterns could be obtained from the concrete blocks. The exact locations of hold fasts could be established and this may provide a more complete description of the impact of grazers and topography on algal biomass. Blocks of similar designs could also be placed into locations experiencing different environmental conditions such as wave exposures and tidal heights. Settlement on to secondary substrata could be examined further by the manipulation of this habitat type. Mussel beds, varying in their overall size and degree of topographic complexity could be monitored throughout periods of recruitment. In general terms the identification of processes structuring the succession of communities requires long term sampling combined with manipulative experiments.

The distribution of mobile invertebrates also requires measurements on a much shorter time scale than those sampled here, if their roles in structuring community patterns are to be assessed. These species are typically either grazers or predators, they therefore have the potential to determine the abundance and distribution patterns of species at lower trophic levels. The feeding patterns of the three larger mobile species could only be inferred from the video analysis, quantification of actual predation rates would therefore be more informative. To establish a more direct link between movement patterns and prey distributions the gut contents of these predators could be examined at the time of the study. Similarly areas where predators and grazers are excluded can provide useful insights into the roles of these species. Within the intertidal zone there is an entire suite of predators and grazers from a number of different taxonomic backgrounds. Research which serves to examine the individual roles of such species and the interactions between them will help to describe the processes shaping rocky shore communities.

(8.5.) Concluding Remarks

The substratum upon which organisms live and move can vary considerably in both physically and biologically generated complexity across a number of spatial and temporal scales. The complexity of a habitat may influence a number of environmental parameters such as wave action, temperature and rates of sedimentation. As a consequence community structure is altered by the changing effects of competition, consumer pressure and physical stress imposed on intertidal organisms. In particular I found that the settlement and recruitment of species was influenced by the topography of the substratum. The distribution and movement patterns of grazers and predators were also concentrated around set topographic features. Interactions between species, environmental parameters and complexity varied in strength depending on the exact system and habitat studied. Until recently the effects of architectural complexity have remained largely uninvestigated but more currently the subject has become widely appreciated. The development of standardised measurement techniques and indices can only help to enhance our understanding of this complex issue. While advances have been made regarding the role of topographic complexity in structuring rocky shore communities there is still considerably more to be learnt about the generalities of the processes that are in operation.

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