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Biodiversity of the invertebrate community associated with the turf-forming red alga Corallina officinalis in tide pools

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Biodiversity of the Invertebrate Community Associated with the Turf-Forming Red Alga *Corallina officinalis* in Tide Pools

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SUMMARY

The invertebrate communities associated with the turf-forming red alga *Corallina officinalis* were investigated in tide pools on rocky shores of the coasts of England, Ireland and Wales. A total of 212 different taxa, including representatives from 14 phyla, were identified.

There was significant small scale (between pools and within pools) variability and large scale variability (regional, between shores) in the diversity and community patterns of invertebrates associated with *Corallina* turf. These patterns were often not consistent between different shores and at different times. For example, greater numbers of species were found amongst *Corallina* turf from shallow depth in tide pools in winter than in summer. At regional scales, differences in the community pattern are correlated with temperature, though overall differences appear to be driven by a complex and interacting arrangement of biotic and abiotic factors such as habitat complexity and the hydrodynamic regime of the area. These patterns are also found when working at taxonomic levels other than species.

Distinct temporal variation in the community was observed that followed a seasonal cyclic template. The observed temporal pattern is produced primarily by the behavioural adaptations and life history characteristics of the associated invertebrates. Assemblages associated with the tide pools frequently contained invertebrates that are small in size, produce few juveniles and have a tendency to brood their offspring or reproduce without a pelagic larval stage. These characteristics result in a clearly distinct community associated within *Corallina* turf on the coasts of the UK and Ireland.

Patterns of the invertebrates associated with *Corallina* turf make an important contribution to our understanding of marine biodiversity. By examining such patterns in similar habitats at similar scales it is possible to make decisions concerning the conservation of the inshore marine environment.

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Chapter 1

General Introduction

General Introduction

What is biodiversity?

Since the Earth Summit held in Rio de Janeiro in 1992 interest in biodiversity has been reawakened. Although studies of biological diversity have advanced over many years (Clements, 1916; Colman, 1940; Hanson, 1961; MacArthur and MacArthur, 1961) the new interest in biodiversity has focused attention on its study at a global need for conservation by action plans implemented on a local scale (Moore, 2002). Biodiversity has many comprehensive definitions in the literature (Reid and Miller, 1989; McNeely *et al.*, 1990; McAllistair, 1991; Fiedler and Jain, 1992; Sandlund *et al.*, 1992; Johnson, 1993; di Castri and Younès, 1996) but put most simply biodiversity is the variety of organisms considered at all levels, from genetic variants belonging to the same species, through arrays of species, genera, families and still higher taxonomic levels, including variety of ecosystems, which comprise both the communities of organisms within particular habitats and the physical conditions under which they live (Wilson, 1994). There are generally considered to be three main levels of biodiversity: genetic, taxonomic and ecological, and these can be observed at different scales, ultimately within patch (alpha), between patch (beta) and continental or regional (gamma) diversity (Gaston, 1996). Genetic diversity is the variability of genes within species covering genetic variation between distinct populations of the same species and the number and frequency of genetically different populations (McAllistair, 1991). Taxonomic diversity refers to the number of different taxa which can be classified into three groups of measurement; richness, abundance and phylogenetic diversity (Magurran, 1988). Ecological diversity encompasses the number and frequency of different communities of organisms and their environments (McAllistair, 1991). Alpha diversity is the diversity within a site, or sample and is termed local diversity. Beta diversity is the change in species composition form site to site or species turnover. Gamma diversity is the diversity of a landscape or all sites combined or regional diversity (Gaston, 1996).

The three components of biodiversity interact so that overall biodiversity is the ensemble of genetic, species and ecological diversity, in a given place, at a given time. Biodiversity at these levels is then nested within habitat and or landscape diversity. These interactions like many ecological situations are of a hierarchical nature (di Castri and Younès, 1996). Biological systems are complex because they involve the interaction of differently scaled processes (Allen and Starr, 1982). Scaling the different levels into different hierarchies allows better interpretation of results from biodiversity studies. The hierarchy is not clearly defined as genes, species and ecosystems do not belong all together in the same hierarchical category. In each hierarchical category there exists a variety of scales. The genetic level can be separated into community, population, organism, cell and molecular diversity. The taxonomic level can be considered from diversity at kingdom level all the way to sub-species level, and ecological diversity can be measured over scales from the biosphere to habitat or niche diversity. Properties not at the gene level appear when focus changes to the species level and similarly from species to the ecosystem level (McAllistair, 1991). Population (genetics), species (taxonomic), and ecosystem (ecological) are usually the cornerstones of interaction between the three hierarchies (Solbrig, 1991).

Biodiversity must be understood from the level and scale at which it is measured, and structural and functional aspects of systems stability, productivity and sustainability as well as patterns of ecosystem functioning can only be clarified if scales and hierarchies are considered in terms of their interactions (di Castri and Younès, 1996). In essence, biodiversity encompasses multiple scales of space and time, from the smallest virus to the earth itself, from seconds to aeons, biodiversity is the hierarchy of living systems that together constitute and support all life on our planet (Lugo, 1996).

Why biodiversity?

Most scientists agree that biodiversity is of high value and its loss could cause unknown global changes. The use of biodiversity throughout history has contributed enormously to the social, economic and academic progression of humanity. Many species have already provided humanity with products that are of immense use in our lives. We depend on biodiversity to supply us with natural products including food, clothes, fibres, gums, dyes and oils (Nations, 1986) and currently more than three quarters of the third world population rely upon plant-based drugs (Farnsworth, 1986; Tickell, 1996). Genetic diversity has led to 'miracle' strains of crops that make up a large proportion of our sustainable diet (Tickell, 1996). Knowledge of the diversity of crops provides the opportunity to produce crops that are resistant to disease and pests (Iltis *et al.*, 1979; Iltis, 1986).

Many authors have noted a human interest in obtaining information on, and maintaining, biodiversity because people feel connected to the natural world (Solbrig *et al.*, 1994; Hawksworth *et al.*, 1996). The popularity of activities like ecotourism and bird watching bring economic production along with rewards for those that pursue them (Ehrlich and Wilson, 1991). There is also an increasing awareness that humans have some kind of ethical responsibility for the welfare of our only known companions in the universe (Solbrig *et al.*, 1994; Hawksworth *et al.*, 1996)

Sustained biodiversity plays a key role in ecosystem function. Forests and vegetation produce soil and regulate water supply by preserving catchment basins, recharging ground water and buffering extreme conditions (Ehrlich and Wilson, 1991). Coral reefs and mangrove swamps provide defence from hurricanes and spawning ground for fish and wetlands on deltas are shock absorbers for floods (Tickell, 1996). Species that have co-evolved depend on the functions of the ecosystem in which they live, therefore each individual species depends upon the same set of other species for its continued existence (Norton, 1986). The removal of one or many species in an ecosystem may remove a vital ecological pathway that permanently alters ecosystem function and structure. For example, in the rocky intertidal zone of northern temperate shores the limpet, *Patella vulgata*, grazes early stages of macroalgae. The removal of *P. vulgata* leads to the shore becoming swamped with a few species of macroalgae (Jones, 1948; Southward, 1956), drastically changing the appearance of the shore. Biodiversity and ecosystem stability has been a matter of academic concern for some time (Odum, 1971). The rivet popper analogy proposed by Ehrlich and Ehrlich (1981) suggests that continually removing or changing species will eventually compromise ecosystem services, in that removal of twelve species might have no effect but the removal of a thirteenth may be catastrophic. Another frequently considered hypothesis concerns the functional importance of keystone species that by definition are not redundant (Chapin *et al.*, 1992). Keystone species (e.g. Paine, 1966, 1968) affect community or ecosystem processes to a degree that appears greater than their relative abundance in the community would indicate (Bond, 1994). If a keystone species is experimentally removed, changes in abundance or composition of the system result (Paine, 1980). Identifying which species are keystone is often a matter of debate and the ‘uniqueness hypothesis’ (Martinez, 1996) suggests that a function can be found for every species which leads to its designation as keystone. For example it is plausible that every species has host specific symbiotic viral, microbial and metazoan endemics whose survival depends on the host. However, if specific keystone species can be identified then they can be used in management of pristine ecosystems, and also for building up biodiversity in natural and managed ecosystems (Ramakrishnan, 1996).

Decline in biodiversity

The current decline in biodiversity can be attributed to several causes, the most prominent of which is the massive growth in human population (Swanson, 1995). Population growth contributes factors that act along with the human population which include; development, institutional failure, policy failure (especially third world) and ecological implications of *Homo sapiens sapiens* occupying a greater range of niche space (Ehrlich, 1988). To conserve biodiversity at all levels requires knowledge of the existence, identity, characteristics, numbers, condition, status, location, distribution, and ecological relationships between biotic species and biological communities or assemblages and their individual occurrence (Jenkins, 1986). It is also essential to record the physical and chemical properties of the environment to define ecosystem relationships (Tickell, 1996). Biodiversity present within a geographically related area is rarely static and therefore the changes need to be monitored over time (Chalmers, 1996). Taxonomic lists serve as a point of departure for studying food webs, patterns in the relative abundance of species, patterns in the numbers of individuals in different categories of physical size, and general trends in the commonness and rarity of organisms (May, 1988). Biologists currently only estimate the total number of species that exist on earth and many of them will be lost to extinction before they can be identified. Around 1.4 million species have currently been identified (Parker, 1982; Wilson, 1986). Approximately 750 000 of these are insects, 41 000 are vertebrates and 250 000 are plants, the remainder being other invertebrates, algae, fungi and micro-organisms (Wilson, 1986). Estimates of the total number of species have been placed at 5 million (Wilson, 1986), 10 million (May, 1988), even up to a 100 million species (Ehrlich and Wilson, 1991). If conservation of biodiversity at the global scale is the main aim of the science then the need for greater knowledge of what exists is essential.

Marine biodiversity

The are fewer marine species presently known than terrestrial species by about seven to one but there are more Orders and Phyla (higher taxonomic levels representing broader genetic variation) in the sea (Lasserre, 1994). Eighty eight percent of all phyla are represented in the marine environment whilst thirteen phyla are endemic (Thorne-Miller and Catena, 1991). In addition, the relative abundance of marine species may be considerably greater, since most marine species are relatively unknown and the importance of bacteria, viruses and other primitive species as important components of the marine biota has only recently been recognised (e.g. Sherr and Sherr, 1991, 1994; Pierce and Turner, 1992). There is also a greater diversity in body sizes in the marine environment when compared to terrestrial systems, and food webs tend to be more complex (Ray, 1988).

Many patterns of biodiversity have already been characterised in marine communities usually alongside a recognised physical gradient. Sanders (1968) presented data that showed that the diversity of macro-invertebrates in soft sediments was greater in tropical than in boreal regions. The diversity of habitats also increases along this gradient, presumably because there is more area at low latitudes (Thorne-Miller and Catena, 1991). In terrestrial environments, increasing diversity with decreasing latitude is a fairly consistent and regularly described pattern (Gaston and Spicer, 1988). The same is not always true for marine environments. Rex *et al.* (1993) found an increase in diversity towards the equator in the northern hemisphere for deep-sea benthic organisms. However, no similar pattern was evident in the southern hemisphere (Brey *et al.*, 1994) and others have found no such pattern in the northern hemisphere (Kendall and Aschan, 1993). The general rule for the marine environment has been questioned (Clarke, 1992) and Gee and Warwick (1996) dismiss the pattern altogether stating that mammals reach their highest diversity at the poles, macroalgae in temperate regions and corals in the tropics. They also note that the patterns in the marine environment may be different from that in the terrestrial environment, partly because strictly comparative data are lacking and because environmental variation in the sea extends over longer ecological and evolutionary time scales.

Diversity generally decreases with increasing water depth, and therefore with decreasing temperature, light and increasing pressure (Lasserre, 1994). This also is not a general rule as benthic species off the Atlantic coast of North America increase in diversity to a maximum at a depth of 1800 metres (Grassle, 1989). In the Pacific diversity at 5000-6000 metres is apparently as high as at shallower depths (Thorne-Miller and Catena, 1991). Other workers have suggested that diversity increases from shallow areas to the deep sea (Sanders, 1968; Grassle and Maciolek, 1992).

Diversity can also change along a concentration gradient of dissolved solutes as it deviates from normal seawater (Wildish, 1977). Estuaries and other brackish habitats typically have low species diversity (Atrill *et al.*, 1996) although they may be highly productive and support dense populations of some species (Kinne, 1971).

With many geographical contradictions in the literature Hutchings (1998) suggests that the presence or absence of gradients of marine diversity may only be of importance regionally. There are a number of localised areas of high species diversity in the sea. These include: coral reefs, deep sea, hydrothermal vents and kelp forests. As knowledge and intensity of research grows, more areas have been recognised as having high diversity. In the deep sea recent samples are revealing a previously unimagined species richness (Etter *et al.*, 1999). Deep-sea hydrothermal vents have revealed around 200 new species and support approximately 200 more (Tunnicliffe, 1991). These specialised communities also feature a low amount of phyletic diversity and a high degree of endemism (Dover, 1990). Ray (1988) concludes that it would be better to describe each marine habitat as having a 'characteristic' diversity rather than look for 'characteristic gradients of diversity'.

In rocky intertidal systems primary substratum is ultimately limiting (Dayton, 1971; Connell, 1972) and many organisms live among mussels and other organisms, which can provide additional substratum. Such biologically generated habitat is important in enhancing biodiversity on rocky shores (Lohse, 1993; Seed, 1996; Thompson *et al.*, 1996). Ecosystem engineers, therefore, are organisms that directly or indirectly control the availability of resources to other species by causing changes in biotic and/or abiotic materials (Jones *et al.*, 1994) and the amount of available substratum can be greatly increased by their presence (Lohse, 1993). Habitat structure influences the conditions of environment and composition of species associated with it and different habitats therefore have different associated faunas. For example, for intertidal organisms, increased structural complexity can alleviate environmental stresses during low tide. Invertebrates are protected form wave action inside mussel beds (Seed, 1996) and clumps of *Fucus* provide shelter for a variety of macro-invertebrates (Thompson *et al.*, 1996).

Algal epifaunas

In this thesis, invertebrates that live on or amongst marine macroalgae are termed the algal epifauna, as distinct from algae growing upon other algae which are collectively called algal epiphytes. The association of invertebrates on marine intertidal algae has been well documented (Seed and O'Connor, 1981; Hicks, 1985; Williams and Seed, 1992 for reviews). Different algae and different parts of the algae provide a mosaic of resources for colonisation by invertebrates; for example, brown algae with wide fronds and large sediment accumulating holdfasts support diverse assemblages of mobile and sessile organisms (Boaden *et al.*, 1975, 1976; Moore, 1985).

Algae attempt to maximise associations with beneficial epiphytes and minimise encounters with those that impose excessive cost (Williams and Seed, 1992). Many invertebrate-algal associations are detrimental to the host algae either by direct grazing e.g. *Helcion* on kelp stipes and holdfasts (Kain and Svendson, 1969), overgrowth by encrusting species, e.g. bryozoans (Oswald and Seed, 1986), leading to reduced photosynthetic rate (Oswald, 1986), removal of nutrients, e.g. bryozoans (Oswald and Seed, 1986) or increased damage from excessive drag (D'Antonio, 1985). However, others are substantially beneficial to the host algae. Many grazers prune senescing tissue from the host algae (Salemma, 1987) thereby reducing unnecessary drag and others even facilitate the release of spores from the algae, mirroring the role of some terrestrial insects (Norton, 1992).

Some of the first work on the fauna associated with seaweed was undertaken by Colman (1940) who, in an earlier study had noted important associations of invertebrates with macroalgae (Colman, 1933). Wieser (1952) conducted a similar study to Colman and demonstrated some similarity in the distribution of amphipods, polychaetes and nematodes on the shore, noting that three critical intertidal zones might exist for their distribution and stressing the importance of plant morphology and accumulation of sediments on the diversity of the epifauna.

Within an ecosystem, the numbers and kinds of organisms present are determined by the availability of resources, competition, predation, environmental disturbances, colonisation and extinction, all acting on an ecological scale in space and time (Barnes and Hughes, 1988). In order to examine processes responsible for community organisation in any system the potential sources of variation (temporally and spatially) should be described (Metaxas *et al.*, 1994).

There are many factors that can influence the patterns of spatial and temporal variability in the invertebrate communities associated with algae. Habitat heterogeneity has a marked effect on species diversity and richness, and phytal habitat complexity has been shown to affect both density and abundance of associated invertebrate species (Hicks, 1980, 1985; Jarvis and Seed, 1996). Gunnill (1983) showed that seasonal variations in the epifauna of *Pelvetia fastigiata* coincided with variations of water temperature and low water temperatures have been related to low densities of animals on large subtidal algae (Hagerman, 1966). Variations in exposure to waves affects the form of intertidal algae (Norton *et al.*, 1982) and consequently the associated faunas (Edgar, 1983b). Many algae produce chemicals that can either attract or repel invertebrates (Norton *et al.*, 1990). Also, polyphenolic compounds in fucoid algae can inhibit the production of bacteria and epiphytic algae (Conover and Sieburth, 1964) which can both be an important food source for invertebrates (Trotter and Webster, 1984) and influence the settlement behaviour of some planktonic larvae for example *Mytilus edulis* (Dobretsov, 1999) and *Abalone* spp. (Roberts, 2001). Moreover, abundance of other epiphytic algae show seasonal patterns of growth (Edgar, 1983a) increase opportunities for attachment (Johnson and Scheibling, 1987) and increase microhabitat complexity providing spatial refuges that may reduce predation on the associated invertebrates (Coull and Wells, 1983).

Although patterns of species occurrence on rocky shores are well described, many studies have focused on larger more conspicuous invertebrates such as barnacles and limpets (Hartnoll and Hawkins, 1985) other gastropods (Underwood, 1979) and mussels. Some studies have approached the associations of invertebrates with other biological structures such as mussel beds (Seed, 1996), barnacles (de Murguia and Seed, 1987; Thompson *et al.*, 1996) and large foliose algae (Seed and O'Connor, 1981; Johnson and Scheibling, 1987). In contrast relatively little work has focused on species associated with mat-like or turf-forming algae. Turf-forming algae are relatively common around the British coast providing a complex structural habitat and also providing food directly for grazers and indirectly by the accumulation of sediments for microalgal grazers and detritivores. Their characteristic compound structure also provides a refuge from predation and physical stresses like wave exposure and desiccation. In addition, turf algae in tide pools have received even less attention, presumably because of the complexities in design of sampling in this habitat.

Intertidal algal turf – *Corallina officinalis*

Turf-forming algae are abundant on many shores around the world and they are especially common in physically stressful habitats or habitats subject to moderate herbivory (Hay, 1981). When grazing pressure and desiccation rate are low, fronds tend to be sparsely branched and loosely arranged, while in desiccated or highly grazed areas the fronds are shorter, more erect, highly branched and more compact (Stewart, 1968; Munda, 1972; Liddle, 1975). The densely packed thalli and low-lying form of algal turfs cause accumulations of sediments (Whorff *et al.*, 1995) which fill spaces between the axes and prevents the settlement of other algal spores on the rock (Sousa, 1979). The ability of turf to pre-empt space in the intertidal despite their low-lying form ensures their success (Lobban and Harrison, 1994).

Articulated coralline algae are of the Order Corallinales with *Corallina officinalis* placed in the family Corallinaceae and sub family Corallinoideae (Woelkerling, 1997). *Corallina officinalis* is a turf-forming alga that consists of calcified (calcium carbonate in the form of calcite) intergenicula separated by non calcified genicula (Johansen, 1974). *Corallina* is the most widespread genus of all the articulated corallines appearing in the literature for the north east Pacific (Smith, 1944; Doty, 1947), south east Pacific (Smith, 1944) north west Atlantic (Edelstein and McLauchlan, 1966), tropical north west Atlantic (Taylor, 1960), north east Atlantic (Gayral, 1966), Atlantic Islands (Munda, 1972), Mediterranean and Red Sea (Feldmann, 1941; Erchegovic, 1957), and also for the north west Pacific, south west Pacific and south Atlantic (references in Johansen, 1969). *Corallina officinalis* occurs in tide pools on north east Atlantic rocky shores and often physical conditions can affect the form of the plant. For example, relatively sheltered tide pools contain longer and less branched plants compared with those on wave-battered areas which form dense cushions (Munda, 1972).

The first descriptive studies on the fauna of turf forming coralline algae found 34 species and upto 376, 800 individulas in the Azores (Chapman, 1955). In *Corallina officinalis,* Dommasnes (1968, 1969) focused on the changes in fauna with wave exposure and found 70 species and several higher taxonomic groups. Hagerman (1968) studied the ostracod fauna of the same samples collected from open rock in the littoral and sublittoral zones. In sheltered localities high sediment accumulations prevent settlement of bryozoans (Dommasnes, 1969). In wave exposed sites some other animals are characterised by shorter legs and stronger terminal claws

(Dommasnes, 1968). Mwaiseje (1977) recorded 91 species associated with *Corallina* around Anglesey, North Wales and found grazers to be the most dominant feeding form followed by filter feeders, deposit feeders and carnivores. The fauna of *Corallina officinalis* is characterised by the small size of the organisms compared with those on the surrounding rocks (Dommasnes, 1969).

Corallina officinalis provides a suitable substrate for the settlement of juveniles for some species. Primary settlement of the Greenshell mussel, *Perna canaliculus*, can dominate *Corallina* reaching levels of up to 85% of the associated fauna in field and laboratory studies (Buchanen and Babcock, 1997). The presence of coralline turf increased recruitment of the colonial ascidian *Pseudodistoma novaezelandiae* in New Zealand (Stocker and Bergquist, 1987), and turfs of *Corallina* facilitate the recruitment of the kelp *Lessonia nigrescens,* a key organising and structuring component of the intertidal zone in northern Chile, by providing a refuge from herbivory (Camus, 1994).

The fauna associated with *Corallina* may be valuable in pollution monitoring. Goss-Custard *et al*., (1979) suggest that on the fronds of *Corallina*, bryozoans in particular may be useful environmental indicators in that there are a large number of species represented, they cannot escape during collection and they are easily preserved. Experimental release of oil into tide pools caused a reduction in individual inhabitants of *Corallina* from 1400 animals/10ml water to 800 animals/10ml water (Bonsdorff, 1983), however, recovery to pre-oil exposure levels took only one week although recovery time would be longer with incresing scale of the pollution incident.

Long-term seasonal studies on the fauna of *Corallina* have been rare. Recently, Hull (1997) attributed the seasonal changes in the density of ostracods within *Corallina* to reproductive cycles of the component species within the assemblage. Other studies have collected samples throughout the period of one year but did not focus on the assemblage with particular reference to temporal heterogeneity (Dommasnes, 1968, 1969; Hagerman, 1968; Grahame and Hanna, 1989).

In the UK only the ostracod fauna of *Corallina* in tide pools has been studied at an appropriately wide range of spatial scales (Hull, 1999). There was significant variability in species richness at the scale of kilometres and significant variability in assemblage diversity over the kilometre and 100-200m scale but not at the 5-10m scale. Alternatively, in Australia, significant variation was detected between low and mid shore areas and between sites separated by tens of metres (Kelaher *et al*., 2001). These differences were often caused by relatively few taxa and were consistent at different times of sampling (Kelaher *et al.*, 2001) and are most likely due to an effect of shore height rather than an effect of differing structural complexity of habitat (Kelaher, 2003b). The structuring forces in spatial variability have been attributed to physical and biological factors. Grahame and Hanna (1989) found increasing species abundance towards a backwall in the tide pools sampled and hypothesised that a 'quiet water effect' was responsible for the patterns observed.

Corallina officinalis is relatively complex structurally having two distinct growth forms. The crustose holdfast or base is perennial and grows apically, similar to encrusting corallines such as *Lithothamnia* sp.. The basal crust may grow continuously until stimulated to produce fronds (Colthart and Johansen, 1973). The fronds have a high surface area to volume ratio when compared to other algae (Hicks, 1977b; Coull and Wells, 1983) and is characterised by high accumulations of sediments (Hicks, 1977a, b). *Corallina* can provide an effective refuge from predation for meiofauna (Coull and Wells, 1983) and conversely a reduction in diversity can occur after artificial reduction in complexity by trampling (Brown and Taylor, 1999). The structural complexity of *Corallina* can be enhanced by the presence of attached epiphytes, particularly the tube worm *Spirorbis corallinae*, by increasing the number and variety of microhabitats within the algae (Crisp and Mwaiseje, 1989). Also, Kelaher *et al.* (2001) described an increase in richness of polychaetes with an increase in sediment but not in gastropods or amphipods. The physical structure of *Corallina*, however, did have a marked influence on the fauna when controlling for biological characteristics using an artificial turf (Kelaher, 2002). Moreover, while frond length of turf could not explain differences in assemblages between different tidal heights or patches separated by tens of metres it did cause large differences in the structure of gastropod assemblages in low shore areas (Kelaher, 2003a).

Tide pools

There are numerous definitions and classification of rock pool types in the literature (Droop, 1953; Ganning, 1971; Mwaiseje, 1977). However the definition of tide pools, as distinct from rock pools are "pools in the intertidal region that are subject to isolation and inundation by the sea on almost every tide" (Mwaiseje, 1977).

Tide pools offer unique possibilities for following the dynamics of ecosystems if the biological and non-biological variations can be measured over very short time intervals (Ganning, 1971). The physical conditions in a tide pool (e.g. temperature, pH, DO_2 and salinity) can exhibit large diurnal variation of differing magnitude seasonally, and often over a small scale within each pool (Morris and Taylor, 1983). The existence of local variation is dependent on the meteorological conditions, duration of emersion and size of the pool (Morris and Taylor, 1983). Dissolved oxygen can increase to over 200% saturation diurnally due to increased photosynthesis in the late afternoon and this can be accompanied by pH changes ranging from 8-10 (Pyefinch, 1943; Ambler and Chapman, 1950; Ganning, 1971; Goss-Custard *et al.*, 1979). Daytime temperature fluctuations can also be relatively large with changes of over 4°C in the space of an hour (Mwaiseje, 1977) and 11°C during the total period of emersion (Daniel and Boyden, 1975). Over a seasonal scale, temperature generally shows the largest variation with annual extremes of 35°C and below 0°C in Sweden (Ganning, 1971). Salinity changes are generally small with greatest effect in high shore pools that are not inundated on every tide (Daniel and Boyden, 1975). Huggett and Griffiths (1986) generalised that an oxygen minimum will occur immediately before flooding after a nocturnal low tide, and a combined oxygen and temperature maximum before flooding after a daytime high tide. Dissolved oxygen variation is greatest in the summer months and higher pH values have been recorded during this time (Morris and Taylor, 1983).

Despite the paucity of literature on tide pool communities an excellent review is provided by Metaxas and Scheibling (1993). The tide pool environment favours small as well as tolerant animal species (Morris and Taylor, 1983; Emson, 1985) which tend to live within the fronds and holdfasts of the algae. Few species are restricted to pool systems but many are characteristic of the environment (Goss-Custard *et al.*,1979; Emson, 1985). Species that are adapted to life within rock pools are often at a competitive advantage to others. Species composition of tide pools varies greatly from pool to pool and from time to time but often with one species dominant (Dethier, 1984). Recent studies have shown that there is marked variability in the tide pool faunal and floral assemblage composition with tidal elevation (Huggett and Griffiths, 1986; Metaxas *et al.*, 1994) and within and between shores (Hicks, 1980; Hull, 1999). Each tide pool is considered unique (due to variation in physical characteristics) which may account for the high degree of variability between tide pool assemblages from similar locations (Metaxas and Scheibling, 1994). The structure of tide pool communities may exhibit large temporal variability mostly related to season (Hicks, 1985; Metaxas and

Scheibling, 1994) and patterns of recruitment (Emson, 1985; Metaxas and Scheibling, 1993).

Aims of this study

The current study investigates the patterns of macro-invertebrates associated with turf-forming algae in the British Isles, predominantly *Corallina officinalis* in intertidal tide pools, through a series of observational and manipulative field experiments in order to determine:

- The number and identity of the species associated with *Corallina officinalis.*
- The change in the fauna associated with *Corallina* turf around the British Isles.
- Patterns of change in the fauna associated with *Corallina* turf at small spatial scales.
- Temporal variations in diversity and community structure of invertebrates associated with *Corallina* turf.
- The influence of certain environmental variables on observed patterns in biodiversity.
- The influence and importance of tide pools on structuring the community of Corallina turf.

At the outset of this study it was necessary to establish a protocol for appropriately sampling the invertebrate fauna within *Corallina* turf in the tide pool environment and to consider the statistical techniques appropriate for these types of data. Chapter 2 therefore describes the methodology, sample sites and statistical techniques employed throughout this study. The aim of this chapter is to avoid unnecessary repetition of methods used in the subsequent chapters. Chapter 2 also provides a general description of the invertebrate fauna associated with *Corallina* turf. As *Corallina officinalis* is common around the U.K., it may be possible to extrapolate the results of local studies (in Wales) to the wider geographical scale. Chapter 3 tests the hypothesis that there is no difference in the community of *Corallina* turf on different shores of the UK and Ireland. The aim of this chapter is to establish the levels of variability in the fauna associated with *Corallina* turf at regional scales. This chapter also investigates the effects of working at taxonomic levels other than that of the species in studies of this type and discusses the implications such results may have on similar studies where taxonomic knowledge of the fauna is insufficient to work at the species level. Changes in small scale variability have large implications for ecological interpretation of experiments at larger scales. In Chapter 4, patterns of small scale variability in the invertebrate fauna associated with *Corallina* turf at different depths within tide pools, and between tide pools of different size and at different heights on the shore are examined. Differences in the patterns of diversity are investigated on different shores and at two different times of sampling. The aim of this chapter is to establish whether there is consistent variability in the fauna of *Corallina* turf over relatively small spatial scales at different locations and at different times. Chapter 5 investigates patterns of temporal variability on three shores in North Wales over 2 years and tests the hypothesis that there is significant temporal variation in the fauna associated with *Corallina* turf. This chapter aims to establish how the turf community changes over time and what species are primarily responsible for the observed changes. The last experimental chapter (Chapter 6) investigates the effect of tide pools on the fauna associated with mat-like habitats such as algal turfs. This chapter tests the hypothesis that there will be no difference in the fauna that colonises identical artificial substrate whether in tide pools or on open rock. It also compares the fauna of two similar red algal turfs *Corallina officinalis* in tide pools and *Laurencia pinnatifida* on open rock. The aim of this chapter is to establish to what extent the tide pool environment influences the types of species found amongst the algal turf in comparison to those assemblages on open rock using carefully designed artificial substrates. Finally, in chapter 7, I discuss the results of this work in terms of the overall contribution the invertebrate community associated with *Corallina* turf makes to biodiversity with suggestions for the long-term conservation.

Chapter 2

The study sites, general methodology and associated fauna of *Corallina officinalis*

Introduction

As many of the methods involved in collecting, sorting and processing of samples in this thesis are identical, an overview is provided here to avoid unnecessary repetition. Details of sites used, collection methods, sorting methods and statistical tools to analyse the data collected are provided. The chapter ends with a brief description of the fauna found throughout the thesis and the habitat in which it occurs. This serves as a starting point for the rest of the thesis that investigates the patterns of change in the fauna associated with *Corallina* turf in more detail.

Site descriptions

In this study tide pools on rocky shores containing turf of the red alga *Corallina officinalis* were sampled extensively around the coasts of the British Isles and Ireland to study patterns of spatial and temporal variability in the associated fauna. Each shore selected had numerous tide pools containing greater than 50% cover of *Corallina* turf and were subject to similar degrees of wave exposure. Detailed below are descriptions of the overall conditions experienced on these shores. A map indicating the locations of each study site is shown in Figure 1. Sites were selected from similar latitude to ensure no latitudinal gradients were influenceing the fauna.

Porth Ysgaden, Lleyn Peninsula, Gwynedd, Wales (52° 54.4' N 4° 38.8' W)

A northerly facing headland on the north coast of the Lleyn Peninsula in North Wales. The shore is rated as semi exposed on the biologically defined scale proposed by (Ballantine, 1961). Formed from Precambrian schist, the shore drops away from the cliff quickly into a shallow kelp bed. There are many tide pools upto 10m in length containing around 50-70% cover of *Corallina* turf, where present. Barnacles and limpets dominate the emergent rock surface with relatively little macroalgal growth until below mean low water springs, where red algae predominate.

Porth Cwyfan, Anglesey, Wales, (53° 10.9' N 4° 29.3' W)

A southwesterly facing shore on the west coast of Anglesey, North Wales. The shore is rated as semi exposed by the biologically defined exposure scale. Formed from

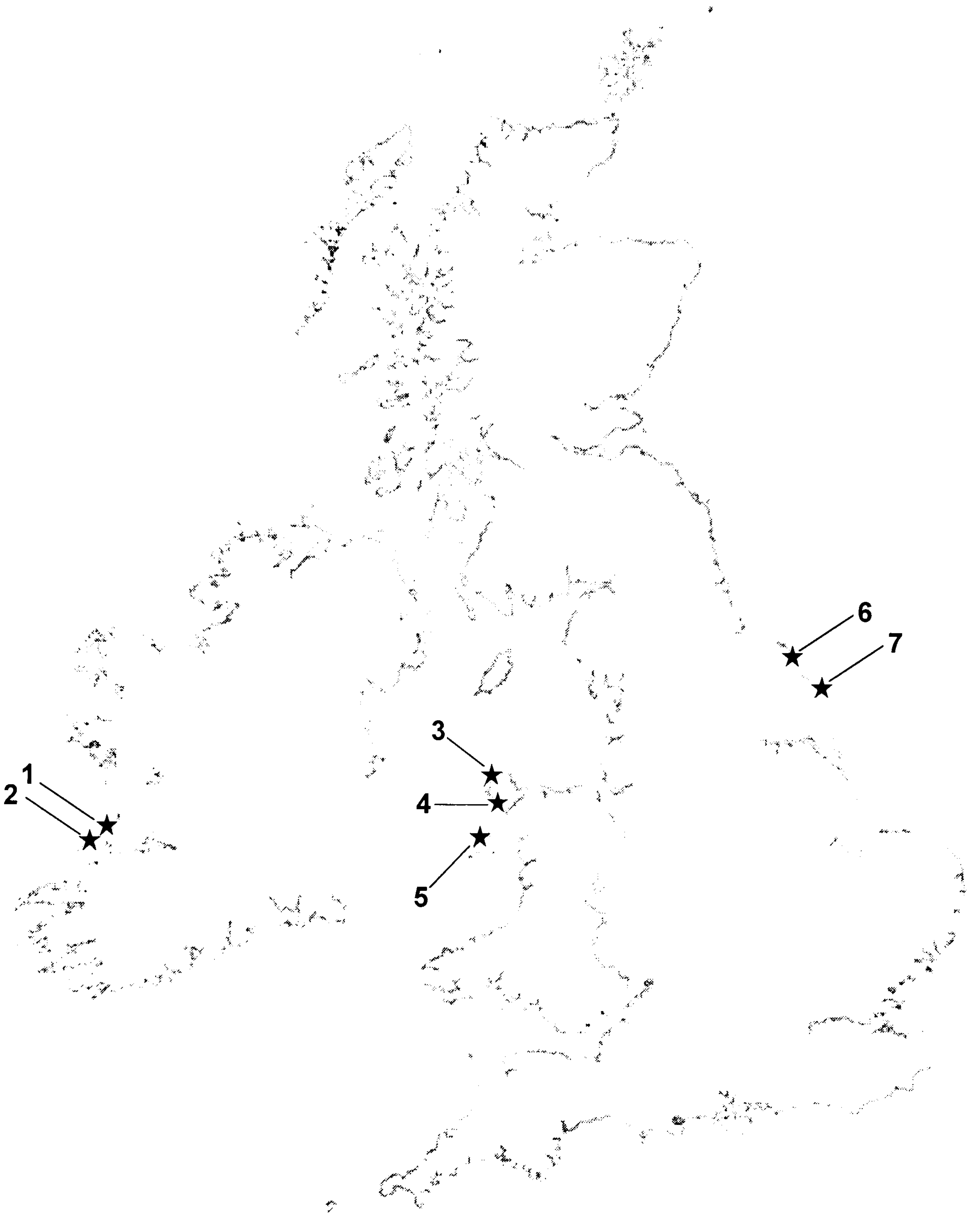


Figure 1. Map of the United Kingdom and Ireland indicating positions of rocky shores used throughout this study. 1-Doonbeg, 2-Kilkee, 3-Cemlyn, 4-Porth Cwyfan, 5-Porth Ysagden, 6-Robin Hood's Bay, 7-Filey Brigg.

metamorphic Precambrian schist, the shore is approximately 500m long with many wide and flat platforms. A wide range of tide pools occur containing up to 100% *Corallina* cover occur from mid tide level and below. A mosaic of barnacles, limpets and fucoids dominates the open rock, with lithothamnion becoming dominant at low shore levels.

Cemlyn, Anglesey, Wales, (53° 24.9' N 4° 31.00' W)

A northerly facing shore on the north coast of Anglesey. The shore is semi-exposed and formed from Precambrian granite schist. The whole shore is nearly 2km long and forms ledges that run out into the sea, normal to the land. Tide pools range in size from less than a metre to over 25 metres long. *Corallina* is present in nearly all pools below mean high water neap tide level, usually with near 100% cover. Barnacles and limpets dominate the emergent rock with many young fucoids growing amongst the barnacle matrix.

Robin Hood's Bay, North Yorkshire, England, (54° 27.11' N 00° 31.01' W)

A predominantly north east facing shore on the east coast of England. Robin Hoods Bay extends from Ness Point, southwards 6km to Ravenscar. Gently shelving soft clay bedrock is exposed at low tide revealing a large number of shallow tide pools in which *Corallina* dominates. The open rock is also dominated by dense stands of *Corallina* which retain a large volume of water at low tide. Boulders and loose rocks are also a defining feature of this site.

Filey Brigg, North Yorkshire, England (54° 12.46' N 00° 15.02' W)

A rocky outcrop about 1km long on the east coast of England. A variety of tide pools are abundant on the northerly facing shore with near 100% *Corallina* cover. The open rock has an abundance of barnacles, limpets, mussels and littorinids but a low occurrence of macroalgae.

Kilkee, County Clare, Irish Republic (09° 39.29'W 52° 41.01'N)

An exposed rocky spit experiencing wave swell in the outer reaches of a very small north-west facing bay on the west coast of Ireland. Large rock platforms extend out into the sea with varying degrees of exposure due to there large size. There is an extensive barnacle/limpet community in the mid-eulittoral with many deep tidepools with brown algae and patches of *Fucus* sp. across the shore. A dense mussel community with attached algae completely covers the lower shore and lower midshore. The shore is a popular recreational area and is fished for edible crabs (*Cancer pagurus*). Tide pools are frequent and reach a size of upto 50m. *Corallina* occurs in some but not all tide pools but where present is almost 100% cover.

Doonbeg, County Clare, Irish Republic (52° 44.47' N 09° 31.57' W)

A north-west facing rocky shore on the west coast of Ireland. The shore may be exposed to west and north-west winds it is moderately protected from prevailing south-west winds by a minor headland and from swell by the presence of rocky breakwaters immediately offshore. The substratum is primarily gently sloping bedrock with some areas of scattered rounded boulders and cobbles. Gullies traverse the shore horizontally between these ridges which form many long tide pools. *Corallina* turf averages around 50% cover in tide pools as lithothamnion becomes the dominant space occupier at a depth of around 30cm.

Field collection and processing of samples

The method for field collection and sorting of samples was the same for most of the study and the criteria are outlined below. Additional methods will be dealt with in the appropriate chapters.

Appropriate shores were chosen on the basis of containing suitable tide pools, which in turn contained a reasonable cover (>50%) of *Corallina officinalis* turf. *Corallina* turf was removed from tide pools by random placement of a 25cm^2 sharpened stainless steel corer. This size sampling unit is practical on irregular rocky shores, minimising effects caused by changes in surface topography. Taking many small samples has also previously been shown to be better for sampling patchy habitats as the combination of many small areas will give a higher species count than a contiguous area of the same size (Pringle, 1984). The corer was placed over the turf, and the turf removed from the rock using a paint scraper. Once the paint scraper was under the corer the whole sample could be lifted out intact. This allowed the method to be standardised for every occasion. The other end of the corer was covered with 63µm plankton mesh to prevent motile animals from escaping. The samples were then stored in a labelled watertight container for return to the laboratory where they were fixed with 5% buffered formalin. The dimensions of tide pools were recorded as maximum length, maximum width along the longest length and maximum depth as an aid to ensure similar sized pools were sampled. Temperature (°C), pH, and salinity (%) of the pools were also recorded at the time of sampling. The physical/chemical conditions of one tide pool at Cemlyn, North Wales, were measured over spring neap tidal cycles on four occasions throughout one year (April, July, October 2000 and January 2001). Temperature, pH and salinity were recorded every fifteen minutes from the time of isolation (on the ebb tide) to the period of inundation. This provided a background of the variability encountered in these variables in this environment.

In the laboratory, samples were washed, the algae removed and the remaining sediment sieved through 500μm mesh to separate the macrofauna. Invertebrates were sorted under a dissecting microscope and identified to species using the appropriate taxonomic key. Species names and authorities were checked using The Species Directory (Howson and Picton, 1997). When identification to species was not possible the lowest taxonomic group attainable was deemed sufficient. Where species did not conform to any available description or identification was not possible, the specimens were drawn to scale, notes taken and each assigned to a morpho-species. Animals attached to the fronds of *Corallina* were identified and counted in the same way whilst still attached to the substratum.

Once all the organisms had been removed form the sample the alga was measured in the following ways; the average frond length based on the length of three longest fronds measured from holdfast to tip, number of branches per mm upon these fronds and number of branchlets per branch. Branchlets are defined as those branches of 4 genicula or less in length, to include the reproductive bodies or rodoliths (a geniculum is one articulation of the *Corallina* frond). Length was measured using a steel rule and branches and branchlets were counted under a dissecting microscope. The number of holdfasts (holdfasts is defined as the number of fronds directly attatched to the basal crust collected in the sample) were counted using a dissection microscope. Volume (cm^3) of algae was measured by first surface drying the fronds and then placing in a measuring cylinder to calculate the displacement of a known volume of water. To aid comparison with other work, volume was divided by the area of the sample to give a measure of the *Corallina* density (CDENS, Grahame and Hanna, 1989). Surface area (cm^2) was calculated based on the methods of Harrod and Hall (1962). Dry weight (g) measurements were obtained for the algae and associated sediment in fractions of

>63um and <63um. Dry weight was measured after drying in an oven for 48 hours at 60°C and then cooling in a desiccator for 12 hours.

Throughout this thesis the following abbreviations are use in relation to environmental variables in the text and in tables: Temperature (Temp °C), pH, Salinity (Sal), *Corallina* density or Volume/Area (CDENS), Number of branches per mm (Brchs), number of branchlets per branch (Brts), number of holdfasts (Holds), dry weight of *Corallina* (Coral), dry weight of sediment greater than 63µm (>63), dry weight of sediment less than 63µm (<63) and surface area of algae (SA).

Sample size

Biodiversity is ultimately concerned with cataloguing what species occur where, when and how. This is rarely if ever possible because this would require an impossibly large amount of time and sampling effort. Many studies have attempted to calculate on optimum number of replicates that would sample most of the species in a community. However, Gage and Coghill (1977) describe species area plots that do not reach asymptotes even after 64 samples. They concluded that collecting fully census data in nearly all marine contexts is impossible. However, a sample size still needs to be large enough to give any subsequent statistical test sufficient 'power' to be able to detect a difference between samples. The multivariate approach to hypothesis testing used in this thesis requires at least four samples in order to generate enough permutations of sample sizes to obtain significantly different results (any less would result in the frequent possibility of making a type II error). Hence, the number of replicates collected in this thesis is five per treatment to ensure that type II errors are not made and that laboratory sorting time is kept to a minimum thus allowing a greater range of habitats to be sampled. The only exception to this is in Chapter 5 where pseudoreplication led to samples needing to be pooled to create one sample per treatment.

Species data analyses

The main aim of this thesis is to investigate the patterns of biodiversity of macro invertebrates associated with *Corallina officinalis*. An exploratory, investigative approach has thus been largely adopted using a combination of univariate, multivariate and graphical techniques. Where necessary the appropriate univariate and or multivariate technique has been used to test *a priori* conceived hypotheses. Many of the statistical methods implemented in this thesis are repeated in several chapters, thus the method and rationale for the uses of these methods are outlined below. Any statistical method specific to a chapter will be referred to in the appropriate section.

Univariate techniques

Various ways of defining and measuring diversity have been proposed. Diversity, however defined, is a single statistic in which the number of species and the evenness are confounded. An assemblage has high diversity if it has many species and abundances are even. Conversely, diversity is low when species are few and abundances uneven. Since diversity depends on two independent properties of a collection, the number of species and their relative abundance, ambiguity is inevitable. Thus a collection with few species and high evenness could have the same diversity as another collection with many species and low evenness.

Describing a community mathematically inherently places more weight to different parts of the community depending upon what statistic is chosen. For the purposes of this thesis a range of descriptive univariate statistics are used to measure of diversity, dominance, richness, evenness and graphical representation of the species/abundance distribution. The choices of statistic are outlined below.

Six univariate measures of diversity were calculated for replicate samples of species abundance data. These were: number of species, number of individuals, Margalef's diversity (d) (Magurran, 1988), the exponential of the Shannon Index (exp H') (Shannon and Weaver, 1964), the complement of Simpson's Dominance Index (1-Simpson) (Simpson, 1949) and Pielou's evenness (J) (Pielou, 1974). Number of species, exp H' and 1-Simpsons have been described by Hill (1953) as specific diversity numbers, namely Hill's N_0, N_1 and N_2 respectively. Hill's N_0 (hereafter referred to as number of species) is a measure of all the species in a community while Hills N_1 is effectively a measure of the number of abundant species in a sample and Hills N_2 is a measure of the very abundant species within a sample. Margalef's d is sensitive to rare species in the community and is therefore dominated by the richness of a community. Pielou's evenness (J') is a measure of how evenly the abundance of different species is distributed throughout the community, such that high evenness indicates high diversity.

Analysis of variance was used to test hypotheses on changes in diversity amongst different shores and in changes of measured environmental variables where appropriate. These analyses were preceded by an Anderson-Darling test of normality and Bartlett's test for homogeneity of variances. Where variances showed significant heterogeneity data were transformed using Log_{10} (x+1) transformation (Underwood, 1997). If after transformation the data were not normally distributed or variances remained heterogeneous then an analysis of variance was carried out any way as ANOVA is generally robust from departure of these assumptions and the results interpreted accordingly and with caution (Underwood, 1997).

Pearson's product-moment correlation was used to identify any significant relationship between univariate measures of diversity and measured environmental variables. As this involved many repeated tests, comparisons were only considered significant if $p<0.01$, thus reducing the possibility of type I errors.

Many attempts have been made to fit empirical models to underlying species abundance patterns. Four models are commonly recognised, geometric, log, log normal and broken stick. The ecological theories on which the models are built often have rather tenuous links to ecological reality and there are many mathematical and statistical problems associated with model fitting to ecological data (Gray, 1996). There does not seem to be any single distribution that is universal and models of species abundance distributions are probably adequate statistical descriptors. Faced with this lack of consensus on the basic principles and the sensitivity of methods in practice the best approach would appear to be to refrain from attempting to fit empirical models and look at the patterns of species abundance themselves. The method used in this study to provide an overview of the organisation of species abundance patterns is plotting of *k*-dominance plots (Clarke and Warwick, 1994). The *k*-dominance curves aid interpretation on the relative diversity of different communities showing low diversity communities to have high dominance and high diversity communities to have low dominance. If two curves should intersect, it is then difficult to separate communities in terms of their intrinsic diversity.

Multivariate techniques

A two stage approach to analysing multivariate data has been adopted (Field *et al.*, 1982). This involves exploring the sample and species associations and then comparing the findings with the environmental information in order to search for consistent patterns in interpretation the community patterns.

All multivariate analysis on species abundance data were carried out using Bray-Curtis similarity matrices of species sample data (Bray and Curtis, 1957). The species sample matrices were first subject to two transformations, square root and presence/absence. Square root transformation down weights the relative contributions of the extremely abundant species in a sample. Presence/absence transformation allows the rare or transient species to influence community pattern by giving them equal weighting as the dominant members of the fauna. All multivariate routines were implemented in the computer software package PRIMER (Plymouth Routines in Multivariate Ecological Research, Primer-E Ltd, Plymouth Marine Laboratory).

For graphical indications of the similarity of samples dendrograms were produced by Cluster analysis using group average linking (Clifford and Stephenson, 1975). This was followed by ordination of the data using 2-dimensional non metric multi dimensional scaling (nMDS, Field *et al.*, 1982; Clarke, 1993). Ordination by nMDS places each individual sample on a 2-dimensional map such that the relative distance between samples indicates their relative similarity (or dissimilarity). The nMDS ordination effectively forces high dimensional species data into 2-dimensional space such that distances between them can be distorted, hence an associated stress value serves as a measure of the goodness of fit of an nMDS ordination to the overall similarity matrix. A stress value greater than 0.2 indicates that the ordination poorly represents the sample dissimilarities.

Analysis of similarities (ANOSIM, Clarke, 1993) is a multivariate test of hypothesis that is analogous with univariate ANOVA. The main advantage of ANOSIM is that it makes no assumptions about the data and only requires that groups of samples to be tested are defined *a priori*. ANOSIM is used to test hypotheses about differences in the composition of communities between treatments using the associated Bray-Curtis similarities. Specific details of each test will be handled in the corresponding chapter.

Similarity percentage analysis (SIMPER) was performed on species abundance data to determine species contributing most to similarity within groups, and species contributing most to dissimilarity between groups (Clarke, 1993). This process elucidates those species that are most responsible for observed differences between groups of samples. In some cases the patterns of change occur along a gradient, for example temporal. In these cases it is necessary to adopt a holistic approach in identifying the species that cause the multivariate pattern. To detect species groupings responsible for the observed multivariate pattern the routine BVSTEP was implemented (Clarke and Warwick, 1998a). BVSTEP searches for a subset or subsets of species that best match the overall multivariate pattern by calculation of a Spearman rank correlation coefficient (rho). The resulting set of species would therefore produce a dendrogram and ordination that closely resemble those for the overall data set.

A similar procedure also using a Spearman rank correlation coefficient was used to test the sample data against a theoretical similarity matrix that resembles data found in a cyclic pattern. The Primer programme RELATE was used for this (Somerfield and Gage, 2000).

Multivariate analysis of environmental variables requires the data to first be normalised (subtract the mean and then divide by the standard deviation). Normalisation places the variables of different units on a common, dimensionless measurement scale. Environmental variables were then plotted against one another and those with a skewed distribution were log (x+1) transformed to better approximate multivariate normality. A similarity matrix was then constructed using Euclidean distance followed by ANOSIM tests of hypothesis in the same way as for the species abundance data. Principal Component Analysis (PCA) was used to display the multivariate biotic pattern using the first two principal components.

Matching of biotic multivariate patterns to species abundance multivariate pattern was done using a weighted Spearman rank correlation coefficient (rho) in the PRIMER routine BIO-ENV (Clarke and Ainsworth, 1993). This approach detects patterns of variation in the species data, which can be best explained by the observed environmental variables. BIO-ENV attempts to find the fewest environmental parameters that best match the species abundance data. To reduce the computational time required for this process all environmental parameters were analysed using Pearson product moment correlation coefficients to see if any were co-linear. If variables were found to be co-linear then only one was used in the analysis and acted as surrogate for the other.

Table 1. Mean, standard deviation and maximum and minimum of some environmental variables measured through the course of the thesis from investigations on small and large scale spatial variability and temporal variability within the fauna associated with *Corallina officinalis*.

	Mean	Standard Deviation	Maximum	Minimum
pH	9.05	0.53	10.18	7.63
Temperature (°C)	16.70	3.47	21.90	7.20
Salinity	35.4	2.20	45.00	31.60
Volume (cm^3)	6.68	3.89	23.00	2.50
Branches/mm	0.87	0.32	1.87	0.23
Branchlets/Branch	5.01	2.14	13.17	0.85
Holdfasts	45.09	56.69	277	0
Weed weight (g)	4.55	2.36	14.46	1.39
Sediment > 500μm	1.82	1.99	9.10	0.15
Sediment < 500μm	2.06	4.69	37.48	0.09
Surface area (cm^2/g)	179.08	77.40	430.12	44.48

Corallina officinalis, tide pools and associated fauna

Corallina turf has many different growth forms providing a variety of complexities of habitat. Generally, environmental factors showed high degree of variability throughout the scales measured (Table 1). For example the number of holdfastscontained in a $25cm^2$ sampled ranged from 0 in several samples upto 277 in one sample taken at Filey Brigg in Yorkshire. The volume of algae ranged between $2.5cm^3$ from samples taken from edge of pool and $23cm^3$ from samples taken at 10 cm depth at Cemlyn. This reflects differences in the growth form of these two habitats from short tightly packed mats at the edges of pools to longer more foliose turf deeper in the pools.

Tide pools undergo many physical and chemical changes in a relatively short space of time which can influence the fauna and flora found within them. The results of monitoring of certain conditions in tide pools are presented in Figure 2. Changes in the conditions of the tide pools monitored at Cemlyn, North Wales appear to follow the patterns from previous studies (Ganning, 1971; Daniel and Boyden, 1975; Goss-Custard *et al.*, 1979; Huggett and Griffiths, 1986). Dissolved oxygen concentration and pH show increases in tide pools during isolation in daylight hours, but decreases in darkness. Both parameters are closely linked the floristic component in the tide pools and will increase during periods of net photosynthesis but decrease during periods of net respiration. All tide pools had extensive cover of *Corallina* turf, but other algae were also present within samples or occurred in the tide pools but not in the samples (Table 2). Temperature shows little fluctuation during the period of isolation, only on extremely hot or cold days, in small pools high on the shore does this parameter differ markedly from sea surface temperature. Patterns of change are evident though during isolation in spring tides the pool temperature drops, as spring tides in North Wales occur during the evening. The opposite pattern is true for neap tides as neap tides tend to occur around midday. However, pool temperature on springs and neaps falls during isolation in October. This is due to elevated sea surface temperatures at the end of the summer which retain their heat longer than the surrounding air. The result is for a rapid decline in temperature due to cooler air temperatures when isolated in a tide pool. Another obvious pattern is the gradual change in temperature throughout the year giving rise to a strong seasonal pattern. Salinity in the tide pools does not appear to change markedly throughout the year. High rainfall levels are expected to lower salinity in winter and evaporation due to high temperatures is thought to increase salinity in the summer (Goss-Custard *et al.*, 1979). This does not appear to happen

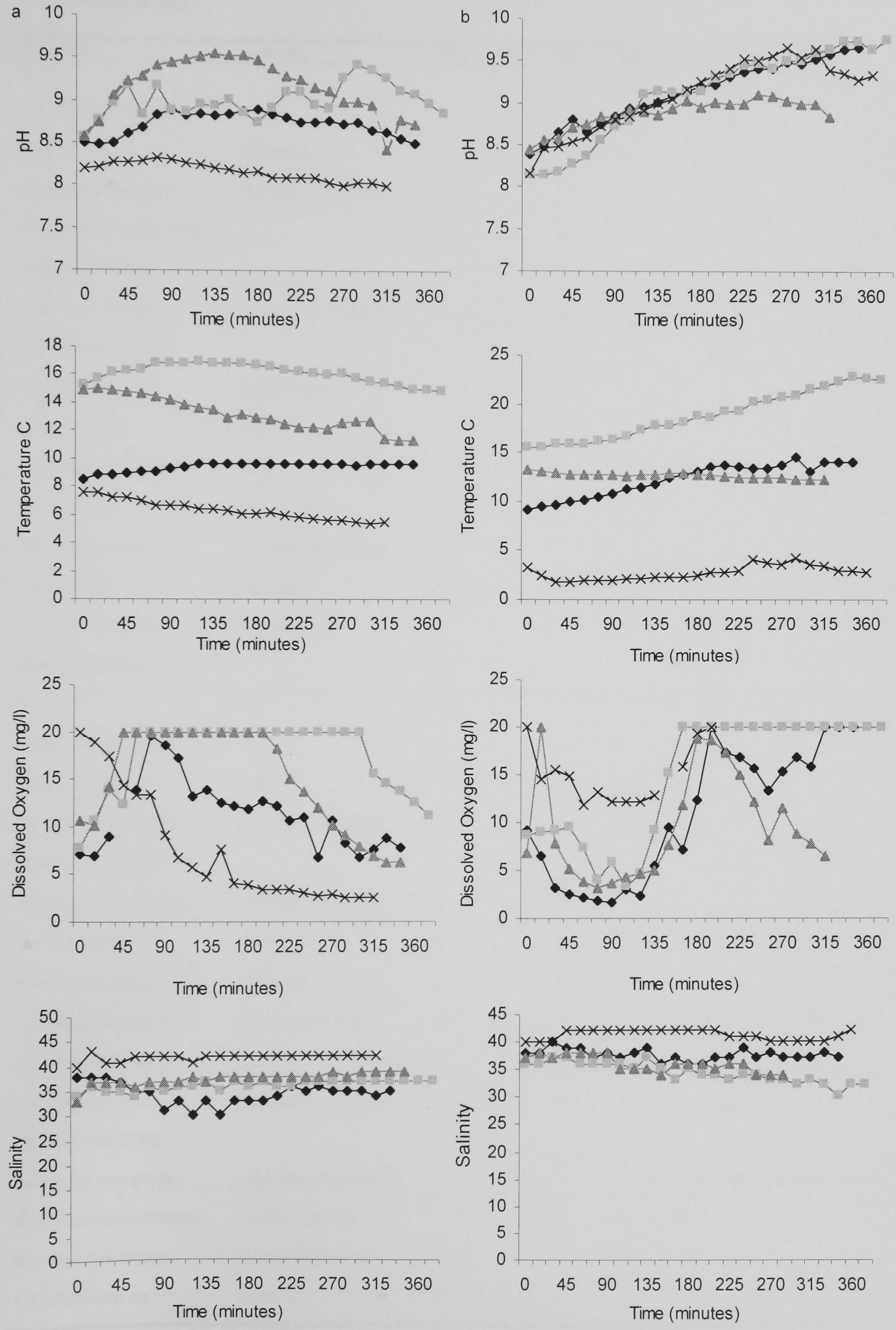


Figure 2. Changes in physical/chemical conditions in tide pools at Cemlyn during isolation from tidal influence during a) one spring tide and b) one neap tide at different times of the year. ♦ April 00, ■ Jul 00, ▲ Oct 00, x Jan 01.

Table 2. Algae found in a.) samples and b.) pools but not samples other than *Corallina officinalis,* and their location around the British Isles and Ireland. (CM, Cemlyn; PC, Porth Cwyfan; PY, Porth Ysgaden; DB, Doonbeg; KK, Kilkee; FB, Filey Brigg; RHB, Robin Hood's Bay).

SPECIES	Authority	CM	PC	PY	DB	KK	FB	RHB
a.								
CHLOROPHYCEAE								
Ulva sp.	Linnaeus	+	+	+	+			
Cladophora rupestris	(Linnaeus) Kützing	+						
Filamentous Green unid.		+	+	+		+	+	+
PHAEOPHYCEAE								
Leathesia difformis	(Linnaeus) Areschoug	+	+	+	+	+	+	+
RHODOPHYCEAE								
Chondrus crispus	Stackhouse	+	+	+				
Ceramium sp.	Roth	+	+	+	+			
Mastocarpus stellatus	(Stackhouse) Guiry	+	+	+				
Gelidium sp.	Lamouroux		+	+				
Palmaria palmata	(Linnaeus) Kuntze	+						
Gracilaria sp.	Greville	+						
Lithothamnion spp.	Heydrich				+			
Filamentous Red unid.		+	+			+	+	+
b.								
CHLOROPHYCEAE								
Enteromorpha sp.	Link				+	+		
Himanthalia elongata	(Linnaeus) S Gray					+		
PHAEOPHYCEAE								
Ascophyllum nodosum	(Linnaeus) Le jolis	+		+				
Fucus serratus	Linnaeus	+		+	+		+	+
Fucus vesiculosus	Linnaeus			+				
Laminaria hyperborea	(Gunnerus) Foslie	+		+				
Laminaria saccharina	(Linnaeus) Lamouroux			+				
Halidrys siliquosa	(Linnaeus) Lyngbye	+	+	+			+	
RHODOPHYCEAE								
Laurencia pinnatifida	(Hudson) Stackhouse						+	
Nemalion helminthoides	(Velley) Batters				+	+		
Polysiphonia lanosa	(Linnaeus) Tandy	+		+				
Lithothamnion sp.	Heydrich	+	+		+			

Table 3. List of taxa identified from *Corallina* turf within tide pools from all sites within the study area encountered during this thesis. (CM, Cemlyn; PC, Porth Cwyfan; PY, Porth Ysgaden; DB, Doonbeg; KK, Kilkee; FB, Filey Brigg; RHB, Robin Hood's Bay).

TAXA	Authority	CM	PC	PY	DB	KK	FB	RHB
PROTISTA								
Foraminifera		+	+	+	+	+		+
CNIDARIA								
Anemone indet1.		+	+		+	+	+	
Anemone indet2.		+						
Urticina sp.	Ehrenberg, 1834	+	+					
PLATYHELMINTHES								
Platyhelmith indet.						+		
Prostheceraeus vittatus	(Montagu, 1813)		+					
Stylochoplana maculata	(Quatrefages, 1845)	+	+	+				
Convoluta convoluta	(Abildgaard)	+	+	+				
NEMERTEA		+	+	+	+	+		+
NEMATODA		+	+	+	+	+	+	+
SIPUNCULA								
Aspidosiphon muelleri	Diesing, 1851	+	+	+				
POLYCHAETA								
Trichobranchus glacialis	Malmgren, 1866	+						
Lanice conchilega	(Pallas, 1766)	+						
Nicolea venustula	(Montagu, 1819)			+				
Sabellaria alveolata	(Linnaeus, 1767)		+					
Sabellaria spinulosa	Leukart, 1849	+	+				+	+
Amphicteis gunneri	(M Sars, 1835)							+
Caulleriella sp.	Chamberlain, 1919						+	
Cirratulus cirratus	(O F Müller, 1776)			+			+	+
Cirratulus filiformis	Keferstein, 1862	+	+	+				
Dodecaria concharum	Oersted, 1843	+	+	+				+
Tharyx sp.	(see Cauleriella)	+		+				
Malacoceros sp.	Quatreages, 1843	+		+	+			+
Polydora caeca	(Oersted, 1843)	+	+	+				+
Polydora ciliata	(Johnston, 1838)	+		+				
Polydora flava	Claparède, 1870	+	+	+				+
Scolelepis foliosa	(Edwards, 1833)					+		+
Scolelepis squamata	(Abildgaard, 1806)	+						
Spionid indet.		+						+
Janua pagenstecheri	(Quatrefages, 1865)	+	+	+	+	+	+	+
Spirorbis corallinae	De Silva & Knight-Jones, 1962	+	+	+	+	+	+	+

TAXA	Authority	CM	PC	PY	DB	KK	FB	RHB
Pomatoceros lamarckii	(Quatrefages, 1866)	+						+
Amphiglena mediterranea	(Leydig, 1851)	+	+	+	+	+		
Demonax langerhansi	Knight-Jones, 1983	+	+	+				
Demonax brachyona	(Claparède, 1870)	+	+					
Fabricia stellaris	(Blainville)	+	+	+	+		+	
Fabriciola baltica	Friedrich, 1940	+		+				
Fabriciola berkelyii	Banse, 1956	+						
Laonome kroyeri	Malmgren, 1866		+					
Oriopsis armandi	(Claparède, 1864)			+				
Perkinsiana rubra	(Langerhans, 1880)	+						
Pseudopotamilla reniformis	(Bruguiere, 1789)	+						
Brania indet.	Quatrefages, 1865	+						
Brania clavata	(Claparède, 1863)	+	+	+				
Brania pusilla	(Dujardin, 1851)	+						
Eurysyllis tuberculata	Ehlers, 1864	+						
Exogone	Oersted, 1845	+	+	+	+			
Exogone naidina	Oersted, 1845	+						
Ehlersia cornuta	(Rathke, 1843)		+					
Odontosyllis ctenostoma	Claparède, 1863	+	+	+				
Odontosyllis gibba	Claparède, 1863	+		+				
Sphaerosyllis bulbosa	Southern, 1914	+						
Syllis gracilis	Grube, 1840	+	+					
Typosyllis brevipennis	(Grube, 1863)		+					
Typosyllis armarillis	(O F Müller, 1771)	+						
Typosyllis prolifera	(Krohn, 1852)	+						
Typosyllis sp.	Langerhans, 1879	+	+	+	+	+		
Sphaerodoridium claperedii	(Greeff, 1866)	+						
Sphaerodorum gracilis	(Rathke, 1843)	+	+	+				
Lepidonotus sp.	Leach, 1816		+	+				
Mysta picta	(Quatrafages, 1866)	+	+	+				
Eulalia bilineata	(Johnston, 1839)	+	+					
Eulalia sp.	Savigny, 1817	+	+		+			
Anaitides maculata	(Linnaeus, 1767)						+	+
Phyllodocid unid		+	+					
Harmothoe (Lagisca)	(Grube, 1840)	+						
Harmothoe impar	(Johnston, 1839)	+	+					
Harmothoe lunulata	(Chiaje, 1841)				+			
Harmothoe spinifera	(Ehlers, 1864)		+					
Pholoe sp.	Johnston, 1839	+	+	+	+	+	+	+
Nereis pelagica	Linnaeus, 1758		+	+				

TAXA	Authority	CM	PC	PY	DB	KK	FB	RHB
Platynereis dumerilii	Edwards, 1833	+	+	+	+	+		
Kefersteinia cirrata	(Keferstein, 1862)	+	+	+	+	+	+	+
Ophelina modesta	Stop-Bowitz, 1958				+	+		
Micromaldane ornithochaeta	Mesnil, 1897	+	+	+	+	+		
Nicomache lumbricalis	(Fabricius, 1780)	+	+	+				
Capitellid indet		+	+	+		+		+
Arenicola defoidens	Cadman & Nelson-Smith 1993		+					
Arenicoloides ecaudata	(Johnston, 1865)	+		+				
OLIGOCHAETA		+	+	+		+	+	+
PYCNOGONIDA								
Achelia echinata	Hodge, 1864	+	+	+				
Achelia hispida	Hodge, 1864	+	+	+				+
Achelia laevis	Hodge, 1864	+	+					
Achelia longipes	(Hodge, 1864)	+	+					+
Achelia simplex	(Giltay, 1934)	+	+					
Anoplodactylus angulatus	(Dohrn, 1881)	+	+	+	+			
Anoplodactylus petiolatus	(Kröyer, 1844)	+	+					
Anoplodactylus pygmaeus	(Hodge, 1864)	+	+				+	
Anoplodactylus virescens	(Hodge, 1864)	+						
Phoxichilidium femoratum	(Rathke, 1799)		+					
Nymphon sp.	Fabricius, 1794	+	+					
Endeis sp.	Philippi, 1843	+						
ARACHNIDA		+	+	+		+		
THORACIA								
Balanus crenatus	Brugière, 1789	+						
Chthamalus montagui	Southward, 1976	+						
Elminus modestus	Darwin, 1854		+	+				
Semibalanus balanoides	(Linnaeus, 1767)	+	+	+				
Verruca stroemia	(O F Müller, 1776)	+	+					+
HARPACTICOIDA		+	+	+	+	+		
OSTRACODA		+	+	+	+	+	+	+
AMPHIPODA								
Talitridae indet.			+					
Stenothoe monoculoides	(Montagu, 1815)	+	+	+	+	+	+	+
Melita sp.	Leach, 1814		+					
Leucothoe sp.	Leach, 1814						+	
Parajassa pelagica	(Leach, 1814)		+					
Hyale perieri	(Lucas, 1846)		+					
Hyale prevostii	(Milne Edwards)	+	+	+			+	
Hyale stebbingi	Chevreux, 1888		+					

TAXA	Authority	CM	PC	PY	DB	KK	FB	RHB
Chaetogammarus sp.	Martynov, 1925	+	+					
Eulimnogammarus obtusatus	(Dahl, 1938)	+						
Gammarellus indet.			+	+				
Eusirus longipes	Boek, 1861	+						
Apherusa bispinosa	(Bate, 1856)	+		+	+			
Apherusa cirrus	(Bate, 1862)	+	+					
Apherusa jurenei	(H Milne-Edwards, 1830)	+	+	+	+			+
Campecopea hirsuta	(Montagu, 1804)		+					
Dexamine spinosa	(Montagu, 1813)	+	+	+	+			
Corophium sp.	Latrielle, 1806				+		+	
Calliopius laeviusculus	(Kröyer, 1838)			+				+
Lembos websteri	Bate, 1857				+	+		
Ampithoe helleri	G Karaman, 1975	+	+	+	+	+		+
Ampithoe ramondi	Audouin, 1826	+	+	+				
Ampithoe rubricata	(Montagu 1808)	+	+	+	+	+		+
Sunampithoe pelagica	(H Milne-Edwards, 1830)	+		+				
Ampeliscidae indet.				+				
Lysianassidae indet		+						
Caprella acanthifera	Leach, 1814	+	+	+				
Caprella linearis	(Linnaeus, 1767)	+						
ISOPODA								
Idotea baltica	(Pallas, 1772)	+	+					
Idotea granulosa	Rathke, 1843	+	+	+			+	
Idotea neglecta	G O Sars, 1897	+						
Idotea pelagica	Leach, 1815	+	+	+	+			+
Jaera albifrons	Leach 1814	+		+		+	+	+
Janiropsis brevipennis	G O Sars, 1899		+					
Dynamene bidentata	(Adams, 1800)	+	+	+	+			
Munna kroyeri	Goodsir, 1842	+	+	+				
Gnathia maxillaris	(Montagu, 1804)	+	+	+				
Paragnathia formica	(Hesse, 1864)		+					
TANAIDACEA								
Apseudes talpa	(Montagu, 1808)	+		+				
Parasinelobus chevreuxi	(Dollfus, 1898)	+						
Tanais dulongii	(Audouin, 1826)	+	+	+	+	+		
DECAPODA								
Cancer pagurus	(Linnaeus, 1758)	+						
Carcinus maenas	(Linnaeus, 1758)	+	+	+	+	+	+	+
Pirimela denticulata	(Montagu, 1808)		+					
Pisida longicornis	(Linnaeus, 1767)		+					

TAXA	Authority	CM	PC	PY	DB	KK	FB	RHB
Porcellana platycheles	(Pennant, 1777)	+						
Palaemon sp.	Weber, 1795					+		
POLYPLACOPHORA								
Acanthochitona crinita	(Pennant, 1777)		+		+			
Leptohiton assellus	(Gmelin, 1791)						+	
Lepidochitona cinerea	(Linnaeus, 1767)				+	+		
GASTROPODA								
Helcion pellucidum	(Linnaeus, 1758)	+	+	+				
Patella vulgata	(Linnaeus, 1758)	+	+	+				
Hinia sp.	J E Gray, 1847		+					+
Nucella lapillus	(Linnaeus, 1758)	+	+	+	+	+		
Raphitoma sp.	Bellardi, 1847		+		+	+		
Skeneopsis planorbis	(O Fabricius, 1780)	+	+	+		+		
Cingula sp.	Fleming, 1818	+						
Onoba semicostata	(Montagu, 1803)	+	+	+	+	+	+	+
Rissoa parva	(da Costa, 1778)	+	+	+	+	+	+	+
Pusillina sarsi	(Lovèn, 1846)	+			+			
Juv Gastro		+	+	+				
Lacuna crassior	(Montagu, 1803)						+	
Lacuna parva	(da Costa, 1778)	+						
Lacuna vincta	(Montagu, 1803)	+				+		
Littorina littorea	(Linnaeus, 1758)	+	+		+		+	+
Littorina mariae	(Sacchi & Rastelli, 1966)	+	+	+			+	+
Littorina neglecta	(Bean in Thorpe, 1844)	+	+	+				
Littorina obtusata	(Linnaeus, 1758)	+						+
Littorina sp.	Fèrussac, 1822	+	+	+	+	+	+	+
Coriandria fulgida	(J Adams, 1797)				+	+		
Barleeia unifascata	(Montagu, 1803)	+		+	+	+		
Rissoella indet.	J E Gray, 1847	+	+	+				
Rissoella diaphana	(Alder, 1848)	+	+	+		+		
Rissoella opalina	(Jeffreys, 1848)	+						
Odostomia plicata	(Montagu, 1803)	+	+	+	+	+		
Ondina diaphana	(Jeffreys, 1848)					+		
Omalogyra atomus	(Philippi, 1841)	+	+	+		+		+
Tricolia pullus	(Linnaeus, 1758)	+	+	+				
Gibbula cinereia	(Linnaeus, 1758)	+				+		
Gibbula magus	(Linnaeus, 1758)		+		+	+		
Gibbula umbilicalis	(da Costa, 1778)	+	+		+	+		
Skenea serpuloides	(Montagu, 1808)		+		+			
Aplysia punctata	(Cuvier, 1803)		+					

TAXA	Authority	CM	PC	PY	DB	KK	FB	RHB
Limapontia sp.	Johnston, 1836	+	+	+	+	+		
Nudibranchia indet.			+					
PELECYPODA								
Lasaea adansoni	(Gmelin, 1791)	+	+	+	+	+	+	+
Turtonia minuta	(Fabricius, 1780)	+	+	+				
Venerupis sp.	Lamarck, 1818	+	+	+			+	+
Anomia ephippium	Linnaeus, 1758	+	+					
Modiolarca tumida	(Hanley, 1843)					+		
Modiolus modiolus	(Linnaeus, 1758)	+	+	+	+	+	+	+
Musculus costulatus	(Risso, 1826)					+		
Musculus discors	(Linnaeus, 1767)	+	+	+	+	+		+
Mytilus edulis	(Linnaeus, 1758)	+	+	+	+			
Hiatella arctica	(Linnaeus, 1767)		+		+	+		
ECHINODERMATA								
Amphipholis squamata	(Chiaje, 1829)	+	+	+	+	+	+	+
Ophiopholis aculeata	(Linnaeus, 1767)		+					
Asterina gibbosa	(Pennant, 1777)	+	+	+	+	+		
Asterina phylactica	Emson & Crump, 1979	+						
INSECTA								
Clunio sp.	Haliday	+	+	+	+	+		
Tipula sp.			+	+				
ASCIDIACEA								
Molgula sp.	Hanley, 1848	+	+	+				
Ascidia sp.	Linnaeus, 1767	+						
Ascidiella aspersa	(O F Müller, 1776)		+					
Aplidium sp.	Savigny, 1816	+	+	+				
OSTEICTHYES								
Nerophis lumbricornis	Jenyns, 1835		+					

with these data, and given the climate, there are very few extremely hot days in the summer and rainfall has been shown to run directly off the top of a tide pool in calm conditions, thus having little influence over the salinity (A. B. Yule pers. comm.).

During this study 212 different species were collected and identified from 14 phyla at locations in Ireland, the UK (Table 3). The most common taxa are polychaete worms with 68 representatives. There were 35 species of gastropod molluscs and 28 species of amphipod crustacean. 70 species (33%) were identified at only one site, or at only one time. Others were common to all sites and all times of sampling. As is normal in invertebrate communities, some species are either common or permanent members of the *Corallina officinalis* community while other members were rare or transient in their occurrence. Species may appear as transient in the community because they are naturally rare, or at least rare in that habitat and only occur by chance. Some species may only occur at certain times of the year and may be missed or not recorded at other times. Other species may only utilise the coralline turf at certain periods in their life cycle, for example as juveniles, while some species will not occur at certain sites because it is beyond their geographical range. Details of the changes in the occurrence, abundance and distribution of the species in Table 3 through space and time are provided in the subsequent chapters.

The greatest number of taxa were recorded from sites in Wales at Cemlyn, Porth Cwyfan and Porth Ysgaden. These sites were the most intensively sampled as part of the study into changes in the patterns of biodiversity with time (Chapter 5) and the effect of small scale spatial patterns (Chapter 4). Lower numbers of species were recorded from sites in Ireland and North Yorkshire, yet these sites were only sampled once as part of the study into large scale or regional spatial variation in community patterns (Chapter 3)

The rest of this thesis details how the fauna associated with *Corallina* turf varies in space and time and with differing associated factors within the turf and tide pool environments.

Chapter 3

Regional diverstiy of the macroinvertebrate community associated with *Corallina* turf.

ABSTRACT

Replicate samples of *Corallina officinalis* turf were collected form three locations in the UK and Ireland. Sites on the North Sea coast of Yorkshire, the Irish Sea coast of North Wales and the Atlantic coast of Ireland were sampled once in the summer of 2001 to investigate regional differences in the fauna associated with the turf forming alga. The data were also used to investigate the effect of working at taxonomic levels higher than species in studies of biodiversity. Of the 107 species recorded, only 11 were common to all sites. Generally highest diversity was found at the Irish sites where the highest numbers of species were found. The fewest species were recorded at the Yorkshire sites while the site with the highest measures of dominance was at Cemlyn in North Wales. These differences can largely be explained by variations in the abundance of the most common taxa as well as the presence or absence of certain taxa from certain sites, i.e. those that are beyond a species' geographical boundary. The single most consistent variable that explained community pattern at the regional scale was temperature, though overall differences appear to be driven by a complex and interacting arrangement of biotic and abiotic factors acting at regional and local scales. Reasons for these patterns of variation at the scales measured are discussed. Aggregating data to taxonomic levels above species revealed different degrees of breakdown in the interpretation of community patterns. In general it is considered that in studies where taxonomic expertise is lacking, working at the Family level results in little loss of information in the observed results.

Introduction

Coastal macroalgae in temperate waters, often host a wide range of animal species from virtually all the main phyla (Williams and Seed, 1992). While the associations of species with large foliose algae such as fucoids (Seed *et al.,* 1981; Seed and O' Connor, 1981; Williams and Seed, 1992) and kelps (Seed and Harris, 1980; Smith *et al.*, 1996) is well studied, relatively little is known about the fauna associated with short turf-forming or mat-like algae such as *Corallina officinalis* Linnaeus.

Turf-forming algae are abundant on many shores around the world and are especially common in physically stressful habitats such as wave-exposed rocky shores, or habitats subject to moderate herbivory (Hay, 1981). When grazing pressure, desiccation rate and wave energy is low, fronds of turf algae are sparsely branched and loosely arranged, while in desiccated, highly grazed and wave exposed shores the fronds are shorter, erect, highly branched and more compact (Stewart, 1968; Munda, 1972; Liddle, 1975). The densely-packed and low-lying form of algal turf cause accumulations of sediments (Whorff *et al.*, 1995) which fills spaces between the algal axes and prevents settlement of other algal spores on the substratum (Sousa, 1979). The ability of turf to pre-empt space in the intertidal despite the low-lying from ensures their success (Lobban and Harrison, 1994). These characteristics provide a mosaic of habitats ideal for an extensive and varied colonisation by invertebrates. *Corallina officinalis* is an articulated coralline turf-forming red alga with a global distribution (Feldmann, 1941; Smith, 1944; Doty, 1947; Erchegovic, 1957; Taylor, 1960; Papenfuss, 1964; Salim, 1965; Edelstein and McLauchlan, 1966; Gayral, 1966; Munda, 1972) making an ideal species to study wide-scale patterns in the biodiversity of its associated invertebrate fauna.

Around Britain, *Corallina* turf is predominantly found in tide pools and on open rock below the mean low water spring tide level. The highly branched and densely packed fronds provide habitat for a diverse assemblage of invertebrates and may contain in excess of 200 000 individuals m^{-2} (Brown and Taylor, 1999). The frequent occurrence of *Corallina* turf and the diverse associated fauna indicates a high contribution to biodiversity for these habitats worldwide. Other mat-like habitats on the rocky intertidal shores also support diverse assemblages of invertebrates, for example mussel beds (Seed, 1996), ascidians (Monteiro *et al.*, 2002) and lichens (Healy, 1996) and it is likely that the fauna associated with *Corallina* makes a large contribution to the biodiversity of rocky shores around the British Isles. Despite this there has only been a limited amount of research on this type of habitat (Dommasnes, 1968, 1969; Hagerman, 1968; Bonsdorff, 1983; Ballesteros, 1988; Crisp and Mwaiseje, 1989; Grahame and Hanna, 1989; Hull, 1997; Davenport *et al.,* 1999; Hull, 1999) with an increased interest recently on Australian shores (Davenport *et al.,* 1999; Kelaher *et al.,* 2001; Olabarria and Chapman 2001a, b; Kelaher, 2002; Olabarria, 2002).

Differences in community structure throughout geographical regions have long been a major concern for ecologists (Menge and Lubchenco, 1981). Many large-scale marine diversity studies have focussed on descriptions of species assemblages and the search for consistent patterns along latitudinal gradients (Sanders, 1968; Clarke, 1992; Kendall and Aschan, 1993; Rex *et al.*, 1993; Brey *et al.*, 1994; Gee and Warwick, 1996), or patterns associated with depth (Sanders, 1968; Grassle, 1989; Grassle and Maciolek, 1992; Poore and Wilson, 1993). Alternatively, diversity studies on the regional scale have observed community changes in response to fluctuations in salinity (Wildish, 1977; Atrill *et al.*, 1996) wave exposure (e. g. Lewis 1964) and shore height (e. g. Paine 1974). Diversity at the scale of 100s km could also incorporate a longitudinal gradient. A longitudinal gradient at regional scales may for example show patterns of distribution along shorelines (Archambault and Bourget, 1996), or between groups of islands (Smith, 2001). Relatively little work has been done concerning invertebrate diversity of identical algal habitats along a longitudinal gradient at regional scales, especially in the British Isles. Diversity at these scales is likely to be influenced not only by local processes, but also by larger scale regional influences, such as transport processes, governing recruitment from local and regional species pools (Karlson and Cornell, 1998). It is also commonly held that samples closer to each other in space should be more similar to each other than those farther apart (Underwood and Chapman, 1996). Thus the expectation here is for a pattern of increasing dissimilarity between different sites with increasing distance between those sites.

In studies encompassing a wide geographical area it is not always possible to identify invertebrates fully to the level of species. This is often due to insufficient taxonomic expertise, lack of taxonomic keys in areas where the fauna and flora are poorly described, and time and cost constraints (Furse *et al.*, 1984). Where these conditions persist, studies have considered taxonomic levels higher than species. For example at the level of Family, when assessing the impacts of pollution (Warwick, 1988b), selecting areas for conservation (Vanderklift *et al.*, 1998), constructing food webs

(Thompson and Townsend, 2000) and describing patterns of community variation (James *et al.*, 1995; Bowman and Bailey, 1997). However, whether or not the benefits outweigh the costs, such as loss of information, in all cases of working at taxonomic level higher than species is a matter of contention amongst ecologists (Ferraro and Cole, 1990).

This chapter investigates the patterns of macroinvertebrate diversity associated with *Corallina* turf at a regional scale (10s-100s km) using a selection of univariate and multivariate techniques. In addition some environmental variables are identified that best describe the associated pattern of invertebrates. The data collected in this study are also used to determine the benefits of working at taxonomic levels other than species in descriptive experiments which describe patterns of biodiversity, using both a multivariate and univariate approach.

Methods

Tide pools were chosen haphazardly at mid tide level on five shores in the UK and Ireland. The criteria for pool selection were that tide pools must be greater than 1m long, greater than 0.5m wide and greater than 30cm deep. The shores chosen were Doonbeg and Kilkee in Ireland, Cemlyn in North Wales and Robin Hood's Bay and Filey Brigg in Yorkshire, UK. These shores were selected as they occur at roughly the same latitude allowing comparisons to be based on the geography of the British Isles rather than any distinct latitudinal gradient. Sites in Wales were sampled on the 14th August, those in Yorkshire on the 16th and 17th August and those in Ireland on the 18th August 2001. One 25cm^2 sample was collected from five randomly selected tide pools on each of the shores. Samples were otherwise processed and sorted according to the methods outlined in Chapter 2.

In addition to the methods in Chapter 2 the data collected are aggregated to higher taxonomic groups of Genus, Family, Order, Class and Phylum. At each of these resolutions ANOVA is performed on the Univariate measures of diversity (Number of species (Hill's N_0), Hill's N_1, Hill's N_2 and Pielou's evenness only). Multivariate Cluster and nMDS analysis are also applied, the results of nMDS are then correlated with the original nMDS based on species level data using the PRIMER programme RELATE which generates a value rho with an associated probability. Finally, one way ANOSIM is carried out on the data to investigate the consistency of the community relationships at higher taxonomic levels.

Results

Despite attempting to collect only samples containing *Corallina officinalis* some other algae often occurred in samples. These included unidentified filamentous green and red algae at all sites, *Leathesia difformis* (Linnaeus) Areschoug at Robin Hood's Bay and Doonbeg and *Ceramium* indet. and *Ulva lactuca* Linnaeus at Doonbeg. Other common species of algae present in the pools and in the samples are presented in Chapter 2.

A total of 5101 invertebrates were collected, counted and identified from the five British and Irish shores. Contributions came from 107 species, in 64 Families, 32 Orders, 21 Classes and 12 Phyla. The dominant phyla in descending order were, Mollusca (37 species), Annelida (32 species) and Crustacea (23 species). Other groups represented were chelicerates, platyhelminths, echinoderms, sipunculans, nemerteans, nematodes, hexapods, cnidarians and protists. Eleven species, or 10% of the total number of species recorded, were common to all sites. These species were amongst the 33 most abundant and were dominated by polychaetes (54% of all individuals – almost entirely due to the sedentary spirorbids, *Sprirorbis corallinae* and *Janua pagenstecheri*) with the single echinoderm, *Amphipholis squamata,* contributing 29% of the individuals and lesser contributions from molluscs (8%), crustaceans (5%) and nematodes (3%). 38 species or 36% of the total number were unique, i.e. restricted to a single sample, with 23 (61%) containing only one individual. Fifty seven percent of the unique species were crustaceans with the proportions of polychaetes, molluscs and a sipunculan being 19%, 16% and 6% respectively.

Significant differences in univariate diversity indices were shown between all shores (Table 1). There were significantly fewer species at Filey Brigg in Yorkshire than at any other location in Wales or Ireland and significantly fewer species were found at Robin Hood's Bay that at Doonbeg, Ireland (Fig 1a). The lowest numbers of individuals were collected at Filey Brigg and these were significantly lower than the numbers collected at Cemlyn in Wales and Kilkee in Ireland (Fig. 1b). The highest richness using Margalef's d was recorded at Doonbeg, with the lowest at Filey Brigg. Overall Doonbeg had a significantly higher richness than all non Irish sites, while Kilkee was significantly higher than Filey (Fig. 1c). Only Doonbeg (J'=0.7502) had significantly higher evenness than that at Cemlyn (J'=0.5203) (Fig. 1d). Hill's N_1 (Exp H'), shows the Irish site to have the highest richness while Cemlyn the lowest. Only Doonbeg has

Table1. Analysis of variance on univariate measures of invertebrate diversity from samples collected in tide pools at five locations in the British Isles and Ireland. *,p<0.05; **p<0.01; ***, p<0.001; ns=not significant. CM=Cemlyn, KK=Kilkee, DB=Doonbeg, RHB=Robin Hood's Bay, FB=Filey Brigg.

		(N=5) Number of species		Number of individuals		Margalef's d	
Transformation		None		None		None	
	Df	MS	F	MS	F	MS	F
Depth	4	249.5	9.14**	47001	5.63**	6.562	8.35***
Residual	20	27.3		8343		0.786	
Tukey's		CM KK DB > FB & DB > FB		CM KK > FB		DB > CM RHB FB & KK > FB	

		Pielous evenness J'		Hill's N_1		Hill's N_2	
Transformation		None		None		None	
	Df	MS	F	MS	F	MS	F
Depth	4	0.0361	3.23*	72.2	6.39**	28.55	4.64**
Residual	20	0.0112		11.1		6.15	
Tukey's		DB >CM		DB > CM RHB FB		DB > CM RHB FB	

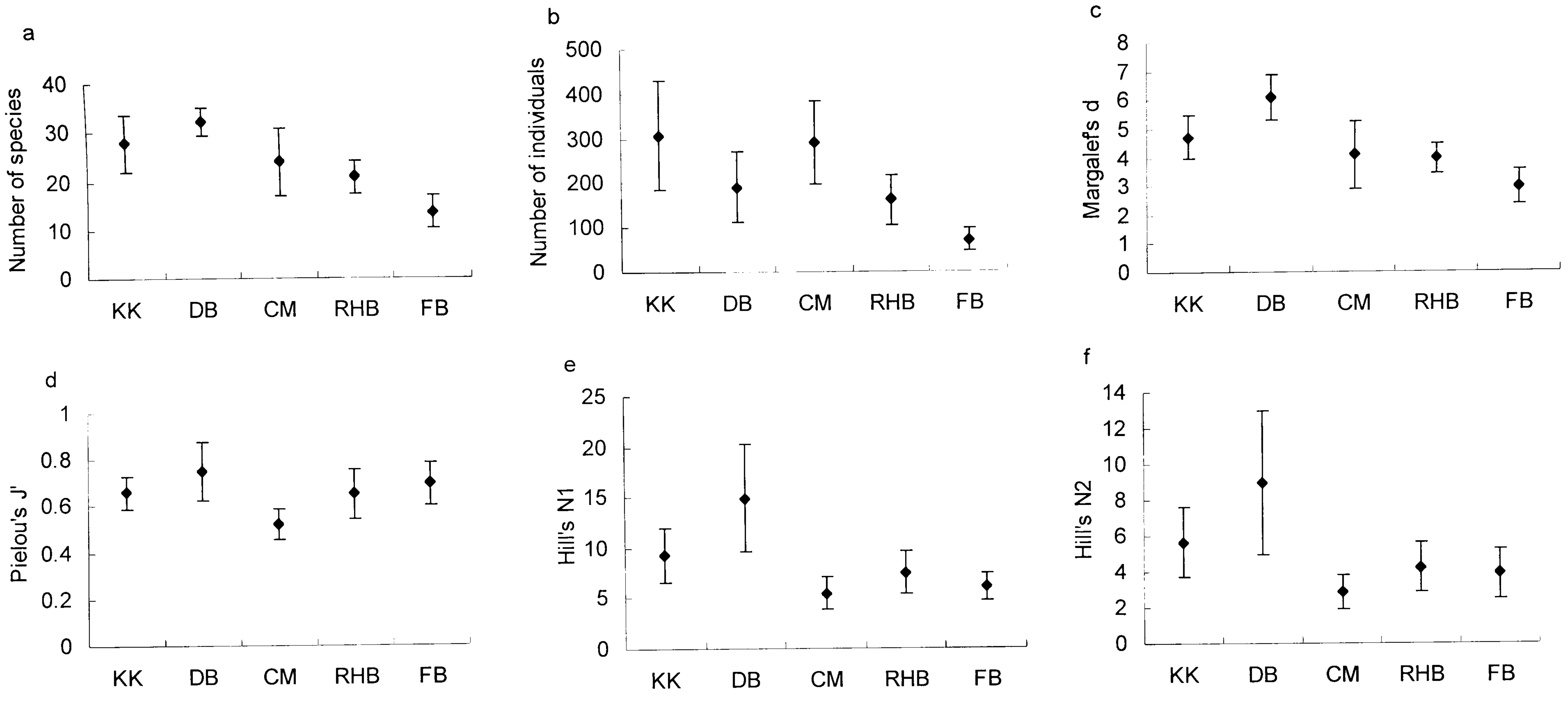


Figure 1 a-f. Mean and 95% confidence intervals of univariate measures of invertebrate diversity associated with *Corallina officinalis* in tide pools from five locations around the U. K. and Ireland. (KK = Kilkee, DB = Doonbeg, CM = Cemlyn, RHB = Robin Hoods Bay, FB = Filey Brigg).

significantly higher value of Hill's N_1 than Cemlyn, Filey and Robin Hood's Bay (Fig. 1e). Hill's N_2 shows the same pattern as Hill's N_1 with the Irish sites having the highest dominance and Cemlyn the lowest. Doonbeg again has significantly higher diversity of very abundant species than Cemlyn (Fig. 1f).

K-dominance curves indicate Doonbeg is the most diverse site with lowest dominance as its curve is below all others with no crossing over (Fig. 2). Also Robin Hood's Bay and Kilkee are more diverse than Cemlyn and Filey Brigg although no further distinction can be made as both these pairs of lines intersect. These data show that while there is much variability in the patterns of diversity, those samples from the Irish site at Doonbeg tend to have highest diversity while those samples from the East coast of England site at Filey Brigg have the lowest diversity.

Cluster analysis of square root transformed data indicates a clear separation of samples between Irish and Welsh sites, while the two sites in Yorkshire are separated from those in other geographical locations but group together themselves (Fig 3). This pattern of separation is more clearly viewed on a 2-dimensional nMDS ordination (Fig. 4). A one-way ANOSIM and pairwise comparisons (Table 2) reveals that all shores contain significantly different communities associated with *C. officinalis* (Global R = 0.881 $p<0.001$). Similarity percentage analysis (SIMPER) shows that similarity within shores between replicate samples was highest at Cemlyn and lowest at Filey Brigg; in all cases the echinoderm, *Amphipholis squamata,* made a large contribution to average similarity within shore (Table 3), indicating that this species has the most even distribution within all the shores. Measures of average dissimilarity between pairs of shores do not increase with increasing geographic distance (Table 4). Between every pair of samples at least one or other of the tubeworms *Spirorbis corallinae* or *Janua pagenstecheri* was the highest contributor to dissimilarity between pairs of samples except for those between Kilkee and Robin Hood's Bay (Table 4) These two polychaetes can attain high abundances and are often the numerically dominant animals in the sample, especially in samples from Cemlyn. *Spirorbis corallinae* contributed more than 3% to the total dissimilarity between all ten pairs of samples, *Janua pagenstecheri* in 7 pairs and *Amphipholis squamata* 6 pairs. Contributions to similarity of less than 3% were numerous and included many species so this was arbitrarily chosen as the cut off percentage for this test. Other species having a high contribution to dissimilarity between samples can be seen in Table 4.

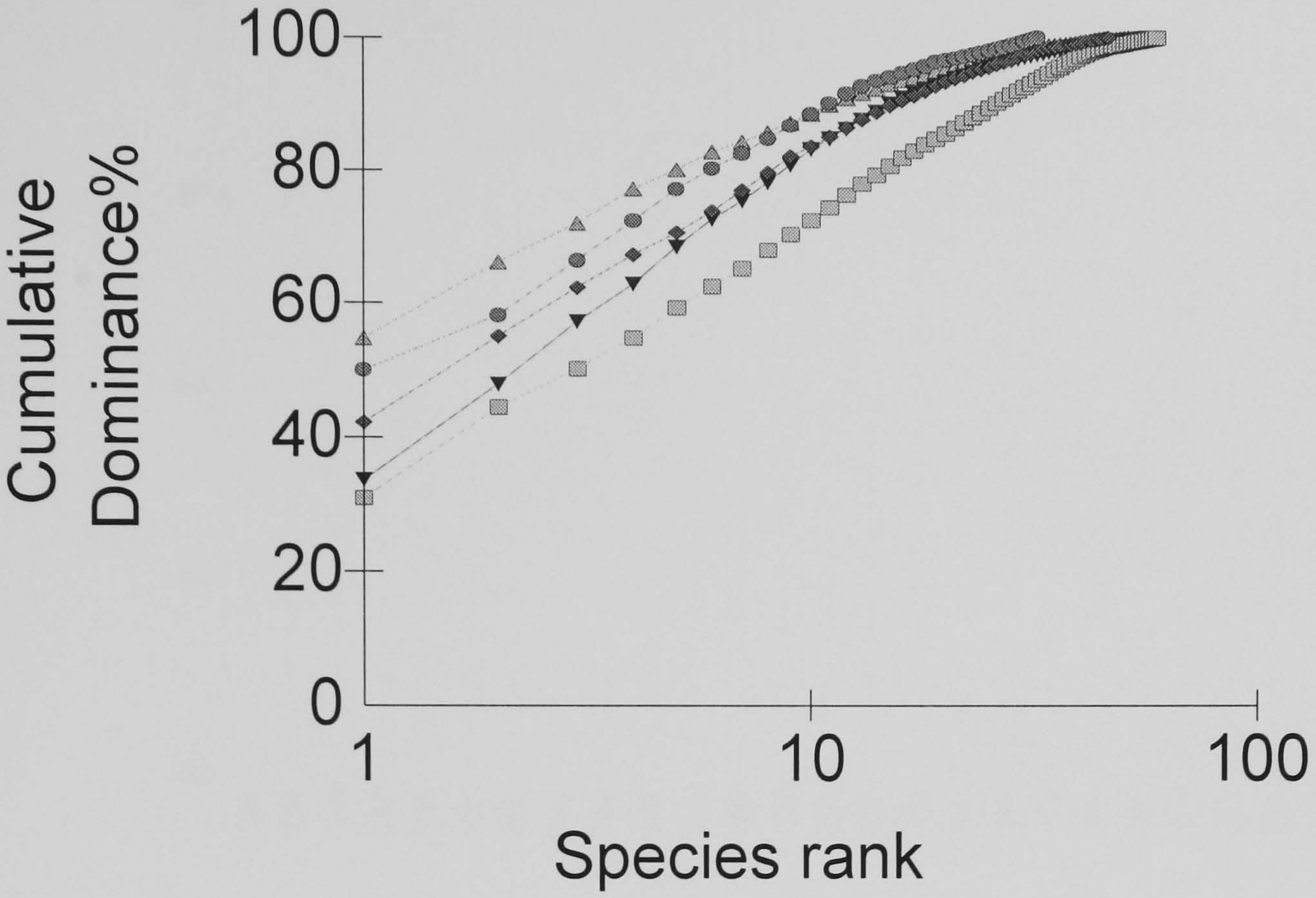


Figure 2. k-dominance curve of species rank against cumulaitve dominance for five shores in the U.K. and Ireland. ▲ = Cemlyn, ▼ = Kilkee, ▨ = Doonbeg, ♦ = Robin Hood's Bay, ● = Filey Brigg.

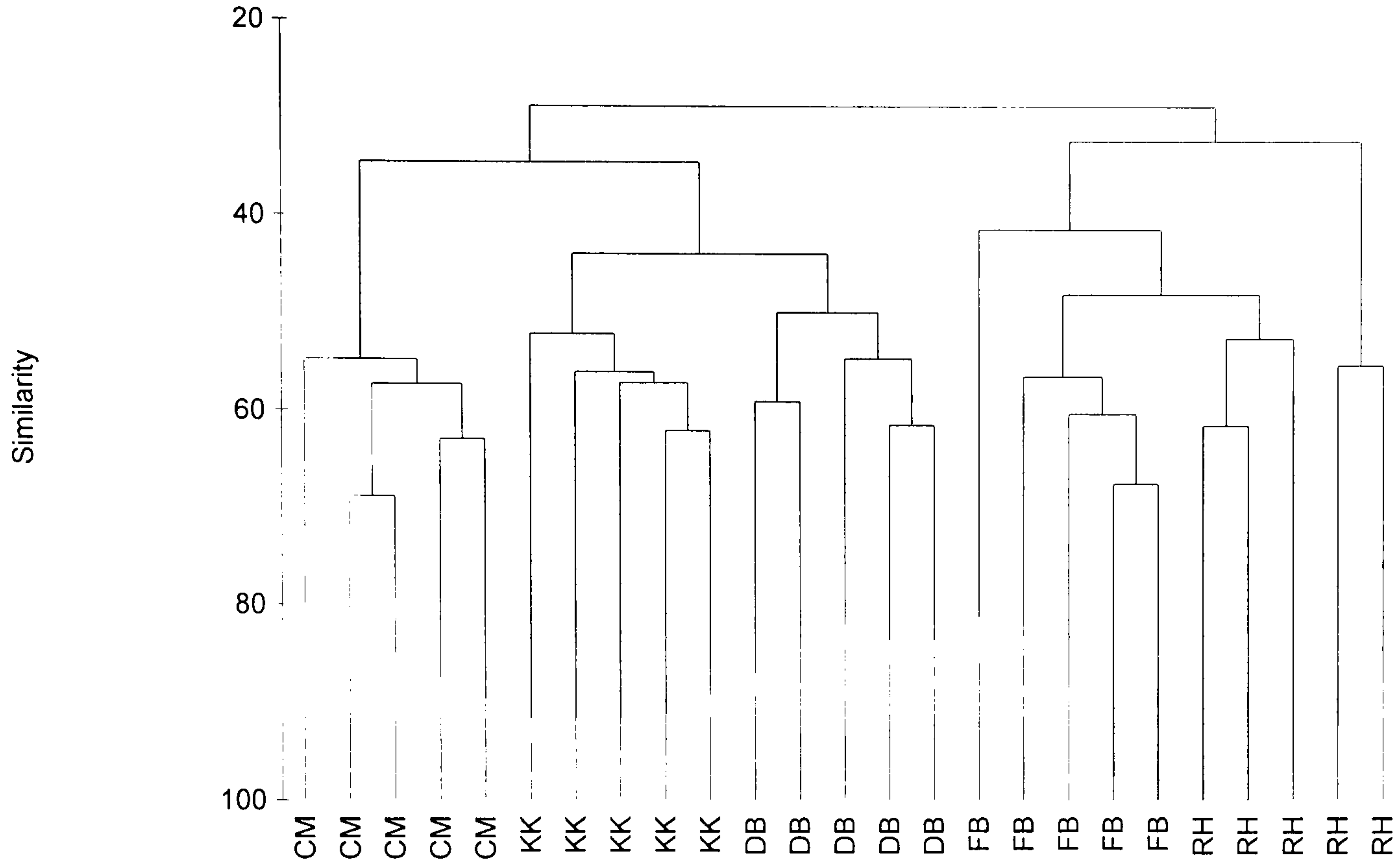


Figure 3. Dendrogram for group average clustering of Bray–Curtis similarities of square root transformed species abundance data from *Corallina officinalis* turf in tide from five shores in th U. K. and Ireland. (CM = Cemlyn, KK = Kilkee, DB = Doonbeg, FB = Filey Brigg, RH = Robin Hood's Bay).

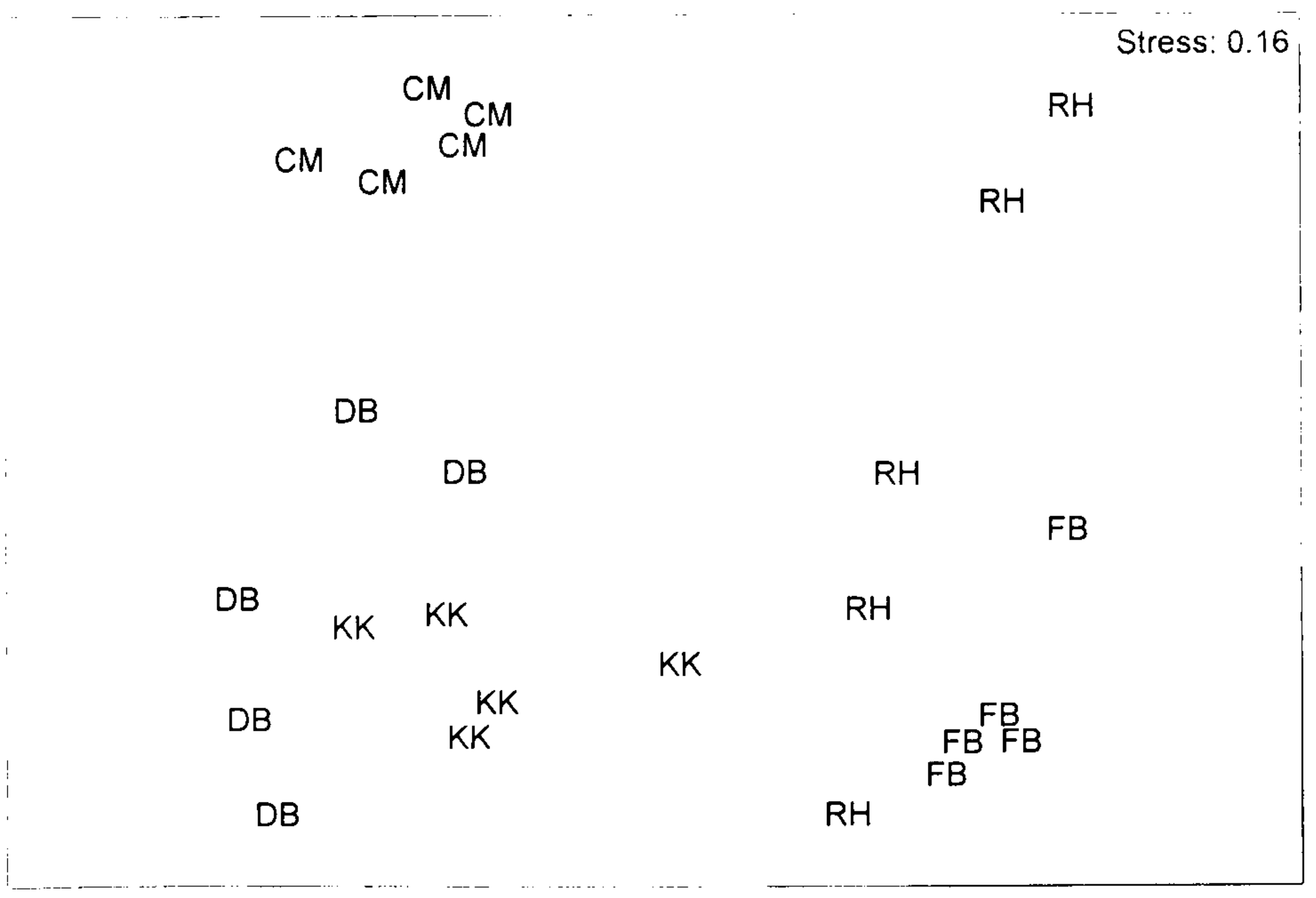


Figure 4. 2-dimensional nMDS ordination on Bray–Curtis similarity of square root transformed species abundance data from *Corallina officinalis* in tide pools from five shores in the UK and Ireland. (CM = Cemlyn, KK = Kilkee, DB = Doonbeg, FB = Filey Brigg, RH = Robin Hood's Bay).

Table 2. Results of pairwise test after ANOSIM on square root transformed species abundance data, all values significant at $p<0.01$. CM = Cemlyn, KK = Kilkee, DB = Doonbeg, RH = Robin Hood's Bay, FB = Filey Brigg.

Pairwise groups	R statistic
CM – KK	1.000
CM – DB	0.872
CM – RH	0.948
CM – FB	1.000
KK – DB	0.852
KK – RH	0.776
KK – FB	0.980
DB – RH	0.900
DB – FB	1.000
RH – FB	0.512

Table 3. Highest contributing species found amongst *Corallina officinalis* to average Bray-Curtis similarity after a square root transformation and average abundance between replicate samples taken from five shores around the UK and Ireland.

Shore	**Species**	**Average abundance 25cm^{-2}**	**Contribution to similarity %**
Cemlyn	*Spirorbis corallinae*	158.4	36.44
	Amphipholis squamata	15.0	9.46
	Musculus discors	32.8	7.37
Filey	*Amphipholis squamata*	35.4	34.67
	Modiolus modiolus	5.8	16.87
	Carcinus maenas	3.4	11.83
Robin Hood's Bay	*Janua pagenstecheri*	68.2	17.72
	Amphipholis squamata	20.8	14.31
	Carcinus maenas	5.2	8.46
Doonbeg	*Amphipholis squamata*	26.0	14.74
	Ampithoe helleri	8.8	7.48
	Spirorbis corallinae	59.2	5.70
Kilkee	*Amphipholis squamata*	103.4	21.49
	Janua pagenstecheri	43.8	14.24
	Spirorbis corallinae	28.6	11.27

Table 4. Similarity percentage analysis of square root transformed species abundance data showing highest percent contribution of species to dissimilarity between pairs of samples. Highlighted species indicates highest abundance found at first quoted shore. CM, Cemlyn; KK, Kilkee; DB, Doonbeg; RH, Robin Hood's Bay; FB, Filey Brigg.

CM+KK	%contribution	CM+DB	% Contribution	CM+RH	% Contribution	CM+FB	% Contribution	KK+DB	% Contribution
Spirorbis corallinae	9.22	*Spirorbis corallinae*	10.67	*Spirorbis corallinae*	13.7	*Spirorbis corallinae*	19.5	*Janua pagenstecheri*	6.71
Amphipholis squamata	7.23	*Musculus discors*	4.40	*Janua pagenstecheri*	7.77	*Musculus discors*	7.02	*Spirorbis corallinae*	6.62
Janua pagenstecheri	5.62	*Onoba semicostata*	3.36	*Musculus discors*	5.41	*Onoba semicostata*	4.29	*Amphipholis squamata*	6.42
Musculus discors	5.00	*Modiolus modiolus*	3.12	*Gammarus finmarchius*	3.65	*Modiolus modiolus*	4.10	*Typosyllis sp.*	3.73
Modiolus modiolus	3.53	*Amphiglena*	3.11	*Onoba semicostata*	3.56	*Amphipholis squamata*	3.86	*Ampithoe helleri*	3.69
Typosyllis sp.	3.31	*Ampithoe helleri*	3.11	Nematodes	3.12	*Convoluta convoluta*	3.70	*Platynereis dumerelli*	3.49
Platynereis dumerelli	3.28	*Convoluta convoluta*	3.06	*Convoluta convoluta*	3.04	Nematodes	3.27		
Coriandria fulgida	3.07								
Average total dissimilarity between sites = 68.26%		Average total dissimilarity between sites =62.68%		Average total dissimilarity between sites = 74.50%		Average total dissimilarity between sites = 74.81%		Average total dissimilarity between sites = 56.15%	

KK+RH	%Contribution	KK+FB	% Contribution	DB+RH	% Contribution	DB+FB	% Contribution	RH+FB	% Contribution
Amphipholis squamata	7.79	*Janua pagenstecheri*	9.15	*Janua pagenstecheri*	7.57	*Spirorbis corallinae*	7.99	*Janua pagenstecheri*	14.72
Janua pagenstecheri	6.44	*Amphipholis squamata*	6.76	*Spirorbis corallinae*	6.10	*Ampithoe helleri*	4.66	*Gammarus finmarchius*	6.41
Platynereis dumerilii	4.42	*Spirorbis corallinae*	6.44	*Ampithoe helleri*	6.51	*Amphiglena*	3.85	*Amphipholis squamata*	5.53
Typosyllis sp.	3.85	*Platynereis dumerilii*	5.01	*Gammarus finmarchius*	3.48	*Onoba semicostata*	3.29	*Lasaea adonsoni*	4.60
Gammarus finmarchius	3.77	*Typosyllis sp.*	4.39	*Amphiglena*	3.12	*Ophelina modesta*	3.19	*Spirorbis corallinae*	4.49
Spirorbis corallinae	3.67	*Coriandria fulgida*	4.19			*Odostomia plicata*	3.00	Ostracods	3.41
Coriandria fulgida	3.57	*Tanais dulongii*	3.33					*Onoba semicostata*	3.31
Nematodes	3.26	Nematodes	3.29					*Polydora caeca*	3.27
Jaera albifrons	3.16	*Jaera albifrons*	3.12					*Jaera albifrons*	3.23
								Nematodes	3.11
Average total dissimilarity between sites = 65.21%		Average total dissimilarity between sites = 68.01%		Average total dissimilarity between sites = 72.83%		Average total dissimilarity between sites = 71.83%		Average total dissimilarity between sites = 61.22%	

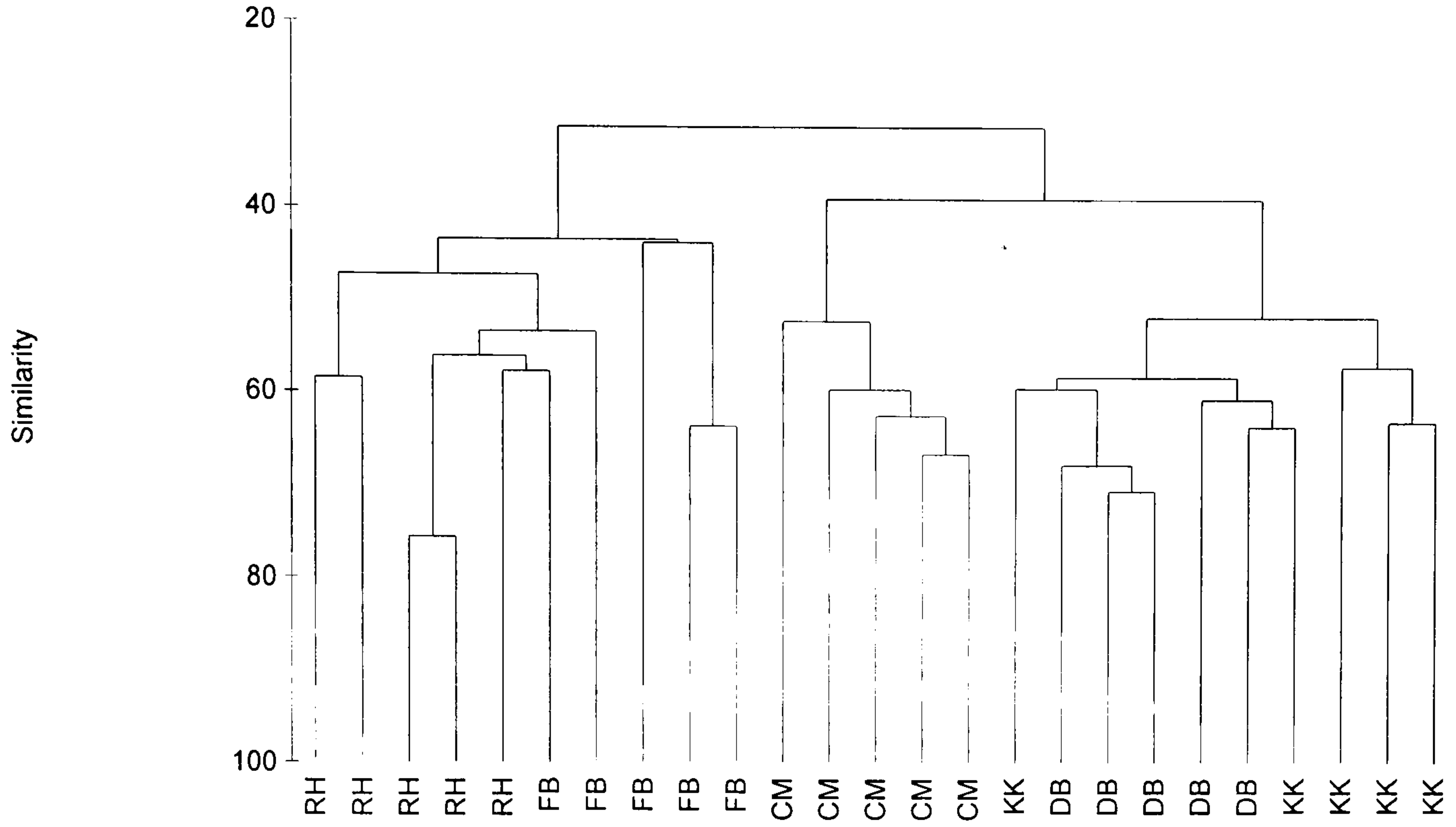


Figure 5. Dendrogram for group average clustering of Bray–Curtis similarities of presence-absence transformed species abundance data from *Corallina officinalis* turf in tide pools from five shores in th U. K. and Ireland. (CM = Cemlyn, KK = Kilkee, DB = Doonbeg, FB = Filey Brigg, RH = Robin Hood's Bay).

Cluster analysis under presence/absence transformation showed a separation of samples on a regional scale, but less so on a local scale (Fig. 5). Ordination by 2D nMDS on the presence/absence transformed data reveals how each region is markedly separated from each other, whereas the separation between shores in the same region breaks down at this level of resolution (Fig. 6). However, a one-way ANOSIM and pairwise comparisons (Table 5) indicated that all shores are again significantly different from each other (Global R=0.867 p<0.001). Similarity percentage analysis revealed the highest average within group similarity was at Doonbeg with the lowest again at Filey Brigg. Under presence/absence transformation more species had higher contributions to similarity within samples than after square root transformation (Table 6). Similarly, there were fewer species contributing to the same levels of dissimilarity between pairs of samples. The highest contributions to dissimilarity generally came from those species that were present in all samples at one site and absent from samples at the compared site (Table 7). The only comparison when this was not the case was between the nearby shores of Robin Hood's Bay and Filey Brigg when *Lasaea adonsoni* was present in every sample at Robin Hood's Bay but only one sample at Filey Brigg. It is clear form these results that *Corallina* turf from different geographic locations in the UK and Ireland supports very different communites and that even on the local scale, especially in terms of those species that dominate the sample, thes communites can be different from shore to shore.

Measured environmental variables showed different degrees of variability and pattern between sites (Fig. 7). All environmental variables were approximately normally distributed. Non homogeneity of variance in the dry weight data was overcome by a $\log_{10}$ (x+1) transformation. When transforming data did not overcome the problem of heterogeneity of variance (as for temperature, CDENS, and number of holdfasts) ANOVA was carried out anyway as there were equal numbers of observations in each sample and care was taken in interpretation of the results (Underwood, 1997). The results of one way ANOVA on the environmental data to test for differences between shore is presented in Table 8. Salinity measures fall in the range 32 to 36 saline, a natural variability that at this scale is unlikely to affect the distributions of the organisms. However, these differences were large enough for the salinty to be significantly greater at Kilkee, Cemlyn and Robin Hood's bay than at Doonbeg and also on the same coast the salinity at Robin Hood's Bay was greater than that measured at Filey Brigg. Patterns of change in pH and temperature seemed to mirror each other (Fig 7 a+b) yet pH was significantly higher at Cemlyn than all other sites and Robin Hood's Bay had significantly lower pH than all other sites. Irish sites and Cemlyn all

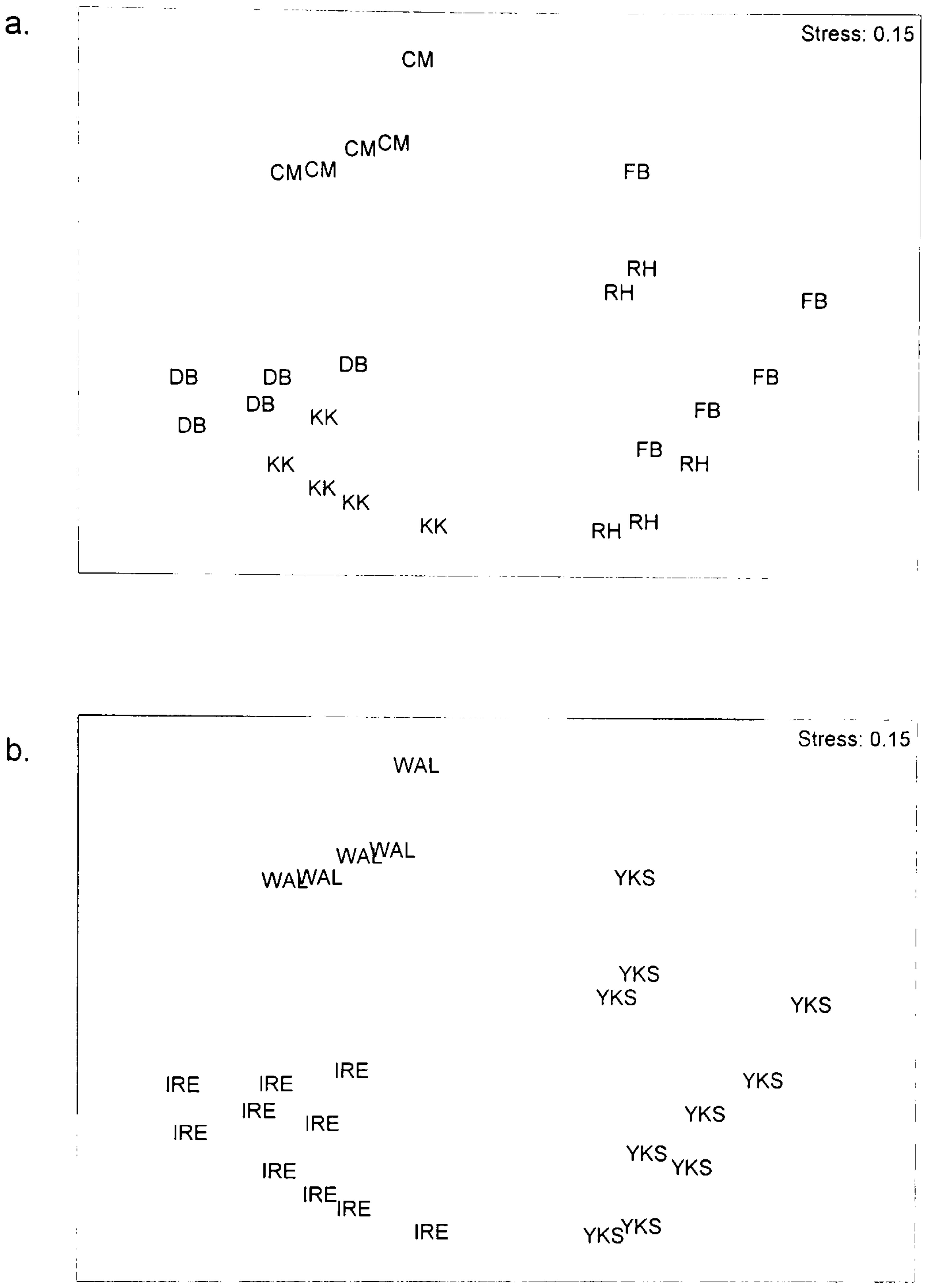


Figure 6a-b. 2-dimensional nMDS ordination on Bray–Curtis similarity of presence/absence transformed species abundance data from *Corallina officinalis* in tide pools from five shores in the UK and Ireland. a) shows each shore separately, (CM = Cemlyn, KK = Kilkee, DB = Doonbeg, FB = Filey Brigg, RH = Robin Hood's Bay). b. shows tha grouping in terms of geographic region (WAL=Wales, IRE=Ireland, YKS=Yorkshire).

Table 5. Results of pairwise test after ANOSIM on presence/absence transformed species abundance data, all values significant at $p<0.01$. CM = Cemlyn, KK = Kilkee, DB = Doonbeg, RH = Robin Hood's Bay, FB = Filey Brigg.

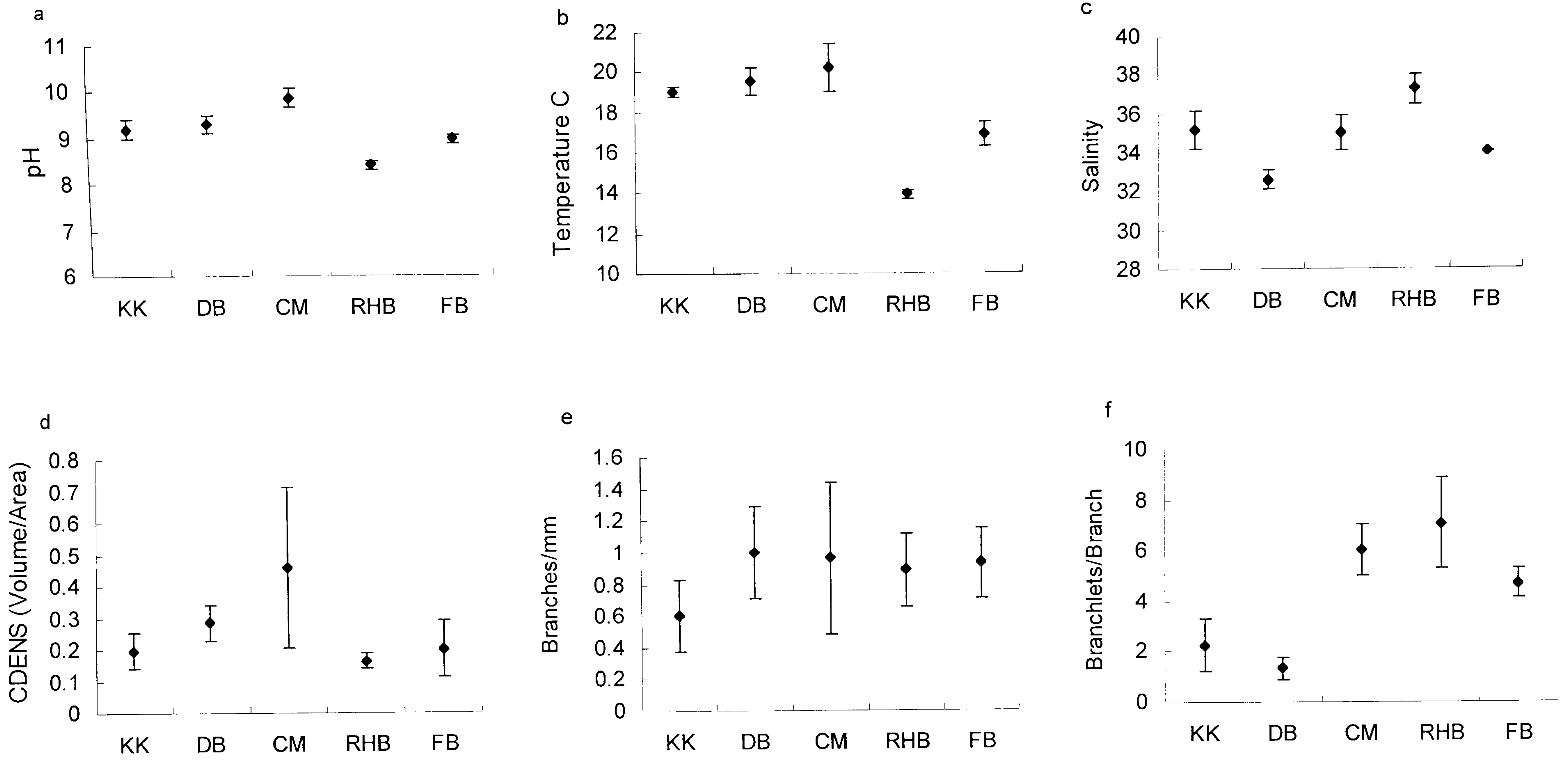
Pairwise groups	R statistic
CM – KK	1.000
CM – DB	0.996
CM – RH	0.984
CM – FB	0.990
KK – DB	0.436
KK – RH	0.976
KK – FB	0.976
DB – RH	0.988
DB – FB	0.996
RH – FB	0.464

Table 6. Highest contributing species found amongst *Corallina officinalis* to average similarity after presence/absence transformation between replicate samples taken from five shores around the British Isles and Ireland

Shore	**Species**	**Average abundance 25 cm^{-2}**	**Contribution to similarity %**
Cemlyn	*Convoluta convoluta*	8.4	7.43
	Carcinus maenas	4.4	7.43
	Harpacticoid copepods	2.0	7.43
	Spirorbis corallinae	158.4	7.43
	Janua pagenstecheri	2.8	7.43
	Amphipholis squamata	15.0	7.43
	Nematodes	7.8	7.43
Filey	*Amphipholis squamata*	35.4	14.64
	Modiolus modiolus	5.8	14.64
	Carcinus maenas	3.4	14.64
Robin Hood's Bay	*Spirorbis corallinae*	20.8	9.02
	Littorina indet.	2.4	9.02
	Amphipholis squamata	20.8	9.02
	Lasaea adonsoni	5.0	9.02
	Carcinus maenas	5.2	9.02
Doonbeg	*Amphipholis squamata*	26.0	5.07
	Nematodes	2.6	5.07
	Asterina gibbosa	1.	5.07
	Micromaldane sp.	1.6	5.07
	Ophelina modesta	4.6	5.07
	Modiolus modiolus	6.0	5.07
	Lasaea adonsoni	3.6	5.07
	Ampithoe helleri	8.8	5.07
	Stenothoe monoculoides	3.8	5.07
Kilkee	*Amphipholis squamata*	103.4	6.35
	Nematodes	8.2	6.35
	Modiolus modiolus	8.6	6.35
	Coriandria fulgida	7.4	6.35
	Onoba semicostata	4.6	6.35
	Janua pagenstecheri	43.8	6.35
	Spirorbis corallinae	28.6	6.35

Table 7. Similarity percentage analysis of square root transformed species abundance data showing highest percent contribution of species to dissimilarity between pairs of samples. Highlighted species indicates highest abundance found at first quoted shore. CM, Cemlyn; KK, Kilkee; DB, Doonbeg; RH, Robin Hood's Bay; FB, Filey Brigg. * = values of similarity only below the arbitrary 3% cut off were found.

CM+KK	%contribution	**CM+DB**	% Contribution	**CM+RH**	% Contribution	**CM+FB**	% Contribution	**KK+DB**	% Contribution
Modiolus modiolus	3.18	*Modiolus modiolus*	3.09	*Harpacticoid Copepods*	3.39	*Convoluta covoluta*	3.98	*Stenothoe monoculoides*	2.99*
Coriandria fulgida	3.18	*Convoluta convoluta*	3.09	*Convoluta covoluta*	3.39	Harpacticoid Copepods	3.98	*Ampithoe helleri*	2.98*
Convoluta convoluta	3.18	*Ophelina modesta*	3.09	Littorinid indet.	3.39	*Musculus discors*	3.98	*Musculus costulatus*	2.31*
						Modiolus modiolus	3.98		
						Platyneris dumerelli	3.20		
						Littorinid indet.	3.18		
						Stenothoe monoculoides	3.16		
Average total dissimilarity between sites = 63.06%		Average total dissimilarity between sites =58.76%		Average total dissimilarity between sites = 68.17%		Average total dissimilarity between sites = 70.45%		Average total dissimilarity between sites = 46.22%	
KK+RH	%Contribution	**KK+FB**	% Contribution	**DB+RH**	% Contribution	**DB+FB**	% Contribution	**RH+FB**	% Contribution
Coriandria fulgida	3.29	*Coriandria fulgida*	3.70	*Asterina gibbossa*	2.73*	*Asterina gibbosa*	3.02	*Lasaea adonsoni*	4.43
Polydora caeca	2.70*	*Rissoella diaphana*	3.05	*Micromaldane sp.*	2.73*	*Micromaldane sp.*	3.02	*Polydora caeca*	4.42
Rissoella diaphana	2.69*	Foraminifera	3.00	*Ophelina modesta*	2.73*	*Ophelina modesta*	3.02	*Gammarus finmarchius*	4.22
		Odostomia plicata	3.00			*Ampithoe helleri*	3.02	*Littorina littorea*	3.69
								Oligochaete	3.61
								Phyllodoce maculata	3.06
								Ostracods	3.04
Average total dissimilarity between sites = 63.93%		Average total dissimilarity between sites = 67.22%		Average total dissimilarity between sites = 69.53%		Average total dissimilarity between sites = 72.83%		Average total dissimilarity between sites = 55.45%	


a
pH
11
10
9
8
7
6
KK
DB
CM
RHB
FB
b
Temperature C
22
20
18
16
14
12
10
KK
DB
CM
RHB
FB
c
Salinity
40
38
36
34
32
30
28
KK
DB
CM
RHB
FB
d
CDENS (Volume/Area)
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
KK
DB
CM
RHB
FB
e
Branches/mm
1.6
1.4
1.2
1
0.8
0.6
0.4
0.2
0
KK
DB
CM
RHB
FB
f
Branchlets/Branch
10
8
6
4
2
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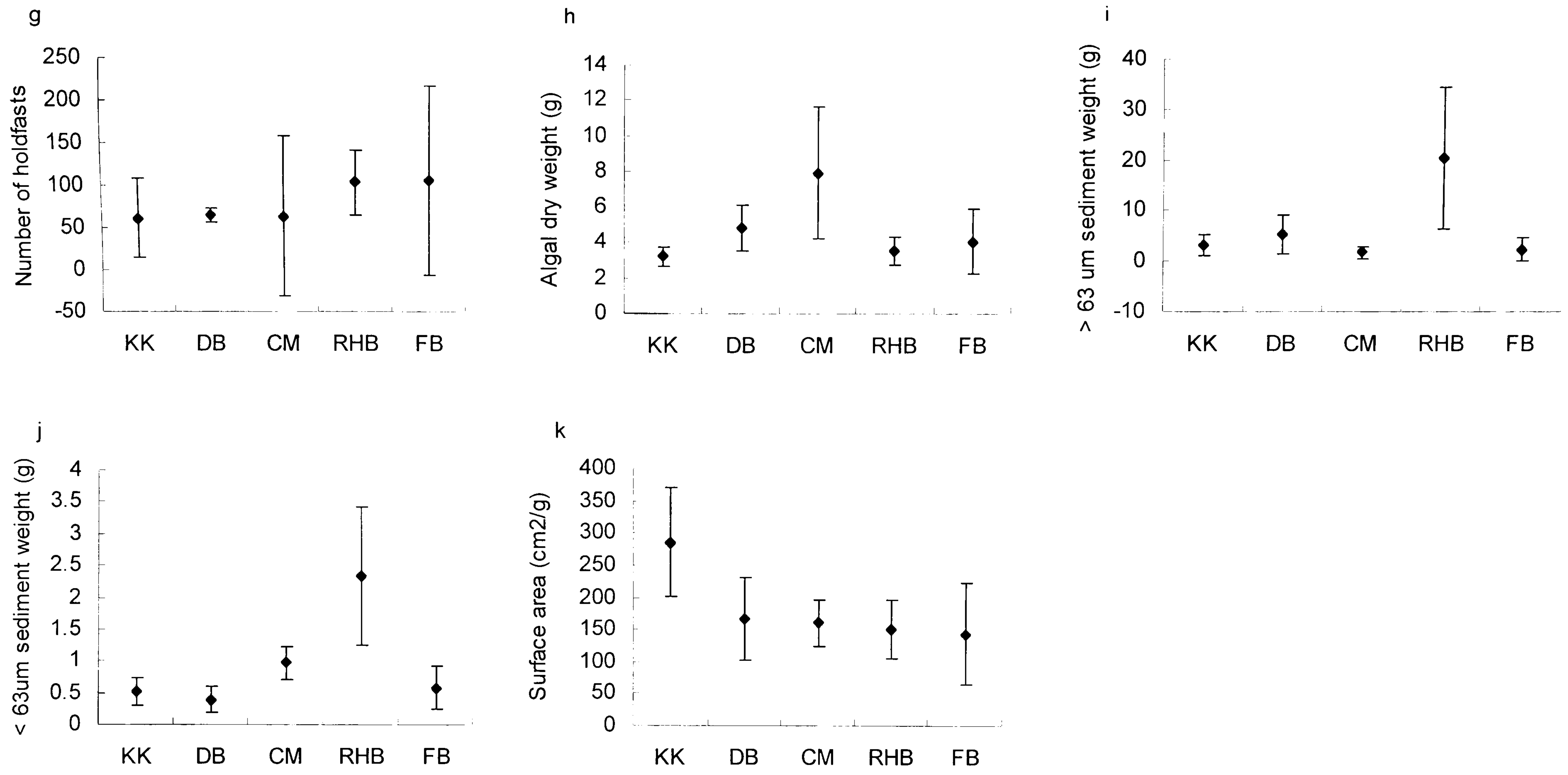


Figure 7 a-k. Mean and 95% confidence intervals for abiotic variables associated with the turf forming algae *Corallina officinalis* in tide pools from five locations around the UK and Ireland. (KK = Kilkee, DB = Doonbeg, CM = Cemlyn, RHB = Robin Hood's Bay, FB = Filey Brigg).

Table 8. Analysis of variance of environmental measures from *Corallina officinalis* habitat from samples collected in tide pools at five different geographical locations. *, $p<0.05$; **,$p<0.01$; ***, $p<0.001$; ns, not significant. CM=Cemlyn, KK=Kilkee, DB=Doonbeg, RHB=Robin Hood's Bay, FB=Filey Brigg. Variables in bold indicate failure to meet assumption of homogeneity of variance. (n=5).

		PH		**Temperature**		Salinity	
Transformation		None		None		None	
	df	MS	F	MS	F	MS	F
Shore	4	1.4188	43.9***	32.487	53.91***	0.14300	22.34***
Residual	20	0.0323		0.603		0.00640	
Tukey's		CM > KK DB FB > RHB		CM KK DB > FB RHB		CM KK RHB > DB + RHB > FB	

		CDENS		Branches		Branchlets	
Transformation		None		None		None	
	df	MS	F	MS	F	MS	F
Depth	4	0.0726	3.62*	0.126	1.08 ns	29.56	20.07***
Residual	20	0.02		0.116		1.47	
Tukey's		CM > RHB				RHB FB CM > DB KK + RHB > FB	

continued:

		Number of holdfasts		Weed weight		Sediment > 63um	
Transformation		Log$_{10}$ (x+1)		Log$_{10}$ (x+1)		Log$_{10}$ (x+1)	
	df	MS	F	MS	F	MS	F
Shore	4	0.578	1.58 ns	0.0679	4.09*	0.5855	8.57***
Residual	20	0.365		0.0166		0.0683	
Tukey's				CM >KK RHB		RHB > CM KK DB FB	

		Sediment < 63um		Surface area	
Transformation		Log$_{10}$ (x+1)		None	
	df	MS	F	MS	F
Shore	4	0.10702	11.35***	17472	3.33*
Residual	20	0.00943		5254	
Tukey's		RHB > CM KK DB FB		KK >FB	

have significantly higher temperature than Filey Brigg and Robin Hood's Bay. Caution must be used when interpreting these differencesas the values obtained rely upon the time of day the pools were sampled but the high F ratio suggests that these are clear differences observed between the sites. The F ratio associated with CDENS is fairly low in comparison. Due to failure of the data to meet the assumptions of analysis of variance caution is implied when stating that Cemlyn has significantly higher density of *Corallina* than Robin Hood's Bay. Other measures of complexity of the alga produced conflicting results. While there was no difference in the number of branches and number of holdfasts, the number of branchlets was significantly higher in non-Irish sites compared to Irish sites. Further there was significantly higher surface area of *Corallina* turf at Kilkee than at Filey Brigg and significantly more sediment at Robin Hood's Bay than elsewhere.

Measured environmental factors were correlated with univariate measures of diversity. Few variables were well correlated with patterns of diversity when considered on an individual shore basis only Hill's N_2 was significantly positively correlated with number of holdfasts at Cemlyn ($r=0.976$ $p<0.01$). When data from all the sites were aggregated there were few more significant correlations. There was significant negative correlation between number of branchlets and Hill's N_1 ($r=-0.522$, $p<0.01$) and Hill's N_2 ($r=-0.508$, $p<0.01$). There was a significant positive correlation between *Corallina* density (CDENS) and Margalef's d ($r=0.545$, $p<0.01$) and number of species ($r=0.575$, $p<0.01$) and also number of species and temperature ($r=0.515$, $p<0.01$) over all shores. These data indicate that there are many complex relationships between the structure of *Corallina* turf and its corresponding invertebrate diversity. For example, one measure of habitat complexity, number of branchlets, is negatively correlated with diversity, while increased *Corallina* density is positively correlated with diversity.

Before using multivariate analyses on the environmental data collected, all dry weights were $\log_{10}(x+1)$ transformed to better approximate multivariate normality as techniques such as PCA and BIOENV work better this way (Clarke & Gorley 2001). Principal Component Analysis was performed on the environmental data (Fig. 8) and the first two principal components capture a relatively low 58.9% (rising to 72.2% with the addition of PC3) of the variability. In very broad terms PC1 represents an axis on which pH temperature, CDENS, and dry weight of *Corallina* are increasing from left to right, while sediment weights tend to decrease from left to right. Principal component 2 is harder to interpret but pH, temperature and surface area will decrease from top to bottom though not on a large scale while all other variables increase in the following

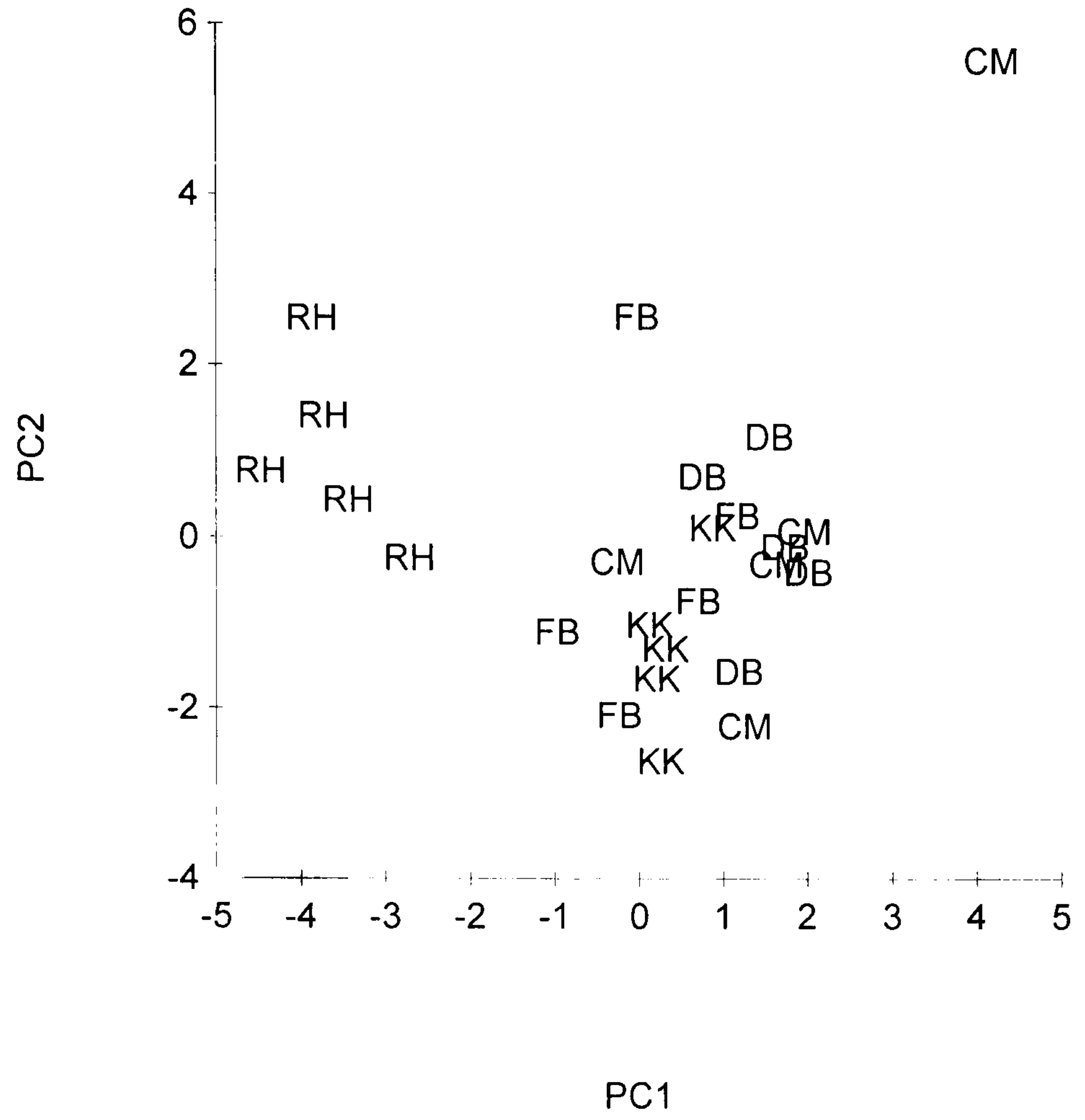


Figure 8. Ordination by PCA based on normalised Euclidean distance of environmental varibles measured in tide pools and associated with *Corallina officinalis* from five shores around the UK and Ireland. (CM = Cemlyn, KK = Kilkee, DB = Doonbeg, FB = Filey Brigg, RH = Robin Hood's Bay).

descending rank order: holdfasts, branches, algae dry weight, CDENS, >63um, <63, branchlets and salinity, which barely features. There is a clear seperation of the samples of Robin Hood's Bay from all others. Also one sample form Cemlyn is wildly separated from all others and this is probably due to a combination of high number of holdfasts and density of *Corallina* which is twice as high as the next value. The result of a one way ANOSIM performed using, normalised Euclidean distance as the similarity measure, indicated significant differences between all shores when comparing the multivariate pattern of the environmental parameters (Global R=0.645 p<0.001).

Matching of multivariate environmental patterns, to multivariate biotic patterns across the five shores was achieved by using the BIOENV routine in PRIMER for square root (Table 9) and presence/absence (Table 10) transformed data. In all cases the highest correlations were produced by matching the physical variable of temperature (which showed large differences between sites regions, (see Fig. 7b) and the measures of habitat complexity like CDENS, dry weight of weed and number of branchlets per branch. These results give an indication of the environmental variables, or combinations of variables, that may have some influence over the observed differences in community pattern.

Aggregation to higher taxonomic groups

As the taxonomic resolution is reduced, the visual representation of the multivariate pattern begins to break up. Boundaries between different shores are less defined on the 2d-nMDS ordination (Fig. 9). The pattern is fairly consistent up to order level and then the samples begin to cluster much more readily with those from different shores rather than those from the same shore. RELATE analysis of subsequent aggregations back to the original square root transformed similarity matrix reveals a trend of weakening correlation, yet the value of rho remains significantly similar to the original similarity matrix, even at the phylum level (Table 11). This suggests that even at the relatively high taxonomic level of phylum, there is still some similarity in pattern to that obtained at the species level. Results of ANOSIM remain consistent up to aggregations at the class level. Only when the data are aggregated into phyla is there a small separation in the results and then only one pairwise test (Doonbeg and Robin Hood's Bay) loses significance (Table 12). However, even at phylum level ANOSIM is able to detect differences when the shores are pooled into the geographic regions of

Table 9. Combinations of environmental variables yielding the best matches of biotic (square root transformed) and abiotic similarity matrices as measured by Spearman rank correlation (rho), bold type indicates overall optimum. See Methods (Chapter 2) for variable abbreviations.

k	Best variable combinations (rho)		
2	°C Brts (0.550)		
3	pH °C Brts (0.572)	°C Cdens Brts (0.567)	PH Cdens Brts (0.550)
4	**pH °C Cdens Brts** **(0.589)**	°C Cdens Brts Holds (0.544)	
5	pH °C Cdens Brts Holds (0.563)	pH °C Cdens Brts <63 (0.554)	

Table 10. Combinations of environmental variables yielding the best matches of biotic (presence/absence transformed) and abiotic similarity matrices as measured by Spearman rank correlation (rho), bold type indicates overall optimum. See Methods (Chapter 2) for variable abbreviations.

k	Best variable combinations (rho)		
1	**°C** **(0.572)**		
2	°C Brts (0.528)	pH °C (0.523)	
3	pH °C Brts (0.535)	°C Cdens Brts (0.490)	
4	pH °C Cdens Brts (0.510)	pH °C Brts Holds (0.493)	pH °C Brts >63 (0.492)
5	pH °C Cdens Brts >63 (0.488)	pH °C Cdens Brts SA (0.487)	

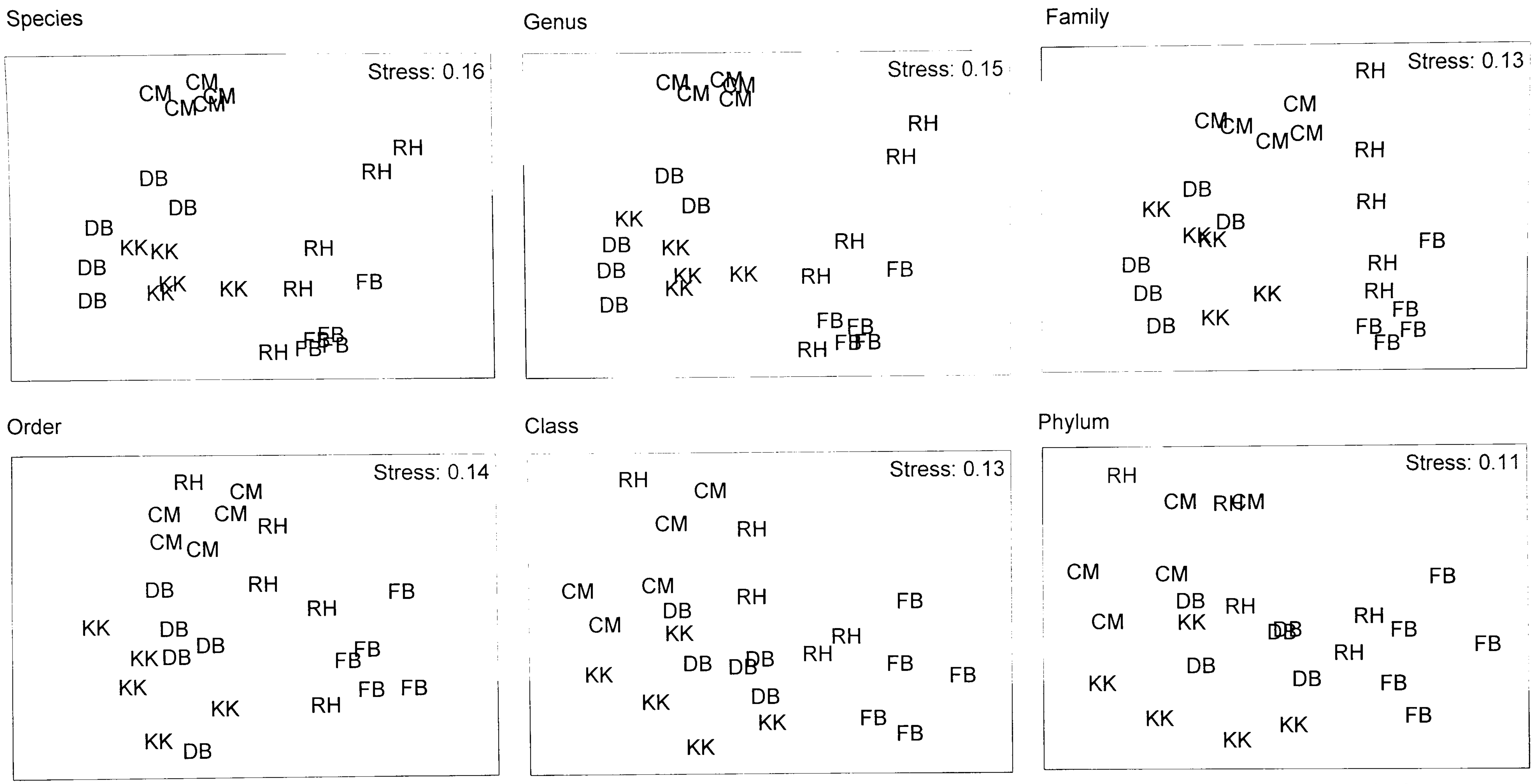


Figure 9. 2-dimensional nMDS ordinations based on Bray-Curtis similarity of species abundance data, aggregated to higher taxonomic levels, from *Corallina officinalis* in tide pools. (CM = Cemlyn, KK = Kilkee, DB = Doonbeg, FB = Filey Brigg, RH = Robin Hood's Bay).

Table 11. Spearman rank correlation coefficients and associated probabilities from RELATE analysis matching square root transformed similarity matrices of species against those aggregated to a higher taxonomic level.

Species v Genus	0.987 $p<0.001$
Species v Family	0.869 $p<0.001$
Species v Order	0.701 $p<0.001$
Species v Class	0.659 $p<0.001$
Species v Phylum	0.586 $p<0.001$

Table 12. ANOSIM R values generated from a one way test of differences between shores. (*=$p<0.05$, **=$p<0.01$)

Comparison	Species	Genus	Family	Order	Class	Phylum
Global R	0.881**	0.876**	0.884**	0.801**	0.625**	0.556**
CM : KK	1.000**	1.000**	0.972**	0.936**	0.536**	0.527**
CM : DB	0.872**	0.896**	0.876**	0.844**	0.632**	0.600**
CM : RH	0.948**	0.920**	0.788**	0.428**	0.500**	0.344*
CM : FB	1.000**	1.000**	1.000**	1.000**	1.000**	1.000**
KK : DB	0.852**	0.872**	0.720**	0.612**	0.344*	0.328*
KK : RH	0.776**	0.772**	0.904**	0.852**	0.512**	0.404*
KK : FB	0.980**	0.976**	0.996**	0.972**	0.956**	0.952**
DB : RH	0.900**	0.892**	0.920**	0.708**	0.372*	0.156
DB : FB	1.000**	0.996**	1.000**	1.000**	0.952**	0.916**
RH : FB	0.512**	0.512**	0.664**	0.620**	0.512**	0.364**

Table 13. One way ANOSIM between communites associated with *Corallina* turf aggregated to the major geographic regions (West Ireland, North Wales and East Engalnd) in this study.

Comparison	R - value
Wales : Ireland	0.524**
Wales : Yorkshire	0.507**
Yorkshire : Ireland	0.399**

Ireland, Wales and England (Table 13). It appears that the multivariate pattern of community differences is statistically fairly robust to changes in the taxonomic resolution implemented in identifying the samples.

At higher taxonomic scales the univariate pattern of diversity is also subject to change. The same aggregations were performed and diversity was measured by number of species (or the taxonomic level aggregated to), Pielou's evenness (J'), Hill's N_1 and Hill's N_2. A general decrease in the value of Hill's numbers N_0 (Fig. 10), N_1 (Fig.11)and N_2 (Fig. 12) was evident yet values of evenness remained fairly constant (Fig 13). When aggregated to higher taxonomic levels, results of one way ANOVA remained consistent upto and including family level for Pielou's measure of evenness (Table 14). However, the patterns were variable for Hill's numbers and number of species. Number of species needs to be considered separately because at higher taxonomic levels this is asking a specific question about the organisation of the community. The results are the same for species and genus level but at the family level Cemlyn loses its significance only to regain it at the level of class. Neither of Hill's calculated measures of diversity (N_1 and N_2) retained any level of significance above the level of Order. Below and including this level patterns of significance varied a little but the site with the highest diversity always remained significantly higher than Cemlyn, the site with the lowest diversity (and Filey Brigg for Hill's N_1) (Table 14).

Discussion

Patterns of biodiversity

Corallina officinalis turf in tide pools supports a diverse assemblage of macrofaunal invertebrates around the rocky coast of the Britain and Ireland. Prior to this study, relatively little was known about the biodiversity of macrofauna in coralline turf communities. In this study 107 macrofaunal taxa were identified and these exceeded densities of 200 000 individuals m^{-2}. Given that *Corallina* turf is common in intertidal pools and subtidally around the coasts of Britain and Ireland it is clear that this assemblage makes a large contribution to biodiversity in these habitats. Compared with other studies in northern temperate localities the fauna in coralline turf in this study appears to be relatively rich. Only 34 species were recoreded in the Azores but the fauna did reach densities of over 376, 000 individual $^{m-2}$ (Chapman, 1955). Dommasnes (1969) found some 81 species and higher taxa in *Corallina officinalis* from

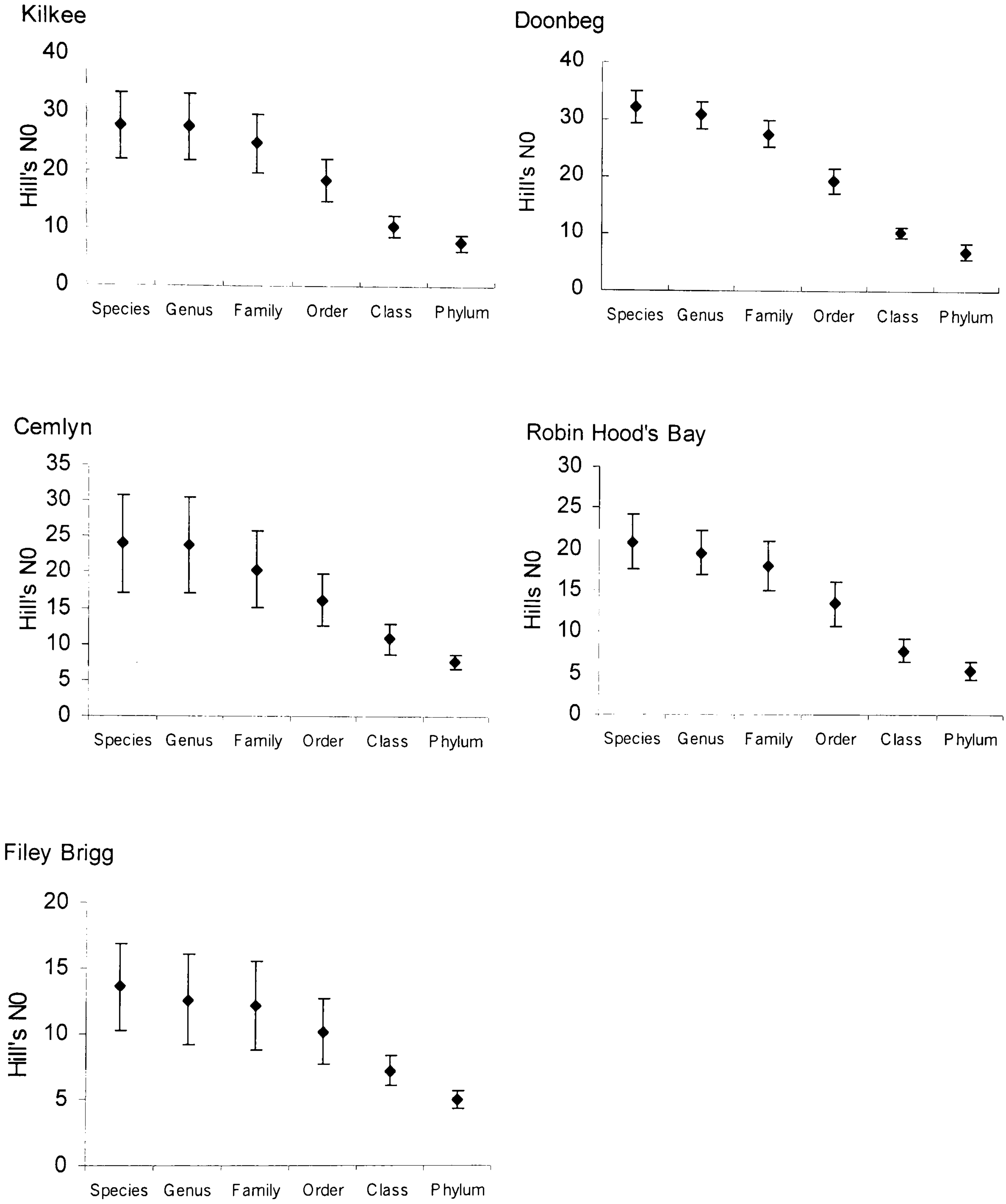


Figure 10. Change in Hill's N0 (number of taxa), calculated fom invertebrates associated with *Corallina officinalis* turf in tide pools, when aggregated to taxonomic levels higher than species from five shores in the UK and Ireland.

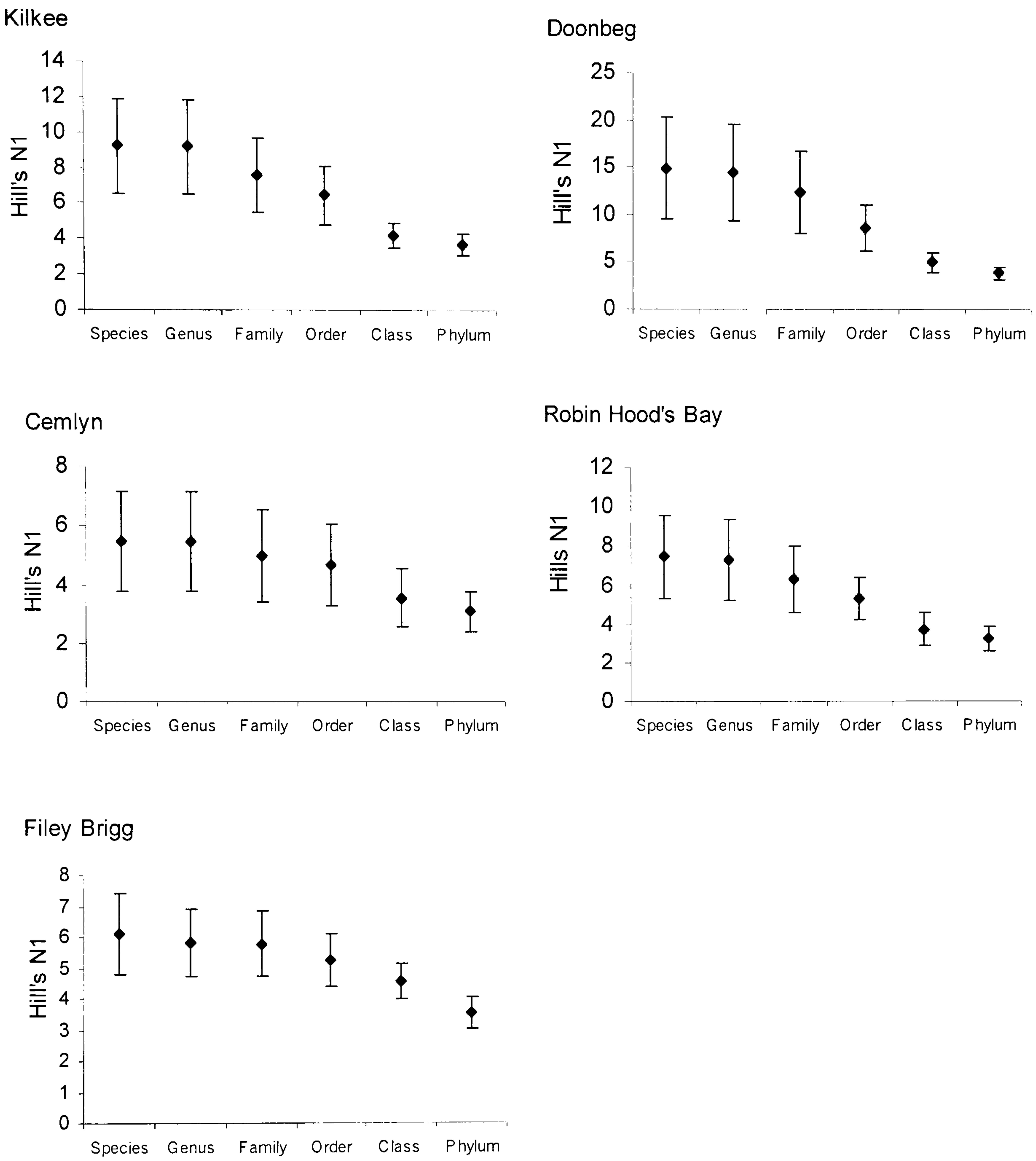


Figure 11 . Change in Hill's N1 (exp H'), calculated fom invertebrates associated with *Corallina officinalis* turf in tide pools, when aggregated to taxonomic levels higher than species, on five shores in the UK and Ireland.

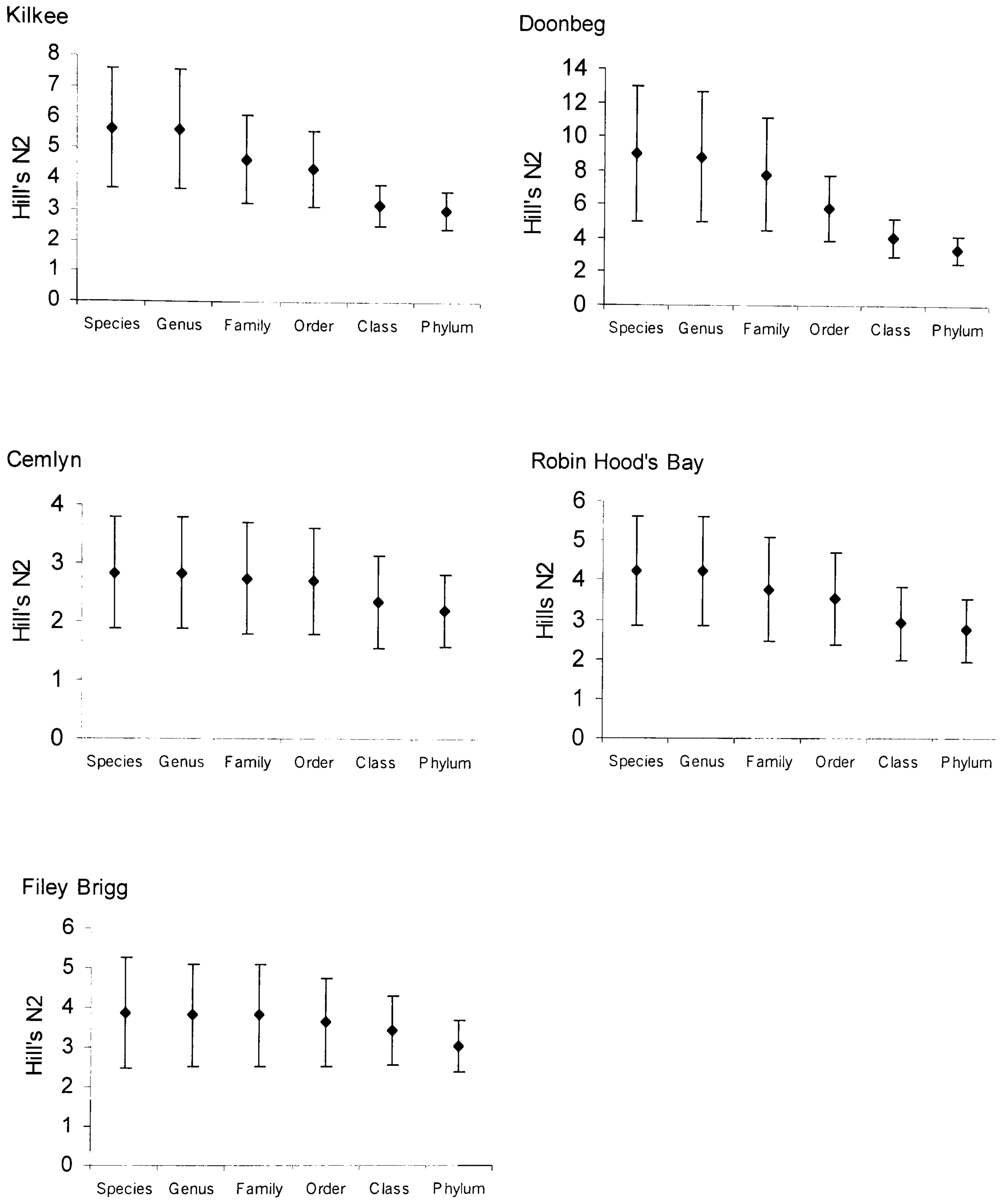


Figure 12 Change in Hill's N2 (1/Simpsons), calculated fom invertebrates associated with *Corallina officinalis* turf in tide pools, when aggregated to taxonomic levels higher than species, on five shores in the UK and Ireland.

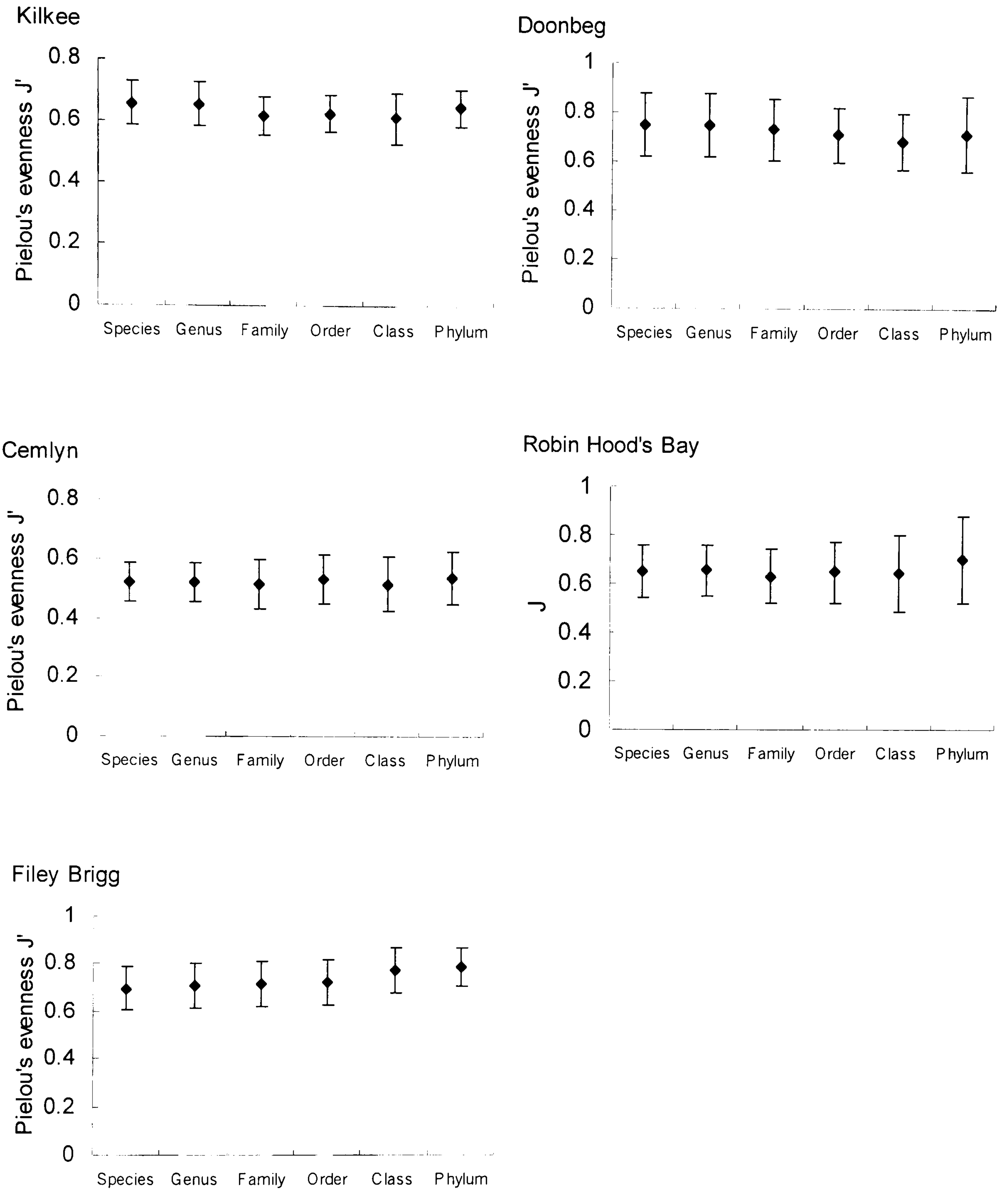


Figure 13. Change in Pielou's evenness (J), calculated fom invertebrates associated with *Corallina officinalis* turf in tide pools, when aggregated to taxonomic levels higher than species, on five shores in the UK and Ireland.

Table 14. F ratios and pairwise differences from one way ANOVA on univariate measures of diversity at increasing scales of taxonomic resolution. *=p<0.05, **=p<0.01, ***=p<0.001

		Species	Genus	Family	Order	Class	Phylum
Evennes	F	3.23*	3.25*	3.12*	2.38	2.83	2.34
		CM<DB	CM<DB	CM<DB	-	-	-
Hill's N0	F	9.14***	10.03***	8.99***	6.47**	4.52**	5.28**
		CM KK DB>FB DB>RHB	CM KK DB>FB DB>RHB	KK DB>FB DB>RHB	KK DB>FB	CM>FB	CM KK>FB CM>RHB
Hill's N1	F	6.39**	4.79**	5.79**	4.01*	1.94	1.24
		DB>CM RHB FB	DB>CM FB	DB>CM RHB FB	DB>CM FB	-	-
Hill's N2	F	3.49*	4.68**	4.34*	3.13*	2.01	1.60
		DB>CM	DB>CM FB RHB	DB>CM FB RHB	DB>CM	-	-

three locations of varying wave exposure in Norway. The sites in this study were comparable in terms of wave exposure and even on the west coast of Ireland where wave exposure was generally higher, pools containing *Corallina* turf tended to be in more sheltered areas of the shore. Previously, 91 species have been recorded amongst *Corallina* turf from several shores on Anglesey in North Wales (Mwaiseje, 1977). For locations ouside of the British Isles, the biodiversity recorded in this study compares well to the 36 taxa found in Chile (Lopez and Stotz, 1997) and 91 taxa in Japan (Akioka *et al.*, 1999). However, more taxa have been recorded from New Zealand, 152 taxa (Hicks, 1971) with up to 250 000 individuals m^{-2} (Brown and Taylor, 1999); and in Australia, 147 taxa (Kelaher *et al.*, 2001).

In terms of multivariate community pattern, clear regional differences were obvious when investigated using species abundance and presence/absence information. Many of these differences can be accounted for by variation in relaitvely few abundant taxa. Of these taxa, the small sedentary polychaete, *Spirorbis corallinae*, made the largest contributions to dissimilarity between shores. This was not unexpected as *S. corallinae* is common, highly abundant and is almost exclusively found on the fronds of *C. officinalis* (De Silva, 1962; De Silva and Knight-Jones, 1962). Other than *S. corallinae*, *Janua pagenstecheri,* another sedentary spirorbid polychaete, and the echinoderm, *Amphipholis squamata,* were also good discriminators between sites. Again these two species occurred in higher densities than most other species collected in the samples and variations in their abundance resulted in differences between samples. Removal of abundance via presence/absence transformation reveals a somewhat different picture. Differences in communities are caused by species that are present at one site, but absent or nearly so from another. These types of species have in the past been referred to as 'transient' species (Seed and Brotohadikusumo, 1994) and their absence from one site could reflect differences in their geographical range or responses to different environmental conditions at that site. Therefore differences in community are attributed to large differences in abundances of species between sites, or the occurrence of transient species between sites.

Discernible patterns of diversity were variable despite clear differences demonstrated between all shores in multivariate community composition but with variable differences detected using univariate measures of diversity and a consistent clear pattern was not found. For example, dominance curves suggest that Doonbeg has the highest diversity while the adjacent site of Kilkee has the lowest. However, Hill's numbers suggest that Kilkee is the second most diverse site after Doonbeg. Measures of dissimilarity between sites from similarity percentage analysis showed a similar confusing pattern with samples from Filey Brigg being more similar to samples in Kilkee than samples in the geographically closer site of Cemlyn. It is a commonly held assumption that samples closer together in space should be more similar than those further apart, due to responses of organisms to patchy habitats and other organisms (Underwood and Chapman, 1996). The absence of such a clear pattern in this instance indicates no common process is responsible for influencing the patterns of diversity in macroinvertebrates at the regional scales measured. Hence, local smaller scale processes are important for structuring some aspects of the macrofaunal assemblage along with broader regional influences.

It is not possible to determine specific factors responsible for changes in community pattern in this study as the data are essentially descriptive. Nevertheless, correlations between environmental variables and macrofauna may provide indications of their importance and have implications for future research.

Sea and air temperature variation is thought to be the most important abiotic determinant on marine community composition at larger scales (Southward *et al.*, 1995; Engle and Summers, 1999). Many authors have shown that changes in temperature can have a marked effect on the distribution of organisms within a community (e.g. Johnson and Scheibling 1987). Gunnill (1983) found that seasonal variations in the fauna of *Pelvetia fastigiata* coincided with variations of water temperature and low water temperatures have been related to low densities of animals on large subtidal algae (Hagerman, 1966). The primary influence of temperature on marine biota is through its constraints on metabolic rates, as almost all marine invertebrates are poikilotherms (Zacharias and Roff, 2001). Underwood (1979) concluded that the temperature regime of an area can affect distributions of species since it can affect gametogenesis, spawning and larval survival such that species have geographical boundaries. In this study multivariate analysis identified water temperature at time of sampling as being a good discriminator of community pattern both when species abundances were included and when purely using presence/absence of species. Temperature was also positively correlated with the number of species at the regional scale (across all sites). Fewer species were recorded from the cooler tide pools of the North Sea (average temperatures in pool 15.4°C) than from tide pools in the Irish Sea (20.96°C) or on the west coast of Ireland (19.24°C). While these temperatures were recorded at the time of sampling it follows that also the historic summer and winter average sea surface temperatures are higher on western coasts than in the North Sea (Anonymous, 1962). In the summer, average sea surface temeratures reach 13.5°C in the North Sea and are slightly higher 14.5°C and 15°C on Irish and Welsh coasts respectively. In the winter the temperature differences are much greater falling to 5.5°C in the North Sea but holding at 7°C and 9.5°C on Welsh and Irish sites respectively. This could be a direct effect of cooler temperatures limiting the survival of species or some other factor could be influenced by temperature and itself correlated with it. In the English Channel the northern limit of certain warmer water species is reached as is the southern limit of many Arctic/Boreal species (Lewis, 1964). In this region there is a particularly well pronounced biogeographical boundary (Southward *et al.*, 1995). This may prevent some of the invertebrates associated with *C.officinalis* on western shores warmed by the Gulf Stream from inhabiting the cooler waters of the North Sea due to their thermal tolerances being reached. There is some evidence of this effect in the results found here as most of the species identified as being good discriminators between Irish and North Sea sites have a limited distribution and have never been recorded from the North Sea (see Table 8), for example the gastropods *Coriandria fulgida* and *Rissoella diaphana,* the echinoderm *Asterina gibbosa* and the polychaete *Micromaldane ornithochaeta* (Hayward and Ryland, 1995).

Another influence on this type of geographical isolation could also be the role of larval supply and survival. As noted above, temperature can influence marine larval life histories directly and this may be also evident in the observed pattern. For example, Southward and Crisp (1954) noted the importance in both geographic distributions and relative abundance of barnacles in response to warm and cold annual temperatures. The recruitment of species with larvae that spend considerable time in the plankton will depend on the hydrodynamic regime and variations in larval food supply (Raffaelli and Hawkins, 1999 see below). Thus, chance events offshore are likely to influence new recruits into a population emphasising the importance of chance or stochastic events. Variations in recruitment have long been acknowledged (Brosnan, 1992) and in the last two decades there have been experimental studies into variations of recruitment and its implications for community structure (Denley and Underwood, 1979; Gaines *et al.*, 1985; Gaines and Roughgarden, 1985). Variation in recruitment can also help initiate events, for example species that are keystone in a community will have a marked effect on the other species present and their absence due to unpredictable larval supply will show a large departure in community composition than the simple removal of one species. Various stimuli are thought to control the control the settlement of marine larvae and these have been outlined by Underwood (1979). Random settlement and subsequent mortality may be responsible for variations in community structure at a large scale with the increased likelihood of stochastic events influencing settlement patterns. Responses of larvae to chemical and biological cues, and species that do not produce pelagic larvae, are more likely to influence community structure on a smaller scale. For example, the spirorbid tubeworm, *Spirorbis corallinae,* has been identified as a good discriminator between sites at the regional scale examined, mainly due to large differences in abundance between sites. The reproductive strategy of this polychaete is to brood its larvae which, upon release, will seek out a suitable substratum on which to settle. As *S. corallinae* is almost exclusively found on *Corallina officinalis* its release into a tide pool that is dominated by the preferred substratum will restrict the wider range dispersal beyond the pool, especially if larval release is timed to coincide with low tide. While there is no evidence of this, the larvae of *S. corallinae* are more abundant on neap tides (De Silva, 1962) and are not released in respose to light (Jones, 1966). Any area with an already large population of *S.corallinae* could result in large increases in its abundance at times of larval release. Subsequently, a shore with low numbers or no *S. corallinae* adults is unlikely to receive large larval inputs from other shores due to the low dispersal range. Hence any original differences in *S. corallinae* abundance become exaggerated with each subsequent period of recruitment, at least until space becomes limiting on shores with high abundance. This source of variation will implement itself on a scale of the individual pool, as well as in wide spread geographical population differences. The methods of development and reproduction employed by those species that best discriminate the differences between groups in this study are interesting in their implications for wider range dispersal. Half of the species produce young via some method of direct development without a pelagic larval stage (Table 15). Of those that do produce larval stages some have larvae which spend little time in the plankton (see for example the gastropod, *Coriandria fuldiga* (Graham, 1971)) and are unlikely to undergo large-scale regional dispersal (Table 15). These patterns in life histories may represent a response to high levels of predation or as a consequence of the need to be small in the tide pool environment (Emson, 1985).

Community patterns may also be influenced by variation in offshore currents and wind conditions affecting those species dispersed by a pelagic larva on the regional scale (Menge *et al.*, 1997). Karlson and Cornell (1998) concluded that local richness patterns appear to be strongly influenced by transport processes governing recruitment from local and regional species pools along with other effects of geography, climate and history of the region. The North Sea is somewhat separated from western shores

Table 15. Reproductive strategies of those species identified by multivariate analysis as being important in generating differences in community structure between shores.

Species	Reproductive Strategy	Reference
Foraminifera	Limited dispersal of gamonts	Murray (1979)
Convoluta convoluta	Probably larval	Ball & Reynoldson (1981)
Nematoda	Direct development	Warwick *et al.* (1998)
Polydora caeca	Planktotrophic larvae	www.marlin.ac.uk
Spirorbis corallinae	Larval, low dispersal	Gee (1963)
Janua pagenstecheri	Larval, low dispersal	Pers. obs.
Amphigelna mediterranea	Direct development	?
Typosyllis sp.	?	?
Platyneris dumerilii	Direct development	Pers. obs.
Ophelina modesta	?	?
Micromaldane ornithochaeta	?	?
Phyllodoce sp.	Planktotrophic larvae	Pleijel & Dales (1991)
Oligochaetes	Direct development, egg capsule	Brinkhurst (1982)
Harpacticoida	Direct benthic development	Huys *et al.* (1996)
Ostracoda	Direct development from eggs	Athersuch *et al.* (1989)
Gammarus finmarchicus	Direct development (Broods)	Reid (1944)
Ampithoe helleri	Direct development (Broods)	Reid (1944)
Stenothoe monoculoides	Direct development (Broods)	Reid (1944)
Jaera albifrons	Marsupial development	Naylor (1972)
Tanais dulongii	Marsupial development	Holdich & Jones (1983)
Onoba semicostata	Veliger larvae	Graham (1971)
Littorina sp.	Oviparous, planktotrophic	Graham (1971)
Coriandria fulgida	Suppressed larval stage	Graham (1971)
Rissoella diaphana	No free larvae	Graham (1971)
Odostomia plicata	Largely unknown	Graham (1971)
Lasaea adonsoni	Direct development, gregarious	Mackie (1984)
Modiolus modiolus	Direct development	Tyler-Walters (2001a)
Musculus discors	Direct development	Tyler-Walters (2001b)
Amphipholis squamata	Viviparous	Mortensen (1927)
Asterina gibbosa	Direct development	Mortensen (1927)

of the British Isles. The main oceanic current influencing the east coast is derived from a winter inflow from the North Atlantic current via the Faroe/Shetland channel (Anonymous, 1981). Also, a front occurs around Flamborough Head just south of the sites sampled in this study (Said, 1990). This front represents an important combination of physical, chemical and biological boundaries which will influence the fauna found there in relation to different geographical areas. Also, recent studies suggest that links between nearshore nutrients and benthic ecosystems can influence community structure with a positive correlation shown for nutrients, microalgal productivity and invertebrate grazer abundances (Bustamante *et al.,* 1995). More phytoplankton means more food for filter feeders and thus faster growth (Bustamante *et al.*, 1995) and high phytoplankton concentrations could increase recruitment by increasing survival of herbivorous larvae (Menge *et al.*, 1997).

Environmental factors such as the amount and availability of sediment (Whorff *et al.*, 1995), availability and structure of habitat (Hicks, 1980; Stoner and Lewis, 1985) and species interactions are also likely to influence the diversity and abundance of species in an assemblage. Of the environmental variables measured in this study, *Corallina* density (CDENS) was positively correlated with number of species and Margalef's diversity. Conversely, the number of branchlets was negatively correlated with Hill's N_1 and Hill's N_2. Both these variables are measures of habitat complexity. It is generally considered that increase in habitat complexity leads to an increase in diversity (Hicks, 1980, 1985; Jarvis and Seed, 1996). The results here therefore conflict with each other in that one measure of habitat complexity appears to increase diversity while another appears to decrease diversity. Of similar importance is the lack of correlation with other parameters of the habitat such as the number of holdfasts, which are important for the attachment of tube-dwelling species, surface area that signifies area for attachment, and sediment weight. A lack of significant correlation with surface area of the algae indicates that the numbers of attached invertebrates present in the habitat was not optimal and that competition for substrate space is unlikely to be a structuring factor at least in regard to that component of the fauna. The same can be implied for infaunal or deposit feeding species due to a lack of correlation of diversity with sediment weight. It must be noted that these values were based on calculations of diversity from the entire habitat. If each portion of the habitat were to be studied separately, i.e. attached fauna, infauna and mobile fauna then the results may well have been different. Such an approach was beyond the scope of this study, which is concerned with general large-scale patterns of biodiversity.

These results draw interesting comparisons from other studies of biologically generated habitat when increasing habitat complexity increased species diversity (Gee and Warwick, 1994; Thompson *et al.*, 1996; Beck, 2000). The lack of any overriding discernible pattern implies that other environmental parameters and biological processes may act on community structure other than the role of habitat complexity (Kelaher *et al.*, 2001) or that increasing compllexity of habitat actually reduces the intersticial space in which the fauna can inhabit (Kelaher, 2003c). This argument is further compounded when the environmental variables that best describe the multivariate pattern are considered. Again *Corallina* density and branchlets, together with pH and temperature, best match the species pattern, indicating that a combination of factors acting alongside one another could be responsible for the observed species distribution. When species abundance is removed, however, the pattern of temperature alone has the best match to the multivariate pattern, indicating that this variable as discussed above may have the greatest influence on species diversity patterns.

Other factors that control diversity at a fine scale but may vary in intensity at larger scales are, that of species interactions and modifications of habitat. These factors can include ecological processes such as predation and competition (Menge and Sutherland, 1976; Russ, 1980; Barkai and Branch, 1988) although the effects of these interactions are not discernible in the present study. The presence of one species can also modify the habitat in such a way as to influence diversity. The dominant species in this study, *S. corallinae,* appears to have a major influence on the associated fauna of *Corallina* by an increased abundance leading to increased habitat complexity (Crisp and Mwaiseje, 1989). The effect of increasing numbers of *S. corallinae* on community structure was not tested here but could potentially be treated as an environmental variable in future studies in the same way as other measures of habitat complexity. It is interesting to note, however, that the dominance of a filter-feeding species in the upper levels of the turf matrix may not only reduce the amount of sediment reaching the bottom levels of the turf matrix, but also the numbers of spores and larvae of other species, preventing their recruitment to the habitat. This would be an interesting focus for future study.

Aggregation to higher taxonomic groups

The multivariate pattern of community data over regional scales remains reasonably consistent even when aggregated to the level of phylum. There is a gradual breakdown in the observed visual patterns in the dendrograms and nMDS plots but the results of statistical tests remain the same to the Ordinal level.

Evidence of the breakdown in multivariate pattern is shown by the trend of weakening correlation of the similarity matrices at higher taxonomic levels back to the original similarity matrix based on species level data. The taxonomic resolution of family is a reasonably obtainable one for inexperienced of taxonomists. This is often the best achievable definition if studies are to be done in areas with which the worker is unfamiliar or in areas where the fauna is poorly described and adequate taxonomic keys are not available. Identifying macrofaunal samples to families also reduces the amount of time required for sorting allowing a larger number of samples to be processed than if a lower taxonomic resolution is used.

The multivariate pattern for the family level in this study has a high correlation with that at the species level and the dendrogram and nMDS plots show similar patterns of clustering. R-values generated by ANOSIM tests retain the same level of significance and are close to those generated by the species level tests. Univariate measures of diversity show justification for choosing the level of family as a suitable resolution for community studies. All measures of diversity retained significance at this level although there was some variation in the results and therefore the conclusions reached.

In wide ranging regional studies where identification to family level is used, particular care must be made when interpreting the results (Wright *et al.*, 1995; Warwick, 1988b). Univariate measures of diversity used in assessing pollution levels have shown a similar breakdown in reliability above the level of family aggregations (Warwick, 1988a, b). Equally these studies demonstrated that aggregating to higher taxonomic levels even phyla, might actually produce better results using multivariate techniques (Warwick, 1988b). Similar patterns have been shown in freshwater streams in response to effluent input (Wright *et al.*, 1995). This approach can be considered particularly useful when planning experiments and carrying out pilot studies to prepare the design of cost-effective sampling programmes for subsequent larger investigations (James *et al.*, 1995) and may be more accurate when the fauna of a region is not well known and distinguishing species may be difficult (Ellis, 1985). Caution must be used though, as aggregating to higher taxonomic levels can seriously affect interpretation of other factors of community organisation such as food webs (Thompson and Townsend, 2000). In 41 rivers around the U. K., Furse *et al.* (1984) found that classification of unpolluted streams is best done at the species level due to higher measures of beta diversity and the importance of individual environmental requirements for single species which is lost when communities are catalogued at higher taxonomic levels.

Other studies have attempted to correlate species diversity with diversity at higher levels when selecting areas for conservation (Vanderklift *et al.*, 1998). The potential for using higher taxonomic groups as indicators for special areas of conservation has attracted some scrutiny in terrestrial conservation biology. Williams and Gaston (1994) found that the spatial pattern of family richness correlated well with that of species richness for several groups of taxa. However, Prance (1994) found that centres of high species diversity in the neotropics were not reflected in family level data and suggested the focus should remain at species level for conservation planning. Marine areas using derived assemblages at the genus or family level have been shown to contain a similar number of species to areas selected on the basis of species level assemblages for several biotic groups (Vanderklift *et al.*, 1998). As with the data presented here, the use of Class level resulted in a very poor representation of species (Vanderklift *et al.*, 1998).

Chapter 4

Small-scale spatial patterns of community change in the fauna of *Corallina officinalis* with tide pool size, depth and tidal height

ABSTRACT

Ecological studies of diversity at different scales are important for our understanding of community processes. Here the changes in the fauna associated with the turf-forming red alga, *Corallina officinalis*, at small spatial scales are presented. Sampling was done at different depths in tide pools and between tide pools of different size and at different heights on the shore where there was a continous cover of turf. In order to investigate the consistency of changes at these small spatial scales, sampling was carried out on two shores and at two different times (summer and winter). More species were found at shallow depth in tide pools in winter but not in summer. The community structure was, however, significantly different at shallow depths at all times of sampling. Significant differences in measures of diversity are also shown between pools of different size and at different heights on the shore although these differences were variable depending on the shore or time of sampling. Patterns in community structure at these scales differed markedly between different shore height, but less so between pools of different size. Environmental data collected alongside the biological data was a poor discriminator of diversity and community patterns at the scales measured except for between height on the shore. The main factors contributing to patterns of biodiversity in this study appear to represent a complex suite of parameters that interact with each other producing variable results. For example, differences in patch size bring about differences in physical parameters, which in turn influence the structure and nature of the biologically generated habitat. This study demonstrates the need for well-structured manipulative field experiments to elucidate the main factors responsible for structuring community assemblages in tide pools at small spatial scales.

Introduction

Studies of patterns of community change at small spatial scales are common in ecological literature for terrestrial (Botkin, 1990), freshwater (Hildrew and Giller, 1994) and marine (Archambault and Bourget, 1996; Underwood and Chapman, 1996, 1998; Coleman, 2002) communities (and see Begon *et al.*, 1990 for overview). Ecological studies of diversity at different scales are important for our understanding of community processes (Underwood *et al.*, 2000) and understanding these scales is a conceptual problem in ecology (Levin, 1992). Descriptive studies of species patterns is an important starting point from which other models and hypotheses arise (Underwood *et al.*, 2000).

There have been many studies describing the occurrence and abundance of marine organisms in the intertidal zone and large-scale changes in community patterns in response to emersion and wave exposure gradients are well documented (Southward, 1958; Lewis, 1964; Connell, 1972; Raffaelli and Hawkins, 1999 for reviews). Most studies of species occurrence have investigated patterns associated with a gradient such as zonation patterns down the shore or horizontal gradients along the shore in response to wave action (Raffaelli and Hawkins, 1999). More recently patterns of species abundance at small scales other than along an obvious environmental gradient have also received much attention (Underwood and Chapman, 1996; Benedetti-Cecchi, 2001). These types of study are important to elucidate patterns of diversity that are not associated with obvious gradients and therefore detect other potentially important sources of variation (Benedetti-Cecchi, 2001). For example, Archamboult & Bourget (1996) demonstrated that on emergent rocky shores, variance in species abundance was due to small-scale substrate heterogeneity whereas much of the variance in species richness occurred at larger scales of kilometres. For this reason there has been increased emphasis on studying community patterns over a range of spatial scales (Thompson *et al.*, 1996; Underwood and Chapman, 1998).

Biologically generated habitats such as mussel beds and algae provide suitable habitats for many marine invertebrate species. Species associations with such habitats have been well studied at many scales of space and time, for example, mussel beds (Seed, 1996), barnacles (de Murguia and Seed, 1987; Thompson *et al.*,

1996) and large foliose algae (Seed and O'Connor, 1981; Johnson and Scheibling, 1987). In contrast, relatively little work has focused on species associated with mat-like or turf-forming algae at small spatial scales (but see Kelaher, 2001). Turf-forming algae are a relatively common habitat around the British coast providing a complex structural habitat and also providing food directly for grazers and indirectly, by the accumulation of sediments, for microalgal grazers and detritivores. Their characteristic compact structure also provides a refuge from predation (Coull and Wells, 1983) and physical stresses like wave exposure (Domasnes, 1968) and desiccation (Gibbons, 1988). Turf-forming algae in tide pools have received even less attention than those on open rock, presumably because of the complexities in design of sampling in this habitat (but see Hull, 1999).

Corallina officinalis is a turf-forming alga that is very common in tide pools around the British coast. Its complex overlying fronds and perennial occurrence encourages the development of a diverse associated fauna. Tide pools have not been as extensively studied as the emergent substrata of rocky shores (Metaxas and Scheibling, 1994). The tide pool environment also has a strong influence on the patterns and processes of the associated assemblage which is strongly influenced by the tidal cycle. The physical and chemical conditions of a tide pool are strongly influenced by its volume, surface area and depth as well its height on the shore, degree of shading, drainage pattern exposure to waves and its biota (Metaxas and Scheibling, 1994).

This chapter involves two experiments that describe the patterns of species abundance in association with different types of tide pool and tests the hypothesis that i) patterns of community organisation vary at different depths within tide pools, i.e. within pool variation, and ii) patterns of community organisation differ significantly between tide pools of different size, and at different heights on the shore, i.e. between pool variation. Some of the environmental variables associated with these habitats and pools are also measured and attempts made to link differences in these to the structure of the community. Finally, because patterns of distribution over small spatial scales are known to vary with the time of sampling and with shores (Underwood and Chapman, 1998) sampling was carried out at two different times on one shore (summer and winter) and at one other time on one other shore.

Methods

Samples of *Corallina* turf and associated infauna were collected on three occasions, at Cemlyn during June 2001 and February 2002, and at Porth Cwyfan during February 2002. Tide pools were sampled in two ways. First, five large tide pools were haphazardly selected on the mid shore. These pools were greater than 5m long and 1m wide and deeper than 30cm. Within these tide pools one sample was randomly collected from depths of 0, 10, 20 and 30cm using the methodology outlined in Chapter 2. Second, small tide pools, i.e. less than 1m long and less than 1m wide with a depth not exceeding 15cm and large pools (as defined aboved) were randomly selected on the mid and low shore. Mid-shore is here defined as being the area on the shore where tide pools begin to contain *Corallina* turf covering greater than 50% of the pool in a continous turf; this area generally coincided with the top of the barnacle zone. Low shore is defined as the area as close to the low water mark as possible at extreme low water of low tides. Five pools of each type were sampled on each occasion (i.e. low shore small pool, low shore large pool, high shore small pool and high shore large pool). Overall, 120 samples were collected, returned to the laboratory, sorted for macrofauna and measured for environmental variables as outlined in Chapter 2.

Results

Variations in community structure in response to changing pool depth

A total of 15 556 individuals encompassing 109 species or higher taxa were counted and identified from different depths in tide pools. The dominant phyla were annelids (31 species), crustaceans (28 species) and molluscs (27 species). Other contributions came from chelicerates (10 species), echinoderms (3 species), chordates (2 species) and one species from each of the following phyla; Porifera, Cnidaria, Protista, Hexapoda, Platyhelminthes, Nemertea, Nematoda and Sipunculida. Overall 22 species were recorded from only one sample with 19 of these comprised only a single individual.

No significant differences at different depths were shown between any of the univariate measures of diversity for the depth transects at Cemlyn on the first sampling date (June 2001) (Table 1; Fig 1a-f). There were significantly more species

Table 1. Analysis of univariate measures of diversity from samples collected at different depths in tide pools from amongst coralline turf at Cemlyn, North Wales in June 2001. ns=not significant

Cemlyn June 01		(N=5)					
		Number of species		Number of individuals		Margalef's d	
Transformation		None		Square Root		None	
	df	MS	F	MS	F	MS	F
Depth	3	1.3	0.03 ns	11	0.5 ns	0.182	0.21 ns
Residual	16	43.2		22.1		0.852	
Tukey's							
		Pielou's Eveness J'		Hill's N_1		Hill's N_2	
Transformation		None		None		None	
	df	MS	F	MS	F	MS	F
Depth	3	0.0096	0.54 ns	7	0.62 ns	1.07	0.14 ns
Residual	16	0.0179		11.3		7.62	
Tukey's							

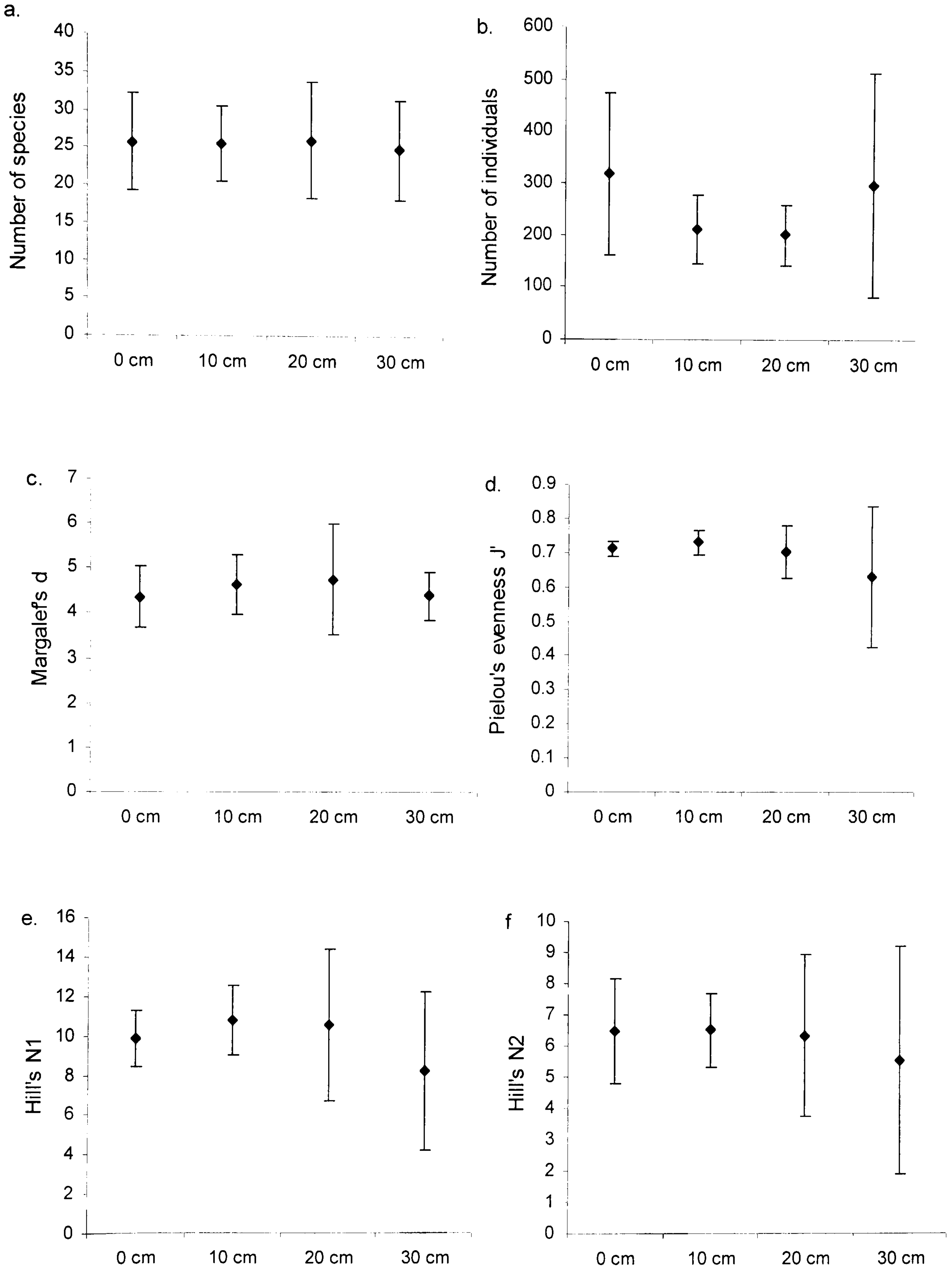


Figure 1 a-f. Mean and 95% confidence intervals for univariate measures of diversity from samples collected at different depths in tide pools from amongst coralline turf at Cemlyn in June 2001

Table 2. Analysis of univariate measures of diversity from samples collected at different depths in tide pools from amongst coralline turf at Cemlyn, North Wales in Feb2002. *,p<0.05; **p<0.01; ***, p<0.001; ns=not significant.

Cemlyn Feb 2002	(N=5)	Number of species		Number of individuals		Margalef's d	
Transformation		None		None		None	
	df	MS	F	MS	F	MS	F
Depth	3	160.7	8.68**	16007	2.04 ns	3.736	10.79***
Residual	16	18.5		7844		0.346	
Tukey's		0cm & 10cm > 20cm & 30cm				0cm & 10cm > 20cm & 30cm	

		Pielou's evenness J'		Hill's N_1		Hill's N_2	
Transformation		None		$\mathrm{Log}_{10}(n+1)$		$\mathrm{Log}_{10}(n+1)$	
	df	MS	F	MS	F	MS	F
Depth	3	0.0185	1.25 ns	0.0988	5.07*	0.1152	4.19*
Residual	16	0.0148		0.0195		0.0275	
Tukey's				0cm >20cm & 30cm		0cm > 20cm &30cm	

Table 3. Analysis of univariate measures of diversity from samples collected at different depths in tide pools from amongst coralline turf at Porth Cwyfan, North Wales in Feb2002. *, $p<0.05$; ns, not significant.

Porth Cwyfan, Feb 2002	(N=5)	Number of species		Number of individuals		Margalef's d	
Transformation		None		None		None	
	df	MS	F	MS	F	MS	F
Depth	3	69.3	3.47*	23184	0.61 ns	1.568	1.93 ns
Residual	16	20		38122		0.813	
Tukey's		0cm > 20cm					
		Pielou's evenness J'		Hill's N_1		Hill's N_2	
Transformation		None		None		$\text{Log}_{10}(n+1)$	
	df	MS	F	MS	F	MS	F
Depth	3	0.0293	1.00 ns	8.55	1.59 ns	0.0481	2.24 ns
Residual	16	0.0293		5.37		0.0215	
Tukey's							

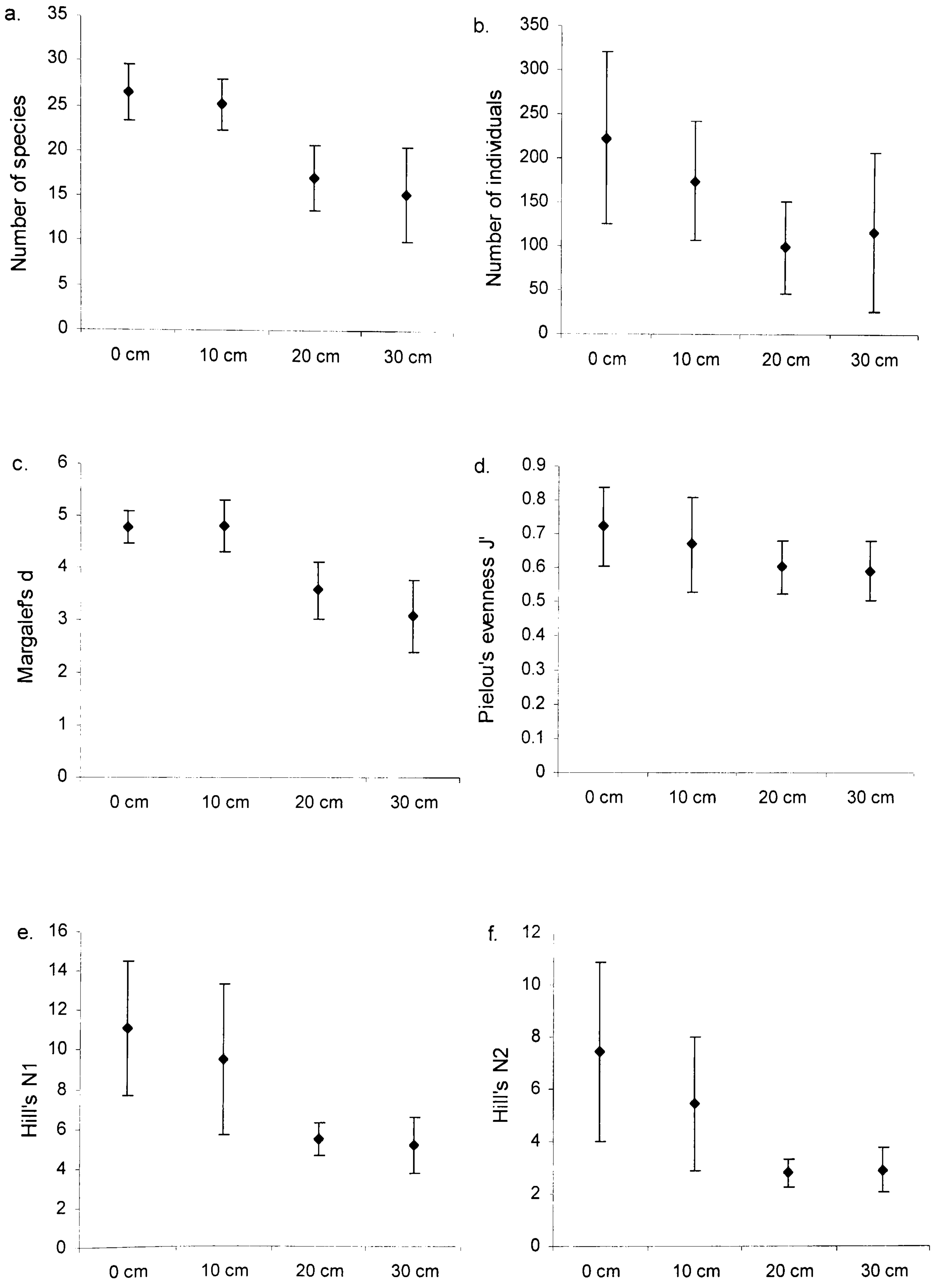


Figure 2 a-f. Mean and 95% confidence intervals for univariate measures of diversity from samples collected at different depths in tide pools from amongst coralline turf at Cemlyn in February 2002.

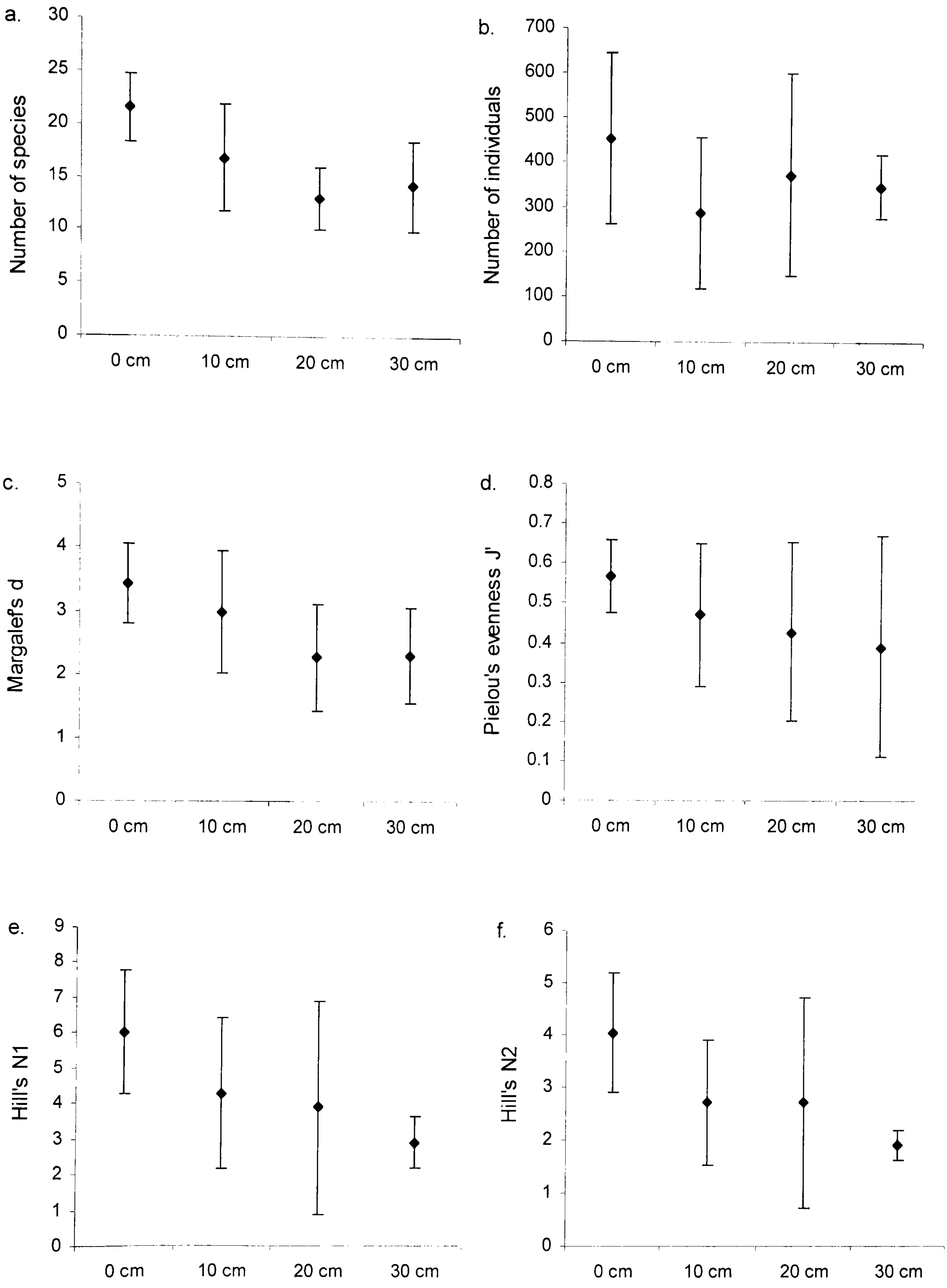


Figure 3 a-f. Mean and 95% confidence intervals for univariate measures of diversity from samples collected at different depths in tide pools from amongst coralline turf at Porth Cwyfan in February 2002.

at shallower depths on the second sampling occasion (Feb 2002) on both shores sampled (Table 2, Table 3; Fig. 2, Fig, 3) although the patterns were not identical. Only at Cemlyn on the second sampling occasion were significant differences at different depths shown between different univariate measures of diversity (Table, 2; Fig. 2). Margalef's d, Hill's N_1 and Hill's N_2 all revealed significantly higher diversity at shallower depths although the differences are less obvious for Hill's numbers than for Margalef's measure of diversity, d. Although there was large variability across depths for all measures of diversity there is a general trend for an increase in variance to be accompanied with an increase in depth when using evenness or Hill's numbers as diversity measures.

Graphical summaries of the data show that on the first sampling occasion in the summer at Cemlyn, samples from the greatest depth, 30 cm, had a high dominance component, while all other samples are inseparable in terms of their intrinsic diversity (Fig. 4a). On the second sampling occasion, in winter, the pattern had changed and samples from the shallowest depth, 0 cm, now separate from all other samples by their lower dominance component (Fig. 4b+c).

A clear separation of samples in community structure between 0 cm and all other depths is clear on both square root transformed (Fig. 5) and presence/absence (Fig. 6) data using cluster analysis and nMDS ordinations. Significant multivariate differences in community structure were demonstrated by an ANOSIM test for both square root transformed and presence/absence data at some level on all shores and at different times of sampling (Table 4). On all occasions community structure at the shallowest depth was different from the community structure in at least one other depth. On two occasions no significant differences were demonstrated using the global test, but significant differences were apparent from the subsequent pairwise tests. Values of significance attributed to pairwise tests are somewhat limited in their use for their limit is fixed by the number of possible permutations in the randomisation procedure. The corresponding value of R is of more use yielding better information. Any value of $R > 0.5$ indicates that the samples are clearly different and only a value of $R < 0.25$ can be said to be barely separable at all. In this case all significant pairwise values of R are greater than 0.25 indicating that there is a separation of these samples.

The bivalve, *Musculus discors* and the sedentary spirorbid polychaete, *Spirorbis corallinae*, were consistently the most common discriminator species within each

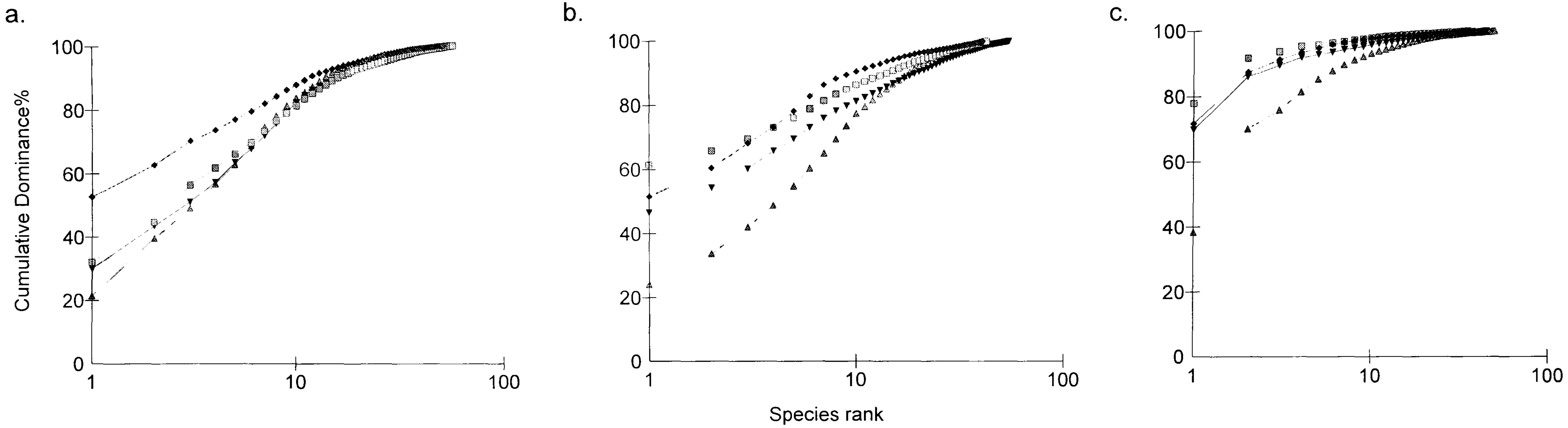


Figure 4. k-dominance curves of species rank against cumulative dominance for samples taken at different depths amongst coralline turf in tide pools, a. Cemlyn, June 2001, b. Cemlyn February, 2002, c. Porth Cwyfan, February 2002. ▲ = 0cm, ▼ = 10cm, ▨ = 20cm, ◆ = 30cm

Figure 5. Dendrograms (i) for group average clustering and nMDS (ii) ordinations of Bray-Curtis similarities based on square root transformed species abundance data from depth profiles in tide pools from a) Cemlyn June 2001, b) Cemlyn February 2002 c) Porth Cwyfan February 2002. (0 = 0cm depth group, 1 = 10cm, 2 = 20cm, 3 = 30cm).

Figure 6. Dendrograms (i) for group average clustering and nMDS (ii) ordinations of Bray-Curtis similarities based on presence/absence transformed species abundance data from depth profiles in tide pools from a) Cemlyn June 2001, b) Cemlyn February 2002 c) Porth Cwyfan February 2002. (0 = 0cm depth group, 1 = 10cm, 2 = 20cm, 3 = 30cm).

Table 4. Results of one-way ANOSIM tests on species abundance data from the three shores sampled using both square root transformed and presence/absence data. *,p<0.05; **p<0.01; ***, p<0.001; ns=not significant. Values in bold indicate a significant pairwise test found after a non significant global test.

Square Root	Cemlyn Jun 2001	Cemlyn Feb 2002	P. Cwyfan 2002
Global-R	0.284***	0.152 ns	0.178*
Pairwise:			
0cm – 10cm	0.712**	0.144 ns	0.376**
0cm – 20cm	0.764**	**0.552****	0.416**
0cm – 30cm	0.628**	**0.380***	0.596**
10cm – 20cm	-0.320 ns	-0.028 ns	-0.088 ns
10cm – 30cm	0.144 ns	0.108 ns	-0.048 ns
20cm – 30cm	-0.076 ns	-0.292 ns	0.000 ns
Presence/Absence			
Global-R	0.231**	0.190*	0.096 ns
Pairwise:			
0cm – 10cm	0.596**	0.286 ns	0.176 ns
0cm – 20cm	0.508*	0.434 *	**0.554** **
0cm – 30cm	0.730**	0.426**	0.198 ns
10cm – 20cm	-0.380 ns	-0.118 ns	-0.080 ns
10cm – 30cm	0.060 ns	0.202 ns	-0.208 ns
20cm – 30cm	-0.198 ns	-0.234 ns	- 0.038 ns

depth group at Cemlyn in June 2001. These two species accounted for over a quarter of the similarity within each depth group. At Porth Cwyfan in February 2002 a similar pattern was observed when *S. corallinae* and the bivalve, *Modiolus modiolus*, provided the highest contribution to similarity within groups. At shallow depth these two species contributed over 50% of the similarity, increasing to over 75% at 30cm depth. However, although *S. corallinae* alone was consistently a high contributor to similarity at Cemlyn in February 2002 there was no single species that also stood out. A similar pattern of increasing contributions to similarity with increasing depth was observed on this occasion. When the influence of species abundance was removed, species that were present in every sample now accounted for the greatest similarity within each depth group. Apart from the abundant and ubiquitous *S. corallinae*, which had the highest contribution to similarity in all groups at all times of sampling, other contributions came from many other species that varied a little between depth, shore and time.

For those species that contribute to dissimilarity between groups, only those that were shown to be significantly different using ANOSIM are presented and discussed. Average dissimilarity between groups generally increases as differences in depth increase. The only time when this was not the case is between 0cm and 30 cm at Porth Cwyfan February 2002. The top five species contributing to dissimilarity between each group is presented for square root transformed data (Table 5) and presence/absence data (Table 6). Differences between groups under square root transformation were caused by similar species on each occasion (Table 5). *S. corallinae* was always the highest contributor to dissimilarity between groups but it was not consistently more abundant in one group than another. For example, *S. corallinae* attained highest abundance at shallow depths in the pools at Cemlyn on the first sampling occasion except at the greatest depth, but was more abundant deeper in the pools on all other occasions. At Porth Cwyfan, differences between groups were caused consistently by three species; the polychaete *S. corallinae*, and the bivalves *Modiolus modiolus* and *Lasaea adonsoni*. These species were responsible for over 30% of the total dissimilarity between significantly different groups.

After presence/absence transformation species contributions to dissimilarity were lower than for square root transformed data. This indicates that more species were responsible for differences between groups. On the first sampling occasion at Cemlyn, differences between groups can be attributed to the consistent occurrence of

Table 5. Top five species contributions to Bray-Curtis dissimilarity between significantly different depth groups and their contribution to dissimilairity based on square root transformation. CM =Cemlyn, PC=Porth Cwyfan. Highlighted species indicate highest abundance found in first quoted depth group.

CM Jun 01 0cm – 10cm		CM Jun 01 0cm – 20cm		CM Jun 01 0cm – 30cm		CM Feb 02 0cm – 20cm	
Spirorbis corallinae	6.74%	*Spirorbis corallinae*	6.75%	*Spirorbis corallinae*	14.53%	*Spirorbis corallinae*	6.05%
Stenothoe monoculoides	5.25%	*Convoluta convoluta*	5.74%	*Convoluta convoluta*	6.06%	*Onoba semicostata*	5.79%
Hyale prevostii	5.10%	*Hyale pevostii*	5.08%	*Janua pagenstecheri*	4.68%	Nematodes	4.63%
Fabricia stellaris	3.85%	*Fabricia stellaris*	3.98%	*Hyale prevostii*	4.43%	*Hyale prevostii*	4.40%
Convoluta convoluta	3.65%	*Musculus discors*	3.96%	*Musculus discors*	4.42%	*Stenothoe monoculoides*	4.33%
Average dissimilarity	53.61%	Average dissimilarity	54.83%	Average dissimilarity	63.77%	Average dissimilairty	58.50%
CM Feb 02 0cm – 30cm		PC Feb 02 0cm – 10cm		PC Feb 02 0cm – 20cm		PC Feb 02 0cm – 30cm	
Spirorbis corallinae	6.65%	*Spirorbis corallinae*	11.10%	*Spirorbis corallinae*	14.02%	*Spirorbis corallinae*	9.62%
Onoba semicostata	5.16%	*Modiolus modiolus*	9.39%	*Modiolus modiolus*	9.44%	*Modiolus modiolus*	8.87%
Stenothoe monoculoides	4.40%	*Lasaea adonsoni*	7.58%	*Lasaea adonsoni*	7.67%	*Lasaea adonsonii*	8.65%
Nematodes	4.39%	*Rissoa parva*	5.96%	*Rissoa parva*	4.70%	*Amphipholis squamata*	5.07%
Hyale prevostii	4.17%	*Amphipholis squamata*	4.06%	Nematodes	4.58%	*Platynereis dumerilii*	4.80%
Average dissimilarity	59.38%	Average dissimilarity	51.38%	Average dissimilarity	54.17%	Average dissimilarity	46.83%

Table 6. Top five species contributions to Bray-Curtis dissimilarity between significantly different depth groups and their contribution to dissimilairity based on presence/absence transformation. CM =Cemlyn, PC=Porth Cwyfan. Highlighted species indicate highest abundance found in first quoted depth group.

CM Jun 01 0cm – 10cm		CM Jun 01 0cm – 20cm		CM Jun 01 0cm – 30cm	
Convoluta convoluta	3.18%	*Fabricia stellaris*	3.19%	*Idotea pelagica*	3.54%
Hyale prevostii	3.01%	*Hyale prevostii*	2.99%	*Fabricia stellaris*	2.94%
Amphithoe neglecta	3.00%	*Tanais dulongii*	2.95%	*Convoluta convoluta*	2.91%
Nemerteans	2.97%	*Idotea pelagica*	2.88%	*Dexamine spinosa*	2.90%
Tanais dulongii	2.97%	*Rissoella diaphana*	2.88%	*Hyale prevostii*	2.75%
Average dissimilarity	51.16%	Average dissimilarity	51.62%	Average dissimilarity	57.30%
CM Feb 02 0cm – 20cm		CM Feb 02 0cm – 30cm		PC Feb 02 0cm – 20cm	
Clunio sp.	3.52%	*Clunio* sp.	4.43%	Nematodes	4.90%
Littorina mariae	3.52%	Foraminifera	4.43%	*Musculus discors*	3.97%
Ostracods	3.49%	Ostracods	3.72%	*Chaetogammarus* sp.	3.33%
Hyale prevostii	3.48%	*Lasaea adonsoni*	3.60%	*Tanais dulongii*	3.11%
Lasaea adonsoni	3.48%	*Littorina mariae*	3.57%	*Hyale prevostii*	3.05%
Average dissimilarity	53.94%	Average dissimilarity	54.91%	Average dissimilarity	59.69%

the amphipod *Hyale prevostii*, the polychaete worm *Fabricia stellaris* and the tanaid crustacean *Tanais dulongii,* and at shallower depths in the tide pools with the platyhelminth *Convoluta convoluta* and the isopod *Idotea pelagica* occupying greater depths. On the second sampling occasion at Cemlyn differences were generally due to the more consistent occurrence in samples of the insect larvae *Clunio* sp., the gastropod *Littorina mariae*, ostracods and *Lasaea adonsoni* at shallower depths in samples. As there was only one significant pairwise difference from Porth Cwyfan discernible patterns are difficult to achieve but some similar species were responsible for the differences observed here including *Tanais dulongii* and *Hyale prevostii*, both of which were also more common at shallower depths.

Overall, these data show that there are clear differences in the assemblages associated with *Corallina* turf at different depths in tide pools. The observed patterns are variable and depend on the time and location of sampling, as well as whether it is diversity or community structure that is being investigated. In most cases, however, it is the samples collected from the shallowest depths that are different form all others.

Variations in community structure in response to changes in shore height and pool size.

A total of 20 509 individuals from 122 different species or higher taxa were counted and identified from tide pools of different sizes and from different heights on the shore. The dominant phyla in terms of species represented were annelids of which all but one species were polychaetes (34 species). Crustaceans (32 species – 14 from the order Amphipoda) and molluscs (30 species – 24 from the class Gastropoda) were also well represented along with chelicerates (11 species – 10 from the class Pycnogonida). Other contributions came from Echinodermata, Chordata, Platyhelminthes, Sipunculida, Nematoda, Nemertea, Protista, Cnidaria and Hexapoda.

On the first sampling occasion at Cemlyn only a few measures of diversity showed significant differences between different tide pools (Table 7, Fig. 7). Large pools low on the shore had significantly more individuals associated with *Corallina* turf than small pools either on the high shore or the adjacent low shore (Table 7; Fig. 7b). Small pools had significantly higher evenness than large pools on the low shore (Table 7; Fig. 7d) and small pools on the low shore had significantly higher diversity, in terms of the abundant species, than large pools anywhere on the shore (Table 7;

Table 7. Analysis of univariate measures of diversity from samples collected in different tide pools at small spatial scales from amongst coralline turf at Cemlyn, North Wales in June 2001. *, $p<0.05$; ns, not significant. LS =Low shore small pool, LL=Low shore large pool, HS=high shore small pool, HL=High shore large pool.

Cemlyn, June 2001	(N=5)	Number of species		Number of individuals		Margalef's d	
Transformation		None		None		None	
	df	MS	F	MS	F	MS	F
Pool type	3	45.8	1.36 ns	93351	4.43*	1.339	1.57 ns
Residual	16	33.7		21091		0.851	
Tukey's				LL > LS & HS			
		Pielou's evenness J'		Hill's N_1		Hill's N_2	
Transformation		None		None		None	
	df	MS	F	MS	F	MS	F
Pool type	3	0.04867	5.33*	24.97	5.29*	9.61	3.10 ns
Residual	16	0.00911		4.72		3.10	
Tukey's		LS & HS > LL		LS > LL & HL			

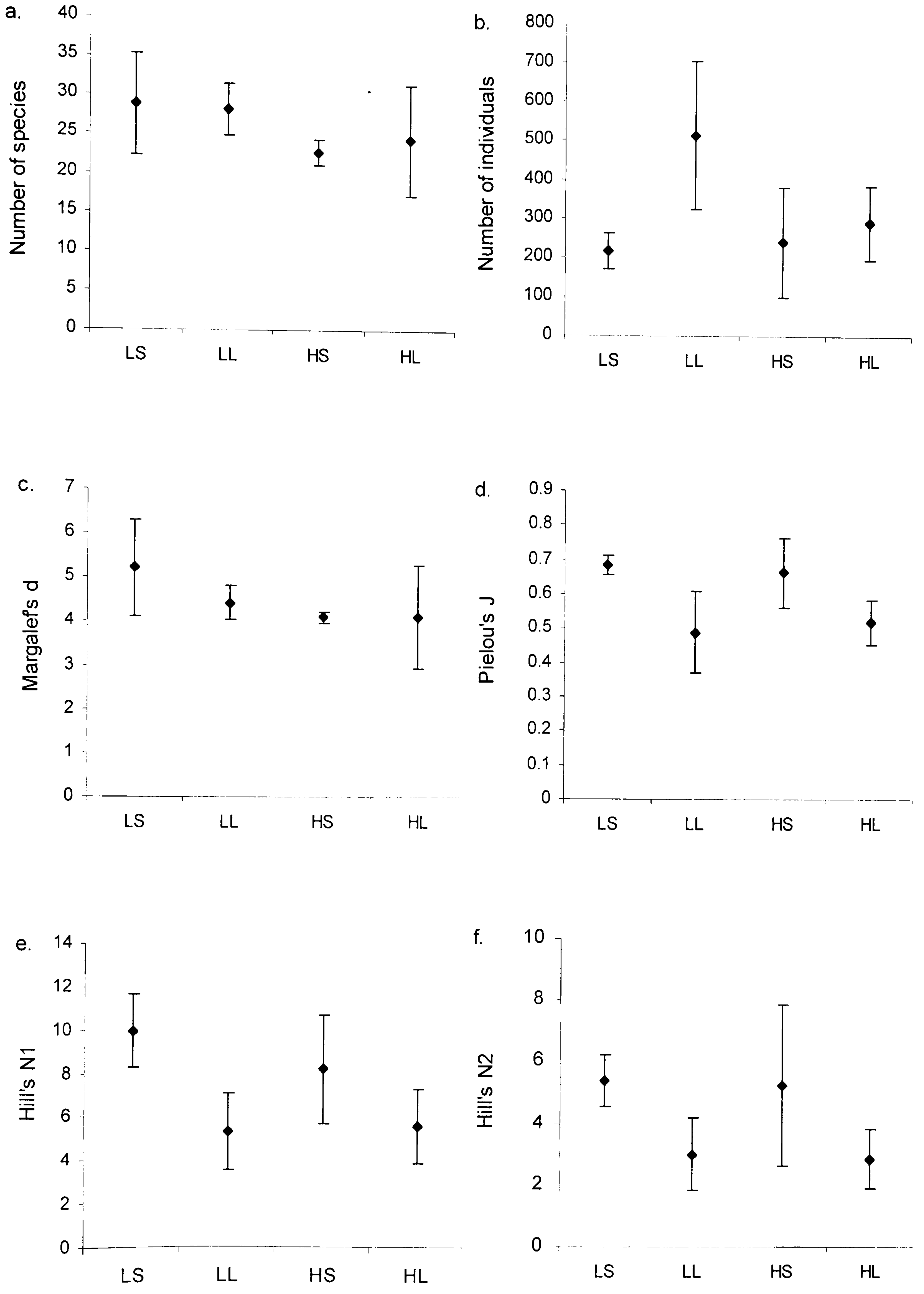


Figure 7 a-f. Mean and 95% confidence intervals for univariate measures of diversity from samples collected on a smal spatial scale amongst coralline turf in tide pools at Cemlyn in June 2001. LS=Low shore small pool, LL=Low shore large pool, HS=High shore small pool, HL=High shore large pool.

Table 8. Analysis of univariate measures of diversity from samples collected in different tide pools at small spatial scales from amongst coralline turf at Cemlyn, North Wales in February 2002. *, p<0.05; ns, not significant. LS =Low shore small pool, LL=Low shore large pool, HS=high shore small pool, HL=High shore large pool. Values in bold indicate data did not meet assumptions of analysis of variance.

Cemlyn, February 2002	(N=5)	Number of species		Number of individuals		Margalef's d	
Transformation		None		None		None	
	df	MS	F	MS	F	MS	F
Pool type	3	25.3	0.67 ns	25994	2.20 ns	0.490	0.54 ns
Residual	16	37.5		11838		0.907	
Tukey's							
		Pielou's evenness J'		Hill's N_1		Hill's N_2	
Transformation		None		None		None	
	df	MS	F	MS	F	MS	F
Pool type	3	0.0631	4.48*	18.90	3.11 ns	**12.77**	**3.32***
Residual	16	0.0141		6.08		**3.86**	
Tukey's		HS > HL		HS > HL		**HS > HL**	

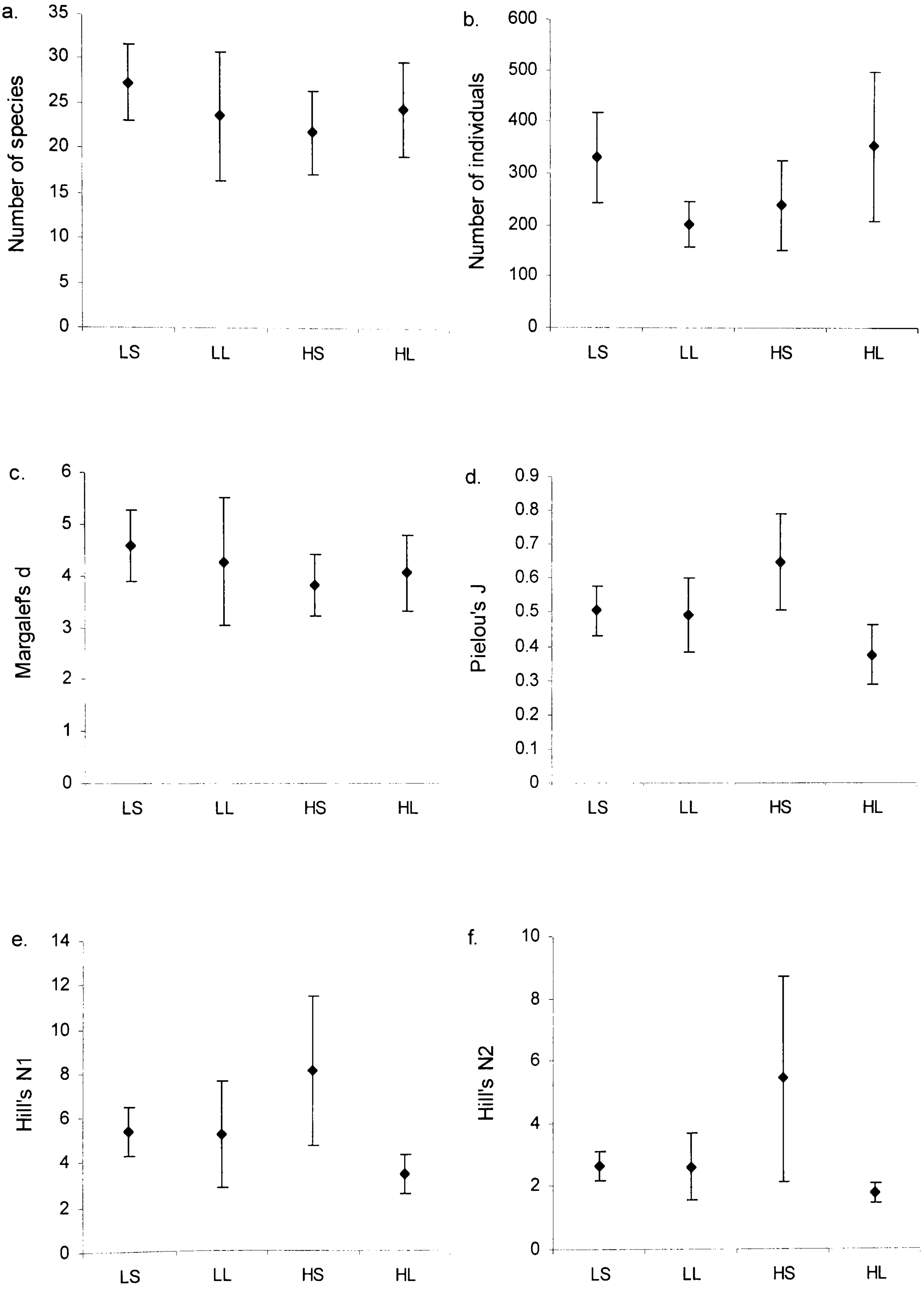


Figure 8 a-f. Mean and 95% confidence intervals for univariate measures of diversity from samples collected on a smal spatial scale amongst coralline turf in tide pools at Cemlyn in February 2002. LS=Low shore small pool, LL=Low shore large pool, HS=High shore small pool, HL=High shore large pool.

Fig; 7e). On the second sampling occasion at Cemlyn the patterns were somewhat different (Table 8, Fig. 8). There was higher evenness in small pools on the high shore than large pools at the same height (Table 8; Fig 8d). Although there were significant pairwise differences for both Hill's measures of diversity these differences are difficult to interpret as there was no overall significance for Hill's N_1. Also, Hill's N_2 did not meet the assumption of homogenous variance for ANOVA and the low F-ratio does not permit a positive interpretation of the results (Table 8; Fig. 8e+f). At Porth Cwyfan, results of ANOVA again reveal different patterns (Table 9, Fig. 9). High shore small pools were now shown to have significantly higher evenness and diversity (Hill's N_1 and N_2) than low shore small pools (Table 9; Fig. 9d-f). Again, Hill's N_2 did not meet the assumption of homogeneity of variances and so this result, due to a low F-ratio, must be treated with caution.

Graphical summaries (k-dominance plots) of the data show that on both sampling occasions at Cemlyn, large pools low on the shore had the highest measures of dominance (Fig. 10 a+b). The lowest measure of dominance on the first sampling occasion at Cemlyn was from small pools on the low shore (Fig. 10a) while these pools carried the highest measure of dominance in samples from Porth Cwyfan, with the lowest dominance from high shore small pools (Fig. 10c). All other lines on the graphs intersect indicating that they have intrinsically similar diversity.

Pools of different types did not consistently form discrete groups under group average clustering (Fig. 11+12 ai-ci). Ordination by nMDS showed that for square root transformed and presence/absence data, samples from different shore heights separated from each other but samples from different pool sizes within the same height on the shore were grouped together (Fig. 11+12 aii-cii). On the second sampling occasion at Cemlyn, the only separation visible on the nMDS was that of high shore small pools from all others (Fig. 11bii). This can be seen by two wildly dissimilar samples, only clustering with all others at less than 40% similarity (Fig. 11 bi). Significant multivariate differences in community structure from different sized pools at different heights on the shore were shown for all shores sampled except for presence/absence data at Cemlyn on the second sampling occasion (Table 10). However, even on this occasion pairwise differences were still detected between high shore small pools and all pools on the low shore. In fact, the biggest pairwise difference was between low shore large pools and high shore small pools on both sampling occasions at Cemlyn, while at Porth Cwyfan the greatest difference was between low shore small pools and high shore large pools attaining an r-value of

Table 9. Analysis of univariate measures of diversity from samples collected in different tide pools at small spatial scales from amongst coralline turf at Porth Cwyfan, North Wales in February 2002. *, p<0.05; ns, not significant. LS =Low shore small pool, LL=Low shore large pool, HS=high shore small pool, HL=High shore large pool. Values in bold indicate data did not meet the assumptions of analysis of variance.

Porth Cwyfan, February 2002	(N=5)	Number of species		Number of individuals		Margalef's d	
Transformation		None		None		None	
	df	MS	F	MS	F	MS	F
Pool type	3	84.6	1.68 ns	82110	2.09 ns	2.88	2.17 ns
Residual	16	503		39198		1.32	
Tukey's							

		Pielou's evenness J'		Hill's N_1		Hill's N_2	
Transformation		None		Log_{10} (n+1)		None	
	df	MS	F	MS	F	MS	F
Pool type	3	0.1085	4.90*	0.1453	4.77*	**7.31**	**3.78***
Residual	16	0.0222		0.0304		**1.93**	
Tukey's		HS > LS		HS > LS		**HS > LS**	

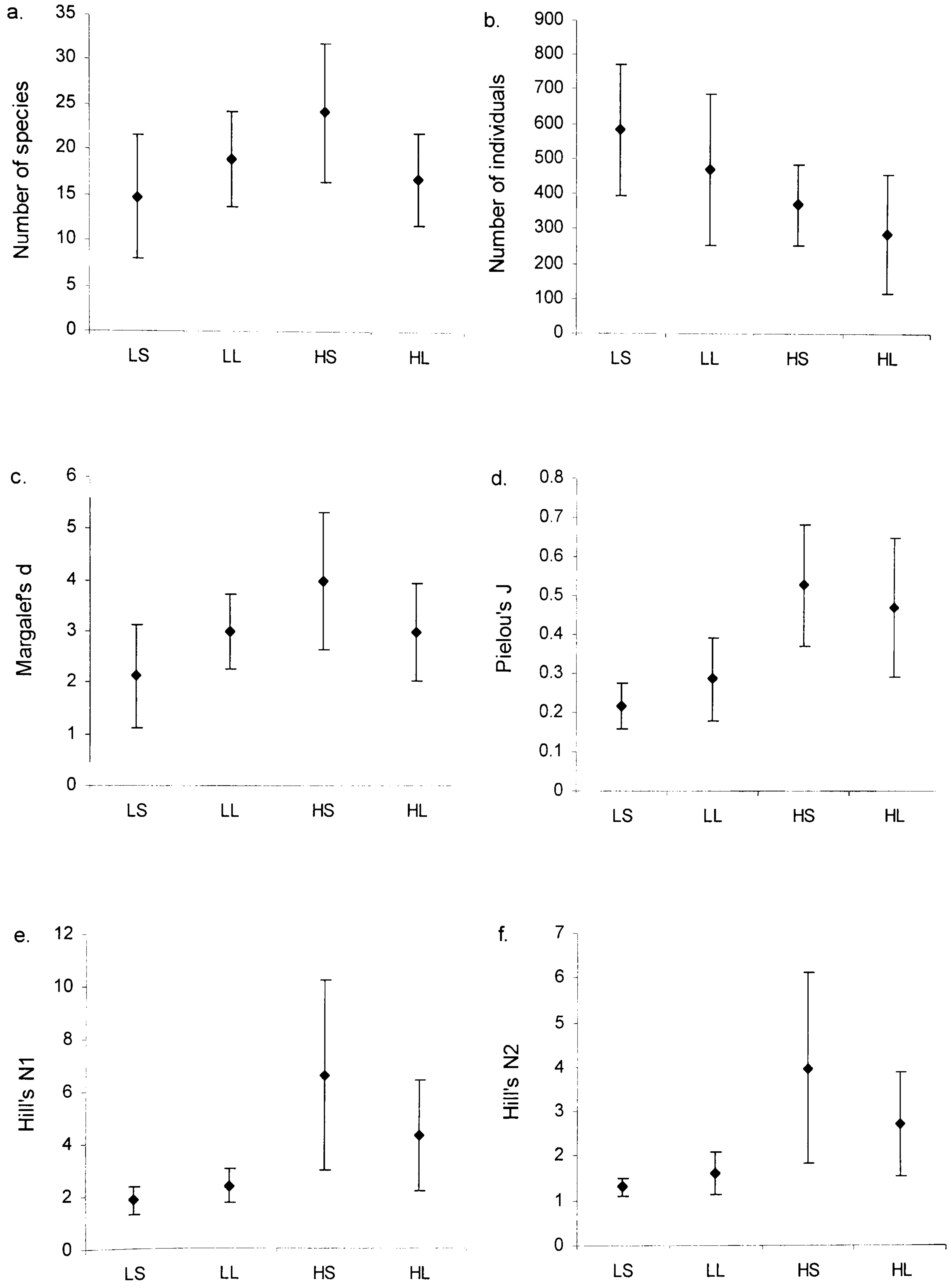


Figure 9 a-f. Mean and 95% confidence intervals for univariate measures of diversity from samples collected on a smal spatial scale amongst coralline turf in tide pools at Porth Cwyfan in February 2002. LS=Low shore small pool, LL=Low shore large pool, HS=High shore small pool, HL=High shore large pool.

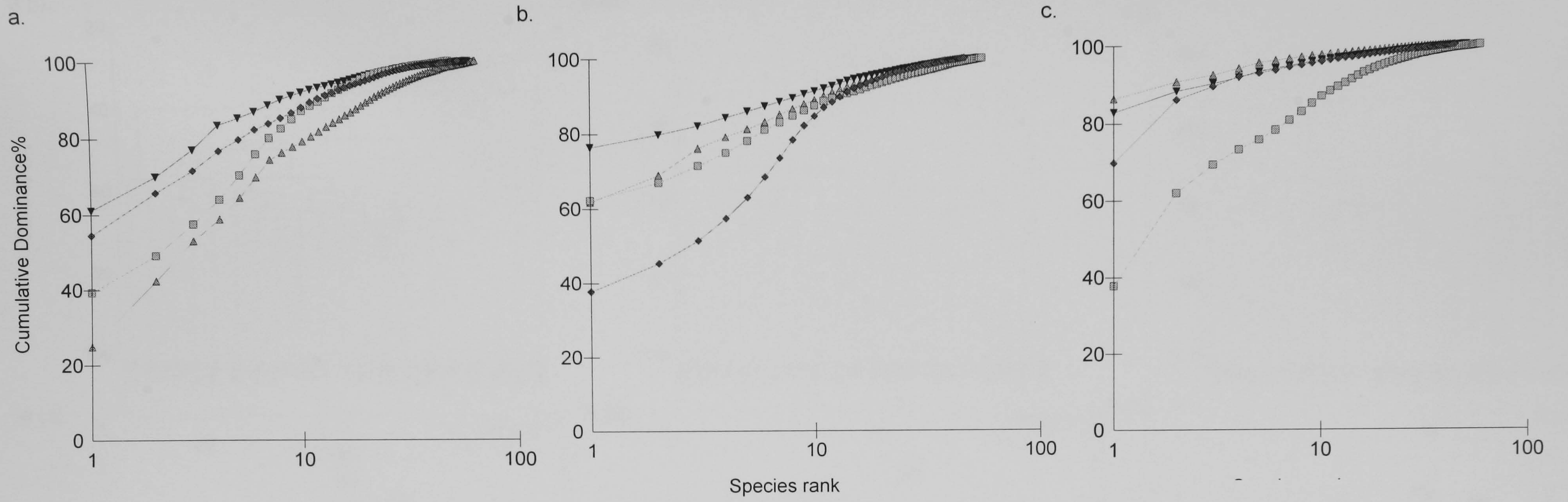


Figure 10. k-dominance curves of species rank aginst cumulative dominance for samples taken from different tide pools at small spatial scales amongst coralline turf. a. Cemlyn, June 2001, b. Cemlyn February, 2002, c. Porth Cwyfan, February 2002.
▲ = Small pool low shore, ▼ = Large pool low shore, ▨ = High shore small pool, ◆ = High shore large pool.

Figure 11. Dendrograms (i) for group average clustering and nMDS (ii) ordinations of Bray-Curtis similarities based on square root transformed species abundance data from coralline turf in tidepools at small spatial scales taken from: a) Cemlyn June 2001, b) Cemlyn February 2002, c) Porth Cwyfan February 2002. LS=Low shore small pool, LL=Low shore large pool, HS=High shore small pool, HL=High shore large pool.

Figure 12. Dendrograms (i) for group average clustering and nMDS (ii) ordinations of Bray-Curtis similarities based on presence absence transformed species abundance data from coralline turf in tidepools at small spatial scales taken from: a) Cemlyn June 2001, b) Cemlyn February 2002, c) Porth Cwyfan February 2002. LS=Low shore small pool, LL=Low shore large pool, HS=High shore small pool, HL=High shore large pool.

Table 10. Results of one-way ANOSIM tests on square root and presence/absence transformed species abundance data from coralline turf in tide pools, collected at small spatial scales from three shores. *,p<0.05; **p<0.01; ***, p<0.001; ns=not significant. Values in bold indicate a significant pairwise test found after a non significant global test. LS=Low shore small pool, LL=Low shore large pool, HS=High shore small pool, HL=High shore large pool.

Square Root	Cemlyn Jun 2001	Cemlyn Feb 2002	P. Cwyfan 2002
Global-R	0.473***	0.238**	0.486***
Pairwise:			
LS -LL	0.416*	0.104 ns	-0.052 ns
LS – HS	0.488**	0.412**	0.546*
LS – HL	0.564**	0.172 ns	0.984**
LL – HS	0.724**	0.424*	0.352*
LL – HL	0.584**	0.036 ns	0.616*
HS – HL	0.272*	0.368*	0.280 ns
Presence/Absence			
Global-R	0.469***	0.136 ns	0.303**
Pairwise:			
LS -LL	0.078 ns	-0.054 ns	-0.004 ns
LS – HS	0.580**	**0.424****	0.354*
LS – HL	0.470**	-0.018 ns	0.656**
LL – HS	0.832**	**0.500****	0.342*
LL – HL	0.400**	-0.218 ns	0.350*
HS – HL	0.468**	0.282 ns	0.192 ns

0.984 after square root transformation (Table 10). Significant differences were demonstrated between high shore small pools and low shore small and large pools on every sampling occasion and under both transformations. Small and large pools on the low shore were only significantly different at Cemlyn June 2001 after square root transformation, while small and large pools on the high shore were never significantly different at Porth Cwyfan, and only just significant at Cemlyn with relative low values of R.

Species contributing most to similarity within groups on both sampling occasions at Cemlyn are the polychaete, *S. corallinae*, and the bivalve, *Musclus discors.* In high shore pools on the first sampling occasion other high contributions to similarity were recorded for nematodes in small pools and the brittlestar, *Amphipholis squamata,* in large pools. In high shore large pools on the second sampling occasion, nematodes and the small amphipod, *Stenothoe monoculoides*, also had high contributions to similarity, otherwise the patterns were fairly consistent. At Porth Cwyfan, the bivalve, *Modiolous modiolus,* contributed to 23% of the similarity in high shore large pools and to over 70% of the similarity in low shore small pools. *Spirorbis corallinae* only had a relatively large contribution to similarity in high shore large pools (40%). Average similarity within groups showed no clear pattern but consistently fell between 50 and 60% similarity. When the importance of species abundance is removed many more species contributed to the similarity within groups on both occasions at Cemlyn with average similarity values remaining consistent between 50-60%. At Porth Cwyfan, however, relatively fewer species contributed to similarity within groups under presence/absence transformation. *Modiolus modiolus* again contributed the highest values of similarity within all groups with different species in different groups. Average similarity was also reduced falling between 40-50%.

For those species that contribute to dissimilarity between groups, only those that were significantly different using ANOSIM are presented and discussed. On both occasions at Cemlyn average dissimilarity was highest between large pools on the low shore and small pools on the high shore. This was not unexpected as these pools are the most extreme in terms of their vulnerability to environmental fluctuations. Low shore large pools will be very stable in terms of temperature and salinity changes and similar to a subtidal habitat based on the algal groups they support. High shore small pools on the other hand will be exposed for longer periods and contain a much smaller volume of water that will respond to changes in the surrounding environment more quickly than large pools. However, at Porth Cwyfan, the largest dissimilarity was between small pools on the low shore and large pools on the high shore indicating that some factor other than the physico-chemical conditions of the tide pool are having a marked effect on community structure. When species abundance is retained as an important feature in analysis, the abundant *S. corallinae* again makes a consistently high contribution to dissimilarity between all combinations of pools on all shores. The distribution of *S. corallinae* is highly variable between pools and no one class of pool has consistently higher abundance of this tubeworm. On the first sampling occasion at Cemlyn, the platyhelminth, *Convoluta convoluta*, the amphipod, *Stenothoe monoculoides*, and the bivalve, *Musculus discors*, were also consistently found to be good discriminator species, particularly between low and high shore pools reaching their maximum abundance on the low shore. By the second sampling occasion, at Cemlyn in the winter, good discriminator species were now found to have highest abundance in high shore pools (except for *S. corallinae*) and included the sabellid polychaete, *Fabricia stellaris*, the brittlestar, *Amphipholis squamata*, the amphipod, *Hyale prevostii* and the tanaid, *Tanais dulongii*. Indeed, overall numbers of individuals were reduced in low shore pools in winter (Fig. 7b +8b). At Porth Cwyfan in winter additional differences were due to large numbers of the horse mussel, *Modiolus modiolus*, in low shore pools (Table 11). Under presence/absence transformation more species contribute to dissimilarity between groups and patterns are difficult to generalise. The occurrence of *Idotea granulosa* appears to be a good discriminator between low shore small pools and high shore pools at both times of sampling at Cemlyn, as does *Modiolus modiolus* and *Polydora caeca* for low shore large pools and high shore pools (Table 12). At Porth Cwyfan, *Hyale perieri*, *Stenothoe monoculoides* and *Rissoa parva* are good discriminators between low shore small pools and high shore pools, with *H. perieri* being more common in low shore pools. Also, nemerteans are more common in low shore large pools while *Stenothoe monoculoides* is most common in high shore pools (Table 12).

These data highlight the differences in diversity and community composition of invertebrates associated with *Corallina* turf in pools of different size and at different heights on the shore, whilst in terms of community structure, differences between pools at different heights are often clear, differences in diversity are not as evident as might be expected. Also, patterns of differences are not necessarily consistent between shores or at different times of sampling.

Table 11. Top five species contributions to Bray-Curtis dissimilarity between significantly different communities in tide pools at small spatial scales and their percentage contribution to dissimilairity based on square root transformation. Highlighted species indicate highest abundance found in first quoted pool type. CM =Cemlyn, PC=Porth Cwyfan. LS=Low shore small pool, LL=Low shore large pool, HS=High shore small pool, HL=High shore large pool.

CM Jun 01 LS – LL		CM Jun 01 LS – HS		CM Jun 01 LS – HL		CM Jun 01 LL – HS		CM Jun 01 LL – HL	
Spirorbis corallinae	15.5%	*Spirorbis corallinae*	7.44%	*Spirorbis corallinae*	9.61%	*Spirorbis corallinae*	11.5%	*Spirorbis corallinae*	8.64%
Convoluta convoluta	8.1%	*Stenothoe monoculoides*	4.61%	*Musculus discors*	5.54%	*Convoluta convoluta*	8.22%	*Convoluta convoluta*	6.51%
Apherusa jurenei	3.75%	*Micromaldane ornithochaeta*	4.5%	*Stenothoe monoculoides*	4.75%	*Stenothoe monculoides*	4.97%	*Stenothoe monoculoides*	5.89%
Stenothoe monoculoides	3.14%	*Janua pagenstecheri*	4.33%	*Apherusa jurenei*	4.28%	*Micromaldane ornithochaeta*	4.14%	*Musculus discors*	5.55%
Musculus discors	3.02%	*Musculus discors*	4.29%	*Onoba semicostata*	3.99%	*Musculus discors*	3.98%	*Onoba semicostata*	4.47%
Average dissimilarity	51.4%	Average dissimilarity	58.6%	Average dissimilarity	56.7%	Average dissimilarity	58.3%	Average similarity	48.5%

CM Jun 01 HS – HL		CM Feb 02 LS – HS		CM Feb 02 LL – HS		CM Feb 02 HS – HL		PC Feb 02 LS – HS	
Spirorbis corallinae	8.64%	*Spirorbis corallinae*	12.3%	*Spirorbis corallinae*	9.75%	*Spirorbis corallinae*	15.3%	*Modiolus modiolus*	15.5%
Micromaldane ornithochaeta	5.41%	*Fabricia stellaris*	5.16%	*Hyale prevostii*	5.21%	*Hyale prevostii*	5.04%	*Spirorbis corallinae*	9.46%
Musculus discors	4.59%	*Tanais dulongii*	4.28%	*Fabricia stellaris*	4.92%	*Tanais dulongii*	4.74%	*Lasaea adonsonii*	5.44%
Onoba semicostata	4.24%	*Amphipholis squamata*	3.97%	*Tanais dulongii*	4.81%	*Amphipholis squamata*	4.37%	*Mytilus edulis*	4.32%
Covoluta convoluta	4.11%	*Hyale prevostii*	3.85%	*Amphipholis squamata*	3.98%	*Fabricia stellaris*	4.22%	Nematodes	3.31%
Average dissimilarity	50.6%	Average dissimilarity	53.4%	Average dissimilarity	59.1%	Average dissimilarity	56.3%	Average dissimilarity	62.3%

PC Feb 02 LS – HL		PC Feb 02 LL – HS		PC Feb 02 LL – HL	
Modiolus modiolus	24.8%	*Modiolus modiolus*	12.6%	*Modiolus modiolus*	21%
Spirorbis corallinae	18.5%	*Spirorbis corallinae*	9.55%	*Spirorbis corallinae*	16.8%
Mytilus edulis	6.01%	*Lasaea adonsoni*	6.4%	Nematodes	4.13%
Amphipholis squamata	3.76%	*Skeneopsis planorbis*	2.92%	*Amphipholis squamata*	3.6%
Nematodes	3.08%	Nematodes	2.75%	*Mytilus edulis*	3.41%
Average dissimilarity	72.5%	Average dissimilarity	61.3%	Average dissimilarity	64.4%

Table 12. Top five species contributions to Bray-Curtis dissimilarity between significantly different communities in tide pools at small spatial scales and their percentage contribution to dissimilairity based on presence/absence transformation. Highlighted species indicate highest abundance found in first quoted pool type. CM =Cemlyn, PC=Porth Cwyfan. LS=Low shore small pool, LL=Low shore large pool, HS=High shore small pool, HL=High shore large pool.

CM Jun 01 LS – HS		CM Jun 01 LS – HL		CM Jun 01 LL – HS		CM Jun 01 LL – HL		CM Jun 01 HS – HL	
Idotea granulosa	3.74%	*Janua pagenstecheri*	3.23%	*Convoluta convoluta*	3.55%	*Modiolus modiolus*	4.11%	*Convoluta convoluta*	4.37%
Janua pagenstecheri	3.14%	*Idotea granulosa*	3.16%	Harpacticoid Copepods	3.55%	*Polydora caeca*	3.03%	Harpacticoid Copepods	4.37%
Idotea pelagica	3.02%	*Clunio* sp.	2.95%	*Polydora caeca*	2.85%	*Skeneopsis planorbis*	2.88%	*Platynereis dumerilii*	3.49%
Polydora caeca	2.63%	*Modiolus modiolus*	2.95%	*Modiolus modiolus*	2.83%	*Littorina mariae*	2.85%	*Lasaea adonsonni*	2.96%
Lasaea adonsonii	2.53%	*Platynereis dumerilii*	2.61%	*Lasaea adonsoni*	2.83%	*Lacuna vincta*	2.77%	Foraminifera	2.84%
Average dissimilarity	52.5%	Average disimilarity	50.5%	Average dissimilarity	55.3%	Average dissimilarity	47.3%	Average dissimilarity	50.0%

CM Feb 02 LS – HS		CM Feb 02 LL – HS		PC Feb 02 LS – HS		PC Feb 02 LS – HL		PC Feb 02 LL – HS	
Idotea granulosa	3.5%	Mites	3.21%	*Hyale perieri*	4.27%	*Hyale perieri*	4.89%	*Lasaea adonsoni*	3.72%
Fabricia stellaris	3.48%	*Lasaea adonsonni*	3.21%	*Stenothoe monoculoides*	3.61%	*Stenothoe monoculoides*	3.68%	*Musculus discors*	2.34%
Rissoella diaphana	3.39%	*Idotea granulosa*	3.05%	*Musculus discors*	2.99%	*Amphipholis squamata*	3.35%	*Stenothoe monoculoides*	2.34%
Mites	3.25%	*Hyale prevostii*	2.84%	*Hyale prevostii*	2.82%	*Rissoa parva*	3.25%	Nemerteans	2.18%
Lasaea adonsonni	3.25%	*Polydora caeca*	2.74%	*Rissoa parva*	2.62%	*Mytilus edulis*	3.07%	*Hyale prevostii*	2.18%
Average dissimilarity	48.7%	Average dissimilarity	53.9%	Average dissimilarity	65.7%	Average dissimilarity	69.9%	Average dissimilarity	65.0%

PC Feb 02 LL – HL	
Nemerteans	3.5%
Apherusa jurenei	2.97%
Nematodes	2.83%
Aspidosiphon muelleri	2.8%
Stenothoe monoculoides	2.63%
Average dissimilarity	64.8%

Table 13. Analysis of environmental measures of habitat from samples collected ifrom different depths in tide pools from amongst coralline turf at Cemlyn, North Wales in June 2001. *, $p<0.05$; **, $p<0.01$; ***, $p<0.001$; ns, not significant. LS =Low shore small pool, LL=Low shore large pool, HS=high shore small pool, HL=High shore large pool.

Cemlyn, June 2001	(N=5)	pH		Temperature		Salinity	
Transformation		None		None		None	
	df	MS	F	MS	F	MS	F
Depth	3	0.009	0.03 ns	4.32	2.5 ns	0.0133	1.03 ns
Residual	16	0.103		1.72		0.0130	
Tukey's							

		CDENS		Branches		Branchlets	
Transformation		None		None		None	
	df	MS	F	MS	F	MS	F
Depth	3	0.0149	0.88 ns	0.358	2.09 ns	4.95	2.81 ns
Residual	16	0.0169		0.171		1.76	
Tukey's							

continued:

Cemlyn, June 2001		(N=5) Number of holdfasts		Weed weight		Sediment > 63um	
Transformation		None		None		None	
	df	MS	F	MS	F	MS	F
Depth	3	1632	3.32*	3.67	1.05 ns	10.8	0.86 ns
Residual	16	493		3.51		12.6	
Tukey's		0cm > 30cm					

		Sediment < 63um		Surface area	
Transformation		Log_{10} (x+1)		None	
	df	MS	F	MS	F
Depth	3	0.0304	1.53 ns	5319	0.36 ns
Residual	16	0.0199		14731	
Tukey's					

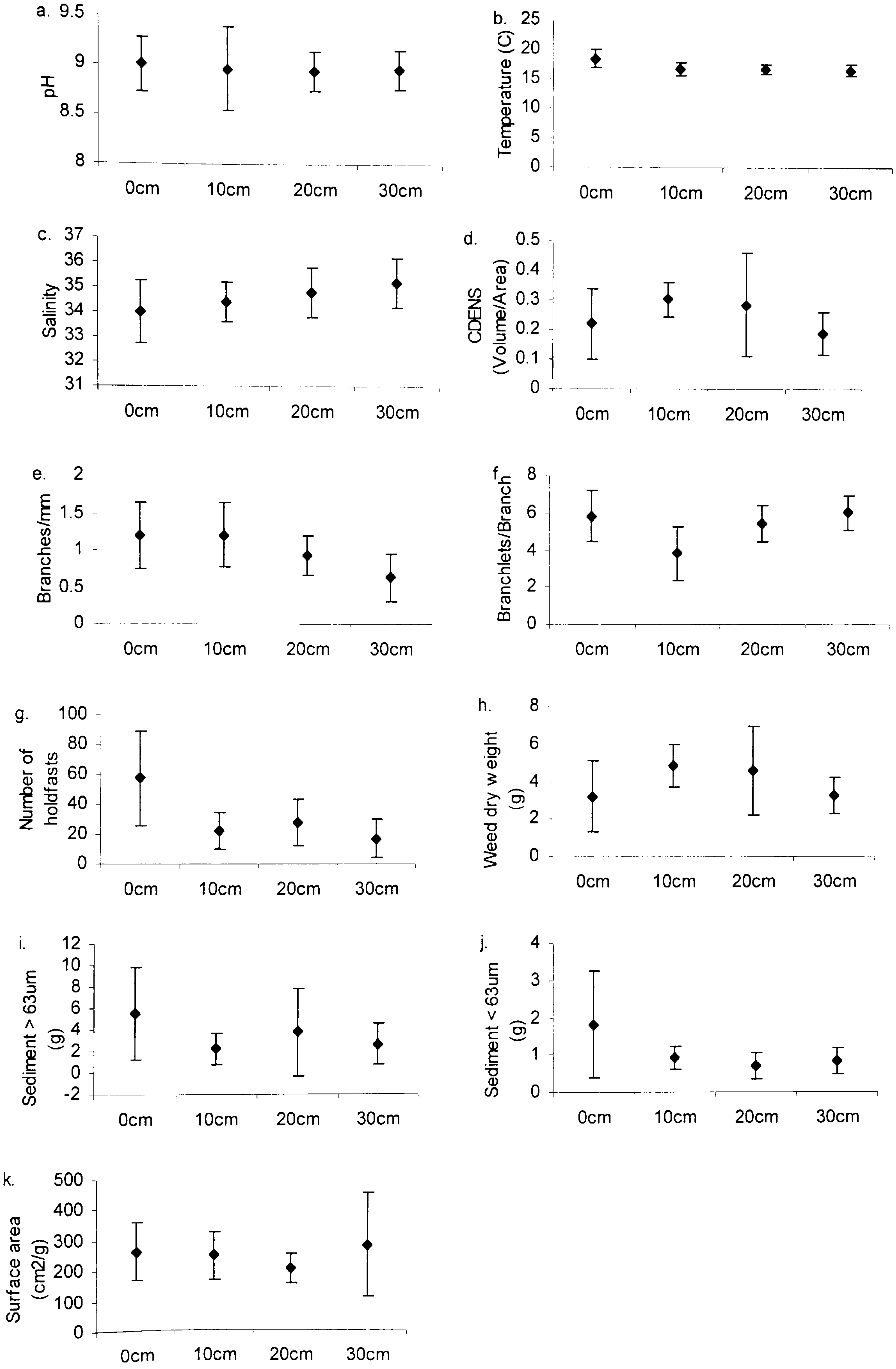


Figure 13a-k. Mean and 95% confidence intervals for environmental measures of habitat from samples collected at different depths amongst coralline turf in tide pools at Cemlyn in June 2001.

Environmental Data

Significant differences in measured environmental variables were only shown between the number of holdfasts at different depths (Table 13, Fig. 13). Although not significant there was a general trend of increasing salinity with increasing depth (Fig. 13c). For small and large pools on the high and low shore there was significantly higher pH and temperature in high shore pools compared to low shore pools (Table 14, Fig. 14a+b). More large sediment fraction (>63um) was collected from high shore small pools than all other pools (Table 14, Fig 14i) and low shore small pools had significantly higher surface area per gram dry weight than high shore pools (Table 14, Fig. 14k). However, only the number of holdfasts were significantly correlated with the number of individuals at different depths within a tide pool (Table 15).

Before multivariate analysis, the number of holdfasts were square root transformed and dry weight measurements were $\log_{10}$ (x+1) transformed to approximate multivariate normality. The first two principal components of the environmental data capture relatively little of the variability, 47% for those associated with samples from depth profiles (Fig. 15a) and 56% for those associated with pools at small spatial scales (Fig. 15b). Environmental samples from depth profiles show some separation of samples from 0cm away from all other samples along PC2 though none were significantly different (Table 16). Broadly speaking PC2 appears to represent an increase in temperature, sediment weight and number of branchlets, or a combination of theses factors. For example, samples at shallow depthes had higher temperatures and high sediment loads. Principal component 1 represents decreasing *Corallina* density, number of holdfasts and dry weight of algae (Fig. 15a). Environmental samples form pools at small spatial scales show some separation of samples based on pool type but are predominantly separated by height on the shore. An ANOSIM test revealed all pairwise combinations of pool type to be significantly different except small and large pools on the high shore (Table 16). PC1 represents an axis of decreasing pH and temperature while PC2 predominantly represents decreasing density, number of branches and algal weight (Fig. 15b).

Matching of overall biotic and abiotic multivariate patterns after square root transformed and presence/absence species data and for both experiments produce some similar results (Table 17a-d). Temperature was consistently identified as were measures of sediment weight. Other measures of habitat complexity were also indicated such as number of branches and holdfasts for those samples from different

Table 14. Analysis of environmental measures of habitat from samples collected in different tide pools at small spatial scales from amongst coralline turf at Cemlyn, North Wales in June 2001. *, $p<0.05$; **,$p<0.01$; ***, $p<0.001$; ns, not significant. LS =Low shore small pool, LL=Low shore large pool, HS=High shore small pool, HL=High shore large pool.

Cemlyn, June 2001	(N=5)	pH		Temperature		Salinity	
Transformation		None		None		None	
	df	MS	F	MS	F	MS	F
Pool type	3	2.668	28.85***	25.07	17.71***	0.0405	1.98 ns
Residual	16	0.0925		1.42		0.0205	
Tukey's		HS & HL > LS & LL		HS & HL > LS, HS > LL			
		CDENS		Branches		Branchlets	
Transformation		None		None		None	
	df	MS	F	MS	F	MS	F
Pool type	3	0.0566	1.52 ns	0.204	1.72 ns	4.33	1.39 ns
Residual	16	0.0372		0.119		3.10	
Tukey's							

continued:

Cemlyn, June 2001	(N=5)	Number of holdfasts		Weed weight		Sediment > 63um	
Transformation		Square root		None		Log_{10} (x+1)	
	df	MS	F	MS	F	MS	F
Pool type	3	24.4	1.62 ns	14.34	1.81 ns	0.4026	7.66**
Residual	16	15.1		7.90		0.0526	
Tukey's						HS > LS & LL & HL	

		Sediment < 63um		Surface area	
Transformation		None		None	
	df	MS	F	MS	F
Pool type	3	0.182	1.09 ns	15163	3.57*
Residual	16	0.167		4247	
Tukey's				LS > HS & HL	

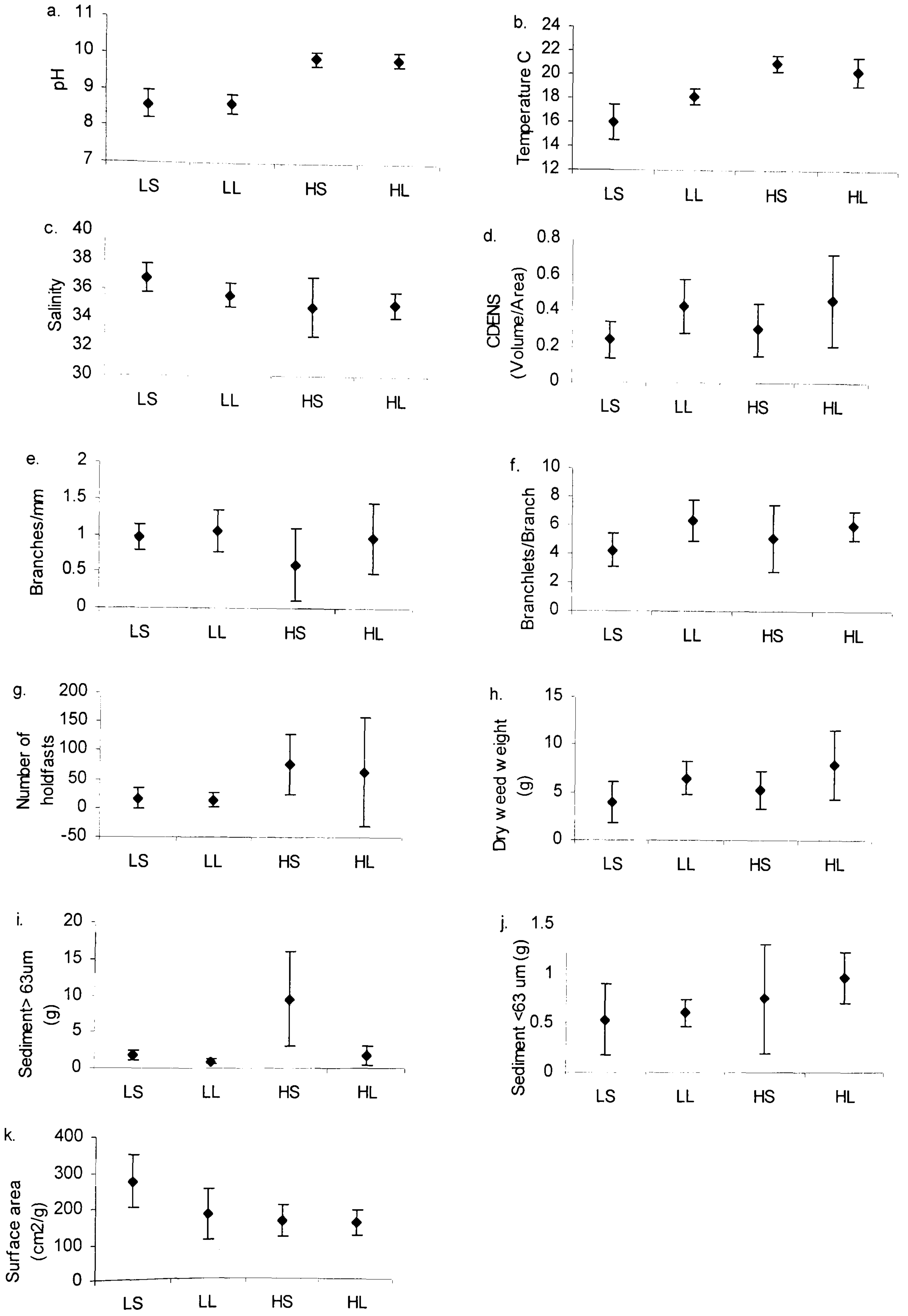


Figure 14a-k. Mean and 95% confidence intervals for environmental measures of habitat from samples collected on a small spatial scale amongst coralline turf in tide pools at Cemlyn in June 2001. LS=Low shore small pool, LL=Low shore large pool, HS=High shore small pool, HL=High shore large pool.

Table 15. Pearson product moment correlation coefficients between measured environmental variables and univariate measures of diversity at Cemlyn in June 2001for a) samples from different depths, and b) samples from pools at different small spatial scales. Significant correlation's where $p<0.01$ are indicated by bold type. *, $p<0.05$; **, $P<0.01$. S=number of species, n=number of individuals, d=Margalef's dominance, J=Pielou's evenness, N1=Hill's N1, N2=Hill's N2.

a.	pH	Temp °C	Salinity	CDENS	Branches	Branchlets	Holdfasts	Weed Wt (g)	Sediment >63um (g)	Sediment <63um (g)	Surface Area
S	0.116	0.228	0.027	0.282	-0.121	-0.062	0.447*	0.293	0.527*	0.201	0.094
n	0.003	0.155	0.141	0.321	-0.203	0.179	**0.569****	0.294	0.33	0.159	0.203
d	0.169	0.223	-0.007	0.137	-0.088	-0.148	0.260	0.167	0.488*	0.135	0.016
J	0.322	0.248	-0.233	-0.34	0.451*	-0.22	-0.257	-0.332	-0.180	-0.138	-0.237
N1	0.383	0.331	-0.148	-0.254	0.408	-0.317	-0.099	-0.239	0.056	-0.093	-0.243
N2	0.384	0.313	-0.111	-0.417	0.449*	-0.238	-0.205	-0.417	-0.061	-0.118	-0.213

b.	pH	Temp °C	Salinity	CDENS	Branches	Branchlets	Root Holdfasts	Weed Wt (g)	Sediment >63um (g)	Sediment <63um (g)	Surface Area
S	-0.329	-0.259	0.140	0.414	0.403	0.013	0.190	0.365	-0.139	-0.026	0.143
n	-0.324	-0.018	-0.219	0.503*	0.245	0.4	0.107	0.464*	0.033	0.209	0.081
d	-0.232	-0.294	0.295	0.216	0.309	-0.202	0.177	0.169	-0.162	-0.151	0.123
J	0.129	-0.173	0.445*	-0.363	-0.107	-0.451*	0.286	-0.364	0.250	-0.260	0.082
N1	-0.017	-0.240	0.501*	-0.295	0.063	-0.494*	0.333	-0.319	0.147	-0.222	0.191
N2	0.03	-0.132	0.461*	-0.348	-0.009	-0.488*	0.407	-0.38	0.192	-0.276	0.124

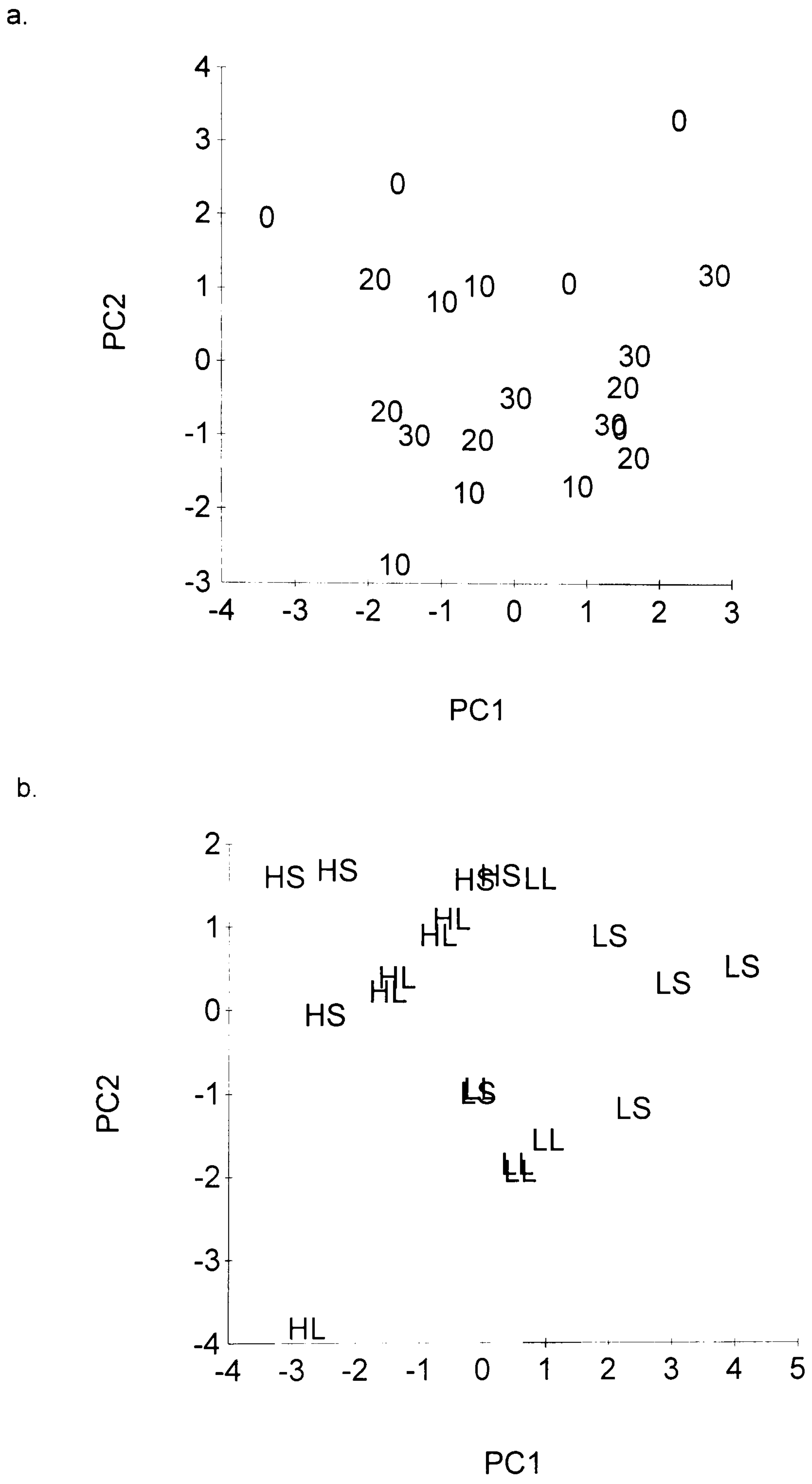


Figure 15. Principal component analysis of environmental variables collected at Cemlyn in June 2001 from a) different depths in tide pools, b) different tide pools at small spatial scales. 0=0cm deep, 10=10cm, 20=20cm, 30=30cm; LS=Low shore small pool, LL=Low shore large pool, HS=High shore small pool, HL=High shore large pool.

Table 16. Results of one-way ANOSIM tests on environmental data from coralline turf in tide pools at Cemlyn in June 2001 based on normalised Euclidean distance for samples collected from a) different depths in tide pools, b) small spatial scales from three shores. *,p<0.05; **p<0.01; ***, p<0.001; ns=not significant. Values in bold indicate a significant pairwise test found after a non significant global test. LS=Low shore small pool, LL=Low shore large pool, HS=High shore small pool, HL=High shore large pool.

a.

	Cemlyn Jun 2001
Global-R	0.064
Pairwise:	
0cm – 10cm	0.144
0cm – 20cm	0.062
0cm – 30cm	0.192
10cm – 20cm	-0.064
10cm – 30cm	0.092
20cm – 30cm	-0.124

b.

Global-R	0.403***
Pairwise:	
LS –LL	0.416*
LS – HS	0.652**
LS – HL	0.560**
LL – HS	0.544**
LL – HL	0.400*
HS – HL	0.060

Table 17a. Combinations of environmental variables yielding the best matches of biotic (square root transformed) and abiotic similarity matrices from different depths in tide pools at Cemlyn June 2001 as measured by Spearman rank correlation (rho), bold type indicates overall optimum. See Chapter 2 for variable abbreviations.

k	Best variable combinations (rho)		
3	0.344 °C Hold <63	0.307 Sal Hold <63	
4	**0.369** **°C Brchs Hold <63**	0.317 °C Hold >63 <63	0.311 °C Sal Hold <63
5	0.344 °C Sal Brchs Hold <63	0.339 °C Brchs Hold >63 <63	0.311 °C Brchs Hold Coral <63

Table 17b. Combinations of environmental variables yielding the best matches of biotic (presence/absence transformed) and abiotic similarity matrices from different depths in tide pools at Cemlyn June 2001 as measured by Spearman rank correlation (rho), bold type indicates overall optimum. See Chapter 2 for variable abbreviations.

k	Best variable combinations (rho)		
3	0.307 °C Hold <63		
4	**0.325** **°C Brchs Hold <63**	0.298 °C Brchs Hold >63	0.294 °C Brchs >63 <63
5	0.319 °C Brchs Hold >63 <63	0.301 °C Brchs Brts Hold <63	0.299 °C Brchs Hold Coral <63

Table 17c. Combinations of environmental variables yielding the best matches of biotic (square root transformed) and abiotic similarity matrices from tide pools at small apstial scales at Cemyln June 2001as measured by Spearman rank correlation (rho), bold type indicates overall optimum. See Chapter 2 for variable abbreviations.

k	Best variable combinations (rho)		
5	**0.559** **pH °C Brts Coral >63**	0.595 pH °C Sal Brts Coral	0.594 pH °C Sal Coral >63

Table 17d. Combinations of environmental variables yielding the best matches of biotic (presence/absence transformed) and abiotic similarity matrices from tide pools at small spatial scales at Cemlyn June 2001 as measured by Spearman rank correlation (rho), bold type indicates overall optimum. See Chapter 2 for variable abbreviations.

k	Best variable combinations (rho)		
2	**0.545** **°C >63**		
3	0.521 pH °C >63	0.520 °C Sal >63	
4	0.520 pH °C Sal >63	0.496 pH °C Brts >63	0.493 °C Sal Brts >63
5	0.510 pH °C Sal Brts >63	0.501 pH °C Sal >63 <63	0.492 pH °C Sal Coral >63

depths in tide pools (Table 17a-b) or branchlets and dry weight of algae form samples collected from different sized pools at different heights on the shore (Table 17c). These environmental data appear to be poor discriminators of differences in diversity and community structure at different depths in tide pools. They do, however, show some clearer differences between pools from different heights on the shore.

Discussion

In this study, patterns of diversity at small scales were different depending on the time of sampling and on the shore from on which they were collected. For example, no patterns were detected along a depth gradient in pools sampled at Cemlyn in the summer, while on the same shore in the winter, samples from greater depth produced higher measures of diversity than those from deeper depths. At Porth Cwyfan in winter the pattern appears similar to that at Cemlyn in the winter but with somewhat weaker evidence. Similarly, diversity measures between pools of different sizes and at different heights on the shore revealed inconsistent patterns related to the time and location of sampling.

Patterns associated with overall multivariate community assemblages also showed differences produced from different sampling times and different shores. However, community differences associated with depth gradients within pools, remained relatively consistent. Pairwise comparisons were always between those samples collected for shallow depths and deeper depths suggesting that the community in shallow areas of tide pools is consistently different from that in any other area of the turf (see below for discussion). The only time when this definitely was not the case was under presence/absence transformation at Porth Cwyfan in the winter. When assemblages were compared between pools of different size and at different heights on the shore, all combinations were different at Cemlyn in the summer. In winter samples only high shore small pools were significantly different from any other pool type. At Porth Cwyfan the pattern was again different with no differences between pools within the same height on a shore but all combinations of pools at different heights supported significantly different communities. Collecting these data highlights the high degree of variability in the fauna of *Corallina* turf and demonstrates the need for well structured sampling designs that can elucidate patterns as well as the causes and consequences of such patterns.

An important point to note is that pairwise differences in ANOSIM tests between depths of 10cm and below often produce negative R values. R values less than 0 indicate greater dissimilarity among replicates within a treatment than between replicates from different treatments (Clarke, 1993). In some comparisons negative R values can arise from very patchy assemblages among each set of treatments or as a result of outliers within the assembly data (Chapman and Underwood, 1999). In this study, the negative values of R are generally low but six out of the thirteen negative values are significantly different from 0. This suggests that variability between pools at the same depth is at least similar to the variability observed within pools at different depths in some cases. It could also suggest that below the shallowest depths, community patterns are particularly patchy within the *Corallina* turf. Negative R values in relation to pool size and height on the shore are fewer with only one out of five significant (between large pools under presence/absence transformation at Cemlyn Feb 2002). When the values of R are generally this close to 0 they can be easily interpreted as showing no difference in the structure of the two communities sampled (Chapman and Underwood, 1999).

Variable patterns of diversity at small spatial scales have been shown in similar habitats before. In a study of the assemblages associated with *Corallina officinalis* on open rock platforms in Australia, Kelaher *et al.* (2001) found significant differences between sites at each height on the shore but these differences varied from time to time. Also differences between different heights on the shore were inconsistent with differences detected in the number of species of gastropods between shore heights on some shores but not others (Kelaher *et al.*, 2001). Different patterns of variation in abundance of individual species of ostracods and in the structure of the assemblage have also been shown for coralline tide pools in North East England (Hull, 1999). On sheltered rocky shores in Australia similar variable patterns have been described (Underwood and Chapman, 1998) and components of midshore and lowshore assemblages that contributed most to spatial differences were not the same at every time of sampling. These results add to the already commonly held view that variability is usual (Underwood and Chapman, 1996) and that these would confound any interpretation of differences form shore to shore. This study suggests that lack of generality in patterns indicates that no common process is responsible for structuring high shore and low shore assemblages between the two shores studied and between the two times sampled, a conclusion similar to that reached by Kelaher *et al.* (2001) studying *Corallina* turf on Australian shores. It follows that local processes such as recruitment, predation and competition, that are themselves variable in space and time must be extremely important for structuring some aspects of the macrofaunal assemblage.

Patterns and distributions of species in this study are observational and therefore no experimental control of single factors was carried out. Coupled with high variability and inconsistent patterns it is not possible to determine the underlying processes that determine these patterns. It is possible to suggest potential mechanisms that may influence the observed pattern and stimulate future research. The pattern of different communities at shallow depths in tide pools from those at greater depth has several explanations. Firstly, there were significantly more holdfasts of *Corallina* at shallow depths in the pool. This indicates greater complexity of habitat at the base of the turf. Also, the turf at these depths was visibly different from that at all other depths although this was not revealed in the analysis of environmental variables. Most turf at greater depths in the pools was long and foliose with relatively long secondary branching. At shallow depths, by contrast, the turf was much shorter and densely packed, forming a moss-like cushion. Spaces between fronds in this case were much smaller, limiting the size of the invertebrates that live between them. Indeed, individuals form shallow depths were generally smaller than those from greater depth in the pools (pers. obs.). This obvious difference in habitat structure probably accounted for much of the difference in community structure between shallow depths and the rest of the pool. Habitat complexity has been shown to be a strong influence on community structure previously, especially in marine phytal communities (Hicks, 1980, 1985; Jarvis and Seed, 1996; Davenport *et al.*, 1999). Other measures of habitat complexity identified by BIOENV were, number of branches and amount of fine sediment, in combination with temperature and number of holdfasts (see above). This lends support to the view that increases in sediment load affects the diversity of invertebrate communities associated with marine macroalgae (Gibbons, 1988; Whorff *et al.*, 1995), as does increased structural complexity like branching (Hicks, 1980; Stoner and Lewis, 1985). It is also apparent from PCA of environmental variables that there was at least some separation of the samples at 0cm from those at deeper areas within the pool. Pools can also be stratified and show marked within pool variation for example in oxygen concentrations (Daniel and Boyden, 1975) temperature (Pyefinch, 1943) and salinity (Ganning, 1971) although this is often only at the shallowest depths (Morris and Taylor, 1983). The spatial variation in the environmental conditions of tide pools may make it possible for motile animals to avoid the most extreme conditions by moving to other areas of the pool. Behavioural adaptations may therefore be as important as physiological adaptations in enabling animals to tolerate unfavourable conditions within tide pools. However, the most common and abundant species associated with *Corallina* tend to be restricted in their movement. Only a few amphipods, like *Stenothoe monoculoides,* are common active swimmers. Most other species tend to be either permanently or temporarily attached to the alga making use of the rigid nature of *Corallina* fronds and their large surface area.

There is also a complex gradient with depth in tide pools that will affect the structure of the habitat as well as the epifauna found within it. Distinct bands in the zonation of algae with increasing depth in tide pools have been demonstrated on the Atlantic coasts of France by Kooistra *et al.* (1989) who suggested that extremes of temperature set the upper limits of zonation while lower limits were due to increased algal shading. In the present study it is likely that the observed pattern is due to the environmental parameters that act directly on the alga thus structuring the habitat differently at different depths. The most important of these is probably limited vertical space in the water colum of tide pools at shallow depths. *Corallina* is very rarely found on the emergent rock surface in the mid tide zone on the shores studied here, and then only in gullies and crevices that experience water run off from tide pools. The growth form of these patches resembles that seen at shallow depths in tide pools. *Corallina* turf has a low tolerance to desiccation and often bleaches when exposed to high summer temperatures, a phenomenen often observed at the edges ot tide pools (Johansen, 1974 and pers. obs.). It is probable that shallow water limits the growth of *Corallina* to short fronds that do not grow beyond the surface of the tide pool thus exposing the alga to extremes of desiccation.

The observed community differences with pool depth could also be influenced by an edge of patch effect, which in turn can also influence habitat complexity. For instance, mussels from the edge of patches attain larger sizes than mussels in the middle of the patch (Svane and Ompi, 1993). Samples from shallow depths are also invariably collected from the edge of a patch of habitat as shallow depths nearly always occur at the edge of tide pools. Many studies of diversity associated with mussel beds have demonstrated a significant edge of patch effect, generally documenting reduced diversity in the peripheral areas of the patch (Suchanek, 1980; Seed and Brotohadikusumo, 1994). Lower diversity was attributed to lower complexity of habitat at the edge of mussel patches as well as reduced protection from extremes of light, wave action and temperature. This was not the case in this study where diversity was at least as high or higher at the edge of a patch than from further into the pool. However Svane and Setyobudiandi (1996) demonstrated no edge of patch in effect in mussel beds and concluded that inherent variability amongst samples at the smallest scale concealed patterns found at higher spatial scales while only differences in multivariate community structure were shown for patch edges in seagrass beds (Bowden *et al.*, 2001). In the present study differences in multivariate community pattern associated with edge of patch were relatively consistent whereas the corresponding univariate measures produced variable results. It would appear therefore, that edge of patch effect does exert some influence on the faunal assemblages in this study but larger scale regional and temporal variations in diversity and the factors acting upon it have greater influence on the community.

The patterns associated with pools of different size and from different tidal heights also have several explanations. The most obvious factor explaining some of the observed variability is that different heights on the shore invariably lead to different communities and different diversity due to prolonged periods of emersion high on the shore as has been documented before many times for communities on emergent substrata (see Southward, 1958; Raffaelli and Hawkins, 1999). Differences in tidal height were often more pronounced than differences between pools of different sizes as interpreted by larger R-values from ANOSIM tests. This pattern was not consistent and indicates that height on the shore is only able to explain some of the variability in communities associated with tide pools along this gradient. Explanations of vertical zonation in tide pools have centred on the change in environmental and physical characteristics with shore height and with pools size or volume. Huggett and Griffiths (1986) found a clear increase in biomass of animals and plants in tide pools further down the shore in South Africa. These differences were attributed mainly to changes in temperature and rate of heat input (pool size was not considered). Temperature has on several occasions been shown to be the primary factor in structuring tide pool communities (Pyefinch, 1943; Ambler and Chapman, 1950; Naylor and Slinn, 1958).

Fluctuations in temperature and salinity can vary with different tidal heights (Pyefinch, 1943; Metaxas and Scheibling, 1993) and in pools of different size related to their depth (Goss-Custard *et al.*, 1979). Daily fluctuations in dissolved oxygen concentration and pH have been recorded which are a result of biological processes in tide pools (Pyefinch, 1943; Ganning, 1971). These fluctuations invariably depend on the period of emersion which is controlled by tidal height and the amount of algae contained within the pool, which is in turn limited by the size of the pool. Although neither pH nor temperature was significantly correlated with diversity, both were significantly higher in high shore pools than in low shore pools, and high shore small pools had the highest temperatures with the least variability. Also, both of these parameters, in combination with the number of branchlets and dry weight of alga and fine sediments, had the best correlations for matching multivariate community pattern.

The size of a pool could have an area effect on community composition. In ecology it is a generally accepted phenomenon that patches of larger size support greater numbers of species (MacArthur and Wilson, 1967). However, in marine communities this generalisation has been questioned (e.g. Anderson, 1999) and in the present study, number of species was not significantly different for any combination of pool sizes. This is somewhat unexpected but lends some support to the elimination of certain theories. The habitat diversity hypothesis suggests that number of species is greater in larger areas because of related increase in diversity of habitats or niche space (Connor and McCoy, 1979) and this effect has been shown in mussel patches (Svane and Ompi, 1993; Lintas and Seed, 1994; Svane and Setyobudiandi, 1996). This would suggest that in this study, habitat diversity remained relatively homogenous independently of patch size (in fact only coarse sediment had higher concentrations in high shore small pools). Also PCA and subsequent ANOSIM revealed much stronger separation of samples in relation to height on the shore rather than to patch size (but see chemical parameters of habitat discussion below).

An overemphasis on number of species and the species area relationship in the literature has detracted from the issue of how assemblages may differ in composition between patches of different size (Keough, 1984). Differences were shown here in terms of assemblage composition. Causes for such variation in species composition may include differences in life history characteristics and adaptations of different species for different sized patches (Anderson, 1999). Small patches can provide refuge for species that are poorer competitors and would be out-competed in larger areas (Jackson, 1977; Keough, 1984) and other causes may include variation in levels of disturbance. Thus, species in small patches will most likely be poor competitors with wide dispersal and rapid colonisation ('r' strategists, see Pianka, 1970; Begon *et al.*, 1996), whereas species in large patches will tend to be 'K' strategists with limited dispersal and good competitive abilities (Bowden *et al.*, 2001). The dominant species in all pools, *S. corallinae* could be considered a K strategist as its larvae often settle without a pelagic stage (Gee, 1963) particularly on *Corallina* (De Silva, 1962). In fact the majority of species within the turf have limited dispersal and release of offspring is often directly into the habitat (Emson, 1985). This is likely to be due to the relative stability of the habitat. *Corallina* turf represents a climax community (Littler and Littler, 1980) and is a very stable habitat in space and time. Thus, perhaps the size of patch on this scale is less relevant as the patch is still very stable forming a continuous turf covering the base of pools.

It is clear from this study that the biodiversity and structure of the invertebrate assemblage associated with *Corallina* turf in tide pools is highly variable. Differences were detected on both shores and at both times of sampling although the patterns of these differences were not consistent. The main factors contributing to patterns of biodiversity in this study appear to represent a complex suite of parameters that interact with each other producing variable results. For example, differences in patch size bring about differences in physical parameters which influence the nature of the biologically generated habitat. This study demonstrates the need for well-structured manipulative field experiments to elucidate the main factors responsible for structuring community assemblages in tide pools at small spatial scales.

Chapter 5

Temporal variability in the invertebrate fauna associated with *Corallina officinalis*

ABSTRACT

The description of temporal change in community patterns is essential to understand the processes that structure assemblages. Bimonthly samples over a one year period, and 6 monthly samples over a two year period were collected to identify the temporal patterns in the diversity and community structure of macroinvertebrate species associated with *Corallina officinalis* turf in tide pools on the coast of North Wales, UK. While many measures of univariate diversity remained constant over the scales measured, number of individuals increased during summer months across all shores. Multivariate measures of the community show a strong seasonal signal in the community patterns. The strength of this signal is not, however, consistent between shores. Certain suites of species are identified as being the main cause of the observed patterns, largely due to their behavioural adaptations and life history characteristics within the tide pool environment. Other seasonally influenced factors, such as, temperature and reproductive state of the alga also directly influence the community. The seasonal signals within the first year seem to be replicated in the next, though the actual community in the second year is somewhat different to that of the previous year. Hence, there is a largely noticeable pattern of within year variability but a more subtle pattern of between year variability in the fauna. The results of this study are consistent with those of previous studies in that temporal variation of the invertebrate fauna of *Corallina* turf must be considered when designing sampling designs for experiment or environmental monitoring.

Introduction

The description of species abundance and community patterns over time is essential to understanding processes that structure assemblages of organisms in marine communities (Hartnoll and Hawkins, 1980; Southward, 1991; Southward *et al.*, 1995). The effect of a seasonal gradient on species diversity has often been noted alongside the gradient of different latitudes (Begon *et al.*, 1996). In tropical areas, seasonal variability may not be evident in terms of species richness (Barletta *et al.*, 2000) or may only be limited to variation between wet and dry seasons (Stoner and Lewis, 1985). In such regions variation between years is often more marked than variation within years (Lubchenco *et al.*, 1984). In more temperate regions, seasonal variability, along with changing climate increase variability within years, often giving rise to a seasonal pattern (e.g. Edgar, 1983a; Gunnill, 1983; Hicks, 1977c; Hull, 1997). This pattern is evident even in subtidal sediment communities (Flach and Heip, 1996) which are sustained largely by organic matter settling from the euphotic zone (Gooday, 2002).

Studies of seasonal change in invertebrate species richness and diversity have long been an integral part of marine phytal research (Colman, 1940; Hagerman, 1966; Fine, 1970; Gunnill, 1983; Johnson and Scheibling, 1987 and see review by Hicks 1985). There also continue to be frequent studies into temporal variability of invertebrate species associated with large macroalgae on rocky shores (Farnsworth and Ellison, 1996; Menconi *et al.*, 1999; Olabarria and Chapman, 2002), and with other biogenic structures including mat-like habitats such as mussel beds (Peake and Quinn, 1993; Smith, 2001). The study of community change within and between years is important if a complete species list is to be obtained for an assemblage (Warwick, 1977).

Causes of seasonal variability in marine algal epifaunas has been attributed to a variety of factors, for example, seasonal changes in temperature (Hagerman, 1966; Metaxas and Scheibling, 1994), desiccation (Colman, 1940), algal growth (Hagerman, 1966; Seed and O'Connor, 1981; Seed, 1985) and decay (Edgar, 1983a; Hicks, 1985), abundance of epiphytes (Colman, 1940; Edgar, 1983a; Gunnill, 1983), food supply (Hicks, 1985; Preston and Moore, 1989), periodicity of life cycles (Connell, 1985; Hicks, 1985; Hull, 1997), immigration and emigration (Gunnill, 1983; Hull, 1997), behaviour e.g. of *Nucella* (Hartnoll and Hawkins, 1980), and seasonal disturbances such as storms (Oswald and Seed, 1986) and frosts that may lead to over-wintering within the shelter of algal fronds (Preston and Moore, 1989).

Several studies have observed distinct seasonal occurrence of algae within tide pools (Goss-Custard *et al.*, 1979; Underwood and Jernakoff, 1984; Metaxas *et al.*, 1994) and of the physico-chemical conditions within tide pools (Morris and Taylor, 1983) but few have gone on to study the seasonality of the fauna associated with algae tide pool algae (but see Preston and Moore, 1989).

This chapter tests the hypothesis that there is significant seasonal (within year variation) and annual (between year variation) in the macroinvertebrate fauna associated with *Corallina officinalis* turf in tide pools. Which species are responsible for any observed pattern are investigated with probable causes for their significance outlined. A second hypothesis is that various environmental variables associated with *Corallina* turf in tide pools will also show significant within year variability in a similar way to the species assemblage. It has been shown previously that studies of community patterns measured over seasonal scales can be expected to show a pattern of cyclicity (Warwick, 1977; Clarke and Gorley, 2001). Such a pattern might arise In this instance as samples taken from adjacent months will be more similar to each other than those taken from months that are further apart in time. This pattern continues until the sampling proceeds beyond six months and the months start to become closer together again, i.e. December, is only one step away from January not eleven. Hence, this study tests the hypotheses that there is a seasonal pattern of cyclicity in the multivariate community pattern of macroinvertebrates associated with *Corallina* turf. The possible influence of environmental variables over the observed variation in the macroinvertebrate community is also investigated. In addition it has been shown previously that in multivariate analyses of the effects of natural variability on community composition, many species are interchangeable in the way that they characterise the samples, giving rise to the concept of structural redundancy (Clarke and Warwick, 1998a). Redundancy in community composition implies that many species are interchangeable in the way that characterise an assemblage (Mistri *et al.*, 2001). Therefore, a community with high structural redundancy may in effect be an indirect measure of the resilience or compensation potential within an assemblage to disturbance or unnatural change such as those caused by oil pollution events (Clarke and Warwick, 1998a). A multivariate routine is therefore employed here to investigate the levels of structural redundancy over a temporal scale on each of the shores studied.

This chapter attempts to describe temporal patterns in the fauna and environmental variables associated with *Corallina* turf. Which species and which environmental variables best explain the observed patterns are identified and as such the level of structural redundancy in each habitat is determined.

Methods

One large pool on each of three different shores (Porth Ysgaden, Porth Cwyfan and Cemlyn) in North Wales was chosen for this study. To determine the within year variability, pools were sampled bimonthly for 12 months starting in April 2000 and finishing in April 2001. All pools were then resampled in October 2001 and April 2002 in order to investigate the patterns of between year variability in the associated fauna. For the purpose of the analyses the samples collected as part of the within year study in April 2000 and October 2000 were also used as part of the between year study. On each sampling occasion only one pool was studied on each shore to minimise the amount of spatial variability in the data. This led to each set of samples effectively being pseudoreplicates; thus for analysis samples for each tide pool on each sampling occasion were pooled then averaged to produce one average sample per pool per sampling occasion.

Samples were sorted and analysed according to the methodology described in Chapter 2 with some modifications due to the experimental deisign. Due to pseudoreplication of samples, normal Analysis of Variance was not appropriate and therefore each of the two analyses was carried out in the following way. Univariate measures of diversity and environmental variables were analysed using a two-way ANOVA without replication (Scheffe test, Dytham, 1999) with shore and month (or season) as factors. Changes in multivariate pattern of biotic and environmental variables were analysed using an two-way analysis of similarities without replication (ANOSIM2) test, again with shore and month (or season) as factors. To test the hypothesis that there is a seasonal cyclic pattern in the community, a multivariate Spearman rank correlation technique was used on the species sample similarity matrix (RELATE, Clarke and Gorley, 2001).

To identify those species responsible for any observed temporal patterns a multivariate algorithm was used (BVSTEP). The procedure can be thought of as a generalisation of the SIMPER approach (Chapter 2) to the case of continuous multivariate patterns rather than a clearly defined clustering of samples (Clarke and Warwick, 1994, 1998a). Species subsets are derived using a forward selection, backward elimination procedure to find the smallest set of species that best matches the overall pattern using a Spearman rank correlation coefficient rho. For a subset to be selected it must exceed a predetermined level of rho (rho>0.95). Selected subsets of species will have an underlying similarity matrix that is highly correlated with the similarity matrix for the overall data. It follows that any ordination produced would be similar in appearance to that of the ordination of all the data. Having found the first species subset, the routine is repeated in order to investigate whether there are further subsets that replicate the full community pattern. The species constituting the first subset are excluded and the routine re-run for the reduced species matrix against the full set. This procedure was continued until no further subsets were detected with a rho ≥ 0.95. In this way all mutually exclusive subsets of species that act as a 'proxy' for the full data are detected. This technique is also used as an indication of the level of structural redundancy within an assemblage. The higher the number of selected subsets of species that match the overall multivariate pattern, the higher the level of structural redundancy in that assemblage. All other sampling and analysis was carried out according to the methodology in Chapter 2.

Results

A total of 38 685 individuals were counted and identified during the course of this study. This included 147 species and higher groups of which 32 were found in only one sample, 28 of which contained only one individual. There were representatives from 12 phyla with most species coming from the Annelida (49 species), Crustacea (38 species) and Mollusca (34 species). The dominant faunal groups were polychaetes (48 species), gastropods (25 species), amphipods (19 species) and pycnogonids (10 species).

A two way analysis of variance (ANOVA) without replication (Scheffe test) revealed significant differences for some univariate measures of diversity over a twelve month period or one full seasonal cycle (Table 1). Number of individuals, Pielou's evenness and Hill's N_1 and N_2 all showed significant variation between shores while only the number of individuals showed significant variation with season (Table 1). Number of species recorded and Margalef's richness measure remained relatively consistent between shores and over time (Fig. 1a & 1c) while number of individuals increased during the summer months to a maximum in October before falling off again in the winter (Fig. 1b). This pattern was most pronounced at Porth Cwyfan, which had higher numbers of individuals than Porth Ysgaden or Cemlyn on nearly all sampling

Table 1. Two way analysis of variance without replication (Scheffe test) on univariate measures of diversity from samples collected at bi monthly intervals from Porth Ysgaden, Porth Cwyfan and Cemlyn between April 2000 and April 2001 inclusive. *, p<0.05; **, p<0.01; ***, p<0.001; ns, p>0.05.

		Number of species			Number of individuals			Margalef's d		
	df	SS	MS	F	SS	MS	F	SS	MS	F
Shore	2	128.38	64.19	3.21 ns	6430887	3215443	10.77**	1.4675	0.7338	2.13 ns
Season	6	317.24	52.87	2.65 ns	5626558	937760	3.14*	4.0556	0.6759	1.96 ns
Residual	12	239.62	19.97		3583904	298659		4.1320	0.3443	

		Pielou's evenness J'			Hill's N_1			Hill's N_2		
	df	SS	MS	F	SS	MS	F	SS	MS	F
Shore	2	0.241	0.120	21.23***	192.21	96.105	20.58***	39.123	19.561	14.16**
Season	6	0.026	0.004	0.77 ns	17.315	2.886	0.62 ns	1.979	0.330	0.24 ns
Residual	12	0.068	0.006		56.03	4.669		16.577	1.381	

Table 2. Two way analysis of similarites without replication on square root and presence absence transformed species abundance data collected from three shores, Porth Ysgaden, Porth Cwyfan and Cemlyn at bi monthly intervals between April 2000 and April 2001 inclusive.

	Global R	
	Square Root	Presence Absence
Season	0.275*	0.371*
Shore	0.333 ns	-0.143

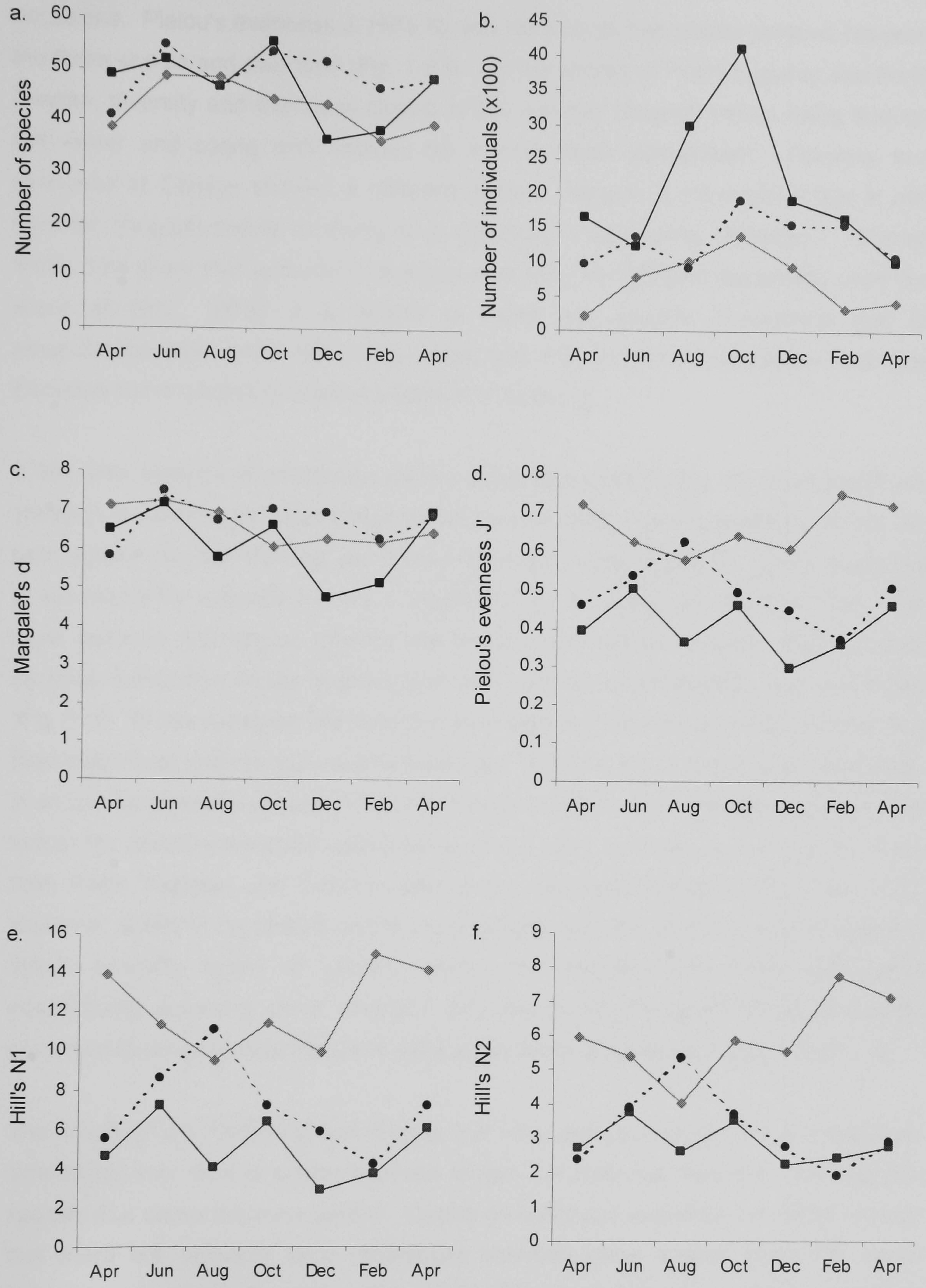


Figure 1 a-f. Univariate measures of diversity for invertebrates collected from three tide pools on three shores (Porth Ysgaden, Porth Cwyfan and Cemlyn) in North Wales over a 12 month period from April 2000 until April 2001. ◆ Porth Ysgaden, ■ Porth Cwyfan, ● Cemlyn.

occasions. Pielou's evenness J, Hill's N_1 and Hill's N_2 all had similar patterns between the three shores and over time (Fig. 1 d-f). On the shores of Porth Ysgaden and Porth Cwyfan, diversity and evenness dipped in mid summer (August) before rising through the winter and spring with another dip in mid winter (December). Diversity and evenness at Cemlyn showed a different pattern, rising to a maximum value in mid summer (August) before declining to a minimum in late winter (February). Overall these data show that patterns in diversity over time are different depending upon the shore studied. While it is difficult to reach any specific conclusions due to peseudoreplication within tide pools, in general, the number of individuals within the *Corallina* turf is subject to marked seasonal fluctuations.

A two way analysis of similarities without replication (ANOSIM2) indicated significant variation in community assemblage structure over time, but not between shores, for both square root transformed and presence/absence data (Table 2). Some clustering of samples from adjacent months is apparent from dendrograms (Fig 2+3 ai-ci). The most common and largest clusters are formed from winter samples; while summer samples sometimes cluster together they also cannot be left isolated, e.g. at Cemlyn (Fig 2 ci). It was expected that samples from adjacent months would be more similar than those from months that were furthest apart, and that the community would change in an annual seasonal pattern. This would produce nMDS plots that were circular. Only two of the nMDS ordinations appeared to exhibit such a pattern at first glance, those from Porth Ysgaden and Cemlyn after square root transformation (Fig 2 aii + cii). However, a test of correlation on the underlying Bray-Curtis similarity matrix against a model similarity matrix of cyclicity, where the sample relationships are placed equidistantly around a circle, revealed only the community at Porth Cwyfan under presence absence transformation to have a non cyclic or seasonal pattern (Table 3).

The results of the ANOSIM2 test reveals that the pattern of change in the invertebrate community over time is similar between shores. It does not, however, infer that the species that cause them are similar. Cluster analysis and ordination by nMDS indicate that there are probably clear differences between these shores given the visual separation of samples from them (Fig 4 a+b). Therefore each shore will be considered individually when searching for the species responsible for seasonal patterns and levels of structural redundancy.

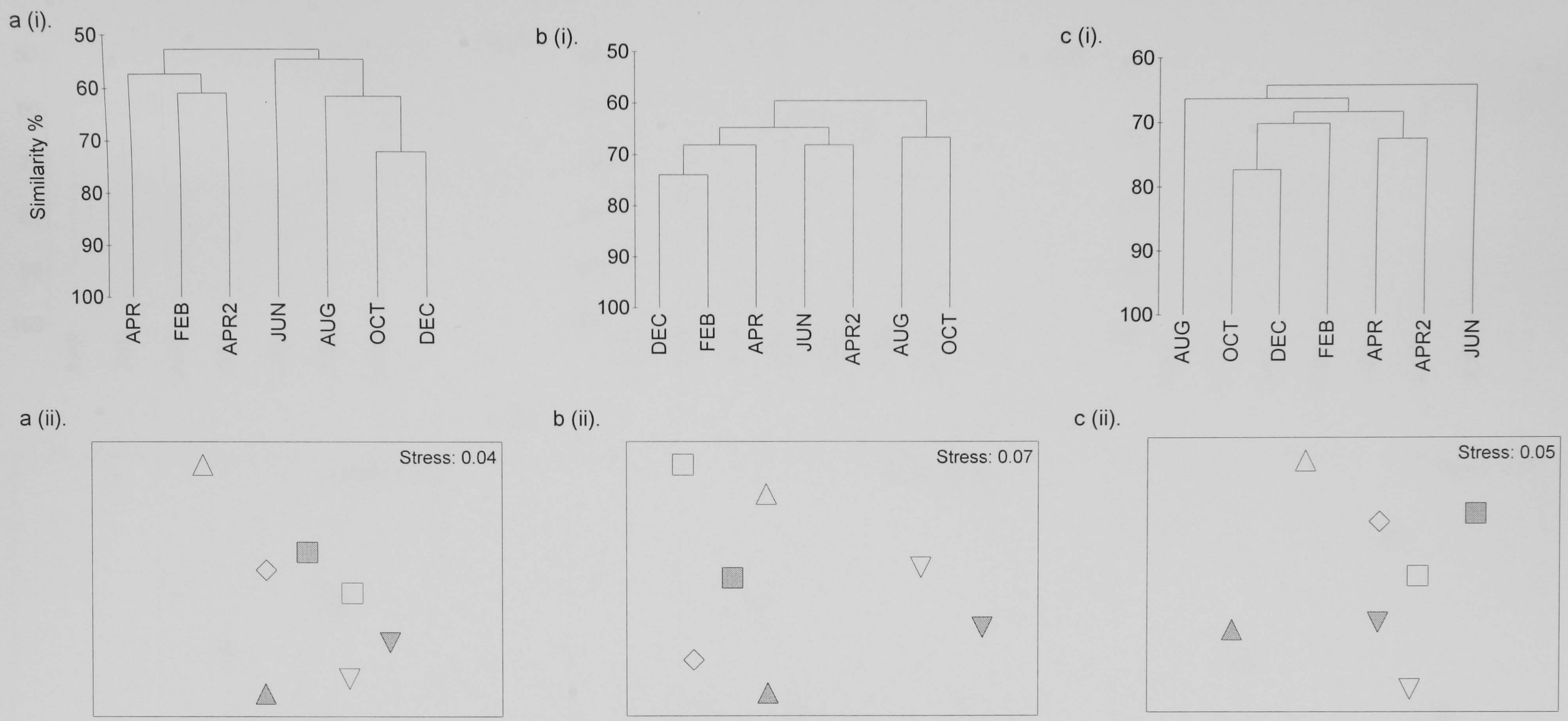


Figure 2 a-c. Dendrograms (i) for group average clustering and nMDS (ii) ordinations of Bray-Curtis similarities based on square root transformed species abundance data from coralline turf in tidepools taken at bimonthly intervals from April 2000 until April 2001 inclusive, on three shores a) Porth Ysgaden, b) Porth Cwyfan, c) Cemlyn. Δ April 2000, ▲June 2000, ▽August 2000, ▼October 2000,□ December 2000 ■ February 2001, ◊ April 20001.

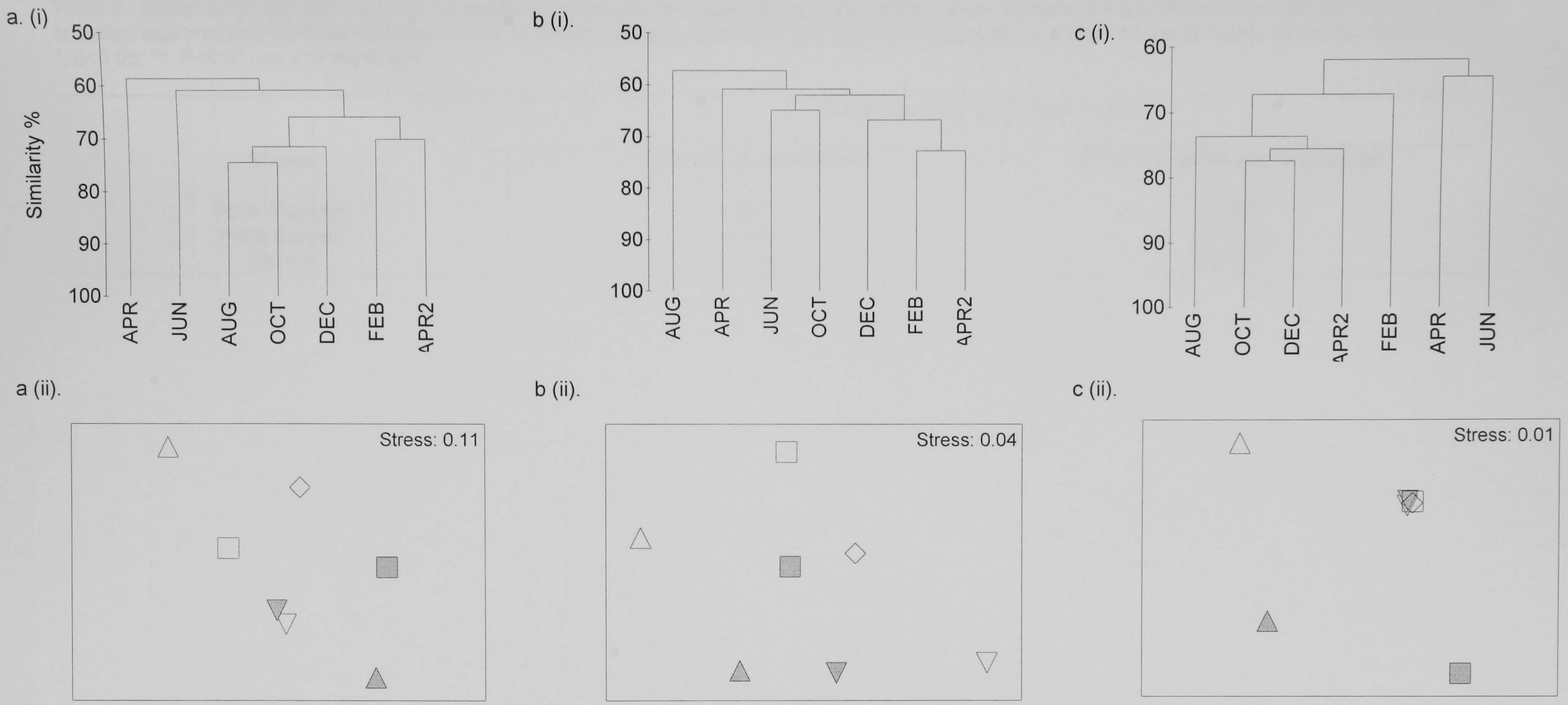


Figure 3 a-c. Dendrograms (i) for group average clustering and nMDS (ii) ordinations of Bray-Curtis similarities based on presence absence transformed species abundance data from coralline turf in tidepools taken at bimonthly intervals from April 2000 until April 2001 inclusive, on three shores, a) Porth Ysgaden, b) Porth Cwyfan, c) Cemlyn. Δ April 2000, ▲June 2000, ▽August 2000, ▼October 2000,□ December 2000 ■ February 2001. ◊ April 20001.

Table 3. Correlations between Bray Curtis similartiy measures from species abundance data under square root and presence/absence transformed data collected at bi monthly intervals on three shores in Wales between April 2000 and April 2001, against the model similarity matrix for cyclic seasonal data. *, $p<0.05$; **, $P<0.01$; ns, not significant.

	Spearman rank correlation (ρ (rho))	
Shores	Square root transformed	Presence absence transformed
Porth Ysgaden	0.597**	0.265*
Porth Cwyfan	0.318*	0.111 ns
Cemlyn	0.472**	0.371**

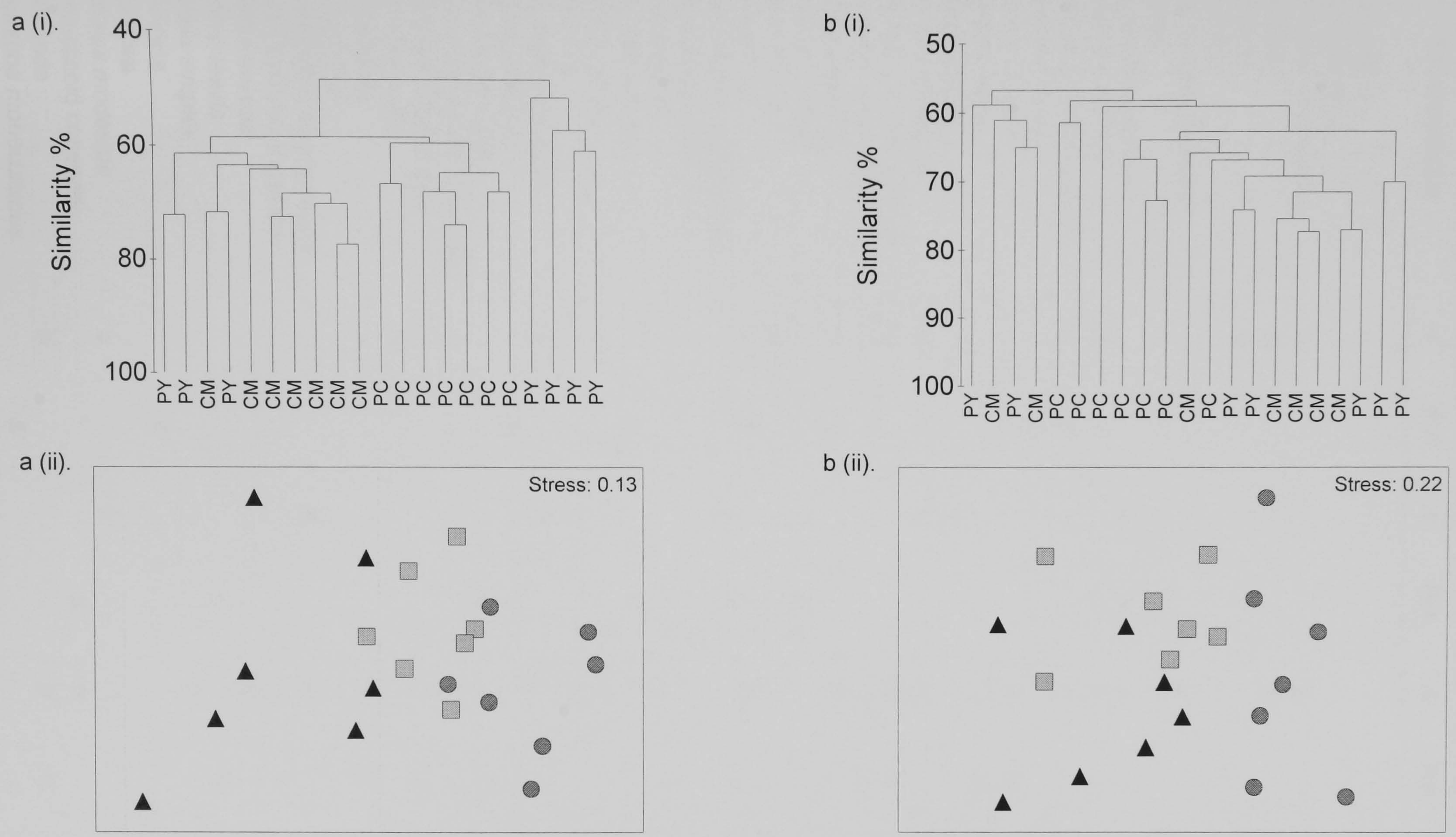


Figure 4. Dendrograms (i) for group average clustering and nMDS (ii) ordinations of Bray-Curtis similarities based on a) square root and b) presence/absence transformed species abundance data from coralline turf in tidepools taken at bimonthly intervals from April 2000 until April 2001 inclusive, on three shores in North Wales.
▲ Porth Ysgaden, ● Porth Cwyfan, ▨ Cemlyn.

Table 4. Species identified by BVSTEP analysis as indicators of overall cylclic multivariate pattern from the three shores and under both square root and presence/absence transformation. 'a' indicates species identified on first run of analysis, 'b' second run and so on.

Species	Porth Ysgaden		Porth Cwyfan		Cemlyn		Total times selected
Transformation:	√	P/A	√	P/A	√	P/A	
Foraminifera	d						1
Platyhelminthes							
Convoluta convoluta	c				b		2
Nematoda	b				a		2
Nemertea	d						1
Sipuncula							
Aspidosiphon muelleri					c		1
Annelida							
Sabellaria spinulosa			a	a	d		3
Cirratulus filiformis	d				d	c	3
Dodecaceria concharum	c	a			d		3
Malacoceros sp.		a					1
Polydora ciliata					b	b	2
Polydora flava					b	a	2
Polydora caeca			a				1
Spirorbis corallinae	c		a		d		3
Amphiglena mediterranea	d				a	a	3
Demonax langerhansi	c				c	a	3
Fabriciola baltica	d	a			d		3
Laonome kroyeri				a			1
Brania clavata	a						1
Exogone sp.	b	a		a	d		4
Odontosyllis ctenostoma			a	a			2
Odontosyllis gibba						c	1
Syllis gracilis					b		1
Lepidonotus sp.		a					1
Phyllodoce sp.					c		1
Pholoe sp.			a		d		2
Platynereis dumerilii	c		a				2
Nereis pelagica		a					1
Kefersteinia cirrata				a		b	2
Micromaldane ornithochaeta	d				b		2
Nicomache lumbricalis	c				d	c	3
Capitellid indet.	c						1
Oligochaeta						b	1
Pycnogonida							
Anaplodactylus pygmaeus			a		c		2
Anaplodactylus angulatus					c	b	2
Achelia hispida					c		1
Achelia laevis						b	1
Achelia simplex					c		1
Arachnida		a					1
Crustacea							
Elminius modestus	a		a				2
Harpacticoid copepods				a	d		2
Ostracoda	b				b	c	3
Stenothoe monoculoides		a					1
Melita sp.			a				1

Species	Porth Ysgaden		Porth Cwyfan		Cemlyn		Total
Transformation:	√	P/A	√	P/A	√	P/A	
Hyale prevostii	c						1
Hyale stebbingi				a			1
Gammarellus sp.				a			1
Apherusa bispinosa	a						1
Apherusa jurinei	b		a	a			3
Dexamine spinosa					d		1
Calliopius laeviusculus		a					1
Ampithoe helleri	b				b		2
Ampithoe ramondii					c		1
Ampithoe rubricata		a	a	a	c		4
Sunampithoe pelagica					d	b	2
Ampeliscidae indet.	a						1
Caprella linearis						b	1
Caprella acanthifera				a	a	c	3
Idotea pelagica					b	b	2
Idotea granulosa					a		1
Jaera albifrons					b	b	2
Dynamene bidentata	d				c	a	3
Parasinelobus chevreuxi						c	1
Tanais dulongii	a						1
Mollusca							
Helcion sp.			a	a			2
Nucella lapillus				a			1
Onoba semicostata	a				d	c	3
Rissoella diaphana	b						1
Rissoa sarsi					d		1
Gastropoda juv.					a		1
Lacuna vincta					c		1
Littorina mariae					c	b	2
Littorina neglecta		a	a				2
Littorina indet.					d		1
Tricolia pullus						c	1
Barleeia unifascata	d	a			d		3
Odostomia plicata	c				b		2
Omalogyra atomus	a						1
Gibbula umbilicalis			a				1
Limapontia sp.					d	c	2
Lasaea adonsoni					b	c	2
Turtonia minuta	b			a		a	3
Venerupis sp.					d	c	2
Anomia ephippium					c	b	2
Modiolus modiolus	c		a		a		3
Musculus discors	c	a	a		a	b	5
Echinodermata							
Asterina gibbosa					a		1
Amphipholis squamata	d		a		d		3
Ascidiacea							
Ascidiella sp.			a				1
Molgula sp.	d						1
TOTAL	35	13	19	14	50	28	

A total of 89 species were identified by BVSTEP as being important in determining the overall multivariate pattern (Table 4). At Porth Ysgaden 35 species were identified in four subsets of BVSTEP without replacement after square root transformation, and 13 species were detected in one subset under presence/absence transformation. At Porth Cwyfan 19 species were identified under square root transformation and 14 under presence/absence transformation, both in only one subset of species. At Cemlyn 50 species were identified in four subsets under square root transformation and 28 species in three subsets under presence/absence transformation. 19 species were found in 50% of the samples. Thus, it appears that the invertebrate community associated with *Corallina* turf at Cemlyn has a high degree of structural redundancy, while at Porth Ysgaden there is only a high degree of structural redundancy when the most abundant species are influencing the analysis. At Porth Cwyfan there is a low degree of structural redundancy for both the abundant and rare components of the community.

All subsets of species produce similar ordinations to those for the entire set of species (Fig. 5). This indicates that the species in the subsets have a strong influence over the observed cyclic pattern of the overall ordination. Bubble plots of relative abundance for four species selected by BVSTEP are shown in Figure 6. These species were selected *a posteriori* to give a general indication of the abundance patterns in the data. Each species is from a separate taxonomic group and was isolated by the BVSTEP procedure on all three shores. The ordinations suggest that these species vary markedly in abundance throughout the year often having increased abundance only at certain times of the year (Fig. 6).

A two-way analysis of variance without replication on samples collected every 6 months revealed a similar pattern of differences for univariate measures of diversity as the data taken at bimonthly intervals over one year (Table 5). Again, number of individuals, Pielou's evenness and Hill's N_1 and N_2 showed significant differences between shores and number of individuals showed significant differences between season (Table 5). Number of species and Margalef's richness remained relatively consistent between shores and through time (Fig 7. a+c). Number of individuals was also higher in both October samples for all shores, only Porth Ysgaden in October 2001 and April 2000, not showing a large difference (Fig. 7b). Patterns in measures of evenness, Hill's N_1 and Hill's N_2 all had the same pattern with values for Porth Ysgaden being consistently higher than on the other two shores (Fig. 7 d-f). Although these patterns suggest some consistency in patterns of diversity between shores over time,

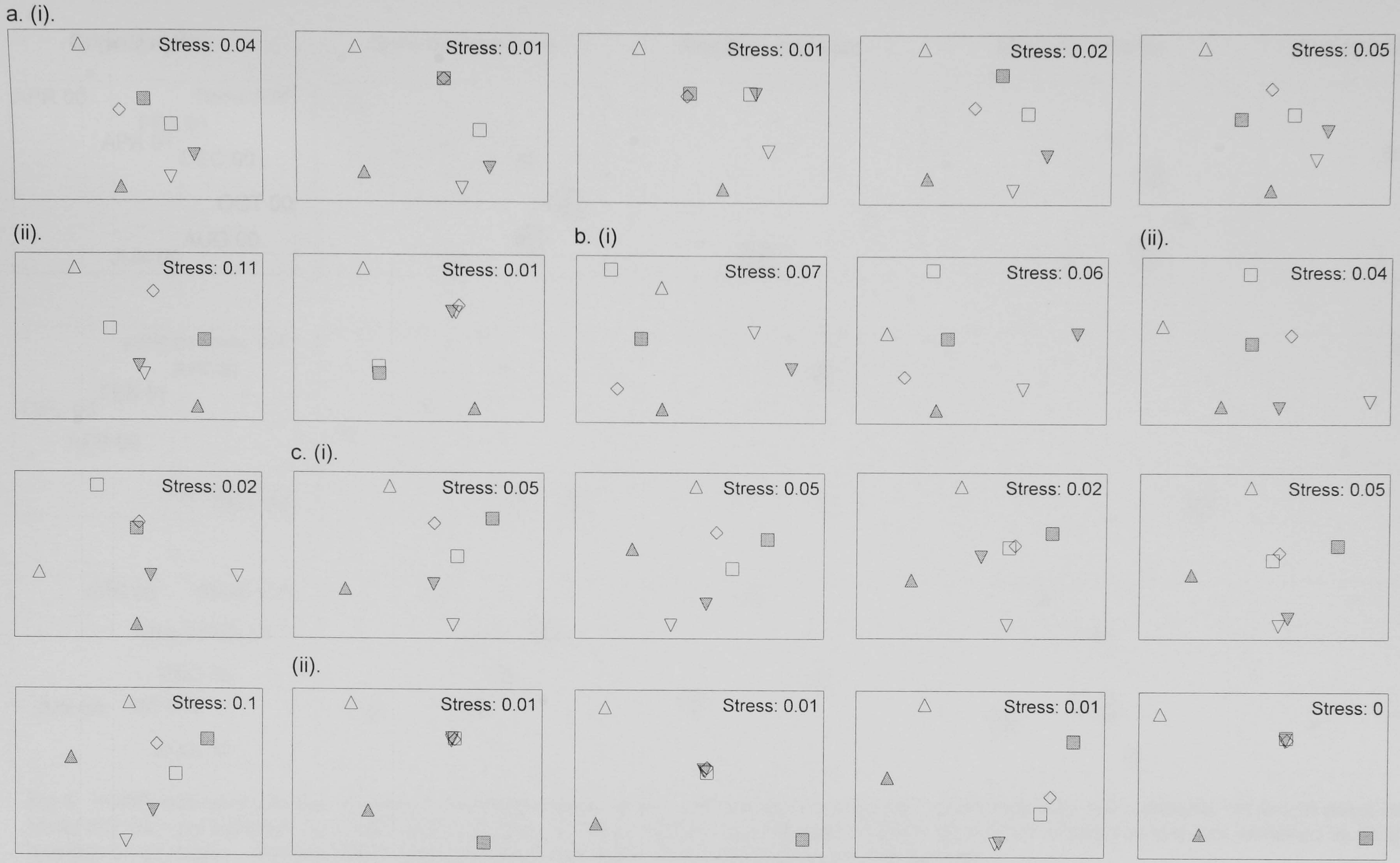


Figure 5. Ordination by nMDS based on Bray-Curtis similarity produced from subsets of species after i) square root transformation ii) presence/absence transformation, that best match overall species data for species abundance data from three shores, a) Porth Ysgaden b) Porth Cwyfan c) Cemlyn. Overall species ordination is shown first for ease of comparison with each subsequent ordination based on the subset of species. Δ April 2000, ▲ June 2000, ▽ August 2000, ▼ October 2000, □ December 2000 ■ February 2001, ◊ April 20001.

Fig 6. nMDS ordinations of Bray-Curtis similarities based on square root transformed species abundance data from coralline turf in tide pools taken at bimonthly intervals between April 2000 and April 2001 inclusive. Bubble size indicates relative abundance of species that was identified by BVSTEP analysis on all shores. Original nMDS ordination is shown first for date reference to the bubble plots.

Table 5. Two way analysis of variance without replication (Scheffe test) on univariate measures of diversity from samples collected every six months for two years from Porth Ysgaden, Porth Cwyfan and Cemlyn between April 2000 and April 2001 inclusive. *, p<0.05; **, p<0.01; ***, p<0.001; ns, p>0.05.

		Number of species			Number of individuals			Margalef's d		
	df	SS	MS	F	SS	MS	F	SS	MS	F
Shore	2	85.73	42.87	1.66 ns	5172156	2586078	6.19*	0.8390	0.4195	0.10 ns
Season	6	153.33	38.33	1.49 ns	7169498	1792374	4.29*	0.1877	0.0469	0.90 ns
Residual	12	206.27	25.78		3340778	417597		3.7374	0.4672	

		Pielou's evenness J'			Hill's N_1			Hill's N_2		
	df	SS	MS	F	SS	MS	F	SS	MS	F
Shore	2	0.092960	0.046480	9.36**	89.330	44.665	9.39**	15.496	7.748	6.31*
Season	6	0.015126	0.003782	0.76 ns	19.402	4.851	1.02ns	7.523	1.881	1.53 ns
Residual	12	0.039719	0.039719		38.051	4.756		9.819	1.227	

Table 6. Two way analysis of similarites without replication on square root and presence/absence transformed species abundance data collected from three shores, Porth Ysgaden, Porth Cwyfan and Cemlyn at six monthly intervals over two years between April 2000 and April 2002 inclusive.

	Global R	
	Square Root	Presence Absence
Season	0.491**	0.830**
Shore	0.400 ns	-0.200 *

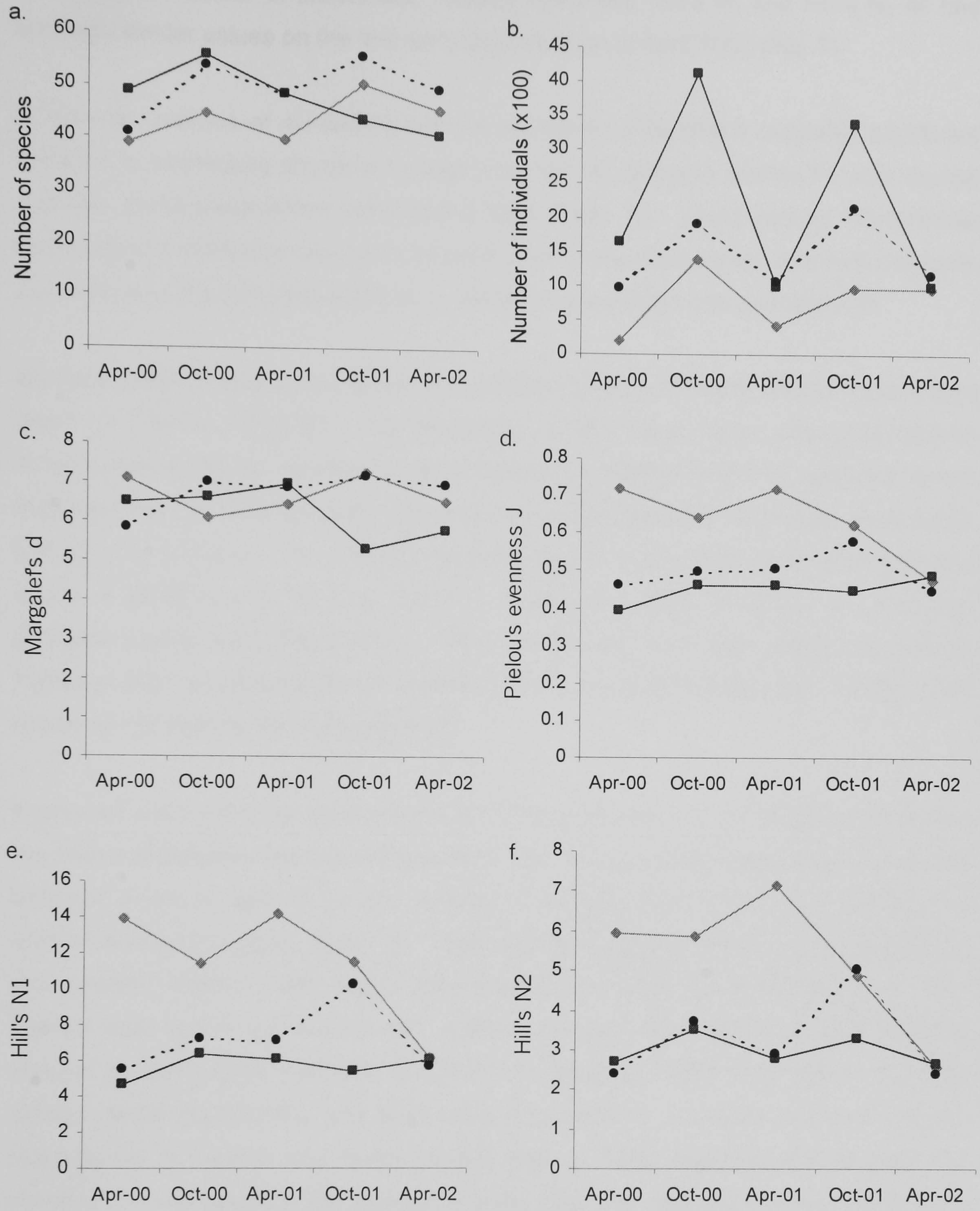


Figure 7. Univariate measures of diversity associated with community assemblages in *Corallina* turf collected from three tide pools on three shores in North Wales at 6 monthly intervals over two years. ♦ = Porth Ysgaden, ■ = Porth Cwyfan, ● = Cemlyn.

all values of number of individuals, Pielou's evenness, Hill's N_1 and Hill's N_2 all had strikingly similar values on the last sampling occasion in April 2002 (Fig. 7).

A two-way analysis of similarities without replication (ANOSIM2) indicated significant variation in community structure through time but not between shores for both square root and presence/absence transformed data (Table 6). These results mirror those found when considering bimonthly samples over a one year period and indicate some consistency in the temporal patterns in the fauna associated with *Corallina* turf.

Samples taken in April after square root transformation are clearly different from those taken in October (Fig 8). The separation is less clear under presence/absence transformation (Fig 9). However, a similar pattern is evident in all April samples, where samples taken in 2000 are more dissimilar to samples taken in 2002 than those taken in 2001 (Fig 8 and 9). Also October samples tend to cluster with each other at higher levels of similarity than do April samples, indicating greater variability in community structure during April (Fig 8 ai-ci). The only exception to this pattern is at Porth Ysgaden after presence/absence transformation where April 2002 and October 2001 cluster at the highest similarity (Fig 9 ai).

Measured environmental variables showed different patterns of variation throughout the year and between the three shores (Fig. 10). There were no significant differences between shore or season for pH, number of branches/mm, number of holdfasts or surface area of the algae (Table 7). There was a significant difference in temperature over season (Table 7) with higher temperatures recorded in the summer (Fig. 10b). Salinity also varied significantly with season although this difference was probably caused by one higher measure at Cemlyn in February 2001 (Fig. 10c). *Corallina* density varied significantly with both shore and season. *Corallina* was consistently more dense at Cemlyn and Porth Cwyfan than at Porth Ysgaden and all sites had elevated density values in the summer months (Fig. 7d). Numbers of branchlets were significantly different with season with the highest values recorded in April at all shores (Fig. 10f). Dry weight of alga and sediment (>63µm and <63µm) all varied significantly with shore but not season (Table 7) with highest weights recorded at Cemlyn and Porth Cwyfan (Fig 10h-j). Overall these data indicate that the environmental variables associated with *Corallina* turf vary at different scales of space and time depending on the variable being considered.

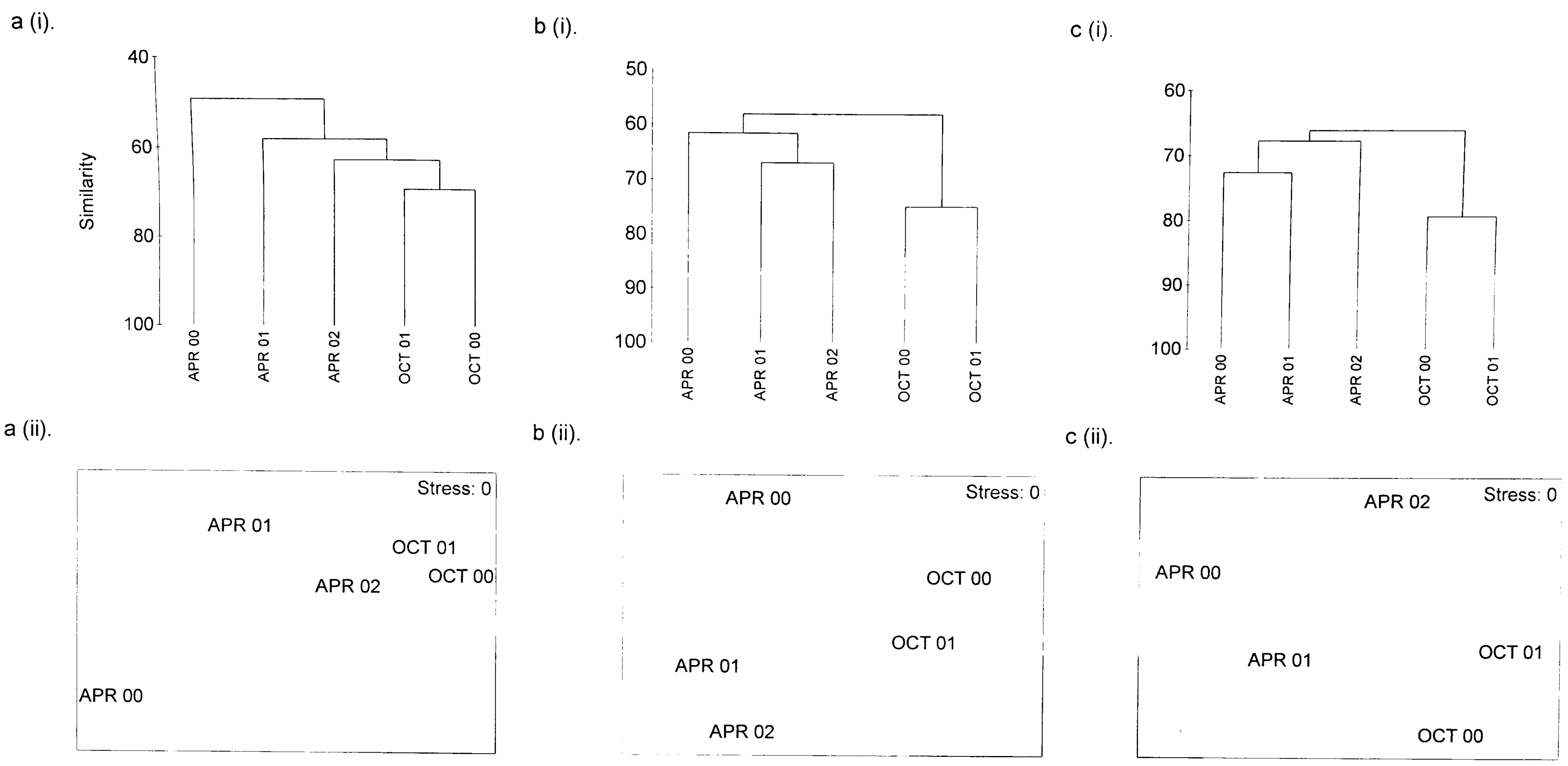


Figure 8 a-c. Dendrograms (i) for group average clustering and nMDS (ii) ordinations of Bray-Curtis similarities based on square root transformed species abundance data from coralline turf in tide pools taken at six monthly intervals from April 2000 until April 2002 inclusive, on three shores in North Wales. a) Porth Ysgaden, b) Porth Cwyfan, c) Cemlyn.

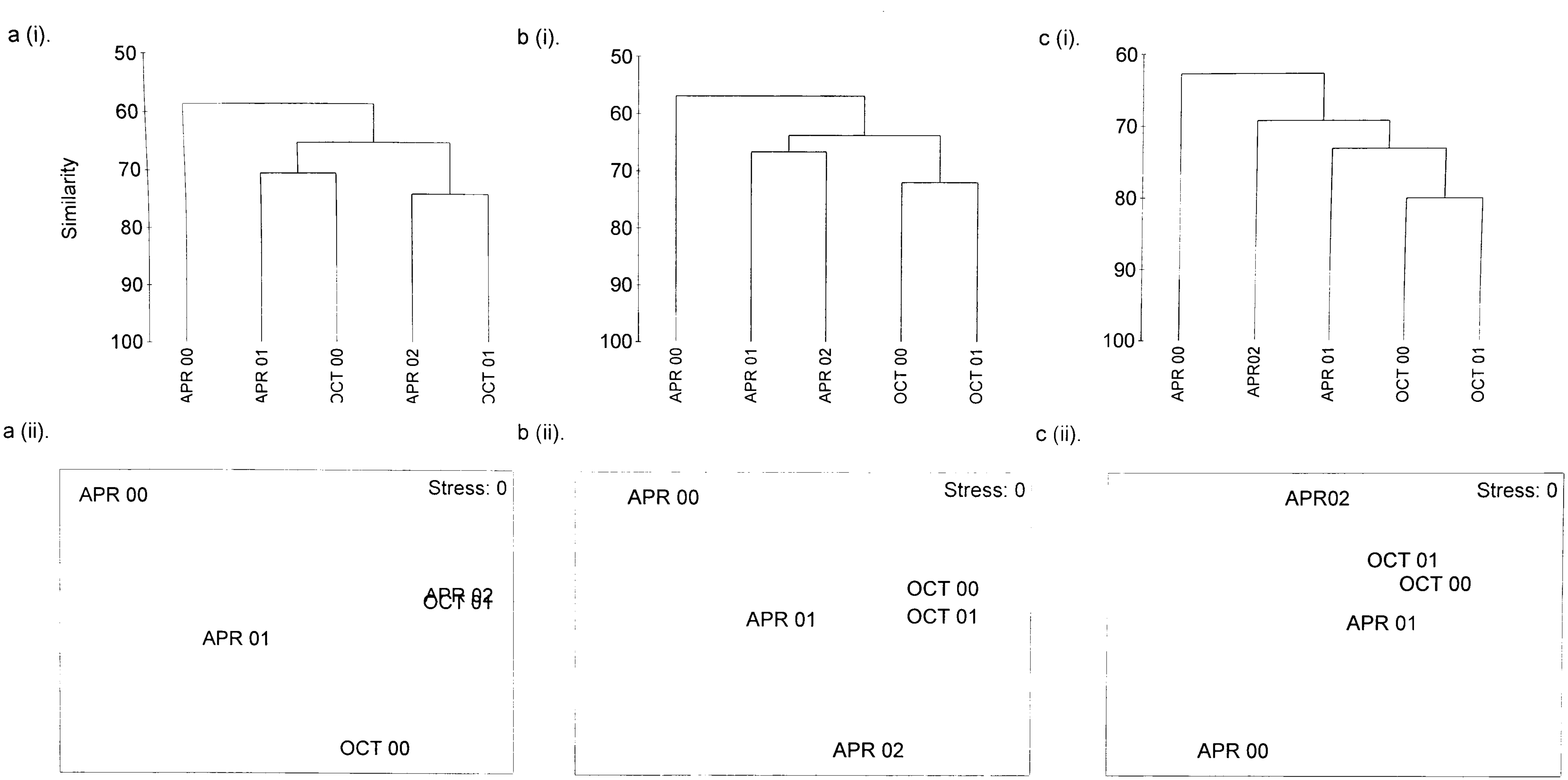
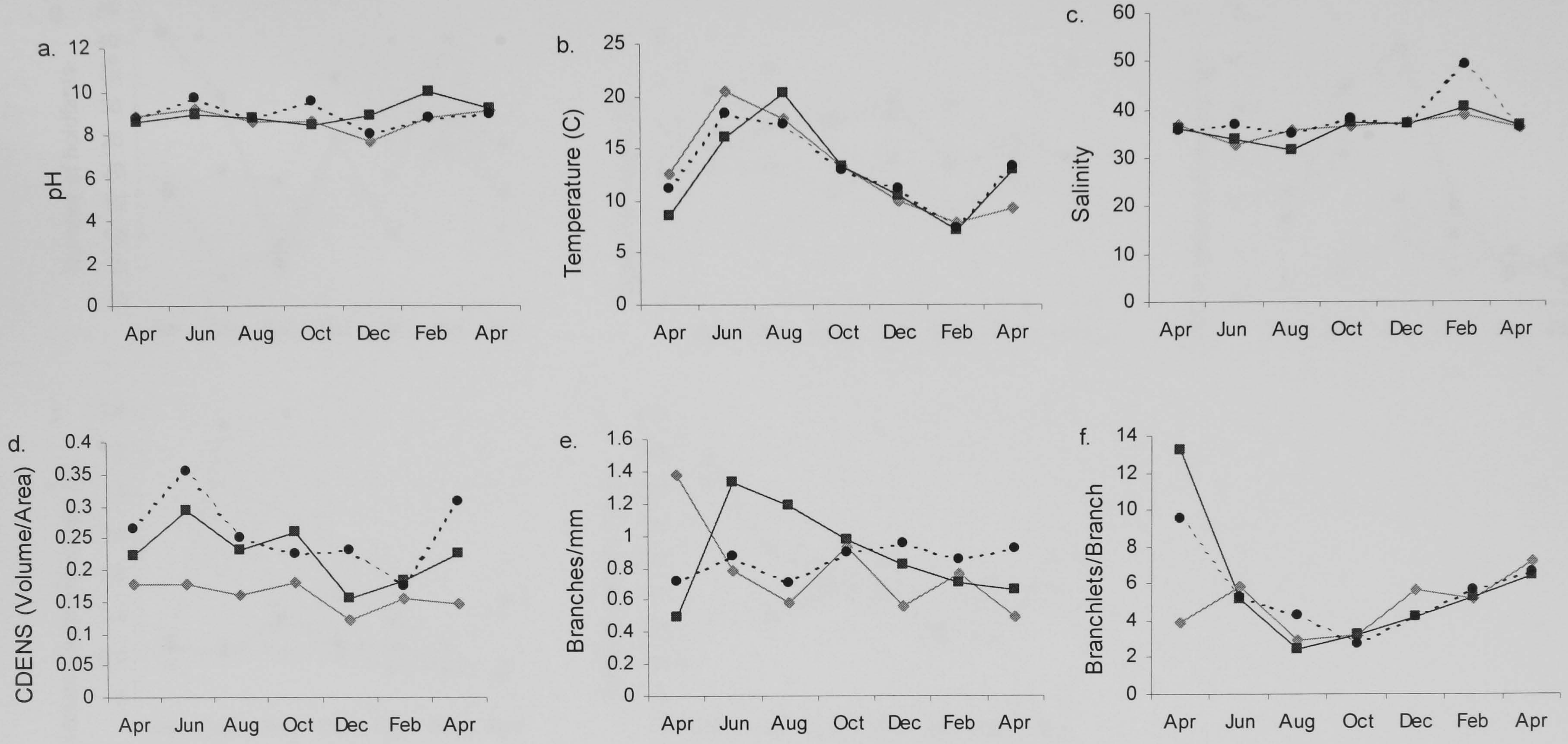


Figure 9 a-c. Dendrograms (i) for group average clustering and nMDS (ii) ordinations of Bray-Curtis similarities based on presence/absence transformed species abundance data from coralline turf in tide pools taken at six monthly intervals from April 2000 until April 2002 inclusive, on three shores in North Wales. a) Porth Ysgaden, b) Porth Cwyfan, c) Cemlyn.



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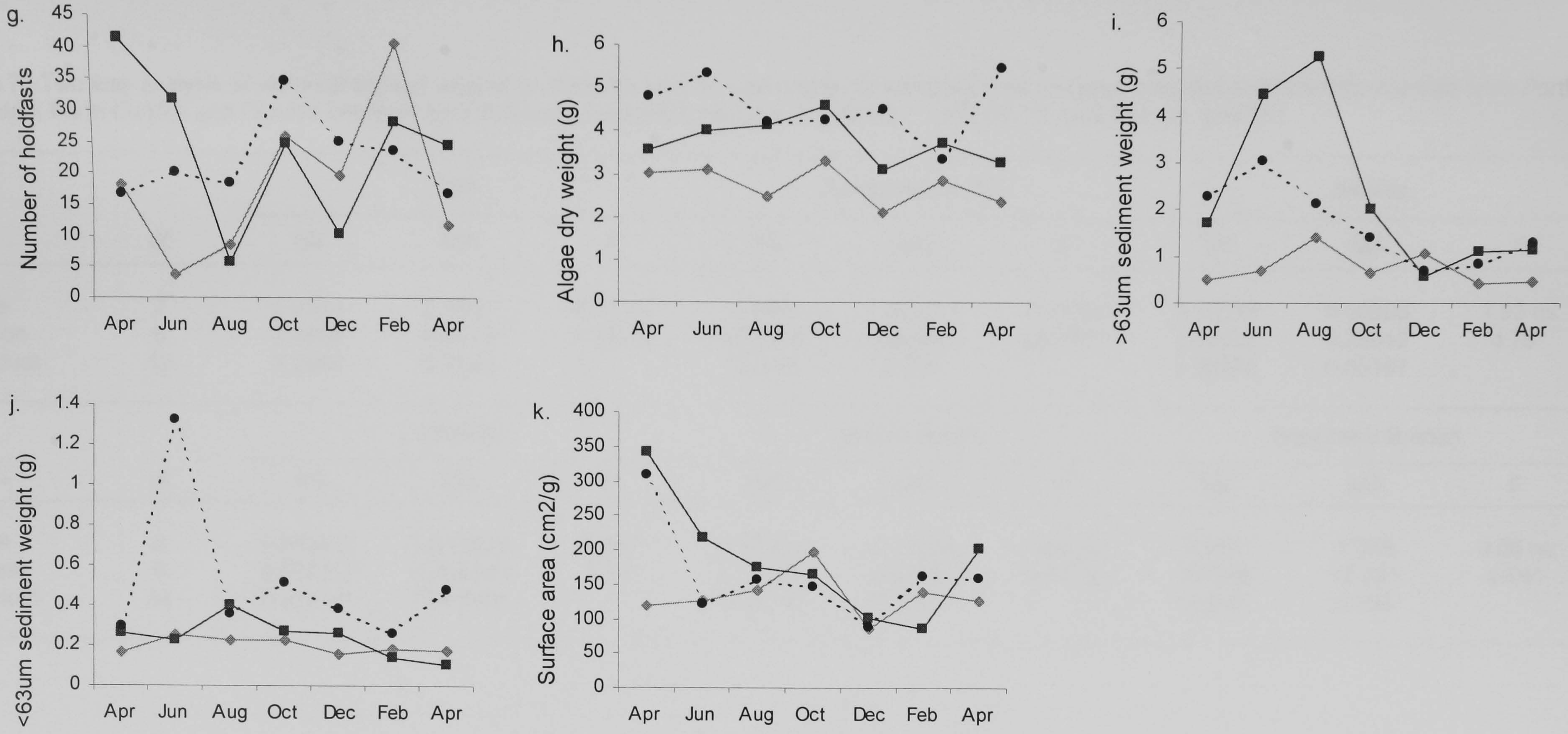

Figure. 10. Change in environmental variables measured bimonthly over one year (April 2000 – April 2001) in *Corallina* turf collected from three tide pools. Values recorded are means from one tide pool and therefore standard errors are not given due to pseudoreplication. ◆ = Porth Ysgaden, ■ = Porth Cwyfan, ● = Cemlyn.

Table 7. Two way analysis of variance without replication (Scheffe test) on environmental variables from samples collected at bi monthly intervals from Porth Ysgaden, Porth Cwyfan and Cemlyn between April 2000 and April 2001 inclusive. *, $p<0.05$; **, $p<0.01$; ***, $p<0.001$; ns, $p>0.05$.

		pH			Temperature (°C)			Salinity		
	df	SS	MS	F	SS	MS	F	SS	MS	F
Shore	2	0.3314	0.1657	0.77 ns	0.642	0.321	0.11 ns	0.19972	0.09986	1.93 ns
Season	6	2.4865	0.4144	1.92 ns	302.410	50.402	18.01***	1.47672	0.24612	4.76*
Residual	12	2.5950	0.2163		33.584	2.799		0.62008	0.05167	

		CDENS			Branches/mm			Branchlets/Branch		
	df	SS	MS	F	SS	MS	F	SS	MS	F
Shore	2	0.035671	0.017836	17.26***	0.03237	0.01629	0.20 ns	2.755	1.378	0.36 ns
Season	6	0.024135	0.004023	3.89*	0.19411	0.03235	0.41 ns	73.989	12.331	3.25*
Residual	12	0.012401	0.001033		0.95000	0.07917		45.546	3.796	

		Holdfasts			Dry weight of alga (g)			Dry weight of sediment >63um (g)		
	df	SS	MS	F	SS	MS	F	SS	MS	F
Shore	2	110.48	55.24	0.57 ns	11.5349	5.7675	17.87***	8.7946	4.3973	5.26*
Season	6	884.40	147.40	1.53 ns	2.1004	0.3501	1.08 ns	14.5713	2.4285	2.90 ns
Residual	12	1156.59	96.38		3.8739	0.3228		10.0414	0.8368	

		Dry weight of sediment <63um (g)			Surface area (cm^2/g)		
	df	SS	MS	F	SS	MS	F
Shore	2	0.42213	0.21106	4.61*	8839	4419	1.55 ns
Season	6	0.32290	0.05382	1.18 ns	45108	7518	2.63 ns
Residual	12	0.54948	0.04579		34251	2854	

Pearson product-moment correlation indicates a significant positive association between *Corallina* density and number of species ($r=0.630$ $p<0.01$). All other combinations of diversity and environmental variable remained non significant at the $p<0.01$ level.

Before carrying out multivariate analysis of environmental data, surface area, dry weight of alga and sediments and salinity were $\log_{10}(x+1)$ transformed to better approximate multivariate normality (Clarke & Gorley 2001). Principal component analysis was carried out on the first twelve months of data for each of the three shores individually (Fig. 11). The first two principal components capture a relatively large amount of the variation (>70% rising to >83% on the addition of the third principal component) on each of the three ordinations suggesting that the PCA is a relatively good indicatior of the actual relationships amongst samples. There appears to be little consistency in the relative placing of samples on the PCA between shores and indeed there is little visual evidence for a consistent cyclic pattern in the data. Only the environmental variables at Porth Cwyfan (Fig. 11b) have a significant correlation with cyclicity ($rho=0.568$, $p<0.01$). An analysis of similarities without replication on the three shores, however, reveals a significant effect of season ($rho=0.410$, $p<0.01$) but not of shore ($rho=0$, $p>0.05$).

Matching of multivariate environmental variable pattern to multivariate biotic variable pattern (BIOENV) was done separately for each shore (Table 8-10). Each shore and transformation has different combinations of environmental variables that best match the biotic data. However, number of branchlets and dry weight of sediment <63µm are selected the most, 4 and 3 times out of six respectively. This technique gives some indication of those environmental parameters that may be influencing the community pattern. This is especially relevant since while the environmental data do not necessarily follow the same pattern as the community data they do vary significantly with season.

Discussion

In this study there is some evidence of inter-annual variation in the diversity of the macrofauna associated with *Corallina officinalis*. From all the univariate measures of diversity only number of individuals showed any significant variation with the time of sampling. There were, however, large spatial differences in diversity between the three

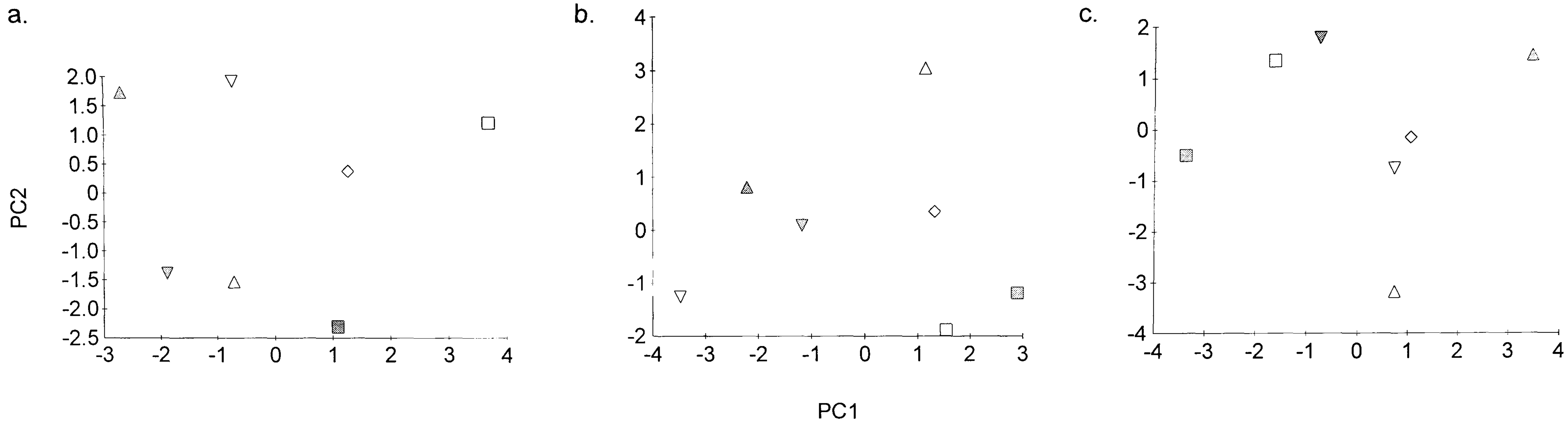

Fig 11. Ordination by Principal component analysis based on normalised Euclidean distance of environmental variables measured every two months for one year in tide pools and associated with *Corallina officinalis* from three pools on three shores in North Wales.
a = Porth Ysgaden, b = Porth Cwyfan, c = Cemlyn.
Δ April 2000, ▲ June 2000, ▽ August 2000, ▼ October 2000, □ December 2000 ■ February 2001, ◊ April 20001.

Table 8. Combinations of environmental variables yielding the best matches with biotic (a. square root transformed, b. presence/absence transformed) similarity matrices at Porth Ysgaden for samples taken bimonthly over twelve months between April 2000 and April 2001 as measured by Spearman rank correlation (rho), bold type indicates overall optimum. See Methods (Chapter 2) for variable abbreviations.

a.

k	Best variable combinations (rho)		
2	°C Brchs (0.601)	Brchs Brts (0.534)	
3	<63 Brch Brts (0.595)	°C Brchs Brts (0.595)	<63 °C Brchs (0.560)
4	**<63 °C Sal Brchs** **(0.616)**	<63 Holds Sal Brchs (0.557)	>63 <63 Sal Brchs (0.530)
5	>63 <63 Sal Brchs Brts (0.553)	<63 Holds °C Sal Brchs (0.542)	

b.

k	Best variable combinations (rho)		
2	**Brchs Brts** **(0.603)**	°C Brchs (0.506)	
3	<63 Sal Brchs (0.600)	°C Sal Brchs (0.554)	pH Sal Brchs (0.520)
4	°C pH Sal Brchs (0.570)	>63 <63 Sal Brchs (0.535)	<63 pH Sal Brchs (0.527)
5	<63 °C pH Sal Brch (0.518)		

Table 9. Combinations of environmental variables yielding the best matches with biotic (a. square root transformed, b. presence/absence transformed) similarity matrices at Porth Cwyfan for samples taken bimonthly over twelve months between April 2000 and April 2001 as measured by Spearman rank correlation (rho), bold type indicates overall optimum. See Methods (Chapter 2) for variable abbreviations.

a.

k	Best variable combinations (rho)		
1	**Coral** **(0.614)**		
2	Coral Holds (0.574)	Coral >63 (0.564)	Coral <63 (0.538)
3	CDENS Coral <63 (0.555)		
4	CDENS Coral <63 Brts (0.605)	CDENS Coral <63 Holds (0.545)	CDENS Coral >63 <63 (0.544)

b.

k	Best variable combinations (rho)		
3	>63 Holds Brts (0.737)		
4	**Coral >63 Holds Brts** **(0.761)**	Coral Holds °C Brts (0.729)	CDENS >63 Holds Brts (0.724)
5	Coral >63 <63 Holds Brts (0.750)	Coral >63 Holds °C Brts (0.726)	
6	Coral >63 <63 Holds °C Brts (0.748)		

Table 10. Combinations of environmental variables yielding the best matches with biotic (a. square root transformed, b. presence/absence transformed) similarity matrices at Cemlyn for samples taken bimonthly over twelve months between April 2000 and April 2001 as measured by Spearman rank correlation (rho), bold type indicates overall optimum. See Methods (Chapter 2) for variable abbreviations.

a.

k	Best variable combinations (rho)		
2	°C Brts (0.721)		
3	**<63 °C Brts** **(0.853)**	CDENS °C Brts (0.732)	>63 <63 Brts (0.716)
4	<63 >63 °C Brts (0.791)	CDENS <63 °C Brts (0.752)	CDENS >63 °C Brts (0.722)
5	CDENS >63 <63 °C Brts (0.769)		

b.

k	Best variable combinations (rho)		
3	<63 >63 Brts (0.785)		
4	**<63 >63 Sal Brts** **(0.853)**	Coral >63 <63 Brts (0.809)	>63 <63 °C Brts (0.781)
5	SA >63 <63 Sal Brts (0.817)	SA >63 <63 °C Brts (0.795)	
6	SA Coral >63 <63 °C Brts (0.798)	CDENS SA >63 <63 °C Brts (0.781)	

different shores sampled. Many previous studies have detected significant variation in species density while species richness and diversity have remained relatively constant. Flach and Heip (1996) observed significantly higher densities of macrofauna along a continental slope in the North East Atlantic during springtime sampling, while Rossi *et al.* (2001) noted increases in abundance of different deposit feeding species at different times of the year. Both these studies relate to benthic sediment habitats that can expect to remain relatively homogenous at all times of the year.

In marine intertidal communities, which are subject to strong climatic temporal variability, Johnson and Scheibling (1987) found pronounced seasonal changes in species density and composition of the invertebrate assemblage associated with the large macroalgae *Ascophyllum nodosum* and *Fucus vesiculosus*. Preston & Moore (1989) also noted seasonal changes in the density of fauna associated with *Cladophora albida* in tide pools but no changes in the total number of species, while Hull (1997) observed pronounced changes in the abundance and diversity of ostracod species associated with *Corallina officinalis* turf. Metaxas & Scheibling (1994) demonstrated temporal patterns of abundance that suggest seasonality for tide pool copepods, foraminferans and nematodes. Diversity of these groups also increased alongside abundance in two peaks at late spring and late summer, while Edgar (1983a) showed that the abundance of all animal groups associated with intertidal algae in Tasmania peaked in the late summer and early autumn. This pattern is also concurrent with equilibrium theory of MacArthur and Wilson (1967) which states that species number in a patch of habitat should remain approximately constant but the identities of these species should change over time. In this study, species number in the fauna associated with *Corallina* turf does remain approximately constant and the patterns observed within the multivariate techniques indicates clearly that the composition of the species varies over time. It should be noted, however, that this pattern does not always occur. Astles (1993) found no significant temporal trend in individual species mean abundance in tide pools within sites but species within individual pools did show random fluctuations. Also, number of species within clumps of the bivalve *Brachidontes rostratus* have been shown to vary temporally while total number of individuals remained relatively constant (Peake and Quinn, 1993). When this pattern is evident it could indicate that the overall density of organisms within any given patch of habitat may be fixed by the availability of resources such as food and space (Seed, 1996).

The observed pattern of cyclicity is often expected in the multivariate analysis of seasonal samples (Clarke and Gorley, 2001) where the expectation is for samples from adjacent months to be more similar than from months that are further apart. It is not an uncommon observation that samples closer together in time (or space) are more similar than those from farther away (Underwood and Chapman, 1996). Indeed, Warwick (1977) observed a cyclical pattern in the seasonal changes in abundance of nematodes associated with intertidal seaweed in the Isles of Scilly. In the present study, species subsets that are responsible for the cyclical pattern observed in the nMDS were isolated by the multivariate technique, BVSTEP. There was a high degree of variability in the results in the levels of structural redundancy for each of the shores studied. Only Cemlyn had consistently high structural redundancy with upto 4 subsets of species being able to adequately describe the overal community patterns. Porth Cwyfan exhibited consistently low structural redundancy with only 1 subset of species able to describe the overall community pattern. Consistently high levels of structural redundancy have been demonstrated for subtidal macrobenthic infauna in the Bay of Morlaix, France, and off the Northumberland coast (Clarke and Warwick, 1998a). Conversely, structural redundancy was low for the macrobenthos within eutrophic lagoons (Mistri *et al.*, 2001). The lack of consistent patterns in structural redundancy in the present study does not permit the formulation of specific hypotheses on the potential resilience of the fauna associated with *Corallina* turf to disturbance at regional scales. Hence, more specific work needs to be done investigating the levels of structural redundancy at a variety of temporal and spatial scales.

Of those species selected by BVSTEP analysis, the tendency is for their abundance to be increased at certain times of the year, and reduced or absent at other times of the year. Several factors could explain the observed pattern of increased abundance at certain times of the year. Differential reproductive strategies can alter the abundance dramatically of some species (Hicks, 1985). Species that do not have pelagic larvae, and reproduce via direct development such as all amphipods (Reid, 1944) and isopods (Naylor, 1972) will dramatically alter in abundance at the time of recruitment. Also, species that have larvae that preferentially settle on the substratum will also add to increased abundance at time of settlement e.g. *Spirorbis corallinae* (De Silva, 1962). The timing of reproduction will also influence seasonal patterns, especially if reproduction is itself seasonal or increased at certain times of the year. Hull (1997) concluded that the temporal patterns of ostracod abundance in *Corallina* turf could largely be explained by differences in the reproduction components of the different species creating maximum densities during certain months. The variation in timing of

Table 11. Reproductive strategies of those species identified by multivariate analysis as being responsible for the seasonal pattern in community structure.

Species	Reproductive Strategy	Reference
Foraminifera	Limited dispersal of gamonts	Murray (1979)
Platyhelminthes		
Convoluta convoluta	Probably larval	Ball and Reynoldson (1981)
Nematoda	Direct development	Warwick *et al.* (1998)
Nemertena	Direct development or non planktotrohic larvae	Gibson (1972)
Sipuncula		
Aspidosiphon muelleri	Short pelagic larvae	Gibbs (1977)
Annelida		
Sabellaria spinulosa	Planktonic larvae	Jackson (1999)
Cirratulus filiformis	Planktotrophic larvae	Pers. Comm. Walker
Dodecaceria concharum	Planktotrophic larvae	Pers. Comm. Walker
Malacoceros sp.	Plantonic larvae	Gravely (1909)
Polydora ciliata	Planktotrophic development	Hill (2000)
Polydora flava	Planktotrophic development	www.marlin.ac.uk
Polydora caeca	Planktotrophic development	www.marlin.ac.uk
Spirorbis corallinae	Larvae, low dispersal	Gee (1963)
Amphiglena mediterranea	Direct development	
Demonax langerhansi	?	?
Fabriciola baltica	?	?
Laonome kroyeri	?	?
Brania clavata	Planktonic larvae	Gravely (1909)
Exogone sp.	Planktonic larvae	Gravely (1909)
Odontosyllis ctenostoma	Planktonic larvae	Gravely (1909)
Odontosyllis gibba	Planktonic larvae	Gravely (1909)
Syllis gracilis	Planktonic larvae	Gravely (1909)
Lepidonotus sp.	?	?
Phyllodoce sp.	Planktonic larvae	Pleijel & Dales (1991)
Pholoe sp.	Planktonic larvae	Chambers & Muir (1997)
Platynereis dumerilii	Direct development	Pers. obs.
Nereis pelagica	Demersal or pelagic larvae	Clark (1977)
Kefersteinia cirrata	?	?
Micromaldane ornithochaeta	?	?
Nicomache lumbricalis	?	?
Capitellid indet.	Some planktonic development	Dales (1963)
Oligochaeta	Probably direct development	Brinkhurst (1982)
Pycnogonida		
Anaplodactylus pygmaeus	Egg released as protonymph	King (1974)
Anaplodactylus angulatus	Egg released as protonymph	King (1974)
Achelia hispida	Egg released as protonymph	King (1974)
Achelia laevis	Egg released as protonymph	King (1974)
Achelia simplex	Egg released as protonymph	King (1974)

	Reproductive Strategy	Reference
Arachnida	?	?
Crustacea		
Elminius modestus	Planktonic larvae	
Harpacticoid Copepods	Direct benthic development	Huys *et al.* (1996)
Ostracoda	Direct development	Athersuch *et al.* (1989)
Stenothoe monoculoides	Direct development, broods	Reid (1944)
Melita sp.	Direct development, broods	Reid (1944)
Hyale prevostii	Direct development, broods	Reid (1944)
Hyale stebbingi	Direct development, broods	Reid (1944)
Gammarellus sp.	Direct development, broods	Reid (1944)
Apherusa bispinosa	Direct development, broods	Reid (1944)
Apherusa jurinei	Direct development, broods	Reid (1944)
Dexamine spinosa	Direct development, broods	Reid (1944)
Calliopius laeviusculus	Direct development, broods	Reid (1944)
Ampithoe helleri	Direct development, broods	Reid (1944)
Ampithoe ramondii	Direct development, broods	Reid (1944)
Ampithoe rubricata	Direct development, broods	Reid (1944)
Sunampithoe pelagica	Direct development, broods	Reid (1944)
Ampeliscidae indet.	Direct development, broods	Reid (1944)
Caprella linearis	Direct development, broods	Harrison (1944)
Caprella acanthifera	Direct development, broods	Harrison (1944)
Idotea pelagica	Direct development, broods	Naylor (1972)
Idotea granulosa	Direct development, broods	Naylor (1972)
Jaera albifrons	Direct development, broods	Naylor (1972)
Dynamene bidentata	Direct development, broods	Naylor (1972)
Parasinelobus chevreuxi	Direct development, broods	Holdich & Jones (1983)
Tanais dulongii	Direct development, broods	Holdich & Jones (1983)
Mollusca		
Helcion sp.	Planktonic larvae	Graham (1988)
Nucella lapillus	Direct from egg capsule	Graham (1988)
Onoba semicostata	Direct from egg capsule	Graham (1988)
Rissoella diaphana	Direct from egg capsule	Graham (1988)
Rissoa sarsi	Planktonic lavae	Graham (1988)
Gastropoda juv.	?	
Lacuna vincta	Planktonic larvae	Graham (1988)
Littorina mariae	Direct from egg capsule	Graham (1988)
Littorina neglecta	Direct from egg capsule	Graham (1988)
Littorina indet.	?	
Tricolia pullus	Planktonic larvae	Graham (1988)
Barleeia unifascata	Direct from egg capsule	Graham (1988)
Odostomia plicata	?	
Omalogyra atomus	Direct fom egg capsule	Graham (1988)
Gibbula umbilicalis	Pelagic larvae	Graham (1988)
Limapontia sp.	Planktonic larvae	Thompson (1988)
Lasaea adonsoni	Direct development, broods	Mackie (1984)
Turtonia minuta	Direct development	Mackie (1984)
Tapes sp.	Probably larval	Mackie (1984)

Species	Reproductive Strategy	Reference
Anomia ephippium	Probably larval	Mackie (1984)
Modiolus modiolus	Planktonic larvae	Tyler-Walters (2001a)
Musculus discors	Direct development	Tyler-Walters (2001b)
Echinodermata		
Asterina gibbosa	Direct development	Mortensen (1927)
Amphipholis squamata	Viviparous	Mortensen (1927)
Ascidiacea		
Ascidiella sp.	Planktonic larvae	Hiscock (2003)
Molgula sp.	Planktonic larvae	Miller (1970)

reproduction and recruitment of ostracods was largely temperature dependant. In the current study, the temperature in tide pools at the time of sampling varied significantly with season and thus could have a marked effect on life history patterns of the associated fauna. Amongst the 89 species deemed important in structuring the overall multivariate pattern across the three shores studied many different life history strategies are represented (Table 11). 46 species show some sort of direct development where there is no pelagic larval stage and the young are released as individuals that either resemble the adult or develop directly in the same habitat as the adults. These life history characteristics are not uncommon in tide pools (Emson, 1985).

Seasonal timing of reproduction is common for many of these species and is particularly well known for the gastropods. For example, within the genus *Littorina, Littorina mariae* reproduces all year round but fecundity is reduced in summer (Graham, 1988); *Littorina neglecta* has maximal development in spring. Variations in the timing of reproduction in these species that have direct development can markedly alter their abundance and occurrence giving rise to a strong seasonal signal in the assemblage. This can be especially marked if these species occur only transiently within the *Corallina* turf, thus altering the presence/absence relationships. For example, the gastropod, *Rissoella diaphana*, develops directly from eggs in the spring and summer when it can reach high abundance. Eggs are then laid at the end of the summer which over-winter within the turf and hatch the following year (Graham, 1988; Hayward and Ryland, 1995). Even those species that have a pelagic larval stage can have a strong influence on the seasonal pattern. The gastropod, *Lacuna vincta*, dies after spawning in the spring (Graham, 1988) causing a sudden reduction in the number observed. The abundance of *L. vincta* subsequently increases as the larvae settle and grow resulting in a seasonal cyclic pattern. The larvae of some species can also exhibit preferential settlement on *Corallina* turf. The gastropod *Tricolia pullus* may reproduce all year but will settle preferentially on red algae (Graham, 1988). Also, whilst the polychaete, *Spirorbis corallinae,* has a pelagic larvae, its time in the plankton is either short or non existent, preferentially settling on *Corallina officinalis* on which it is almost exclusively found (De Silva and Knight-Jones, 1962).

Other species can also contribute to a seasonal pattern by their perceived transient occurrence in the assemblage. For example, the decapod crustacean, *Carcinus maenas,* occurs only as a juvenile in the *Corallina* turf which it uses as a refuge from predation as well as being a good source of food. As the size of *C. maenas* increases it will no longer require the turf as a refuge, and or, its increased size makes it difficult to move amongst the tightly packed fronds therby reducing foraging efficiency. It appears, therefore, that the species found within *Corallina* turf, and the timing, method and strategy of reproduction and patterns of behaviour can have a significant influence on the seasonal fluctuation in community patterns, driving them not only by changes in abundance but also, in some cases, by their presence or absence due to the transient nature of some of the fauna.

As species abundance was largely increased in summer months during both years of the current study, reproductive strategies alone are unlikely to be the sole cause of the observed pattern. Number of branchlets and *Corallina* density both varied significantly with season. Higher values for both these variables were obtained in early summer and are probably due to increased number of reproductive conceptacles on *Corallina* at this time (Johansen, 1981 and pers. obs.). Conceptacles produced by the genus, *Corallina*, protrude more than on other coralline algae (Johansen, 1981) and therefore increase habitat complexity. While growth of the *Corallina* is unlikely to be sufficiently rapid (2.2mm/month according to Colthart and Johansen, 1973) to influence significantly the associated fauna as in other similar studies (e.g. Oswald and Seed, 1986), the seasonal production of reproductive conceptacles may well do so. Gunnill (1983) found a positive correlation between the reproductive cycle of the alga *Pelvetia fastigiata* and variations in its associated fauna but assumed that such variations were caused by external environmental parameters other than the reproductive state of the alga. However, it seems likely that an increase in complexity of the *Corallina* turf linked to its reproductive cycle could cause variations in the fauna associated with it for example by providing increased refuge from predation (Coull and Wells, 1983) or by restricting foraging ability of larger more mobile animals (Edgar, 1983a).

Abundance of algal epiphytes can also create the same functional response in the invertebrate fauna associated with marine algae. Edgar (1983a) found almost identical patterns of monthly variation in epiphyte weight and animal abundance on the host plant. Indeed, some studies of invertebrates associated with marine algae have focussed entirely on the invertebrates associated with the phytal epiphytes themselves (Jarvis and Seed, 1996). Seasonal increases in phytal epiphyte abundance may allow populations of invertebrates to spread into tide pools from other refuge areas to exploit opportunistically the increased resource (Edgar, 1983a; Johnson and Scheibling, 1987). Although algal epiphytes on *Corallina* turf were not measured directly in the current study, there were large increases in abundance and diversity of algae, especially *Ulva* spp. and *Ceramium* spp., during June 2000, although this was largely decreased by the next time of sampling in August and had reached an approximately constant 'winter' level by October. This pattern also coincides with the increases in the observed number of individuals across the three pools.

The indications from the univariate and multivariate data in the present study are that the patterns observed in one year are repeated the next. Number of individuals was highest during October of both years and nMDS ordinations generally place the same months in different years closer together than those months closer to them in time, i.e. October 2000 is generally more similar to October 2001 than either April 2000 or April 2001 which are closer to it in terms of time between samples. However, the equivalent months from separate years never support exactly the same community. This is most marked in the samples from April taken on three separate years. In terms of these samples alone similarity between April 2000 and April 2001 and between April 2001 and April 2002 is always higher than the similarity between April 2000 and April 2002, on all shores and after both square root and presence/absence transformation. This is not surprising in that those samples closer in time are more similar than those further apart as has been observed previously (at shorter time scales earlier in this chapter). Hence, although the communities tend to show a cyclic pattern of seasonality, the pattern can be considered as having a different start point each year (theoretically at least, since the pattern is continuous and there is no real start or end point). The variations in the fauna throughout the year cause changes that are seen at the larger scale between years. For example, should one year favour settlement of *S. corallinae* on the fronds of *Corallina* this will not only influence the within year pattern as discussed above, but also increased settlement will show between year variation. An increase in the number of adult worms in one year can result in a bigger increase in population the following year again as more adults produce more larvae. Variations in the theoretical 'starting point' can also be caused by chance events such as intense storms and habitat damage (Oswald and Seed, 1986) that dramatically alter the identity and abundance of the fauna, especially in winter when reproduction is generally lower than in summer.

Chapter 6

The effect of tide pools on recruitment patterns of invertebrates to intertidal algal turf

ABSTRACT

Many factors interact to create, maintain and increase diversity in marine algal epifaunas, including type of alga, habitat complexity and height on the shore. There is also common belief that tide pools contain different suites of species than can be found on the adjacent open rock both in terms of their macroalgae and associated invertebrate assemblages. However, the effect of tide pool on the invertebrate fauna found within it while controlling for other external influences on biodiversity has never been tested. This study uses an artificial substratum (ASU) to mimic intertidal algal turf and to control for habitat complexity, habitat characteristics (such as exudates) and height on the shore in an investigation into the communities that form in tide pools and on open rock. Comparisons are also made between two natural turf algae occurring in tide pools, *Corallina officinalis* and *Laurencia pinnatifida*. While the artificial substrata do not recruit communities that mimic the natural turf, they do provide useful means for testing hypotheses about the invertebrate faunas associated with intertidal algae. Clear differences in community structure exist between natural turfs of *Corallina* and *Laurencia* year round. These differences appear to be largely attributable to differences in the form and function of the algae as well as the presence or absence of tide pools. Clear differences also exist in the fauna that colonises artificial substrata. As there is no difference in the structure of the artificial substrata the differences in their associated fauna must be caused by different methods of colonisation and subsequent patterns of community evolution within tide pools and on open rock.

Introduction

In the rocky intertidal, tide pools can be considered as unique islands of habitat that lie somewhere between the physical characteristics of the classical intertidal habitat and the adjacent subtidal (Raffaelli and Hawkins, 1999). The physical environment of tide pools does not fluctuate as much as that of emergent substrata and the inhabitants of tide pools remain submerged for the entire tidal cycle; however, the fluctuations within tide pools are larger than would be encountered during constant submergence in the subtidal zone (Metaxas and Scheibling, 1993).

Although there are few species that are restricted entirely to tide pools, many species can be considered as characteristically belonging to the tide pool environment (Emson, 1985). Differences between the communites in tide pools and on open rock may arise because of smaller fluctuations in the physical conditions and/or more intense biological interactions in the pools (Metaxas and Scheibling, 1993). Tide pools also provide an extra habitat dimension for their occupants in the form of a permanent water column (Metaxas and Scheibling, 1993). Phytoplankton, zooplankton and fish can be encountered in pools at all times as opposed to only at high tide on emergent substrata. In particular, tide pools may provide a refuge for fish of varying sizes (Thompson and Lehner, 1976; Moring, 1990). Another component of variability in the physical conditions of pools is the macroalgae. Several algae have been documented as more abundant in tide pools; these include the sea-oak *Halidrys siliquosa* (Tyler-Walters and Pizzolla, 2003), and the turf forming *Corallina* and *Ceramium* (Johnson and Skutch, 1928). Other species such as *Fucus vesiculosus* and *Ascophyllum nodosum*, however, are more abundant on open rock (Lubchenco, 1982). Algae influence the variability of invertebrate species in tide pools by reducing water movement, creating microhabitat, trapping accumulated sediments and by altering the dissolved oxygen concentrations in the pool through photosynthesis and respiration. They can also directly influence the invertebrate fauna by providing food for grazers, by attracting or repelling species through the production of exudates (Galanidi, 2001) and by providing refugia from predators such as fishes (Coull and Wells, 1983).

Due to these factors, the tide pool environment favours small as well as tolerant animal species which tend to live amongst the fronds and holdfasts of the algae (Morris and Taylor, 1983; Emson, 1985). Coralline algal turf is a relatively common habitat within tide pools on the rocky shores of the United Kingdom while it is virtually absent from open rock except on the extreme low shore. This turf supports a diverse community of invertebrate species. As *Corallina* is virtually absent form the open rock of the intertidal zone it is unclear as to whether a similar community would be supported if coralline turf was abundant on the open rock as in other areas of the world, e.g. Australia (Underwood, 1981). Although *Corallina* turf is virtually absent from the open rock, other turf and mat like habitats, such as mussel beds, predominate (e.g. Smith, 2001). *Laurencia pinnatifida* (Hudson) Lamouroux, a turf forming red alga that is the closest algal habitat structurally, on open rock, to that of *Corallina officinalis* in tide pools. Other studies have shown that the fauna associated with mat-like habitats formed from different biogenic habitats but in the same location can be similar (Kelaher pers. comm.). Thus it might be expected that on structural grounds the faunas associated with turfs, of *Corallina* and *Laurencia* would be similar in their composition. However, the chemical exudates of the two algae are likely to be different (Palmero *et al.*, 1991; Tariq, 1991).

Artificial substrata provide a useful inert mimic of macroalgae that allow hypotheses to be tested regarding the structural and physical components of macroalgae independently from the biological characteristics of these biogenic habitats (Kelaher, 2002). Artificial habitat mimics have been utilised in a variety of intertidal and subtidal studies and in general, invertebrate species have colonised these substrata readily. Schoener (1974) tested some aspects of island biogeography using spherical plastic mesh scrubbers to simulate subtidal sponges while Russ (1980) added pieces of nylon fish net to simulate bryozoan colonies. In the intertidal Smith (2001) used mussel shells filled with epoxy resin to simulate different packing densities and therefore different degrees of habitat complexity in mat-like mussel beds. Many other methods have been used to simulate mat-like habitats on intertidal rocky shores, e.g. modified polypropylene rope (Dean and Connell, 1987; Edgar, 1991), plastic sheet (Dean and Connell, 1987), plastic pan scourers (Myers and Southgate, 1980; Gibbons, 1988; Worthington and Fairweather, 1989) and artificial grass or astroturf (Kelaher, 2002, 2003a; Olabarria, 2002).

In this study artificial substrata are used to mimic natural mat-like turf algae. Turf algae are a common feature of the rocky shores in the UK both within tide pools and on open rock, although the species of algae differ between the two habitats. It has been shown previously that the fauna associated with mat-like habitats formed from different constituent species on open rock, do not differ markedly (Kelaher pers. com.). This study was designed to test two main hypotheses. Firstly, that there is no difference in the fauna that colonises artificial turf in tide pools or on open rock. Secondly, that there is no difference in the fauna found in natural turf both within tide pools (*Corallina officinalis*) and on adjacent open rock (*Laurencia pinnatifida*). If the first hypothesis is true then it can be inferred that the nature of the habitat is important for structuring the associated assemblage irrespective of tide pools. If the second hypothesis is true then it can be inferred that the communites of mat-like habitats are largely similar at similar heights on the shore, irresepctive of tide pools. A further hypothesis was tested but using a multivariate approach only, due to differences in sample size between the size of core used on natural turf and the size of artificial substratum. This was that there is no difference between the community in artificial and natural turf in a) tide pools and b) on open rock after 3, 6 and 9 months of colonisation. This hypothesis goes some way to determining the relative merits and future implications for using artificial habitats of this sort to test future hypotheses on the diversity of faunas associated with natural algae.

Methods

The study was done on the rocky intertidal at Cemlyn Bay, North Wales (see Chapter 2). Five large tide pools were selected around mid tide level with a good cover of *Corallina officinalis* turf within the tide pool, and good examples of *Laurencia pinnatifida* turf on the adjacent open rock. Artificial substrata were constructed from pads of astroturf mats (The Original Astroturf™, Belgium) and nylon pan scourers held together with cable ties (Fig. 1). The astroturf base measured 15cm by 13cm and was consisdered to be a good representation of the holdfast of *Corallina* turf and *Laurencia* turf. The pan scourers were 9cm in diameter and more closely replicated the more foliose fronds of the two algae.

The artificial substratum units (ASU) were secured to the rock surface by drilling a hole in the rock and screwing the four corners of the astroturf securely with a stainless steel screw and washer. This proved to be an effective method as only one complete ASU was lost in storms and 3 pan scourers were lost form the tops of astroturf out of 50 deployments (Fig 2). Sufficient ASU were placed on the shore to compensate for such losses. ASU were placed in the tide pools during August 2001. At the same time five replicate samples of *Corallina* turf in the tide pools and five replicate samples of *Laurencia* turf from the adjacent rock surface were collected. These samples therefore represented the fauna in the natural turf at the start of the experiment. Each plot was

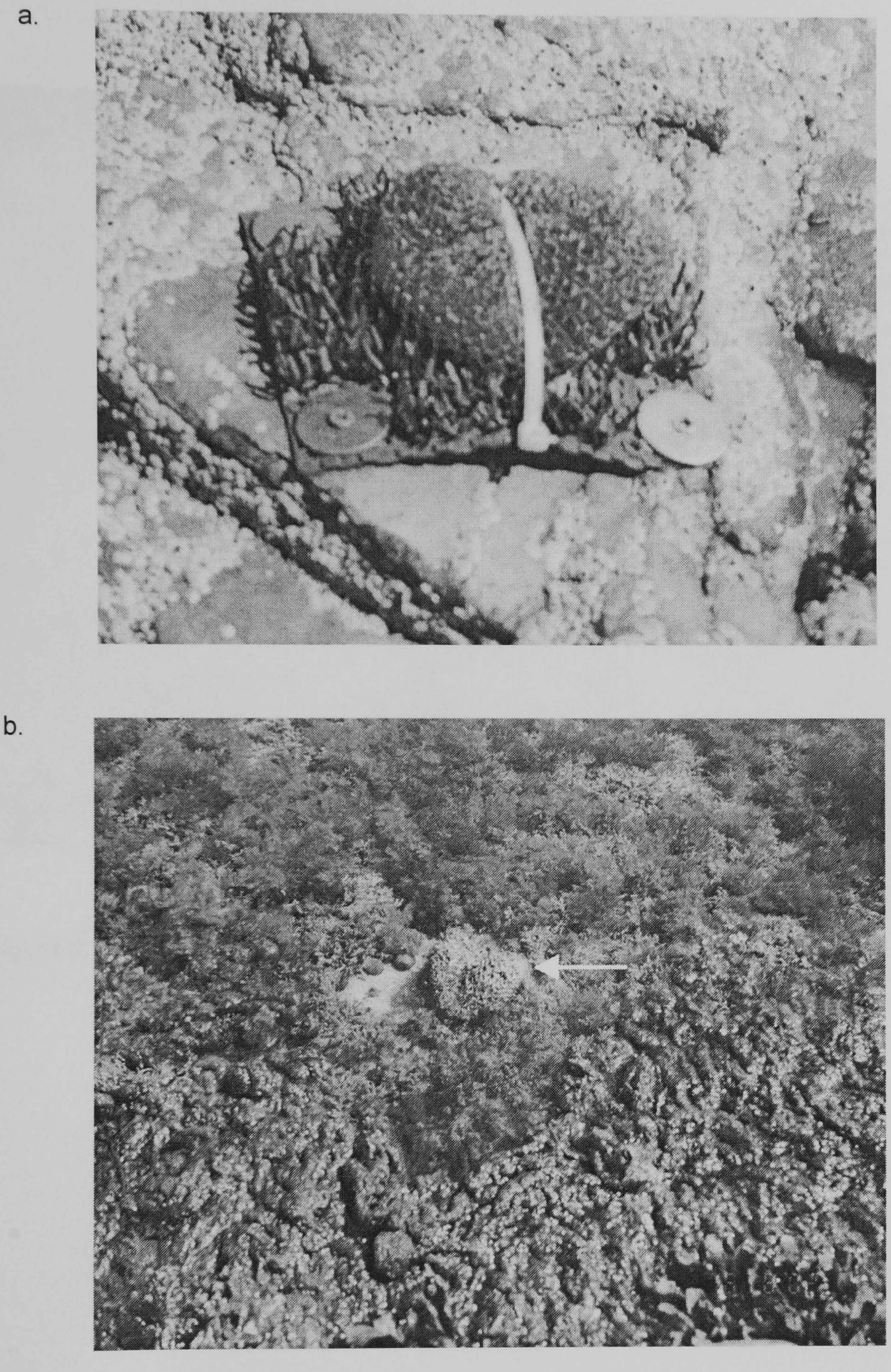

Figure 1. Artificial turf on a) on open rock and b) in tide pool.

Figure 2. Artificial substratum, with pan scourer removed, on open rock.

then sampled every three months, in November 2001, February and May 2002. Natural turf samples were collected according to the methodology described in Chapter 2. Artificial turf was removed form the rock by unscrewing the fastenings and then transferred to a large container for their return to the laboratory. Animals were removed from the artificial turf, by carefully washing over a 0.5mm mesh. The pan scourers easily unravelled into a flat sheet and the astroturf could then be cut into small pieces to ensure that the entire fauna and associated sediments were removed. The resultant fauna were then stored in 4% buffered formalin and sorted and identified according to the methodology in Chapter 2. Permanently attached fauna (e.g. spirorbids) were not included in the analysis as the methods used were not sufficient to quantify this component accurately. Environmental data were collected for each habitat; from artificial turf it was only possible to collect dry weight of relative large sediment fractions of >0.5mm, >1mm and >2 mm whereas from the natural turf of *Corallina* and *Laurencia* it was possible to collect data on the density (volume/area), algal dry weight of, small sediment fraction (<63) and large sediment fraction (>63), actual surface area (cm^2) and relative surface area per gram dry weight (cm^2/g).

The effect of tide pool on the diversity of artificial and natural turf, was analysed using a repeated measures ANOVA. The same techniques were also applied to the environmental data. An Anderson-Darling test was used to test for normality followed by Bartlett's test for homogeneity of variance. Where variance was not homogenous a Log_{10} (x+1) transformation was performed; if variances were still not homogenous, ANOVA was carried out as it was deemed there was sufficient observations to make the test sufficiently powerful with adequate care taken in the interpretation of the results (Underwood, 1997). ANOVA was not used to test hypotheses between artificial and natural turf due to the non-comparability brought about by very different sample sizes, these comparisons were carried out using multivariate techniques only.

Ordinations by non-metric Multidimensional scaling and dendrograms by group average clustering were produced for the data under both square root and presence/absence transformation based on Bray-Curtis similarity. Ordinations by Principal component analysis were produced for the measured environmental variables based on noramalised Euclidean distance as the similarity measure. Differences in biotic community pattern were tested using a one-way analysis of similarities with a combined treatment and time as the factor. This approach was thought better than the two-way crossed ANOSIM as the design produces more interpretable information in terms of the *a posteriori* pairwise comparisons. When testing hypotheses between natural and artificial turf the data were first standardised to convert the species abundance data to percentages and account for differences in sample size (Clarke and Warwick, 1994). Differences in the environmental variables for each hypothesis were, however, tested using a two-way crossed ANOSIM design with treatment and time as individual factors and normalised Euclidean distance as the similarity measure. The environmental data from natural algal communites was further investigated using the BIOENV technique to search for the best combination of environmental variables that match the biotic patterns in natural turf. This technique was only applied to the comparison purely between natural turf as it was only possible to collect a greater suite of environmental data from these habitats.

Results

A total of 16350 individuals belonging to 120 species and higher groups were counted and identified during the course of this study (Table 1). 18 species were found in only one sample, 15 of which comprised only one individual. There were representatives from 14 phyla with most species coming from the Annelida (36 species), Mollusca (30 species) and Crustacea (30 species). The dominant faunal groups were polychaetes (35 species) gastropods (19 species), amphipods (15 species), bivalves (9 species) pycnogonids (7 species) and isopods (7 species). Although biomass was not measured, individuals from artificial substrata were consistently larger than their natural turf counterparts.

Repeated measures ANOVA showed significant differences between treatments for all measures of diversity on artificial substrata within tide pools and open rock except for evenness (Table 2). Only the number of individuals showed significant difference over time. There was no significant difference in the interaction term for any of the measures of diversity indicating that each treatment showed a similar pattern through time. It can be seen that diversity and number of individuals are consistently higher amongst artificial substrata within tide pools than on open rock (Fig. 3).

Patterns in the data of artificial turf, were not obviously repeated in natural turf, in and out of tide pools. Significant differences were demonstrated for all measures of diversity and abundance except for number of species. There was, however, a significant difference through time for number of species and Margalef's d and evenness (Table 3). While there were no significant interactions between artificial turf,

Table 1. List of taxa identified from *Corallina* turf and artificial substrata in tide pools, and, *Laurencia* turf and artificial substrata on open rock.

TAXA	Authority	*Corallina* turf	*Laurencia* turf	Artificial substratum in pool	Artificial substratum open rock
PROTISTA					
Foraminifera		+	+	+	+
PORIFERA					
Sycon sp.		+		+	
CNIDARIA					
Anemone indet.		+	+	+	+
Anemonia sulcata.	Pennant, 1777			+	
PLATYHELMINTHES					
Stylochoplana maculata	(Quatrefages, 1845)			+	
Convoluta convoluta	(Abildgaard)	+	+		+
NEMERTENA		+	+	+	+
NEMATODA		+	+	+	+
SIPUNCULA					
Aspidosiphon muelleri	Diesing, 1851	+	+	+	+
POLYCHAETA					
Trichobranchus glacialis	Malmgren, 1866	+			
Sabellaria spinulosa	Leukart, 1849	+		+	
Sabellid indet.				+	
Cirratulus cirratus	(O F Müller, 1776)	+	+		+
Cirratulus filiformis	Keferstein, 1862	+	+		+
Dodecaceria concharum	Oersted, 1843	+	+		
Polydora caeca	(Oersted, 1843)	+	+	+	+
Polydora flava	Claparède, 1870	+	+	+	
Scolelepis squamata	(Abildgaard, 1806)	+			
Amphiglena mediterranea	(Leydig, 1851)	+	+	+	
Demonax sp.	Kinberg, 1867	+			
Fabricia stellaris	(Blainville)	+	+	+	+
Brania clavata	(Claparède, 1863)	+	+	+	
Exogone naidina	Oersted, 1845	+	+		
Odontosyllis ctenostoma	Claparède, 1863	+	+		
Odontosyllis gibba	Claparède, 1863	+			
Syllis gracilis	Grube, 1840		+		+
Typosyllis sp.	Langerhans, 1879	+	+	+	+
Sphaerodoridium claparedii	(Greeff, 1866)	+			
Sphaerodorum gracilis	(Rathke, 1843)			+	
Lepidonotus sp.	Leach, 1816	+			

TAXA	Authority	*Corallina* turf	*Laurencia* turf	Artificial substratum in pool	Artificial substratum open rock
Eulalia sp.	Savigny, 1817	+	+		
Phyllodocid indet.				+	
Harmothoe (Lagisca)	(Grube, 1840)			+	
Harmothoe sp.	Kinberg, 1855		+	+	
Pholoe sp.	Johnston, 1839	+	+	+	
Nereis pelagica	Linnaeus, 1758			+	
Platynereis dumerilii	Edwards, 1833	+	+	+	+
Kefersteinia cirrata	(Keferstein, 1862)	+		+	
Micromaldane ornithochaeta	Mesnil, 1897	+	+	+	
Nicomache lumbricalis	(Fabricius, 1780)	+	+		
Neanthes sp.				+	
Capitellid indet		+	+	+	
Terebellid indet.		+		+	
OLIGOCHAETA		+	+	+	+
PYCNOGONIDA					
Achelia echinata	Hodge, 1864	+		+	
Achelia longipes	(Hodge, 1864)	+			
Anoplodactylus angulatus	(Dohrn, 1881)	+	+	+	
Anoplodactylus petiolatus	(Kröyer, 1844)			+	
Anoplodactylus pygmaeus	(Hodge, 1864)	+			
Anoplodactylus virescens	(Hodge, 1864)	+			+
Phoxichilidium femoratum	(Rathke, 1799)			+	
ARACHNIDA		+	+	+	+
THORACIA					
Elminus modestus	Darwin, 1854		+		+
Semibalanus balanoides	(Linnaeus, 1767)		+	+	+
HARPACTICOIDA		+	+	+	+
OSTRACODA		+	+	+	+
AMPHIPODA					
Stenothoe monoculoides	(Montagu, 1815)	+	+	+	+
Hyale prevostii	(Milne Edwards)	+	+	+	+
Eulimnogammarus obtusatus	(Dahl, 1938)	+		+	+
Gammarus finmarchicus	Dahl, 1938			+	+
Apherusa bispinosa	(Bate, 1856)			+	
Apherusa jurinei	(H Milne-Edwards, 1830)	+	+		+
Campecopea hirsuta	(Montagu, 1804)		+		+
Dexamine spinosa	(Montagu, 1813)	+	+	+	

TAXA	Authority	*Corallina* turf	*Laurencia* turf	Artificial substratum in pool	Artificial substratum open rock
Corophium sp.	Latrielle, 1806			+	
Lembos websteri	Bate, 1857			+	
Ampithoe helleri	G Karaman, 1975	+		+	
Ampithoe ramondi	Audouin, 1826	+	+	+	
Ampithoe rubricata	(Montagu 1808)	+		+	
Lysianassidae *indet*				+	+
Jassa falcata	(Montagu, 1808)			+	
Caprella acanthifera	Leach, 1814	+		+	
ISOPODA					
Idotea granulosa	Rathke, 1843	+	+	+	+
Idotea pelagica	Leach, 1815	+	+	+	+
Jaera albifrons	Leach 1814	+	+	+	+
Dynamene bidentata	(Adams, 1800)	+	+		+
Gnathia maxillaris	(Montagu, 1804)				+
TANAIDACEA					
Apseudes talpa	(Montagu, 1808)			+	
Tanais dulongii	(Audouin, 1826)	+	+	+	+
DECAPODA					
Cancer pagurus	(Linnaeus, 1758)			+	
Carcinus maenas	(Linnaeus, 1758)	+	+	+	+
Pirimela denticulata	(Montagu, 1808)			+	
POLYPLACOPHORA					
Lepidochitona cinerea	(Linnaeus, 1767)		+		
GASTROPODA					
Patella vulgatta	(Linnaeus, 1758)			+	+
Nucella lapillus	(Linnaeus, 1758)	+	+	+	+
Skeneopsis planorbis	(O Fabricius, 1780)	+	+	+	+
Onoba semicostata	(Montagu, 1803)	+	+	+	+
Rissoa parva	(da Costa, 1778)	+	+	+	+
Lacuna vincta	(Montagu, 1803)	+	+	+	+
Littorina littorea	(Linnaeus, 1758)	+	+	+	+
Littorina mariae	(Sacchi & Rastelli, 1966)	+	+	+	+
Littorina neglecta	(Bean in Thorpe, 1844)	+	+	+	+
Littorina obtusata	(Linnaeus, 1758)			+	+
Littorina sp.	Fèrussac, 1822	+	+	+	+
Coriandria fulgida	(J Adams, 1797)	+	+		
Rissoella diaphana	(Alder, 1848)	+	+	+	+
Rissoella opalina	(Jeffreys, 1848)	+			

TAXA	Authority	*Corallina* turf	*Laurencia* turf	Artificial substratum in pool	Artificial substratum open rock
Tricolia pullus	(Linnaeus, 1758)	+	+	+	+
Gibbula cineraria	(Linnaeus, 1758)			+	
Gibbula magus	(Linnaeus, 1758)			+	
Gibbula umbilicalis	(da Costa, 1778)	+	+	+	
Skenea serpuloides	(Montagu, 1808)			+	+
Aplysia punctata	(Cuvier, 1803)				
Limapontia sp.	Johnston, 1836	+	+	+	+
PELECYPODA					
Lasaea adansoni	(Gmelin, 1791)	+	+	+	+
Turtonia minuta	(Fabricius, 1780)	+	+	+	+
Venerupis sp.	Lamarck, 1818		+	+	
Anomia ephippium	Linnaeus, 1758			+	
Modiolarca tumida	(Hanley, 1843)		+	+	
Modiolus modiolus	(Linnaeus, 1758)	+	+	+	+
Musculus discors	(Linnaeus, 1767)	+	+	+	+
Mytilus edulis	(Linnaeus, 1758)		+		+
Hiatella arctica	(Linnaeus, 1767)				+
ECHINODERMATA					
Amphipholis squamata	(Chiaje, 1829)	+	+	+	+
Ophiothrix fragilis	(Abildgaard, 1789)			+	
Asterina gibbosa	(Pennant, 1777)	+	+	+	
INSECTA					
Clunio sp.	Haliday	+	+	+	+
Tipula sp.				+	+
Anurida maritima	(Guerin)		+	+	+
ASCIDIACEA					
Molgula sp.	Hanley, 1848	+		+	

Table 2. Repeated measures ANOVA tables for total numbers of species, individuals and diversity associated with artificial substrata from samples collected every three months for nine months. Treatment was either tide pool or open rock. Results in italics indicate Log (x+1) transformation applied. * $p<0.05$, ** $p<0.01$, *** $p<0.001$, ns=not significant.

		d. f.	SS	MS	*F*
Number of species					
Between subjects	Treatment	1	1320.03	1320.03	31.93***
	Residual	8	164.80	20.60	
Within subjects	Time	2	291.20	145.60	3.52 ns
	Treatment*Time	2	17.87	8.93	0.22 ns
	Residual	16	661.60	41.35	
Number of individuals					
Between subjects	Treatment	1	107162	107162	14.98**
	Residual	8	85216	10652	
Within subjects	Time	2	175421	87710	12.26**
	Treatment*Time	2	51032	25516	3.57 ns
	Residual	16	114490	7156	
Margalef's d					
Between subjects	Treatment	1	28.335	28.335	27.07***
	Residual	8	4.410	0.551	
Within subjects	Time	2	4.567	2.283	2.18 ns
	Treatment*Time	2	1.538	0.769	0.73 ns
	Residual	16	16.750	1.047	
Pielou's J					
Between subjects	*Treatment*	*1*	*0.03079*	*0.03079*	*2.94 ns*
	Residual	*8*	*0.16229*	*0.02029*	
Within subjects	*Time*	*2*	*0.00221*	*0.00111*	*0.11 ns*
	*Treatment*Time*	*2*	*0.01267*	*0.01048*	*0.60 ns*
	Residual	*16*	*0.16774*	*0.01048*	
Hill's N1					
Between subjects	Treatment	1	118.549	118.549	15.17**
	Residual	8	120.552	15.065	
Within subjects	Time	2	9.970	4.985	0.64 ns
	Treatment*Time	2	21.479	10.739	1.37 ns
	Residual	16	125.036	7.815	
Hill's N2					
Between subjects	Treatment	1	38.180	38.180	10.63**
	Residual	8	72.098	9.012	
Within subjects	Time	2	2.405	1.202	0.33 ns
	Treatment*Time	2	13.688	6.844	1.91 ns
	Residual	16	57.447	3.590	

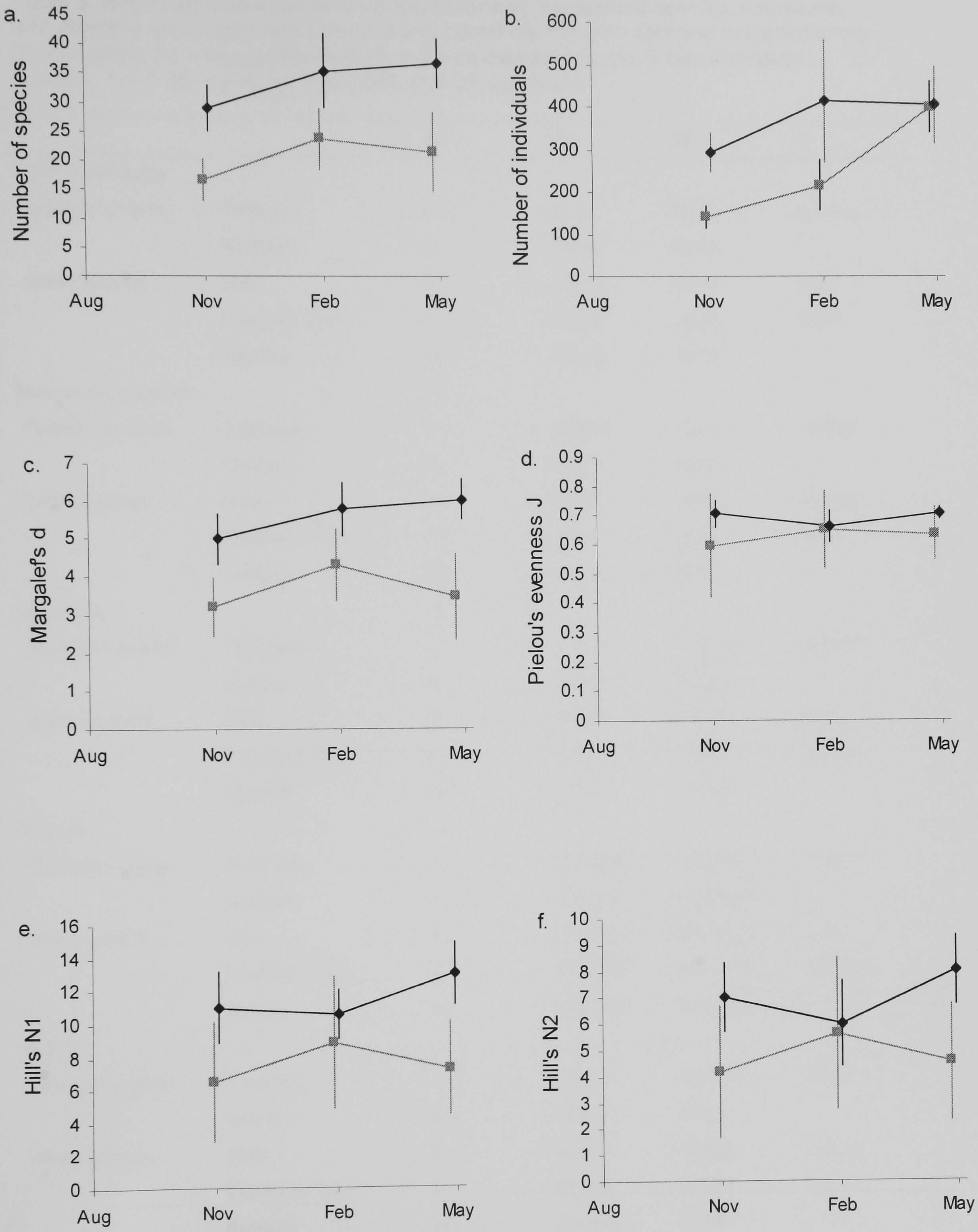

Figure 3 (a-f).Univariate measures of diversity and 95% confidence intervals associated with artificial substratum collected every three months from date of initiation in August 2001. ◆ Tide pool, ■ Open rock.

Table 3. Repeated measures ANOVA tables for total numbers of species, individuals and diversity associated with *Corallina* and *Laurencia* turf from samples collected every three months for nine months. Results in italics indicate Log (x+1) transformation applied. * $p<0.05$, **$p<0.01$, **$p<0.001$, ns=not significant.

		d. f.	SS	MS	F
Number of species					
Between subjects	Treatment	1	62.50	62.50	4.14 ns
	Residual	8	388.50	48.56	
Within subjects	Time	3	177.30	59.10	3.91*
	Treatment*Time	3	138.90	46.30	3.07*
	Residual	24	362.30	15.10	
Number of individuals					
Between subjects	Treatment	1	138415	138415	15.74**
	Residual	8	47821	5978	
Within subjects	Time	3	56916	18972	2.16 ns
	Treatment*Time	3	3474	1158	0.13 ns
	Residual	24	211030	8793	
Margalef's d					
Between subjects	Treatment	1	11.2765	11.2765	24.83***
	Residual	8	6.3254	0.7907	
Within subjects	Time	3	4.3658	1.4553	3.20*
	Treatment*Time	3	4.0454	1.3485	2.97 ns
	Residual	24	10.9001	0.4542	
Pielou's J					
Between subjects	Treatment	1	0.064870	0.064870	17.39***
	Residual	8	0.058152	0.007269	
Within subjects	Time	3	0.041724	0.013908	3.73*
	Treatment*Time	3	0.019399	0.006466	1.73 ns
	Residual	24	0.089530	0.003730	
Hill's N1					
Between subjects	Treatment	1	136.278	136.278	17.32***
	Residual	8	78/016	9.752	
Within subjects	Time	3	40.467	13.489	1.71 ns
	Treatment*Time	3	80.034	26.678	3.39*
	Residual	24	188.802	7.867	
Hill"s N2					
Between subjects	*Treatment*	1	*70.256*	*70.256*	*11.95***
	Residual	8	*60.383*	*7.548*	
Within subjects	*Time*	3	*33.493*	*11.164*	*1.90 ns*
	*Treatment*Time*	3	*44.903*	*14.968*	*2.55 ns*
	Residual	24	*141.147*	*5.881*	

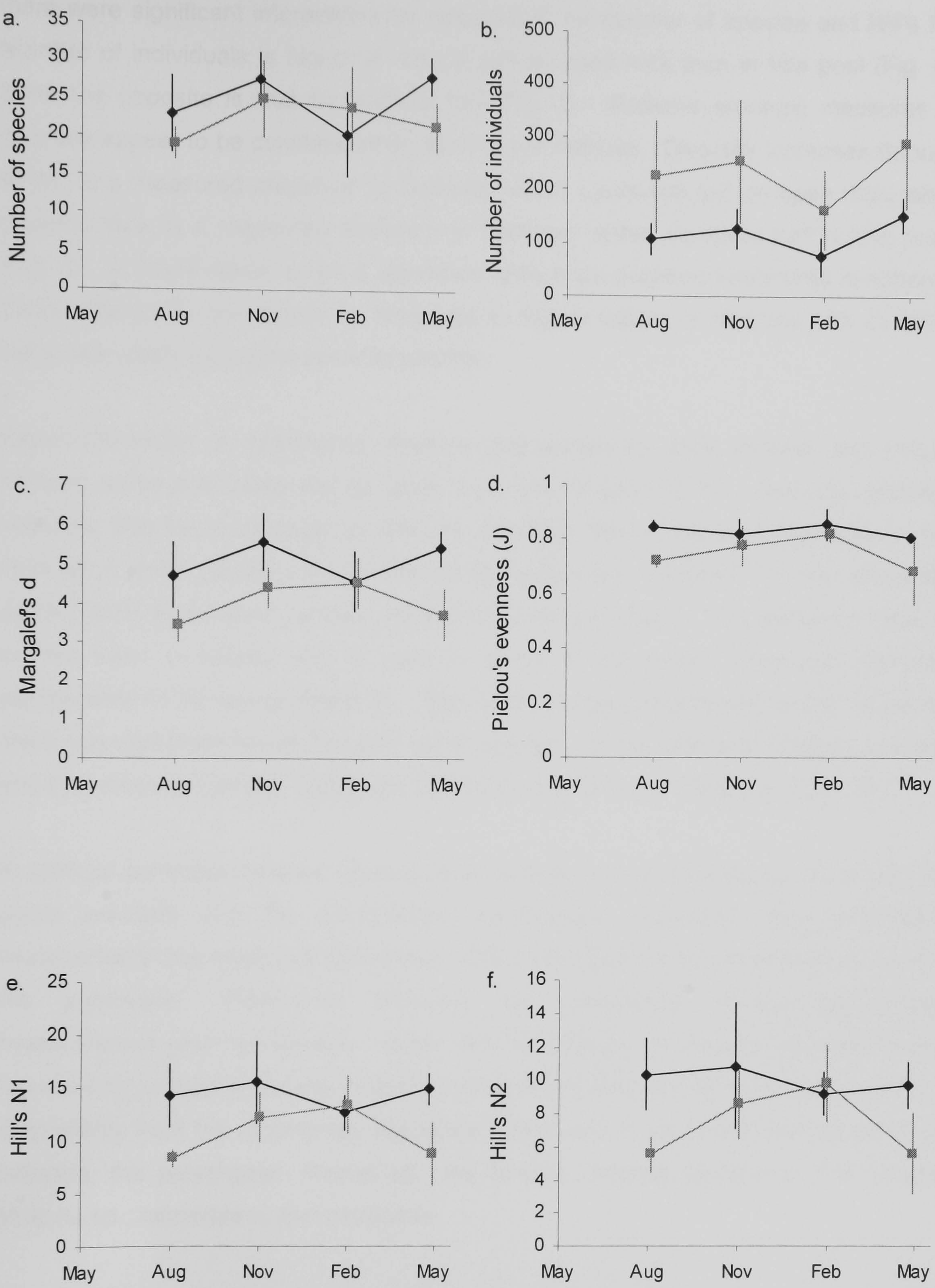

Figure 4 (a-f). Univariate measures of diversity and 95% confidence intervals from fauna associated with *Corallina officinalis* and *Laurencia pinnatifida* over 12 months.
♦ *Corallina*, ▨ *Laurencia.*

there were significant interactions for natural turf, for number of species and Hill's N_1. Number of individuals is higher in natural turf on open rock than in tide pool (Fig. 4), while the opposite is true for artificial turf (Fig. 3). Patterns amongst measures of diversity appear to be constant within the two turf habitats. Diversity increases through winter to a measured maximum in February within *Laurencia* turf on open rock, while diversity falls to a measured minimum in February within *Corallina* turf in tide pools (Fig. 4). In those cases where a significant difference between treatments is obtained these differences can largely be attributed to higher values of diversity with *Corallina* turf in tide pools during the summer months.

Clear differences in community structure are shown for both artificial and natural habitats within tide pools and on open rock (Fig. 5 and Fig. 6). One-way ANOSIM indicates that the community of artificial substrata fails to achieve significance only between 3 and 6 months after the start of the experiment on open rock and within tide pools (Table 4); all other pairwise comparisons are significant. This pattern is identical to that seen in natural turf, at least in terms of the more numerically dominant components of the fauna (Table 5). After presence/absence transformation there are more non-significant results but only within habitat. All comparisons between *Corallina* and *Laurencia* turf remain significantly different at all times of sampling (Table 5).

In artificial substrata between treatments at different times of sampling the amphipod, *Hyale prevostii*, and the echinoderm, *Amphipholis squamata*, were consistently responsible for the observed differences. Other contributions to dissimilarity came from the polychaete, *Platynereis dumerilii*, the gastropod, *Onoba semicostata*, foraminiferans and nematodes. When the importance of species abundance was removed by presence/absence transformation there were further high contributions to dissimilarity from the amphipods, *Ampithoe helleri*, and *A. ramondii*, the isopod *Idotea pelagica*, the polychaete, *Pholoe* sp., the bivalve, *Anomia ephippium*, the ascidian *Molgula* sp., nemerteans and ostracods.

At different times of sampling the amphipods, *Hyale prevostii* and *Stenothoe monoculoides*, and the polychaete, *Fabricia stellaris*, were consistently high contributors to dissimilarity between the communities associated with *Corallina* turf and *Laurencia* turf. Other high contributions came from the tanaid, *Tanais dulongii*, the platyhelminth, *Convoluta convoluta*, and midge larvae *Clunio* sp. When the importance of species abundance was removed by presence/absence transformation overall

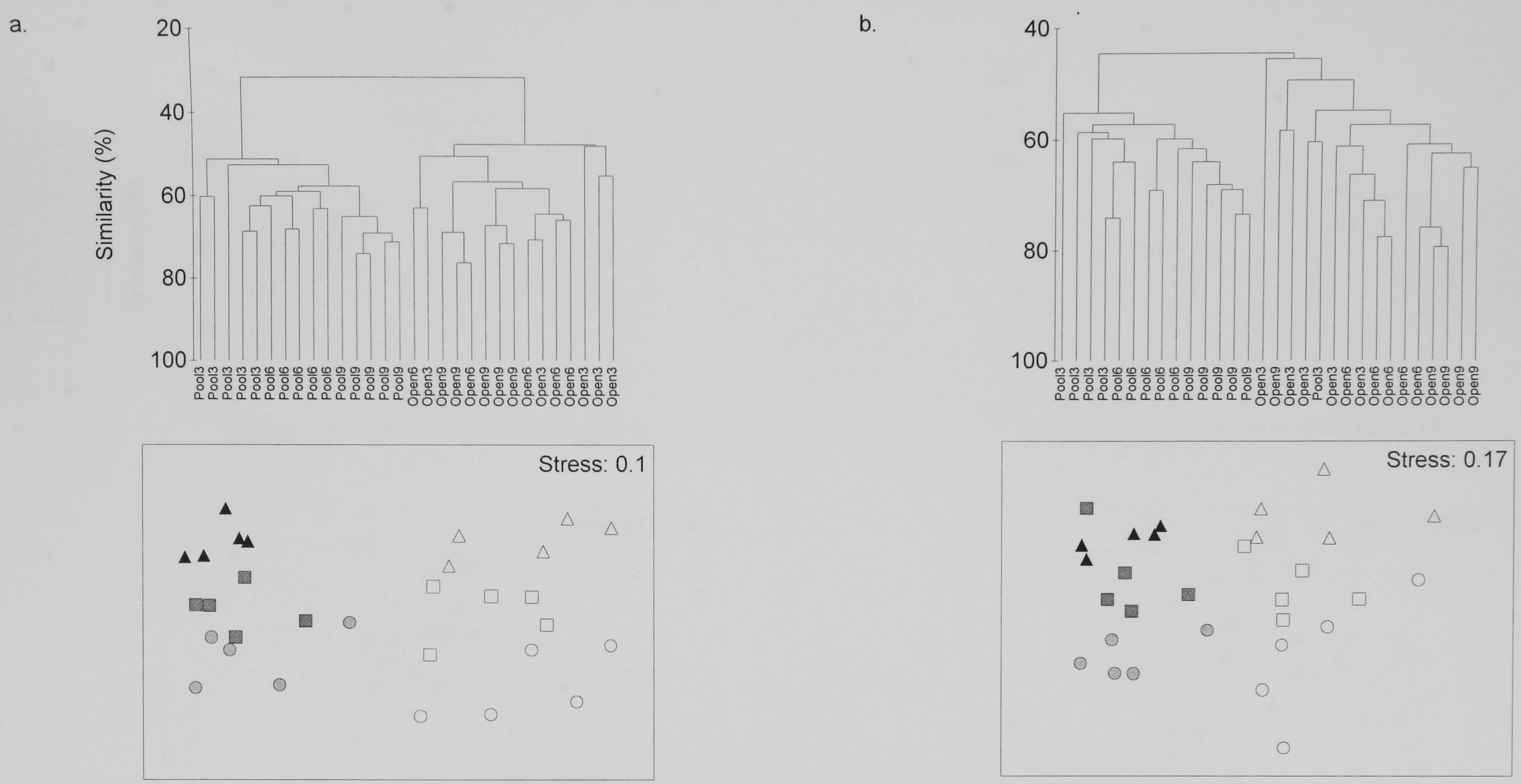

Figure 5. Cluster and nMDS of community pattern associated with artificial substrata in tide pools and on open rock after, a)square root and b)presence/absence transformed data. For dendrograms, Open indicates samples from open rock, Pool indicates samples from inside tide pool, numeric values relates to number of months in field for colonisation. For nMDS plots, ▲ Δ 9 mths ■ □ 6 mths ● ○ 3 Mths Filled symbols indicate samples from inside tide pool, open symbols samples from on open rock on open rock.

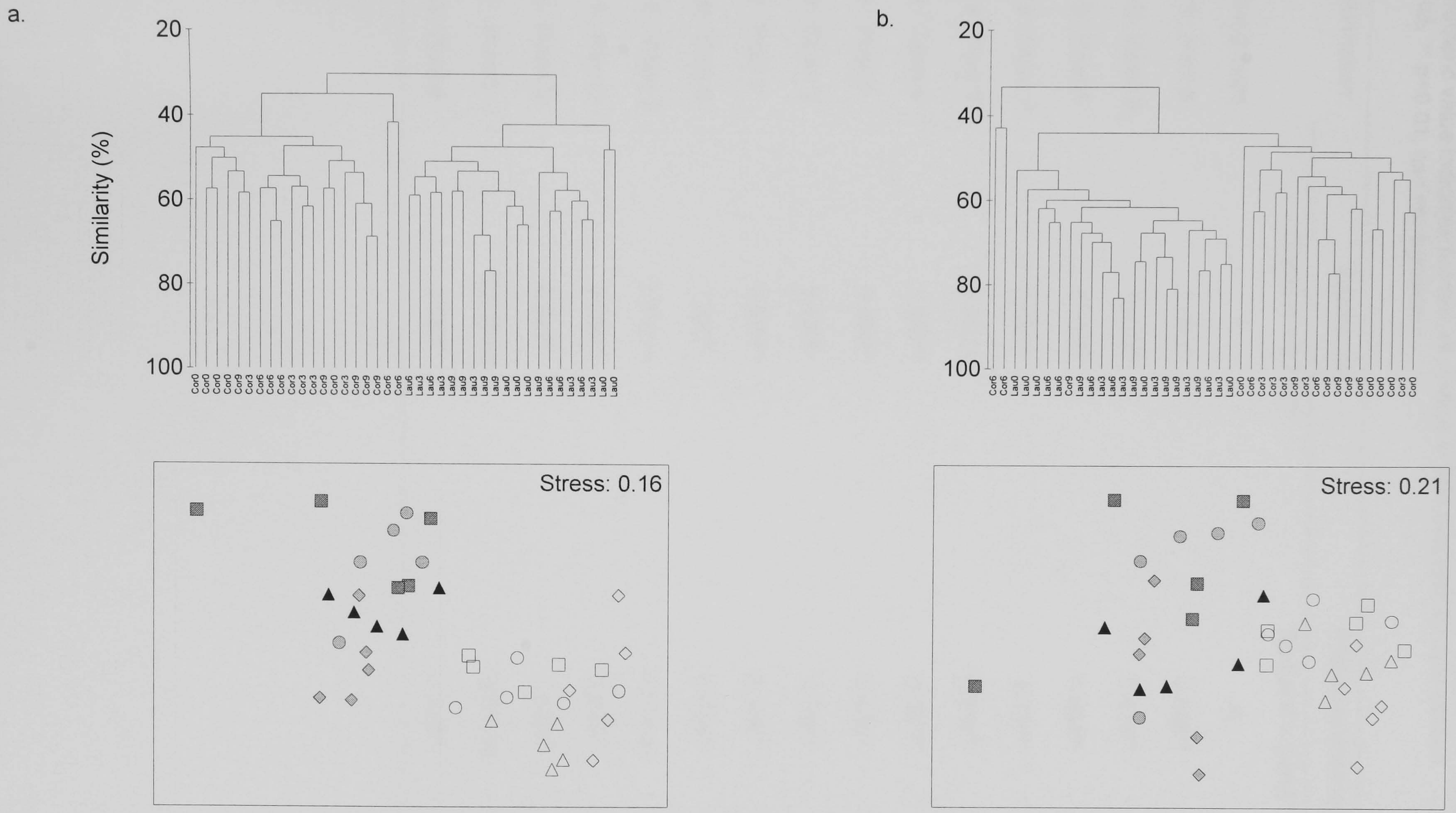

Figure 6. Cluster and nMDS of community pattern associated with *Corallina officinalis* and *Laurencia pinnatifida* turf in tide pools and on open rock after a) square root and b) presences/absence transformation. For dendrograms, Cor indicates samples of *Corallina officinalis*, Lau indicates samples of *Laurencia pinnatifida*, numeric values relates to number of months from start of experiment. For nMDS plots, ▲ Δ 9 mths ■ □ 6 mths ● ○ 3 Mths ◆ ◊ 0 mths. Filled symbols indicate samples of*Corallina*, open symbols indicate samples of *Laurencia*.

Table 4. One way ANOSIM between community found associated with artificial substratum unit within tide pool and on open rock after 3, 6 and 9 months of colonisation. For pairwise groups, Open indicates samples taken from open rock, Pool indicates samples taken from within tide pool, numeric value indicates number of months in field available for colonisation.
* p<0.05, ** p<0.01, ns= not significant.

Transformation:	Square root	Presence/absence
	Global R = 0.741**	Global R = 0.618**
Pairwise groups	R	R
Open 9 : Pool 9	1.000**	0.846**
Open 9 : Open 6	0.428*	0.414**
Open 9 : Pool 6	1.000**	0.904**
Open 9 : Open 3	0.620**	0.330*
Open 9 : Pool 3	0.952**	0.916**
Pool 9 : Open 6	1.000**	0.986**
Pool 9 : Pool 6	0.436**	0.408**
Pool 9 : Open 3	1.000**	0.742**
Pool 9 : Pool 3	0.576**	0.738**
Open 6 : Pool 6	1.000**	0.894**
Open 6 : Open 3	0.264 ns	0.122 ns
Open 6 : Pool 3	0.940**	0.860**
Pool 6 : Open 3	0.940**	0.672**
Pool 6 : Pool 3	0.036 ns	0.166 ns
Open 3 : Pool 6	0.880**	0.570**

Table 5. One way ANOSIM between community associated with *Corallina* in tide pools and *Laurencia* turf on open rock from samples taken every three months for nine months. For pairwise groups, 'Cor' indicates samples of *Corallina* turf, 'Lau' indicates samples of *Laurencia* turf, associated numerical value indicates number of months from start of experiment. $p<0.05$, ** $p<0.01$, ns= not significant.

Transformation;	Square root	Presence/absence
	Global R = 0.682**	Global R = 0.500**
Pairwise groups	R	R
Cor 9 : Lau 9	1.000**	0.670**
Cor 9 : Cor 6	0.312**	0.140 ns
Cor 9 : Lau 6	0.892**	0.604**
Cor 9 : Cor 3	0.488*	0.416*
Cor 9 : Lau 3	0.936**	0.624**
Cor 9 : Cor 0	0.484*	0.188 ns
Cor 9 : Lau 0	1.000**	0.888**
Lau9 : Cor 6	0.948**	0.776**
Lau9 : Lau 6	0.628**	0.362ns
Lau9 : Cor 3	0.980**	0.896**
Lau9 : Lau 3	0.420*	0.264ns
Lau9 : Cor 0	0.988**	0.844**
Lau9 : Lau 0	0.396*	0.074 ns
Cor 6 : Lau 6	0.724**	0.580**
Cor 6 : Cor 3	0.044 ns	0.142 ns
Cor 6 : Lau 3	0.764**	0.534**
Cor 6 : Cor 0	0.460**	0.430**
Cor 6 : Lau 0	0.984**	0.884**
Lau 6 : Cor 3	0.900**	0.778**
Lau 6 : Lau 3	0.104 ns	0.144 ns
Lau 6 : Cor 0	0.896**	0.804**
Lau 6 : Lau 0	0.704**	0.398**
Cor 3 : Lau 3	0.952**	0.666**
Cor 3 : Cor 0	0.376*	0.282 ns
Cor 3 : Lau 0	1.000**	0.936**
Lau 3: Cor 0	0.900**	0.630**
Lau 3 : Lau 0	0.276*	0.338**
Cor 0 : Lau 0	1.000**	0.904**

contributions to dissimilarity were reduced but with relatively high contributions from the gastropods, *Rissoa parva, Skeneopsis planorbis, Lacuna vincta* and *Littorina mariae*, the bivalve, *Lasaea adonsoni,* the amphipods, *Apherusa jurinei* and *Caprella acanthifera*, the isopods, *Idotea pelagica* and *Jaera albifrons*, and the echinoderm, *Amphipholis squamata*. Artificial turf and natural turf also supported clearly different communities throughout the course of this study in tide pools and on open rock for both the numerically dominant members of the community and the rare species (Fig. 7 and Fig. 8). One-way ANOSIM confirmed that natural turf and artificial turf communities were different at all times of sampling (Table 6 and Table 7). Non significant pairwise differences were only shown within the same habitat type and between adjacent months for the numerically dominant members of the community. After presence/absence transformation there were more non significant results indicating that the component species of the community are more stable between adjacent months after colonisation, in comparrison to their fluctuating abundances through time.

Despite these clear community differences, some species did occur in artificial substrata in similar proportions to natural turf when considering the relative species rank even after only three months deployment. The echinoderm, *Amphipholis squamata*, was consistently the most abundant species found in artificial substrata within pools and was also found in high abundance within *Corallina* turf (Table 8). The gastropod, *Onoba semicostata,* was also found in high abundance in *Corallina* turf and was present in artificial turf at the first time of sampling. Juveniles of the bivalves, *Modiolus modiolus* and *Musculus discors*, the amphipod, *Ampithoe helleri,* mites and nematodes were also found in both habitats in relatively high abundance (Table 8). The pattern is similar on open rock. In artificial substrata the amphipod, *Hyale prevosti,* consistently attained the highest abundance while remaining one of the top ranking species in natural *Laurencia* turf (Table 9). Other species common in both habitats in terms of their relative rank were the bivalves *Modiolus modiolus* and *Musculus discors*, the gastropod, *Onoba semicostata* and foraminiferans (Table 9).

More sediment accumulated in artificial substrata that were in tide pools rather than on open rock (Fig. 9, Table 10). This was also significantly different through time for sediment fractions of >0.5mm and greater than >2mm. This can be attributed to an increase in the dry weight of sediment between 3 and 6 months (November-February).

Of the environmental variables measured within the two natural turfs, only the relative density of alga (CDENS) failed to show a significant difference between treatments

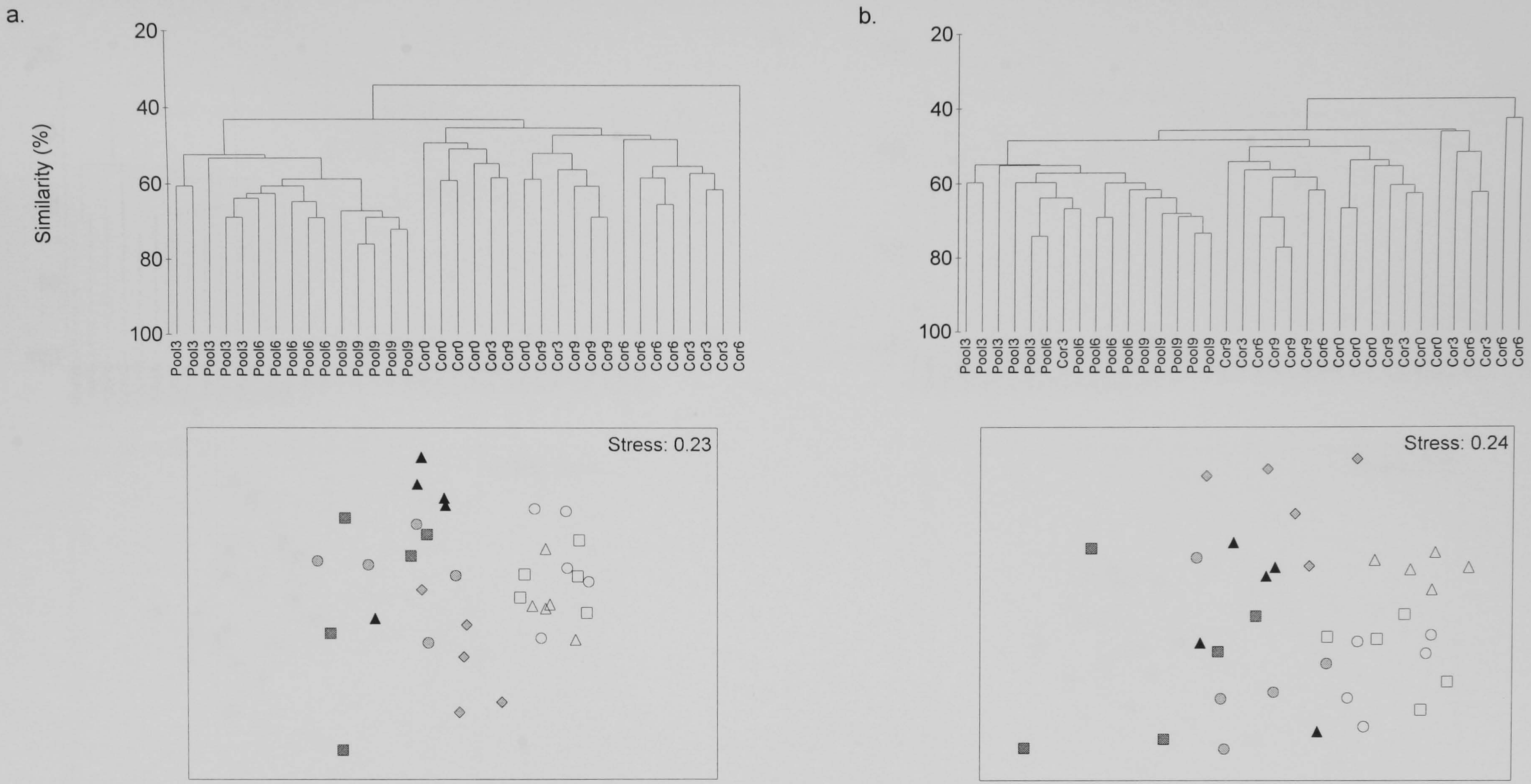

Figure 7. (a-b). Cluster and nMDS ordinations of a.) standardised square root and b) presence/absence transformed species abundance data from *Corallina officinalis* and artificial substratum in tide pools. ▲-9 months, ▨-6 months, ●-3 months ◆-0 months; open symbols relate to samples from artificial substrata.

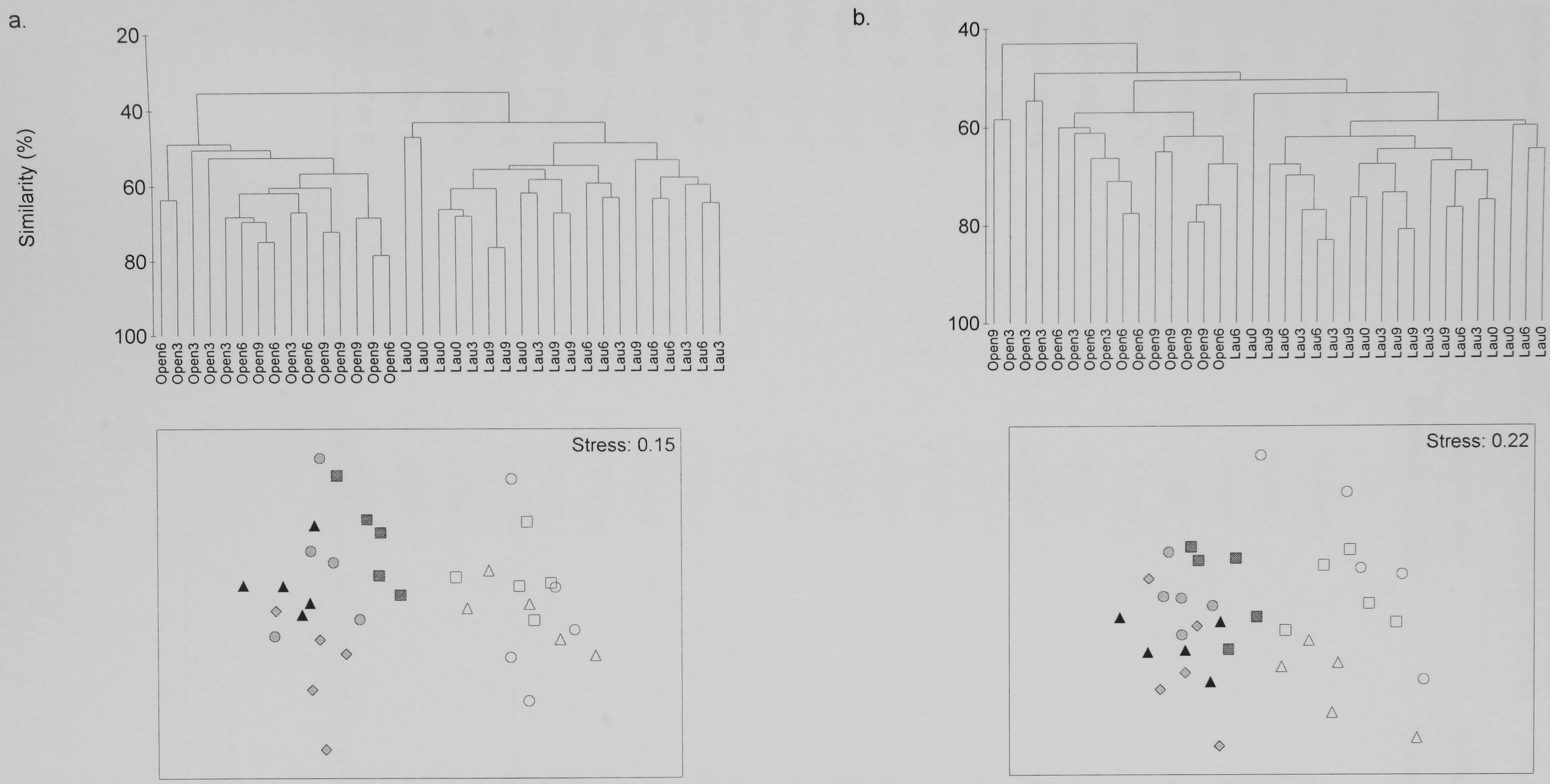

Figure 8. Cluster and nMDS ordinations of a.) standardised square root and b) presence/absence transformed species abundance data from *Laurencia pinnatifida* and artificial substratum on open rock. ▲-9 months, ■-6 months, ●-3 months ◆-0 months; open symbols relate to samples from artificial substratum.

Table 6. One way ANOSIM between community associated with artificial substratum and *Corallina* turf in tide pools at 0, 3, 6 and 9 months after colonisation. For pairwise groups, 'Cor' indicates samples of *Corallina* turf, 'Asu' indicates artificial substratum unit, associated numerical value indicates number of months from start of experiment. $p<0.05$, ** $p<0.01$, ns=not significant.

Transformation:	Square root	Presence/absence
	Global R = 0.569**	Global R = 0.491**
Pairwise groups	R	R
Cor 9 : Asu 9	0.964**	0.820**
Cor 9 : Cor 6	0.284*	0.140 ns
Cor 9 : Asu 6	1.000**	0.812**
Cor 9 : Asu 3	1.000**	0.790**
Cor 9 : Cor 3	0.520*	0.416*
Cor 9 : Cor 0	0.500*	0.188 ns
Asu 9 : Cor 6	0.700**	0.744**
Asu 9 : Asu 6	0.576**	0.408**
Asu 9 : Asu 3	0.568**	0.738**
Asu 9 : Cor 3	0.828**	0.818**
Asu 9 : Cor 0	0.552**	0.728**
Cor 6 : Asu 6	0.600**	0.512**
Cor 6 : Asu 3	0.704**	0.652**
Cor 6 : Cor 3	0.008 ns	0.142 ns
Cor 6 : Cor 0	0.400**	0.430**
Asu 6 : Asu 3	0.012 ns	0.166 ns
Asu 6 : Cor 3	0.732**	0.524**
Asu 6 : Cor 0	0.716**	0.730**
Asu 3 : Cor 3	0.836**	0.470*
Asu 3 : Cor 0	0.624**	0.630**
Cor 3 : Cor 0	0.376*	0.282 ns

Table 7. One way ANOSIM between community associated with artificial substratum and *Laurencia* turf on open rock after 0, 3, 6 and 9 months after colonisation. For pairwise groups, 'Lau' indicates samples of *Laurencia* turf, 'Asu' indicates artificial substratum unit, associated numerical value indicates number of months from start of experiment.
$p<0.05$, ** $p<0.01$, ns=not significant.

Transformation:	Square root	Presence/absence
	Global R = 0.658**	Global R = 0.523**
Pairwise groups	R	R
Lau 9 : Asu 9	1.000**	0.720**
Lau 9 : Lau 6	0.580*	0.362 ns
Lau 9 : Asu 6	1.000**	0.932**
Lau 9 : Asu 3	0.984**	0.662**
Lau 9 : Lau 3	0.420*	0.264 ns
Lau 9 : Lau 0	0.360**	0.074 ns
Asu 9 : Lau 6	0.896**	0.598**
Asu 9 : Asu 6	0.192 ns	0.414**
Asu 9 : Asu 3	0.364**	0.330*
Asu 9 : Lau 3	0.956**	0.848**
Asu 9 : Lau 0	0.956**	0.644**
Lau 6 : Asu 6	0.860**	0.866**
Lau 6 : Asu 3	0.800**	0.444*
Lau 6 : Lau 3	0.024 ns	0.144 ns
Lau 6 : Lau 0	0.584**	0.398**
Asu 6 : Asu 3	0.100 ns	0.122 ns
Asu 6 : Lau 3	0.948**	0.948**
Asu 6 : Lau 0	0.976**	0.894**
Asu 3 : Lau 3	0.936**	0.662**
Asu 3 : Lau 0	0.948**	0.632**
Lau 3 : Lau 0	0.176 ns	0.338**

Table 8. Species occurring within natural *Corallina* turf and artificial substrata in order of their rank abundance at three monthly intervals from start of sampling.

Corallina at Start	*Corallina* 3 months	*Corallina* 6 months	*Corallina* 9 months
Amphipholis squamata	*Amphipholis squamata*	*Stenothoe monoculoides*	*Stenothoe monoculoides*
Musculus discors	*Stenothoe monoculoides*	*Amphipholis squamata*	*Convoluta convoluta*
Onoba semicostata	*Musculus discors*	*Musculus discors*	*Onoba semicostata*
Nematode	*Idotea granulosa*	*Onoba semicostata*	Nematode
Stenothoe monoculoides	*Onoba semicostata*	*Idotea granulosa*	*Amphipholis squamata*
Apherusa jurenei	*Polydora flava*	*Modiolus modiolus*	*Micromadane ornithochaeta*
Polydora flava	Nematode	*Rissoa parva*	*Musculus discors*
Ampithoe helleri	*Rissoa parva*	Nematode	*Rissoa parva*
Ostracods	*Micromadane ornithochaeta*	*Polydora caeca*	Mites
Platynereis dumerilli	*Aspidosiphon muelleri*	*Caprella acanthifera*	*Polydora caeca*
	ASU 3 months	ASU 6 months	ASU 9 months
	Amphipholis squamata	*Amphipholis squamata*	*Amphipholis squamata*
	Onoba semicostata	*Musculus discors*	Nematode
	Musculus discors	*Onoba semicostata*	*Onoba semicostata*
	Ampithoe ramondii	Foraminiferan	*Musculus discors*
	Hyale prevostii	*Platynereis dumerilii*	*Platynereis dumerilii*
	Foraminiferan	*Modiolus modiolus*	Foraminiferan
	Platynereis dumerilii	*Ampithoe ramondi*	*Ampithoe ramondii*
	Carcinus maenas	*Rissoa parva*	Mites
	Modiolus modiolus	Nematode	*Limapontia* sp.
	Nematode	*Ampithoe helleri*	*Clunio* sp.

Table 9. Species occurring within natural *Laurencia* turf and artificial substrata in order of their rank abundance at three monthly intervals from start of sampling.

Laurencia at Start	*Laurencia* 3 months	*Laurencia* 6 months	*Laurencia* 9 months
Clunio sp.	*Tanais dulongii*	*Lasaea adonsoni*	*Fabricia stellaris*
Fabricia stellaris	*Micromadane ornithochaeta*	*Musculus discors*	Nematode
Hyale prevostii	*Fabricia stellaris*	*Hyale prevostii*	*Hyale prevostii*
Tanais dulongii	*Hyale prevostii*	Nematode	*Skeneopsis planorbis*
Skeneopsis planorbis	*Musculus discors*	*Fabricia stellaris*	*Lasaea adonsoni*
Nematode	*Stenothoe monoculoides*	*Modiolus modiolus*	*Onoba semicostata*
Lasaea adonsoni	Nematode	*Onoba semicostata*	*Jaera albifrons*
Modiolus modiolus	*Clunio* sp.	Foraminiferan	*Tanais dulongii*
Capitellid Juv	*Lasaea adonsoni*	*Amphiglena mediterranea*	*Modiolus modiolus*
Musculus discors	*Modiolus modiolus*	*Amphipholis squamata*	*Clunio* sp.
	ASU 3 months	ASU 6 months	ASU 9 months
	Hyale prevostii	*Hyale prevostii*	*Hyale prevostii*
	Modiolus modiolus	*Modiolus modiolus*	*Modiolus modiolus*
	Littorina mariae	*Musculus discors*	Mites
	Musculus discors	*Gammarus finmarchius*	*Littorina neglecta*
	Eulimnogammarus obtusatus	*Onoba semicostata*	*Littorina mariae*
	Littorina indet.	*Littorina mariae*	*Onoba semicostata*
	Carcinus maenas	*Littorina neglecta*	*Littorina* indet.
	Foraminiferan	Foraminiferan	*Gammarus finmarchius*
	Onoba semicostata	*Littorina* indet.	*Lasaea adonsoni*
	Idotea granulosa	*Carcinus maenas*	*Musculus discors*

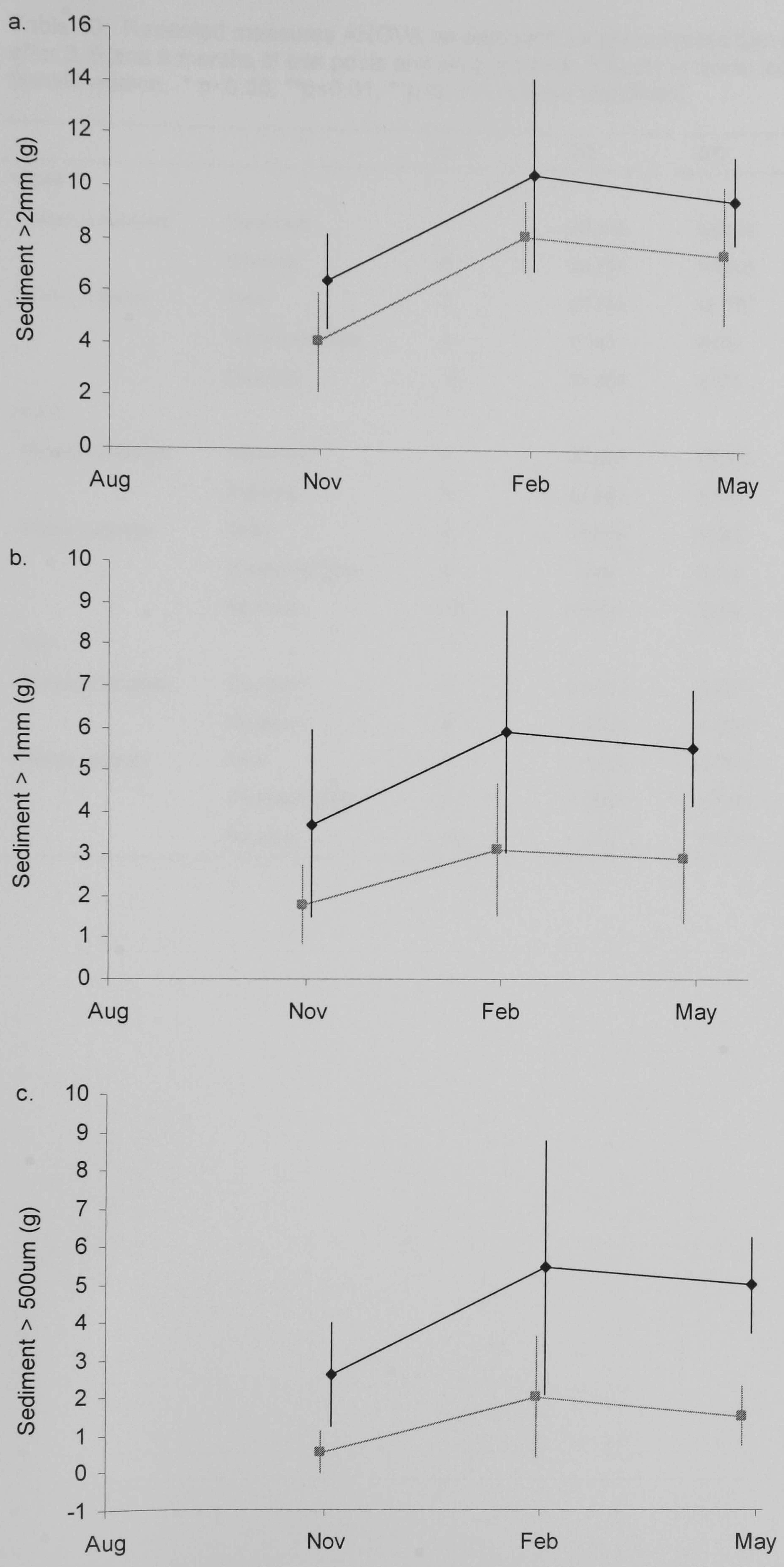

Figure 9. Mean dry weight and 95% confidence intervals of sediment of different fractions collected from artificial substrata in tide pools and on open rock. ♦-tide pool, ■-open rock.

Table 10. Repeated measures ANOVA on sediment weight collected fom artificial substratum after 3, 6 and 9 months in tide pools and on open rock. Results in italics indicate Log (x+1) transformation. * p<0.05, **p<0.01, **p<0.001, ns=not significant.

		d. f.	SS	MS	*F*
>2000					
Between subjects	Treatment	1	39.342	39.342	7.75*
	Residual	8	82.766	10.346	
Within subjects	Time	2	96.504	48.252	9.51**
	Treatment*Time	2	0.145	0.073	0.01 ns
	Residual	16	81.202	5.075	
>1000					
Between subjects	Treatment	1	45.559	45.559	16.25**
	Residual	8	62.847	7.859	
Within subjects	Time	2	18.105	9.052	3.23 ns
	Treatment*Time	2	1.049	0.525	0.19 ns
	Residual	16	44.871	2.804	
>500					
Between subjects	*Treatment*	*1*	*2.9212*	*2.9212*	*26.61****
	Residual	*8*	*1.4763*	*0.1845*	
Within subjects	*Time*	*2*	*1.4812*	*0.7406*	*6.75***
	*Treatment*Time*	*2*	*0.2081*	*0.1041*	*0.95 ns*
	Residual	*16*	*1.7561*	*0.1098*	

Table 11. Repeated measures ANOVA on environmental variables collected from *Corallina officinalis* in tide pools and *Laurencia pinnatifida* on open rock on four occasions every three months. Varaibles in bold type did not meet the assumptions of analysis of variance.
* p<0.05, **p<0.01, **p<0.001, ns=not significant.

		d. f.	SS	MS	F
CDENS					
Between subjects	Treatment	1	0.001440	0.001440	0.28 ns
	Residual	8	0.039870	0.004984	
Within subjects	Time	2	0.061290	0.020430	4.01*
	Treatment*Time	2	0.009340	0.00113	0.61 ns
	Residual	16	0.122370	0.005099	
Algae Dry Weight					
Between subjects	Treatment	1	5.41483	5.41483	231.30***
	Residual	8	0.19569	0.02446	
Within subjects	Time	2	0.02970	0.00990	0.42 ns
	Treatment*Time	2	0.01764	0.00588	0.25 ns
	Residual	16	0.56210	0.02342	
Sediment >63um					
Between subjects	Treatment	1	54.967	54.967	8.71 **
	Residual	8	218.168	27.271	
Within subjects	Time	2	41.557	13.852	2.20 ns
	Treatment*Time	2	54.999	18.333	2.91 ns
	Residual	16	151.409	6.309	
Sediment <63um					
Between subjects	Treatment	1	0.7812	0.7812	4.94 *
	Residual	8	5.9940	0.7943	
Within subjects	Time	2	2.9748	0.9916	6.27**
	Treatment*Time	2	1.9406	0.6469	4.09*
	Residual	16	3.7934	0.1581	
Surface Area of Algae					
Between subjects	Treatment	1	2680019	2680019	65.52***
	Residual	8	166393	20799	
Within subjects	Time	2	1137469	379156	8.84***
	Treatment*Time	2	924038	308013	7.19**
	Residual	16	1028818	42867	
Relative Surface Area (cm^2/g)					
Between subjects	Treatment	1	1601845	1601845	85.40***
	Residual	8	107723	13465	
Within subjects	Time	2	66470	22157	1.18 ns
	Treatment*Time	2	82340	27447	1.46 ns
	Residual	16	450163	18757	

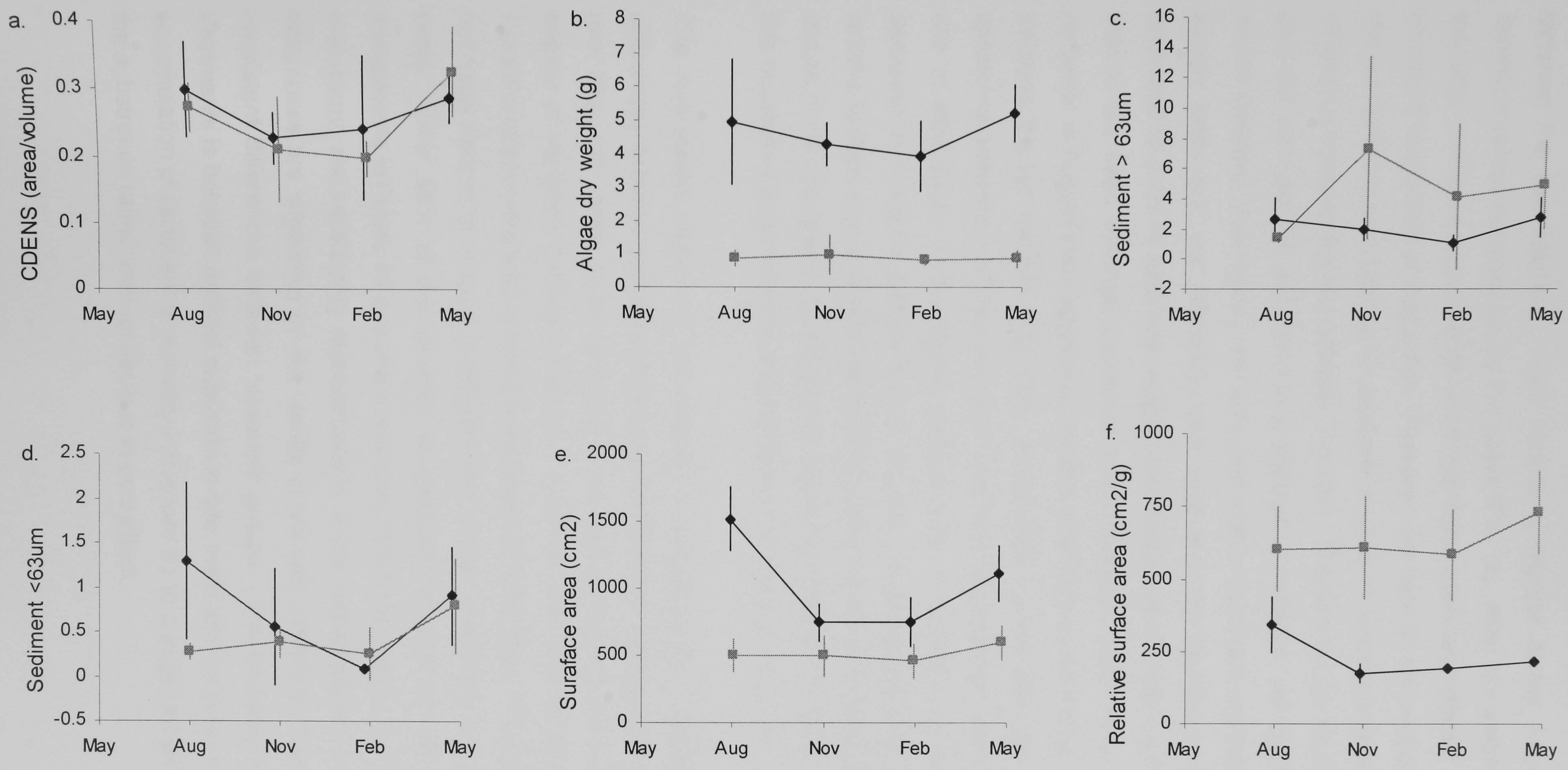

Figure 10. Mean and 95% confidence intervals of measured environmental variables within *Corallina officinalis* and *Laurencia pinnatifida* turf taken at 3 monthly intervals form August 2001 to May 2002. ♦-*Corallina officinalis*, ■-*Laurencia pinnatifida*.

(Table 11). CDENS does show significant variability through time that is consistent between the two habitats. Algal density is highest during August and May with minimum values obtained during the winter (Fig 10). Algal dry weight and dry weight of the large sediment fraction both show significant treatment effects, with no significant change through time or interaction. However, the data for the >63µm sediment fraction did not meet the assumptions for analysis of variance and there appears to be little real difference between the two habitats (Fig 10c). The data for the small sediment fraction also did not meet the assumptions of analysis of variance, yet significant results were shown between treatments, over time and with a significant interaction (Table 11). It seems likely that the difference over time and the significant interaction can be attributed to a fall in sediment weight associated with *Corallina* turf during the winter that is not seen amongst *Laurencia* turf. However, apart from the first sampling occasion in August there appears to be little difference in the actual weight of sediment between the two habitats (Fig 10d). Actual algal surface area also shows significant difference between samples and over time with a significant interaction term. Again this is attributable to the higher surface area of *Corallina* in the summer with a decrease in winter, a pattern that is not seen in *Laurencia* (Fig 10e). In terms of relative surface area a significant treatment effect exists only where the relative weight of *Laurencia* (per gram) is consistently higher than that of *Corallina*; again, the data on this occasion did not meet the assumptions of analysis of variance.

The multivariate pattern of the measured environmental variables indicates clear differences between artificial substrata and natural turf algae in tide pools and on open rock (Fig. 11). Most of the ordinations are well spread indicating a relatively similar degree of variability between habitats. However, the tight clustering of samples for *Corallina* when compared to artificial substrata in pools (Fig. 11c) indicates that natural turf traps sediments in quite a different way to that of artificial turf, at least within tide pools. Over 95% of the variation is captured by each of the first two principal components in Figure 11 a, c and d and over 75% for Figure 11 b, indicating that these ordinations are satisfactory representations of the overall pattern in the data. These differences are supported by the results of two-way ANOSIM (Table 12) which show consistent differences between treatment groups. The weakest difference between treatments is between artificial substrata in tide pools and on open rock, indicating that accumulation of sediment is probably influenced by to a larger extent than expected by the substratum rather than an obvious in pool effect.

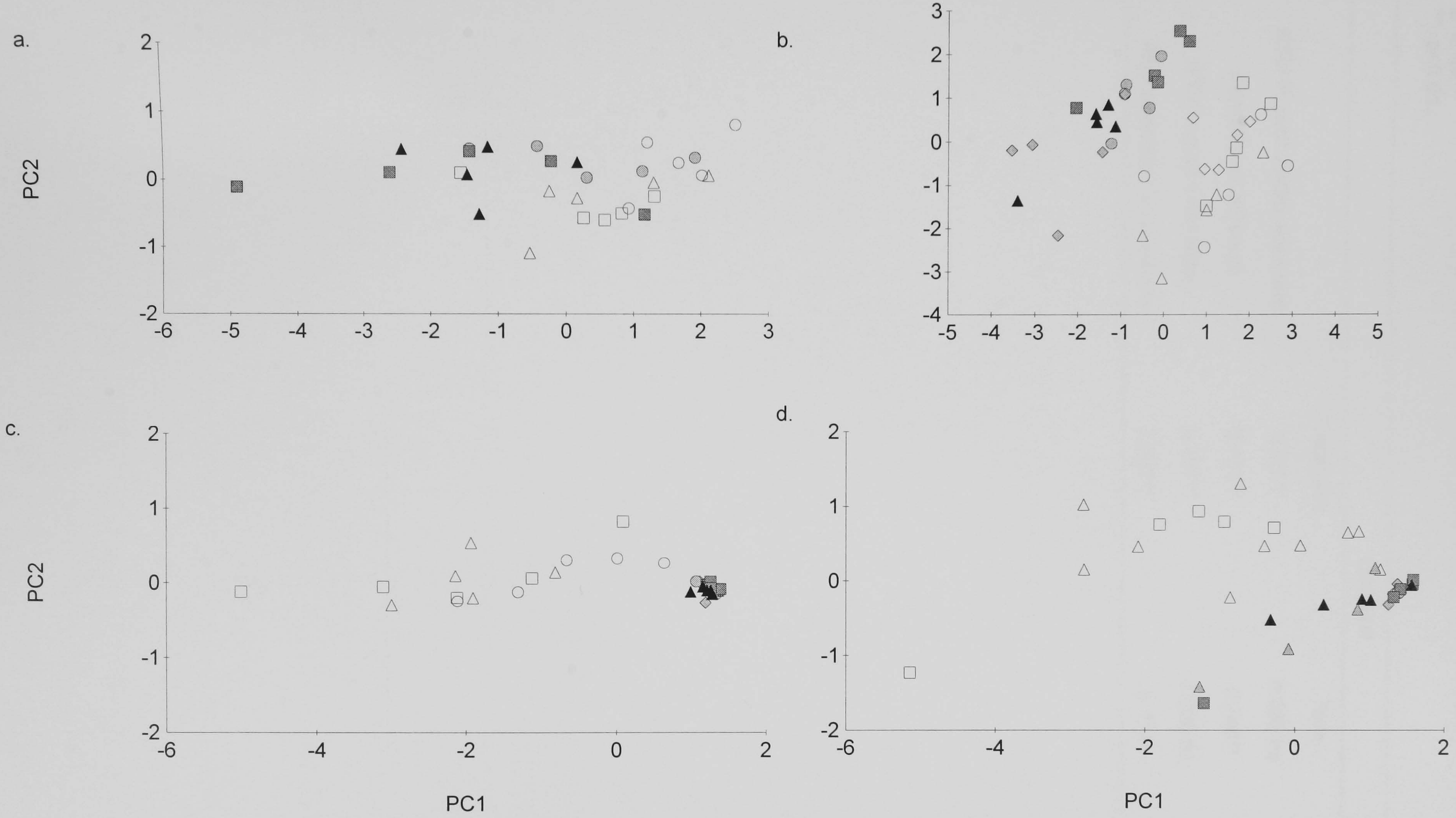

Figure 11. Principal component analysis (PCA) of environemental variables collected from a) artificial substrata in pool and on open rock, b) *Corallina officinalis* and *Laurencia pinnatifida*, c) *Corallina officinalis* and artificial substratum in tide pools, d) *Laurencia pinnatifida* and artificial substratum on open rock. ▲-9 months, ▨-6 months, ●-3 months, ◆ 0-months after start of experiment, open symbol indicates second named habitat .

Table 12. Two-way analysis of similarities on environmental variables measured amongst natural and artificial turf in tide pools and on open rock. ASU=Artificial substratum unit. *, p<0.05;
**, p<0.01.

	Global R	
	Treatment	Time
ASU In pool v ASU open rock	0.200*	0.085 ns
Corallina v *Laurencia*	0.731**	0.240**
ASU in pool v *Corallina*	0.767**	0.008 ns
ASU open rock v *Laurencia*	0.367**	0.114*

Table 13. Combinations of environmental variables measured amongst *Corallina* and *Laurencia* turf that best match the observed biotic communities associated with each habitat after a) sqaure root and b) presence absence transformation. Optimum value of rho indicated in bold type.

a.

	Best variable combination (rho)		
1	**Weed (0.628)**		
2	Weed SA/g (0.618)	Weed SA (0.535)	
3	Weed SA SA/g (0.583)	Weed <63 SA/g (0.562)	Weed >63 SA/g (0.532)
4	Weed <63 SA SA/g (0.535)	Weed >63 SA SA/g (0.533)	

b.

	Best variable combination (rho)		
1	**Weed (0.487)**		
2	Weed SA (0.477)	Weed SA/g (0.436)	Weed <63 (0.434)
3	Weed SA SA/g (0.469)	Weed <63 SA/g (0.456)	Weed >63 SA/g (0.425)
4	Weed <63 SA SA/g (0.470		

A multivariate analysis of environmental variables associated with natural turf algae (BIOENV) (Table 13) indicates that algal dry weight is best correlated with the multivariate biotic pattern in the data with surface area and relative surface area also having an influence. These results highlight the difference in the structure of the two algae and it seems likely that observed differences in the fauna of these two habitats is strongly influenced by this factor as well as the tide pool effect.

Discussion

During the course of this study artificial substrata were successfully colonised by a wide range of invertebrate taxa. Although not tested statistically, due to unequal sample sizes, there were similar numbers of individuals and species in artificial substrata and natural turf after 3 months and a greater number in artificial turf after 6 and 9 months, although this could be due to the difference in size of the sampling units. However, despite the numerical similarities between artificial habitat and natural turf, clear differences were demonstrated in terms of the actual community structure. Dean and Connell (1987) demonstrated similar results using artificial habitat mimics to elucidate patterns of diversity in algal succession. In the present study, of the 118 species found on artificial algae, all but two also occurred on natural algae. Despite this, the fauna found in artificial habitats were clearly much more similar within treatments than to the fauna found amongst the natural algae. At the start of experiments the artificial substrata are relatively inert with none of the exudates or microbial or microalgal biofilms that would be present on natural algae (Norton and Manley, 1990). However, as the artificial substrata age they can become covered in a similar suite of microfauna as natural surfaces as well as accumulating detritus and broken fronds of the larger macroalgae. This change in the state of the artificial substrata could affect the associated invertebrate fauna. Cummings and Ruber (1987) found that plastic polypropylene rope used to mimic the saltmarsh grass *Spartina alterniflora* was more attractive than the natural habitat once it had aged in the environment. This phenomenon was attributed to the colonisation by microflora and the accumulation of detritus, which can provide a source of food for colonising invertebrates (Worthington and Fairweather, 1989; Brawley, 1992; Williams and Seed, 1992) and microflora can produce exudates that may attract or repel invertebrates (Underwood, 1979).

Using astroturf to mimic coralline algal turf Kelaher (2002) found that there was no difference between artificial and natural turf after 4 months of colonisation and suggested that by this time the difference in associated biofilms between the two habitats was negligible. The present study suggests that the artificial substrata used showed a similar pattern to that decribed by Kelaher, over similar time scales, yet beyond the three month period the number of individuals and species diverged again and increased to levels greater than in natural turf, as was predicted in Kelaher's study, and as observed in recolonisation of patches of sediment over similar time scales (Beukema *et al.*, 1999; Lu and Wu, 2000). However, whether these relatively short time scales produce communities that can appropriately be described as the same as the initial community would require much longer periods of deployment. Studies following patterns of recovery after oil spills, for example, show that the communities continue to fluctuate many years after the event despite giving an initial appearance of maximum recovery after only a relatively short time (Southward and Southward, 1978; Southward, 1979). Also the fauna associated with algal turf communities on artificial reefs may take 10-15 years before they are similar to those found on natural reefs (Aseltine-Neilson *et al.*, 1999). Despite these differences, artificial substrata still provide a useful tool in ecology and have been used successfully to test hypotheses on habitat complexity (Kelaher, 2003a), colonisation and island biogeography (Olabarria, 2002) and behaviour of associated invertebrates (Worthington and Fairweather, 1989).

Because the artificial turf in this study was not an exact mimic of the two natural turf algae it is also possible that differences in community between these two natural turf habitats was caused by variations in the structure of the habitat itself. The fronds of *Corallina* are calcareous, complex, long and highly branched, while those of *Laurencia* are shorter and partly gelatinous. The astroturf base of the artificial units closely resembled *Laurencia* in appearance but was less dense and much more rigid. The pan scourers have a relatively high surface area and high complexity, but little variability in the nature of the complexity due to their manufactured nature. Differences in the samples could therefore be caused by increases in surface area thereby increasing the relative size of the sample (Parker *et al.*, 2001) as well as differences in the structural component of the habitats (see Beck, 2000).

Differences between communities associated with *Corallina* and *Laurencia* turf can be attributed to many factors. For example, increases in the fractal dimension of algae (Gee and Warwick, 1994) or changes in the length of fronds (Kelaher, 2003a; Kelaher *et al.*, 2001) can explain variations in diversity. Different algae also produce different exudates or support different biofilms that may either attract or repel grazing molluscs (Norton and Manley, 1990) and these effects may be enhanced within tide pools

(Galanidi, 2001). Extracts of *Corallina officinalis* in tide pools have been shown to be lethal to the larvae of the barnacle *Elminius modestus* and inhibit the feeding behaviour of adults (Galanidi, 2001). Also, polyphenolic compounds in fucoid algae can inhibit the production of bacteria and epiphytes (Conover and Sieburth, 1964) and while this is unlikely to inhibit production of a biofilm in the intertidal, in tide pools the concentration of these chemicals at low tide may have a deleterious effect. The presence of a biofilm is well known to have an effect on the choice of settlement position and substratum for marine larvae (Zobell and Allen, 1935; Wieczorek and Todd, 1998). Planktotrophic larvae of most specialist sessile invertebrates have evolved mechanisms which ensure correct selection of specific benthic substrata on which to settle (Morse, 1992). An artificial substratum may not possess the necessary cues with which to induce settlement of these larvae particularly during their early stages of deployment. In the natural turf the environmental variable that best matched the multivariate community pattern was algal dry weight. This probably reflects clear differences in the structure of the two habitats and indeed, albeit at lower levels of correlation, surface area combined with algal dry weight is also a good predictor of the observed community pattern. In the comparison between artificial algae however, both these factors were identical. Amongst turf forming algae in the Azores, mollusc density is strongly influenced by algal dry weight while abundance and diversity were influenced by the species composition of the turf (Azevedo, 1992). However, despite supporting different communities, *Corallina* and *Laurencia* turf support relatively similar numbers of species. It would be interesting to study whether other mat like habitats under similar conditions also support similar number of species and to determine therefore whether these habitats have an optimum carrying capacity for the species they support. The comparison between *Corallina* and *Laurencia* turf is insufficient to explain fully the differences between these two algal species; nevertheless it does go some way to elucidating the potential effect of tide pools on the associated invertebrate faunas.

There was consistently higher diversity in artificial substrata in tide pools than on open rock. Of all the measures used only number of individuals increased significantly from the initial time of sampling. An increase in the number of individuals may indicate an increase in the amount of food in the habitat that could be attributed to colonisation of the artificial substratum surface by microflora and accumulated detritus. While microflora were not measured there were significant differences in the amount of coarse sediments (>500µm, >1000µm and > 2000µm) associated with the artificial substrata over time. Increasing the amount of sediment increases habitat complexity thus influencing the diversity of the associated invertebrates. Olabarria and Chapman

(2001b), for example, show how variations in the amount of sediment can explain variations in the distribution of different species of intertidal gastropods. Given the time scales involved in this study any pattern could be influenced by a pattern of seasonality (Chapter 5). As the artificial substrata were only recovered up to 9 months after deployment in the field this is difficult to determine. Nevertheless, in natural turf there is some evidence for a seasonal pattern in the number of individuals and in some of the measured environmental variables (CDENS, fine sediment and surface area). If there were a seasonal trend in the fauna of artificial substrata then it appears to take longer than 3 months to develop. Number of individuals increases through November to February in both habitats while during this period there is a noticeable decline in the number of individuals associated with natural turf. This pattern is reflected in the accumulation of sediments between the two habitats and it has previously been shown that the sediments associated with artificial algae can mimic seasonal fluctuations (Southgate, 1982). A further indication that the artificial substrata had not reached equilibrium was the greater mass of coarse sediment associated with artificial substrata in tide pools than out of pools yet in natural turf; higher amounts of coarse sediment were found amongst *Laurencia* turf on open rock. If artificial substrata had reached equilibrium with their environment it might have been expected that those artificial substrata on open rock would contain greater levels of sediment than those in tide pools.

As differences between the two artificial habitats could not be due to initial differences in structural complexity the effect of either the tide pool or open rock must have a major role in structuring the community. Differences between artificial habitat and natural turf were greatest between *Laurencia* and open rock. R-values derived from ANOSIM tests were much higher between these two habitats than between *Corallina* and artificial substrata in tide pools at the same time. Similarly, although not shown, average dissimilarity was also higher between pairwise groups on open rock than in tide pools. It is likely that these differences can be attributed to the difference in time available for colonisation. Artificial substrata on open rock will only be susceptible to immigration by larvae and mobile invertebrates at high tide. Also while the tide is out, the invertebrates in tide pools will have a much more restricted area for dispersal, increasing the likelihood of encountering the artificial substrata. Thus it would appear that the artificial substrata may be a better mimic of *Corallina* turf than *Laurencia* turf at least within their respective habitats. Many species have previously been described as being characteristic of tide pools (Emson, 1985) yet until now no study had been done that has controlled for substratum complexity in tide pools and on open rock. It has been shown previously that tide pools can greatly increase the growth and diversity of macroalgae species in the rocky intertidal (Underwood and Jernakoff, 1984).

This study clearly shows that differences in diversity and community structure in marine algal invertebrate fauna in tide pools and on open rock is not simply due to differences in the types of algae and structural complexity between the two habitats. These results can be explained by several factors. Firstly more individuals and species colonising artificial habitats in tide pools may reflect the time available for colonisation. As explained above, tide pools remain submerged for the entire tidal cycle and thus mobile species and larvae have a greater time for movement into the new substratum. Moreover, at low tide, the pool acts as a barrier against wide range dispersal, encouraging colonisation of the artificial habitat by common species within the tide pool. Studies of re-colonisation of pools have shown that although ephemeral algae are quick to recolonise, as are highly mobile animals such as amphipods, many less mobile species, particularly those associated with turf-forming algae may take several years to become established (Mwaiseje, 1977).

Many authors have demonstrated that the nature of colonisation of bare habitat in marine benthic communities following disturbance or defaunation is dependent on the species present at the time of disturbance. For example, in intertidal algae there is considerable variation in the early arrivals depending on the timing of grazer removal (Raffaelli and Hawkins, 1999) and colonisation of the short-lived red alga *Ceramium rubrum* by harpacticoid copepods proceeds as an invasion from other nearby algae and sediments (Hicks, 1985). Seasonality has been shown to affect the community that colonises patches of cleared bare rock (Kaehler and Williams, 1998) and disturbed patches of mussel bed (Dean, 1981). The fauna of natural *Corallina* turf has a strong seasonal pattern associated with it (Chapter 5) and this is probably reproduced in the fauna of *Laurencia* turf (this chapter).

In this study, the echinoderm, *Amphipholis squamata*, attained its highest levels of abundance in the artificial turf in tide pools while the amphipod, *Hyale prevostii*, was most abundant in artificial turf on open rock. Although benthic marine research has emphasised species that colonise areas as planktonic larvae, individuals of many taxa disperse as adults or juveniles (Martel and Chia, 1991; Norkko *et al.*, 2001). High rates of post-settlement movement are considered important in rapid dispersal and colonisation of patches by macrofauna (Cummings *et al.*, 1995). In addition, transport of sediments may move post-settlement juvenile and adult benthic stages of macrofauna (Commito *et al.*, 1995; Cummings *et al.*, 1995; Norkko *et al.*, 2001).

Animals typical of tide pools tend to be small and reproductively favour direct development or brooding juveniles (Emson, 1985). Unpredictable environments like the rocky intertidal by contrast are usually characterised by a predominance of species with a high reproductive potential (Todd, 1985). Emson (1985) suggests that typical tide pool species do not adopt this strategy as they tend to be small enabling them to live amongst the interstices of algae but reducing their reproductive output. A good example of this is the harpacticoid copepod, *Scutellidium lamellipes*, which when colonising individual plants reached an equilibrium level through immigration and emigration together with direct *in situ* reproduction (Gunnill, 1982). Thus the species present in tide pools tend to be restricted in their ability to colonise new patches other than within their own tide pool. Also many invertebrates on open rock which have a planktonic larva and should be able to colonise tide pools as well as open rock surfaces are often absent or rare in tide pools while being highly abundant on the adjacent open rock e.g. barnacles, see discussion above. Post-settlement drifting and rafting have been proposed as potential dispersal mechanisms for invertebrates without a pelagic larval stage (Highsmith, 1985; Martel and Chia, 1991) along with floating on the meniscus of tide pools, e. g. *Anurida* (pers. obs.); in the confines of a tide pool, even the dispersal range of this method would be low. Thus, those species already present in pools are likely to be the suppliers of juveniles to the new habitat. Furthermore, intertidal environments are often dominated by physically robust organisms able to survive the constant drying out effect at low tide (Olsgard, 1999) and thus may be expected to have rapid rates of recolonisation. Colonisation of artificial substrata on open rock has also been shown to vary at many scales with no consistent patterns in terms of distance from parent patch or mode of colonisation (adults/juveniles) (Olabarria, 2002).

Of those species that are most responsible for differences between the two artificial habitats in this study, those that are most active, such as *Hyale prevostii*, attain the highest levels of abundance in suitable algal habitats on the open rock. This indicates that these species probably arrived in the new habitat as adults seeking the structure as a place of attachment during high tide and a refuge during low tide. In tide pools, slower moving species such as the gastropod *Onoba semicostata,* and the echinoderm *Amphipholis squamata,* or even temporarily attached species such as *Platynereis dumerilii* attained their highest levels of abundance. *Amphipholis squamata* and *Onoba* *semicostata* were present in artificial turf after only three months exposure and at sizes similar to those found in the natural turf indicating a probable direct effect of migration into the artificial turf. *Platynereis dumerilii*, however, only became established in the turf in February after six months exposure. *Platynereis dumerilii* is known to reproduce during late autumn and winter where it broods juveniles inside the sediment or algal tubes in which it lives (Chapters 3 and 5). It seems likely that this species recruited to the artificial turf as juveniles.

Once the initial colonisation has occurred, the initial settlers can dictate subsequent patterns of community development. For example, mussel settlement on bare rock, changes the hydrodynamic regime and microclimate encouraging settlement of species that would previously have been absent (Seed, 1996 and references therein). Thrush *et al.* (1992) also demonstrated that addition of the bivalve *Tellina liliana,* or the polychaete, *Aonides oxycephala,* facilitated the arrival of other species into defaunated patches of sediment. Therefore, if there are differences in the initial period of colonisation between two habitats, the modification of the habitat by these different colonists is likely to lead to further divergences in community structure.

Ultimately this experiment shows that there are clear differences in the community associated with natural turf-forming algae within tide pools and those on open rock. Moreover, when the complexity of habitat is controlled for, these differences are maintained. The differences therefore, are probably caused by variations in the physical regime within tide pools and on open rock surfaces. Variations in colonisation of artificial bare patches can also be explained by the influence of the life histories, reproductive strategies, larval and post-settlement dispersal as well as adult migration and immigration of the resident species in these habitats. These behavioural patterns are apparently strongly influenced by the nature of the habitat, whether tide pool or open rock surface.

Chapter 7

General Discussion

General discussion

The primary purpose of ecological investigation is to understand and explain natural phenomena, ecological processes and, therefore, the resultant patterns of distribution, abundance, diversity and interactions of species (Underwood *et al.*, 2000). Despite the widespread belief in the 'balance of nature', it is well known that natural assemblages in marine (Underwood, 1996), terrestrial (Botkin, 1990) and freshwater habitats (Likens, 1992) have patchy distributions and are unpredictably variable through space and time. The present study focuses on such patterns amongst the invertebrate fauna associated with the turf-forming red alga, *Corallina officinalis*, in tide pools. *Corallina* turf is common in tide pools on moderately wave-exposed shores of the British Isles and is also common in tide pools and on open rock throughout the world (Chapter 1). *Corallina* turf is structurally complex with calcified fronds which provide a surface for attachment, form a matrix of interstitial spaces and trap sediments making them ideal for colonisation by a wide suite of invertebrate species. The turf provides food, directly so for grazers and indirectly for microalgal grazers and detritivores.

In this study there was a high degree of variability in the patterns of diversity and community structure in the invertebrates associated with *Corallina* turf. Numbers of individuals reached over 330,000 m^{-2} at one time of sampling (Porth Cwyfan, Chapter 5) but only 16,000 individuals m^{-2} at Filey Brigg (Chapter 3). However, numbers of individuals reached over 200,000 m^{-2} in at least one sample of all experiments and this compares favourably with other studies on *Corallina* turf (200,000 m^{-2} in New Zealand, Brown and Taylor, 1999) and 250,000 m^{-2} in Australia (Kelaher *et al.*, 2001). Even considering differences in methods of sampling the number of taxa identified amongst *Corallina* turf in this study (212 taxa from 14 phyla) also compares favourably with those in other studies in other countries (Japan 91 taxa (Akioka *et al.*, 1999); Chile, 36 taxa (Lopez and Stotz, 1997); Norway, 72 taxa (Dommasnes, 1969); New Zealand, 106 taxa (Hicks, 1971) and Australia 147 taxa (Kelaher *et al.*, 2001)).

Patterns in the biodiversity of invertebrates associated with *Corallina* turf were often very variable at small and large temporal and spatial scales. At regional scales (Chapter 3) there were clear differences in the community of invertebrates in different geographic areas of the British Isles. While measures of diversity showed some conflicting results there was a general trend for decreasing diversity from East to West. In this case, temperature was consistently well correlated with the observed pattern.

This makes sense, as the temperature regime of the three areas are different at different times of the year (Anonymous, 1962). The three sites studied are also somewhat isolated by variations in the direction of offshore currents (Anonymous, 2001), which can influence larval supply and survival (e.g. Southward and Crisp, 1954; Raffaelli and Hawkins, 1999). However, many of the species found at each site did not disperse via a pelagic larva which can lead to further differences in the assemblages. Most interestingly in this chapter, while some measures of habitat complexity produced a positive correlation with species richness (e.g. density of turf) others did not (e.g. number of branches). Other studies have described an increase in habitat complexity with an associated increase in species richness (Gee and Warwick, 1994; Thompson *et al.*, 1996; Beck, 2000) but the results here suggest that biological processes other than habitat complexity and environmental parameters must act on the community structure.

At smaller spatial scales (Chapter 4) patterns of community structure and diversity were variable from time to time and place to place with no single clear pattern evident. For example, no patterns in diversity were detected along a depth gradient in pools sampled at Cemlyn in the summer, whereas on the same shore in the winter, samples from shallow water depth produced higher measures of diversity. Similarly, diversity measures between pools of different sizes and at different heights on the shore revealed inconsistent patterns related to the time and location of sampling. Samples from large pools on the low shore at Cemlyn in the summer supported more individuals than small pools anywhere on the shore. In winter samples, however, there was little significant variation in measures of diversity at this site. On another shore, Porth Cwyfan, the pattern appeared to be reversed, high shore small pools now having significantly higher diversity than low shore small pools. Other studies have recently detected similar variations in small-scale patterns from place to place and at different times e.g. (Underwood and Chapman, 1996; Hull, 1999; Kelaher *et al.*, 2001). Studies that do not find consistent patterns are extremely important in ecology (Underwood *et al.*, 2000) as inconsistent patterns are in themselves patterns and provide new knowledge for broader understanding of variability in assemblages. Studies that have detected high variability at very small scales have found different explanations for the observed patterns. In some cases, the physical features of habitat are sufficient to explain the patterns (Archambault and Bourget, 1996; Thompson *et al.*, 1996) while in others, complex behavioural interactions are important in determining patterns of abundance at different spatial scales (Underwood and Chapman, 1996). In some areas, variability in species richness and species abundance are best explained by the processes acting at different spatial scales (e.g. richness at the kilometre scale but abundance at the cebtimetre scale, Archambault and Bourget, 1996). In others small scales alone explain most variability in diversity (Underwood and Chapman, 1996). It is clear from this study that local processes operating on the invertebrate fauna must themselves be very variable in space and time and manipulative experiments are required to elucidate which of these are important.

Over temporal scales (two years, Chapter 5) clear repeatable patterns were evident in the community structure, of the fauna associated with *Corallina* turf, which showed a cyclical pattern that follows a yearly sequence. While diversity remained relatively constant, number of individuals fluctuated attaining highest values in the summer. In this case, the pattern of community change was similar between different shores even if the structure of the communities causing the patterns were different between shores. This temporal pattern was also evident in the second year of sampling, but at this point the communities were slightly different to those of the previous year. Similar patterns in similar habitats have previously been described (e.g. Johnson and Scheibling, 1987; Preston and Moore, 1989; Metaxas and Scheibling, 1994; Hull, 1997) as well as other examples of the clear pattern of cyclicity (Warwick, 1977). In the present study the observed patterns seemed to be influenced by the timing, method and strategy of reproduction and patterns of behaviour in the fauna, a similar conclusion to that reached by Hull (1997) when studying the ostracod fauna associated with *Corallina* turf in tide pools. However, in the current study, increase in the number of individuals also occurred against a backdrop of increasing number of branchlets and density of turf that were in turn linked to the reproductive cycle of the alga as well as increases in the growth of algal epiphytes. This result is interesting as the number of branchlets was previously negatively correlated with diversity while density of turf was positively correlated at regional scales (Chapter 3). On rocky shores there is generally a positive relationship between complexity of algal structure and richness and abundance of the associated fauna (e.g., Hicks, 1985; Gibbons, 1988; Gee and Warwick, 1994). However these results suggest that the relationship between algal complexity and faunal diversity is not simple. It has been shown experimentally that decreasing the amount of structure in extremely complex habitats may have positive effects on abundance's of individual species by increasing resource availability (Sullivan and Klenner, 2000). Recently, Kelaher (2003c) demonstrated that large increases in habitat complexity of *Corallina* fronds using artificial substrata can have a negative effect on the associated gastropod assemblage and suggested that there may be distinct upper thresholds in the relationship between structural complexity and faunal species richness. Clearly more work needs to be done to elucidate the relationships between different environmental variables that structure the temporal patterns of invertebrate diversity associated with *Corallina* turf.

Finally, Chapter 6 shows that the fauna associated with *Corallina* turf is different to that of another turf-forming alga, *Laurencia pinnatifida,* at similar heights on the shore. Although such differences are normally explained by variations in the physical and chemical components of the two algae, here it is shown, using artificial habitat mimics, that the effect of the tide pool increases the diversity in algal turf habitats and results in markedly different communities irrespective of habitat structure and chemical composition of the algae. Increased diversity in tide pools is matched by higher concentrations of sediment which has previously been correlated with increases in diversity (e.g. Gibbons, 1988). However, differences in the community structure and diversity of invertebrate assemblages in tide pools and on open rock appear to be dictated by the behavioural responses of the animals that settle there. Tide pools tend to favour species that are small and with limited dispersal mechanisms (Emson, 1985) while on open rock there are more instances of species with higher reproductive potential (Todd, 1985). Also, some species on open rock may produce larvae that arrive in tide pools but, due sensitivity to the specialised conditions within tide pools may inhibit their survival (Galanidi, 2001). Thus the fauna of the two habitats is separated into different fractions, those that can tolerate tide pools, those that can tolerate open rock and those that can succeed in either habitat.

Corallina turf clearly influences the overall levels of biodiversity on rocky shores in the British Isles. Therefore, this habitat is important when considering global and local patterns of, and contributions to, biodiversity. Currently there are many initiatives to identify, record and promote areas of high diversity at species and habitat levels (www.ukbap.org.uk). Already in the U. K. there are Biodiversity Action Plans for at least six marine habitats that are similar in their physical characteristics to the mat-like *Corallina* turf (*Modiolus modiolus* beds, maerl beds and seagrass beds as well as of *Sabellaria alveolata*, *Sabelleria spinulosa* and serpulid reefs (UK Biodiversity Group 1998)). These habitats are selected for the important contributions they make to the biodiversity of the UK as well as the suites of associated species they support. *Sabellaria alveolata* reefs in Northern France, for example, support 63 species found in 24 samples (Dubois *et al.*, 2002), while in a study similar to this thesis 192 taxa have been identified from subtidal maerl beds in Northern Ireland (S. Vize pers. comm.). Subtidal *Modiolus modiolus* beds off the coast of the Llyn Peninsula, North Wales are specifically monitored for their biodiversity by the Countryside Council for Wales and these have been shown to have upwards of 65 associated taxa (B. Sanderson pers. comm.). While these numbers will differ from those found in this study due to differences in sampling techniques and sample size, it is clear that the fauna associated with *Corallina* turf is at least as important as in other protected habitats. Although the link between biodiversity and ecosystem functioning is strongly debated, ecosystem function seems to be positively correlated with biodiversity (Schwartz *et al.*, 2000). Other mat-like habitats on rocky shores, such as mussel beds, support similar numbers of species to *Corallina* turf on British coasts (192 taxa associated with beds of the mussel *Mytilus edulis*, Smith, 2001). Given that the fauna associated with *Corallina* turf varies around the coast of the British Isles and the sensitivity of the fauna to anthropogenic impacts such as trampling in areas of high tourist activity (Brown and Taylor, 1999) and pollution events (Bonsdorff, 1983) it is clear that there is a need for conservation and management of mat-like habitats on a nationwide scale.

The Convention on Biological Diversity requires that its signatory nations undertake to make inventories of their biodiversity, monitor changes and make plans as to how biodiversity can be conserved (Groombridge, 1992). This requires the knowledge of how to measure biodiversity, but as yet, no single convention has been agreed upon (Gray, 2000). In this study the approach taken was to use a suite of different measures of diversity using both univariate and multivariate techniques as suggested in the literature (Field *et al.*, 1982; Gray, 2000). Different indices of diversity often give conflicting results because they measure different aspects of diversity. This can lead to one community being considered more diverse than another purely because of the statistic chosen (Magurran, 1988) and most of the commonly used indices of diversity have the unfortunate property of being sample-size dependent (Warwick and Clarke, 1995). In this thesis, multivariate analysis of community pattern often provided clearer and more consistent differences between the various assemblages under investigation. Multivariate statistics are therefore extremely useful in our understanding of the communities as has previously been shown in studies on the effects of pollution and disturbance on communities (Warwick and Clarke, 1993). However, as these techniques do not measure diversity it is essential that we continue to use indices of diversity, whilst at the same time bearing in mind their constraints and precisely what they measure (Magurran, 1988).

As attention focuses more and more on monitoring biodiversity, indices used should ideally indicate how different the inhabitants of a community are from each other

(Hawksworth *et al.*, 1996). Also, as biodiversity does not only encompass species diversity, ecologists should strive to measure genetic and taxonomic diversity in studies of biodiversity. Such measures are currently being developed based on the taxonomic relatedness of the species found (Clarke and Warwick, 1998b, 1999, 2001; Warwick and Clarke, 1995, 2001). Two main new indices have been proposed, taxonomic diversity and taxonomic distinctness. Taxonomic diversity measures the average path length along Linnean taxonomic classification of individuals of different species and measures whether any two organisms selected at random from the full set of individuals are from the same species. Taxonomic distinctness is the expected path length of any two randomly chosen individuals from the sample provided they belong to different species. These indices were not used in this thesis as they are still relatively new and as yet have only been applied to data sets to illustrate the effects of environmental impacts rather than of diversity per se. Other authors have commented that their use should be cautioned until they have been more widely applied (Gray, 2000). However, these indices highlight the need to measure biodiversity using a variety of statistical tools to elucidate patterns in highly variable and diverse communities.

Overall this thesis shows the biodiversity of invertebrate communities associated with *Corallina* turf to be high. However, patterns in this biodiversity along some common gradients are variable. The invertebrate community associated with *Corallina* turf shows high variability at regional scales around the UK and Ireland and these differences are maintained when working at taxonomic levels higher than that of species. Much of this variation may be attributed to variations in temperature and the hydrodynamic regime of the region as well as some complex relationships between diversity and habitat complexity. Clear consistent patterns in the biodiversity of invertebrates associated with *Corallina* turf at small spatial scales were not found between different heights on the shore, pools of different size and at different depths within pools. Local processes operating on the fauna at these scales and manipulative experiments are required to elucidate the causes of such high variability in the associated fauna. A distinct temporal pattern was identified in changes in the community associated with *Corallina* turf which showed, using multivariate statistics, a seasonal cyclical pattern . This pattern was caused by many small subsets of species and was influenced by the reproductive strategy and life history characteristics of these species as well as by seasonal changes in the structure of the turf itself. Less clear patterns were evident from univariate measures of diversity, which highlights the need to measure biodiversity with a variety of statistical tools at a hierarchy of different levels. Finally, turf algae in tide pools support clearly different communities from turf algae on open rock, irrespective of habitat complexity and differences in the physiology of different algae. These differences are caused by those species that can tolerate the unique physical conditions experienced in tide pools. This thesis highlights the need to describe patterns of spatial and temporal variation in marine communities before experimental studies can be undertaken to elucidate the mechanisms responsible for these patterns (Underwood *et al.*, 2000). Studies of this type perform an important baseline function when carrying out monitoring programmes to assess the ecological health of inshore marine ecosystems. They provide information that prevents sites being designated as impacted (i.e. from pollution events) when in fact they are simply undergoing natural patterns of variation.

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