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Biodiversity of the invertebrate communities associated with intertidal mussel beds on rocky shores

A thesis presented to the University of Wales for the degree of Doctor of Philosophy

By

Kate Smith BSc (Wales)

April 2001

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SUMMARY

The invertebrate communities associated with intertidal mytilid mussel species were investigated on a variety of wave-exposed rocky shores around the coasts of the British Isles, Irish Republic (*Mytilus edulis*) and Chile, South America (*Perumytilus purpuratus*). A total of 192 different taxa were identified in *Mytilus edulis* beds at various rocky shore sites in the British Isles and Irish Republic, while 35 taxa were identified to higher taxonomic levels in *Perumytilus purpuratus* beds in Chile, South America.

Significant small-scale spatial variations in community structure were observed at two locations in Wales, while significant large-scale spatial variations in community structure were observed within mussel beds both in the British Isles and Irish Republic and in Chile. Additionally, the communities associated with *M. edulis* and *P. purpuratus* differed significantly, when compared at the same taxonomic levels. The structure of the invertebrate communities associated with *M. edulis* populations showed significant intra-annual variation, while those associated with *M. edulis* and *P. purpuratus* displayed significant inter-annual variation.

The spatial and temporal variation observed in the structure of the invertebrate communities associated with intertidal mussel beds were deemed to be the result of a variety of natural processes, along with stochastic events. Variation in measured environmental factors in the mussel beds did not fully account for the observed variation in community structure, although some factors, such as mussel density were shown to have some structuring effect.

It is concluded that the structure of the invertebrate communities associated with intertidal mussel on rocky shores are highly variable, both spatially and temporally. However, a small subset of taxa often display the same multivariate patterns as the entire data set; a phenomenon which could be utilised in any monitoring or impact studies involving mussel communities.

LIST OF TABLES AND FIGURES

		PAGE
	Chapter 2	
Figure 1	Map of the British Isles and Irish Republic, showing location of sample sites.	12
Figure 2	Map of Chile, showing location of sample sites.	13
Figure 3	Photographs of sample sites in the British Isles.	14-16
Figure 4	Photographs of study sites in Chile, South America.	17-19
Table 1	Observed species/area relationship for mussel communities at White Beach and Criccieth.	31
Table 2	Probability of occurrence of taxa in mussel bed communities at White Beach and Criccieth.	32
Figure 5	Taxa/area curves for mussel communities at White Beach and Criccieth.	34
	Chapter 3	
Figure 1	Size distributions of *Mytilus edulis* at the sample sites in the British Isles and Irish Republic in July 1999.	39
Table 1	Mussel densities, volume and mass at the sample sites in the British Isles and Irish Republic in July 1999.	40
Figure 2	Temporal variation in the size distribution of *Mytilus edulis* at Point Lynas in 1999.	42
Figure 3	Temporal variation in size distribution of *Mytilus edulis* at White Beach throughout 1998.	43
Table 2	Temporal variation in mussel densities, volume and mass at Point Lynas, White Beach and Criccieth during 1998 and1999.	44
Figure 4	Temporal variation in size distribution of *Mytilus edulis* at Criccieth during 1998 and 1999.	45
Figure 5	Annual variation in the size distribution of *Mytilus edulis* between 1998 and 1999.	46
Figure 6	Size structure of *Perumytilus purpuratus* at sample sites in Chile.	47
Figure 7	Mean mussel density at the sample sites in Chile.	48

Figure 8	Annual variation in the size structure of *Perumytilus purpuratus* at four sites in Chile.	49
Figure 9	Annual variation in mussel density of *Perumytilus purpuratus* at four sites in Chile.	50
Figure 10	*Mytilus edulis* and *Perumytilus purpuratus* shell sections.	52
Table 3	Size at age data for *Mytilus edulis* and *Perumytilus purpuratus.*	53
Table 4	Results of GLM regression analysis performed on growth data for *Mytilus edulis* and *Perumytilus purpuratus.*	54
Table 5	Results of ANOVA analysis performed on growth data for *Mytilus edulis* and *Perumytilus purpuratus.*	56
Table 6	Full taxa list for mussel communities at sample sites in the British Isles and Irish Republic.	57-61
Figure 11	Abundance of the main taxa in mussel beds at study sites in the British Isles and Irish Republic.	62
Table 7	Full taxa list for mussel communities at sample sites in Chile.	64
Figure 12	Abundance of the main taxa in mussel beds at study sites in Chile.	65

Chapter 4

Table 1	Environmental parameters measured in mussel beds at Point Lynas and White Beach.	75
Table 2	Results of ANOVA analysis performed between univariate measures of community diversity in mussel beds at Point Lynas and White Beach.	76
Figure 1	Univariate measures of community diversity in mussel beds at Point Lynas.	77
Figure 2	Univariate measures of diversity in mussel beds at White Beach.	79
Figure 3	Cluster analysis of square-root transformed mussel bed community data at Point Lynas.	80
Figure 4	Cluster analysis of presence/absence transformed mussel bed community data at Point Lynas.	81

Figure 5	Cluster analysis of square-root transformed mussel bed community data at White Beach.	82
Figure 6	Cluster analysis of presence/absence transformed mussel bed community data at White Beach.	83
Figure 7	Multidimensional scaling of square-root transformed mussel bed community data at Point Lynas.	84
Table 3	Results of ANOSIM analysis performed on mussel bed community data at Point Lynas and White Beach.	85
Table 4	SIMPER analysis of square-root transformed mussel bed community data at Point Lynas.	87-89
Table 5	SIMPER analysis of presence/absence transformed mussel bed community data at Point Lynas.	90-92
Table 6	SIMPER analysis of square-root transformed mussel bed community data at White Beach.	93-94
Table 7	SIMPER analysis of presence/absence transformed mussel bed community data at White Beach.	95-96
Table 8	Correlation between environmental parameters and univariate measures of diversity in mussel beds at Point Lynas and White Beach.	97
Table 9	Correlation between environmental parameters in mussel beds at Point Lynas and White Beach.	98
Table 10	BIOENV analysis performed on mussel community data at Point Lynas and White Beach.	99
Figure 8	Principal component analysis performed on environmental data in mussel beds at Point Lynas and White Beach.	100

Chapter 5

Table 1	Results of ANOVA analysis performed between univariate measures of community diversity in mussel beds at sample sites in the British Isles and Irish Republic.	112
Figure 1	Univariate measures of community diversity in mussel beds at sample sites in the British Isles and Irish Republic.	113
Figure 2	Cluster analysis of square-root transformed mussel bed community data at sample sites in the British Isles and Irish Republic.	114

Figure 3	Cluster analysis of presence/absence transformed mussel bed community data at sample sites in the British Isles and Irish Republic.	115
Figure 4	Multidimensional scaling of square-root transformed mussel bed community data at sample sites in the British Isles and Irish Republic.	116
Table 2	Results of ANOSIM analysis performed on mussel bed community data at sample sites in the British Isles and Irish Republic.	118
Figure 5	Multidimensional scaling of presence/absence transformed mussel bed community data at sample sites in the British Isles and Irish Republic.	119
Table 3	SIMPER analysis of square-root transformed mussel bed community data at sample sites in the British Isles and Irish Republic.	120-124
Table 4	SIMPER analysis of presence/absence transformed mussel bed community data at sample sites in the British Isles and Irish Republic.	126-130
Figure 6	Environmental parameters measured in mussel beds at sample sites in the British Isles and Irish Republic.	131
Table 5	Correlation between environmental parameters and selected taxa in mussel beds at sample sites in the British Isles and Irish Republic.	132
Table 6	Correlation between environmental parameters and univariate measures of diversity in mussel beds at sample sites in the British Isles and Irish Republic.	133-134
Figure 7	Principal component analysis performed on environmental data in mussel beds at sample sites in the British Isles and Irish Republic.	136
Table 7	Correlation between environmental parameters in mussel beds at sample sites in the British Isles and Irish Republic.	137
Table 8	Results of BIOENV analysis performed on mussel community data at sample sites in the British Isles and Irish Republic.	138
Figure 8	Multidimensional scaling of square-root transformed mussel bed community data at sample sites in the British Isles and Irish Republic with wave-exposure overlaid.	139

Figure 9	Univariate measures of community diversity in mussel beds at sample sites in the Chile.	141
Figure 10	Cluster analysis of square-root transformed mussel bed community data at sample sites in Chile.	142
Figure 11	Cluster analysis of presence/absence transformed mussel bed community data at sample sites in Chile.	143
Figure 12	Multidimensional scaling of square-root transformed mussel bed community data at sample sites in Chile.	144
Table 9	Results of ANOSIM analysis performed between mussel bed community data at sample sites in Chile.	145
Figure 13	Multidimensional scaling of presence/absence transformed mussel bed community data at sample sites in Chile.	146
Table 10	SIMPER analysis of square-root transformed mussel bed community data at sample sites in the British Isles and Irish Republic.	148-153
Table 11	SIMPER analysis of presence/absence transformed mussel bed community data at sample sites in the British Isles and Irish Republic.	154-159
Table 12	Results of t-tests performed between univariate measures of community diversity in mussel beds at sample sites in the British Isles and Irish Republic and in Chile.	160
Figure 14	K-dominance plots for mussel communities at sample sites in the British Isles and Irish Republic and in Chile.	162
Figure 15	Multidimensional scaling of square-root and presence/absence transformed mussel bed community data at sample sites in the British Isles and Irish Republic and in Chile.	163
Table 13	Results of ANOSIM analysis performed on mussel bed communities at sample sites in the British Isles and Irish Republic and in Chile.	164
Table 14	SIMPER analysis of square-root transformed mussel bed community data at sample sites in the British Isles and Irish Republic and in Chile.	165
Figure 16	Multidimensional scaling of square-root transformed mussel bed community data at sample sites in the British Isles and Irish Republic and in Chile with mussel density overlaid.	167

Chapter 6

Figure 1	Temporal variation in univariate measures of community diversity in mussel beds at Point Lynas.	185
Figure 2	Cluster analysis of square-root and presence/absence transformed mussel community data at Point Lynas during 1999.	186
Figure 3	Multidimensional scaling of square-root and presence/absence transformed mussel community data at Point Lynas during 1999.	187
Table 1	Results of ANOSIM analysis performed between mussel bed community data at Point Lynas, throughout 1999.	188
Table 2	SIMPER analysis of square-root transformed mussel bed community data at Point Lynas, throughout 1999.	190
Table 3	SIMPER analysis of presence/absence transformed mussel bed community data at Point Lynas, throughout 1999.	191
Figure 4	Abundance of selected taxa (identified by BVStep analysis) in mussel beds at Point Lynas throughout 1999.	192
Table 4	Correlation between environmental parameters and univariate measures of diversity in mussel beds at Point Lynas throughout 1999.	194
Figure 5	Principal component 1 plotted against univariate measures of community diversity for mussel beds at Point Lynas, throughout 1999.	195
Figure 6	Temporal variation in univariate measures of community diversity in mussel beds at White Beach.	197
Figure 7	Cluster analysis of square-root and presence/absence transformed mussel community data at White Beach during 1999.	198
Figure 8	Multidimensional scaling of square-root and presence/absence transformed mussel community data at White Beach during 1999.	199
Table 5	Results of ANOSIM analysis performed on mussel bed communities at White Beach, throughout 1999.	200
Table 6	SIMPER analysis of square-root transformed mussel bed community data at White Beach, throughout 1999.	202

Table 7	SIMPER analysis of square-root transformed mussel bed community data at White Beach, throughout 1999.	203
Figure 9	Abundance of selected taxa (identified by BVStep analysis) in mussel beds at White Beach throughout 1999.	204
Table 8	Correlation between environmental parameters and univariate measures of diversity in mussel beds at White Beach throughout 1999.	205
Figure 10	Principal component 1 plotted against univariate measures of community diversity for mussel beds at White Beach, throughout 1999.	207
Figure 11	Temporal variation in univariate measures of community diversity in mussel beds at Criccieth.	209
Figure 12	Cluster analysis of square-root and presence/absence transformed mussel community data at Criccieth during 1999.	210
Figure 13	Multidimensional scaling of square-root and presence/absence transformed mussel community data at Criccieth during 1999.	211
Table 9	Results of ANOSIM analysis performed between mussel bed community data at Criccieth, throughout 1999.	212
Table 10	SIMPER analysis of square-root transformed mussel bed community data at Criccieth, throughout 1999.	213
Table 11	SIMPER analysis of square-root transformed mussel bed community data at Criccieth, throughout 1999.	215
Figure 14	Abundance of selected taxa (identified by BVStep analysis) in mussel beds at Criccieth throughout 1999.	216
Table 12	Correlation between environmental parameters and univariate measures of diversity in mussel beds at Criccieth throughout 1999.	217
Figure 15	Principal component 1 plotted against univariate measures of community diversity for mussel beds at Criccieth, throughout 1999.	219
Figure 16	Multidimensional scaling of square-root and presence/absence transformed mussel community data at Point Lynas, White Beach and Criccieth during 1999 and 2000.	220

Table 13	Results of ANOSIM analysis performed between mussel bed community data at Point Lynas, White Beach and Criccieth during 1999 and 2000.	221
Table 14	Results of ANOVA analysis performed between univariate measures of community diversity in mussel beds at four sites in Chile, between 1997-2000.	223
Figure 17	Temporal variation in univariate measures of community diversity in mussel beds at four sites in Chile, between 1997-2000.	224
Figure 18	Multidimensional scaling of square-root transformed mussel community data at four sites in Chile from 1997-2000.	225
Figure 19	Multidimensional scaling of presence/absence transformed mussel community data at four sites in Chile from 1997-2000.	226
Table 15	Results of ANOSIM analysis performed between mussel bed community data at four sites in Chile from 1997-2000.	227
Table 16	SIMPER analysis of square-root transformed mussel bed community data at four sites in Chile from 1997-2000.	228
Table 17	SIMPER analysis of presence/absence transformed mussel bed community data at four sites in Chile from 1997-2000.	229

Chapter 7

Figure 1	Multidimensional scaling performed on square-root and presence/absence transformed biotic data and PCA performed environmental data in mussel beds of manipulated density.	244
Table 1	SIMPER analysis of square-root transformed mussel bed community data in mussel beds of manipulated density.	246
Table 2	SIMPER analysis of presence/absence transformed mussel bed community data in mussel beds of manipulated density.	247
Table 3	T-tests performed between environmental parameters in mussel beds of manipulated density.	248
Figure 2	Correlation between environmental parameters and univariate measures of diversity in mussel beds of manipulated density.	249
Table 4	Correlation between environmental parameters in mussel beds of manipulated density.	251

Chapter 8

Table 1	Lists of taxa responsible for spatial and temporal multivariate patterns in square-root transformed biotic data.	261
Table 2	Lists of taxa responsible for spatial and temporal multivariate patterns in presence/absence transformed biotic data.	262

CONTENTS

		Page
Chapter 1	General Introduction.	1-8
Chapter 2	General Methodology.	9-34
Chapter 3	Size structure and growth rate of *Mytilus edulis* and *Perumytilus purpuratus* populations together with a brief note on their associated invertebrate communities.	35-69
Chapter 4	Small-scale spatial variations in the structure of the invertebrate communities associated with *Mytilus edulis.*	70-106
Chapter 5	Large-scale spatial variation in the structure of the Invertebrate communities associated with *Mytilus edulis* and *Perumytilus purpuratus.*	107-179
Chapter 6	Temporal variation in the structure of the invertebrate communities associated with *Mytilus edulis* and *Perumytilus purpuratus.*	180-238
Chapter 7	Investigations into the effect of substratum heterogeneity on the invertebrate communities associated with *Mytilus edulis.*	239-255
Chapter 8	General Discussion.	256-264
References		265-285
Appendix		296-301

Chapter 1

General Introduction

GENERAL INTRODUCTION

Mussel biology and distribution

Mytilid mussels, especially those belonging to the genus *Mytilus*, are amongst the most intensively researched marine organisms with entire books devoted solely to their study (e.g. Bayne, 1976; Stefano, 1990; Gosling, 1992). There are many reasons for such scientific interest; e.g. these mussels are widely distributed and exceedingly abundant throughout the world's oceans; they are important ecologically as dominant space-occupying organisms, particularly in coastal and estuarine waters (e.g. Seed and Suchanek, 1992); they are important economically as food and fouling organisms (e.g. Hickman, 1992). In addition, from as early as 1976, when the Mussel Watch Monitoring Program was initiated, mussels have been widely used as sentinels or biomonitors of coastal water quality (e.g. Goldberg, 1986; Widdows and Donkin, 1992). Some species, such as the common blue mussel (*Mytilus edulis* Linnaeus), have also proved to be a model organisms in studies of physiology, biochemistry and population genetics (see relevant chapters in Gosling, 1992).

Mussels of the genus *Mytilus* are widely distributed throughout the cooler waters of the northern and southern hemispheres, where they occur in a variety of shore habitats, ranging from sediment shores of unprotected bays to gravel or pebble shores in semi-exposed conditions, true rocky shores exposed to considerable wave action and sublittorally in natural sediment or attached to pier pilings etc. (Bayne, 1976). Their success is most pronounced in exposed or moderately wave-exposed locations in temperate seas, particularly on horizontal or gently shelving rocky substrata, where they commonly dominate the communities of littoral and sub-littoral shores as the primary space occupier (Seed and Suchanek, 1992), often forming long-lived beds with discrete boundaries (Geesteranus, 1942; Kuenen, 1942; Verwey, 1952; Seed, 1976). In tropical and sub-tropical latitudes, this genus is replaced by other dominant zone-forming genera such as *Perna* and *Septifer*, while dense populations of highly specialised species have also been reported from cold-seep areas and sites of hydrothermal vent activity in the deep sea (e.g. Hessler *et al*, 1988; Jahnke *et al*, 1995; Van Dover and Trask, 2000). Of the many factors that are responsible for the success of mytilid mussels, the evolution of the heteromyarian form associated with the neotenous retention of the byssus is of particular significance (Seed, 1983; Morton, 1992). The secretion of byssus threads by a special gland at the base of the foot provided an effective means of attachment onto hard surfaces and enabled various bivalve classes, including mussels, to become independent of the soft sediments inhabited by their ancestors. The broadly

triangular heteromyarian form of the 'typical' mussel coupled with secure byssal attachment throughout life enabled bivalves like epibyssate mussels to live in high population densities on hard or moderately consolidated substrata. Other factors contribute to the success of mytilid mussels, including their supreme efficiency as filter-feeding organisms (e.g. Shumway, 1989) and high fecundity, producing large numbers of planktotrophic larvae which ensure rapid and widespread dispersal (further facilitated by bysso-pelagic drifting of juveniles) (e.g. Seed and Suchanek, 1992).

Several factors affect local distribution patterns of mussels, including predation and competition, along with physical factors such as exposure, substratum type and angle and tidal elevation (Sanders, 1968, 1969). In general the upper distributional limits for *Mytilus* spp. are constant over long periods of time and set by physiological intolerance to extremes of temperature and desiccation (Suchanek, 1985; Almada-Villela *et al*, 1982; Tsuchiya, 1983; Seed and Suchanek, 1992). The lower distributional limits are under strong influence from biological factors such as competition with other sessile organisms (e.g. Suchanek, 1981) and predation, for example by predatory starfish and gastropods (e.g. Seed, 1969a; Kitching and Ebling, 1967; Menge, 1983; Paine, 1974; Paine, 1971; Paine *et al*, 1985). Once established, mussels, by virtue of their competitive superiority, quickly become the dominant space-occupying members of the community, with the potential to completely eliminate most other sessile species. After larval settlement on the rock, a monolayer mussel bed is formed in the early stages of patch growth (Tsuchiya and Nishihira, 1986). With growth, mussels require more space for attachment, and some individuals on the periphery of the patch are pushed outward while some inside the patch are shifted upward, resulting in the formation of a double or multi-layered mussel bed. Mussel bed populations are among the most dense of all suspension-feeding bivalves, reaching densities of 21000 individuals.m^{-2} (Nixon *et al*, 1971) and can range from a complete cover of mussels to a mosaic of patches or islands of different size (Seed, 1996). Seed (1968) stated that the highest densities of mussels tend to be associated with:

1. Shores receiving moderate to severe wave action - probably a direct influence of the amount of water (and larval stages) passing over them;
2. The lower levels of the shore;
3. Slow draining, horizontal platforms, especially where surfaces are roughened or broken by discontinuities.

It is clear that in the absence of adequate levels of disturbance, mussels as superior spatial competitors, can effectively monopolise large areas of the rocky

intertidal zone by denying access to the weaker more opportunistic species. Such loss of species richness, however, applies only to those species that compete for the primary resource – attachment space – on the rock surface. Aggregations of mussels can drastically modify the local environment through enhanced water retention, biodeposition of faecal and pseudofaecal material (= 'mussel mud'), and the provision of additional attachment surface and shelter by the mussel themselves (e.g. Bayne, 1976) – features which serve to encourage species enrichment in habitats wherever mussels are present in abundance. Mussels are thus keystone species within the rocky intertidal (Seed, 1996) and effective 'ecosystem engineers', a term used by Lawton and Jones (1995) to describe species that either directly or indirectly modulate the availability of resources to other species by causing physical state changes in biotic or abiotic materials, thereby modifying, maintaining and creating habitats. Levin and Paine (1974) suggested that it is appropriate to view communities of sessile biota, such as mussels, as being composed of a mosaic of small patches with differing species compositions and developmental histories. In addition, since such mussel patches are isolated from similar patches, they can be treated as islands for associated communities (Tsuchiya and Nishihira, 1985, 1986).

Invertebrate communities associated with mussel beds

Mussel bed communities are extremely well delineated, bounded by the physical limits of the mussels, which, in the intertidal, are in turn restricted by physical and biological factors to a well definable zone (Suchanek, 1980). As structurally and functionally complex entities mussel patches provide refuge and suitable habitat for a broad suite of associated organisms, while the majority of taxa occurring in mussel beds cannot exist without the protection provided by the mussels, especially on wave-exposed shores (Tokeshi and Romero, 1995). Many authors have stated that the associates of mussel communities show a marked pattern of distribution throughout the matrix, derived from the microhabitat differences encountered by associated fauna (e.g. Tsuchiya and Bellan-Santini, 1989; Ong Che and Morton, 1992; Lintas and Seed, 1994). The biota associated with mytilid beds can thus be divided into three major functional categories, with some of these organisms living attached to the mussel shells (epibiota), others typically living amongst the rich sediments and shell fragments which accumulate at the base of the bed (infauna) and mobile organisms roving freely through the complex matrix of shells and interconnecting byssus threads (Suchanek, 1985). Several authors have documented the communities associated with *Mytilus edulis* from a variety of habitats. For example, up to 96 taxa have been identified from *Mytilus edulis* beds

on rocky substrata at a variety of intertidal locations (e.g. Briggs, 1982; Tsuchiya and Nishihira, 1985, 1986; Lintas and Seed, 1994; Svane and Setyobudiandi, 1996). In addition, similar numbers of taxa have been identified from *Mytilus edulis* beds on soft substrata at a variety of locations (e.g. Asmus, 1987; Commito, 1987; Dittman, 1990). Other authors have investigated the communities associated with other mussel species; Suchanek (1980) identified 303 taxa from *Mytilus californianus* beds on the Pacific coast of North America, up to 171 taxa have been identified from subtidal *Modiolus modiolus* beds in the UK (Brown and Seed, 1977; Witman, 1980), up to 52 from intertidal *Septifer virgatus* beds in Hong Kong (Ong Che and Morton, 1992; Seed and Brotohadikus, 1994), 56 from intertidal *Brachidontes rostratus* beds in south-eastern Australia (Peake and Quinn, 1993) and 28 from deep-sea *Bathymodiolus* spp. at hydrothermal vents.

A striking feature of many of these studies is that similar taxa, often from the same genus, regularly recur within these communities worldwide. Moreover, with the exception of *Mytilus californianus* – a much larger bodied mussel, which forms thick multi-layered beds – the number of associated taxa is broadly comparable between species, with representatives from most of the main phyla. Such observations suggest that the pattern of parallel communities on rocky shores may be replicated on a much finer scale within mussel patches (Seed, 1996). Despite these high levels of diversity, mussel communities are typically dominated by a few very abundant species (e.g. Seed, 1996). For example, Ong Che and Morton (1992) demonstrated that *Septifer virgatus* beds in Hong Kong were dominated by three species, accounting for 75% of the total numbers. In the same mussel beds, more than 90% of the associated molluscan fauna was comprised of three bivalve species (*Hormomya mutabilis*, 37%; *Isognomon legumen*, 30%; *Lasaea nipponica*, 27%) (Seed and Brotohadikusumo, 1994). Suchanek (1978, 1980) found that in studies of *Mytilus californianus* beds in western North America, in some cases, a single species dominated the sample by more than 50%. Many taxa associated with mussel beds often occur only occasionally and may be considered to be accidental or transient, rather than permanent members of the community (e.g. Seed and Brotohadikusumo, 1994).

Biodiversity

Biodiversity has recently become an important issue, both in scientific (Wilson, 1988; Ehrlich and Wilson, 1991) and political (United Nations Environment Programme, 1992; World Resources Institute, 1993; Heywood and Watson, 1995) terms. Most scientists agree that biodiversity is of inestimable value and that its loss

or enforced change could invoke currently inestimable changes upon many aspects of the globe. In addition, sustained biodiversity plays a key role in ecosystem function and species that have co-evolved depend on functions of the ecosystem in which they live. Each species depends upon other species for its continued existence so that the removal of one or many species in an ecosystem may remove a vital ecological pathway that permanently alters ecosystem function and structure (Norton, 1986).

There are generally considered to be three main components of biodiversity; genetic, specific or taxonomic and ecological or habitat diversity, along with a wide variety of definitions of the term, although in its most basic form, biodiversity refers to the numbers of species in different places (Ricklefs and Schulter, 1993). Wilson (1992) defined biodiversity as 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 the variety of ecosystems, which comprise both the communities of organisms within particular habitats and the physical conditions under which they live. This definition allows biodiversity to be considered at all levels from global (gamma diversity) to local (alpha diversity) and take into account species turnover between habitats (beta diversity) (Gaston, 1996).

Many relationships have been investigated between biodiversity and latitude, climate, biological productivity, habitat heterogeneity, habitat complexity and disturbance. Any complete theory of species numbers must explain how the number of species in a particular area is regulated; how the species are formed; where they come from and how interactions between species set an upper limit to their number (Ricklefs, 1980).

Aims of the current study

Due to the small size and immobility of sessile invertebrate species of marine epifaunal communities, such as mussels, these habitats are ideal for studying patterns of change in species composition and diversity (Osman, 1977). Since mussels, particularly of the genus *Mytilus*, occur throughout the cooler waters of the northern and southern hemispheres, in a variety of shore habitats (Bayne, 1976), these communities might prove to be ideal for investigating the effects of anthropogenic activities in coastal seas. However, it is clear from many recent empirical studies, that a complete understanding of the structure of any community is possible only when temporal variation is encompassed (Morris, 1990). Many authors have pointed out the difficulty, in studies of intertidal benthic communities, in

discriminating between community changes due to anthropogenic activities and those caused by natural variation (e.g. DelValls *et al*, 1998).

This thesis aims to provide a detailed description of the invertebrate communities associated with two intertidal mytilid mussel species on rocky shores; *Mytilus edulis* in the British Isles and Irish Republic and *Perumytilus purpuratus* in Chile, South America. Initially, it was necessary to establish a suitable sampling protocol, including an appropriate sample size and methodology with which to investigate accurately the structure of these communities (Chapter 2). Habitat structure and heterogeneity are known to affect the structure of such communities, so Chapter 3 provides information on the size structure of all the mussel populations studied, along with information on the age structure and growth rates of *Mytilus edulis* and *Perumytilus purpuratus*. This information is used in later chapters, in an attempt to relate structure of the associated communities to the physical parameters of the mussel matrices themselves. Chapter 3 also provides a basic description of the communities associated with the two mussel species, at the different sites in this study. Chapter 4 will deal with the small-scale (intra-site) variation in the structure of communities associated with *Mytilus edulis* on two rocky shores on the coast of Anglesey, North Wales. The effects of tidal elevation, position within a mussel patch, angle of substratum and epifloral covering, on the structure of the associated invertebrate communities are investigated. Chapter 5 will deal with larger-scale spatial variations in the structure of the communities associated with *Mytilus edulis* and *Perumytilus purpuratus* on rocky shores at a variety of sites throughout the British Isles and Irish Republic and Chile, South America respectively. Inter-site variations in community structure are investigated for each mussel species, while larger, geographical comparisons are made between the communities associated with *Mytilus edulis* and *Perumytilus purpuratus*. Chapter 6 deals with the temporal (seasonal and annual) variation in the structure of the invertebrate community associated with *Mytilus edulis* on three rocky shores on the coast of North Wales. Chapter 7 involves an experimental investigation using panels of manipulated mussel density, to investigate the effect of mussel density and habitat heterogeneity on the structure of the invertebrate associates of *Mytilus edulis* on a rocky shore on Anglesey, North Wales, where the mussel species is already present in established beds. Attempts are made in each of the above investigations, to relate spatial and temporal variations in community structure to measured abiotic parameters of the mussel matrices. Finally, I discuss the results and implications of this work, with particular reference to the potential use of the invertebrate communities associated with intertidal mussel beds in monitoring the effect of anthropogenic activities in

coastal areas. In writing this thesis my intention was that each chapter should stand on its own, whilst attempting to avoid excessive repetition.

Chapter 2

General Methodology

INTRODUCTION

Many investigations have found that a prerequisite to precise estimates of the abundance of organisms in any habitat is a prior knowledge of the sampling variability (e.g. Elliot, 1977; Green, 1979; Vezina, 1988). Since most ecological communities are too large to be studied in their entirety, for practical and conservation purposes, representative samples must be taken (Weinberg, 1978). Various authors have pointed out the importance of both the size of the area sampled (quadrat) in any ecological study and the overall sample size (number of quadrats) (e.g. Greig-Smith, 1952; Wiegert, 1962). The optimal sample size should be large enough to include most or all of the species in the community, but as small as possible to reduce the time required for laboratory sorting (Hawkins and Hartnoll, 1980). There are three basic formats for data collection in such species/area studies (Goodall, 1952), these are to collect:

1. Random quadrats of different sizes within the community under study, and to determine the number of species within each quadrat. However, using this technique, the provision of satisfactory confidence limits of the organisms within each area would involve considerable time and labour.
2. The smallest quadrat at random and then to add to it increasing contiguous areas in order to provide data from larger quadrats. The data gained might be quite atypical, and an assumption with this approach is that there is homogeneity in the community.
3. A large number of small quadrats taken at random within the community, and combine the information from them in order to derive the species content of larger areas.

The third approach was chosen in the present study because of the practical and theoretical considerations, listed below:

1. It is the most economical in the use of field and laboratory time.
2. It permits an accurate description of the change of species number with sample size.
3. It is practicable on very irregular terrain, and in areas of mixed communities whose boundaries are not evident, both of which are often typical of mussel beds.
4. The data obtained in this way are also valuable for the determination of species abundance and confidence limits and species distribution patterns, much more so than data obtained by the other two sampling approaches mentioned.
5. It is the least intrusive sampling method on the habitat, since only small samples are taken.

This chapter details the calculation of a suitable sample size, along with field and laboratory procedures undertaken in order to describe the temporal and small and large-scale spatial variation in the structure of invertebrate infaunal assemblages associated with intertidal mussel populations. Descriptions and photographs where available, are provided of the study sites within the British Isles, Irish Republic and Chile, South America, from which field samples were collected during the course of the study. Details are provided on the main statistical techniques and procedures utilised to describe both the biotic and environmental data in the present study.

GENERAL METHODOLOGY

Site Details

During this study a number of rocky intertidal shores with extensive mussel communities, both in the British Isles and Irish Republic (Figure 1) and in Chile, South America (Figure 2), were investigated in order to study the temporal, spatial and small and large-scale geographical variation associated with mussel bed communities. The selection criteria for the shores were that they were subject to similar conditions of wave-exposure and that *Mytilus edulis* and *Perumytilus purpuratus* formed continuous beds on rocky substrata in the mid-shore area. Communities of *M. edulis* in the British Isles and Irish Republic and *P. purpuratus* in Chile, were chosen because of the mussels similar overall morphology and the fact that they formed similar multi-layered beds on each shore, such that, at each site the mussels and their associated communities could be compared using similar sampling techniques. A description of each site follows.

Point Lynas, Anglesey (Wales) Position: 53°25.13'N 04°17.20'W

A north-easterly facing headland on the north coast of Anglesey, exposed to moderate wave action. *M. edulis* occurs as tightly packed beds at this site, both on the sloping rocks of the headland and in crevices and gullies. For much of the year, the mussel shells themselves are covered by thick growths of ephemeral green algae, such as *Ulva lactuca*. The waters immediately surrounding this site were often observed to contain a large amount of suspended sediment, which during low tide settled out of suspension and covered parts of the shore. The mean tidal range at Amlwch, 3km to the west, is 6.3m during spring tides and 3.2m at neaps (Admiralty Tide Tables, 1999).

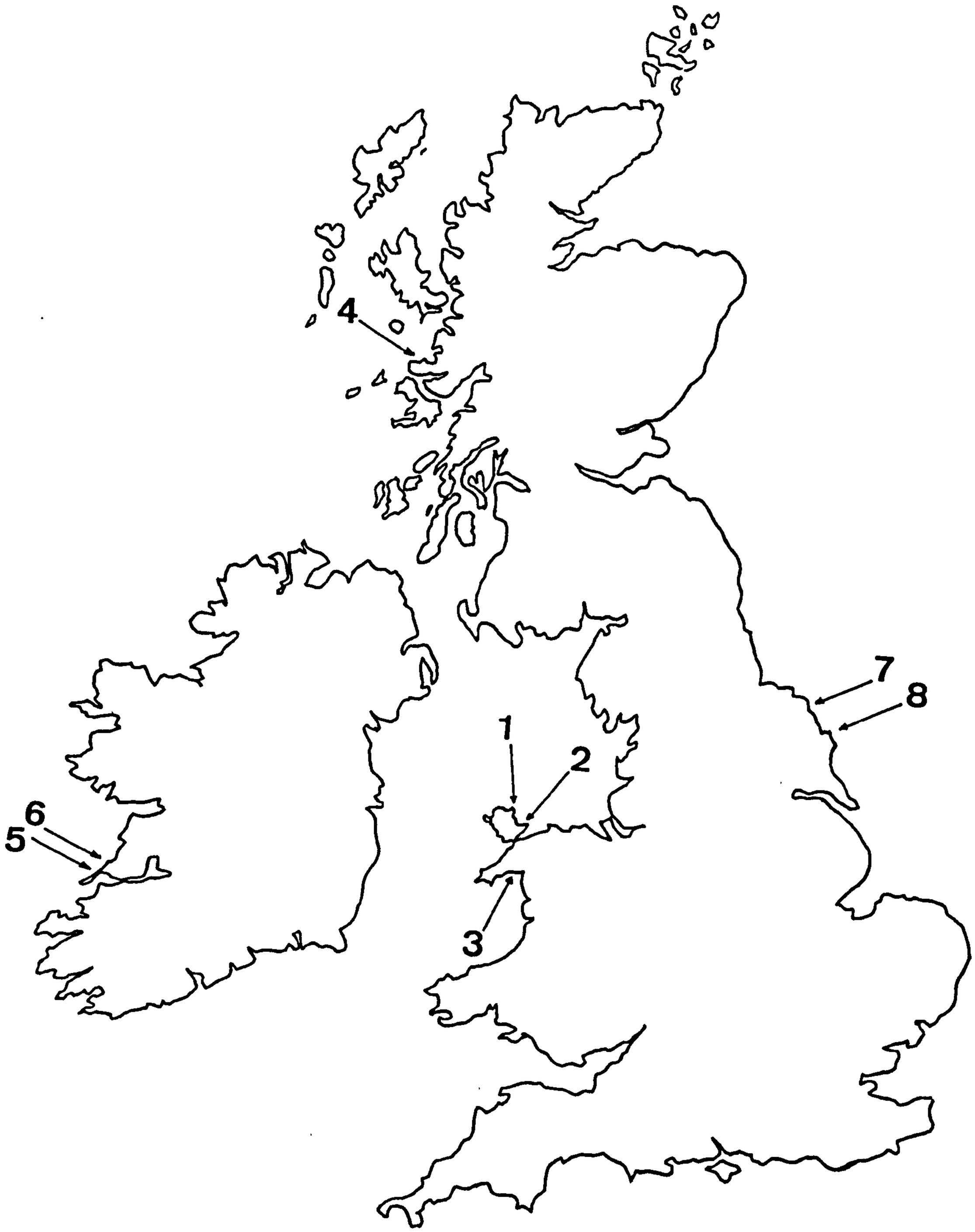


Figure 1 Map of the British Isles and Irish Republic showing the location of sample sites. 1 = Point Lynas, 2 = White Beach, 3 = Criccieth, 4 = Arisaig, 5 = Kilkee, 6 = Doonbeg, 7 = Robin Hood's Bay, 8 = Filey Brigg.

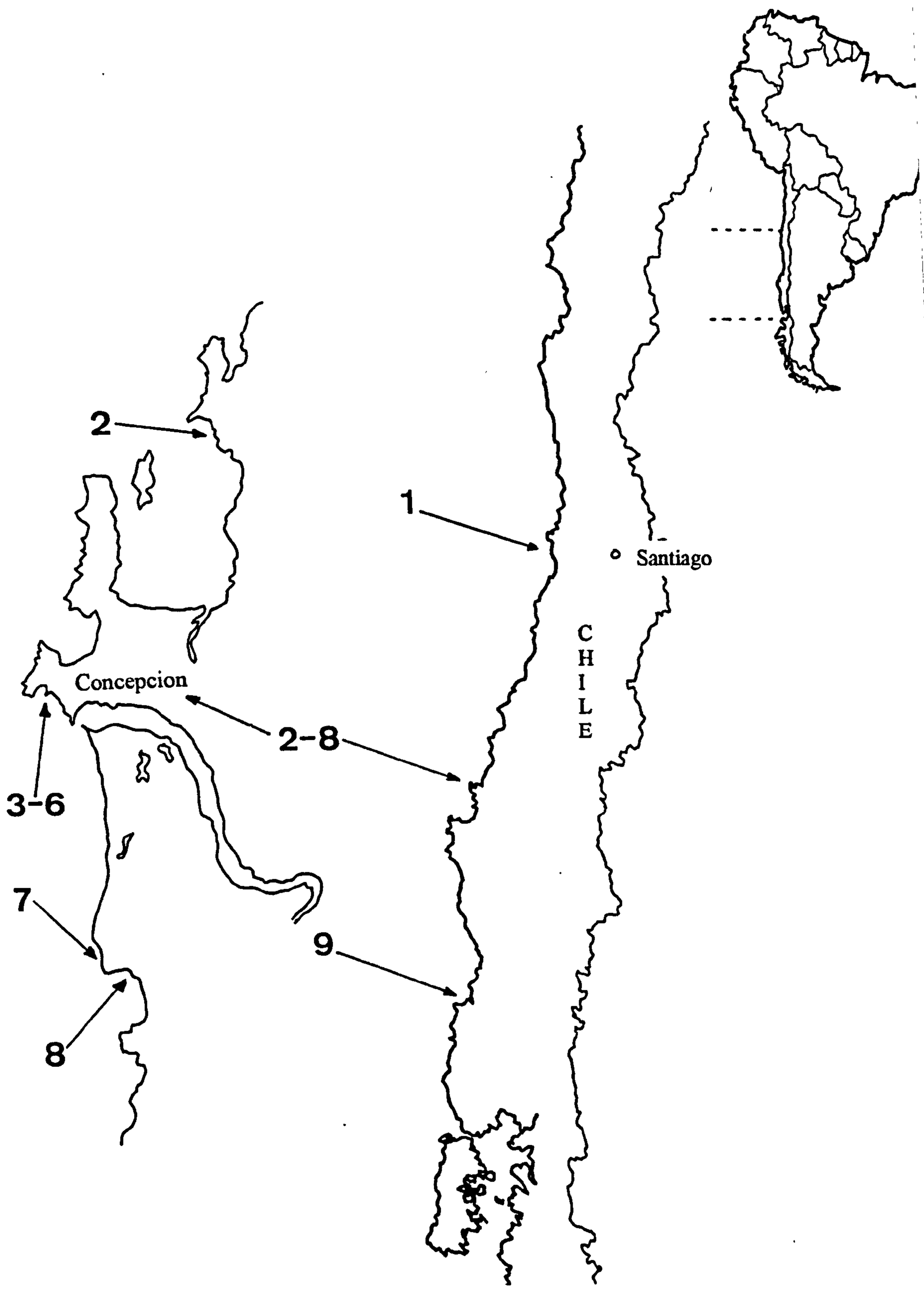


Figure 2 Map of Chile, South America showing the location of sample sites. Geographical range of sites is indicated on large-scale map of South America, while distribution of sample sites are shown in maps of Chile and Concepcion area. 1 = Las Cruces, 2 = Cocholgue, 3 = Desembocadura exposed site 1, 4 = Desembocadura exposed site 2, 5 = Desembocadura sheltered site 1, 6 = Desembocadura sheltered site 2, 7 = Maule, 8 = Coronel, 9 = Valdivia.

Figure 3 Photographs of sample sites in the British Isles used in the present study. a) Point Lynas, Wales, b) White Beach, Wales, c) Criccieth, Wales, d) Robin Hood's Bay, England, e) Filey Brigg, England. (Note that photographs of sample sites in Scotland and the Irish Republic are not available).

Point Lynas, Wales

b) White Beach, Wales

c) Criccieth, Wales

d) Robin Hood's Bay, England

e) Filey Brigg, England

Figure 4 Photographs of sample sites in Chile, South America used in the present study. a) Las Cruces, b) Cocholgue, c*i*) Desembocadura sheltered site, c*ii*) Desembocadura exposed site, d) Maule, e) Coronel. (Note that photographs of sample sites in Scotland and the Irish Republic are not available).

a) Las Cruces, VI Region

b) Cocholgue, VIII Region

c*i*) Las Desembocadura, VIII Region

c*ii*) Las Desembocadura, VIII Region

d) Maule, VIII Region

e) Coronel, VIII Region

White Beach, Anglesey (Wales) Position: 53°19.05'N 04°05.35'W

A northerly facing shore at the north-eastern corner of Anglesey, only exposed to moderate wave action. *M. edulis* forms solid, tightly packed beds, which extensively cover the gently sloping rock platforms present at this site. Mussels in the mid-shore are covered with epifloral species such as *Ulva lactuca* to varying degrees throughout the year, although to a lesser extent during the summer when bleaching occurs. This site is popular with local fishermen and it is possible that the mussels and their associated communities are subject to disturbance through trampling. The mean tidal range at Trwyn Dinmor, 2.5km to the east, is 6.6m during spring tides and 3.4m at neaps (Admiralty Tide Tables, 1999).

Criccieth, Gwynedd (Wales) Position: 53°54.58'N 04°14.00'W

A south-westerly facing shore at the southern base of the Llyn Peninsula, in the far north-eastern corner of Porthmadog Bay. This site is subject to a considerable amount of fetch from Porthmadog Bay and is thus exposed to moderate to high wave action. *M. edulis* forms solid beds, coverings the large boulders, which are strewn across the middle and lower levels of the shore. Mussels also form patches higher on the shore on the vertical rocky cliffs, which border the shore. The mean tidal range at Criccieth, is 4.6m during spring tides and 1.6m at neaps (Admiralty Tide Tables, 1999).

Arisaig, Ardnamurchan Peninsula (Scotland) Position: 56°49.89'N 05°46.51'W

An exposed site on the north coast of the Ardnamurchan Peninsula, on the West Coast of Scotland. Here mussels form tightly packed beds on the gently sloping rock platform, which descends into deep water. Despite being sheltered to a small extent, by offshore islands such as Eigg, the site is exposed to a high degree of wave action. The mean tidal range at Loch Moidart, 10km to the east, is 4.3m during spring tides and 1.9m at neaps (Admiralty Tide Tables, 1999).

Kilkee, Co. Clare (Irish Republic) Position: 52°41.01'N 09°39.29'W

A large, westerly facing bay on the West Coast of Ireland. Mussels form extensive beds covering the horizontal rock platforms, which surround the bay. The site is exposed to the full fetch of the Atlantic and thus a high degree of wave action. Samples were collected from a wave exposed location on the north-west end of the platform on the southern side of the bay. The mean tidal range at Liscanor, 20km to the north, is 4.1m during spring tides and 1.6m at neaps (Admiralty Tide Tables, 1999).

Doonbeg, Co. Clare (Irish Republic) Position: 52°44.47'N 09°31.57'W

A westerly facing 2km long sandy beach on the West Coast of Ireland. Mussels form thick, extensive beds on a large rocky platform at the far northern end of the Bay. The site is exposed to the full fetch of the Atlantic and thus a high degree of wave action. Mussel samples were collected from one of the many horizontal rock platforms, which surround the bay. The mean tidal range at Liscanor, 15km to the north, is 4.1m during spring tides and 1.6m at neaps (Admiralty Tide Tables, 1999).

Robin Hoods Bay, Yorkshire (England) Position: 54°27.11'N 00°31.01'W

A predominantly north-easterly facing shore, on the East Coast of England. Robin Hoods Bay extends from Old Peak, or South Cheek, about 6km to Ness Point, or North Cheek. Mussel samples and their associated infauna were collected from the far north end of the Bay, where they form solid, tightly packed beds, which extensively cover the horizontal wave cut shale platforms. The sampling area was beyond the main protected part of the Bay and thus was subject to a high degree of wave-action. The mean tidal range at Whitby, 7km to the north-west, is 4.8m during spring tides and 2.4m at neaps (Admiralty Tide Tables, 1999).

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

A northerly facing promontory, around 1km long, at the far northern end of Filey Bay, on the east coast of England. The site is exposed to a high degree of wave action. Mussels form thick extensive beds over the entire lower levels of the stepped rocky platform on the exposed north side of the Brigg. This site is very popular with local fishermen and it is possible that the mussels and their associated communities might be subject to disturbance through trampling. The mean tidal range at Filey Bay, is 4.8m for springs and 2.5m for neaps (Admiralty Tide Tables, 1999).

Las Cruces, VI Region, Chile Position: 33°29.30'S 71°39.20'W

A highly wave exposed westerly facing shore due west of Santiago. *P. purpuratus* forms thick beds on the sloping rock platforms and boulders of the middle and lower shore areas, where there is considerable surge and wave action.

Cocholgue, VIII Region, Chile Position: 36°35.15'S 72°58.30'W

An enclosed, westerly facing fishing bay 20km north of Concepcion. *P. purpuratus* forms extensive beds on the horizontal rock platforms, which form the

substantial part of the middle to lower intertidal area. The rock surfaces are highly eroded and interspersed with many pools of varying sizes, along with surge gullies. The site is sheltered to some extent from the full force of the Pacific waves, since it lies within a protected bay. However, the mussels are still exposed to a high degree of wave action at this site.

Las Desembocadura, VIII Region, Chile Position: 36°48.20'S 73°10.05'W

A large circular sandy bay situated to the west of Concepcion, near the mouth of the River Bio Bio. The bay is interspersed with large rocky outcrops and lined by rock platforms to the north and south. *P. purpuratus* forms consolidated beds attaching to rocks in the mid and low shore levels. The large size of the bay and range of exposure conditions it encompasses, enabled mussel samples to be collected from a variety of habitats, ranging from highly wave-exposed rock platforms at the far north and south ends of the bay (Desembocadura exposed sites 1 and 2, respectively), to more sheltered locations within the bay itself, to the north (Desembocadura sheltered site 1) and south (Desembocadura sheltered site 2).

Maule, VIII Region, Chile Position: 37°01.25'S 73°10.05'W

A small enclosed, westerly facing bay, close to the site at Coronel (below). *P. purpuratus* forms extensive beds on the horizontal rock platforms that occur throughout the intertidal area of the shore. The site is sheltered to some extent from the full force of the Pacific waves, since it lies within a protected bay. However, the mussels are still exposed to a high degree of wave action at this site.

Coronel, VIII Region, Chile Position: 37°03.38'S 73°09.50'W

A large westerly facing 2km long sandy bay, 20km South of Concepcion. *P. purpuratus* forms beds on the gently sloping rocky platforms, extending into the lower shore area at the far northern end of the bay. The site is subject to a high degree of wave action. This site is located in the heart of the main coal producing area of Chile and coal dust and fragments are mixed in with the sand of the bay. In addition, the bay is a popular beach, lined with many bars and cafes and can be very crowded, particularly during the summer.

Valdivia, X Region, Chile Position: 39°51.00'S 73°24.00'W

A long, west facing 2km long sandy bay, lined by rock platforms to the north and south. Mussel samples were collected from the highly wave exposed rock

platforms at the south end of the bay, where *P. purpuratus* formed thick, tightly packed multilayered beds on the middle and lower shore areas.

Field collection and processing of samples

The selection criteria for all the sites in the British Isles, Irish Republic and Chile, from which samples were collected, were that *M. edulis* and *P. purpuratus* of similar overall size and shape, formed continuous beds on rocky substrata in the mid-shore area, such that the habitat provided by each mussel population for colonisation by infaunal invertebrates was broadly similar. Sites were selected such that as far as possible, conditions of wave-exposure were similar between all locations. More detailed descriptions of sampling procedures are provided, where necessary, in relevant chapters. On each occasion, eight replicate areas of $25cm^2$ were scraped from the rock surfaces using a paint scraper and placed in labelled containers. With the exception of the investigation of small-scale spatial variations in community structure, the quadrats were taken randomly from horizontal surfaces within the central areas of the mussel beds at mid shore level, thus ensuring that any spatial variation effects, due to differing topographies within each shore were minimised. On collection, samples were placed immediately in a cool box and returned to the laboratory. Where this was not possible (samples from England, Scotland and Ireland), samples were placed immediately in 7% formalin.

Each sample of mussels and its associated macro- and meiofauna from the sites in the British Isles and Irish Republic, were sieved through a 63µm mesh, with 63µm filtered seawater. All material passing through the sieve was retained and placed in containers to settle for 48 hours, after which the seawater was decanted and any remaining material (classed as fine sediment) dried to constant weight at 60^0C for 48 hours. The mussels and their associated fauna retained on the sieve were then fixed in 7% formalin, placed in labelled containers, and stored in the laboratory to await sorting. Samples were placed in 7% formalin, in order that the organisms retained their true colour, which facilitated identification. Prior to sorting, samples were removed from their labelled containers and washed through a 63µm sieve with copious quantities of freshwater, in order to remove all traces of formalin. The material retained on the sieve was washed into a Bogorov tray and sorted under a dissecting microscope, while larger material, including mussels was sorted in Petri dishes. Samples from Chile and those taken in Wales as part of the study of temporal variation associated with the mussel communities, were not sieved or preserved in formalin, but were sorted immediately after collection by dividing into

smaller sub-samples in Petri dishes containing 63μm filtered seawater and examining under a dissecting microscope.

All organisms, including small mussels (<5mm) present in the samples from the British Isles, Irish Republic and Chile were removed, identified to the lowest taxonomic category possible and counted. Where species did not conform to any available description or identification was not possible, the specimens were scale drawn, notes taken and each assigned to a morpho-species. Keys to most of the species in Chile were not available, while many of the species present in the samples had not been previously described. In addition, time was the limiting factor during this study, so to reduce sorting times and enable a greater volume of material to be processed; identification of organisms was generally only made to higher taxonomic levels. Polychaetes were identified to family level, while most other organisms were identified to class level. Others, such as nematodes and nemerteans were identified to phylum level. To reduce sorting time again, a measurement scale was assigned for the abundance of infauna. Taxa present in quadrats in numbers <25 were counted individually, while greater abundance were placed in various categories, as follows;

- approximately 25-50 individuals per quadrat = 25
- approximately 50-100 individuals per quadrat = 50
- greater than 100 individuals per quadrat = 100

Where samples were collected at sites in the British Isles and Irish Republic to provide a comparison with samples collected in Chile, species identification and enumeration was conducted in the same way, in order to standardise methodologies as much as possible, for comparative purposes.

Once all organisms had been removed from each of the samples from the British Isles and Irish Republic, all remaining material (small stones, shell fragments and byssal threads, classed as coarse sediment) was dried to constant weight at 60^0C for 48 hours. This material was not collected from Chilean mussel samples. The sediment content of mussel samples collected in the investigation of small-scale variation in the structure of the communities was further subdivided into the following fractions, using graded sieves, and weighed; <63μm, 63-125μm, 125-250μm, 250-500μm and >500μm.

The length (anterior-posterior axis) of each mussel >5mm, was measured with vernier callipers, to the nearest 0.1mm and length-frequency distributions constructed. The total volume of the mussels from each quadrat was measured by calculating their displacement in a 200ml measuring cylinder. Total biomass of

mussels in British samples only, was obtained by drying the mussels in an oven at 60^{0}C for 48 hours and then weighing. Small mussels <5mm were not included in the size distributions, since these individuals are scaled to the same size as the rest of the associated fauna and thus play an interactive, rather than a structural, role at this stage in their life.

Age structure of mussel populations

In order to investigate the growth history of populations of *M. edulis* in the British Isles and *P. purpuratus* in Chile, samples of the largest individuals were collected from the mid shore zones of mussel beds at several locations in each country. Mussels were collected from Point Lynas, White Beach and Criccieth in the British Isles, during July 1998 and Desembocadura exposed sites 1 and 2, Desembocadura sheltered site 2 and Coronel in Chile, during January 1997. Only shells with an intact periostracum were selected, since the analysis of external growth rings and internal growth bands is often difficult and frequently impossible in severely abraded shells or those damaged by the action of shell-boring algae. Since determination of the age of individual mussels by counting the number of surface growth rings was often difficult or impossible, it was necessary to study the internal microgrowth bands present in the prismatic layer of the shells. Mussels were boiled to remove all the flesh, whilst the external surfaces were scraped and scrubbed clean. One shell valve was then selected for embedding in Metaset resin (Buehler UK Ltd). All embedded shells were sectioned through the umbone, along the anterior-posterior axis, using a diamond saw. The cut surface of one section from each mussel was then ground smooth on increasingly finer grades of wet and dry paper, using a rotating table. The ground surface of each section was polished using household Brasso and washed in mild liquid detergent, before being placed in 1% Decal for 30 minutes, in order to etch the exposed surface of the mussel shell. Acetate peel replicas of the dry and etched shell sections were then prepared, by immersing replication material (Agar Scientific Ltd, UK) in ethyl acetate solvent for a few seconds, before applying it to the etched surface of the shell section. Dry acetate peels were removed, trimmed and mounted onto glass microscope slides and viewed using a light microscope. Twenty *M. edulis* shells were prepared in this manner from each site in the British Isles, whilst only ten *P. purpuratus* shells were prepared from each site in Chile, since these shells were highly eroded and numbers of shells with an intact periostracum were limited.

The annual growth and longevity of individual mussels was established by observing changes in the tidal microgrowth band patterns present in the middle

prismatic layer of each shell. Annual checks within each shell were identified by the narrow banding deposited during the winter (November to April in the British Isles, May to September in Chile). Each winter growth cessation was marked directly onto the acetate peel replica. The age of each mussel was noted and the distance between each successive check and the umbo measured to the nearest 0.1mm using vernier callipers. Von Bertalanffy Growth (VBG) constants in the VBG equation $L_t=L_{max}(1-e^{-kt})$ were determined from the measurements of size at age using the software package Fishparm, and fitted growth curves were subsequently generated and plotted for all mussel populations. (L_t = length at time (t); L_{max} = asymptotic growth maximum; k = the VBG constant and t_0 = the estimated date of settlement when length is zero).

Species data analyses

Species data were analysed using the PRIMER 5 (Plymouth Routines in Multivariate Ecological Research) package for multivariate community data analysis. Various procedures within this package were utilised to describe both the biotic and environmental data.

Univariate measures of mussel community structure

The limitations of single-figure diversity indices for describing ecological data have been stated by many authors (e.g. Green, 1979); however their use in the present study is justified as a method to facilitate the comparison of equally sized samples between sites. Univariate measures calculated were: number of taxa, the total number of individuals and the following diversity indices: Shannon-Weiner diversity (H'), Margalef's species richness (d) and Pielou's evenness (J). In order to compare infaunal communities over various temporal, spatial and geographical scales, each univariate measure was calculated for all eight replicate quadrats, comprising one complete sample. A one-way ANOVA/Mood's median test was used to test the significance of spatial or temporal differences in univariate measures of diversity. Where applicable, diversity indices were also calculated from pooled data across sample replicates.

Inter-relationships between the measured environmental variables from each of the sample replicates and diversity indices were examined using Pearson product moment correlation coefficients. All environmental variables used in the analysis were first log transformed to reduce the characteristically skewed nature of such environmental data.

Multivariate measures of mussel community structure

The two-stage approach advocated by Field *et al* (1982) for analysing multivariate data has been followed. This involves exploring the sample and species associations and then comparing the findings with the environmental information in order to search for an environmental interpretation of the community patterns.

A range of non-parametric multivariate techniques included in the PRIMER V5 package was applied to the species/sample matrices in order to summarise the faunal community data at each of the sites in the British Isles, Irish Republic and Chile. This involved initially constructing a triangular similarity matrix from the biotic data matrix using the Bray-Curtis similarity coefficient. Species abundance in the data matrix was first subject to either a square-root transformation, where emphasis in the analysis is placed on abundant species, or a presence/absence transformation, which allows the rarer species to influence the analyses (Elliot, 1977).

Similarity coefficients were then grouped using group average linkage cluster analysis, a hierarchical classification technique (Lance and Williams, 1967), and the results displayed as dendrograms. The Bray-Curtis similarity matrix was further employed to produce non-metric multidimensional scaling (MDS) ordinations of inter-sample relationships (Kruskal and Wish, 1978). Such ordination methods serve to summarise community data by producing a "map" or configuration in a two-dimensional space in which similar samples are close together and dissimilar samples are further apart. The non-metric solution seeks for an ordination in as few dimensions as possible (preferably two) which minimises the stress value. A large stress value (>0.2) indicates that the configuration or "map" for a particular dimension poorly represents the sample dissimilarities. As such, stress values can be regarded as a measure of the goodness of fit of an ordination diagram in representing the similarity values (Clarke and Green, 1988). Ordinations produced using non-metric MDS at each site were tested, where applicable, against ordinations showing cyclic patterns of seasonal change, seriation patterns indicating underlying gradients in the data, or against other independent similarity matrices. This was achieved by defining them in only one dimension, so that the correlation of their ranks can be used as a measure of their agreement. The RELATE routine achieves this by calculating Spearman rank correlation between each of the corresponding similarity matrices, the significance of which is then ascertained through a permutation procedure (Clarke and Ainsworth, 1993).

The triangular similarity matrices were further utilised in the ANOSIM procedure to test for significant differences in community structure between samples. ANOSIM generates a value of R, which is scaled to lie between -1 and +1, a value

of zero representing the null hypothesis, such that there is no significant difference in community structure between samples. A value of +1 indicates significant differences, while a value of –1 indicates greater dissimilarity among replicate units within samples than occurs between samples (Chapman and Underwood, 1999).

Similarity percentage analyses (SIMPER) were performed on the species/sample matrices to elucidate characteristic faunal groupings and to determine which species contribute to the Bray-Curtis dissimilarity between samples (Clarke, 1993). However, where a holistic approach was required to identify species contributing to sample differences, such as when community changes are occurring in a continuum, the BVSTEP procedure in PRIMER was used. This procedure undertakes a stepwise selection of species from the main biotic data matrix, in an attempt to search for a species subset which, when subject to ordination techniques, displays the same pattern as the entire data set.

Analysis of environmental parameters in the mussel bed

To search for initial relationships between environmental variables measured in the mussel beds and the infaunal communities, Pearson product moment correlation coefficients were calculated between all environmental variables and univariate measures of diversity.

The second stage in analysing the multivariate data was to test whether the community patterns found at each site could be related to environmental gradients. Correlation-based principal components analysis (PCA) was used to ordinate the environmental variables, the data having previously undergone a log transformation. PC1 was then plotted against each of the univariate measures of community diversity at each of the three locations and Pearson product moment correlation coefficients calculated to search for any relationships. Triangular similarity matrices based on normalised Euclidean distance were constructed from the environmental data obtained from each of the mussel bed samples. These ordinations derived from environmental data and the averaged biotic data from each sample were then compared using the RELATE routine.

Relationships between environmental measures and biological variation were further explored using the BIOENV procedure in PRIMER (Clarke and Ainsworth, 1993). This approach detects patterns of variation in the species data, which can be "best", explained by the observed environmental variables, using rank correlation coefficients. Prior to inclusion in the BIOENV procedure, Pearson product moment correlation coefficients were calculated between all log-transformed environmental parameters at each site to establish whether any of them were co-linear. If any co-

linear relationships were seen to exist ($r>0.95$), a single variable was used as a representative of the correlated variables in the analysis.

Sample size calculation

A quadrat size of $25cm^2$ (5x5cm) was selected, since it has been shown previously that in communities, such as those associated with mussel beds, where species are patchily distributed, the combination of separate small areas will give a higher species count than a contiguous area of the same size (Pringle, 1984).

There are various methods by which the data in the form of the species count of a number of random quadrats of equal size can be used to determine the species content of areas of larger size. The simplest of these is to order the samples randomly and then construct a straightforward cumulative species/area curve (Ursin, 1960). However, these curves are irregular, and their shape is dependent on the position in the sequence of those quadrats containing numbers of the rarer species; a re-randomisation of the quadrats can totally change the curve. It was thus suggested by Ursin (1960) that totally independent samples at each size enabled improved statistical analysis. However, the number of samples required to construct such curves is very high, being 210 for one replicate for each point on the curve from one to twenty quadrats. In addition, irregular curves will still result for the same reasons described earlier. In an attempt to reduce the irregularities of the curve, Ursin (1960) suggested the construction of 'semi-cumulative' curves, where the mean number of species is determined for all mutually independent sets of quadrats taken 1,2,3,4...n at a time from the pool of n quadrats. However, this method can still lead to irregularities in the curve for sets of $>n/2$ quadrats, where only one mutually independent set can be drawn from the pool. Various methods using probability theory have been used in the derivation of species/ area curves, most of which are lengthy, cannot be extrapolated beyond the original sample size and make no compensation for species with zero counts in the original sample. Hawkins and Hartnoll (1980) suggested a method using the frequency of occurrence in random quadrats, which permits indefinite extrapolation beyond the original sample size and permits a partial compensation for zero counts. This method was used to calculate sample size in this study and is summarised as follows.

Assume that N quadrats contain a total of S species, and that the ith species occurs in n_i quadrats. The probability of the ith species occurring in a quadrat is n_i/N, and the probability of it not appearing is $1-(n_i/N)$. The probability of it not occurring in q quadrats is $[1-(n_i/N)]^q$, and of it not occurring $1-[1-(n_i/N)]^q$. Thus the number of species expected in q quadrats will be:

$$\sum_{i=1}^{S}\left(1-\left[1-\frac{n_i}{N}\right]^q\right)$$

This formula may be used to calculate the expected species number in any number of quadrats, either smaller or larger than N and would be expected to provide an acceptable prediction if the sample of N quadrats contained information on the frequency of all the species in the community. Some species will have a zero frequency in the sample, but have a finite probability of appearing in a sample of that size. The number of species with low probability of occurrence in a quadrat (i.e. of 1/N or 2/N) will be underestimated. This will substantially affect the predicted species number at sample sizes up to N quadrats. The number of species with even lower probabilities, of less than 1/N, will not be indicated by the sample. Thus a correction factor must be applied to the formula to allow for rarer species within the community. The correction factor is as follows and is only necessary for those frequencies where;

$$[1-(n_i/N)]^N > 0.1$$

No correction can be made with regard to species with a frequency of less than 1/N on the basis of information in the sample, although the effects of not doing so will be minimal for areas up to N quadrats.

Thus for each value of q an increment must be made to the predicted number of species in respect of each of the frequency classes where it is required. This is the probability of occurrence of one species of that frequency in q quadrats multiplied by the number of un-represented species as calculated above, namely:

$$\left(1-\left[1-\frac{ni}{N}\right]^q\right) x \left(\left[\frac{x}{1-\left[1-\left(ni/N\right)\right]^N}\right]-x\right)$$

In order to use this probability theory method to calculate the predicted species/area relationship for mussel bed communities, fifteen replicate $25cm^2$ quadrats were collected from mussel patches at both Criccieth and White Beach and the resulting species abundance data entered into the model.

RESULTS

Table 1 details the number of taxa encountered in increasing numbers of $25cm^2$ quadrats at White Beach and Criccieth, while Table 2 provides information on

Table 1 Observed taxa/area relationship of infaunal communities associated with mussel beds at a) White Beach, Anglesey and b) Criccieth, Gwynedd.

a) White Beach

Quadrat No.	No. Taxa	Cumulative Area (cm^2)	Cumulative Taxa	% Increase (Taxa)
1	8	25	8	100.0
2	11	50	12	50.0
3	7	75	15	25.0
4	7	100	16	6.7
5	9	125	20	25.0
6	12	150	25	25.0
7	12	175	28	12.0
8	5	200	28	0.0
9	5	225	30	7.1
10	5	250	30	0.0
11	11	275	32	6.7
12	9	300	33	3.1
13	6	325	33	0.0
14	6	350	34	3.0
15	10	375	34	0.0

b) Criccieth

Quadrat No.	No. Taxa	Cumulative Area (cm^2)	Cumulative Taxa	% Increase (Taxa)
1	14	25	14	100.0
2	12	50	21	50.0
3	10	75	24	14.3
4	13	100	29	20.8
5	5	125	29	0.0
6	4	150	29	0.0
7	10	175	32	10.3
8	4	200	32	0.0
9	6	225	33	3.1
10	3	250	33	0.0
11	11	275	33	0.0
12	15	300	33	0.0
13	10	325	33	3.0
14	11	350	34	2.9
15	6	375	35	0.0

Table 2 Probability of occurrence in quadrats, of each infaunal taxon found in mussel beds at a) White Beach, Anglesey and b) Criccieth, Gwynedd. Taxa marked * are found in only 1 or 2 quadrats, so correction factors must be applied to these taxa in the model.

a) White Beach

Taxa No.	No.[1]	Prob.[2]	Prob.[3]
1	15	1.0	0.000
2*	2	0.133	0.867
3	13	0.867	0.133
4	4	0.267	0.733
5*	1	0.067	0.933
6*	2	0.133	0.867
7	3	0.200	0.800
8	3	0.200	0.800
9*	1	0.067	0.933
10*	2	0.133	0.867
11	6	0.400	0.600
12	3	0.200	0.800
13*	2	0.133	0.867
14	13	0.867	0.133
15*	2	0.133	0.867
16*	2	0.133	0.867
17*	2	0.133	0.867
18*	1	0.067	0.933
19*	1	0.067	0.933
20*	1	0.067	0.933
21	5	0.333	0.667
22*	1	0.067	0.933
23*	1	0.067	0.933
24	4	0.267	0.733
25	4	0.267	0.733
26	4	0.267	0.733
27*	2	0.133	0.867
28*	1	0.067	0.933
29*	2	0.133	0.867
30*	1	0.067	0.933
31	12	0.800	0.200
32*	2	0.133	0.867
33*	1	0.067	0.933
34	3	0.200	0.800

b) Criccieth

Taxa No.	No.[1]	Prob.[2]	Prob.[3]
1	15	1.000	0.000
2	9	0.600	0.400
3*	2	0.133	0.867
4*	1	0.067	0.933
5	3	0.200	0.800
6*	1	0.067	0.933
7*	1	0.067	0.933
8*	1	0.067	0.933
9*	1	0.067	0.933
10*	1	0.067	0.933
11	4	0.267	0.733
12*	1	0.067	0.933
13	5	0.333	0.667
14	4	0.267	0.733
15	6	0.400	0.600
16	4	0.267	0.733
17*	2	0.133	0.867
18	9	0.600	0.400
19*	1	0.067	0.933
20	8	0.533	0.467
21*	1	0.067	0.933
22	13	0.867	0.133
23	6	0.400	0.600
24*	1	0.067	0.933
25	4	0.267	0.733
26	4	0.267	0.733
27*	1	0.067	0.933
28*	1	0.067	0.933
29*	2	0.133	0.867
30	3	0.200	0.800
31	4	0.267	0.733
32*	2	0.133	0.867
33*	2	0.133	0.867
34	3	0.200	0.800
35	8	0.533	0.467

1 Number of quadrats in which each taxon occurred
2 Probability taxon occurs in a quadrat
3 Probability taxon does not occur in a quadrat

calculated values of the probability of occurrence of each of these taxa in a quadrat. These data were then entered into the probability theory model described earlier, and resulting taxa/area curves plotted for each location (Figure 3). At both sites, the model predicts that eight to nine $25cm^2$ quadrats should be taken in order to sample adequately the communities associated with the mussel populations. As such, in studies of the temporal, spatial and geographical variation in the structure of invertebrate communities associated with *M. edulis* in the British Isles and Irish Republic and *P. purpuratus* in Chile, eight replicate $25cm^2$ quadrats were taken from mussel beds.

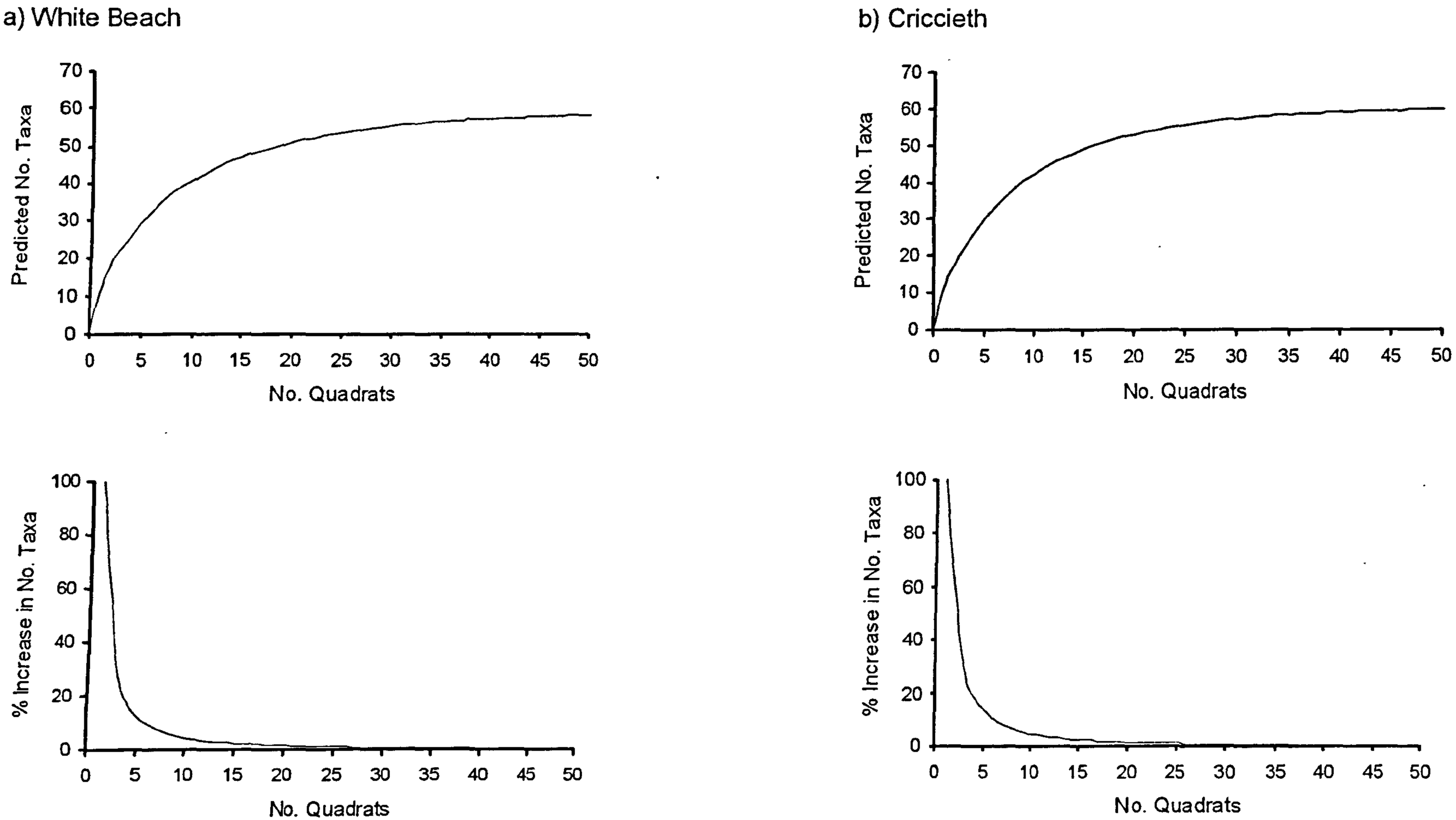


Figure 5 Taxa/area curves for infaunal communities associated with mussel beds and predicted % increase in the number of taxa encountered with increasing sample size in mussel beds at a) White Beach, Anglesey and b) Criccieth, Gwynedd, as predicted using probability theory.

Chapter 3

Size structure and growth rate of *Mytilus edulis* and *Perumytilus purpuratus* populations together with a brief note on their associated invertebrate communities

ABSTRACT

The size structure and growth rates of *Mytilus edulis* and *Perumytilus purpuratus* were investigated at a variety of locations throughout the British Isles, Irish Republic and Chile, South America. Investigations showed inter-site differences in the size structure of *M. edulis* populations throughout the British Isles and Irish Republic during the summer of 1999, although smaller (<10mm) mussels dominated most of the mussel populations. The maximum length attained was 33mm, at Criccieth and White Beach, North Wales and Filey Brigg, NE England while few individuals larger than 25mm were found at any of the other sites. Mussel density varied between 55 and 176 individuals per 25cm^2, while mussel volume and biomass also showed significant inter-site variations. *P. purpuratus* populations in Chile showed considerable inter-site variations in size structure. The maximum size attained was 37mm at Desembocadura exposed site 1, although mussels greater than 20mm were common at all sites. These mussel populations contained fewer small individuals than their British and Irish counterparts. Mussel density did not vary significantly between sites, with around 20-30 individuals per 25cm^2 at all sites. The size structure of mussel populations in North Wales, along with mussel density, volume and biomass showed some seasonal variation, while *M. edulis* and *P. purpuratus* populations both showed annual variations in size structure. *M. edulis* showed significantly different growth rates at three different sites in North Wales, while the growth rate of *P. purpuratus* also showed significant inter-site variation. *M. edulis* displayed a significantly faster growth rate than Perumytilus purpuratus, although *P. purpuratus* attained a greater maximum age. A total of 182 taxa were identified from the *M. edulis* communities in the British Isles and Ireland, while substantially fewer were identified to higher taxonomic levels, from the *P. purpuratus* beds in Chile.

INTRODUCTION

Structural complexity of the environment has often been considered an important determinant of biotic diversity and biologists have long held the view that structurally complex habitats support more species than structurally simple ones (Smith, 1972; Kohn and Leviten, 1976). The notion that the number of species able to survive in any one habitat is directly proportional to the number of microhabitats has been quantified for a variety of communities including rocky intertidal shores (Archambault and Bourget, 1996), subtidal reefs (Pimm, 1994), groups of birds (MacArthur, 1972), chydorid cladocerans (Whiteside and Harmsworth, 1967), gastropods of the genus *Conus* (Kohn, 1967; Kohn and Leviten, 1976) and lizards (Pianka, 1966). Harner and Harper (1976) illustrated in a study of plant species diversity that environmental heterogeneity was strongly correlated with species diversity and accounted for 84% of the variation in species numbers. Thus, in this study of mussel community structure, any variation in the density and size distributions of the mussels might result in changes in the diversity of the associated invertebrate communities.

Size-frequency distributions within some bivalve populations are characteristically polymodal, each mode representing an individual year class (Richardson *et al*, 1995). In many mussel populations however, size classes may overlap to such an extent that while size-frequency distributions provide information on the heterogeneity of the habitat provided by the mussels, they are of limited value for estimating population growth rate (e.g. Kautsky, 1982; Richardson *et al*, 1990). Growth in *Mytilus* has been extensively documented. The growth history of each mussel is permanently recorded in the shell, either as a series of annual checks in the periostracum (Seed, 1969a; Davenport *et al*, 1984) and/or inner nacreous layers (Lutz, 1976; Kautsky, 1982), or as microgrowth bands present in the middle prismatic layer (Richardson, 1989; Richardson *et al*, 1990). Surface growth rings produced during periods of suspended shell growth have previously been used to determine the age of individual *M. edulis* (Seed and Richardson, 1990). However, periods of suspended shell growth may also be associated with seasonal changes in temperature or food availability, prolonged stormy weather, or even with the annual reproductive cycle and cannot therefore be assumed to be of annual origin (Seed, 1976).

Several authors have demonstrated that mussel growth rates and population structure vary according to environmental conditions, such as temperature (Richardson *et al*, 1990; Sukhotin and Kulakowski, 1992), food supply (Incze *et al*, 1980; Page and Ricard, 1990) and aerial exposure (Rodhouse *et al*, 1984; Sukhotin

and Maximovich, 1994). Longevity of mussels in areas of rapid growth has been shown to be considerably less than in those areas where they display slow growth (Seed, 1968). Sanders (1968) concluded that, with increasing habitat age and prolonged habitat stability, diversity increases and the community evolves into a set of species that are biologically accommodated. In contrast, young communities, which are controlled primarily by physical factors, have eurytopic species, wide population fluctuations and many opportunistic species. Thus, the age structure of the mussel populations might also affect community diversity and as such, has been determined in this study for some of the mussel populations from the British Isles and Irish Republic and Chile.

Details of the size distribution of mussel populations at all of the sample sites in both the British Isles, Irish Republic and in Chile, South America are provided in this chapter. Growth rates of *M. edulis* and *P. purpuratus* have been determined, by examination of the tidal microgrowth bands present in the prismatic layer of the shells. A brief summary of the suite of species associated with these mussel beds is also provided.

METHODOLOGY

Details of the methodology for this work are provided in Chapter 2.

RESULTS

Size structure of mussel populations

Sites in the British Isles and Irish Republic

The mussel populations from eight study sites in the British Isles and Irish Republic did not exhibit polymodal size distributions (Figure 1). The populations at Arisaig, Kilkee, Filey Brigg and Robin Hood's Bay were dominated by smaller mussels with a shell length of between 5mm and 10mm and had relatively few large mussels. Populations at Point Lynas, Criccieth and Doonbeg were dominated by medium sized mussels (12mm to 20mm) with few small mussels. The population at White Beach, however, was exceptional in having a relatively uniform distribution of mussel sizes. The maximum size observed was 33mm, at White Beach, Criccieth and Filey Brigg. Mussel density (per 25cm^2) was highly variable between each location, with highest densities at Filey Brigg and lowest densities at White Beach (Table 1). Mussel volume and biomass per unit area were highest at White Beach and Filey Brigg and lowest at Point Lynas and Doonbeg.

Little seasonal variation in size structure of the mussel populations at Point Lynas and White Beach was apparent between January 1998 and November 1998

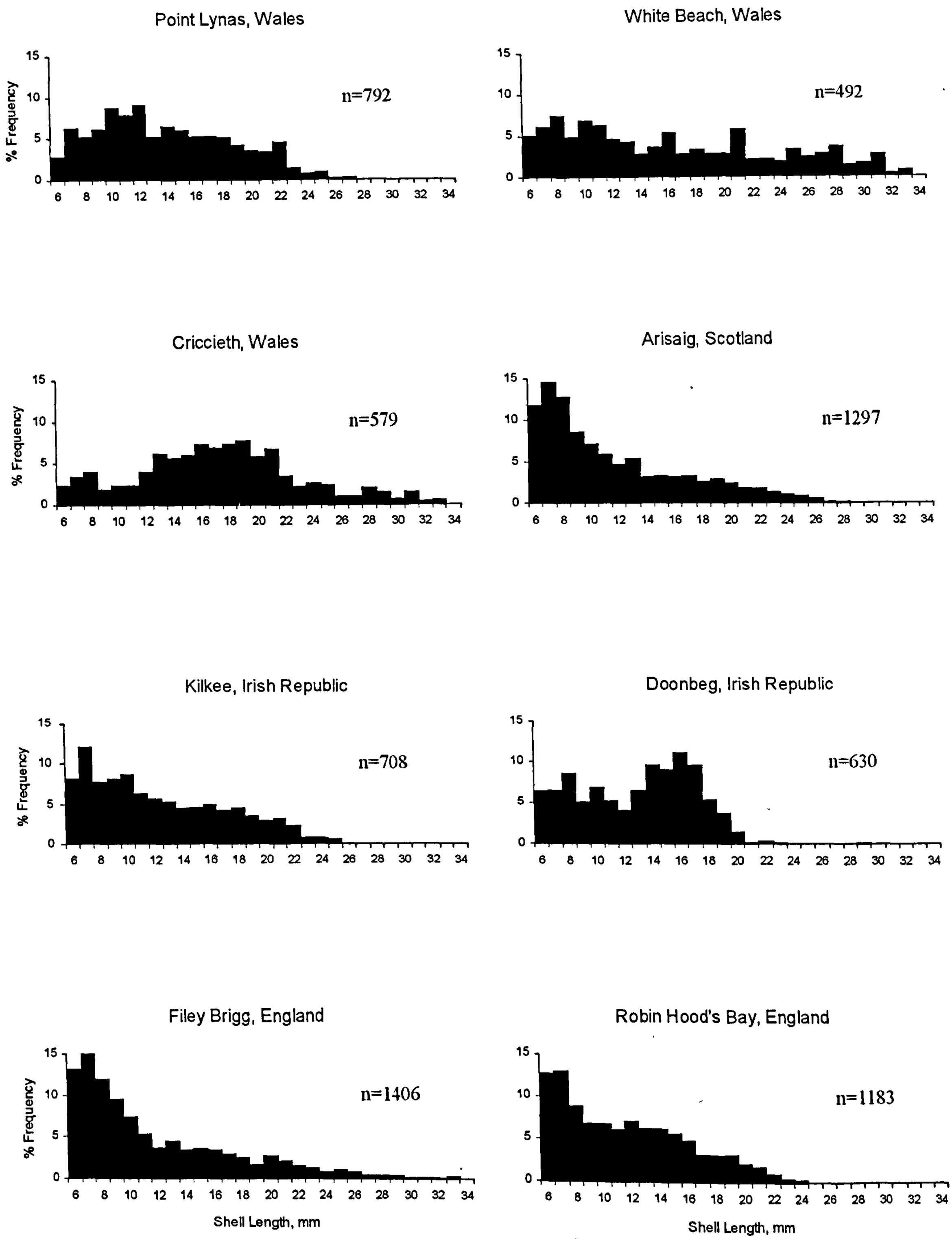


Figure 1 Size distributions of *Mytilus edulis* from eight sites in the British Isles and Irish Republic, in July 1999. Distributions are based on a mussel bed sample area of 200cm^2.

Table 1 Mean density, volume and biomass of mussels per $25cm^2$ area of mussel bed at eight sites in the British Isles and Irish Republic. 95% confidence intervals are marked, such that significant differences ($p<0.05$) are represented by non-overlapping intervals.

Site	Mussel Density	Mussel Volume (ml)	Mussel Biomass (g)
Point Lynas, Wales	64±11	19.1±3.0	11.64±2.24
White Beach, Wales	55±3	34.3±1.7	25.30±1.33
Criccieth, Wales	96±7	24.5±2.0	19.83±2.24
Arisaig, Scotland	163±9	19.4±2.4	19.67±1.26
Kilkee, Irish Republic	87±8	19.8±2.7	14.48±0.97
Doonbeg, Irish Republic	79±5	19.1±0.9	14.46±0.64
Robin Hood's Bay, England	149±8	27.9±2.1	17.34±1.29
Filey Brigg, England	176±10	31.5±3.3	22.49±1.73

(Figure 2 and 3), although slight variations were observed in the frequency of mussels at the smaller end of the size range (5 to 10mm). The mean density of mussels at the two locations, particularly White Beach, showed little seasonal variation, while mussel volume and biomass per unit area displayed slight monthly fluctuations, although with little consistency between sites or seasons (Table 2). By contrast, however, the mussel population at Criccieth showed considerable seasonal variation in size structure between January 1998 and November 1998, notably with an absence of large mussels (>24mm) in July and small mussels (<16mm) in September (Figure 4). The modal size increased gradually throughout the year, from 12mm in January to 30mm in November. Mussel density also showed considerable seasonal fluctuations, with higher values during the summer months (May and July) than in the winter months (November and January) (Table 2). By contrast, mussel volume and biomass were greater during the winter months than the summer. These seasonal patterns in mussel density, volume and biomass were similar between 1998 and 1999. The size structure of the populations at Point Lynas and White Beach remained relatively stable between 1998 and 1999 (Figure 5). However, the population at Criccieth fluctuated in density, particularly between summer and winter, while there was an overall trend towards increasing maximum size between July 1998 and January 1999.

Sites in Chile

Mussel populations from the Chilean sites did not display any apparent polymodal size distributions (Figure 6). The populations at Las Cruces, Desembocadura sheltered site 1, Cocholgue and Valdivia were generally dominated by large mussels (16mm to 27m), with few small mussels. Populations at Desembocadura (exposed sites), along with Maule and Coronel had much more uniform size distributions. The largest mussels occurred at the Desembocadura exposed sites, where they reached a maximum length of 37mm.

Mussel density did not vary greatly between the nine sites (Figure 7). However, there was a great deal of within site variation in the density of mussels within mussel beds at each of the locations, with the exception of Desembocadura exposed site 1. The size structure of the mussel populations at the three sites at Desembocadura and Coronel showed slight annual differences between 1997 and 2000 (Figure 8), whilst mean mussel density did not vary significantly (Figure 9).

The size structure of the mussel populations in the UK and Chile did not differ greatly. However, mussel beds in the British Isles and Irish Republic generally had more small, juvenile mussels, while the density of *P. purpuratus* in the Chilean

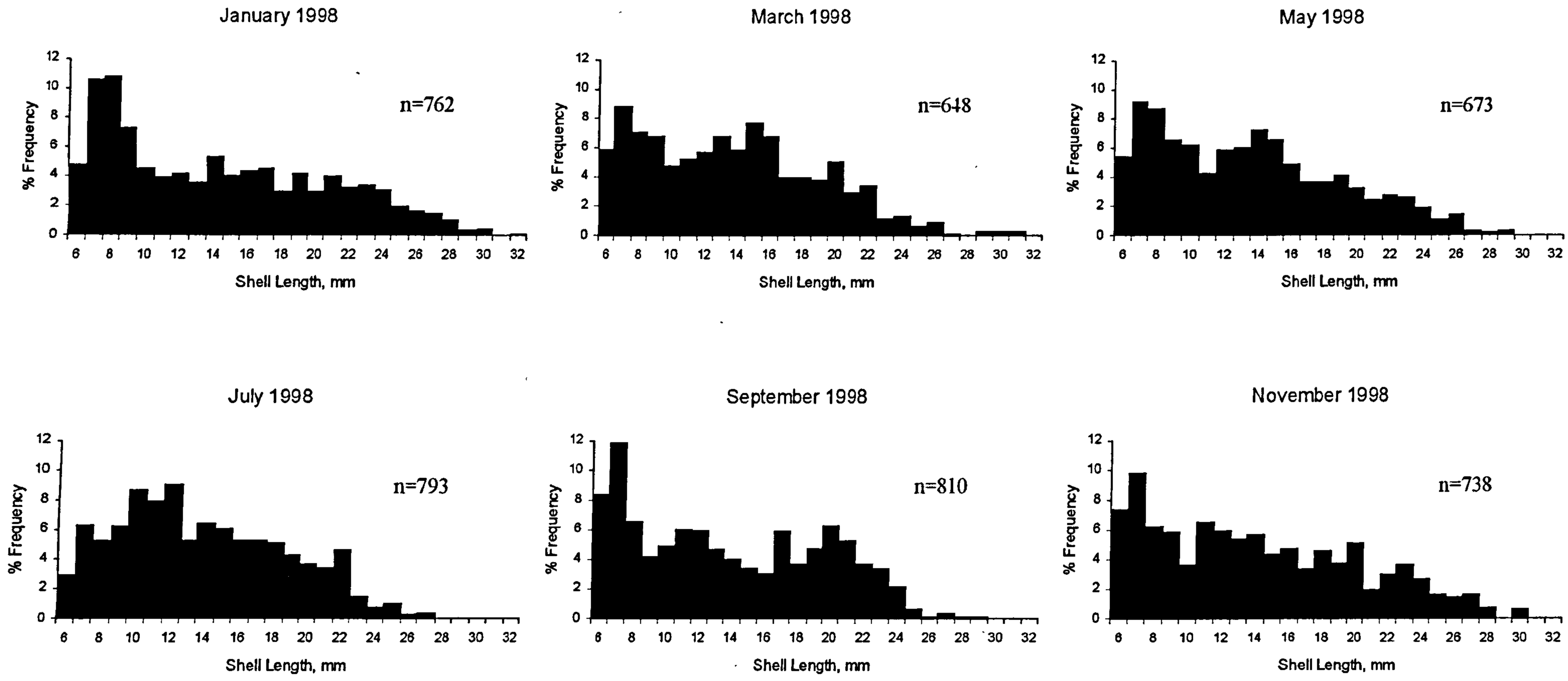


Figure 2 Size distributions of *Mytilus edulis* from Point Lynas, Anglesey, collected at bimonthly intervals during a twelve-month period between January 1998 and November 1998. Distributions are based on a mussel bed sample area of 200cm^2.

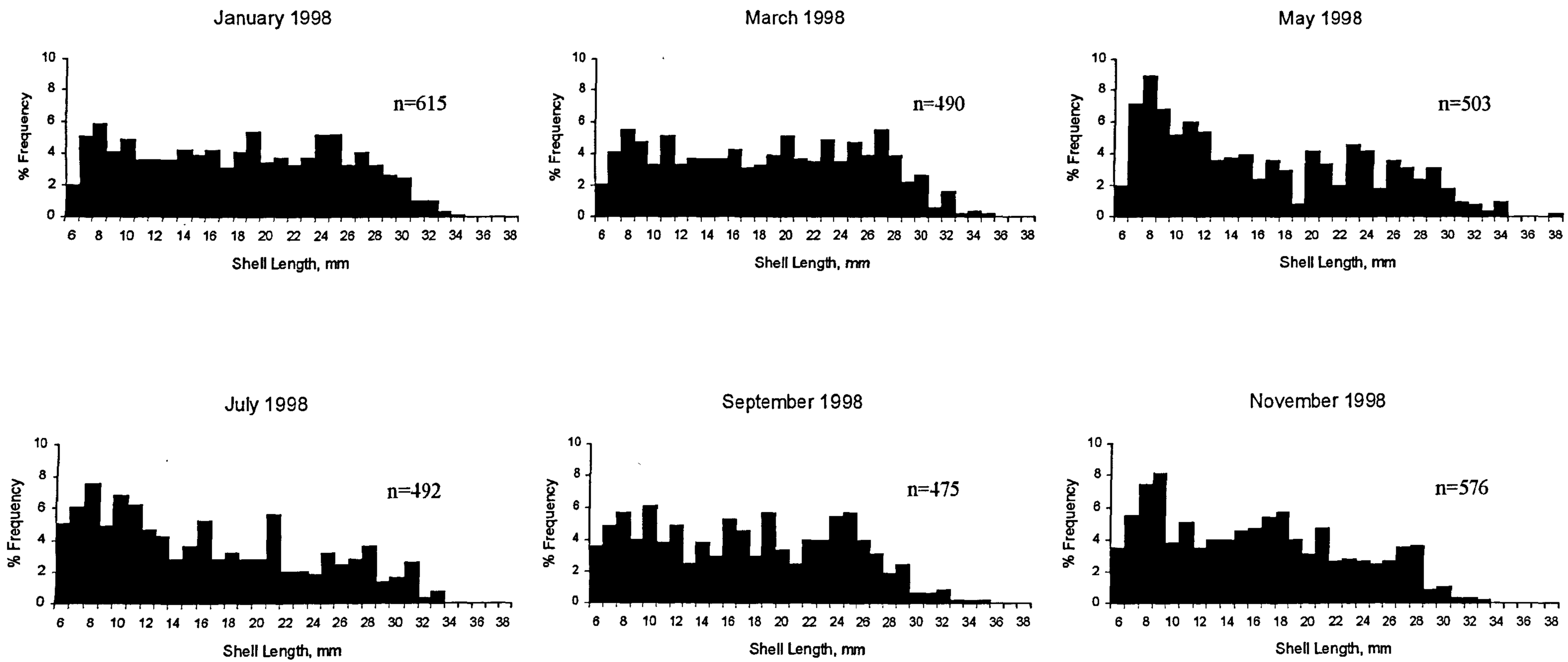


Figure 3 Size distributions of *Mytilus edulis* from White Beach, Anglesey, collected at bimonthly intervals during a twelve-month period between January 1998 and November 1998. Distributions are based on a mussel bed sample area of 200cm^2.

Table 2 Mean density, volume and biomass of mussels per 25cm^2 in mussel beds from Point Lynas, White Beach and Criccieth, Wales at intervals between January 1998 and July 1999. 95% confidence intervals are marked, such that significant differences ($p<0.05$) are represented by non-overlapping intervals.

Site	Date	Mussel Density	Mussel Volume (ml)	Mussel Biomass (g)
Point Lynas	January 1998	96±7	23.4±2.2	22.72±1.55
	March 1998	78±5	17.5±1.5	11.97±2.53
	May 1998	84±9	28.3±0.7	16.54±0.86
	July 1998	100±12	17.0±1.3	15.91±0.92
	September 1998	102±8	25.4±2.2	21.38±1.48
	November 1998	93±9	23.6±3.1	19.57±1.32
	January 1999	92±14	19.1±2.2	13.55±1.91
	July 1999	64±11	19.1±3.0	11.64±2.24
White Beach	January 1998	79±6	51.9±4.2	46.8±4.09
	March 1998	60±4	45.5±3.9	42.72±4.12
	May 1998	63±6	36.0±3.3	35.27±2.69
	July 1998	62±7	35.1±2.2	26.71±1.96
	September 1998	59±4	35.0±4.0	34.58±4.00
	November 1998	72±6	31.5±2.5	31.90±1.67
	January 1999	67±5	33.5±2.0	28.83±1.70
	July 1999	55±3	34.3±1.7	25.30±1.33
Criccieth	January 1998	35±3	26.1±2.5	22.75±2.58
	March 1998	35±3	25.2±1.2	26.06±1.31
	May 1998	79±10	24.8±2.8	19.64±1.25
	July 1998	76±8	19.38±2.1	12.07±0.37
	September 1998	39±2	20.5±1.6	20.83±1.06
	November 1998	31±2	38.3±3.3	28.77±1.26
	January 1999	35±4	42.9±2.0	40.16±1.75
	July 1999	96±7	24.5±2.0	19.83±2.24

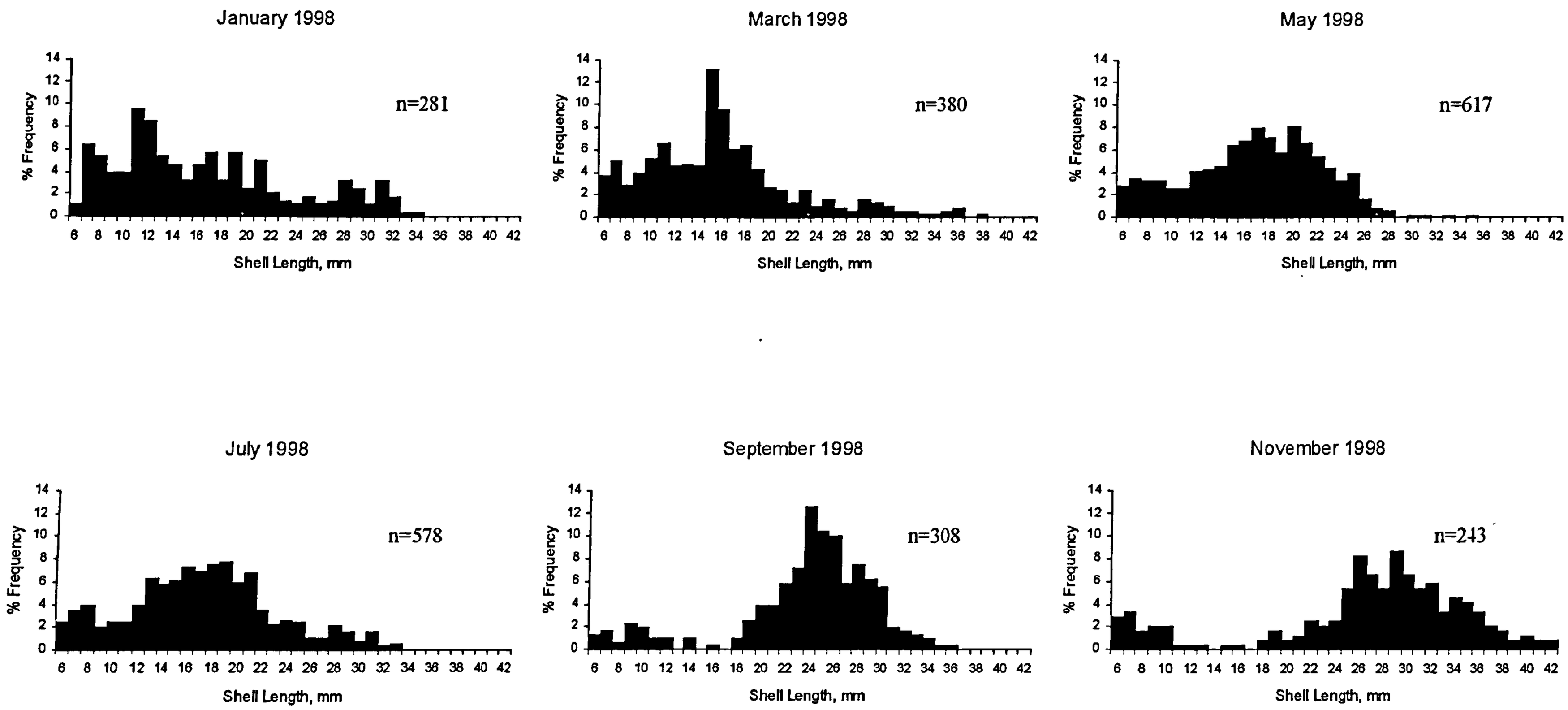
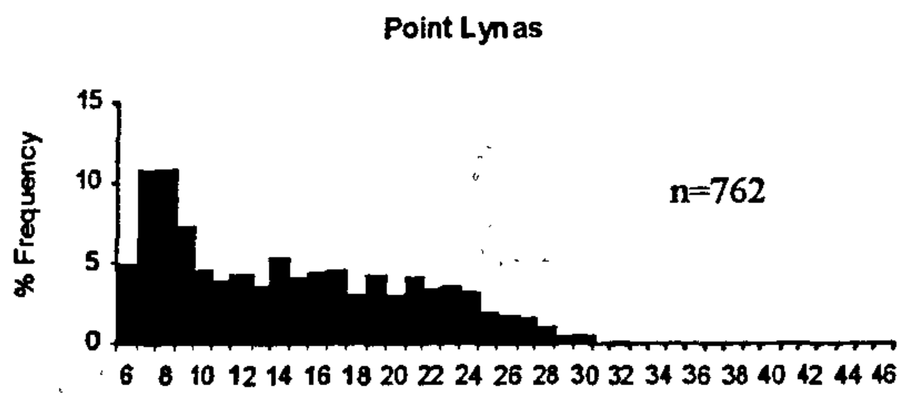


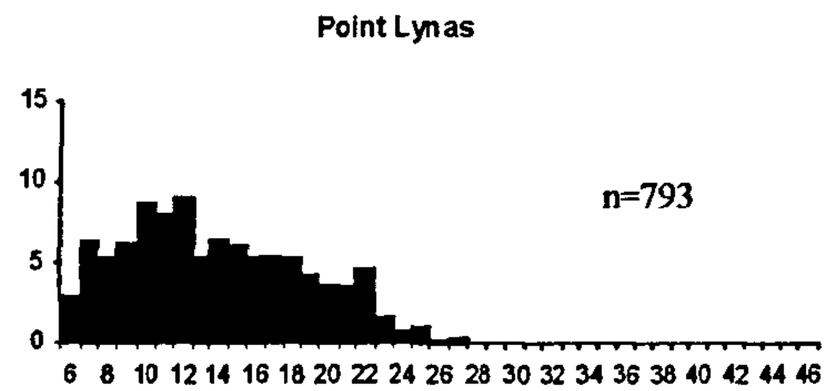
Figure 4 Size distributions of *Mytilus edulis* from Criccieth, North Wales, collected at bimonthly intervals during a twelve-month period between January 1998 and November 1998. Distributions are based on a mussel bed sample area of 200cm^2.

Figure 5 Size distributions of *Mytilus edulis* from three sites in North Wales; Point Lynas and White Beach, Anglesey and Criccieth, Gwynedd, during a) January 1998, b) July 1998, c) January 1999 and d) July 1999. Distributions are based on a mussel bed sample area of $200cm^2$.

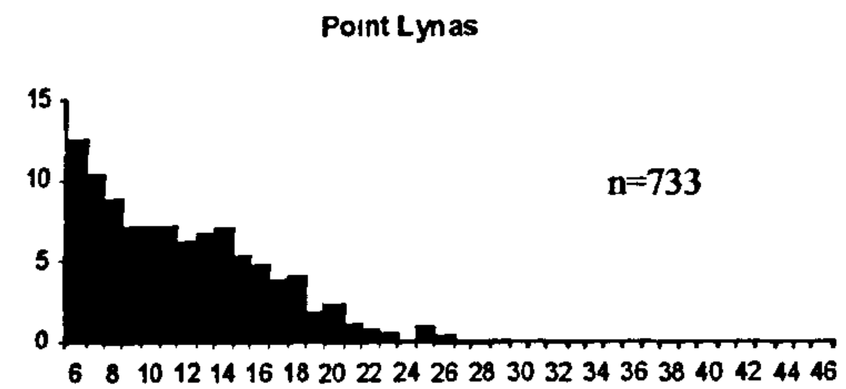
a) January 1998



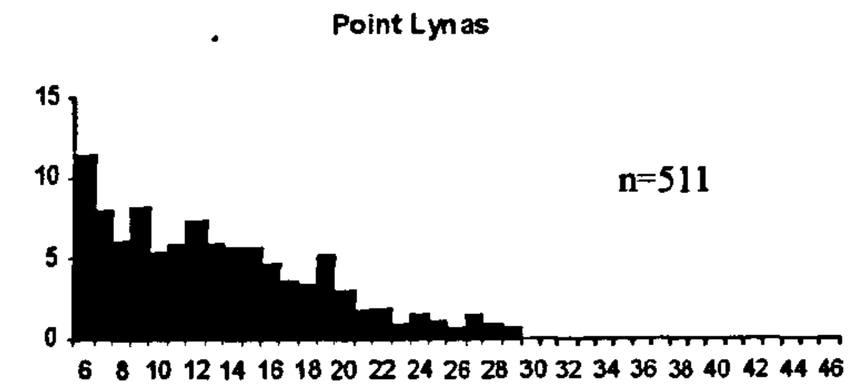
b) July 1998

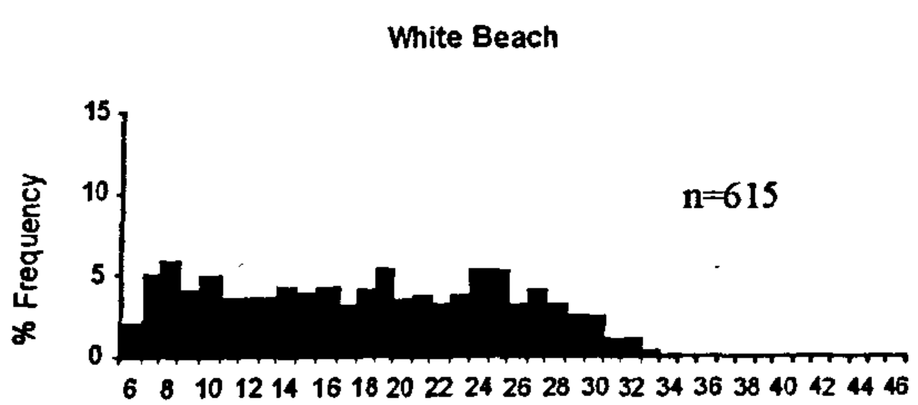


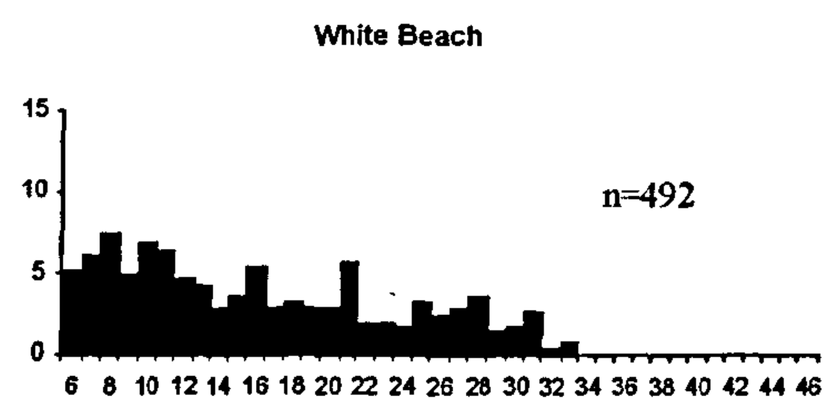
c) January 1999

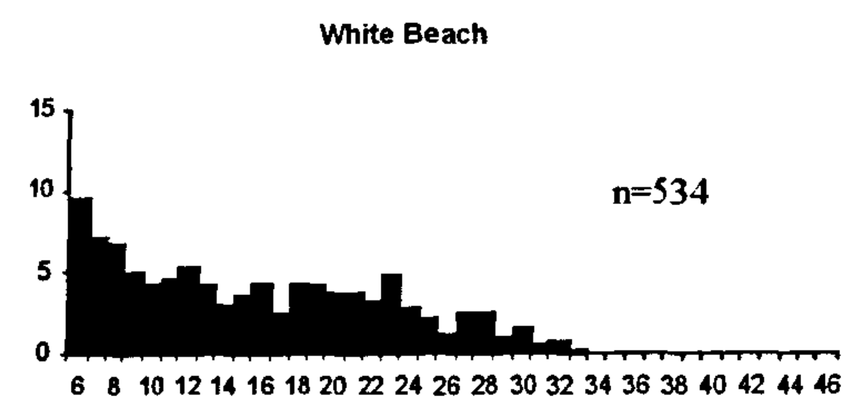


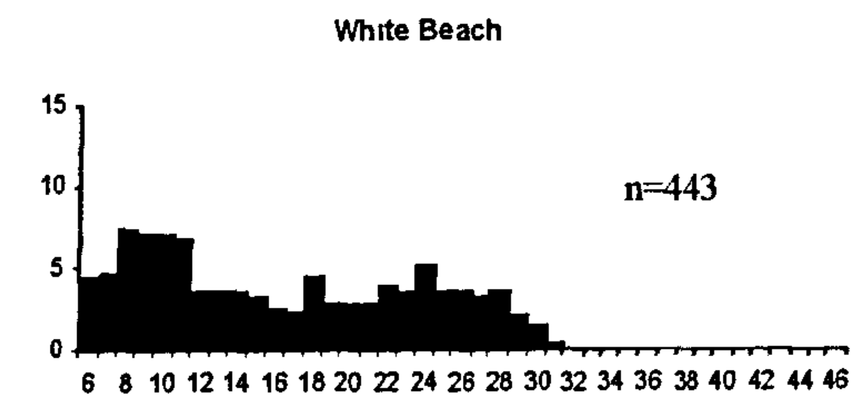
d) July 1999

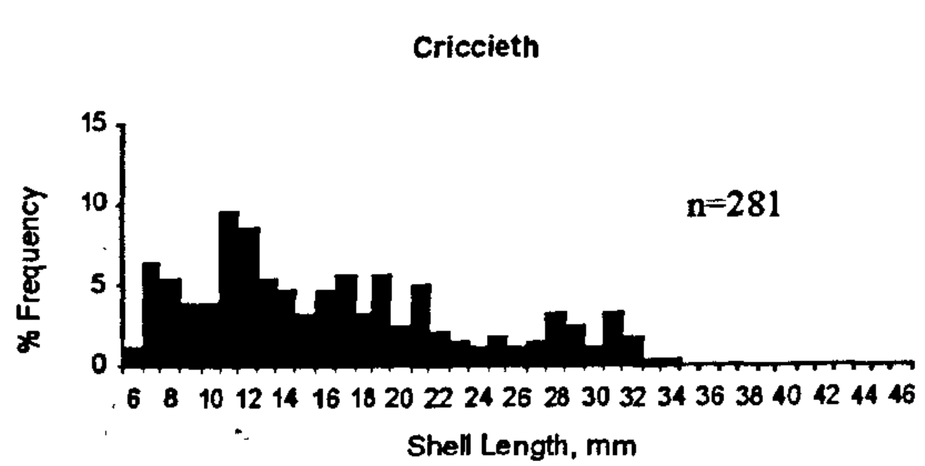


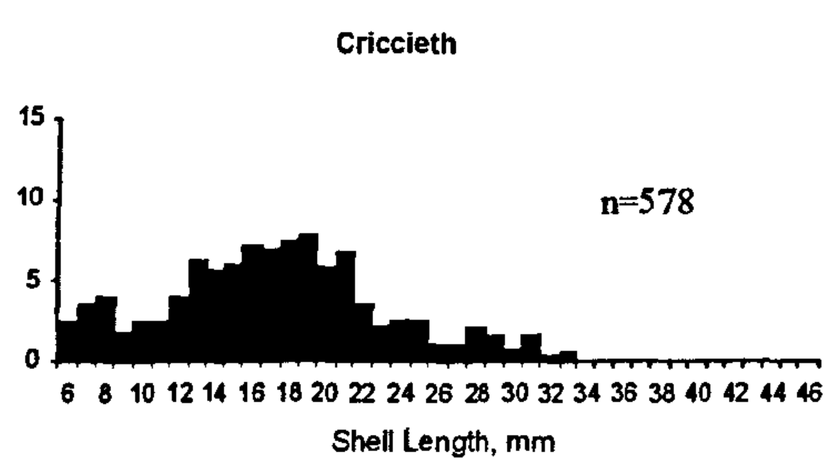


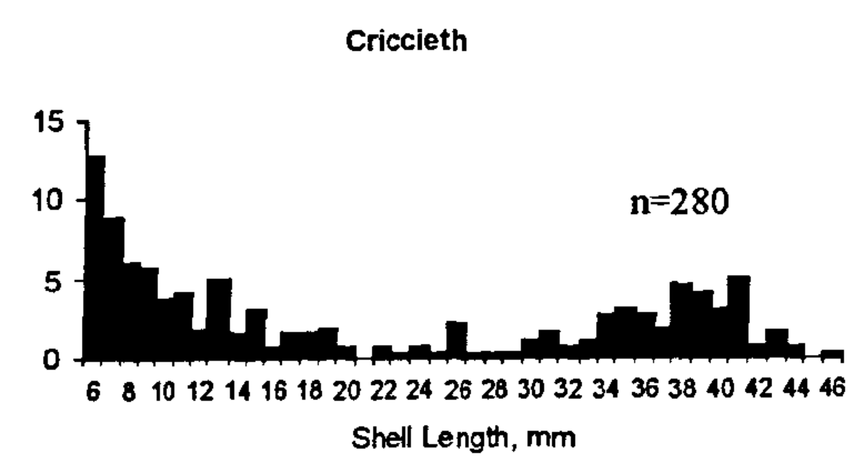


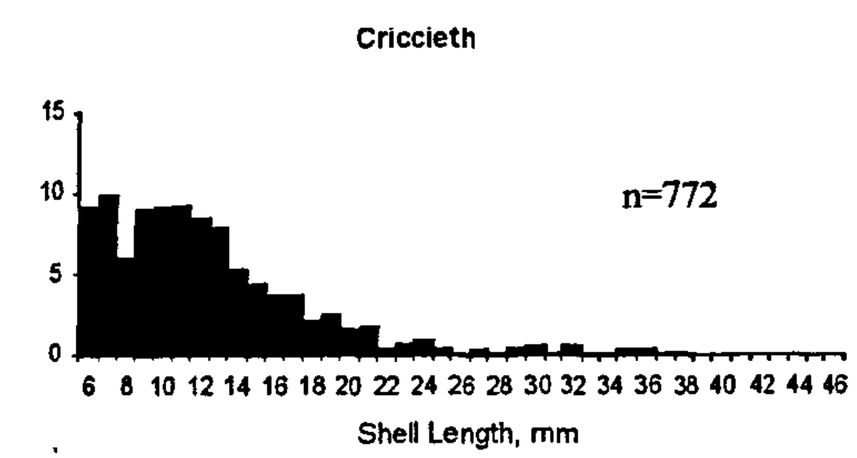












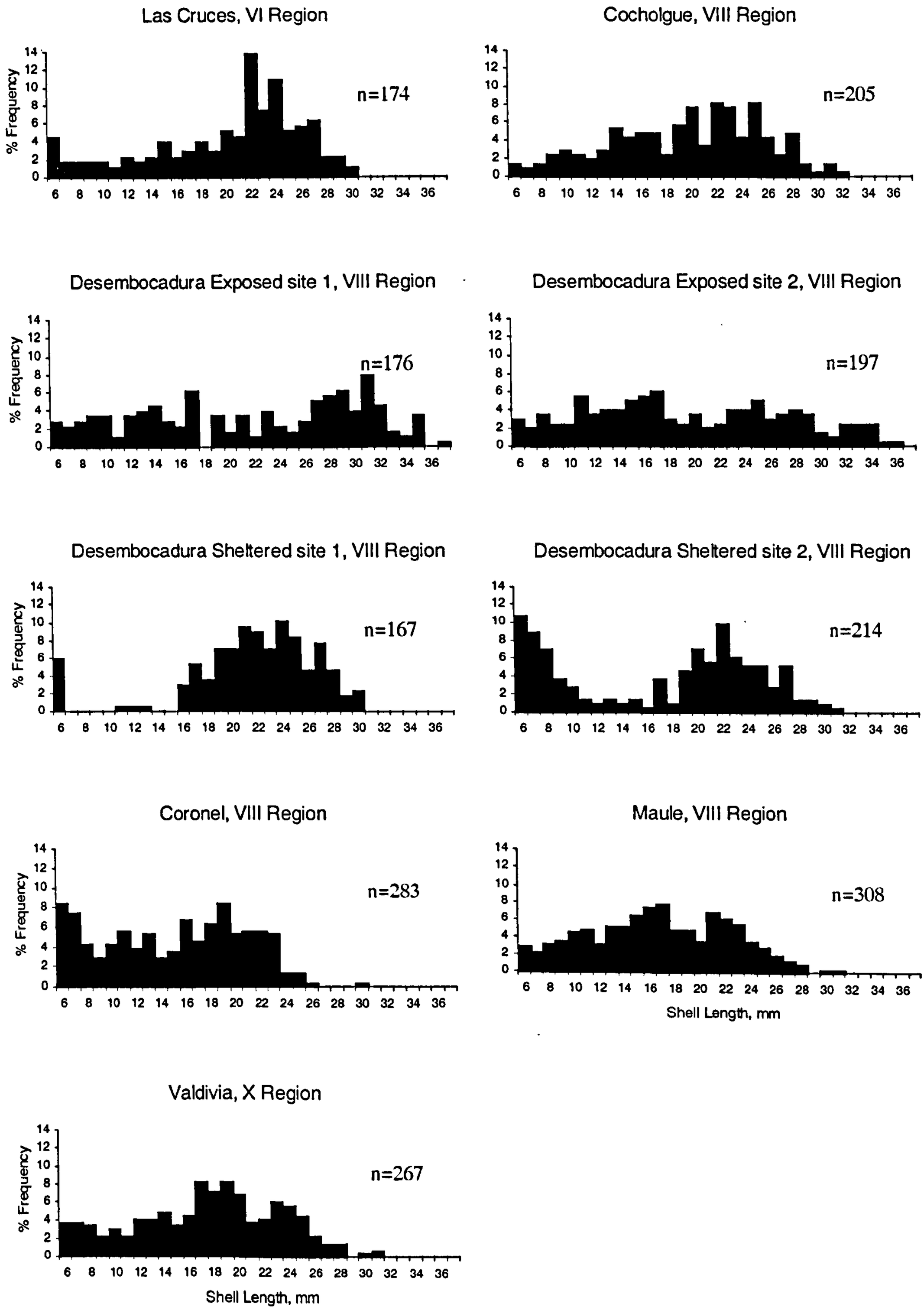


Figure 6 Size distributions of *Perumytilus purpuratus* from nine sites in Chile, South America. All mussels were collected in January 1999, with the exception of Valdivia, where mussels were collected in January 1998. Distributions are based on a mussel bed sample area of 200cm^2.

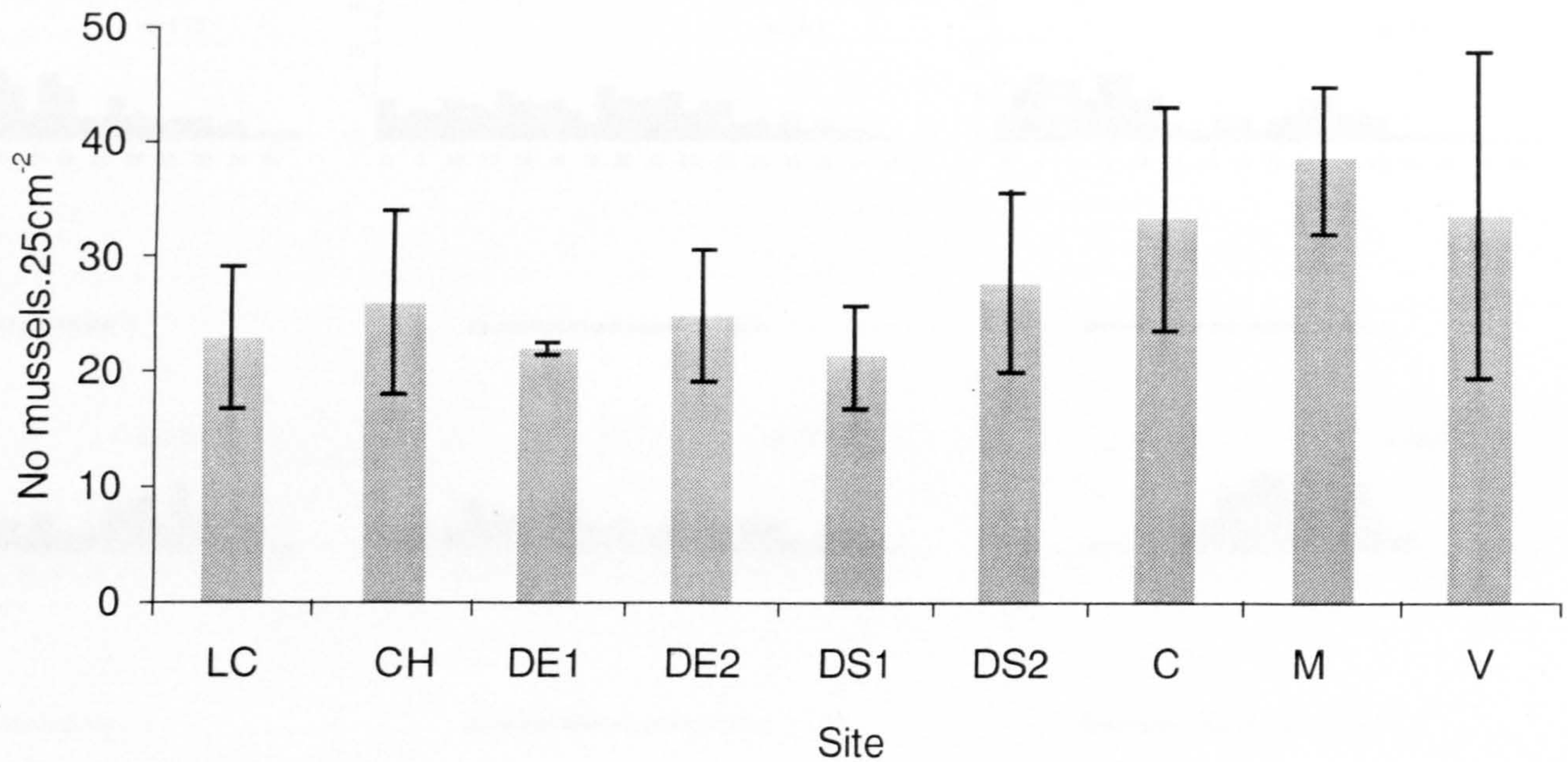


Figure 7 Mean density of *Perumytilus purpuratus*, per 25cm^2 area of mussel bed at nine sites in Chile, South America (LC = Las Cruces, VI Region; CH = Cocholgue, VIII Region; DE1 = Desembocadura exposed site 1, VIII Region; DE2 = Desembocadura exposed site 2, VIII Region; DS1 = Desembocadura sheltered site 1, VIII Region; DS2 = Desembocadura sheltered site 2, VIII Region; C = Coronel, VIII Region; M = Maule, VIII Region; V = Valdivia, X Region). 95% confidence intervals are marked, such that significant differences ($p<0.05$) are represented by non-overlapping intervals.

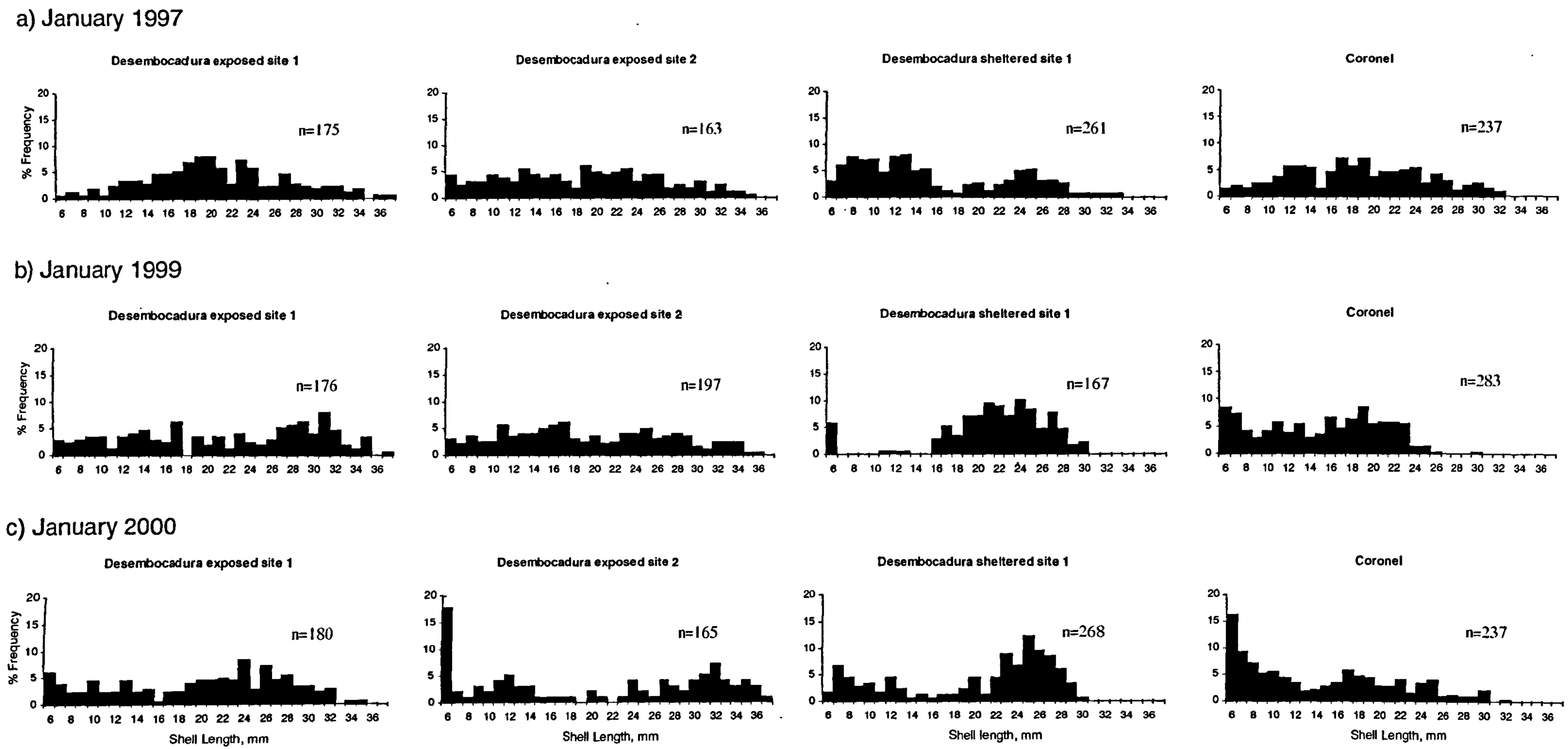


Figure 8 Size distributions of *Perumytilus purpuratus* from four sites in the VIII Region of Chile, South America; Desembocadura exposed site 1, Desembocadura exposed site 2, Desembocadura sheltered site 1 and Coronel, during a) January 1997, b) January 1999 and c) January 2000.

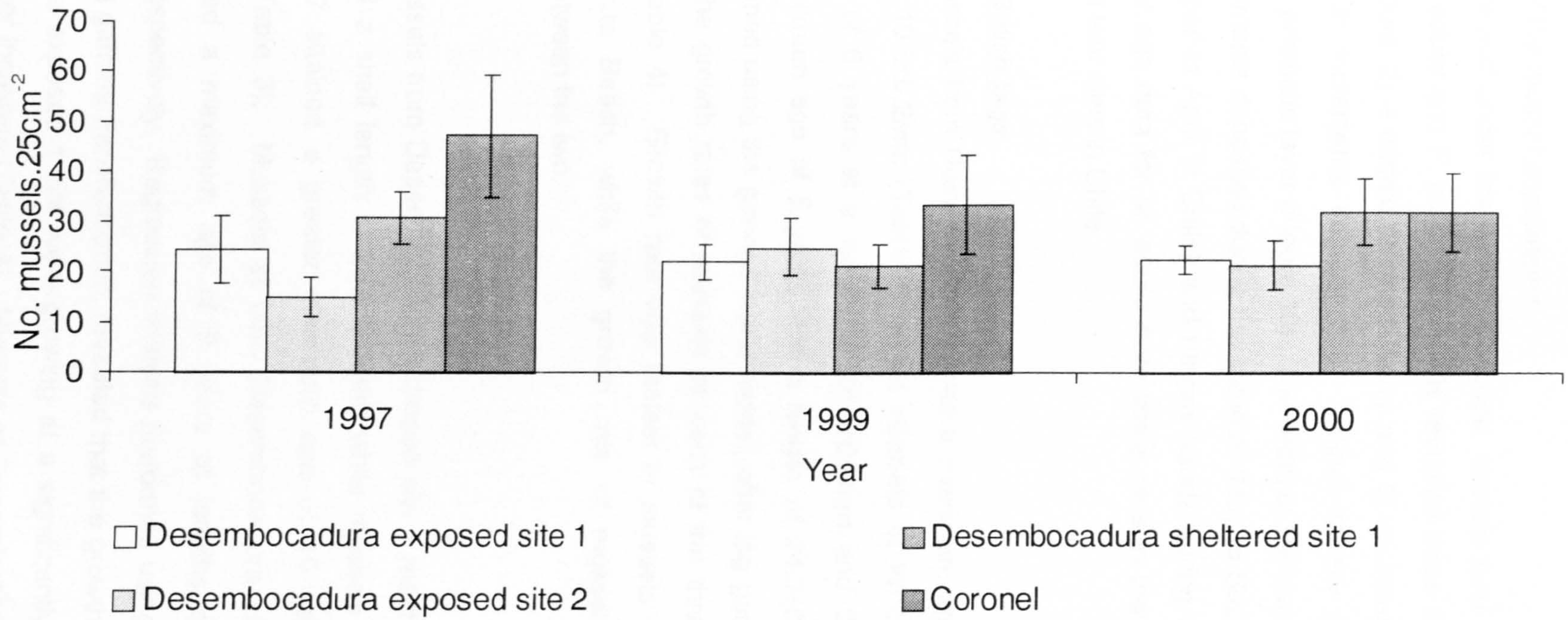


Figure 9 Mean density of *Perumytilus purpuratus*, per 25cm^2 area of mussel bed at Desembocadura exposed sites 1 and 2, sheltered site 1 and Coronel, during January 1997, 1999 and 2000. 95% confidence intervals are marked, such that significant differences ($p<0.05$) are represented by non-overlapping intervals.

mussel beds was substantially less than that of *M. edulis* in the British Isles and Irish Republic.

Age structure of the mussel populations

When viewed under the light microscope, acetate peel replicas of polished and etched *M. edulis* and *P. purpuratus* shells revealed three shell layers; 1) a thin outer periostracum, 2) a middle prismatic layer and 3) an inner nacreous layer. A series of growth increments separated by distinct narrow growth bands were observed in the prismatic layer (Figure 10). The width of the bands varied seasonally with wider increments deposited during the summer (May to September in the British Isles and October to April in Chile) and narrow bands during the winter. Table 3 contains size at age data for *M. edulis* from three sites in the British Isles and *P. purpuratus* from four sites in Chile.

Sites in the British Isles

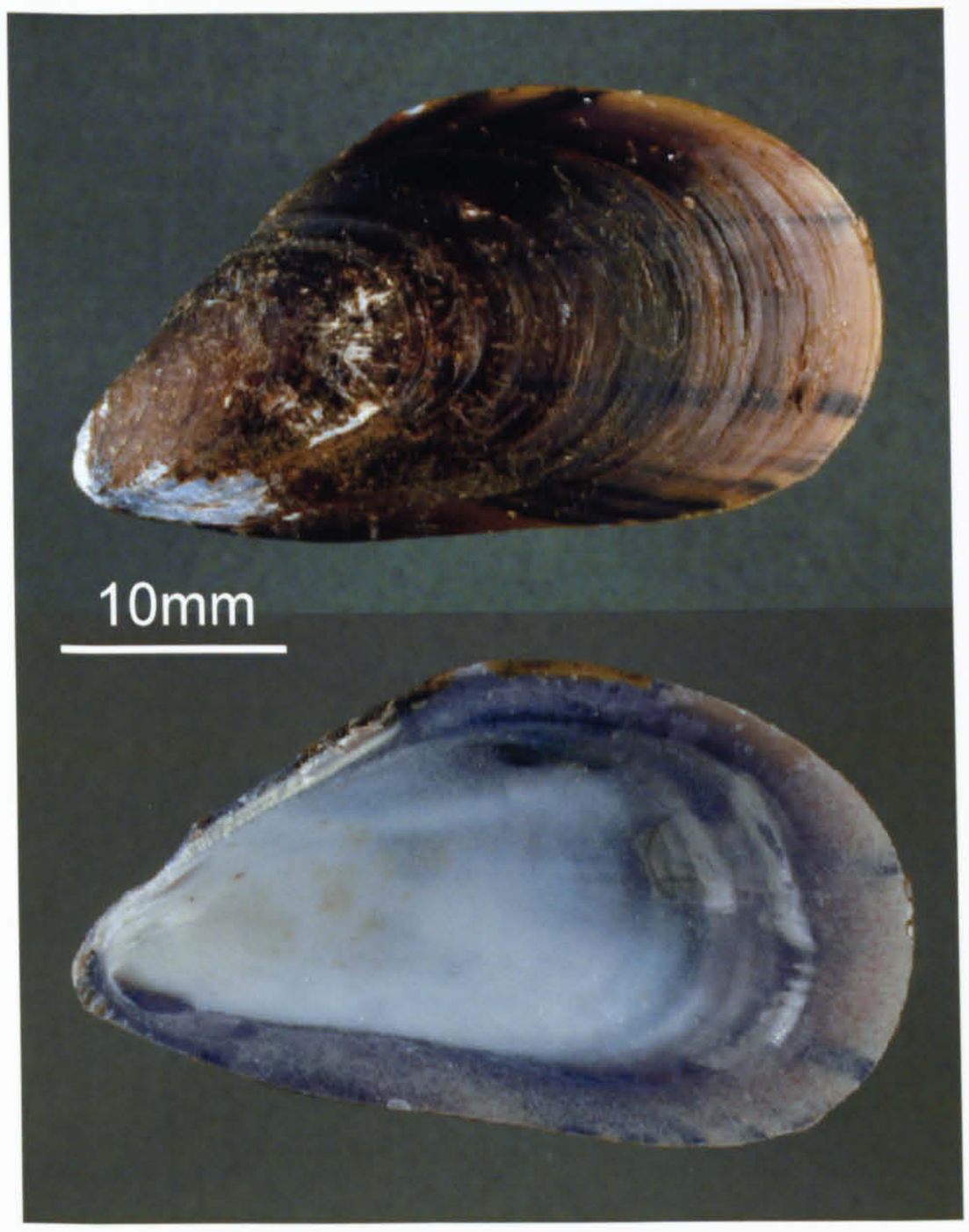
The mussels from Point Lynas reached a maximum age of 3 years and a shell length of 19.5±0.2mm (Table 3), whilst mussels at White Beach reached a maximum age of 6 years at a length of 24.6±0.5mm and those from Criccieth reached a maximum age of 5 years and a length of 24.0±0.0mm. Regression analysis performed using the general linear model, after log gamma transformation, revealed that the growth rates of mussels at each of the three locations differed significantly (Table 4). Growth rate was fastest in mussels at Point Lynas and slowest at White Beach, while the growth rate of mussels at Criccieth was intermediate between the two.

Sites in Chile

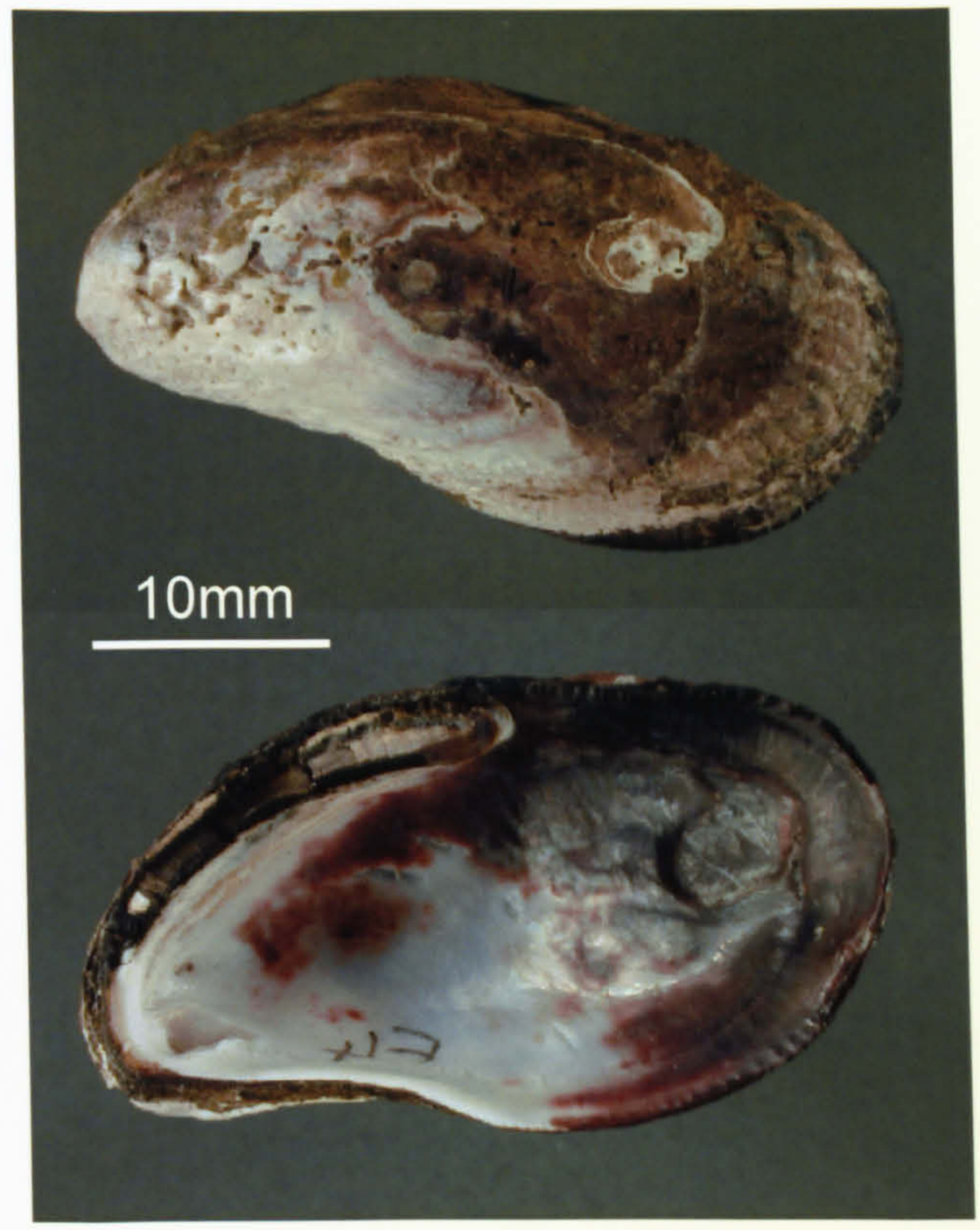
The mussels from Desembocadura exposed site 1 reached a maximum age of 8 years and a shell length of 25.2±0.8mm, while mussels at Desembocadura exposed site 2 attained a greater maximum age of 10 years at a length of 27.1±0.3mm (Table 3). Mussels at both Desembocadura sheltered site 1 and Coronel reached a maximum age of 9 years at lengths of 24.3±0.0mm and 22.3±0.0mm, respectively. Regression analysis performed using the General Linear Model, after log gamma transformation, revealed that the growth rates of mussels at Desembocadura exposed 1 site were growing at a significantly faster rate than at each of the other locations (Table 4). Mussels at Desembocadura sheltered site 1 and Coronel had a significantly slower growth rate than mussels at the other two

Figure 10 a), b) Photographs of *Mytilus edulis* and *Perumytilus purpuratus* shells, c) Photomicrograph of an acetate peel replica of *M. edulis* and *P. purpuratus* shell sections, e) Schematic diagram of a mussel shell section to illustrate the layers of the shell: p, periostracum; pl, prismatic layer; n, nacreous layer; u, umbo, f) position of a winter growth check (arrow) in the shell of *M. edulis*.

a) *Mytilus edulis* shell



b) *Perumytilus purpuratus* shell



c) *Mytilus edulis* section

d) *Perumytilus purpuratus* section

e) Schematic diagram

f) Position of winter growth check

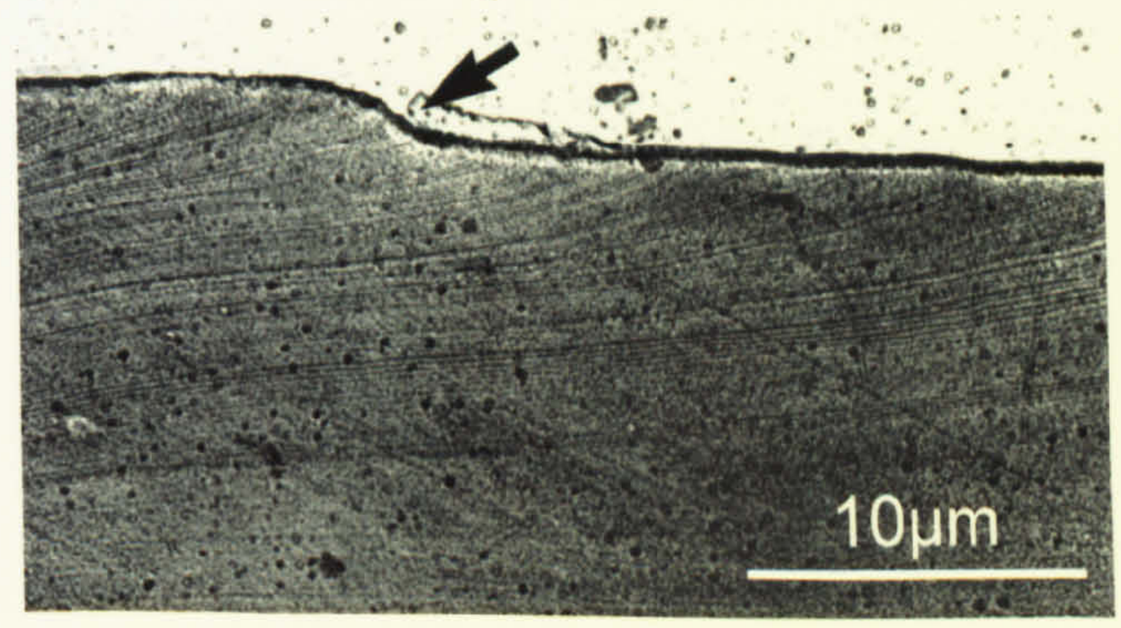


Table 3 Shell length (mm) at age (years) of *Mytilus edulis* (British Isles) and *Perumytilus purpuratus* (Chile) derived from internal growth bands.

Site	Shell length (mean±s.e.) at age									
	1	2	3	4	5	6	7	8	9	10
Point Lynas (British Isles)	7.3±0.2	13.3±0.3	19.5±0.2							
White Beach (British Isles)	7.3±0.2	11.6±0.2	15.6±0.3	19.5±0.5	22.4±0.5	24.6±0.5				
Criccieth (British Isles)	7.5±0.3	13.2±0.4	18.5±0.3	23.5±0.4	24.0±0.0					
Desembocadura exposed 1 (Chile)	4.2±0.5	8.0±0.4	11.5±0.3	14.7±0.3	17.7±0.3	20.4±0.4	22.9±0.2	25.2±0.8		
Desembocadura exposed 2 (Chile)	3.0±0.2	6.0±0.3	8.8±0.2	11.6±0.2	14.4±0.3	17.0±0.2	19.6±0.2	22.2±0.3	24.6±0.3	27.1±0.3
Desembocadura sheltered 1 (Chile)	4.8±0.3	8.8±0.4	12.3±0.2	15.2±0.2	17.6±0.3	19.7±0.2	21.5±0.2	23.0±0.1	24.3±0.0	
Coronel (Chile)	3.0±0.3	5.9±0.2	8.6±0.3	11.2±0.3	13.7±0.2	16.0±0.2	18.2±0.2	20.3±0.3	22.3±0.0	

Table 4 a) ANOVA performed between regression slopes for the growth rates of mussels and b) the departure of single regression slopes from the average slope, using the general linear model, at i) Point Lynas, White Beach and Criccieth, British Isles and ii) Desembocadura exposed site 1, Desembocadura exposed site 2, Desembocadura sheltered site 1 and Coronel, Chile.

a)
i)

Source	DF	SS	MS	F	p
Age	1	2240.3	2240.3	2825.3	<0.05
Site	2	16.1	8.05	10.2	<0.05
Age*Site	2	133.7	66.8	84.3	<0.05
Error	8	6.3	0.8		
Total	13				

ii)

Source	DF	SS	MS	F	p
Age	1	10372.8	10372.8	5027.88	<0.05
Site	3	69.8	23.3	11.28	<0.05
Age*Site	3	104.1	34.7	16.82	<0.05
Error	28	57.8	2.1		
Total	35				

b)
i)

Term of Regression	Coefficient	Standard deviation	t-value	p
Constant	-5.5469	0.6155	-9.01	<0.05
Age	12.7898	0.2406	53.15	<0.05
Age*Site				
Point Lynas	2.5748	0.4360	5.91	<0.05
White Beach	-3.2458	0.2702	-12.01	<0.05
Criccieth	0.6709	0.2904	2.31	0.05

ii)

Term of Regression	Coefficient	Standard deviation	t-value	P
Constant	-5.9787	0.5240	-11.41	<0.05
Age	6.7010	0.0945	70.91	<0.05
Age*Site				
Desembocadura exposed site 1	1.0703	0.1830	5.85	<0.05
Desembocadura exposed site 2	0.1910	0.1464	1.30	0.20
Desembocadura sheltered site 1	-0.4040	0.1616	-2.50	<0.05
Coronel	-0.8573	0.1616	-5.30	<0.05

sites, while the growth rate of mussels at Desembocadura exposed site 2 was intermediate between the other sites. Regression analysis performed using the general linear model, revealed that growth rates of *M. edulis* at locations in the UK were significantly greater than for *P. purpuratus* at locations in Chile (Table 5).

Species composition of communities associated with mussel populations

Sites in the British Isles and Irish Republic

Between January 1998 and July 1999, a total of 87 taxa were identified from mussel beds at Point Lynas, with 94 at White Beach and 94 at Criccieth (Table 6). At Point Lynas, the most numerically abundant taxa were nematodes, nemerteans, mites, *Clunio* sp. larvae, bivalves (predominantly juvenile mussels) and various small species of gastropods. At White Beach the dominant taxa were nematodes, *Clunio* sp. larvae, bivalves (predominantly small mussels) and various crustaceans including ostracods, barnacles, isopods, amphipods, tanaids and crabs. The community at Criccieth was characterised by nematodes, *Clunio* sp. larvae, isopods, barnacles, bivalves (predominantly small mussels) and various polychaete species. A more detailed analysis of the invertebrate communities associated with each of the mussel populations is provided in later chapters.

During the summer of 1999 (June and July), 29 taxa were associated with the mussel population at Arisaig, with 43 at Kilkee, 35 at Doonbeg, 52 at Robin Hood's Bay and 46 at Filey Brigg (Table 6). During the summer of 1999 at the three main study sites in Wales, 36 taxa were identified at Point Lynas, 28 at White Beach and 39 at Criccieth during July 1999. The invertebrate communities associated with mussel populations at the different locations in the UK were dominated to varying degrees, by taxa including nematodes, bivalves, gastropods, insects (mainly *Clunio* sp. larvae) and mites (Figure 11). Bivalves (mainly juvenile mussels) dominated mussel communities from all sites, while many of the dominant taxa varied in abundance and identity between sites (e.g. ostracods, isopods, and insects). Other taxa, such as nemerteans, gastropods and mites were found in consistently high numbers at all or most of the sites.

Sites in Chile

Identification of infaunal associates of *P. purpuratus* was only carried out to relatively broad taxonomic categories, since taxonomic keys to most of the species were not available, and many of the species present in the samples had not been previously described. In addition, time was a limiting factor during this study, so to reduce sorting times and enable a greater volume of material to be processed;

Table 5 a) ANOVA performed between regression slopes for the growth rates of *Mytilus edulis* at 3 sites in the British Isles (Point Lynas, White Beach and Criccieth) and *Perumytilus purpuratus* at four sites in Chile (Desembocadura exposed site 1, Desembocadura exposed site 2, Desembocadura sheltered site 1 and Coronel), using the general linear model; b) the departure of single regression slopes, representing growth rates, from the average slope.

a)

Source	DF	SS	MS	F	p
Age	1	5847.4	5847.4	3283.57	<0.05
Site	6	90.1	15.0	8.43	<0.05
Age*Site	6	801.2	133.5	74.99	<0.05
Error	36	64.1	1.8		
Total	49				

b)

Country	Term of regression	Coefficient	Standard deviation	t-value	p
	Constant	-5.7937	0.4834	-11.99	<0.05
	Age	9.3105	0.1625	57.30	<0.05
	Age*Site				
British Isles	Point Lynas	6.0541	0.8139	7.44	<0.05
	White Beach	0.2336	0.3148	0.74	>0.05
	Criccieth	4.1502	0.3919	10.59	<0.05
Chile	Desembocadura exposed 1	-1.5392	0.2381	-6.49	<0.05
	Desembocadura exposed 2	-2.4185	0.2045	-11.83	<0.05
	Desembocadura sheltered site 1	-3.0134	0.2182	-13.81	<0.05
	Coronel	-3.4668	0.2182	-15.89	<0.05

Table 6 List of taxa identified from mussel beds at each of the study sites in the British Isles and Irish Republic, throughout the entire study period (PL, Point Lynas; WB, White Beach; C, Criccieth; A, Arisaig, K, Kilkee; D, Doonbeg; RHB, Robin Hood's Bay; FB, Filey Brigg). Taxa are listed alphabetically within main taxonomic groupings. Taxa at Point Lynas, White Beach and Criccieth marked *, were present in samples collected during July 1999, as part of the study of large-scale spatial variation in the structure of mussel communities.

TAXA	PL	WB	C	A	K	D	RHB	FB
FORAMINIFERANS								
Foraminifera indet.	• *	• *	• *					
ANEMONES								
Actinia equina	•	•	•					
Actinia fragacea			•					
Anthopleura balli	•	•						
Stomphia coccinea	•	•	•					
White anemone							•	•
PLATYHELMINTHES								
Platyhelminthe indet.	•	•	• *	•				
NEMATODES								
Nematoda indet.	• *	• *	• *	•	•	•	•	•
NEMERTEANS								
Nemertea indet.	• *	• *	• *	•	•	•	•	•
Amphiporidae indet.	•	•						
Cephalothricidae indet.	•	•	•					
Emplectonematidae indet.	•	•	•					
Lineidae indet.	•	•	•					
Tetrastemmatidae indet.	•	•	•					
Tubulanidae indet.	•	•	•					
POLYCHAETES								
Alentia gelatinosa			•					
Amblyosyllis formosa		•	•					
Anaitides maculata	•		•					
Aphelochaeta marioni	•							
Brania pusilla		• *			•			
Capitella capitata			• *				•	
Capitella sp.					•			
Cirratulus cirratus	• *	•	• *		•	•		
Cirratulus filiformis	•	•	•					
Cirriformia tentaculata	•	•	•					
Drilonereis filum	•	•	•		•	•		
Eulalia viridis	•	•	• *	•	•	•	•	•
Eumidia sanguinea			•					
Eunicid sp. 1		•						
Eunicid sp. 2	•							

TAXA	PL	WB	C	A	K	D	RHB	FB
Eusyllis blomstrandi							●	●
Fabricia stellaris	● *	● *			●	●	●	
Harmothoe sp.	●	●	●				●	●
Harmothoe extenuata		●	● *					
Lepidontus clava	●		●					
Lepidontus squamata	●		●					
Lumbrineris spp.			●					
Maldanidae spp.		●			●		●	
Neanthes furcata			●					
Nepthys hombergii								●
Nepthys sp.							●	
Odontosyllis sp.	●		●					
Ophelia bicornis	●	●	●					
Ophelia rathkei	●	●	●	●	●			
Paralaeospira malardi		●						
Perinereis cultrifera			●					
Pherusa plumosa							●	●
Pholoe inoculata							●	●
Pholoe inornata								●
Phyllodocid sp.		●						
Polydora ciliata		●						
Polychaete indet.								
Polychaete larvae indet.		●						
Pomatoceros triqueter								●
Scolelepis squamata	● *	●	● *			●	●	●
Scoloplos armiger			●					
Spirorbis spirorbis	● *							●
Syllid sp. 1		●						
Syllid sp. 2		●			●			
Typosyllis prolifera		●	●	●	●	●		
Typosyllis sp.		●						
OLIGOCHAETES								
Oligochaeta indet.	● *	● *	● *	●	●	●	●	●
SIPHUNCULIDS								
Golfingia vulgaris	● *							
OSTRACODS								
Heterocythere albomaculata	● *	● *	● *		●	●	●	●
Leptocythere pellucida	●	● *	● *		●	●		●
Semicytherura nigrescens		●	● *					
Ostracod sp. 4		● *						

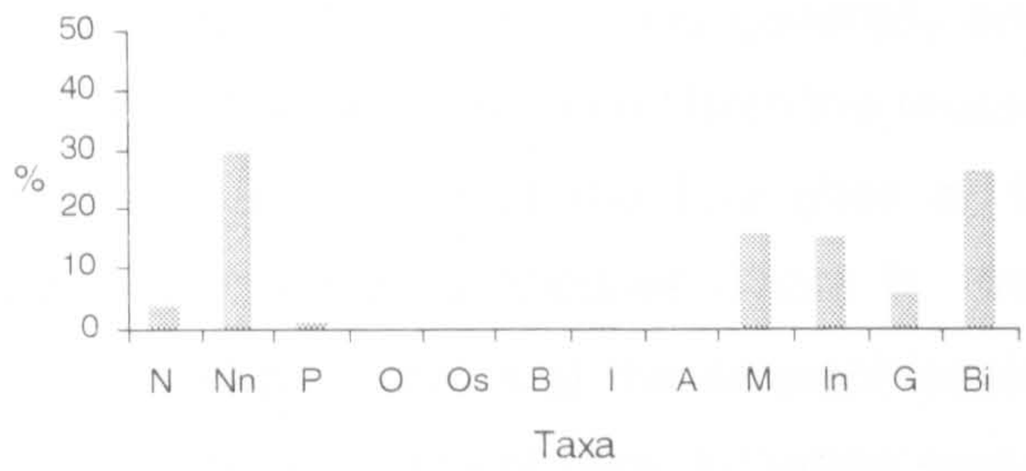
TAXA	PL	WB	C	A	K	D	RHB	FB
BARNACLES								
Chthamalus montagui		●	● *	●	●		●	●
Elminius modestus	● *	● *	● *	●			●	●
Semibalanus balanoides		●	● *	●			●	●
Juvenile barnacles indet.				●				
TANAIDS								
Tanais dulongii	● *	●		●	●	●		
ISOPODS								
Idotea baltica	●	●	●					
Idotea chelipes	●	●						
Idotea emarginata			●					
Idotea granulosa	● *		●					
Idotea linearis		●						
Idotea neglecta		●						
Idotea pelagica	● *	● *	● *	●			●	●
Jaera albifrons	● *	● *	● *	●	●	●	●	●
Jaera marina		●						
Jaera nordmanni							●	
Janira maculosa		●						
Janiropsis breviremis	●	●	●					
AMPHIPODS								
Abludomelita obtusata		●						
Atylus swammerdami								
Calliopius laeviusculus	●	●						
Echinogammarus marinus	●	● *						
Ericthonius punctatus		●	●					
Hyale prevostii	●	●	● *	●	●	●	●	●
Iphimedia minuta	●		●					
Iphimedia obesa			●					
Jassa falcata								●
Orchestia gammarellus		●		●				
Parajassa pelagica	●							
Pontocrates altamarinus			●					
Stenothoe monoculoides		●						
Sunamphitoe pelagica		● *						
DECAPODS								
Cancer pagurus	● *							
Carcinus maenas	● *	● *	● *			●	●	●
Crab larvae indet.		●						
Necora puber	●							
Pilumnus hirtellus	●	●	●				●	
Pinnotheres pisum	●	●						

TAXA	PL	WB	C	A	K	D	RHB	FB
MITES								
Mite sp. 1	● *	● *	● *	●	●	●	●	●
Mite sp. 2	●	●	● *	●	●		●	
Mite sp. 3	●	● *	● *	●		●	●	
Mite sp. 4	●		●					
Mite sp. 5	● *	●	● *			●		
Mite sp. 6								
Mite sp. 7		●		●	●		●	●
Mite sp. 8	●	●	●					
Mite sp. 9		●						
Mite sp. 10	●	●						
Mite sp. 11	●					●	●	●
Mite sp. 12		●						
INSECTS								
Clunio sp. larvae indet.	● *	● *	● *	●	●	●	●	●
Dipteran larvae indet.	● *	●	● *		●	●		
Anurida maritima	● *							
Petrobius marinus			●					
CHITONS								
Acanthochitona crinata			●					
Lepidochitona asellus			● *					
Lepidochitona cinerea			●					
Acanthocardia echinata							●	●
BIVALVES								
Angulus tenuis		●						
Arca tetragona							●	●
Chlamys varia	●							
Epilepton clarkiae							●	
Hiatella arctica							●	●
Lasaea adansoni	● *	● *	● *	●	●	●		
Modiolula phaseolina		● *	● *		●	●	●	●
Mytilus edulis	● *	● *	● *	●	●	●	●	●
Tellina spp.							●	
Turtonia minuta	● *		●					
Venerupis rhomboides					●			
Venerupis saxatilis							●	
Venerupis senegalensis					●			
GASTROPODS								
Alvania beani						●	●	
Alvania punctura			●					
Barleeia unifasciata			●					
Brachystomia scalaris	● *	● *	● *		●		●	●

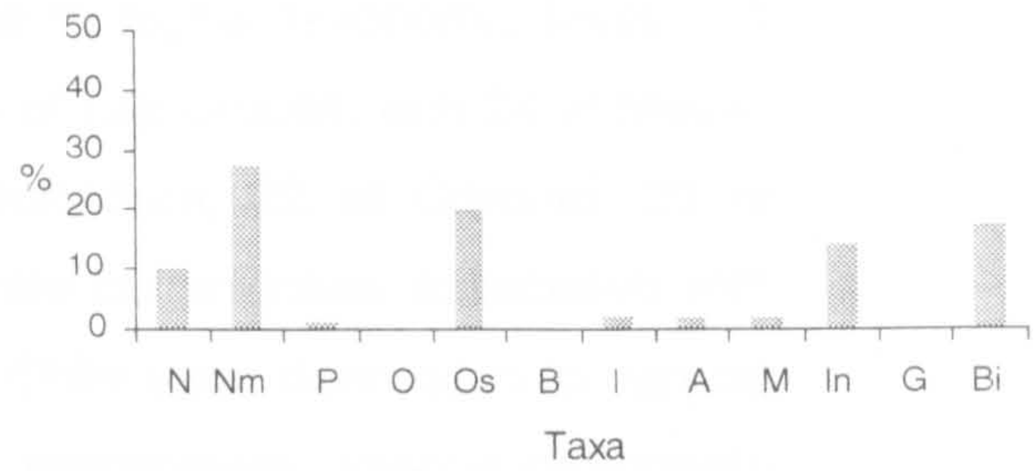
TAXA	PL	WB	C	A	K	D	RHB	FB
Buccinum undatum	●		●					
Cerithiopsis tubercularis			●		●			
Chauvetia brunnea			●					
Chrysallida interstincta	●							
Cingula cingullus	●							
Coriandria fulgida			● *		●	●		●
Eatonina fulgida	● *							
Epitonium clathrus					●		●	●
Eulimella laevis			●					
Gibbula magus			● *					
Hydrobia ulvae	●	●						
Juvenile gastropods indet.	● *	●	● *		●	●	●	●
Lacuna pallidula						●	●	●
Lacuna parva							●	
Lacuna vincta	● *							●
Limapontia depressa	● *			●			●	●
Littorina littorea	●		●					
Littorina mariae	● *				●			
Littorina neglecta			● *					
Littorina obtusata			●					
Littorina rudis	● *	●	● *			●		
Manzonia crassa		●						
Nucella lapillus	● *	● *	●	●	●	●	●	●
Obtusella intersecta	●							
Ocinebrina edwardsi		●						
Omalogyra atomus					●			
Ondina diaphina			●					
Onoba semicostata	● *	● *	● *		●		●	●
Patella ulyssiponensis			●					
Patella vulgata	●	● *		●		●		
Propilidium exiguum					●			
Rissoa membranacea			●					
Rissoa parva	● *	•	●	●	●	●	●	●
Rissoa violacea			●					●
Rissoella opalina		● *	● *				●	
Skenea serpuloides	●	● *	● *	●	●	●	●	●
Skeneopsis planorbis					●	●	●	
Tectura testudinalis	●	●			●		●	
Tricolia pullus				●		●		
ECHINODERMS								
Amphiura chiajei								●
Ophiothrix fragilis	● *							
TOTAL TAXA	87	94	94	29	43	35	52	46

Figure 11 Abundance of main taxa in the mussel beds at eight sites in the British Isles and Irish Republic during the summer of 1999. Taxa are restricted to those contributing to >5% of individuals present in the community at at least one of the eight sites.

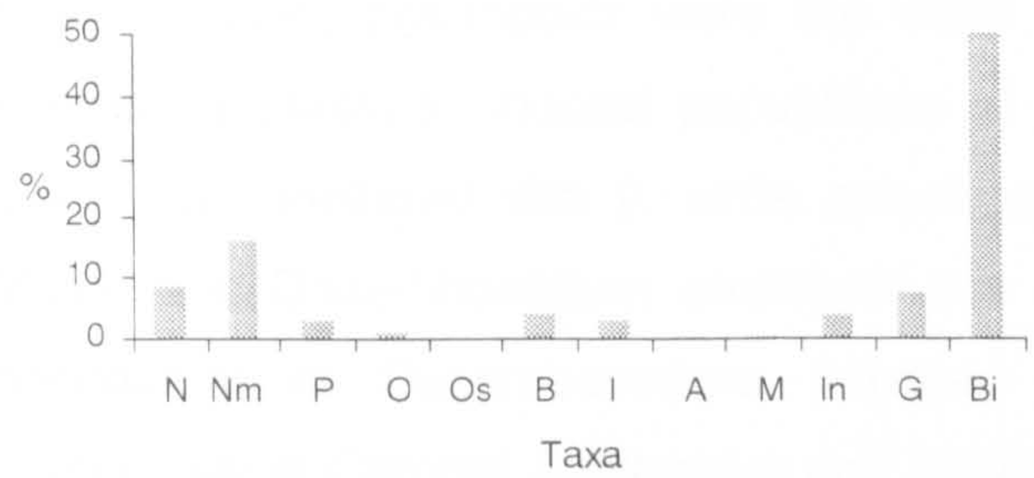
Point Lynas, Wales



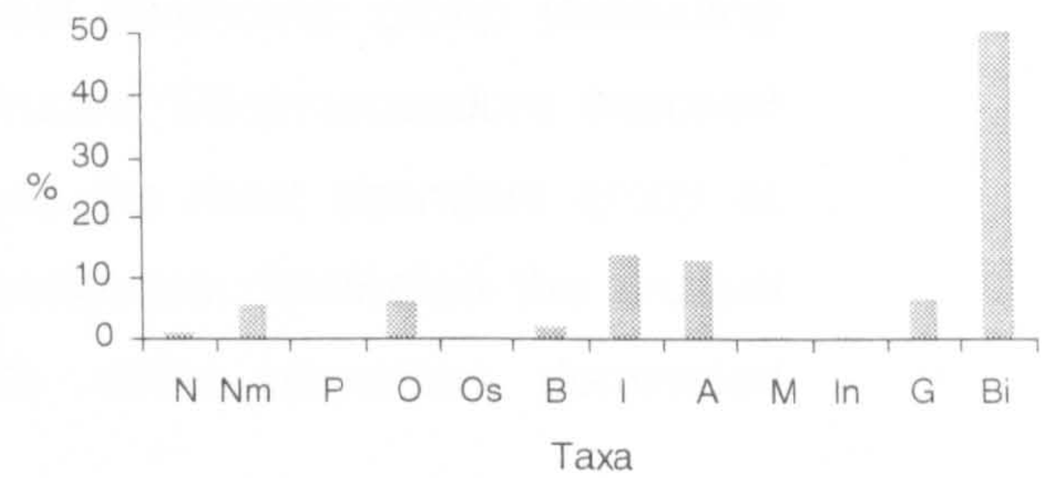
White Beach, Wales



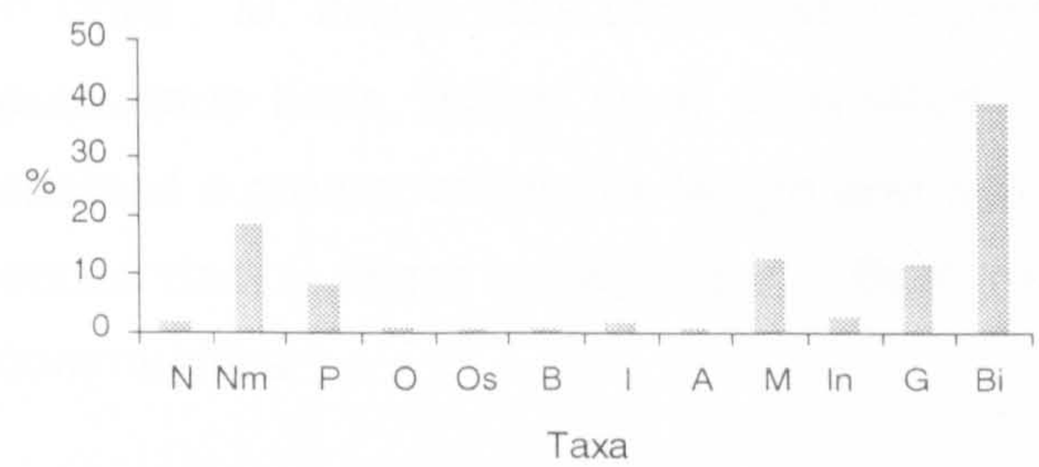
Criccieth, Wales



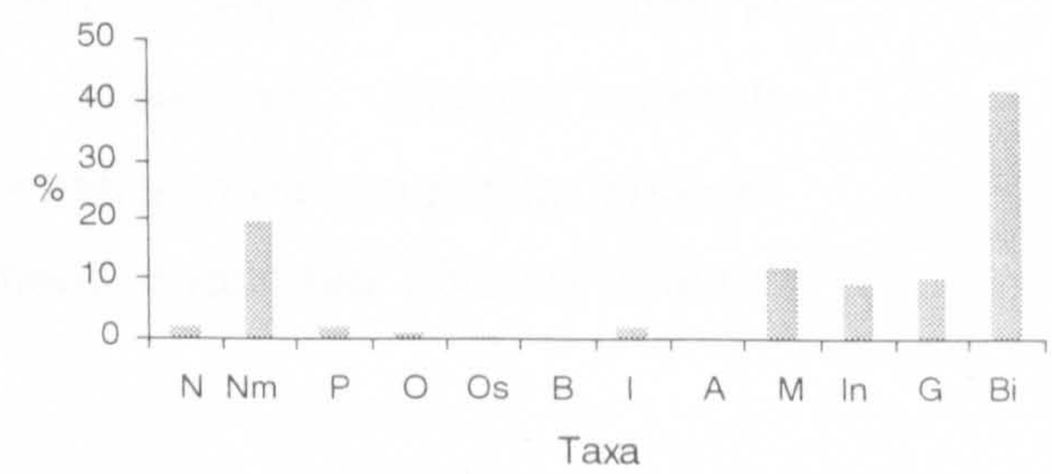
Arisaig, Scotland



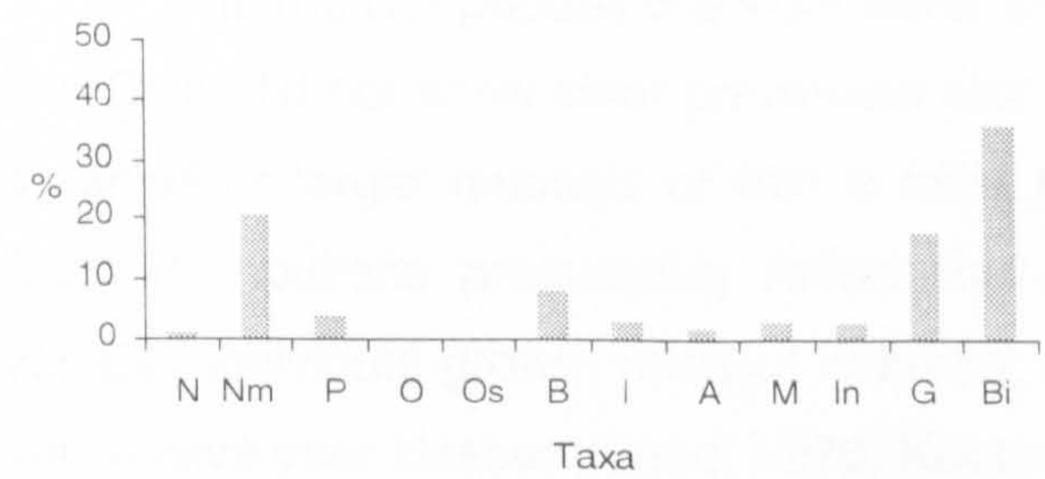
Kilkee, Irish Republic



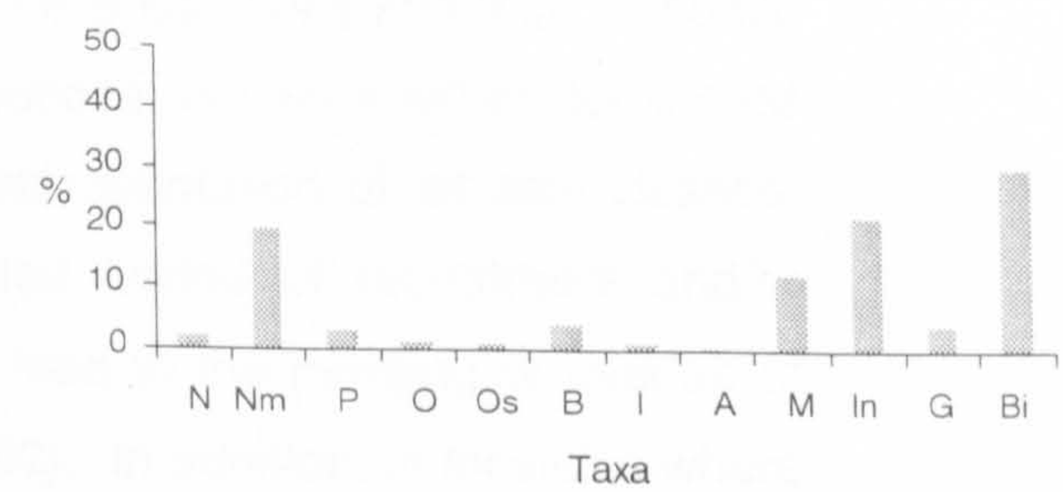
Doonbeg, Irish Republic



Filey Brigg, England



Robin Hood's Bay, England



Taxa Key

N	Nematodes	I	Isopods
Nm	Nemerteans	A	Amphipods
P	Polychaetes	M	Mites
O	Oligochaetes	In	Insects
Os	Ostracods	G	Gastropods
B	Barnacles	Bi	Bivalves

identification of organisms was generally only made to higher taxonomic levels. A total of 21 taxa were identified from the mussel beds at Las Cruces, with 24 at Maule, between 19 and 29 at the four sites at Desembocadura, 22 at Coronel, 20 at Cocholgue and 21 at Valdivia (Table 7). Invertebrate communities associated with the mussel populations at the different locations in Chile were dominated to varying degrees, by a variety of taxa, including nematodes, nemerteans, various polychaete families, oligochaetes, barnacles, isopods, amphipods, crabs, gastropods and juvenile mussels (Figure 12). The dominant taxonomic groups varied greatly between sites; gastropods were the most abundant taxonomic group (excluding juvenile mussels) in mussel populations at Las Cruces, Desembocadura exposed site 1 and sheltered site 2, while polychaetes were the most abundant group at Maule and Desembocadura sheltered site 1. Nematodes dominated the mussel community at Desembocadura exposed site 2, while barnacles dominated numerically at Coronel, Cocholgue and Valdivia.

In summary, intersite differences were observed in the size structure and growth rate of both *M. edulis* in the British Isles and Irish Republic and *P. purpuratus* in Chile. *M. edulis* beds contained a higher proportion of smaller mussels than *P. purpuratus* beds, which were dominated by larger individuals. Chilean mussels attained a greater maximum length and age than British and Irish mussels, while *M. edulis* had a faster growth rate. Both mussel beds supported diverse infaunal communities.

DISCUSSION

Size structure of mussel populations

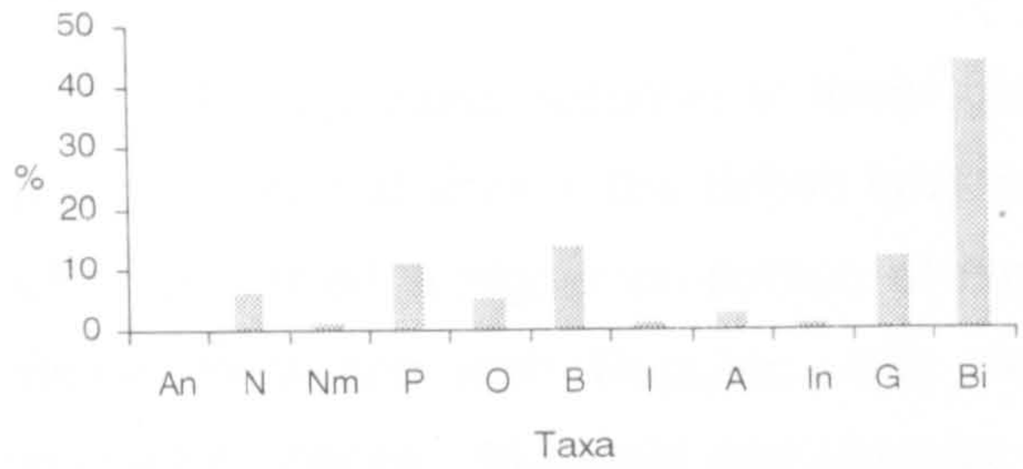
The mussel populations from study sites in the British Isles and Irish Republic and Chile did not show clear polymodal size distributions, but were either dominated by small or larger mussels or had a fairly even representation of all size classes. Such distributions presumably reflect the extended period of recruitment and/or variable individual growth rates of mussels, which lead to the merging or overlap of successive year classes (Seed, 1976; Kautsky, 1982). In addition, in localities where the life expectancy of mussels is increased due to the absence of predators, a high incidence of old individuals occurs, whereas in populations in which the mussel turnover is more rapid there is a preponderance of relatively young mussels (Seed, 1968). Despite some intersite differences, the size-frequency distributions of *M. edulis* and *P. purpuratus* were broadly similar across all sites within the British Isles and Irish Republic and in Chile, respectively. It would thus appear that, in terms of size structure alone, mussel populations within the British Isles and Irish Republic

Table 7 List of taxa identified from mussel beds at each of the study sites in Chile throughout the entire study period (LC, Las Cruces; M, Maule; DE1, Desembocadura Exposed site 1; DE2, Desembocadura Exposed site; DS1, Desembocadura Sheltered site 1; DS2, Desembocadura Sheltered site 2; C, Coronel; CH, Cocholgue; V, Valdivia).

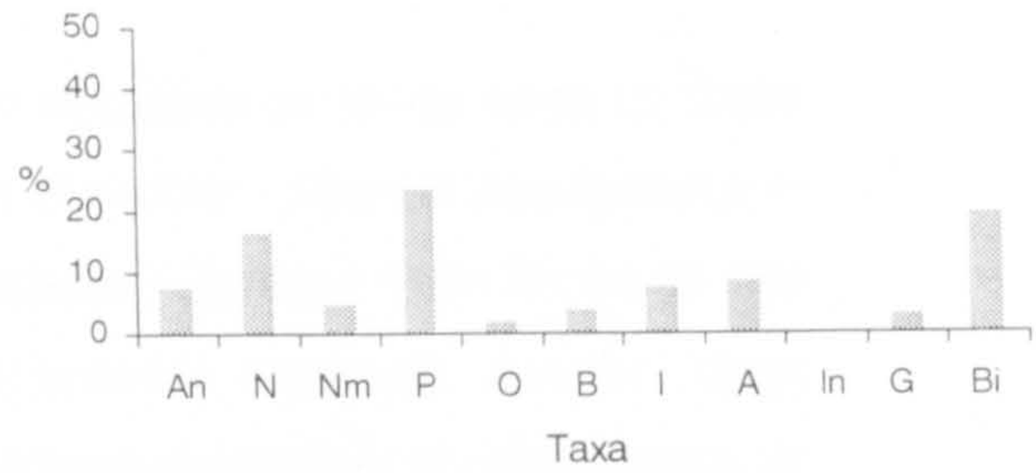
TAXA	LC	M	DE1	DE2	DS1	DS2	C	CH	V
Anemones indet.		•	•	•	•	•	•	•	•
Turbellaria indet.	•	•	•	•	•	•	•	•	•
Nemertea indet.	•	•	•	•	•	•	•	•	•
Nematoda indet.	•	•	•	•	•	•	•	•	•
Aphroditidae polychaetes		•		•	•	•			
Cirratulidae polychaetes	•	•	•	•	•		•		
Eunicidae polychaetes	•	•	•	•	•	•	•	•	
Hesionidae polychaetes			•	•	•				
Nepthydae polychaetes			•						
Nereidae polychaetes	•	•	•	•	•	•	•	•	•
Ophelidae polychaetes		•							•
Orbinidae polychaetes						•		•	
Phyllodocidae polychaetes		•	•	•		•			
Spionidae polychaetes	•	•	•	•	•	•	•	•	•
Syllidae polychaetes	•	•	•	•	•	•	•	•	•
Terebellidae polychaetes			•	•					
Spirorbidae polychaetes									•
Oligochaeta indet.	•	•	•	•	•	•	•	•	•
Ostracoda indet.	•								•
Barnacles indet.	•	•	•	•	•	•	•	•	•
Tanais sp.	•	•	•	•				•	
Isopoda indet.	•	•	•	•	•	•	•	•	•
Amphipoda indet.	•	•	•	•	•	•	•	•	•
Crabs	•	•	•	•	•	•	•	•	•
Spiders	•								
Mites	•		•	•			•	•	•
Sea spiders		•	•	•			•		
Chironomidae larvae	•	•	•	•	•		•	•	•
Insects indet.			•	•					•
Chitons		•	•	•	•		•	•	
Limpets	•	•	•	•	•	•	•	•	•
Gastropoda indet.		•	•	•	•	•	•		
Juvenile mussels	•	•	•	•	•	•	•	•	•
Bivalves indet.	•		•	•	•		•		•
Ophiuroids			•						
Total Taxa	21	24	29	28	22	19	22	20	21

Figure 12 Abundance of main taxa in the mussel beds at nine sites Chile during the Austral summer of 1999. Taxa are restricted to those contributing to >5% of individuals present in the community at at least one of the nine sites.

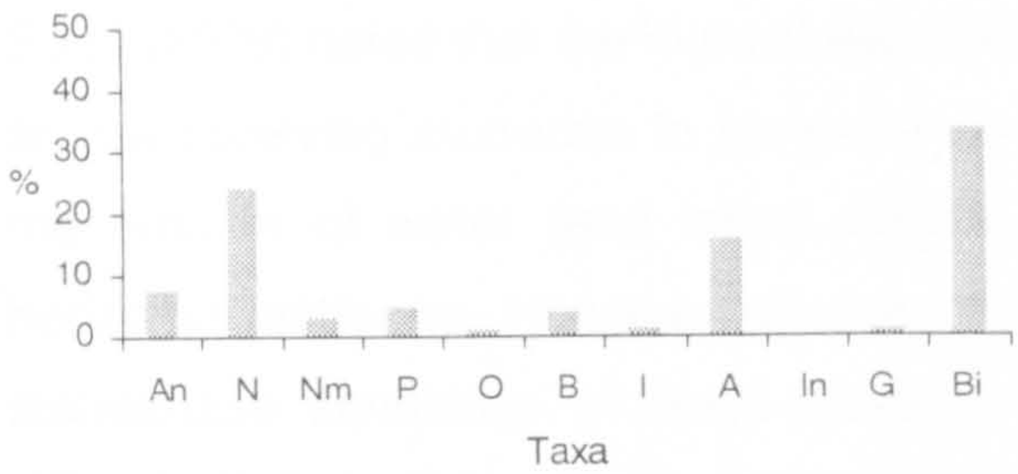
Las Cruces, VI Region



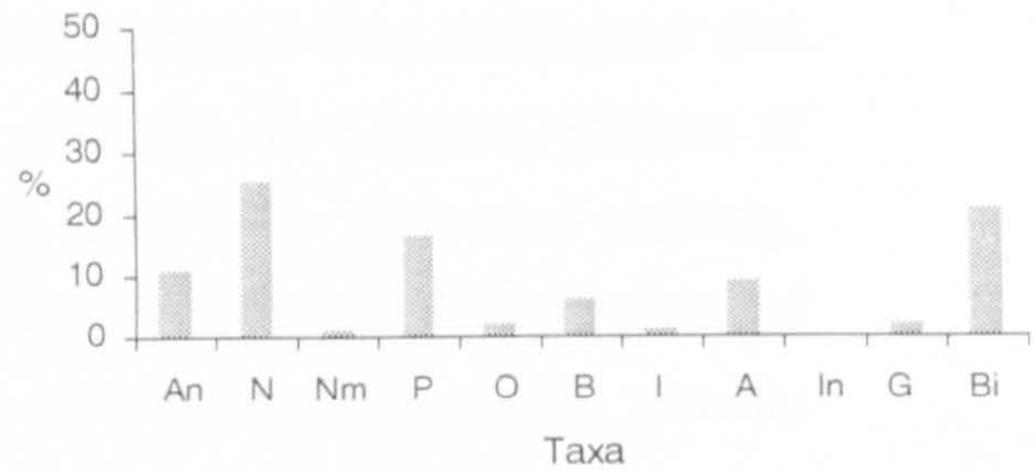
Maule, VIII Region



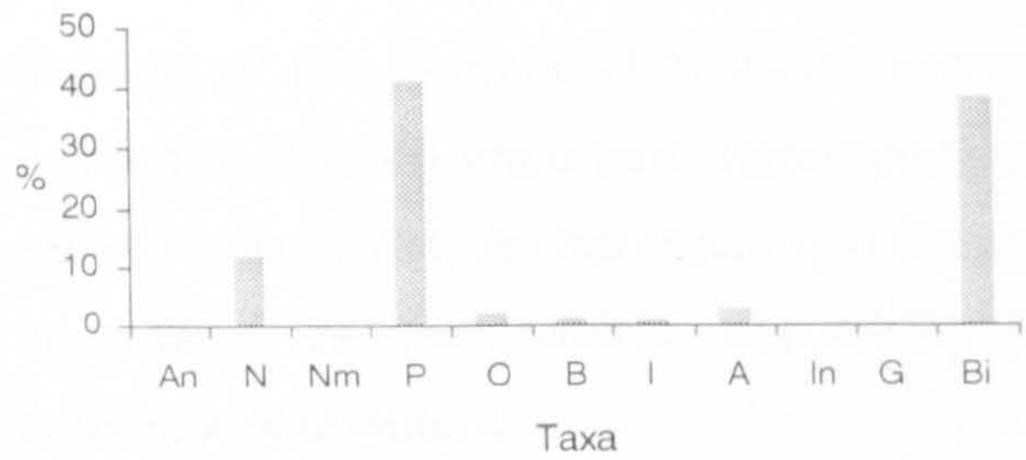
Desembocadura Exposed site 1, VIII Region



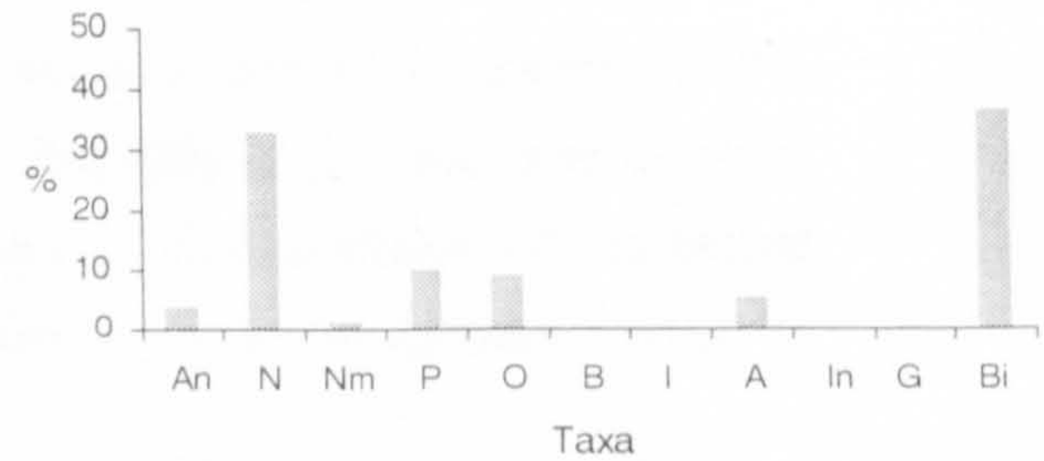
Desembocadura Exposed site 2, VIII Region



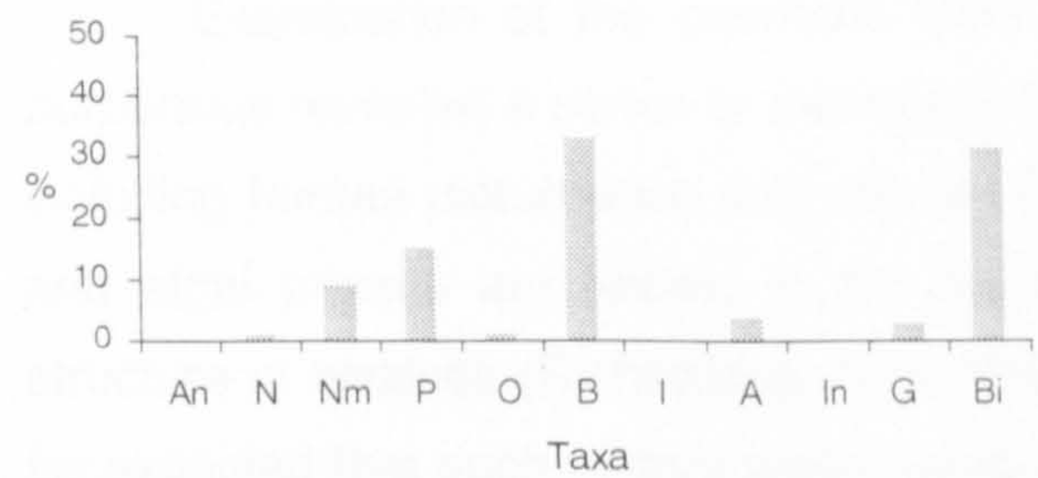
Desembocadura Sheltered site 1, VIII Region



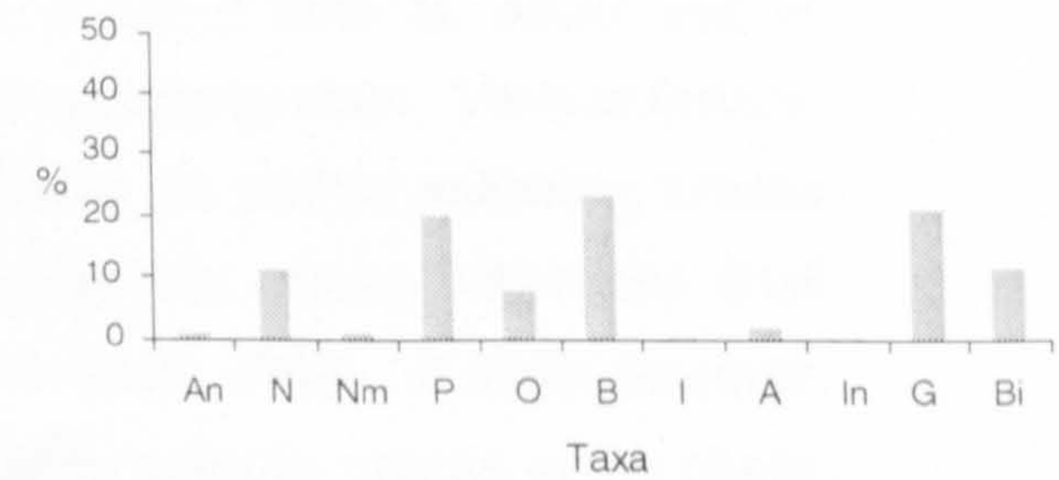
Desembocadura Sheltered site 2, VIII Region



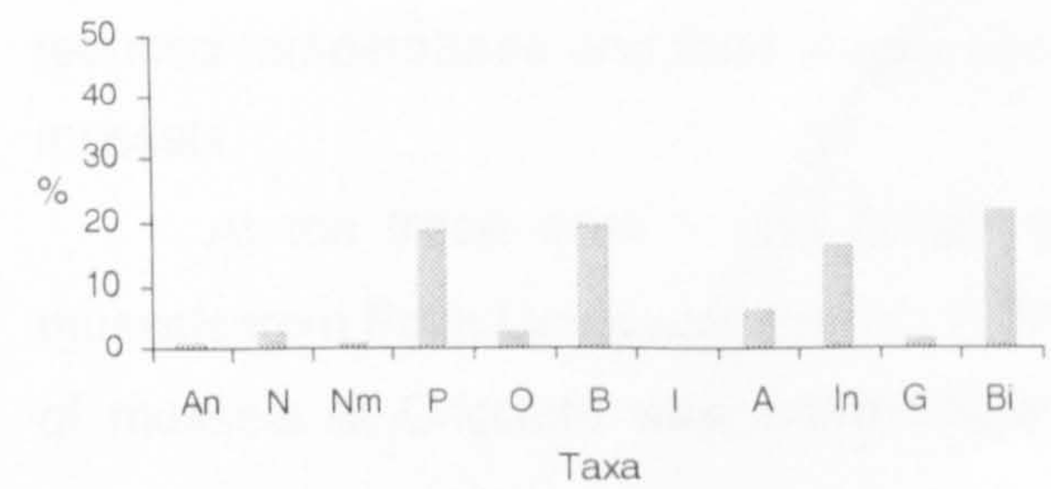
Coronel, VIII Region



Cocholgue, VIII Region



Valdivia, X Region



Taxa Key

An	Anemones	I	Insects
N	Nematodes	A	Amphipods
Nm	Nemerteans	In	Insects
P	Polychaetes	G	Gastropods
O	Oligochaetes	Bi	Bivalves
B	Barnacles		

and Chile, provide a habitat similar in structural complexity for species colonisation at all sites.

P. purpuratus occurred in lower population densities at study sites in Chile than *M. edulis* at sites in the British Isles and Irish Republic. Mussel populations in Chile contained a higher proportion of larger mussels (>20mm) than those in the British Isles and Irish Republic, with very few smaller mussels, despite large interstitial spaces. McQuaid and Lindsay (2000) found in studies of populations of *Perna perna* around the South African coastline, that wave-exposed shores supported larger mussels and had higher mortality rates than sheltered shores. Seed (1968) noted that the highest densities of mussels tended to be associated with shores receiving moderate to severe wave action, probably as a direct influence of the amount of water (and larval stages) passing over them and slow draining, horizontal platforms. However, effort was made during the selection of study sites, to standardise conditions of wave-exposure. It is unlikely that population density differences between mussels in the British Isles and Irish Republic, and Chile were due to differences in wave-exposure. The different size-frequency distributions of mussels from the British Isles and Irish Republic, and Chile might be reflected in the diversity of the associated infaunal communities, since structural complexity of the environment is an important determinant of biotic diversity (e.g. Kohn and Leviten, 1976; Pimm, 1994; Archambault and Bourget, 1996). This hypothesis will be tested in relation to communities associated with mussel beds in greater detail in subsequent chapters.

Age structure of mussel populations

Examination of the prismatic layer of the shells of both *M. edulis* and *P. purpuratus* revealed a series of microgrowth bands and increments. Various factors, including human disturbance and attacks by predators, as well as spawning breaks and algal blooms are known to be recorded as growth checks within the shell structure of bivalves (Richardson *et al*, 1990; Richardson, 1993). It might however, be expected that such factors would produce random, irregular checks in the shells; the observed checks in the mussel shells in this study occurred in regular patterns. These checks correspond to the slowing of growth during winter seasons, due to reduced temperatures and food supply and were used to estimate the age of these mussels.

At the three sites in the British Isles, shell growth rates were fastest in mussels from Point Lynas and slowest in White Beach mussels, while the growth rate of mussels at Criccieth was intermediate. In Chile, mussels at Desembocadura

(sheltered site 1) and Coronel had a significantly slower growth rate than mussels at the other two sites, while the growth rate of mussels at Desembocadura (exposed site 2) was intermediate between the other sites. Overall the mussels in Chile had significantly slower growth rates than those from the British Isles. Seed (1976) pointed out that mussel growth rate varies, not only between localities but also within similar size and age groups in the same population; even mussels grown under apparently identical conditions can exhibit widely different rates. *M. edulis* can reach lengths of 60-70mm in a twelve to eighteen month period (Mason, 1969, 1972), while other authors have measured much slower growth rates in less favourable conditions, of only 20-30mm in 15 to 20 years (e.g. Pike, 1971).

Various factors are important in affecting growth rates in bivalves, and are such that, in temperate waters, growth is rapid during the spring and summer and slight or absent during the colder winter months (Dare, 1969, Mason, 1969). Food supply is thought to be the single most important factor influencing growth in mussels (Wallace, 1980; Loo and Rosenberg, 1983; Rodhouse *et al*, 1984; Page and Ricard, 1990). Although other factors are also known to be important in controlling growth rate in mussels, including temperature (Sukhotin *et al*, 1992; Tomalin, 1995; Babarro *et al*, 2000) and light (Seed, 1969b), it is unlikely that any of these factors varied between the 3 Welsh sites on a large enough scale to produce the observed differences in growth rate. Similarly in Chile, the four sites were all located within 10-15 miles of each other. It is possible that differences in food supply, temperature or light might contribute to the faster growth rates of *M. edulis* in the British Isles and *P. purpuratus* in Chile. Various authors have shown that tidal height and wave-exposure can influence the growth rate of mussels (e.g. van Erkom Schurink and Griffiths, 1993; Richardson *et al*, 1995; Gray *et al*, 1997; McQuaid and Lindsay, 2000). However, conditions of wave-exposure and tidal height from which samples were collected were standardised across all study sites, these factors are unlikely to be the cause of the observed growth rate differences.

Longevity of mussels was greater in Chile than in the British Isles as well as growth rate being slower. Similarly, Gray *et al* (1997) found, in populations of *M. edulis chilensis* in the Falkland Islands, that the longer living individuals also exhibited the lowest growth rates. It has been suggested that faster growing mussels may be shorter-lived because they will attain the size limit imposed by the environment much more rapidly than those living in habitats where growth rates are much slower (Seed and Suchanek, 1992). Seed (1969b) found that in populations of *M. edulis* from the east coast of England, the absence of major predators in the upper shore resulted in enhanced survival and therefore the occurrence of relatively

old individuals. *P. purpuratus* populations in Chile might be subject to lower levels of predation than *M. edulis* in the British Isles and Irish Republic, although the communities associated with the sampled mussel populations in Chile were diverse and contained several species, including crabs, which might be predatory on mussels (see later chapters).

The difference in growth rate between *P. purpuratus* in Chile and *M. edulis* in the British Isles is the result of a combination of various physical, biological or environmental factors. Without studying the growth of the two mussel species in identical physical and environmental conditions, it would be impossible to deduce exact causes for the observed differences in growth rate between *P. purpuratus* and *M. edulis.* Mussels in Chile are slower growing and longer lived than their British counterparts, thus, it might be expected that the Chilean mussel beds would support a more diverse associated fauna, since Sanders (1968) concluded that, with increasing age and prolonged habitat stability; diversity increases.

Species composition of communities associated with mussel populations

Mussel populations at all sites, both in the British Isles and Irish Republic and in Chile supported diverse invertebrate assemblages. Numerous studies have described the diverse infaunal assemblages associated with intertidal mussel beds (e.g. Suchanek, 1979; Tsuchiya and Nishihira, 1985, 1986; Lintas and Seed, 1994; Seed, 1996). In the present study, 182 different invertebrate taxa were identified over the course of several months from *Mytilus edulis* beds at various locations in the British Isles and Irish Republic, while in *Perumytilus purpuratus* beds in Chile, around 35 different taxa were identified, although identification was to higher taxonomic levels and did not cover as wide a temporal period as the studies of *M. edulis.* Over a twelve-month period, a total of 79 taxa were identified from mussel beds at Point Lynas, with 92 at White Beach and 85 at Criccieth. These figures exceed those of previous studies of the communities associated with *M. edulis* beds on rocky shores. For example, Briggs (1982) identified 34 taxa associated with mussel beds in Loch Foyle, Northern Irish Republic, while Lintas and Seed (1994) found representatives from 59 taxa in mussel beds on a wave-exposed rocky shore on Anglesey. Tsuchiya and Nishihira (1985, 1986) identified 69 species from 8 phyla in mussel beds in Japan. Similar results have been obtained in studies of the communities associated with populations of different mussel species. For example, Ong Che and Morton (1992) found 52 macro-invertebrate species in *Septifer virgatus* beds in Hong Kong, while Seed and Brotohadikusumo (1994) identified 29 molluscan taxa from the same mussel beds. Peake and Quinn (1993) identified 56 macroinvertebrate species, from

8 phyla in *Brachidontes rostratus* beds in south-eastern Australia. In addition, similar numbers of taxa have been reported to be associated with *M. edulis* on soft sediments in the Wadden Sea (Dittman, 1990) and subtidal *Modiolus modiolus* beds (Brown and Seed, 1976). Thus, more taxa were associated with mussel beds on rocky substrata in this study than have been previously reported, with the exception of *M. californianus*, a much larger-bodied mussel which forms particularly thick multilayered beds which have been shown to support around 270 invertebrate taxa (Suchanek, 1979).

Chapter 4

Small-scale spatial variations in the structure of the invertebrate communities associated with *Mytilus edulis*

ABSTRACT

Small-scale spatial, or intra-site variation in the structure of the invertebrate community associated with *Mytilus edulis* beds was investigated on two rocky shores on the coast of Anglesey, North Wales. Communities associated with *M. edulis* showed significant small-scale spatial variation at the two study sites. Intra-site variations were more pronounced when data were analysed at the multivariate level, although many of the univariate measures of diversity did differ significantly between habitats. Multivariate differences in mussel bed community structure at both sites were the result of differences in abundance of around 16 of the more common members of the communities. The identity of many of these taxa were the same at each site, for example, juvenile *M. edulis*, mites, ostracods and oligochaetes, while others were restricted to one site or the other. When emphasis was removed from taxa abundance, clear intra-site differences still emerged between mussel communities, with many more taxa contributing to the dissimilarities between habitats. Some taxa appeared ubiquitous to all habitats at both sites, while others were site or habitat specific in their occurrence and abundance. Environmental parameters measured in the mussel bed showed some significant small-scale spatial variation within each site, although differences in individual parameters between habitats were not always consistent at the two sites. Multivariate analysis of the abiotic data showed a clear separation of mussel beds from each of the habitats at the two sites. However, the abiotic data did not show a high degree of correlation with the biotic data at either site. It was concluded that most of the intra-site variations in the structure of the *M. edulis* communities were the complex result of many different processes, together with stochastic events.

INTRODUCTION

Several studies have described the diverse infaunal assemblages associated with intertidal mussel beds (e.g. Suchanek, 1979; Tsuchiya and Nishihira, 1985, 1986; Lintas and Seed, 1994; Seed, 1996). Mussel beds represent an extremely well delineated community, bounded by the physical limits of the mussels, which in the intertidal, are in turn restricted by physical and biological factors to a clearly definable zone (Suchanek, 1980). In addition, due to the small size and immobility of sessile invertebrate species of marine epifaunal communities, these habitats are ideal for studying patterns of change in species composition and diversity (Osman, 1977).

Many workers have described the natural variability in patterns in intertidal communities (e.g. Lewis, 1964; Stephenson and Stephenson, 1972; Paine, 1974; Underwood and Chapman, 1996, 1998). Many of these studies have been very general, while patterns of structure of specific intertidal assemblages have usually been described from one sample, in a very restricted spatial scale of sampling (e.g. Foster, 1990; Warwick and Clarke, 1993). A complete understanding of the structure of any community can only be possible, when small-scale spatial variation is encompassed (Morris, 1990). In addition, Underwood and Chapman (1998) stated that understanding processes in complex assemblages depends on a clear understanding of spatial and temporal patterns of structure at various spatial scales. Other studies have stressed the importance of documenting spatial patterns in species abundance, in order to understand scales at which organisms interact with one another or with their environment, and the relative importance of different ecological processes which may determine these patterns (e.g. Underwood, 1991a; Underwood, 1992; Underwood and Chapman, 1996).

Spatial variation in species distributions can operate over a wide range of scales, from small-scale patchiness on shores to pan-continental variation and as such, multi-scale investigations should be carried out in community studies since different scales may influence community characteristics differently (Levin, 1992). Several investigations have been carried out into spatial variations, on a variety of scales, in the structure of marine assemblages. For example, Menge (1983) studied small-scale spatial patterns in tropical intertidal assemblages, while Underwood and Chapman (1998) studied small-scale spatial variation in sheltered rocky shore assemblages in south-eastern Australia. Archambault and Bourget (1986), Bergeron and Bourget (1986) and Bourget *et al* (1994) undertook several studies of coastal heterogeneity and benthic intertidal species richness, diversity and abundance in the intertidal zone on a variety of spatial scales. Hopner and Wonneberger (1985) have investigated patchiness in the epi-phytobenthos on intertidal flats, while Morrisey *et al*

(1992) studied spatial variation in soft-sediment benthos in Australia and Hixon and Beets (1993) studied small-scale spatial variability in coral reef assemblages.

Small-scale spatial variations in the structure of communities associated with intertidal mussel beds have been studied in some detail in the past. Many studies have investigated the effect of various factors, which show small-scale, or intra-site spatial variations, on the structure of invertebrate assemblages associated with intertidal mussel populations. The factors investigated have included mussel patch size (Suchanek, 1979; Tsuchiya and Nishihira, 1985, 1986; Peake and Quinn, 1993), mussel patch thickness (Tsuchiya and Nishihira, 1985, 1986; Svane and Ompi, 1993), position within the mussel patch (Okamura, 1986; Tsuchiya and Nishihira, 1986; Dittman, 1990); Lintas and Seed, 1994), inclination of the rock surface (Lintas and Seed, 1994), elevation on the shore (Suchanek, 1979, 1980; Tsuchiya and Nishihira, 1985; Jacobi, 1987a; Tsuchiya and Bellan-Santini, 1989, Lintas and Seed, 1994; Seed and Brotohadikusumo, 1994). However, most of these studies have considered only univariate techniques in the analysis of the effects of such sources of spatial variation on the structure of mussel bed communities. Efficient description of overall sample patterns require multivariate analyses of the community as a whole, rather than simple, univariate studies, which can often fail to identify, or oversimplify, patterns in data sets (Clarke, 1999).

In this chapter a range of univariate and multivariate techniques are used to investigate the small-scale spatial variations, or intra-shore variations, amongst the fauna associated with *Mytilus edulis* from several physically contrasting habitats at two different sites on Anglesey, North Wales. Taxa are investigated for evidence of positive or negative associations. Hypotheses for possible causes of spatial variations in community structure are suggested.

METHODS

Samples, each comprising of eight replicate 25cm^2 quadrats, were collected from *M. edulis* beds at Point Lynas and White Beach during two consecutive spring tides in July 1999, from each of the following habitats;

1) Low shore area within the mussel zone, flat surface, middle of the mussel patch,
2) Mid shore area within the mussel zone, flat surface, middle of the mussel patch,
2) High shore area within the mussel zone, flat surface, middle of the mussel patch,
4) Mid shore area within the mussel zone, flat surface, edge of the mussel patch,
5) Mid shore area within the mussel zone, vertical surface, middle of the mussel patch,

6) Mid shore, flat surface, middle of the mussel patch, covered with epiflora (Point Lynas only, since epifloral covering did not occur on mussel beds at White Beach). Samples were processed and sorted according to the methodologies described in Chapter 2.

RESULTS

The mussel populations and environmental factors

A total of 8908 mussels were collected and measured from the shores at Point Lynas and White Beach during this investigation. The relative abundance, size, volume and biomass of mussels from each of these habitats, together with the weight of each of the sediment fractions associated with these mussels are presented for both sites in Table 1. At Point Lynas, the population density, volume, biomass and mean length of *M. edulis* showed little variation with habitat, although values in the high-shore were slightly, although not always significantly, reduced. The two finest sediment fractions were significantly reduced in mussel beds on the low-shore and on vertical surfaces, compared to elsewhere, while the larger sediment fractions were similar in mussel beds from all habitats, except for those covered with epiflora, where quantities were elevated. The amounts of very coarse sediment and shell fragments were similar in mussel beds from all habitats. At White Beach, mussel population density decreased significantly with increasing tidal elevation, while mean mussel length, by contrast, increased with tidal elevation. The volume and biomass of mussels did not differ significantly across habitats. The weight of sediment fractions were generally elevated in mussel beds on vertical surfaces and the middle of patches on the mid shore and lower elsewhere. The weight of shell fragments and very coarse sediment was greatest in the high-shore mussel beds.

The Associated Fauna

A total of 47459 individual organisms were collected and identified from the mussel beds at Point Lynas, while 19708 specimens were collected from those at White Beach. At Point Lynas, each of the univariate measures of community diversity showed some significant variation in mussel beds across habitats (Table 2a). The total number of taxa, along with Margalef's richness were significantly lower in the middle of the mussel beds in the mid shore than elsewhere (Figure 1). Values of Shannon's diversity and Pielou's evenness were significantly elevated in mussel beds on vertical surfaces compared to other habitats. At White Beach, the total number of taxa, individuals and Margalef's richness showed significant variation in mussel beds from different habitats, while other univariate measures of community

Table 1 Mean values of environmental variables per 25cm^2 area of mussel bed from a) six different habitats on the shore at Point Lynas, Anglesey and b) five different habitats on the shore at White Beach, Anglesey. 95% confidence intervals are marked, such that significant differences ($p<0.05$) are represented by non-overlapping intervals.

a)

	MUSSEL PARAMETERS				MASS SEDIMENT FRACTIONS (g)				
Habitat	Density	Mean length (mm)	Volume (ml)	Mass (g)	<63μm	63-125μm	125-250μm	250-500μm	>500μm
Low shore	148±11	11.1±0.5	21±1	12.74±1.17	1.22±0.71	0.08±0.05	0.15±0.14	0.22±0.17	3.58±0.83
Mid shore	141±33	11.3±0.8	29±4	20.45±2.12	2.68±0.84	0.13±0.10	0.21±0.17	0.33±0.10	7.08±1.76
High shore	106±19	10.6±1.1	17±6	12.26±4.17	2.08±0.99	0.42±0.23	0.17±0.15	0.23±0.17	6.11±2.63
Edge of patch	167±12	10.1±0.5	23±5	17.10±2.96	3.38±2.31	0.29±0.19	0.14±0.08	0.20±0.14	4.83±1.03
Vertical surface	126±13	10.5±0.8	19±4	12.34±2.33	1.66±0.34	0.06±0.03	0.06±0.02	0.14±0.05	5.91±1.27
Epifloral covered	109±23	12.0±0.4	28±4	20.13±3.53	2.93±0.74	0.42±0.21	0.33±0.21	0.98±0.85	6.46±1.66

b)

	MUSSEL PARAMETERS				MASS SEDIMENT FRACTIONS (g)				
Habitat	Density	Mean length (mm)	Volume (ml)	Mass (g)	<63μm	63-125μm	125-250μm	250-500μm	>500μm
Low shore	93±18	13.4±1.1	32±3	24.30±2.88	1.64±0.79	0.16±0.06	0.11±0.06	0.20±0.17	3.59±1.68
Mid shore	62±14	15.9±2.1	35±5	26.71±4.10	2.05±0.85	0.27±0.28	0.21±0.26	0.19±0.25	5.01±1.85
High shore	39±11	17.2±1.4	28±6	22.66±4.76	1.65±0.66	0.17±0.13	0.08±0.04	0.08±0.04	9.59±2.25
Edge of patch	55±7	16.0±0.6	34±4	25.43±2.80	1.44±0.41	0.31±0.11	0.14±0.21	0.06±0.04	2.04±0.45
Vertical surface	69±5	14.0±0.8	31±5	24.54±3.55	2.19±0.99	0.43±0.26	0.41±0.28	0.30±0.17	7.51±3.15

Table 2 One-way ANOVA/Moods median tests between univariate measures of diversity for mussel beds from six different habitats at Point Lynas, Anglesey and five different habitats at White Beach, Anglesey. Significant differences are indicated by * ($p<0.05$).

	Point Lynas		White Beach	
Univariate Measure	F-value	χ^2-value	F-value	χ^2-value
Total taxa	14.25*	-	9.11*	-
Total individuals	-	12.00*	-	13.00*
Margalef's richness	16.91*	-	5.32*	-
Shannon diversity	8.47*	-	2.35	-
Pielou's evenness	5.89*	-	0.55	-

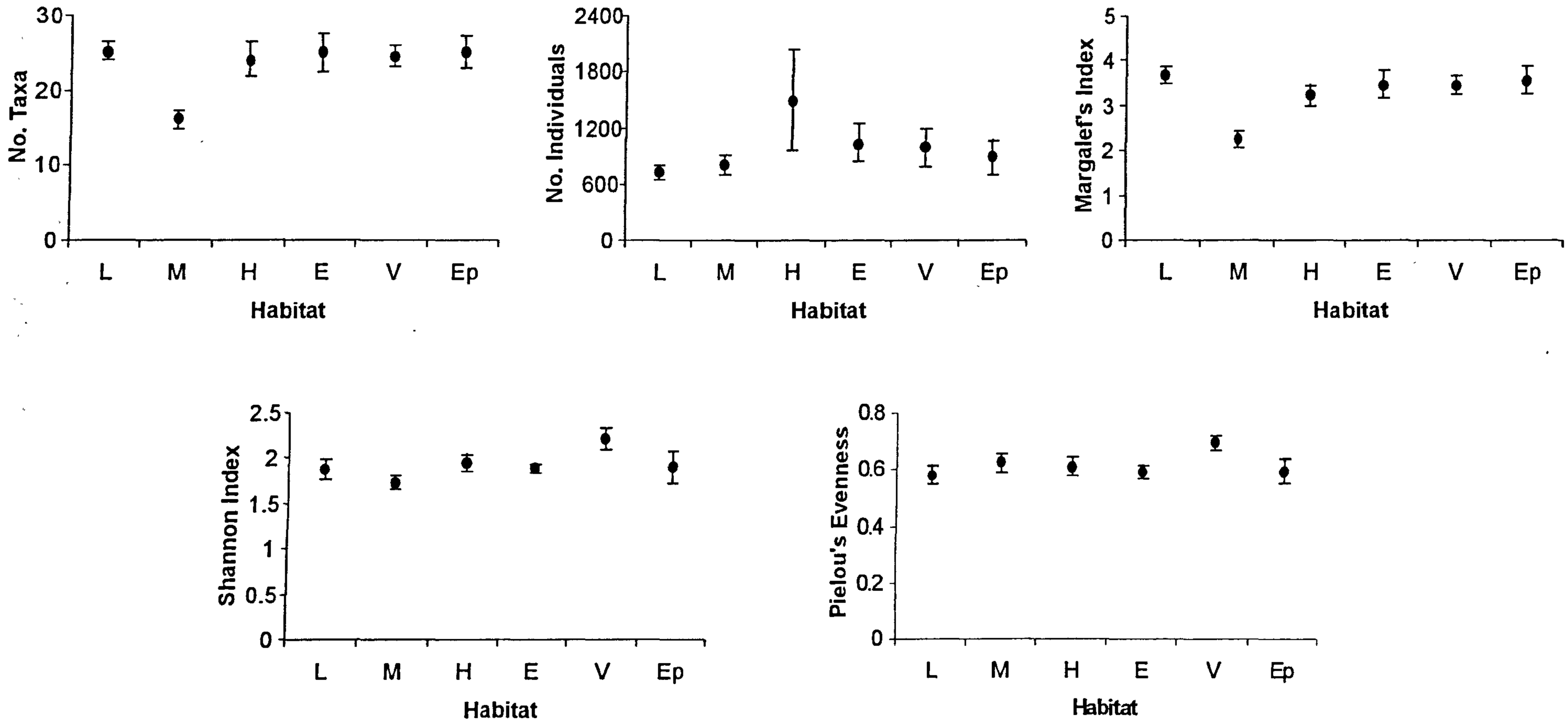


Figure 1 Mean values and 95% confidence intervals for univariate measures of mussel bed community structure from six different habitats on the shore at Point Lynas, Anglesey. (L = Low shore, mid patch; M = Mid shore, mid patch; H = High shore, mid patch; E = Edge of patch, mid shore; V = Vertical surface, mid shore; Ep = Epifloral covering, mid patch, mid shore).

diversity did not vary significantly (Table 2). The total number of taxa were significantly lower in the middle and on the edge of mid shore mussel patches than in other habitats (Figure 2), while the total number of individuals was reduced on the edge of mid shore patches. Margalef's index of richness was greatest in mussel beds on the low shore. However, the majority of the univariate measures of community diversity did show significant intra-site variation in mussel beds at either Point Lynas or White Beach.

Correlation coefficients calculated between abundance values for taxa at both sites, from all habitats, showed high levels of a positive correlation between some taxa, for example between the limpet *Tectura testudinalis* and the crab *Hyas areneas* and between the polychaete *Drilonereis filum* and *Cancer pagurus* (Appendix I). Such correlation did not necessarily suggest a relationship between the two species, but was probably a reflection of the fact that many of the members of the mussel community were rare, or transient in nature. Other more common taxa, such as turbellarians and the polychaete *Brania pusilla* and the polychaetes *Tharyx marioni* and *Lagisca extenuata* showed more intermediate levels of significantly positive correlation.

Cluster analysis of square-root transformed infaunal data from mussel beds at Point Lynas revealed a clear separation of samples from each of the six different habitats (Figure 3). The same analysis performed with a presence/absence transformation revealed a less clear separation of samples (Figure 4). The separation of samples from each of the five habitats at White Beach was relatively clear with both transformations, when cluster analysis was performed (Figure 5 and 6). MDS ordination of square-root transformed infaunal abundance at Point Lynas illustrated a clear separation of mussel bed samples from each of the six habitats (Figure 7ai). A one-way ANOSIM test and pairwise comparisons performed on the data confirmed that the community structure of mussel beds in each of the six habitats were significantly different ($R=0.641$, $p<0.05$) (Table 3ai). MDS ordination of presence/absence transformed infaunal abundance revealed a less distinct separation, with samples from each of the six habitats, except for those from the middle of mussel patches on the mid shore, showing a high degree of overlap (Figure 7aii). However, a one-way ANOSIM test and pairwise comparisons performed on the data showed that the community structure of mussel beds in each of the six locations did differ significantly ($R=0.580$, $p<0.05$) (Table 3aii). MDS ordination of square-root transformed infaunal abundance at White Beach illustrated a separation of mussel bed samples from the five habitats (Figure 7bi). A one-way ANOSIM test and pairwise comparisons performed on the data confirmed that the structure of the

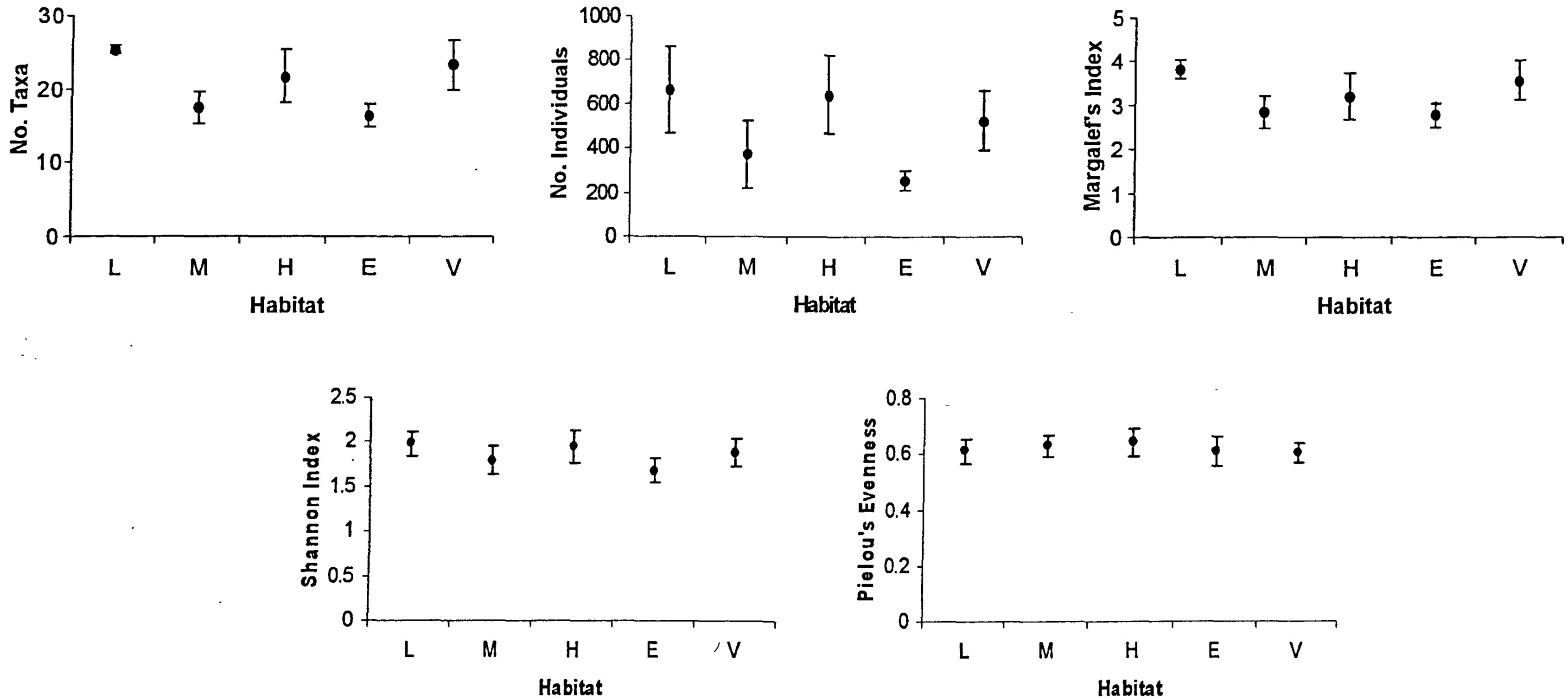


Figure 2 Mean values and 95% confidence intervals for univariate measures of mussel bed community structure from five different habitats on the shore at White Beach, Anglesey. (L = Low shore, mid patch; M = Mid shore, mid patch; H = High shore, mid patch; E = Edge of patch, mid shore; V = Vertical surface, mid shore).

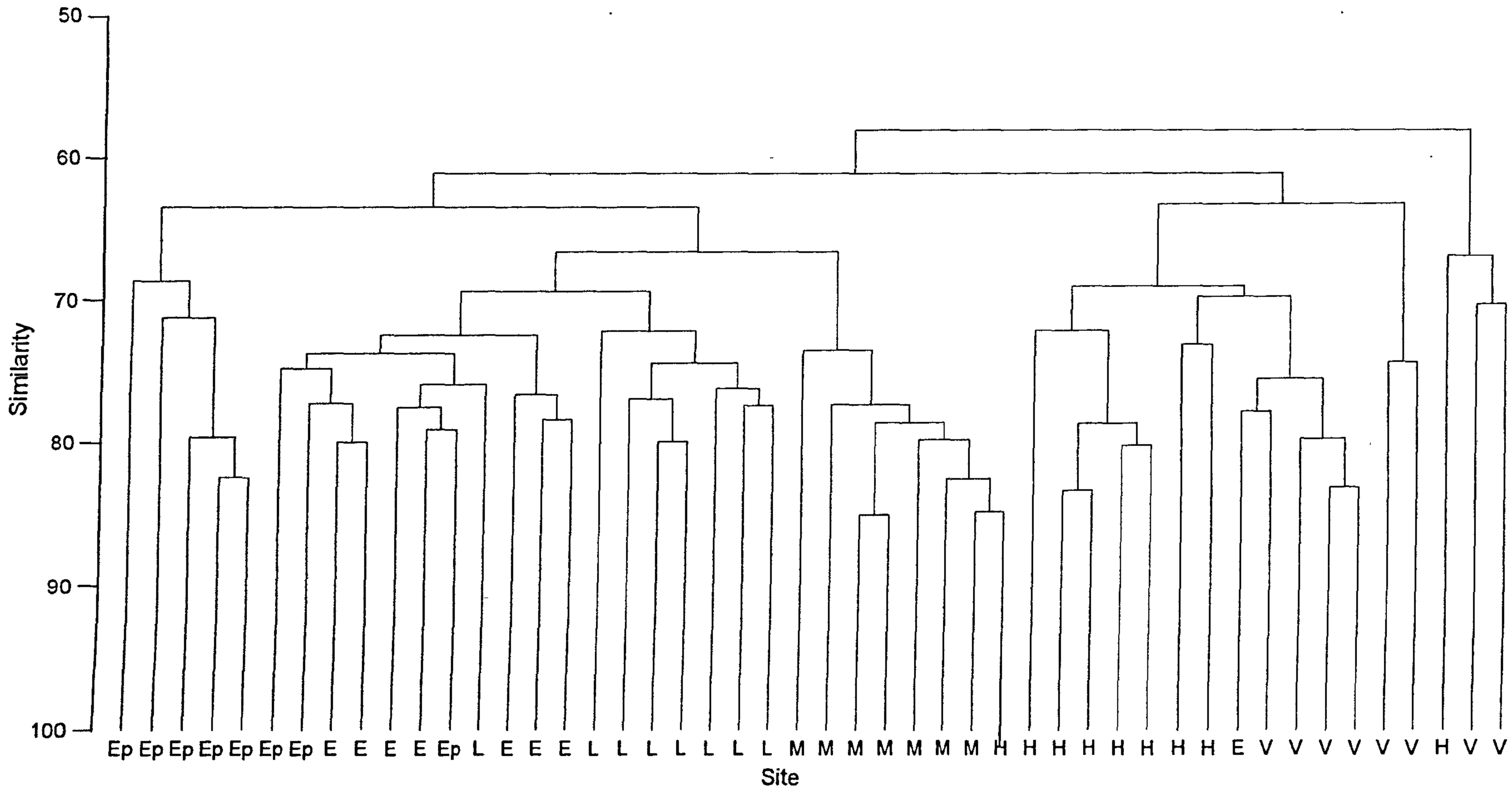


Figure 3 Dendrogram for group average clustering of Bray-Curtis similarities based on square-root transformed biotic data for mussel beds from six different habitats on the shore at Point Lynas, Anglesey. (L = Low shore, mid patch; M = Mid shore, mid patch; H = High shore, mid patch; E = Edge of patch, mid shore; V = Vertical surface, mid shore; Ep = Epifloral covering, mid patch, mid shore).

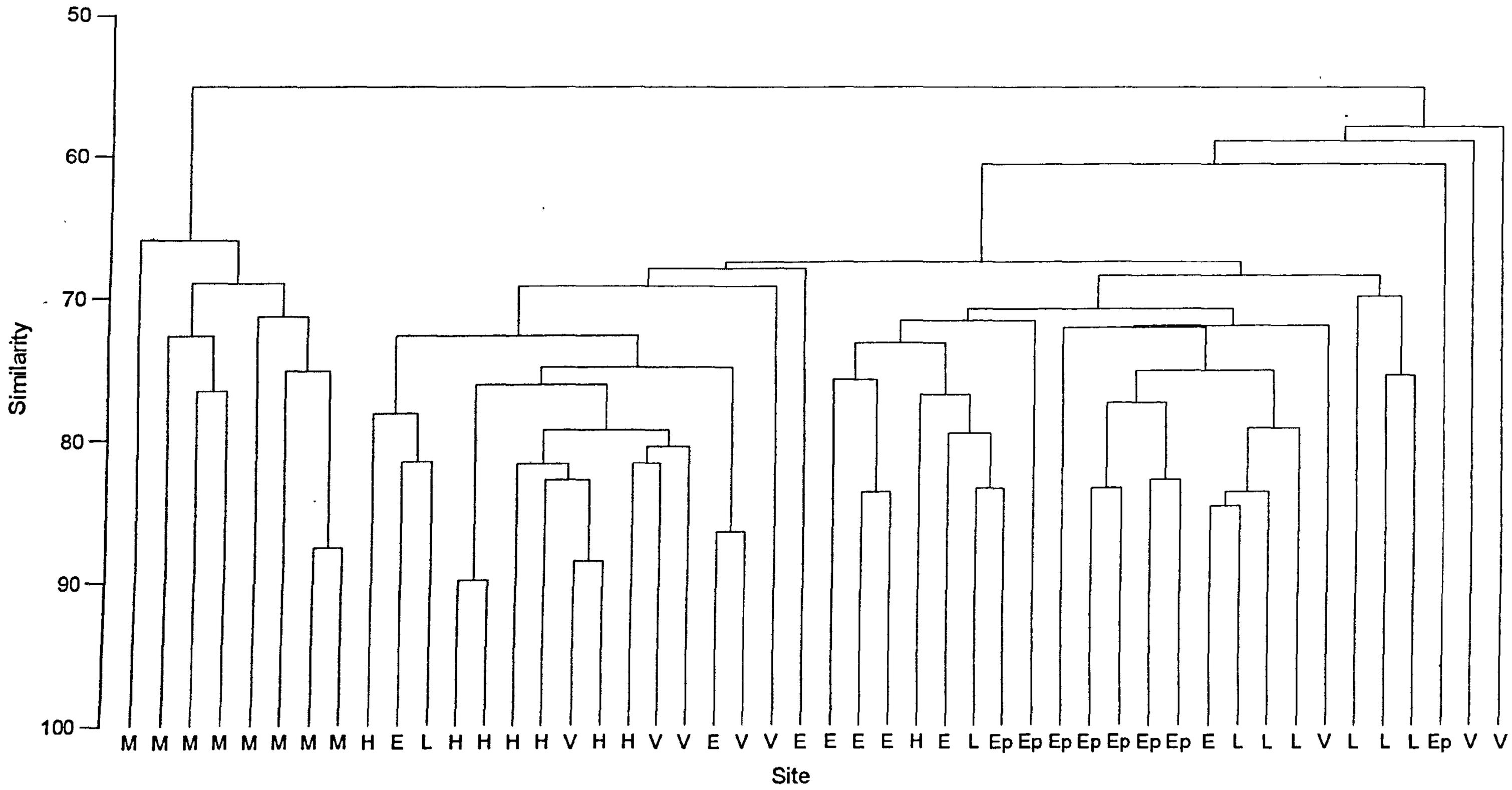


Figure 4 Dendrogram for group average clustering of Bray-Curtis similarities based on presence/absence transformed biotic data for mussel beds from six different habitats on the shore at Point Lynas, Anglesey. (L = Low shore, mid patch; M = Mid shore, mid patch; H = High shore, mid patch; E = Edge of patch, mid shore; V = Vertical surface, mid shore; Ep = Epifloral covering, mid patch, mid shore).

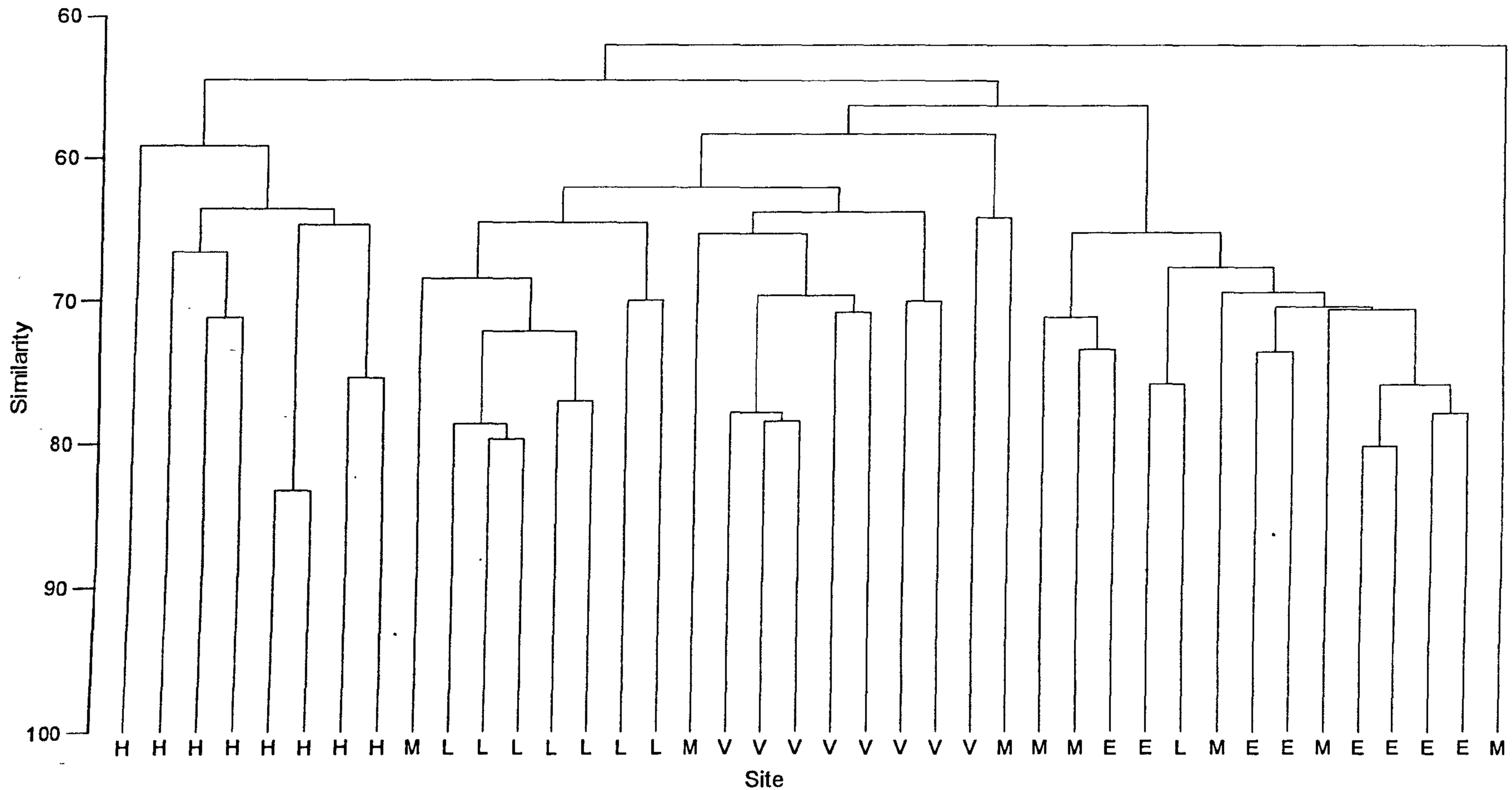


Figure 5 Dendrogram for group average clustering of Bray-Curtis similarities based on square-root transformed biotic data for mussel beds from five different habitats on the shore at White Beach, Anglesey. (L = Low shore, mid patch; M = Mid shore, mid patch; H = High shore, mid patch; E = Edge of patch, mid shore; V = Vertical surface, mid shore).

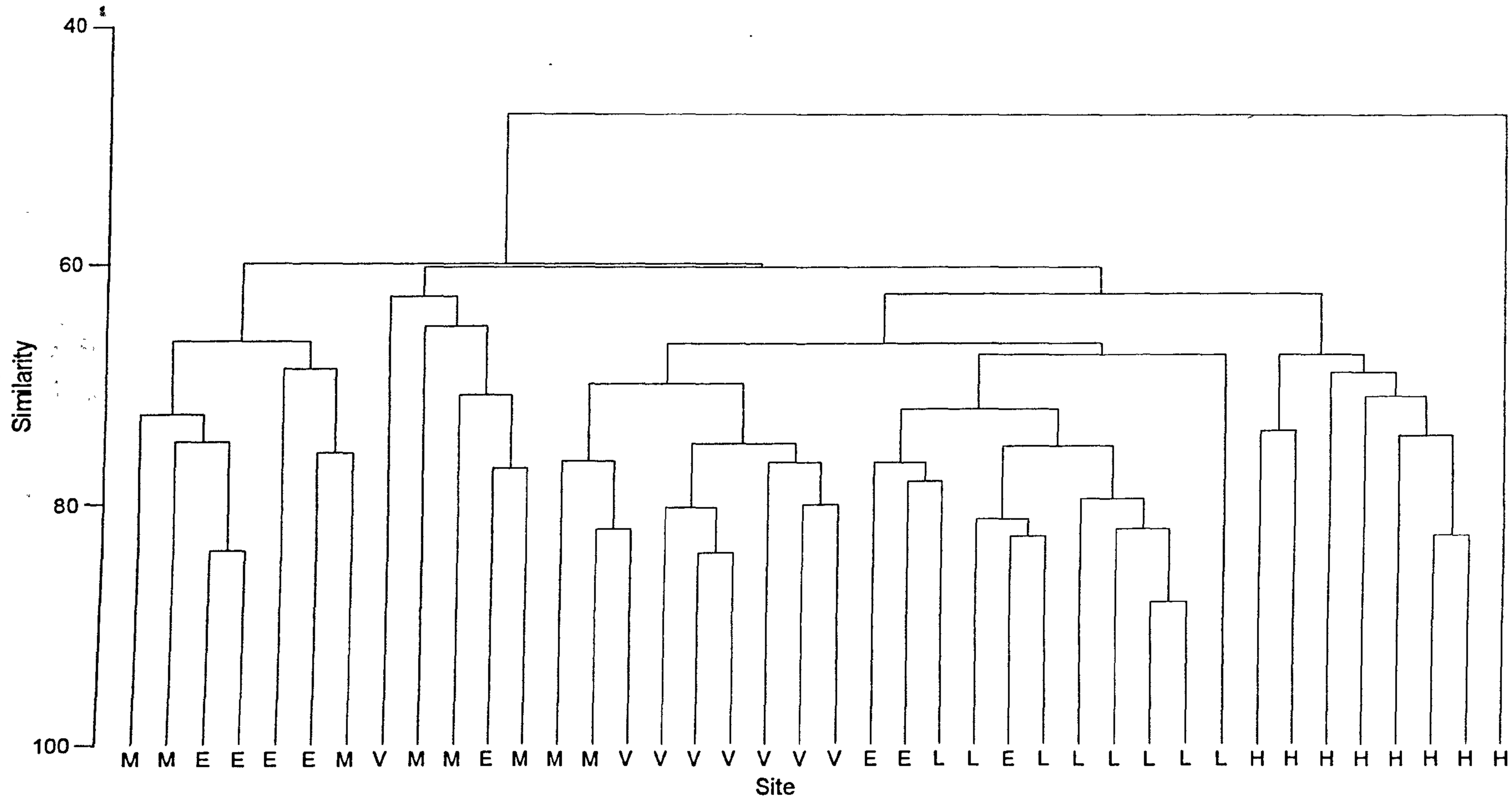
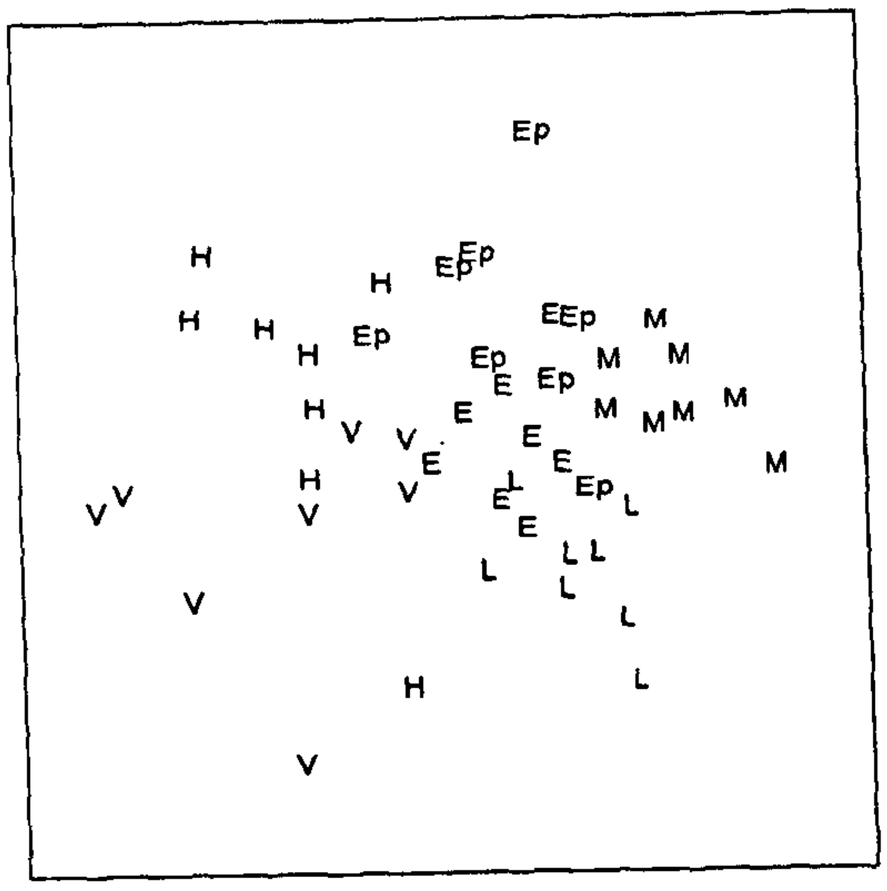
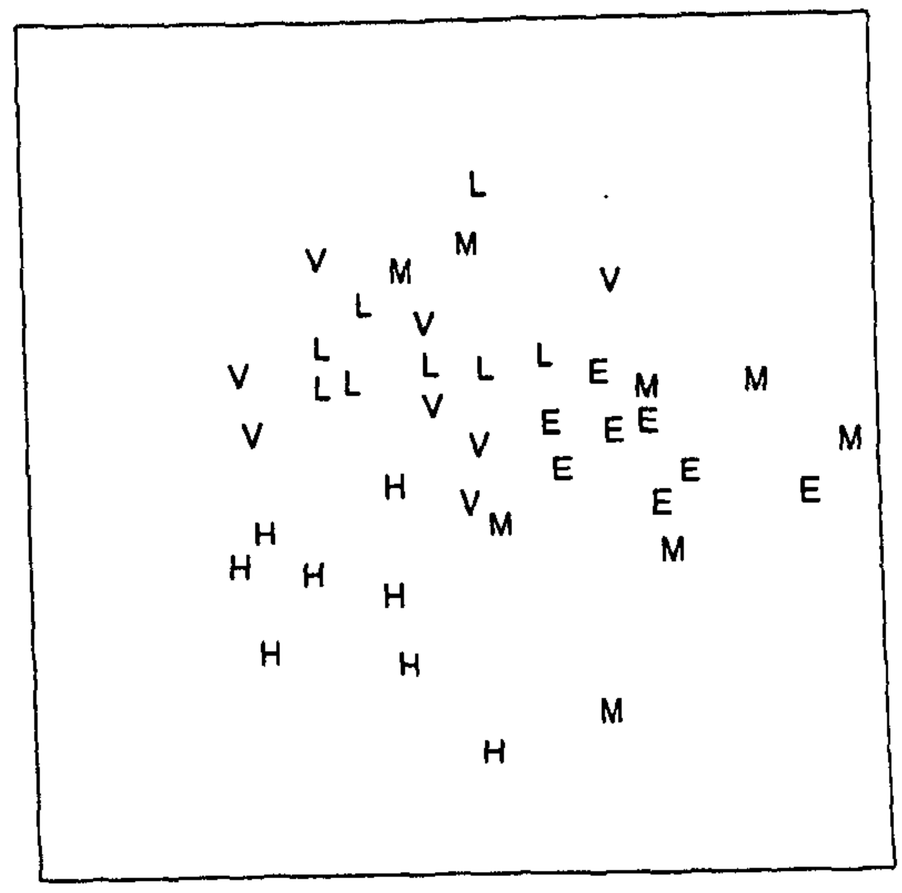


Figure 6 Dendrogram for group average clustering of Bray-Curtis similarities based on presence/absence transformed biotic data for mussel beds from five different habitats on the shore at White Beach, Anglesey. (L = Low shore, mid patch; M = Mid shore, mid patch; H = High shore, mid patch; E = Edge of patch, mid shore; V = Vertical surface, mid shore).

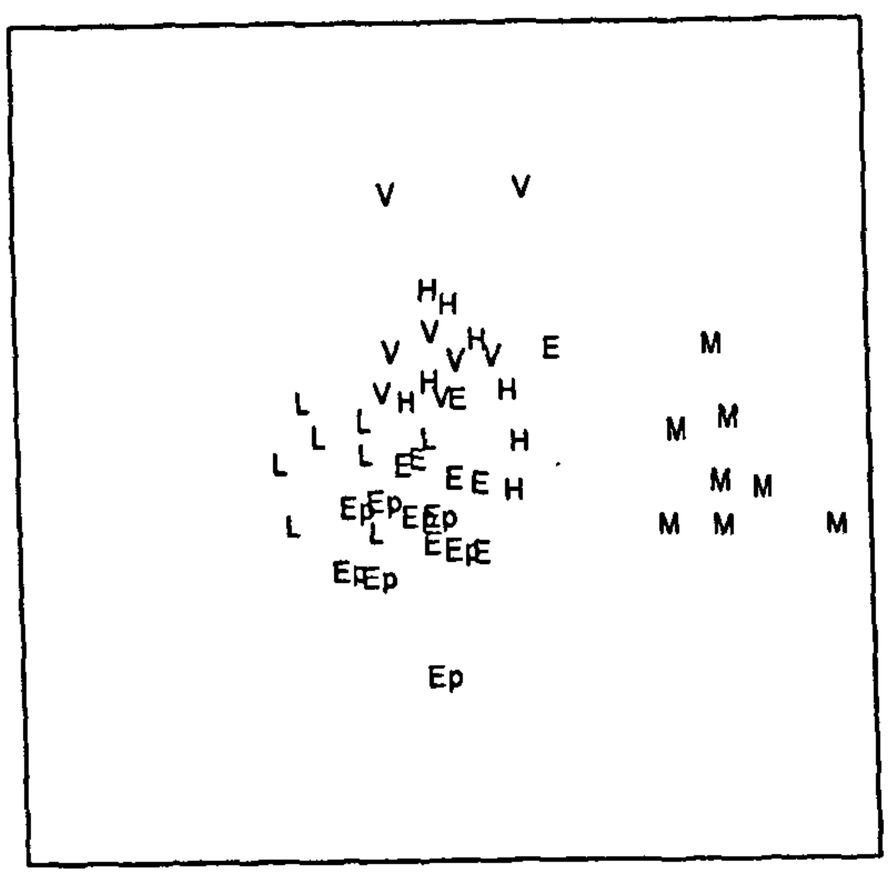
a) Point Lynas
i) Stress = 0.20



ii) Stress = 0.20



b) White Beach
i) Stress = 0.20



ii) Stress = 0.20

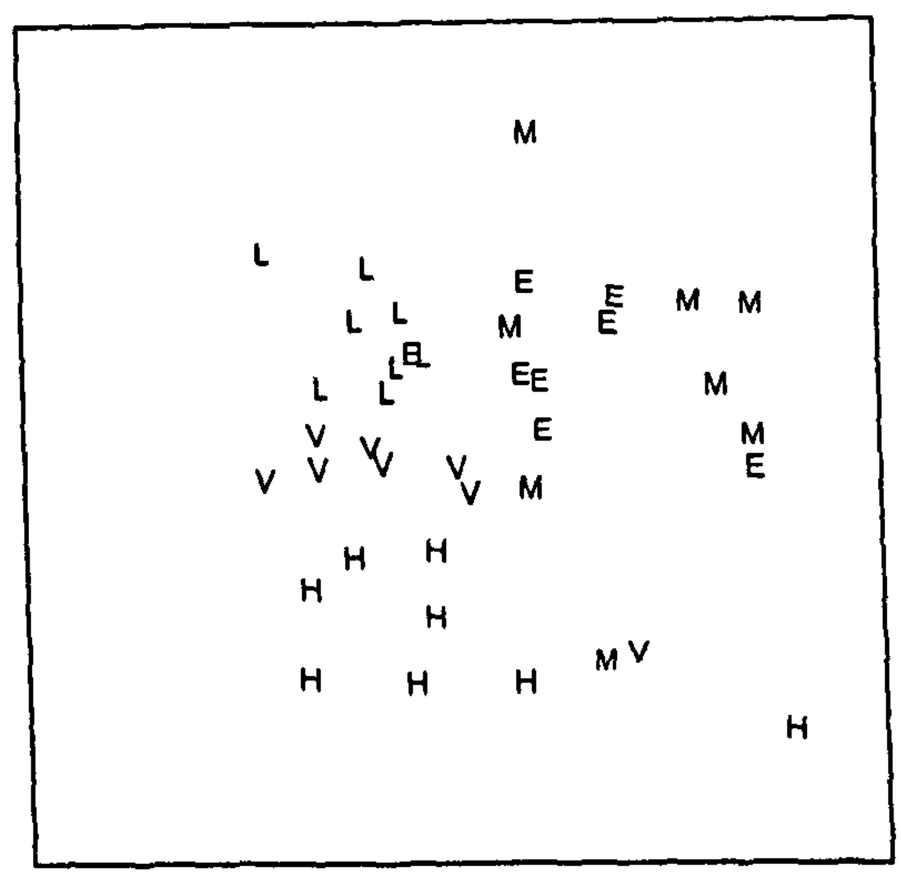


Figure 7 MDS ordination of Bray-Curtis similarity matrix of i) square-root and ii) presence/absence transformed taxa abundance data from mussel beds from a) six different habitats on the shore at Point Lynas, Anglesey and b) five different habitats on the shore at White Beach, Anglesey. (L = Low shore, mid patch; M = Mid shore, mid patch; H = High shore, mid patch; E = Edge of patch, mid shore; V = Vertical surface, mid shore; Ep = Epifloral covering, mid patch, mid shore).

Table 3 Global R-values for ANOSIM pairwise comparisons between samples of mussel bed communities from a) six different habitats Point Lynas, Anglesey and b) five different habitats at White Beach, Anglesey, based on i) square-root transformations and ii) presence/absence transformations of taxa abundance. Unless stated otherwise, samples were collected from the mid shore, from the middle of mussel patches and from horizontal rock surfaces. Significant differences in community structure are indicated by bold type.

a)
i.

	Low shore	*Mid shore*	*High shore*	*Edge of patch*	*Vertical surface*
Mid shore	**0.912**				
High shore	**0.803**	**0.845**			
Edge of patch	**0.568**	**0.774**	**0.712**		
Vertical surface	**0.751**	**0.841**	**0.287**	**0.496**	
Epifloral covering	**0.550**	**0.706**	**0.612**	**0.348**	**0.654**

ii.

	Low shore	*Mid shore*	*High shore*	*Edge of patch*	*Vertical surface*
Mid shore	**0.993**				
High shore	**0.644**	**0.926**			
Edge of patch	**0.315**	**0.906**	**0.592**		
Vertical surface	**0.496**	**0.919**	**0.169**	**0.372**	
Epifloral covering	**0.397**	**0.975**	**0.664**	**0.294**	**0.528**

b)
i.

	Low shore	*Mid shore*	*High shore*	*Edge of patch*
Mid shore	**0.491**			
High shore	**0.756**	**0.671**		
Edge of patch	**0.706**	0.103	**0.875**	
Vertical surface	**0.578**	**0.374**	**0.686**	**0.716**

ii.

	Low shore	*Mid shore*	*High shore*	*Edge of patch*
Mid shore	**0.607**			
High shore	**0.684**	**0.629**		
Edge of patch	**0.352**	0.123	**0.633**	
Vertical surface	**0.581**	**0.499**	**0.482**	**0.554**

mussel communities differed significantly between all habitats, except for in the middle and on the edge of mussel patches on the mid shore (R=0.570, $p<0.05$) (Table 3bi). The same pattern was revealed when MDS ordination was performed on presence/absence transformed infaunal abundance (Figure 7bii), along with a one-way ANOSIM test and pairwise comparisons (R=0.491, $p<0.05$) (Table 3bii).

Similarity percentage analysis (SIMPER), performed with a square-root transformation, revealed that a small number of taxa, namely small mussels, nematodes, mites, ostracods, oligochaetes, and chironomid larvae accounted for a large degree of the dissimilarity between habitats at the two shores (Table 4 and 5). The abundance of other taxa appeared to consistently characterise certain habitats. For example, the tanaid, *Tanais dulongii* and the ostracod, *Heterocythereis albomaculata* were present in elevated numbers in mussel beds in the high shore at the two shores, while *Fabricia stellaris* was abundant in the low shore at both sites and *Idotea pelagica* was consistently found in mid shore mussel patches. SIMPER analysis performed on data from the two shores, with a presence/absence transformation revealed many more taxa were responsible for habitat differences in community composition at both sites, when abundance was not taken into account (Table 6 and 7). Differences in taxa composition between habitats was much less clear, as the majority of taxa were present in all habitats.

Biotic and environmental relationships

Univariate measures of the diversity of the mussel bed community at the two shores failed to show any high degree of correlation with any of the measured environmental factors in the mussel beds, although some of the relationships were significant (Table 8).

Determination of correlation coefficients between environmental variables measured in mussel beds at Point Lynas and White Beach failed to reveal any strong relationships ($r>0.95$) , although there was some significant correlation (Table 9). As such, all environmental factors measured in the mussel beds were entered into the BIOENV procedure. This analysis revealed that square-root and presence/absence transformed biotic data at Point Lynas showed little correlation with environmental variables in the mussel matrix (Table 10a). Biotic data at White Beach showed a higher degree of correlation with a combination of increasing values of mussel density, length and coarse sediment content of the mussel matrix (Table 10b). Ordination by PCA of the environmental data from mussel samples showed that samples from each of the different habitats did not separate out as clearly as the biotic data from Point Lynas and White Beach (Figure 8). RELATE analysis between

Table 4 Results of similarity percentage analysis (SIMPER) performed on square-root transformed abundance of infaunal taxa in mussel bed communities from six different habitats on the shore at Point Lynas, Anglesey, showing a breakdown of % contributions of infaunal taxa (% Cont.) to average dissimilarity between habitats. Taxa highlighted in grey indicate higher abundance in the first listed habitat.

Low shore Mid shore	% Cont.	Low shore High shore	% Cont.	Low shore Edge of patch	% Cont.	Low shore Vertical surface	% Cont.	Low shore Epifloral cover	% Cont.
Turbellaria indet.	7.32	Mite sp. 1	14.49	Mite sp. 1	9.86	Mite sp. 1	8.52	Oligochaeta indet.	9.86
Oligochaeta indet.	7.27	*Tanais dulongii*	8.99	Juvenile *Mytilus edulis*	7.57	*Clunio* sp. larvae	7.62	Mite sp. 1	7.88
Modiolula phaseolina	6.87	*Clunio* sp. larvae	6.98	Turbellaria indet.	7.07	*Lasaea adansoni*	6.79	Nematoda indet.	5.90
Mite sp. 1	6.48	Nematoda indet.	6.43	Nematoda indet.	6.46	Nematoda indet.	6.46	Juvenile *Mytilus edulis*	5.75
Copepoda indet.	6.23	Oligochaeta indet.	6.40	Oligochaeta indet.	6.39	Oligochaeta indet.	6.36	*Modiolula phaseolina*	5.10
Nematoda indet.	4.80	Juvenile *Mytilus edulis*	3.56	Nemertea indet.	4.70	*Tanais dulongii*	5.59	Turbellaria indet.	4.70
Nemertea indet.	4.51	*Leptocythere pellucida*	3.42	*Clunio* sp. larvae	4.62	Turbellaria indet.	3.85	*Leptocythere pellucida*	3.72
Clunio sp. larvae	4.14	*Modiolula phaseolina*	3.05	*Modiolula phaseolina*	4.35	*Elminius modestus*	3.77	*Clunio* sp. larvae	3.48
Elminius modestus	3.88	*Anurida maritima*	2.96	Copepoda indet.	3.56	*Heterocythereis albomaculata*	3.58	Nemertea indet.	3.40
Juvenile *Mytilus edulis*	3.79	Nemertea indet.	2.78	Benthic foraminifera indet.	2.58	Juvenile *Mytilus edulis*	3.03	*Elminius modestus*	3.38
Benthic foraminifera indet.	3.28	Turbellaria indet.	2.67	*Leptocythere pellucida*	2.49	*Leptocythere pellucida*	2.76	*Heterocythereis albomaculata*	3.09
Other foraminifera indet.	2.71	*Heterocythereis albomaculata*	2.65	*Fabricia stellaris*	2.45	*Modiolula phaseolina*	2.67	Copepoda indet.	2.88
Leptocythere pellucida	2.63	Copepoda indet.	2.55	*Heterocythereis albomaculata*	2.20	*Semibalanus balanoides*	2.50	*Skenea serpuloides*	2.38
Heterocythereis albomaculata	2.54	*Lasaea adansoni*	2.47	*Tanais dulongii*	2.17	Nemertea indet.	2.41	Dipteran larvae indet.	2.30
Fabricia stellaris	2.35	Mite sp. 2	2.00	*Elminius modestus*	2.08	Copepoda indet.	2.30	*Fabricia stellaris*	2.18
Juvenile gastropoda indet.	2.29			Ostracod sp. 4	2.05	Benthic foraminifera indet.	2.12	Benthic foraminifera indet.	2.10
								Lasaea adansoni	1.98
Average dissimilarity between habitats = 35.90%		Average dissimilarity between habitats = 40.91%		Average dissimilarity between habitats = 30.62%		Average dissimilarity between habitats = 40.96%		Average dissimilarity between habitats = 34.75%	

Mid shore High shore	% Cont.	Mid shore Edge of patch	% Cont.	Mid shore Vertical surface	% Cont.	Mid shore Epifloral cover	% Cont.	High shore Edge of patch	% Cont.
Mite sp. 1	12.07	Juvenile *Mytilus edulis*	7.27	*Clunio* sp. larvae	7.99	Oligochaeta indet.	10.74	Mite sp. 1	11.46
Tanais dulongii	8.20	Nematoda indet.	6.43	Nematoda indet.	6.98	*Leptocythere pellucida*	6.22	*Tanais dulongii*	7.97
Clunio sp. larvae	7.73	*Clunio* sp. larvae	6.00	Oligochaeta indet.	6.82	Juvenile *Mytilus edulis*	5.68	Nematoda indet.	7.28
Oligochaeta indet.	7.43	Mite sp. 1	5.49	*Elminius modestus*	6.56	*Heterocythereis albomaculata*	5.49	*Clunio* sp. larvae	6.87
Nematoda indet.	5.96	Copepoda indet.	5.48	*Lasaea adansoni*	6.39	*Modiolula phaseolina*	5.02	Juvenile *Mytilus edulis*	6.77
Leptocythere pellucida	5.32	Oligochaeta indet.	5.23	*Heterocythereis albomaculata*	5.38	Nematoda indet.	4.96	Oligochaeta indet.	6.61
Heterocythereis albomaculata	4.50	*Heterocythereis albomaculata*	4.46	Mite sp. 1	4.94	*Clunio* sp. larvae	4.72	Turbellaria indet.	4.33
Juvenile *Mytilus edulis*	3.73	Turbellaria indet.	4.38	*Tanais dulongii*	4.83	Mite sp. 1	4.70	*Leptocythere pellucida*	3.08
Copepoda indet.	3.50	*Modiolula phaseolina*	4.37	*Leptocythere pellucida*	4.47	Copepoda indet.	4.62	*Anurida maritima*	3.08
Turbellaria indet.	3.49	*Elminius modestus*	4.24	Copepoda indet.	3.98	Benthic foraminifera indet.	3.90	*Heterocythereis albomaculata*	2.45
Modiolula phaseolina	3.05	*Leptocythere pellucida*	3.69	Turbellaria indet.	3.76	Other foraminifera indet.	3.25	Copepoda indet.	2.33
Anurida maritima	2.91	Ostracod sp. 4	3.56	*Semibalanus balanoides*	3.08	Nemertea indet.	2.89	Nemertea indet.	2.25
Ostracod sp. 4	2.73	Nemertea indet.	2.85	*Modiolula phaseolina*	2.99	*Skenea serpuloides*	2.69	*Elminius modestus*	2.19
		Other foraminifera indet.	2.43	Juvenile *Mytilus edulis*	2.84	Turbellaria indet.	2.46	*Lasaea adansoni*	2.17
		Juvenile gastropoda indet.	2.41			*Rissoella opalina*	2.12	Mite sp. 2	2.09
		Benthic foraminifera indet.	2.36			Juvenile gastropoda indet.	2.05		
Average dissimilarity between habitats = 42.05%		Average dissimilarity between habitats = 31.38%		Average dissimilarity between habitats = 43.55%		Average dissimilarity between habitats = 36.14%		Average dissimilarity between habitats = 36.91%	

High shore Vertical surface	% Cont.	High shore Epifloral cover	% Cont.	Edge of patch Vertical surface	% Cont.	Edge of patch Epifloral cover	% Cont.	Vertical surface Epifloral cover	% Cont.
Mite sp. 1	11.32	Mite sp. 1	11.60	*Clunio* sp. larvae	7.47	Oligochaeta indet.	10.01	Nematoda indet.	8.10
Nematoda indet.	9.61	*Tanais dulongii*	8.82	Nematoda indet.	7.11	Juvenile *Mytilus edulis*	8.81	*Clunio* sp. larvae	7.47
Clunio sp. larvae	5.92	*Clunio* sp. larvae	7.45	Juvenile *Mytilus edulis*	7.09	Nematoda indet.	6.96	*Elminius modestus*	6.33
Lasaea adansoni	5.90	Nematoda indet.	6.38	*Lasaea adansoni*	6.78	*Clunio* sp. larvae	4.86	*Lasaea adansoni*	5.96
Elminius modestus	5.48	Oligochaeta indet.	5.17	Oligochaeta indet.	6.08	Turbellaria indet.	4.72	Oligochaeta indet.	5.75
Tanais dulongii	5.32	Juvenile *Mytilus edulis*	4.95	*Tanais dulongii*	4.90	Mite sp. 1	4.45	*Tanais dulongii*	5.19
Oligochaeta indet.	4.13	*Modiolula phaseolina*	3.20	Turbellaria indet.	4.84	*Modiolula phaseolina*	4.04	Juvenile *Mytilus edulis*	4.24
Turbellaria indet.	3.64	Turbellaria indet.	2.81	*Elminius modestus*	4.10	*Elminius modestus*	3.58	Mite sp. 1	4.14
Juvenile *Mytilus edulis*	3.42	*Anurida maritima*	2.76	Mite sp. 1	3.64	*Leptocythere pellucida*	3.08	*Semibalanus balanoides*	3.50
Heterocythereis albomaculata	3.02	Benthic foraminifera indet.	2.51	*Heterocythereis albomaculata*	3.38	Nemertea indet.	3.07	Turbellaria indet.	3.44
Anurida maritima	2.71	*Heterocythereis albomaculata*	2.38	*Semibalanus balanoides*	2.98	Benthic foraminifera indet.	3.04	*Heterocythereis albomaculata*	2.88
Nemertea indet.	2.46	*Semibalanus balanoides*	2.36	Nemertea indet.	2.80	*Heterocythereis albomaculata*	2.99	*Modiolula phaseolina*	2.80
Ostracod sp. 4	2.31	Nemertea indet.	2.21	*Leptocythere pellucida*	2.64	*Skenea serpuloides*	2.46	Benthic foraminifera indet.	2.67
Mite sp. 2	2.22	Mite sp. 2	2.04	Copepoda indet.	1.99	Dipteran larvae indet.	2.45	Nemertea indet.	2.28
Leptocythere pellucida	2.22	Ostracod sp. 4	2.02	Ostracod sp. 4	1.95	Copepoda indet.	2.37	Other foraminifera indet.	2.16
Copepoda indet.	2.01	*Skenea serpuloides*	2.01	Benthic foraminifera indet.	1.65	*Tanais dulongii*	2.17	*Skenea serpuloides*	1.97
		Copepoda indet.	1.95	Dipteran larvae indet.	1.63	Ostracod sp. 4	1.99	*Leptocythere pellucida*	1.65
Average dissimilarity between habitats = 35.50%		Average dissimilarity between habitats = 38.21%		Average dissimilarity between habitats = 36.16%		Average dissimilarity between habitats = 31.65%		Average dissimilarity between habitats = 39.94%	

Table 5 Results of similarity percentage analysis (SIMPER) performed on presence/absence transformed abundance of infaunal taxa in mussel bed communities from six different habitats on the shore at Point Lynas, Anglesey, showing a breakdown of % contributions of infaunal taxa (% Cont.) to average dissimilarity between habitats. Taxa highlighted in grey indicate higher abundance in the first listed habitat.

Low shore Mid shore	% Cont.	Low shore High shore	% Cont.	Low shore Edge of patch	% Cont.	Low shore Vertical surface	% Cont.	Low shore Epifloral cover	% Cont.
Other foraminifera indet.	4.95	*Tanais dulongii*	5.33	*Tanais dulongii*	4.83	*Tanais dulongii*	4.47	*Semibalanus balanoides*	3.90
Copepoda indet.	4.95	*Anurida maritima*	4.42	*Modiolula phaseolina*	4.36	Other foraminifera indet.	4.31	*Elminius modestus*	3.79
Heterocythereis albomaculata	4.95	*Rissoella opalina*	4.25	Turbellaria indet.	4.35	*Rissoella opalina*	3.96	*Nucella lapillus*	3.74
Turbellaria indet.	4.95	*Brachystomia scalaris*	3.82	*Hyale prevostii*	4.28	Benthic foraminifera indet.	3.60	*Modiolula phaseolina*	3.68
Benthic foraminifera indet.	4.36	*Modiolula phaseolina*	3.81	*Idotea pelagica*	4.20	*Modiolula phaseolina*	3.57	*Idotea pelagica*	3.55
Leptocythere pellucida	3.81	Mite sp. 2	3.68	*Nucella lapillus*	3.98	*Brachystomia scalaris*	3.41	*Hyale prevostii*	3.49
Ostracod sp. 4	3.75	*Skenea serpuloides*	3.41	*Brachystomia scalaris*	3.73	*Limapontia depressa*	3.24	*Jaera albifrons*	3.33
Elminius modestus	3.68	*Nucella lapillus*	3.27	*Semibalanus balanoides*	3.69	*Nucella lapillus*	3.24	*Brania pusilla*	3.08
Rissoella opalina	3.40	Other foraminifera indet.	3.13	*Skenea serpuloides*	3.54	*Skenea serpuloides*	3.23	*Fabricia stellaris*	3.07
Tanais dulongii	3.36	Benthic foraminifera indet.	3.10	*Brania pusilla*	3.50	*Idotea pelagica*	2.86	*Onoba semicostata*	3.07
Modiolula phaseolina	3.10	*Fabricia stellaris*	3.07	*Fabricia stellaris*	3.46	*Fabricia stellaris*	2.86	*Anurida maritima*	2.99
Juvenile gastropoda indet.	3.09	*Jaera albifrons*	3.04	*Limapontia depressa*	3.23	Ostracod sp. 4	2.85	*Skenea serpuloides*	2.95
Skenea serpuloides	3.09	*Brania pusilla*	3.02	*Jaera albifrons*	2.81	*Jaera albifrons*	2.84	*Brachystomia scalaris*	2.95
Jaera albifrons	2.94	*Cirratulus cirratus*	2.96	Benthic foraminifera indet.	2.70	*Brania pusilla*	2.84	*Limapontia depressa*	2.91
Brachystomia scalaris	2.80	Nemertea indet.	2.50	Nemertea indet.	2.61	*Anurida maritima*	2.82	Nemertea indet.	2.54
Semibalanus balanoides	2.79	*Semibalanus balanoides*	2.46	*Rissoella opalina*	2.31	*Littorina rudis*	2.81	*Littorina mariae*	2.53
Idotea pelagica	2.48	*Limapontia depressa*	2.44	*Lasaea adansoni*	2.21	*Carcinus maenas*	2.17	*Cirratulus cirratus*	2.46
Nucella lapillus	2.47	Mite sp. 3	2.38	Ostracod sp. 4	2.15	Nemertea indet.	2.14	Ostracod sp. 4	2.38
Hyale prevostii	2.46	*Hyale prevostii*	2.32	Mite sp. 3	2.08	*Semibalanus balanoides*	2.14	*Lasaea adansoni*	1.96
Brania pusilla	2.45	*Elminius modestus*	2.28	*Pholoe inornata*	1.74	*Semicytherura nigrescens*	2.13	*Tanais dulongii*	1.95
Fabricia stellaris	2.44	*Idotea pelagica*	2.24	*Polydora ciliata*	1.73	Turbellaria indet.	2.11	*Littorina rudis*	1.85
		Podocoryne carnea	2.21	*Rissoa parva*	1.68	Mite sp. 5	2.08	Dipteran larvae indet.	1.66
		Ostracod sp. 4	1.92	White anemone indet.	1.66	Mite sp. 3	1.79	*Pomatoceros triqueter*	1.66
						Lasaea adansoni	1.78	Turbellaria indet.	1.66
						Polydora ciliata	1.78	Juvenile gastropoda indet.	1.63
								Oligochaeta indet.	1.62
Average dissimilarity between habitats = 48.96%		Average dissimilarity between habitats = 33.38%		Average dissimilarity between habitats = 28.64%		Average dissimilarity between habitats = 35.17%		Average dissimilarity between habitats = 31.91%	

High shore Vertical surface	% Cont.	High shore Epifloral cover	% Cont.	Edge of patch Vertical surface	% Cont.	Edge of patch Epifloral cover	% Cont.	Vertical surface Epifloral cover	% Cont.
Limapontia depressa	4.79	*Semibalanus balanoides*	5.05	*Hyale prevostii*	4.57	*Brania pusilla*	4.78	*Semibalanus balanoides*	5.34
Mite sp. 2	4.00	*Idotea pelagica*	4.33	Other foraminifera indet.	4.30	*Tanais dulongii*	4.13	Other foraminifera indet.	4.03
Idotea pelagica	3.49	*Tanais dulongii*	4.28	*Brania pusilla*	4.14	*Elminius modestus*	4.00	*Rissoella opalina*	3.71
Anurida maritima	3.48	*Fabricia stellaris*	4.20	*Semibalanus balanoides*	3.86	*Jaera albifrons*	3.98	*Tanais dulongii*	3.67
Fabricia stellaris	3.47	*Rissoella opalina*	3.99	*Rissoella opalina*	3.83	Turbellaria indet.	3.67	Benthic foraminifera indet.	3.37
Jaera albifrons	3.46	*Brachystomia scalaris*	3.47	*Limapontia depressa*	3.54	*Brachystomia scalaris*	3.49	Hyale nilssoni	3.32
Benthic foraminifera indet.	3.44	Mite sp. 2	3.30	Turbellaria indet.	3.32	*Skenea serpuloides*	3.33	*Elminius modestus*	3.25
Ostracod sp. 4	3.44	*Hyale prevostii*	3.20	Benthic foraminifera indet.	3.30	*Onoba semicostata*	3.25	*Brachystomia scalaris*	3.11
Other foraminifera indet.	3.41	*Skenea serpuloides*	3.15	*Fabricia stellaris*	3.10	*Anurida maritima*	3.16	*Limapontia depressa*	3.01
Littorina rudis	3.40	*Elminius modestus*	3.01	Ostracod sp. 4	3.10	*Limapontia depressa*	3.06	*Skenea serpuloides*	2.97
Cirratulus cirratus	3.38	Other foraminifera indet.	2.93	*Idotea pelagica*	3.09	*Hyale nilsonni*	2.91	*Jaera albifrons*	2.69
Carcinus maenas	3.04	*Anurida maritima*	2.90	*Anurida maritima*	3.07	*Cirratulus cirratus*	2.77	*Anurida maritima*	2.67
Turbellaria indet.	2.99	Benthic foraminifera indet.	2.90	*Jaera albifrons*	3.06	Benthic foraminifera indet.	2.55	Ostracod sp. 4	2.66
Nucella lapillus	2.98	*Jaera albifrons*	2.86	*Littorina rudis*	3.04	*Semibalanus balanoides*	2.51	*Idotea pelagica*	2.66
Mite sp. 3	2.95	*Cirratulus cirratus*	2.84	*Skenea serpuloides*	3.01	*Littorina mariae*	2.46	*Fabricia stellaris*	2.65
Skenea serpuloides	2.60	*Onoba semicostata*	2.81	*Carcinus maenas*	2.56	White anemone indet.	2.44	*Littorina rudis*	2.64
Elminius modestus	2.58	*Limapontia depressa*	2.32	*Brachystomia scalaris*	2.44	Dipteran larvae indet.	2.18	*Onoba semicostata*	2.63
Semicytherura nigrescens	2.58	*Nucella lapillus*	2.26	*Semicytherura nigrescens*	2.32	*Rissoella opalina*	2.16	Turbellaria indet.	2.35
Rissoella opalina	2.52	Mite sp. 3	2.22	Mite sp. 3	2.28	Ostracod sp. 4	2.16	*Littorina mariae*	2.33
Mite sp. 5	2.52	Turbellaria indet.	2.17	Mite sp. 5	2.27	*Idotea pelagica*	1.98	Mite sp. 5	2.28
Podocoryne carnea	2.51	*Littorina mariae*	2.13	*Nucella lapillus*	2.25	Mite sp. 3	1.95	*Cirratulus cirratus*	2.25
Hyale prevostii	1.76	*Podocoryne carnea*	2.07	*Tanais dulongii*	1.91	*Nucella lapillus*	1.94	*Semicytherura nigrescens*	2.17
Odontosyllis ctenostoma	1.74	Ostracod sp. 4	1.90	*Littorina mariae*	1.53	*Pomatoceros triqueter*	1.76	*Carcinus maenas*	2.03
				Capitella capitata	1.51	Juvenile gastropoda indet.	1.72	Dipteran larvae indet.	1.72
						Oligochaeta indet.	1.71	Oligochaeta indet.	1.71
Average dissimilarity between habitats = 29.82%		Average dissimilarity between habitats = 35.76%		Average dissimilarity between habitats = 32.47%		Average dissimilarity between habitats = 30.42%		Average dissimilarity between habitats = 37.72%	

Mid shore High shore	% Cont.	Mid shore Edge of patch	% Cont.	Mid shore Vertical surface	% Cont.	Mid shore Epifloral cover	% Cont.	High shore Edge of patch	% Cont.
Heterocythereis albomaculata	5.86	*Heterocythereis albomaculata*	5.86	Copepoda indet.	5.52	Other foraminifera indet.	5.21	*Idotea pelagica*	5.84
Leptocythere pellucida	5.07	Other foraminifera indet.	5.11	*Heterocythereis albomaculata*	5.52	Copepoda indet.	5.21	*Anurida maritima*	4.78
Copepoda indet.	5.03	Ostracod sp. 4	5.11	*Leptocythere pellucida*	4.78	*Heterocythereis albomaculata*	5.21	*Brania pusilla*	4.44
Ostracod sp. 4	5.03	Copepoda indet.	5.05	*Semibalanus balanoides*	4.17	Benthic foraminifera indet.	4.59	*Fabricia stellaris*	4.09
Turbellaria indet.	4.47	*Jaera albifrons*	4.63	*Limapontia depressa*	4.17	*Leptocythere pellucida*	4.51	*Rissoella opalina*	4.07
Semibalanus balanoides	4.09	*Leptocythere pellucida*	4.46	*Elminius modestus*	4.10	Turbellaria indet.	3.80	*Hyale prevostii*	4.06
Fabricia stellaris	3.96	*Elminius modestus*	4.35	Turbellaria indet.	3.49	Ostracod sp. 4	3.78	Mite sp. 2	3.97
Juvenile gastropoda indet.	3.66	*Brania pusilla*	3.90	Juvenile gastropoda indet.	3.45	*Rissoella opalina*	3.60	*Semibalanus balanoides*	3.90
Anurida maritima	3.58	Juvenile gastropoda indet.	3.66	*Jaera albifrons*	2.82	*Tanais dulongii*	3.23	Turbellaria indet.	3.72
Mites sp. 2	3.50	*Rissoella opalina*	3.57	Ostracod sp. 4	2.78	*Skenea serpuloides*	3.15	Other foraminifera indet.	3.36
Elminius modestus	3.29	Benthic foraminifera indet.	3.42	*Nucella lapillus*	2.78	Juvenile gastropoda indet.	2.91	Benthic foraminifera indet.	3.31
Jaera albifrons	2.96	*Nucella lapillus*	2.95	*Idotea pelagica*	2.76	*Brachystomia scalaris*	2.88	*Jaera albifrons*	3.27
Nucella lapillus	2.94	*Hyale prevostii*	2.94	*Fabricia stellaris*	2.74	*Nucella lapillus*	2.63	*Cirratulus cirratus*	3.22
Idotea pelagica	2.94	*Idotea pelagica*	2.93	*Anurida maritima*	2.74	*Hyale prevostii*	2.61	*Skenea serpuloides*	3.20
Hyale prevostii	2.92	*Skenea serpuloides*	2.71	*Hyale prevostii*	2.73	*Idotea pelagica*	2.60	*Nucella lapillus*	2.82
Benthic foraminifera indet.	2.89	*Semibalanus balanoides*	2.58	*Littorina rudis*	2.70	*Onoba semicostata*	2.55	Mite sp. 3	2.77
Other foraminifera indet.	2.84	*Brachystomia scalaris*	2.49	*Carcinus maenas*	2.28	*Anurida maritima*	2.54	*Limapontia depressa*	2.60
Cirratulus cirratus	2.82	Turbellaria indet.	2.21	Benthic foraminifera indet.	2.21	*Elminius modestus*	2.34	*Elminius modestus*	2.46
Rissoella opalina	2.15	*Tanais dulongii*	2.20	*Semicytherura nigrescens*	2.06	*Littorina mariae*	2.11	*Podocoryne carnea*	2.39
Podocoryne carnea	2.11			*Rissoella opalina*	2.05	*Cirratulus cirratus*	2.08	*Brachystomia scalaris*	2.36
				Mite sp. 5	2.00	*Jaera albifrons*	2.07		
				Tanais dulongii	1.77	*Limapontia depressa*	1.96		
				Littorina mariae	1.70				
Average dissimilarity between habitats = 42.72%		Average dissimilarity between habitats = 41.72%		Average dissimilarity between habitats = 44.59%		Average dissimilarity between habitats = 46.70%		Average dissimilarity between habitats = 31.06%	

Table 6 Results of similarity percentage analysis (SIMPER) performed on square-root transformed abundance of infaunal taxa in mussel bed communities from five different habitats on the shore at White Beach, Anglesey, showing a breakdown of % contributions of infaunal taxa (% Cont.) to average dissimilarity between habitats. Taxa highlighted in grey indicate higher abundance in the first listed habitat.

Low shore Mid shore	% Cont.	Low shore High shore	% Cont.	Low shore Edge of patch	% Cont.	Low shore Vertical surface	% Cont.	Mid shore High shore	% Cont.
Juvenile *Mytilus edulis*	11.29	Juvenile *Mytilus edulis*	9.99	Juvenile *Mytilus edulis*	11.71	*Elminius modestus*	6.81	Nematoda indet.	9.00
Nematoda indet.	6.43	Nematoda indet.	6.95	Nematoda indet.	8.04	Nematoda indet.	6.55	Juvenile *Mytilus edulis*	6.64
Clunio sp. larvae	5.85	*Elminius modestus*	5.76	Mite sp. 1	6.60	Juvenile *Mytilus edulis*	5.93	Copepoda indet.	6.42
Benthic foraminifera indet.	5.33	Turbellaria indet.	4.37	*Clunio* sp. larvae	5.36	Copepoda indet.	5.76	*Elminius modestus*	6.07
Mite sp. 1	5.04	Benthic foraminifera indet.	4.14	Copepoda indet.	4.46	*Idotea pelagica*	4.60	Mite sp. 1	5.83
Copepoda indet.	4.51	*Leptocythere pellucida*	3.83	Benthic foraminifera indet.	4.37	*Clunio* sp. larvae	4.41	Turbellaria indet.	5.20
Other foraminifera indet.	4.01	*Clunio* sp. larvae	3.79	Other foraminifera indet.	4.21	Benthic foraminifera indet.	3.73	*Clunio* sp. larvae	5.14
Oligochaeta indet.	3.76	*Idotea pelagica*	3.75	Ostracod sp. 4	3.71	Mite sp. 1	3.68	Oligochaeta indet.	4.33
Ostracod sp. 4	3.63	Mite sp. 1	3.67	*Idotea pelagica*	3.65	*Modiolula phaseolina*	3.59	*Leptocythere pellucida*	4.14
Rissoella opalina	3.37	*Hyale prevostii*	3.59	*Jaera albifrons*	3.50	Oligochaeta indet.	3.08	*Hyale prevostii*	3.94
Jaera albifrons	3.35	Copepoda indet.	3.59	Nemertea indet.	3.31	Ostracod sp. 4	2.98	*Idotea pelagica*	3.80
Idotea pelagica	3.35	Ostracod sp. 4	2.75	Oligochaeta indet.	3.20	*Heterocythereis albomaculata*	2.94	*Heterocythereis albomaculata*	2.83
Modiolula phaseolina	3.06	*Jaera albifrons*	2.71	*Rissoella opalina*	3.06	*Brania pusilla*	2.90	*Modiolula phaseolina*	2.59
Brania pusilla	2.50	Other foraminifera indet.	2.55	Dipteran larvae indet.	2.91	Other foraminifera indet.	2.70	Nemertea indet.	2.50
Dipteran larvae indet.	2.45	*Rissoella opalina*	2.54	*Modiolula phaseolina*	2.69	*Jaera albifrons*	2.55	*Echinogammarus marinus*	2.23
Echinogammarus marinus	2.22	Oligochaeta indet.	2.44			*Cirratulus cirratus*	2.30		
		Brania pusilla	2.43			*Rissoella opalina*	2.11		
		Heterocythereis albomaculata	2.27			*Leptocythere pellucida*	2.10		
						Brachystomia scalaris	1.95		
Average dissimilarity between habitats = 44.23%		Average dissimilarity between habitats = 44.01%		Average dissimilarity between habitats = 40.60%		Average dissimilarity between habitats = 38.86%		Average dissimilarity between habitats = 48.96%	

Mid shore Edge of patch	% Cont.	Mid shore Vertical surface	% Cont.	High shore Edge of patch	% Cont.	High shore Vertical surface	% Cont.	Edge of patch Vertical surface	% Cont.
Juvenile *Mytilus edulis*	10.45	Juvenile *Mytilus edulis*	9.52	Nematoda indet.	11.08	Copepoda indet.	7.83	Juvenile *Mytilus edulis*	8.34
Nematoda indet.	7.61	*Elminius modestus*	7.00	Mite sp. 1	7.42	Juvenile *Mytilus edulis*	7.81	*Elminius modestus*	7.97
Clunio sp. larvae	7.11	*Clunio* sp. larvae	5.86	*Elminius modestus*	7.14	Nematoda indet.	7.61	Nematoda indet.	6.61
Copepoda indet.	5.38	Oligochaeta indet.	5.64	Copepoda indet.	6.12	*Elminius modestus*	5.97	Oligochaeta indet.	5.97
Oligochaeta indet.	5.36	Nematoda indet.	5.63	Turbellaria indet.	5.92	Turbellaria indet.	5.15	*Idotea pelagica*	5.39
Idotea pelagica	4.74	*Idotea pelagica*	4.68	*Leptocythere pellucida*	4.88	Mite sp. 1	4.24	*Clunio* sp. larvae	5.19
Modiolula phaseolina	4.66	Mite sp. 1	4.30	*Clunio* sp. larvae	4.55	*Leptocythere pellucida*	4.10	Mite sp. 1	4.63
Nemertea indet.	4.53	*Modiolula phaseolina*	3.87	*Hyale prevostii*	4.49	*Hyale prevostii*	3.89	*Modiolula phaseolina*	4.47
Mite sp. 1	4.43	*Heterocythereis albomaculata*	3.51	*Idotea pelagica*	4.46	*Heterocythereis albomaculata*	3.70	Copepoda indet.	4.45
Echinogammarus marinus	3.44	*Rissoella opalina*	3.36	Oligochaeta indet.	4.43	Oligochaeta indet.	3.61	*Heterocythereis albomaculata*	3.57
Leptocythere pellucida	3.39	Copepoda indet.	3.33	*Mytilus edulis*	4.40	*Modiolula phaseolina*	3.23	*Lasaea adansoni*	2.83
Benthic foraminifera indet.	3.09	*Lasaea adansoni*	2.93	*Heterocythereis albomaculata*	2.69	*Clunio* sp. larvae	3.21	*Cirratulus cirratus*	2.81
Rissoella opalina	2.84	*Cirratulus cirratus*	2.52	Juvenile barnacles indet.	2.44	*Rissoella opalina*	2.41	*Rissoella opalina*	2.77
Heterocythereis albomaculata	2.83	*Echinogammarus marinus*	2.44			*Semibalanus balanoides*	2.23	*Leptocythere pellucida*	2.75
Jaera albifrons	2.77	Other foraminifera indet.	2.40			*Lasaea adansoni*	2.23	Nemertea indet.	2.56
		Leptocythere pellucida	2.25			Juvenile barnacles indet.	2.15		
		Nemertea indet.	2.11			*Cirratulus cirratus*	2.03		
Average dissimilarity between habitats = 38.12%		Average dissimilarity between habitats = 44.21%		Average dissimilarity between habitats = 45.94%		Average dissimilarity between habitats = 43.62%		Average dissimilarity between habitats = 42.84%	

Table 7 Results of similarity percentage analysis (SIMPER) performed on presence/absence transformed abundance of infaunal taxa in mussel bed communities from five different habitats on the shore at White Beach, Anglesey, showing a breakdown of % contributions of infaunal taxa (% Cont.) to average dissimilarity between habitats. Taxa highlighted in grey indicate higher abundance in the first listed habitat.

Low shore Mid shore	% Cont.	Low shore High shore	% Cont.	Low shore Edge of patch	% Cont.	Low shore Vertical surface	% Cont.	Mid shore High shore	% Cont.
Ostracod sp. 4	5.69	*Hyale prevostii*	5.17	Ostracod sp. 4	5.52	*Elminius modestus*	6.13	*Hyale prevostii*	5.71
Benthic foraminifera indet.	5.00	*Elminius modestus*	5.17	*Skenea serpuloides*	5.07	*Brania pusilla*	4.63	Turbellaria indet.	4.77
Skenea serpuloides	4.97	*Rissoella opalina*	4.05	*Rissoella opalina*	4.40	Ostracod sp. 4	4.05	*Elminius modestus*	4.41
Lasaea adansoni	3.95	Ostracod sp. 4	3.97	*Brachystomia scalaris*	4.36	*Idotea pelagica*	4.00	*Echinogammarus marinus*	4.29
Echinogammarus marinus	3.92	Benthic foraminifera indet.	3.40	*Lasaea adansoni*	4.17	*Cirratulus cirratus*	3.81	*Semibalanus balanoides*	3.52
Rissoella opalina	3.91	*Semibalanus balanoides*	3.35	Other foraminifera indet.	3.74	*Skenea serpuloides*	3.75	*Idotea pelagica*	3.49
Other foraminifera indet.	3.68	*Brania pusilla*	3.32	*Modiolula phaseolina*	3.72	*Nucella lapillus*	3.48	Other foraminifera indet.	3.16
Brachystomia scalaris	3.37	*Idotea pelagica*	3.30	Oligochaeta indet.	3.70	*Brachystomia scalaris*	3.28	*Heterocythereis albomaculata*	2.86
Brania pusilla	3.20	*Brachystomia scalaris*	3.23	Crab larvae indet.	3.67	Crab larvae indet.	3.07	*Fabricia stellaris*	2.85
Heterocythereis albomaculata	2.89	Turbellaria indet.	3.04	Dipteran larvae indet.	3.66	Mite sp. 3	2.96	Juvenile gastropoda indet.	2.83
Crab larvae indet.	2.84	*Skenea serpuloides*	3.02	Nemertea indet.	3.59	*Cirriformia tentaculata*	2.56	*Tanais dulongii*	2.73
Juvenile gastropoda indet.	2.83	*Lasaea adansoni*	2.86	*Brania pusilla*	3.24	*Modiolula phaseolina*	2.37	Dipteran larvae indet.	2.72
Jaera albifrons	2.43	Crab larvae indet.	2.59	*Pholoe inornata*	2.78	*Anurida maritima*	2.36	*Jaera albifrons*	2.60
Dipteran larvae indet.	2.33	*Fabricia stellaris*	2.58	Mite sp. 3	2.75	*Heterocythereis albomaculata*	2.35	*Brania pusilla*	2.46
Modiolula phaseolina	2.21	*Tanais dulongii*	2.50	*Ophelia rathkei*	2.74	*Pholoe inornata*	2.32	Nemertea indet.	2.45
Fabricia stellaris	2.17	*Heterocythereis albomaculata*	2.37	*Heterocythereis albomaculata*	2.73	*Ophelia rathkei*	2.29	*Lasaea adansoni*	2.42
Pholoe inornata	2.16	Mite sp. 3	2.20	Turbellaria indet.	2.72	Turbellaria indet.	2.28	Oligochaeta indet.	2.39
Oligochaeta indet.	2.15	Dipteran larvae indet.	2.18	*Jaera albifrons*	2.35	*Fabricia stellaris*	2.23	*Modiolula phaseolina*	2.35
Ophelia rathkei	2.12	Nemertea indet.	2.18	*Fabricia stellaris*	2.31	*Lasaea adansoni*	1.97	*Skenea serpuloides*	2.23
Turbellaria indet.	2.11	*Pholoe inornata*	2.11	*Echinogammarus marinus*	2.27	Juvenile gastropoda indet.	1.97	Mite sp. 3	2.19
Mite sp. 3	1.77	*Modiolula phaseolina*	2.06	*Nucella lapillus*	2.25	*Eulalia viridis*	1.84	Benthic foraminifera indet.	2.13
Scolelepis squamata	1.77	Juvenile barnacles indet.	2.01			Copepoda indet.	1.68	Crab larvae indet.	1.97
Cirriformia tentaculata	1.73	*Ophelia rathkei*	1.93			Benthic foraminifera indet.	1.57	Juvenile barnacles indet.	1.97
Eulalia viridis	1.73	*Cirratulus cirratus*	1.82			*Cirratulus filiformis*	1.55	*Cirratulus cirratus*	1.97
						Harmothoe sp.	1.53		
Average dissimilarity between habitats = 41.11%		Average dissimilarity between habitats = 41.43%		Average dissimilarity between habitats = 32.65%		Average dissimilarity between habitats = 33.66%		Average dissimilarity between habitats = 45.75%	

Mid shore Edge of patch	% Cont.	Mid shore Vertical surface	% Cont.	High shore Edge of patch	% Cont.	High shore Vertical surface	% Cont.	Edge of patch Vertical surface	% Cont.
Benthic foraminifera indet.	5.73	*Elminius modestus*	4.73	*Hyale prevostii*	6.44	*Hyale prevostii*	5.99	*Elminius modestus*	6.17
Echinogammarus marinus	5.29	*Lasaea adansoni*	4.71	*Elminius modestus*	5.61	Turbellaria indet.	5.04	*Idotea pelagica*	4.67
Brania pusilla	4.44	*Echinogammarus marinus*	4.23	Turbellaria indet.	5.38	*Rissoella opalina*	4.59	*Cirratulus cirratus*	4.39
Heterocythereis albomaculata	4.29	Benthic foraminifera indet.	4.19	*Semibalanus balanoides*	4.22	Benthic foraminifera indet.	3.45	*Brania pusilla*	4.34
Modiolula phaseolina	4.26	*Rissoella opalina*	4.14	*Idotea pelagica*	4.15	*Semibalanus balanoides*	3.45	*Lasaea adansoni*	4.21
Oligochaeta indet.	4.22	*Idotea pelagica*	3.82	Benthic foraminifera indet.	3.72	*Lasaea adansoni*	3.43	*Rissoella opalina*	4.20
Dipteran larvae indet.	4.21	*Cirratulus cirratus*	3.80	*Brania pusilla*	3.62	*Nucella lapillus*	3.26	*Nucella lapillus*	3.83
Other foraminifera indet.	4.18	Other foraminifera indet.	3.69	*Modiolula phaseolina*	3.24	*Cirratulus cirratus*	3.21	Other foraminifera indet.	3.59
Juvenile gastropoda indet.	4.17	*Nucella lapillus*	3.44	Other foraminifera indet.	3.24	*Fabricia stellaris*	2.99	*Modiolula phaseolina*	3.58
Nemertea indet.	4.12	*Heterocythereis albomaculata*	3.10	Oligochaeta indet.	3.24	Mite sp. 3	2.91	Oligochaeta indet.	3.57
Jaera albifrons	3.86	Juvenile gastropoda indet.	3.05	Dipteran larvae indet.	3.22	*Tanais dulongii*	2.89	Dipteran larvae indet.	3.53
Rissoella opalina	3.64	Mite sp. 3	2.87	*Fabricia stellaris*	3.22	*Skenea serpuloides*	2.80	Nemertea indet.	3.44
Lasaea adansoni	3.30	*Cirriformia tentaculata*	2.73	Nemertea indet.	3.21	*Heterocythereis albomaculata*	2.76	Mite sp. 3	3.39
Fabricia stellaris	2.73	*Jaera albifrons*	2.49	*Tanais dulongii*	3.08	*Idotea pelagica*	2.72	*Skenea serpuloides*	2.97
Mite sp. 3	2.62	*Modiolula phaseolina*	2.46	*Lasaea adansoni*	3.05	Ostracod sp. 4	2.45	Ostracod sp. 4	2.94
Nucella lapillus	2.59	*Brachystomia scalaris*	2.39	*Heterocythereis albomaculata*	2.99	*Modiolula phaseolina*	2.44	*Cirriformia tentaculata*	2.80
Elminius modestus	2.50	Dipteran larvae indet.	2.32	*Skenea serpuloides*	2.86	Dipteran larvae indet.	2.38	*Brachystomia scalaris*	2.74
Crab larvae indet.	2.16	Oligochaeta indet.	2.32	Crab larvae indet.	2.73	Nemertea indet.	2.38	*Heterocythereis albomaculata*	2.73
Ostracod sp. 4	2.08	*Brania pusilla*	2.32	Mite sp. 3	2.72	*Cirriformia tentaculata*	2.35	Benthic foraminifera indet.	2.73
		Fabricia stellaris	2.24	*Rissoella opalina*	2.56	*Anurida maritima*	2.26	*Anurida maritima*	2.41
		Eulalia viridis	2.19			Other foraminifera indet.	2.14		
		Skenea serpuloides	2.11			*Brachystomia scalaris*	2.13		
		Anurida maritima	2.09			Crab larvae indet.	2.10		
Average dissimilarity between habitats = 34.45%		Average dissimilarity between habitats = 40.65%		Average dissimilarity between habitats = 41.62%		Average dissimilarity between habitats = 37.92%		Average dissimilarity between habitats = 36.10%	

Table 8 Correlation coefficients between environmental variables and univariate measures of diversity in mussel beds from a) six different habitats on the shore at Point Lynas, Anglesey and b) five different habitats on the shore at White Beach, Anglesey. *NT* number of taxa, *NI* number of individuals, *d* Margalef's species richness, *H'* Shannon-Weiner diversity, *J* Pielou's evenness. Values in bold indicate significant correlation.

a)

	NT	*NI*	*d*	*H'*	*J*
Σmussels	0.043	-0.022	0.018	-0.088	-0.112
Mass mussels	-0.255	-0.219	-0.233	**-0.351**	-0.188
Volume mussels	-0.272	-0.268	-0.231	**-0.300**	-0.125
Mean mussel size	-0.163	**-0.414**	-0.031	-0.228	-0.138
Mass <63μm sediment	0.070	0.156	0.006	**-0.297**	**-0.352**
Mass 63-125μm sediment	0.247	0.192	0.191	-0.193	**-0.367**
Mass 125-250μm sediment	0.084	0.061	0.077	**-0.285**	**-0.371**
Mass 250-500μm sediment	0.167	0.005	0.174	-0.137	-0.242
Mass >500μm sediment	-0.073	**0.364**	-0.197	-0.100	-0.042

b)

	NT	*NI*	*d*	*H'*	*J*
Σmussels	**0.384**	**0.340**	**0.326**	0.136	-0.172
Mass mussels	0.000	-0.001	0.015	-0.174	-0.259
Volume mussels	-0.028	-0.063	0.010	-0.186	-0.251
Mean mussel size	**-0.454**	**-0.470**	**-0.349**	-0.235	0.089
Mass <63μm sediment	-0.103	-0.008	-0.132	-0.207	-0.168
Mass 63-125μm sediment	0.067	-0.158	0.129	-0.003	-0.068
Mass 125-250μm sediment	0.202	0.213	0.138	-0.034	-0.209
Mass 250-500μm sediment	**0.372**	**0.368**	0.284	0.070	-0.216
Mass >500μm sediment	0.250	**0.392**	0.129	0.307	0.190

Table 9 Correlation coefficients between various environmental variables measured in mussel beds from a) six different habitats on the shore at Point Lynas, Anglesey and b) five different habitats on the shore at White Beach, Anglesey. Values in bold indicate significant correlation.

a)

	No. mussels	*Mass mussels*	*Volume mussels*	*Mean mussel size*	*Mass <63μm sediment*	*Mass 63-125μm sediment*	*Mass 125-250μm sediment*	*Mass 250-500μm sediment*
Mass mussels	0.137							
Volume mussels	0.098	**0.915**						
Mean mussel size	**-0.497**	**0.569**	**0.632**					
Mass <63μm sediment	-0.051	**0.313**	**0.296**	0.121				
Mass 63-125μm sediment	-0.203	0.062	0.054	0.059	**0.479**			
Mass 125-250μm sediment	**-0.327**	0.070	0.055	0.267	**0.372**	**0.372**		
Mass 250-500μm sediment	**-0.331**	0.105	0.067	**0.312**	**0.367**	0.236	**0.742**	
Mass >500μm sediment	-0.187	**0.353**	**0.323**	0.216	0.226	0.150	**0.308**	0.242

b)

	No. mussels	*Mass mussels*	*Volume mussels*	*Mean mussel size*	*Mass <63μm sediment*	*Mass 63-125μm sediment*	*Mass 125-250μm sediment*	*Mass 250-500μm sediment*
Mass mussels	**0.452**							
Volume mussels	**0.510**	**0.876**						
Mean mussel size	**-0.776**	0.040	**0.510**					
Mass <63μm sediment	0.056	0.069	0.069	-0.165				
Mass 63-125μm sediment	**-0.313**	-0.143	-0.175	0.306	0.096			
Mass 125-250μm sediment	0.076	-0.158	-0.243	-0.265	**0.349**	**0.323**		
Mass 250-500μm sediment	0.306	0.010	-0.063	**-0.346**	0.258	0.173	**0.797**	
Mass >500μm sediment	**-0.391**	-0.295	**-0.480**	0.202	0.156	0.223	**0.367**	**0.368**

Table 10 Results of BIOENV analysis, comparing environmental variables with biotic data in mussel beds from a) six different habitats on the shore at Point Lynas, Anglesey and b) five different habitats on the shore at White Beach, Anglesey. 'Best' variable combinations are based on Spearman rank correlation's between square root and presence/absence transformed biotic data and environmental parameters are given for each site.

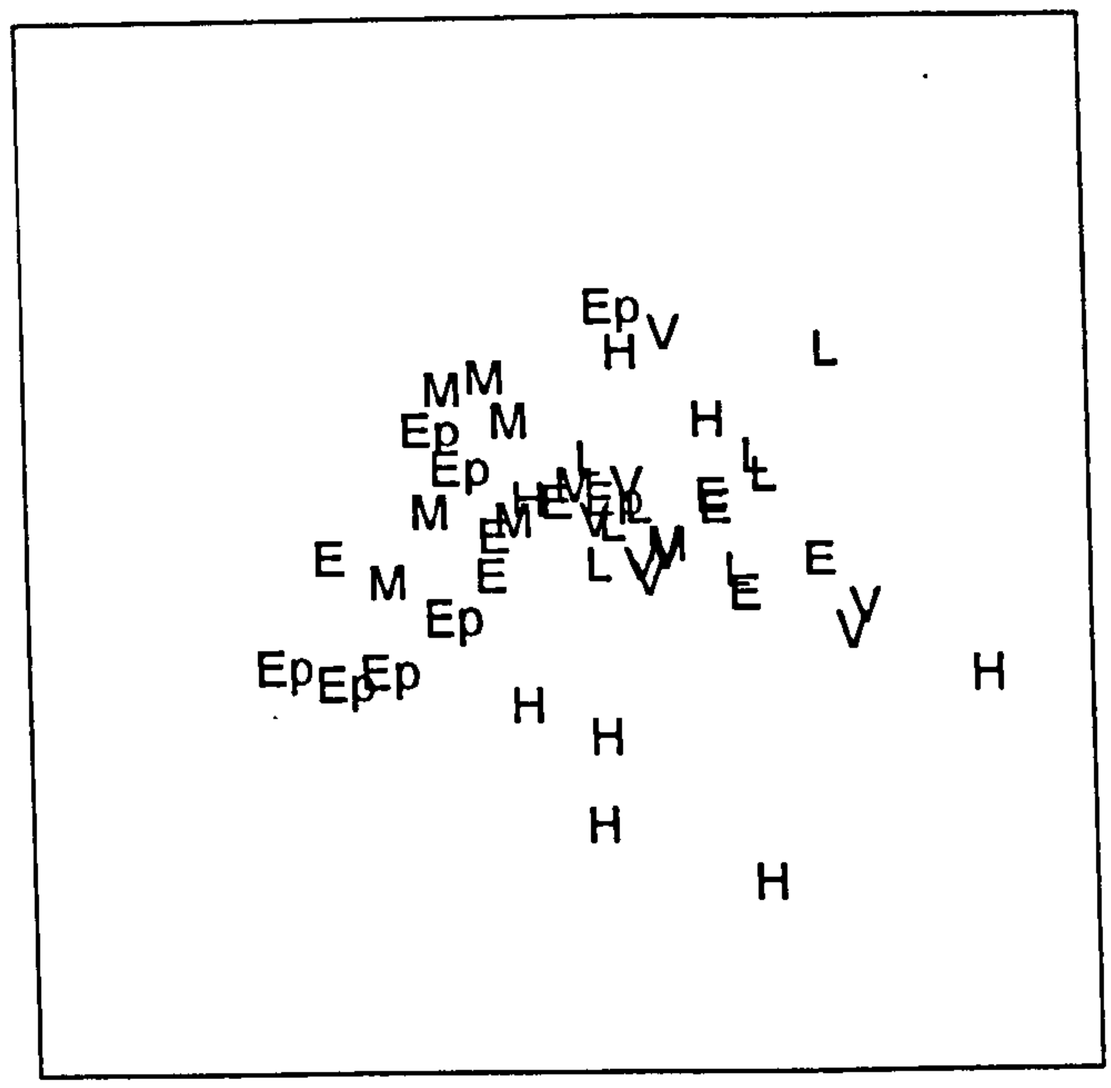
a)

Best Variable Combination	
Square-root transformation (r_s = 0.285)	Presence/absence transformation (r_s = 0.129)
Total number of mussels	Total number of mussels
Mass of mussels	Mass 125-250μm sediment
Mass 125-250μm sediment	Mass 250-500μm sediment

b)

Best Variable Combination	
Square-root transformation (r_s = 0.431)	Presence/absence transformation (r_s = 0.456)
Total number of mussels	Total number of mussels
Mean size of mussels	Mean size of mussels
Mass 250-500μm sediment	Mass of mussels
Mass >500μm sediment	Mass <63μm sediment
	Mass 125-250μm sediment
	Mass 250-500μm sediment

a)



b)

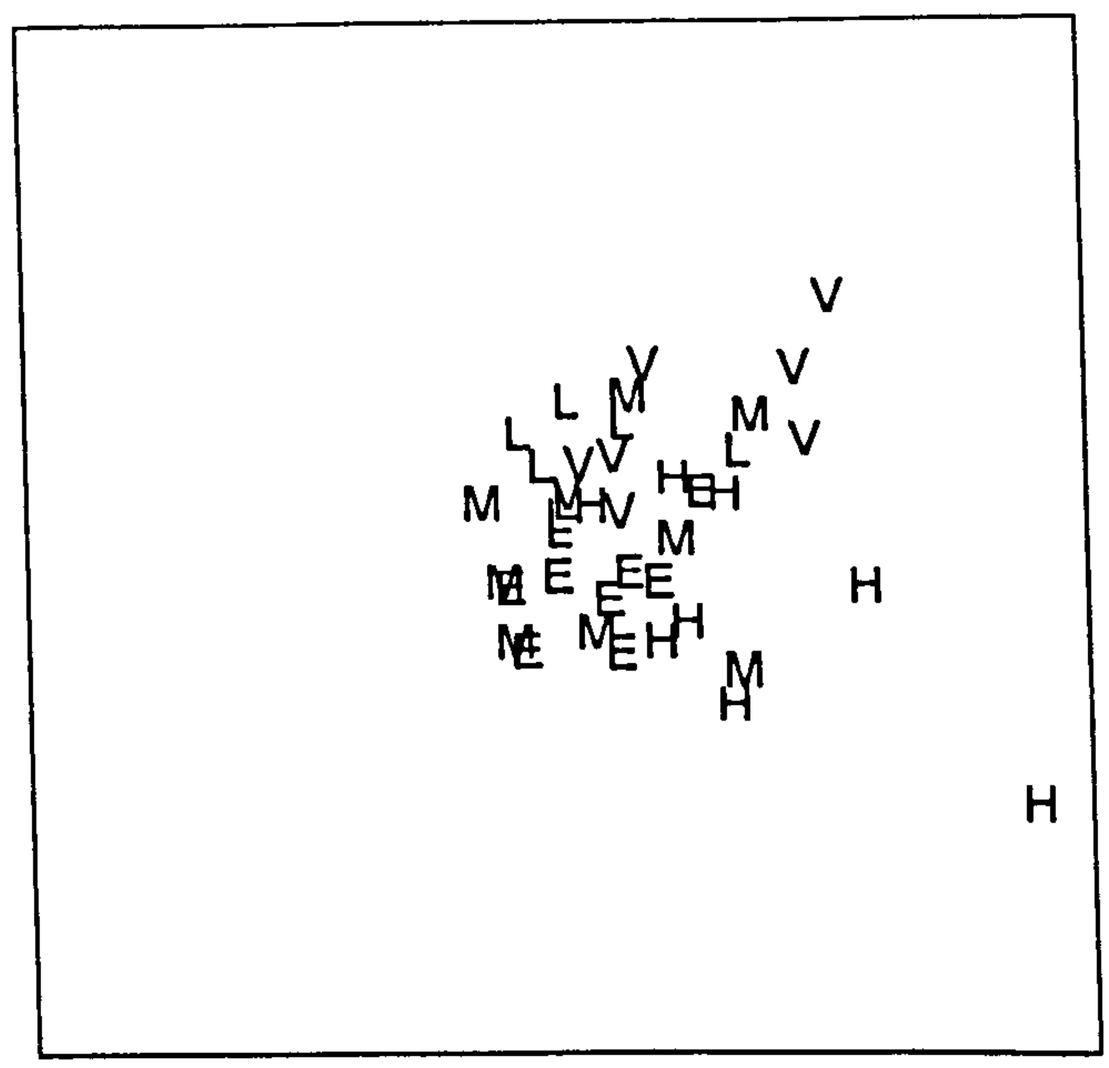


Figure 8 Ordination by PCA, using normalised Euclidean distance, of environmental variables measured in mussel beds from a) six different habitats on the shore at Point Lynas, Anglesey and b) five different habitats on the shore at White Beach, Anglesey. (L = Low shore, mid patch; M = Mid shore, mid patch; H = High shore, mid patch; E = Edge of patch, mid shore; V = Vertical surface, mid shore; Ep = Epifloral covering, mid patch, mid shore).

the Point Lynas environmental data similarity matrix, produced using normalised Euclidean distance and the biotic data similarity matrix, produced using Bray-Curtis similarity with a square-root transformation showed the two to be significantly different ($R=0.253$, $p<0.05$). The same analysis performed between the environmental data matrix and the biotic data matrix produced using a presence/ absence transformation revealed that the two were significantly correlated ($R=0.037$, $p>0.05$). RELATE analysis between the White Beach environmental data similarity matrix, produced using normalised Euclidean distance and the biotic data similarity matrices, produced using Bray-Curtis similarity with a square-root and presence/absence transformation showed significant differences ($R=0.344$, $p<0.05$; $R=0.431$, $p<0.05$).

In summary, communities associated with *M. edulis* showed significant small-scale spatial variation at two sites on Anglesey, both at the univariate and multivariate level. Differences in the abundance of around 16 of the more common members of the community were responsible for intra-site variation at both Point Lynas and White Beach. When data were analysed at the presence/absence level, clear intra-site differences still emerged. Environmental factors measured in the mussel beds did not fully account for the observed variations in community structure.

DISCUSSION

Small-scale spatial variations amongst the fauna associated with *M. edulis* on a wave-exposed rocky shore in North Wales, similar to those described in this study have been described elsewhere. For example, Lintas and Seed (1994) observed marked intersite variations both in the abundance and distribution of the mussel and its associated fauna; the highest diversity was found in mussel patches on the low shore. Similarly, Tsuchiya and Nishihira (1985, 1986) reported significant small-scale variations in the structure of invertebrate communities associated with *M. edulis* on rocky shores in Japan whilst Jacobi (1987a) noted small-scale variations in the distribution of amphipods in intertidal *Pema pema* beds in Brazil. Ong Che and Morton (1992) found that a large degree of local patchiness occurred in the communities associated with *Septifer virgatus* on wave-exposed rocky shores in Hong Kong. Seed and Brotohadikusumo (1994) found marked small-scale spatial variations in the abundance and distribution of the molluscan faunal associates of the same mussel populations. Tokeshi (1995) found significant spatial variations in the polychaete assemblages associated with *Perumytilus purpuratus* beds on a Pacific South American shore.

Mussel communities at Point Lynas and White Beach were diverse, but were dominated by a small number of taxa, some of which were common to the two locations, for example, small mussels, nematodes, mites, ostracods, oligochaetes and chironomid larvae. Other were specific to one shore or the other, for example, barnacles were much more prevalent at Point Lynas than White beach, which in turn supported a greater number of isopods and amphipods. These same taxa were those primarily responsible for small-scale variations in community structure, both between different habitats on the shores and between replicates within habitats. Similarly, Underwood and Chapman (1998) found, in a study of the spatial variation in rocky intertidal assemblages in south-eastern Australia, that few species characterised the assemblages, while even fewer discriminated between different levels on a shore. Although, Peake and Quinn (1993) found a total of 56 macroinvertebrates species associated with clumps of *Brachidontes rostratus* in south-eastern Australia, they found that the mussel community was dominated by a few every abundant species, namely the bivalves, *Lasaea australis* and *Xenostrobus pulex*, the barnacle *Chthamalus antennatus*, and the gastropod *Nodolittorina unifasciata*. Ong Che and Morton (1992) recorded at least 52 macroinvertebrate species associated with the mussel *Septifer virgatus* at a wave-exposed site in Hong Kong. They found that 75% of the individuals present comprised of three species, namely, *Lasaea nipponica*, *Chthamalus sinensis* and *Hyale* sp. The same pattern was found in communities associated with deep-sea hydrothermal vent mussels, with large numbers of individuals from a small number of species (Van Dover and Trask,. 2000).

Since the data are of an observational nature, it is not possible to explain the spatial variations in the structure of the assemblages associated with mussels at Point Lynas and White Beach, in terms of specific ecological mechanisms. However, it is possible to hypothesise about some potential causes. Bowers and Brown (1982) stated that local communities are non-random assemblies of those available and patterns of local assembly are predictable in the context of microhabitat variation. In addition, Tokeshi (1995) stated that spatial dispersion patterns are considered to reflect the behavioural response of organisms to a range of biotic/abiotic environmental factors, often mediated by some stochasticity in dispersal patterns.

Mussel patches are isolated from similar patches on rocky shores and as such can be treated as islands for their associated communities, so that many of the species-area theories developed using island ecosystems can be applied to mussel bed communities (Tsuchiya and Nishihira, 1985). It is generally accepted that larger islands support more species (MacArthur and Wilson, 1967; MacArthur, 1972).

Tsuchiya and Nishihira (1985) demonstrated that increasing mussel patch size significantly increased the diversity of the community associated with *M. edulis* and concluded that this effect was probably due to the increased environmental heterogeneity and favourable conditions in larger patches. However, in the present study, samples were collected from mussel patches of a similar size in order to reduce such effects of patch size. It is unlikely therefore that the observed small-scale variations in mussel community structure were due to different patch sizes. In addition, during their study of patch size effects on mussel bed diversity, Tsuchiya and Nishihira (1985) did not consider the effects of tidal level on community structure. Svane and Setyobudiandi (1996) concluded that species diversity, abundance and distribution of the organisms associated with *M. edulis* in Danish fjords were not correlated with patch size.

Environmental heterogeneity has often been suggested as a possible cause for spatial variations in community structure and it has been shown to be the case for a variety of marine communities, including those of subtidal reefs (Pimm, 1994), and temperate rocky intertidal shores (Bergeron and Bourget, 1986; Bourget *et al*, 1994; Archambault and Bourget, 1996; Thompson *et al*, 1996). In addition, studies have demonstrated that the rocky substratum can influence the structure of assemblages (e.g. McGuiness, 1988, 1990; Underwood and Chapman, 1998). However, in the present study, geological differences cannot be used as an explanation for the differences in assemblage structure, since the two shores were both characterised by the same igneous rock-type. However, small-scale topographical heterogeneity provided by interstices and crevices underlying the mussel matrix might in part account for the observed spatial variations in community structure, since other studies have demonstrated the positive effects of such features on diversity of communities in the intertidal environment (Emson and Faller-Fritsch, 1976; Raffaelli and Hughes, 1978; Menge, 1983, Archambault and Bourget, 1996). Some significant spatial variation was observed in the measured environmental variables in the present study, such as sediment fractions and mussel density, biomass and volume, which appeared to account to some extent, for variations in community structure in the mussel assemblages. Correlation's calculated between the environmental variables measured and the biotic data in the BIOENV procedure were not exceptionally high, although there did appear to be some correlation between increasing mussel density and length and sediment content and the structure of the associated community. Similarly, Svane and Ompi (1993) reported differential size distributions of mussels related to position within a patch, which might account for variations in the associated community. In addition, Svane and Setyobudiandi (1996)

concluded that in mussel beds in Danish fjords, the dominant taxa were associated with the organically enriched sediment (faeces or pseudofaeces) found between the mussels. Jacobi (1987a) concluded that spatial differences in the amphipods associated with *Perna perna* in Brazil were due mainly to differences in the sediment content of the mussel beds. The author concluded that a certain amount of fine sediment appeared to enhance diversity while an excess had the opposite effect, by hampering the settlement of some species and clogging respiratory or feeding structures. In the present study, fine sediments in the mussel bed probably result in increased abundance of infaunal taxa such as nemerteans and nematodes.

Tsuchiya and Nishihira (1985) demonstrated that the position in the mussel patch had a significant effect on the diversity of the associated community. The authors found that species richness and equitability were greater in central portions of the mussel bed than around the periphery. This, they concluded was a reflection of the increased amounts of sediment, shell fragments and byssal threads in the central, older, more stable portion of the bed. In the present study, peripheral areas of the mussel beds had lower coarse sediment contents than other areas, and this might have accounted for the observed reduced values of univariate measures of community diversity. In addition, lower diversity in the peripheral areas of the mussel beds probably reflected a reduction in protection from extremes of light, temperature and wave action provided on the perimeter of patches compared to the central portion (Suchanek, 1980; Seed and Brotohadikusumo, 1994).

Many patch dynamic models describe processes occurring within patches and successional mechanisms of species replacement, including stochastic processes (Connell, 1978; Connell and Keough, 1985; Sousa, 1984). Svane and Setyobudiandi (1996) concluded that the observed differences in the numbers and abundance of species in mussel beds in Danish fjords could largely be explained by differences in food and seston dynamics throughout the mussel bed. However, in mussel beds the food resource for the associated fauna is complex and competitive abilities of the individual species are difficult to quantify and thus difficult to link to assemblage structure. Underwood and Chapman (1998) suggested that differences in the recruitment of various conspicuous species might be the cause of spatial variations in the structure of intertidal communities at different sites on a sheltered rocky shore in south-eastern Australia. These investigations concluded that some sites had received more recruits of a particular species than at other sites on the same shore. Such variations in larval recruitment are a possible cause for the observed spatial differences in mussel community structure in the present study and would require further investigation. Behavioural differences in the species present in

the mussel beds might account in part for the observed spatial differences in community structure. Such a phenomenon was observed on rocky shores in south-eastern Australia, where the gastropods *Nerita atramentosa* and *Morula marginalba* were crevice bound during inclement weather, but foraged when they could, creating patchiness in the surrounding fauna (Fairweather, 1988; Underwood and Chapman, 1998). In mussel beds in the present study, foraging behaviours of many of the mobile taxa such as *Nucella lapillus*, *Hyale prevostii*, *Idotea pelagica* and nemerteans for example, probably account for some of the observed spatial distributions.

Many workers have documented positive and negative species associations within intertidal assemblages. Hacker and Gaines (1997) stated that they are generally accepted as important processes in communities and are most common in environments with relatively high levels of physical disturbance, stress or predation. In a study of spatial variations in the structure of intertidal assemblages in south-eastern Australia, Underwood and Chapman (1998) found that many of the species showed large interactions between sites. The authors went on to conclude that given these species were those ones contributing most to differences among assemblages, the whole assemblages were also likely to be interacting. The community structure in any place was largely an outcome of the interactions among components of an assemblage that happen to be present or numerous in different places. Hacker and Gaines (1997) demonstrated a number of species interactions, in an experimental study of species interactions in a salt marsh habitat in New England, North America. Several interactions were observed between taxa in the present study, the strongest of which were all positive associations, for example, between the two polychaete species *Tharyx marioni* and *Lagisca extenuata* and turbellarians and the polychaete *Brania pusilla*. Since data were all of an observational nature, it is not possible to conclude whether the presence of one taxa encouraged the presence of another, or if both were simply present due to mutually favourable environmental conditions.

The present study demonstrates the importance of using a small-scale resolution to measure biodiversity in assemblages such as those associated with mussel beds. The results demonstrate the great natural variability in patterns of intertidal assemblages. Although there was a subset of taxa that tended to characterise and/or differentiate mussel communities in habitats within each of the shores, the results generally support the view that assemblages on rocky shores are spatially dynamic in composition. Despite a few general features, most of the taxa are present or absent independently of the construction of the assemblage. This is consistent with the findings of many other studies of rocky shore communities, for example, in California (Foster, 1990), New South Wales, Australia (Kennelly and

Underwood, 1992; Underwood and Chapman, 1998) and Canada (Bourget *et al*, 1994; Archambault and Bourget, 1996).

Chapter 5

Large-scale spatial variation in the structure of the invertebrate communities associated with *Mytilus edulis* and *Perumytilus purpuratus*

ABSTRACT

Communities associated with *Mytilus edulis* and *Perumytilus purpuratus*. *purpuratus* showed significant inter-site variation, when analysed using both univariate and multivariate techniques. Inter-site differences in community structure were partially the result of differences in the suite of taxa present and partially the result of differences in the abundance of taxa common to all sites. The mussel communities at different sites were often characterised by quite different assemblages, although some taxa such as nematodes, nemerteans, larvae of the insect genus *Clunio*, mites, juvenile mussels and the isopod *Jaera albifrons* in *M. edulis* beds and nematodes, juvenile mussels, nereid polychaetes and anemones in *P. purpuratus* beds, were consistently present, often in similar numbers, at all or most sites. Other taxa were present in mussel beds only at certain sites. Some of the measured environmental factors of the mussel beds also showed significant inter-site variations, although analysis failed to reveal any strong relationships between the abiotic and biotic parameters of the mussel beds. When analysed at higher taxonomic levels, the structure of the communities associated with *M. edulis* and *P. purpuratus* showed significant differences. Univariate measures of community structure diversity were greater in *M. edulis* beds, although dominance curves for the two species were remarkably similar. Multivariate analysis revealed significant differences in community structure and showed that *M. edulis* beds were characterised by an abundance of nematodes, nemerteans, juvenile mussels, insect larvae, mites, isopods and gastropods, while *P. purpuratus* beds were characterised by nematodes, oligochaetes, juvenile mussels, barnacles, amphipods and syllid and nereid polychaetes. Environmental factors measured in the mussel beds failed to account for all of the observed large-scale spatial variation in the structure of these mussel communities. It is thus likely that in the present study, the geographic differences in community structure at each of the sites in the British Isles, Irish Republic and Chile are due to many different processes, together with stochastic events.

INTRODUCTION

Mussels, particularly of the genus *Mytilus*, occur throughout the cooler waters of the northern and southern hemispheres, along a variety of shore habitats (Bayne, 1976). Several studies have described the diverse infaunal assemblages associated with such intertidal mussel beds (e.g. Suchanek, 1979; Tsuchiya and Nishihira, 1985, 1986; Lintas and Seed, 1994; Seed, 1996). Due to the small size and immobility of sessile invertebrate species of marine epifaunal communities, such as those associated with mussel beds, these habitats are ideal for studying patterns of change in species composition and diversity (Osman, 1977). In addition, intertidal mussels form very similar matrices on wave-exposed rocky shores throughout the world, providing a similar habitat for colonisation by a suite of species (Seed and Suchanek, 1992; Seed *et al*, 2000). Thus, the infaunal communities associated with intertidal mussel beds offer an ideal opportunity to study variations in community structure across a wide geographical range.

The analysis of spatial patterns in species abundance is an essential basis for understanding scales at which organisms interact with one another or with their environment, and the relative importance of different ecological processes which may determine these patterns (Underwood and Chapman, 1996). Thus a complete understanding of the structure of any community can only be possible when geographical variation is encompassed (Morris, 1990). However in the past, small-scale patterns of community structure have been erroneously extrapolated to landscape and geographic scales (Murdoch and Aronson, 1999), although geographical variation in the structure of communities has been noted in a wide variety of habitats, including ant communities in Costa Rica (Longino, 1989); amphibian communities in Borneo forests (Inger and Voris, 1993) and freshwater fish in the Wet Tropics of Queensland, Australia (Pusey and Kennard, 1996). This phenomenon has also been documented for various intertidal marine habitats, such as temperate and tropical intertidal flats in Australia (Dittman, 1990; 1995), rocky shore communities in New England (Menge, 1991a), intertidal sediments in the northern Wadden Sea (Reise *et al*, 1994), intertidal rocky shore communities in New South Wales, (Underwood and Chapman, 1996) and brackish water fauna (Cognetti and Maltagliati, 2000).

Information regarding the geographical variation in the diverse invertebrate communities associated with intertidal mussel beds is somewhat lacking, although a number of studies describing these infaunal assemblages have been undertaken in various geographical locations for example, in North America (Suchanek, 1979), Japan (Tsuchiya and Nishihira, 1985, 1986) and the UK (Lintas and Seed, 1994).

Kanter (1980) did conduct a study of patterns in the structure of communities associated with *Mytilus californianus* from the southern Californian Bight. However, none of these studies of mussel bed communities investigated patterns of change across a range of locations, thus encompassing a variety of environmental conditions. In addition, very different sampling protocols were employed for each of the studies. Many authors have highlighted the importance of standardised sampling procedures in comparative ecological studies. For example, Underwood (1992) pointed out, that in studies of community structure, an appropriate combination of replicated sampling, at appropriate scales is absolutely mandatory before any attempt to determine potential impact is likely to succeed. Similarly, other authors have stated that simple decisions about sampling approach in ecological field studies can influence species abundance estimates significantly (e.g. Green, 1979; Hurlbert, 1984; Andrew and Mapstone, 1987; Eberhardt and Thomas, 1991; Miller and Ambrose, 2000). In addition, the infaunal communities associated with mussel beds have been shown to vary temporally. Briggs (1982) reported significant seasonal variation in the fauna associated with *M. edulis* in Loch Foyle, Ireland, while Tsuchiya and Nishihira (1985) found similar patterns in associates of the same mussel species in Japan. Peake and Quinn (1993) have reported seasonal variations in the infaunal associates of *Brachidontes rostratus* in Australia, while Jacobi (1987a) found seasonal differences in the abundance of amphipod associates of mussel beds from the Bay of Santos, Brazil. Similarly, Tokeshi (1995) reported significant differences in the abundance of polychaetes associated with mussel beds on South American shores. Thus, comparisons of the structure of the infaunal communities associated with mussel beds, based on the results of individual studies in different locations, should be undertaken with caution, since temporal variation or differences due to inconsistent sampling or sorting protocols might confound any geographical variation in community structure. It is clear that any investigation of the geographical variation associated with the structure of mussel bed communities must eliminate such possible sources of variation.

In this chapter the variation in the invertebrate communities associated with *Mytilus edulis* and *Perumytilus purpuratus* on eight rocky shores around the coast of the British Isles (England, Wales and Scotland) and Irish Republic and nine along the coastline of Chile, South America, is investigated, using both a univariate and a multivariate approach. Comparisons are made between sites in each country, to investigate geographical patterns of variation in community structure, on a similar temporal scale. The extent to which various environmental parameters of the mussel beds influence community structure, such as mussel density and the volume and

mass of sediment fractions, together with conditions of wave-exposure, is also investigated in the UK. In addition, inter-continental variation in mussel community structure is investigated, by comparing mussel communities in the UK and Chile.

METHODS

Samples were collected on spring tides from *M. edulis* beds at eight sites in the British Isles and Ireland during June and July 1999 and from *P. purpuratus* beds at nine sites in Chile, South America during January 1999, with the exception of samples at Valdivia, which were collected during January 1998. Details of each of these sites are provided in Chapter 2. Samples were processed and sorted according to the methodology described in Chapter 2.

RESULTS

Large-scale spatial variation in the community associated with M. edulis

A total of 45339 infaunal organisms representing 168 different taxa were collected and identified from mussel beds at the eight locations within the UK. All of the univariate measures of community diversity, i.e., total number of taxa, total number of individuals, Margalef's Index of richness, Shannon's Index of diversity and Pielou's evenness showed significant variation between the eight sites (Table 1). Significantly more taxa were present in mussel beds at sites in England, Ireland and Criccieth than at Point Lynas, White Beach and Arisaig in Scotland (Figure 1). A similar pattern was observed for the total number of individuals present in the mussel beds, with significantly fewer individuals at Point Lynas and White Beach than at all the other sites. Margalef's index of richness was greatest for mussel bed communities from the Irish sites and Robin Hood's Bay and lowest at Point Lynas, White Beach and Arisaig. Similarly, Shannon's index of diversity was greatest at the Irish sites and Robin Hood's Bay and lowest at Point Lynas, White Beach and Filey Brigg. Pielou's Eveness was similar at all sites, except for a particularly low value at Filey Brigg.

Cluster analysis of square-root transformed infauna abundance showed clear differences in community structure between the eight locations, in terms of the more dominant taxa in the community (Figure 2). Similar clear differences in community structure emerged between the eight locations when cluster analysis was performed with a presence/absence transformation, thus removing emphasis from taxa abundance (Figure 3). MDS ordination of square-root transformed infaunal abundance illustrated a clear separation of mussel bed communities at each of the eight locations, in terms of the more dominant taxa in the community (Figure 4a).

Table 1 One-way ANOVA/Mood median tests between univariate measures of diversity calculated for mussel bed communities at eight locations in the British Isles and Irish Republic. Significant differences are indicated by * ($p<0.05$).

Univariate Measure	*F- value*	χ^2 *- value*
Total taxa	7.24*	-
Total individuals	-	32.00*
Margalef's richness	4.28*	-
Shannon's diversity	-	29.00*
Pielou's evenness	9.89*	-

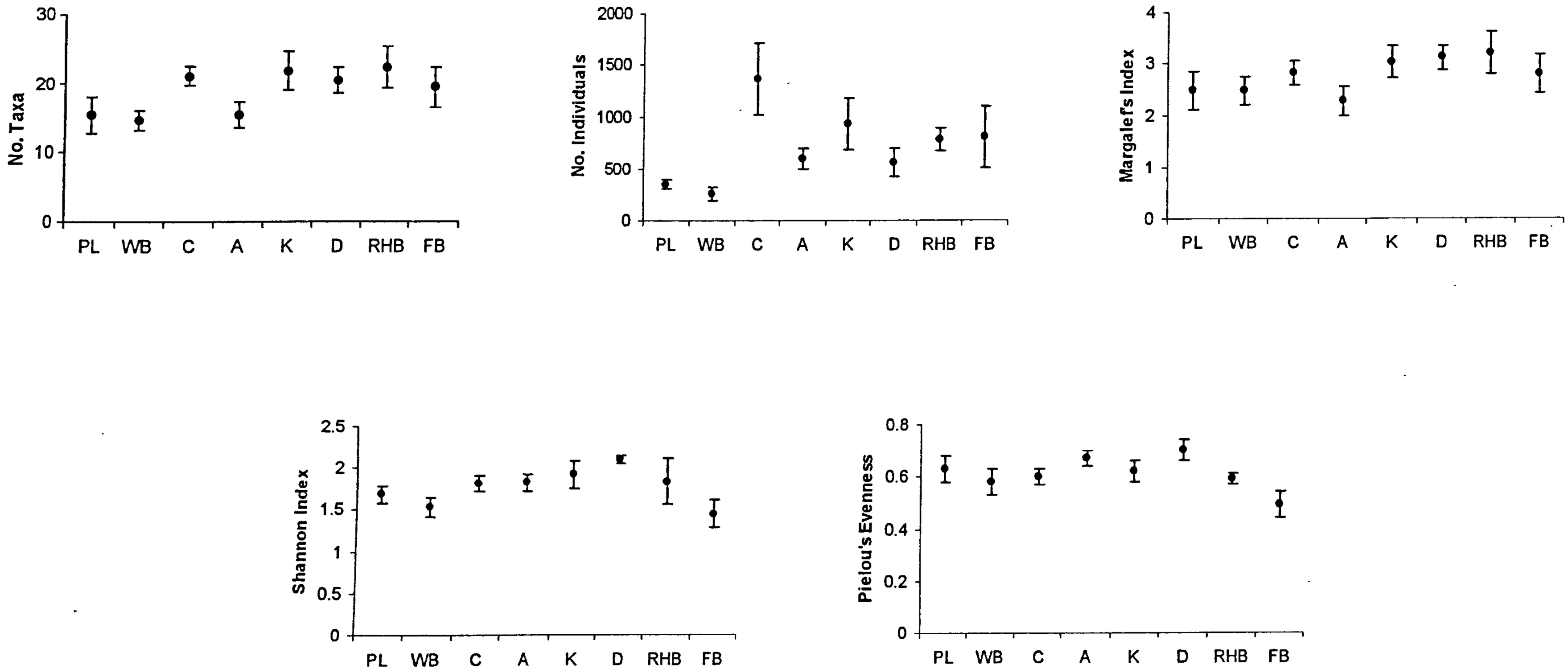


Figure 1 Univariate measures of mussel bed community diversity at Point Lynas (PL), White Beach (WB), Criccieth (C), Arisaig (A), Kilkee (K), Doonbeg (D), Robin Hood's Bay (RHB) and Filey Brigg (FB). Values are based on 25cm^2 replicates. 95% confidence intervals are marked, such that significant differences are represented by non-overlapping intervals.

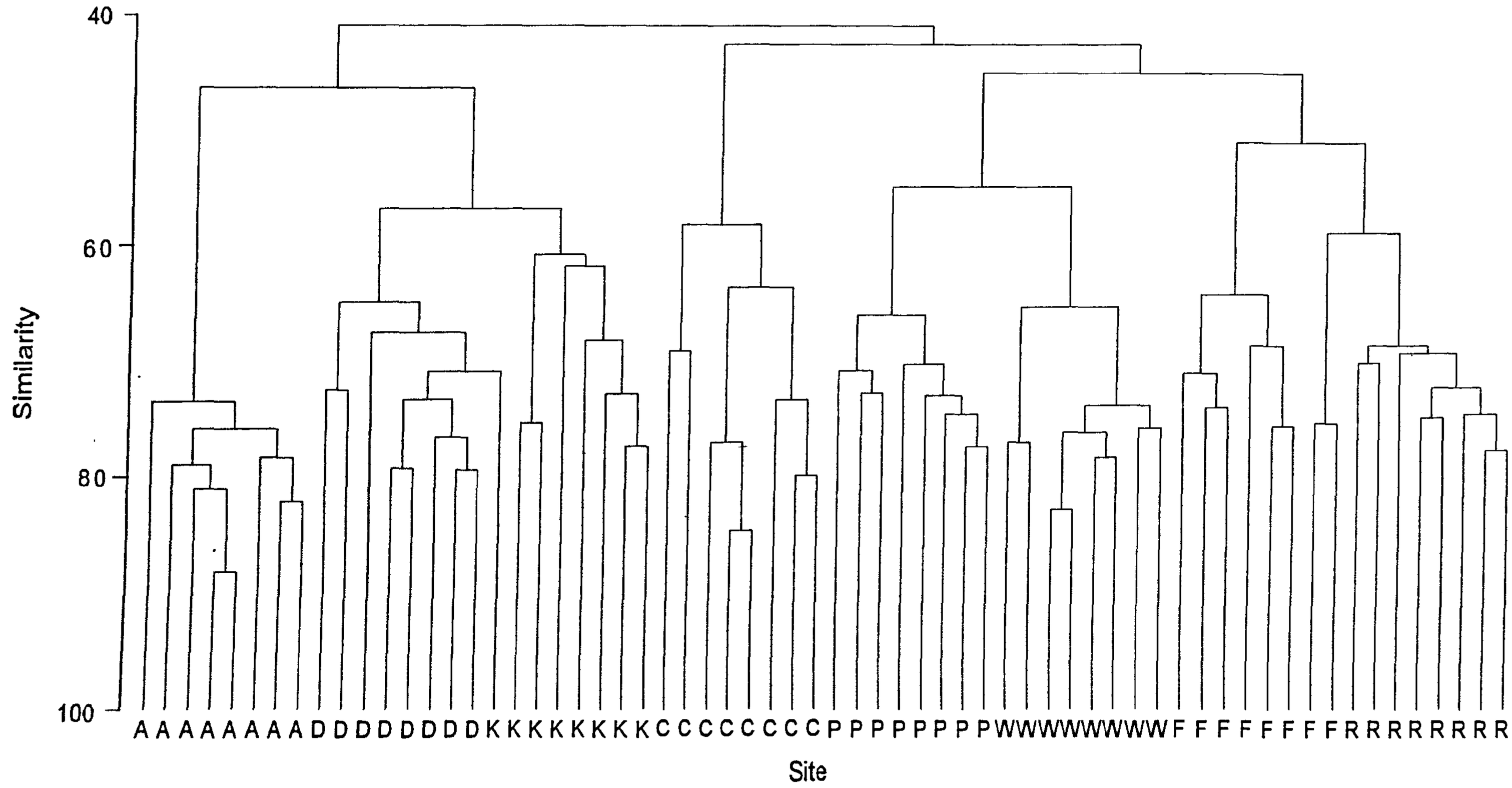


Figure 2 Dendrogram for group average clustering of Bray-Curtis similarities based on square-root transformed biotic data from mussel beds at eight locations in the British Isles and Irish Republic. (P = Point Lynas, Wales; W = White Beach, Wales; C = Criccieth, Wales; A = Arisaig, Scotland; K = Kilkee, Irish Republic; D = Doonbeg, Irish Republic; R = Robin Hood's Bay, England; F = Filey Brigg, England).

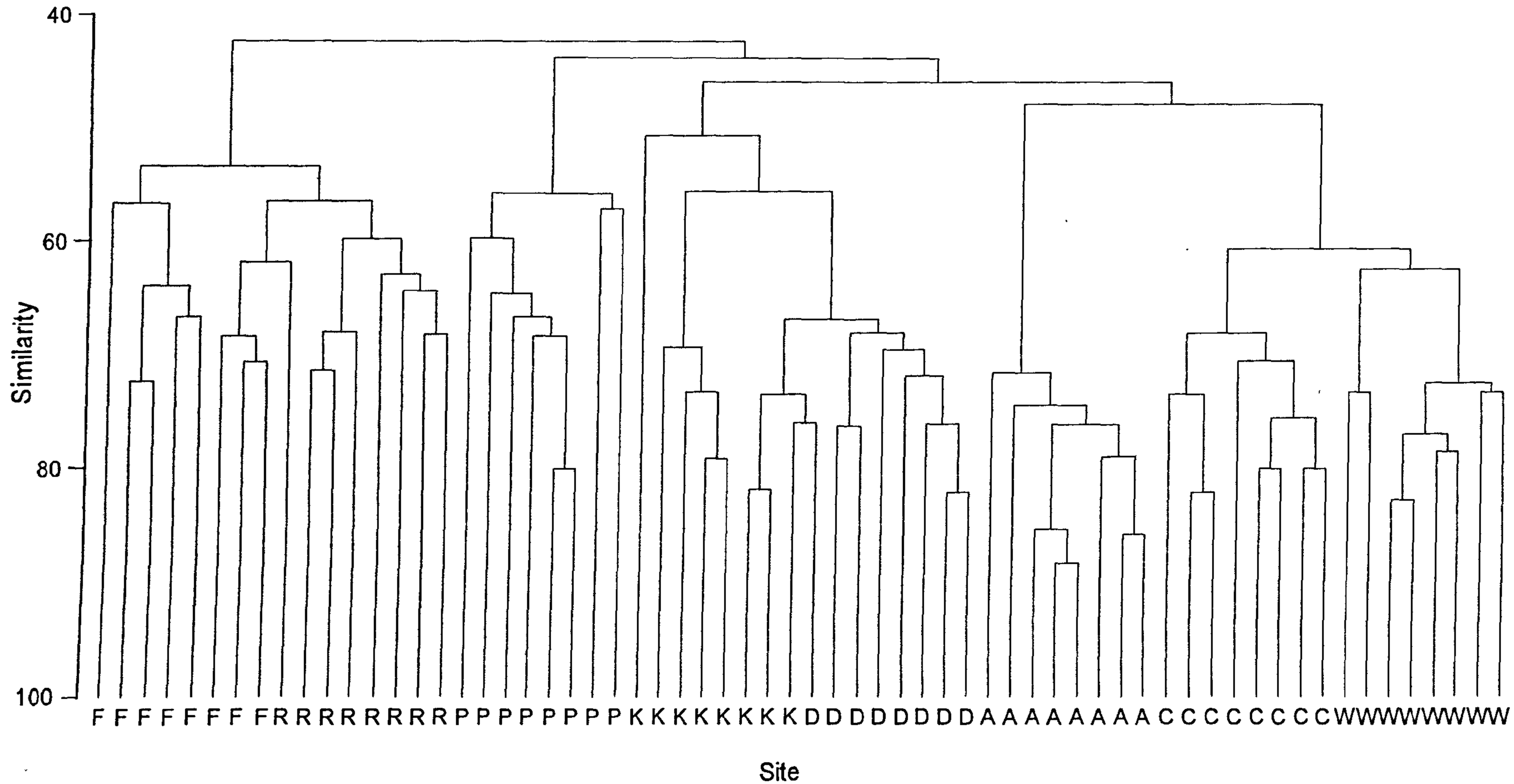


Figure 3 Dendrogram for group average clustering of Bray-Curtis similarities based on presence/absence transformed biotic data from mussel beds at eight locations in the British Isles and Irish Republic. (P = Point Lynas, Wales; W = White Beach, Wales; C = Criccieth, Wales; A = Arisaig, Scotland; K = Kilkee, Irish Republic; D = Doonbeg, Irish Republic; R = Robin Hood's Bay, England; F = Filey Brigg, England).

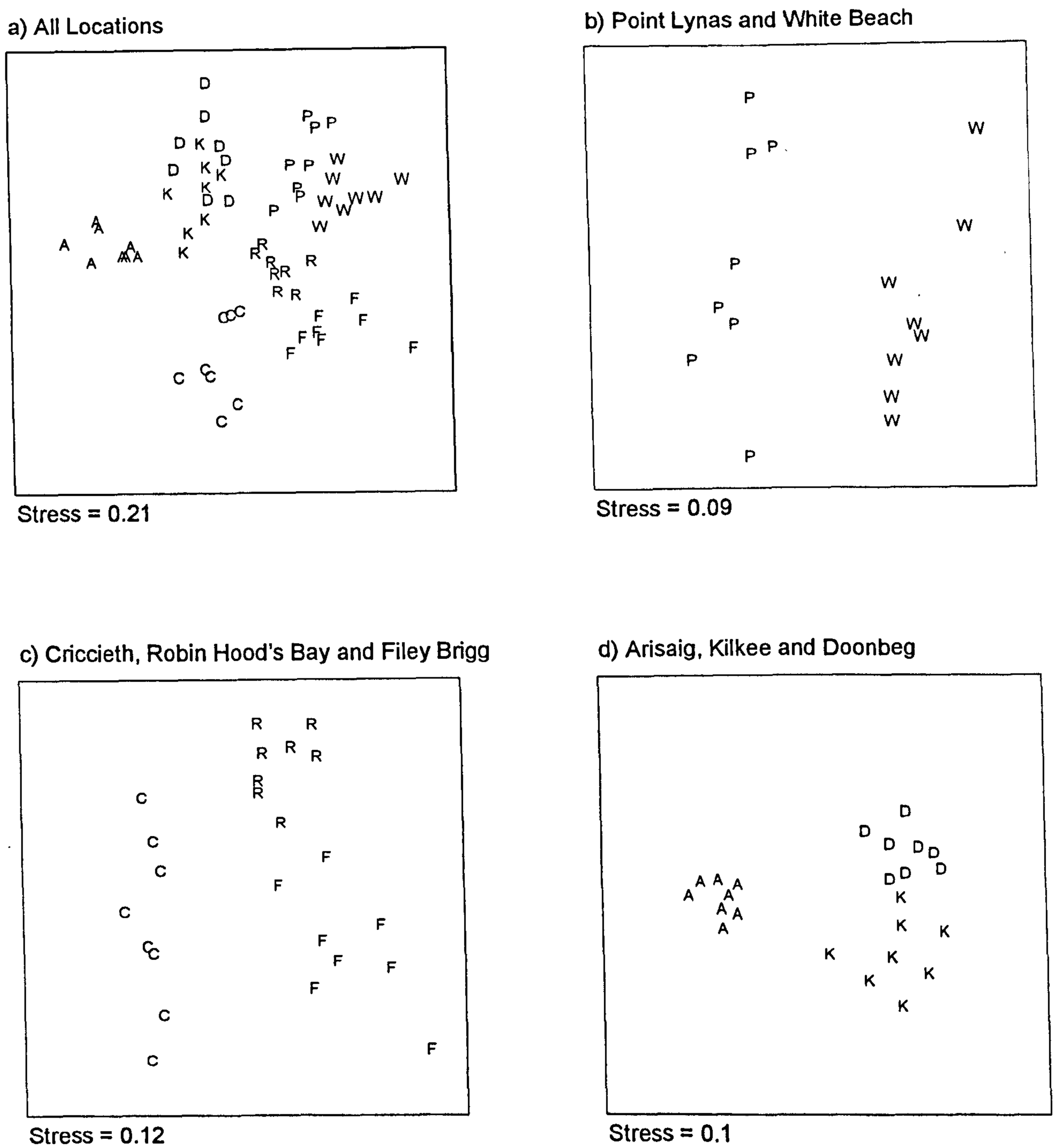


Figure 4 Ordination by MDS based on Bray-Curtis similarity, of square-root transformed taxa abundance data from mussel beds at a) eight different locations in the British Isles and Irish Republic (50 most important taxa), b) Point Lynas and White Beach (all taxa), c) Criccieth, Robin Hood's Bay and Filey Brigg (all taxa) and d) Arisaig, Kilkee and Doonbeg (all taxa). (P = Point Lynas, Wales; W = White Beach, Wales; C = Criccieth, Wales; A = Arisaig, Scotland; K = Kilkee, Irish Republic; D = Doonbeg, Irish Republic; R = Robin Hood's Bay, England; F = Filey Brigg, England).

The high stress value of the MDS plot (0.21) reflected the difficulty of condensing such a large data set into two dimensions, despite only the 50 most important taxa (in terms of contribution to site differences) in the community being used in the analysis. Different sites were grouped according to clustering patterns in the original plot and re-plotted using the complete data set, for increased accuracy of interpretation (Figure 4b-d). A one-way ANOSIM test performed on the data confirmed that there were significant inter-site differences in community structure ($R=0.951$, $p<0.05$). ANOSIM pairwise comparisons revealed that the structure of the mussel community differed significantly between all of the eight sites (Table 2a). However, RELATE analysis showed that there was no significant pattern of seriation, or gradient underlying the MDS ordination of data ($R=0.382$, $p<0.05$).

MDS ordination performed with a presence/absence transformation on the 50 most important taxa abundance indicated similar patterns (Figure 5a), with replicates from each of the eight locations clustering together. Again, the plot had a high associated stress value (0.23), so sites were grouped together and re-plotted using the complete taxa data set (Figure 5b-d). A one-way ANOSIM test performed on the data confirmed that there were significant differences in community structure between some of the sites ($R=0.893$, $p<0.05$). Pairwise comparisons revealed that the structure of the mussel community was significantly different at all of the eight sites (Table 2b). RELATE analysis showed that there was no significant pattern of seriation, or gradient underlying the MDS ordination of data ($R=0.487$, $p<0.05$).

MDS ordination performed on square-root transformed biotic data did, however, show that sites generally clustered out into groups supplied by the same surface water currents (for surface water current details, see MAFF, 1981). Mussel communities at the sites on the west coast of the Irish Republic and Arisaig in Scotland cluster together, while Point Lynas and White Beach on Anglesey and Robin Hood's Bay and Filey Brigg on the NE coast of England form two groups; Criccieth remains quite distinct. Such patterns correspond closely to patterns of surface water movement around the coast of the British Isles. MDS ordination performed on presence/absence transformed biotic data does not correlate so closely with surface water patterns (Figure 5).

Similarity Percentage analysis (SIMPER), performed with a square-root transformation indicated that mussel bed communities at each of the eight sites in the UK were characterised by a quite different assemblage of numerically dominant taxa. However, some taxa were consistently dominant members of the infaunal communities at most or all sites, namely, nematodes, juvenile *Mytilus edulis*, Mite sp. 1, *Clunio* sp. larvae, nemerteans, and the isopod *Jaera albifrons*. Table 3 provides

Table 2 Global R-values for ANOSIM pairwise comparisons between samples of mussel bed communities at eight locations throughout the British Isles and Irish Republic, based on a) square-root transformations and b) presence/absence transformations of species abundance. Significant differences in community structure ($p<0.05$) are indicated by bold type (all differences are significant).

a)

	Point Lynas	*White Beach*	*Criccieth*	*Arisaig*	*Kilkee*	*Doonbeg*	*Robin Hood's Bay*
White Beach	**0.954**						
Criccieth	**0.995**	**0.944**					
Arisaig	**1.000**	**1.000**	**0.996**				
Kilkee	**0.977**	**1.000**	**0.996**	**0.987**			
Doonbeg	**0.994**	**1.000**	**0.987**	**1.000**	**0.681**		
Robin Hood's Bay	**0.961**	**0.999**	**0.973**	**1.000**	**0.966**	**0.991**	
Filey Brigg	**0.935**	**0.943**	**0.954**	**0.976**	**0.945**	**0.977**	**0.748**

b)

	Point Lynas	*White Beach*	*Criccieth*	*Arisaig*	*Kilkee*	*Doonbeg*	*Robin Hood's Bay*
White Beach	**0.905**						
Criccieth	**0.931**	**0.637**					
Arisaig	**0.964**	**0.990**	**0.960**				
Kilkee	**0.786**	**0.968**	**0.909**	**0.947**			
Doonbeg	**0.930**	**0.992**	**0.976**	**1.000**	**0.578**		
Robin Hood's Bay	**0.969**	**0.983**	**0.963**	**0.992**	**0.899**	**0.959**	
Filey Brigg	**0.912**	**0.921**	**0.884**	**0.952**	**0.943**	**0.980**	**0.513**

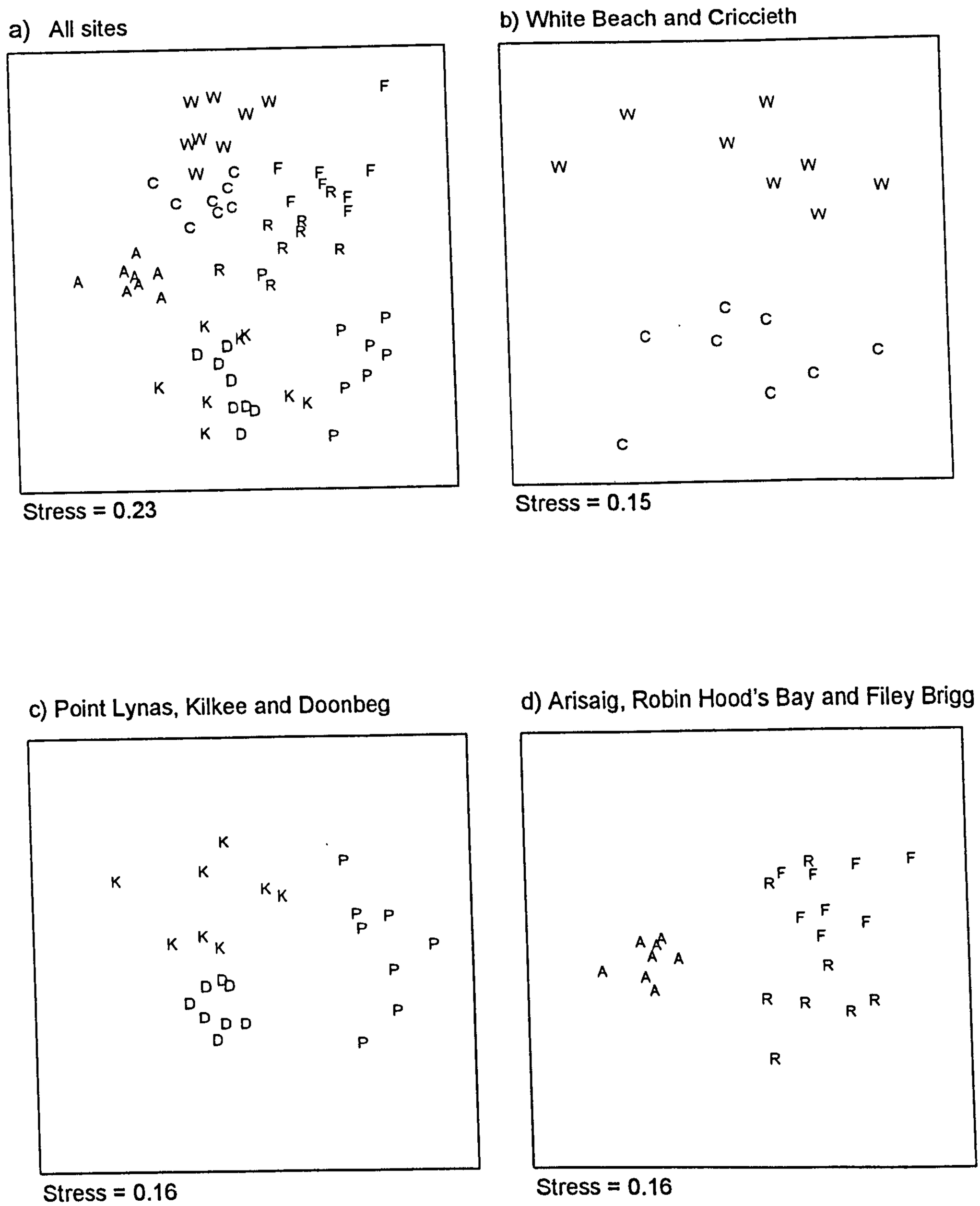


Figure 5 Ordination by MDS based on Bray-Curtis similarity, of presence/absence transformed taxa abundance data from mussel beds at a) eight different locations in the British Isles and Irish Republic (50 most important taxa), b) White Beach and Criccieth (all taxa), c) Point Lynas, Kilkee and Doonbeg (all taxa) and d) Arisaig, Robin Hood's Bay and Filey Brigg (all taxa). (P = Point Lynas, Wales; W = White Beach, Wales; C = Criccieth, Wales; A = Arisaig, Scotland; K = Kilkee, Irish Republic; D = Doonbeg, Irish Republic; R = Robin Hood's Bay, England; F = Filey Brigg, England).

Table 3 Results of similarity percentage analysis (SIMPER) performed on square-root transformed abundance of infaunal taxa present in mussel beds at eight locations in the British Isles and Irish Republic, showing a breakdown of % contributions of infaunal taxa (% Cont.) to average dissimilarity between locations. Taxa highlighted in grey indicate higher abundance at the first listed site.

Point Lynas, White Beach	% Cont.	Point Lynas, Criccieth	% Cont.	Point Lynas, Arisaig	% Cont.	Point Lynas, Kilkee	% Cont.	Point Lynas, Doonbeg	% Cont.	Point Lynas, Robin Hood's Bay	% Cont.	Point Lynas, Filey Brigg	% Cont.
Mite sp. 1	13.79	*Elminius modestus*	12.75	*Lasaea adansoni*	14.66	*Lasaea adansoni*	17.79	*Lasaea adansoni*	16.15	Juvenile *Mytilus edulis*	9.87	Juvenile *Mytilus edulis*	14.69
Leptocythere pellucida	7.01	*Jaera albifrons*	12.23	Mite sp. 1	8.94	Juvenile *Mytilus edulis*	6.78	*Skeneopsis planorbis*	7.26	*Modiolula phaseolina*	8.78	Mite sp. 1	7.14
Nematoda indet.	6.68	Nematoda indet.	10.93	*Jaera albifrons*	8.78	Nematoda indet.	6.13	Nematoda indet.	6.75	*Clunio* sp. larvae	8.48	Nematoda indet.	6.62
Idotea pelagica	6.04	*Leptocythere pellucida*	7.11	*Hyale prevostii*	8.71	*Fabricia stellaris*	5.81	*Modiolula phaseolina*	6.67	Nematoda indet.	6.89	*Clunio* sp. larvae	6.57
Clunio sp. larvae	5.68	Oligochaeta indet.	5.74	Nematoda indet.	6.46	*Clunio* sp. larvae	4.45	Mite sp. 5	4.68	*Elminius modestus*	5.49	*Brachystomia scalaris*	6.36
Nemertea indet.	5.55	Juvenile *Mytilus edulis*	4.82	*Tricolia pullus*	6.24	*Omalogyra atomus*	3.91	*Skenea serpuloides*	4.06	Mite sp. 1	5.01	*Modiolula phaseolina*	5.47
Juvenile *Mytilus edulis*	5.02	Mite sp. 1	4.65	*Clunio* sp. larvae	5.93	Mite sp. 1	3.83	Mite sp. 1	3.98	Oligochaeta indet.	3.45	*Pholoe inornata*	4.81
Brachystomia scalaris	4.14	*Skenea serpuloides*	3.15	Oligochaeta indet.	5.72	*Modiolula phaseolina*	3.71	*Tricolia pullus*	3.61	*Jaera albifrons*	2.78	*Semibalanus balanoides*	4.39
Foraminifera indet.	3.5	Foraminifera indet.	3.09	Juvenile *Mytilus edulis*	4.62	*Skenea serpuloides*	3.47	*Clunio* sp. larvae	3.48	*Leptocythere pellucida*	2.53	*Idotea pelagica*	3.86
Juvenile gastropoda indet.	3.48	*Clunio* sp. larvae	2.85			*Eulalia viridis*	3.40	*Jaera albifrons*	3.23	Nemertea indet.	2.46	Nemertea indet.	3.46
Jaera albifrons	2.64	*Idotea pelagica*	2.46			*Jaera albifrons*	2.63	Juvenile *Mytilus edulis*	3.01	*Eusyllis blomstrandi*	2.45	*Skenea serpuloides*	2.89
Carcinus maenas	2.30	*Rissoella opalina*	2.35			*Skeneopsis planorbis*	2.50	Nemertea indet.	2.99	*Skeneopsis planorbis*	2.26	*Hyale prevostii*	2.85
Dipteran larvae indet.	2.30					Oligochaeta indet.	2.42	*Brachystomia scalaris*	2.55	*Brachystomia scalaris*	2.24	*Elminius modestus*	2.58
Brania pusilla	2.29					Nemertea indet.	2.17	Oligochaeta indet.	2.24	*Semibalanus balanoides*	1.91		
						Hyale prevostii	2.12			Juvenile gastropoda indet.	1.89		
										Pholoe inornata	1.85		
										Rissoa parva	1.81		
Average dissimilarity between sites = 45.12%		Average dissimilarity between sites = 60.71%		Average dissimilarity between sites = 68.32%		Average dissimilarity between sites = 52.84%		Average dissimilarity between sites = 50.06%		Average dissimilarity between sites = 48.15%		Average dissimilarity between sites = 58.07%	

White Beach, Criccieth	% Cont.	White Beach, Arisaig	% Cont.	White Beach, Kilkee	% Cont.	White Beach, Doonbeg	% Cont.	White Beach, Robin Hood's Bay	% Cont.	White Beach, Filey Brigg	% Cont.
Elminius modestus	14.84	*Lasaea adansoni*	17.85	*Lasaea adansoni*	17.39	*Lasaea adansoni*	15.91	*Clunio* sp. larvae	10.64	Juvenile *Mytilus edulis*	15.52
Nematoda indet.	13.18	*Hyale prevostii*	10.12	Mite sp. 1	6.85	*Skenea serpuloides*	6.77	Mite sp. 1	8.72	*Brachystomia scalaris*	9.53
Jaera albifrons	13.00	*Jaera albifrons*	8.80	Juvenile *Mytilus edulis*	6.07	Nematoda indet.	6.16	Juvenile *Mytilus edulis*	8.66	Nematoda indet.	7.08
Oligochaeta indet.	6.52	*Tricolia pullus*	7.25	Nematoda indet.	5.66	Mite sp. 1	5.95	*Modiolula phaseolina*	6.87	*Pholoe inornata*	5.22
Juvenile *Mytilus edulis*	5.44	Nematoda indet.	6.94	*Fabricia stellaris*	5.41	*Modiolula phaseolina*	5.07	Nematoda indet.	6.30	*Modiolula phaseolina*	5.19
Leptocythere pellucida	5.36	Oligochaeta indet.	6.27	*Omalogyra atomus*	3.67	Mite sp. 5	4.73	*Elminius modestus*	5.05	*Clunio* sp. larvae	4.74
Skenea serpuloides	3.48	Juvenile *Mytilus edulis*	5.00	*Idotea pelagica*	3.33	*Idotea pelagica*	3.97	*Leptocythere pellucida*	3.98	*Semibalanus balanoides*	4.71
Clunio sp. larvae	3.30	*Leptocythere pellucida*	4.11	*Skenea serpuloides*	3.26	*Clunio* sp. larvae	3.92	*Idotea pelagica*	3.35	*Leptocythere pellucida*	4.25
Rissoella opalina	2.73	*Clunio* sp. larvae	3.84	*Eulalia viridis*	3.19	*Leptocythere pellucida*	3.84	Nemertea indet.	3.18	*Skenea serpuloides*	3.27
Foraminifera indet.	2.63			*Leptocythere pellucida*	3.19	*Skenea serpuloides*	3.45	Oligochaeta indet.	2.79	*Hyale prevostii*	3.07
				Nemertea indet.	2.95	*Tricolia pullus*	3.38	*Brachystomia scalaris*	2.29	*Idotea pelagica*	2.78
				Modiolula phaseolina	2.85	Juvenile *Mytilus edulis*	2.92	*Eusyllis blomstrandi*	2.22	*Elminius modestus*	2.77
				Skeneopsis planorbis	2.33	Nemertea indet.	2.62	Foraminifera indet.	2.15	Foraminifera indet.	2.36
				Clunio sp. larvae	2.23	*Carcinus maenas*	2.34	*Skeneopsis planorbis*	2.04		
				Jaera albifrons	2.14			*Carcinus maenas*	2.00		
Average dissimilarity between sites = 55.18%		Average dissimilarity between sites = 63.04%		Average dissimilarity between sites = 59.86%		Average dissimilarity between sites = 57.30%		Average dissimilarity between sites = 56.53%		Average dissimilarity between sites = 57.56%	

Criccieth, Arisaig	% Cont.	Criccieth, Kilkee	% Cont.	Criccieth, Doonbeg	% Cont.	Criccieth, Robin Hood's Bay	% Cont.	Criccieth, Filey Brigg	% Cont.
Nematoda indet.	14.10	*Lasaea adansoni*	10.64	*Elminius modestus*	10.96	*Jaera albifrons*	9.51	*Jaera albifrons*	9.83
Elminius modestus	11.01	*Elminius modestus*	10.46	Nematoda indet.	9.56	*Elminius modestus*	8.39	*Elminius modestus*	9.71
Lasaea adansoni	10.61	*Jaera albifrons*	8.19	*Jaera albifrons*	8.54	Nematoda indet.	8.36	Nematoda indet.	9.56
Leptocythere pellucida	6.40	Nematoda indet.	7.18	*Lasaea adansoni*	8.42	*Leptocythere pellucida*	6.52	Juvenile *Mytilus edulis*	6.11
Hyale prevostii	5.64	*Leptocythere pellucida*	5.43	*Leptocythere pellucida*	5.73	*Clunio* sp. larvae	5.84	*Leptocythere pellucida*	6.08
Jaera albifrons	4.83	Oligochaeta indet.	4.41	Oligochaeta indet.	4.75	*Modiolula phaseolina*	5.25	*Brachystomia scalaris*	5.03
Oligochaeta indet.	4.76	*Fabricia stellaris*	3.81	Juvenile *Mytilus edulis*	4.28	Mite sp. 1	5.18	Oligochaeta indet.	5.03
Tricolia pullus	4.76	Mite sp. 1	3.74	*Skeneopsis planorbis*	4.06	Oligochaeta indet.	4.99	*Clunio* sp. larvae	3.92
Clunio sp. larvae	4.03	*Skenea serpuloides*	3.04	*Modiolula phaseolina*	3.51	Juvenile *Mytilus edulis*	3.13	*Modiolula phaseolina*	3.50
Foraminifera indet.	2.97	*Clunio* sp. larvae	2.76	Foraminifera indet.	2.78	Foraminifera indet.	3.03	*Skenea serpuloides*	3.49
Juvenile *Mytilus edulis*	2.72	Foraminifera indet.	2.65	Mite sp. 5	2.69	*Skenea serpuloides*	2.72	*Pholoe inornata*	3.06
		Juvenile *Mytilus edulis*	2.52	Mite sp. 1	2.63	*Rissoella opalina*	2.22	*Semibalanus balanoides*	2.94
		Omalogyra atomus	2.44	*Idotea pelagica*	2.33	*Idotea pelagica*	2.21	Foraminifera indet.	2.86
		Modiolula phaseolina	2.25			*Hyale prevostii*	2.11		
		Idotea pelagica	2.22			*Semibalanus balanoides*	2.04		
Average dissimilarity between sites = 59.88%		Average dissimilarity between sites = 59.31%		Average dissimilarity between sites = 61.51%		Average dissimilarity between sites = 53.66%		Average dissimilarity between sites = 60.64%	

Arisaig, Kilkee	% Cont.	Arisaig, Doonbeg	% Cont.	Arisaig, Robin Hood's Bay	% Cont.	Arisaig, Filey Brigg	% Cont.
Nematoda indet.	9.70	*Hyale prevostii*	8.16	*Lasaea adansoni*	12.67	*Lasaea adansoni*	14.20
Mite sp. 1	8.33	Nematoda indet.	7.08	*Clunio* sp. larvae	10.18	Juvenile *Mytilus edulis*	7.52
Hyale prevostii	6.44	Mite sp. 1	7.06	Nematoda indet.	7.78	*Jaera albifrons*	6.90
Jaera albifrons	6.12	*Jaera albifrons*	6.44	Mite sp. 1	7.34	*Brachystomia scalaris*	6.86
Tricolia pullus	5.91	*Clunio* sp. larvae	6.40	*Hyale prevostii*	5.93	Nematoda indet.	6.79
Fabricia stellaris	5.24	*Skeneopsis planorbis*	5.77	*Modiolula phaseolina*	5.63	*Hyale prevostii*	5.63
Oligochaeta indet.	4.24	Oligochaeta indet.	5.38	*Jaera albifrons*	5.24	*Tricolia pullus*	5.58
Idotea pelagica	4.20	*Modiolula phaseolina*	5.30	*Tricolia pullus*	4.97	Oligochaeta indet.	5.39
Lasaea adansoni	3.87	Juvenile *Mytilus edulis*	5.17	*Idotea pelagica*	3.20	*Modiolula phaseolina*	4.36
Omalogyra atomus	3.42	*Idotea pelagica*	4.51	Oligochaeta indet.	3.13	*Pholoe inornata*	3.74
Modiolula phaseolina	3.30	*Lasaea adansoni*	4.30	*Elminius modestus*	2.97	*Semibalanus balanoides*	3.54
Skenea serpuloides	3.09	Mite sp. 5	4.01	Juvenile *Mytilus edulis*	2.85		
Juvenile *Mytilus edulis*	2.65	*Tricolia pullus*	3.53				
Clunio sp. larvae	2.54						
Eulalia viridis	2.36						
Average dissimilarity between sites = 52.80%		Average dissimilarity between sites = 54.62%		Average dissimilarity between sites = 65.42%		Average dissimilarity between sites = 63.67%	

Kilkee, Doonbeg	% Cont.	Kilkee, Robin Hood's Bay	% Cont.	Kilkee, Filey Brigg	% Cont.	Doonbeg, Robin Hood's Bay	% Cont.	Doonbeg, Filey Brigg	% Cont.	Robin Hood's Bay, Filey Brigg	% Cont.
Nematoda indet.	7.78	*Lasaea adansoni*	15.84	*Lasaea adansoni*	14.52	*Lasaea adansoni*	13.50	*Lasaea adansoni*	11.45	*Clunio* sp. larvae	12.46
Juvenile *Mytilus edulis*	7.52	*Clunio* sp. larvae	9.37	Juvenile *Mytilus edulis*	5.74	Juvenile *Mytilus edulis*	8.33	Juvenile *Mytilus edulis*	11.22	Mite sp. 1	7.59
Fabricia stellaris	5.75	Nematoda indet.	5.18	Nematoda indet.	5.72	Nematoda indet.	6.48	*Brachystomia scalaris*	6.05	Nematoda indet.	6.94
Lasaea adansoni	5.56	*Fabricia stellaris*	4.82	*Brachystomia scalaris*	5.26	*Clunio* sp. larvae	6.32	Nematoda indet.	5.52	Juvenile *Mytilus edulis*	5.97
Skeneopsis planorbis	5.37	Mite sp. 1	4.31	Mite sp. 1	5.13	Mite sp. 1	4.58	*Clunio* sp. larvae	4.96	*Brachystomia scalaris*	5.93
Clunio sp. larvae	4.91	*Elminius modestus*	4.16	*Fabricia stellaris*	4.55	*Elminius modestus*	4.55	*Skeneopsis planorbis*	4.70	*Modiolula phaseolina*	4.88
Mite sp. 5	4.39	*Modiolula phaseolina*	4.00	*Skenea serpuloides*	3.71	*Skeneopsis planorbis*	3.90	Mite sp. 1	3.79	*Elminius modestus*	4.04
Skenea serpuloides	4.36	*Omalogyra atomus*	3.23	*Pholoe inornata*	3.42	Mite sp. 5	3.54	*Skenea serpuloides*	3.54	*Semibalanus balanoides*	3.90
Mite sp. 1	4.28	*Skenea serpuloides*	3.00	*Semibalanus balanoides*	3.26	*Modiolula phaseolina*	3.08	*Pholoe inornata*	3.47	*Idotea pelagica*	3.51
Omalogyra atomus	4.03	*Skeneopsis planorbis*	2.69	*Modiolula phaseolina*	3.23	Oligochaeta indet.	2.88	Mite sp. 5	3.27	*Skenea serpuloides*	3.14
Modiolula phaseolina	3.48	Juvenile *Mytilus edulis*	2.50	*Idotea pelagica*	2.97	*Tricolia pullus*	2.75	*Semibalanus balanoides*	3.27	Nemertea indet.	3.11
Tricolia pullus	3.13	Oligochaeta indet.	2.32	*Omalogyra atomus*	2.97	*Skenea serpuloides*	2.65	*Modiolula phaseolina*	3.03	*Pholoe inornata*	3.04
Oligochaeta indet.	2.81	*Eulalia viridis*	2.27	*Clunio* sp. larvae	2.81	*Eusyllis blomstrandi*	1.93	*Idotea pelagica*	3.01	Oligochaeta indet.	2.93
Jaera albifrons	2.59	*Jaera albifrons*	1.84	Nemertea indet.	2.46	*Brachystomia scalaris*	1.89	*Tricolia pullus*	2.33	*Heterocythereis albomaculata*	2.09
Eulalia viridis	2.45	*Eusyllis blomstrandi*	1.76	*Eulalia viridis*	2.30	*Heterocythereis albomaculata*	1.87	Nemertea indet.	2.00	*Skeneopsis planorbis*	1.94
Mite sp. 3	2.26	*Heterocythereis albomaculata*	1.66	*Elminius modestus*	1.97	Nemertea indet.	1.83				
		Dipteran larvae indet.	1.62								
Average dissimilarity between sites = 42.87%		Average dissimilarity between sites = 50.51%		Average dissimilarity between sites = 59.32%		Average dissimilarity between sites = 50.91%		Average dissimilarity between sites = 65.16%		Average dissimilarity between sites = 47.52%	

details of the taxa, contributing to differences in mussel bed community composition between sites. Similarity Percentage analysis (SIMPER), performed with a presence/absence transformation indicated that the mussel bed communities at each of the eight sites in the UK were characterised by quite different sets of taxa. However, some taxa were consistently present in mussel bed communities at most or all sites, namely, juvenile *M. edulis*, *Clunio* sp. larvae, Mite sp. 1, nemerteans, nematodes, the isopod *Jaera albifrons* and the amphipod *Hyale prevostii*. Table 4 provides details of the taxa contributing to differences in mussel bed community composition between sites. Mussel beds at the more sheltered locations (Point Lynas, White Beach and Criccieth) were dominated by meiofaunal taxa associated with the sediment portion of the mussel matrix (nematodes, nemerteans, *Clunio sp.* larvae and various mites). At the other, more wave-exposed locations, macrofaunal and mobile taxa such as *Jaera albifrons*, *Lasaea adansoni*, *Hyale prevostii* and *Omalgyra atomus* were much more abundant with meiofaunal taxa proportionally less abundant.

Many of the environmental variables measured in the mussel beds showed significant variation both within and across the eight sites (Figure 6). Mussel density was greater at Robin Hood's Bay, Filey Brigg and Arisaig than at all other sites. The mass and volume of mussels, per unit area of mussel bed was lower at Point Lynas than sites on the NE coast of England and White Beach, while between other sites, these variables did not differ significantly. The mean length of mussels at each site was similar at all sites, except at White Beach where mussels were slightly larger. The fine sediment content of the mussel beds was generally greater in mussel beds at the more sheltered locations. A subset of taxa, randomly selected, such that epibiotic, mobile and infaunal organisms were represented, were tested for relationships between their abundance and various environmental parameters of the mussel beds. Various relationships were found, of which the most obvious was the finding that the abundance of all the taxa tested was negatively correlated with the mean size of mussels in the patch (Table 5). However, although significant, none of these relationships was highly correlated.

Univariate measures of the diversity of mussel bed communities did not show a high degree of correlation with many of the environmental variables measured within the mussel beds (Table 6b-i) when data at each site were tested separately. However, when data from all sites were pooled, coarse sediment content was shown to be an important factor influencing univariate measures of community diversity (Table 6a), while other factors were seen to have varying effects.

Table 4 Results of similarity percentage analysis (SIMPER) performed on presence/absence transformed abundance of infaunal taxa present in mussel beds at eight locations throughout the British Isles and Irish Republic, showing a breakdown of % contributions of infaunal taxa (% Cont.) to average dissimilarity between locations. Taxa highlighted in grey indicate higher abundance at the first listed site.

Point Lynas, White Beach	% Cont.	Point Lynas, Criccieth	% Cont.	Point Lynas, Arisaig	% Cont.	Point Lynas, Kilkee	% Cont.	Point Lynas, Doonbeg	% Cont.	Point Lynas, Robin Hood's Bay	% Cont.	Point Lynas, Filey Brigg	% Cont.
Leptocythere pellucida	6.18	*Leptocythere pellucida*	4.88	*Tricolia pullus*	5.37	*Eulalia viridis*	5.05	*Skeneopsis planorbis*	5.22	*Modiolula phaseolina*	4.41	*Pholoe inornata*	5.01
Brachystomia scalaris	4.81	*Jaera albifrons*	4.36	*Hyale prevostii*	5.37	*Modiolula phaseolina*	4.35	*Modiolula phaseolina*	5.22	*Jaera albifrons*	3.93	*Modiolula phaseolina*	4.25
Foraminifera indet.	4.73	*Elminius modestus*	4.36	*Jaera albifrons*	4.81	*Fabricia stellaris*	4.00	*Skenea serpuloides*	4.56	*Elminius modestus*	3.93	*Hyale prevostii*	4.25
Juvenile gastropoda indet.	4.57	*Eulalia viridis*	4.27	Oligochaeta indet.	4.81	*Cerithiopsis tubercularis*	3.90	*Tricolia pullus*	4.47	*Heterocythereis albomaculata*	3.46	*Semibalanus balanoides*	3.80
Idotea pelagica	4.37	*Idotea pelagica*	3.81	*Brachystomia scalaris*	4.62	*Carcinus maenas*	3.67	*Jaera albifrons*	1.14	*Hiatella arctica*	3.33	*Lasaea adansoni*	3.60
Heterocythereis albomaculata	4.30	Foraminifera indet.	3.73	*Idotea pelagica*	4.22	*Jaera albifrons*	3.46	Mite sp. 5	3.88	*Tectura testudinalis*	3.30	*Idotea pelagica*	3.53
Jaera albifrons	4.25	Juvenile gastropoda indet.	3.62	Mite sp. 1	4.16	*Hyale prevostii*	3.14	*Brachystomia scalaris*	3.61	*Eusyllis blomstrandi*	3.29	*Harmothoe* sp.	3.18
Brania pusilla	3.74	*Skenea serpuloides*	3.59	Juvenile gastropoda indet.	3.97	Oligochaeta indet.	3.01	*Carcinus maenas*	3.49	*Skeneopsis planorbis*	3.28	*Hiatella arctica*	3.17
Onoba semicostata	3.65	*Heterocythereis albomaculata*	3.41	Mite sp. 3	3.91	*Onoba semicostata*	2.84	Mite sp. 3	3.27	*Lasaea adansoni*	3.18	Nemertea indet.	3.11
Lasaea adansoni	3.46	Oligochaeta indet.	2.96	*Carcinus maenas*	3.88	*Brachystomia scalaris*	2.60	*Onoba semicostata*	3.23	Oligochaeta indet.	3.08	Dipteran larvae indet.	2.96
Nucella lapillus	3.32	*Onoba semicostata*	2.88	*Onoba semicostata*	3.32	Juvenile gastropoda indet.	2.57	*Lacuna pallidula*	3.23	*Carcinus maenas*	2.73	Juvenile gastropoda indet.	2.85
Cirratulus cirratus	3.26	*Nucella lapillus*	2.85	*Elminius modestus*	3.18	*Omalogyra atomus*	2.55	*Typosyllis prolifera*	3.19	*Hyale prevostii*	2.73	*Elminius modestus*	2.84
Dipteran larvae indet.	3.09	*Littorina rudis*	2.63	Dipteran larvae indet.	3.15	*Nucella lapillus*	2.53	*Eulalia viridis*	3.13	Dipteran larvae indet.	2.62	*Onoba semicostata*	2.84
Oligochaeta indet.	3.06	Dipteran larvae indet.	2.56	*Limapontia depressa*	2.97	*Rissoa parva*	2.53	*Nucella lapillus*	2.82	*Nucella lapillus*	2.49	*Jaera albifrons*	2.80
Modiolula phaseolina	3.00	*Cirratulus cirratus*	2.52	*Cirratulus cirratus*	2.83	*Skenea serpuloides*	2.50	*Tanais dulongii*	2.59	*Onoba semicostata*	2.47	*Cirratulus cirratus*	2.63
Nemertea indet.	3.00	Mite sp. 3	2.52	*Eulalia viridis*	2.66	*Epitonium clathrus*	2.44	*Cirratulus cirratus*	2.58	Juvenile gastropoda indet.	2.30	*Rissoa parva*	2.50
Rissoa parva	2.90	*Brachystomia scalaris*	2.51	*Rissoa parva*	2.56	Mite sp. 3	2.44	*Hyale prevostii*	2.56	*Cirratulus cirratus*	2.30	*Nucella lapillus*	2.41
Rissoella opalina	2.46	*Hyale prevostii*	2.47	*Nucella lapillus*	2.48	*Cirratulus cirratus*	2.44	*Rissoa parva*	2.50	*Rissoa parva*	2.22	*Limapontia depressa*	2.14
Anurida maritima	2.23	*Semicytherura nigrescens*	2.47	*Tanais dulongii*	2.30	*Heterocythereis albomaculata*	2.41	Dipteran larvae indet.	2.36	*Semibalanus balanoides*	2.17	*Eusyllis blomstrandi*	1.99
		Semibalanus balanoides	2.41			Dipteran larvae indet.	2.30	*Coriandria fulgida*	2.17	*Pholoe inornata*	2.13	*Scolelepis squamata*	1.97
		Platyhelminthe indet.	2.41			*Coriandria fulgida*	2.11	*Fabricia stellaris*	2.17	*Scolelepis squamata*	1.91	*Carcinus maenas*	1.97
		Rissoella opalina	2.37			*Anurida maritima*	1.85			*Idotea pelagica*	1.82	*Spirorbis spirorbis*	1.87
		Rissoa parva	2.32			*Skeneopsis planorbis*	1.84			Mite sp. 5	1.79	*Coriandria fulgida*	1.87
						Littorina rudis	1.83			*Epilepton clarkiae*	1.75	*Skenea serpuloides*	1.83
										Jaera nordmanni	1.65	*Anurida maritima*	1.82
Average dissimilarity between sites = 54.76%		Average dissimilarity between sites = 56.62%		Average dissimilarity between sites = 61.35%		Average dissimilarity between sites = 54.20%		Average dissimilarity between sites = 54.09%		Average dissimilarity between sites = 61.16%		Average dissimilarity between sites = 58.41%	

White Beach, Criccieth	% Cont.	White Beach, Arisaig	% Cont.	White Beach, Kilkee	% Cont.	White Beach, Doonbeg	% Cont.	White Beach, Robin Hood's Bay	% Cont.	White Beach, Filey Brigg	% Cont.
Eulalia viridis	6.26	*Tricolia pullus*	5.97	*Carcinus maenas*	4.86	*Skeneopsis planorbis*	5.08	*Leptocythere pellucida*	4.70	*Pholoe inornata*	5.12
Elminius modestus	6.22	*Carcinus maenas*	5.97	*Eulalia viridis*	4.86	Mite sp. 5	5.08	Foraminifera indet.	4.09	*Leptocythere pellucida*	4.56
Littorina rudis	4.51	*Hyale prevostii*	5.97	*Cirratulus cirratus*	4.22	*Carcinus maenas*	4.44	*Elminius modestus*	4.09	*Brachystomia scalaris*	4.53
Skenea serpuloides	4.44	*Leptocythere pellucida*	5.97	Foraminifera indet.	4.22	Foraminifera indet.	4.42	*Carcinus maenas*	3.59	Foraminifera indet.	4.45
Brania pusilla	4.35	Foraminifera indet.	5.18	*Idotea pelagica*	4.20	*Idotea pelagica*	4.40	*Hiatella arctica*	3.55	*Hyale prevostii*	4.34
Lasaea adansoni	4.32	Mite sp. 1	4.62	*Fabricia stellaris*	3.78	*Tricolia pullus*	4.36	*Tectura testudinalis*	3.52	*Semibalanus balanoides*	3.88
Mite sp. 3	3.63	*Heterocythereis albomaculata*	4.49	*Cerithiopsis tubercularis*	3.75	*Leptocythere pellucida*	3.90	*Eusyllis blomstrandi*	3.51	*Heterocythereis albomaculata*	3.29
Hyale prevostii	3.62	*Lasaea adansoni*	3.83	*Leptocythere pellucida*	3.75	Juvenile gastropoda indet.	3.78	*Skeneopsis planorbis*	3.50	*Harmothoe* sp.	3.25
Semicytherura nigrescens	3.60	*Nucella lapillus*	3.78	*Lasaea adansoni*	3.10	*Skenea serpuloides*	3.51	*Brachystomia scalaris*	3.15	*Hiatella arctica*	3.24
Oligochaeta indet.	3.59	Mite sp. 3	3.67	*Hyale prevostii*	3.02	*Lasaea adansoni*	3.25	*Hyale prevostii*	2.91	*Brania pusilla*	3.11
Dipteran larvae indet.	3.58	*Brania pusilla*	3.61	*Brania pusilla*	2.69	*Lacuna pallidula*	3.14	*Idotea pelagica*	2.88	*Elminius modestus*	2.89
Nemertea indet.	3.54	*Limapontia depressa*	3.56	*Heterocythereis albomaculata*	2.50	*Cirratulus cirratus*	3.14	*Rissoa parva*	2.87	*Nucella lapillus*	2.85
Rissoella opalina	3.54	*Elminius modestus*	3.50	*Modiolula phaseolina*	2.47	*Typosyllis prolifera*	3.11	*Brania pusilla*	2.86	*Modiolula phaseolina*	2.60
Semibalanus balanoides	3.54	Oligochaeta indet.	3.02	*Rissoa parva*	2.45	*Brania pusilla*	3.09	*Modiolula phaseolina*	2.40	Nemertea indet.	2.58
Platyhelminthes indet.	3.54	Dipteran larvae indet.	2.98	*Omalogyra atomus*	2.45	*Eulalia viridis*	3.05	Oligochaeta indet.	2.36	Dipteran larvae indet.	2.56
Modiolula phaseolina	3.53	*Eulalia viridis*	2.96	Oligochaeta indet.	2.43	*Heterocythereis albomaculata*	2.92	Dipteran larvae indet.	2.34	Oligochaeta indet.	2.54
Brachystomia scalaris	3.47	Nemertea indet.	2.93	Dipteran larvae indet.	2.43	Mite sp. 3	2.87	*Semibalanus balanoides*	2.31	*Rissoa parva*	2.52
Littorina littorea	2.79			*Skenea serpuloides*	2.42	*Modiolula phaseolina*	2.60	Nemertea indet.	2.29	*Jaera albifrons*	2.37
				Mite sp. 3	2.39	Dipteran larvae indet.	2.54	*Pholoe inornata*	2.28	*Skenea serpuloides*	2.21
				Nucella lapillus	2.38	Oligochaeta indet.	2.53	Juvenile gastropoda indet.	2.12	*Eusyllis blomstrandi*	2.04
				Nemertea indet.	2.37			*Rissoella opalina*	1.87	*Limapontia depressa*	1.88
				Epitonium clathrus	2.35			*Epilepton clarkiae*	1.77	*Rissoella opalina*	1.88
				Brachystomia scalaris	2.35			*Skenea serpuloides*	1.76	*Lasaea adansoni*	1.84
								Jaera nordmanni	1.73		
								Lasaea adansoni	1.70		
Average dissimilarity between sites = 39.32%		Average dissimilarity between sites = 56.26%		Average dissimilarity between sites = 57.34%		Average dissimilarity between sites = 56.48%		Average dissimilarity between sites = 58.36%		Average dissimilarity between sites = 58.18%	

Criccieth, Arisaig	% Cont.	Criccieth, Kilkee	% Cont.	Criccieth, Doonbeg	% Cont.	Criccieth, Robin Hood's Bay	% Cont.	Criccieth, Filey Brigg	% Cont.
Tricolia pullus	5.73	*Idotea pelagica*	4.42	*Skeneopsis planorbis*	4.64	*Leptocythere pellucida*	4.44	*Pholoe inornata*	4.54
Leptocythere pellucida	5.73	*Elminius modestus*	4.42	*Idotea pelagica*	4.64	*Lasaea adansoni*	3.87	*Leptocythere pellucida*	4.03
Foraminifera indet.	4.94	*Fabricia stellaris*	3.86	*Elminius modestus*	4.64	Foraminifera indet.	3.84	*Lasaea adansoni*	3.95
Mite sp. 1	4.41	Foraminifera indet.	3.83	Mite sp. 5	4.06	*Modiolula phaseolina*	3.37	Foraminifera indet.	3.92
Nucella lapillus	4.36	*Cirratulus cirratus*	3.43	Foraminifera indet.	4.01	*Hiatella arctica*	3.35	*Eulalia viridis*	3.20
Heterocythereis albomaculata	4.33	*Cerithiopsis tubercularis*	3.40	*Tricolia pullus*	3.99	*Tectura testudinalis*	3.33	*Modiolula phaseolina*	3.09
Carcinus maenas	4.25	*Leptocythere pellucida*	3.40	*Leptocythere pellucida*	3.55	*Eusyllis blomstrandi*	3.32	*Heterocythereis albomaculata*	2.91
Littorina rudis	3.61	*Carcinus maenas*	3.29	*Modiolula phaseolina*	3.52	*Skeneopsis planorbis*	3.31	*Harmothoe* sp.	2.87
Skenea serpuloides	3.57	*Modiolula phaseolina*	3.04	Juvenile gastropoda indet.	3.46	*Idotea pelagica*	2.88	*Hiatella arctica*	2.86
Limapontia depressa	3.45	*Littorina rudis*	2.79	*Carcinus maenas*	3.17	*Littorina rudis*	2.80	*Littorina rudis*	2.86
Semicytherura nigrescens	2.90	Dipteran larvae indet.	2.48	*Lacuna pallidula*	2.88	*Carcinus maenas*	2.79	*Nucella lapillus*	2.78
Eulalia viridis	2.88	*Heterocythereis albomaculata*	2.27	*Typosyllis prolifera*	2.85	*Skenea serpuloides*	2.74	Oligochaeta indet.	2.74
Semibalanus balanoides	2.84	*Semicytherura nigrescens*	2.23	*Littorina rudis*	2.77	*Eulalia viridis*	2.74	*Skenea serpuloides*	2.55
Hyale prevostii	2.83	*Rissoa parva*	2.23	*Cirratulus cirratus*	2.73	*Rissoa parva*	2.72	Nemertea indet.	2.53
Platyhelminthes indet.	2.83	*Omalogyra atomus*	2.23	*Heterocythereis albomaculata*	2.66	Mite sp. 3	2.26	*Brachystomia scalaris*	2.35
Mite sp. 3	2.83	*Skenea serpuloides*	2.22	Dipteran larvae indet.	2.63	*Brachystomia scalaris*	2.25	Mite sp. 3	2.33
Rissoella opalina	2.76	Mite sp. 3	2.22	Oligochaeta indet.	2.50	*Semicytherura nigrescens*	2.24	*Semicytherura nigrescens*	2.29
Brachystomia scalaris	2.76	*Brachystomia scalaris*	2.21	*Semicytherura nigrescens*	2.34	*Semibalanus balanoides*	2.22	*Semibalanus balanoides*	2.28
Littorina littorea	2.23	*Hyale prevostii*	2.21	*Hyale prevostii*	2.32	*Hyale prevostii*	2.22	*Hyale prevostii*	2.25
Elminius modestus	2.18	*Semibalanus balanoides*	2.19	Mite sp. 3	2.30	Platyhelminthes indet.	2.20	Platyhelminthes indet.	2.24
		Platyhelminthes indet.	2.19	*Semibalanus balanoides*	2.30	*Rissoella opalina*	2.16	*Rissoa parva*	2.24
		Epitonium clathrus	2.15	Platyhelminthes indet.	2.30	*Pholoe inornata*	2.16	*Rissoella opalina*	2.19
		Rissoella opalina	2.14			*Scolelepis squamata*	2.04	*Scolelepis squamata*	1.98
		Nucella lapillus	2.13			Juvenile gastropoda indet.	2.03	*Jaera albifrons*	1.88
		Juvenile gastropoda indet.	2.13			Oligochaeta indet.	1.92	*Elminius modestus*	1.85
		Oligochaeta indet.	2.07			*Littorina littorea*	1.72	*Eusyllis blomstrandi*	1.78
Average dissimilarity between sites = 48.04%		Average dissimilarity between sites = 53.20%		Average dissimilarity between sites = 52.07%		Average dissimilarity between sites = 52.30%		Average dissimilarity between sites = 54.91%	

Arisaig, Kilkee	% Cont.	Arisaig, Doonbeg	% Cont.	Arisaig, Robin Hood's Bay	% Cont.	Arisaig, Filey Brigg	% Cont.
Tricolia pullus	5.01	*Skeneopsis planorbis*	5.49	*Tricolia pullus*	4.70	*Tricolia pullus*	4.93
Idotea pelagica	5.01	*Modiolula phaseolina*	5.49	*Modiolula phaseolina*	4.70	*Brachystomia scalaris*	4.93
Fabricia stellaris	4.38	Mite sp. 5	5.49	*Lasaea adansoni*	4.70	*Lasaea adansoni*	4.93
Cirratulus cirratus	4.36	*Idotea pelagica*	5.49	*Heterocythereis albomaculata*	4.08	*Pholoe inornata*	4.93
Modiolula phaseolina	4.32	Mite sp. 1	4.23	*Hiatella arctica*	3.55	Oligochaeta indet.	4.39
Cerithiopsis tubercularis	3.87	Dipteran larvae indet.	4.16	*Tectura testudinalis*	3.52	*Modiolula phaseolina*	4.18
Mite sp. 1	3.86	Juvenile gastropoda indet.	4.09	*Eusyllis blomstrandi*	3.51	Mite sp. 1	3.80
Dipteran larvae indet.	3.69	*Skenea serpuloides*	3.83	*Skeneopsis planorbis*	3.50	*Carcinus maenas*	3.62
Elminius modestus	3.10	Oligochaeta indet.	3.54	*Brachystomia scalaris*	3.40	Mite sp. 3	3.61
Limapontia depressa	3.02	*Nucella lapillus*	3.44	*Nucella lapillus*	3.30	*Semibalanus balanoides*	3.44
Nucella lapillus	2.56	*Elminius modestus*	3.40	Mite sp. 1	3.28	*Harmothoe sp.*	3.13
Mite sp. 3	2.54	*Lacuna pallidula*	3.40	Mite sp. 3	3.13	*Hiatella arctica*	3.12
Omalogyra atomus	2.53	*Cirratulus cirratus*	3.39	*Idotea pelagica*	3.07	Nemertea indet.	2.90
Eulalia viridis	2.52	*Typosyllis prolifera*	3.36	*Rissoa parva*	2.74	*Limapontia depressa*	2.59
Rissoa parva	2.52	*Limapontia depressa*	3.30	*Limapontia depressa*	2.73	*Eulalia viridis*	2.45
Skenea serpuloides	2.49	*Hyale prevostii*	2.79	*Eulalia viridis*	2.34	*Rissoa parva*	2.44
Epitonium clathrus	2.43	*Eulalia viridis*	2.75	*Semibalanus balanoides*	2.32	*Elminius modestus*	2.36
Juvenile gastropoda indet.	2.40	*Tanais dulongii*	2.73	*Pholoe inornata*	2.28	*Nucella lapillus*	2.18
Brachystomia scalaris	2.40			Juvenile gastropoda indet.	2.12	*Skenea serpuloides*	2.11
Heterocythereis albomaculata	2.36			Mite sp. 7	2.01	*Jaera albifrons*	2.08
Tanais dulongii	1.93			*Hyale prevostii*	1.79	*Eusyllis blomstrandi*	1.86
Hyale prevostii	1.89			*Elminius modestus*	1.79		
Oligochaeta indet.	1.89			*Epilepton clarkiae*	1.77		
Average dissimilarity between sites = 54.32%		Average dissimilarity between sites = 51.10%		Average dissimilarity between sites = 57.06%		Average dissimilarity between sites = 58.97%	

Kilkee, Doonbeg	% Cont.	Kilkee, Robin Hood's Bay	% Cont.	Kilkee, Filey Brigg	% Cont.	Doonbeg, Robin Hood's Bay	% Cont.	Doonbeg, Filey Brigg	% Cont.	Robin Hood's Bay, Filey Brigg	% Cont.
Mite sp. 5	5.64	*Lasaea adansoni*	4.25	*Lasaea adansoni*	4.02	*Lasaea adansoni*	4.41	*Skeneopsis planorbis*	4.04	*Tectura testudinalis*	3.90
Tricolia pullus	4.85	*Elminius modestus*	4.22	*Pholoe inornata*	4.02	*Elminius modestus*	4.41	*Lasaea adansoni*	4.04	*Skeneopsis planorbis*	3.87
Cerithiopsis tubercularis	4.34	*Cirratulus cirratus*	3.69	*Fabricia stellaris*	3.51	*Tricolia pullus*	3.79	Mite sp. 5	4.04	*Heterocythereis albomaculata*	3.66
Skeneopsis planorbis	3.61	*Fabricia stellaris*	3.29	*Cirratulus cirratus*	3.50	Dipteran larvae indet.	3.34	*Pholoe inornata*	4.04	Oligochaeta indet.	3.62
Lacuna pallidula	3.49	*Cerithiopsis tubercularis*	3.25	*Idotea pelagica*	3.47	*Hiatella arctica*	3.33	*Idotea pelagica*	3.49	*Carcinus maenas*	3.24
Fabricia stellaris	3.29	*Hiatella arctica*	3.17	*Eulalia viridis*	3.11	*Tectura testudinalis*	3.30	*Tricolia pullus*	3.47	Nemertea indet.	3.23
Typosyllis prolifera	3.16	*Eusyllis blomstrandi*	3.14	*Cerithiopsis tubercularis*	3.10	Mite sp. 5	3.30	*Brachystomia scalaris*	3.08	*Idotea pelagica*	3.17
Oligochaeta indet.	3.01	Dipteran larvae indet.	3.12	*Semibalanus balanoides*	3.04	*Eusyllis blomstrandi*	3.30	Dipteran larvae indet.	3.06	*Nucella lapillus*	3.05
Juvenile gastropoda indet.	2.87	*Tectura testudinalis*	2.86	Dipteran larvae indet.	2.96	*Skenea serpuloides*	3.02	*Semibalanus balanoides*	3.06	*Harmothoe* sp.	2.95
Omalogyra atomus	2.84	*Eulalia viridis*	2.75	*Carcinus maenas*	2.96	*Cirratulus cirratus*	2.73	*Carcinus maenas*	2.73	*Eusyllis blomstrandi*	2.88
Mite sp. 3	2.84	*Skeneopsis planorbis*	2.46	*Harmothoe* sp.	2.55	*Brachystomia scalaris*	2.73	*Harmothoe* sp.	2.56	*Pholoe inornata*	2.67
Rissoa parva	2.84	*Heterocythereis albomaculata*	2.25	*Hiatella arctica*	2.54	*Typosyllis prolifera*	2.71	*Hiatella arctica*	2.55	*Semibalanus balanoides*	2.62
Skenea serpuloides	2.84	*Brachystomia scalaris*	2.13	Nemertea indet.	2.50	*Heterocythereis albomaculata*	2.67	Mite sp. 3	2.53	*Rissoa parva*	2.61
Hyale prevostii	2.83	*Omalogyra atomus*	2.12	Oligochaeta indet.	2.39	Mite sp. 3	2.60	*Cirratulus cirratus*	2.50	Juvenile gastropoda indet.	2.53
Tanais dulongii	2.79	*Rissoa parva*	2.10	*Elminius modestus*	2.38	*Rissoa parva*	2.59	*Typosyllis prolifera*	2.48	*Skenea serpuloides*	2.26
Heterocythereis albomaculata	2.77	*Skenea serpuloides*	2.09	*Brachystomia scalaris*	2.09	Oligochaeta indet.	2.52	*Skenea serpuloides*	2.43	*Hiatella arctica*	2.25
Nucella lapillus	2.77	Juvenile gastropoda indet.	2.09	*Omalogyra atomus*	2.03	*Lacuna pallidula*	2.49	*Lacuna pallidula*	2.39	*Scolelepis squamata*	2.25
Brachystomia scalaris	2.76	*Semibalanus balanoides*	2.07	*Nucella lapillus*	2.03	*Eulalia viridis*	2.34	*Elminius modestus*	2.39	Mite sp. 7	2.24
Epitonium clathrus	2.74	Mite sp. 3	2.06	*Rissoa parva*	2.01	Juvenile gastropoda indet.	2.29	Juvenile gastropoda indet.	2.30	*Hyale prevostii*	2.16
Cirratulus cirratus	2.32	*Epitonium clathrus*	2.05	*Skenea serpuloides*	2.00	*Hyale prevostii*	2.21	Nemertea indet.	2.27	*Jaera albifrons*	2.15
Eulalia viridis	2.23	*Pholoe inornata*	2.04	*Epitonium clathrus*	1.99	*Tanais dulongii*	2.18	*Eulalia viridis*	2.25	*Eulalia viridis*	2.14
Dipteran larvae indet.	2.13	*Nucella lapillus*	2.04	Juvenile gastropoda indet.	1.99	*Semibalanus balanoides*	2.18	*Nucella lapillus*	2.24	*Elminius modestus*	2.12
Coriandria fulgida	2.06	*Hyale prevostii*	1.98	Mite sp. 3	1.95	*Pholoe inornata*	2.15	*Hyale prevostii*	2.04	*Limapontia depressa*	2.06
		Oligochaeta indet.	1.84	*Heterocythereis albomaculata*	1.95	*Scolelepis squamata*	1.86	*Rissoa parva*	2.00	*Epilepton clarkiae*	1.96
		Mite sp. 7	1.79	*Jaera albifrons*	1.84	*Fabricia stellaris*	1.83	*Tanais dulongii*	1.99	*Epitonium clathrus*	1.93
		Epilepton clarkiae	1.58	*Hyale prevostii*	1.66					*Jaera nordmanni*	1.92
		Jaera nordmanni	1.55	*Eusyllis blomstrandi*	1.58					*Onoba semicostata*	1.87
		Onoba semicostata	1.54	*Limapontia depressa*	1.48						
Average dissimilarity between sites = 42.43%		Average dissimilarity between sites = 54.77%		Average dissimilarity between sites = 61.35%		Average dissimilarity between sites = 53.53%		Average dissimilarity between sites = 62.68%		Average dissimilarity between sites = 46.76%	

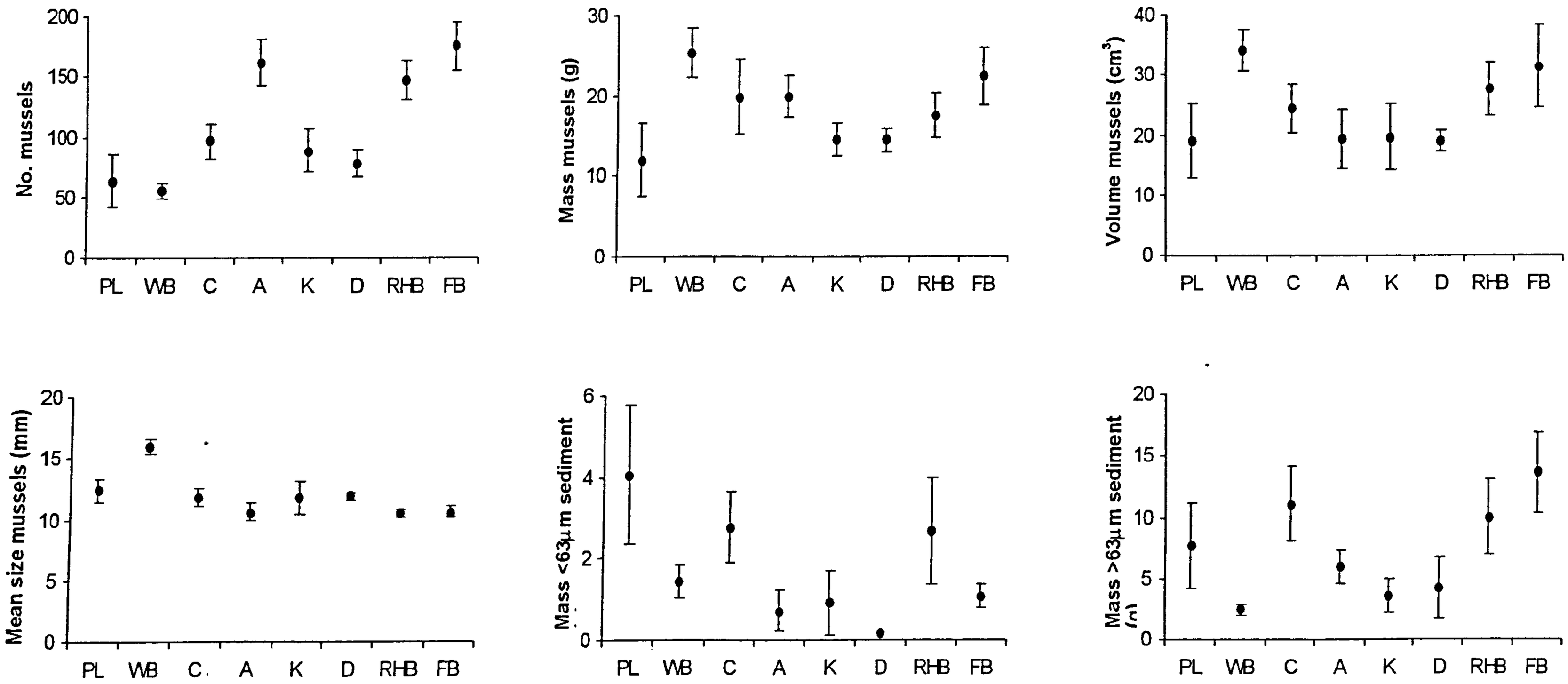


Figure 6 Environmental variables measured in mussel beds at Point Lynas (PL), White Beach (WB), Criccieth (C), Arisaig (A), Kilkee (K), Doonbeg (D), Robin Hood's Bay (RHB) and Filey Brigg (FB). Values are based on 25cm^2 replicates. 95% confidence intervals are marked, such that significant differences are represented by non-overlapping intervals.

Table 5 Correlation coefficients calculated between the abundance of selected a) infaunal, b) mobile and c) epibiotic taxa and environmental variables deemed relevant to their lifestyle, in mussel beds at eight locations in the British Isles and Irish Republic. Significant correlation is indicated by bold type.

a) Infaunal taxa

	Mass <63μm sediment	Mass >63μm sediment
Platyhelminthe indet.	0.197	0.231
Nematoda indet.	0.235	**0.386**
Nemertea indet.	0.081	0.061
Oligochaeta indet.	0.101	0.169
Brania pusilla	0.037	**-0.254**
Heterocythere albomaculata	0.113	0.123
Pholoe inornata	0.008	**0.427**
Clunio sp. larvae	0.220	0.223
Mite sp. 1	0.155	0.034
Juvenile gastropoda indet.	0.080	-0.026
Foraminifera indet.	0.039	-0.064

b) Mobile taxa

	No Mussels	Mean Size Mussels	Mass >63μm sediment
Cirratulus cirratus	-0.240	-0.008	-0.072
Eulalia viridis	-0.091	-0.204	-0.097
Pholoe inornata	**0.474**	**-0.248**	**0.427**
Oligochaeta indet.	0.069	-0.169	0.169
Heterocythere albomaculata	0.051	-0.009	0.123
Tanais dulongii	-0.001	-0.087	-0.187
Idotea pelagica	0.241	-0.057	0.117
Jaera albifrons	0.014	-0.056	0.052
Hyale prevostii	**0.354**	-0.245	-0.051
Carcinus maenas	**-0.305**	**0.526**	-0.030
Mite sp. 1	-0.020	-0.164	0.034
Clunio sp. larvae	0.126	-0.205	0.223
Lasaea adansoni	-0.003	-0.141	**-0.363**
Modiolula phaseolina	0.264	-0.203	0.205
Brachystomia scalaris	**0.408**	-0.200	**0.443**
Coriandria fulgida	-0.178	0.026	-0.065
Juvenile gastropoda indet.	-0.166	-0.030	-0.026
Littorina rudis	-0.146	-0.028	-0.050
Skenea serpuloides	-0.063	-0.002	0.070

c) Epibiotic taxa

	No. Mussels	Mean Size Mussels
Elminius modestus	-0.047	-0.022
Semibalanus balanoides	**0.287**	-0.223
Chthamalus montagui	0.010	-0.068

Table 6 Correlation coefficients calculated between environmental variables and univariate measures of diversity in mussel beds at a) Point Lynas, b) White Beach, c) Criccieth, d) Arisaig, e) Kilkee, f) Doonbeg, g) Robin Hood's Bay and h) Filey Brigg. (*NT*=Number of taxa, *NI*=Number of individuals, *d*=Margalef's index, *H'*=Shannon's diversity, *J*=Pielou's evenness). Values in bold indicate significant correlation ($p<0.05$).

a) Point Lynas, Wales

	NT	*NI*	*d*	*H'*	*J*
∑mussels	0.404	0.442	0.297	0.003	-0.290
Mussel mass	0.436	0.628	0.287	-0.517	-0.703
Mussel volume	0.415	0.605	0.264	-0.467	-0.628
Mean mussel size	0.195	0.352	0.102	**-0.724**	-0.659
Mean size*∑ mussels	0.464	0.516	0.345	-0.130	-0.428
Mass fine sediment	-0.411	-0.462	-0.328	-0.063	0.314
Mass coarse sediment	0.577	0.780	0.467	-0.280	**-0.807**

b) White Beach, Wales

	NT	*NI*	*d*	*H'*	*J*
∑mussels	-0.187	0.502	-0.334	0.183	0.199
Mussel mass	-0.505	0.650	**-0.739**	-0.324	-0.070
Mussel volume	-0.387	**0.758**	-0.644	-0.333	-0.137
Mean mussel size	-0.538	0.198	-0.586	-0.540	-0.216
Mean size*∑ mussels	-0.381	0.616	-0.557	0.007	0.135
Mass fine sediment	-0.399	-0.125	-0.259	0.704	**0.801**
Mass coarse sediment	0.009	-0.684	0.290	0.422	0.398

c) Criccieth, Wales

	NT	*NI*	*d*	*H'*	*J*
∑mussels	-0.642	0.297	-0.648	-0.365	-0.097
Mussel mass	0.383	0.308	0.132	0.694	0.583
Mussel volume	0.481	0.199	0.263	**0.713**	0.558
Mean mussel size	0.610	-0.358	0.618	0.541	0.309
Mean size*∑ mussels	-0.629	0.185	-0.603	-0.272	0.002
Mass fine sediment	0.568	0.166	0.444	-0.261	-0.574
Mass coarse sediment	0.275	-0.428	0.483	-0.433	-0.615

d) Arisaig, Scotland

	NT	*NI*	*d*	*H'*	*J*
∑mussels	-0.207	**-0.831**	-0.047	-0.433	-0.286
Mussel mass	0.154	-0.345	0.229	0.128	-0.053
Mussel volume	-0.203	-0.379	-0.117	-0.268	-0.171
Mean mussel size	0.521	0.479	0.433	**0.715**	0.296
Mean size*∑ mussels	0.047	**-0.886**	0.221	-0.139	-0.210
Mass fine sediment	-	-	-	-	-
Mass coarse sediment	0.243	0.654	0.113	0.362	0.144

e) Kilkee, Irish Republic

	NT	*NI*	*d*	*H'*	*J*
∑mussels	-0.501	-0.617	-0.437	-0.332	-0.171
Mussel mass	-0.246	-0.005	-0.329	-0.171	-0.087
Mussel volume	-0.157	-0.025	-0.201	-0.160	-0.124
Mean mussel size	0.651	**0.808**	0.556	0.391	0.157
Mean size*∑ mussels	-0.467	-0.494	-0.442	-0.280	-0.120
Mass fine sediment	-0.056	-0.222	0.010	0.114	0.178
Mass coarse sediment	**0.910**	0.682	**0.936**	0.588	0.239

f) Doonbeg, Irish Republic

	NT	*NI*	*d*	*H'*	*J*
∑mussels	0.459	0.438	0.306	**-0.796**	-0.631
Mussel mass	0.127	-0.013	0.190	-0.553	-0.308
Mussel volume	0.074	-0.010	0.137	-0.645	-0.322
Mean mussel size	-0.238	-0.323	-0.113	**0.732**	0.491
Mean size*∑ mussels	0.468	0.449	0.308	**-0.779**	-0.625
Mass fine sediment	0.251	0.487	0.038	-0.395	-0.326
Mass coarse sediment	0.194	0.210	0.124	-0.271	-0.265

g) Robin Hood's Bay, England

	NT	*NI*	*d*	*H'*	*J*
∑mussels	0.135	0.500	0.069	0.124	-0.087
Mussel mass	0.059	0.112	0.052	-0.210	-0.187
Mussel volume	0.002	0.148	-0.018	-0.358	-0.159
Mean mussel size	0.179	-0.073	0.196	-0.372	-0.365
Mean size*∑ mussels	0.205	0.514	0.140	0.049	-0.199
Mass fine sediment	0.303	-0.204	0.362	0.319	-0.185
Mass coarse sediment	0.472	-0.093	0.526	0.298	-0.368

h) Filey Brigg, England

	NT	*NI*	*d*	*H'*	*J*
∑mussels	0.061	-0.323	0.174	-0.409	-0.519
Mussel mass	0.031	-0.234	0.110	-0.346	-0.415
Mussel volume	0.017	-0.562	0.216	-0.585	-0.664
Mean mussel size	-0.341	-0.411	-0.237	-0.591	-0.459
Mean size*∑ mussels	-0.037	-0.400	0.092	-0.537	-0.600
Mass fine sediment	-0.327	-0.211	-0.325	0.179	0.401
Mass coarse sediment	0.446	0.280	0.362	0.597	0.435

Ordination by PCA of the environmental data from the mussel samples (Figure 7) showed that replicate samples from each of the eight sites did not cluster out as distinctly as ordinations using biotic data (Figures 4 and 5). This may be due in part to the high degree of intra-site variation in measurements of each of these variables (Figure 6). Over 90% of the geographical variability in the environmental data was accounted for by the first three Principal Components, while the first two Principal Components accounted for 72% of the variability. PC1 was seen to be a linear combination of the environmental parameters, with increasing values of all variables, except for mean mussel size.

Determination of correlation coefficients for all environmental variables measured in the mussel beds at each of the eight sites failed to reveal any high levels of correlation between any of the variables ($r>0.95$), although some correlation's were significant (Table 7). As such, all the measured environmental variables were entered into BIOENV analysis, to identify the most appropriate combinations of variables explaining the square-root and presence/absence transformed biotic data. BIOENV analysis failed to identify any high levels of correlation between any environmental parameters and square-root or presence/absence transformed biotic data (Table 8). The BIOENV procedure was repeated, using only the important site-characterising taxa identified under each transformation by SIMPER, and with taxa present at greater than 50% of sites, since the original data set was so large that any patterns in the data might be masked. However, this procedure did not increase the correlation between environmental and either square-root or presence/absence transformed biotic data.

RELATE analysis between the environmental data similarity matrix, produced using normalised Euclidean distance and the biotic data similarity matrices, produced using Bray-Curtis similarity with a square-root and a presence/absence transformation showed significant differences ($R=0.296$, $p<0.05$; $R=0.321$, $p<0.05$). Thus, the physical and environmental factors measured in mussel beds at each of the eight locations in this study were not solely responsible for producing the observed differences in community structure between locations.

An arbitrary, ranked scale of wave-exposure was applied to each of the eight sites in the present study, which were then overlaid onto the averaged MDS ordination of square-root and presence/absence transformed infauna abundance, which revealed clear patterns in the data (Figure 8). In addition, the univariate measures of diversity were generally greater at the more exposed sites (Figure 1).

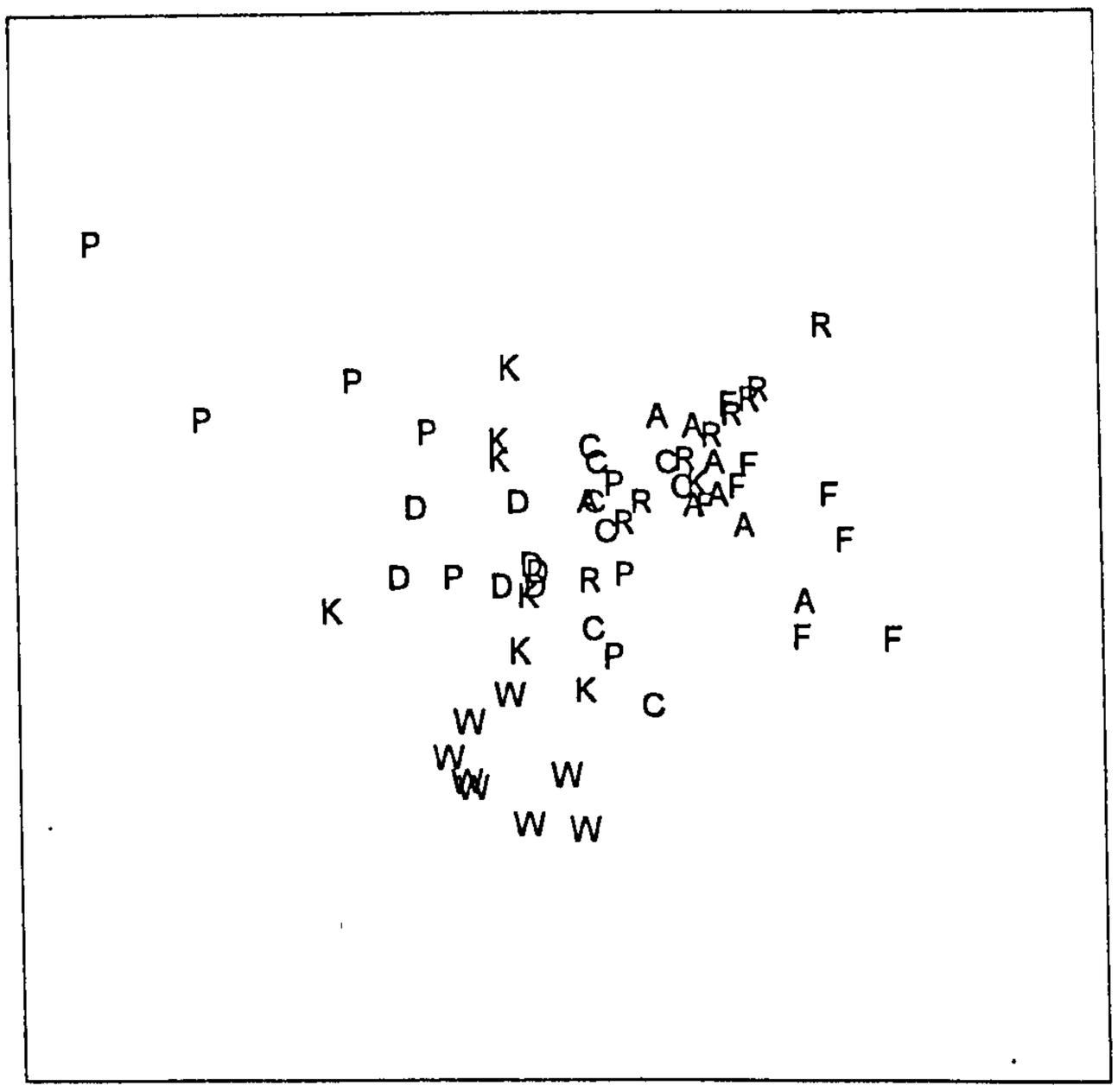


Figure 7 Ordination by PCA, using normalised Euclidean distance, of environmental variables measured in mussel beds at each of the eight locations in the British Isles and Irish Republic. (P = Point Lynas, Wales; W = White Beach, Wales; C = Criccieth, Wales; A = Arisaig, Scotland; K = Kilkee, Irish Republic; D = Doonbeg, Irish Republic; R = Robin Hood's Bay, England; F = Filey Brigg, England).

Table 7 Correlation coefficients calculated between various environmental variables measured in mussel beds at eight locations in the British Isles and Irish Republic. Significant correlation ($p<0.05$) is indicated by bold type.

	No. mussels	*Mussel volume*	*Mussel mass*	*Mean size mussels*	*Mean size*No. mussels*	*Mass fine sediment*
Mussel volume	**0.255**					
Mussel mass	**0.307**	**0.851**				
Mean size mussels	**-0.684**	**0.356**	**0.353**			
*Mean size*No. mussels*	**0.974**	**0.419**	**0.471**	**-0.526**		
Mass fine sediment	**-0.256**	-0.120	**-0.268**	0.023	**-0.297**	
Mass coarse sediment	**0.359**	0.054	0.011	**-0.341**	**0.325**	**0.295**

Table 8 Results of BIOENV analysis, comparing environmental variables with biotic data in mussel beds at the eight locations in the British Isles and Irish Republic. 'Best' variable combinations are based on Spearman rank correlation's between a) square-root and b) presence/absence transformed biotic data and environmental parameters are given. For each transformation, the entire biotic data set is used in the analysis, along with data sets comprising of taxa identified by SIMPER analysis as important in characterising the communities and taxa present at >50% locations.

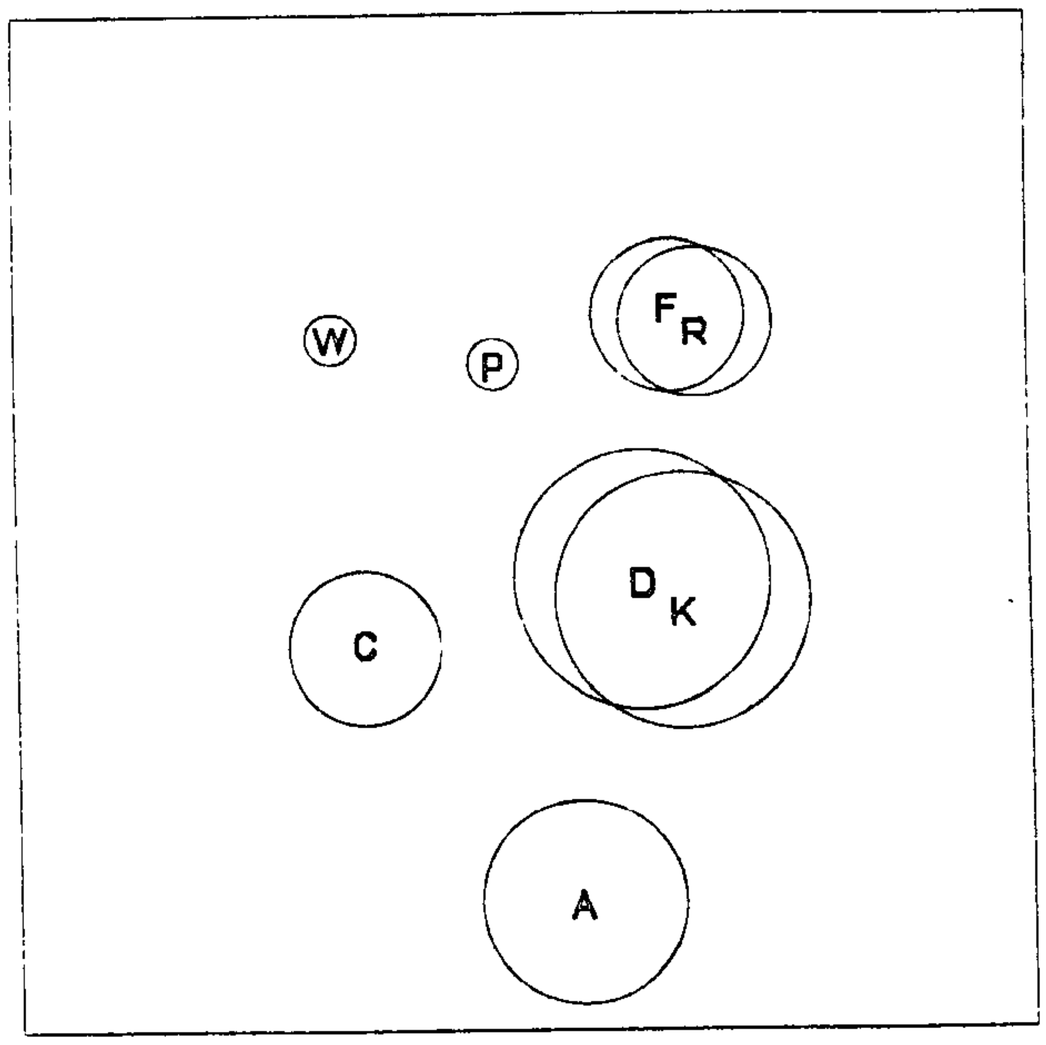
a)

Biotic data set	*Best variable combination*	*Correlation*
Full data set	Total number of mussels Mussel volume Mean size*total number of mussels Mass course sediment	0.277
SIMPER taxa only	Total number of mussels Mussel volume Mean size of mussels Mean size*total number of mussels Mass course sediment	0.273
Taxa present at >50% locations only	Total number of mussels Mussel volume Mean size of mussels Mean size*total number of mussels Mass course sediment	0.271

b)

Biotic data set	*Best variable combination*	*Correlation*
Full data set	Total number of mussels Mussel volume Mean size*total number of mussels Mass fine sediment	0.341
SIMPER taxa only	Total number of mussels Mussel volume Mean size of mussels Mean size*total number of mussels Mass fine sediment	0.309
Taxa present at >50% locations only	Total number of mussels Mussel volume Mean size of mussels Mean size*total number of mussels Mass fine sediment	0.358

a) Stress = 0.11



b) Stress = 0.13

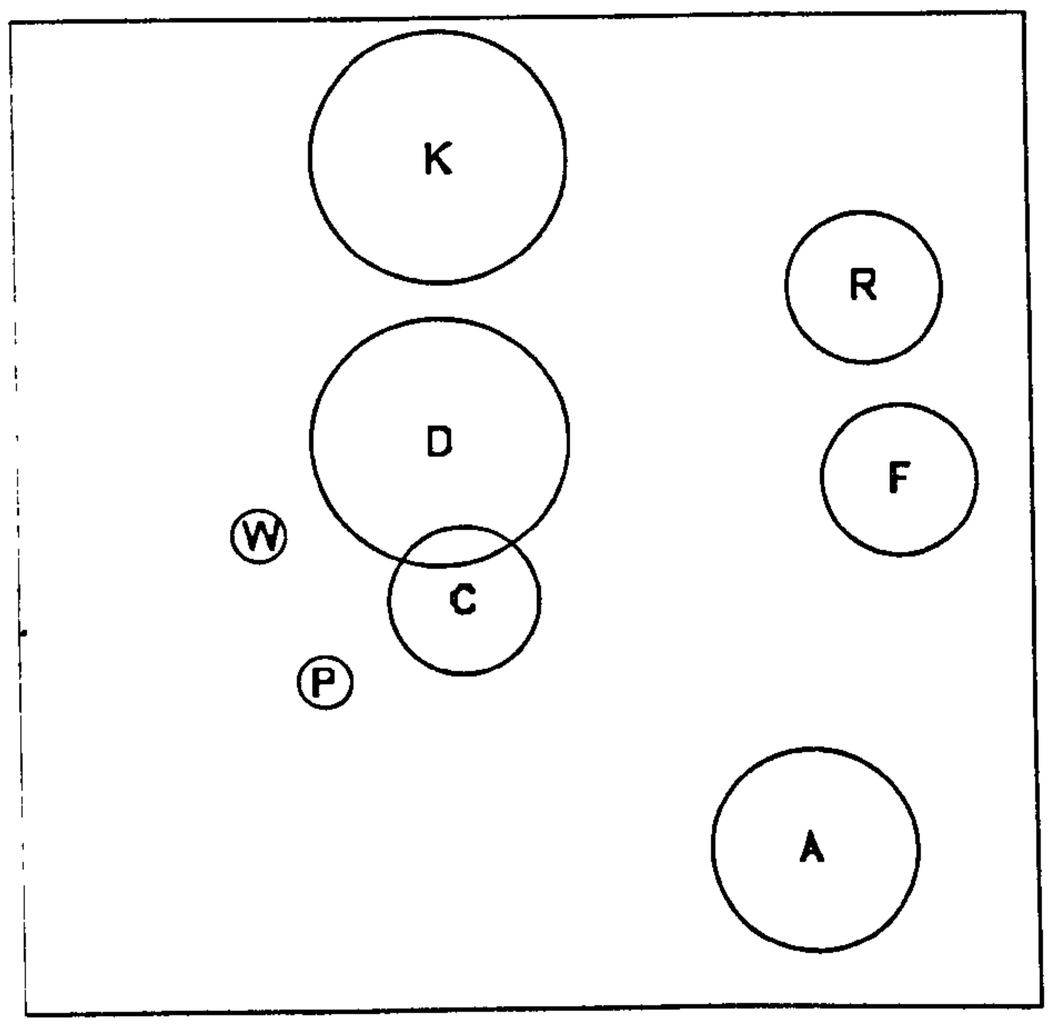


Figure 8 Ordination by MDS based on Bray-Curtis similarity, of a) square-root and b) presence absence transformed average taxa abundance data from the mussel beds at eight locations in the British Isles and Irish Republic. (P = Point Lynas, Wales; W = White Beach, Wales; C = Criccieth, Wales; A = Arisaig, Scotland; K = Kilkee, Irish Republic; D = Doonbeg, Irish Republic; R = Robin Hood's Bay, England; F = Filey Brigg, England). Superimposed circles are scaled in size to represent the relative values of degree of wave exposure at each of the locations.

Large-scale spatial variation in the community associated with P. purpuratus

All of the univariate measures of community diversity, i.e., total number of taxa, total number of individuals, Margalef's index of richness, Shannon's index of diversity and Pielou's evenness showed significant variation between the nine sample sites. With few exceptions, univariate measures of diversity were greater at Valdivia, Maule and the exposed locations at Desembocadura and lower at the sheltered Desembocadura locations (Figure 9). Values at the other sites were intermediate.

Cluster analysis of square-root transformed infauna abundance illustrated clear differences in community structure between the nine different sites, in terms of the more dominant taxa in the community (Figure 10). Similar clear differences in community structure emerged between the nine sites when cluster analysis was performed with a presence/absence transformation, thus removing emphasis from taxa abundance (Figure 11). MDS ordination of square-root transformed infaunal abundance illustrated a clear separation of mussel communities at each of the nine locations, in terms of the more dominant taxa in the community (Figure 12a). The high stress value of the original MDS plot (0.22) reflects the difficulty in condensing a large data set into two dimensions, so sites were re-grouped according to general cluster patterns and re-plotted to increase the accuracy of interpretation (Figure 12b-e). A one-way ANOSIM performed on the data confirmed that there were significant differences in community structure between some of the sites ($R=0.742$, $p<0.05$). ANOSIM pairwise comparisons revealed that the structure of the community associated with *P. purpuratus* was significantly different between each of the nine sites (Table 9a). RELATE analysis showed that there was no significant pattern of seriation, or gradient, underlying the MDS ordination of data ($R=0.349$, $p<0.05$).

MDS ordination performed with a presence/absence transformation illustrated a less clear separation of communities at each of the nine sites (Figure 13a). The plot had a high stress value (0.23), so sites were grouped together and re-plotted to facilitate the accuracy of interpretation. In general, the communities associated with *P. purpuratus* at each of the nine locations appeared less dissimilar when emphasis was removed from abundance of taxa (Figure 13b-e). However, a one-way ANOSIM test revealed that community structure was significantly different between at least some of the sites ($R=0.531$, $p<0.05$). Pairwise comparisons showed that the structure of the mussel community was significantly different at all of the nine sites, although R-values were generally lower than those obtained using a square-root transformation, indicating less pronounced differences (Table 9b). RELATE analysis

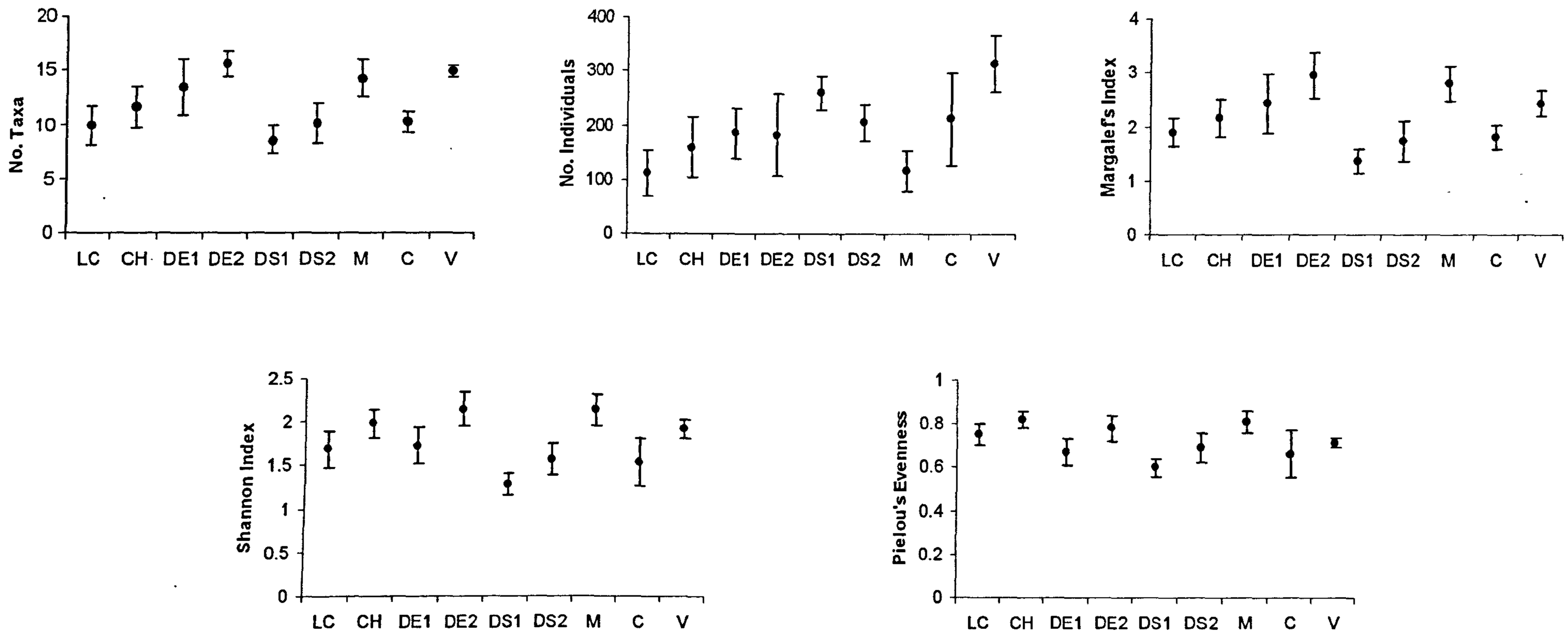


Figure 9 Univariate measures of mussel bed community diversity at Las Cruces (LC), Cocholgue (CH), Desembocadura exposed site 1 (DE1), Desembocadura exposed site 2 (DE2), Desembocadura sheltered site 1 (DS1), Desembocadura sheltered site 2 (DS2), Maule (M), Coronel (C) and Valdivia (V). Values are based on 25cm^2 replicates. 95% confidence intervals are marked, such that significant differences are represented by non-overlapping intervals.

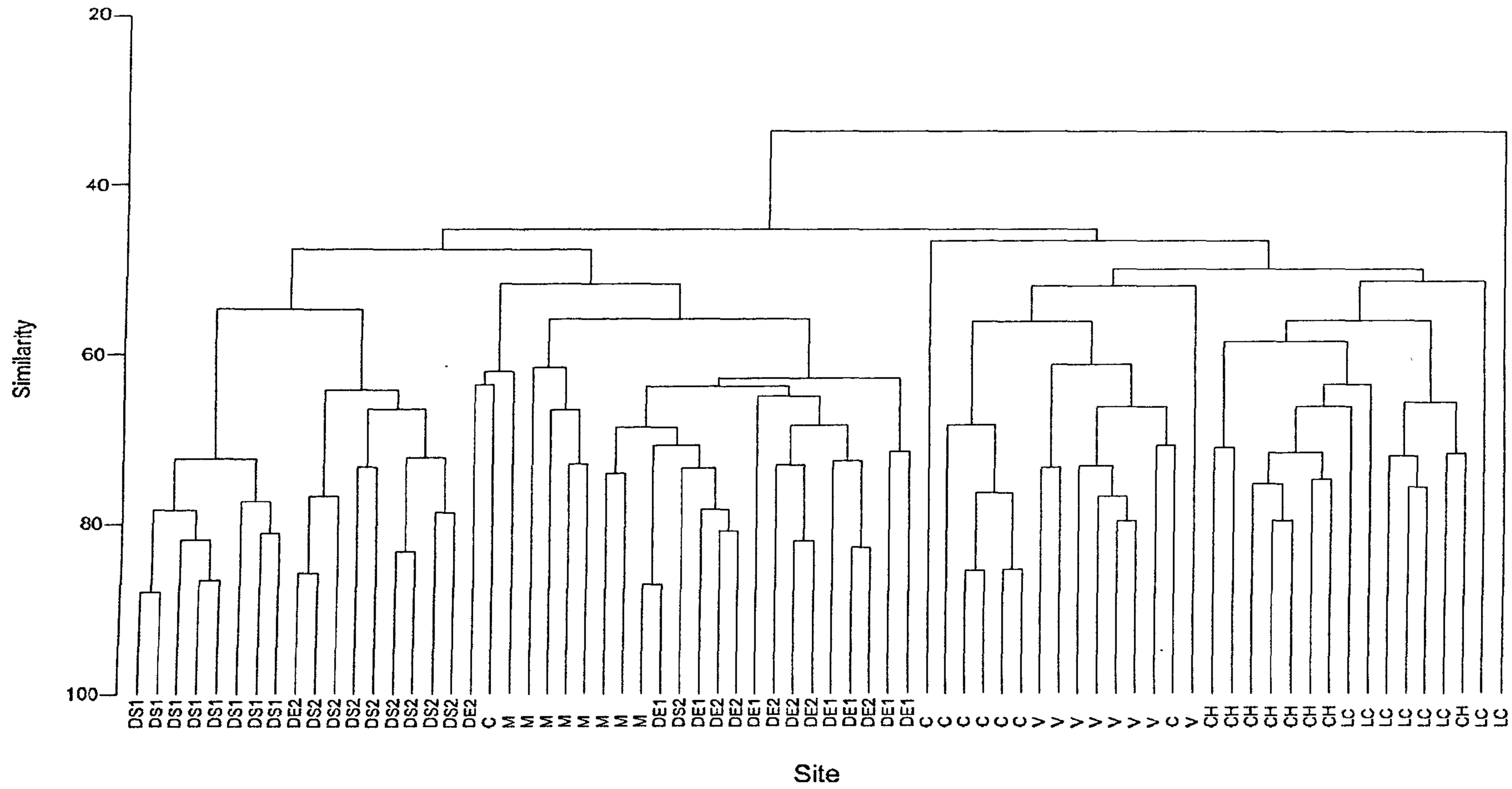


Figure 10 Dendrogram for group average clustering of Bray-Curtis similarities based on square-root transformed biotic data from mussel beds at nine locations in Chile, South America. (LC = Las Cruces; CH = Cocholgue; DE1 = Desembocadura exposed site 1; DE2 = Desembocadura exposed site 2; DS1 = Desembocadura sheltered site 1; DS2 = Desembocadura sheltered site 2; M = Maule; C = Coronel; V = Valdivia).

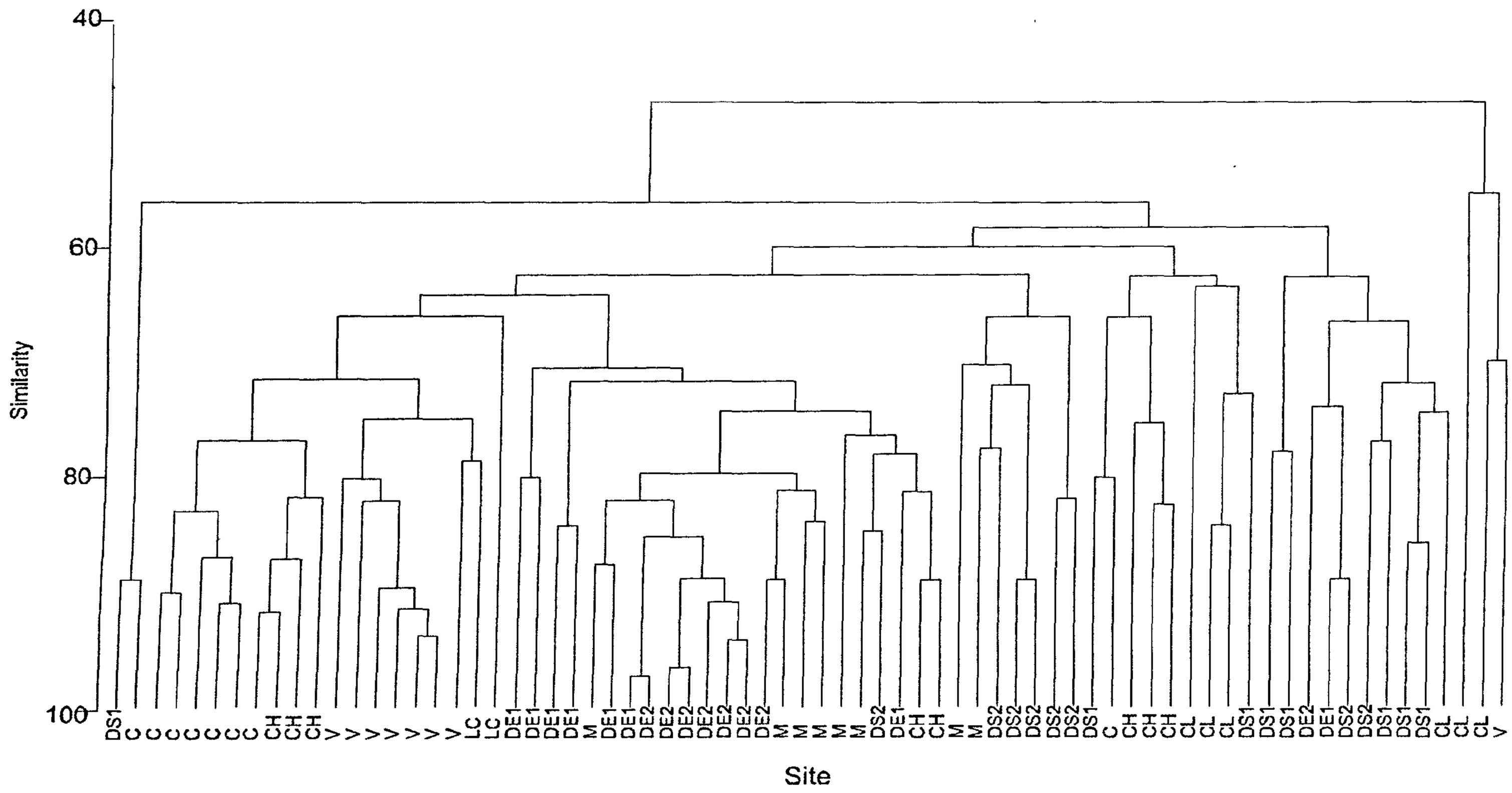
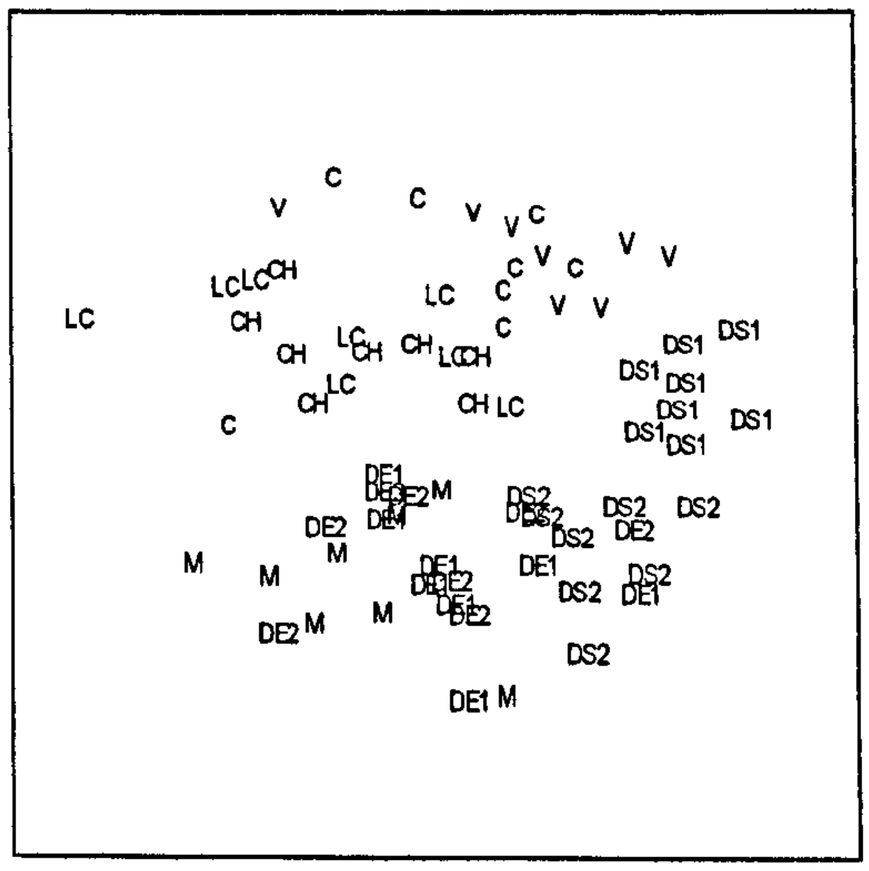


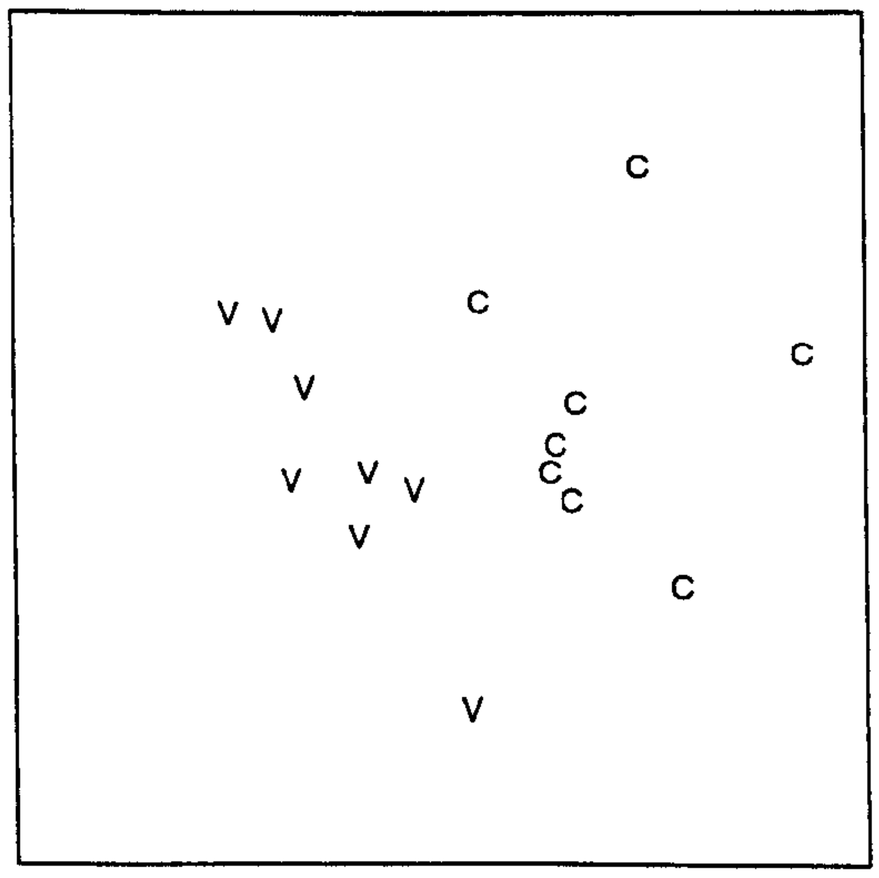
Figure 11 Dendrogram for group average clustering of Bray-Curtis similarities based on presence/absence transformed biotic data from mussel beds at nine locations in Chile, South America. (LC = Las Cruces; CH = Cocholgue; DE1 = Desembocadura exposed site 1; DE2 = Desembocadura exposed site 2; DS1 = Desembocadura sheltered site 1; DS2 = Desembocadura sheltered site 2; M = Maule; C = Coronel; V = Valdivia).

Figure 12 Ordination by MDS based on Bray-Curtis similarity, of square-root transformed taxa abundance data from mussel beds at a) nine locations in Chile, South America and b), c), d), e) at selected locations for ease of interpretation. (LC = Las Cruces; CH = Cocholgue; DE1 = Desembocadura exposed site 1; DE2 = Desembocadura exposed site 2; DS1 = Desembocadura sheltered site 1; DS2 = Desembocadura sheltered site 2; M = Maule; C = Coronel; V = Valdivia).

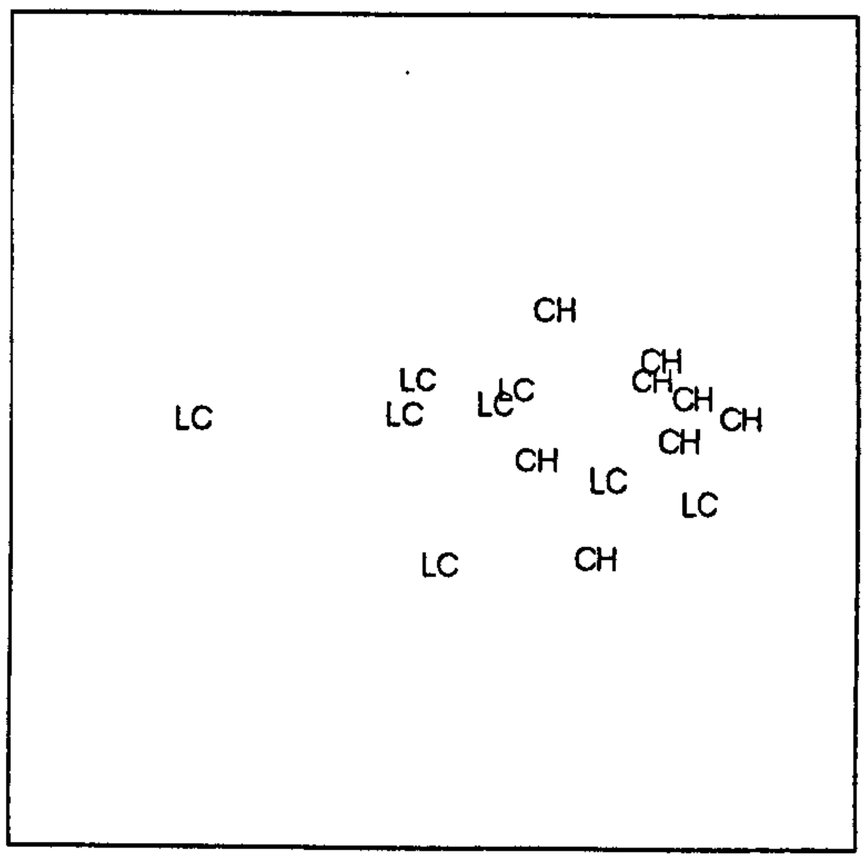
a) Stress = 0.22



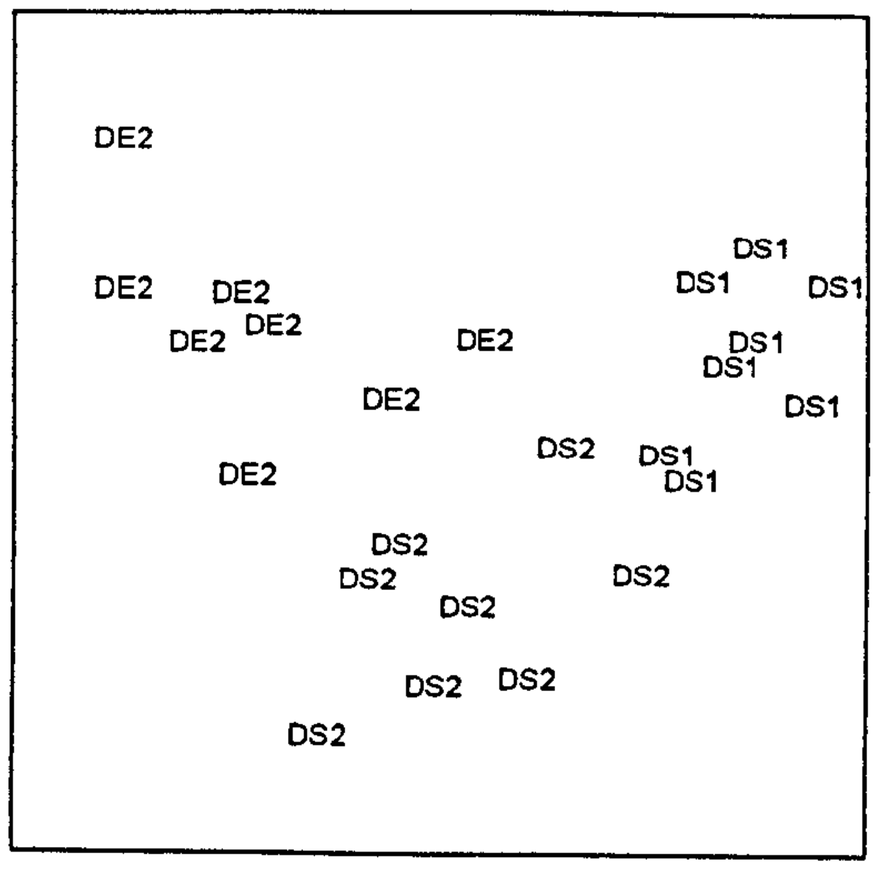
b) Stress = 0.15



c) Stress = 0.13



d) Stress = 0.12



e) Stress = 0.16

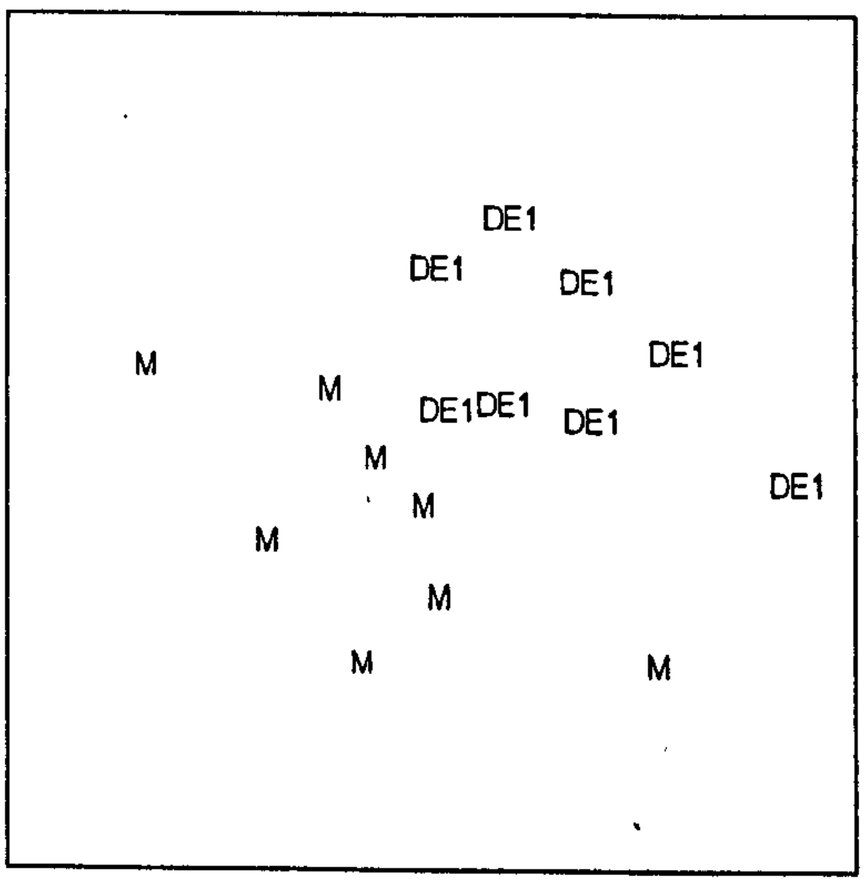


Table 9 Global R-values for ANOSIM pairwise comparisons between samples of mussel bed communities taken in January 1999 at nine locations in Chile, South America, based on a) square-root transformations of taxa abundance and b) presence/absence transformations. Significant differences in community structure are indicated by bold type (all differences are significant).

a)

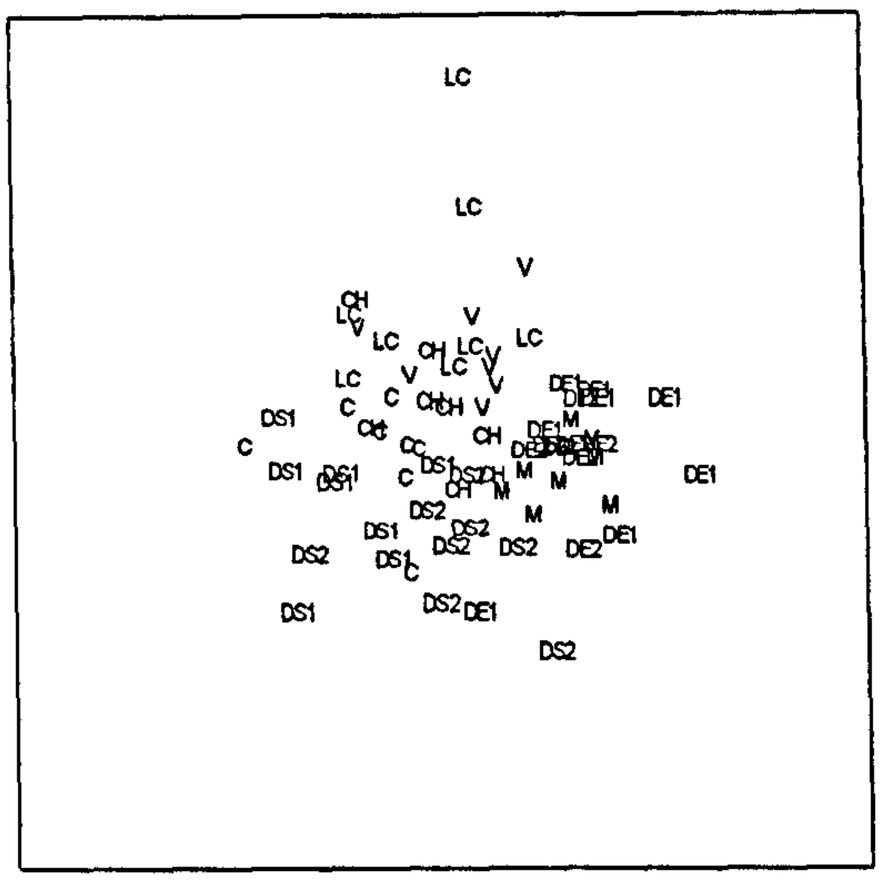
	Las Cruces	*Cocholgue*	*Desembocadura exposed site 1*	*Desembocadura exposed site 2*	*Desembocadura sheltered site 1*	*Desembocadura sheltered site 2*	*Maule*	*Coronel*
Cocholgue	**0.323**							
Desembocadura exposed site 1	**0.741**	**0.894**						
Desembocadura exposed site 2	**0.739**	**0.783**	**0.114**					
Desembocadura sheltered site 1	**0.839**	**0.971**	**0.932**	**0.943**				
Desembocadura sheltered site 2	**0.754**	**0.890**	**0.642**	**0.749**	**0.815**			
Maule	**0.672**	**0.821**	**0.353**	**0.366**	**0.953**	**0.708**		
Coronel	**0.535**	**0.562**	**0.859**	**0.843**	**0.719**	**0.853**	**0.824**	
Valdivia	**0.655**	**0.754**	**0.900**	**0.910**	**0.841**	**0.927**	**0.914**	**0.510**

b)

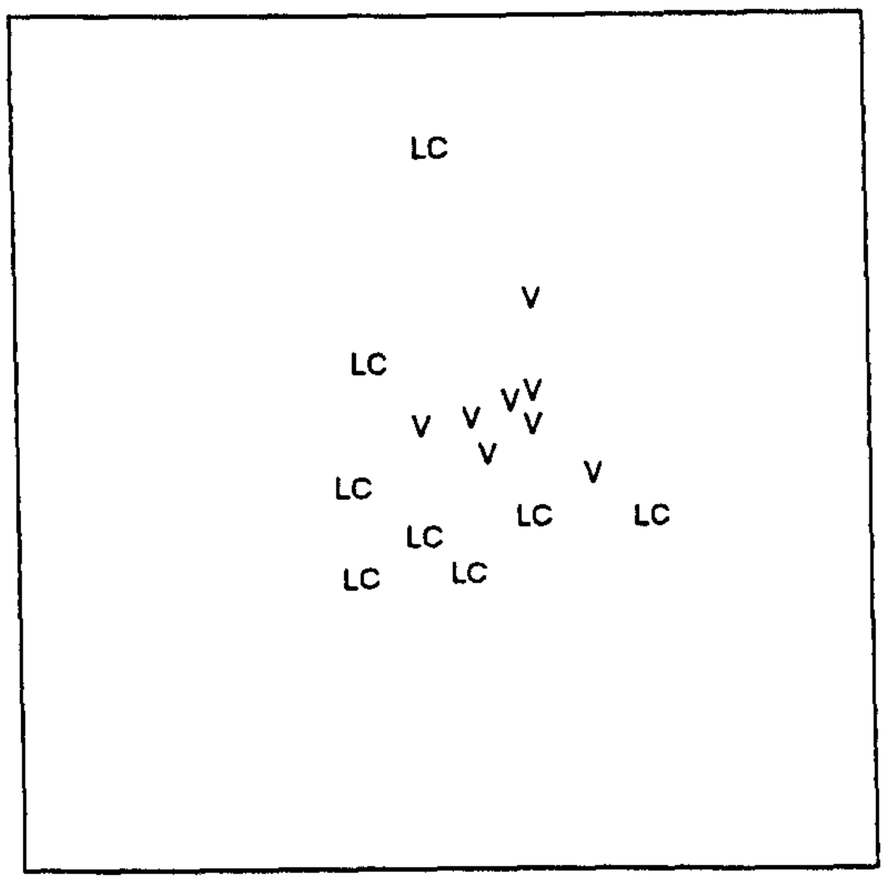
	Las Cruces	*Cocholgue*	*Desembocadura exposed site 1*	*Desembocadura exposed site 2*	*Desembocadura sheltered site 1*	*Desembocadura sheltered site 2*	*Maule*	*Coronel*
Cocholgue	**0.234**							
Desembocadura exposed site 1	**0.465**	**0.528**						
Desembocadura exposed site 2	**0.577**	**0.609**	**0.199**					
Desembocadura sheltered site 1	**0.398**	**0.461**	**0.743**	**0.803**				
Desembocadura sheltered site 2	**0.494**	**0.385**	**0.600**	**0.694**	**0.274**			
Maule	**0.529**	**0.558**	**0.177**	**0.338**	**0.748**	**0.502**		
Coronel	**0.416**	**0.300**	**0.859**	**0.946**	**0.414**	**0.428**	**0.895**	
Valdivia	**0.321**	**0.542**	**0.672**	**0.921**	**0.741**	**0.730**	**0.842**	**0.630**

Figure 13 Ordination by MDS based on Bray-Curtis similarity, of presence/absence transformed taxa abundance data from mussel beds at a) nine locations in Chile, South America and b), c), d), e) at selected locations for ease of interpretation. (LC = Las Cruces; CH = Cocholgue; DE1 = Desembocadura exposed site 1; DE2 = Desembocadura exposed site 2; DS1 = Desembocadura sheltered site 1; DS2 = Desembocadura sheltered site 2; M = Maule; C = Coronel; V = Valdivia).

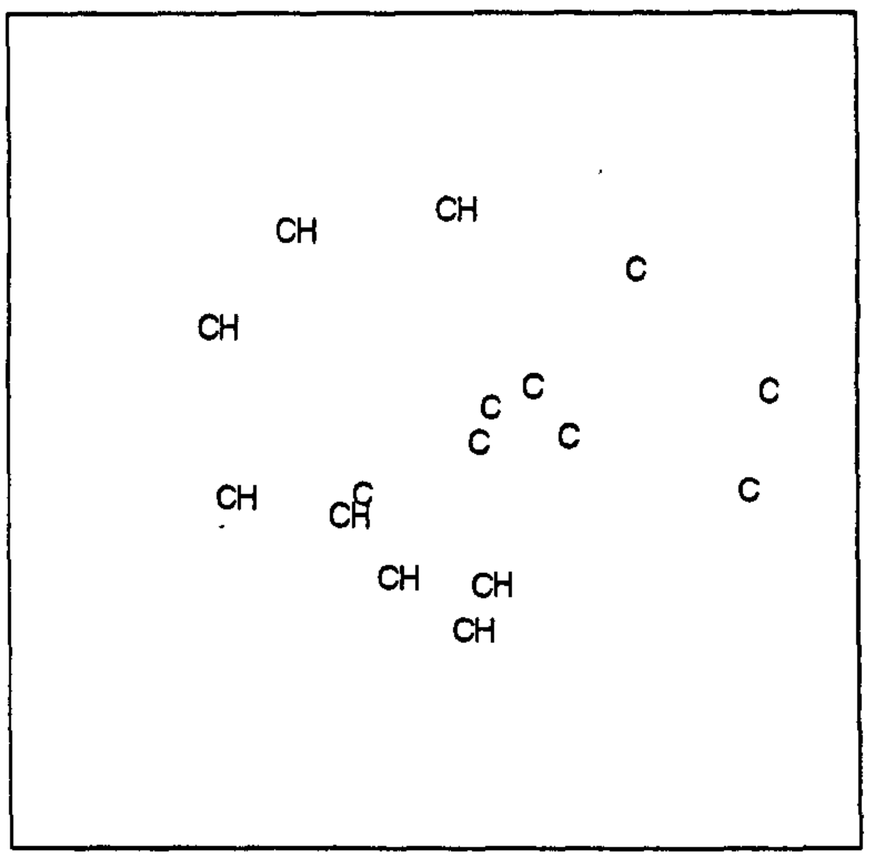
a) Stress = 0.23



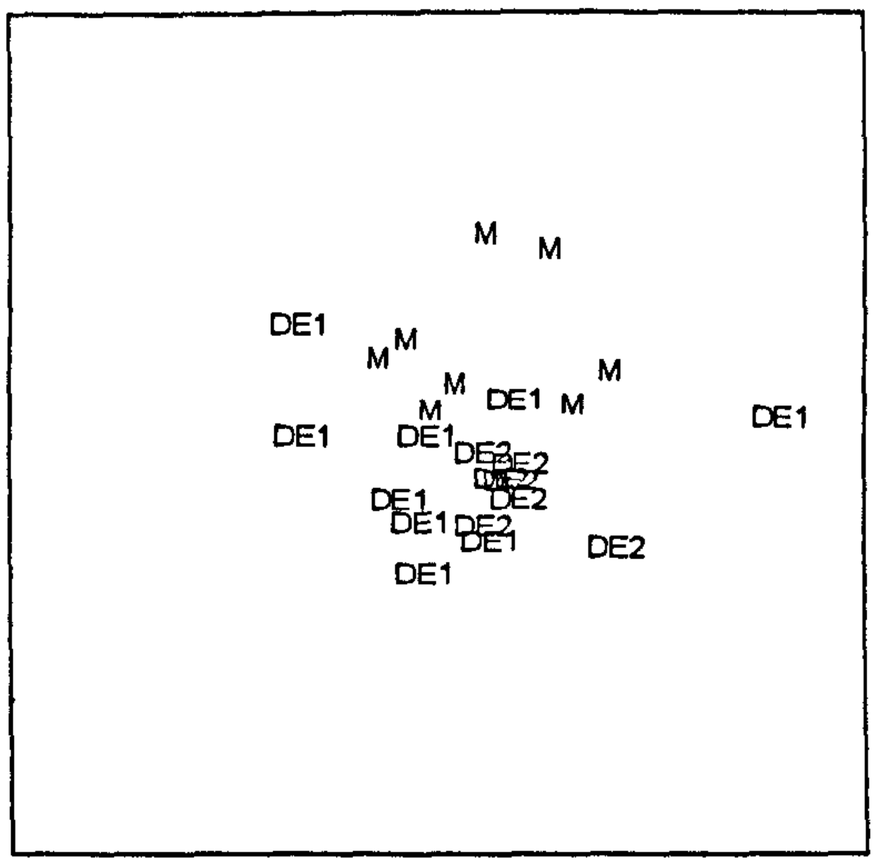
b) Stress = 0.14



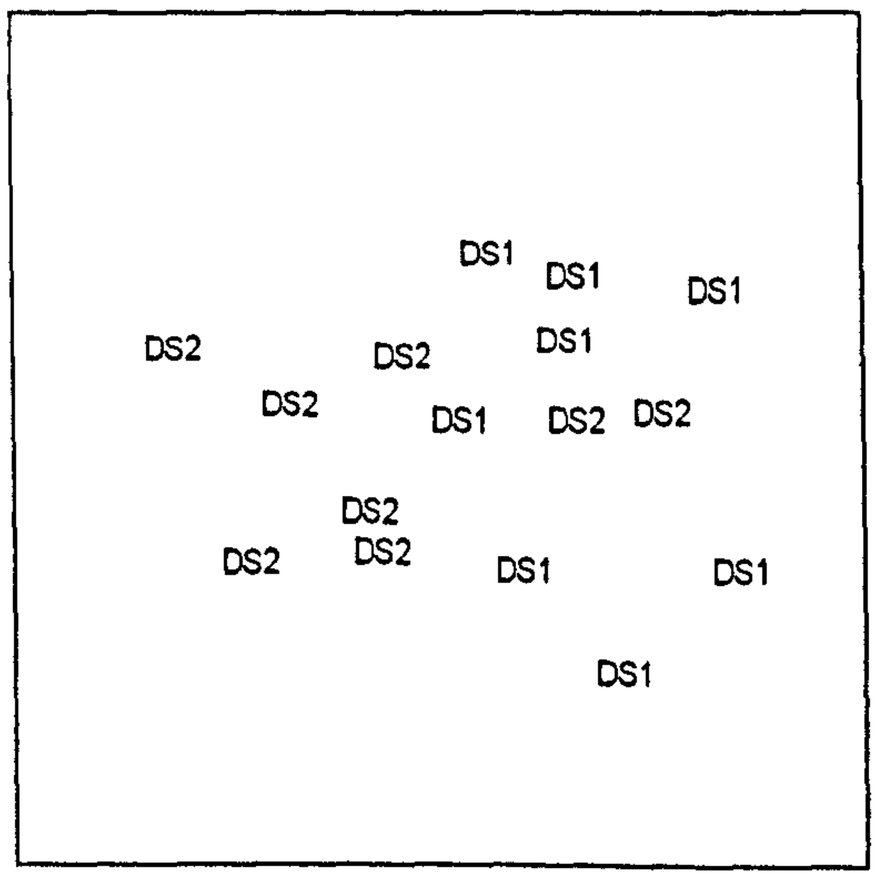
c) Stress = 0.14



d) Stress = 0.20



e) Stress = 0.15



showed that there was no significant pattern of seriation, or gradient, underlying the MDS ordination of data ($R=0.244$, $p<0.05$).

Similarity Percentage analysis (SIMPER), performed with a square-root transformation indicated that many of the taxa characterising the mussel bed communities were the same across each of the nine sites in Chile, such as nematodes, juvenile mussels, nereid polychaetes and anemones. Other dominant taxa were site-specific, such as sea spiders, isopods and various polychaete families. Table 10 provides details of the taxa contributing to differences in mussel bed community composition across sites. SIMPER analysis performed with a presence/absence transformation indicated that the mussel bed communities at each of the nine sites throughout Chile were characterised by quite different taxa, with few taxa consistently present in mussel beds at all sites (Table 11). Given the highly variable structure of the communities, it was difficult to ascertain any pattern in the data. However in general, most taxa were found in greater abundance at the more wave-exposed sites (e.g. Valdivia and Desembocadura exposed sites), than the sheltered (Desembocadura sheltered sites and at Las Cruces), with the exception of a few selected taxa, including anemones, isopods and nereid and hesionid polychaetes. Such mobile taxa might be excluded from the more exposed locations, as a result of 'flushing' by severe wave action, while anemones might not be able to feed effectively in such conditions.

The population density of mussels in the beds has been shown not to vary significantly between each of the nine Chilean sites (see ANOVA, Chapter 3). It was thus unlikely, statistically, that the observed differences in community diversity between each of the nine sites were a reflection of mussel density and no further analysis was performed on the data.

Comparison of the communities associated with M. edulis and P. purpuratus

Values of all the univariate measures of community diversity, with the exception of Shannon's index, showed significant differences between mussel beds in the British Isles and Irish Republic and Chile, when data were pooled for each of the two geographical areas and compared at the same taxonomic level (Table 12). The total number of taxa and individuals present in the mussel beds, along with Margalef's index of richness were all higher in British and Irish mussel beds than their counterparts in Chile. In contrast, Pielou's evenness was greater in *P. purpuratus* beds (refer to Figures 1 & 9).

Infaunal abundance data from *P. purpuratus* and *M. edulis* communities were plotted as *k*-dominance plots, based on the ranking of taxa in decreasing order of

Table 10 Results of similarity percentage analysis (SIMPER) performed on square-root transformed abundance of infaunal taxa present in mussel beds at nine locations throughout Chile, South America, showing a breakdown of % contributions of infaunal taxa (% Cont.) to average dissimilarity between locations. Taxa highlighted in grey indicate higher abundance at the first listed site.

Las Cruces Cocholgue	% Cont.	Las Cruces Des. Exp. 1	% Cont.	Las Cruces Des. Exp. 2	% Cont.	Las Cruces Des. Shelt. 1	% Cont.	Las Cruces Des. Shelt. 2	% Cont.	Las Cruces Maule	% Cont.	Las Cruces Coronel	% Cont.	Las Cruces Valdivia	% Cont.
Barnacles	10.11	Nematodes	13.20	Nematodes	11.86	Spionidae polychaetes	26.57	Nematodes	18.31	Anemones	8.60	Barnacles	15.87	Spionidae polychaetes	13.39
Juvenile mussels	9.60	Anemones	9.99	Anemones	11.52	Juvenile mussels	10.72	Barnacles	8.79	Nematodes	8.04	Juvenile mussels	11.76	Chironomid larvae	13.25
Nematodes	9.33	Amphipods	9.68	Terebellidae polychaetes	8.26	Nematodes	9.62	Limpets	8.27	Cirratulidae polychaetes	7.18	Spionidae polychaetes	10.34	Barnacles	10.56
Limpets	8.11	Limpets	7.46	Juvenile mussels	7.20	Limpets	8.53	Juvenile mussels	7.46	Barnacles	7.09	Nemerteans	7.54	Mites	6.54
Nereidae polychaetes polychaetes	7.85	Juvenile mussels	7.02	Amphipods	6.50	Barnacles	7.05	Anemones	7.24	Isopods	6.68	Oligochaetes	5.94	Other Bivalves	5.71
Oligochaetes	6.65	Barnacles	5.82	Limpets	5.20	Oligochaetes	4.95	Oligochaetes	6.65	Juvenile mussels	6.39	Turbellarians	5.71	Amphipods	5.67
Spionidae polychaetes	6.63	Nemerteans	5.59	Barnacles	5.15	Amphipods	4.51	Amphipods	5.89	Limpets	5.94	Nereidae polychaetes	5.22	Juvenile mussels	5.27
Syllidae polychaetes	6.24	Nereidae polychaetes	4.56	Spionidae polychaetes	4.51	Syllidae polychaetes	4.45	Nereidae polychaetes	5.18	Amphipods	5.87	Limpets	5.01	Nematodes	5.05
Amphipods	4.80	Syllidae polychaetes	4.39	Sea spiders	4.50	Nereidae polychaetes	4.07	Syllidae polychaetes	4.95	Nemerteans	5.52	Syllidae polychaetes	4.97	Oligochaetes	4.10
Other Bivalves	4.36	Oligochaetes	3.87	Nereidae polychaetes	4.43	Other Bivalves	3.50	Spionidae polychaetes	3.87	Syllidae polychaetes	5.16	Amphipods	4.95	Turbellarians	3.70
Nemerteans	4.00	Other Bivalves	3.58	Syllidae polychaetes	4.13	Isopods	3.00	Other Bivalves	3.56	Oligochaetes	4.64	Nematodes	4.90	Syllidae polychaetes	3.44
Chitons	3.36	Isopods	3.28	Nemerteans	3.84	Hesionidae polychaetes	2.09	Nemerteans	3.02	Nereidae polychaetes	4.62	Other Bivalves	3.97	Nemerteans	3.41
Isopods	3.01	Terebellidae polychaetes	2.88	Oligochaetes	3.48	Chironomid larvae	1.93	Isopods	2.24	Crabs	3.82	Chironomid larvae	2.29	Nereidae polychaetes	3.29
Chironomid larvae	2.94	Crabs	2.81	Other Bivalves	3.36			Chironomid larvae	2.14	Other Bivalves	3.78	Isopods	2.16	Limpets	3.27
Crabs	2.48	Mites	2.42	Isopods	3.21			Phyllodocidae polychaetes	1.97	Eunicidae polychaetes	2.33			Other Insects	3.24
Mites	2.19	Cirratulidae polychaetes	4.25	Crabs	2.86			Crabs	1.82	Spionidae polychaetes	2.22			Anemones	2.71
		Chironomid larvae	1.87							Chironomid larvae	2.19				
Average dissimilarity between sites = 46.57%		Average dissimilarity between sites = 54.62%		Average dissimilarity between sites = 54.73%		Average dissimilarity between sites = 57.48%		Average dissimilarity between sites = 56.04%		Average dissimilarity between sites = 54.59%		Average dissimilarity between sites = 52.33%		Average dissimilarity between sites = 53.06%	

Cocholgue Des. Exp. 1	% Cont.	Cocholgue Des. Exp. 2	% Cont.	Cocholgue Des. Shelt. 1	% Cont.	Cocholgue Des. Shelt. 2	% Cont.	Cocholgue Maule	% Cont.	Cocholgue Coronel	% Cont.	Cocholgue Valdivia	% Cont.
Limpets	10.51	Anemones	9.80	Spionidae polychaetes	19.55	Barnacles	13.95	Barnacles	10.89	Juvenile mussels	13.68	Chironomid larvae	12.44
Juvenile mussels	9.69	Limpets	9.42	Juvenile mussels	15.35	Juvenile mussels	12.68	Limpets	9.94	Barnacles	11.25	Spionidae polychaetes	10.55
Amphipods	9.42	Nematodes	8.41	Limpets	11.46	Limpets	12.02	Cirratulidae polychaetes	6.64	Limpets	9.60	Juvenile mussels	8.18
Nematodes	8.36	Barnacles	8.14	Barnacles	10.14	Nematodes	11.54	Isopods	6.45	Spionidae polychaetes	8.87	Barnacles	7.08
Barnacles	8.20	Terebellidae polychaetes	8.10	Nematodes	7.25	Oligochaetes	6.97	Anemones	6.43	Nematodes	8.05	Limpets	6.39
Anemones	7.32	Amphipods	7.52	Oligochaetes	5.41	Amphipods	5.86	Amphipods	6.12	Nemerteans	7.31	Other Bivalves	6.18
Syllidae polychaetes	5.55	Juvenile mussels	7.14	Nereidae polychaetes	4.68	Anemones	5.59	Nematodes	6.10	Oligochaetes	6.86	Mites	6.07
Nereidae polychaetes	5.17	Spionidae polychaetes	5.90	Amphipods	4.60	Spionidae polychaetes	5.50	Oligochaetes	5.61	Amphipods	5.88	Amphipods	5.77
Spionidae polychaetes	4.86	Oligochaetes	4.99	Syllidae polychaetes	3.98	Syllidae polychaetes	3.51	Spionidae polychaetes	5.36	Turbellarians	4.69	Nereidae polychaetes	5.09
Oligochaetes	4.72	Sea spiders	4.43	Nemerteans	2.54	Nemerteans	3.32	Juvenile mussels	5.19	Nereidae polychaetes	4.45	Oligochaetes	4.84
Nemerteans	3.71	Syllidae polychaetes	3.67	Chitons	2.35	Nereidae polychaetes	2.97	Nereidae polychaetes	4.80	Syllidae polychaetes	4.31	Nematodes	4.71
Isopods	2.67	Crabs	3.34	Isopods	2.27	Chitons	2.54	Crabs	4.00	Chitons	2.81	Turbellarians	3.17
Crabs	2.67	Nereidae polychaetes	3.14	Anemones	1.89	Orbinidae	1.87	Nemerteans	3.98	Anemones	2.28	Other Insects	2.98
Terebellidae polychaetes	2.49	Isopods	3.12			Phyllodocidae polychaetes	1.83	Syllidae polychaetes	3.08			Syllidae polychaetes	2.84
Mites	2.14	Nemerteans	2.84					Chitons	2.47			Nemerteans	2.62
Chitons	2.11	Chironomid larvae	1.79					Eunicidae polychaetes	2.12			Anemones	2.52
Cirratulidae polychaetes	1.94							Chironomid larvae	1.91				
Average dissimilarity between sites = 55.97%		Average dissimilarity between sites = 49.60%		Average dissimilarity between sites = 58.03%		Average dissimilarity between sites = 53.29%		Average dissimilarity between sites = 52.55%		Average dissimilarity between sites = 47.74%		Average dissimilarity between sites = 51.86%	

Des. Exp. 1 Des. Exp. 2	% Cont.	Des. Exp. 1 Des. Shelt. 1	% Cont.	Des. Exp. 1 Des. Shelt. 2	% Cont.	Des. Exp. 1 Maule	% Cont.	Des. Exp. 1 Coronel	% Cont.	Des. Exp. 1 Valdivia	% Cont.
Nematodes	12.79	Spionidae polychaetes	24.81	Nematodes	11.47	Nematodes	12.19	Barnacles	12.79	Spionidae polychaetes	11.64
Juvenile mussels	11.63	Nematodes	10.17	Amphipods	9.61	Juvenile mussels	10.61	Nematodes	11.39	Chironomid larvae	11.46
Terebellidae polychaetes	7.32	Anemones	7.56	Oligochaetes	8.54	Amphipods	8.19	Spionidae polychaetes	8.73	Barnacles	9.68
Amphipods	7.10	Amphipods	7.14	Juvenile mussels	7.71	Cirratulidae polychaetes	7.28	Juvenile mussels	8.63	Nematodes	7.67
Spionidae polychaetes	5.93	Juvenile mussels	6.52	Barnacles	6.54	Syllidae polychaetes	6.35	Anemones	7.55	Amphipods	6.56
Barnacles	5.34	Nemerteans	5.32	Nemerteans	5.58	Isopods	6.02	Nemerteans	6.57	Other bivalves	5.51
Nereidae polychaetes	4.93	Oligochaetes	4.13	Syllidae polychaetes	5.55	Barnacles	4.49	Amphipods	6.45	Juvenile mussels	5.05
Sea spiders	4.87	Barnacles	4.12	Nereidae polychaetes	5.02	Anemones	4.39	Turbellarians	4.54	Mites	4.82
Syllidae polychaetes	4.79	Crabs	3.25	Anemones	4.72	Nemerteans	4.38	Syllidae polychaetes	3.52	Anemones	4.80
Anemones	4.37	Nereidae polychaetes	3.10	Spionidae polychaetes	3.91	Nereidae polychaetes	4.09	Nereidae polychaetes	3.46	Oligochaetes	3.89
Nemerteans	4.11	Syllidae polychaetes	3.09	Crabs	3.63	Limpets	3.33	Limpets	3.24	Limpets	3.17
Oligochaetes	3.81	Isopods	3.04	Isopods	3.14	Oligochaetes	3.32	Crabs	3.14	Turbellarians	3.15
Limpets	3.51	Terebellidae polychaetes	2.56	Terebellidae polychaetes	3.08	Terebellidae polychaetes	3.25	Oligochaetes	2.98	Other insects	2.66
Isopods	3.29	Mites	2.03	Mites	2.45	Eunicidae polychaetes	2.86	Isopods	2.66	Nemerteans	2.57
Mites	2.78	Limpets	2.03	Cirratulidae polychaetes	2.40	Crabs	2.81	Terebellidae polychaetes	2.47	Nereidae polychaetes	2.42
Cirratulidae polychaetes	2.73	Cirratulidae polychaetes	1.99	Phyllodocidae polychaetes	2.20	Mites	2.58	Mites	1.96	Syllidae polychaetes	2.33
Crabs	2.18			Eunicidae polychaetes	2.12	Sea spiders	2.13			Isopods	2.06
				Limpets	2.08	Tanaids	1.90			Terebellidae polychaetes	1.97
				Turbellarians	1.82						
Average dissimilarity between sites = 36.97%		Average dissimilarity between sites = 54.21%		Average dissimilarity between sites = 44.73%		Average dissimilarity between sites = 43.56%		Average dissimilarity between sites = 57.52%		Average dissimilarity between sites = 56.81%	

Des. Exp. 2 Des. Shelt. 1	% Cont.	Des. Exp. 2 Des. Shelt. 2	% Cont.	Des. Exp. 2 Maule	% Cont.	Des. Exp. 2 Coronel	% Cont.	Des. Exp. 2 Valdivia	% Cont.
Spionidae polychaetes	19.34	Juvenile mussels	11.36	Nematodes	11.53	Barnacles	12.20	Chironomid larvae	11.36
Juvenile mussels	11.60	Nematodes	10.49	Terebellidae polychaetes	9.75	Nematodes	10.88	Spionidae polychaetes	9.40
Nematodes	9.28	Terebellidae polychaetes	8.66	Juvenile mussels	7.87	Juvenile mussels	9.94	Barnacles	8.81
Anemones	8.88	Barnacles	7.09	Cirratulidae polychaetes	7.31	Anemones	9.27	Nematodes	7.13
Terebellidae polychaetes	7.26	Oligochaetes	6.87	Amphipods	5.49	Terebellidae polychaetes	7.38	Juvenile mussels	6.38
Barnacles	4.67	Amphipods	6.71	Barnacles	5.43	Spionidae polychaetes	7.02	Anemones	5.84
Amphipods	4.56	Spionidae polychaetes	5.48	Spionidae polychaetes	5.39	Nemerteans	5.73	Terebellidae polychaetes	5.75
Oligochaetes	4.03	Anemones	5.10	Isopods	5.23	Turbellarians	4.45	Mites	5.45
Sea spiders	3.97	Sea spiders	4.74	Anemones	4.82	Amphipods	4.27	Other bivalves	5.29
Crabs	3.55	Syllidae polychaetes	4.00	Sea spiders	4.72	Sea spiders	4.03	Amphipods	5.11
Nemerteans	3.47	Nemerteans	3.91	Syllidae polychaetes	4.24	Oligochaetes	3.90	Oligochaetes	3.39
Limpets	3.03	Crabs	3.89	Oligochaetes	4.15	Crabs	3.61	Sea spiders	3.15
Syllidae polychaetes	3.03	Isopods	3.17	Nemerteans	3.71	Isopods	3.15	Turbellarians	3.03
Isopods	2.90	Limpets	3.12	Nereidae polychaetes	2.86	Syllidae polychaetes	2.95	Other Insects	2.55
Nereidae polychaetes	2.16	Nereidae polychaetes	2.36	Limpets	2.83	Limpets	2.26	Nereidae polychaetes	2.44
		Chitons	2.16	Crabs	2.67			Isopods	2.32
		Phyllodocidae polychaetes	1.94	Eunicidae polychaetes	2.32			Limpets	2.22
								Nemerteans	1.99
Average dissimilarity between sites = 55.05%		Average dissimilarity between sites = 45.93%		Average dissimilarity between sites = 41.87%		Average dissimilarity between sites = 55.43%		Average dissimilarity between sites = 56.40%	

Des. Shelt. 1 Des. Shelt. 2	% Cont.	Des. Shelt. 1 Maule	% Cont.	Des. Shelt. 1 Coronel	% Cont.	Des. Shelt. 1 Valdivia	% Cont.
Spionidae polychaetes	26.76	Spionidae polychaetes	22.90	Spionidae polychaetes	18.51	Chironomid larvae	13.15
Nematodes	14.64	Juvenile mussels	13.44	Barnacles	17.62	Barnacles	13.08
Oligochaetes	8.55	Nematodes	7.62	Nematodes	9.88	Spionidae polychaetes	8.50
Anemones	6.56	Cirratulidae polychaetes	5.75	Juvenile mussels	9.45	Nematodes	7.12
Amphipods	6.44	Anemones	5.57	Nemerteans	6.87	Mites	6.83
Syllidae polychaetes	4.79	Isopods	5.24	Oligochaetes	5.18	Other Bivalves	6.34
Juvenile mussels	4.56	Nemerteans	4.63	Limpets	4.96	Juvenile mussels	5.88
Barnacles	4.55	Amphipods	4.19	Turbellarians	4.94	Amphipods	5.53
Nereidae polychaetes	3.95	Oligochaetes	3.96	Amphipods	4.63	Oligochaetes	4.65
Nemerteans	2.57	Crabs	3.91	Syllidae polychaetes	3.93	Limpets	4.54
Isopods	2.56	Syllidae polychaetes	3.73	Nereidae polychaetes	3.15	Turbellarians	3.36
Hesionidae polychaetes	2.30	Barnacles	3.36	Isopods	2.23	Nemerteans	3.25
Phyllodocidae polychaetes	2.12	Limpets	3.04			Other Insects	3.06
		Nereidae polychaetes	1.97			Anemones	2.49
		Hesionidae polychaetes	1.79			Syllidae polychaetes	2.28
Average dissimilarity between sites = 45.63%		Average dissimilarity between sites = 60.31%		Average dissimilarity between sites = 48.92%		Average dissimilarity between sites = 50.38%	

Des. Shelt. 2 Maule	% Cont.	Des. Shelt. 2 Coronel	% Cont.	Des. Shelt. 2 Valdivia	% Cont.	Maule Coronel	% Cont.	Maule Valdivia	% Cont.	Coronel Valdivia	% Cont.
Nematodes	14.33	Barnacles	17.89	Barnacles	13.27	Barnacles	14.57	Chironomid larvae	11.49	Chironomid larvae	14.50
Juvenile mussels	11.77	Nematodes	17.34	Chironomid larvae	11.93	Juvenile mussels	10.71	Spionidae polychaetes	10.97	Spionidae polychaetes	9.68
Oligochaetes	8.39	Juvenile mussels	8.71	Nematodes	10.36	Spionidae polychaetes	8.58	Barnacles	10.59	Juvenile mussels	8.43
Cirratulidae polychaetes	6.86	Oligochaetes	8.45	Spionidae polychaetes	10.14	Nemerteans	6.68	Juvenile mussels	6.03	Barnacles	7.93
Isopods	6.83	Spionidae polychaetes	7.65	Mites	5.90	Isopods	6.68	Mites	5.77	Mites	7.29
Amphipods	6.22	Nemerteans	6.34	Other Bivalves	5.48	Anemones	6.18	Other Bivalves	5.35	Other Bivalves	6.34
Nemerteans	4.97	Anemones	5.67	Amphipods	5.46	Cirratulidae polychaetes	6.11	Amphipods	4.77	Nemerteans	5.98
Crabs	4.37	Amphipods	5.33	Oligochaetes	4.40	Nematodes	6.11	Isopods	4.76	Amphipods	5.66
Barnacles	4.33	Limpets	3.88	Juvenile mussels	4.05	Turbellarians	4.53	Cirratulidae polychaetes	4.58	Oligochaetes	5.62
Syllidae polychaetes	3.90	Syllidae polychaetes	3.70	Limpets	3.54	Amphipods	4.19	Nematodes	4.51	Nematodes	4.65
Spionidae polychaetes	3.79	Turbellarians	3.68	Anemones	3.41	Crabs	4.17	Oligochaetes	3.92	Turbellarians	3.33
Nereidae polychaetes	3.42	Nereidae polychaetes	2.76	Nereidae polychaetes	3.15	Syllidae polychaetes	3.49	Anemones	3.55	Other Insects	3.27
Anemones	3.27			Nemerteans	2.82	Oligochaetes	3.18	Turbellarians	2.96	Nereidae polychaetes	3.11
Limpets	3.18			Turbellarians	2.69	Nereidae polychaetes	2.57	Other Insects	2.59	Anemones	2.70
Eunicidae polychaetes	2.55			Other Insects	2.64	Limpets	2.45	Nemerteans	2.54	Syllidae polychaetes	2.62
Phyllodocidae polychaetes	2.15			Syllidae polychaetes	2.61			Syllidae polychaetes	2.45		
								Limpets	2.28		
								Nereidae polychaetes	1.90		
Average dissimilarity between sites = 50.32%		Average dissimilarity between sites = 55.93%		Average dissimilarity between sites = 58.09%		Average dissimilarity between sites = 58.24%		Average dissimilarity between sites = 60.78%		Average dissimilarity between sites = 48.17%	

Table 11 Results of similarity percentage analysis (SIMPER) performed on presence/absence transformed abundance of infaunal taxa present in mussel beds at nine locations in Chile, South America, showing a breakdown of % contributions of infaunal taxa (% Cont.) to average dissimilarity between locations. Taxa highlighted in grey indicate higher abundance at the first listed site.

Las Cruces Cocholgue	% Cont.	Las Cruces Des. Exp. 1	% Cont.	Las Cruces Des. Exp. 2	% Cont.	Las Cruces Des. Shelt. 1	% Cont.	Las Cruces Des. Shelt. 2	% Cont.	Las Cruces Maule	% Cont.	Las Cruces Coronel	% Cont.	Las Cruces Valdivia	% Cont.
Chitons	8.86	Anemones	9.66	Terebellidae polychaetes	9.00	Limpets	8.88	Anemones	9.05	Anemones	9.59	Turbellarians	9.59	Other Insects	8.20
Nereidae polychaetes	6.58	Nemerteans	6.63	Anemones	9.00	Spionidae polychaetes	8.06	Chironomid larvae	6.70	Nemerteans	6.69	Spionidae polychaetes	8.17	Turbellarians	7.46
Nemerteans	6.56	Terebellidae polychaetes	5.54	Sea Spiders	7.80	Chironomid larvae	6.41	Barnacles	6.53	Isopods	5.83	Oligochaetes	7.26	Mites	7.35
Chironomid larvae	6.43	Chironomid larvae	5.24	Chitons	6.65	Nereidae polychaetes	6.33	Nereidae polychaetes	5.87	Chironomid larvae	5.73	Chironomid larvae	7.23	Spionidae polychaetes	6.81
Spionidae polychaetes	6.30	Isopods	5.19	Nemerteans	6.26	Oligochaetes	6.12	Limpets	5.62	Cirratulidae polychaetes	5.51	Nemerteans	6.79	Nemerteans	6.79
Amphipods	6.14	Syllidae polychaetes	5.15	Isopods	5.46	Other Bivalves	5.87	Spionidae polychaetes	5.37	Nereidae polychaetes	5.08	Nereidae polychaetes	6.46	Anemones	6.64
Other Bivalves	5.99	Crabs	4.90	Chironomid larvae	5.37	Crabs	5.78	Other Bivalves	5.31	Crabs	4.87	Other Bivalves	6.03	Nereidae polychaetes	5.58
Crabs	5.96	Nereidae polychaetes	4.88	Spionidae polychaetes	4.85	Isopods	5.51	Crabs	5.26	Other Bivalves	4.76	Crabs	5.91	Crabs	5.54
Isopods	5.18	Other Bivalves	4.79	Nereidae polychaetes	4.83	Syllidae polychaetes	5.37	Turbellarians	5.14	Oligochaetes	4.13	Nematodes	5.53	Other Bivalves	5.52
Nematodes	4.92	Cirratulidae polychaetes	4.63	Crabs	4.59	Nematodes	5.16	Syllidae polychaetes	4.90	Syllidae polychaetes	4.11	Syllidae polychaetes	5.50	Nematodes	4.71
Syllidae polychaetes	4.87	Mites	4.56	Other Bivalves	4.47	Barnacles	4.92	Amphipods	4.56	Spionidae polychaetes	4.01	Other Gastropods	4.84	Chironomid larvae	4.49
Mites	4.73	Limpets	4.30	Syllidae polychaetes	4.05	Amphipods	4.57	Isopods	4.52	Nematodes	3.87	Amphipods	4.62	Syllidae polychaetes	4.38
Turbellarians	4.53	Nematodes	3.91	Nematodes	3.61	Hesionidae	4.18	Nemerteans	4.44	Eunicidae polychaetes	3.58	Isopods	4.28	Isopods	4.25
Oligochaetes	4.22	Tanaids	3.75	Cirratulidae polychaetes	3.57	Anemones	4.09	Nematodes	4.39	Aphroditidae polychaetes	3.41	Mites	3.39	Amphipods	4.25
Anemones	3.96	Spionidae polychaetes	3.71	Tanaids	3.44	Turbellarians	3.49	Phyllodocidae polychaetes	3.70	Amphipods	3.34	Anemones	3.05	Ostracods	4.15
Ostracods	2.97	Oligochaetes	3.39	Amphipods	3.15	Mites	3.35	Eunicidae polychaetes	3.11	Tanaids	2.80	Ostracods	2.98	Oligochaetes	3.55
Orbinidae polychaetes	2.63	Amphipods	3.35	Mites	2.93	Ostracods	2.92	Mites	3.01	Mites	2.64			Ophelidae polychaetes	2.79
		Sea Spiders	3.10	Ostracods	2.22			Ostracods	2.64	Ophelidae polychaetes	2.39				
		Ostracods	2.38							Ostracods	2.36				
		Eunicidae polychaetes	2.17							Sea Spiders	2.30				
										Other Gastropods	2.27				
										Chitons	2.27				
Average dissimilarity between sites = 39.61%		Average dissimilarity between sites = 46.14%		Average dissimilarity between sites = 44.16%		Average dissimilarity between sites = 46.82%		Average dissimilarity between sites = 48.11%		Average dissimilarity between sites = 44.34%		Average dissimilarity between sites = 41.80%		Average dissimilarity between sites = 37.21%	

Cocholgue Des. Exp. 1	% Cont.	Cocholgue Des. Exp. 2	% Cont.	Cocholgue Des. Shelt. 1	% Cont.	Cocholgue Des. Shelt. 2	% Cont.	Cocholgue Maule	% Cont.	Cocholgue Coronel	% Cont.	Cocholgue Valdivia	% Cont.
Crabs	7.10	Terebellidae polychaetes	11.34	Limpets	9.91	Chitons	9.48	Crabs	7.91	Chitons	10.33	Other Bivalves	9.64
Syllidae polychaetes	6.92	Sea Spiders	9.83	Chitons	9.70	Barnacles	8.44	Isopods	7.61	Turbellarians	9.36	Other Insects	8.22
Anemones	6.78	Crabs	8.84	Nemerteans	7.67	Anemones	7.97	Anemones	7.38	Oligochaetes	8.50	Chitons	8.11
Chitons	6.41	Isopods	7.77	Amphipods	6.83	Nemerteans	6.76	Chitons	6.93	Amphipods	7.87	Mites	7.54
Terebellidae polychaetes	5.88	Anemones	7.50	Oligochaetes	6.71	Limpets	6.75	Cirratulidae polychaetes	6.64	Nemerteans	7.32	Crabs	6.95
Isopods	5.74	Amphipods	5.85	Chironomid larvae	6.07	Amphipods	6.59	Spionidae polychaetes	6.02	Spionidae polychaetes	6.45	Chironomid larvae	6.53
Spionidae polychaetes	5.70	Spionidae polychaetes	5.43	Anemones	5.88	Spionidae polychaetes	6.47	Amphipods	5.75	Anemones	6.34	Turbellarians	6.25
Amphipods	5.28	Nemerteans	4.89	Isopods	5.83	Turbellarians	6.35	Oligochaetes	5.07	Chironomid larvae	6.11	Anemones	5.87
Cirratulidae polychaetes	4.86	Chironomid larvae	4.55	Spionidae polychaetes	5.66	Isopods	4.80	Nemerteans	4.82	Other Gastropods	6.07	Amphipods	5.64
Mites	4.77	Tanaids	4.43	Turbellarians	5.54	Chironomid larvae	4.79	Chironomid larvae	5.45	Syllidae polychaetes	4.05	Nemerteans	5.03
Chironomid larvae	4.65	Chitons	4.38	Barnacles	5.02	Orbinidae polychaetes	4.55	Turbellarians	4.24	Nematodes	4.05	Spionidae polychaetes	4.81
Limpets	4.48	Cirratulidae polychaetes	4.19	Hesionidae	4.69	Phyllodocidae polychaetes	4.49	Eunicidae polychaetes	4.17	Mites	3.88	Oligochaetes	4.32
Nemerteans	4.44	Turbellarians	3.98	Mites	3.37	Eunicidae polychaetes	3.77	Aphroditidae polychaetes	3.96	Isopods	3.88	Nereidae polychaetes	4.22
Oligochaetes	4.15	Oligochaetes	3.84	Syllidae polychaetes	3.23	Oligochaetes	3.76	Tanaids	3.40	Other Bivalves	3.59	Isopods	3.38
Nereidae polychaetes	4.13	Mites	3.52	Orbinidae polychaetes	2.85	Syllidae polychaetes	3.67	Mites	2.82	Orbinidae polychaetes	3.33	Ostracods	2.85
Tanaids	4.04			Crabs	2.79	Crabs	3.54	Ophelidae polychaetes	2.77			Ophelidae polychaetes	2.79
Turbellarians	3.54							Sea Spiders	2.68				
Sea Spiders	3.31							Other Gastropods	2.64				
								Phyllodocidae polychaetes	2.58				
Average dissimilarity between sites = 40.58%		Average dissimilarity between sites = 32.79%		Average dissimilarity between sites = 38.26%		Average dissimilarity between sites = 36.59%		Average dissimilarity between sites = 35.60%		Average dissimilarity between sites = 30.51%		Average dissimilarity between sites = 34.64%	

Des. Exp. 1 Des. Exp. 2	% Cont.	Des. Exp. 1 Des. Shelt. 1	% Cont.	Des. Exp. 1 Des. Shelt. 2	% Cont.	Des. Exp. 1 Maule	% Cont.	Des. Exp. 1 Coronel	% Cont.	Des. Exp. 1 Valdivia	% Cont.
Chitons	8.74	Crabs	8.12	Crabs	7.83	Syllidae polychaetes	7.55	Turbellarians	8.12	Other Bivalves	7.78
Sea Spiders	8.63	Spionidae polychaetes	8.12	Barnacles	6.60	Terebellidae polychaetes	7.09	Crabs	7.94	Spionidae polychaetes	6.75
Spionidae polychaetes	8.12	Nemerteans	8.12	Nemerteans	6.13	Cirratulidae polychaetes	6.12	Spionidae polychaetes	7.94	Other Insects	6.63
Syllidae polychaetes	8.09	Anemones	6.24	Syllidae polychaetes	5.85	Oligochaetes	5.55	Anemones	6.99	Turbellarians	6.50
Cirratulidae polychaetes	6.87	Syllidae polychaetes	5.71	Terebellidae polychaetes	5.83	Limpets	5.48	Isopods	5.89	Syllidae polychaetes	5.97
Tanaids	6.36	Terebellidae polychaetes	5.48	Isopods	5.76	Mites	5.38	Syllidae polychaetes	5.46	Chironomid larvae	5.48
Mites	6.34	Isopods	5.10	Spionidae polychaetes	5.07	Nereidae polychaetes	5.20	Terebellidae polychaetes	5.38	Isopods	5.34
Limpets	6.21	Limpets	5.04	Limpets	5.06	Tanaids	5.19	Oligochaetes	5.20	Terebellidae polychaetes	5.19
Terebellidae polychaetes	5.76	Oligochaetes	4.86	Turbellarians	4.86	Sea Spiders	5.00	Cirratulidae polychaetes	4.46	Mites	4.82
Isopods	5.58	Cirratulidae polychaetes	4.55	Cirratulidae polychaetes	4.83	Isopods	4.90	Limpets	4.14	Cirratulidae polychaetes	4.27
Nereidae polychaetes	5.56	Chironomid larvae	4.26	Mites	4.37	Eunicidae polychaetes	4.77	Mites	4.05	Nereidae polychaetes	4.23
Chironomid larvae	5.22	Nereidae polychaetes	4.16	Nereidae polychaetes	4.14	Chironomid larvae	4.55	Nereidae polychaetes	4.03	Limpets	3.83
Oligochaetes	4.73	Mites	4.09	Phyllodocidae polychaetes	3.83	Aphroditidae polychaetes	4.35	Nemerteans	3.92	Oligochaetes	3.50
Nemerteans	3.31	Barnacles	3.63	Tanaids	3.64	Chitons	4.33	Other Gastropods	3.71	Anemones	3.49
Crabs	2.01	Tanaids	3.43	Chironomid larvae	3.37	Spionidae polychaetes	3.97	Chironomid larvae	3.47	Tanaids	3.21
		Hesionidae	3.41	Sea Spiders	3.26	Phyllodocidae polychaetes	3.49	Tanaids	3.35	Nemerteans	3.01
		Sea Spiders	3.05	Eunicidae polychaetes	3.23	Ophelidae polychaetes	3.03	Sea Spiders	3.02	Crabs	2.95
		Turbellarians	2.34	Oligochaetes	2.98	Nemerteans	2.90	Chitons	2.71	Sea Spiders	2.94
		Chitons	2.11	Amphipods	2.64	Other Gastropods	2.89	Nematodes	2.47	Ostracods	2.30
				Orbinidae polychaetes	2.43					Ophelidae polychaetes	2.25
Average dissimilarity between sites = 25.31%		Average dissimilarity between sites = 49.01%		Average dissimilarity between sites = 43.43%		Average dissimilarity between sites = 30.61%		Average dissimilarity between sites = 46.44%		Average dissimilarity between sites = 40.50%	

Des. Exp. 2 Des. Shelt. 1	% Cont.	Des. Exp. 2 Des. Shelt. 2	% Cont.	Des. Exp. 2 Maule	% Cont.	Des. Exp. 2 Coronel	% Cont.	Des. Exp. 2 Valdivia	% Cont.
Crabs	9.51	Terebellidae polychaetes	10.02	Terebellidae polychaetes	13.28	Crabs	9.84	Terebellidae polychaetes	8.66
Terebellidae polychaetes	9.51	Crabs	8.90	Sea Spiders	9.16	Terebellidae polychaetes	9.84	Other Bivalves	7.58
Sea Spiders	8.24	Sea Spiders	8.69	Chitons	8.31	Isopods	8.63	Sea Spiders	7.52
Nemerteans	8.24	Chitons	7.41	Spionidae polychaetes	7.43	Turbellarians	8.55	Isopods	6.87
Chitons	7.03	Isopods	6.97	Cirratulidae polychaetes	6.99	Sea Spiders	8.53	Mites	6.83
Limpets	6.49	Barnacles	6.49	Oligochaetes	5.64	Anemones	7.36	Chironomid larvae	6.77
Anemones	6.16	Nemerteans	6.09	Tanaids	5.61	Chitons	6.70	Other Insects	6.46
Isopods	5.63	Limpets	5.14	Aphroditidae polychaetes	4.77	Oligochaetes	5.90	Chitons	6.41
Oligochaetes	4.88	Spionidae polychaetes	5.01	Eunicidae polychaetes	4.62	Other Gastropods	4.15	Turbellarians	6.35
Chironomid larvae	3.64	Turbellarians	4.83	Syllidae polychaetes	4.32	Nemerteans	4.08	Spionidae polychaetes	3.56
Spionidae polychaetes	3.62	Syllidae polychaetes	3.92	Other Gastropods	4.09	Syllidae polychaetes	3.78	Anemones	3.39
Barnacles	3.60	Cirratulidae polychaetes	3.70	Ophelidae polychaetes	3.31	Spionidae polychaetes	3.74	Nereidae polychaetes	3.31
Syllidae polychaetes	3.58	Phyllodocidae polychaetes	3.53	Phyllodocidae polychaetes	3.12	Cirratulidae polychaetes	3.64	Cirratulidae polychaetes	3.21
Cirratulidae polychaetes	3.51	Tanaids	3.51	Nemerteans	3.01	Tanaids	3.45	Tanaids	3.07
Hesionidae	3.41	Amphipods	2.60	Limpets	3.01	Nematodes	2.58	Nemerteans	2.87
Tanaids	3.32	Orbinidae polychaetes	2.41	Isopods	2.88			Oligochaetes	2.76
		Eunicidae polychaetes	2.41	Chironomid larvae	2.69			Crabs	2.27
								Ostracods	2.23
Average dissimilarity between sites = 43.75%		Average dissimilarity between sites = 39.26%		Average dissimilarity between sites = 25.54%		Average dissimilarity between sites = 39.52%		Average dissimilarity between sites = 37.98%	

Des. Shelt. 1 Des. Shelt. 2	% Cont.	Des. Shelt. 1 Maule	% Cont.	Des. Shelt. 1 Coronel	% Cont.	Des. Shelt. 1 Valdivia	% Cont.
Anemones	8.83	Crabs	8.83	Limpets	11.54	Other Bivalves	8.67
Barnacles	7.87	Nemerteans	8.77	Turbellarians	10.59	Mites	8.67
Oligochaetes	7.68	Spionidae polychaetes	7.51	Nemerteans	9.44	Limpets	7.42
Spionidae polychaetes	7.30	Limpets	6.90	Oligochaetes	7.59	Other Insects	7.39
Limpets	7.13	Anemones	6.54	Anemones	6.53	Crabs	7.26
Turbellarians	7.12	Cirratulidae polychaetes	5.99	Other Gastropods	6.18	Nemerteans	7.15
Isopods	6.39	Isopods	5.96	Syllidae polychaetes	5.87	Turbellarians	6.10
Syllidae polychaetes	5.74	Oligochaetes	5.06	Isopods	5.84	Chironomid larvae	6.04
Hesionidae	5.17	Barnacles	4.08	Barnacles	5.84	Anemones	5.24
Phyllodocidae polychaetes	5.02	Aphroditidae polychaetes	3.89	Chironomid larvae	5.80	Oligochaetes	5.04
Nemerteans	5.02	Chironomid larvae	3.82	Hesionidae	5.45	Nereidae polychaetes	4.12
Chironomid larvae	4.97	Hesionidae	3.60	Nematodes	5.09	Isopods	4.00
Amphipods	4.78	Eunicidae polychaetes	3.42	Nereidae polychaetes	3.68	Barnacles	3.75
Eunicidae polychaetes	3.47	Syllidae polychaetes	3.25	Other Bivalves	3.59	Hesionidae	3.54
Orbinidae polychaetes	3.47	Turbellarians	3.01			Ostracods	2.57
Aphroditidae polychaetes	2.81	Ophelidae polychaetes	2.51			Ophelidae polychaetes	2.51
		Sea Spiders	2.42			Syllidae polychaetes	2.43
		Other Gastropods	2.38				
		Chitons	2.38				
Average dissimilarity between sites = 37.41%		Average dissimilarity between sites = 44.34%		Average dissimilarity between sites = 34.84%		Average dissimilarity between sites = 43.30%	

Des. Shelt. 2 Maule	% Cont.	Des. Shelt. 2 Coronel	% Cont.	Des. Shelt. 2 Valdivia	% Cont.	Maule Coronel	% Cont.	Maule Valdivia	% Cont.	Coronel Valdivia	% Cont.
Crabs	8.89	Anemones	9.17	Other Bivalves	8.30	Crabs	9.13	Other Bivalves	7.79	Mites	10.51
Isopods	7.79	Barnacles	8.93	Mites	8.30	Isopods	9.13	Mites	7.79	Chironomid larvae	9.36
Barnacles	6.93	Oligochaetes	8.74	Chironomid larvae	8.19	Turbellarians	8.24	Isopods	7.06	Other Insects	8.96
Nemerteans	6.84	Nemerteans	7.30	Other Insects	7.07	Anemones	7.80	Chironomid larvae	6.97	Crabs	8.82
Cirratulidae polychaetes	6.68	Limpets	7.15	Crabs	6.46	Spionidae polychaetes	7.78	Other Insects	6.65	Other Bivalves	8.37
Limpets	5.77	Turbellarians	7.06	Barnacles	6.14	Cirratulidae polychaetes	6.22	Turbellarians	6.06	Oligochaetes	6.81
Spionidae polychaetes	5.61	Spionidae polychaetes	6.82	Nemerteans	5.35	Oligochaetes	5.48	Spionidae polychaetes	6.06	Anemones	6.63
Turbellarians	5.42	Other Gastropods	5.76	Limpets	4.91	Other Gastropods	4.65	Cirratulidae polychaetes	5.35	Nemerteans	5.37
Phyllodocidae polychaetes	4.69	Syllidae polychaetes	5.44	Turbellarians	4.81	Nemerteans	4.32	Oligochaetes	4.01	Nereidae polychaetes	4.97
Eunicidae polychaetes	4.67	Phyllodocidae polychaetes	4.73	Spionidae polychaetes	4.74	Aphroditidae polychaetes	3.71	Nereidae polychaetes	3.67	Other Gastropods	4.73
Oligochaetes	4.53	Amphipods	4.35	Anemones	4.03	Eunicidae polychaetes	3.57	Anemones	3.49	Turbellarians	3.97
Aphroditidae polychaetes	4.34	Nematodes	3.64	Nereidae polychaetes	3.64	Syllidae polychaetes	3.48	Ophelidae polychaetes	3.35	Nematodes	3.95
Syllidae polychaetes	3.85	Isopods	3.25	Phyllodocidae polychaetes	3.33	Chitons	3.13	Aphroditidae polychaetes	3.20	Syllidae polychaetes	3.16
Other Gastropods	3.30	Orbinidae polychaetes	3.25	Amphipods	3.02	Nematodes	2.75	Eunicidae polychaetes	3.09	Ostracods	3.11
Amphipods	2.91	Eunicidae polychaetes	3.25	Isopods	2.80	Ophelidae polychaetes	2.60	Nemerteans	2.95	Ophelidae polychaetes	3.04
Ophelidae polychaetes	2.79	Other Bivalves	3.20	Syllidae polychaetes	2.63	Sea Spiders	2.51	Crabs	2.87		
Sea Spiders	2.69			Ostracods	2.46	Other Bivalves	2.47	Ostracods	2.30		
Orbinidae polychaetes	2.69			Oligochaetes	2.41	Tanaids	2.45	Sea Spiders	2.16		
				Ophelidae polychaetes	2.40	Phyllodocidae polychaetes	2.41	Other Gastropods	2.13		
								Chitons	2.13		
								Tanaids	2.12		
Average dissimilarity between sites = 37.52%		Average dissimilarity between sites = 36.60%		Average dissimilarity between sites = 42.69%		Average dissimilarity between sites = 39.79%		Average dissimilarity between sites = 39.00%		Average dissimilarity between sites = 33.28%	

Table 12 T-tests performed between univariate measures of diversity calculated for pooled data from mussel bed communities at eight sites in the British Isles and Irish Republic and eight in Chile, South America. Mean values of each univariate measure per 25cm^2 quadrat are given. Significant differences are marked * ($p<0.05$).

Univariate Measure	British Isles and Irish Republic	Chile	t
Total taxa	19	12	-9.60*
Total individuals	708	193	-9.35*
Margalef's richness	2.780	2.235	-5.03*
Shannon's diversity	1.770	1.806	0.63
Pielou's evenness	0.610	0.726	6.96*

their importance in terms of biomass. The *k*-dominance plot for mussel communities in both Chile and the British Isles and Irish Republic were very similar, such that, although the specific taxa present in each of the mussel communities may be very different, the patterns of dominance in each were remarkably similar (Figure 14).

MDS ordination of square-root transformed infaunal taxa abundance illustrated a clear separation of mussel communities from Chile and the British Isles and Irish Republic, in terms of the more dominant taxa in the community (Figure 15a). A one-way ANOSIM test performed between the pooled data for each geographical area confirmed that the structure of the infaunal community associated with *P. purpuratus* was significantly different from the *M. edulis* community ($R = 0.680$, $p<0.05$). Additionally, when sites in Chile were tested individually against sites in the British Isles and Irish Republic, a one-way ANOSIM test confirmed that there were significant inter-site differences in community structure ($R = 0.847$, $p<0.05$). ANOSIM pairwise comparisons revealed that the structure of the mussel community was significantly different between all the sites in Chile and those in the British Isles and Irish Republic (Table 13a). MDS ordination performed with a presence/absence transformation on the same data set showed a slightly less clear, but still distinct, separation of sites from Chile and the British Isles and Irish Republic (Figure 15b). A one-way ANOSIM test performed between the pooled data for each of the two geographical areas confirmed that the structure of the infaunal community associated with *P. purpuratus* was significantly different from the *M. edulis* community ($R = 0.723$, $p<0.05$). Additionally, when sites in Chile were tested individually against sites in the British Isles and Irish Republic, a one-way ANOSIM test confirmed that there were significant differences in community structure between some of the sites ($R = 0.783$, $p<0.05$). ANOSIM pairwise comparisons revealed that the structure of the mussel community was significantly different between all the sites in Chile and those in the British Isles and Irish Republic (Table 13b).

Prior to Similarity Percentage analysis (SIMPER), samples from each geographical area were spilt so that data from only 50% of the replicate samples from each site were used in the analysis, so that unbiased statistical tests could be performed on the remaining 50% of the data. SIMPER analysis performed with a square-root transformation indicated that communities associated with *M. edulis* were characterised predominantly by juvenile mussels and other bivalves, nematodes, nemerteans, chironomids, mites, isopods and various gastropod taxa. Communities associated with *P. purpuratus* were characterised mainly by juvenile mussels, nematodes, barnacles, limpets, amphipods, oligochaetes and syllid and nereid polychaetes. Table 14 indicates those taxa contributing to differences between

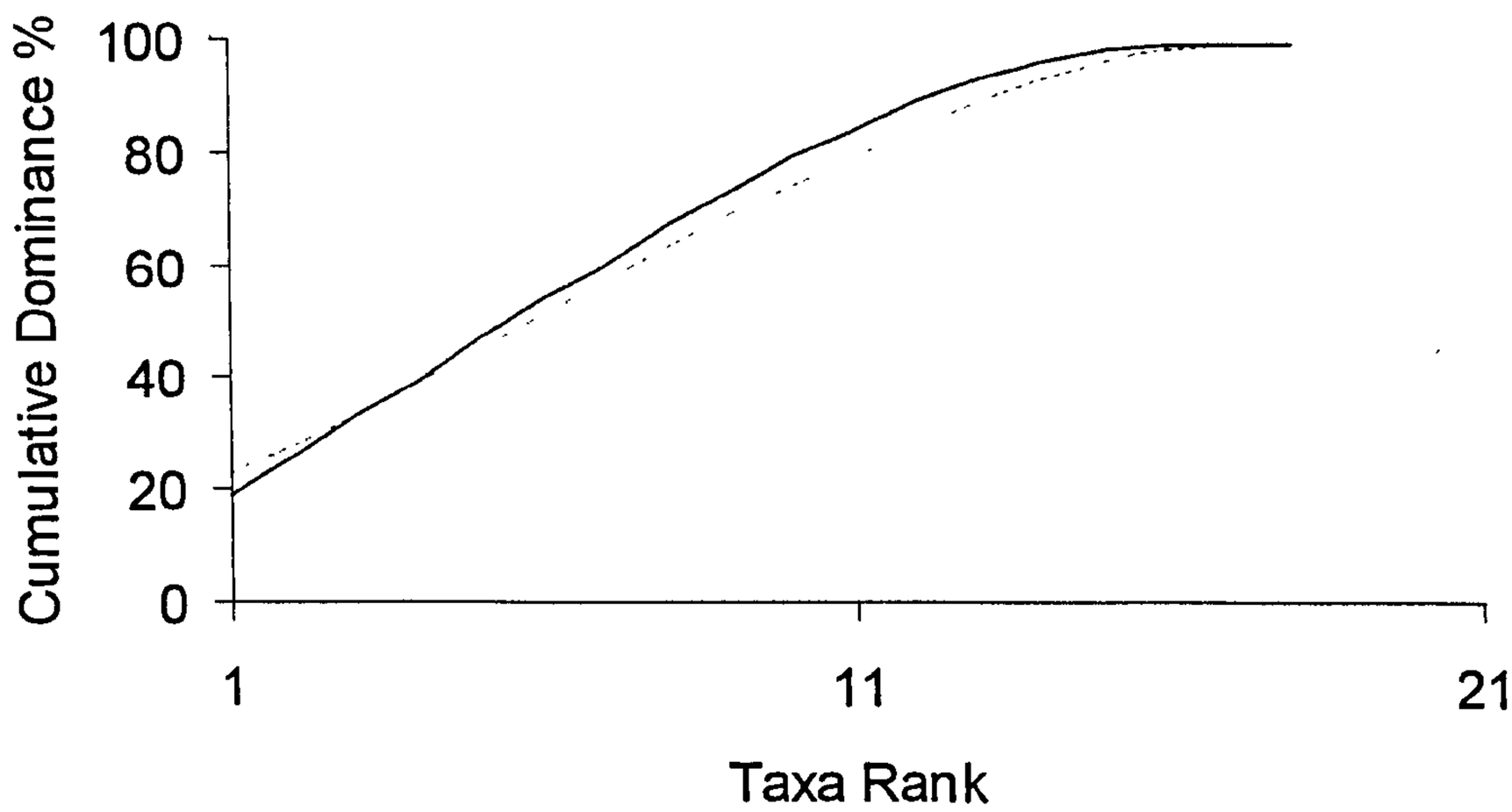
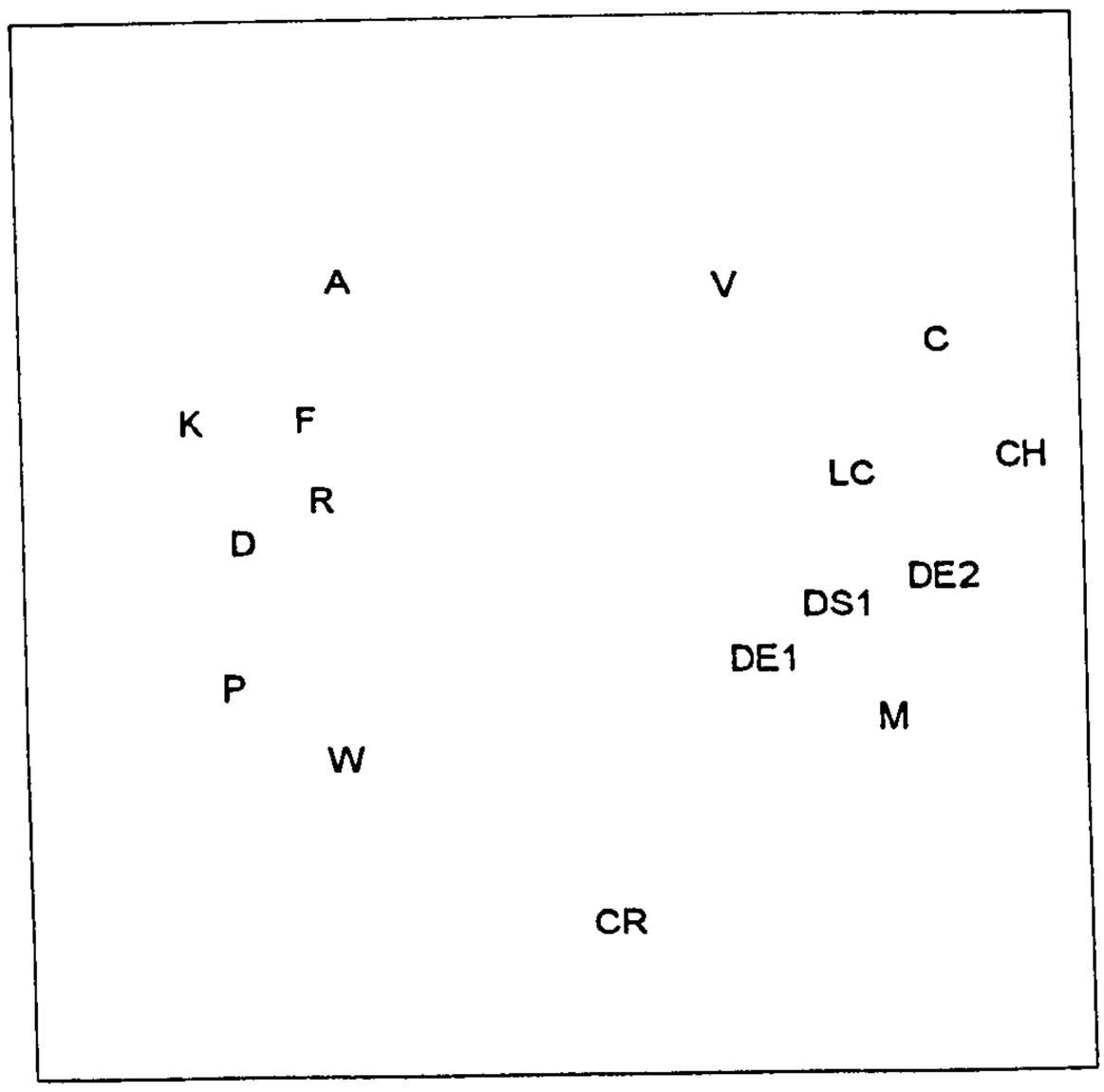


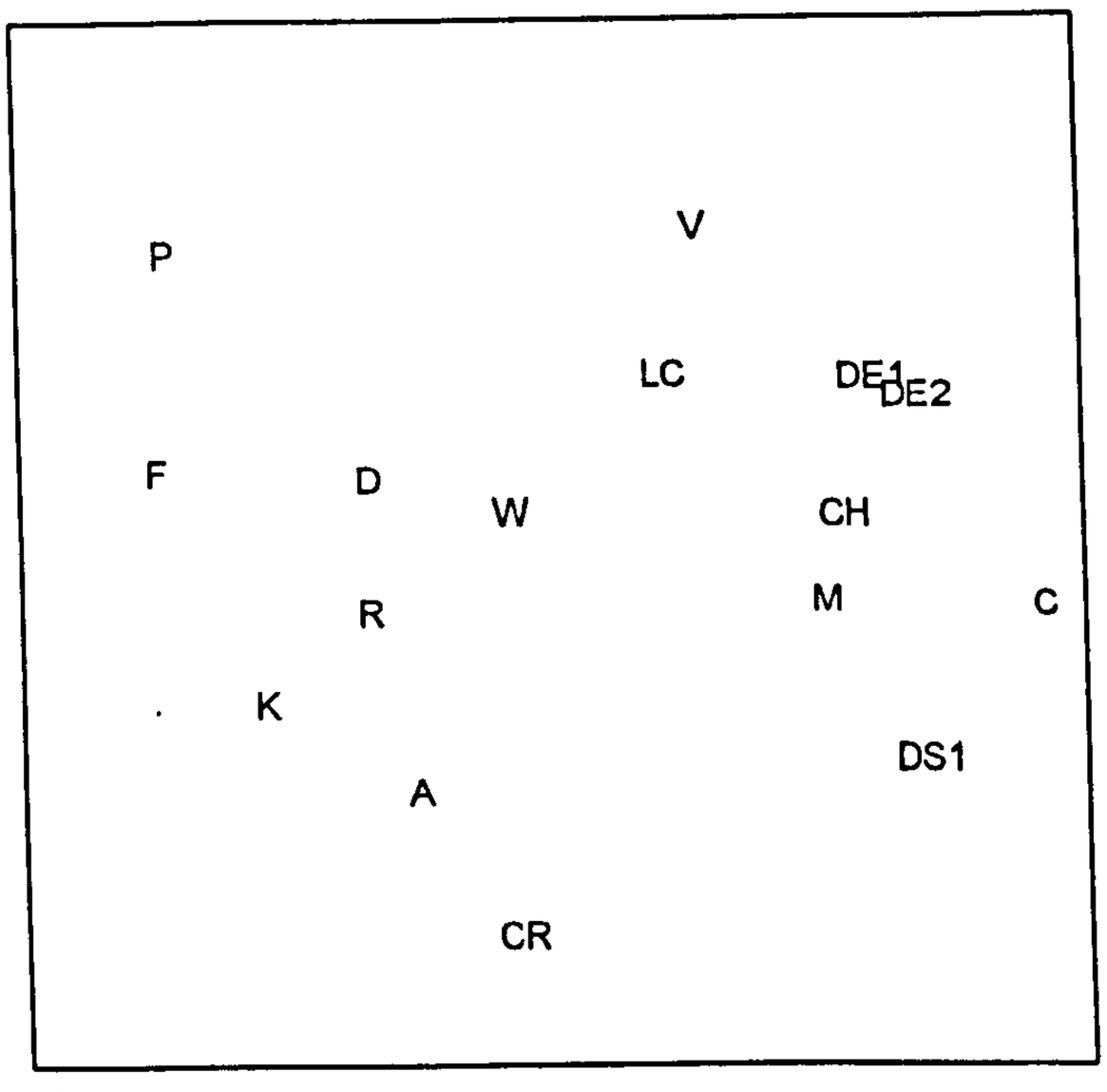
Figure 14 *k*-dominance curves for taxa abundance in *Mytilus edulis* beds in the British Isles and Irish Republic (—) and *Perumytilus purpuratus* beds in Chile, South America (····).

a) Square-root transformation



b) Stress = 0.11

b) Presence/absence transformation



Stress = 0.15

Figure 15 Ordination by MDS based on Bray-Curtis similarity, of averaged abundance of infauna from mussel beds at eight locations in the British Isles and Irish Republic; Point Lynas (P), White Beach (W), Criccieth (CR), Arisaig (A), Kilkee (K), Doonbeg (D) Robin Hood's Bay (R) and Filey (F) and eight locations in Chile, South America; Las Cruces (LC), Cocholgue (CH), Desembocadura exposed site 1 (DE1), Desembocadura exposed site 2 (DE2), Desembocadura sheltered site 1 (DS1), Maule (M), Coronel (C) and Valdivia (V), using a) square-root transformation and b) presence/absence transformation.

Table 13 Global R-values for ANOSIM pairwise comparisons between samples of mussel communities taken in summer 1999 at eight different locations in the British Isles and Irish Republic and eight locations in Chile, South America, based on a) square-root transformations of taxa abundance and b) presence/absence transformations. Significant differences in community structure ($p<0.05$) are indicated by bold type.

a)

	Las Cruces	*Cocholgue*	*Desembocadura exposed site 2*	*Desembocadura exposed site 2*	*Desembocadura sheltered site 1*	*Maule*	*Coronel*	*Valdivia*
Point Lynas	**0.979**	**1.000**	**1.000**	**1.000**	**1.000**	**0.989**	**0.999**	**0.932**
White Beach	**0.963**	**1.000**	**0.954**	**0.992**	**0.993**	**0.950**	**0.999**	**0.939**
Criccieth	**0.860**	**0.935**	**0.813**	**0.951**	**0.858**	**0.874**	**0.896**	**0.922**
Arisaig	**0.906**	**1.000**	**0.978**	**1.000**	**0.998**	**0.972**	**0.978**	**0.931**
Kilkee	**0.968**	**1.000**	**0.996**	**0.999**	**0.996**	**0.987**	**0.998**	**0.945**
Doonbeg	**0.965**	**1.000**	**0.997**	**1.000**	**1.000**	**0.987**	**0.999**	**0.924**
Robin Hood's Bay	**0.905**	**1.000**	**0.992**	**0.997**	**1.000**	**0.977**	**0.965**	**0.821**
Filey Brigg	**0.943**	**1.000**	**0.962**	**0.987**	**0.979**	**0.961**	**0.955**	**0.915**

b)

	Las Cruces	*Cocholgue*	*Desembocadura exposed site 1*	*Desembocadura exposed site 2*	*Desembocadura sheltered site 1*	*Maule*	*Coronel*	*Valdivia*
Point Lynas	**0.929**	**1.000**	**0.988**	**1.000**	**1.000**	**1.000**	**1.000**	**0.995**
White Beach	**0.783**	**0.977**	**0.769**	**0.964**	**0.98**	**0.914**	**0.999**	**0.948**
Criccieth	**0.628**	**0.856**	**0.808**	**0.939**	**0.915**	**0.905**	**0.921**	**0.889**
Arisaig	**0.672**	**0.989**	**0.881**	**1.000**	**0.972**	**0.998**	**1.000**	**0.973**
Kilkee	**0.838**	**1.000**	**0.954**	**1.000**	**0.996**	**0.998**	**1.000**	**0.994**
Doonbeg	**0.848**	**0.992**	**0.959**	**1.000**	**0.994**	**0.998**	**0.998**	**0.963**
Robin Hood's Bay	**0.641**	**0.965**	**0.899**	**1.000**	**0.967**	**0.993**	**0.979**	**0.915**
Filey Brigg	**0.840**	**0.999**	**0.959**	**0.999**	**0.998**	**0.994**	**0.997**	**0.966**

Table 14 Taxa identified by similarity percentage analysis (SIMPER) performed on square-root and presence/absence transformed abundance as those contributing to differences in community structure between mussel beds in the British Isles and Irish Republic and Chile, South America. SIMPER analysis has been performed on only 50% of samples from each location. The remaining 50% of samples have been entered into statistical analyses to test for abundance differences between locations. Significant differences in abundance ($p<0.05$) are indicated by * next to taxa.

	Mean abundance per 25cm^2 quadrat	
Taxa	**British Isles and Irish Republic**	**Chile**
Anemones*	0.06	5.97
Nemerteans	10.00	3.06
Nematodes*	68.22	23.19
Nereidae polychaetes*	0.00	4.09
Spionidae polychaetes*	0.69	7.03.
Syllidae polychaetes*	1.28	3.97
Oligochaetes*	3.47	5.44
Chironomid larvae*	30.44	4.47
Mites*	31.13	2.91
Barnacles*	7.56	27.56
Amphipods*	9.16	13.47
Isopods*	11.41	2.59
Crabs	1.41	1.03
Juvenile mussels*	79.69	40.69
Other bivalves*	44.78	3.03
Limpets*	0.28	7.28
Predatory gastropods	0.72	0.00
Other gastropods*	17.91	0.34
Opisthobranchs*	5.25	0.00

communities associated with *P. purpuratus* and *M. edulis*, as identified by SIMPER analysis using both a square-root and presence/absence transformation. Data from the remaining 50% of replicate samples from each of the sites in both the British Isles and Irish Republic and Chile were pooled and the abundance of each of the taxa identified by SIMPER analysis tested for significant differences between countries. Results of these analyses are indicated in Table 14.

The density of mussels in the *P. purpuratus* beds was significantly lower than the density of mussels in the *M. edulis* beds (t-test; $t = 16.22$, $p<0.05$) (for details of mussel densities, see Chapter 3). The total number of taxa within mussel beds in the British Isles and Chile was significantly correlated with mussel density ($r = 0.503$), although none of the other univariate measures of community diversity showed significant correlation with this variable. Mean values of mussel density at each of the sites in Chile and the British Isles and Irish Republic were overlaid onto the MDS plot obtained from square-root transformed biotic data analysis to illustrate the influence of mussel density on the multivariate data set (Figure 16). BIOENV analysis revealed low levels of correlation between mussel density and the square-root and presence/absence transformed data derived from the mussel bed infauna (0.374, 0.384, respectively).

In summary, communities associated with both *M. edulis* and *P. purpuratus* showed significant intersite, large-scale spatial variation. Such intersite differences within the British Isles and Irish Republic and in Chile were observed when data were analysed at a presence/absence level and when species abundance was taken into account, although different species accounted for these differences in each case. When analysed at the same high taxonomic level, the communities associated with *M. edulis* and *P. purpuratus* displayed significant differences; *M. edulis* beds supported a greater number of meiofaunal species, while *P. purpuratus* beds were characterised by macrofaunal species. Although some of the environmental parameters of the mussel beds did correlate with the biotic data, they failed to fully account for the observed large-scale spatial variation.

DISCUSSION

M. edulis and *P. purpuratus* both supported diverse invertebrate communities at a variety of locations in the British Isles and Irish Republic and Chile, South America. The communities were characterised by a diversity of macrofaunal and meiofaunal taxa such as nematodes, nemerteans, polychaetes, gastropods, anemones and bivalves. Such communities compare with those described for *M.*

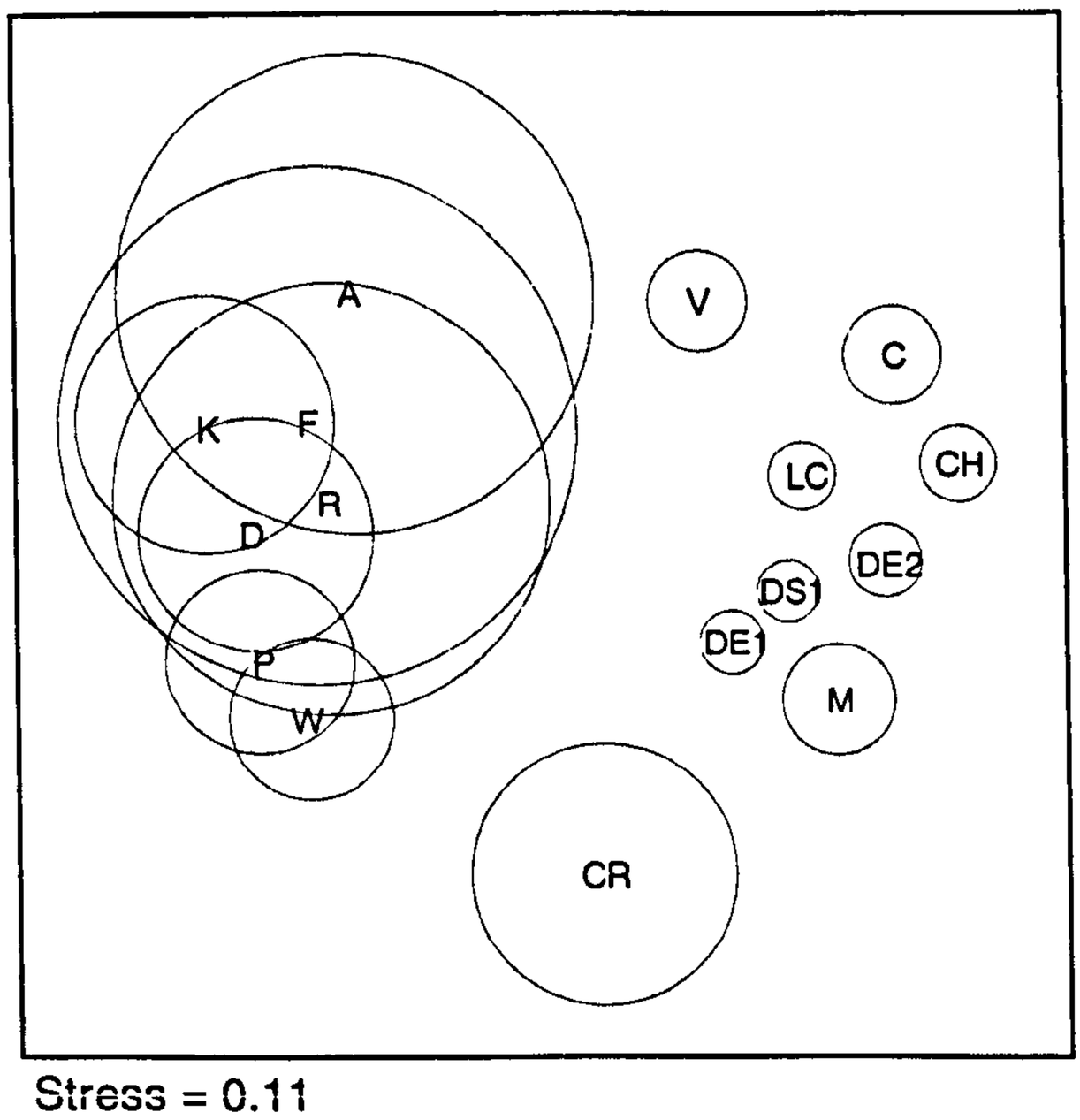


Figure 16 Ordination by MDS based on Bray-Curtis similarity, of averaged abundance of infauna from mussel beds at eight locations in the British Isles and Irish Republic Chile and eight locations in South America, using a square root transformation. Superimposed circles are scaled in size to represent the density of mussels in beds at each of the sites (i.e., the larger the circle diameter, the higher the mussel density per unit area). (LC = Las Cruces; CH = Cocholgue; DE1 = Desembocadura exposed site 1; DE2 = Desembocadura exposed site 2; DS1 = Desembocadura sheltered site 1; M = Maule; C = Coronel; V = Valdivia; P = Point Lynas; W = White Beach; CR = Criccieth; A = Arisaig; K = Kilkee; D = Doonbeg; R = Robin Hood's Bay; F = Filey Brigg).

edulis, by other authors (e.g. Lintas and Seed, 1994; Tsuchiya and Nishihira, 1985, 1986) and *P. purpuratus* (e.g. Amesti, 1994; Tokeshi, 1995).

Communities associated with the mussel beds in the British Isles and Irish Republic showed significant large-scale spatial variation between the eight locations in the present study. In addition, the invertebrate community associated with *P. purpuratus* showed significant large-scale spatial variation, at a number of sites along the coastline of Chile. Kanter (1980) similarly reported significant differences in the structure of the invertebrate community associated with *Mytilus califomianus* across various sites in the southern Californian Bight. In addition, various studies have reported large-scale spatial variation in the structure of a variety of marine intertidal communities, such as intertidal flats in Australia (Dittman, 1990; 1995); rocky shore communities in New England (Menge, 1991a) and rocky shore communities in New South Wales, Australia (Underwood and Chapman, 1996).

Mussel beds at all locations in the British Isles and Irish Republic and Chile in the present study were dominated by a few very abundant taxa. In the British Isles and Irish Republic, these taxa included nematodes, nemerteans, juvenile mussels, *Clunio sp.* larvae, the isopod *Jaera albifrons* and the opisthobranch *Brachystomia scalaris*, while in Chile, polychaetes, gastropods, bivalves and anemones were dominant. Such dominance of mussel communities by a few very abundant taxa is well documented in the literature and many authors have observed similar dominance patterns in mussel beds at various geographical locations. For example, Ong Che and Morton (1992) demonstrated that *Septifer virgatus* beds in Hong Kong were dominated by three infaunal species, accounting for 75% of the total numbers. In studies of the same mussel beds, Seed and Brotohadikusumo (1994) found that more than 90% of the molluscan fauna associated with the mussels was comprised of three bivalve species (*Hormomya mutabilis*, *Isognomon legumen* and *Lasaea nipponica*). Suchanek (1979,1980) found that in *Mytilus californianus* beds on the north-west coast of America, a single species dominated the sample by more than 50%, in some cases, although the identity of this species did vary with location. Mussel beds at hydrothermal vents have been seen to share this attribute of very uneven distributions, with a large number of individuals reported from a small number of species (Van Dover and Trask, 2000). Similar phenomena have been reported in other marine benthic communities. For example, Reise *et al* (1994) reported that the most common species in subtidal sandy habitats, in Konigshafen in the northern Wadden Sea were also the most common species elsewhere in the Wadden Sea. Kanter (1980) reported the presence of several ubiquitous species in mussel beds throughout the southern California Bight.

Analysis showed that variations in numbers of many of the most abundant taxa already listed above, characterised mussel bed communities at each of the sites in the British Isles and Irish Republic and Chile. Kanter (1980) found similar results from analysis of communities associated with *Mytilus californianus* at sites throughout the southern Californian Bight. Similarly, Reise *et al* (1994) reported significant regional differences in the structure of benthic communities in the Wadden Sea, in terms of the more abundant species; the numerical abundance of *Hydrobia ulvae* at northern sites was an order of magnitude higher than at western sites, while *Arenicola marina* abundance was particularly high in the north.

Many taxa encountered in the present study occurred only at some sites and in the past, such taxa have been considered to be either accidental or transient, rather than permanent members of the community (e.g. Seed and Brotohadikusumo, 1994). However, multivariate analyses, particularly when performed with a presence/absence transformation, indicate that these transient taxa may be important in defining large-scale spatial differences in the structure of such communities, along with the more numerically abundant taxa. For example, certain taxa were only encountered in mussel beds at selected locations, probably as a result of their limited geographical range (e.g. in the British Isles and Irish Republic, the gastropod *Tricolia pullus*, Hayward and Ryland, 1990).

Explanations for large-scale spatial variation

It is well known that biological substrata, such as mussel beds are affected by both biotic and abiotic factors, and that this will modify the composition of the faunal associates (Hagermann, 1966; Crooks, 1998; Crooks and Khim, 1999). Several authors have attempted to explain such large-scale spatial variations in community structure, and relate them to various biological and environmental factors; such factors include:

Larval recruitment and dispersal

Dispersal of planktonic larvae by currents and water masses is a hypothesis often put forth to explain biogeographic patterns of species distribution (MacArthur and Wilson, 1967; Johnson, 1975). Many authors have suggested that the supply of larval recruits to benthic marine habitats are subject to considerable variation in time and space and have a major influence on the structure and dynamics of local populations (e.g. Roughgarden *et al*, 1985; Underwood and Fairweather, 1989; Caley *et al*, 1996; Hughes *et al*, 2000). Most mussel community members reproduce either by releasing gametes into the surrounding waters where external fertilisation and larval development occurs, or by releasing larvae after partial development in an egg

capsule or within the adults (Kanter, 1980). These planktonic larvae drift with prevailing currents and water masses. Passive drifting ends when the larva has matured sufficiently to seek out an appropriate substratum. Settlement and metamorphosis, however, can only occur when this substratum is within the behavioural and physiological tolerances of the larva. Larvae may drift a considerable distance (up to hundreds of kilometres) from source areas prior to settlement (Scheltema, 1974). Kanter (1980) stated that mussel community similarities at various sites in the southern Californian might have been the result of receiving larval recruits from similar source waters (source parental stock). Such species distribution patterns corresponded in part to known patterns of current flow. Analysis of data in the present study, particularly in the British Isles and Irish Republic, suggests that the structure of the mussel bed communities, in terms of the more abundant, dominant taxa, was determined by the supply of larval recruits. Mussel beds receiving larval recruits from the same source waters had more similar community structures than those sites with different source waters. Main surface currents and source waters appear to dictate the presence or absence of the rarer, more transient members of the communities to a lesser extent, while other biotic and abiotic factors, or stochastic events were also important.

For most intertidal species, which disperse via a planktonic larval stage but which have limited adult mobility, variations in recruitment and mortality will lead to variations in abundance from one shore to another i.e. at a scale of kilometres (Dayton, 1971; Underwood and Denley, 1984; Menge *et al*; 1985). Spatial and temporal variations in the densities of populations of marine invertebrates can be expected to be large in those species which produce dispersing larvae (Underwood, 1979). Menge (1991b) postulated that recruitment limitation has been advocated as a major cause of community structure on rocky shores and that, particularly when low, recruitment density is a very important factor in influencing the structure of these communities. Similarly, Underwood and Fairweather (1989) and Raimondi (1990) noted that the stochastic nature of settlement and mortality that often typifies many marine species should be fully recognised when considering global patterns of marine biodiversity. A wide variety of stimuli may be involved in the selection of a suitable substratum on which to settle. The spatial patterns of settlement shown by larvae of intertidal marine invertebrates follows the scheme outlined by Underwood (1976):

1) completely random spatial settlement over the entire area of the shore, with subsequent mortality in, or migration from, unfavourable areas;

2) responses to physical, chemical or biochemical cues which attract larvae to a particular habitat; these cues cause spatial variations in the number of larvae settling;
3) responses to physical, chemical or biochemical cues from adults of their own or of closely related species, which result in larvae settling in areas occupied, or previously occupied, by adults;
4) species, which have no pelagic dispersal larvae and reproduce by direct development in benthic egg capsules, or by viviparity usually produce juveniles within the normal habitat of the adults.

Underwood and Chapman (1996) similarly, concluded that variations in the structure of rocky shore communities at various sites in New South Wales, Australia were due to differences in recruitment and/or mortality, which, in turn were determined by processes that vary between sites.

Species Interactions

Many authors have emphasised the importance of post-juvenile factors such as predation and competition, as causes of variation in survival of post-settled benthic, as well as adult stages, thus having the potential to structure rocky shore communities (Underwood and Denley, 1984; Watanabe, 1984; Caffey, 1985; Gaines and Roughgarden, 1985; Sutherland and Ortega, 1986; Sutherland, 1990). In addition, in a study of the geographical variation in the structure of rocky shore communities on the coast of New England, Menge (1991a) suggested that between site variation was due to site differences in the relative importance of predation and competition, along with physical disturbance. It is likely that such factors play a structuring role, to a certain extent, in the mussel communities in the present study, but are not the sole cause of the large-scale spatial variation.

Habitat heterogeneity

Habitat structure has long been considered an important determinant of the number, identity and abundance of species present in many biological communities (e.g. MacArthur and Wilson, 1967; Abele, 1974; Menge and Sutherland, 1976; McGuiness and Underwood, 1986; Archambault and Bourget, 1996). Suchanek (1979, 1980) stated that the structural complexity and heterogeneity of a mussel bed is the most important factor promoting biodiversity and depends on two factors; the size of mussels and the number of mussels within the matrix. These in turn, are a function of tidal elevation, age of the mussel bed and the relative degree of wave exposure. As the structural complexity of mussel beds increases, the number of

microhabitats under, between and around the mussels also increases, producing structurally complex entities capable of harbouring a diverse assemblage of associated fauna (Newcombe, 1935; Kanter, 1980).

The abundance of some of the taxa inhabiting mussel beds in the present study showed significant correlation with various environmental parameters of the mussel matrix. However, data analysis, using a multivariate approach, failed to identify any strong relationships between the heterogeneity of the mussel beds at each of the sites within the British Isles and Irish Republic and the structure of the infaunal communities. However, positive and negative correlation, did occur between various environmental and biotic components of the mussel beds in the British Isles and Irish Republic and Chile. The various measurements of substratum heterogeneity varied between sites within each of the two geographical locations, although differences were often not significant. As such, mussels at each of the sites within the British Isles and Irish Republic and within Chile were generally of similar size, shape and packing densities and provided a similar habitat with substratum heterogeneity for colonisation by a suite of taxa. These taxa were generally similar in mussel beds within the British Isles and Irish Republic and Chile, but probably varied according to local physical and biological factors acting on the mussel bed. Behavioural responses to habitat can account for community variations on a small spatial scale (tens of metres), but other processes probably account for larger-scale variations (Underwood, 1976; Underwood and Denley, 1984; Chapman and Underwood, 1994; Underwood and Chapman, 1996).

Patch size

Patch size has been suggested as an important factor affecting biodiversity in mussel beds. Tsuchiya and Nishihira (1985) demonstrated that the number of species per unit area in *M. edulis* beds in Japan decreased with patch size, possibly because species endemic to larger patches might suppress other animals via predation or competition, or create unsuitable physico-chemical environments for other species. In another study of the same mussel beds, Tsuchiya and Nishihira (1986) found that species richness was greatest in larger beds. Similarly, Lintas and Seed (1994) found species diversity and richness to be greater in larger, more extensive (and presumably more spatially complex) areas of *M. edulis* beds on Anglesey, North Wales. Positive species-area relationships have also been reported for the macro-invertebrate fauna within clumps of *Brachidontes rostratus* in Australia (Peake and Quinn, 1993). However, since mussel patches were of similar size on

shores at each of the sites in the present study, it is unlikely that the observed differences in community structure were due to differences in patch size.

Wave exposure

Suchanek (1979) demonstrated that the diversity of communities associated with *M. californianus* increased with wave exposure, despite wave forces being greatly diminished inside the mussel bed due to the wave-buffering role played by the matrix itself. In extremely wave-exposed habitats, mussel beds become perturbed at a more frequent rate and thus may not reach full diversity potential (Suchanek, 1980). Many other authors have stressed the important structuring role that water motion produced by breaking waves plays in structuring intertidal communities (e.g. Lewis, 1964; Dayton, 1971; Levin and Paine, 1974; Lubchenco and Menge, 1978; Paine and Levin, 1981; Sousa, 1985, Gaylord, 1999). In intertidal regions, species assemblages and the rates of turnover of both plants and animals may be influenced as much by the level of wave exposure typical of a site as by biological factors such as predation or competition (Lewis, 1964; Paine, 1979; McQuaid and Branch, 1985). Alternatively, wave action may interact critically with biological features to affect the persistence of organisms; for example by limiting the activity or distribution of important grazers and predators (Lubchenco and Menge, 1978; Menge, 1978; Underwood and Jernakoff, 1984). Attempts were made to standardise the conditions of wave-exposure at the sites in the present study. However, some sites were subject to slightly different degrees of wave-exposure, and univariate and multivariate analyses of community structure suggested this was an important factor in structuring these communities in the British Isles and Irish Republic. Certain species, such as *Hyale prevostii*, juvenile *Mytilus edulis*, *Lasaea adansoni* and *Omalgyra atomus*, were present in elevated abundance at the more exposed locations, such as sites on the west coast of Ireland, while the abundance of most taxa varied with exposure. Similarly, Jacobi (1987a) stated that in mussel beds in the Bay of Santos, Brazil, certain amphipod species only occurred at more wave-exposed sites. The author went on to state that at mussel beds in sheltered locations, large quantities of sediment filled interstitial cavities and produced a tight arrangement, while exposed mussel beds showed a loose multi-layered structure with large, abundant interstices and little sediment. Suchanek (1979, 1980) suggested that since the amount of sediment, which accumulates on a mussel bed, is dependent on the degree of wave exposure, differences in mussel bed community structure between exposed and sheltered locations might be in part, a result of sediments. Hagermann (1966) showed that the number of nematodes associated with seaweed fronds increased

with increased sedimentation, while the number of creeping and clinging animals decreased. The amount of sedimentation was in turn affected by the amount of water movement, or wave action. Various authors have highlighted the importance of fine sediments on the abundance and diversity of benthic community structure in estuaries (Chester *et al*, 1983; Flint and Kalke, 1985; Mannino and Montagna, 1997). Similarly, Boesch (1973) found that sediment composition was responsible for species distribution and diversity in Chesapeake Bay. Mussel beds at the more wave-exposed locations in the British Isles and Irish Republic, such as those on the east coast of England and the west coast of Ireland, in the present study had lower fine and coarse sediment contents than the more sheltered locations, such as those on Anglesey. However, univariate and multivariate analyses failed to identify strong relationships between sediment content of the mussel beds and the associated communities. Thus, differences in community structure due to wave-exposure are not simply due to differences in sediment content, although the exact mechanisms behind the structuring role that wave exposure plays on mussel bed communities in the present study is unclear.

Climatic differences

Various authors have proposed that climatic differences might explain variations in diversity in different parts of the world (e.g. Fischer, 1960; Pianka, 1966). Underwood (1979) stated that the temperature regime of an area can affect distributions of species, since it can affect gametogenesis, spawning and larval or embryonic survival, such that species have geographical boundaries. It is unlikely that such a factor would cause the observed differences in diversity of mussel bed communities at each of the eight sites in the British Isles and Irish Republic or between the nine sites in Chile, since the locations did not cover a sufficiently wide geographical range to encounter significant differences in climatic conditions or stability. Few of the taxa encountered in mussel beds were present only at some sites and absent at others, probably as a result of limited geographical range, with the possible exception of the gastropod, *Tricolia pullus*, which has a distribution limited to the west coasts of Scotland and Ireland (Hayward and Ryland, 1990).

Latitudinal differences

Latitudinal gradients in diversity were unlikely to contribute to the observed large-scale spatial differences in mussel community structure at sites within the British Isles and Irish Republic. However, such factors may affect the structure of the *P. purpuratus* community, since Chile is 4329 km long, extending from 18°S to 56°S

and the present study encompassed sites from Region VI in the north, to Region X in the south of Chile, ranging from 33°S to 39°S, a distance of approximately 1000km. Latitudinal gradients in biodiversity are well documented and are commonly associated with environmental gradients related to solar energy and temperature (e.g. Gee and Warwick, 1996; Lambshead *et al,* 2000). In nearly all groups of organisms, the number of species within a given area increases markedly towards the equator, reaching a maximum in tropical latitudes and decreasing both northward and southward towards the poles (e.g. Fischer, 1960; Stehli, 1968; Ricklefs, 1993; Blackburn and Gaston, 1996). This phenomenon has been demonstrated in many taxa, for example, polychaetes (Sanders, 1968), bivalves (Stehli *et al*, 1967) and according to Thorson (1957) is most pronounced in epifaunal communities. As such, geographical differences in mussel community structure in the present study might be a reflection of latitudinal gradients in diversity. Lancellotti and Vasquez (2000) noted, in a study of the zoogeography of benthic macroinvertebrates of the Chilean coast that biodiversity showed a mild but progressive increase along the latitudinal gradient from north to south. Within the limits of the study, univariate measures of diversity were greater at southern Chilean sites than those further north, so latitudinal gradients in diversity appeared to exist in the data, but these appear to contradict the more usual trend of increased diversity towards the equator (e.g. Blackburn and Gaston, 1996).

Stochastic factors and unpredictable events

While many of the aforementioned biotic and abiotic factors are probably important in structuring the communities associated with mussel beds in the British Isles and Irish Republic and Chile, it is likely that much of the large-scale spatial variation is not accounted for by such predictable processes. A large amount of the intersite variation is probably due to stochastic factors and unpredictable events, such as random variation in the order of larval arrival or predation pressure. Kiørboe (1979) concluded that although the structure of subtidal benthic communities on mixed sediment substrata in Holbæk Fjord, Denmark was influenced by both biotic and abiotic conditions, it was not exactly predictable, due to environmental and demographic stochasticity. Hughes and Jackson (1992) concluded that geographical differences in reef fish species along the Caribbean coast of Panama were unlikely to be the result of high sensitivity to local conditions, but were more likely to have a stochastic and historical basis. Other authors have emphasised the importance of unpredictable events for the structure of benthic communities (e.g. Lewis, 1964; Eagle, 1974; Gutt, 2000).

Comparison of the communities associated with mussel beds in the British Isles and Irish Republic and in Chile

General predictions of species distribution patterns in the sea are relatively easy, in comparison to terrestrial patterns (MacArthur and Connell, 1966). The general circulation in the oceans carries heat away from the equator in the western parts of the oceans (along the eastern shores of the continents), so that tropical marine organisms are found up to about 30°N and S latitude. In contrast, the colder waters from high latitude flows towards the equator along the western shores of the continents, and tropical organisms, such as coral reefs, extend to only 10° or 15°N and S latitude. In the present study, mussel beds in the British Isles and Irish Republic and Chile all occurred on rocky shores at temperate latitudes. In addition, although the size, age and packing densities of *P. purpuratus* and *M. edulis* did show slight differences, the habitat provided for colonisation by infaunal taxa by the two mussels are very similar in nature, in terms of habitat structure and environmental conditions. Thus, it might be expected that the invertebrate communities associated with *P. purpuratus* and *M. edulis* would be very similar, particularly at higher taxonomic levels. This phenomenon of 'parallel communities', due to convergent evolution, has been observed in a variety of habitats, for example, crab fauna of mangrove areas in Florida and Australia (McIvor and Smith, 1995), coral assemblages in the Atlantic and Indo-Pacific (Karlson and Cornell, 1998, 1999), Atlantic asteroids (Price *et al*, 1999), deep-sea nematodes across the North Atlantic (Lambshead *et al*, 2000) and brackish water fauna (Cognetti and Maltagliati, 2000).

At the species level, the faunal associates of *P. purpuratus* and *M. edulis* are quite distinct, as might be expected, given that the assemblages occurred on different continents. Myers (1994) stated that the proximate cause of pan-continental scale patterns of species richness and diversity is origination through speciation, balanced by global extinction and TECO (tectonic, eustatic, climatic and oceanographic) events and is thus largely caused by processes operating through historical time. High species richness is promoted by high rates of origination, either through *in situ* speciation or through colonisation, or alternatively by low rates of extinction or a combination of both. In contrast, small-scale spatial differences are defined by recent ecological processes such as competition and predation (e.g. Underwood and Denley, 1984; Gaines and Roughgarden, 1985; Sutherland, 1990).

When plotted graphically, the patterns of dominance in mussel bed communities in the British Isles and Irish Republic and Chile are remarkably similar; both are dominated by a few common taxa. Such a phenomenon has previously

been documented in communities associated with intertidal mussel species (e.g. Lintas and Seed, 1992; Ong Che and Morton, 1992). Furthermore, Seed and Brotohadikusumo (1994) noted that in the case of *Septifer virgatus* in Hong Kong, this dominance pattern applied not only to the total fauna associated with this mussel, but also the molluscan fauna when this was considered separately. Seed (1996) noted that while data from previous studies of communities associated with different intertidal mussel species around the world (e.g. Tsuchiya and Nishihira, 1985, 1986; Peake and Quinn, 1993; Lintas and Seed, 1994) could not be scaled for sampling effort, it appeared that the number of associated taxa is broadly comparable between mussel species. Moreover, Seed (1996) went on to note that functionally similar taxa, often within the same genus (e.g. *Lasaea*, *Hyale*, and *Typosyllis*) regularly recurred in mytilid communities worldwide. Similar biogeographic observations have been made in other communities, such as decapod crustacean fauna in the Southeast Atlantic (MacPherson, 1991), asteroid taxa across the Atlantic (Price *et al*, 1999) and the fauna of brackish water habitats (Cognetti and Maltagliati, 2000). The results of the present study agree, to some extent, with these findings, although significant differences were observed between communities associated with the two mussel species. When analyses were carried out at higher taxonomic levels, clear differences were observed in the structure of the invertebrate communities associated with *P. purpuratus* in Chile and *M. edulis* in the British Isles and Irish Republic, both at a univariate and multivariate level. British and Irish mussel beds tended to be dominated by many meiofaunal taxa, such as nematodes, nemerteans, mites and chironomids, probably as a result of the increased sediment content, while Chilean mussel beds had a much greater proportion of macrofaunal taxa, particularly anemones, polychaetes, barnacles and limpets. However, many of the differences in community composition between the two mussel species were due to variability in the proportional abundance of mutually occurring taxa. Thus, to a certain extent, the invertebrate assemblages associated with *P. purpuratus* and *M. edulis* populations appeared to be examples of 'parallel communities', showing similar patterns of dominance. However, in many cases, the identity of dominant taxa was very different from one mussel species to the other or even from one location to another, within populations of the same mussel species.

Differences in the structure of communities associated with *P. purpuratus* and *M. edulis* might have been, in part, due to different size, age and packing densities of the mussels. Many studies have highlighted the relationship between mussel packing density and the diversity of the associated infaunal communities. Various studies have shown that the abundance of associated fauna in mussel beds is often

positively correlated with density of mussels (Commito, 1987; Seed and Suchanek, 1992). Commito and Boncavage (1989) demonstrated that oligochaete abundance in *M. edulis* beds in New England was positively correlated with mussel density. However, in studies of mussel beds in the northern Wadden Sea, Asmus (1987) failed to find any correlation between *M. edulis* density and the biomass of associated invertebrates. In addition, Seed and Brotohadikusumo (1994) found no significant correlation between the density of mussels and that of the associated fauna in *Septifer virgatus* beds in Hong Kong. *P. purpuratus* occurred in lower densities and achieved a generally greater size and age than *M. edulis*; *P. purpuratus* beds also contained a lower proportion of juvenile mussels than beds of *M. edulis*. The present study found that univariate measures of diversity were greater in British and Irish mussel beds than those in Chile, when compared at the same taxonomic level. The small interstitial spaces provided by *M. edulis* beds would favour greater numbers of meiofaunal taxa, which were observed here in significantly greater numbers. In addition, the increased packing density and greater proportion of smaller mussel in British and Irish mussel beds might help to reduce water flow and favour the retention of sediments within the mussel bed (Theisen, 1968; Dittman, 1987). Mussels in Chilean beds were more loosely packed, such that water movement would prevent any sediment retention and as such, sediment content was negligible. This factor might account for the lower abundance of meiofaunal and deposit feeding taxa such as nematodes, nemerteans and mites, which were abundant in British and Irish mussel beds. The greater interstitial space in *P. purpuratus* beds, given the larger size of mussels and lower packing densities, would favour the presence of larger bodied and mobile taxa, such as nereid polychaetes, limpets, barnacles and anemones, which were observed in much higher abundance here. The lack of small mussels in *P. purpuratus* beds might be due to a high degree of predation pressure, since Navarette and Castilla (1988) documented a high predation pressure on small *P. purpuratus* (3-6mm shell length) by the carnivorous intertidal crabs *Acanthocyclus gayi* (Milne-Edwards et Lucas) and *A. hassleri* (Rathbun). In addition, Mendez and Cancino (1990) and Dye (1991) reported a strong selection for small *P. purpuratus*, <10mm, by juveniles of the muricid gastropod *Concholepas concholepas*, another key intertidal predator on Chilean rocky shores (Castilla *et al*, 1979; Guisado and Castilla, 1983; Moreno *et al*, 1986; Alvarado and Castilla, 1996). Alternatively, the lack of juvenile mussels could simply reflect the timing of settlement periods.

Differences in packing densities and sediment content of mussel beds in Chile and the British Isles and Irish Republic might be a function of wave exposure in

the two geographical locations. Attempts were made to select sites in each location with similar wave exposure and the majority of sites, with the possible exception of those on Anglesey were deemed to conform to this requirement. Previous studies have shown that the highest densities of mussels tend to be associated with shores receiving moderate to severe wave action, probably a direct influence of the amount of water (and larval stages) passing over them and slow draining, horizontal platforms, especially where surfaces are roughened or broken by discontinuities (Seed, 1968). Jacobi (1987a, 1987b) demonstrated that mussel beds protected from wave action, on the coast of Brazil retained large quantities of sediment which obliterated cavities and produced a tight arrangement, while those in more exposed conditions showed a loose multilayered structure with large, abundant interstices and little sediment.

In conclusion, while the invertebrate communities associated with *P. purpuratus* in Chile and *M. edulis* in the British Isles and Irish Republic show similar general patterns of dominance by a few common taxa, the identity of many of these more dominant taxa differs between the British Isles and Irish Republic and Chile. Other taxa are commonly found in mussel beds in each of the two main geographical locations. Chilean mussel beds are dominated by mobile, macrofaunal taxa, while British and Irish mussel beds have a higher abundance of meiofaunal taxa. Such differences might be attributed in part, to the very different packing densities and sediment content of the two mussel species, which in turn, may be a function of the degree of wave exposure. However, a full understanding of the dynamics of mussel communities and their biogeographical variation, requires the integration of local ecological perspective with large-scale phenomena.

Chapter 6

Temporal variation in the structure of the invertebrate communities associated with *Mytilus edulis* and *Perumytilus purpuratus*

ABSTRACT

The invertebrate communities associated with *Mytilus edulis* at all three locations in Wales showed significant temporal variation, which was much more pronounced when data were analysed using multivariate techniques, than when using a univariate approach; the latter often failing to show any significant differences. The structure of the mussel communities at each of the sites showed significant intra-annual multivariate changes, although these differences were not always of a cyclic, progressional nature. The mussel bed communities at each site also showed significant inter-annual variation, such that community structures differed both between different months in a yearly cycle and between the same month from year to year. The invertebrate communities associated with *Perumytilus purpuratus* in Chile also showed significant inter-annual variations at the four study sites. Temporal differences in the structure of the invertebrate communities associated with *M. edulis* and *P. purpuratus* were generally the result of differences in the abundance of less than 10 common taxa, when emphasis was placed on taxa abundance in the analysis. The identity of many of these, numerically dominant taxa was the same at each site, for example, in the Welsh sites, juvenile *M. edulis*, nematodes, mites, larvae of the insect genus *Clunio* and various nemertean families and in the Chilean sites, juvenile *P. purpuratus*, nematodes, barnacles and nemerteans. Clear differences in community structure were also seen, when data were analysed with a presence/absence transformation, although many more taxa contributed to such temporal differences. Some taxa were temporally ubiquitous, while others appeared to be only transient members of the communities. Many of the measured environmental factors of the mussel beds at each of the study sites showed significant temporal variation, but did not show a high degree of correlation with the biotic data, either on a univariate or multivariate level. It is concluded that the intra- and inter-annual variation in the structure of the mussel communities both in Wales and Chile, are the result of complex interactions between many different processes, together with stochastic events.

INTRODUCTION

Many studies have demonstrated temporal variation, both seasonal and annual, in various benthic marine communities. Beukema (1974) reported considerable seasonal variation in the abundance of macrobenthos on a tidal flat area in the Dutch Wadden Sea, while Persson (1983) showed significant within year differences in the structure of coastal macrobenthic assemblages in the southern Baltic. During a twelve-month study, Nickell and Sayer (1998) found significant seasonal variation in the occurrence of mobile macrofauna on a sublittoral reef on the West Coast of Scotland. A significantly higher abundance of macro-crustacean species was recorded on algal plants in the tropics between wet and dry seasons (Stoner, 1985). In a study of the fauna associated with a Brazilian intertidal mangrove forest, Barletta *et al* (2000) found that although total fish densities did not differ significantly with time, total biomass did show significant seasonal variation. Maurer *et al* (1979) reported significant seasonal differences in coastal benthic assemblages on the East Coast of America, which were found to be so marked, that the authors suggested these seasonal differences should be taken into account in environmental impact studies of such communities. In studies of tropical rocky intertidal communities in the Bay of Panama, Lubchenco *et al* (1984) found that seasonal changes in community structure were small or lacking, whilst annual changes were larger, but still small in comparison to those communities in temperate regions. By contrast, Buchanan *et al* (1978) demonstrated that benthic macrofaunal communities off the south Northumberland coast remained essentially stable for more than a decade, although seasonal variations within years were observed. Estacio *et al* (1999) detected significant temporal changes in species abundance, diversity and evenness in estuarine benthic communities in southern Spain, whilst Keough and Butler (1983) demonstrated that the number of epifaunal species on individual *Pinna bicolor* shells in South Australia showed large temporal fluctuations.

Temporal changes in the structure of communities can result in the occurrence of taxonomically related species at different times, such that seasonal or annual variations only become apparent at more refined taxonomic levels. For example, Jarvis and Seed (1996) demonstrated that the abundance of meiofaunal species on epiphytes of the intertidal macroalga, *Ascophyllum nodosum*, displayed little temporal variation at high taxonomic levels, whereas seasonal changes were apparent at the species level. Thus, it is important in any studies of temporal (and spatial) variation in invertebrate communities to identify organisms in the community to the lowest possible taxonomic category.

Temporal variation in mussel bed communities is somewhat less extensively covered in the literature. Briggs (1982) observed significant seasonal variation in the fauna associated with *M. edulis* in Loch Foyle, while Tsuchiya and Nishihira (1985) found similar patterns in associates of this mussel species in Japan. Peake and Quinn (1993) have reported seasonal variations in the infaunal associates of *Brachidontes rostratus* in Australia, while Jacobi (1987a) found seasonal differences in the abundance of amphipod associates of mussel beds from the Bay of Santos, Brazil. Similarly, Tokeshi (1995) reported significant differences in abundance of polychaetes associated with mussel beds on South American shores, while Ong Che and Morton (1992), reported significant seasonal and annual variation in the invertebrate communities associated with the mussel *Septifer virgatus* on the Hong Kong coast.

In this chapter the seasonal and annual variation associated with mussel bed communities at three contrasting rocky shore sites on the coast of North Wales and four sites in Chile, South America is investigated, using both a univariate and a multivariate approach. Comparisons are made within and between sites to investigate patterns of seasonal and annual variation in community structure. The extent to which various environmental parameters of the mussel bed, such as mussel density and volume and mass of sediment fractions affect community structure over the course of the study is also investigated.

METHODS

Samples of *M. edulis* and their associated fauna were collected during spring tides between January and November 1998 at bimonthly intervals from the mussel beds at each of three study sites in North Wales. Each site was visited on consecutive days within a three-day period, in order to reduce the possibility of small-scale temporal variations between sites. Such variations might occur due to factors such as strong onshore winds, or invasions by predators such as *Asterias rubens* or *Nucella lapillus.* Further samples were collected from each of the three sites during January and July 1999 to allow inter-annual comparisons to be made. Samples of *P. purpuratus* were collected each January between 1997 and 2000, from four sites in Chile. Samples were processed and sorted according to the methodology described in Chapter 2.

RESULTS

Temporal variation in communities associated with Mytilus edulis

For ease of interpretation of the data and statistical analysis, each site in the UK is dealt with separately in this section, while at the end of the section there is an overall analysis of the data.

Point Lynas

Over the twelve-month sampling period a total of 14210 infaunal organisms representing 79 different taxa were collected and identified from mussel beds at Point Lynas. These included representatives from 10 phyla, 16 classes, 31 orders and 54 different families. None of the univariate measures of diversity, i.e. number of taxa (NT), number of individuals (NI), Margalef's richness (d), Shannon's diversity (H') and Pielou's evenness (J) showed any significant variation over the twelve-month sampling period. However, the variability associated with total taxa and richness was greater among replicates during the winter months (November and January) than the rest of the year. The variability associated with Shannon's diversity and Pielou's evenness was similar among replicates at all times of the year (Figure 1).

Cluster analysis of square-root transformed infaunal data revealed three major groups, with March and May clustered together, July, September and November as another group and January as a distinct group on its own (Figure 2a). When cluster analysis was performed on presence/absence transformed infaunal data, the bimonthly samples clustered as two main groups, representing spring/summer (March to July) samples and autumn/winter (September to January) samples (Figure 2b). MDS ordination of square-root transformed infauna abundance illustrated a change in community structure over the twelve-month period, in terms of the more dominant taxa in the community (Figure 3a). A one-way ANOSIM test performed on the data confirmed that significant differences in community structure did exist between some of the bimonthly samples ($R=0.315$, $p<0.05$). Pairwise comparisons revealed that the structure of the mussel community was significantly different between all months, with the exception of January/November and July/September (Table 1a). When tested using the RELATE procedure this seasonal progression in community structure was seen to be of a cyclic nature ($R=0.454$, $p>0.05$). MDS ordination and an ANOSIM performed with a presence/absence transformation on taxa abundance indicated there were also significant seasonal differences in the mussel bed community, with regard to the rarer members of the community (ANOSIM, $R=0.246$, $p<0.05$) (Figure 3b). Pairwise comparisons of monthly samples showed that differences were less pronounced than when analysis

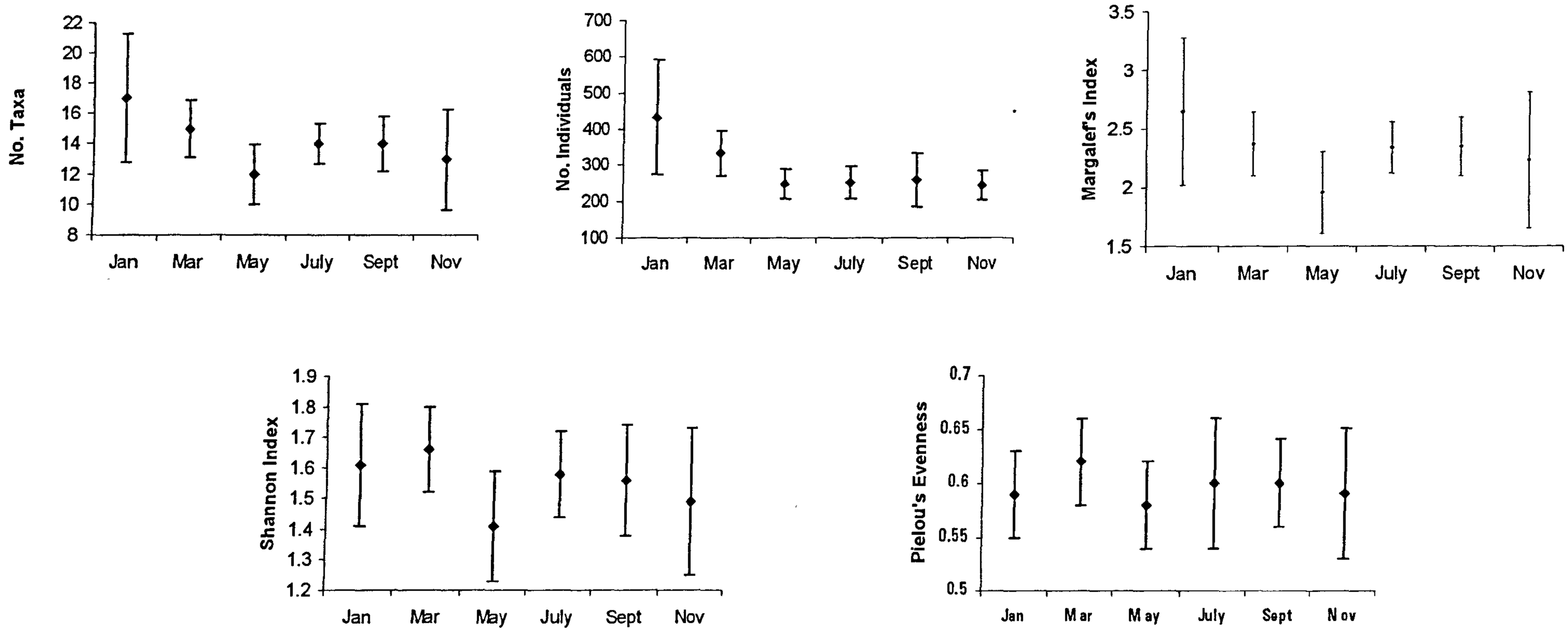
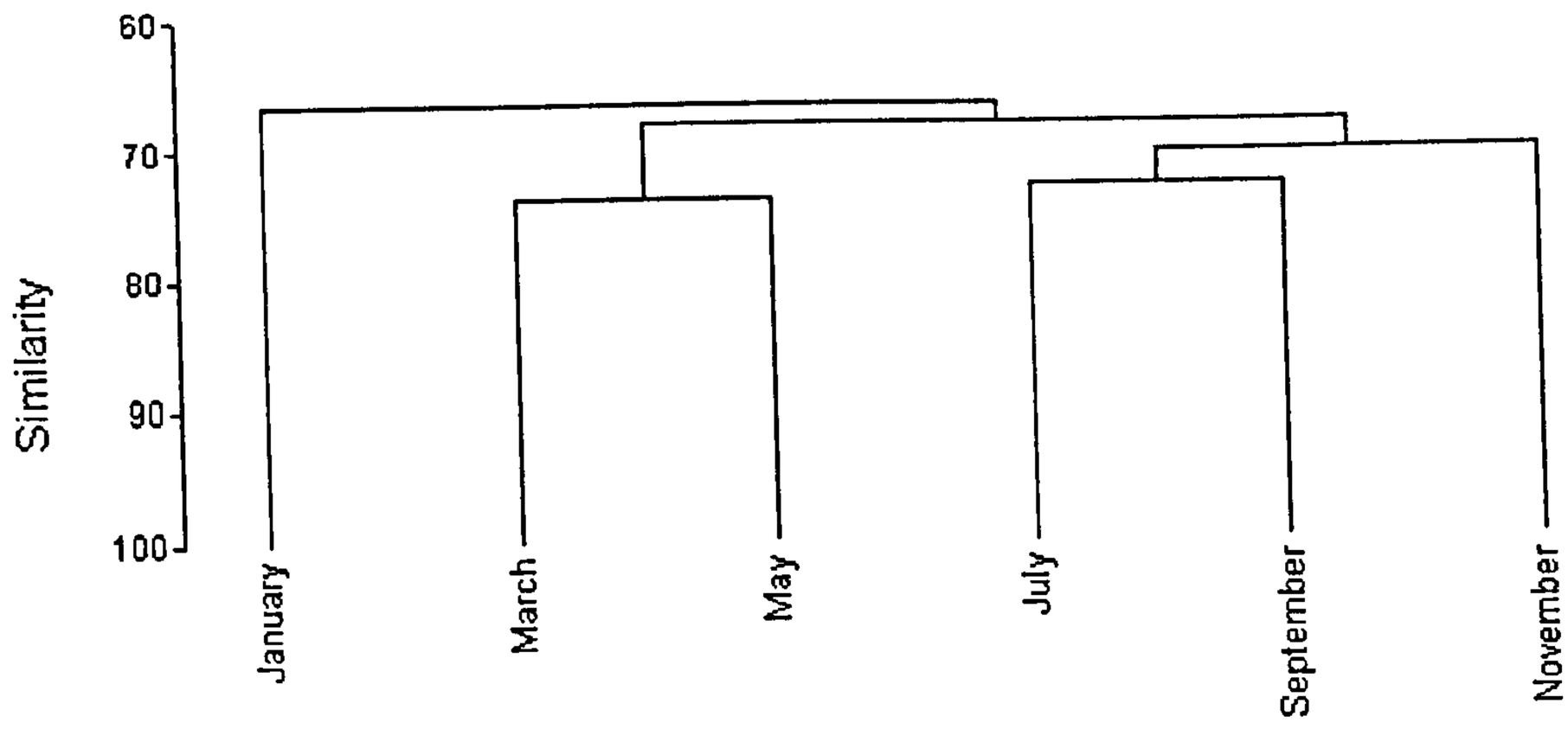


Figure 1 Univariate measures of mussel bed community structure at Point Lynas, Anglesey at bimonthly intervals between January and November 1998. Values are based on 25cm^2 replicates. 95% confidence intervals are marked, such that significant differences ($p<0.05$) are represented by non-overlapping intervals.

a) Square-root transformation



b) Presence/absence transformation

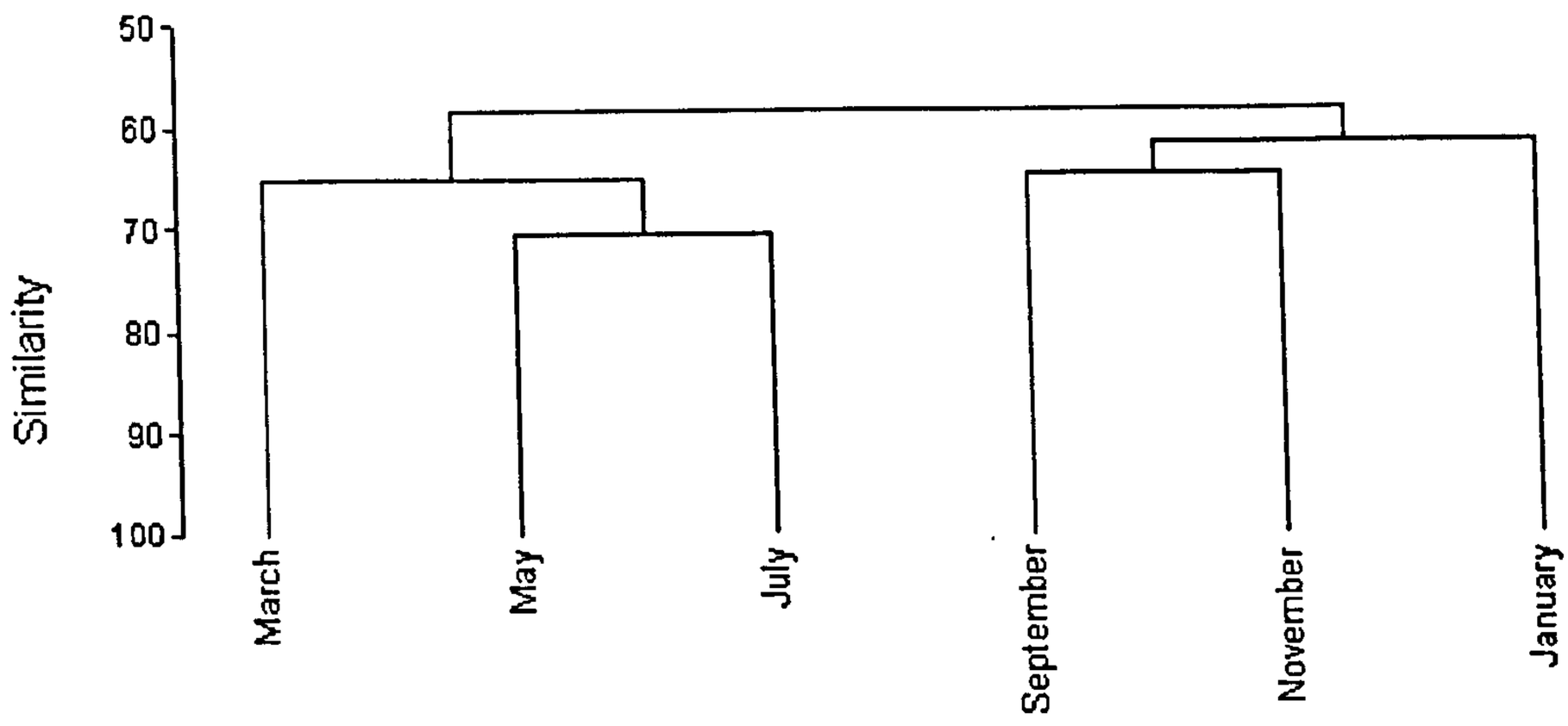


Figure 2 Dendrograms for group average clustering of Bray-Curtis similarities based on a) square-root transformed and b) presence/absence transformed biotic data from mussel beds at Point Lynas, Anglesey at bimonthly intervals between January and November 1998.

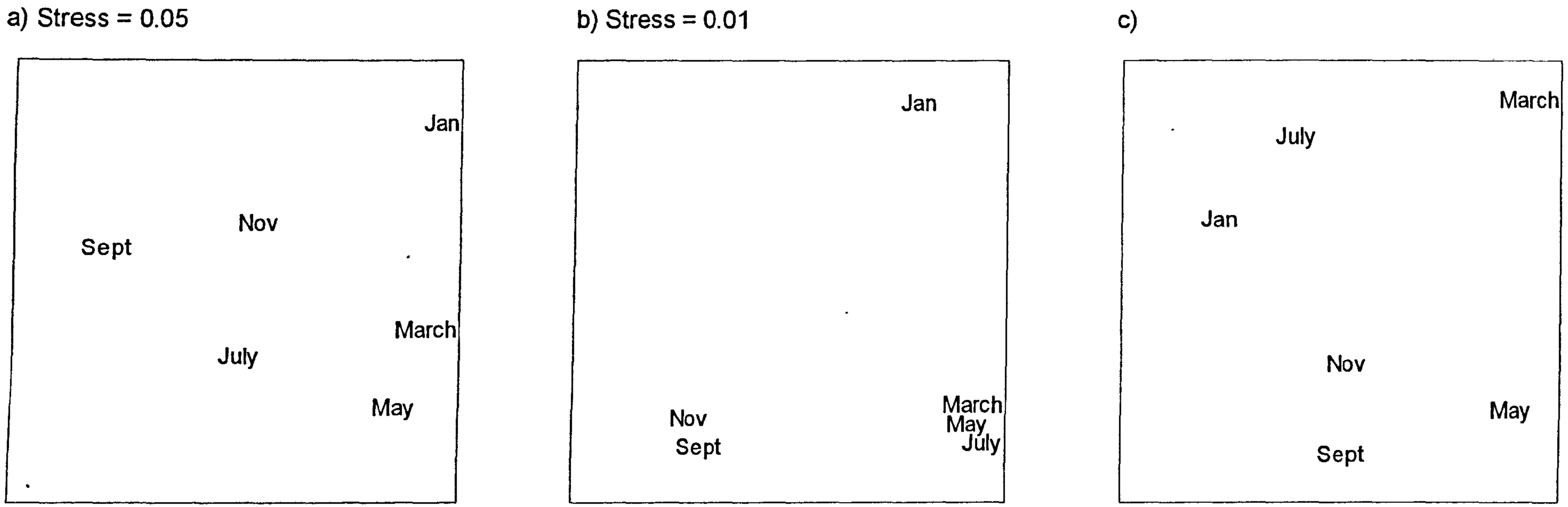


Figure 3 Ordination by MDS based on Bray-Curtis similarity, of averaged abundance of infauna from the mussel beds at Point Lynas, Anglesey at bimonthly intervals between January and November 1998, using a) square-root transformation, b) presence/absence transformation and c) ordination by PCA of environmental variables based on normalised Euclidean distance.

Table 1 Global R-values for ANOSIM pairwise comparisons between bimonthly samples of the mussel bed communities at Point Lynas, Anglesey based on a) square-root transformation of species abundance and b) presence/absence transformation of species abundance. Significant differences in community structure ($p<0.05$) are indicated by bold type.

a)

	January	*March*	*May*	*July*	*September*
March	**0.164**				
May	**0.41**	**0.199**			
July	**0.175**	**0.332**	**0.503**		
September	**0.256**	**0.57**	**0797**	0.126	
November	0.136	**0.262**	**0.407**	**0.145**	**0.296**

b)

	January	*March*	*May*	*July*	*September*
March	**0.249**				
May	**0.354**	**0.396**			
July	0.096	**0.224**	**0.263**		
September	0.129	**0.436**	**0.488**	**0.177**	
November	0.137	**0.206**	0.125	**0.299**	**0.238**

places emphasis on the more numerically abundant members of the community (Table 1b). RELATE analysis showed that there was also a significant pattern of cyclic seasonal progression in the less common constituents of the mussel community($R = 0.745$, $p>0.05$).

Similarity percentage analysis (SIMPER), performed with a square-root transformation (Table 2), highlighted the more abundant taxa principally responsible for structuring each of the bimonthly sample groupings illustrated in Figure 3a. It can be seen that similarities within replicates for each bimonthly sample were primarily caused by changes in the abundance of 7 dominant taxa throughout the year, namely small mussels, mite sp. 1, nematodes, *Clunio* sp. larvae, nemertean families, the ostracod *Heterocythereis albomaculata* and the bivalve *Lasaea adansoni*. Many of these taxa were the most numerically abundant over the twelve-month study period. SIMPER analysis performed on presence/absence transformed data illustrated that many more taxa (up to 15) contributed to similarities within replicates for each of the bimonthly samples when emphasis was removed from taxa abundance (Table 3). Some of the taxa contributing to these similarities were the same as those identified using the square-root transformation, while many of the less numerically abundant taxa such as the crab, *Pilumnus hirtellus*, and the gastropods, *Onoba semicostata*, *Rissoa parva* and *Coriandria fulgida*, also contributed.

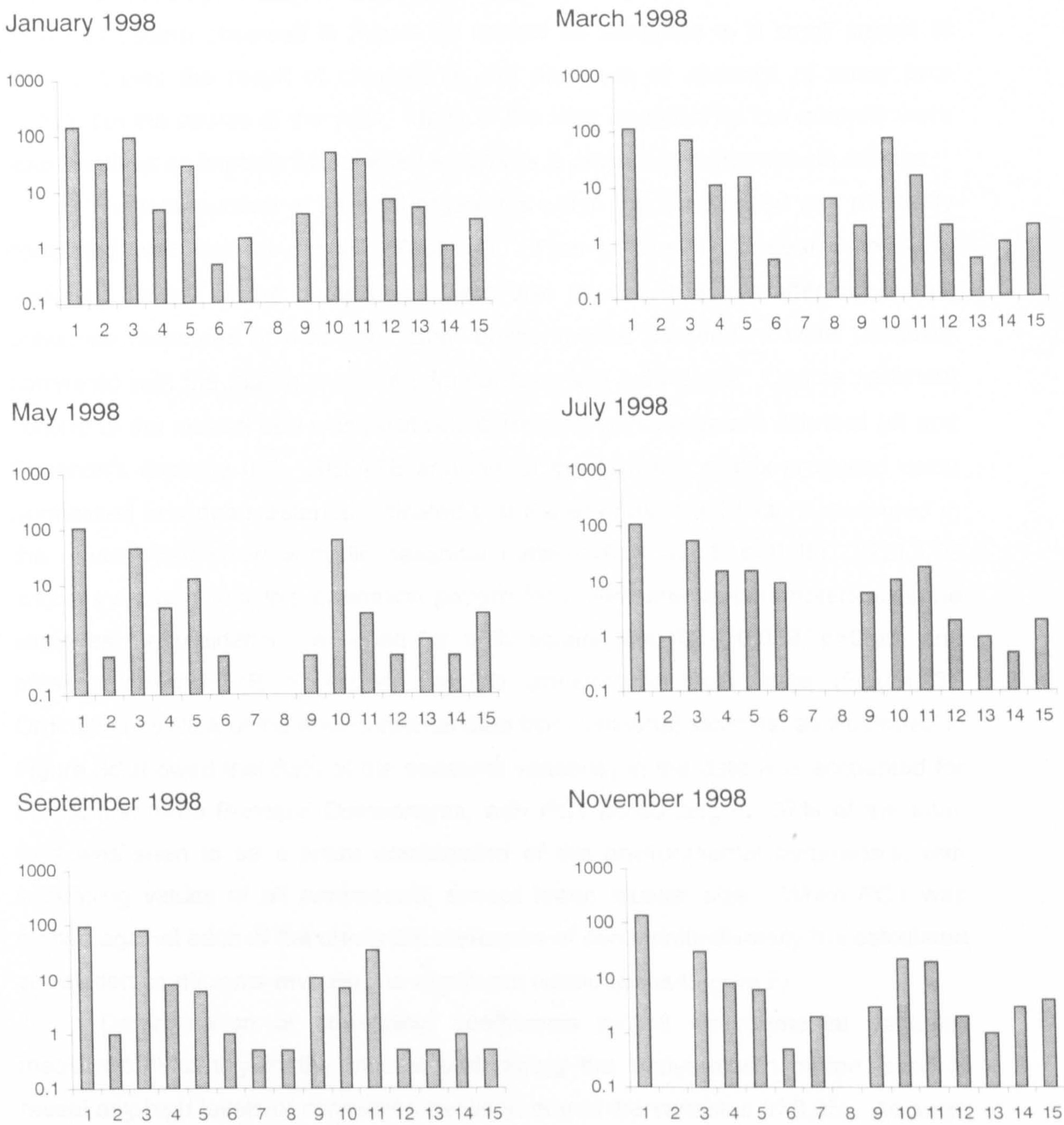
Since the pattern in the biotic data was of a cyclic, seasonal nature, it can be assumed that the community changes in structure were occurring in a continuum. Thus a holistic approach was required to identify taxa contributing to these differences, rather than pairwise comparisons between sample groups. BVSTEP analysis was performed on the data using a square-root transformation to identify which predominant taxa contributed to the observed cyclic seasonal progression in community structure (Figure 3a). Analysis revealed a subset of 15 taxa; small mussels, platyhelminthes, nematodes, tubulanid nemerteans, lineid nemerteans, tetrastemmatid nemerteans, *Cirratulus cirratus*, *Drilonereis filum*, *Heterocythereis albomaculata*, mite sp. 1, *Clunio* sp. larvae, *Cingula trifasciata*, *Coriandria fulgida*, *Nucella lapillus* and *Brachystomia scalaris*. Changes in abundance of this subset of taxa over the twelve-month study period are illustrated in Figure 4. Second-stage BVSTEP analysis performed on the data set, with these 15 taxa excluded failed to identify any further taxa subsets, which explained the seasonal pattern, observed in community structure. Thus, there was a great deal of structural redundancy within the data patterns of the mussel infaunal community; many of the taxa present did not react to any seasonal gradients. When BVSTEP analysis was repeated with a presence/absence transformation, to search for patterns in the rarer members of the

Table 2 Results of similarity percentage analysis (SIMPER) performed on bimonthly data from mussel beds at Point Lynas, Anglesey, using a square-root transformation. The taxa are listed in descending order of importance; figures in brackets represent cumulative % similarity with 90% chosen as the upper limit. Figures in bold in row 1 show average similarity within monthly replicates.

January **64**	March **67**	May **66**	July **59**	September **62**	November **61**
Juvenile *Mytilus edulis* (33)	Juvenile *Mytilus edulis* (29)	Juvenile *Mytilus edulis* (37)	Juvenile *Mytilus edulis* (38)	Juvenile *Mytilus edulis* (35)	Juvenile *Mytilus edulis* (42)
Mite sp. 1 (50)	Mite sp. 1 (55)	Mite sp. 1 (64)	Nematoda indet. (50)	Nematoda indet. (60)	*Clunio* sp. larvae (57)
Nematoda indet. (65)	Nematoda indet. (69)	Nematoda indet. (83)	*Clunio* sp. larvae (61)	*Clunio* sp. larvae (77)	Mite sp. 1 (70)
Clunio sp. larvae (78)	*Clunio* sp. larvae (79)	*Clunio* sp. larvae (87)	Mite sp. 1 (69)	*Heterocythereis albomaculata* (82)	Nematoda indet. (82)
Lasaea adansoni (82)	Lineidae indet. (84)	Lineidae indet. (91)	Tubulanidae indet. (75)	Lineidae indet. (86)	*Nucella lapillus* (86)
Heterocythereis albomaculata (86)	*Cingula trifasciata* (87)		Lineidae indet. (81)	Tubulanidae indet. (89)	Tubulanidae indet. (89)
Lineidae indet. (89	Tubulanidae indet. (90)		*Heterocythereis albomaculata* (85)	*Lasaea adansoni* (91)	Lineidae indet. (91)
Tubulanidae indet. (91)			*Lasaea adansoni* (89)		
			Brachystomia scalaris (92)		

Table 3 Results of similarity percentage analysis (SIMPER) performed on bimonthly data from mussel beds at Point Lynas, Anglesey, using a presence/absence transformation. The taxa are listed in descending order of importance; figures in brackets represent cumulative % similarity with 90% chosen as the upper limit. Figures in bold in row 1 show average similarity within monthly replicates.

January **51.9**	March **59.6**	May **53.5**	July **60**	September **54**	November **53**
Clunio sp. larvae	*Cingula trifasciata*	*Clunio* sp. larvae	Lineidae indet.	*Clunio* sp. larvae	*Clunio* sp. larvae
(12)	(12)	(16)	(12)	(14)	(15)
Mite sp. 1	*Clunio* sp. larvae	Mite sp. 1	Juvenile *Mytilus edulis*	Nematoda indet.	Mite sp. 1
(24)	(23)	(33)	(24)	(27)	(30)
Juvenile *Mytilus edulis*	Mite sp. 1	Nematoda indet.	Tubulanidae indet.	Juvenile *Mytilus edulis*	Juvenile *Mytilus edulis*
(36)	(35)	(49)	(34)	(41)	(45)
Nematoda indet.	Nematoda indet.	Juvenile *Mytilus edulis*	*Lasaea adansoni*	Lineidae indet.	Nematoda indet.
(45)	(46)	(65)	(42)	(51)	(56)
Lasaea adansoni	Juvenile *Mytilus edulis*	Lineidae indet.	*Clunio* sp. larvae	*Heterocythereis albomaculata*	*Nucella lapillus*
(54)	(58)	(73)	(52)	(60)	(67)
Heterocythereis albomaculata	*Lasaea adansoni*	*Rissoa parva*	Mite sp. 1	*Lasaea adansoni*	Tubulanidae indet..
(63)	(66)	(78)	(60)	(67)	(74)
Lineidae indet.	Lineidae indet.	Tubulanidae indet.	Nematoda indet.	Tubulanidae indet.	*Brachystomia scalaris*
(68)	(72)	(84)	(69)	(74)	(79)
Brachystomia scalaris	*Heterocythereis albomaculata*	*Brachystomia scalaris*	*Heterocythereis albomaculata*	Oligochaeta indet.	*Carcinus maenas*
(72)	(76)	(87)	(76)	(79)	(81)
Coriandria fulgida	*Brachystomia scalaris*	*Anurida maritima*	*Brachystomia scalaris*	*Nucella lapillus*	Lineidae indet.
(75)	(80)	(91)	(82)	(83)	(84)
Tubulanidae indet.	*Onoba semicostata*		*Carcinus maenas*	Mite sp. 1	*Lasaea adansoni*
(79)	(84)		(86)	(88)	(86)
Nucella lapillus	Tubulanidae indet.		*Cingula trifasciata*	Tetrastemmatidae indet.	*Cingula trifasciata*
(82)	(88)		(89)	(90)	(89)
Pilumnus hirtellus	Cephalothricidae indet.		*Pilumnus hirtellus*		*Heterocythereis albomaculata*
(85)	(92)		(92)		(91)
Platyhelminthe indet.					
(87)					
Oligochaeta indet.					
(89)					
Onoba semicostata					
(91)					



Key

1	Juvenile *Mytilus edulis*	9	*Heterocythere albomaculata*
2	Platyhelminthes indet.	10	Mite sp. 1
3	Nematoda indet.	11	*Clunio* sp. larvae
4	Tubulanidae indet.	12	*Cingula trifasciata*
5	Lineidae indet.	13	*Coriandria fulgida*
6	Tetrastemmatidae indet.	14	*Nucella lapillus*
7	*Cirratulus cirratus*	15	*Brachystomia scalaris*
8	*Drilonereis filum*		

Figure 4 Bimonthly log mean abundance per 25cm^2 quadrat, of taxa identified by BVSTEP analysis as those contributing to the seasonal patterns of diversity in the mussel beds at Point Lynas, Anglesey.

mussel community, a subset of 35 taxa from the 79 present was identified. The seasonal pattern observed in Figure 3b cannot be attributed to a small subset of taxa, but was the result of changes in the presence or absence of many taxa throughout the course of the year. Many of the taxa identified by this analysis were also identified as important taxa when emphasis is placed on numerical abundance.

The total number of infaunal organisms within the mussel bed was positively correlated with mussel density (Table 4). Fine (<63μm) and coarse (>63μm) sediment content of the mussel bed were also important factors affecting certain univariate measures of diversity. Both environmental parameters were positively correlated with the total number of infaunal taxa and individuals. Coarse sediment content of the mussel bed was positively correlated with Margalef's richness (d) and Shannon's diversity (H'). RELATE analysis of the similarity matrix produced using normalised Euclidean distance indicated that the environmental factors measured in the mussel bed show a cyclic seasonal pattern ($R = -0.11$, $p>0.05$). RELATE analysis showed that this ordination pattern for environmental parameters was the same as the ordination described for both square-root ($R = 0.089$, $p>0.05$) and presence/absence ($R = -0.084$, $p>0.05$) transformed biotic data (Figure 3). Ordination by PCA of the environmental data from seasonal samples, as illustrated in Figure 3c showed that 83% of the seasonal variability in the data was accounted for by the first three Principal Components, with PC1 accounting for 37% of the total. PC1 was seen to be a linear combination of the environmental parameters, with increasing values of all parameters, except mean mussel size. When PC1 was plotted against each of the univariate measures of community diversity the calculated correlation coefficients revealed no significant relationships (Figure 5).

Determination of correlation coefficients for all environmental variables measured bimonthly in the mussel bed during the twelve-month period failed to reveal any high levels of correlation between any of the variables ($r>0.95$). As such, all the measured environmental variables were entered into BIOENV analysis, to identify the most appropriate combinations of variables explaining the square-root and presence/absence transformed biotic data. The BIOENV procedure revealed that the highest correlation of square-root transformed infauna data was only 0.178, with the mass of coarse sediment. A similarly low correlation of 0.199 was obtained for presence/absence transformed infauna data, with a combination of the mass of coarse and fine sediment.

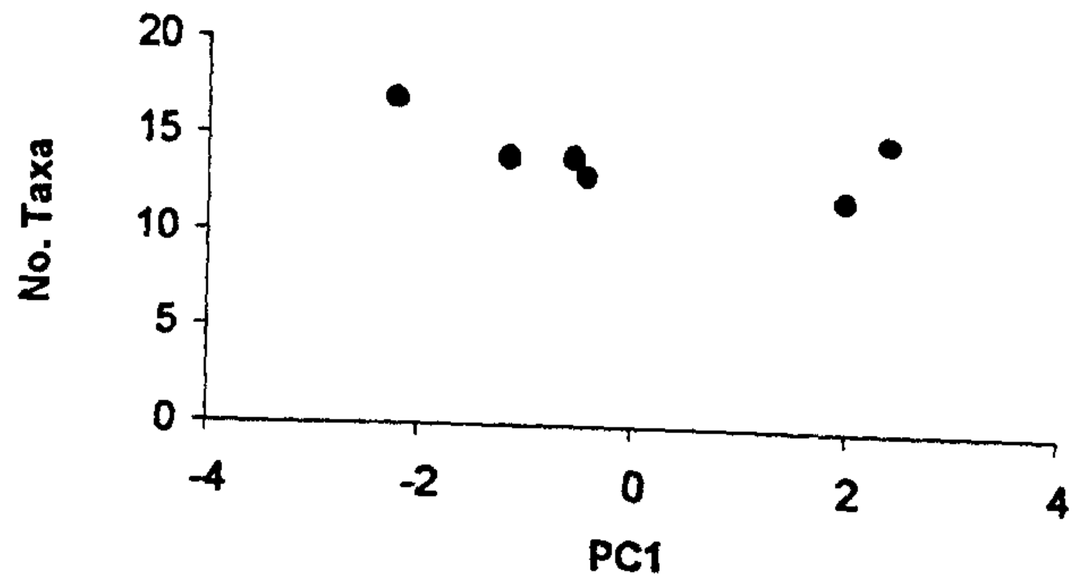
It can be concluded that at this particular site, the physical and environmental factors measured in the mussel bed did not have a significant structuring effect on

Table 4 Correlation coefficients calculated between environmental variables and univariate measures of diversity in the mussel beds at Point Lynas, Anglesey. Values in bold indicate significant correlation ($p<0.05$).

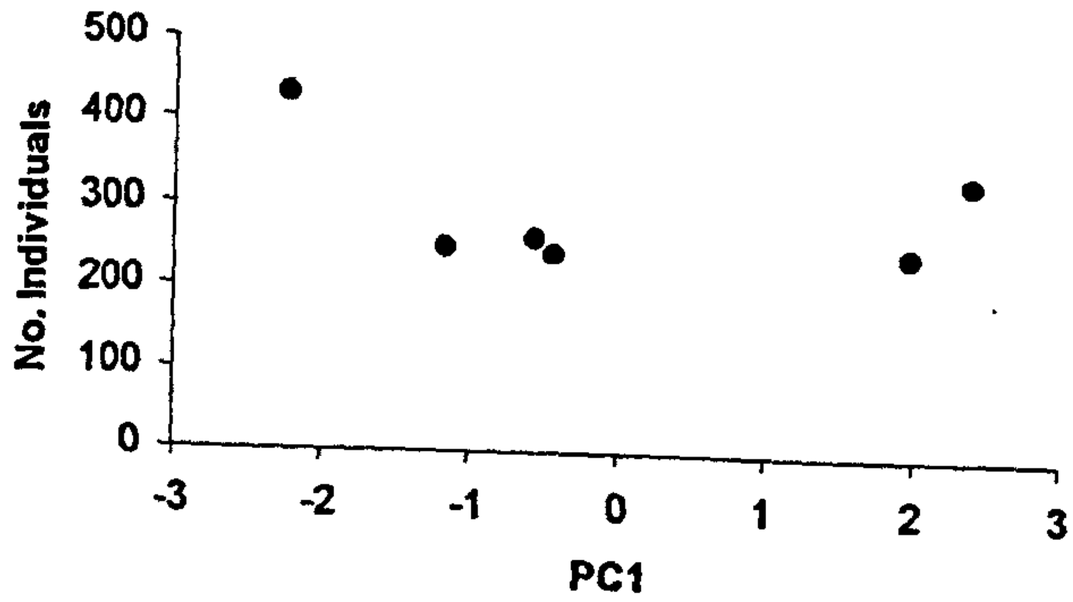
	NT	*NI*	*d*	*H'*	*J*
∑mussels	0.141	**0.302**	0.083	0.006	-0.142
Mussel mass	0.262	0.166	0.247	-0.033	-0.216
Mussel volume	-0.079	-0.025	-0.103	-0.263	-0.177
Mean mussel size	0.093	-0.208	0.162	0.083	0.080
Mean size*∑ mussels	0.203	0.263	0.162	0.020	-0.161
Mass fine sediment	**0.302**	**0.403**	0.225	0.166	-0.030
Mass coarse sediment	**0.454**	**0.555**	**0.360**	**0.326**	0.039

NT Number of taxa
NI Number of individuals
d Margalef's index
H' Shannon's diversity
J Pielou's evenness

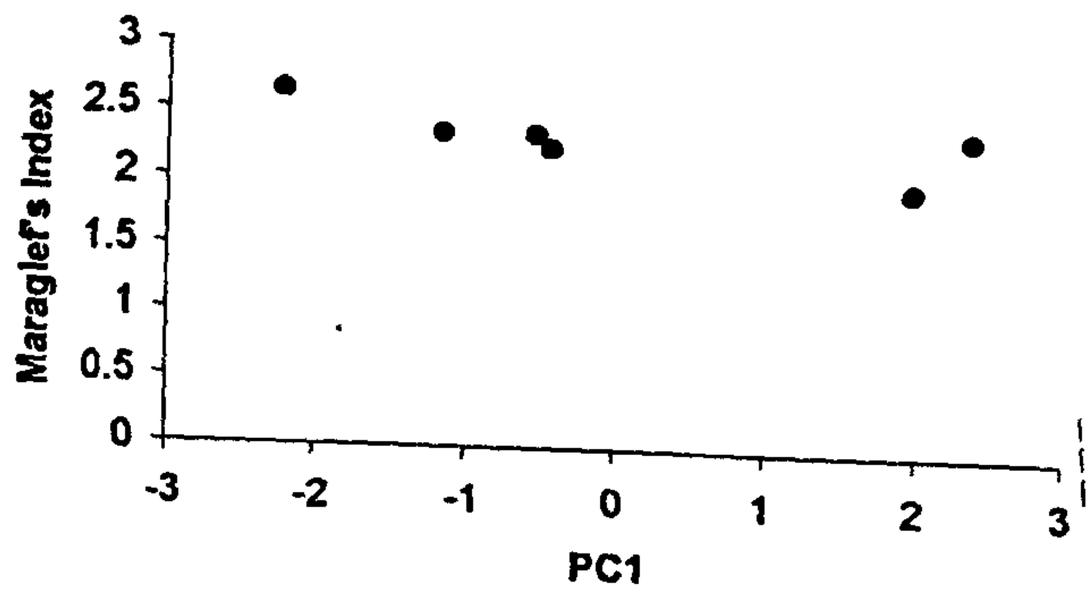
Figure 5 Principal Component 1 (PC1) plotted against each of the univariate measures of mussel bed community structure at Point Lynas, Anglesey. Correlation coefficients (r) and significance levels between the variables are shown.



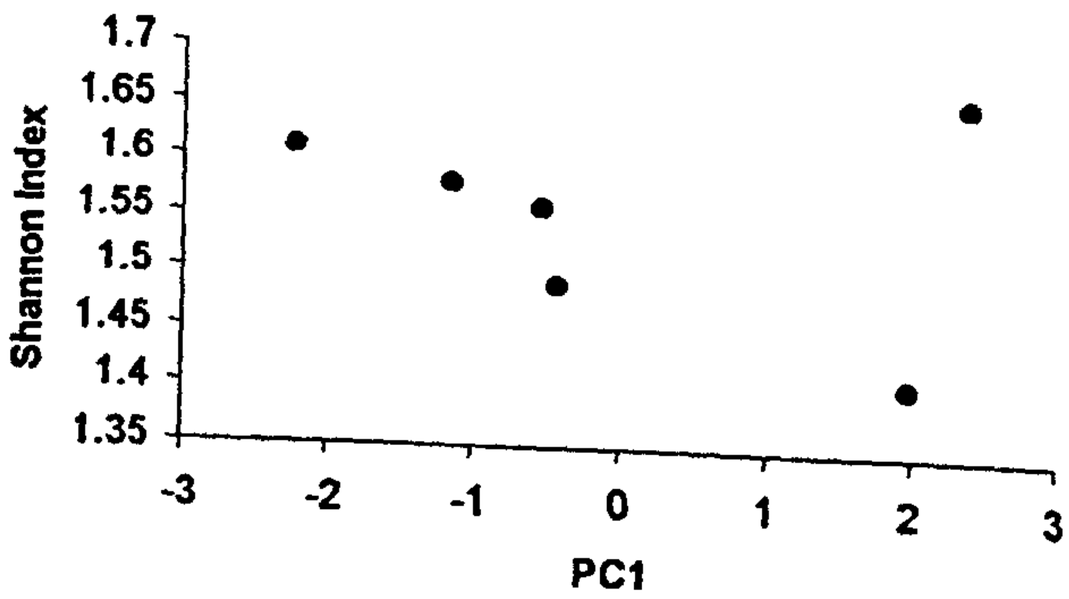
r = -0.503
p > 0.05



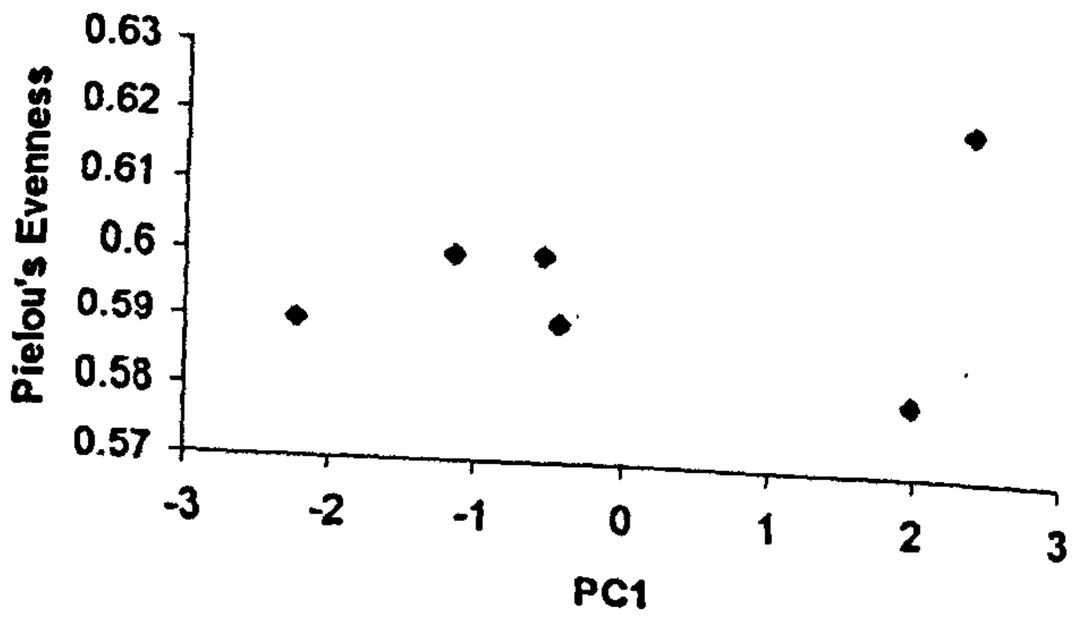
r = -0.319
p > 0.05



r = -0.661
p > 0.05



r = -0.202
p > 0.05



r = 0.280
p > 0.05

the multivariate characteristics of the associated community. Although some of the environmental variables measured did significantly affect the structure and diversity of the mussel bed community at Point Lynas, their main effects were masked by the stronger influencing factor of seasonal variation, which underlies the data.

White Beach

Over the twelve month sampling period a total of 16169 infaunal organisms from 93 different taxa were collected and identified from mussel beds at White Beach. These taxa included representatives from 10 phyla, 15 classes, 30 orders and 59 different families. The univariate measures of diversity i.e., number of taxa (NT), number of individuals (NI) and Shannon's diversity (H') showed no significant variation over the twelve month study period. Margalef's richness (d) was significantly greater in July than in March, while Pielou's evenness (J) was significantly lower in November than in either March or September (Figure 6). The variability associated with all univariate measures of community diversity varied greatly amongst replicate quadrats throughout the year.

Cluster analysis of square-root transformed infaunal data revealed only one major grouping, between autumn/winter (September to January) samples (Figure 7a). The other bimonthly samples remained separate. Almost identical results were obtained when cluster analysis was performed on presence/absence transformed infaunal data (Figure 7b). MDS ordination of square-root transformed infaunal abundance illustrated, in terms of the more dominant taxa in the community, a change in community structure during the twelve-month period (Figure 8a). A one-way ANOSIM test performed on the data confirmed that significant differences existed in community structure between some of the bimonthly samples ($R=0.611$, $p<0.05$), whilst pairwise comparisons revealed that the structure of the mussel community was significantly different between all months (Table 5a). When tested using the RELATE procedure no seasonality was apparent in community structure, ($R=0.363$, $p<0.05$). MDS ordination and ANOSIM performed with a presence/absence transformation on taxa abundance indicated there were also significant seasonal differences in the mussel bed community, with regard to the less dominant members of the community (ANOSIM, $R=0.523$, $p<0.05$) (Figure 8b). Pairwise comparisons of the bimonthly samples revealed that the community structure was significantly different between all months when emphasis was placed on the less common members of the community (Table 5b). However, RELATE analysis showed that there was no significant seasonality in the less common constituents of the mussel community ($R = 0.476$, $p<0.05$).

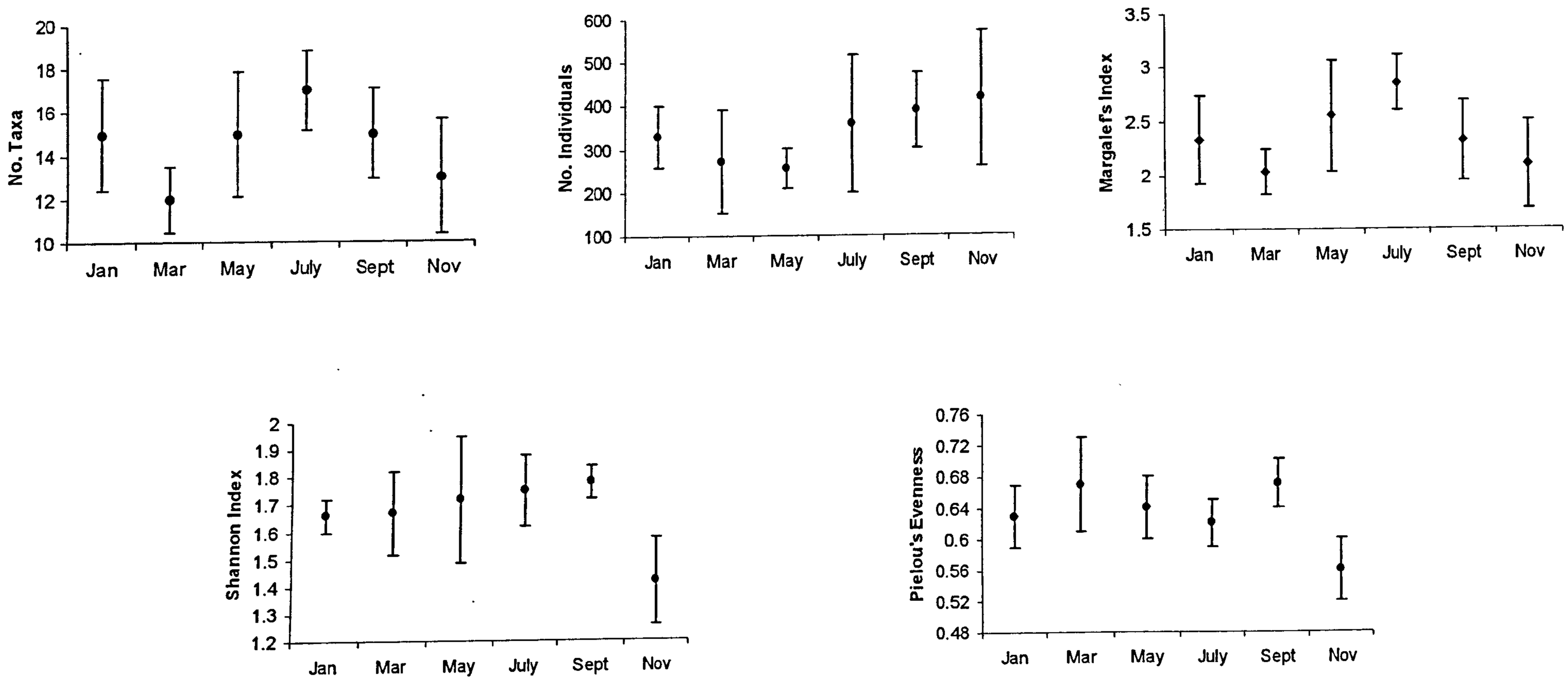
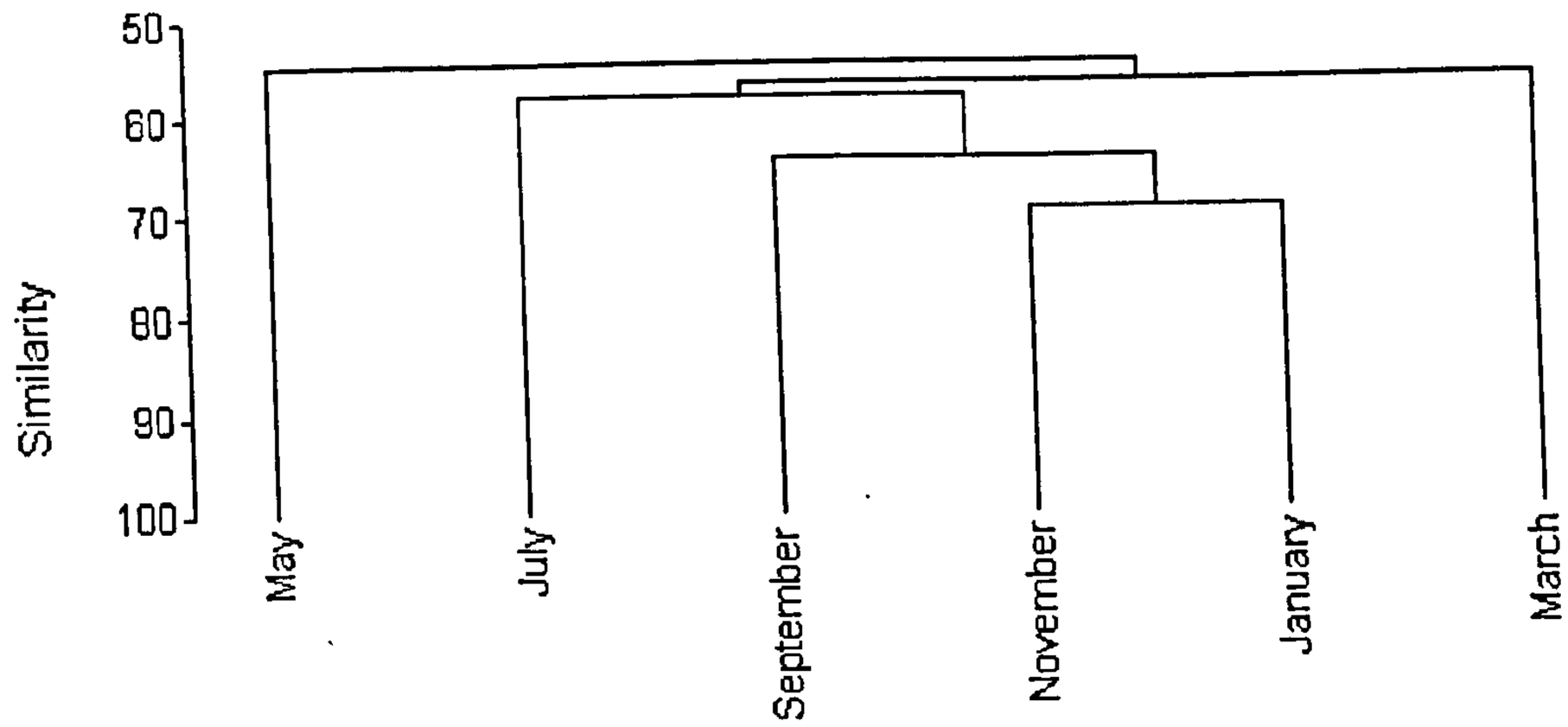


Figure 6 Univariate measures of mussel bed community structure at White Beach, Anglesey at bimonthly intervals between January and November 1998. Values are based on 25cm^2 replicates. 95% confidence intervals are marked, such that significant differences ($p<0.05$) are represented by non-overlapping intervals.

a) Square-root transformation



b) Presence/absence transformation

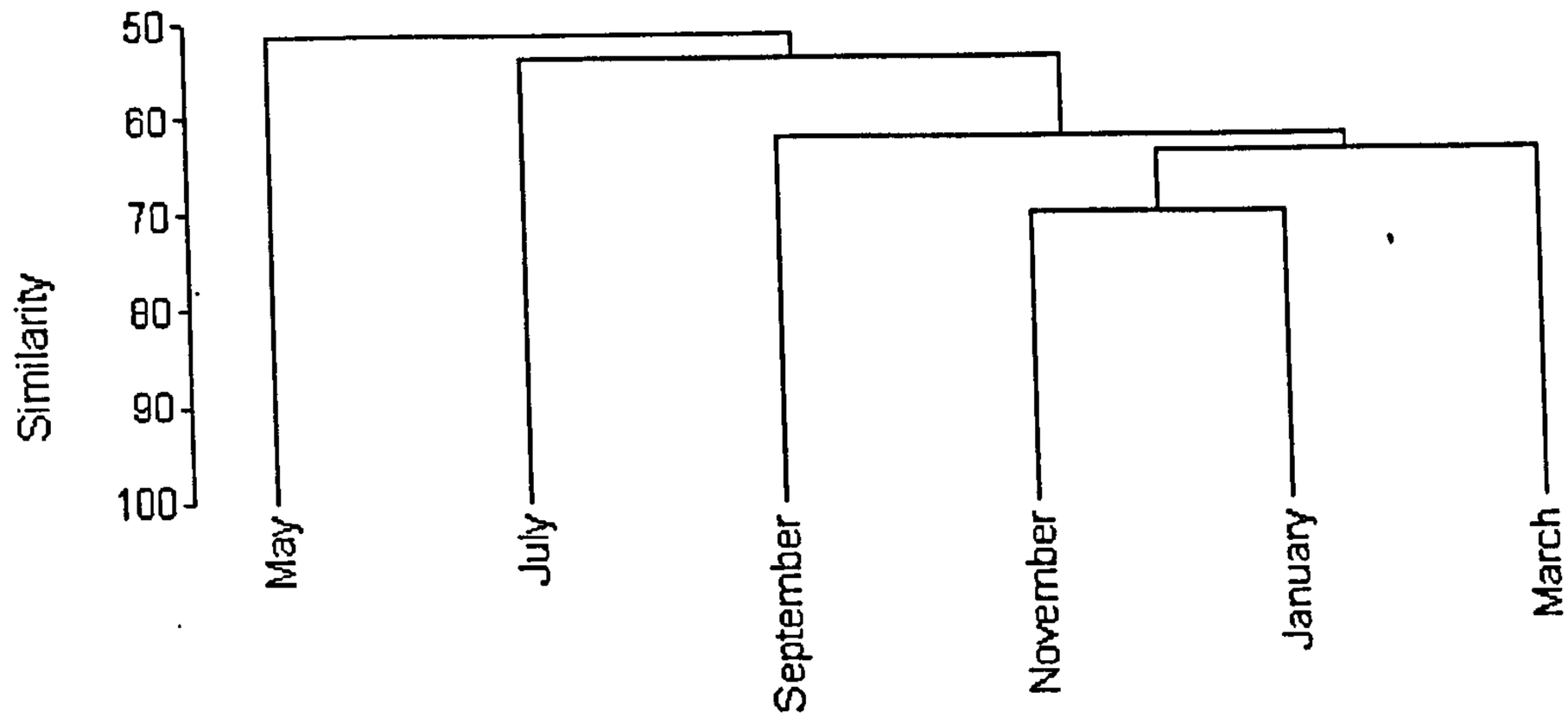


Figure 7 Dendrograms for group average clustering of Bray-Curtis similarities based on a) square-root transformed and b) presence/absence transformed biotic data from White Beach, Anglesey at bimonthly intervals between January and November 1998.

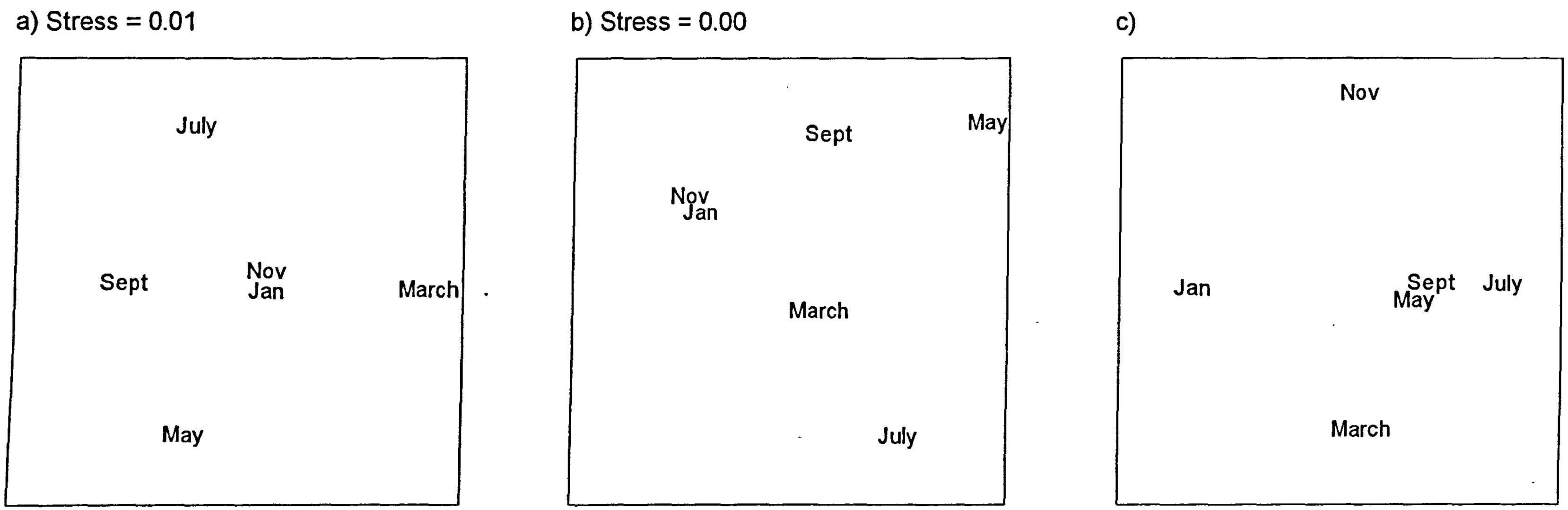


Figure 8 Ordination by MDS based on Bray-Curtis similarity, of averaged abundance of infauna from the mussel beds at White Beach, Anglesey at bimonthly intervals between January and November 1998, using a) square-root transformation, b) presence/absence transformation and c) ordination by PCA of environmental variables based on normalised Euclidean distance.

Table 5 Global R-values for ANOSIM pairwise comparisons between bimonthly samples of the mussel bed communities at White Beach based on a) square-root transformation of species abundance and b) presence/absence transformation of species abundance. Significant differences in community structure ($p<0.05$) are indicated by bold type (all differences are significant).

a)

	January	*March*	*May*	*July*	*September*
March	**0.456**				
May	**0.497**	**0.591**			
July	**0.756**	**0.862**	**0.576**		
September	**0.788**	**0.939**	**0.460**	**0.830**	
November	**0.469**	**0.800**	**0.296**	**0.645**	**0.327**

b)

	January	*March*	*May*	*July*	*September*
March	**0.278**				
May	**0.613**	**0.500**			
July	**0.711**	**0.724**	**0.805**		
September	**0.355**	**0.298**	**0.646**	**0.811**	
November	**0.183**	**0.195**	**0.624**	**0.756**	**0.267**

Similarity percentage analysis (SIMPER), performed with a square-root transformation (Table 6), highlighted the more abundant taxa principally responsible for structuring each of the bimonthly sample groupings illustrated in Figure 8a. Changes in the abundance of 4 dominant taxa throughout the year; small mussels, mite sp. 1, nematodes and *Clunio* sp. larvae were primarily responsible for similarities within replicates of each bimonthly sample. Other taxa including *Jaera albifrons*, *Orchestia gammarellus*, the ostracod *Heterocythereis albomaculata* and nemertean families were also important to varying extents throughout the year. Many of these taxa were the most numerically abundant at all times of the year. SIMPER analysis performed on presence/absence transformed data illustrated that many more taxa (up to 15) contributed to similarities within replicates for each of the bimonthly samples when emphasis was removed from overall abundance of taxa (Table 7). Some of the taxa contributing to these similarities were the same as those identified using a square-root transformation. However, many of the less numerically abundant taxa such as the ostracod *Leptocythere pellucida*, mite sp. 3 and various polychaete taxa also contributed to differences between the bimonthly samples.

BVSTEP analysis using a square-root transformation revealed a subset of 14 taxa explaining differences in community structure throughout the year; small mussels, platyhelminthes, nematodes, Cephalothricidae nemerteans, oligochaetes, *Clunio* sp. larvae, and small arthropods, e.g. *Heterocythereis albomaculata*, *Leptocythere pellucida*, *Elminius modestus*, *Idotea pelagica*, *Stenothoe monoculoides*, *Carcinus maenas*, mite sp. 1 and mite sp. 3. Changes in the abundance of this taxa subset throughout the year are illustrated in Figure 9. Second stage BVSTEP analysis performed on the data set with these 14 taxa excluded failed to identify any further taxa subsets, which might have explained the seasonal pattern observed in the community structure. BVSTEP analysis performed on the same data, with a presence/absence transformation, to search for patterns in the rarer members of the community identified a subset of 37 taxa from the 93 present. Second stage BVSTEP analysis failed to identify any further subsets of taxa explaining the seasonal pattern in biotic data. The seasonal pattern observed in Figure 8b cannot be attributed to a small subset of taxa, but was the result of changes in the presence or absence of many different taxa throughout the year. Many of the taxa identified by this analysis were also identified as important taxa when emphasis was placed on numerical abundance.

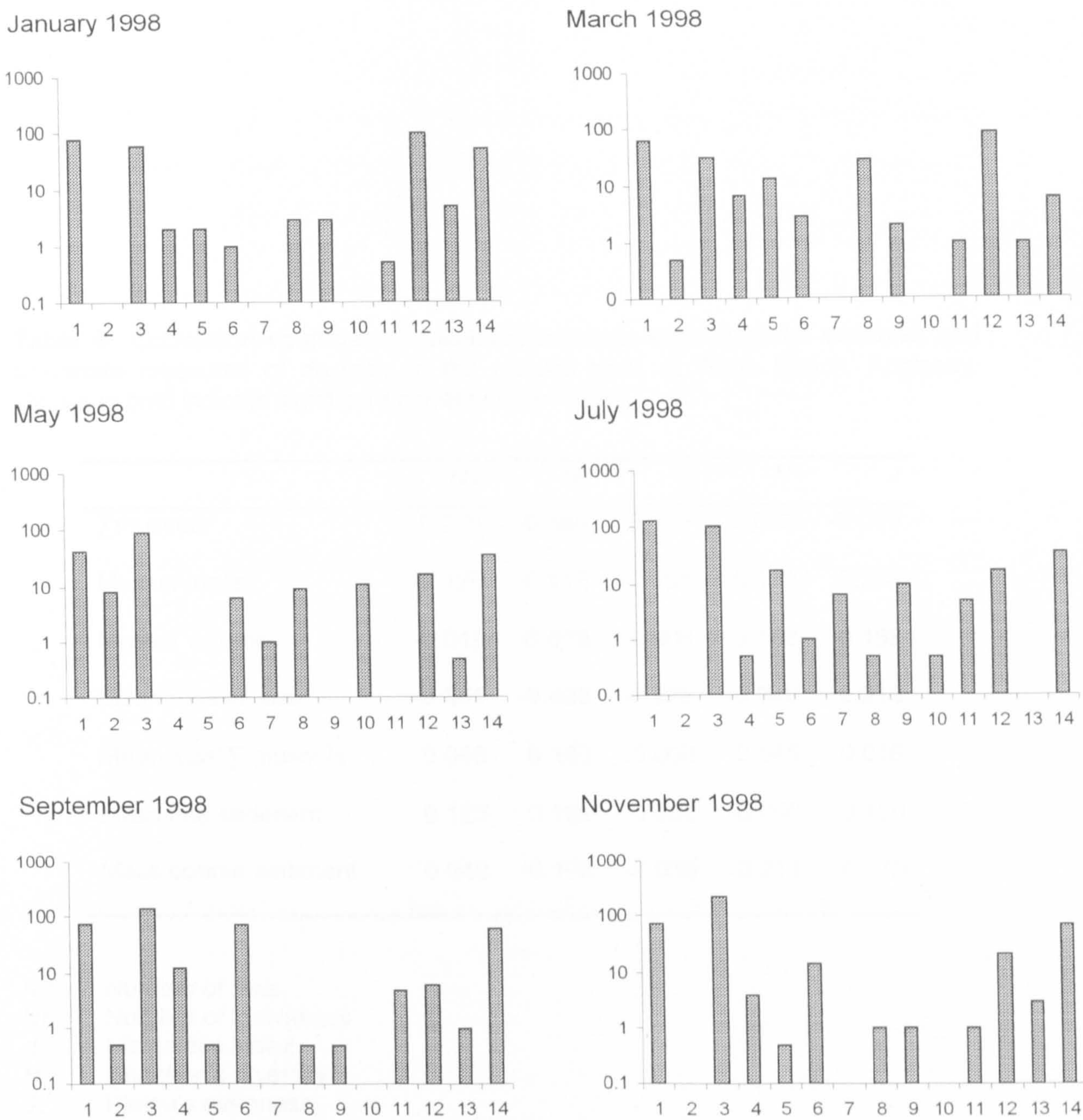
The total number of infaunal taxa and individuals within the mussel bed were negatively correlated with the mean size of mussels, while the total number of individuals was also positively correlated with mussel density (Table 8). None of the

Table 6 Results of similarity percentage analysis (SIMPER) performed on the bimonthly data from mussel beds at White Beach, Anglesey, using a square-root transformation. The taxa are listed in descending order of importance; figures in brackets represent cumulative % similarity with 90% chosen as the upper limit. Figures in bold in row 1 show average similarity within monthly replicates.

January **64**	March **63**	May **52**	July **60**	September **65**	November **59**
Mite sp. 1	Mite sp. 1	Nematoda indet.	Juvenile *Mytilus*	Nematoda indet.	Nematoda indet.
(27)	(28)	(25)	*edulis*	(26)	(36)
Juvenile *Mytilus*	Juvenile *Mytilus*	*Clunio* sp. larvae	(27)	*Heterocythereis*	Juvenile *Mytilus*
edulis	*edulis*	(43)	Nematoda indet.	*albomaculata*	*edulis*
(53)	(55)	Juvenile *Mytilus*	(48)	(47)	(59)
Nematoda indet.	Nematoda indet.	*edulis*	*Clunio* sp. larvae	Juvenile *Mytilus*	*Clunio* sp. larvae
(70)	(67)	(62)	(59)	*edulis*	(75)
Clunio sp. larvae	*Elminius modestus*	Mite sp. 1	*Idotea pelagica*	(67)	Mite sp. 1
(85)	(80)	(71)	(65)	*Clunio* sp. larvae	(85)
Jaera albifrons	*Clunio* sp. larvae	*Lasaea adansoni*	*Leptocythere*	(83)	*Heterocythereis*
(88)	(87)	(78)	*pellucida*	Cephalothricidae	*albomaculata*
Idotea pelagica	*Orchestia*	Platyhelminthe indet.	(71)	indet.	(90)
(90)	*gammarellus*	(84)	Mite sp. 1	(88)	
	(90)	*Heterocythereis*	(78)	Mite sp. 1	
		albomaculata	*Carcinus maenas*	(91)	
		(90)	(82)		
			Modiolus modiolus		
			(86)		
			Chaetogammarus		
			marinus		
			(88)		
			Oligochaeta indet.		
			(91)		

Table 7 Results of similarity percentage analysis (SIMPER) performed on the bimonthly data from mussel beds at White Beach, Anglesey, using a presence/absence transformation. The taxa are listed in descending order of importance; figures in brackets represent cumulative % similarity with 90% chosen as the upper limit. Figures in bold in row 1 show average similarity within monthly replicates.

January **52**	March **60**	May **54**	July **60**	September **54**	November **53**
Clunio sp. larvae	*Clunio* sp. larvae	*Lasaea adansoni*	*Clunio* sp. larvae	*Clunio* sp. larvae	*Clunio* sp. larvae
(13)	(14)	(13)	(9)	(13)	(15)
Mite sp. 1	Mite sp. 1	*Clunio* sp. larvae	Mite sp. 1	*Heterocythereis*	Mite sp. 1
(30)	(28)	(26)	(18)	*albomaculata*	(30)
Nematoda indet.	*Elminius modestus*	Nematoda indet.	*Carcinus maenas*	(26)	Nematoda indet.
(40)	(42)	(39)	(28)	Nematoda indet.	(45)
Juvenile *Mytilus edulis*	Nematoda indet.	Juvenile *Mytilus edulis*	*Idotea pelagica*	(40)	Juvenile *Mytilus edulis*
(54)	(56)	(52)	(37)	Juvenile *Mytilus edulis*	(60)
Jaera albifrons	Juvenile *Mytilus edulis*	Mite sp. 1	*Leptocythere pellucida*	(53)	Mite sp. 3
(64)	(70)	(62)	(46)	*Carcinus maenas*	(71)
Heterocythereis	*Heterocythereis*	Platyhelminthe indet.	Nematoda indet.	(63)	*Heterocythereis*
albomaculata	*albomaculata*	(71)	(55)	Cephalothricidae indet.	*albomaculata*
(69)	(77)	*Heterocythereis*	Juvenile *Mytilus edulis*	(72)	(76)
Idotea pelagica	Oligochaeta indet.	*albomaculata*	(64)	Mite sp. 1	*Ophelia bicornis*
(74)	(82)	(79)	*Chaetogammarus*	(79)	(79)
Cephalothricidae indet.	*Carcinus maenas*	*Leptocythere pellucida*	*marinus*	*Tanais dulongii*	Tubulanidae indet.
(76)	(86)	(84)	(69)	(83)	(82)
Fabricia stellaris	Tubulanidae indet.	*Elminius modestus*	Oligochaeta indet.	*Idotea baltica*	*Carcinus maenas*
(79)	(89)	(89)	(74)	(87)	(85)
Elminius modestus	*Orchestia gammarellus*	Oligochaeta indet.	*Jaera albifrons*	Eunicid sp. 1	*Idotea pelagica*
(82)	(92)	(91)	(79)	(90)	(88)
Lasaea adansoni			*Modiolus modiolus*		Cephalothricidae indet.
(84)			(84)		(90)
Mite sp. 3			Dipteran larvae indet		
(87)			(87)		
Eulalia viridis			Lineidae indet.		
(89)			(90)		
Cirriformia tentaculata					
(90)					



Key

1	Juvenile *Mytilus edulis*	8	*Elminius modestus*
2	Platyhelminthes indet.	9	*Idotea pelagica*
3	Nematoda indet.	10	*Stenothoe monoculoides*
4	Cephalothricidae indet.	11	*Carcinus maenas*
5	Oligochaeta indet.	12	Mite sp. 1
6	*Heterocythere albomaculata*	13	Mite sp. 3
7	*Leptocythere pellucida*	14	*Clunio* sp. larvae

Figure 9 Bimonthly log mean abundance per 25cm^2 quadrat, of taxa identified by BVSTEP analysis as those contributing to seasonal patterns of diversity in the mussel beds at White Beach, Anglesey.

Table 8 Correlation coefficients calculated between environmental variables and univariate measures of diversity in the mussel beds at White Beach, Anglesey. Values in bold indicate significant correlation ($p<0.05$).

	NT	*NI*	*d*	*H'*	*J*
∑mussels	0.276	**0.384**	0.168	0.092	-0.099
Mussel mass	-0.127	-0.119	-0.101	0.139	0.245
Mussel volume	-0.015	-0.078	0.006	0.168	0.188
Mean mussel size	**-0.351**	**-0.425**	-0.223	-0.040	0.213
Mean size*∑ mussels	0.046	0.180	-0.009	0.045	0.016
Mass fine sediment	0.123	0.192	0.066	-0.050	-0.150
Mass coarse sediment	0.048	0.178	-0.036	-0.211	-0.270

NT Number of taxa
NI Number of individuals
d Margalef's index
H' Shannon's diversity
J Pielou's evenness

other environmental variables measured had a significant effect on any of the univariate measures of community diversity. RELATE analysis on the similarity matrix produced using normalised Euclidean distance indicated that the environmental factors measured in the mussel bed showed a cyclic seasonal progression ($R = 0.209$, $p>0.05$). RELATE analysis showed that the ordination pattern for the environmental parameters was the same as the ordination described for both square-root ($R = -0.493$, $p>0.05$) and presence/absence ($R = -0.046$, $p>0.05$) transformed biotic data (Figure 8). Ordination by PCA of the environmental data from seasonal samples, as illustrated in Figure 8c, showed that 82% of this seasonal variability in the data could be accounted for by the first three Principal Components, with PC1 accounting for 42% of the total. PC1 was seen to be a linear combination of the environmental parameters, with increasing values of all parameters, except mean mussel size. When PC1 was plotted against each of the univariate measures of community diversity the correlation coefficients revealed no significant relationships (Figure 10).

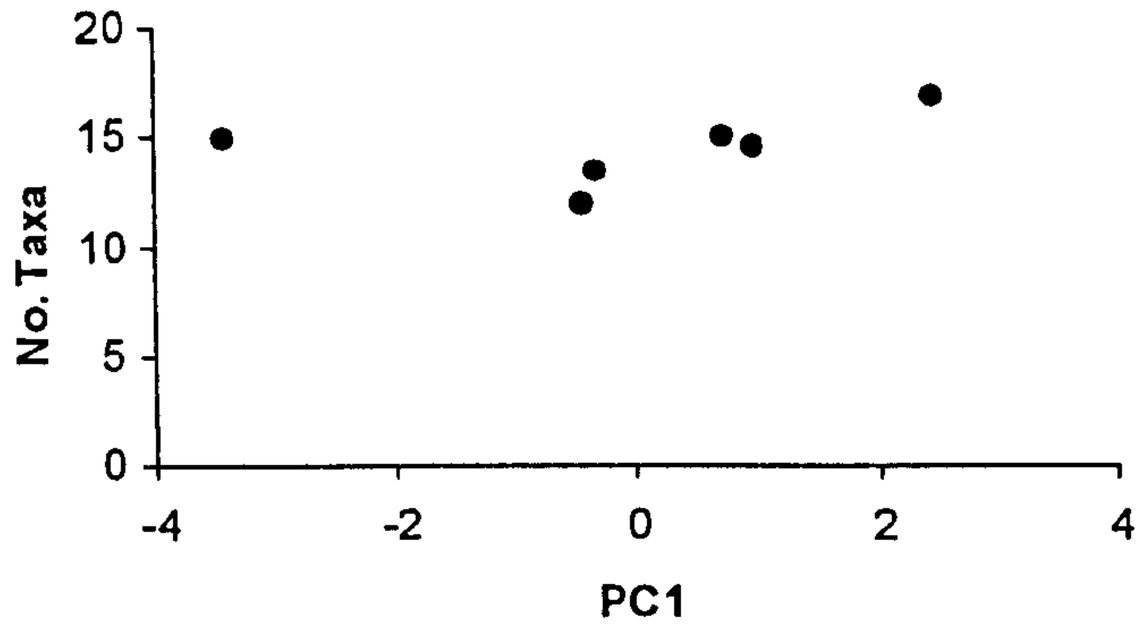
Determination of correlation coefficients for all environmental variables measured bimonthly in the mussel bed during the twelve-month period failed to reveal any high levels of correlation between any of the variables ($r>0.95$). As such, all the measured environmental variables were entered into BIOENV analysis, to identify the most appropriate combinations of variables explaining the square-root and presence/absence transformed biotic data. The BIOENV procedure revealed that the highest correlation of square-root transformed data was only 0.287, with the mass of fine and coarse sediments. A similarly low correlation of 0.117 was obtained between the presence/absence transformed infauna data and the mass of fine and coarse sediments.

Thus, it appears that, like the mussel beds at Point Lynas, the strongest influencing force on the structure of the infaunal communities at White Beach was season. Although there was no significant seasonality in the data, there was a clear difference in the structure of the communities throughout the year. Some of the environmental variables measured correlated with certain univariate measures of community diversity, although any influencing effect they might have had on the multivariate data was probably being masked by the strong seasonal effect underlying the data.

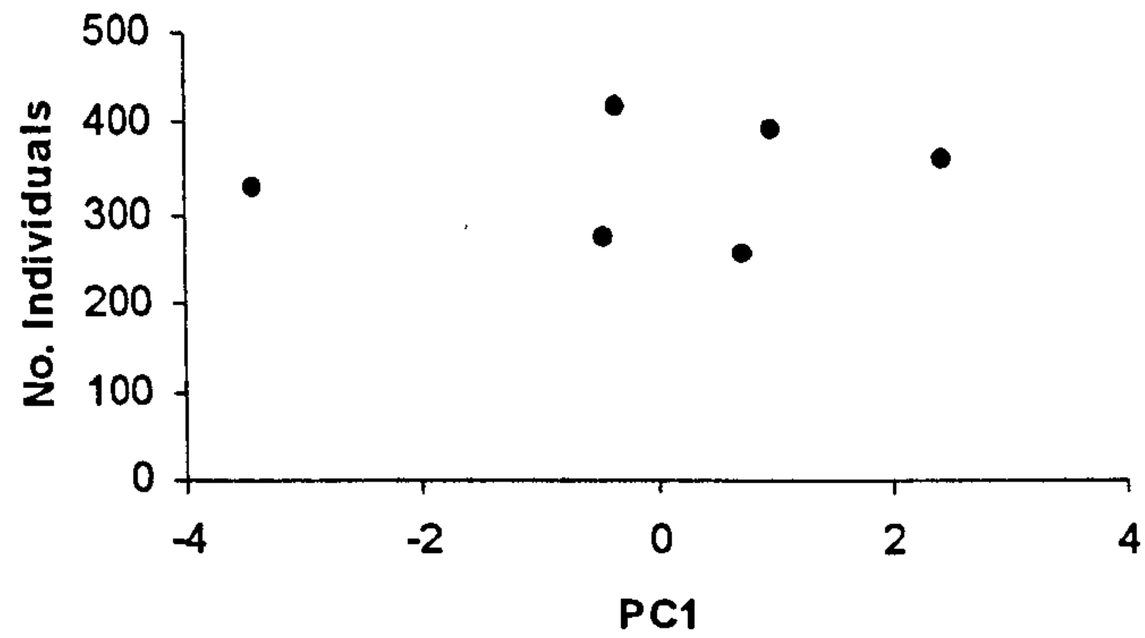
Criccieth

Over the twelve-month sampling period a total of 9576 infaunal organisms from 85 different taxa were collected and identified from mussel beds at Criccieth.

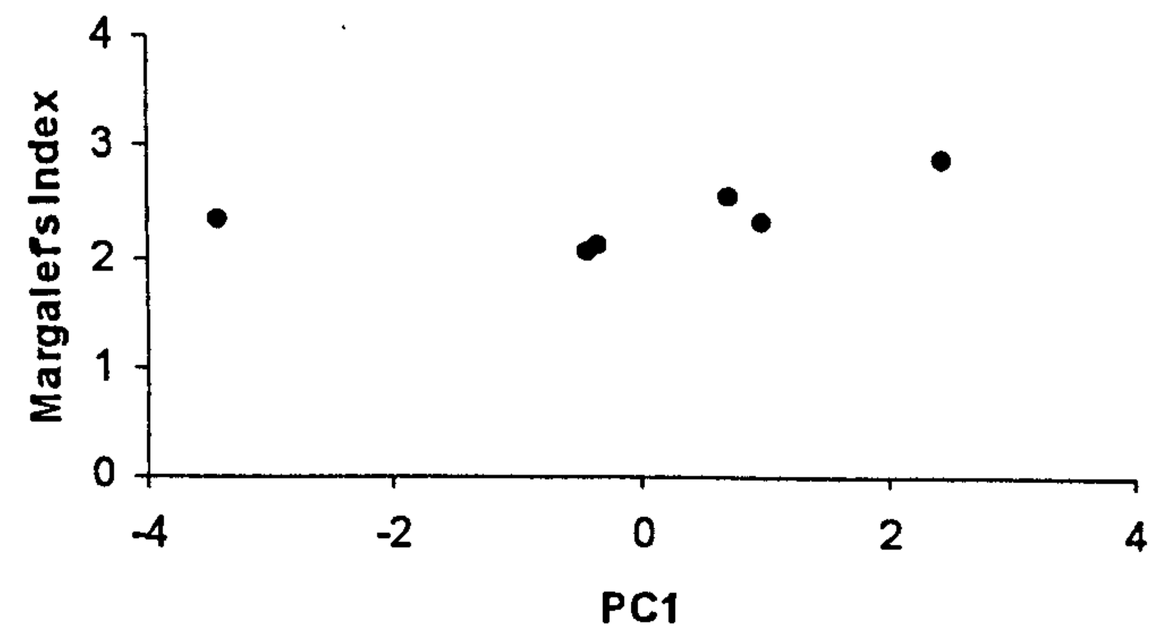
Figure 10 Principal Component 1 (PC1) plotted against each of the univariate measures of community structure at White Beach, Anglesey. Correlation coefficients (r) and significance levels between the variables are shown.



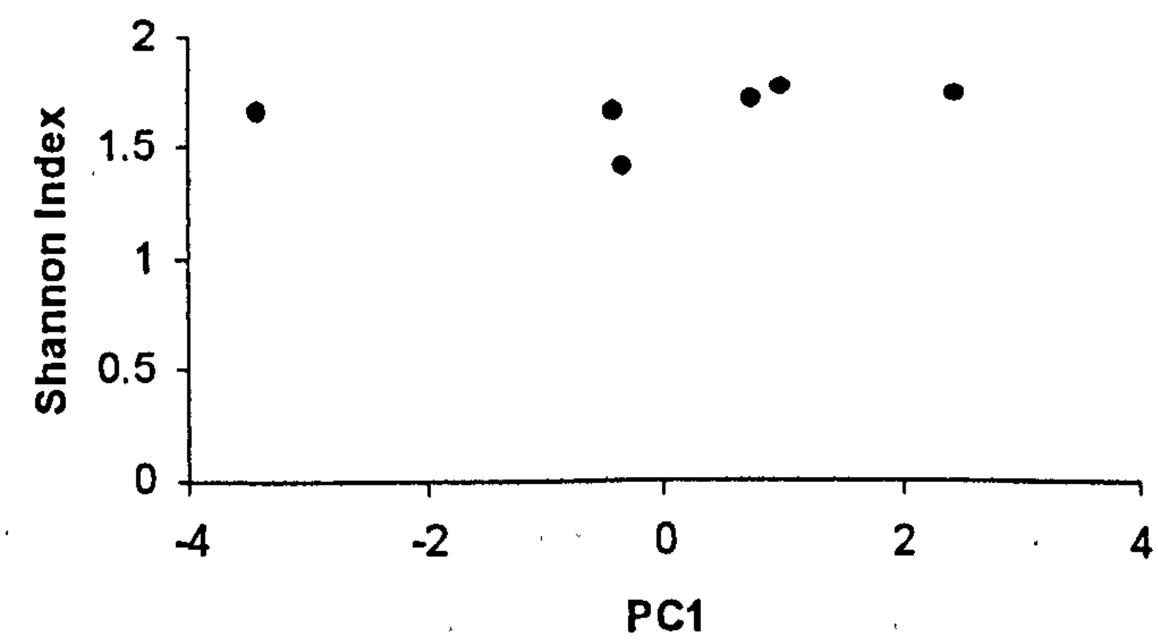
r = 0.378
p > 0.05



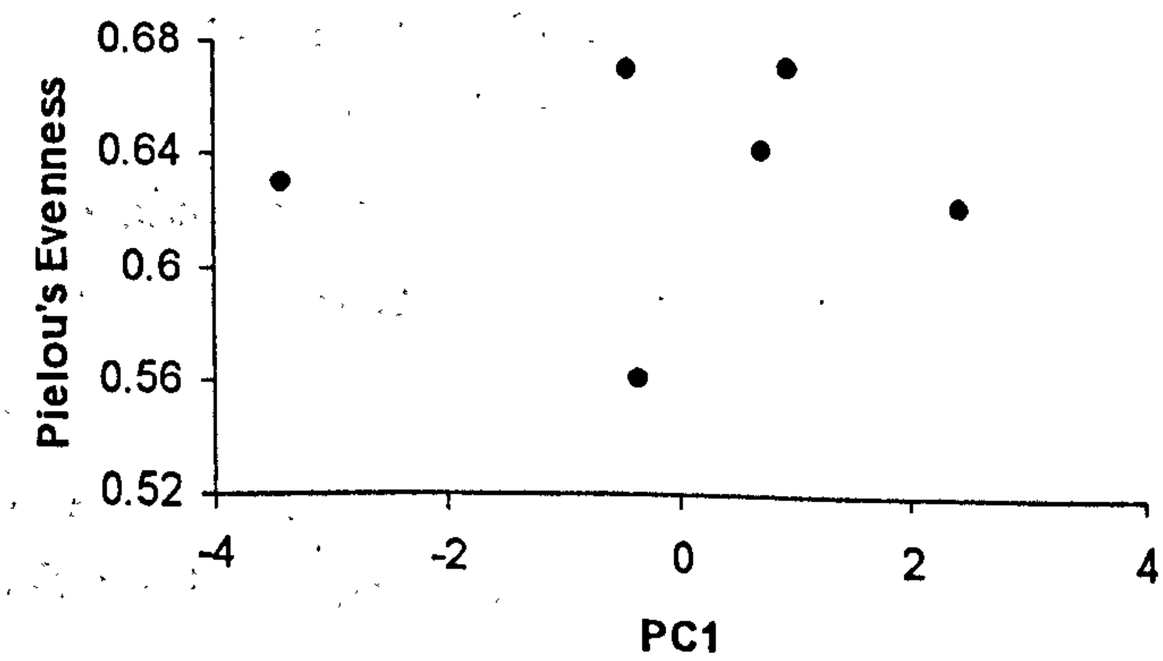
r = 0.110
p > 0.05



r = 0.548
p > 0.05



r = 0.358
p > 0.05



r = 0.070
p > 0.05

These taxa included representatives from 10 phyla, 16 classes, 30 orders and 51 different families. Values of Shannon's diversity index (H') showed no significant variation during the twelve-month study period. However, all other univariate measures of diversity; number of taxa (NT), number of individuals (NI), Margalef's richness (d) and Pielou's evenness (J) did show significant variation over the twelve-month period. Values of these indices showed an oscillation throughout the year, with peaks in March and November and troughs in May/July (Figure 11).

Cluster analysis of square-root transformed infaunal data revealed three major groups, representing spring (January and March), summer (May and July) and autumn/winter (September and November) samples (Figure 12a). At a slightly lower level of similarity (55%), the autumn/winter and spring groups merged such that two main groups remained. A similar pattern was revealed when cluster analysis was performed on the same data, with a presence/absence transformation, in that the same three main groups of samples separated out (Figure 12b). However, at a lower similarity level (55%), the spring and summer groups merged, leaving a distinct autumn/winter group.

MDS ordination of square-root transformed infaunal abundance illustrated a change in community structure over the twelve-month period, in terms of the more dominant members of the community (Figure 13a) and the clear separation of three main groups, as identified by cluster analysis. A one-way ANOSIM test performed on the data confirmed that during the twelve-months, there were significant differences in community structure ($R=0.372$, $p<0.05$). Pairwise comparisons revealed that the structure of the mussel community was significantly different between all months, with the exception of January/March, January/July and May/July (Table 9a). When tested using the RELATE procedure this seasonal progression in community structure was seen to be cyclic ($R=0.18$, $p>0.05$). MDS ordination and ANOSIM performed with a presence/absence transformation indicated that the seasonal differences in community structure were also apparent at Criccieth, when emphasis was removed from abundant taxa (ANOSIM, $R=0.437, p<0.05$) (Figure 13b). Pairwise comparisons revealed that differences between monthly samples were more pronounced than when abundance was taken into account, with all but May/July showing significant differences (Table 9b). RELATE analysis showed that there was a significant pattern of cyclic seasonal progression in community structure throughout the year.

Similarity percentage analysis (SIMPER) performed with a square-root transformation (Table 10) highlighted the dominant taxa principally responsible for

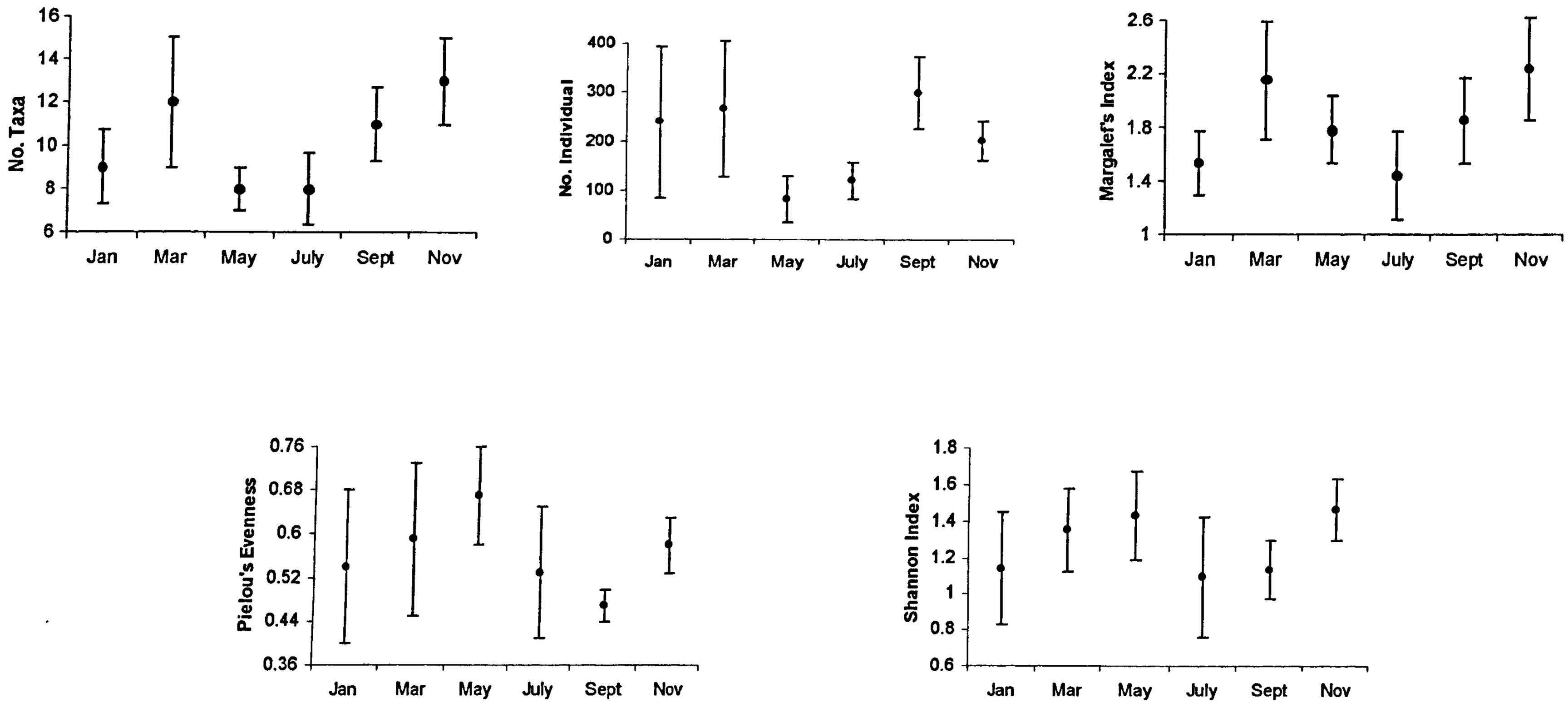
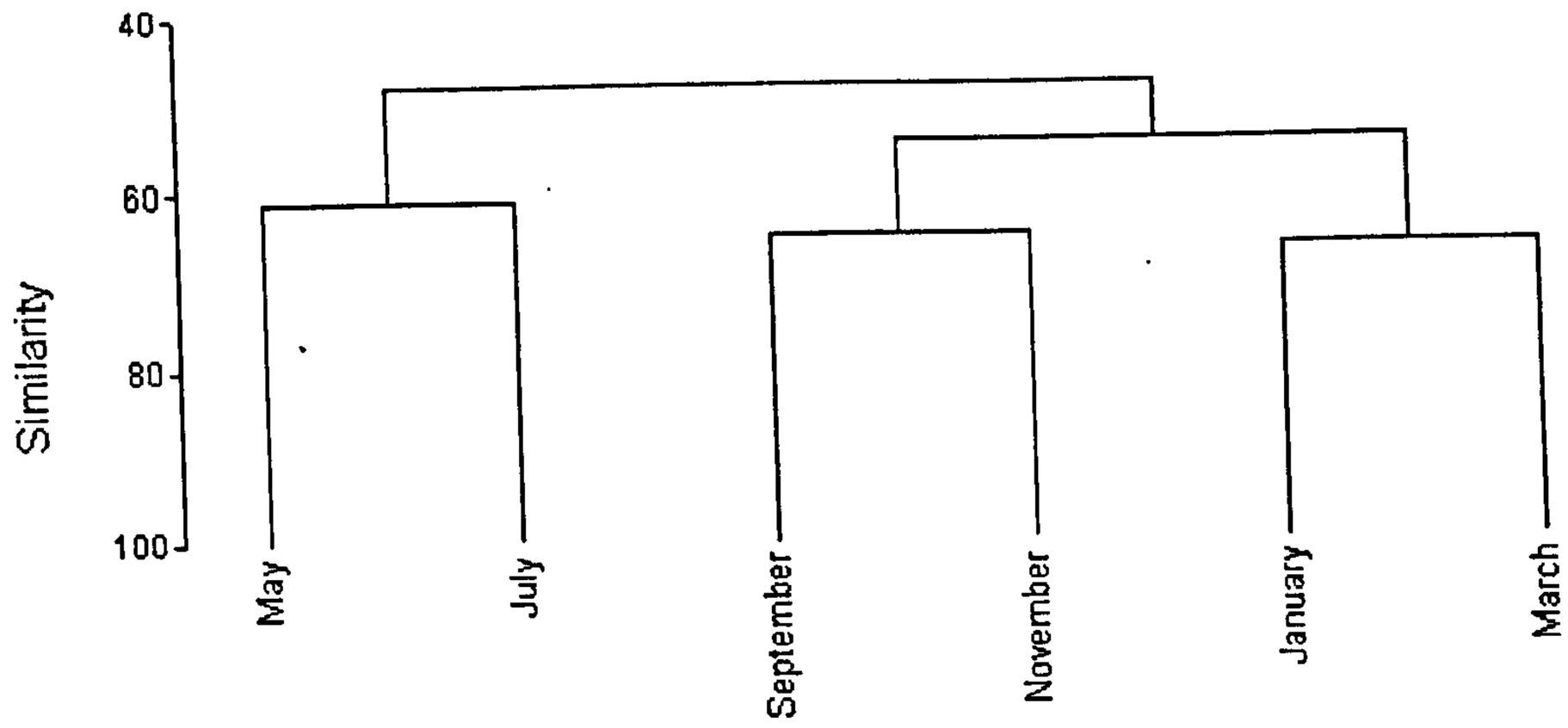


Figure 11 Univariate measures of mussel bed community diversity at Criccieth, Gwynedd measured at bimonthly intervals between January and November 1998. Values are based on 25cm^2 replicates. 95% confidence intervals are marked, such that significant differences are represented by non-overlapping intervals.

a) Square-root transformation



b) Presence/absence transformation

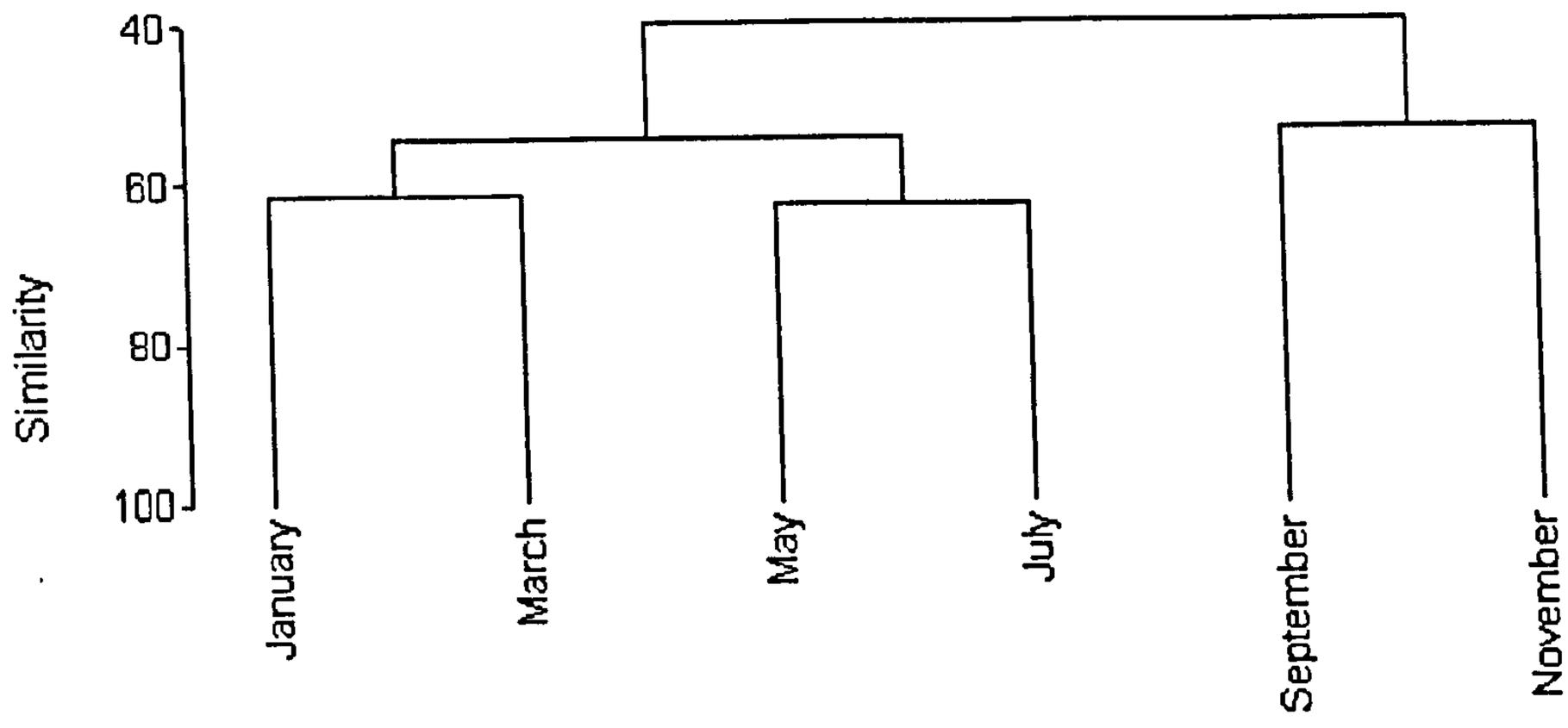


Figure 12 Dendrograms for group average clustering of Bray-Curtis similarities based on a) square-root transformed and b) presence/absence transformed biotic data from mussel beds at Criccieth, Gwynedd at bimonthly intervals between January and November 1998.

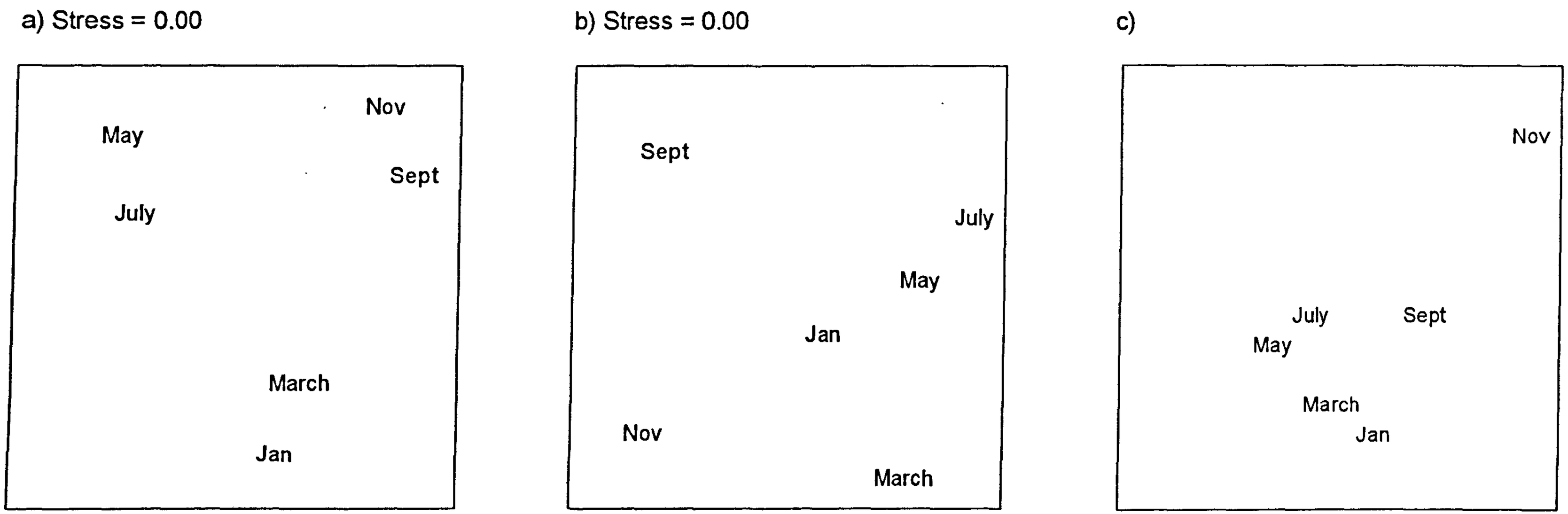


Figure 13 Ordination by MDS based on Bray-Curtis similarity, of averaged abundance of infauna from the mussel beds at Criccieth, Gwynedd at bimonthly intervals between January and November 1998, using a) square-root transformation, b) presence/ absence transformation and c) ordination by PCA of environmental variables based on normalised Euclidean distance.

Table 9 Global R-values for ANOSIM pairwise comparisons between bimonthly samples of the mussel bed communities at Criccieth, Gwynedd, based on a) square-root transformation of species abundance and b) presence/absence transformation of species abundance. Significant differences in community structure ($p<0.05$) are indicated by bold type.

a)

	January	*March*	*May*	*July*	*September*
March	0.104				
May	**0.256**	**0.425**			
July	-0.004	**0.245**	0.134		
September	**0.362**	**0.46**	**0.85**	**0.513**	
November	**0.406**	**0.468**	**0.796**	**0.513**	**0.295**

b)

	January	*March*	*May*	*July*	*September*
March	**0.243**				
May	**0.404**	**0.285**			
July	**0.134**	**0.269**	0.099		
September	**0.574**	**0.776**	**0.842**	**0.542**	
November	**0.491**	**0.587**	**0.619**	**0.462**	**0.33**

Table 10 Results of similarity percentage analysis (SIMPER) performed on the bimonthly data from mussel beds at Criccieth, Gwynedd, using a square-root transformation. The taxa are listed in descending order of importance; figures in brackets represent cumulative % similarity with 90% chosen as the upper limit. Figures in bold in row 1 show average similarity within monthly replicates.

January **35**	March **50**	May **50**	July **47**	September **58**	November **54**
Juvenile *Mytilus edulis* (53)	Juvenile *Mytilus edulis* (36)	Juvenile *Mytilus edulis* (49)	Juvenile *Mytilus edulis* (64)	Juvenile *Mytilus edulis* (47)	Juvenile *Mytilus edulis* (38)
Nematoda indet. (71)	Nematoda indet. (61)	Nematoda indet. (64)	Nematoda indet. (77)	Nematoda indet. (76)	Nematoda indet. (74)
Elminius modestus (80)	*Clunio* sp. larvae (68)	*Clunio* sp. larvae (75)	*Elminius modestus* (86)	*Scololepis squamata* (81)	*Harmothoe* sp. (83)
Clunio sp. larvae (86)	*Elminius modestus* (75)	*Brachystomia scalaris* (85)	*Clunio* sp. larvae (95)	Mite sp. 1 (85)	*Scololepis squamata* (87)
Jaera albifrons (92)	*Brachystomia scalaris* (80)	*Lepidontus clava* (91)		*Drilonereis filum* (89)	*Elminius modestus* (91)
	Platyhelminthes indet. (83)			*Elminius modestus* (93)	
	Lineidae indet. (86)				
	Lepidontus squamata (88)				
	Idotea pelagica (90)				

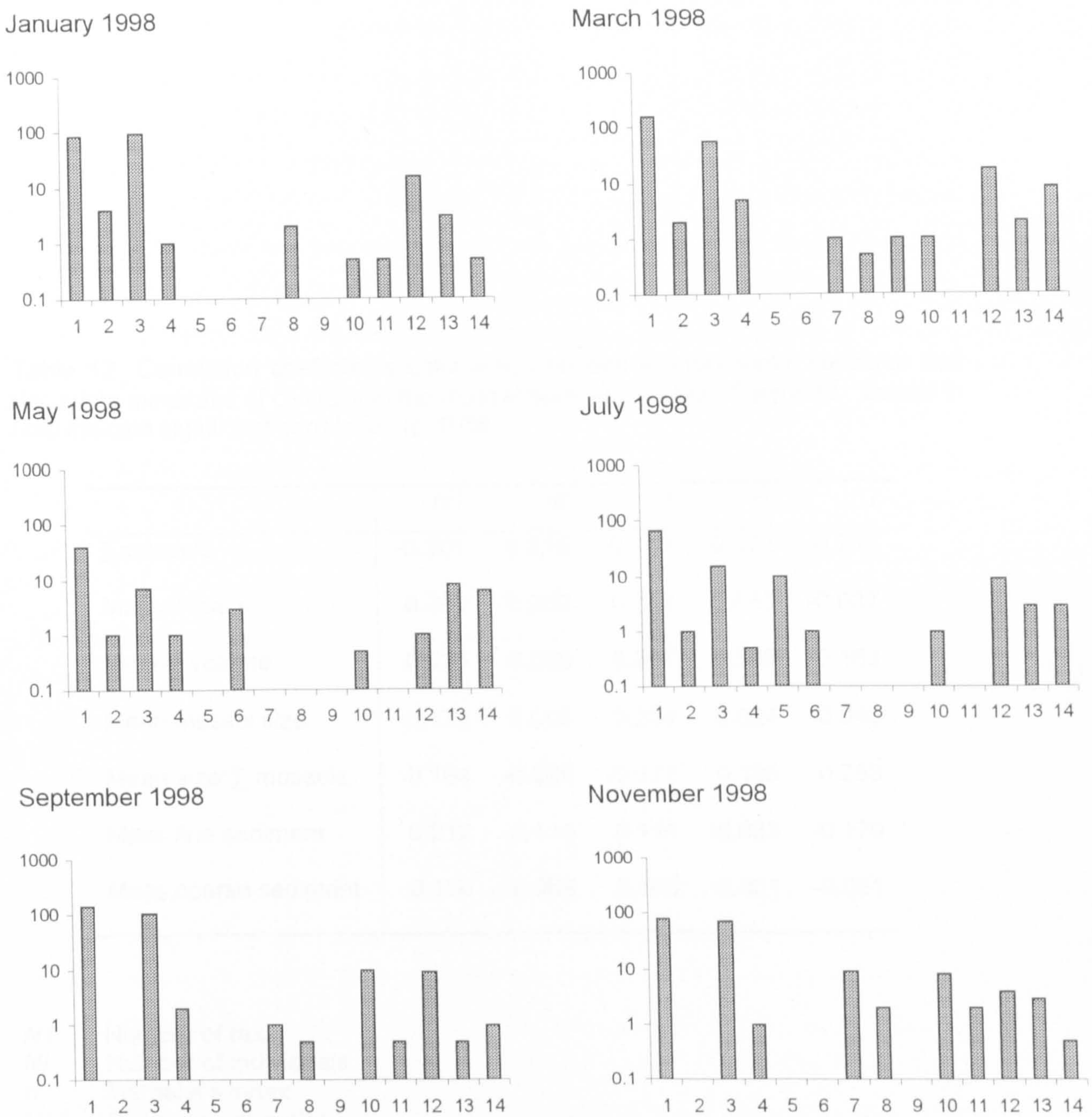
structuring each of the bimonthly sample groupings illustrated in Figure 13a. Similarities within replicates for each bimonthly sample were primarily caused by changes in abundance of 4 dominant taxa throughout the year; small mussels, nematodes, the barnacle *Elminius modestus* and the chironomid *Clunio* sp. larvae, with further contributions from less abundant taxa. When the same analysis was repeated with a presence/absence transformation, thus removing the emphasis from abundance similar taxa were seen to contribute to group similarities (Table11).

BVSTEP analyses was performed on the data to identify which members of the community were predominantly contributing to the cyclic progression of community structure over the year. When emphasis was placed on taxa abundance with a square-root transformation, a subset of 14 taxa; small mussels, platyhelminthes, nematodes, lineid nemerteans, emplectonematid nemerteans, the polychaetes, *Lepidontus clava*, *Harmothoe* sp., *Capitella capitata*, *Cirratulus cirratus*, *Scolelepis squamata*, the arthropods *Heterocythereis albomaculata*, *Elminius modestus*, *Clunio* sp. larvae and the gastropod, *Brachystomia scalaris.* Changes in the abundance of this taxa subset throughout the year are illustrated in Figure 14. Second stage BVSTEP analysis performed on the same data set, with the exclusion of these 14 taxa, failed to identify any further taxa subsets, which adequately explained the seasonal variation in community structure. Thus, many members of the mussel community at Criccieth did not respond to any seasonal gradients. BVSTEP analysis performed with presence/absence transformation identified a subset of 32 taxa from the 85 present, explaining the seasonal variation observed (Figure 13b). Thus the community patterns observed are the result in changes in the presence or absence of many taxa in the mussel bed.

The total number of taxa present in the mussel bed was positively correlated with both the mass and volume of mussels. (Table 12). Margalef's (d) and Shannon's (H') indices were also positively correlated with the total volume of mussels. The total number of individual organisms present is negatively correlated with the mean size of mussels*mussel density. RELATE analysis of the similarity matrix produced using normalised Euclidean distance indicated that the environmental factors measured in the mussel bed did not show any seasonality ($R=0.498$, $p<0.05$). RELATE analysis showed that this ordination pattern for environmental parameters was significantly different to the ordination described for both square-root ($R = 0.568$, $p<0.05$) and presence/absence ($R = 0.756$, $p<0.05$) transformed biotic data (Figure 13). Ordination by PCA of the environmental data, as illustrated in Figure 13c showed that 83% of the seasonal variability in the data was accounted for by the first three Principal Components, with PC1 accounting for 38%

Table 11 Results of similarity percentage analysis (SIMPER) performed on the bimonthly data from mussel beds at Criccieth, Gwynedd, using a presence/absence transformation. The taxa are listed in descending order of importance; figures in brackets represent cumulative % similarity with 90% chosen as the upper limit. Figures in bold in row 1 show average similarity within monthly replicates.

January **42**	March **55**	May **51**	July **46**	September **51**	November **40**
Juvenile Mytilus edulis	*Clunio* sp. larvae	Juvenile Mytilus edulis	Juvenile Mytilus edulis	Nematoda indet.	Nematoda indet.
(28)	(16)	(24)	(29)	(18)	(20)
Elminius modestus	Juvenile Mytilus edulis	*Clunio* sp. larvae	*Elminius modestus*	Juvenile Mytilus edulis	Juvenile Mytilus edulis
(43)	(33)	(41)	(52)	(35)	(40)
Nematoda indet.	Nematoda indet.	Nematoda indet.	Nematoda indet.	*Drilonereis filum*	*Harmothoe* sp.
(57)	(44)	(58)	(72)	(49)	(56)
Clunio sp. larvae	*Elminius modestus*	*Lepidontus clava*	*Clunio* sp. larvae	Mite sp. 1	*Elminius modestus*
(68)	(53)	(71)	(88)	(59)	(66)
Jaera albifrons	Platyhelminthes indet	*Brachystomia scalaris*	*Lepidontus clava*	*Elminius modestus*	*Scolelepis squamata*
(78)	(61)	(83)	(90)	(69)	(73)
Lasaea adansoni	*Brachystomia scalaris*	Lineidae indet.		*Scolelepis squamata*	*Brachystomia scalaris*
(84)	(68)	(88)		(77)	(78)
Capitella capitata	*Lepidontus squamata*	Platyhelminthes indet.		*Alentia gelatinosa*	*Stomphia coccinea*
(89)	(72)	(93)		(83)	(82)
Mite sp. 1	Tubulanidae indet.			*Rissoa parva*	*Heterocythereis albomaculata*
(94)	(75)			(87)	(85)
	Idotea pelagica			Tubulanidae indet..	Mite sp. 1
	(78)			(91)	(89)
	Cirratulus cirratus				*Rissoa parva*
	(80)				(91)
	Mite sp. 1				
	(83)				
	Eulalia viridis				
	(86)				
	Foraminiferans				
	88)				
	Lineidae sp.				
	(91)				



Key

1	Juvenile *Mytilus edulis*	8	*Capitella capitata*
2	Platyhelminthes indet.	9	*Cirratulus cirratus*
3	Nematoda indet.	10	*Scolelepis squamata*
4	Lineidae nemerteans	11	*Heterocythere albomaculata*
5	Emplectonematidae nemerteans	12	*Elminius modestus*
6	*Lepidontus clava*	13	*Clunio* sp. larvae
7	*Harmothoe* sp.	14	*Brachystomia scalaris*

Figure 14 Bimonthly log mean abundance per 25cm^2 quadrat, of taxa identified by BVSTEP analysis as those contributing to the seasonal patterns of diversity in the mussel beds at Criccieth, Gwynedd.

Table 12 Correlation coefficients calculated between environmental variables and univariate measures of diversity in the mussel beds at Criccieth, Gwynedd. Values in bold indicate significant correlation ($p<0.05$).

	NT	*NI*	*d*	*H'*	*J*
∑mussels	-0.201	-0.216	-0.144	0.172	0.258
Mussel mass	**0.302**	0.206	0.258	0.083	-0.037
Mussel volume	**0.323**	0.000	**0.301**	**0.308**	0.163
Mean mussel size	0.179	0.007	0.204	0.024	-0.046
Mean size*∑ mussels	-0.184	**-0.286**	-0.111	0.185	0.253
Mass fine sediment	0.212	0.119	0.111	-0.033	-0.170
Mass coarse sediment	0.150	0.058	0.109	0.021	-0.081

NT Number of taxa
NI Number of individuals
d Margalef's index
H' Shannon's diversity
J Pielou's evenness

of the total. PC1 was seen to be a linear combination of the environmental factors, with increasing values of all parameters. When PC1 was plotted against each of the univariate measures of community diversity the correlation coefficients revealed no significant relationships (Figure 15).

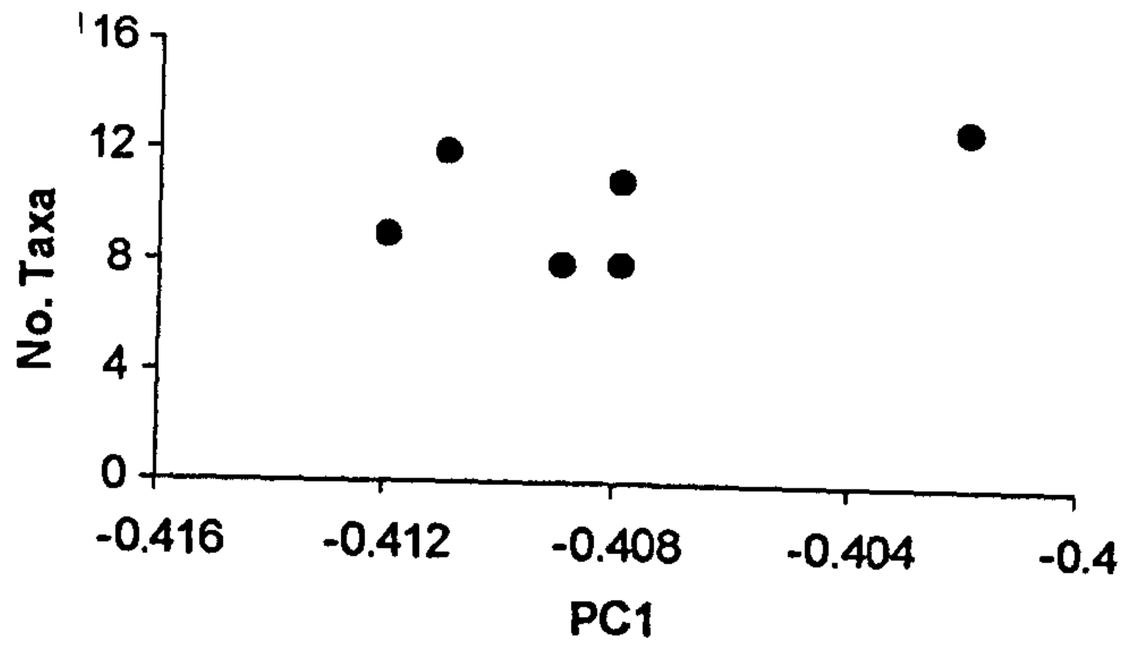
Determination of correlation coefficients for all environmental variables measured bimonthly in the mussel bed during the twelve-month period failed to reveal any high levels of correlation between any of the variables ($r>0.95$). As such, all the measured environmental variables were entered into BIOENV analysis, to identify the most appropriate combinations of variables explaining the square-root and presence/absence transformed biotic data. The BIOENV procedure revealed that the highest correlation of square-root transformed data was 0.232, with a combination of mussel density, mass and mean size and the mass of fine sediments. A correlation of 0.334 was obtained between the presence/absence transformed biotic data and the mean size of mussels and the mass of fine sediments.

Thus, the physical and environmental parameters measured in the mussel bed appear to have some effect on the structure of the mussel bed community. Although some of the environmental variables measured do significantly affect the structure and diversity of the mussel bed community at Criccieth, as indicated by comparisons with univariate measures of diversity, they are not wholly responsible for producing the seasonal progression in multivariate community structure observed.

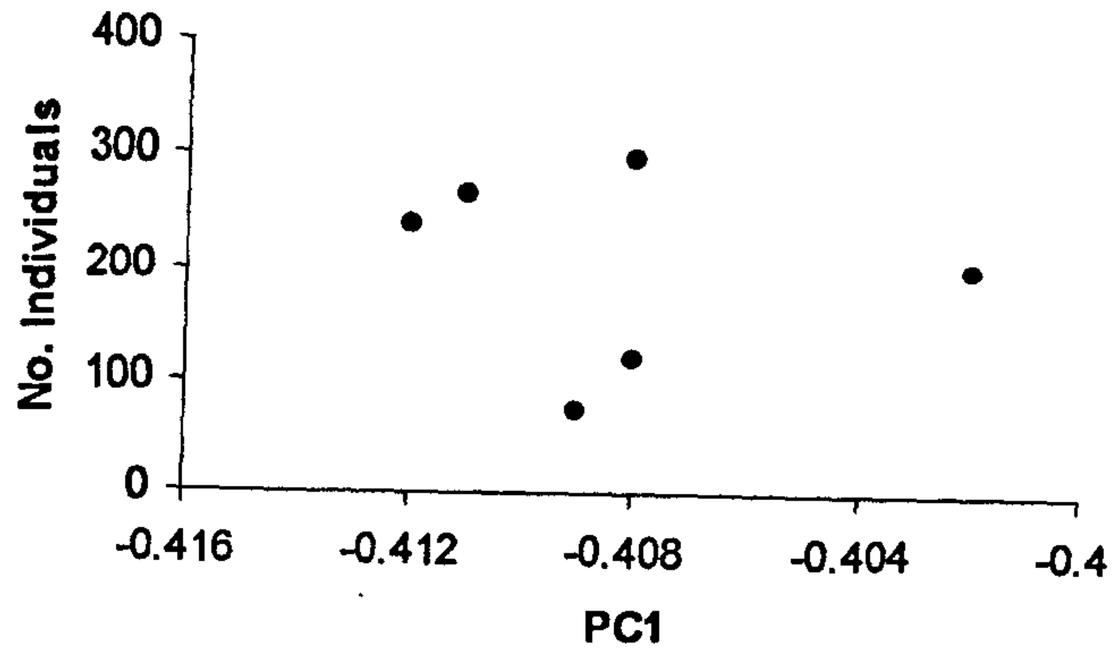
MDS ordination of the data collected from the mussel beds at Point Lynas during the summer and winter in two consecutive years failed to illustrate any clear annual patterns in community structure, either with a square-root or a presence/absence transformation (Figure 16a). This was also the case for similar data collected at White Beach (Figure 16b) and Criccieth (Figure 16c). ANOSIM tests performed on the data confirmed differences between the summer and winter of consecutive years' samples were significant at all locations (Table 13). Thus, whilst there was an annual cyclic progression in community structure during 1998 and 1999, the structure of the communities at each of the locations were quite different from one year to the next.

SIMPER analysis, performed with a square-root transformation revealed that the taxa responsible for the annual differences in community structure at all three sites were the same taxa characterising the structure of the mussel bed throughout the year (see Table 2 & 3, 6 & 7 and 10 & 11). Thus, annual changes at the three sites were not caused by the appearance of new taxa, but changes in the abundance of those that were already common. Similar results were found when SIMPER analysis was performed with a presence/absence transformation, although

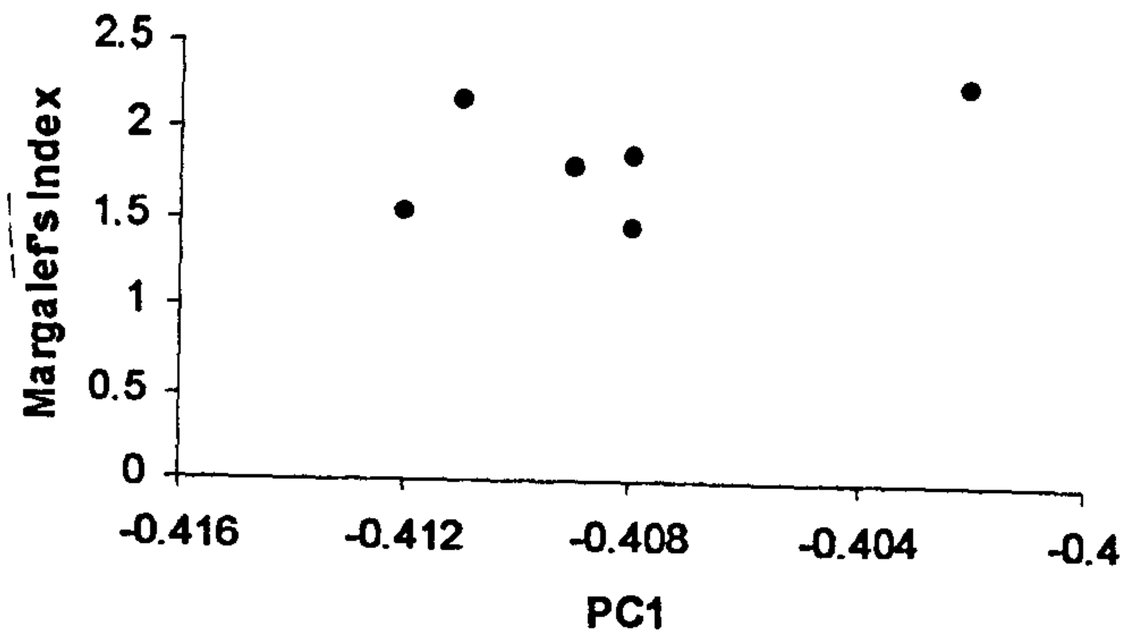
Figure 15 Principal Component 1 (PC1) plotted against each of the univariate measures of mussel bed community structure at Criccieth, Gwynedd. Correlation coefficients (r) and significance levels between the variables are shown.



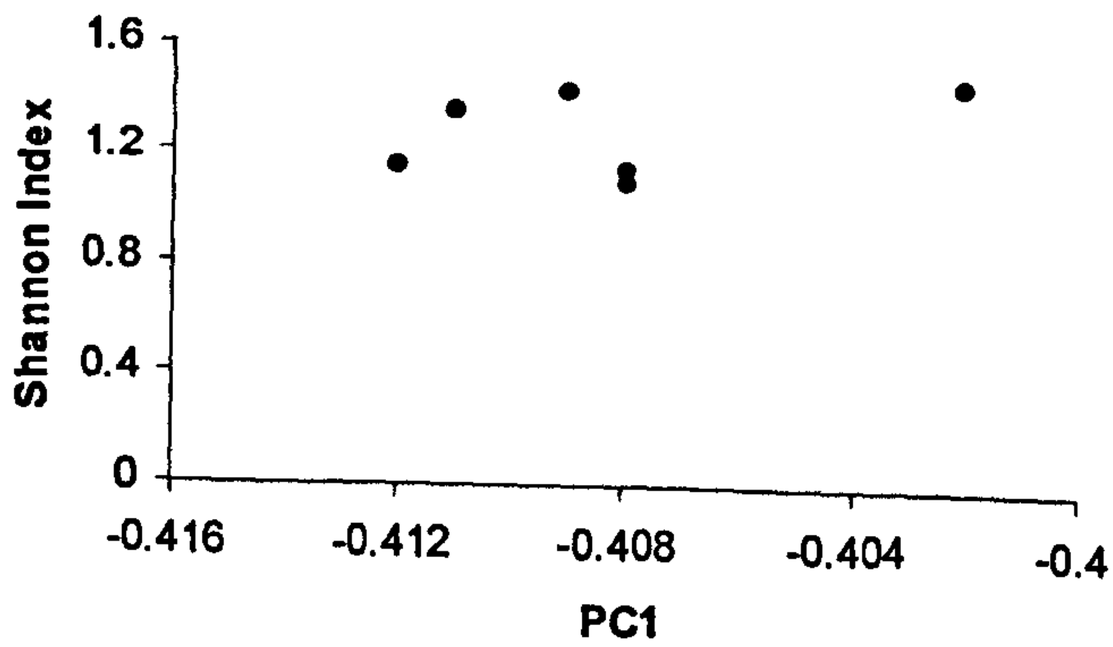
r = 0.490
p > 0.05



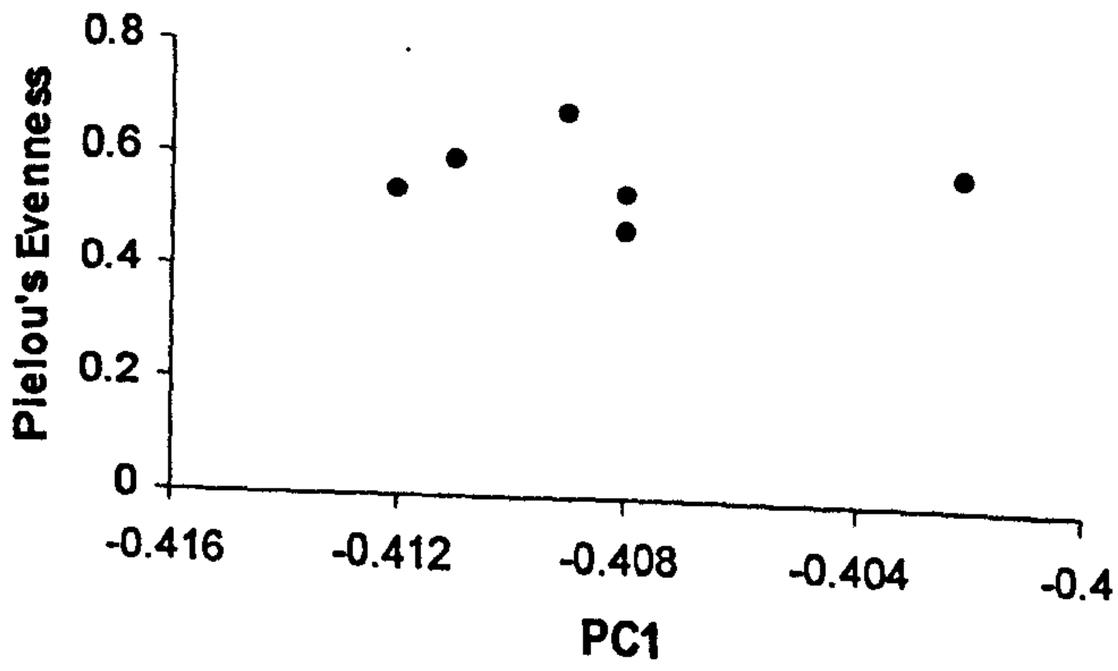
r = -0.143
p > 0.05



r = 0.490
p > 0.05



r = 0.432
p > 0.05

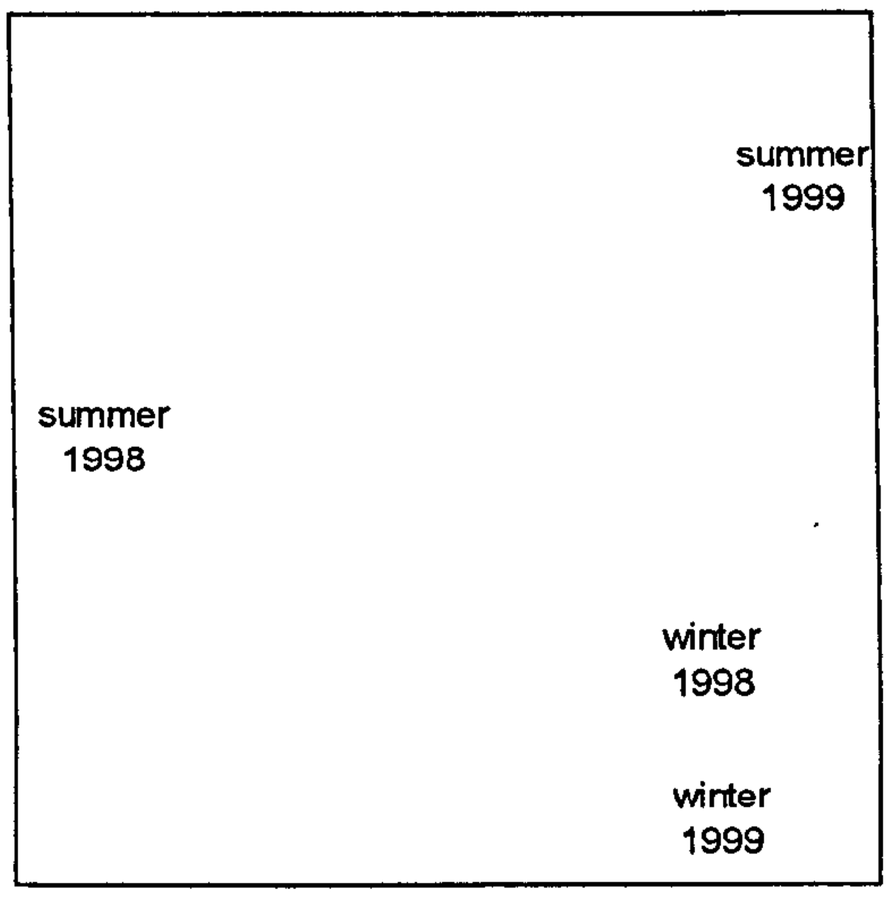


r = 0.006
p > 0.05

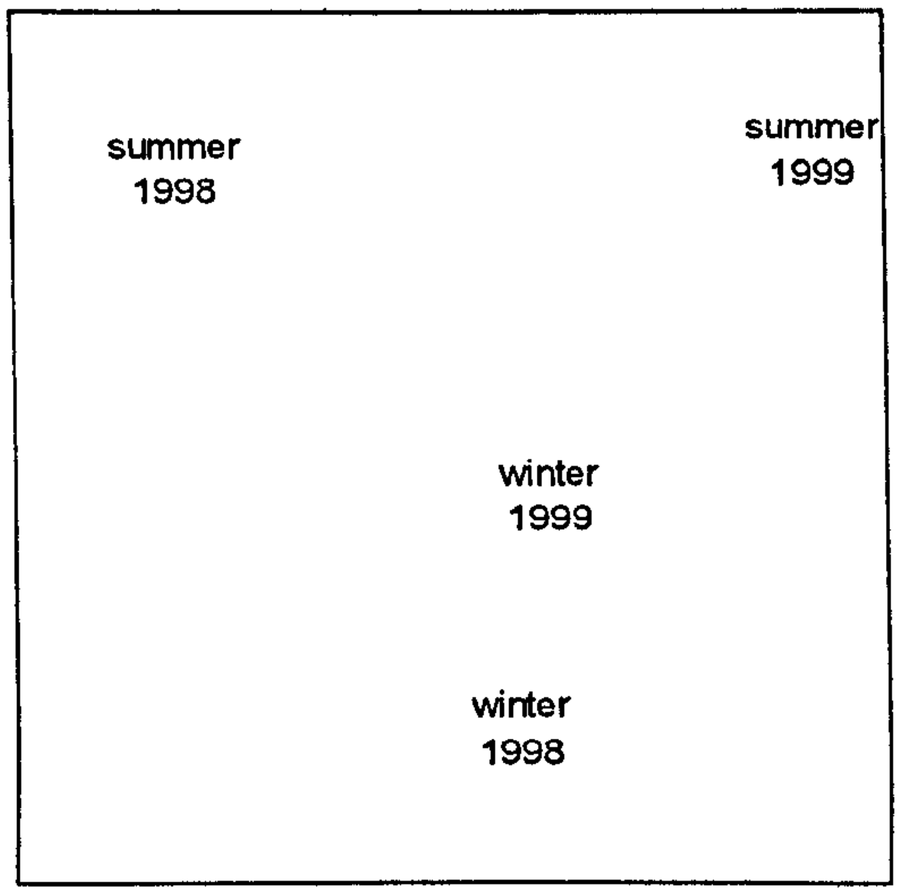
Figure 16 Ordination by MDS of averaged abundance of infauna from the mussel beds during the summer and winter in two consecutive years (1998 and 1999) at a) Point Lynas, Anglesey, b) White Beach, Anglesey and c) Criccieth, Gwynedd, based on square-root and presence/absence transformations. Stress values for all plots = 0.0

a) Point Lynas

Square-root transformed data

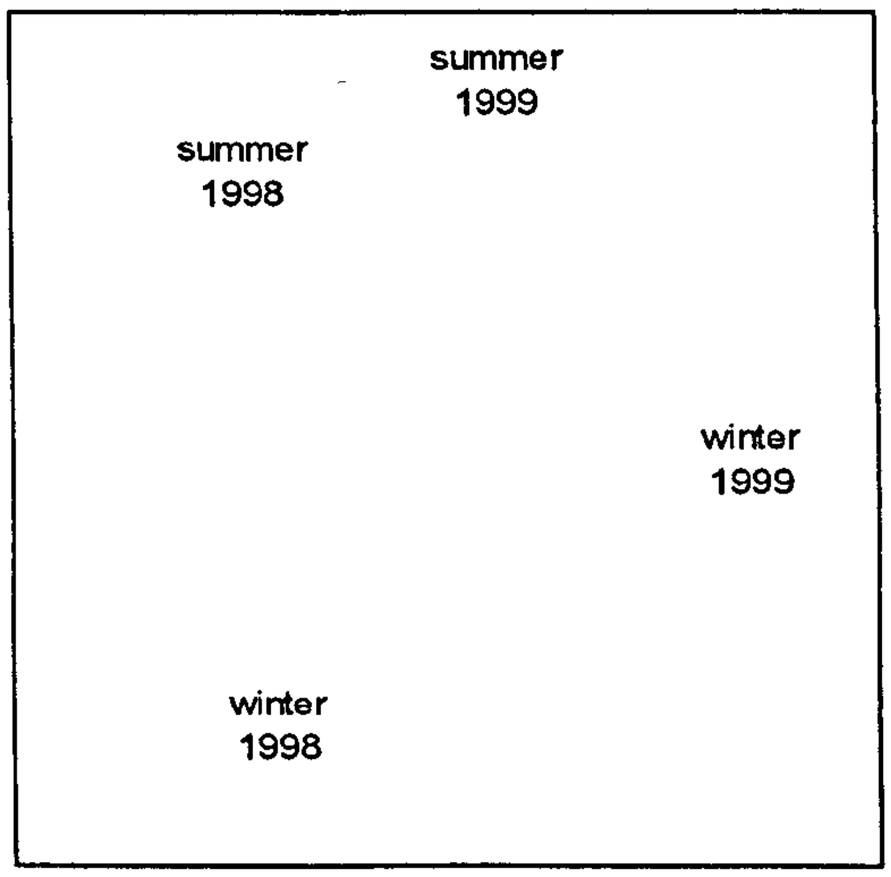


Presence/absence transformation

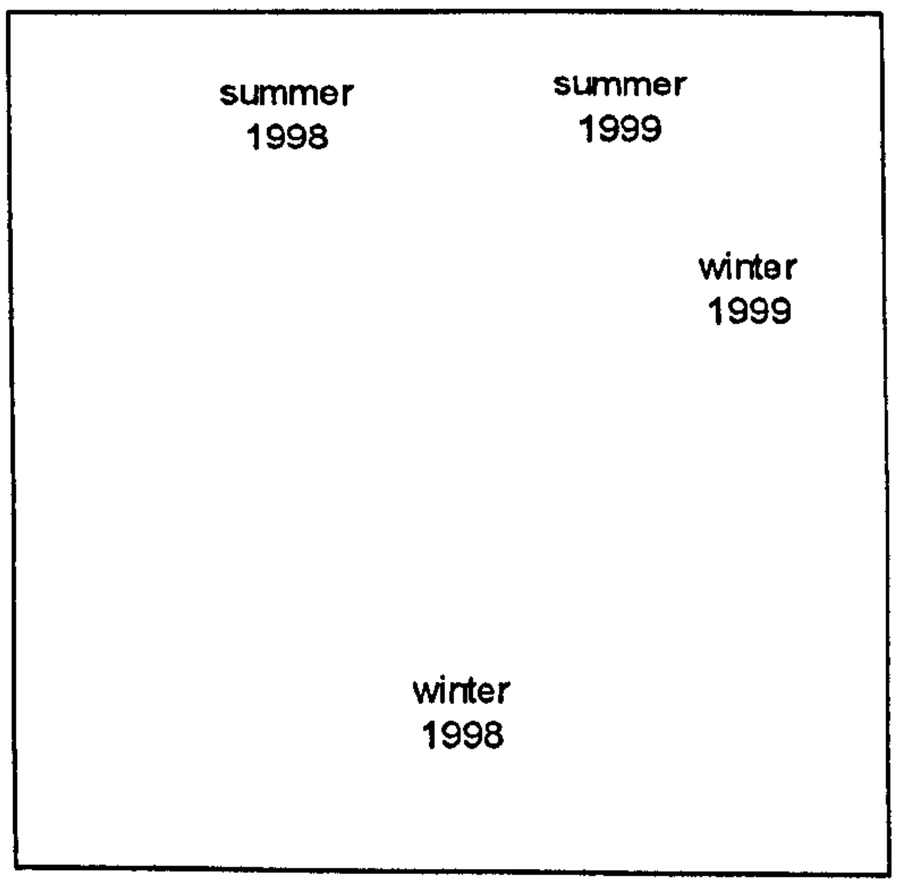


b) White Beach

Square-root transformed data

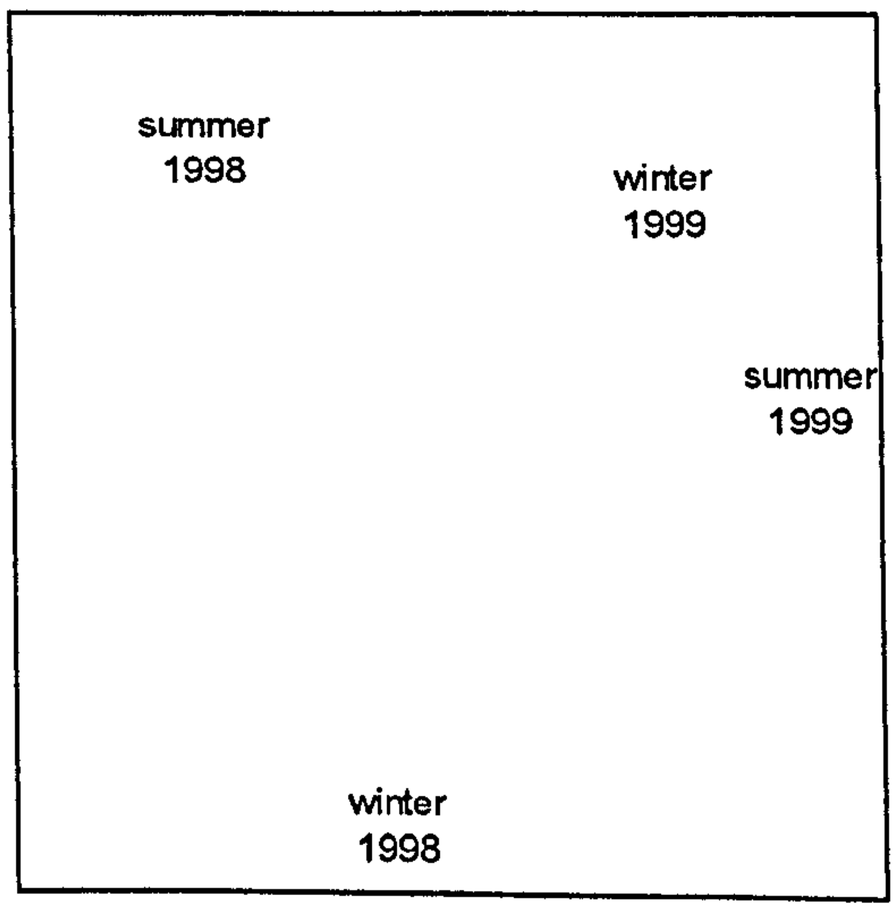


Presence/absence transformation



c) Criccieth

Square-root transformation



Presence/absence transformation

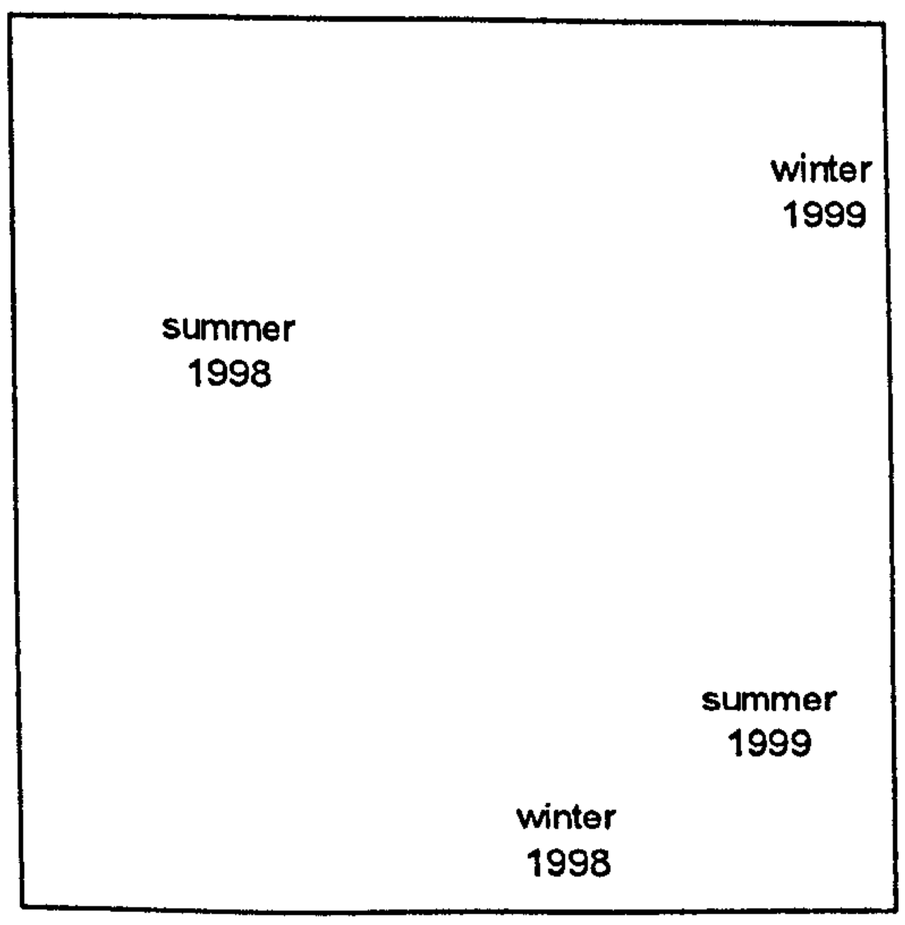


Table 13 ANOSIM pairwise comparisons between the mussel bed communities during the summer and winter in two consecutive years (1998 and 1999) at Point Lynas and White Beach, Anglesey and Criccieth, Gwynedd, based on square-root and presence/absence (italicised values in brackets) transformations. Significant differences in community structure ($p<0.05$) are indicated by bold type (all differences are significant).

	Summer 1998/1999	Winter 1998/1999
Point Lynas	**0.513** ***(0.563)***	**0.417** ***(0.513)***
White Beach	**0.283** ***(0.388)***	**0.765** ***(0.740)***
Criccieth	**0.958** ***(0.781)***	**0.634** ***(0.585)***

differences here were also due in part, to the appearance of new taxa in the mussel bed, since emphasis was removed from abundance in this analysis. Foraminifera, ostracods, oligochaetes, *Brania pusilla* and *Modiolula phaseolina* were common at all sites in the 1999 samples at all sites, but virtually absent from the 1998 samples.

Temporal variation in communities associated with P. purpuratus

Several of the univariate measures of community diversity showed significant annual variation at each of the four sites (Table 14). At Coronel and Desembocadura sheltered site 1, univariate measures were generally lower during 1999 than other years (Figure 17). At the two exposed sites at Desembocadura, for many of the measures, this pattern was reversed. At each of the sites, measures for 1999 were often quite different to values during 1997 and 2000.

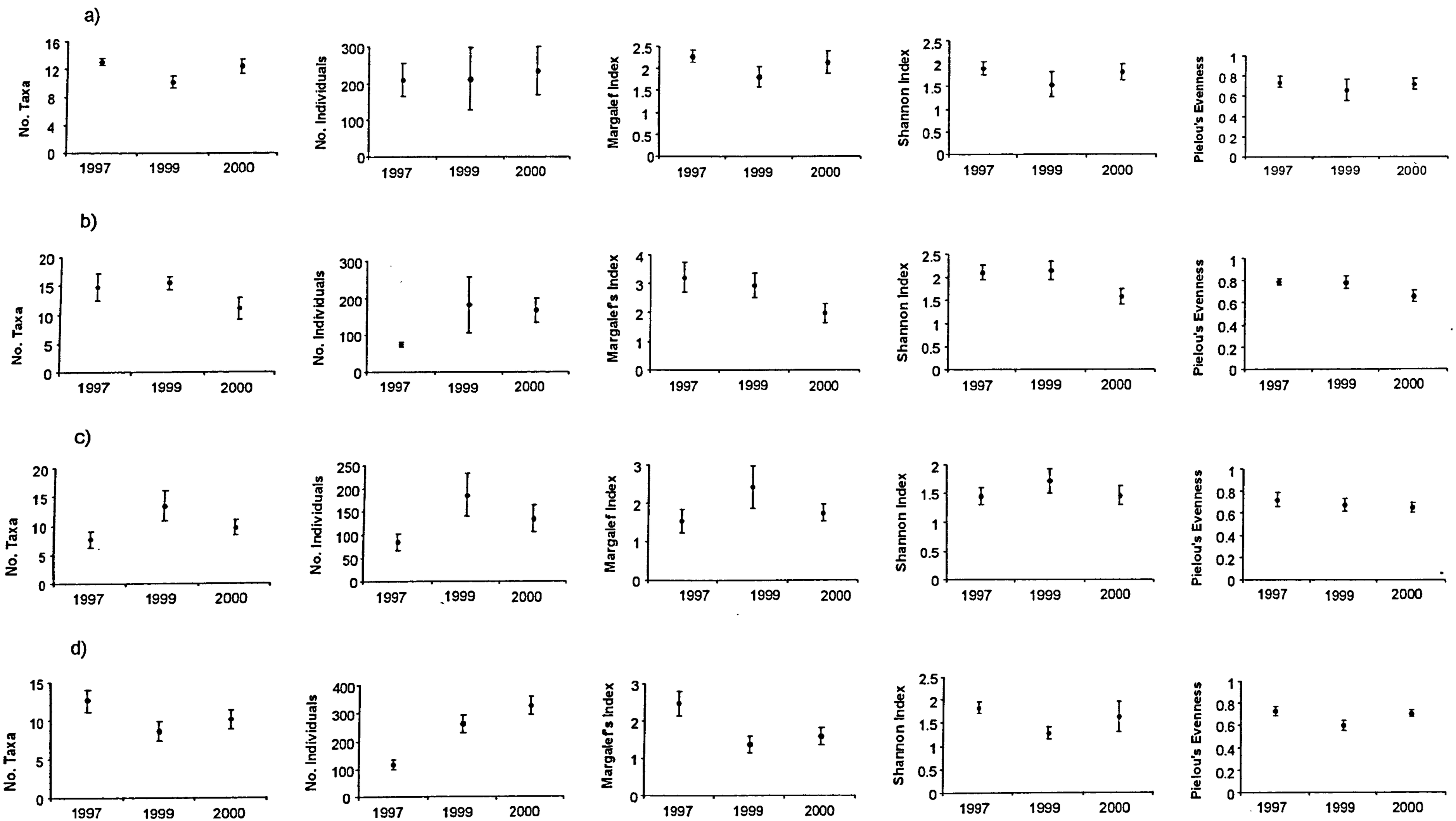
MDS ordination of the data collected from *P. purpuratus* beds at the four sites illustrated a clear separation of samples taken in 1997, 1999 and 2000, when performed with both a square-root and a presence/absence transformation (Figure 18 & 19). A one-way ANOSIM test confirmed that at each of the sites, there was significant annual variation in community structure, both in terms of the more common and rarer members of the community (Table 15). ANOSIM pairwise comparisons revealed that annual variation was significant at all sites, between all years, with both transformations.

Similarity percentage analysis (SIMPER), performed with a square-root transformation on inter-annual data from each site, indicated that the dominant taxa characterising the mussel bed communities at the sites were the same from year to year. The mussel community at Coronel was mainly characterised by an abundance of anemones, nematodes, barnacles, small mussels and other bivalves. The mussel community at Desembocadura exposed site 1 was characterised predominantly by nematodes, small mussels and barnacles, while Desembocadura exposed site 2 was characterised by these taxa along with anemones and various polychaete families. The mussel community at Desembocadura sheltered site 1 was characterised mainly by small mussels, barnacles, spionid polychaetes and nematodes. Inter-annual differences in community structure at each of the sites were due mainly to variations in the abundance of these main dominant taxa (Table 16). Similar results were obtained when SIMPER analysis was performed on the same data, with a presence/absence transformation, to remove the emphasis from numerical abundance of taxa (Table 17). Thus, the same taxa were seen to characterise each site whether emphasis was placed on numerical abundance or simply just presence.

Table · 14 One-way ANOVA tests between univariate measures of diversity calculated for mussel bed communities in Chile during January 1997, 1999 and 2000 at a) Coronel, b) Desembocadura exposed site 1, c) Desembocadura exposed site 2 and Desembocadura sheltered site 1. Significant differences are marked * ($p<0.05$).

Univariate Measure	Coronel *F*	Des. Exp. 1 *F*	Des. Exp. 2 *F*	Des. Shelt. 1 *F*
Total taxa	10.56*	9.23*	6.12*	8.95*
Total individuals	0.17	8.75*	13.00*	54.60*
Margalef's richness	4.96*	5.73*	8.63*	19.10*
Shannon's diversity	3.36	2.98	13.74*	20.59*
Pielou's evenness	1.05	1.49	8.48*	11.53*

Figure 17 Univariate measures of mussel bed community diversity at a) Coronel, b) Desembocadura exposed site 1, c) Desembocadura exposed site 2 and d) Desembocadura sheltered site 1 (Chile) in January 1997, 1999 and 2000. Values are based on 25cm^2 replicates. 95% confidence intervals are marked, such that significant differences are represented by non-overlapping intervals.


a)
No. Taxa
No. Individuals
Margalef Index
Shannon Index
Pielou's Evenness
b)
No. Taxa
No. Individuals
Margalef's Index
Shannon Index
Pielou's Evenness
c)
No. Taxa
No. Individuals
Margalef Index
Shannon Index
Pielou's Evenness
d)
No. Taxa
No. Individuals
Margalef's Index
Shannon Index
Pielou's Evenness
1997
1999
2000

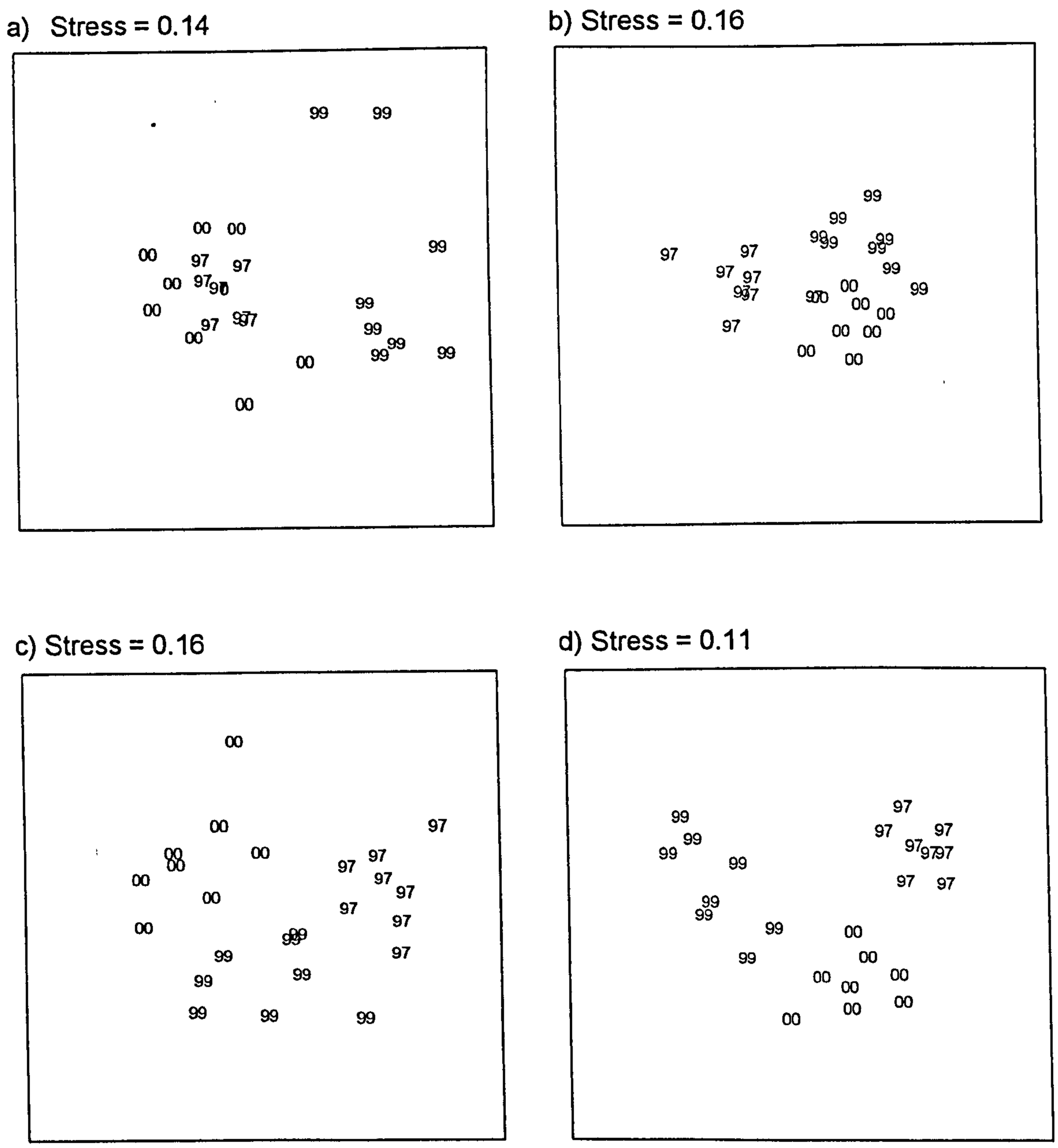


Figure 18 Ordination by MDS based on Bray-Curtis similarity, of square-root transformed abundance of taxa from the mussel beds at a) Coronel, b) Desembocadura exposed site 1, c) Desembocadura exposed site 2 and d) Desembocadura sheltered site 1, in January 1997, 1999 and 2000.

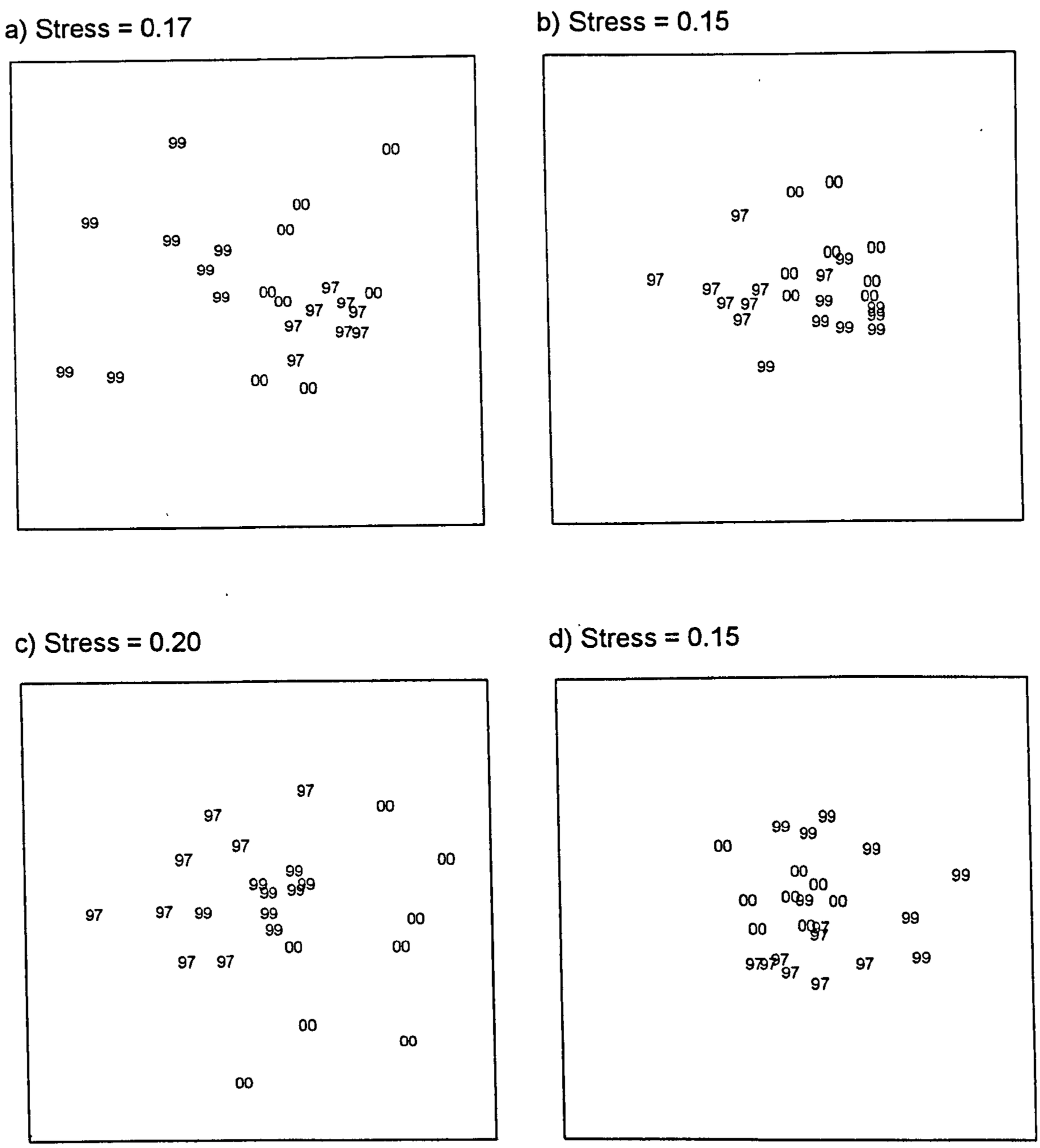


Figure 19 Ordination by MDS based on Bray-Curtis similarity, of presence/absence transformed abundance of taxa from the mussel beds at a) Coronel, b) Desembocadura exposed site 1, c) Desembocadura exposed site 2 and d) Desembocadura sheltered site 1, in January 1997, 1999 and 2000.

Table 15 Global R-values for ANOSIM tests and pairwise comparisons between mussel bed communities in January 1997, 1999 and 2000 at Coronel, Desembocadura exposed site 1, Desembocadura exposed site 2 and Desembocadura sheltered site 1, based on a) square-root and b) presence/absence transformations of taxa abundance. Significant differences in community structure pairwise comparisons are indicated by bold type (all differences are significant).

a)

All sites ANOSIM

Site	*Global R-value*	*p*
Coronel	0.521	<0.05
Desembocadura exposed site 1	0.691	<0.05
Desembocadura exposed site 2	0.744	<0.05
Desembocadura sheltered site 1	0.917	<0.05

ANOSIM Pairwise Comparisons

Coronel

	1997	*1999*
1999	**0.680**	
2000	**0.293**	**0.676**

Desembocadura exposed site 1

	1997	*1999*
1999	**0.824**	
2000	**0.725**	**0.520**

Desembocadura exposed site 2

	1997	*1999*
1999	**0.714**	
2000	**0.867**	**0.656**

Desembocadura sheltered site 1

	1997	*1999*
1999	**0.996**	
2000	**0.920**	**0.815**

b)

Site	*Global R-value*	*p*
Coronel	0.453	<0.05
Desembocadura exposed site 1	0.430	<0.05
Desembocadura exposed site 2	0.359	<0.05
Desembocadura sheltered site 1	0.358	<0.05

	1997	*1999*
1999	**0.707**	
2000	**0.280**	**0.439**

	1997	*1999*
1999	**0.568**	
2000	**0.492**	**0.210**

	1997	*1999*
1999	**0.388**	
2000	**0.484**	**0.378**

	1997	*1999*
1999	**0.508**	
2000	**0.450**	**0.162**

Table 16 Results of similarity percentage analysis (SIMPER) performed on square-root transformed abundance of infaunal taxa, showing a breakdown of % contributions of infaunal taxa (% Cont.) to average dissimilarity between mussel bed communities during January 1997, 1999 and 2000 at a) Coronel, b) Desembocadura exposed site 1, c) Desembocadura exposed site 2 and d) Desembocadura sheltered site 1. Taxa are ordered in decreasing contribution to the average dissimilarity (cut-off at 70% average dissimilarity) and those highlighted in grey indicate higher abundance in the first listed year.

a) Coronel

1997 1999	% Cont.	1997 2000	% Cont.	1999 2000	% Cont.
Bivalves indet.	18.34	Bivalves indet.	13.68	Nematodes	15.67
Nematodes	10.88	Barnacles	12.55	Barnacles	12.85
Barnacles	10.51	Nematodes	10.08	Anemones	9.68
Small mussels	10.11	Small mussels	9.14	Bivalves indet.	9.63
Anemones	8.75	Spionidae	8.65	Small mussels	9.33
Nemerteans	6.47	Amphipods	7.15	Spionidae	6.72
Spionidae	6.10	Anemones	5.32	Nemerteans	6.01
		Turbellarians	4.05	Amphipods	5..36
Average dissimilarity between years = 46.45%		Average dissimilarity between years = 30.72%		Average dissimilarity between years = 50.02%	

b) Desembocadura exposed site 1

1997, 1999	% Cont.	1997, 2000	% Cont.	1999, 2000	% Cont.
Nematodes	17.44	Nematodes	24.07	Amphipods	14.69
Amphipods	10.74	Barnacles	12.56	Nematodes	13.01
Barnacles	9.55	Anemones	8.23	Small mussels	9.87
Small mussels	8.91	Small mussels	8.18	Barnacles	7.57
Nemerteans	6.47	Amphipods	5.76	Nemerteans	6.17
Anemones	5.75	Mites	5.06	Anemones	4.77
Nereidae	4.33	Bivalves indet.	5.04	Nereidae	4.59
Oligochaetes	3.53	Limpets	4.14	Mites	4.30
Isopods	3.31			Oligochaetes	3.72
				Isopods	3.67
Average dissimilarity between years = 53.18%		Average dissimilarity between years = 48.90%		Average dissimilarity between years = 42.75%	

c) Desembocadura exposed site 2

1997 1999	% Cont.	1997 2000	% Cont.	1999 2000	% Cont.
Nematodes	15.37	Nematodes	17.43	Small mussels	11.63
Amphipods	9.97	Small mussels	12.33	Nematodes	10.26
Small mussels	7.14	Barnacles	7.17	Amphipods	9.89
Terebellidae	5.39	Other gastropods	5.35	Terebellidae	9.03
Spionidae	5.33	Anemones	4.87	Barnacles	6.35
Barnacles	5.03	Syllidae	4.73	Spionidae	5.18
Other gastropods	5.01	Terebellidae	4.63	Oligochaetes	4.84
Oligochaetes	4.93	Nemerteans	3.88	Sea spiders	4.51
Nemerteans	4.20	Crabs	3.74	Syllidae	4.21
Syllidae	4.06	Limpets	3.73	Limpets	4.07
Sea spiders	3.97	Mites	3.60	Nemerteans	4.05
Average dissimilarity between years = 43.61%		Average dissimilarity between years = 50.29%		Average dissimilarity between years = 43.99%	

d) Desembocadura sheltered site 1

1997 1999	% Cont.	1997 2000	% Cont.	1999 2000	% Cont.
Spionidae	23.28	Nematodes	16.50	Spionidae	18.24
Small mussels	13.09	Small mussels	14.18	Nematodes	17.27
Barnacles	10.82	Oligochaetes	13.72	Barnacles	15.63
Nematodes	10.09	Barnacles	7.89	Oligochaetes	11.58
Oligochaetes	5.24	Anemones	7.37	Anemones	6.10
Amphipods	4.39	Spionidae	5.67	Syllidae	4.91
Anemones	3.85	Syllidae	4.70		
Average dissimilarity between years = 45.78%		Average dissimilarity between years = 36.50%		Average dissimilarity between years = 39.42%	

Table 17 Results of similarity percentage analysis (SIMPER) performed on presence/absence transformed abundance of infaunal taxa, showing a breakdown of % contributions of infaunal taxa (% Cont.) to average dissimilarity between mussel bed communities during January 1997, 1999 and 2000 at a) Coronel, b) Desembocadura exposed site 1, c) Desembocadura exposed site 2 and d) Desembocadura sheltered site 1. Taxa are ordered in decreasing contribution to the average dissimilarity (cut-off at 70% average dissimilarity) and those highlighted in grey indicate higher abundance in the first listed year.

a) Coronel

1997 1999	% Cont.	1997 2000	% Cont.	1999 2000	% Cont.
Crabs	14.70	Predatory gastropods	11.70	Crabs	13.11
Bivalves indet.	11.22	Turbellarians	11.15	Anemones	11.32
Anemones	11.00	Nemerteans	9.82	Bivalves indet.	9.57
Predatory gastropods	9.16	Cirratulidae	9.61	Nemerteans	7.62
Turbellarians	8.74	Limpets	7.73	Oligochaetes	6.98
Nemerteans	7.41	Chitons	7.33	Chitons	6.09
Cirratulidae	7.16	Oligochaetes	7.13	Other gastropods	6.00
Other gastropods	5.82	Syllidae	6.42	Limpets	5.98
				Syllidae	5.90
Average dissimilarity between years = 29.24%		Average dissimilarity between years = 19.92%		Average dissimilarity between years = 29.26%	

b) Desembocadura exposed site 1

1997 1999	% Cont.	1997 2000	% Cont.	1999 2000	% Cont.
Nematodes	9.51	Nematodes	11.42	Oligochaetes	7.77
Nemerteans	8.22	Spionidae	8.10	Isopods	6.68
Oligochaetes	7.50	Sea spiders	7.95	Terebellidae	6.57
Spionidae	6.32	Amphipods	6.72	Sea spiders	6.42
Terebellidae	6.09	Bivalves indet.	6.45	Amphipods	6.36
Nereidae	6.08	Limpets	6.36	Nemerteans	5.98
Isopods	5.41	Mites	6.33	Bivalves indet.	5.97
Cirratulidae	5.19	Nemerteans	6.28	Nereidae	5.95
Limpets	4.95	Isopods	6.26	Limpets	5.92
Mites	4.53	Nereidae	6.05	Mites	5.90
Tanaids	3.82			Cirratulidae	5.69
Crabs	3.70			Tanaids	4.67
Average dissimilarity between years = 45.90%		Average dissimilarity between years = 45.90%		Average dissimilarity between years = 37.87%	

c) Desembocadura exposed site 2

1997 1999	% Cont.	1997 2000	% Cont.	1999 2000	% Cont.
Other gastropods	10.09	Other gastropods	9.17	Terebellidae	9.61
Oligochaetes	8.05	Terebellidae	8.18	Oligochaetes	8.32
Nemerteans	8.01	Limpets	5.56	Isopods	7.72
Cirratulidae	6.48	Chitons	5.19	Limpets	7.33
Isopods	5.82	Nemerteans	5.11	Sea spiders	7.26
Spionidae	5.77	Cirratulidae	5.07	Chitons	6.05
Syllidae	5.27	Sea spiders	4.95	Spionidae	6.00
Sea spiders	5.04	Spionidae	4.66	Amphipods	5.69
Amphipods	4.66	Amphipods	4.62	Mites	5.33
Nematodes	4.50	Isopods	4.58	Cirratulidae	5.04
Tanaids	4.47	Mites	4.56	Nemerteans	4.50
Chitons	4.37	Syllidae	3.98		
		Nematodes	3.57		
		Barnacles	3.57		
Average dissimilarity between years = 28.60%		Average dissimilarity between years = 43.00%		Average dissimilarity between years = 35.13%	

d) Desembocadura sheltered site 1

1997 1999	% Cont.	1997 2000	% Cont.	1999 2000	% Cont.
Bivalves indet.	9.94	Bivalves indet.	12.86	Limpets	12.70
Limpets	9.36	Oligochaetes	11.17	Oligochaetes	9.49
Anemones	8.93	Chitons	10.79	Anemones	9.15
Chitons	8.34	Predatory gastropods	10.58	Nemerteans	9.01
Predatory gastropods	8.17	Anemones	9.19	Chironomids	7.86
Nemerteans	7.99	Nemerteans	8.88	Isopods	7.05
Oligochaetes	6.69	Turbellarians	7.35	Barnacles	7.05
Isopods	6.03			Syllidae	6.92
Turbellarians	5.77			Turbellarians	6.63
Average dissimilarity between years = 34.82%		Average dissimilarity between years = 25.12%		Average dissimilarity between years = 29.16%	

The density of mussel populations did not vary significantly at each of the four sites in Chile, between 1997 and 2000 (see Chapter 2). Thus, it was statistically unlikely that the observed annual differences in community diversity between each of the sites were a reflection of mussel density and no further analysis was performed on the data.

Overall, these data show that the invertebrate communities associated with *M. edulis* display significant intra- and inter-annual variations, while those associated with *P. purpuratus* also display significant inter-annual variation. Temporal differences in community structure of both mussel species were generally the result of changes in the abundance of no more than 10 of the most common taxa, while many more taxa contributed to temporal differences when data were analysed using a presence/absence transformation. Such temporal differences did not correlate with differences in the measured environmental parameters of the mussel beds.

DISCUSSION

At each of the sites around the coast of North Wales and Chile, *M. edulis* and *P. purpuratus* remained the dominant primary space occupiers during this study. Thus, in terms of the main space occupiers, these rocky shore communities exhibit a strong temporal consistency. Many earlier studies documenting the major components of rocky shore communities have found similar temporal patterns. For example, Berlow and Navarrete (1997) found in studies of the main primary space occupiers in rocky intertidal communities on the west coast of America, that patterns of community structure remained virtually unchanged from early 1990 through the early spring of 1993. Other authors, including Dayton (1971) and Paine (1974) have obtained similar results in studies of rocky shore communities. However, when these mussel bed communities were studied in greater detail, by examining associations between infaunal and epifaunal taxa and the primary space occupiers, seasonal differences in community structure did emerge.

Mussel beds at each of the study sites in this investigation, both in the Wales and Chile were observed to support diverse infaunal communities, with representatives from most of the main animal phyla. Seasonal and annual differences in the abundance of many of the associated taxa, resulted in temporal patterns of community structure in each of the mussel beds. Seasonal differences in the structure of the infaunal communities associated with the *M. edulis* and *P. purpuratus* beds were much more evident when analysed using multivariate, rather than univariate techniques. In general, the total number of taxa and individuals present in the beds remained relatively constant with time, although the actual

species composition changed. In contrast to these findings, using graphical techniques Peake and Quinn (1993) to study of the invertebrate communities inhabiting clumps of the intertidal mussel, *Brachidontes rostratus* in Australia, found fewer species for a given area in autumn and summer compared with winter and spring. The equilibrium theory of MacArthur and Wilson (1967) states that the number of species in a patch of habitat should remain approximately constant, at its equilibrium value, although the identities of species should change with time. This phenomenon, referred to as species turnover, appears to apply to the mussel bed communities at each of the sites in the present study. It should be noted, however, that the application of general ecological models to new habitats is difficult, since ecological processes vary from one habitat to another (Crowe and Underwood, 1999). It is likely that the total number of taxa and individuals present within the mussel patches, are more or less fixed by the availability of resources such as food and space.

When the taxa composition of the mussel bed infaunal communities were analysed using multivariate techniques, a clear temporal variation was demonstrated at all sites. The structure of the communities at Point Lynas and Criccieth changed throughout the year in a cyclic progression, while the community at White Beach showed significant seasonal differences, although the progression of community change over the year did not appear to be cyclic. Significant annual variation was observed in the mussel communities in the UK and Chile. Such temporal variations at each of the sites were due mainly to fluctuations in the presence and abundance of taxa such as nematodes, nemerteans, platyhelminthes, juvenile mussels and various polychaete, gastropod and crustacean taxa. Other studies of mussel beds, based on a multivariate approach have demonstrated similar seasonal variations in community structure. For example, Jacobi (1987a) found amphipods in Brazilian mussel beds to be more abundant in summer, while Tokeshi (1995) found a general tendency towards reduced polychaete population densities in mussel beds on Pacific South American rocky shores in the austral winter. In addition, Ong Che and Morton (1992) found large temporal macro-invertebrate population fluctuations in *Septifer virgatus* beds in Hong Kong.

Several authors have attempted to explain the development and change of marine epifaunal communities over time, and relate them to various biological and environmental factors, as detailed below.

Reproduction and Larval Recruitment

The seasonality of the climate has a marked effect on the reproduction and growth of infaunal and epifaunal species, such that most species produce larvae over a limited period of time (Osman, 1977). Underwood and Fairweather (1989) have pointed out the stochastic nature of marine communities, emphasising the considerable temporal variation in recruitment of species with planktonic larval stages as a major cause. Many studies, have demonstrated that this seasonality in reproduction and immigration (settlement of larvae) causes a cycle in the equilibrium number of species present on or in a substratum (e.g. Osman, 1978). Schoener and Schoener (1981) concluded, in a study of the marine fouling communities on artificial panels, that settling species were somewhat dependent upon season. Osman (1977) concluded that seasonal fluctuations in larval abundance was an important factor in the development of a marine epifaunal community, since colonisation was directly dependent on the abundance of settling larvae, which in turn was a function of seasonality and selectivity and as such would be highly variable. Osman (1977) found that the peak abundance of larval production and settlement in rocky shore epifaunal communities on the East Coast of America occurred during the late summer. Following this, both the number of species reproducing and the number of larvae produced per species declined to a minimum level in the late winter. This resulted in a fluctuation in the number of species between a high point at the end of the summer and a low point at the end of the winter. Stoner (1985) suggested that priority of arrival as recruits might determine the species composition of crustaceans associated with calcareous green algae in Puerto Rico, in a similar manner to the lottery system proposed by Sale (1978) for reef fishes.

Various intertidal marine benthic invertebrates have been shown to display seasonal patterns of reproduction, for example, gastropods (Underwood, 1979; Parry, 1982) and barnacles (Caffey, 1985; Raimondi, 1990). In addition, Hull (1997) demonstrated that several intertidal ostracod species (similar to taxa found in mussel beds in this study) reproduced in early spring. The reproductive cycle of *M. edulis* itself, exhibits marked seasonal patterns (Seed and Suchanek, 1992), which might explain the seasonal variation in juvenile mussel densities in each of the mussel beds. Spawning normally occurs in early spring and if environmental conditions are favourable, periods of redevelopment and spawning may occur throughout the summer (Dix and Ferguson, 1984; Gray *et al*, 1997). Jarvis and Seed (1996) suggested that the seasonal pattern displayed by meiofaunal taxa, such as ostracods and nematodes, inhabiting epiphytic algae on *Ascophyllum nodosum* could be attributed to annual life cycles and reproductive activity. Colman (1940) and later

Kito (1982) drew similar conclusions in studies of the fauna inhabiting intertidal seaweeds.

Hughes *et al* (2000) have pointed out the importance of variable larval input in determining the size of local adult populations in marine benthic communities, although for most marine organisms, the spatial scale at which adult stocks and recruitment are coupled is unknown. In addition, Renaud *et al* (1999) suggested that post-settlement processes, such as predation, are also important in structuring marine benthic communities. Woodin (1976) predicted that successful larval recruitment might be rare in the presence of densely packed suspension-feeding bivalves, since the probability of successful larval settlement is reduced either due to ingestion or burial in faeces and pseudofaeces. Persson (1983) and Dittman (1990) agreed that adult populations of suspension- and deposit-feeders might consume or disturb any settling larvae, while Mileikovsky (1974) additionally stated that larvae that pass through the mussels alive, subsequently have little chance of survival in the mussel deposits. Thus, the arrival of settling pelagic larvae is probably not an important structuring factor in mussel bed communities.

Various researchers have identified methods of reproduction adopted by infaunal taxa, which may affect their presence and abundance within mussel bed communities and produce seasonal patterns in community structure. Tokeshi (1995) and Tokeshi and Romero (1995) have suggested that temporal variations in diversity and abundance of macroinvertebrates associated with mussel patches probably reflect prolonged reproductive cycles, along with the stochastic nature of settlement and mortality that often typifies many marine species with planktonic larvae (Underwood and Fairweather (1989). Dittman (1990) noted that only infauna with a benthic larval development, rather than pelagic development successfully recruited and established populations in mussel beds in the Wadden Sea. For example, oligochaetes form cocoons from which juveniles emerge (Hunter and Arthur, 1978); some oligochaetes and polychaetes fragment asexually (Levinton and Stewart, 1982; Oliver, 1984); some polychaetes, bivalves and crustaceans brood their young (Pechenik, 1979); and many taxa disperse as larvae, juveniles and adults (Commito, 1982; Ambrose, 1986). Best (1978) found that most brooding species were not adversely affected by densely packed populations of the clam, *Mercenaria mercenaria*. Amphipods, which brood their young and nematodes, which encapsulate their developing embryos, are abundant in mussel beds from several localities (Radziejewska, 1986; Tsuchiya and Nishihira 1986; Jacobi, 1987a). Commito (1987) suggested that the oligochaete *Tubificoides benedeni* was abundant in *M. edulis* beds because it produced cocoons, which liberate juvenile worms

directly into the community. Dean (1981) stated that gregarious settling behaviour might partially account for species abundance patterns on mussel beds. Such behaviour is generally mediated by chemical signals (Crisp, 1979) and responsible for aggregation of barnacles, serpulid polychaetes, hydroids, and a host of other sessile invertebrates (Buss, 1979).

It is likely, therefore, that the main taxa contributing to seasonal differences in the mussel communities in the present study are those that reproduce by non-pelagic methods.

Species Immigration and Emigration

It has been suggested that the eventual competitive outcome and development of a marine epifaunal community will depend on which species have immigrated into the community (Osman, 1977). Similarly, Schoener and Schoener (1981) concluded that immigration-related processes were probably responsible over the short-term for initiating a relatively stable species-area relationship in marine fouling communities. Individual species may alter actual species counts. Thus, different functional groups of species might be replaced by others through time, yet stability in the species-area slope is maintained. Stoner (1985) stated that changes in species composition over time on the calcareous green alga, *Penicillus capitatus*, were indicative of some non-random effects, such as differential immigration and/or emigration rates, while Beukema (1974) concluded that the observed spring and summer increases in macrobenthos biomass on a tidal flat in the Dutch Wadden Sea were due mainly to species immigration. Keough and Butler (1983) noted that species of sessile invertebrates on the shells of the fan mussel, *Pinna pinna* in Australia were never gained and lost simultaneously and sometimes successive immigrations occurred by chance before corresponding extinction's occurred and *vice versa*. Persson (1983) concluded that the observed seasonal variations, repeated from year to year, in macrobenthic community structure in the Southern Baltic, might result from biological events such as reproduction and migration. In addition, Jarvis and Seed (1997) suggested that seasonal patterns in ostracod abundance on epiphytes of *Ascophyllum nodosum* in North Wales might be attributed to seasonal migrations into the sublittoral zone.

The suggestion that seasonal changes in the mussel community at the three sites were due to species immigration and emigration would imply that the taxa present in the mussel beds were also present on other areas of the shore. However, several studies have shown that the presence of mussel beds on rocky shores serves to encourage species enrichment through provision of a structurally complex

habitat (e.g. Bayne, 1976; Suchanek, 1979; Seed, 1996). Mussel beds thus represent an extremely well delineated community bounded by the physical limits of the mussels, which in the intertidal are in turn restricted to a clearly definable zone by physical and biological factors (Suchanek, 1985). It is unlikely that many of the taxa present in the mussel matrix could survive elsewhere on the shore, without the protection provided by the mussels (Tokeshi and Romero, 1995). As such, immigration of taxa into the mussel beds in this study from elsewhere on the three rocky shores is highly unlikely to be causing the observed seasonal variations in community structure.

Species Interactions

The biological interactions within a species and between species may be important to the developing species composition, structure and the diversity of marine benthic communities (Osman, 1977). Haines and Maurer (1980) established that seasonal changes in faunal associates of the serpulid worm *Hydroides dianthus* were due to interactions of associates and predators. Similarly, Stoner (1985) concluded that changes in species composition over time of *Penicillus capitatus* may be due to species interactions, including displacement of certain taxa, positive or negative associations and differential susceptibility to predation. Various authors have suggested that seasonal decreases in abundance in various intertidal marine habitats might be the result of predation and spatial competition (Maurer *et al*, 1979). Keough and Butler (1983) demonstrated that the actions of a few species of resident organisms and predators could be shown to influence fluctuations in the number of species residing on the shells of the bivalve *Pinna bicolor*, but were not sufficient to account for the observed seasonal fluctuations. They decided it was more likely that, rather than the interactions between adult organisms, the important sources of variation were those processes that involved the dispersive stages of these species.

Little is known of species interactions within mussel beds, although many of the species show very close relationships. For example, on *M. edulis* beds in the Broadkill Estuary, Delaware, the nudibranchs *Doridella obscura* and *Cratena* sp. were found almost exclusively on the bryozoan *Membranipora tenuis* and the hydroid *Tubularia crocea*, respectively (Dean, 1981). In the same study, the predatory flatworm, *Stylochus ellipticus* was always associated with barnacles. Dean (1981) found a positive correlation between mobile species richness and sessile species richness on *M. edulis* beds, while a negative relationship was noted between mobile species richness and sessile species dominance. Such dominance of the community by certain sessile species may be the result of sessile adults inhibiting settlement of

other species (both mobile and sessile) by engulfing potential larval propagules (Sutherland and Karlson, 1977).

Environmental Factors

Physical disturbance of marine epibenthic communities, with the resultant local extinction of their fauna is an important factor, which might result in seasonal changes in community structure (Osman, 1977). Other authors such as Shelford (1930) and Kawahara (1965) have emphasised the importance of seasonal and annual changes in the physical environment, in causing change in species composition.

Buchanan *et al* (1978) found that benthic macrofaunal assemblages off the Northumberland coast showed significant seasonal and annual variation only when subject to an unstable temperature regime. Warmer winter water temperatures resulted in the replacement of larger bodied species (e.g. the polychaete, *Chaetozone setosa*) with species of a smaller body size (e.g. the polychaete, *Paraonis gracilis*). They concluded that different suites of species enjoyed competitive advantage at different points of the temporal range of temperature variability, which in turn allowed the community to maximise its performance throughout a broad range of environmental variability. Similarly, Peake and Quinn (1993) concluded that the seasonal differences observed in clumps of the mussel, *Brachidontes rostratus*, in Australia were probably due to physical stress on shores in summer and autumn, when high temperatures often coincide with low tides in the middle of the day, thus resulting in reduced species numbers.

Surface water temperatures for the North Wales coast over the temporal scale of this study ranged from 8.0°C at the beginning of the study, in March 1998 to 17.0°C in August 1998 and back to 7.5°C in January 1999. Temperatures in the following twelve months, covering the period of the annual study were virtually identical to these. Within a mussel bed, physical conditions can be very different to those outside the matrix, with less extreme temperatures and humidity (Seed and Suchanek, 1992; Lintas and Seed, 1994). Suchanek (1980) found that on a sunny day, the temperature at the base of a 25cm thick *Mytilus californianus* bed was between 5° to 13°C cooler than at the surface. Thus, although *M. edulis* and *P. purpuratus* beds in this study would not provide the same protection from temperature fluctuations as the multi-layered *M. califomianus* beds in Suchanek's study, it is still unlikely that the observed temperature changes (7.5°C to 17.0°C) would result in any major species extinctions. In addition, none of the environmental

parameters measured over the course of the study were seen to affect community structure patterns at any of the three sites in the UK.

A possible cause of the observed temporal and spatial variation in the structure of the community associated with *P. purpuratus* was the El Niño-Southern Oscillation (ENSO), which occurs every four to seven years, with varying intensity (Philander, 1990). This phenomenon is characterised by a reduction in the amount of upwelling of nutrient-rich, cold waters along the eastern Pacific, caused by warmer, nutrient-poor surface waters flowing from the western Pacific. This results in a drastic decline in primary productivity, which adversely affects all levels of the food chain (NOAA, 2000). It is widely accepted that pelagic systems are physically driven by large-scale, low frequency events, such as El Niño and more recently, the importance of such large-scale processes in structuring benthic communities has been recognised (e.g. Gomez-Gutierrez *et al*, 1995; Hernandez-Trujillo, 1999; Davis, 2000). Many authors have shown that temporal and spatial patterns of benthos at all latitudes are determined by primary productivity (e.g. Alongi, 1990), while it is suggested that coastal upwelling promotes enrichment of littoral communities due to increased nutrient supply (Camus and Andrade, 1999). El Niño has been observed to affect significantly larval recruitment, and thus the structure of kelp forest communities in California (Tegner *et al*, 1997; Dayton *et al*, 1999), rocky intertidal communities in California (Sagarin *et al*, 1999), tide-pool fish assemblages in Southern California (Davis, 2000) and coral communities in the tropical eastern Pacific (Fong and Glynn, 2000). Since the El Niño event in 1997-1998 was particularly strong (NOAA, 2000), the phenomenon would probably affect the structure of mussel communities over the course of the present study, by influencing the reproduction and recruitment of constituent taxa.

In summary, the multivariate analysis of the structure of the infaunal communities associated with *M. edulis* beds at three sites on the North Wales coast and *P. purpuratus* at four sites on the coast of Chile, showed significant intra- and inter-annual variations. Such variations in community structure are clearly the result of complex biological interactions and processes within the mussel matrix. However, it is most likely that such variations are predominantly due to seasonal patterns of reproduction of infaunal species, leading to fluctuations in larval abundance and recruitment into the mussel bed. It is also probable that many of the taxa responsible for seasonal changes in community structure do not utilise pelagic larvae as a means of reproduction. Other influencing processes such as species immigration and emigration, species interactions or extinctions due to temperature fluctuations probably play minor roles in structuring the communities. Peake and Quinn (1993),

similarly, concluded that seasonal variation in the structure of infaunal communities associated with *B. rostratus* were the result of a combination of unpredictable seasonal recruitment patterns and mortality patterns.

Chapter 7

Investigations into the effect of substratum heterogeneity on the invertebrate communities associated with *Mytilus edulis*

Abstract

Artificial mussel patches of manipulated low and high mussel density were placed, in the middle of the mussel zone at a site already colonised by naturally occurring *Mytilus edulis* beds. During a three-month period on the shore, manipulated mussel patches were colonised by 46 invertebrate taxa. The communities associated with mussel patches of low and high density differed, although not significantly, at either a univariate or multivariate level. The community structure of low density mussel patches showed more variability than high density patches. Nine dominant taxa characterised the structure of the community associated with the artificial mussel patches; nematodes, nemerteans, juvenile *M. edulis*, *Modiolula phaseolina*, chironomid larvae, *Carcinus maenas*, *Hyale prevostii*, *Idotea pelagica* and *Jaera albifrons*. Mussel density and mussel mass were the only environmental variables measured, to show significant differences between low and high density patches. The total number of organisms present in patches showed significant correlation with mussel density, while the total number of taxa showed significant correlation with the mass of coarse sediment. Multivariate analysis suggested a high degree of correlation between the environmental characteristics of the mussel patches and the structure of the associated community. It was concluded that habitat heterogeneity did have a structuring effect on the community associated with mussel patches of manipulated low and high mussel density at a multivariate level. It is unlikely that the communities associated with the artificial mussel patches were at the final point of colonisation, since they were less diverse than mussel communities previously sampled from the shore at the same site, in terms of species richness. The structure of the communities was probably the result of those taxa who reproducing during the time of the experiment, along with mobile taxa who recruited as adults from neighbouring natural mussel beds.

INTRODUCTION

Several studies have demonstrated the pervasive effects of habitat structure on community composition and diversity. Biologists have long held the view that physically complex habitats often contain more species than physically simple ones. This notion has been found to be true and quantified for a variety of marine habitats and communities, including intertidal boulder communities (McGuinness and Underwood, 1986), rocky intertidal shores (Bergeron and Bourget, 1986; Bourget *et al*, 1994; Archambault and Bourget, 1996; Thompson *et al*, 1996), subtidal reefs (Pimm, 1994), tropical intertidal habitats (Kohn and Leviten, 1976), the epifaunal associates of intertidal algae (Gee and Warwick, 1994; Jarvis and Seed, 1996) and intertidal rockpools (Willis and Roberts, 1996). In addition, several studies have highlighted the effect of substratum heterogeneity on the colonisation of various marine habitats following either natural or artificial defaunation. For example Beukema *et al* (1999) and Ford *et al* (1999) investigated such processes in the infaunal associates of sandy intertidal habitats, while Kim and DeWreede (1996) conducted studies of recolonisation in rocky intertidal habitats. Similar studies have been conducted into recolonisation of subtidal reefs (Airoldi, 2000), littoral rockpools (Benedetti-Cecchi and Cinelli, 1996; Benedetti-Cecchi, 2000a), intertidal oyster reefs in the south-eastern United States (Meyer and Townsend, 2000) and estuarine fouling assemblages in Botany Bay, Australia (Anderson and Underwood, 1994).

The mechanisms driving recolonisation processes are poorly understood, but a complicating problem is that different sources of habitat structure can be confounded in both surveys and experiments (Berlow, 1997). Ecologists appreciate that many factors concurrently influence the distribution and abundance of organisms and that single factor analyses or experiments are insufficient to understand how populations, groups of species or communities are structured (Rotenberry and Wiens, 1985). As such, field experiments have proven to be powerful tools used by ecologists to elucidate causal processes of community organisation (Paine, 1977; Hairston, 1989; Lubchenco and Real, 1991). However, field experiments can be difficult to interpret if the effects of spatial and temporal variation are unknown. The most effective experiments are therefore those designed and interpreted in the context of a well-known system (Polis *et al*, 1997). Field experiments must deal with both chance chaotic changes and with large random or directional variation in factors and forces over scales from hours to decades (Rotenberry and Wiens, 1985).

Various authors have demonstrated experimentally, the importance of substratum heterogeneity as a controlling factor in community diversity, through the colonisation of objects in marine areas (e.g. Anderson and Underwood, 1994; Jacobi

and Langevin, 1996; Pugh, 1996). A variety of artificially created substrata have been used to investigate the effects of substratum heterogeneity on colonisation and diversity, including artificial crevices (Kensler and Crisp, 1965), concrete blocks (Kawahara, 1965) and panels of various types (e.g. Turner *et al*, 1969; Haderlie, 1971), while Petraitis (1990) demonstrated that surface rugosity (i.e., surface heterogeneity) played an important role in enhancing mussel recruitment on rocky shores in Maine, USA.

In this chapter, the influence of substratum heterogeneity on the establishment and diversity of the invertebrate communities associated with *M. edulis* is investigated experimentally, using panels to which are attached mussel patches of manipulated density. A univariate and multivariate approach is taken to compare the communities associated with mussel patches of low and high mussel density. The extent to which various environmental parameters of the mussel matrix such as mussel volume and the mass of fine and coarse sediment fractions, affect community structure, which themselves, might be a reflection of differences in mussel density are also investigated.

METHODS

Fourteen cages, of dimensions ≈100x100x20mm were constructed using 'Twiweld' 10mm^2 PVC-covered wire mesh. These cages were designed to enclose a 100x100mm slate slotted into the base, thus creating a completely enclosed mesh box. Slate was chosen as it provided a substratum similar to the rock surface on the shore at Point Lynas. Slightly larger Perspex panels were constructed, such that the entire mesh cage and slate unit could be attached using screws and held in place on the panels. A month prior to the commencement of the experiment, during spring tides in May 2000, small patches of intertidal substratum at Point Lynas were cleared using a paint scraper of all biota, and washed with freshwater. Patches were cleared such that they were equally interspersed throughout the mid-shore area, on substratum already extensively colonised by beds of *Mytilus edulis*. The Perspex panels without mesh cages were cemented to the shore, using quick-setting cement and left for one month, in order to test their strength of attachment.

Mussels (shell lengths >5mm) were collected from the shore at Point Lynas and cleaned and sorted into 1mm-size categories in the laboratory. Each of the fourteen mesh cages were then filled with these mussels, such that seven of the cages were packed with mussels (shell length 25-35mm), providing a low mussel density of restricted size. The remaining seven cages were filled with mussels from the available size range (shell length 5-35mm) and were thus packed at higher

densities, thereby providing greater structural complexity and substratum heterogeneity. Once the mesh cages had been filled with mussels, the slate base was slotted into place in the base of the mesh cage and the units placed in running seawater in the laboratory, to allow the mussels to lay down byssal attachments. During this time, the mussels were fed daily on a mixture of *Tetraselmis suecica* and *Rhinomonas reticulata*. After one month, the fourteen artificial mussel patches were placed in buckets of seawater, transported to the shore at Point Lynas and screwed onto the pre-cemented Perspex panels. These manipulated mussel patch densities were randomly allocated to the Perspex panels. The panels were then left, undisturbed for a period of three months, in order to allow colonisation to take place. After this time, each, containing its mussels and all associated organisms were removed from the panels and immediately returned to the laboratory for sorting.

In the laboratory, the contents of each mesh cage, including the mussels and associated macro- and meiofauna were sieved through a 63µm mesh, with 63µm filtered seawater. All material passing through the sieve was retained, placed in containers and allowed to settle for 48 hours, after which time the seawater was decanted and any remaining material dried in at oven at 60°C for 48 hours, to calculate the dry weight. The mussels and their associated fauna were then fixed in 7% formalin, placed in labelled containers, and stored in the laboratory to await sorting. Samples were then washed and sorted and data analysed according to methods previously described.

RESULTS

A total of 6216 infaunal organisms representing 46 different taxa had colonised the artificially created mussel patches at Point Lynas, during a period of three months. None of the univariate measures of community diversity (total number of taxa, total number of individuals, Margalef's index of richness, Shannon's index of diversity and Pielou's evenness) was significantly different between the artificially created patches with manipulated low and high mussel densities.

MDS ordination of square-root transformed infaunal abundance indicated that there was a small degree of separation between the mussel bed communities from the artificially created patches of high and low packing densities (Figure 1a). The communities associated with the high density mussel patches were, in general, more similar to each other than those communities associated with the low density patches, implying a greater variability in community structure at low mussel packing densities. A one-way ANOSIM test performed on the data, however, revealed that there were no significant differences in community structure between the mussel patches with high and low packing densities ($R=-0.032$, $p>0.05$). The negative R-

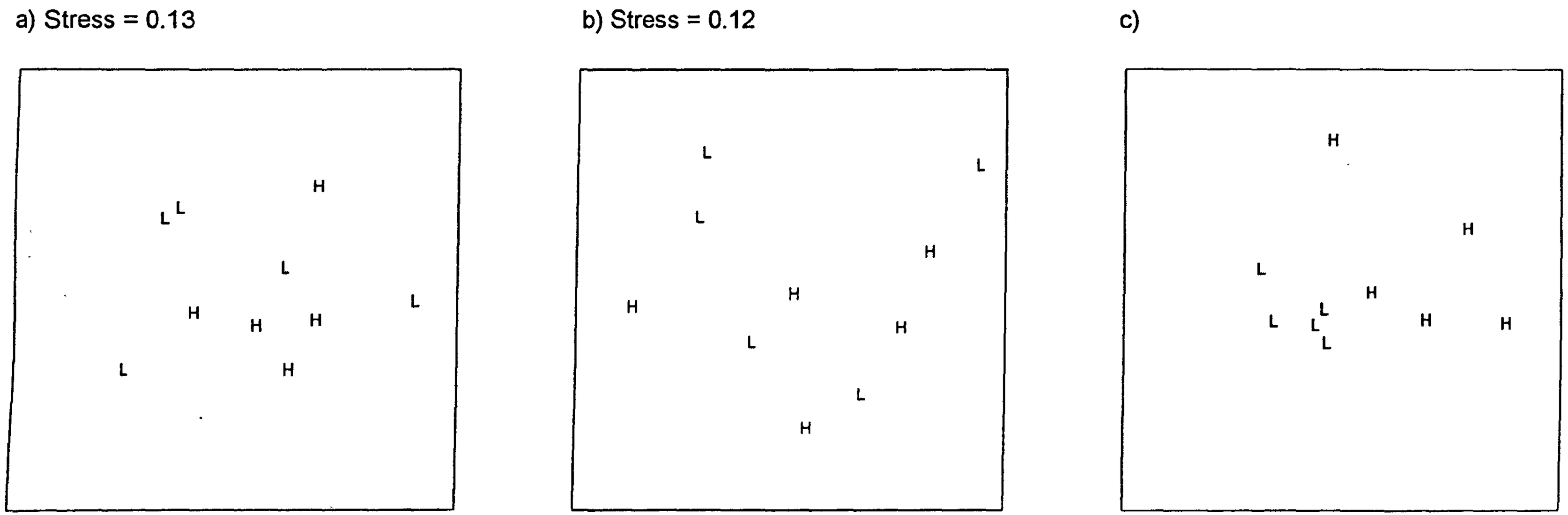


Figure 1 MDS ordination of Bray-Curtis similarity matrix of a) square-root and b) presence/absence transformed taxa abundance data from panels placed on the rocky shore at Point Lynas, Anglesey, with manipulated low (L) and high (H) packing density and c) ordination by PCA of environmental variables based on normalised Euclidean distance.

value indicates a high degree of variation in community structure between panels with the same packing density, as suggested by the pattern of ordination in Figure 1a. MDS ordination performed using a presence/absence transformation on infaunal abundance failed to demonstrate any clear separation of the mussel bed communities amongst the artificially created patches at high and low packing densities (Figure 1b). This was confirmed by a one-way ANOSIM performed on the data, which showed there were no significant differences between mussel patches at high and low packing densities ($R=-0.148$, $p>0.05$). As was the case for square-root transformed data, a negative R-value indicated a high degree of variation in community structure between panels of the same packing density, as suggested by the pattern of ordination in Figure 1b.

Similarity percentages analysis (SIMPER), performed with a square-root transformation indicated that the communities associated with the mussel patches of different density were characterised, to varying degrees, by the same nine dominant taxa (nematodes, nemerteans, juvenile *M. edulis*, *Modiolula phaseolina*, chironomid larvae, *Carcinus maenas*, *Hyale prevostii*, *Idotea pelagica* and *Jaera albifrons*). Variations in the abundance of these taxa between the mussel patches and their contribution to differences in community structure are shown in Table 1. A similar result was obtained when SIMPER analysis was performed using a presence/absence transformation, although more taxa characterised the mussel communities of each packing density. While some taxa were consistently present in mussel patches of high and low packing density, others appeared to have more restricted distributions. In particular, epifaunal organisms such as barnacles and anemones were present mainly in mussel beds at low packing density, while many infaunal organisms, such as oligochaetes, benthic Foraminifera and *Lasaea adansoni* were found at greater abundance in the high packing density mussel beds. A breakdown of the contributions of various taxa to differences in community structure between mussel beds of high and low packing densities is given in Table 2.

The total number of mussels per unit area of mussel bed was significantly greater in mussel beds where there was a high packing density, while the mass of mussels was greater in the low density beds (Table 3). None of the other environmental variables showed significant variation at the two packing densities. Univariate measures of community diversity did not show a high degree of correlation with environmental factors measured in the mussel beds; many showed relatively constant values, regardless of changing environmental conditions (Figure 2). However, the total number of infaunal organisms in the mussel beds did show significant positive correlation with the total number of mussels ($r = 0.644$). In

Table 1 Results of similarity percentage analysis (SIMPER) performed on square-root transformed abundance of taxa present in the manipulated low and high density mussel patches at Point Lynas, Anglesey. A breakdown is provided of % contribution (% Cont.) of taxa to average dissimilarity between mussel beds of low and high density; taxa are ordered in decreasing contribution to the average dissimilarity (cut-off at 90% average dissimilarity).

Taxa	Mean No. 100cm^{-2}		%	Cumulative %
	Low density	High density		
Nemertea indet.	39.4	78.8	12.07	12.07
Juvenile *Mytilus edulis*	284.0	393.2	10.53	22.60
Idotea pelagica	10.4	47.4	7.41	30.02
Hyale prevostii	20.8	33.4	6.47	36.49
Nematoda indet.	27.4	33.2	6.16	42.64
Chironomid larvae indet.	67.0	61.8	5.34	47.98
Leptocythere pellucida	13.8	3.2	4.71	52.69
Nucella lapillus	1.6	9.8	4.03	56.72
Mite sp. 1	7.6	4.2	3.45	60.18
Juvenile barnacles indet.	3.4	0.2	3.07	63.25
Modiolula phaseolina	10.2	11.4	2.76	66.01
Jaera albifrons	6.4	8.2	2.75	68.76
Copepoda indet.	2.8	1.0	2.31	71.07
Carcinus maenas	21.2	16.0	2.16	73.23
Elminius modestus	2.0	1.4	1.86	75.09
Oligochaeta indet.	0.6	1.4	1.78	76.87
Platyhelminthe indet.	3.0	0.2	1.57	78.44
Lasaea adansoni	0.2	1.2	1.41	79.85
Limapontia depressa	0.6	0.8	1.38	81.23
Benthic foraminifera indet.	0.2	1.6	1.29	85.52
Pinnotheres pisum	0.6	0.0	1.25	83.77
Rissoa parva	0.2	0.8	1.25	85.02
Littorina obtusata	0.8	0.0	1.13	86.15
Dipteran pupae indet.	0.6	0.2	1.12	87.27
White anemone indet.	0.6	0.0	1.11	88.38
Typosyllis prolifera	0.6	0.2	1.04	89.42
Brania pusilla	1.6	0.0	0.93	90.36

Average dissimilarity between mussel patches of low and high packing densities = 33.64%

Table 2 Results of similarity percentage analysis (SIMPER) performed on presence/absence transformed abundance of taxa present in the manipulated low and high density mussel patches at Point Lynas, Anglesey. A breakdown is provided of % contribution (% Cont.) of taxa to average dissimilarity between mussel beds of low and high density; taxa are ordered in decreasing contribution to the average dissimilarity (cut-off at 90% average dissimilarity).

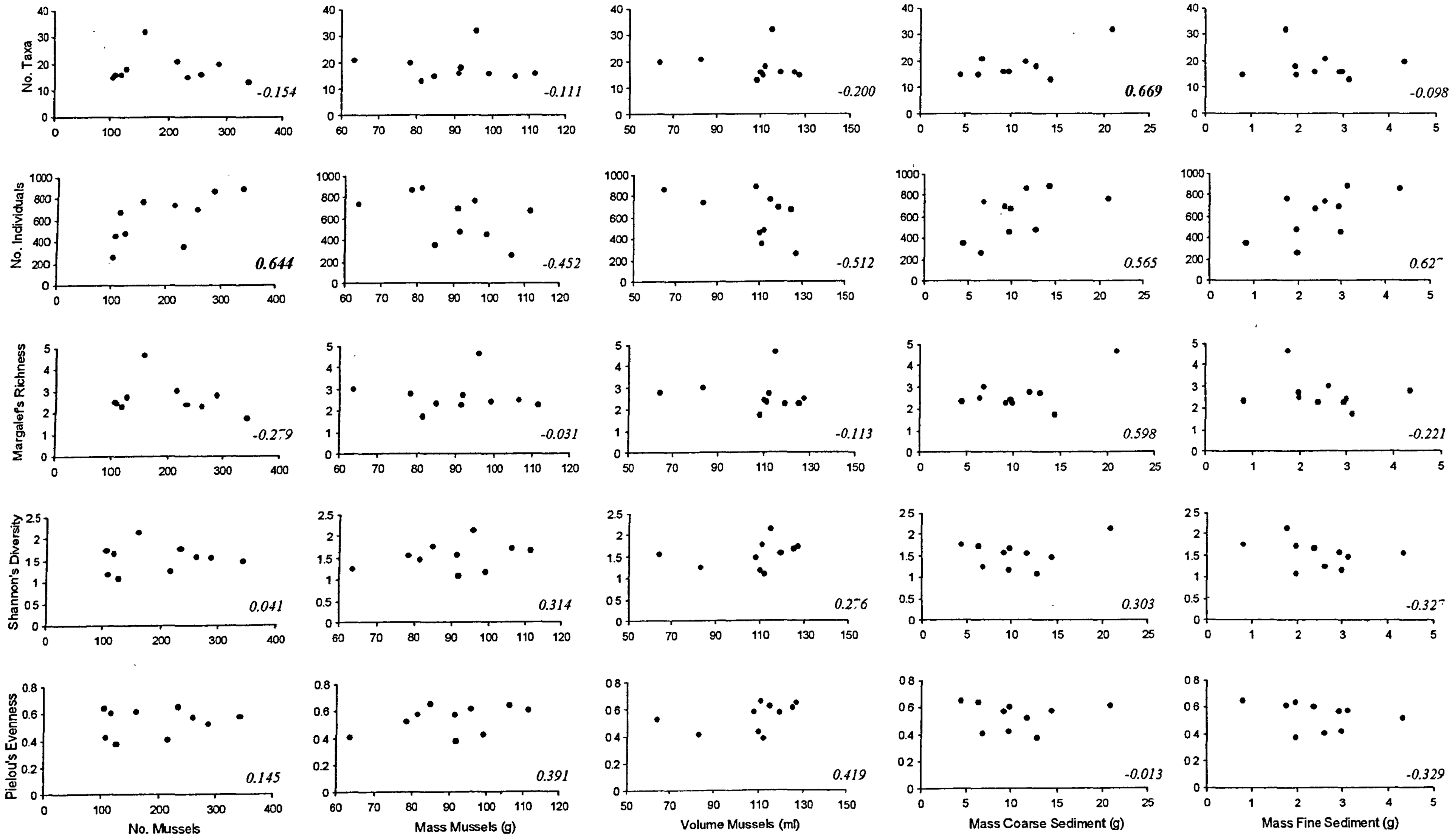
Taxa	Mean No. 100cm^{-2}		%	Cumulative %
	Low density	High density		
Juvenile barnacles indet.	3.4	0.2	4.73	4.73
Leptocythere pellucida	13.8	3.2	4.73	9.47
Pinnotheres pisum	0.6	0.0	4.62	14.09
Copepoda indet.	2.8	1.0	4.26	18.35
Oligochaeta indet.	0.6	1.4	4.02	22.38
Limapontia depressa	0.6	0.8	3.79	26.17
Elminius modestus	2.0	1.4	3.77	29.94
Rissoa parva	0.2	0.8	3.63	33.57
Lasaea adansoni	0.2	1.2	3.48	37.05
White anemone indet.	0.6	0.0	3.44	40.49
Mite sp. 1	7.6	4.2	3.44	43.93
Dipteran pupae indet.	0.6	0.2	3.40	47.32
Typosyllis prolifera	0.6	0.2	3.29	50.61
Brachystomia scalaris	0.2	0.4	3.27	53.88
Littorina obtusata	0.8	0.0	2.96	56.84
Ophiothrix fragilis	0.4	0.0	2.85	56.69
Nucella lapillus	1.6	9.8	2.81	62.51
Nemertea indet.	39.4	78.8	2.65	65.15
Idotea granulosa	0.4	0.2	2.63	67.78
Littorina mariae	0.2	0.2	2.61	70.39
Turbellaria indet.	0.2	0.4	2.38	72.77
Benthic foraminifera indet.	0.2	1.6	2.24	75.01
Harmothoe sp.	0.2	0.2	2.24	77.26
Platyhelminthe indet.	3.0	0.2	2.21	79.47
Scolelepis squamata	0.0	0.4	1.84	81.31
Hyale prevostii	20.8	33.4	1.84	83.16
Omalogyra atomus	0.2	0.0	1.77	84.93
Juvenile gastropoda indet.	0.0	0.6	1.68	86.61
Heterocythereis albomaculata	0.0	0.2	1.68	88.29
Orchestia gammarellus	0.2	0.0	1.67	89.95
Dynamena pumila	0.0	0.2	1.46	91.42

Average dissimilarity between mussel patches of low and high packing densities = 34.53%

Table 3 T-tests between environmental variables measured in mussel beds of manipulated low and high packing densities at Point Lynas, Anglesey. Significant differences are marked * ($p<0.05$).

Environmental Variable	Mean Value at Low Density	Mean Value at High Density	t
Number mussels	122	266	-5.95*
Mass mussels (g)	100.79	79.70	3.60*
Volume mussels (ml)	117.8	97.0	1.93
Mass coarse sediment (g)	11.90	9.27	0.87
Mass fine sediment (g)	2.20	2.75	-0.90

Figure 2 Environmental variables measured in mussel beds (per 100cm^2 mussel bed) plotted against various univariate measures of diversity. Correlation coefficients are shown in italics. Values in bold type and larger font indicate significant correlation.


No. Taxa
-0.154
-0.111
-0.200
0.669
-0.098
No. Individuals
0.644
-0.452
-0.512
0.565
0.62
Margalef's Richness
-0.279
-0.031
-0.113
0.598
-0.221
Shannon's Diversity
0.041
0.314
0.276
0.303
-0.32
Pielou's Evenness
0.145
0.391
0.419
-0.013
-0.329
No. Mussels
Mass Mussels (g)
Volume Mussels (ml)
Mass Coarse Sediment (g)
Mass Fine Sediment (g)

addition, the total number of taxa was significantly correlated with the mass of coarse sediment ($r = 0.669$).

Ordination by PCA of the environmental data from the mussel samples (Figure 1c) showed that replicate samples from mussel beds of manipulated low packing density clustered more distinctly than those of manipulated high density. The first two Principal Components accounted for 78% of the variability in the environmental data. PC1 was a linear combination of the environmental parameters, with increasing values of mussel density and sediment content and decreasing values of mussel mass and volume.

Determination of correlation coefficients between environmental variables measured in the mussel beds of manipulated packing density failed to reveal any high levels of correlation ($r>0.95$), although there was some significant correlation between variables (Table 4). Subsequently, all environmental variables measured in the mussel beds were entered into the BIOENV procedure. However, this analysis failed to identify any high levels of correlation between environmental parameters and square-root or presence/absence transformed biotic data. The mass of coarse sediment was the most important factor influencing the square-root transformed biotic data set ($r_s=0.307$), while the mass of mussels and the mass of coarse sediment gave the highest correlation with the presence/absence transformed data set ($r_s=0.032$).

RELATE analysis performed between the environmental data similarity matrix, produced using normalised Euclidean distance and the biotic data similarity matrices, produced using Bray-Curtis similarity, with a square-root and a presence/absence transformation failed to reveal significant differences ($R=0.006$, $p>0.05$; $R=-0.356$, $p>0.05$). Thus, there is a high degree of correlation between the combined physical and environmental characteristics of the mussel beds and the multivariate structure of the associated communities.

These results indicate that although the communities, which had colonised panels of manipulated low and high density, did differ, such differences were not significant. The community associated with low density patches showed greater variability than high density patches. Multivariate analysis suggested a high degree of correlation between the environmental characteristics of the mussel patches and the structure of the associated community.

DISCUSSION

During the three-month period that the manipulated mussel patches of low and high density were present on the rocky shore at Point Lynas, both were

Table 4 Correlation coefficients calculated between environmental variables measured in mussel patches of manipulated low and high mussel density at Point Lynas, Anglesey. Figures in bold indicate significant correlation ($p<0.05$).

	Mass Mussels	Volume Mussels	Mass Coarse Sediment	Mass Fine Sediment
No. Mussels	**-0.682**	-0.510	0.068	0.423
Mass Mussels		**0.776**	0.095	-0.265
Volume Mussels			-0.001	-0.610
Mass Coarse Sediment				0.166

successfully colonised by a wide variety of invertebrate taxa. Since intertidal environments are often dominated by physiologically 'robust' organisms, they might be expected to have relatively rapid rates of colonisation (Olsgard, 1999) and this has been demonstrated by a number of workers, in a variety of intertidal habitats. For example, in a study of faunal utilisation of artificially created intertidal oyster reefs in the south-eastern United States, Meyer and Townsend (2000) found that the reefs could quickly acquire functional ecological attributes of their natural counterparts and were rapidly colonised by infaunal species. Similarly, in a study of the recolonisation of a sandy, intertidal habitat in Florida, following a massive outbreak of red tide, Simon and Dauer (1994) found that the fauna made a rapid recovery in terms of species numbers and composition. They found that polychaetes were the most rapid colonists both in terms of the number of species and individuals, while other groups, such as molluscs and amphipods were slower to appear since they were significantly affected by seasonal patterns of reproduction, and thus dispersal. Within a mussel bed however, physical conditions can be very different to those outside the matrix, with reduced wave action, less extreme temperatures and an increase in sedimentation and humidity (Lintas and Seed, 1994). As such, the species occupying the mussel beds might be less robust and may not be capable of such rapid rates of recolonisation. Several workers have shown that the recovery of mussel beds from disturbance is a long-term process and varies from one assemblage to another. For example, when *Mytilus californianus* were removed from the rocky intertidal, complete recolonisation took around 60-80 months, although this figure refers to recolonisation by the mussels themselves, along with the associated community (Suchanek, 1979). Paine and Levin (1981) however, found that very small patches created in *M. californianus* beds were colonised almost immediately due to a leaning response of the border mussels, in which surrounding mussels encroach into the space. However, both these studies relate to complete recovery of mussel communities from cleared bare rock, rather than recovery from defaunated intact mussel patches. In a study of the colonisation of artificial mussel patches, Suchanek (1979) demonstrated that within one year, an associated community equivalent to real mussel beds of comparable structural complexity had become established. It is likely therefore, that the communities in the present study were not at the final point of recolonisation, since they were less diverse than mussel communities previously sampled from the shore at Point Lynas, in terms of species richness (see Chapters 2-5).

Analyses of the mussel bed communities, which had developed on the experimental panels, revealed that patches of low and high mussel density were

characterised by the same subset of around ten taxa. Such observations might simply reflect the availability of those taxa reproducing during the term of the experiment. Many authors have demonstrated that the nature of the recolonisation process in marine benthic communities, following disturbance or defaunation is dependent on the species present around the time of cessation of the disturbance. For example, Suchanek (1979) stated that when *Mytilus californianus* populations were artificially or naturally disrupted, season was an important factor in determining the identity and timing of colonising fauna and flora that occupied the recovering disturbance gaps. In addition, Dean (1981) showed that species settling into a recovering *Mytilus edulis* community in the Broadkill Estuary, Delaware, displayed highly seasonal settlement patterns that determined much of the development sequence. Similarly, Kaehler and Williams (1998) and Willis and Roberts (1996) found that in colonisation studies on rocky shores in Hong Kong and New Zealand, respectively, the timing of liberation of rock space was important for the development of floral and faunal assemblages. Settlement and metamorphosis of pelagic larvae are generally considered the most critical phases in the development of marine benthic assemblages (Olsgard, 1999). Variation in the recruitment of benthic marine invertebrates is often attributed to the interaction between the supply of new individuals to a habitat and the availability of space for colonisation when they arrive (Minchinton, 1997). Also important in determining variation in recruitment is the response of the larvae to the characteristics of the habitat, since larvae of many benthic marine invertebrates show a high degree of specificity of requirements when selecting a habitat (e.g. Benedetti-Cecchi, 2000a; Downes *et al*, 2000).

Previous studies of patterns of recolonisation have demonstrated that variability in species recruitment at early stages of colonisation can dictate much of the subsequent dynamics in the system (e.g. Dayton, 1971; Menge, 1976; Osman, 1977; Lubchenco and Menge, 1978; Benedetti-Cecchi, 2000b). In a study of the dynamics of space occupancy on a mussel-dominated shore in subtropical South America, Tokeshi and Romero (1995) demonstrated a clear trade-off between colonisation ability and competitive ability amongst many taxa, which affected community structure. For example, while the barnacle *Jehlius cirratus* showed much higher colonisation rates than the gallery-building polychaete, *Phragmatopoma moerchi*, the latter species was competitively superior. Similarly, in a study of colonisation patterns on intertidal sand-flats, Thrush *et al* (1992) highlighted the importance of facilitatory interactions in macrofaunal recolonisation, with the presence of certain taxa affecting the abundance of others. Similar interactions have been observed on rocky shores in South Africa (Vanzyl and Robertson, 1991) and

Oregon, North America, where Farrell (1991) noted that both direct and indirect interactions between species determined community structure.

It is highly probable in the present study, that some or all of these common taxa did not colonise the mussel patches as juveniles, but migrated as adults from the surrounding mussel beds. Peterson *et al* (1986) stated, that in mussel beds, only those species which can migrate to recently opened patches will be common in the community, whether they migrate from older patches or from areas that are not dominated by mussels. Similarly, Reed *et al* (1997) pointed out the importance of adult dispersal in the recovery of populations that have been locally disturbed and that many sessile species, which have limited dispersal potential, often rapidly colonise areas that have been recently disturbed. In the present study, many of the more common taxa, such as nemerteans, isopods, amphipods and gastropods probably recruited to the mussel patches in this manner, rather than as juveniles, since panels were placed on the shore in areas already colonised by mussels.

The present study, conducted for only three months, was unable to identify any significant differences in community structure between the mussel patches of manipulated low and high density, with the same abundant taxa dominating both. Community recovery from pollution events, such as oil spills has been shown to proceed through a series of severe fluctuations of a few dominant interacting species, before diversity and equilibrium are restored (Southward, 1982). Thus, as previously suggested, it is possible that the mussel patches in the present study were at an early stage of community development and any differences in community structure due to substratum heterogeneity were masked by this factor. Therefore, had it been possible to leave the panels on the shore for a longer period of time, differences in community structure might have emerged. Analyses of the data did however, suggest that there was some link between environmental parameters and the associated infaunal community. Many studies have demonstrated the important effects of substratum heterogeneity on the structure of a variety of benthic assemblages. For example, in studies of the diversity of colonising mobile epifauna on artificial panels, Jacobi and Langevin (1996) found that the effect of the original substratum complexity seemed to be restricted to the early stages of colonisation, since after this initial period, the substratum became modified by organisms themselves. Jones and Boulding (1999) demonstrated both with the use of natural and artificial substrata, that significantly more intertidal littorinid snails recruited to topographically complex microhabitats than less complex ones. In a study of the effect of artificial macrophyte beds of varying structure on fish assemblages in southern Australia, Jenkins and Sutherland (1997) concluded that the physical

structure of the habitat influenced fish assemblages beyond the simple presence or absence of structure. In addition, several workers have demonstrated the important effect of substratum heterogeneity on the communities associated with mussel beds. Suchanek (1980) concluded that the physical structure of the mussel matrix was the single most important factor in promoting biological diversity. In both *Mytilus edulis* and *M. californianus* beds, species richness and diversity were shown to be positively correlated with age and structural complexity of the mussel matrix (Suchanek, 1979, 1985; Tsuchiya and Nishihira, 1985, 1986; Lintas and Seed, 1994). Possible mechanisms for this apparent positive effect of habitat heterogeneity on benthic community species diversity have been suggested and include; the provision of spatial refuges from predators or physical stress (Kohn and Leviten, 1976; Lubchenco and Menge, 1981) and reduction of competitive interactions, through the provision of a variety of substrata for feeding and shelter (Abele, 1974; Ricklefs, 1980). In addition, Ricklefs (1980) stated that it is probable that the heterogeneity created by the presence of many species provides further opportunity for the diversification of life, i.e. that diversity tends to breed more diversity.

In the present study, the mass of mussels, along with the mass of coarse sediment in the mussel patches were seen to be the two most important factors in structuring the community, with mussel density being a secondary, less important factor. Several workers have documented the positive effects of coarse sediments on diversity of rocky intertidal assemblages as a result of increased habitat diversity (e.g. Hicks, 1980; Gibbons, 1988). Using artificially constructed byssal mats, Crooks (1998) concluded that the presence of physical structure alone can produce several of the patterns observed in naturally occurring mussel beds and thus the presence of the mussels themselves was not an important factor. Similarly, Tsuchiya and Nishihira (1986) demonstrated that the observed lower species richness in monolayered *M. edulis* patches in Japan compared with multi-layered patches, was probably due to an increase in sediments and shell fragment contained within the latter. Thus, it would appear from these studies that the substratum provided by the sediments, byssal threads and shell fragments trapped within the mussel beds is more important than the structure provided by the mussels themselves, although these components are themselves dependent on the presence of mussels.

Chapter 8

General Discussion

GENERAL DISCUSSION

The preceding chapters clearly demonstrate that a wide variety of invertebrates inhabit intertidal mussel patches on rocky shores. The two mussel species in the present study; *Mytilus* edulis and *Perumytilus purpuratus* both formed similar, solid beds in the rocky intertidal zone in the British Isles and Irish Republic and Chile, respectively. Significant differences were, however, observed in the size and age structure of populations of the two mussel species (Chapter 3). *M. edulis* beds contained a higher overall density of mussels, with a greater number of small individuals, while *P. purpuratus* beds were more loosely packed and contained fewer small individuals. *M. edulis* had a faster growth rate than *P. purpuratus*, although *P. purpuratus* attained a greater maximum age. A total of 182 different invertebrate taxa were identified in intertidal *M. edulis* beds from various locations around the coasts of the British Isles and Irish Republic, while 61 different taxa were identified, to higher taxonomic levels, from the intertidal *P. purpuratus* beds in Chile, South America. The invertebrate communities associated with the two mussel species showed a high degree of variation over different spatial scales (Chapters 4 and 5), along with temporal variation (Chapter 6). This variation in the structure of the communities is the result both of changes in the abundance of the commoner taxa, along with more fundamental differences in the identify of taxa present. Since mussel bed communities occur in similar habitats, throughout the world, they might prove useful in monitoring studies. However, if they are to prove useful tools for monitoring the effects of anthropogenic activities in the marine environment, establishing the extent of natural variation in community structure is essential, encompassing both spatial and temporal scales.

Aggregations of mussels drastically modify the local environment through enhanced water retention, biodeposition of faecal and pseudofaecal material ('mussel mud'), and the provision of additional attachment surface and shelter by the mussels themselves – features which serve to encourage species enrichment in habitats wherever mussels are present in abundance, such that mussels are effective 'ecosystem engineers' (Lawton and Jones, 1995; Seed *et al*, 2000). Some of the organisms associated with intertidal mussel beds live attached to the mussel shells (epibiota), others typically live amongst the rich sediments and shell fragments which accumulate at the base of the bed (infauna), whilst mobile organisms rove freely through the complex matrix of shells and interconnecting byssus threads (Seed, 1996). The relationship between the mussels and each of the associated species may be negative, neutral or positive, while in general, infauna seem to be of negligible consequence to the health and well-being of the mussel beds, although

competitive abilities of the individual species are difficult to quantify (Svane and Setyobudiandi, 1996). Suchanek (1980) stated that some species are attracted to mussel beds by food resources, while others utilise the space as a refuge from physically imposed stresses (such as wave action or desiccation) or biological stresses (such as predation). As predators and scavengers locate these initial colonisers and other competitors enter the system, trophic links become more complex, thus increasing community stability (MacArthur, 1955; Paine, 1966). Various authors have stated that the increased species diversity on mussel beds produces a more complex food web, which in turn results in enhanced stability of the whole community (Brown and Seed, 1976; Dean and Hurd, 1980).

Mussel patches thus undoubtedly increase biodiversity on rocky shores, through a variety of mechanisms and several studies have described the diverse infaunal assemblages associated with intertidal mussel beds (e.g. Suchanek, 1980; Tsuchiya and Nishihira, 1985, 1986; Jacobi, 1987; Tsuchiya and Bellan-Santini, 1989; Ong Che and Morton, 1992; Peake and Quinn, 1993; Lintas and Seed, 1994; Seed, 1996). The present study generally found intertidal mussel beds on rocky substrata to support a greater number of invertebrate taxa than has previously been described, with the possible exception of *Mytilus californianus* on the west coast of North America (a larger bodied-mussel which forms particularly thick multi-layered beds). This might at least in part, be due to the fact that few of these previous studies have investigated spatial and temporal variability of these communities and have merely provided a spatially or temporally static description of the communities.

Many interacting and complex factors are probably responsible for the observed variation in the structure of the communities associated with intertidal mussel beds in the present study. Amongst them, mussel density is probably an important structuring factor (Chapter 7). However, understanding the dynamics of communities such as those associated with mussels requires integrating the local ecological perspective and traditional niche-based notions, such as resource partitioning, with large-scale phenomena (Myers, 1994) and evolutionary history (Hugueny *et al*, 1997, Karlson and Cornell, 1998, 1999). Such integration will necessarily encompass multiple spatial and temporal scales (Karlson and Cornell, 1999). Sagarin *et al* (1999) concluded that in studies of change in intertidal community structure, climatic warming drove the observed range-related community shifts. The authors concluded that habitat changes anthropogenic effects, indirect biological interactions, El Niño-Southern Oscillation (ENSO) events and upwelling are considered to be less important than climate change.

Mussel beds in the present study were observed to support generally similar overall numbers of taxa, when studied on similar temporal scales. This phenomena is reflected in the literature, in studies of communities associated with mussel beds at different locations and even between intertidal beds of different mussel species (see Seed, 1996; Seed *et al*, 2000 for reviews). Seed (1996) observed that in mussel beds of similar structural complexity and size, in different parts of the world, the total number of associated species and individuals are remarkably similar. To some extent the results of this work support this statement; the macroinvertebrate communities associated with rocky intertidal mussel patches particularly when these patches experience similar physical conditions and are of similar size and structural complexity, often exhibit a remarkable degree of conformity when compared using simple univariate statistics. Such observations suggest that when the associated communities are at, or near, equilibrium, mussel beds are occupied by taxonomically and functionally similar species. It seems therefore, that the pattern of parallel communities on rocky shores may be replicated to a certain extent, on a much finer scale within mussel patches (Seed, 1996). However, such univariate techniques, which collapse the full set of species counts into a single coefficient, tend to grossly oversimplify complex systems and reveal little about community organisation (Ricklefs and Schulter, 1993). Thus, although in many cases, the communities associated with intertidal mussel patches in the present study show little temporal or spatial variation in terms of their species richness, diversity and evenness, significant differences do emerge when multivariate techniques are applied to these same communities. The present study thus illustrates the importance of using a variety of resolutions to measure biodiversity.

Sites in the present study have assumed their distinctive character by virtue of sufficient and consistent differences in emphasis between taxa. Those taxa contributing to spatial and temporal differences when emphasis was placed on abundance, were rarely the same as those contributing to differences based on presence alone, such that diagnostic taxa may or may not be dominant. Whether such differences reflect increasingly optimal conditions for each taxa, or whether what is perceived is a spatial mosaic built up and maintained by differential fecundity and dispersion tendencies of taxa and subject to flux is not clear. For the purposes of this summary of the data presented in the preceding chapters, it was appropriate to take a holistic approach to analysis, to search for influential subsets of taxa, whose among-sample relationships capture nearly the same multivariate pattern as the full taxa set. BVSTEP analysis performed on the data for this purpose (as described in Chapter 2) revealed that there is a great deal of structural redundancy in the

communities associated with intertidal mussel beds (Table 1 and 2). This phenomenon was particularly apparent in small-scale spatial, or intra-shore variations in the structure of mussel communities, where a very small subset of taxa captured the same multivariate pattern as the full taxa set. It is commonly held that samples closer together in space should be more similar to each other than those further apart because of responses of organisms to patchy habitats or other organisms (e.g., Brown, 1984; Palmer, 1988, 1992; Carlile *et al*, 1989, Underwood and Chapman, 1996). In contrast, BVSTEP failed to identify any small subsets of taxa capturing the temporal variation in the communities. This reflects the fact that these data sets encompass fluctuations in presence and abundance due to reproductive cycles, in all taxa present. It is clear that temporal differences at sites do occur, as a result of reproductive patterns of the taxa present and as such, any investigations of patterns in community structure should take both seasonal and annual variation into account.

Analysis revealed a degree of consistency in the presence of certain taxa, such that intertidal *M. edulis* beds support a 'baseline' community characterised by a set of taxa, ubiquitous across spatial and temporal scales, namely nematodes, nemerteans, oligochaetes, cirratulid polychaetes and *Fabricia stellaris*, Clunio sp. larvae, mite sp. 1, the ostracods *Heterocythereis albomaculata* and *Leptocythere pellucida*, the isopods *Idotea pelagica* and *Jaera albifrons*, the amphipod *Hyale nilssoni*, the tanaid *Tanais dulongii*, the decapod *Carcinus maenas*, the gastropods *Rissoa parva*, *Skenea serpuloides* and *Brachystomia scalaris* and the bivalve *Lasaea adansoni*. Similar observations have been made in other marine assemblages, for example, Moore (1986) identified a set of amphipod species found in characteristic low or high abundance in kelp holdfast communities at northern British sites. Such ubiquitous taxa were often the most important in discriminating among assemblages across spatial and temporal scales. The same taxa were also important for measuring small-scale patchiness within each assemblage (i.e. between replicates on a shore). Similar results have been observed in other rocky shore habitats (e.g. Underwood and Chapman, 1998). Thus, investigations of this small subset of species, rather than the entire community structure, might prove to be a useful tool for future monitoring of these communities. In addition, since this study has shown that intertidal mussel beds of similar structure in different geographical locations support similar overall numbers of taxa and individuals, their overall diversity at comparable taxonomic levels might be monitored to reflect the quality of the environment.

Table 1 Taxa responsible for spatial and temporal variation in the community structure of intertidal mussel beds in the British Isles and Irish Republic and Chile, South America. Taxa have been selected as those whose among-sample relationships capture at least 95% of the multivariate pattern of the full taxa set, when subject to a square-root transformation. Figures in bold in Table headings indicate the Chapters to which the data refer.

Type of variation in mussel bed community structure studied					
Intra-shore, Point Lynas (4)	Intra-shore, White Beach (4)	Inter-shore, British Isles and Irish Republic (5)	Inter-shore, Chile (5)	Inter-country, British Isles, Irish Republic and Chile (5)	Temporal, Point Lynas, White Beach, Criccieth (6)
Sagartia ornata	*Harmothoe impar*	White anemone indet.	Anemones indet.	Anemones indet.	*Anthopleura ballii*
Turbellaria indet.	*Leptocythere pellucida*	Nematoda indet.	Nematoda indet.	Nemertea indet.	Nematoda indet.
Nemertea indet.	*Idotea pelagica*	*Eulalia viridis*	Hesionidae indet.	Nematoda indet.	Tubulanidae indet.
Oligochaeta indet.	Mite sp. 1	*Pholoe inornata*	Nereidae indet.	Nereidae indet.	Lineidae indet.
Clunio sp. larvae	*Rissoella opalina*	*Leptocythere pellucida*	Spionidae indet.	Syllidae indet.	Amphiporidae indet.
		Elminius modestus	Oligochaeta indet.	Oligochaeta indet.	*Harmothoe* sp.
		Hyale prevostii	Barnacles indet.	Barnacles indet.	*Cirratulus cirratus*
		Mite sp. 1	Amphipoda indet.	Amphipoda indet.	Eunicidae indet.
		Mite sp. 5	Crabs indet.	Mites indet.	*Scolelepis squamata*
		Lasaea adansoni	Sea spiders indet.	*Clunio* sp. larvae	*Spirorbis spirorbis*
		Brachystomia scalaris	Chironomid larvae indet.	Limpets indet.	*Heterocythereis albomaculata*
		Rissoa parva	Juvenile mussels	Juvenile mussels	*Leptocythere pellucida*
				Bivalves indet.	*Semicytherura nigrescens*
					Chthamalus montagui
					Tanais dulongii
					Idotea chelipes
					Idotea emarginata
					Jaera albifrons
					Janiropsis breviremis
					Hyale prevostii
					Calliopius laeviusculus
					Pinnotheres pisum
					Mite sp. 1
					Mite sp. 8
					Clunio sp. larvae
					Acanthochitona crinatus
					Modiolus modiolus
					Onoba semocostata
					Brachystomia scalaris

Table 2 Taxa responsible for spatial and temporal variation in the community structure of intertidal mussel beds in the British Isles and Irish Republic and Chile, South America. Taxa have been selected as those whose among-sample relationships capture at least 95% of the multivariate pattern of the full taxa set, when subject to a presence/absence transformation. Figures in bold in Table headings indicate the Chapters to which the data refer.

Type of variation in mussel bed community structure studied					
Intra-shore, Point Lynas (4)	Intra-shore, White Beach (4)	Inter-shore, British Isles and Irish Republic (5)	Inter-shore, Chile (5)	Inter-country, British Isles, Irish Republic and Chile (5)	Temporal, Point Lynas, White Beach, Criccieth (6)
Turbellaria indet.	White anemone indet.	Nematoda indet.	Anemones indet.	Anemones indet.	Juvenile mussels
Nematoda indet.	Nemertea indet.	*Brania pusilla*	Nemertea indet.	Turbellaria indet.	*Actinia equina*
Lepidontus clava	*Harmothoe impar*	*Capitella capitata*	Cirratulidae indet.	Nemertea indet.	*Actinia fragacea*
Harmothoe impar	*Cirratulus filiformis*	*Eusyllis blomstrandi*	Eunicidae indet.	Nereidae indet.	*Stomphia coccinea*
Pholoe inornata	*Nereimya punctata*	*Fabricia stellaris*	Nepthydae indet.	Phyllodocidae indet.	Platyhelminthe indet.
Capitella capitata	*Eteone picta*	*Harmothoe extenuata*	Nereidae indet.	Spionidae indet.	Cephalothricidae indet.
Chaetozone setosa	*Polydora ciliata*	Maldanidae indet.	Phyllodocidae indet.	Syllidae indet.	Emplectonematidae indet.
Cirratulus cirratus	*Fabriciola berkeleyi*	Nepthys indet.	Spionidae indet.	Oligochaeta indet.	*Lagisca extenuata*
Brania pusilla	Juvenile barnacles indet.	*Pholoe inoculata*	Terebellidae indet.	Ostracoda indet.	*Harmothoe* sp.
Heterocythereis albomaculata	*Elminius modestus*	*Pholoe inornata*	Oligochaeta indet.	Barnacles indet.	Eunicidae sp. 1
Littorina mariae	*Chaetogammarus marinus*	*Spirorbis spirorbis*	Ostracoda indet.	Isopoda indet.	*Perinereis cultrifera*
Musculus discors	Crab larvae indet.	*Typosyllis* sp.	Barnacles indet.	Amphipoda indet.	*Eulalia viridis*
		Heterocythere albomaculata	Isopoda indet.	Crabs indet.	*Polydora ciliata*
		Semicytherura nigrescens	Mites indet.	Chironomidae larvae indet.	Syllid sp. 1
		Chthamalus montagui	Sea spiders indet.	Chitons indet.	Syllid sp. 2
		Elminius montagui	Chironomid larvae indet.	Limpets indet.	*Fabricia stellaris*
		Elminius modestus	Insecta indet.	Gastropoda indet.	*Chthamalus montagui*
		Juvenile barnacles indet.	Chitons indet.	Opisthobranchia indet.	*Semibalanus balanoides*
		Idotea granulosa	Bivalves indet.	Mussels indet.	*Tanais dulongii*
		Idotea pelagica	Ophiuroids indet.	Bivalves indet.	*Idotea pelagica*
		Hyale prevostii			*Idotea baltica*
		Orchestia gammarellus			*Chaetogammarus laeviusculus*
		Mite sp. 2			*Liocarcinus puber*
		Mite sp. 5			*Pinnotheres pisum*
		Dipteran larvae indet.			Dipteran larvae indet.
		Lasaea adansoni			*Acanthochitona crinatus*
		Venerupis sp.			*Lasaea adansoni*
		Coriandria fulgida			*Chlamys varia*
		Lacuna pallidula			*Patella ulyssiphonensis*
		Patella vulgata			*Littorina saxatilis*
		Rissoa parva			*Littorina littorea*
		Skenea serpuloides			*Hydrobia ulvae*
					Cingula trifasciata
					Coriandria fulgida
					Rissostomia membranacea
					Rissoella opalina
					Nucella lapillus
					Juvenile gastropoda indet.

Mussels have been used extensively as biomonitors of environmental water quality throughout the world (e.g. Phillips, 1980; Bourgoin, 1990). Populations of intertidal mussels possess a variety of attributes, which facilitate their use for such monitoring studies (Widdows and Donkin, 1992). They have a wide geographical distribution and are commonly the dominant primary space occupiers on rocky shores. In addition, mussel populations are relatively stable and can be sufficiently large for repeated sampling, thus providing data on short and long-term community changes arising from anthropogenic activity. Since mussel populations are sedentary, their associated assemblages are therefore better than completely mobile species as integrators of anthropogenic activity in a given area. Mussels themselves are relatively tolerant of a wide range of environmental conditions, including moderately high levels of many types of contaminants, so given that they are suspension-feeders that pump large volumes of water and concentrate many chemicals in their tissues, the measurement of contaminants in mussel tissues provides an assessment of biological availability. Additionally mussels have a low level of activity of those enzyme systems capable of metabolising organic contaminants and thus measurements of such compounds in mussel tissues accurately reflects the magnitude of environmental contamination.

With the gradual acquisition of biological data on individual species along with communities, it becomes possible to understand patterns of distribution and to interpret community organisation. From such an understanding flows a capacity for prediction which is central to any baseline application (Lewis, 1980). Gross changes in the relative abundance of 'standard or indicator' species, or incursions by foreign species would suggest causes beyond those encompassed by such natural spatial or temporal variation, such as described here. Thus, although on initial investigation, the fauna inhabiting intertidal mussel beds might be considered intrinsically too complicated to play a useful role in surveillance and monitoring contexts, this study does suggest that a 'baseline' community occurs in relatively non-impacted mussel beds, many of which can be identified at higher taxonomic levels. In order to investigate whether this baseline community remains unaltered in mussel beds impacted from human activity, further investigations would be necessary. Thus, there appears to be a great deal of structural redundancy in the communities, such that when analyses are performed on the data, this small subset of the species data give a similar result to that of the full species analysis. Other authors have documented similar findings in a variety of marine benthic habitats (e.g. Gray *et al*, 1988; Warwick, 1993; Clarke and Warwick, 1998). Furthermore, many of these studies, concentrating on the effect of anthropogenic activities on the structure of

these communities have highlighted the fact that clear differences in community structure can be seen at relatively high taxonomic levels, thus removing he need to identify all organisms to the species level. It is the author's opinion that some of these baseline members of the community might occur in reduced population density in such an impacted site and as indicator species would serve as a useful monitoring tool. The statement that there is always a need for experimental verification of field hypotheses (Underwood, 1986) would apply here. As biodiversity typically reflects the quality of habitats and communities, mussel patches could prove to be valuable bioindicators of coastal and estuarine water quality. These data provide a rationale for utilising the communities associated with intertidal mussel beds in future monitoring studies, for example in investigations into the effects of anthropogenic activities on coastal areas. They highlight the need to recognise the high degree of temporal and spatial variation in the structure of these communities in such studies.

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Appendix I: Pearson's correlation coefficients (r), calculated between the abundance's of the118 taxa (number in italics) present in the mussel beds at Point Lynas and White Beach, during the study of small-scale spatial variation in community structure (see Chapter 4). The number code for taxa is given in the table following. Significant correlation's are marked in bold; * indicates one individual present only in samples.

	1	*2*	*3*	*4*	*5*	*6*	*7*	*8*
2	-0.034							
3	0.062	-0.017						
4	0.039	-0.050	0.029					
5	0.158	-0.020	-0.031	0.205				
6	0.176	0.066	0.131	-0.090	-0.038			
7	**0.294**	-0.055	0.115	0.029	-0.050	**0.279**		
8	-0.034	-0.011	-0.017	-0.050	-0.020	-0.044	-0.050	
9	-0.034	-0.011	-0.017	-0.050	-0.020	0.100	0.049	-0.011
10	0.339	-0.011	-0.017	-0.050	-0.020	0.077	0.287	-0.011
11	0.327	-0.014	-0.021	-0.052	-0.024	0.055	-0.094	-0.014
12	-0.046	-0.015	-0.024	-0.067	-0.027	-0.064	-0.128	-0.015
13	-0.079	-0.027	-0.041	-0.032	**0.296**	0.003	0.120	-0.027
14	-0.043	-0.015	-0.022	-0.063	0.162	0.336	-0.038	-0.015
15	-0.034	-0.011	-0.017	-0.050	-0.020	0.364	-0.001	-0.011
16	-0.074	-0.032	**0.570**	0.016	-0.040	0.161	0.173	-0.032
17	-0.042	-0.014	-0.022	-0.024	-0.025	-0.084	-0.042	-0.014
18	**0.239**	-0.030	-0.046	-0.131	-0.053	0.025	-0.043	-0.030
19	-0.055	-0.019	-0.028	-0.040	-0.033	0.048	0.074	-0.019
20	-0.034	-0.011	-0.017	-0.050	-0.020	-0.077	-0.102	-0.011
21	-0.034	**1.000**	-0.017	-0.050	-0.020	0.066	-0.055	-0.011
22	-0.034	-0.011	-0.017	-0.050	-0.020	-0.088	0.007	-0.011
23	-0.034	-0.011	-0.017	-0.050	-0.020	0.166	-0.007	-0.011
24	-0.034	-0.011	-0.017	-0.050	-0.020	-0.066	-0.092	-0.011
25	-0.065	-0.022	-0.034	-0.017	-0.039	-0.024	0.090	-0.022
26	0.252	-0.019	-0.029	-0.078	-0.033	-0.031	-0.154	-0.019
27	0.339	-0.011	-0.017	-0.050	-0.020	0.122	0.064	-0.011
28	-0.034	-0.011	-0.017	-0.050	-0.020	-0.066	-0.092	-0.011
29	-0.046	-0.015	-0.024	-0.067	-0.027	0.070	0.050	-0.015
30	-0.048	-0.016	-0.025	0.036	-0.029	-0.070	-0.057	-0.016
31	-0.094	-0.032	-0.048	0.007	-0.056	0.084	0.012	-0.032
32	-0.057	-0.019	-0.029	0.066	-0.034	-0.006	-0.060	-0.019
33	0.339	-0.011	-0.017	-0.035	-0.020	0.166	0.042	-0.011
34	0.272	-0.026	-0.039	-0.103	-0.045	0.063	-0.094	-0.026
35	-0.050	-0.049	-0.064	-0.066	-0.065	-0.167	-0.061	0.025
36	0.312	-0.015	**0.270**	-0.020	-0.026	0.053	**0.297**	-0.015
37	-0.034	-0.011	-0.017	-0.050	-0.020	-0.099	-0.095	-0.011
38	-0.043	-0.015	-0.022	0.100	-0.026	0.011	0.003	-0.015
39	-0.034	-0.011	-0.017	0.150	-0.020	-0.055	-0.094	-0.011
40	-0.034	-0.011	-0.017	-0.050	**0.571**	-0.033	-0.118	-0.011
41	-0.114	-0.042	0.029	0.095	0.070	0.079	0.168	-0.042
42	-0.069	-0.023	-0.036	0.010	**0.260**	-0.010	-0.062	-0.023
43	-0.034	-0.011	-0.017	0.020	-0.020	-0.099	0.084	-0.011
44	**0.217**	-0.016	-0.025	-0.064	-0.029	0.157	0.193	-0.016
45	-0.034	-0.011	-0.017	-0.050	-0.020	0.044	-0.025	-0.011
46	0.015	-0.010	-0.008	0.160	-0.034	**0.239**	**0.254**	-0.075
47	-0.056	0.073	0.058	0.061	0.178	0.167	0.003	-0.054
48	0.006	-0.072	0.315	0.122	0.082	-0.041	**0.289**	0.052
49	-0.054	-0.018	-0.028	-0.059	**0.280**	-0.073	-0.059	-0.018
50	0.027	0.127	**0.678**	0.174	0.016	**0.235**	0.176	-0.061
51	-0.072	-0.093	-0.041	**0.222**	-0.003	-0.161	0.109	-0.005
52	-0.053	-0.018	-0.027	**0.542**	-0.031	-0.149	0.074	-0.018
53	-0.034	-0.011	-0.017	0.105	-0.020	-0.022	-0.136	-0.011
54	-0.034	-0.011	-0.017	0.150	-0.020	-0.055	-0.094	-0.011

	1	2	3	4	5	6	7	8
55	-0.141	-0.029	0.147	0.144	0.012	0.144	-0.000	-0.051
56	-0.126	-0.018	-0.065	0.181	0.077	-0.134	-0.101	-0.047
57	-0.075	-0.027	0.404	0.085	0.011	0.218	0.339	-0.038
58	-0.035	-0.012	-0.018	-0.022	-0.021	-0.090	-0.110	0.036
59	0.339	-0.011	-0.017	-0.045	-0.020	0.022	-0.092	-0.011
60	-0.043	-0.015	-0.022	-0.063	-0.026	-0.076	-0.061	-0.015
61	0.114	-0.046	-0.089	-0.133	-0.041	-0.216	-0.284	0.020
62	-0.075	-0.039	-0.059	0.192	-0.043	-0.095	-0.104	-0.039
63	-0.034	-0.011	-0.017	-0.050	-0.020	0.044	-0.036	-0.011
64	-0.006	-0.022	-0.016	0.488	-0.012	-0.105	0.115	-0.022
65	-0.034	-0.011	-0.017	-0.040	-0.020	-0.066	0.099	-0.011
66	-0.010	0.093	-0.039	-0.111	-0.045	-0.026	-0.187	0.506
67	-0.034	-0.011	-0.017	-0.050	-0.020	-0.055	-0.038	-0.011
68	-0.034	-0.011	-0.017	-0.050	-0.020	-0.088	-0.058	-0.011
69	-0.034	-0.011	-0.017	-0.050	-0.020	0.353	0.091	-0.011
70	-0.009	-0.036	-0.055	0.158	-0.063	-0.213	0.014	-0.036
71	0.339	-0.011	-0.017	-0.050	-0.020	-0.033	-0.081	-0.011
72	-0.043	-0.015	-0.022	-0.063	-0.026	-0.073	-0.038	-0.015
73	-0.128	-0.082	-0.054	0.189	-0.121	-0.301	0.081	0.149
74	-0.048	-0.016	-0.025	-0.025	-0.029	-0.117	0.055	-0.016
75	0.071	0.036	0.329	0.074	0.003	0.444	0.470	-0.064
76	0.188	-0.025	0.187	-0.048	0.250	0.156	0.314	-0.025
77	0.029	-0.052	-0.004	-0.116	0.054	-0.032	0.148	-0.052
78	0.009	-0.032	-0.048	-0.069	0.436	-0.069	-0.105	-0.032
79	*	*	*	*	*	*	*	*
80	0.148	-0.030	0.316	-0.079	-0.053	0.182	0.432	-0.030
81	-0.034	-0.011	-0.017	-0.035	-0.020	-0.022	0.154	-0.011
82	-0.056	-0.077	0.126	0.104	-0.085	0.195	0.214	-0.098
83	-0.019	0.103	0.413	0.326	0.130	0.399	0.304	-0.089
84	-0.041	-0.014	-0.021	0.065	-0.024	0.183	0.175	-0.014
85	0.084	-0.038	-0.058	-0.164	-0.067	0.269	0.063	0.114
86	0.339	-0.011	-0.017	-0.050	-0.020	-0.033	-0.081	-0.011
87	-0.069	-0.023	-0.036	-0.102	-0.041	-0.167	-0.181	-0.023
88	-0.048	-0.016	-0.025	-0.067	-0.029	-0.117	-0.089	-0.016
89	0.055	-0.044	-0.034	-0.067	0.049	0.040	0.058	-0.044
90	0.339	-0.011	-0.017	-0.035	-0.020	0.166	0.042	-0.011
91	-0.034	-0.011	-0.017	-0.045	-0.020	-0.088	-0.024	-0.011
92	-0.089	-0.030	-0.046	0.227	-0.053	-0.093	-0.096	-0.030
93	0.097	-0.033	0.110	0.128	0.096	0.045	-0.085	-0.033
94	-0.034	-0.011	-0.017	-0.035	-0.020	0.111	-0.040	-0.011
95	0.140	-0.031	-0.047	-0.124	-0.054	0.047	0.044	-0.031
96	-0.034	-0.011	-0.017	-0.050	-0.020	-0.077	-0.148	-0.011
97	-0.048	-0.016	-0.025	0.032	-0.029	-0.039	0.101	-0.016
98	-0.034	-0.011	-0.017	0.150	-0.020	-0.055	-0.094	-0.011
99	0.252	-0.019	-0.029	-0.064	-0.033	0.110	-0.008	-0.019
100	-0.048	-0.016	-0.025	-0.071	-0.029	0.204	0.142	-0.016
101	0.142	-0.044	-0.067	-0.090	-0.022	0.054	-0.050	-0.044
102	0.078	-0.053	0.113	-0.068	-0.031	-0.020	0.156	0.053
103	0.083	-0.044	-0.067	-0.148	-0.016	0.161	-0.022	-0.044
104	-0.122	-0.041	0.029	0.006	0.105	0.224	0.083	-0.041
105	-0.045	-0.015	-0.023	-0.067	-0.027	0.022	-0.125	-0.015
106	0.152	0.007	0.002	0.239	0.198	0.279	0.265	-0.144
107	0.076	-0.001	0.024	-0.026	0.027	0.212	0.288	-0.042
108	0.339	-0.011	-0.017	-0.050	-0.020	0.077	0.287	-0.011
109	-0.064	-0.033	-0.027	0.037	0.257	-0.026	-0.192	-0.033
110	-0.034	-0.011	-0.017	-0.050	-0.020	0.000	0.017	-0.011
111	-0.034	-0.011	-0.017	-0.050	-0.020	-0.022	-0.118	-0.011
112	-0.047	-0.016	-0.024	-0.026	-0.028	-0.107	-0.114	-0.016
113	-0.034	-0.011	-0.017	-0.035	-0.020	-0.099	0.142	-0.011
114	-0.034	-0.011	-0.017	-0.050	-0.020	-0.022	-0.118	-0.011
115	-0.034	-0.011	-0.017	-0.045	-0.020	-0.077	0.044	-0.011
116	0.225	-0.057	-0.069	-0.093	-0.101	0.154	0.126	-0.057

	1	2	3	4	5	6	7	8
117	0.112	-0.038	0.065	-0.030	0.063	0.055	0.192	-0.038

	9	10	11	12	13	14	15	16
10	-0.011							
11	-0.014	-0.014						
12	-0.015	-0.015	-0.018					
13	-0.027	-0.027	-0.031	-0.036				
14	-0.015	-0.015	-0.017	-0.020	-0.034			
15	-0.011	-0.011	-0.014	-0.015	-0.027	**0.948**		
16	-0.032	-0.032	-0.027	-0.043	-0.059	-0.040	-0.032	
17	-0.014	-0.014	-0.017	-0.019	-0.033	-0.018	-0.014	**0.245**
18	-0.030	-0.030	0.183	-0.041	-0.071	-0.039	-0.030	0.175
19	-0.019	-0.019	-0.022	-0.025	-0.043	-0.024	-0.019	**0.610**
20	-0.011	-0.011	-0.014	-0.015	-0.027	-0.015	-0.011	-0.032
21	-0.011	-0.011	-0.014	-0.015	-0.027	-0.015	-0.011	-0.032
22	-0.011	-0.011	-0.014	-0.015	-0.027	-0.015	-0.011	-0.032
23	-0.011	-0.011	-0.014	-0.015	-0.027	-0.015	-0.011	0.047
24	-0.011	-0.011	-0.014	-0.015	-0.027	-0.015	-0.011	-0.032
25	-0.022	-0.022	-0.026	-0.030	-0.051	-0.028	-0.022	**0.324**
26	-0.019	-0.019	**0.797**	**0.536**	-0.044	-0.024	-0.019	-0.052
27	-0.011	-0.011	-0.014	-0.015	-0.027	-0.015	-0.011	-0.032
28	-0.011	-0.011	-0.014	-0.015	-0.027	-0.015	-0.011	-0.032
29	-0.015	-0.015	-0.018	-0.021	**0.492**	-0.020	-0.015	-0.043
30	-0.016	-0.016	-0.019	**0.624**	-0.038	-0.021	-0.016	-0.045
31	-0.032	-0.032	-0.038	-0.043	-0.074	-0.040	-0.032	0.011
32	-0.019	-0.019	-0.023	0.144	-0.045	-0.025	-0.019	-0.054
33	-0.011	-0.011	-0.014	-0.015	-0.027	-0.015	-0.011	-0.032
34	-0.026	-0.026	**0.712**	**0.220**	-0.023	-0.033	-0.026	-0.071
35	-0.049	0.062	-0.058	**0.567**	0.094	-0.063	-0.049	-0.118
36	-0.015	-0.015	-0.017	-0.020	-0.034	-0.019	-0.015	-0.040
37	-0.011	-0.011	-0.014	**0.439**	-0.027	-0.015	-0.011	-0.032
38	-0.015	-0.015	-0.017	-0.020	-0.034	-0.019	-0.015	-0.040
39	-0.011	-0.011	-0.014	-0.015	-0.027	-0.015	-0.011	-0.032
40	-0.011	-0.011	-0.014	-0.015	-0.027	**0.306**	-0.011	-0.032
41	-0.012	-0.042	-0.050	-0.057	0.087	0.122	0.112	0.107
42	-0.023	-0.023	-0.028	-0.032	**0.245**	-0.030	-0.023	-0.011
43	-0.011	-0.011	-0.014	-0.015	-0.027	-0.015	-0.011	-0.032
44	-0.016	-0.016	0.122	-0.022	-0.038	-0.021	-0.016	0.029
45	-0.011	-0.011	-0.014	-0.015	-0.027	-0.015	-0.011	-0.032
46	0.114	**0.210**	-0.061	-0.079	-0.044	0.062	0.085	-0.055
47	-0.054	-0.037	-0.038	-0.068	-0.110	0.149	0.050	0.081
48	-0.094	0.023	-0.062	-0.051	-0.074	0.054	-0.014	**0.242**
49	-0.018	-0.018	-0.021	-0.025	-0.042	0.147	-0.018	-0.028
50	-0.061	0.033	0.108	0.128	0.067	-0.011	0.009	**0.471**
51	-0.093	-0.005	-0.054	**0.286**	0.041	0.089	0.104	-0.127
52	-0.018	-0.018	-0.021	-0.024	-0.030	-0.023	-0.018	-0.047
53	-0.011	-0.011	-0.014	-0.015	-0.027	-0.015	-0.011	-0.032
54	-0.011	-0.011	-0.014	-0.015	-0.027	-0.015	-0.011	-0.032
55	-0.051	-0.051	-0.060	-0.068	-0.114	**0.382**	**0.361**	0.128
56	-0.039	-0.039	-0.055	-0.063	-0.081	0.168	0.110	0.149
57	-0.027	-0.020	-0.044	-0.051	-0.087	0.060	0.035	**0.309**
58	-0.012	-0.012	-0.014	-0.016	-0.028	-0.015	-0.012	-0.033
59	-0.011	-0.011	**0.980**	-0.015	-0.027	-0.015	-0.011	-0.032
60	-0.015	-0.015	-0.017	-0.020	-0.034	-0.019	-0.015	0.043
61	-0.032	-0.006	**0.387**	**0.253**	0.014	-0.062	-0.059	-0.154
62	-0.061	-0.061	-0.071	**0.454**	0.165	-0.056	-0.039	-0.103
63	-0.011	-0.011	-0.014	-0.015	-0.027	-0.015	-0.011	-0.032
64	-0.011	-0.011	-0.026	-0.030	-0.041	-0.028	-0.022	-0.050
65	-0.011	-0.011	-0.014	-0.015	-0.027	-0.015	-0.011	-0.032
66	-0.026	-0.026	-0.030	0.019	-0.059	-0.032	-0.026	-0.066
67	-0.011	-0.011	-0.014	-0.015	-0.027	-0.015	-0.011	0.047
68	-0.011	-0.011	-0.014	-0.015	-0.027	-0.015	-0.011	-0.032

	9	10	11	12	13	14	15	16
69	-0.011	-0.011	-0.014	-0.015	-0.027	-0.015	-0.011	-0.032
70	-0.036	-0.036	**0.218**	**0.309**	-0.084	-0.046	-0.036	-0.038
71	-0.011	-0.011	-0.014	-0.015	-0.027	-0.015	-0.011	-0.032
72	-0.015	-0.015	-0.017	-0.020	-0.034	-0.019	-0.015	-0.040
73	0.034	0.034	-0.089	-0.024	0.041	-0.079	-0.043	-0.027
74	-0.016	-0.016	-0.019	-0.022	-0.038	-0.021	-0.016	-0.045
75	-0.006	0.003	-0.021	-0.037	-0.098	0.101	0.093	**0.478**
76	-0.025	-0.025	-0.030	-0.034	-0.059	0.128	-0.025	0.069
77	-0.052	0.196	-0.062	0.097	0.167	-0.066	-0.052	0.035
78	-0.032	-0.032	-0.038	-0.043	0.143	0.138	-0.032	-0.081
79	*	*	*	*	*	*	*	*
80	-0.030	-0.030	-0.036	-0.041	-0.071	-0.001	0.009	0.072
81	-0.011	-0.011	-0.014	-0.015	-0.027	-0.015	-0.011	-0.032
82	0.175	0.049	-0.094	-0.037	0.119	-0.044	-0.014	0.115
83	0.066	-0.067	-0.101	-0.075	-0.074	**0.311**	**0.290**	0.312
84	-0.014	-0.014	-0.016	-0.019	-0.032	-0.018	-0.014	-0.001
85	-0.038	-0.038	-0.045	-0.051	0.089	-0.048	-0.038	-0.078
86	-0.011	-0.011	-0.014	-0.015	-0.027	-0.015	-0.011	-0.032
87	-0.023	-0.023	-0.028	-0.032	-0.054	-0.030	-0.023	0.095
88	-0.016	-0.016	-0.019	-0.022	-0.038	-0.021	-0.016	-0.045
89	-0.044	0.100	0.004	**0.328**	-0.040	-0.010	-0.044	-0.047
90	-0.011	-0.011	-0.014	-0.015	-0.027	-0.015	-0.011	-0.032
91	-0.011	-0.011	-0.014	-0.015	-0.027	-0.015	-0.011	-0.032
92	-0.030	-0.030	-0.035	-0.040	-0.070	-0.038	-0.030	-0.083
93	-0.033	-0.033	-0.039	-0.044	-0.076	0.167	0.099	-0.077
94	-0.011	-0.011	-0.014	-0.015	-0.027	-0.015	-0.011	-0.032
95	-0.031	0.178	0.005	-0.042	-0.072	-0.039	-0.031	-0.026
96	-0.011	-0.011	-0.014	-0.015	-0.027	-0.015	-0.011	-0.032
97	-0.016	-0.016	-0.019	-0.022	0.101	-0.021	-0.016	-0.045
98	-0.011	-0.011	-0.014	-0.015	-0.027	-0.015	-0.011	-0.032
99	-0.019	-0.019	-0.022	-0.026	-0.044	-0.024	-0.019	-0.052
100	-0.016	-0.016	-0.019	-0.022	**0.241**	-0.021	-0.016	-0.045
101	-0.044	0.088	**0.350**	0.162	-0.044	-0.056	-0.044	-0.078
102	0.053	-0.053	-0.063	-0.071	-0.082	-0.034	-0.053	0.021
103	-0.044	0.061	**0.331**	-0.060	0.060	-0.023	-0.044	-0.105
104	-0.041	-0.041	-0.049	-0.056	-0.037	**0.524**	**0.463**	0.053
105	-0.015	-0.015	-0.018	-0.021	-0.036	-0.020	-0.015	-0.042
106	-0.022	0.148	-0.065	0.034	0.092	-0.012	-0.010	-0.029
107	-0.001	-0.021	-0.079	-0.078	-0.080	-0.005	0.006	-0.053
108	-0.011	**1.000**	-0.014	-0.015	-0.027	-0.015	-0.011	-0.032
109	-0.029	-0.014	-0.031	-0.036	-0.071	0.155	-0.002	-0.036
110	-0.011	-0.011	-0.014	-0.015	-0.027	-0.015	-0.011	0.125
111	-0.011	-0.011	-0.014	-0.015	-0.027	-0.015	-0.011	-0.032
112	-0.016	-0.016	-0.019	-0.022	0.014	-0.020	-0.016	-0.044
113	-0.011	-0.011	-0.014	-0.015	0.169	-0.015	-0.011	-0.032
114	-0.011	-0.011	-0.014	-0.015	-0.027	-0.015	-0.011	-0.032
115	-0.011	-0.011	-0.014	-0.015	-0.027	-0.015	-0.011	-0.032
116	-0.057	**0.244**	0.125	0.173	**0.357**	-0.044	-0.027	-0.069
117	-0.056	0.109	0.082	0.106	**0.518**	-0.071	-0.056	0.094

	17	18	19	20	21	22	23	24
18	**0.400**							
19	-0.023	**0.251**						
20	-0.014	-0.030	-0.019					
21	-0.014	-0.030	-0.019	-0.011				
22	-0.014	-0.030	-0.019	-0.011	-0.011			
23	-0.014	-0.030	-0.019	-0.011	-0.011	-0.011		
24	-0.014	0.192	-0.019	-0.011	-0.011	-0.011	-0.011	
25	-0.028	-0.059	**0.490**	**0.303**	-0.022	-0.022	-0.022	-0.022
26	-0.024	0.134	-0.031	-0.019	-0.019	-0.019	-0.019	-0.019
27	-0.014	0.638	-0.019	-0.011	-0.011	-0.011	-0.011	-0.011
28	-0.014	0.192	-0.019	-0.011	-0.011	-0.011	-0.011	**1.000**

	17	18	19	20	21	22	23	24
29	-0.019	0.059	-0.025	-0.015	-0.015	-0.015	-0.015	-0.015
30	-0.020	-0.043	-0.026	-0.016	-0.016	-0.016	-0.016	-0.016
31	0.051	-0.084	-0.051	-0.032	-0.032	-0.032	-0.032	-0.032
32	-0.024	-0.051	-0.031	0.170	-0.019	-0.019	-0.019	-0.019
33	-0.014	-0.030	-0.019	-0.011	-0.011	-0.011	-0.011	-0.011
34	-0.032	0.182	-0.042	-0.026	-0.026	-0.026	-0.026	-0.026
35	-0.062	-0.122	-0.080	-0.049	-0.049	-0.049	0.025	-0.049
36	-0.018	-0.039	-0.024	-0.015	-0.015	-0.015	-0.015	-0.015
37	-0.014	-0.030	-0.019	-0.011	-0.011	-0.011	-0.011	-0.011
38	-0.018	-0.039	-0.024	-0.015	-0.015	-0.015	-0.015	-0.015
39	-0.014	-0.030	-0.019	-0.011	-0.011	-0.011	-0.011	-0.011
40	-0.014	-0.030	-0.019	-0.011	-0.011	-0.011	-0.011	-0.011
41	-0.009	-0.092	0.006	-0.042	-0.042	-0.042	-0.042	-0.042
42	-0.029	-0.062	-0.038	-0.023	-0.023	-0.023	**0.491**	-0.023
43	-0.014	-0.030	-0.019	-0.011	-0.011	-0.011	-0.011	-0.011
44	-0.020	-0.043	-0.026	-0.016	-0.016	-0.016	-0.016	-0.016
45	-0.014	-0.030	-0.019	-0.011	-0.011	-0.011	-0.011	-0.011
46	-0.031	-0.061	-0.059	-0.075	-0.010	0.129	0.062	-0.071
47	-0.025	-0.117	0.013	-0.014	0.073	-0.054	-0.037	-0.048
48	-0.046	-0.119	0.027	-0.021	-0.072	-0.094	-0.079	-0.057
49	-0.023	-0.048	-0.029	-0.018	-0.018	-0.018	-0.018	-0.018
50	-0.014	-0.111	-0.061	-0.038	0.127	-0.061	-0.061	-0.061
51	-0.056	**-0.217**	-0.127	-0.071	-0.093	-0.093	-0.027	-0.038
52	0.038	-0.048	-0.029	0.003	-0.018	-0.018	-0.018	-0.018
53	-0.014	-0.030	-0.019	-0.011	-0.011	-0.011	-0.011	-0.011
54	-0.014	-0.030	-0.019	-0.011	-0.011	-0.011	-0.011	-0.011
55	-0.017	-0.134	0.023	0.144	-0.029	-0.051	-0.051	-0.051
56	-0.008	0.204	**0.346**	**0.239**	-0.018	-0.047	0.007	-0.043
57	-0.047	-0.089	0.093	0.046	-0.027	-0.034	-0.038	-0.038
58	-0.015	-0.032	-0.019	-0.012	-0.012	-0.012	-0.012	-0.012
59	-0.014	0.192	-0.019	-0.011	-0.011	-0.011	-0.011	-0.011
60	-0.018	0.032	0.063	-0.015	-0.015	-0.015	-0.015	-0.015
61	-0.069	-0.039	-0.091	-0.046	-0.046	-0.046	-0.046	-0.059
62	-0.006	-0.122	-0.051	-0.061	-0.039	-0.061	-0.039	-0.039
63	-0.014	0.192	-0.019	-0.011	-0.011	-0.011	-0.011	-0.011
64	-0.000	-0.052	-0.036	-0.022	-0.022	-0.022	0.082	-0.022
65	-0.014	-0.030	-0.019	-0.011	-0.011	-0.011	-0.011	-0.011
66	-0.032	-0.054	-0.041	-0.026	0.093	-0.026	-0.026	0.034
67	-0.014	-0.030	-0.019	-0.011	-0.011	-0.011	-0.011	-0.011
68	-0.014	-0.030	-0.019	-0.011	-0.011	-0.011	-0.011	-0.011
69	-0.014	-0.030	-0.019	-0.011	-0.011	-0.011	-0.011	-0.011
70	-0.045	-0.037	-0.059	-0.036	-0.036	-0.036	-0.036	-0.036
71	-0.014	-0.030	-0.019	-0.011	-0.011	-0.011	-0.011	-0.011
72	-0.018	-0.039	-0.024	**0.948**	-0.015	-0.015	-0.015	-0.015
73	0.008	0.021	-0.039	-0.120	-0.082	0.034	-0.043	0.111
74	-0.020	-0.043	-0.026	-0.016	-0.016	-0.016	-0.016	-0.016
75	-0.068	-0.057	**0.279**	0.053	0.036	-0.043	0.079	-0.045
76	-0.026	-0.067	0.103	-0.025	-0.025	-0.025	-0.025	-0.025
77	-0.021	-0.111	0.050	-0.052	-0.052	-0.052	-0.052	-0.052
78	-0.040	-0.084	-0.052	**0.529**	-0.032	-0.032	-0.032	-0.032
79	*	*	*	*	*	*	*	*
80	-0.024	-0.080	-0.002	0.067	-0.030	-0.011	-0.030	-0.030
81	-0.014	-0.030	-0.019	-0.011	-0.011	-0.011	-0.011	-0.011
82	-0.049	-0.041	0.035	-0.014	-0.077	-0.056	0.028	-0.035
83	-0.092	-0.135	-0.045	0.010	0.103	-0.088	0.011	-0.063
84	-0.017	-0.037	-0.023	-0.014	-0.014	-0.014	-0.014	-0.014
85	0.027	0.302	-0.062	-0.038	-0.038	-0.038	-0.038	0.038
86	-0.014	-0.030	-0.019	-0.011	-0.011	-0.011	-0.011	-0.011
87	-0.029	**0.278**	**0.240**	-0.023	-0.023	-0.023	-0.023	**0.491**
88	-0.020	-0.043	-0.026	**0.703**	-0.016	-0.016	-0.016	-0.016
89	-0.036	-0.077	-0.033	-0.044	-0.044	-0.044	-0.044	-0.044
90	-0.014	-0.030	-0.019	-0.011	-0.011	-0.011	-0.011	-0.011

	17	18	19	20	21	22	23	24
91	-0.014	-0.030	-0.019	-0.011	-0.011	-0.011	-0.011	-0.011
92	-0.038	-0.079	-0.049	-0.030	-0.030	0.300	-0.030	-0.030
93	-0.041	0.174	-0.053	-0.033	-0.033	-0.033	-0.033	-0.033
94	-0.014	-0.030	-0.019	-0.011	-0.011	-0.011	-0.011	-0.011
95	-0.039	-0.082	-0.050	-0.031	-0.031	-0.031	-0.031	-0.031
96	-0.014	-0.030	-0.019	-0.011	-0.011	-0.011	-0.011	-0.011
97	-0.020	-0.043	-0.026	-0.016	-0.016	-0.016	-0.016	-0.016
98	-0.014	-0.030	-0.019	-0.011	-0.011	-0.011	-0.011	-0.011
99	-0.024	0.501	-0.031	-0.019	-0.019	-0.019	-0.019	-0.019
100	-0.020	-0.043	-0.026	-0.016	-0.016	-0.016	-0.016	-0.016
101	-0.049	0.021	-0.021	-0.044	-0.044	-0.044	-0.025	-0.044
102	0.057	-0.000	0.000	-0.053	-0.053	-0.053	-0.053	-0.053
103	-0.055	0.011	-0.015	-0.044	-0.044	0.008	0.008	-0.044
104	-0.052	-0.109	-0.067	-0.041	-0.041	-0.041	-0.041	-0.041
105	-0.019	0.055	-0.025	-0.015	-0.015	-0.015	-0.015	0.420
106	-0.090	-0.072	0.011	-0.058	0.007	-0.014	0.074	-0.181
107	-0.083	0.019	-0.040	0.006	-0.001	-0.062	-0.062	-0.035
108	-0.014	-0.030	-0.019	-0.011	-0.011	-0.011	-0.011	-0.011
109	-0.038	-0.075	-0.011	0.292	-0.033	-0.010	-0.029	-0.033
110	0.166	-0.030	-0.019	-0.011	-0.011	-0.011	-0.011	-0.011
111	-0.014	-0.030	-0.019	-0.011	-0.011	-0.011	-0.011	-0.011
112	-0.020	-0.043	-0.026	-0.016	-0.016	-0.016	-0.016	-0.016
113	-0.014	-0.030	-0.019	-0.011	-0.011	-0.011	-0.011	-0.011
114	-0.014	-0.030	-0.019	-0.011	-0.011	-0.011	-0.011	-0.011
115	-0.014	-0.030	-0.019	-0.011	-0.011	-0.011	-0.011	-0.011
116	-0.014	-0.089	-0.052	-0.057	-0.057	-0.057	-0.042	-0.057
117	0.007	-0.068	-0.027	-0.056	-0.038	-0.056	-0.056	-0.038

	25	26	27	28	29	30	31	32
26	-0.037							
27	-0.022	-0.019						
28	-0.022	-0.019	-0.011					
29	-0.030	-0.026	-0.015	-0.015				
30	-0.031	0.270	-0.016	-0.016	-0.022			
31	-0.061	-0.052	-0.032	-0.032	-0.043	-0.045		
32	0.024	0.046	-0.019	-0.019	-0.026	0.242	-0.054	
33	-0.022	-0.019	-0.011	-0.011	-0.015	-0.016	-0.032	-0.019
34	-0.050	0.814	-0.026	-0.026	0.050	-0.037	-0.071	-0.043
35	0.024	0.255	-0.049	-0.049	0.067	0.564	-0.099	0.230
36	-0.028	-0.024	-0.015	-0.015	-0.020	-0.021	-0.040	-0.025
37	-0.022	0.398	-0.011	-0.011	-0.015	-0.016	-0.032	-0.019
38	-0.028	-0.024	-0.015	-0.015	-0.020	-0.021	-0.040	0.879
39	-0.022	-0.019	-0.011	-0.011	-0.015	-0.016	-0.032	-0.019
40	-0.022	-0.019	-0.011	-0.011	-0.015	-0.016	-0.032	-0.019
41	0.384	-0.070	-0.042	-0.042	-0.016	-0.060	0.146	0.137
42	0.120	-0.039	-0.023	-0.023	-0.032	-0.033	-0.065	-0.040
43	0.627	-0.019	-0.011	-0.011	-0.015	-0.016	-0.032	-0.019
44	-0.031	-0.027	-0.016	-0.016	-0.022	-0.023	-0.045	-0.028
45	-0.022	-0.019	-0.011	-0.011	-0.015	-0.016	0.223	-0.019
46	-0.063	-0.088	-0.021	-0.071	-0.021	-0.085	-0.067	0.156
47	0.107	-0.087	-0.054	-0.048	-0.068	-0.065	0.176	-0.062
48	-0.101	-0.100	-0.094	-0.057	-0.028	-0.092	0.050	-0.077
49	-0.035	-0.030	-0.018	-0.018	-0.025	-0.026	-0.050	-0.031
50	-0.050	0.160	-0.061	-0.061	0.065	0.046	0.155	-0.064
51	-0.009	0.095	-0.093	-0.038	0.037	0.172	0.057	0.044
52	-0.028	-0.030	-0.018	-0.018	-0.005	-0.011	0.141	-0.022
53	-0.022	-0.019	-0.011	-0.011	-0.015	-0.016	-0.032	-0.019
54	-0.022	-0.019	-0.011	-0.011	-0.015	-0.016	-0.032	-0.019
55	0.153	-0.084	-0.051	-0.051	-0.068	-0.057	0.012	-0.045
56	0.043	-0.077	-0.047	-0.043	-0.063	-0.055	-0.007	0.016
57	0.087	-0.062	-0.027	-0.038	-0.051	-0.053	0.147	-0.048
58	-0.023	-0.020	-0.012	-0.012	-0.016	-0.017	-0.033	-0.020

	25	26	27	28	29	30	31	32
59	-0.022	**0.815**	-0.011	-0.011	-0.015	-0.016	-0.032	-0.019
60	-0.028	-0.024	-0.015	-0.015	-0.020	-0.021	-0.040	-0.025
61	**-0.092**	**0.441**	-0.059	-0.059	-0.032	0.170	0.017	0.042
62	0.002	0.159	-0.061	-0.039	0.055	**0.314**	0.197	0.085
63	-0.022	-0.019	-0.011	-0.011	**0.439**	-0.016	-0.032	-0.019
64	-0.025	-0.037	-0.011	-0.022	-0.030	-0.032	0.180	-0.038
65	-0.022	-0.019	-0.011	-0.011	-0.015	-0.016	-0.032	-0.019
66	-0.049	0.007	-0.026	0.034	-0.034	-0.036	0.138	-0.021
67	-0.022	-0.019	-0.011	-0.011	-0.015	-0.016	-0.032	-0.019
68	-0.022	-0.019	-0.011	-0.011	-0.015	-0.016	-0.032	-0.019
69	-0.022	-0.019	-0.011	-0.011	-0.015	-0.016	-0.032	-0.019
70	-0.070	**0.378**	-0.036	-0.036	-0.049	0.137	0.167	-0.011
71	-0.022	-0.019	-0.011	-0.011	-0.015	-0.016	-0.032	-0.019
72	**0.281**	-0.024	-0.015	-0.015	-0.020	-0.021	-0.040	0.156
73	-0.034	-0.071	-0.005	0.111	0.063	0.021	-0.004	-0.001
74	-0.031	-0.027	-0.016	-0.016	-0.022	-0.023	-0.045	-0.028
75	**0.249**	-0.049	0.021	-0.045	-0.056	-0.051	0.152	-0.053
76	0.065	-0.042	-0.025	-0.025	-0.034	-0.036	0.131	-0.043
77	-0.021	0.068	-0.052	-0.052	-0.070	-0.074	0.199	-0.088
78	0.119	-0.053	-0.032	-0.032	-0.043	-0.045	-0.088	0.051
79	*	*	*	*	*	*	*	*
80	0.010	-0.050	-0.030	-0.030	-0.041	-0.043	**0.245**	-0.033
81	-0.022	-0.019	-0.011	-0.011	-0.015	-0.016	-0.032	-0.019
82	0.034	-0.092	0.070	-0.035	-0.028	0.175	0.015	0.072
83	-0.063	-0.129	-0.027	-0.063	-0.081	-0.053	0.087	-0.036
84	-0.027	-0.023	-0.014	-0.014	-0.019	-0.020	**0.271**	-0.024
85	-0.073	-0.063	**0.343**	0.038	**0.223**	-0.054	-0.086	-0.064
86	-0.022	-0.019	-0.011	-0.011	-0.015	-0.016	-0.032	-0.019
87	-0.045	-0.039	-0.023	**0.491**	-0.032	-0.033	-0.065	-0.040
88	**0.430**	-0.027	-0.016	-0.016	-0.022	-0.023	-0.045	0.107
89	-0.073	0.164	-0.044	-0.044	-0.027	0.193	-0.068	0.060
90	-0.022	-0.019	-0.011	-0.011	-0.015	-0.016	-0.032	-0.019
91	**0.303**	-0.019	-0.011	-0.011	-0.015	-0.016	-0.032	-0.019
92	-0.058	-0.050	-0.030	-0.030	-0.040	0.192	-0.083	0.011
93	-0.021	-0.054	**0.362**	-0.033	-0.044	-0.047	-0.091	-0.056
94	-0.022	-0.019	-0.011	-0.011	-0.015	-0.016	-0.032	-0.019
95	-0.060	-0.051	-0.031	-0.031	-0.042	-0.044	0.125	-0.052
96	-0.022	-0.019	-0.011	-0.011	-0.015	-0.016	-0.032	-0.019
97	-0.031	-0.027	-0.016	-0.016	-0.022	-0.023	-0.045	**0.647**
98	-0.022	-0.019	-0.011	-0.011	-0.015	-0.016	-0.032	-0.019
99	-0.037	-0.031	**0.815**	-0.019	-0.026	-0.027	-0.052	-0.032
100	-0.031	-0.027	-0.016	-0.016	-0.022	-0.023	-0.045	-0.028
101	-0.061	**0.365**	-0.044	-0.044	0.017	0.099	**0.259**	0.021
102	-0.102	-0.087	0.053	-0.053	-0.071	-0.075	0.200	**0.209**
103	-0.085	**0.231**	-0.044	-0.044	-0.012	-0.026	0.076	-0.065
104	-0.080	-0.068	-0.041	-0.041	-0.056	0.013	-0.114	0.044
105	-0.030	-0.025	-0.015	**0.420**	-0.021	-0.022	0.188	-0.026
106	0.014	-0.038	0.006	-0.181	0.027	0.082	0.055	0.032
107	0.021	-0.103	0.136	-0.035	-0.032	-0.108	0.002	-0.113
108	-0.022	-0.019	-0.011	-0.011	-0.015	-0.016	-0.032	-0.019
109	0.065	-0.047	-0.033	-0.033	-0.045	-0.039	0.000	0.007
110	-0.022	-0.019	-0.011	-0.011	-0.015	-0.016	**0.477**	-0.019
111	-0.022	-0.019	-0.011	-0.011	-0.015	-0.016	**0.477**	-0.019
112	-0.031	-0.027	-0.016	-0.016	-0.022	-0.023	-0.045	-0.027
113	-0.022	-0.019	-0.011	-0.011	-0.015	-0.016	-0.032	-0.019
114	-0.022	-0.019	-0.011	-0.011	-0.015	-0.016	**0.477**	-0.019
115	-0.022	-0.019	-0.011	-0.011	-0.015	-0.016	-0.032	-0.019
116	-0.028	0.141	-0.057	-0.057	**0.519**	0.122	-0.037	**0.211**
117	-0.091	0.120	-0.056	-0.038	**0.652**	0.025	0.136	0.105

	33	34	35	36	37	38	39	40
34	0.163							
35	-0.049	0.021						
36	-0.015	-0.033	-0.027					
37	-0.011	**0.541**	0.173	-0.015				
38	-0.015	-0.033	0.079	-0.019	-0.015			
39	-0.011	-0.026	0.025	-0.015	-0.011	-0.015		
40	-0.011	-0.026	-0.049	-0.015	-0.011	-0.015	-0.011	
41	-0.042	0.009	-0.096	-0.005	-0.042	0.152	-0.042	0.050
42	-0.023	-0.052	0.164	-0.030	-0.023	-0.030	**0.491**	-0.023
43	-0.011	-0.026	-0.049	-0.015	-0.011	-0.015	-0.011	-0.011
44	-0.016	-0.037	-0.070	-0.021	-0.016	-0.021	-0.016	-0.016
45	-0.011	-0.026	-0.049	-0.015	-0.011	-0.015	-0.011	-0.011
46	-0.071	-0.051	-0.088	0.056	-0.060	**0.278**	**0.467**	-0.058
47	-0.002	-0.111	-0.038	-0.010	-0.054	-0.043	-0.048	**0.320**
48	0.023	-0.135	0.121	0.087	-0.028	-0.045	-0.079	**0.212**
49	-0.018	-0.041	-0.074	-0.023	-0.018	-0.023	-0.018	**0.516**
50	-0.014	0.082	0.055	-0.011	0.080	-0.078	-0.061	-0.061
51	-0.027	-0.091	**0.397**	0.073	-0.022	0.002	0.055	-0.033
52	-0.018	-0.040	-0.028	-0.023	-0.018	-0.023	-0.018	-0.018
53	-0.011	-0.026	-0.049	-0.015	-0.011	-0.015	-0.011	-0.011
54	-0.011	-0.026	0.025	-0.015	-0.011	-0.015	**1.000**	-0.011
55	-0.051	-0.089	-0.153	-0.057	-0.051	-0.064	-0.051	0.122
56	-0.047	-0.102	-0.147	-0.060	-0.047	-0.019	-0.018	0.197
57	-0.038	-0.080	-0.147	0.087	-0.038	-0.046	-0.038	0.084
58	-0.012	-0.027	-0.048	-0.015	-0.012	-0.015	-0.012	-0.012
59	-0.011	**0.730**	-0.049	-0.015	-0.011	-0.015	-0.011	-0.011
60	-0.015	-0.033	-0.063	-0.019	-0.015	-0.019	-0.015	-0.015
61	-0.059	**0.240**	**0.276**	-0.075	-0.032	-0.033	-0.059	-0.019
62	-0.039	-0.095	**0.487**	0.033	0.004	0.033	-0.039	-0.061
63	-0.011	0.163	-0.049	-0.015	-0.011	-0.015	-0.011	-0.011
64	-0.011	-0.048	-0.053	0.027	-0.022	-0.010	-0.022	-0.022
65	-0.011	-0.026	-0.049	-0.015	-0.011	-0.015	-0.011	-0.011
66	-0.026	0.009	-0.023	-0.032	0.093	-0.032	-0.026	-0.026
67	-0.011	-0.026	-0.049	-0.015	-0.011	-0.015	-0.011	-0.011
68	-0.011	-0.026	0.025	-0.015	-0.011	-0.015	-0.011	-0.011
69	-0.011	-0.026	-0.012	-0.015	-0.011	-0.015	-0.011	-0.011
70	-0.036	**0.266**	**0.225**	-0.046	**0.229**	-0.046	-0.036	-0.036
71	-0.011	-0.026	0.025	-0.015	-0.011	-0.015	-0.011	-0.011
72	-0.015	-0.033	-0.063	-0.019	-0.015	-0.019	-0.015	-0.015
73	-0.005	-0.054	0.169	-0.104	0.034	0.079	-0.043	-0.120
74	-0.016	-0.037	-0.070	-0.021	-0.016	-0.021	-0.016	-0.016
75	0.092	-0.041	-0.133	0.130	-0.046	-0.048	-0.058	0.039
76	-0.025	-0.057	-0.082	**0.645**	-0.025	-0.032	-0.025	**0.478**
77	-0.052	0.092	0.100	0.170	**0.321**	-0.066	-0.052	-0.052
78	**0.249**	-0.019	-0.044	-0.040	-0.032	-0.040	-0.032	0.529
79	*	*	*	*	*	*	*	*
80	0.048	-0.050	-0.101	**0.501**	-0.030	-0.039	-0.030	-0.030
81	-0.011	-0.026	-0.049	-0.015	-0.011	-0.015	-0.011	-0.011
82	-0.056	-0.085	0.154	-0.004	-0.056	0.043	0.091	-0.098
83	-0.061	-0.139	-0.195	**0.240**	-0.089	-0.000	0.027	0.110
84	-0.014	-0.031	-0.060	-0.018	-0.014	-0.018	-0.014	-0.014
85	-0.038	0.043	-0.091	-0.048	-0.038	-0.048	-0.038	-0.038
86	-0.011	-0.026	0.025	-0.015	-0.011	-0.015	-0.011	-0.011
87	-0.023	-0.052	-0.082	-0.030	-0.023	-0.030	-0.023	-0.023
88	-0.016	-0.037	0.194	-0.021	-0.016	-0.021	-0.016	-0.016
89	**0.207**	0.062	0.155	-0.056	0.100	0.012	-0.008	0.100
90	**1.000**	0.163	-0.049	-0.015	-0.011	-0.015	-0.011	-0.011
91	-0.011	-0.026	**0.322**	-0.015	-0.011	-0.015	-0.011	-0.011
92	-0.030	-0.067	-0.032	-0.038	-0.030	0.067	-0.030	-0.030
93	0.099	-0.049	-0.083	-0.042	-0.033	-0.042	0.099	**0.230**
94	-0.011	-0.026	-0.049	-0.015	-0.011	-0.015	-0.011	-0.011
95	**0.388**	0.009	-0.094	-0.039	-0.031	-0.039	-0.031	-0.031

	33	34	35	36	37	38	39	40
96	-0.011	-0.026	-0.049	-0.015	-0.011	-0.015	-0.011	-0.011
97	-0.016	0.098	0.035	-0.021	-0.016	**0.664**	-0.016	-0.016
98	-0.011	-0.026	0.025	-0.015	-0.011	-0.015	1.000	-0.011
99	-0.019	-0.042	-0.081	-0.024	-0.019	-0.024	-0.019	-0.019
100	-0.016	-0.037	0.062	-0.021	-0.016	-0.021	-0.016	-0.016
101	0.013	**0.258**	0.024	-0.056	-0.006	0.004	-0.006	-0.044
102	-0.053	-0.119	-0.025	**0.437**	-0.053	**0.235**	0.053	0.053
103	0.061	**0.344**	-0.078	-0.056	-0.044	-0.056	0.008	0.061
104	-0.041	-0.036	0.019	-0.052	-0.041	0.076	-0.041	**0.262**
105	-0.015	-0.034	-0.066	-0.020	-0.015	-0.020	-0.015	-0.015
106	-0.043	-0.056	0.094	0.025	-0.036	0.102	0.018	-0.008
107	-0.021	-0.056	**-0.209**	0.164	-0.021	-0.038	-0.076	-0.035
108	-0.011	-0.026	0.062	-0.015	-0.011	-0.015	-0.011	-0.011
109	0.002	-0.056	-0.124	-0.022	-0.029	-0.042	-0.029	**0.495**
110	-0.011	-0.026	-0.049	-0.015	-0.011	-0.015	-0.011	-0.011
111	-0.011	-0.026	0.025	-0.015	-0.011	-0.015	-0.011	-0.011
112	-0.016	-0.036	0.041	-0.020	-0.016	-0.020	-0.016	-0.016
113	-0.011	0.163	-0.049	-0.015	-0.011	-0.015	-0.011	-0.011
114	-0.011	-0.026	0.025	-0.015	-0.011	-0.015	-0.011	-0.011
115	-0.011	-0.026	-0.049	-0.015	-0.011	-0.015	-0.011	-0.011
116	**0.455**	0.122	**0.235**	-0.058	-0.012	0.190	-0.042	-0.057
117	0.017	0.084	0.150	-0.054	0.128	0.110	0.036	-0.056

	41	42	43	44	45	46	47	48
42	0.008							
43	**0.575**	-0.023						
44	-0.060	-0.033	-0.016					
45	-0.042	-0.023	-0.011	-0.016				
46	0.085	**0.218**	0.027	-0.104	-0.033			
47	0.118	0.104	-0.031	0.050	-0.054	-0.133		
48	0.001	-0.157	-0.072	0.115	-0.021	**-0.219**	**0.265**	
49	-0.018	-0.037	-0.018	-0.026	-0.018	-0.089	**0.223**	0.143
50	**0.267**	-0.125	0.009	-0.021	-0.061	-0.005	0.194	**0.320**
51	0.023	0.134	-0.011	-0.089	-0.055	-0.157	0.037	**0.401**
52	-0.064	-0.037	-0.018	-0.026	-0.018	-0.060	-0.070	0.135
53	-0.042	-0.023	-0.011	-0.016	-0.011	-0.069	**0.620**	0.052
54	-0.042	**0.491**	-0.011	-0.016	-0.011	**0.467**	-0.048	-0.079
55	0.187	-0.070	0.079	-0.072	-0.051	-0.080	**0.435**	0.154
56	-0.018	-0.045	-0.014	-0.061	-0.047	-0.047	0.111	0.102
57	0.131	-0.075	-0.024	-0.053	-0.038	-0.105	**0.502**	**0.394**
58	-0.044	-0.024	-0.012	-0.017	-0.012	-0.077	-0.028	-0.026
59	-0.042	-0.023	-0.011	-0.016	-0.011	-0.048	-0.054	-0.086
60	-0.054	-0.030	-0.015	-0.021	-0.015	-0.087	-0.058	-0.036
61	-0.135	-0.086	-0.032	-0.046	**0.218**	-0.189	-0.185	-0.154
62	-0.033	-0.002	0.026	-0.086	0.199	-0.129	-0.037	-0.049
63	0.050	-0.023	-0.011	-0.016	-0.011	0.089	-0.054	-0.079
64	-0.069	0.031	-0.011	-0.007	-0.022	-0.013	-0.055	0.070
65	-0.042	-0.023	-0.011	-0.016	-0.011	-0.023	-0.014	-0.014
66	-0.091	-0.052	-0.026	-0.036	-0.026	-0.143	-0.008	0.003
67	-0.042	-0.023	-0.011	-0.016	-0.011	-0.069	-0.054	-0.064
68	-0.042	-0.023	-0.011	-0.016	-0.011	-0.073	-0.048	-0.079
69	-0.012	-0.023	-0.011	-0.016	-0.011	0.094	0.050	0.023
70	-0.109	-0.074	-0.036	-0.051	-0.036	-0.188	-0.142	**0.280**
71	-0.042	-0.023	-0.011	-0.016	-0.011	-0.075	-0.025	0.037
72	-0.054	-0.030	-0.015	-0.021	-0.015	0.032	-0.030	-0.049
73	-0.033	-0.069	0.111	-0.089	-0.082	-0.046	**-0.225**	**0.345**
74	-0.060	-0.033	-0.016	-0.023	-0.016	-0.034	-0.024	-0.071
75	**0.313**	-0.028	-0.002	0.037	-0.058	-0.000	**0.350**	**0.322**
76	0.189	-0.051	-0.025	-0.036	-0.025	-0.017	**0.340**	**0.277**
77	0.175	0.020	-0.052	-0.074	0.196	-0.079	0.033	0.187
78	-0.015	0.078	-0.032	-0.045	-0.032	-0.072	**0.297**	0.095
79	*	*	*	*	*	*	*	*

	41	42	43	44	45	46	47	48
80	0.031	-0.062	-0.030	-0.043	-0.030	-0.022	**0.278**	**0.315**
81	-0.042	-0.023	-0.011	-0.016	-0.011	**0.324**	-0.037	0.001
82	0.171	-0.028	-0.014	-0.139	**0.259**	**0.228**	0.177	-0.026
83	**0.291**	-0.043	-0.069	-0.076	-0.004	0.134	**0.444**	**0.318**
84	**0.429**	-0.028	-0.014	-0.020	-0.014	-0.073	**0.252**	0.106
85	-0.141	-0.078	-0.038	0.054	-0.038	0.090	-0.153	-0.183
86	-0.042	-0.023	-0.011	-0.016	-0.011	-0.075	-0.025	0.037
87	-0.071	-0.048	-0.023	-0.033	-0.023	-0.096	-0.034	-0.020
88	-0.038	**0.333**	-0.016	-0.023	-0.016	-0.097	**0.234**	-0.081
89	-0.084	-0.053	-0.044	0.014	-0.044	0.172	**0.267**	0.075
90	-0.042	-0.023	-0.011	-0.016	-0.011	-0.071	-0.002	0.023
91	-0.012	**0.491**	-0.011	-0.016	-0.011	-0.062	**0.344**	-0.094
92	-0.060	-0.061	-0.030	-0.043	-0.030	0.022	**0.478**	0.041
93	0.015	0.067	-0.033	-0.047	-0.033	-0.005	**0.495**	0.143
94	-0.042	-0.023	-0.011	-0.016	-0.011	-0.075	**0.332**	0.059
95	-0.114	-0.063	-0.031	0.105	-0.031	-0.115	-0.039	-0.014
96	-0.012	-0.023	-0.011	-0.016	-0.011	-0.050	0.044	-0.021
97	**0.422**	-0.033	-0.016	-0.023	-0.016	0.193	-0.061	-0.066
98	-0.042	**0.491**	-0.011	-0.016	-0.011	**0.467**	-0.048	-0.079
99	-0.070	-0.039	-0.019	-0.027	-0.019	-0.079	0.082	-0.064
100	-0.038	-0.033	-0.016	-0.023	-0.016	0.021	0.009	0.038
101	-0.075	-0.061	-0.025	0.018	**0.809**	0.012	-0.046	-0.093
102	0.079	-0.054	-0.053	-0.075	-0.053	**0.314**	0.059	0.110
103	-0.120	-0.037	-0.044	0.012	0.114	0.011	-0.072	-0.089
104	**0.272**	-0.084	-0.041	-0.059	-0.041	**0.250**	0.075	0.044
105	-0.057	-0.031	-0.015	-0.022	-0.015	-0.083	0.029	-0.024
106	0.053	-0.056	0.098	-0.125	0.161	**0.393**	0.059	-0.106
107	-0.040	-0.127	0.033	-0.069	-0.049	**0.369**	-0.015	-0.127
108	-0.042	-0.023	-0.011	-0.016	-0.011	**0.210**	-0.037	0.023
109	0.070	-0.064	-0.033	-0.025	-0.033	-0.140	**0.651**	0.142
110	0.204	-0.023	-0.011	-0.016	-0.011	0.123	0.182	0.059
111	-0.012	-0.023	-0.011	-0.016	-0.011	-0.073	-0.037	-0.057
112	-0.051	-0.033	-0.016	-0.023	-0.016	-0.086	-0.041	-0.044
113	**0.420**	-0.023	-0.011	-0.016	-0.011	0.052	-0.048	-0.050
114	-0.012	-0.023	-0.011	-0.016	-0.011	-0.073	-0.037	-0.057
115	-0.042	-0.023	-0.011	-0.016	-0.011	-0.068	-0.025	0.001
116	-0.014	-0.094	0.033	0.197	-0.057	-0.022	-0.056	-0.000
117	0.030	0.035	-0.038	**0.273**	-0.056	-0.004	0.043	0.128

	49	50	51	52	53	54	55	56
50	-0.058							
51	-0.015	0.035						
52	-0.028	-0.058	**0.450**					
53	0.089	-0.061	-0.011	-0.018				
54	-0.018	-0.061	0.055	-0.018	-0.011			
55	0.071	0.188	0.044	0.144	**0.425**	-0.051		
56	0.087	-0.106	0.099	**0.373**	0.119	-0.018	**0.462**	
57	0.051	**0.461**	-0.084	-0.054	**0.261**	-0.038	**0.501**	0.026
58	-0.019	-0.064	-0.049	-0.019	-0.012	-0.012	0.012	0.063
59	-0.018	0.103	-0.038	-0.018	-0.011	-0.011	-0.051	-0.047
60	-0.023	-0.056	-0.090	-0.023	-0.015	-0.015	-0.064	-0.037
61	-0.044	-0.084	0.107	-0.004	-0.059	-0.059	-0.200	-0.139
62	-0.091	0.054	**0.411**	**0.376**	-0.061	-0.039	-0.066	0.049
63	-0.018	-0.061	-0.093	-0.018	-0.011	-0.011	-0.051	-0.047
64	-0.036	-0.081	**0.315**	**0.898**	-0.022	-0.022	0.025	**0.293**
65	-0.018	-0.038	-0.033	-0.018	-0.011	-0.011	-0.051	-0.039
66	-0.040	-0.098	0.075	-0.040	-0.026	-0.026	-0.106	-0.096
67	-0.018	-0.061	-0.071	-0.018	-0.011	-0.011	-0.051	-0.030
68	-0.018	-0.061	-0.066	-0.018	-0.011	-0.011	-0.051	-0.047
69	-0.018	0.056	0.126	-0.018	-0.011	-0.011	-0.051	-0.043
70	-0.057	-0.033	**0.352**	**0.364**	-0.036	-0.036	-0.125	0.010
71	-0.018	-0.061	-0.066	-0.018	-0.011	-0.011	-0.029	-0.047

	49	50	51	52	53	54	55	56
72	-0.023	-0.056	-0.097	-0.003	-0.015	-0.015	0.121	**0.212**
73	-0.024	-0.118	**0.355**	**0.430**	-0.082	-0.043	-0.128	0.003
74	-0.026	-0.021	0.070	-0.026	-0.016	-0.016	-0.057	-0.043
75	0.036	**0.506**	-0.067	-0.077	-0.001	-0.058	**0.285**	-0.033
76	**0.226**	0.120	0.025	-0.039	-0.025	-0.025	0.140	0.040
77	-0.083	0.151	0.042	-0.061	-0.052	-0.052	-0.116	-0.142
78	**0.276**	-0.073	0.002	-0.038	**0.249**	-0.032	0.196	**0.213**
79	*	*	*	*	*	*	*	*
80	-0.026	**0.255**	-0.016	-0.044	0.028	-0.030	**0.291**	-0.040
81	-0.018	-0.014	-0.082	-0.018	-0.011	-0.011	-0.051	-0.047
82	-0.030	**0.332**	-0.107	-0.077	0.196	0.091	0.073	-0.111
83	0.048	**0.561**	-0.009	-0.065	0.196	0.027	**0.425**	0.020
84	-0.022	**0.297**	0.021	-0.022	-0.014	-0.014	0.075	-0.039
85	-0.060	-0.121	-0.123	-0.053	-0.038	-0.038	-0.137	-0.148
86	-0.018	-0.061	-0.066	-0.018	-0.011	-0.011	-0.029	-0.047
87	-0.037	-0.113	-0.050	-0.037	-0.023	-0.023	-0.103	**0.282**
88	-0.026	-0.071	0.098	-0.011	-0.016	-0.016	0.113	0.139
89	0.112	0.092	0.063	-0.068	0.100	-0.008	-0.071	-0.036
90	-0.018	-0.014	-0.027	-0.018	-0.011	-0.011	-0.051	-0.047
91	-0.018	-0.061	**0.208**	-0.018	-0.011	-0.011	0.014	-0.043
92	0.022	-0.068	-0.105	-0.040	**0.631**	-0.030	**0.221**	0.011
93	0.156	0.017	-0.030	-0.051	**0.625**	0.099	**0.446**	0.087
94	-0.018	-0.014	-0.022	-0.018	-0.011	-0.011	-0.051	-0.047
95	**0.482**	-0.068	-0.090	-0.048	-0.031	-0.031	-0.136	-0.113
96	-0.018	-0.038	-0.082	-0.018	-0.011	-0.011	-0.051	-0.039
97	-0.026	-0.054	0.039	-0.026	-0.016	-0.016	-0.057	-0.026
98	-0.018	-0.061	0.055	-0.018	-0.011	1.000	-0.051	-0.018
99	-0.030	-0.082	-0.106	-0.030	-0.019	-0.019	-0.057	-0.031
100	-0.026	0.113	0.078	-0.026	-0.016	-0.016	-0.072	-0.064
101	-0.044	0.003	-0.042	-0.068	0.050	-0.006	-0.116	-0.095
102	-0.028	0.121	0.034	-0.003	-0.053	0.053	-0.016	0.055
103	0.075	0.026	-0.015	-0.067	-0.044	0.008	-0.091	-0.135
104	**0.276**	0.185	0.002	-0.062	-0.041	-0.041	**0.261**	0.089
105	-0.024	-0.082	0.103	-0.024	-0.015	-0.015	-0.068	-0.057
106	-0.003	**0.312**	-0.127	-0.107	-0.008	0.018	-0.031	-0.109
107	-0.070	-0.024	**-0.213**	-0.078	-0.021	-0.076	-0.065	-0.141
108	-0.018	0.033	-0.005	-0.018	-0.011	-0.011	-0.051	-0.039
109	**0.329**	-0.037	-0.080	-0.042	**0.691**	-0.029	**0.431**	**0.273**
110	-0.018	**0.268**	-0.016	-0.018	-0.011	-0.011	0.058	0.036
111	-0.018	-0.014	0.049	-0.018	-0.011	-0.011	-0.051	-0.047
112	-0.026	-0.035	-0.017	-0.025	-0.016	-0.016	-0.003	0.047
113	-0.018	-0.014	0.038	-0.018	-0.011	-0.011	-0.029	-0.030
114	-0.018	-0.014	0.049	-0.018	-0.011	-0.011	-0.051	-0.047
115	-0.018	0.080	**0.274**	-0.018	-0.011	-0.011	-0.051	-0.047
116	-0.048	0.121	0.162	-0.029	-0.012	-0.042	-0.165	-0.144
117	-0.054	**0.309**	0.143	-0.001	-0.019	0.036	-0.097	-0.033

	57	58	59	60	61	62	63	64
58	-0.039							
59	-0.038	-0.012						
60	-0.048	-0.015	-0.015					
61	-0.143	-0.005	**0.403**	-0.058				
62	-0.151	-0.062	-0.061	-0.015	**0.448**			
63	-0.038	-0.012	-0.011	-0.015	-0.006	-0.061		
64	-0.065	-0.023	-0.022	-0.028	-0.004	**0.380**	-0.022	
65	-0.038	-0.012	-0.011	-0.015	0.007	-0.061	-0.011	-0.022
66	-0.082	-0.001	-0.026	0.024	0.088	-0.048	-0.026	-0.050
67	-0.038	-0.012	-0.011	**0.948**	-0.046	-0.017	-0.011	-0.022
68	-0.038	-0.012	-0.011	-0.015	-0.019	-0.039	-0.011	-0.022
69	-0.034	-0.012	-0.011	-0.015	-0.059	0.069	-0.011	0.001
70	-0.117	-0.038	**0.229**	-0.046	0.164	**0.264**	-0.036	**0.446**
71	-0.038	-0.012	-0.011	-0.015	0.152	0.026	-0.011	-0.022

	57	58	59	60	61	62	63	64
72	0.033	-0.015	-0.015	-0.019	-0.049	-0.077	-0.015	-0.021
73	**-0.261**	0.002	-0.082	0.067	-0.096	0.059	-0.005	0.266
74	-0.053	-0.017	-0.016	-0.021	-0.037	-0.086	-0.016	-0.032
75	**0.721**	-0.030	-0.027	-0.065	**-0.211**	-0.170	-0.030	-0.055
76	**0.423**	-0.026	-0.025	-0.032	-0.108	-0.045	-0.025	-0.008
77	-0.030	0.070	-0.052	-0.027	-0.039	0.060	-0.052	-0.072
78	0.092	-0.033	-0.032	-0.040	0.016	0.042	-0.032	-0.049
79	*	*	*	*	*	*	*	*
80	**0.719**	0.007	-0.030	-0.039	-0.149	-0.065	-0.030	-0.024
81	-0.038	-0.012	-0.011	-0.015	-0.006	-0.061	-0.011	0.001
82	0.173	-0.018	-0.077	-0.091	-0.143	0.053	-0.035	-0.063
83	**0.602**	-0.064	-0.092	-0.077	**-0.276**	-0.111	-0.054	-0.053
84	**0.382**	-0.015	-0.014	-0.018	-0.071	-0.074	-0.014	-0.027
85	-0.112	-0.033	-0.038	-0.048	-0.103	-0.129	-0.038	-0.054
86	-0.038	-0.012	-0.011	-0.015	0.152	0.026	-0.011	-0.022
87	-0.077	-0.024	-0.023	-0.030	0.129	0.009	-0.023	-0.046
88	0.008	-0.017	-0.016	-0.021	-0.074	0.022	-0.016	-0.007
89	-0.041	-0.046	-0.008	-0.056	0.019	0.145	-0.044	-0.044
90	-0.038	-0.012	-0.011	-0.015	-0.059	-0.039	-0.011	-0.011
91	-0.034	-0.012	-0.011	-0.015	-0.059	0.091	-0.011	0.012
92	0.148	-0.031	-0.030	-0.038	-0.089	-0.059	-0.030	-0.032
93	**0.343**	-0.034	-0.033	-0.042	-0.151	-0.120	-0.033	-0.049
94	0.011	-0.012	-0.011	-0.015	-0.032	0.069	-0.011	0.001
95	-0.098	-0.032	-0.031	**0.359**	-0.120	-0.100	-0.031	-0.053
96	-0.038	-0.012	-0.011	-0.015	-0.059	0.069	-0.011	-0.022
97	-0.053	-0.017	-0.016	-0.021	-0.065	-0.025	-0.016	-0.032
98	-0.038	-0.012	-0.011	-0.015	-0.059	-0.039	-0.011	-0.022
99	-0.033	**0.397**	-0.019	-0.024	-0.064	-0.046	-0.019	-0.018
100	-0.051	-0.017	-0.016	-0.021	-0.046	0.114	-0.016	-0.015
101	-0.104	0.010	**0.354**	0.016	**0.331**	**0.226**	0.013	-0.068
102	-0.011	0.161	-0.053	**0.269**	-0.138	0.005	-0.053	-0.019
103	-0.125	-0.046	**0.325**	0.011	0.088	-0.042	-0.044	-0.072
104	0.015	0.058	-0.041	-0.052	-0.123	-0.109	-0.041	-0.049
105	-0.050	-0.016	-0.015	-0.020	-0.055	-0.032	-0.015	-0.030
106	0.069	-0.100	-0.056	-0.057	-0.065	0.176	-0.095	-0.032
107	-0.001	-0.003	-0.076	0.164	-0.180	-0.147	0.068	-0.037
108	-0.020	-0.012	-0.011	-0.015	-0.006	-0.061	-0.011	-0.011
109	**0.299**	**0.317**	-0.029	-0.022	-0.104	-0.138	-0.033	-0.056
110	-0.038	-0.012	-0.011	-0.015	-0.046	0.091	-0.011	-0.022
111	-0.038	-0.012	-0.011	-0.015	0.086	0.113	-0.011	-0.022
112	-0.053	**0.956**	-0.016	-0.020	0.083	0.091	-0.016	-0.029
113	-0.038	-0.012	-0.011	-0.015	-0.046	-0.061	-0.011	-0.022
114	-0.038	-0.012	-0.011	-0.015	0.086	0.113	-0.011	-0.022
115	-0.038	-0.012	-0.011	-0.015	-0.046	-0.017	-0.011	-0.022
116	-0.148	-0.060	0.078	-0.044	0.076	**0.247**	-0.057	-0.029
117	-0.067	-0.058	0.054	-0.048	-0.012	**0.209**	-0.056	-0.005

	65	66	67	68	69	70	71	72
66	-0.026							
67	-0.011	0.034						
68	-0.011	-0.026	-0.011					
69	-0.011	-0.026	-0.011	-0.011				
70	-0.036	-0.034	-0.036	-0.036	-0.036			
71	-0.011	0.152	-0.011	-0.011	-0.011	-0.036		
72	-0.015	-0.032	-0.015	-0.015	-0.015	-0.046	-0.015	
73	0.072	0.160	0.034	-0.082	-0.043	0.328	-0.043	-0.104
74	**0.703**	-0.036	-0.016	-0.016	-0.016	-0.051	-0.016	-0.021
75	-0.014	-0.125	-0.049	-0.060	0.020	-0.093	-0.061	0.054
76	-0.025	-0.056	-0.025	-0.025	-0.025	-0.079	-0.025	-0.032
77	0.196	-0.058	-0.052	-0.052	0.072	0.096	-0.052	-0.066
78	-0.032	-0.071	-0.032	-0.032	-0.032	-0.100	-0.032	**0.493**
79	*	*	*	*	*	*	*	*

	65	66	67	68	69	70	71	72
80	-0.030	-0.068	-0.030	-0.030	-0.030	-0.091	-0.030	0.054
81	-0.011	-0.026	-0.011	-0.011	-0.011	-0.036	-0.011	-0.015
82	-0.056	-0.152	-0.077	-0.056	0.028	-0.175	-0.098	-0.031
83	-0.038	-0.039	-0.067	-0.091	0.001	-0.138	-0.098	-0.003
84	-0.014	-0.031	-0.014	-0.014	-0.014	-0.044	-0.014	-0.018
85	0.038	0.076	-0.038	-0.038	-0.038	-0.120	-0.038	-0.048
86	-0.011	0.152	-0.011	-0.011	-0.011	-0.036	**1.000**	-0.015
87	-0.023	0.038	-0.023	-0.023	-0.023	-0.074	-0.023	-0.030
88	-0.016	-0.036	-0.016	-0.016	-0.016	-0.051	-0.016	**0.664**
89	-0.044	-0.079	-0.044	-0.044	-0.008	0.031	-0.044	-0.056
90	-0.011	-0.026	-0.011	-0.011	-0.011	-0.036	-0.011	-0.015
91	-0.011	-0.026	-0.011	-0.011	-0.011	-0.036	-0.011	-0.015
92	**0.300**	-0.067	-0.030	-0.030	-0.030	-0.095	-0.030	-0.038
93	-0.033	-0.073	-0.033	-0.033	-0.033	-0.034	-0.033	-0.042
94	-0.011	-0.026	-0.011	-0.011	-0.011	-0.036	-0.011	-0.015
95	0.178	-0.044	**0.388**	-0.031	-0.031	-0.097	-0.031	-0.039
96	-0.011	-0.026	-0.011	-0.011	-0.011	-0.036	-0.011	-0.015
97	-0.016	-0.036	-0.016	-0.016	-0.016	-0.051	-0.016	-0.021
98	-0.011	-0.026	-0.011	-0.011	-0.011	-0.036	-0.011	-0.015
99	-0.019	-0.042	-0.019	-0.019	-0.019	-0.060	-0.019	-0.024
100	-0.016	-0.036	-0.016	-0.016	**0.703**	-0.051	-0.016	-0.021
101	0.050	-0.091	0.013	-0.044	0.013	0.074	-0.044	-0.056
102	-0.053	-0.025	**0.265**	-0.053	0.053	-0.083	-0.053	-0.034
103	-0.044	-0.092	-0.044	-0.044	-0.044	0.013	-0.044	-0.056
104	-0.041	-0.092	-0.041	-0.041	**0.262**	-0.130	-0.041	-0.052
105	-0.015	**0.742**	-0.015	-0.015	-0.015	-0.048	-0.015	-0.020
106	0.040	-0.203	-0.078	-0.142	0.157	-0.189	-0.014	-0.051
107	**0.491**	0.059	0.191	-0.076	0.081	-0.192	-0.049	0.088
108	-0.011	-0.026	-0.011	-0.011	-0.011	-0.036	-0.011	-0.015
109	-0.018	-0.070	-0.022	-0.025	-0.025	-0.095	-0.033	**0.270**
110	-0.011	-0.026	-0.011	-0.011	-0.011	-0.036	-0.011	-0.015
111	-0.011	-0.026	-0.011	-0.011	-0.011	**0.229**	-0.011	-0.015
112	-0.016	-0.036	-0.016	-0.016	-0.016	-0.051	-0.016	-0.020
113	-0.011	-0.026	-0.011	-0.011	-0.011	-0.036	-0.011	-0.015
114	-0.011	-0.026	-0.011	-0.011	-0.011	**0.229**	-0.011	-0.015
115	-0.011	-0.026	-0.011	-0.011	-0.011	-0.036	-0.011	-0.015
116	-0.012	-0.116	-0.027	-0.042	0.033	0.068	-0.042	-0.073
117	-0.038	-0.070	-0.038	-0.056	-0.001	0.074	-0.056	-0.071

	73	74	75	76	77	78	79	80
74	0.048							
75	**-0.232**	-0.053						
76	**-0.223**	-0.036	**0.575**					
77	0.163	0.102	0.168	**0.231**				
78	-0.184	-0.045	0.039	**0.209**	-0.076			
79	*	*	*	*	*	*		
80	-0.197	-0.043	**0.575**	**0.667**	0.126	0.019	*	
81	0.034	-0.016	-0.009	-0.025	-0.052	**0.249**	*	-0.011
82	-0.140	-0.034	**0.308**	0.094	**0.240**	0.050	*	0.050
83	-0.189	-0.052	**0.629**	**0.388**	0.086	0.106	*	**0.379**
84	-0.146	-0.020	**0.655**	**0.430**	**0.299**	-0.039	*	**0.262**
85	0.007	-0.000	-0.067	-0.084	-0.155	-0.042	*	-0.092
86	-0.043	-0.016	-0.061	-0.025	-0.052	-0.032	*	-0.030
87	0.069	-0.033	-0.101	-0.051	**0.210**	-0.065	*	-0.032
88	-0.116	-0.023	0.005	-0.036	-0.074	**0.354**	*	0.026
89	-0.059	0.014	-0.028	-0.006	-0.046	**0.296**	*	-0.037
90	-0.005	-0.016	0.092	-0.025	-0.052	**0.249**	*	0.048
91	-0.043	-0.016	-0.047	-0.025	-0.052	-0.032	*	-0.030
92	0.025	0.192	-0.041	-0.056	-0.055	0.100	*	-0.022
93	-0.109	-0.047	0.036	0.074	-0.133	**0.310**	*	0.142
94	-0.082	-0.016	-0.033	0.004	-0.052	-0.032	*	0.009
95	0.043	0.105	-0.005	-0.068	0.014	0.030	*	0.019

	73	74	75	76	77	78	79	80
96	0.072	-0.016	-0.057	-0.025	**0.445**	-0.032	*	0.028
97	-0.007	-0.023	-0.057	-0.036	-0.074	-0.045	*	-0.043
98	-0.043	-0.016	-0.058	-0.025	-0.052	-0.032	*	-0.030
99	-0.040	-0.027	-0.007	-0.029	-0.035	-0.053	*	-0.018
100	-0.007	-0.023	-0.017	-0.036	**0.279**	-0.045	*	-0.043
101	-0.107	0.018	-0.102	-0.086	**0.262**	-0.007	*	-0.051
102	0.075	-0.000	0.023	**0.368**	0.202	0.000	*	**0.343**
103	-0.091	0.012	-0.101	-0.043	0.058	0.126	*	-0.058
104	-0.102	-0.059	0.122	0.060	-0.089	0.137	*	-0.066
105	0.148	-0.022	-0.076	-0.034	-0.070	-0.043	*	-0.041
106	-0.169	0.070	**0.211**	0.109	0.179	0.061	*	0.099
107	-0.039	**0.320**	0.122	0.126	0.140	0.025	*	0.096
108	0.034	-0.016	0.003	-0.025	0.196	-0.032	*	-0.030
109	-0.204	-0.031	0.184	**0.307**	0.024	**0.598**	*	0.068
110	0.072	-0.016	-0.025	0.004	0.196	-0.032	*	0.048
111	0.034	-0.016	-0.061	-0.025	-0.052	-0.032	*	-0.030
112	-0.037	-0.023	-0.041	-0.035	0.046	0.054	*	-0.003
113	-0.043	-0.016	-0.041	-0.025	-0.052	-0.032	*	-0.030
114	0.034	-0.016	-0.061	-0.025	-0.052	-0.032	*	-0.030
115	-0.043	-0.016	-0.039	-0.025	-0.052	**0.249**	*	-0.011
116	0.044	0.015	-0.056	-0.107	-0.029	0.146	*	-0.075
117	0.082	-0.041	-0.047	-0.081	0.138	0.002	*	-0.025

	81	82	83	84	85	86	87	88
82	**0.259**							
83	0.101	**0.391**						
84	-0.014	**0.295**	**0.337**					
85	-0.038	-0.032	-0.098	-0.046				
86	-0.011	-0.098	-0.098	-0.014	-0.038			
87	-0.023	-0.103	-0.126	-0.028	-0.039	-0.023		
88	-0.016	-0.064	-0.043	-0.020	-0.054	-0.016	-0.033	
89	**0.674**	**0.282**	0.070	-0.054	-0.119	-0.044	-0.035	-0.037
90	-0.011	-0.056	-0.061	-0.014	-0.038	-0.011	-0.023	-0.016
91	-0.011	-0.077	-0.071	-0.014	-0.038	-0.011	-0.023	**0.703**
92	-0.030	**0.218**	0.179	-0.037	-0.075	-0.030	-0.061	-0.043
93	0.099	0.117	**0.250**	-0.040	0.040	-0.033	-0.067	0.047
94	-0.011	0.133	0.042	-0.014	-0.038	-0.011	-0.023	-0.016
95	-0.031	-0.111	-0.153	-0.038	-0.087	-0.031	-0.063	-0.044
96	-0.011	0.007	-0.027	-0.014	-0.038	-0.011	**0.491**	-0.016
97	-0.016	0.100	-0.026	-0.020	-0.054	-0.016	-0.033	-0.023
98	-0.011	0.091	0.027	-0.014	-0.038	-0.011	-0.023	-0.016
99	-0.019	0.107	-0.030	-0.023	**0.251**	-0.019	-0.039	-0.027
100	-0.016	**0.294**	0.049	-0.020	-0.054	-0.016	-0.033	-0.023
101	0.164	**0.254**	-0.066	-0.036	-0.079	-0.044	0.035	-0.063
102	0.159	0.067	0.064	-0.039	-0.032	-0.053	0.054	-0.075
103	0.114	0.141	-0.051	-0.054	0.131	-0.044	-0.010	-0.063
104	**0.262**	**0.316**	**0.365**	-0.050	-0.137	-0.041	-0.084	-0.059
105	-0.015	-0.046	0.045	-0.019	0.051	-0.015	0.190	-0.022
106	**0.253**	**0.582**	**0.321**	0.122	0.067	-0.014	-0.136	-0.120
107	**0.368**	0.167	0.173	0.051	**0.319**	-0.049	-0.081	-0.030
108	-0.011	0.049	-0.067	-0.014	-0.038	-0.011	-0.023	-0.016
109	-0.014	0.152	**0.266**	0.197	-0.094	-0.033	-0.054	0.184
110	-0.011	-0.056	0.012	-0.014	-0.038	-0.011	-0.023	-0.016
111	-0.011	-0.098	-0.076	-0.014	-0.038	-0.011	-0.023	-0.016
112	-0.016	0.040	-0.077	-0.020	-0.033	-0.016	-0.033	-0.023
113	-0.011	0.091	-0.032	-0.014	-0.038	-0.011	-0.023	-0.016
114	-0.011	-0.098	-0.076	-0.014	-0.038	-0.011	-0.023	-0.016
115	-0.011	0.028	0.024	-0.014	0.191	-0.011	-0.023	-0.016
116	0.048	0.015	-0.164	-0.070	0.102	-0.042	-0.071	-0.071
117	-0.019	-0.023	-0.066	-0.059	0.134	-0.056	0.026	-0.067

	89	90	91	92	93	94	95	96
90	**0.207**							
91	-0.008	-0.011						
92	0.154	-0.030	-0.030					
93	0.145	0.099	0.099	**0.429**				
94	**0.494**	-0.011	-0.011	**0.300**	-0.033			
95	0.119	**0.388**	-0.031	-0.012	-0.034	-0.031		
96	-0.008	-0.011	-0.011	-0.030	-0.033	-0.011	-0.031	
97	0.014	-0.016	-0.016	-0.043	-0.047	-0.016	-0.044	-0.016
98	-0.008	-0.011	-0.011	-0.030	0.099	-0.011	-0.031	-0.011
99	0.149	-0.019	-0.019	0.087	**0.271**	**0.398**	-0.051	-0.019
100	-0.012	-0.016	-0.016	-0.043	-0.047	-0.016	-0.044	-0.016
101	0.181	0.013	-0.044	-0.017	-0.023	-0.044	0.104	0.164
102	0.120	-0.053	-0.053	-0.138	0.014	-0.053	-0.011	0.053
103	0.129	0.061	-0.044	-0.064	-0.058	0.008	0.077	0.061
104	**0.207**	-0.041	-0.041	-0.009	0.092	-0.041	0.014	-0.041
105	-0.059	-0.015	-0.015	-0.040	-0.044	-0.015	-0.041	-0.015
106	**0.254**	-0.043	-0.111	0.069	-0.041	-0.021	-0.031	0.056
107	0.144	-0.021	-0.049	0.112	0.008	-0.049	0.134	0.006
108	0.100	-0.011	-0.011	-0.030	-0.033	-0.011	0.178	-0.011
109	0.106	0.002	-0.033	**0.407**	**0.527**	-0.014	-0.029	-0.014
110	0.064	-0.011	-0.011	-0.030	-0.033	-0.011	-0.031	-0.011
111	-0.044	-0.011	-0.011	-0.030	-0.033	-0.011	-0.031	-0.011
112	-0.037	-0.016	-0.016	-0.042	-0.046	-0.016	-0.043	-0.016
113	-0.008	-0.011	-0.011	-0.030	-0.033	-0.011	-0.031	-0.011
114	-0.044	-0.011	-0.011	-0.030	-0.033	-0.011	-0.031	-0.011
115	0.028	-0.011	-0.011	-0.030	-0.033	-0.011	-0.031	-0.011
116	**0.300**	**0.455**	-0.042	-0.076	-0.047	-0.012	**0.242**	-0.012
117	0.151	0.017	-0.038	-0.063	-0.065	0.036	0.009	0.054

	97	98	99	100	101	102	103	104
98	-0.016							
99	-0.027	-0.019						
100	-0.023	-0.016	-0.027					
101	0.018	-0.006	-0.050	-0.009				
102	0.151	0.053	0.087	-0.000	-0.026			
103	-0.026	0.008	-0.051	0.124	**0.280**	-0.044		
104	**0.228**	-0.041	-0.026	0.157	-0.023	0.095	-0.012	
105	-0.022	-0.015	-0.025	-0.022	-0.059	-0.071	-0.059	-0.055
106	-0.018	0.018	-0.042	**0.298**	**0.268**	0.095	**0.270**	**0.247**
107	-0.093	-0.076	0.092	0.150	0.037	0.172	-0.041	0.059
108	-0.016	-0.011	-0.019	-0.016	0.088	-0.053	0.061	-0.041
109	-0.036	-0.029	0.098	-0.039	-0.001	0.019	-0.035	0.120
110	-0.016	-0.011	-0.019	-0.016	-0.006	**0.583**	-0.044	-0.041
111	-0.016	-0.011	-0.019	-0.016	0.013	-0.053	0.167	-0.041
112	-0.023	-0.016	**0.375**	-0.023	0.001	0.158	-0.021	0.084
113	**0.703**	-0.011	-0.019	-0.016	0.013	-0.053	0.008	**0.262**
114	-0.016	-0.011	-0.019	-0.016	0.013	-0.053	0.167	-0.041
115	-0.016	-0.011	-0.019	-0.016	0.013	0.053	**0.378**	-0.041
116	0.165	-0.042	-0.076	0.058	0.130	-0.017	**0.237**	-0.047
117	0.090	0.036	-0.055	0.012	0.074	0.178	0.041	-0.081

	105	106	107	108	109	110	111	112
106	-0.149							
107	0.102	**0.375**						
108	-0.015	0.148	-0.021					
109	-0.041	-0.023	-0.006	-0.014				
110	-0.015	0.022	-0.028	-0.011	-0.014			
111	-0.015	-0.062	-0.062	-0.011	-0.029	-0.011		
112	-0.022	-0.027	-0.025	-0.016	**0.294**	-0.016	-0.016	
113	-0.015	-0.074	-0.055	-0.011	-0.018	-0.011	-0.011	-0.016
114	-0.015	-0.062	-0.062	-0.011	-0.029	-0.011	1.000	-0.016
115	-0.015	0.127	-0.049	-0.011	-0.033	-0.011	-0.011	0.072

	105	106	107	108	109	110	111	112
116	-0.077	0.180	-0.124	0.244	-0.080	0.018	0.063	-0.005
117	-0.051	0.115	-0.165	0.109	-0.094	0.367	-0.001	-0.030

	113	114	115	116
114	-0.011			
115	-0.011	-0.011		
116	0.018	0.063	0.184	
117	-0.001	-0.001	0.054	0.674

TAXA KEY

1	White anemone indet.	31	*Eulalia viridis*	61	*Idotea pelagica*	91	*Littorina obtusata*
2	*Sagartia ornata*	32	*Polydora ciliata*	62	*Jaera albifrons*	92	*Littorina mariae*
3	*Podocoryne carnea*	33	*Scolelepis foliosa*	63	*Stenothoe* spp.	93	*Littorina rudis*
4	Turbellaria indet.	34	*Scolelepis squamata*	64	*Hyale prevostii*	94	*Cingula trifasciata*
5	Polycladida indet.	35	*Brania pusilla*	65	*Hyale pontica*	95	*Onoba semicostata*
6	Nemertea indet.	36	*Odontosyllis ctenostoma*	66	*Chaetogammarus marinus*	96	*Alvania semistriata*
7	Nematoda indet.	37	*Odontosyllis gibba*	67	*Gammarus locusta*	97	*Rissoa parva*
8	*Lagisca extenuata*	38	*Pionosyllis divaricata*	68	*Sunamphitoe pelagica*	98	*Barleeia unifasciata*
9	*Lepidontus clava*	39	*Sphaerosyllis bulbosa*	69	*Caprella linearis*	99	*Coriandria fulgida*
10	*Lepidontus squamata*	40	*Typosyllis prolifera*	70	Crab larvae indet.	100	*Skeneopsis planorbis*
11	*Harmothoe impar*	41	*Fabricia stellaris*	71	*Hyas araneus*	101	*Rissoella opalina*
12	*Harmothoe* spp.	42	*Fabriciola berkeleyi*	72	*Cancer pagurus*	102	*Nucella lapillus*
13	*Pholoe inornata*	43	*Oriopsis armandi*	73	*Carcinus maenas*	103	*Brachystomis scalaris*
14	*Capitella capitata*	44	*Pomatoceros triqueter*	74	*Pinnotheres pisum*	104	*Limapontia depressa*
15	*Chaetozone setosa*	45	*Paralaeospira malardi*	75	Mite sp. 1	105	Juvenile Bivalves indet.
16	*Cirratulus cirratus*	46	Oligochaeta indet.	76	Mite sp. 2	106	Juvenile *Mytilus edulis*
17	*Cirratulus filiformis*	47	*Heterocythereis albomaculata*	77	Mite sp. 3	107	*Modiolula phaseolina*
18	*Cirriformia tentaculata*	48	Ostracod sp. 2	78	Mite sp. 5	108	*Musculus discors*
19	*Tharyx marioni*	49	Ostracod sp. 3	79	Mite sp. 6	109	*Lasaea adansoni*
20	*Driloneris filum*	50	Ostracod sp. 4	80	*Anurida maritima*	110	*Tapes* spp.
21	*Marphysa sanguinea*	51	Copepoda indet.	81	*Petrobius maritimus*	111	*Venerupis saxatilis*
22	Hesionidae indet.	52	Juvenile barnacles indet.	82	Dipteran pupae indet.	112	*Turtonia minuta*
23	*Kefersteinia cirrata*	53	Barnacle nauplii	83	Chironomid larvae indet.	113	Ophiolepidae indet.
24	*Nereimya punctata*	54	*Balanus balanus*	84	Ant	114	*Ophiocomina nigra*
25	Maldanidae indet.	55	*Semibalanus balanoides*	85	Juvenile gastropods indet.	115	*Ophiothrix fragilis*
26	*Ophelia rathkei*	56	*Elminius modestus*	86	Tectura tessulata	116	Benthic foraminifera indet.
27	*Ophelia bicornis*	57	*Tanais dulongii*	87	*Patella vulgata*	117	Foraminifera indet.
28	Orbiniidae indet.	58	*Idotea baltica*	88	*Patella ulyssiponensis*		
29	*Scoloplos armiger*	59	*Idotea granulosa*	89	*Skenea serpuloides*		
30	*Eteone picta*	60	*Idotea neglecta*	90	*Lacuna vincta*		