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**THE EFFECTS OF THE PRESENCE OF
SEAGRASSES (ZOSTERA SPP.) ON
BENTHIC INTERTIDAL INVERTEBRATE
COMMUNITIES**

N.D.HILLARD

Thesis submitted as part of the requirement
for the degree of M.Sc. by Advanced Course in
Ecology (1992).



24 FEB 1993

ABSTRACT

1. A quantitative investigation of the benthic macrofauna associated with seagrass swards was carried out over a period of four months, on the intertidal mud flats at Lindisfarne, Northumberland.
2. Two species of seagrasses belonging to the genus *Zostera* are present at this site: *Z.noltii*, a perennial species which overwinters as rhizomes, and *Z.marina*, an annual germinating each year from seed.
3. Core samples were collected from three midshore sites at Lindisfarne and from three different habitat types, namely swards of both *Zostera* species and from adjacent bare mud surfaces. The samples were removed to the laboratory and carefully washed through a sieve of mesh size 40 squares per inch, to extract the macrofauna.
4. Comparisons were made between the invertebrate faunas associated with the vegetated and unvegetated sites, as well as between the two species of *Zostera*.
5. Several of the more obvious environmental variables at the sites were measured - *Zostera* biomass, detrital biomass, RPD depth and sediment granulometry - in order to identify any possible causal agents of these variations in community composition.
6. Differences were found in both the densities and the biomass of invertebrates present between vegetated and unvegetated sites and also between the two seagrass species. The highest densities were recorded in *Z.noltii* samples, due largely to the abundance of oligochaetous annelids. *Z.marina* cores, despite having the lowest total densities of benthic macrofauna, showed the highest diversity and biomass of invertebrates.
7. Epifaunal taxa, especially the isopod *Idotea baltica* and the gastropod molluscs, were generally more abundant in the structurally more complex *Z.marina* sites.
8. Polychaetes were often poorly represented in the study, but two sedentary species - *Scoloplos armiger* and *Ampharete balthica* - showed an apparent preference for sediments supporting the annual seagrass species.
9. The data suggested that *Z.noltii* sediments maintained an invertebrate community somewhat intermediate to those of bare mud and *Z.marina* samples.
10. Statistical analysis of the data gathered on several environmental variables, highlighted a number of differences between the different sample sites and also the different habitat types.
11. The influence of the seagrasses on the composition and nature of the sediments was found to account for approximately 26% of the observed variation in species' densities.
12. The presence of *Zostera* species on the surface of intertidal sediments was therefore seen to play a potentially important role in determining the composition of benthic macrofaunal communities.

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CHAPTER 1. INTRODUCTION

1.1 THE SEDIMENTARY INTERTIDAL ENVIRONMENT

Mud flats are expanses of fine intertidal sediments periodically exposed and submerged by the tides and which usually slope gently towards the sea. Sand and mud flats are the most extensive intertidal habitat in the majority of the north-west European countries, occupying over 2000 km² in Great Britain (Wolff, 1987). A transient habitat, these areas nevertheless comprise some of our most biologically fertile land.

The unstable nature of such flats do not allow the establishment of many macrophyte species. As such, they are mostly bare, apart from the brown hue of the sediment surface caused by the presence of innumerable microscopic diatoms.

One notable and very conspicuous exception to this are the seagrass meadows which (outside the polar regions) often characterize photic-zone sand and mud communities. The seagrasses are monocotyledonous angiosperms adapted for marine life both through their physiology and morphology (McRoy and Helfferich, 1977). Their most obvious characters are the extensive rhizome and rooting system to prevent upheaval, and generally the very strap-like leafing pattern to minimise drag (Boaden and Seed, 1985).

There are 49 seagrass species, of which 11 belong to the genus forming the basis of this study, *Zostera*. On a broad geographic scale, it is found that *Zostera* and its subgenus *Zosterella* are widely distributed in the temperate zones of Europe, North America and Asia, as well as the south temperate coasts of Australia (Day et al., 1989). Members of this genus have little capacity for upward rhizome growth and are therefore limited to areas where the deposition and erosion of sediments is more or less in equilibrium.

1.2 RELEVANT PREVIOUS INVESTIGATIONS

Beeftink (1977), in a review of the wet coastal ecosystems of western and northern Europe, defined *Zostera* communities as homogeneous assemblages of one (or two) *Zostera* species. Two types of association are commonly found, one dominated by the broad-leaved annual *Zostera marina*, the other by the finer-leaved perennial species *Zostera noltii*. The former is essentially a sublittoral association penetrating into the intertidal belt at the most to about mean sea level, dependent on the water-holding capacity of the substratum. In Britain, the climate is such that the rhizomes are killed by frost in the eulittoral zone and as a consequence, the assemblage is summer-annual. The *Z.noltii* association is less susceptible to frost damage, developing in intertidal flats of mud or fine sand rich in detritus, between the MLWN and MHWN tide levels.

It has long been recognised that seagrass meadows represent an important source of food and shelter for benthic invertebrates and a nursery ground for fishes. As a result, numerous studies have been conducted to investigate macrofaunal invertebrate assemblages associated with seagrass meadows and to assess differences between vegetated and unvegetated habitats.

Many of the studies that have focussed on this particular ecological aspect have been carried out in near-tropical areas, such as western Australia (Edgar, 1990), Florida (Brook, 1978) and the Seychelles (Taylor and Lewis, 1970). These investigations have in general found both qualitative and quantitative differences among the faunas of sites with different degrees of macrophyte cover, with the number of species and density of invertebrates being significantly lower in the bare sediment environment. However, due to the latitudinal differences between study areas such as these and those around the British Isles, and associated differences in tidal regime, sea temperature, current velocities etc., the results of such analyses are not strictly comparable.

Much previous work has also been on single *Zostera* spp. systems, most commonly *Z.marina*, often in subtidal environments. For example, Stoner (1980) was able to eliminate differences in the granulometric properties of subtidal sediments and isolate the role of seagrass biomass in regulating the community organisation of benthic macrofauna. He concluded that the

biomass of benthic subtidal macrophytes, independent of sediment granulometry and hydrodynamic effects, was an important regulator of species abundances, dominance, diversity and trophic organisation in macrofaunal assemblages.

Reise's extensive work in the Dutch Wadden Sea (for review see Reise, 1985) included studies predominantly concerned with intertidal *Z.noltii* systems in Königshafen. His work, unlike much other research focussing on either the epifaunal (for example, Schneider and Mann, 1991b) or infaunal component, dealt with the whole benthic invertebrate macrofaunal (and meiofaunal) community in relation to sediment characteristics. He found that the most diverse macrofauna of the area (an approximate 70% increase in species number compared to unvegetated sand or mud flats) occurred within the grass beds. Total abundance was also higher in such vegetated sites than anywhere else in Königshafen.

1.3 PURPOSE OF THE PRESENT STUDY

Although Reise (1985) referred to a few localities where *Z.noltii* and *Z.marina* grew together, his studies on invertebrate assemblages did not take account of the two-species situation present at Lindisfarne. Since the two *Zostera* species grew in close proximity to each other at this location, comparisons between the two could be made, as well as those between vegetated and unvegetated sites.

Due to the localised distribution pattern of the *Zostera*, the studies focussed solely on the midshore region. Within the Lindisfarne N.N.R., three suitable areas were identified, within which samples were taken:-

- (a) *Z.noltii* beds
- (b) *Z.marina* beds
- (c) Bare mud surfaces

In quantitative biological surveys the main aim is to estimate the numbers of one or more species or another parameter (such as biomass, RPD depth etc.) per unit area from a series of samples taken from the populations within a defined area. From data gathered on macrofaunal densities and the

measurement of several of the more obvious ecological parameters, it was hoped to be able to compare:

1. Invertebrate community differences between vegetated and unvegetated areas within a particular site.
2. Invertebrate communities associated with the two species of *Zostera*.
3. Any differences in community composition between sites within the Lindisfarne N.N.R..

These studies would ideally identify any differences in faunal dominance and species composition within and between the sites at Lindisfarne and also establish possible explanations for any such dissimilarities.

CHAPTER 2. STUDY AREA

2.1 DESCRIPTION AND HISTORY

The project was carried out within the Lindisfarne National Nature Reserve in northern Northumberland. Lindisfarne (or alternatively Holy Island) is situated approximately 80 kilometres north of Newcastle-upon-Tyne, the nearest town being Berwick-upon-Tweed on the Scottish Borders, 13 kilometres to the north. The tiny island is cut off from the mainland at high tide and was famous in ecclesiastical history as the seat of the Saxon See of Lindisfarne.

Lindisfarne was designated a national nature reserve in 1964 and consists mainly of intertidal mudflats, sandflats, saltmarsh and sand dunes. The importance of the site for wintering wildfowl and shorebirds has been recognised for at least two hundred and fifty years (see for example Perry, 1946). Today the most noteworthy species utilising the area include Pale-bellied Brent Geese (*Branta bernicla*) and large numbers of Wigeon (*Anas penelope*). On the island itself, considerable botanical interest is found in the dune and particularly dune slack areas, where several species of orchid occur. The entire reserve is today protected under legislation outlined in the Nature Conservancy Act (1973) and the Wildlife and Countryside Act (1981) and is managed both for research and for its conservation needs.

Lindisfarne is a particularly important intertidal site since it contains both floral and faunal communities which are not subject to such extremes of salinity fluctuation as might be expected in estuarine localities. The protection from onshore winds afforded by Holy Island itself has in the past been important in the development of mudflats and saltmarsh.

2.2 SELECTION OF STUDY SITES

The particular areas of the Lindisfarne N.N.R. relevant to this study were the intertidal mudflats, stretching from the edge of *Spartina* dominated saltmarsh to Low Water Mark. The nature of the investigations meant that:

- (a) individual sites had to consist of areas of *Zostera* interspersed with bare mud surfaces enabling within site comparisons to be carried out.
- (b) different sample sites had to be as similar as possible in terms of tidal height, granulometric properties etc., to enable between site comparisons to be made.

The actual sites chosen for the study were those which in the past have been noted for having considerable swards of *Zostera* present.

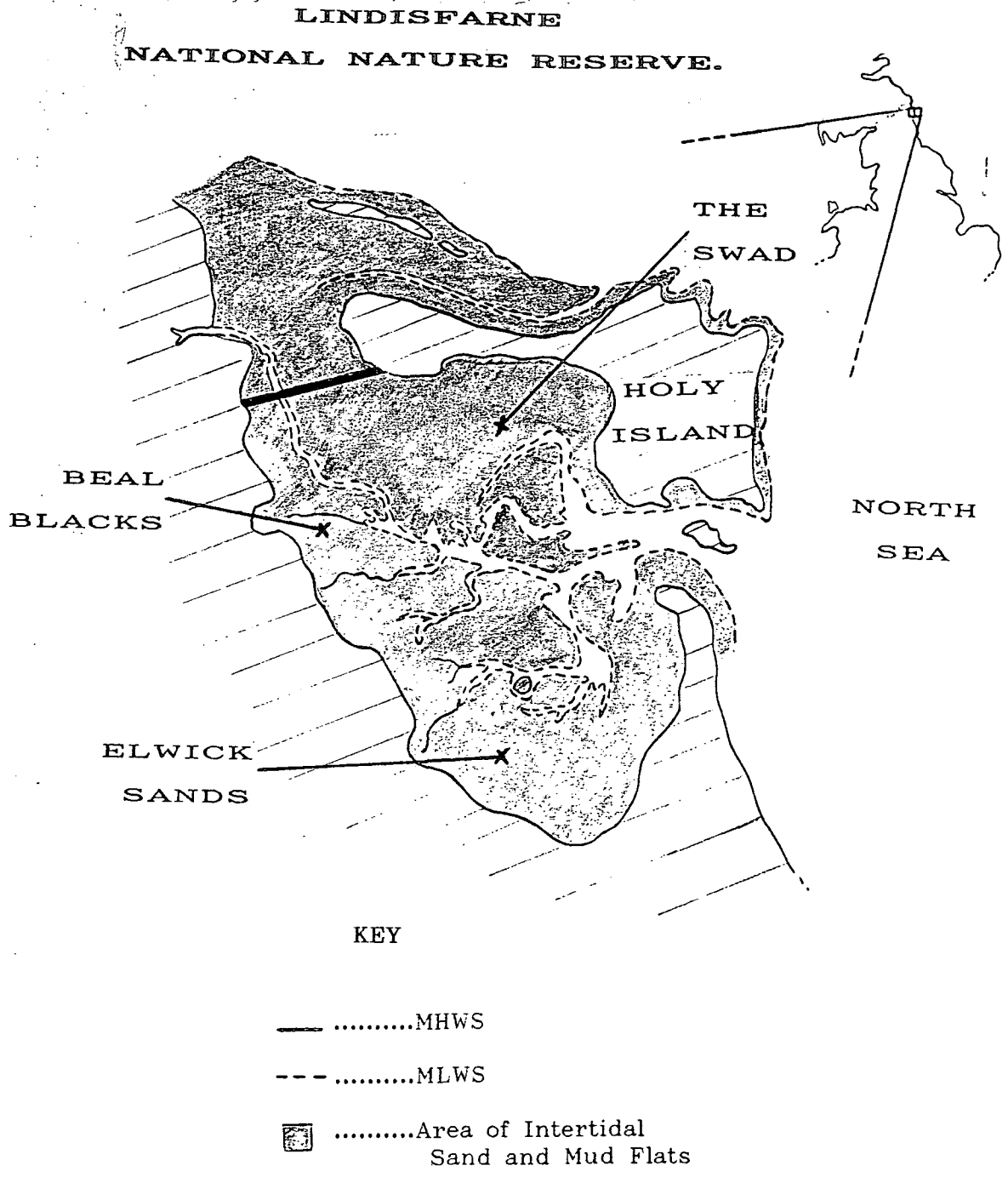
In recent years the extent of the seagrass meadows has gradually decreased leaving three major sites -

- Beal Blacks
- Elwick Sands
- The Swad.

Figure 2.1 shows the three sites selected for the study. They were similar in that they each contained both species of *Zostera*: the perennial *Z.noltii* which overwinters as rhizomes and the annual *Z.marina* which germinates each year from seed.

It was intended that most of the samples should be taken from the midtidal level of the shore within these sites, in order to negate the effects of differences in community structure associated with differences in tidal level. However, due to the patchy nature of the *Zostera* beds, this proved unfeasible. It was possible to select sites at Beal and Elwick which were at very similar tidal levels, towards the upper regions of the midshore. At the Swad, on the other side of South Low (the stream which flows through the flats), it was possible to collect samples only from the lower midshore region. The effects of such disparities will be discussed later.

FIGURE 2.1 : Location of the Study Sites within the Lindisfarne N.N.R.



2.3 NATURE OF THE STUDY SITES

As stated previously, the sites were chosen both out of necessity and for the presence of the two *Zostera* species. It was noticeable from field observations that *Z.marina* showed a marked preference for the areas of sediment that maintained a relatively high water content during periods of emersion viz. the run-off channels and the surface pools. *Z.noltii* was associated with areas that dried out more fully at low water and was seldom found in such channels or pools.

Beal Blacks was the first area to be sampled on May 19th. 1992 (Low Tide: 11.18). The *Zostera* at this site was found growing within twenty metres of the edge of the *Spartina* on relatively muddy, unconsolidated sediments. On this date, both species of the seagrass were distinguished. On return two months later, a dense blanket of *Enteromorpha* was found, overlying the *Z.noltii* in particular. The effects of such an algal mat on benthic macrofauna have been shown to be fairly dramatic in previous studies on saltmarsh (Millard, 1976) and open mud flats (Nicholls *et al.*, 1981).

Elwick Sands as the name suggests is largely an area of muddy sands in the south-west corner of the bay. The *Zostera* beds at this locality were reached by walking approximately 100 metres downshore from the edge of the *Spartina*. Samples were taken on June 5th. 1992 (Low Tide:12.55)

The area of the **Swad** was reached from the causeway. This site in particular has recently shown a dramatic reduction in the extent of the *Zostera* sward. Once again, the sediments are of a muddy-sand type. Sampling of this site was carried out on June 22nd. 1992 (Low Tide: 14.25).

CHAPTER 3. METHODOLOGY

3.1 INVERTEBRATE MACROFAUNA

3.1.1 Sample Collection

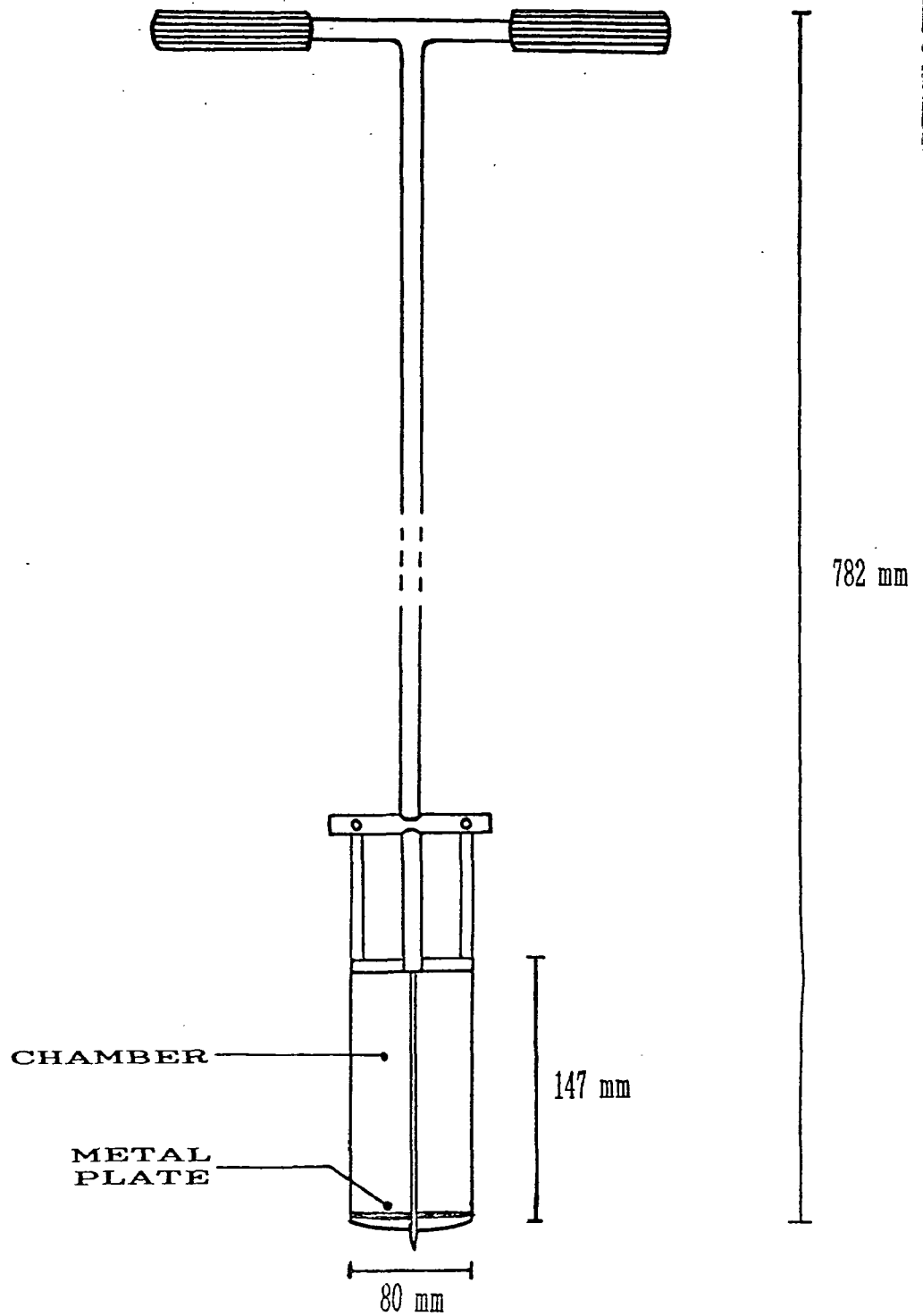
The macrofauna of intertidal sediments are usually defined as "all invertebrate animals retained by a sieve with a mesh size of 0.5 or 1.0mm" (Wolff, 1987).

The standard technique in the collection of benthic macrofauna from intertidal sediments involves the use of hand-held cylindrical corers, as shown in Figure 3.1. Such corers are open at the bottom end, with the lower edge sharpened. The device is driven into the sediment at low tide to the required depth and then twisted and pulled out at an angle. The mud core is then pushed back out of the chamber manually. The nature of the sediments to be sampled at Lindisfarne meant that a corer with diameter of 80 mm and cross-sectional area of 0.005m² was most suited to the task.

Preliminary results showed that approximately 97% of the macrofaunal numbers were located within the top 5cm of sediment. However some of the larger bivalves and oligochaetes were often found below this level, so cores were taken to a depth of approximately 14cm (equivalent to the height of the corer chamber) to ensure adequate sampling. Preliminary investigations also indicated that 12 cores was a sufficient number to provide statistically significant results and to take account of the heterogeneity within the sample areas (see Appendix A). At each of the sample areas therefore, 12 cores were taken in each of the three habitat types ie. *Z.marina* beds, *Z.noltii* beds and the bare mud surfaces.

These cores were placed in plastic tubs with lids, to prevent desiccation, and transported back to the laboratory.

FIGURE 3.1 : Sketch of Hand-Held Corer Used in the Study



3.1.2 Laboratory Analyses

Core samples were placed upright in individual plastic tubs and covered with sea-water for 48 hours. After this time, it was possible to pick off the living, mobile gastropods (ie. *Hydrobia* and *Littorina* spp.) from the mud surface and/or tub sides.

The mud cores were then gently broken down to produce a slurry (method from Nicholls et al., 1981) and sieved with tap water as delicately as possible using a screen with mesh size of 40 squares per inch (0.64 mm). Lewis and Stoner (1980), in an examination of methods used in the sampling of the macrobenthos in seagrass meadows, showed that the common practice of using a 1.0mm screen allowed the passage of 14% of the macrofaunal species and 47% of the macrofaunal number. The material retained by the sieve was washed into a sorting tray and examined.

The benthic samples were sorted by hand and all molluscs, polychaetes, nemertines and crustaceans identified to at least genus level. This enabled both quantitative and qualitative analyses to be carried out. The taxonomy of the oligochaetes was beyond the scope of my investigations, involving electron microscopy, and they were thus counted but not identified. Owing to the problems of numerous empty gastropod shells in the samples, all molluscs were removed into sea-water and observed for a period of a few minutes. If such shells were inhabited, movement could be noted within this time and these individuals removed, counted and preserved. The soft-bodied invertebrates were preserved directly in a 4% formalin-seawater mixture.

Ash-free dry weights were determined for the invertebrates extracted from the sediments by drying at 100°C for 24 hours followed by ashing in a muffle furnace at 450°C for 6 hours. The ash-free dry weights were calculated for the molluscs and for the soft-bodied invertebrates separately, and subsequently combined and used as a measure of biomass.

Several cores were divided horizontally into 2cm deep sections prior to sieving each section separately. This provided data on the vertical distribution of the invertebrate taxa within the sediment cores.

3.2 ZOSTERA BIOMASS

The sieving procedure outlined above also retained the fragments of *Zostera* present within the cores. In the laboratory, it was possible to separate the aerial green parts of the seagrass from the living and dead rhizomes. The latter may be distinguished, since living rhizomes are white or light brown, while dead sections are black and fragmentary (Sand-Jensen, 1975). The remaining largely amorphous material was grouped together with the dead rhizomes and collectively termed "detritus".

The separate parts obtained from each core were dried for 24 hours at 105°C, cooled in a desiccator and weighed. This gave a measure of the above ground and below ground living *Zostera* biomass. The detrital component was ashed at 450°C in a muffle furnace for 6 hours to establish the dead organic component of the sediment. This ash-free dry weight was expressed as a percentage of the total sediment dry weight, minus the *Zostera* biomass.

3.3 SEDIMENTS

At each sampling station, a further two variables were measured.

(a) Twelve cores were taken in the field and split longitudinally in two with a sharp blade. The depth of the Redox Potential Discontinuity (RPD) layer below the surface of the sediment was measured, enabling a mean value and standard error to be derived.

(b) Four cores were extracted in order to investigate the granulometric properties of the sediments. These samples were broken up and oven-dried for 24 hours at 105°C. The dried muds were then passed through a sediment shaker consisting of screens with mesh sizes of 20(1.27mm), 40(0.64mm), 60(0.42mm), 100(0.25mm) and 200(0.12mm) squares per inch. Particles which passed through the 200 squares per inch mesh (ie. had a diameter of less than 0.125 mm), producing the residue at the base of the shaker, were deemed to form the silt-clay fraction. In actual fact, this residue would also contain a very fine sand fraction (since 63 micrometre diameter particles represent the arbitrary division of the sands and clays), but the terminology was sufficient for my investigations.

3.4 BEHAVIOURAL INVESTIGATIONS

In conjunction with the results obtained through other methods of analysis, it was decided to carry out some investigations of behavioural preferences in selected species. Invertebrates were given the opportunity to "choose" between a bare mud sample and one which had *Zostera* growing on it. Simple choice chambers were therefore set up, as shown in Figure 3.2, in which half the tank was lined with mud alone and the other half with sediment supporting the seagrass.

The invertebrates most suitable for a study of this sort were the mobile gastropods *Hydrobia* and *Littorina*. These invertebrates were easily marked to facilitate counting, using a spot of Tipp-Ex positioned on their shell (see Figure 3.3).

Twenty individuals of the same genus were placed along the line dividing the two sediment samples, moistened carefully with a small quantity of sea water, and left in a constant temperature of 8°C for 24 hours. After this time, the numbers of gastropods in each "chamber" (ie. each half of the tank) and those remaining on the start line were counted and recorded.

The experiment was then repeated at least twenty times with different individuals of each of the two genera, so that statistical tests could be confidently applied to the data obtained.

FIGURE 3.2 : Example of the Choice Chamber set up to analyse Behavioural Preferences in Gastropod Molluscs



FIGURE 3.3 : Hydrobiid Snail marked with Tipp-Ex, to Facilitate Counting



CHAPTER 4. RESULTS

4.1 ENVIRONMENTAL VARIABLES

4.1.1 Depth of Redox Potential Discontinuity Layer

The depth of the black anoxic level (RPD layer) below the sediment surface was measured in each of the three vegetation types at each of the three sample sites. Figure 4.1 shows the mean depth of this layer at each location.

Statistical analysis of variance showed that RPD depths below a chosen habitat were not significantly different between sample sites:-

1. Bare mud samples - $F= 1.17$, d.f.= 20 $P>0.05$
2. *Z.noltii* samples - $F= 0.18$, d.f.= 20 $P>0.05$
3. *Z.marina* samples - $F= 2.77$, d.f.= 20 $P>0.05$

This enabled data to be combined for each of the three habitat types (Table 4.1).

Table 4.1 : Mean depths of redox potential discontinuity layer below sediment surface within different habitats of three study sites at Lindisfarne.

SITE [Sample size]	MEAN DEPTH (cm)		
	Bare Mud	<i>Z. noltii</i>	<i>Z. marina</i>
Beal [n= 7]	26.29 (2.64)	13.14 (1.61)	12.01 (2.05)
Elwick [n= 7]	41.14 (7.89)	13.00 (1.59)	15.41 (2.17)
The Swad [n= 7]	28.29 (9.86)	13.57 (2.46)	21.00 (3.54)
Mean Standard error	31.90 cm (4.34)	13.24 cm (1.06)	16.14 (1.68)

Figure 4.1 : Mean Depth of RPD Layer below Surface within Study Areas.

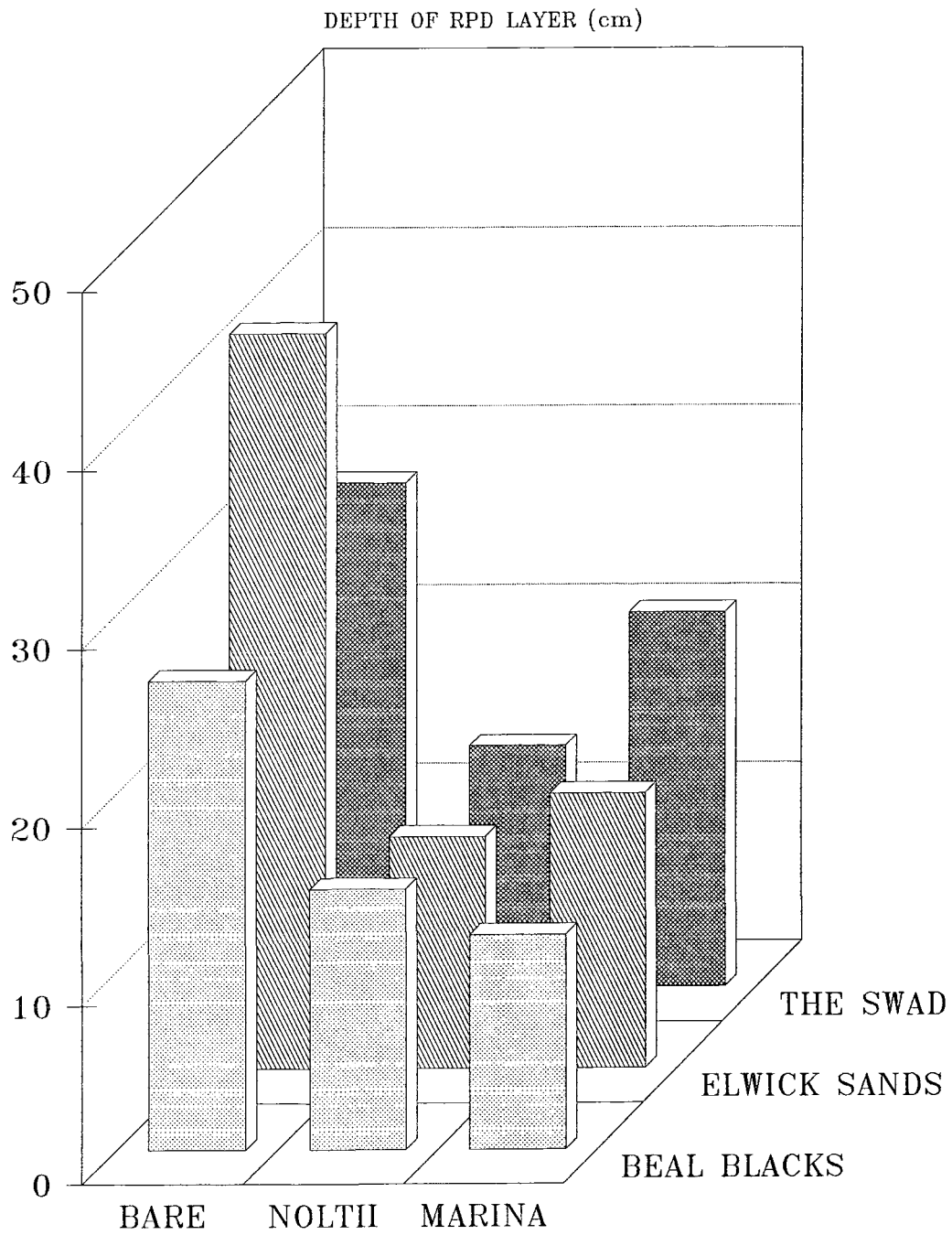
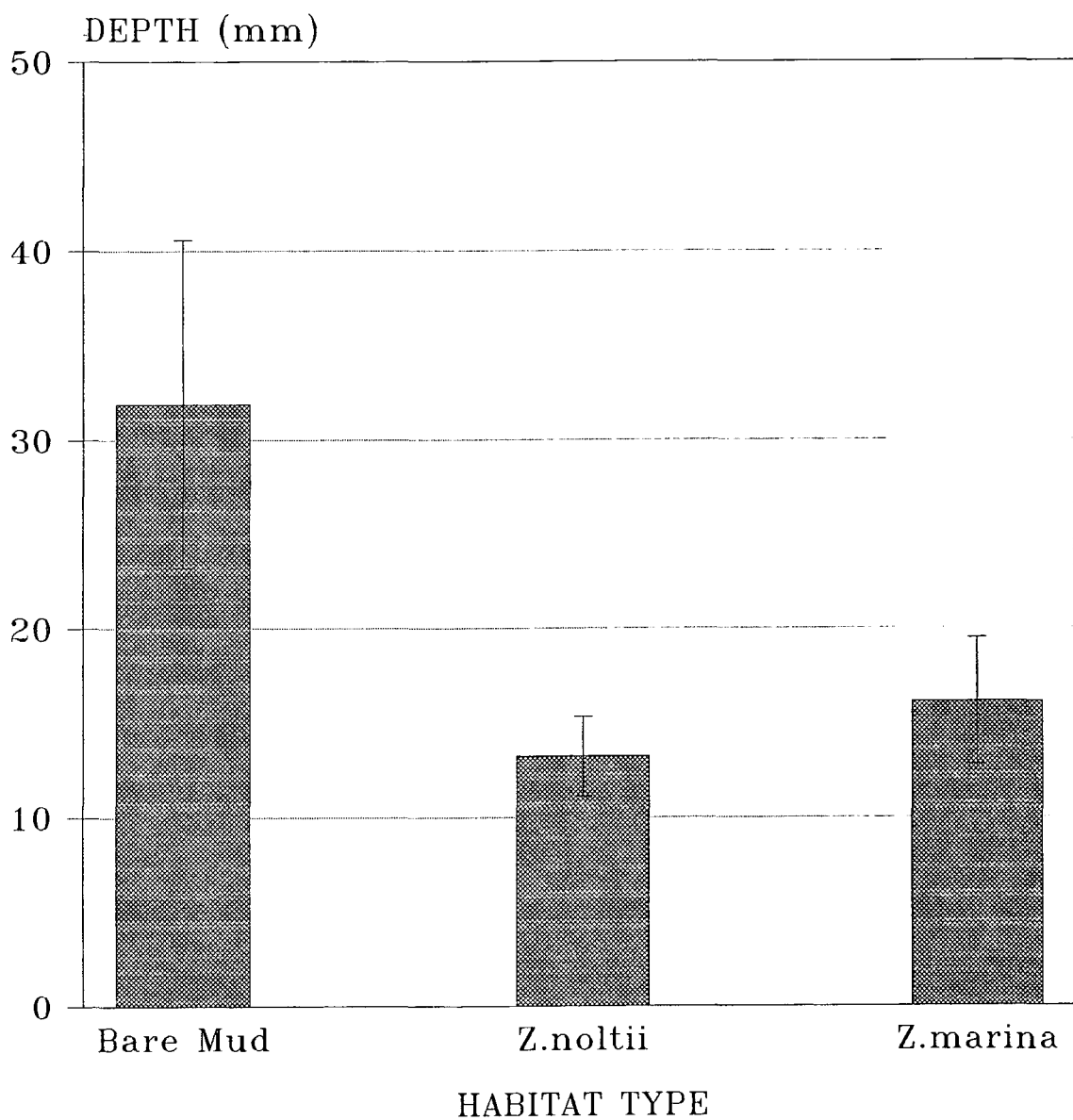


Figure 4.2 : Mean RPD Depths for the
Three Habitat Types at Lindisfarne.
(Data from all three sample sites)



I 2 x S.E █ DEPTH BELOW SURFACE

The mean values for depths of RPD at Lindisfarne are shown in Figure 4.2. T-tests applied to these data provided the following levels of significance :

Table 4.2 : Significance levels of differences in RPD depth between the different vegetation types.

Sample Size (n) = 21	Bare	<i>Z.noltii</i>
Bare	-- -- --	t = 4.18 d.f.= 40 P < 0.01
<i>Z.marina</i>	t = 3.39 d.f.= 40 P < 0.01	t = 1.46 d.f.= 40 n.s.

d.f. - Degrees of Freedom
P - Levels of Significance

From Table 4.2, it can be seen that the depth of the RPD was significantly deeper in sediments supporting no vegetation, than in those supporting either *Zostera noltii* or *Zostera marina*. Sediment cores removed from within swards of the two *Zostera* species did not differ significantly with respect to the depth of the black anoxic layer.

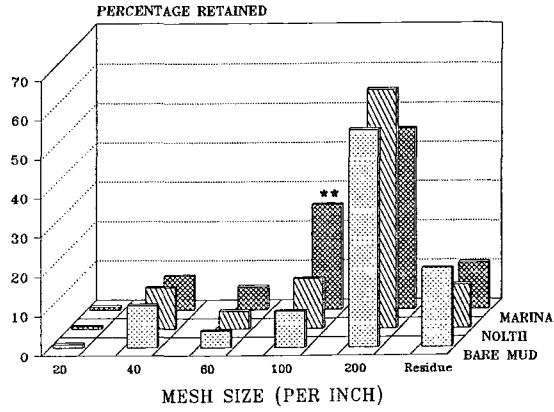
4.1.2 Sediment Granulometry

Despite attempts to sample from sites with similar granulometric properties, statistical analysis of particle size distributions, showed that this had not been achieved.

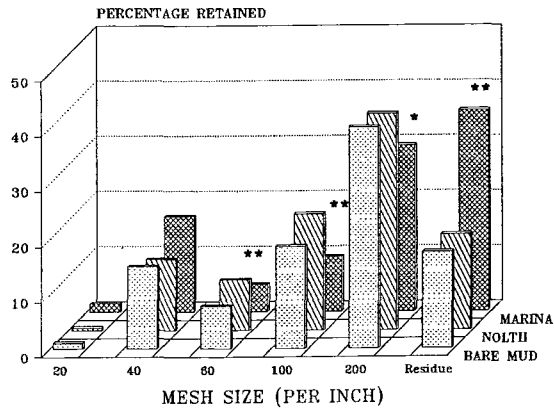
The quantity of sediment retained by each sieve, after passing through the next largest mesh size, was expressed as a percentage of the total. Figure 4.3 illustrates the differences at the three sampling sites. Analysis of variance showed the major differences to be between sediments supporting *Z.marina* compared to the other two habitat types. These differences are illustrated in Table 4.3.

Figure 4.3 : Comparison of the Sediment Granulometry at Different Sites

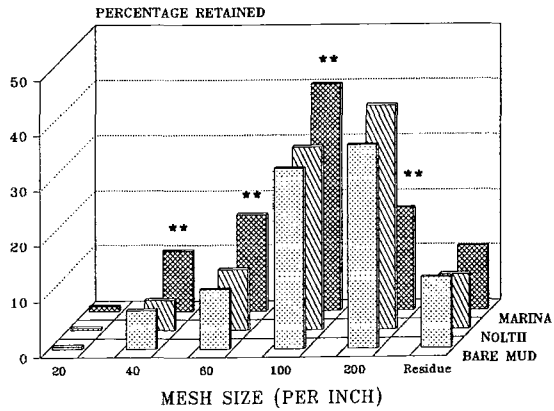
BEAL BLACKS



ELWICK SANDS



THE SWAD



** Z.marina differs significantly from both Z.noltii and bare mud (P < 0.05)

* Z.marina differs from bare mud only (P < 0.05)

Table 4.3 : Significant differences (ANOVA, $P < 0.05$) in sediment grain sizes at each of the sample sites.

SITE [n= 4 per site]	MESH SIZE					
	20	40	60	100	200	Res
Beal	n.s.	n.s.	n.s.	3>>1,2	n.s.	n.s.
F value	0.2	0.4	1.9	37.2	2.2	2.6
d.f.	11	11	11	11	11	11
Elwick	n.s.	n.s.	3<<1,2	3<<1,2	3<<1	3>>1,2
F value	3.3	0.9	18.1	13.2	5.8	8.6
d.f.	11	11	11	11	11	11
The Swad	n.s.	3>>1,2	3>>1,2	3>>1,2	3<<1,2	n.s.
F value	1.8	15.1	13.1	15.6	56.6	1.4
d.f.	11	11	11	11	11	11

1. Bare mud samples 2. Z.noltii 3. Z.marina

>> - significantly greater than ($P < 0.05$)

<< - significantly less than ($P < 0.05$)

n.s. - no significant difference

d.f. - degrees of freedom

There was also substantial between-site variation in particle size distributions, making the combination of results difficult. It was therefore accepted that the effects of sediment granulometry could not be eliminated from the study as a possible contributory source of variation.

4.1.3 Silt/Clay Content

Measures of the sediment silt/clay content (that fraction with particle diameter less than 0.125mm) at the different sites ranged from 7.7% to 44.2%. Table 4.4 illustrates the mean percentage that this fraction comprised within the sediments.

Table 4.4 : Mean percentage silt/clay content (particles less than 0.125mm diameter) of sediments extracted.

SITE [Sample size]	MEAN PERCENTAGE		
	Bare	Z.noltii	Z.marina
Beal	19.90	11.00	11.75
[n= 6]	(4.70)	(1.40)	(1.90)
Elwick	17.50	17.30	36.40
[n= 6]	(1.50)	(1.90)	(6.00)
The Swad	12.70	9.80	11.55
[n= 8]	(1.70)	(0.90)	(1.00)

() Standard errors

Significant differences between habitat types, within sample sites, were restricted to Elwick, where *Z.marina* sediment cores were found to have a statistically greater percentage content of this fraction (ANOVA: $F= 8.6$, $d.f.= 11$; $P<0.05$). The presence of seagrasses at the surface might intuitively slow water speeds down, enabling finer particles to sediment out. However, the data described in this study on the whole do not support this theory.

Variations between the sample sites were evident and are shown in Figure 4.4. Sediments supporting both *Zostera* species had significantly higher proportions of silt/clay particles at Elwick compared to Beal and the Swad.

4.2 ZOSTERA BIOMASS

Figure 4.5 shows the mean aerial and root or rhizome biomass measures for each of the seagrass species at each site. Superimposed on top of these means is a seasonal variation coupled to the growing season. However, even in the perennial *Z.noltii*, there is considerable variation in for example rhizome biomass between the sites, creating problems in making comparisons.

4.2.1 Aerial Biomass

Measures of above-ground biomass were similar for each of the *Zostera* species at both Elwick and the Swad. However, the finer leaved *Zostera noltii* was found to have on average approximately 50% less aerial biomass compared to *Z.marina*.

Samples collected from *Z.marina* beds on 16.07.92 showed an increased aerial biomass, compared to those collected earlier in the growing season (19.05.92), which was similar to both Elwick and the Swad. A seasonal variation in above ground biomass was therefore apparent.

FIGURE 4.4 : Percentage Silt/Clay Content of Lindisfarne Sediments.
(Particles of diameter less than 125 μ m)

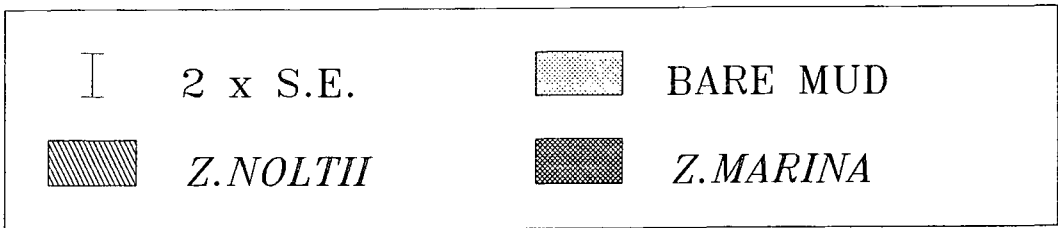
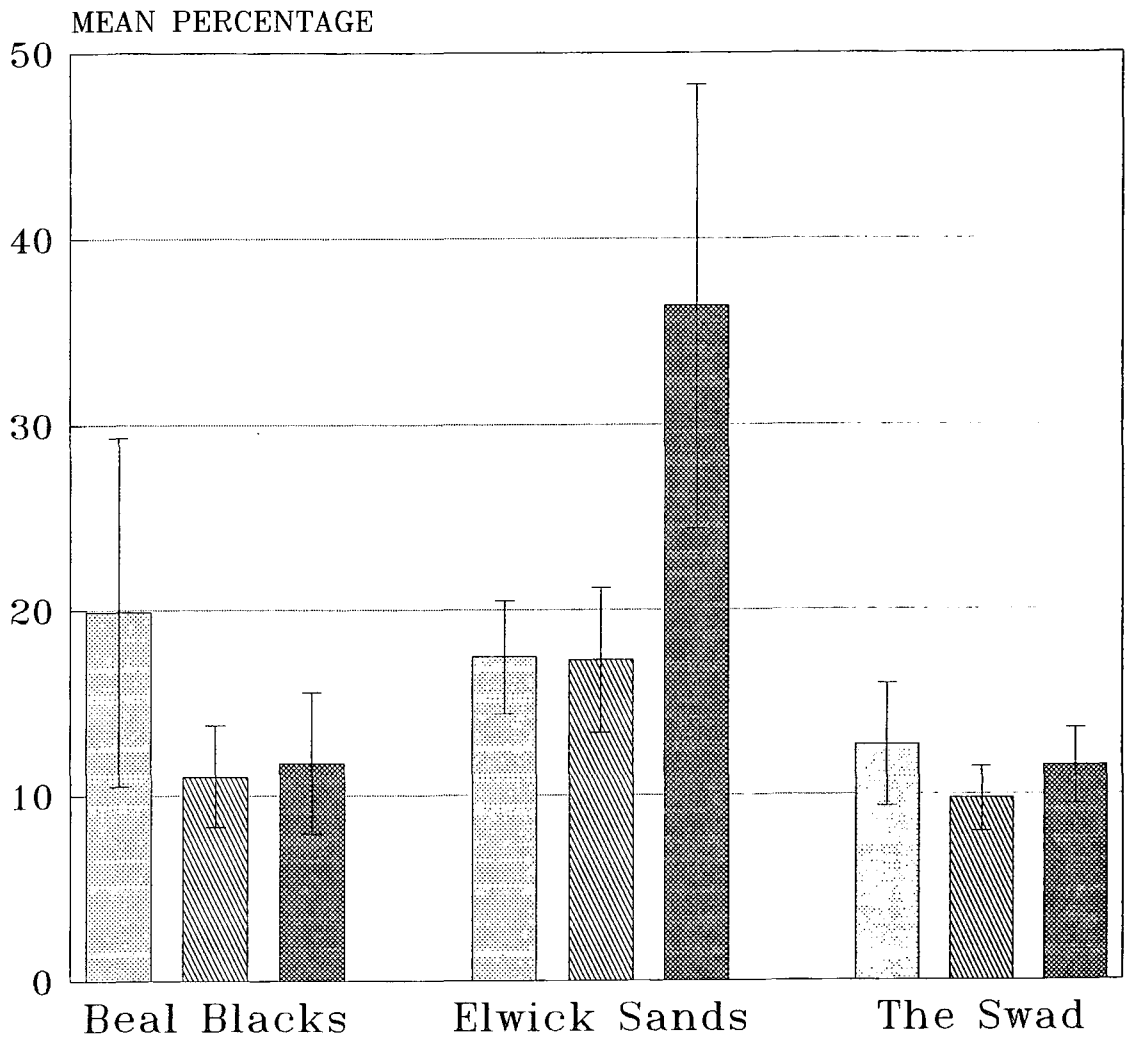


FIGURE 4.5 : Mean Measures of *Zostera* Biomass at Lindisfarne.

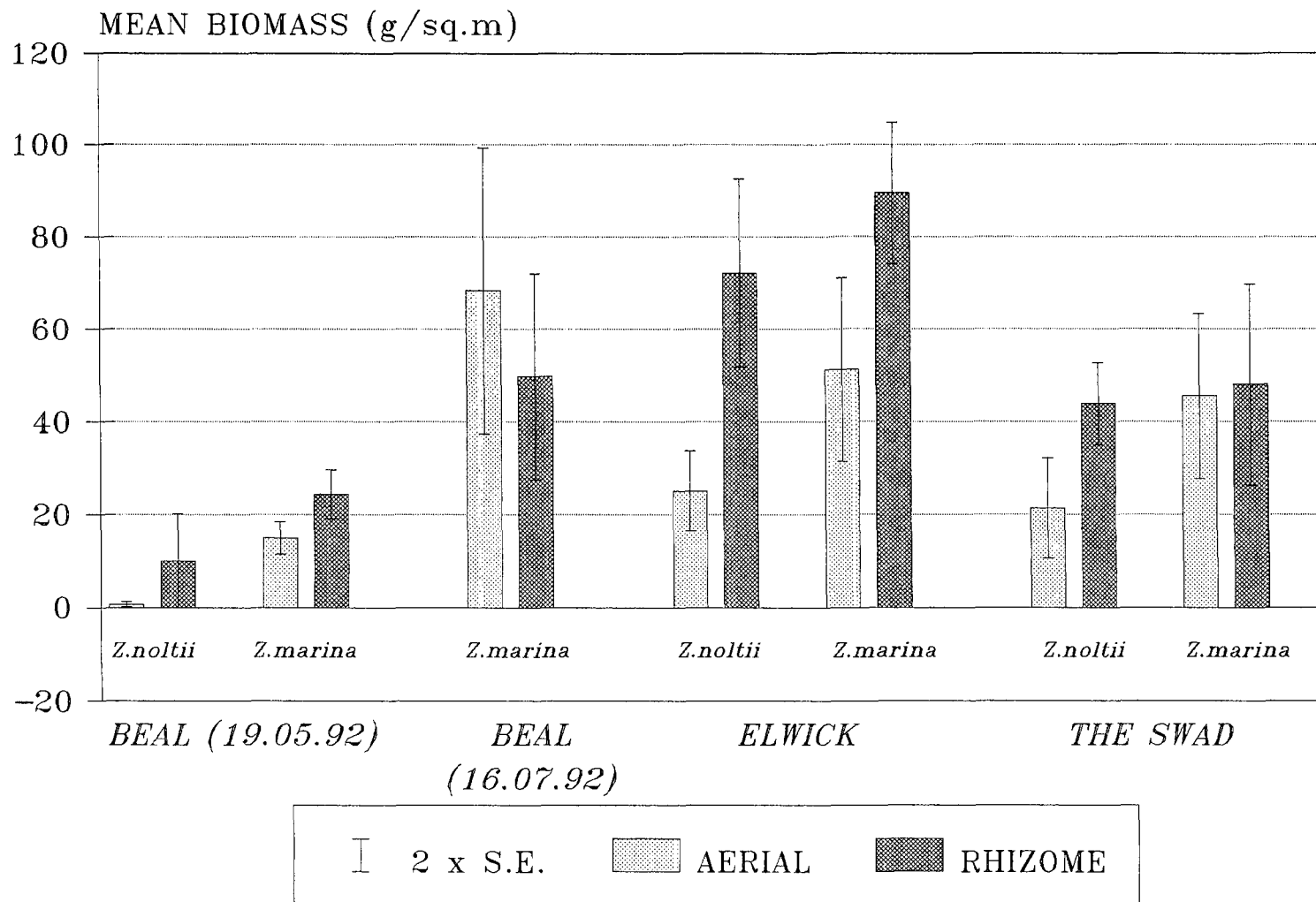


Table 4.5 : Mean aerial biomass of *Zostera* spp. at the three study sites.

SITE [Sample size]	SAMPLING DATE	MEAN BIOMASS (gm ⁻²)	
		<i>Z.noltii</i>	<i>Z.marina</i>
Beal [n= 6]	19.05.92	0.69(0.27)	14.89(1.75)
	[n= 8] 16.07.92	--	68.39(15.48)
Elwick [n= 6]	05.06.92	25.12(4.31)	51.24(9.86)
The Swad [n= 8]	22.06.92	21.39(5.41)	45.51(8.87)

() standard error of mean

4.2.1 Rhizome Biomass

Measurements made of below ground living *Zostera* biomass showed substantial variation both within and between sites (Table 4.6).

Table 4.6 : Mean rhizome biomass of *Zostera* spp. at the three study areas.

SITE [Sample size]	SAMPLING DATE	MEAN BIOMASS(gm ⁻²)	
		<i>Z.noltii</i>	<i>Z.marina</i>
Beal [n= 6]	19.05.92	9.98(5.09)	24.37(2.66)
	[n= 8] 16.07.92	--	49.74(11.10)
Elwick [n= 6]	05.06.92	72.12(10.18)	89.48(7.72)
The Swad [n= 8]	22.06.92	43.77(4.41)	48.00(10.82)

() standard error of mean

There was no significant difference between the two *Zostera* species at any of the three sites in terms of the biomass of their below ground portion.

Between site variation was such that all three sampling areas differed in their *Z.noltii* rhizome biomass. The rhizome biomass in *Z.marina* was significantly greater at the Elwick site compared to the Swad and the two Beal samples.

4.2.3 Dead Organic Component

Measurements of the actual organic detrital component (gm^{-2}) of the sediments were extremely variable, with those removed from the Swad differing from the other sites by an order of magnitude (Table 4.7).

Table 4.7 : Mean detrital biomass and percentage that this component formed in upper 14 cm of sediment at the three study areas.

SITE [Sample size]		Bare Mud	VEGETATION	
			<i>Z.noltii</i>	<i>Z.marina</i>
Beal [n= 6]	g/m^2	87.88 (33.17)	224.5 (26.24)	261.97 (29.78)
	%	2.61 (0.68)	6.17 (1.68)	7.79 (0.64)
Elwick [n= 6]	g/m^2	89.78 (8.08)	146.49 (5.86)	178.57 (17.44)
	%	1.56 (0.03)	2.85 (0.21)	2.78 (0.15)
The Swad [n= 8]	g/m^2	1534.02 (418.23)	644.48 (153.38)	3854.13 (393.30)
	%	11.74 (3.10)	7.24 (1.38)	20.38 (1.29)

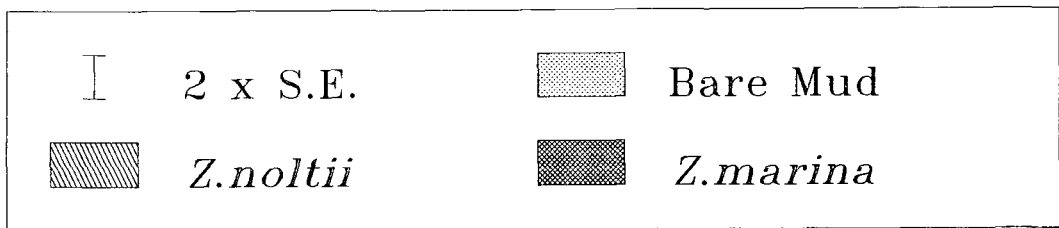
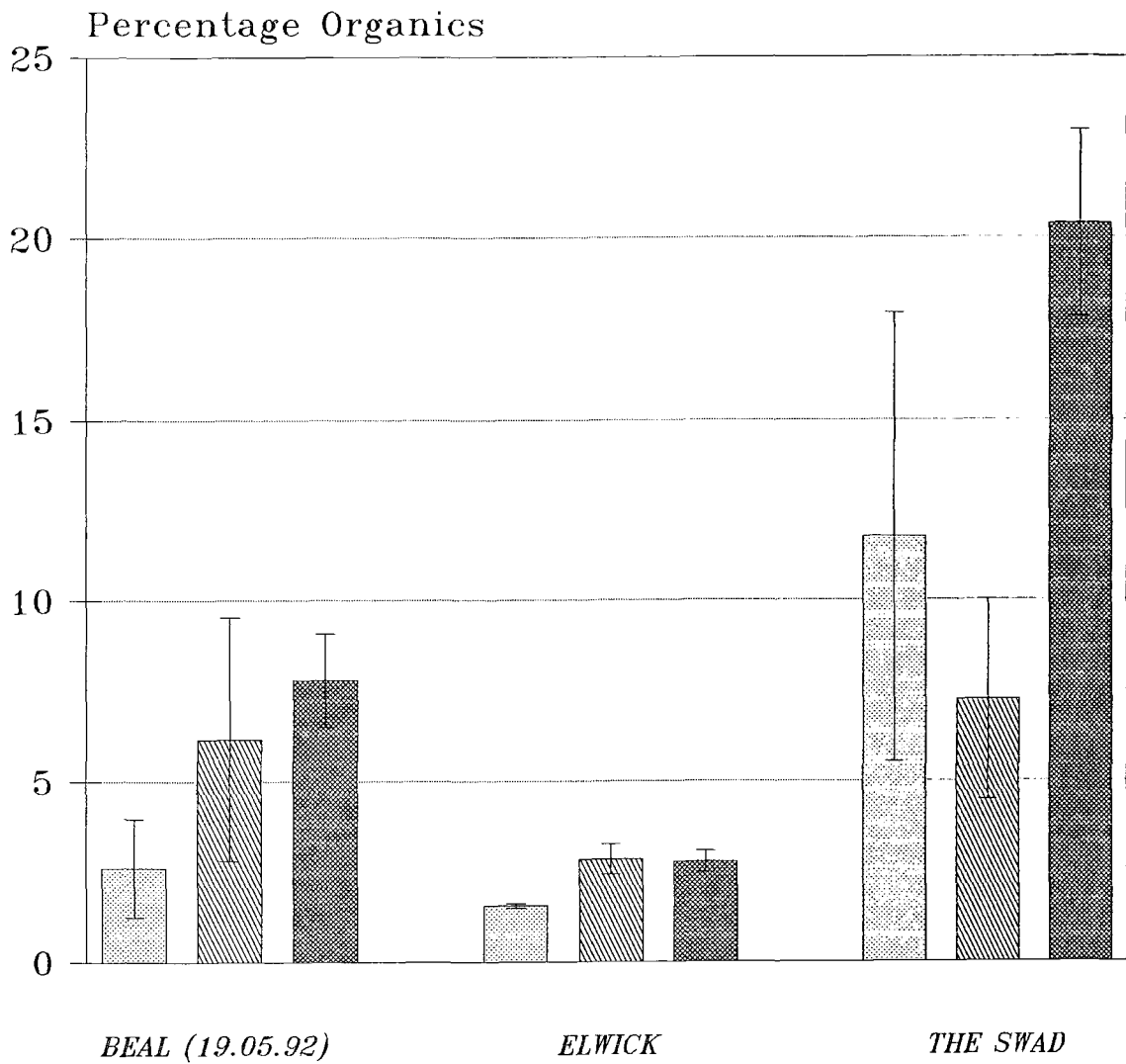
) standard error of mean

g/m^2 - mean biomass % - percentage detrital component

A more appropriate method of presenting the data was to consider the percentage that the detrital component formed within the sediments collected, ie. the top 14 cm.. Figure 4.6 shows that the Swad site, despite considerable variability, had in general a higher percentage of dead organic matter compared to Beal and Elwick.

The general pattern was that the samples removed from the bare mud areas had a substantially lower percentage detrital element compared to those supporting *Zostera*. The bare mud cores differed significantly to *Z.marina* samples at all three sites: Beal ($t= 5.5$, d.f.= 6; $P<0.01$), Elwick ($t= 5.99$, d.f.= 6; $P<0.001$) and the Swad ($t= 2.6$, d.f.= 10; $P<0.05$) Bare mud samples differed from *Z.noltii* cores at Elwick only ($t= 7.91$, d.f.= 6; $P<0.001$). At the Swad, core samples taken from the two seagrass species also differed significantly ($t= 6.97$, d.f.= 10; $P<0.001$), with the bare mud samples showing extreme variation.

FIGURE 4.6 : Mean Measures of Detrital Biomass Within Habitat Types at Lindisfarne.



4.3 CORRELATION OF MEASURED VARIABLES

Mean values for the five variables measured were examined for significant correlation. The five variables are listed in Table 4.8, together with the coefficients of correlation.

Table 4.8 : *Coefficients of Correlation between the different environmental variables measured.*

	RPD	CLAY	AERIAL	RHIZOME	ORGANIC
RPD	1.0000	.0782	-.4373	-.5733	-.1832
CLAY		1.0000	-.4592	.5238	-.4871
AERIAL			1.0000	.8994**	.3157
RHIZOME				1.0000	-.0106
ORGANIC					1.0000

Significance Level

* - $P < 0.05$ ** - $P < 0.01$

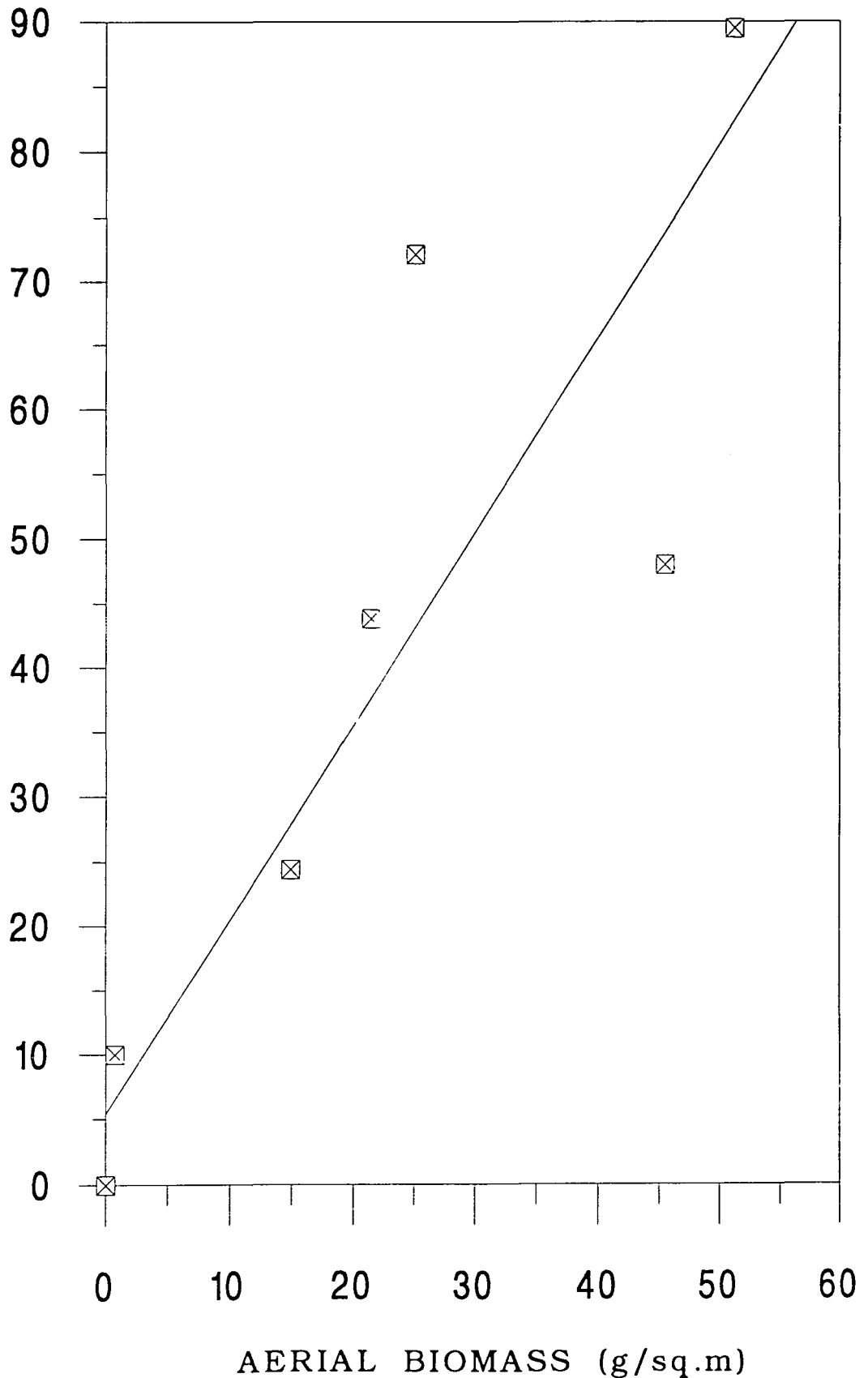
From Table 4.8, it can be seen that the above and below ground *Zostera* biomasses are significantly positively correlated. This is not too surprising, since both biomass measures were gathered from the vegetated sites, but neither from the bare mud samples. Figure 4.7 shows this relationship graphically.

No other significant correlations were found in the data.

Figure 4.7 : Relationship between Aerial and Rhizome Biomass of Zostera

RHIZOME BIOMASS (g/sq.m)

$$y = 5.48032 + 1.50175x \quad r^2 = 0.80882$$



4.4 BENTHIC MACROFAUNA

During the course of the two month study, a total of 116 core samples were removed from Lindisfarne and analysed. These yielded 6167 macrobenthic invertebrates, the majority of which were oligochaetous annelids, the sedentary polychaete *Scoloplos armiger* and several mollusc genera. Table 4.9 shows the list of organisms identified. The major feature of the list is the presence of both substantial epifaunal and infaunal components.

A total of twenty two invertebrates were identified to species level, one to genus, two to family (including the larval and pupal stages of a Dipteran fly), and due to taxonomic difficulties, the oligochaetes were simply grouped together.

4.4.1 Relative Abundance

Table 4.10 illustrates the relative abundance of the different genera in the nine sample sites. It can be seen that the patterns of abundance were generally similar within a habitat, at the different sample sites. For example, *Hydrobia* and the oligochaetes were present in virtually all the cores, irrespective of vegetation type, whilst *Ampharete* and *Lineus* spp. were only found in cores supporting *Zostera*. *Littorina* and *Mytilus* occurred in a greater percentage of cores from the seagrass sward compared to the bare mud samples, whereas the dipteran larvae and pupae were not recovered from *Z.marina* cores at all. The isopod *Idotea baltica* conversely was restricted solely to *Zostera marina* samples

This pattern was not consistent however in the polychaete annelids - a group which was rather poorly represented in the samples. Cores removed from Elwick, for example, yielded only one errant polychaete (a nereid) in total. From Table 4.10, it appears that this group tended to prefer the vegetated habitats and that the Swad appeared to have the highest relative abundance and diversity of errant polychaetes. However, with so few individuals recorded, these conclusions are extremely uncertain.

4.4.2 Density of Invertebrates

Figure 4.8 shows the mean values for total invertebrate number per square metre at each of the three sampling localities and in each of the three

Table 4.9: List of Invertebrates Identified

MOLLUSCA

Hydrobia ulvae
Hydrobia ventrosa
Macoma balthica
Mytilus edulis
Littorina littoralis
Littorina littorea
Littorina saxatilis
Cerastoderma edule
F: Lepidochitonidae (species n.d.)

NEMERTINI

Lineus spp.

ANNELIDA

POLYCHAETA:

Arenicola marina
Eulalia viridis
Eteone longa
Nephtys caeca
Nereis diversicolor
Phyllodoce maculata
Phyllodoce mucosa

Ampharete balthica
Owenia fusiformis
Pectinaria koreni tubes
Pygospio elegans
Scoloplos armiger

OLIGOCHAETA: Species n.d.

ARTHROPODA

CRUSTACEA:

Idotea baltica
Corophium volutator
Urothoë spp.

DIPTERA:

Larvae, F: Dolichopodidae (species n.d.)
Pupae, F: Dolichopodidae (species n.d.)

Table 4.10 : *Invertebrate Abundances at the Different Sample Sites.*

	BEAL			ELWICK			THE SWAD		
	B	N	M	B	N	M	B	N	M
<i>HYDROBIA</i>	**	***	***	***	***	***	***	***	***
<i>MACOMA</i>	***	***	***	*	***	***	**	***	***
<i>LITTORINA</i>	*	**	**	*	**	***	0	**	**
<i>MYTILUS</i>	*	**	**	0	*	***	*	**	**
<i>CERASTO- DERMA</i>	0	0	0	0	0	0	0	*	*
<i>LINEUS</i>	0	0	**	0	0	0	0	*	*
<i>NEREIS</i>	0	0	0	0	0	*	0	0	**
<i>NEPHTYS</i>	0	*	0	0	0	0	0	0	*
<i>ETEONE</i>	0	0	*	0	0	0	**	0	0
<i>EULALIA</i>	0	0	0	0	0	0	0	0	*
<i>PHYLLODOCE</i>	0	0	0	0	0	0	0	*	**
<i>ARENICOLA</i>	0	*	0	0	0	0	0	*	0
<i>SCOLOPLOS</i>	**	**	***	0	***	***	**	**	***
<i>AMPHARETE</i>	0	**	**	0	**	**	0	*	**
<i>OWENIA</i>	0	0	0	0	0	*	0	0	0
<i>PECTINARIA</i>	*	*	*	0	0	0	0	0	0
<i>PYGOSPIO</i>	**	0	0	0	0	0	*	0	0
<i>OLIGO- CHAETA</i>	***	***	***	***	***	***	***	***	***
<i>IDOTEA</i>	0	0	**	0	0	*	0	0	**
<i>COROPHIUM</i>	0	0	0	0	0	0	*	*	0
<i>UROTHOE</i>	0	0	0	0	0	0	0	0	0
<i>DIPTERA</i>	*	**	0	***	**	0	*	**	0

No. of Cores (out of 12) in which the Invertebrate Occurred.

*** ALL

** 1 < NO. < ALL

* 1 ONLY

B-Bare Mud; N-*Z.noltii*; M-*Z.marina*

different vegetation types. This mean number ranged from 1182 to 27772 invertebrates per square metre. Despite this variation, there were statistical differences between the sample sites (ANOVA, $P < 0.05$).

At Beal, *Z.noltii* cores differed statistically from both bare ($t = 2.51$, d.f. = 22; $P < 0.05$) and *Z.marina* ($t = 6.26$, d.f. = 22, $P < 0.001$) cores. At Elwick, the unvegetated cores yielded a significantly lower faunal number than either of those supporting vegetation (*Z.noltii*: $t = 5.67$, d.f. = 22, $P < 0.001$; *Z.marina*: $t = 4.29$, d.f. = 22, $P < 0.001$). At the Swad, the *Z.marina* cores showed a significant difference to unvegetated cores ($t = 3.81$, d.f. = 22; $P < 0.01$) and also to the other species of *Zostera* ($t = 2.28$, d.f. = 22; $P < 0.05$)

Between site differences were restricted to bare mud cores at Elwick and the Swad ($t = 5.16$, d.f. = 22; $P < 0.001$) and *Z.noltii* samples at Beal and the Swad ($t = 3.17$, d.f. = 22; $P < 0.01$). Elwick had a significantly higher mean total invertebrate number inhabiting the *Z.marina* beds than Beal ($t = 2.68$, d.f. = 22; $P < 0.05$) and the Swad ($t = 3.11$, d.f. = 22; $P < 0.01$).

Table 4.11 provides a breakdown of the different invertebrate groups (full details are given in Appendix B). From this it can be seen that the vast majority of the density is made up by oligochaetes. On average, two-thirds of all macrofaunal numbers are provided by this group, but in some samples, this value rose to over 90%. The second most important group with respect to density were the molluscs, followed by the polychaetes, with the other groups forming only a fraction of the number (always less than 5% of the total).

FIGURE 4.8 Mean Numbers of all Invertebrates at the Different Sites

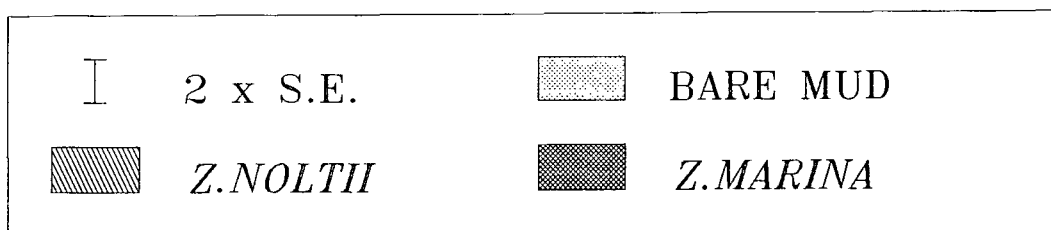
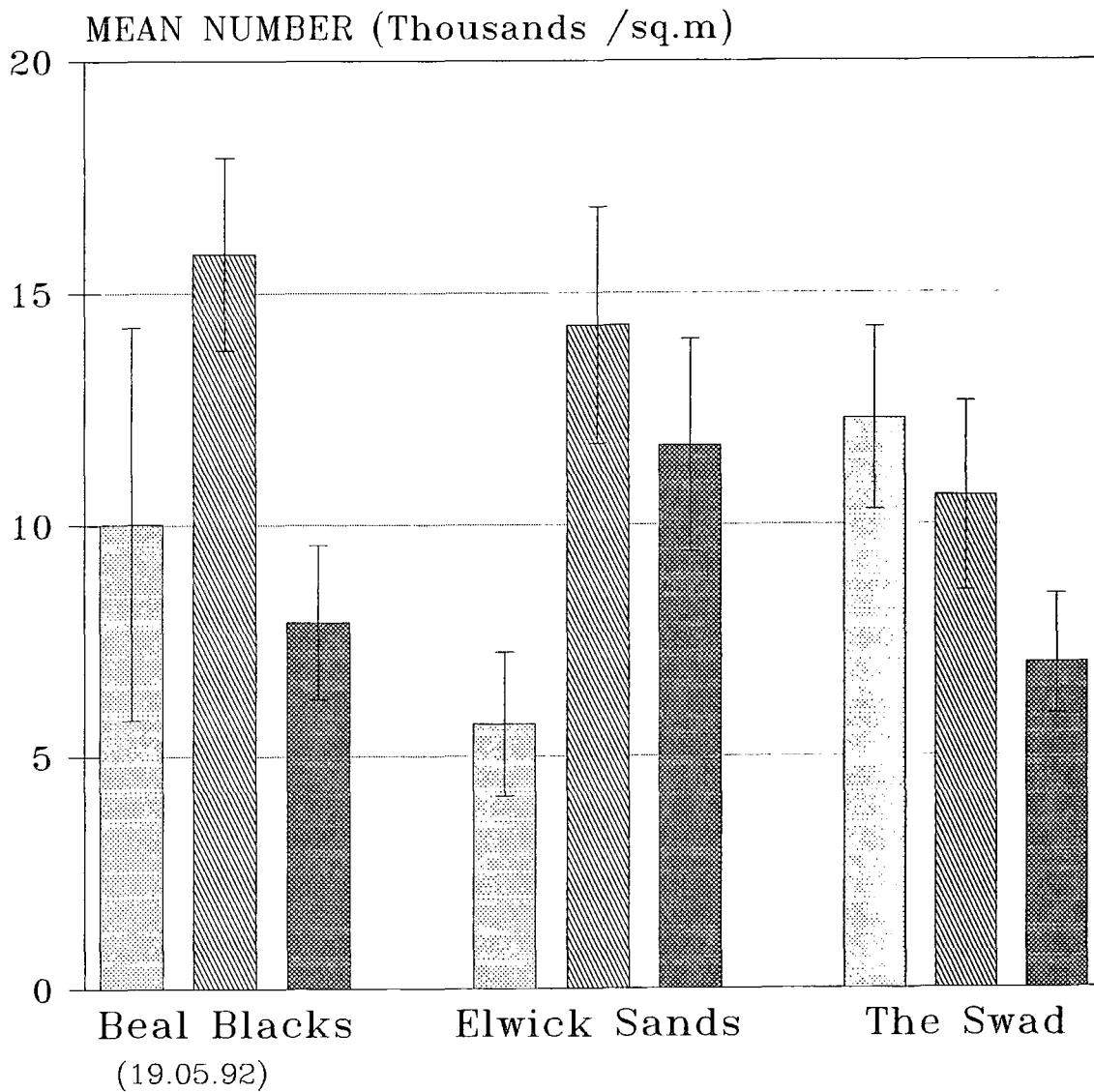


Table 4.11 : Mean Densities (No.m⁻²) of Individuals belonging to Different Invertebrate Groups.

		BEAL	ELWICK	THE SWAD
MOLLUSCA	B	846	275	4941
	N	1282	1424	2947
	M	1575	3238	2848
POLYCHAETA	B	622	--	444
	N	136	1763	228
	M	3839	2412	1248
OLIGOCHAETA	B	8589	5204	6997
	N	14416	11225	7461
	M	2321	6151	2934
OTHERS	B	50	271	33
	N	163	33	88
	M	249	17	53
TOTALS	B	10107	5750	12415
	N	15997	14445	10724
	M	8004	11818	7083

Owing to the considerable differences in relative densities of the different invertebrates within the sample sites, it was appreciated that few of those organisms identified actually occurred in sufficient numbers to be suitable for quantitative analysis. The nine macrofaunal types chosen for the study included four mollusc genera, *Hydrobia*, *Macoma*, *Mytilus* and *Littorina*, two polychaetes, *Scoloplos* and *Ampharete*, the group collectively referred to as the oligochaetes, the isopod *Idotea* and the dipteran larvae and pupae. Table 4.12 below shows the mean densities of these organisms within the study areas (full details are given in Appendix B). The results are shown graphically in Figure 4.9.

**FIGURE 4.9 : Mean Invertebrate Numbers (/sq.m)
at the Different Sites at Lindisfarne**

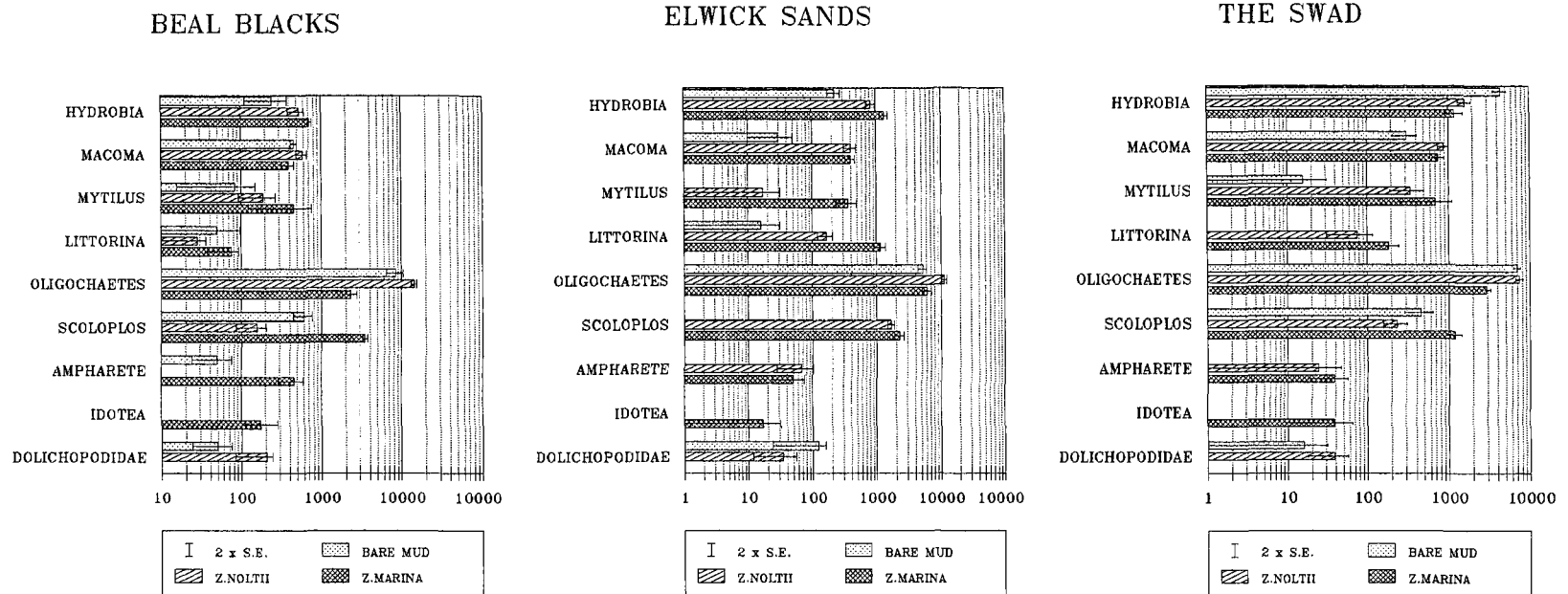


Table 4.12 : Mean densities (No.m⁻²) of the nine invertebrates chosen for analysis, present at the different sample sites.

SITE :	BEAL			ELWICK			THE SWAD		
	BB	BN	BM	EB	EN	EM	SB	SN	SM
<i>HYDROBIA</i>	249	506	680	230	846	1326	4609	1641	1219
<i>MACOMA</i>	464	577	381	31	398	398	315	883	746
<i>MYTILUS</i>	83	181	448	--	17	365	17	348	696
<i>LITTORINA</i>	50	18	66	17	166	1161	--	75	187
OLIGOCHAETES	8589	14416	2321	5204	11225	6151	6997	7461	2935
<i>SCOLOPLOS</i>	613	145	3432	--	1691	2338	464	236	1219
<i>AMPHARETE</i>	50	--	448	--	66	50	--	25	37
<i>IDOTEA</i>	--	--	199	--	--	17	--	--	37
DIPTERA	50	163	--	122	33	--	17	37	--

(a) Variation in the vertical distribution of invertebrates.

Investigations were carried out at the Swad into the vertical distribution of invertebrates within the cores. The vast majority of individuals occurred within the top 6 cm. of sediment, irrespective of RPD depth or any other environmental variable measured. Only the oligochaetes and the tellinid *Macoma balthica* appeared consistently in at measurable densities below this depth. Table 4.13 shows an example of this vertical distribution pattern in core no.4 taken from the *Z.noltii* bed on the Swad.

Table 4.13 : Example of variation in the vertical plane of invertebrate numbers from one core sample.

Swad/Noltii 4	DEPTH (cm)						
	0-2	2-4	4-6	6-8	8-10	10-12	
<i>Hydrobia</i>	2	0	0	0	0	0	
<i>Macoma</i>	1	0	1	0	0	0	
<i>Mytilus</i>	3	0	0	0	0	0	
<i>Littorina</i>	0	0	0	0	0	0	
<i>Scoloplos</i>	5	4	1	0	0	0	
Oligochaetes	56	13	3	7	0	0	
Dipteran	1	0	0	0	0	0	
<i>Phyllococe</i>	1	0	0	0	0	0	
PERCENTAGE	71	17	5	7	0	0	

(b) Between site variations.

It has already been indicated that mudflats represent a very heterogeneous environment. It was hoped that the three study sites chosen within the Lindisfarne N.N.R. for their similarity, would generate statistically comparable invertebrate densities such that differences between habitat types (vegetated and bare) could be examined.

Table 4.14 demonstrates the significant differences for the nine chosen invertebrates between the different study sites. Full details are given in Appendix C(i). These differences refer to mean densities given in Table 4.12.

Table 4.14 : *Levels of significance of variations in mean invertebrate densities within the different habitat types between sample sites at Lindisfarne (ANOVA, all sites).*

	BARE MUD	Z.NOLTII	Z.MARINA
HYDROBIA	3 >> 1,2	1 << 3	n.s.
MACOMA	2 << 1,3	2 << 3	n.s.
MYTILUS	n.s.	n.s.	n.s.
LITTORINA	n.s.	n.s.	2 >> 1,3
OLIGOCHAETES	n.s.	3 << 1,2	2 >> 1,3
SCOLOPLOS	1 >> 2	2 >> 1,3	1 >> 3
AMPHARETE	n.s.	n.s.	1 >> 2,3
IDOTEA	n.s.	n.s.	n.s.
DIPTERA	2 >> 3	n.s.	n.s.

SITE 1 : BEAL BLACKS
 SITE 2 : ELWICK SANDS
 SITE 3 : THE SWAD

Interpretation

1 >> 2 ... Site 1 (Beal) had a significantly (ANOVA, P<0.05) higher density of a given invertebrate than Site 2 (Elwick).

2 << 1,3 ... Site 2 (Elwick) had a significantly lower density of a given invertebrate than either Site 1 (Beal) or Site 3 (The Swad)

From Table 4.12, it can be seen that there was considerable between site variation in the densities of most invertebrates utilising the three habitat types.

The density of hydrobiid gastropods tended to be significantly greater at the Swad, except in those cores removed from *Z.marina* beds. This was linked to the observation that the *Hydrobia* at this location were in general of a smaller size than the other two sites. It was thought possible that this augmented density represented an influx of this year's young. However, no investigations were carried out into hydrobiid shell size distributions at the different sites (see Wood, 1972 for further details relating to this aspect).

The other gastropod studied, *Littorina*, showed moderately low, statistically similar densities at the three sample sites in bare mud samples and *Z.noltii* beds. The density at Elwick within *Z.marina* beds (approximately 1161 individuals m⁻²) was however an order of magnitude greater than either Beal or the Swad.

The hemi-sessile bivalve, *Mytilus edulis*, although exhibiting a rather patchy distribution and occurring in relatively low densities, did not show statistical differences in density within the different habitat types at any of the three sample sites.

Macoma balthica, a deposit-feeding tellinid living within the sediment (see Section 4.4.2 (a)) again showed significant differences in density between the sites supporting no vegetation and the finer-leaved *Zostera noltii*.

Oligochaetes in general showed higher densities within swards of both *Zostera* species at Elwick than at the other two sites.

Scoloplos armiger, a sedentary bacteria-eating polychaete, varied significantly in density between sites in all habitat types.

The other sedentary polychaete, *Ampharete*, was present in rather low numbers, but in general appeared in highest densities at Beal.

Idotea was solely found in *Z.marina* samples and did not show any statistical between site differences.

The dipteran larvae, belonging to the family Dolichopodidae, were found in samples taken from Beal and Elwick. At the Swad only the pupal stage was recovered from cores. This family of Diptera contains several genera that spend their larval and pupal stages in intertidal sediments (see Assis Fonseca, 1978 for further details). Since the Swad was sampled later in the season, it was felt this pattern reflected a natural progression in the life cycle of this invertebrate, with the pupal stage following on from the larval stage. Between site variation was restricted to bare mud samples removed from Elwick and the Swad.

It was therefore apparent that combination of the invertebrate density data from the different sample sites within the Lindisfarne N.N.R. was not possible. The heterogeneous nature of the environment meant that each site had to be treated more or less independently.

(c) Within site variations.

The major aim of the project was to investigate invertebrate community differences between the two *Zostera* habitats and between vegetated and unvegetated sites. Table 4.15 shows the significant differences between vegetation types at each sample site, in terms of mean invertebrate densities recovered. Full details are given in Appendix C(ii).

Table 4.15 : Levels of significance of variations in mean invertebrate densities between habitat types within the different sample sites at Lindisfarne (ANOVA, all sites).

	BEAL BLACKS	ELWICK SANDS	THE SWAD
<i>HYDROBIA</i>	1 << 3	1 << 2,3	1 >> 2,3
<i>MACOMA</i>	n.s.	1 << 2,3	1 << 2
<i>MYTILUS</i>	n.s.	3 >> 1,2	n.s.
<i>LITTORINA</i>	n.s.	3 >> 1,2	1 << 3
OLIGOCHAETES	2 >> 1 >> 3	2 >> 1,3	3 << 1,2
<i>SCOLOPLOS</i>	3 >> 1,2	1 << 2,3	3 >> 1,2
<i>AMPHARETE</i>	3 >> 1,2	n.s.	n.s.
<i>IDOTEA</i>	3 >> 1,2	n.s.	n.s.
DIPTERA	n.s.	1 >> 3	n.s.

SAMPLE 1 : BARE MUD
 SAMPLE 2 : *Z.NOLTII*
 SAMPLE 3 : *Z.MARINA*

Interpretation

1 >> 2 ... Cores removed from vegetation type 1 (Bare mud samples) had a significantly (ANOVA, $P < 0.05$) higher density of a given invertebrate than type 2 (*Z.noltii*).

2 << 1,3 ... Cores removed from vegetation type 2 (*Z.noltii*) had a significantly lower density of a given invertebrate than either type 1 (Bare mud samples) or type 3 (*Z.marina*)

The obvious first impression from the table is that there are many differences in the densities of particular invertebrate groups between the different habitats at a site. A general point is that it is almost solely either communities extracted from bare mud cores or else from *Z.marina* cores which differ significantly from one or either of the other two types of vegetation.

Molluscs

The molluscs collected in this study could be categorized as epifaunal or infaunal. The epiphytic grazer *Littorina* belongs to the epibenthic component,

whereas *Macoma* lives wholly within the sediment but feeds using a long inhalent siphon at the surface. *Hydrobia* is noted for its behavioural pattern of daytime low tide avoidance by remaining buried a few millimetres within the sediment and returning to the surface when the rising tide passes. However, since its feeding behaviour is concentrated at or above the sediment surface, *Hydrobia* may be grouped in the epibenthic component. *Mytilus* also lives half-buried in the sediment, filter feeding during periods of immersion.

Those sediments removed from *Zostera marina* beds, in particular, are notably rich in epibenthic grazers. The observation that this guild was especially abundant in the *Zostera* beds led to the investigation of behavioural preferences discussed in Section 4.4.4. The situation is complicated at the Swad, where vast numbers of the hydrobid snails were recorded in bare mud samples. However a possible reason for this disparity was discussed earlier.

Macoma reached its highest densities within the *Zostera* swards, particularly *Z.noltii*. At both Elwick and the Swad, densities of *Macoma* were significantly lower in bare mud samples than in samples extracted from perennial (*Z.noltii*) seagrass beds. A possible explanation for this preference might lie in the feeding mechanism employed, whereby a long inhalent siphon extends above the sediment surface and is used to suck in food particles comprising diatoms, detritus with bacteria and some protozoans. Such food particles are likely to be more abundant in sediment supporting *Zostera*, since water speeds are likely to be less, reducing the risk of removal by the current. It was also apparent that the majority of the larger *Macoma* (showing more than two annual growth rings on their shells) were present within those samples taken from vegetated sites. This aspect was not investigated in this study, but might provide an interesting topic for future investigation.

Mytilus numbers as stated previously were extremely variable, ranging from mean density values of zero to six thousand per square metre. This variability arose from its very patchy distribution. Despite this, at Elwick, the *Z.marina* beds were found to support a significantly higher density of this bivalve. Mean density values for *Mytilus* were always higher in samples taken from the *Zostera* swards than in the bare mud samples (Table 4.12).

Polychaetes

The rather sparse representation of this group within the mud flats at Lindisfarne restricted the statistical analysis to two sedentary species, *Scoloplos armiger* and *Ampharete balthica*.

Scoloplos is a readily recognisable polychaete owing to its bright red colour, and belongs to the family Orbiniidae. It was easily the most abundant member of this group, occurring at all but one of the sampling locations (bare mud samples at Elwick). It reached particularly high numbers in *Z.marina* cores, showing statistically higher densities than in bare mud samples at all sites. *Scoloplos* was found in general at higher densities in the annual rather than the perennial *Zostera* species. Only at Elwick were mean *Scoloplos* densities within the two seagrass species not statistically different. Indeed at the other two sites, mean densities were in fact lower in *Z.noltii* samples than in bare mud samples.

Ampharete balthica is a creamy coloured polychaete which lives within a membranous tube composed of agglutinated sediment particles. It was abundant only within samples taken from the *Z.marina* beds at Beal. At this location, numbers recovered from the coarse-bladed seagrass cores were significantly greater than either bare mud or *Z.noltii* samples ($F= 6.8$, $d.f.= 34$; $P<0.01$). At the other sites, despite not actually appearing in any of the bare mud cores, mean densities of this polychaete within the habitat types showed no significant difference to one other.

Oligochaetes

The oligochaetes were by far the most densely represented group overall. Subdivision of this group from simple observations of differences might have been possible, but without the taxonomic expertise to back up such divisions, it was deemed most appropriate to leave the group entire. Oligochaetes were recorded in every single core sieved, with mean densities ranging from 800 to 24000 m⁻².

Samples extracted from *Z.noltii* swards yielded the highest densities of oligochaetes at all three sampling localities. Densities were significantly

greater in this vegetation type at Beal ($F=19.1$, d.f.= 34; $P<0.001$) and Elwick ($F= 10.8$, d.f.= 36; $P<0.01$) than in either bare mud samples or sediments supporting *Z.marina*. At the Swad, *Z.marina* cores contained significantly fewer oligochaetes than the other two habitat types ($F= 14.6$, d.f.= 43; $P<0.01$).

Oligochaetes were therefore most abundant in *Z.noltii* sediments and generally least abundant in sediments upon which the annual seagrass was established. The two seagrass species seemed to contrast markedly in their relative attractiveness to this group of invertebrates.

Other Groups

The other two invertebrate groups studied, despite not occurring at very high densities, showed very interesting distributional patterns.

Idotea baltica is an epibenthic isopod, commonly associated with *Zostera*. It often adopts a colouration to blend in with that of the seagrass blades. These investigations showed a distinct preference in this species for *Z.marina*. No individuals of this species were recorded in any other habitat. However, the only statistically significant difference was at Beal, where densities rose to almost 200 m⁻² ($F= 4.8$, d.f.= 34; $P<0.05$). It is understandable that this species might prefer sites containing *Zostera* rather than bare mud patches, due to its scavenging feeding behaviour and food availability. However the distinct preference for the annual ahead of the perennial seagrass warrants further investigation.

The dipteran, recovered from all three sample sites as either larvae or pupae, was absent from all *Z.marina* cores. It was nevertheless found in densities up to 160m⁻² in both bare and *Z.noltii* samples. Due to low densities at the majority of sites however, the only statistical difference was at Elwick where bare mud samples yielded a significantly higher number of the dipteran than *Z.marina* cores ($F=6.4$, d.f.= 36; $P<0.01$)

4.4.3 Invertebrate Biomass

The ash-free dry weights of the invertebrates extracted from the samples were calculated and used as a measure of biomass per square metre for each of the sites at Lindisfarne. The values for molluscan biomass were calculated separately (Table 4.16).

Table 4.16 : Mean invertebrate biomass measures (gm^{-2}) recorded at the different sample sites.

SITE	MOLLUSC	SOFT-BODIED	TOTAL BIOMASS
BEAL			
[n= 6] BB	41.1(14.5)	3.6(0.4)	44.8(15.0)
[n= 6] BN	36.2(7.3)	2.3(1.2)	38.5(8.5)
[n= 6] BM	83.1(20.5)	2.0(1.0)	85.1(21.5)
ELWICK			
[n= 6] EB	3.0(1.0)	11.6(0.7)	18.6(1.8)*
[n= 6] EN	11.6(2.6)	15.9(1.2)	27.5(1.4)*
[n= 6] EM	56.4(28.7)	21.9(3.1)	78.3(31.7)
THE SWAD			
[n= 8] SB	15.4(2.9)	2.6(0.3)	18.1(2.9)
[n= 8] SN	10.4(1.5)	3.7(0.3)	14.2(1.6)
[n= 8] SM	217.2(129.2)	3.0(0.4)	219.9(128.8)

n - Sample Sizes
 () Standard Errors
 * Significant Difference

The size of the standard errors in Table 4.16 provide an indication of the extreme variability within the data. For example, at the Swad, invertebrate biomass derived from *Z.marina* cores varied from a mere 3 gm^{-2} to over 1 kgm^{-2} . This high value coincided with the presence of a number of large *Mytilus* within that particular sample.

From Table 4.15, it can be seen that molluscs contribute most of the biomass at all sites except bare mud and *Z.noltii* samples from Elwick. The majority of the mollusc biomass is provided by bivalves (Lamellibranchia), particularly *Mytilus edulis* and *Macoma balthica*. The abundance of epibenthic gastropods at the Swad does not influence biomass measures greatly.

Significant within-site differences in total biomass were restricted to Elwick, where samples removed from the bare mud had statistically lower invertebrate biomass measures than *Z.noltii* samples.

4.4.4 Behavioural Investigations

The behavioural experiments carried out sought to back up some of the information on distributional patterns. The simple choice chamber enabled counts to be made of individuals' preference for sediments supporting *Zostera* and those devoid of the seagrass (Figure 10). *Hydrobia* and *Littorina* were studied and the results analysed using a Wilcoxon matched-pairs signed ranks test (see Appendix D for full details of observations). A total of 20 gastropods were tested in each experiment and the choice experiment repeated 21 times for *Hydrobia* and 23 times for *Littorina*.

Table 4.17 : Results and Significance Levels for the Behavioural Analyses Conducted

TOTAL			
Genus	+ signed ranks	- signed ranks	Significance
<i>Hydrobia</i> [n= 21]	148	83	n.s.
<i>Littorina</i> [n= 23]	276	0	P < 0.01

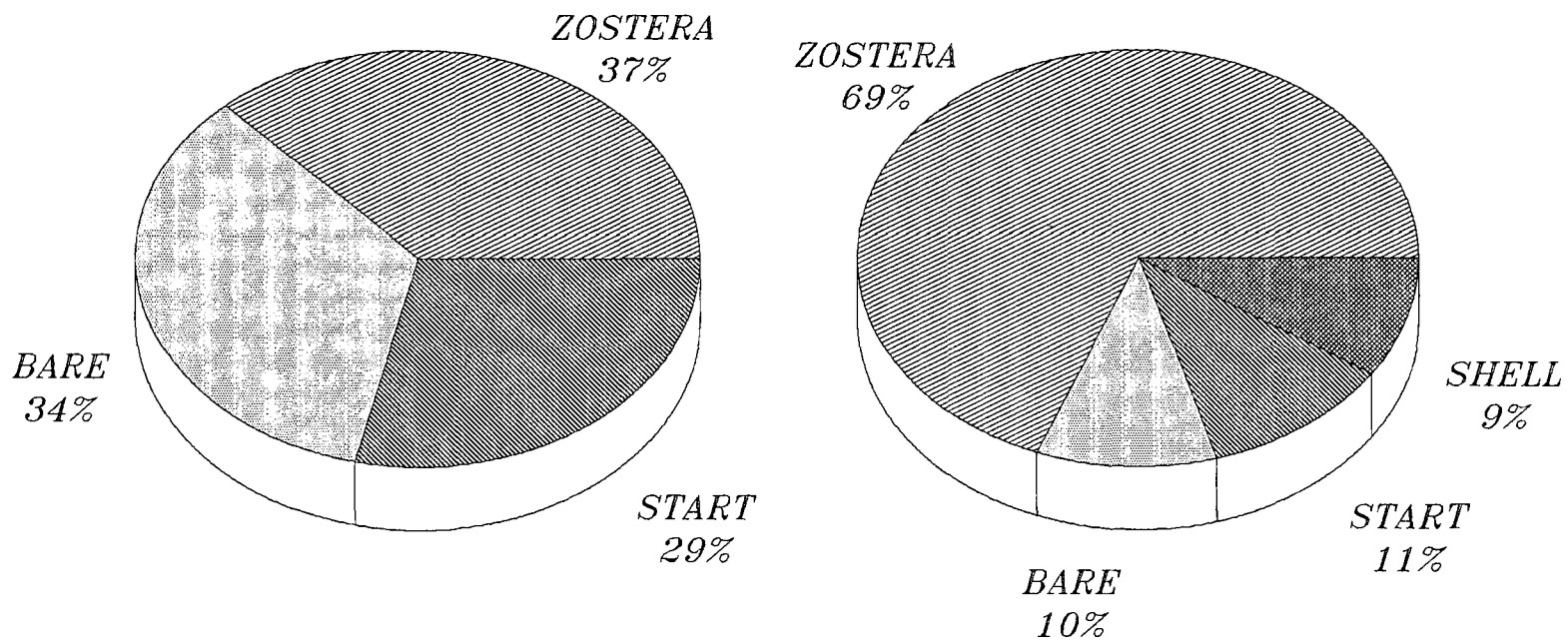
From this table, it can be seen that *Littorina* show a statistically significant preference for the seagrass sediments, as opposed to the bare mud sediments. This agrees with the results achieved from core sampling (Table 4.12), in which the greater densities of this gastropod were always associated with either or both seagrass species, relative to the bare mud samples.

Hydrobia, although numbers observed within the *Zostera* chamber were generally higher, show no significant preference for the seagrass. This result also mirrors the less clear cut density patterns observed for this genus.

FIGURE 4.10 : Pie Charts showing the Percentage of Observations of the Invertebrates in the Different Chambers

HYDROBIA ULVAE

LITTORINA SPP.



Number of Repetitions

Hydrobia - 21 experiments

Littorina - 23 experiments

4.5 RELATIONSHIP BETWEEN ENVIRONMENTAL VARIABLES AND BENTHIC MACROFAUNA.

The relationship between invertebrate densities and the environmental variables measured was investigated statistically.

4.5.1 Correlation and Regression Analysis

(i) Total Density

Total densities of all invertebrates at the nine sample sites were used as the dependent variable in multiple regression analysis. The environmental variables - RPD depth, percentage clay content, aerial biomass, rhizome biomass and percentage organics - were the independent variables in stepwise multiple regression. This procedure removes the independent variable with the largest probability-of-F value from the regression equation, before recomputing the equation omitting this removed variable. In this way, if a single independent variable is very highly significantly related to the dependent variable, then this does not obscure other less evident relationships.

Prior to regression analysis, the correlation coefficients between total densities and the environmental variables were derived (Table 4.18).

Table 4.18 : *Correlation coefficients of mean total invertebrate density and the measured environmental variables*

	RPD	%CLAY	AERIAL	ROOTS	%ORGANICS
MEAN NUMBER	-0.57	0.06	-0.09	0.20	-0.23

From this table, there are no significant correlations between mean density and the environmental variables. However, there is a distinct negative relationship between the RPD depth and density and a slight positive correlation with root and rhizome biomass. Regression analysis subsequently, failed to show any significant relationships in the data.

(ii) Densities of Individual Taxa

Mean densities of the nine individual invertebrate taxa were then regressed against the environmental variables.

Molluscs

The two mollusc genera that showed significant relationships to the environmental variables were *Mytilus* and *Littorina*.

Mytilus edulis densities were found to be significantly correlated with above ground *Zostera* biomass ($r = 0.70$; $P < 0.05$). This species was also strongly (but not significantly) positively correlated with percentage organic content of sediments ($r = 0.67$; $P > 0.05$).

Littorina spp. densities were found to show a significant correlation to the organic content of sediments ($r = 0.79$; $P < 0.05$).

In stepwise multiple regression analysis on *Mytilus*, the first variable removed was aerial biomass, followed by rhizome biomass and finally RPD depth. *Littorina* spp. densities were related significantly to percentage organic content only. Table 4.19 shows the F values and significance levels for these relationships.

Table 4.19 : F values and significance levels for mollusc taxa, derived through stepwise multiple regression of invertebrate density against environmental variables.

	RPD	%CLAY	AERIAL	ROOTS	%ORGANICS
<i>MYTLUS</i>					
F	16.88	--	6.75	8.79	--
d.f.	3,5	--	1,7	2,6	--
P	P< 0.01	--	P<0.05	P<0.05	--
<i>LITTORINA</i>					
F	--	--	--	--	11.5
d.f.	--	--	--	--	1,7
P	--	--	--	--	P<0.05

Annelids

No significant correlations were found between densities of *Ampharete*, *Scoloplos* or oligochaetes and any of the variables measured. However, both the polychaetes showed negative correlations ($r = -0.38$ and $r = -0.52$ respectively) to RPD depth. *Scoloplos* also showed a distinct positive correlation with the two *Zostera* variables, aerial biomass ($r = 0.51$) and rhizome biomass ($r = 0.52$). The oligochaetes showed a negative correlation with all the measured variables.

Stepwise multiple regression failed to highlight any significant relationships.

Other groups

Neither *Idotea* nor the dipteran larvae and pupae showed any significant correlations with the environmental variables. The particularly low correlation ($r = 0.10$) between *Idotea* densities and aerial biomass measures was perhaps a little surprising, since this organism was only ever found on *Zostera marina* blades. Dipteran densities do show strong negative correlations to *Zostera* biomass measures (aerial: $r = -0.61$; rhizome: $r = -0.51$), mirroring some of the distributional patterns described earlier (see Table 4.10)

(iii) Invertebrate Biomass Measures

Correlations between mean invertebrate biomass at the different sample sites and the environmental variables are given in Table 4.20.

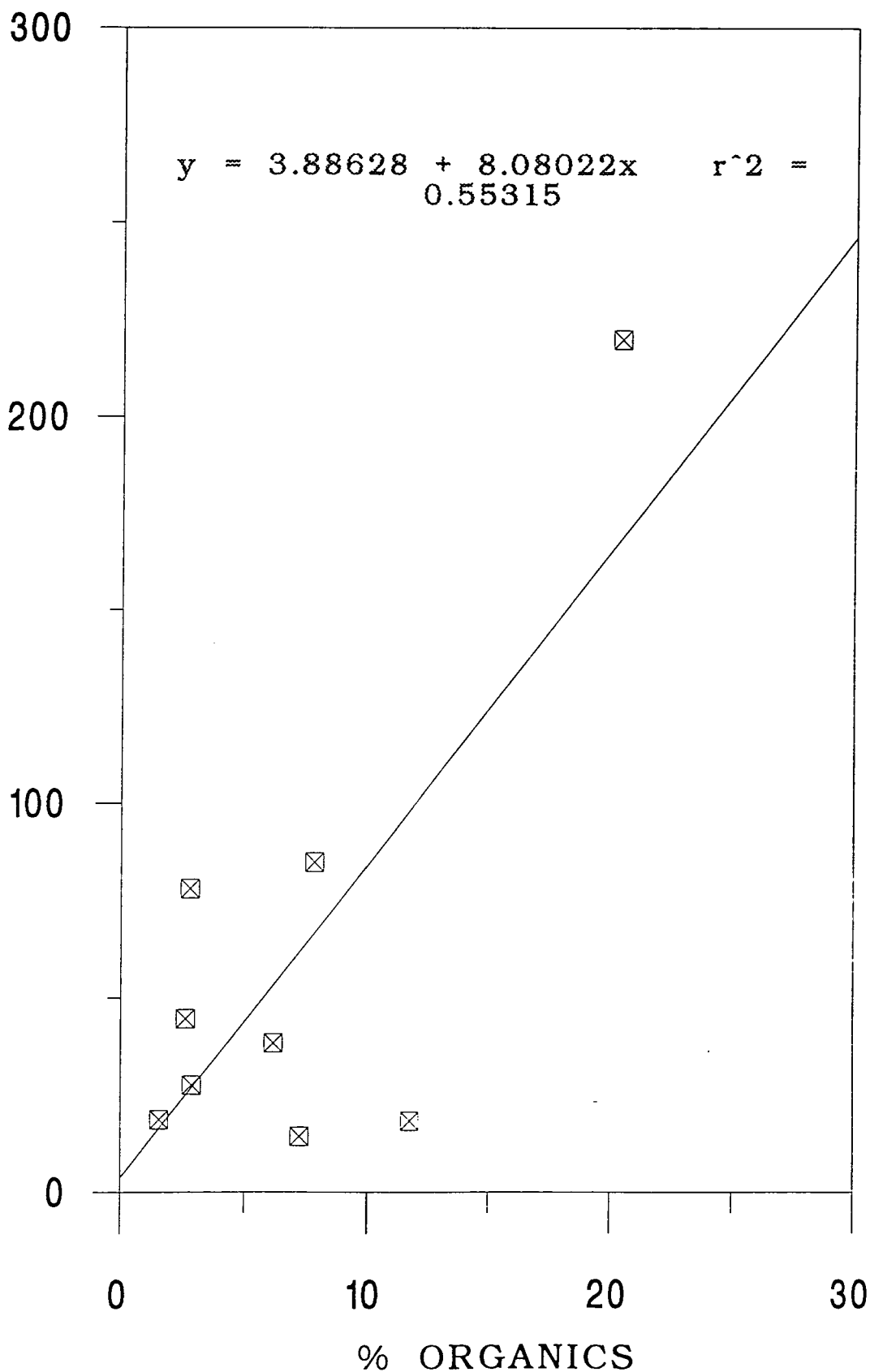
Table 4.20 : Correlation coefficients of mean invertebrate biomass and the measured environmental variables

	RPD	%CLAY	AERIAL	ROOTS	%ORGANICS
BIOMASS	-0.14	-0.58	0.64	0.30	0.75*

* - Significant Correlation ($P < 0.05$)

Figure 4.11 : Graph Illustrating the Relationship Between Invertebrate Biomass and Percentage Organic Component of the Sediments

Invertebrate
Biomass
(g/sq.m)



Invertebrate biomass in this study was therefore seen to be significantly positively correlated with percentage organic content of the sediments (see Figure 4.11). Strong positive correlations were also evident, particularly with aerial *Zostera* biomass but also root and rhizome biomass.

Stepwise multiple regression analysis, with invertebrate biomass as the dependent variable confirmed the significant relationship to percentage organics ($F= 8.67$, $d.f.= 1,7$; $P<0.05$). Removal of this variable failed to reveal any further significant relationships in the data.

4.5.2 Canonical Correspondence Analysis (CANOCO)

CANOCO is a multivariate analysis technique developed to relate community composition to known variation in the environment. It provides an integrated description of species-environmental relationships by assuming a response model that is common to all species, and the existence of a single set of underlying environmental gradients to which all species respond (Ter Braak, 1986)

Data for the different sample sites of the densities of invertebrates present were related to the environmental variables measured (see Appendix E). From the programme results, it was found that approximately 26% of the variation in the species densities recorded could be accounted for by those environmental variables measured (sum of all canonical eigenvalues = 0.25872).

The ordination analysis produced a series of axis scores for each taxon and for each sampling site. For each axis, an eigenvalue is calculated which is proportional to the variation (of the 26%) accounted for by that axis. In this study, four axes were specified, with the following variation accounted for:

Axis 1: 54.1%
Axis 1,2: 82.2%
Axis 1,2,3: 96.9%
Axis 1,2,3,4: 99.4%

Although time did not enable a full analysis of the results achieved through CANOCO, the axis scores for the two primary axes were plotted. It was acknowledged that these plots were two dimensional representations of a multidimensional ordination diagram, but it is convention to display the scores for those canonical axes that account for the greatest variation in the data.

Figure 4.12 shows the species scores for these axes, together with the biplot scores for the environmental variables. The aerial and rhizome biomass measures are reasonably close to one another, indicating the significant positive correlation mentioned previously. The rhizome biomass also appears to show a very close association with percentage clay content. The diagram is however in only two dimensions. Substantial differences between these variables occur in other dimensions.

From Figure 4.12, it can be seen that the various invertebrate groups studied (molluscs, polychaetes etc.) show a degree of aggregation, suggesting they have similar ecological relationships. For example, the two sedentary polychaetes *Scoloplos* and *Ampharete* are in the same sector of the diagram, displaying a positive association with rhizome biomass. The molluscs, except for *Littorina*, are clustered in the top two sectors, and display a positive association with sediment organic content. The dipteran larvae and pupae show a negative association with all variables measured apart from depth of RPD, an observation borne out by correlation analysis. *Idotea* is positively associated with aerial biomass - a feature that was recognised from field observations but not supported by regression analysis.

Figure 4.13 shows the nine site scores for the two primary axes. A distinct clustering is apparent between several of the sites. The sites dominated by *Z.marina* show a distinct positive association to all variables except RPD depth, particularly and not surprisingly to aerial biomass. The *Z.noltii* and bare mud sites produced axis scores analogous to one another, suggesting they had a similar set of underlying gradients in those environmental variables measured. This is interesting since it actually shows the difference between the two *Zostera* species in terms of these ecological variables.

The canonical correspondence analysis showed that the different invertebrate taxa do have different responses to those environmental

variables measured, but that there is a degree of cluster associated with the different groups. Another important result was regarding differences between habitat types, and particular that between the two seagrass species. The inclusion in the analysis of a greater number of variables would undoubtedly highlight these relationships better.

FIGURE 4.12 : Species Scores for the two Primary Axes derived through CANOCO Analysis

AXIS 2

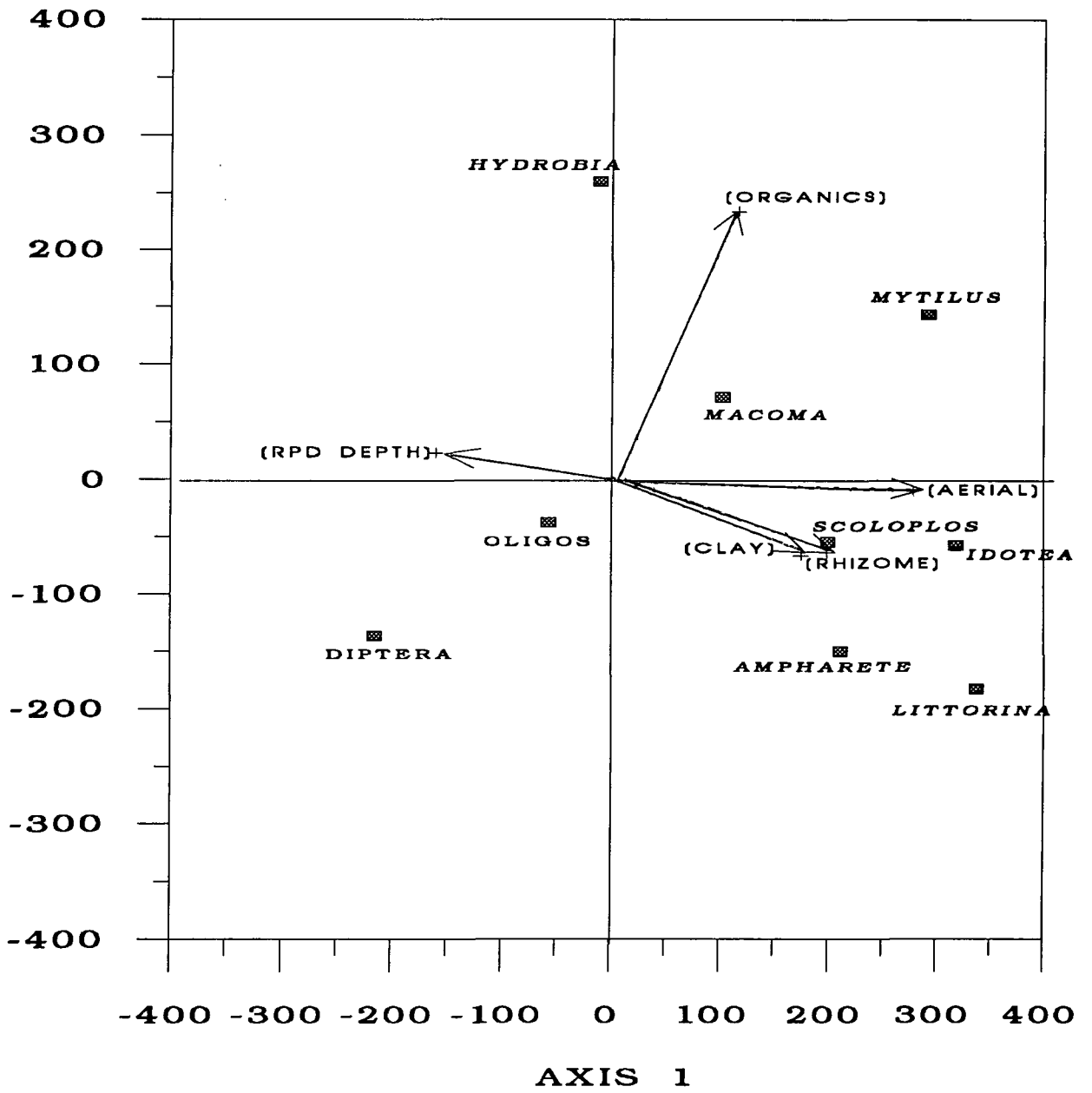
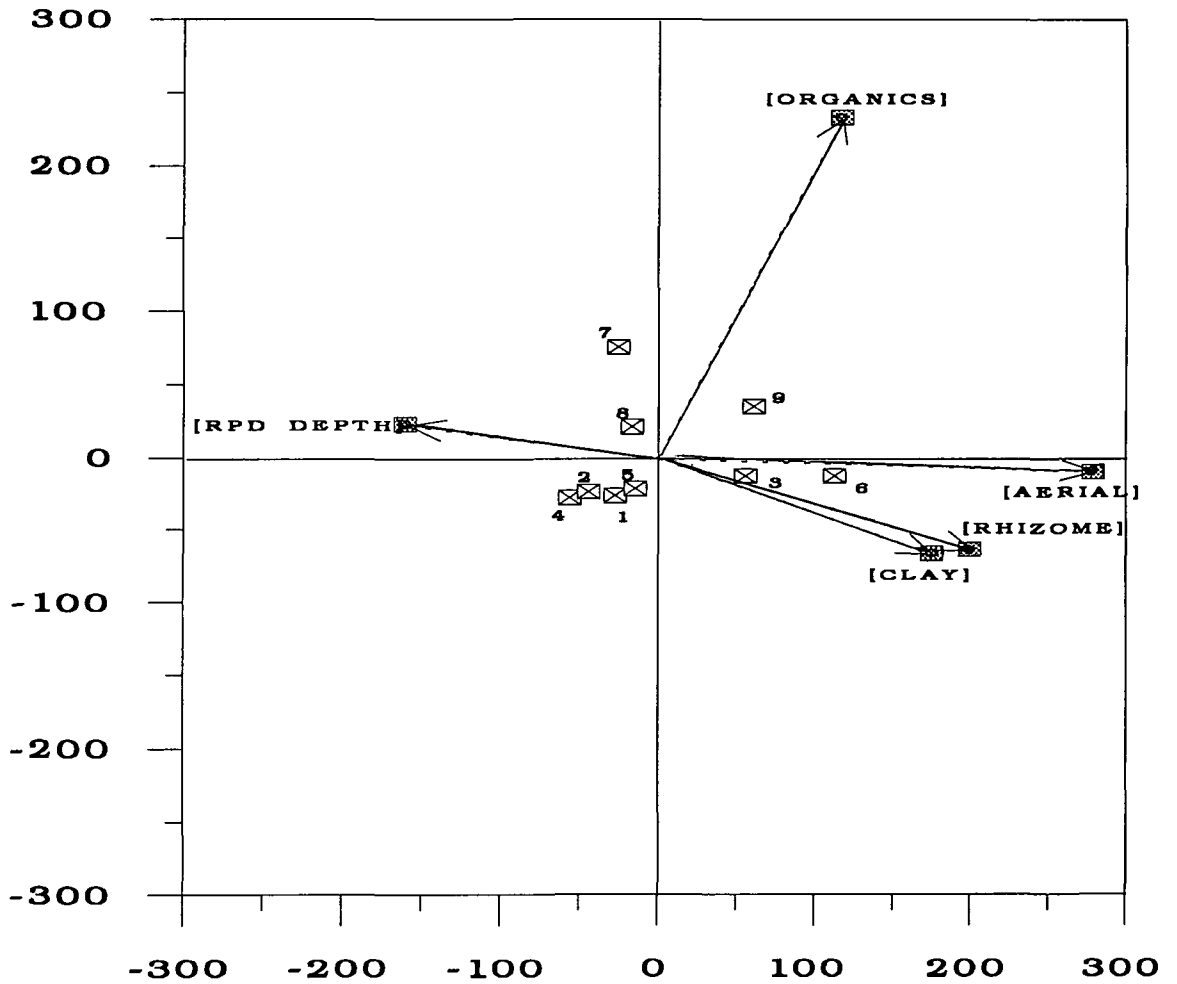


Figure 4.13: Site Scores for the Two Primary Axes derived through CANOCO Analysis

AXIS 2



KEY

AXIS 1

1. BEAL BARE
2. BEAL NOLTII
3. BEAL MARINA
4. ELWICK BARE
5. ELWICK NOLTII
6. ELWICK MARINA
7. SWAD BARE
8. SWAD NOLTII
9. SWAD MARINA

CHAPTER 5. DISCUSSION

The investigations within the different study areas at Lindisfarne were primarily concerned with differences in benthic macrofaunal communities between (a) vegetated and unvegetated sites, and (b) the different species of *Zostera*. Not surprisingly, the heterogeneous nature of the intertidal habitat was such that there were significant differences between the three different sample sites at Lindisfarne, causing problems with respect to combining data.

Multivariate analysis of the data gathered suggested differences between the sample sites in terms of the environmental variables measured and the assemblages of invertebrate taxa present. It appeared from ordination that the two seagrass species differed in terms of their macrofaunal component, such that communities from *Z.noltii* beds showed a greater similarity in composition to those extracted from bare mud, than they did to *Z.marina* beds. There seemed therefore to be a degree of specificity in terms of the communities associated with the two species of seagrass.

Despite these differences in overall community composition, few consistent patterns emerged in the data gathered on invertebrate densities within the different habitat types. However, it was possible with the results achieved, to highlight a number of relationships and to provide tentative explanations of any apparent associations.

5.1 ENVIRONMENTAL HETEROGENEITY

The measurement of several of the more obvious environmental variables was an important aspect of this study, since the specific composition and distribution of the macrofaunal community in any given area is a function of the response of individual species to such environmental factors (Day *et al.*, 1989). These variables provided an indication of the environmental

variability in the habitats under consideration. Few significant differences were documented, between the two *Zostera* species, in terms of those variables measured. Nevertheless, in comparing bare and vegetated sites, a number of interesting dissimilarities were found.

Seagrasses have been shown to influence the nature and depth of their own sediment bed through the trapping and binding of suspended particles associated with damping wave and tidal energy. A reduction in wave action within seagrass beds has been shown to effect the redox potential discontinuity layer, granulometric properties and organic content of sediments (Zieman, 1975), with consequent impacts on the macrofauna.

The depth of the redox potential discontinuity layer dramatically effects vertical distribution of organisms beneath the sediment surface. This phenomenon has been studied in the micro- and meiofauna (Fenchel and Riedl, 1970), but is also evident in the macrofauna. In this study, RPD depths were significantly greater in unvegetated sediments compared to those supporting *Zostera*. This interstitial oxygen deficiency would appear to limit the depth to which obligate aerobic organisms (lacking any adaptive avoidance or endurance mechanisms) could live beneath seagrass swards. This feature of the sediments does represent one possible constraint on invertebrate densities beneath *Zostera* swards. An obvious exception is *Macoma balthica* which lives in anoxic sediments, but draws oxygen and food particles down from the surface by means of a long inhalent siphon.

The two *Zostera* species differ to a great extent in terms of their life histories and ecological requirements. Such differences might have been expected to effect sediment RPD depth. For example, differences in the above ground floral morphology of the two might exert an influence on boundary layer dynamics, reducing current velocities and thereby altering oxygen tensions within the sediments. The difference between the perennial and the annual seagrass species in terms of sediment water content preferences might also lead to variations in depth of this layer. However, no such differences were recorded, with the RPD measured within *Zostera* swards at the three sites showing no significant variation.

Several authors have noted that macrofaunal densities at sites vegetated by seagrasses were higher than nearby unvegetated sites. However, it has often

been difficult in past investigations to differentiate between macrophytic effects and those relating to sediment granulometry. There are many examples in the literature of differences in the relative abundance of benthic taxa being attributed to differences in granulometry (Rhoads, 1974; Dankers and Beukema, 1983). Stoner (1980), working within subtidal (and presumably more stable) seagrass beds, was able to remove this variable from his analyses, thereby isolating the role of seagrass density in regulating community structure.

Attempts to eliminate sediment granulometric differences between the sample sites were unsuccessful. Cores removed from the different habitat types showed significant differences in terms of particle size distributions. It was largely those cores from *Z.marina* beds that differed in this respect, but there was no overall pattern between the sampling areas.

An appreciation of the silt/clay content of the sediments is important, since it is around particles of this approximate diameter that the organic molecules that constitute the food for many of the macrofauna, are associated. The percentage silt/clay contents within the Lindisfarne N.N.R. were very variable and showed no overall correlation to the presence or absence of vegetation. This is again surprising for reasons explained earlier relating to boundary layer dynamics.

Three variables were measured relating to the *Zostera* itself. Values for both above- and below-ground biomass of *Z.marina* were considerably less than those reported from subtidal studies in Denmark by Sand-Jensen (1975), but these might be attributed to differences in tidal level. The biomass measures for *Z.noltii* are of the same order as those of Hoek *et al.*(1983).

In general, the thicker bladed *Z.marina* had on average double the above-ground biomass of the finer-leaved *Z.noltii*. This in itself is not too surprising and could be estimated from simple field observations. Values for living root biomass were similar between the two seagrass species, and were equivalent at most sites to the figure achieved for aerial biomass of *Z.marina*. An extensive rooting and rhizome system is therefore present, preventing upheaval and providing a habitat for infaunal invertebrates.

Variations in seagrass biomass between the sites at Lindisfarne were considerable, reflecting not only the heterogeneity of the environment, but also a seasonal variation during the early part of the growing season.

Measures of detrital biomass throughout the study period were particularly erratic, making it difficult to identify patterns in the data. The Swad emerged as having by far the greatest biomass and percentage of this fraction compared to the other two sites. This was perhaps a consequence of the substantial reduction in recent years in the total area of the seagrass sward at this site. It is thought that the slow decomposition of the plant tissue within the sediments would augment detrital biomass measures substantially, providing much suitable organic material for infaunal deposit-feeding invertebrates such as *Scoloplos*, *Arenicola* and oligochaetes. An increase in the diversity of the polychaetes present at this site was observed, but not on a scale proportional to that recorded in detrital biomass.

Statistical analysis failed to identify any significant correlations between the environmental variables, apart from the obvious relationship between above- and below-ground *Zostera* biomass. Previous investigations have highlighted a correlation between percentage clay content of sediments and percentage organics. Tubbs (1977) reported an increase in the organic composition and nutrient status of sediments associated with the decrease in particle size. However, no such significant correlations were evident in this data.

5.2 QUALITATIVE INVESTIGATIONS

The number of invertebrate taxa collected from Lindisfarne (27) was comparable to that found in other similar studies. For example, Reise (1985) found 32 taxa of similar trophic groups to those in Table 4.9 associated with intertidal seagrass beds in the Wadden Sea.

Table 4.9 is a fairly impressive list of the benthic macroinvertebrates present at Lindisfarne. At first sight, this list may be seen to contain all those organisms that might have been expected - several species of epifaunal and infaunal mollusc, a wide range of annelid genera and several crustaceans. However on closer inspection, although these taxa were present at Lindisfarne, numbers of the vast majority were very low. The number of

different species recovered from any single core rarely exceeded ten and were generally the same groups occurring repeatedly, pointing to a rather high dominance of a select few.

The absence of several often very abundant benthic intertidal mud flat invertebrate species was surprising. The polychaete *Nereis diversicolor* and the amphipod *Corophium volutator*, for example, appeared in less than 1% of all cores taken, despite being known to establish dense assemblages on tidal flats (although not always associated with seagrass swards) and to physically dominate the habitat. However, rather than dwelling on those taxa that were not present at Lindisfarne, it is of greater value to look at those species actually recorded and look at their relation to vegetation/habitat type.

Differences in the species composition of the samples were evident in all three habitat types. Diversity in invertebrate taxa was usually greatest in *Z.marina* cores. The relative abundances of the epifaunal invertebrate groups were generally dependent upon the presence of seagrasses. *Idotea baltica* was only recorded from cores supporting the larger bladed *Zostera marina*, and *Littorina*, in the behavioural analyses, showed a distinct preference for the seagrass habitat. Stoner (1980) suggested this was evidently related to increased surface area and habitat complexity above the sediment provided by grass blades and epiphytes. Schneider and Mann (1991b) suggested that both the degree of epiphyte cover and its shape were important factors in determining the distribution of epifaunal invertebrates. The effects of predation by epibenthic predators have also been shown to be mediated by the spatial resistance offered by the roots and blades of seagrasses (Reise, 1985).

The dipteran larvae and pupae showed an apparent avoidance of *Z.marina* sediments. Their presence in *Z.noltii* and bare mud samples is probably related to the lower water content of such sediments, enabling respiration and feeding in the larvae and respiration in the pupal stage, during periods of low tide.

5.3 QUANTITATIVE ASPECTS

The densities of macrofaunal invertebrates from all stations were of the same order as those reported in other studies. Densities removed from vegetated sites at Lindisfarne were comparable to those reported by a number of authors in the United States (for example, Santos and Simon, 1974) and by Castel *et al.*(1989) in Arcachon Bay, France. Reise (1985) reported densities of macrobenthic organisms of between 4000 and 18000 /m² within sand and mud flats at Königshafen, corresponding to the abundance values recorded for bare mud samples in this study. However, this author's exceptionally high figures for invertebrate densities removed from seagrass beds (> 50000 invertebrates/m²), were not mirrored in these investigations.

At Lindisfarne, densities were generally highest in *Z.noltii* beds, due to the presence of large numbers of oligochaetous annelids, together with the abundance of mollusc taxa. In bare mud samples, densities of molluscs were lower (except at the Swad, where large numbers of hydrobiid snails were recovered), but the abundance of oligochaetes was again responsible for producing large mean total density values. In *Z.marina* cores, the oligochaetes were in general of much lower abundance. Much of the observed total density in this habitat was attributable to the abundance of molluscs and the sedentary polychaete *Scoloplos armiger*. In this case, macrofaunal density was not greater in the vegetated sites compared to nearby bare areas, an observation that contrasts with other studies (Stoner, 1980; Schneider and Mann, 1991a). However, total invertebrate biomass was found to be greatest in amongst the seagrass vegetation, particularly *Z.marina*.

Densities of several individual taxa were directly related to the presence of vegetation. Larger individuals of *Macoma balthica* were particularly abundant in *Zostera* beds (possibly related to their feeding mechanisms), as were *Mytilus edulis* bivalves which rely upon the protection afforded by the seagrass to currents and predators. The presence of the latter is however a possible consequence of the moisture retaining properties of the *Zostera* blades during low tide periods of emersion. The preferences of the epifaunal gastropods *Littorina* and *Hydrobia* have been mentioned and the results backed up by behavioural investigations. The latter species shows an

interesting mechanism of avoidance of daytime low tide conditions by staying buried a few millimetres within the sediment and closing its shell with the operculum. The experimental set-up, mimicking low tide conditions, was therefore perhaps too simplified to take account of such a behavioural pattern.

Differences in the relative abundance of polychaete trophic groups have been shown to be a function of many different environmental variables, including macrophyte biomass (Stoner, 1980). Polychaete densities at all sites were dominated by *Scoloplos armiger*. Numbers recorded from *Z.noltii* sediments were comparable to those reported by Reise (1985) at Königshafen. However, particular abundance at all sites was noted in *Z.marina* samples, where densities rose to over 1000/m². It appeared that this bacterivorous species had a distinct preference for sediments supporting *Z.marina*, possibly related to the rhizomal properties of this seagrass and their effect on bacterial populations.

The increased number within *Z.marina* beds was also reflected in total polychaete densities. Explanations for this and also an apparent avoidance of *Z.noltii* supporting sediments by the group as a whole (except at Elwick), warrant further detailed investigation of the rhizome mats of the respective seagrass species.

5.4 CONCLUDING REMARKS

The intertidal system at Lindisfarne is undoubtedly very complex and variable. The two *Zostera* species present do influence the characteristics of the sediments that support them, and consequently affect the benthic macrofaunal assemblages associated with them. This study showed however, that those invertebrates associated with the two seagrass species are not identical in terms of their community structure. There are obvious differences between vegetated and unvegetated sites and also between *Zostera marina* and *Zostera noltii* sites.

Sediments supporting *Z.marina* were found to contain the highest diversity and biomass of invertebrates, but least overall invertebrate densities. *Z.noltii* samples were found to bear greater similarities to bare mud samples than those supporting *Z.marina* in terms of invertebrate community composition.

Further research could follow seasonal trends in the macrobenthic communities associated with the annual and the perennial species of seagrass. The region of the rhizosphere might also be focussed upon, with studies investigating exudations from root surfaces and possible effects on the microbial organisms upon which much of the macrofauna depends.

In short, there is much scope for further ecological research in this field, which will enable the better understanding of the factors affecting invertebrate communities associated with both species of *Zostera* within this unique ecosystem.

REFERENCES

- Assis Fonseca E.C.M. (1978). *Handbooks for the Identification of British Insects, Volume IX, Part 5: Diptera, Orthorrhapha, Brachycera, Dolichopodidae*. Royal Entomological Society of London.
- Beeftink W.G. (1977). The coastal saltmarshes of western and northern Europe: an ecological and phytosociological approach. In *Wet Coastal Ecosystems*, ed. V.J.Chapman, pp. 109-155. Elsevier, Amsterdam.
- Boaden P.J.S. and Seed R. (1985). *An Introduction to Coastal Ecology*. Blackie, Glasgow.
- Brook I.M. (1978). Comparative macrofaunal abundance in turtlegrass (*Thalassia testudinum*) communities in south Florida characterised by high blade density. *Bull. Mar. Sci.* **28**, 212-217.
- Castel J., Auby I., Labourg P.J., Escaravage V. and Garcia M.E. (1989). Influence of seagrass beds and oyster parks on the abundance and biomass patterns of meiobenthos and macrobenthos in tidal flats. *Est. Coast. Shelf Sci.* **28**, 71-85.
- Dankers N. and Beukema J.J. (1983). Distributional patterns of macrozoobenthic species in relation to some environmental factors. In *Ecology of the Wadden Sea*, ed. W.J. Wolff, Chapter 4.3, pp. 69-103.
- Day J.W., Jr., Hall C.A.S., Kemp W.M. and Yanez-Arancibia A. (1989). *Estuarine Ecology*. Wiley, New York.
- Dekker R. (1989). The macrozoobenthos of the subtidal western Dutch Wadden Sea: I. Biomass and species richness. *Neth. J. Sea Res.* **23**, 57-68.
- Edgar G.J. (1990). The influence of plant structure on the species richness, biomass and secondary production of macrofaunal assemblages associated with western Australia seagrass beds. *J. Exp. Mar. Biol. Ecol.* **137**, 215-240.
- Fenchel T.M. and Riedl R.J. (1970). The sulphide system: a new biotic community underneath the oxidised layer of marine sand bottom. *Mar. Biol.* **7**, 255-268.
- Hoek C. van den, Admiraal W., Colijn F. and de Jonge V.N. (1983). The role of algae and seagrasses in the ecosystem of the Wadden Sea: a review. In *Ecology of the Wadden Sea*, ed. W.J. Wolff, Chapter 3, pp. 8-118.
- Lewis F.G. III and Stoner A.W. (1980). An examination of methods for sampling macrobenthos in seagrass meadows. *Bull. Mar. Sci.* **31**, 31-57.
- McRoy C.P. and Helfferich C. (eds.) (1977). *Seagrass Ecosystems. A Scientific Perspective*. Dekker, New York.

- Millard A.V. (1976). The invertebrate faunas of *Spartina* marshes and their utilisation by shorebirds at Lindisfarne, Northumberland. Ph.D. Thesis, University of Durham.
- Nicholls D.J., Tubbs C.R. and Haynes F.N. (1981). The effect of green algal mats on intertidal macrobenthic communities and their predators. *Kieler Meeresforsch., Sonderh.* **5**, 511-520.
- Perry R. (1946). *A Naturalist on Lindisfarne*. Lindsay Drummond Ltd., London.
- Reise K. (1985). *Tidal Flat Ecology. An Experimental Approach to Species Interactions*. Springer-Verlag, Berlin.
- Rhoads D.C. (1974) Organism-sediment relations on the muddy sea floor. *Ann. Rev. Oceanogr. Mar. Biol.* **12**, 263-300.
- Sand-Jensen K. (1975). Biomass, net production and growth dynamics in an eelgrass (*Zostera marina* L.) population in Vellerup Vig, Denmark. *Ophelia* **14**, 185-201.
- Santos S.L. and Simon J.L. (1974). Distribution and abundance of the polychaetous annelids in a south Florida estuary. *Bull. Mar. Sci.* **24**, 669-689.
- Schneider F.I. and Mann K.H. (1991a). Species-specific relationships of invertebrates to vegetation in a seagrass bed. 1. Correlational studies. *J. Exp. Mar. Biol. Ecol.* **145**, 101-117.
- Schneider F.I. and Mann K.H. (1991b). Species-specific relationships of invertebrates to vegetation in a seagrass bed. 2. Experiments on the importance of macrophyte shape, epiphyte cover and predation. *J. Exp. Mar. Biol. Ecol.* **145**, 119-139.
- Stoner A.W. (1980). The role of seagrass biomass in the organisation of benthic macrofaunal assemblages. *Bull. Mar. Sci.* **30**, 537-551.
- h.* Taylor J.D. and Lewis M.S. (1970). The flora, fauna and sediments of the marine grass beds of Mabe, Seychelles. *J. Nat. Hist.* **4**, 199-220.
- Ter Braak C.J.F. (1986). A new eigenvector technique for multivariate direct gradient analysis. *Ecol.* **67**, 1167-1179.
- Tubbs C.R. (1977). Muddy foreshores. In *The Coastline*, ed. R.S.K. Barnes, pp. 83-93. Wiley, New York.
- Wolff W.J. (1987). Flora and macrofauna of intertidal sediments. In *Biological Surveys of Estuaries and Coasts*, ed. J.M. Baker and W.J. Wolff, pp. 81-130. Cambridge University Press.
- Wood J.B. (1972). Aspects of the ecology of *Hydrobia ulvae*. M.Sc. Thesis, University of Durham.
- Zieman J.C. (1975). Quantitative and dynamic aspects of the ecology of turtlegrass, *Thalassia testudinum*. In *Estuarine Research*, ed. L.E. Cronin, pp. 541-562. Academic, New York.

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APPENDIX

Appendix A: Calculation of Sample Size

Size of sample size required was calculated by considering 95% probability of a standard error equal to 20% of the mean to be a reasonable level of accuracy to aim for.

Samples removed during a preliminary visit to Elwick and Beal yielded the following numbers:

SAMPLE SIZE	MEAN NO.	STANDARD ERROR	PERCENTAGE
n= 8	56	13.88	24.78%
n= 10	54	11.79	21.83%
n= 12	52	9.84	18.92%

The sample size was therefore set at **12** per habitat type.

Appendix B: Invertebrate Densities recovered per core from the three
Sample Sites at Lindisfarne

KEY

z : number per core
z x 198.9654 : number per square metre

B : Bare mud cores
N : *Z.noltii* cores
M : *Z.marina* cores

H - *Hydrobia*
Ma - *Macoma*
My - *Mytilus*
Li - *Littorina*
O - *Oligochaetes*
Sc - *Scoloplos*
A - *Ampharete*
I - *Idotea*
D - Diptera

1. BEAL BLACKS

	H	Ma	My	Li	O	Sc	A	I	D
B1	0	4	0	0	16	6	0	0	0
B2	0	3	0	0	30	5	0	0	0
B3	0	2	1	0	12	5	0	0	0
B4	1	2	0	0	22	1	0	0	0
B5	0	2	0	0	56	8	1	0	0
B6	0	2	0	0	38	4	0	0	1
B7	1	2	0	0	22	1	0	0	0
B8	0	2	0	0	16	5	1	0	1
B9	8	2	4	3	123	0	1	0	0
B10	2	3	0	0	20	0	0	0	0
B11	3	3	0	0	87	0	0	0	0
B12	0	1	0	0	76	2	0	0	1
N1	2	1	4	0	85	0	0	0	0
N2	0	2	0	0	92	0	0	0	0
N3	1	2	0	0	96	0	0	0	0
N4	3	2	2	0	56	0	0	0	0
N5	4	4	0	1	88	0	0	0	1
N6	5	2	1	0	80	0	0	0	2
N7	5	4	0	0	51	3	0	0	0
N8	4	2	0	0	84	2	0	0	4
N9	0	6	3	0	49	1	0	0	2
N10	1	3	0	0	53	0	0	0	0
N11	3	4	0	0	61	1	0	0	0
N12	-	-	-	-	-	-	-	-	-
M1	3	0	1	1	10	28	4	2	0
M2	3	0	0	1	14	18	2	4	0
M3	6	3	1	0	8	19	9	0	0
M4	2	2	0	1	7	11	5	3	0
M5	5	2	20	1	38	10	0	0	0
M6	3	2	2	0	12	23	0	0	0
M7	2	4	1	0	7	24	0	0	0
M8	2	3	0	0	11	21	2	3	0
M9	3	3	1	0	4	9	0	0	0
M10	5	3	1	0	8	16	3	0	0
M11	5	0	0	0	15	21	2	0	0
M12	2	1	0	0	8	9	0	0	0

2. ELWICK SANDS

	H	Ma	My	Li	O	Sc	A	I	D
B1	1	0	0	1	22	0	0	0	1
B2	3	0	0	0	14	0	0	0	1
B3	1	0	0	0	5	0	0	0	0
B4	1	0	0	0	20	0	0	0	1
B5	1	0	0	0	57	0	0	0	1
B6	0	0	0	0	26	0	0	0	0
B7	1	0	0	0	48	0	0	0	0
B8	1	0	0	0	33	0	0	0	1
B9	2	1	0	0	15	0	0	0	0
B10	0	1	0	0	13	0	0	0	0
B11	0	0	0	0	28	0	0	0	0
B12	2	0	0	0	37	0	0	0	1
B13	2	0	0	0	22	0	0	0	2
N1	2	3	0	0	50	4	0	0	0
N2	4	5	0	1	47	11	2	0	0
N3	2	1	0	1	37	9	0	0	0
N4	6	1	0	0	43	8	0	0	0
N5	3	3	0	2	47	5	0	0	0
N6	4	1	0	0	42	7	0	0	0
N7	10	1	0	0	81	11	0	0	0
N8	4	0	1	1	91	15	0	0	0
N9	3	4	0	1	56	6	0	0	1
N10	4	1	0	2	89	14	0	0	0
N11	3	3	0	1	54	5	1	0	0
N12	6	1	0	1	40	7	1	0	1
M1	6	1	3	6	55	12	0	0	0
M2	4	3	1	9	60	9	0	1	0
M3	5	2	2	16	43	28	0	0	0
M4	8	0	1	6	20	17	1	0	0
M5	4	3	0	5	10	22	0	0	0
M6	5	1	6	6	31	7	0	0	0
M7	4	3	0	4	28	6	0	0	0
M8	11	3	4	1	18	9	0	0	0
M9	8	3	0	3	29	10	0	0	0
M10	6	1	0	9	53	3	0	0	0
M11	4	1	0	1	12	13	1	0	0
M12	15	3	5	4	12	5	1	0	0

3. THE SWAD

	H	Ma	My	Li	O	Sc	A	I	D
B1	16	0	0	0	28	3	0	0	0
B2	16	1	0	0	17	5	0	0	0
B3	12	1	0	0	23	9	0	0	0
B4	16	1	0	0	19	7	0	0	0
B5	66	5	0	0	23	1	0	0	0
B6	17	2	0	0	57	1	0	0	0
B7	23	4	0	0	45	0	0	0	1
B8	26	4	0	0	48	1	0	0	0
B9	18	0	0	0	33	1	0	0	0
B10	27	0	0	0	39	0	0	0	0
B11	24	1	0	0	39	0	0	0	0
B12	17	0	1	0	51	0	0	0	0
N1	2	2	3	0	65	2	0	0	0
N2	1	4	0	1	32	2	0	0	0
N3	4	3	11	0	83	1	0	0	1
N4	2	3	2	0	38	5	2	0	0
N5	20	10	4	2	35	2	0	0	0
N6	14	5	2	3	46	1	0	0	0
N7	14	5	2	3	29	4	0	0	0
N8	10	6	0	0	44	0	0	0	0
N9	9	6	0	0	35	0	0	0	1
N10	6	6	0	0	23	0	0	0	0
N11	5	2	0	0	25	0	0	0	0
N12	6	0	0	0	41	0	0	0	0
N13	9	4	0	0	32	1	0	0	0
N14	11	7	0	0	23	0	0	0	0
N15	4	4	0	0	21	0	0	0	0
N16	8	1	0	0	28	0	0	0	1
M1	3	0	0	0	12	4	0	0	0
M2	4	2	0	2	21	4	0	2	0
M3	8	10	1	2	17	17	0	0	0
M4	7	4	0	0	4	6	0	0	0
M5	2	6	18	1	14	4	1	0	0
M6	2	6	0	2	4	6	1	1	0
M7	2	5	32	2	18	18	0	0	0
M8	3	2	0	0	12	9	0	0	0
M9	1	3	0	0	22	4	0	0	0
M10	2	1	0	0	28	2	0	0	0
M11	0	0	0	0	26	6	1	0	0
M12	15	3	3	4	12	8	0	0	0
M13	15	3	3	4	12	4	0	0	0
M14	12	3	2	1	14	3	0	0	0
M15	16	10	0	0	5	0	0	0	0
M16	19	5	0	1	18	3	0	0	0

Appendix C(i): *F-values and levels of significance of variations in mean invertebrate numbers within the different vegetation types between sample sites at Lindisfarne.*

	STATISTIC	BARE MUD	Z.NOLTII	Z.MARINA
<i>HYDROBIA</i>	F d.f. Sig.	3 >> 1,2 28.79 36 P<0.001	1 << 3 6.81 38 P<0.01	n.s. 1.96 39 P>0.05
<i>MACOMA</i>	F d.f. Sig.	2 << 1,3 12.11 36 P<0.001	2 << 3 5.01 38 P<0.05	n.s. 3.1 39 P>0.05
<i>MYTILUS</i>	F d.f. Sig.	n.s. 1.28 36 P>0.05	n.s. 2.12 38 P>0.05	n.s. 0.25 39 P>0.05
<i>LITTORINA</i>	F d.f. Sig.	n.s. 0.73 36 P>0.05	n.s. 3.21 38 P>0.05	2 >> 1,3 19.95 39 P<0.001
<i>OLIGOS.</i>	F d.f. Sig.	n.s. 1.70 36 P>0.05	3 << 1,2 12.67 38 P<0.001	2 >> 1,3 9.61 39 P<0.001
<i>SCOLOPLOS</i>	F d.f. Sig.	1 >> 2 5.98 36 P<0.01	2 >> 1,3 45.45 38 P<0.001	1 >> 3 11.47 39 P<0.001
<i>AMPHARETE</i>	F d.f. Sig.	n.s. 2.83 36 P>0.05	n.s. 1.41 38 P>0.05	1 >> 2,3 7.41 39 P<0.01
<i>IDOTEA</i>	F d.f. Sig.	n.s. -- 36 --	n.s. -- 38 --	n.s. 2.68 39 P>0.05
<i>DIPTERA</i>	F d.f. Sig.	2 >> 3 3.84 36 P<0.05	n.s. 2.67 38 P>0.05	n.s. -- 39 --

SITE 1 : BEAL BLACKS
SITE 2 : ELWICK SANDS
SITE 3 : THE SWAD

Appendix C(ii): *F-values and levels of significance of variations in mean invertebrate densities between habitat types within the different sample sites at Lindisfarne.*

	STATISTIC	BEAL	ELWICK	THE SWAD
<i>HYDROBIA</i>	F d.f. Sig.	1 << 3 3.87 34 P<0.05	1 << 2,3 17.06 36 P<0.001	1 >> 2,3 13.96 43 P<0.001
<i>MACOMA</i>	F d.f. Sig.	n.s. 1.87 34 P>0.05	1 << 2,3 11.72 36 P<0.01	1 << 2 4.16 43 P<0.05
<i>MYTILUS</i>	F d.f. Sig.	n.s. 0.90 34 P>0.05	3 >> 1,2 8.44 36 P<0.01	n.s. 1.27 43 P>0.05
<i>LITTORINA</i>	F d.f. Sig.	n.s. 0.47 34 P>0.05	3 >> 1,2 21.17 36 P<0.001	1 << 3 3.95 43 P<0.05
<i>OLIGOS.</i>	F d.f. Sig.	2 >> 1 >> 3 19.11 34 P<0.001	2 >> 1,3 10.82 36 P<0.001	3 << 1,2 14.63 43 P<0.001
<i>SCOLOPLOS</i>	F d.f. Sig.	3 >> 1,2 58.94 34 P<0.001	1 << 2,3 21.45 36 P<0.001	3 >> 1,2 8.54 43 P<0.001
<i>AMPHARETE</i>	F d.f. Sig.	3 >> 1,2 6.78 34 P<0.05	n.s. 1.86 36 P>0.05	n.s. 0.81 43 P>0.05
<i>IDOTEA</i>	F d.f. Sig.	3 >> 1,2 4.85 34 P<0.05	n.s. 1.04 36 P>0.05	n.s. 1.65 43 P>0.05
<i>DIPTERA</i>	F d.f. Sig.	n.s. 3.21 34 P>0.05	1 >> 3 6.44 36 P>0.05	n.s. 1.72 43 P>0.05

SITE 1 : BARE MUD
 SITE 2 : *Z.NOLTII*
 SITE 3 : *Z.MARINA*

Appendix D: Wilcoxon matched-pairs signed ranks Test for the data gathered during the Behavioural Experiments.

1. HYDROBIA

	OBSERVED		EXPECTED ZOSTERA	DIFFERENCE (d)	RANKED AND SIGNED d
	BARE	ZOSTERA			
1.	8	6	7	-1	-11
2.	12	8	10	-2	-16
3.	8	7	7.5	-0.5	-5.5
4.	12	8	10	-2	-16
5.	6	9	7.5	1.5	14
6.	4	11	7.5	3.5	20.5
7.	9	10	9.5	0.5	5.5
8.	6	7	6.5	0.5	5.5
9.	6	8	7	1	11
10.	7	5	6	-1	-11
11.	9	8	8.5	-0.5	-5.5
12.	6	8	7	1	11
13.	5	5	5	0	1.5
14.	4	8	6	2	16
15.	6	7	6.5	0.5	5.5
16.	5	6	5.5	0.5	5.5
17.	1	7	4	3	19
18.	9	9	9	0	1.5
19.	8	3	5.5	-2.5	-18
20.	3	10	6.5	3.5	20.5
21.	5	7	6	1	11

TOTAL OF POSITIVE SIGNED RANKS = 148

TOTAL OF NEGATIVE SIGNED RANKS = 83 (T)

SIGNIFICANCE LEVEL : n.s.

2. LITTORINA

	OBSERVED BARE	ZOSTERA	EXPECTED ZOSTERA	DIFFERENCE (d)	RANKED AND SIGNED d
1.	1	18	9.5	8.5	18
2.	1	17	9	8	16
3.	0	18	9	9	20.5
4.	1	16	8.5	7.5	14
5.	0	18	9	9	20.5
6.	3	17	10	7	12
7.	1	19	10	9	20.5
8.	0	16	8	8	16
9.	0	19	9.5	9.5	23
10.	3	13	8	5	7
11.	4	12	8	4	3.5
12.	4	11	7.5	3.5	1
13.	2	15	8.5	6.5	10
14.	5	14	9.5	4.5	6
15.	4	16	10	6	9
16.	4	12	8	4	3.5
17.	3	11	7	4	3.5
18.	1	19	10	9	20.5
19.	3	17	10	7	12
20.	2	16	9	7	12
21.	2	13	7.5	5.5	8
22.	5	13	9	4	3.5
23.	2	18	10	8	16

TOTAL OF POSITIVE SIGNED RANKS = 276

TOTAL OF NEGATIVE SIGNED RANKS = 0 (T)

SIGNIFICANCE LEVEL : P < 0.01

Appendix E(i): File containing the Environmental Variable Information used in CANOCO Analysis

meanenvvardec
(I7,6(I2,F6.0))

6

1	1	28	2	20	3	0	4	0	5	2.6	6
2	1	15	2	11	3	1	4	10	5	6.2	6
3	1	12	2	12	3	15	4	24	5	7.8	6
4	1	41	2	18	3	0	4	0	5	1.6	6
5	1	13	2	17	3	25	4	72	5	2.8	6
6	1	16	2	36	3	51	4	89	5	2.8	6
7	1	23	2	13	3	0	4	0	5	11.7	6
8	1	14	2	10	3	21	4	44	5	7.2	6
9	1	21	2	21	3	46	4	48	5	20.4	6
0											

RPDCLAY AERIALRHIZOMEORGANICS

BealB BealN BealM EIB EIN EIM SwadB
SwadN SwadM

Appendix E(ii): File Containing Information on Species Abundances used in CANOCO Analysis

meaninvertsdec
(I7,9(I2,F6.0))

9

1	1	249	2	464	3	83	4	50	5	8589	6	613	7	50	8	0	9	50
2	1	506	2	578	3	181	4	18	5	14416	6	145	7	0	8	0	9	163
3	1	680	2	381	3	448	4	66	5	2321	6	3432	7	448	8	199	9	0
4	1	230	2	31	3	0	4	15	5	5203	6	0	7	0	8	0	9	122
5	1	846	2	398	3	17	4	166	5	11225	6	1691	7	66	8	0	9	22
6	1	1326	2	398	3	365	4	1161	5	6151	6	2338	7	50	8	17	9	0
7	1	4609	2	315	3	17	4	0	5	6997	6	464	7	0	8	0	9	17
8	1	1641	2	883	3	348	4	75	5	7461	6	236	7	25	8	0	9	25
9	1	1218	2	746	3	696	4	187	5	2935	6	1219	7	37	8	37	9	0
0																		

HYDROBLA MACOMA MYTILUS LITT OLIGOS SCOL AMPH IDOTEA
DIPTERA

BealB BealN BealM EIB EIN EIM SwadB SwadN SwadM

Appendix E(iii): Species Scores derived for each Canonical Axis by Canonical Correspondence Analysis

SPECIES	AXIS 1	AXIS 2	AXIS 3	AXIS 4
HYDROBIA	-10	260	69	-64
MACOMA	102	71	-142	154
MYTILUS	292	143	-194	397
LITTORINA	337	-183	555	158
OLIGOS	-57	-38	0	6
SCOLOPLOS	200	-55	-17	-129
AMPHARETE	212	-150	-459	-388
IDOTEA	318	-58	-595	-326
DIPTERA	-215	-137	-156	589

Appendix E(iv): Site Scores derived for each Canonical Axis by Canonical Correspondence Analysis

SITE	AXIS 1	AXIS 2	AXIS 3	AXIS 4
BEAL BARE	-27	-27	-8	7
BEAL NOLTII	-44	-24	-7	18
BEAL MARINA	113	-13	-55	-58
ELWICK BARE	-56	-28	0	17
ELWICK NOLTII	-14	-22	2	-9
ELWICK MARINA	56	-13	45	1
SWAD BARE	-25	75	21	-20
SWAD NOLTII	-16	21	-6	18
SWAD MARINA	61	35	-16	25

Appendix E(v): Biplot Scores of Environmental Variables for each Canonical Axis derived through Canonical Correspondence Analysis

VARIABLE	AXIS 1	AXIS 2	AXIS 3	AXIS 4
RPD DEPTH	-73	10	12	22
% CLAY	92	-33	70	9
AERIAL BIOMASS	350	-11	87	18
ROOT BIOMASS	222	-66	89	2
% ORGANICS	102	189	-40	4

