Meiobenthos of the discovery Bay Lagoon, Jamaica, with an emphasis on nematodes.

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ABSTRACT

Sediment granulometry, microphytobenthos and meiobenthos were investigated at five habitats (white and grey sands, backreef border, shallow and deep thalassinid ghost shrimp mounds) within the western lagoon at Discovery Bay, Jamaica. Habitats were ordinated into discrete stations based on sediment granulometry. Microphytobenthic chlorophyll-*a* ranged between 9.5- and 151.7 mg m^{-2} and was consistently highest at the grey sand habitat over three sampling occasions, but did not differ between the remaining habitats. It is suggested that the high microphytobenthic biomass in grey sands was related to upwelling of nutrient rich water from the nearby main bay, and the release and excretion of nutrients from sediments and burrowing heart urchins, respectively. Meiofauna abundance ranged from 284- to 5344 individuals 10 cm^{-2} and showed spatial differences depending on taxon. Of 22 higher taxa recorded, nematodes dominated followed by copepods, together accounting for ~80 % of all individuals. Both taxa were most abundant in grey sands, suggesting a response, either directly or indirectly, to the high microphyte biomass. Significant within-habitat spatial variability in both meio- and microphytobenthos was found, causes of which are discussed. Nematode feeding groups varied between habitats. Fine white sands and both thalassinid mound habitats were dominated by non-selective deposit feeders. Slender and plump nematode morphotypes were found, yet the plump morphotype was largely absent from coarse sands subjected to high wave swash at the backreef border habitat. Here, nematode lengths were significantly higher than at other habitats. Nematode biomass spectra differed significantly between habitats, with a shift in peak biomass values towards larger size classes in the disturbed sediments. It is suggested that

longer and larger nematodes represent an adaptation to sediment disturbance, helping to prevent being displaced from the benthos by hydrodynamic forces and bioturbation.

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Don't Quit!

When things go wrong, as they sometimes will,
When the road you're trudging seems all uphill,
When the funds are low and the debts are high,
And you want to smile, but you have to sigh,
When care is pressing you down a bit,
Rest if you must, but don't you quit.

Success is failure inside out –
The silver tint of the clouds of doubt,
And you never can tell how close you are,
It may be near when it seems afar;
So stick to the fight when you're hardest hit,
It's when things seem worst that you mustn't quit!

TABLE OF CONTENTS

1. **INTRODUCTION**.....17
1.1. General introduction.....18
1.2. What are meiofauna?.....22
1.3. Aims.....24

2. **STUDY SITES AND GENERAL METHODS**.....25
2.1. Introduction.....25
2.2. Sample habitats.....27
2.2.1. Habitat descriptions.....27
2.2.1.1. Habitat 1.....27
2.2.1.2. Habitat 2.....27
2.2.1.3. Habitat 3.....29
2.2.1.4. Habitat 4.....29
2.2.1.5. Habitat 5.....29
2.3. Sampling design.....30
2.4. Sampling layout.....31
2.5. Statistical analysis.....34
2.5.1. Non-metric Multi-Dimensional Scaling (MDS).....34
2.5.2. Analysis of Similarities (ANOSIM).....35
2.5.3. Similarity Percentages (SIMPER).....35
2.5.4. Principle Components Analysis (PCA).....36

3. **MICROPHYTOBENTHOS AND SEDIMENT GRANULOMETRY**.....37
3.1. Introduction.....37
3.2. Methods.....41
3.2.1. Sample collection.....41
3.2.1.1. Sediment granulometry.....41
3.2.1.2. Microphytobenthos.....42
3.2.2. Statistical analysis.....43
3.2.2.1. Sediment granulometry.....43
3.2.2.2. Microphytobenthos.....44
3.3. Results.....46

3.3.1. Sediment granulometry overview 46
3.3.1.1. Habitat 1 46
3.3.1.2. Habitat 2 46
3.3.1.3. Habitat 3 47
3.3.1.4. Habitat 4 47
3.3.1.5. Habitat 5 48
3.3.2. Ordination of sediment granulometry characteristics and particle size distributions 52
3.3.3. Microphytobenthos 56
3.3.3.1. Spatio-temporal distribution 56
3.3.3.2. Spatio-temporal variation 61
3.3.3.3. Relationship between microphytobenthos and sediment granulometry 64
3.4. Discussion 66
3.4.1. Sediment granulometry 66
3.4.2. Distribution and biomass of microphytobenthos 67
3.4.3. Spatial and temporal variation in microphytobenthos 73
3.5. Summary 76

4. **DISTRIBUTION AND ABUNDANCE OF MEIOBENTHOS** 77
4.1. Introduction 77
4.2. Methods 80
4.2.1. Sample collection 80
4.2.2. Sample processing 81
4.2.3. Statistical analysis 81
4.3. Results 82
4.3.1. Meiofaunal taxa 82
4.3.2. Spatial patterns 88
4.3.3. Multivariate taxonomic assemblage structure 90
4.3.4. Relationship between meiofauna, microphytobenthos and sediment properties 93
4.4. Discussion 97
4.5. Summary 105

5. **NEMATODE FUNCTIONAL GROUPS, MORPHOMETRY, AND BIOMASS SIZE-SPECTRA** 107
5.1. Introduction 107
5.2. Methods 113
5.2.1. Nematode sample processing 113
5.2.2. Nematode functional groups 113
5.2.3. Nematode morphometry 114
5.2.4. Nematode biomass 114
5.2.5. Data processing and analysis 115
5.2.5.1. Nematode functional groups 115
5.2.5.2. Nematode morphometry 115
5.2.5.3. Nematode biomass spectra 116
5.3. Results 117
5.3.1. Nematode functional groups 117
5.3.2. Nematode morphometry 121
5.3.3. Nematode biomass and biomass spectra 132
5.3.3.1. Regular biomass spectra 132
5.3.3.2. Cumulative biomass spectra 133
5.3.3.3. Abundance spectra 137
5.4. Discussion 138
5.4.1. Nematode feeding groups 138
5.4.2. Nematode morphometrics – lengths and widths 143
5.4.3. Nematode morphometrics – plump and slender assemblages 147
5.4.4. Nematode biomass and abundance / biomass spectra 150
5.5. Summary 159

6. **SYNTHESIS AND CONCLUSIONS** 161
6.1. Aim 1: To characterise the sediment granulometry of five characteristic and visibly different habitats within the shallow lagoon 161
6.2. Aim 2: To assess the spatial and temporal variation in microphytobenthos within the shallow lagoon 162
6.3. Aim 3: Assess the spatial variation in meiobenthos within the shallow lagoon 164

6.4. Aim 4: Examine nematode feeding groups among habitats in order to test hypotheses that different groups have affinities for certain benthic conditions ……165
6.5. Aim 5: Examine nematode body size and biomass spectra from communities subjected to different sediment conditions and forms of natural disturbance.....166
6.6. Discussion of methodology 167
6.7. Suggestions for further work 169
6.8. Concluding remarks 170

7. **REFERENCES** 171

LIST OF FIGURES

Figure 2.1. Schematic maps showing the position of Discovery Bay on the north coast of Jamaica and bathymetry of the bay……26

Figure 2.2. Overhead photograph showing the positions of the five sampling habitats within the shallow west lagoon. The numbers (1-5) represent the location of the habitats while the black lines represent the position and orientation of the 30 x 2 m sampling transects…… 28

Figure 2.3. Schematic representation of sampling design showing A: one of the five sampling habitats containing four nested sites (in grey); B: a single site containing three nested plots (in grey); and C: a single plot from which two random replicate core samples were obtained (shown as circles at positions 12 and 24). Note scales…….....33

Figure 3.1. Relative grain size fractions at each habitat. Black bar = sand; light grey bar = gravel; dark grey bar = silt/clay. Note Y axis scale. (*n*=24)……...49

Figure 3.2. Box plots of sediment granulometry characteristics at the five lagoon habitats. Sed = Sediment. (*n*=24)…….50

Figure 3.3. Principal component ordination of sediment granulometry characteristics from the five habitats in the shallow lagoon at Discovery Bay……..….54

Figure 3.4. Principal component ordination of sediment particle size data from the five habitats in the shallow lagoon at Discovery Bay……54

Figure 3.5. Mean (+/- 1SE) microphytobenthic biomass in each Plot for the 3 sampling dates, 1, 2, and 3. (*n*=2 replicate cores). Habitats with the same letter are not significantly different (Tukey's HSD test, α=0.05)…….59

Figure 3.6. Mean coefficient of variation (+SE) in the biomass of microphytobenthos vs. scale for each habitat for the 3 sampling dates. P=plot; S=site; H=habitat. For each date and habitat mean CV is calculated from *n*=12 plots, *n*=4 sites, and *n*=1 habitat with 2, 6 and 24 replicates per scale, respectively……...62

Figure 3.7. Overall pattern of variation in the biomass of microphytobenthos versus scale. Bars are mean coefficient of variation (+SE). Mean CV calculated from 180 plots (*n*=2 per plot); 60 sites (*n*=6 per site); 15 habitats (*n*=24 per habitat) and 3 dates (*n*=120 per date)……..63

Figure 3.8. Relationship between mean biomass of microphytobenthos (*n*=72) and the proportion of sediments < 125 μm in grain size (*n*=24) at the 5 habitats ……..65

Figure 3.9. Relationship between mean biomass of microphytobenthos (*n*=72) and average mean grain size (*n*=24) at the 5 habitats…….. 65

Figure 4.1. Relative abundance of meiofaunal taxa contributing more than 1% (i.e. common taxa) towards total abundance from the five habitats. Taxa contributing less than 1% to total abundance have been pooled into 'Others'…83

Figure 4.2. Mean density of (a) total meiofauna; (b) nematoda; and (c) copepoda. (*n*=2, +1SE). Habitats with the same number above the bars are not significantly different from one another (Tukey HSD, α=0.05, after data transformations as per Table 4.2)……..84

Figure 4.3. Mean density of (a) copepoda nauplii; (b) turbellaria; and (c) polychaeta. (*n*=2, +1SE). Habitats with the same number above the bars are not significantly different from one another (Tukey HSD, α = 0.05, after data transformations as per Table 4.2)…….85

Figure 4.4. Mean density of (a); oligochaeta and (b) ostracoda (*n*=2, +1SE). Habitats with the same number above the bars are not significantly different from one another (Tukey HSD, α=0.05, data transformations as per Table 4.2). Note Tukey *post-hoc* test not carried out for the oligochaeta since ANOVA result not significant at Habitat level……86

Figure 4.5. Multidimensional scaling (MDS) ordination of meiofaunal samples from the five lagoon habitats based on Bray-Curtis similarities calculated from fourth-root transformed data…….90

Figure 4.6. Multidimensional scaling (MDS) ordination of meiofaunal samples from the five lagoon habitats based on Bray-Curtis similarities calculated from fourth-root transformed data. Data have been averaged by site with 6 replicates per site for visual clarity……...91

Figure 4.7. Relationship between mean density of meiofauna and mean biomass of microphytobenthos (date 2) at habitats 1 to 5 (*n*=24; +/- SE)…… 94

Figure 4.8. Relationship between mean grain size and mean density of meiofauna at habitats 1 to 5 (*n*=24; +/- SE)……...94

Figure 4.9. Mean Euclidian distances from normalised sediment granulometry parameter data (a) and Bray-Curtis dissimilarities from untransformed meiofauna data (b) for habitats 1-5 for all pairwise comparisons among replicates within plots (R, white bar), among plots within sites (P, grey bar), and among sites (S, black bar)……..96

Figure 5.1. Mean (±SE) relative abundance (%) of nematode feeding groups from the 5 lagoon habitats at Discovery Bay (*n*=24, 1200 nematodes analysed per habitat)……119

Figure 5.2. MDS ordinations of nematode feeding group relative abundance from the 5 lagoon habitats at Discovery Bay. Each point represents a single site…...120

Figure 5.3. Mean lengths of nematodes from the 5 lagoon habitats at Discovery Bay (*n*=2, ±1SE). Habitats with the same letter are not significantly different from one another (Tukey's HSD test, α=0.05)……...125

Figure 5.4. Mean widths of nematodes from the 5 lagoon habitats at Discovery Bay (*n*=2, ±1SE). Habitats with the same letter are not significantly different from one another (Tukey's HSD test, α=0.05)……...126

Figure 5.5. Boxplots of nematode length for each feeding group from each of the 5 lagoon habitats. Note that box width is proportional to the number of nematodes measured, which varied from 188 to 453 per habitat-group combination. The connecting line represents the mean of each feeding group.....127

Figure 5.6. Scatterplots of body width versus length of nematodes from lagoon habitats 1 to 3 at Discovery Bay (left side), and corresponding frequency distributions of length/width ratios (right side). 1200 nematodes were measured per scatterplot / frequency distribution……...129

Figure 5.7. Scatterplots of body width versus length of nematodes from lagoon habitats 4, 5 and all habitats grouped together at Discovery Bay (left side), and corresponding frequency distributions of length/width ratios (right side). 1200 nematodes per scatterplot or frequency distribution were measured for individual habitats, and 6000 nematodes for all habitats grouped together…….130

Figure 5.8. Plump nematode: *Richtersia* spp……..131

Figure 5.9. Relationship between nematode body width and length and feeding group. Plump nematodes are found nearer the top edge of the triangular area whereas slender nematodes are found nearer the bottom edge……..131

Figure 5.10. Relationship between nematode dry weight (dwt, μg) and length (μm)……132

Figure 5.11. Regular nematode biomass spectra from each of the 5 lagoon habitats at Discovery Bay. Individual spectra represent data from 1200 nematodes……...136

Figure 5.12. Cumulative nematode biomass spectra from each of the 5 lagoon habitats at Discovery Bay . Individual spectra represent data from 1200 nematodes…….……..136

Figure 5.13. Nematode abundance spectra from each of the 5 lagoon habitats at Discovery Bay. Individual spectra represent data from 1200 nematodes……..139

LIST OF TABLES

Table 3.1 Summary of granulometry statistics at each Habitat. Data are mean values with standard deviation in parentheses. (*n*=24)…….49

Table 3.2. Results of Kruskal-Wallis tests evaluating differences in the median of sediment granulometry characteristics between the five lagoon habitats. Differences between individual habitats were determined by *post-hoc* multiple comparisons using the Nemenyi test. (*n*=24)……...51

Table 3.3. *R*-statistic values and significance of pairwise two-way nested ANOSIM tests for differences in sediment conditions between the 5 lagoon habitats. All results are derived from Euclidean dissimilarity matrices. Before analysis sediment particle size distribution (SPSD) data were standardised to % fraction and then cumulated; sediment granulometry parameter (SGC) data were normalised (i.e. values for each variable have their mean subtracted and are then divided by their standard deviation)…….55

Table 3.4. Summary of microphytobenthic biomass values (mg m^{-2}) at each habitat. SD=standard deviation. (*n*=72)……56

Table 3.5. Results of ANOVA used to investigate the spatial and temporal distribution of biomass of microphytobenthos…… 58

Table 3.6. Results of the three-factor nested ANOVA in the distribution of biomass of microphytobenthos at Date 1…… 60

Table 3.7. Results of the three-factor nested ANOVA in the distribution of biomass of microphytobenthos at Date 2…… 60

Table 3.8. Results of the three-factor nested ANOVA in the distribution of biomass of microphytobenthos at Date 3…… ……60

Table 3.9 Variance components estimates (%) of microphytobenthos. Data are derived from the mixed model nested analysis of variance using untransformed data (see Underwood, 1997)…….64

Table 4.1 Mean density (individuals 10 cm^{-2}) and standard deviation (in parenthesis; *n*=24) of meiofaunal taxa from the five habitats, ranked in order of percentage of total meiofauna……...83

Table 4.2. Results of the three-factor nested ANOVA examining differences in the total number of individuals and selected taxa contributing more than 1% to total abundance…….87

Table 4.3. Summary of mixed model 3-factor nested analysis of variance results for difference in mean density at the Habitat scale or significant variability at Site and Plots scales (see Bennington and Thayne, 1994). Dashed line = no significant difference; *p<0.05; **p<0.01; ***p<0.001……...88

Table 4.4. Estimates of variance components of total numbers of individuals and selected taxa contributing more than 1% to total abundance. Data are derived from the mixed model nested analysis of variance using untransformed data (see Underwood, 1997). Total Abund. = total abundance; Nema = nematodes; Cope = copepods; Nauplii = copepod nauplii; Polych. = polychaetes; Turb. = turbellarians; Oligo. = oligochaetes; Ostra. = Ostracods; -: negative estimates...89

Table 4.5. *R*-statistic values and significance of two-way nested ANOSIM tests for differences in meiofaunal taxonomic structure between habitats and sites (using site groups as samples after checking for no significant area effect at the plot spatial scale). All results are derived from Bray-Curtis similarity matrices using fourth-root transformed data.…….92

Table 5.1. Results of One Way ANOVA and Tukey *post-hoc* comparisons (α=0.05) examining differences in the relative abundance (%) of nematode feeding groups within each of the 5 lagoon habitats at Discovery Bay…….118

Table 5.2. *R*-statistic values and significance of pairwise ANOSIM tests for differences in nematode feeding group structure between the 5 lagoon habitats at Discovery Bay……120

Table 5.3. Length, width and biomass characteristics of nematode assemblages from the 5 lagoon habitats at Discovery Bay. Numbers in brackets indicate 1 standard deviation (*n*=1200). Pop. Biomass = Population Biomass, estimated from the product of mean abundance and mean individual biomass per habitat…….123

Table 5.4. Pearson correlation matrix between mean nematode abundance, mean length, mean width, mean L/W ratio, mean individual biomass, and nematode population biomass with mean chlorophyll *a* biomass, mean grain size, mean % porosity and mean % silt/clay for the 5 lagoon habitats at Discovery Bay……124

Table 5.5. Results of the three-factor nested ANOVA examining differences in mean nematode length from the 5 habitats within the shallow lagoon at Discovery Bay……125

Table 5.6. Results of the three-factor nested ANOVA examining differences in mean nematode width from the 5 habitats within the shallow lagoon at Discovery Bay……..126

Table 5.7. *R*-statistic values and significance of pairwise ANOSIM tests for differences in cumulative biomass spectra between the 5 lagoon habitats at Discovery Bay……136

1. INTRODUCTION

1.1. General introduction

Shallow lagoon and bay ecosystems form extensive areas of coastal habitats worldwide. They are highly productive environments and are active sites of decomposition and nutrient recycling, relying on sediment biota to effect material transformations and exchange processes (Knoppers, 1994; Borum, 1996; Alongi, 1998). They provide several essential ecological functions such as habitat, food, and breeding grounds for a wide variety of organisms, many of which are of economic importance to humans, including fish, crustaceans, and molluscs. They are dynamic systems offering many goods and services to mankind, including aesthetic and recreational appeal (Costanza *et al.*, 1997). However due to their proximity to land they are under increasing risk of environmental disturbance due to anthropogenic factors. These factors include nutrient enrichment (e.g. Orive *et al.*, 2002; McGlathery *et al.*, 2007), pollution (e.g. Siung-Chang, 1997; Bigot *et al.*, 2006), trawling (Jennings *et al.*, 2002; Demestre *et al.*, 2008; Olsgard *et al.*, 2008), and aquaculture (Ólafsson *et al.*, 1995; Duplisea and Hargrave, 1996; Mirto *et al.*, 2000) which, amongst other factors, threaten the ecological integrity of shallow water ecosystems. In order to conserve and protect these ecosystems, quantification of the patterns in populations of animals and plants is necessary. At the same time this is a useful biological tool, enabling environmental change and anthropogenic disturbance to be monitored (Coull and Chandler, 1992; Chapman and Underwood, 2008; Moreno *et al.*, 2008).

At Discovery Bay in Jamaica there is a long history of research on the local coral reefs, which are regarded as some of the most extensively studied in the Caribbean (Liddell and Ohlhorst, 1981; Goreau, 1992; Szmant, 2002). However, over the last 30 years many changes have occurred which have severely disturbed and altered the ecology of the fringing reef system, including hurricane damage (Liddell and Ohlhorst, 1986, 1992; Hughes, 1993) and the Caribbean-wide die-off of *Diadema antillarum* Philippi (Echinodermata: Echinoidea) (Lessios *et al.*, 1983, 1984; Hughes *et al.*, 1985). Combined with other stressors, such as over-fishing (Sary, 2001; Munro *et al.*, 2003), these events have contributed to a phase-shift (*sensu* Done, 1992) from a coral dominated reef community to one of macroalgal dominance (Hughes, 1994; Liddell and Ohlhorst, 1986) which largely persists today.

Research conducted at Discovery Bay in the last decade has continued to focus predominantly on the ecology of the reef (e.g. Solandt and Campbell, 2001; Zilderberg and Edmunds, 2001; Macdonald and Perry, 2003; Perry, 1998; Idjadi *et al.*, 2006), as well as the distribution and productivity of seagrass beds (Bramwell, 2000), bay-wide nutrient chemistry (Greenaway and Gordon-Smith, 2006), the fishery (Munro, 2000; Sary, 2001; Munro *et al.*, 2003; Watson and Munro, 2004), and the influence of a bauxite shipping terminal in the south-west corner of the bay on sediment geochemistry and diagenetic processes (Perry and Taylor, 2004, 2006; Perry *et al.*, 2006; Taylor *et al.*, 2007). However the soft-bottom benthos has largely been ignored. Indeed the only published studies on the soft-bottom benthic fauna (Aller and Dodge, 1974) and microflora (Bunt *et al.*, 1972) were conducted more than 30 years ago. In an attempt to redress this

balance this research examines the meiobenthos (i.e. benthic meiofauna) and microphytobenthos (i.e. benthic microalgae) in the shallow lagoon at Discovery Bay, so as to further our knowledge on the ecology of lagoon benthos in this system, and to serve as a baseline for future monitoring, conservation and management programs.

Meiofauna (for definitions see section 1.2) are an abundant and ubiquitous component of the benthos in soft-sediment marine ecosystems and play an important role in their structure and function (see reviews by Higgins and Thiel, 1988; Giere, 1993). They enhance the decomposition rate of organic material and stimulate bacterial production (Tenore *et al.*, 1977; Findlay and Tenore, 1982; Alkemade *et al.*, 1992b, amongst others), thus providing recycled nutrients for new primary production. They act as vertical conveyors within the sediment, increasing the transport of solutes into and out of the benthos due to bioturbation, further stimulating microbial mineralisation and enhancing geochemical activity (Aller and Aller, 1992; Rysgaard *et al.*, 2000; Murray *et al.*, 2002). They are a food source for a wide variety of prey species within the trophic web, spanning several different phyla and size-ranges, such as crustaceans (Pihl and Rosenberg, 1984; Hunter and Feller, 1987; Clark, 2000), fish (St. John *et al.*, 1989; Street *et al.*, 1998), and avifauna (Gaston, 1992; Sutherland *et al.*, 2000). Consequently knowledge of meiofaunal structural dynamics and the spatial scales over which communities change will help in the development of tractable hypotheses about patterns in organism distributions, as well as the many processes that they influence within soft-sediment habitats.

While no attempt has been made to conduct manipulative experiments [this thesis is mensurative in origin (*sensu* Hurlbert, 1984)], as acknowledged by Underwood *et al.* (2000): "[one] can't make progress on processes without understanding the patterns". In ecology the description of pattern is of primary importance as it forms the basis from which models are constructed and hypotheses tested (Andrew and Mapstone, 1987). Indeed, observation of patterns in organism distributions and abundances are fundamental starting blocks for ecological studies, since until they have been described there is no basis for investigators to invoke explanatory models about structuring processes (Underwood *et al.*, 2000).

In view of the fact that soft-sediment benthic marine organism distributions are typically characterised by non-random spatial patterns (Barry and Dayton, 1991; Thrush, 1991; Hall *et al.*, 1994), the distribution of meiobenthos being no exception (e.g. Findlay, 1981; Phillips and Fleeger, 1985; Fleeger and Decho, 1987; Sun and Fleeger, 1991), a sampling design is employed to assess variations in the benthos within the shallow lagoon over several spatial scales. These range from centimetres to hundreds of metres, in five contrasting habitats. The present study shows that the Nematoda are the dominant meiofaunal taxon, as is most often found in marine sediments (Heip *et al.*, 1985). Their feeding groups, morphometry, and biomass size spectra are explored further and compared to environmental parameters in order to unravel the causes of biotic variation in this environment. In the absence of evidence to suggest that sediment communities in the western corner of the bay are directly affected by anthropogenic factors,

benthic community dynamics are presumed to be due to natural environmental variability and results are discussed with this in mind.

This thesis begins with an overview of what constitutes meiofauna before aims and objectives are stated (Chapter 1). Chapter 2 introduces the study habitats and describes the overall experimental designs and methods used, and details some of the univariate and multivariate statistical procedures employed in the analysis of data. The following chapter (Chapter 3) characterises the study environment in terms of sediment granulometry and spatial and temporal distribution in microphytobenthic biomass. The two ensuing chapters form the bulk of the thesis whereby the meiobenthic communities (Chapter 4) and nematode feeding groups, morphometry and biomass size spectra (Chapter 5) are described. The last chapter is a synthesis of the findings and discusses the results in the wider context of current understanding in marine benthic ecology (Chapter 6).

1.2. What are meiofauna?

Derived from the Greek word "μείος" meaning "smaller", meiofauna are subjectively defined by size range as organisms of intermediate size (Mare, 1942), and consist of a taxonomically diverse group of metazoans and protozoans that are smaller than macrofauna (e.g. <1 mm) yet bigger than the nanofauna (e.g. bacteria, microalgae and most protozoans) (Coull and Bell, 1979). For the most part the distinction between macrofauna and meiofauna is defined by the method used to separate one from another (Higgins and Thiel, 1988). This generally involves the passing of sediment through sieves of defined mesh aperture size. By convention, organisms retained on a 500 μm mesh sieve are

regarded as macrofauna, while those passing through this size mesh yet retained on a 63 μm mesh are regarded as meiofauna (Warwick *et al.*, 2006; International Association of Meiobenthologists, 2009). Organisms passing the 63 μm mesh are commonly deemed the nanobenthos. This fraction may, however, still include the smallest of metazoans, especially in deep sea sediments, and hence a lower size limit of 32 μm separating meiofauna from the nanofauna seems to be commonly accepted (Soltwedel, 2000).

As the most phylogenetically diverse group of organisms currently recognised (Baguley *et al.*, 2003), the meiobenthos contains representatives from 24 of the 34 recognised phyla in the Kingdom Animalia as well as 3 from the Kingdom Protista (Giere, 1993) and exhibit diversity comparable to the Insecta (May, 1988). Although some taxa are endemic to the marine environment, such as the Gnathostomulida, Kinoryncha and Loricifera, many occur in both marine and freshwaters. Despite the fact that some phyla are far more diverse and abundant than others, in general densities are often in the order of 1×10^6 m^{-2} (Coull, 1988), which represents a biomass of approximately 0.2 – 2 g C m^{-2} (Heip *et al.*, 1985). As such the metazoan members of the meiofauna are the most abundant, small-sized metazoans known to science, and it is argued that they were the first to appear on earth (Boaden, 1975, 1977, 1989) thus influencing the life traits, histories and strategies of other, larger, macrofaunal organisms (Warwick, 1989). Indeed, Warwick (1984) argued that meiofauna are actually a distinct evolutionary unit consisting of a diverse variety of organisms whose life-histories and feeding adaptations set them apart from the larger macrobenthos. However, while some taxa never outgrow the meiobenthic size range and are deemed

‘permanent meiofauna’, others are juveniles of macrofauna and defined as ‘temporary meiofauna’ (McIntyre, 1964). The temporary component spend only part of their lifecycle within the meiofauna size range, and include species of the Echinodermata, Cnidaria, Priapulida as well as the Polychaeta.

1.3. Aims

The main aim of this thesis is to understand the patterns in the benthos within the shallow west lagoon at Discovery Bay. More specifically this thesis aims to:

1. Characterise the sediment granulometry of five characteristic and visibly different habitats within the shallow lagoon.

2. Assess the spatial and temporal variation in microphytobenthos within the shallow lagoon.

3. Assess the spatial variation in meiobenthos within the shallow lagoon.

4. Examine nematode feeding groups among the five habitats in order to test hypotheses that different groups have affinities for certain benthic conditions.

5. Examine nematode body size and biomass spectra from communities subjected to different sediment conditions and forms of natural disturbance.

2. STUDY SITES AND GENERAL METHODS

2.1. Introduction

Sampling was conducted in the shallow lagoon landward of the west reef crest at Discovery Bay, Jamaica, West Indies. Discovery Bay is located at 18°28’00"N, 77°24’30"W (Figure 2.1) and forms a sharp indentation on the central north coast of Jamaica covering an area of approximately 1.4 km^2 (UNESCO, 1998). The climate is sub-tropical, with an annual air temperature range of 22-32 ºC and sea temperature range of 26-30 ºC (Woodley and Robinson, 1977; Liddell *et al.*, 1984). North-easterly trade winds dominate the coast of north Jamaica and due to a limited tidal range (~ 30 cm), currents within the bay are generally wave-driven (Aller and Dodge, 1974; Porter, 1985; Gayle and Woodley, 2004).

The bay can be divided into two bathymetric areas: shallow lagoon shelf regions (0-8 m) behind the reef crest in the east and western areas, and a deeper basin (8-53 m) (Aller and Dodge, 1974) (Figure 2.1). North-west of the main bay is a shallow shelf between the Discovery Bay Marine Laboratory and the western reef crest (Figure 2.1). The majority of this area is a designated marine reserve. Study habitats (Figure 2.2) were located within the marine reserve, which is generally less than 10 m deep, apart from a drowned caustic silt-filled sink hole known as the ‘Blue Hole’ which reaches 13 m deep (Figure 2.1. & 2.2). Typical features of the sediment within the marine reserve include white and grey sand areas, seagrass beds, thalassinid (ghost) shrimp mounds, small coral knolls and areas of coral rubble (see also Aller and Dodge, 1974).

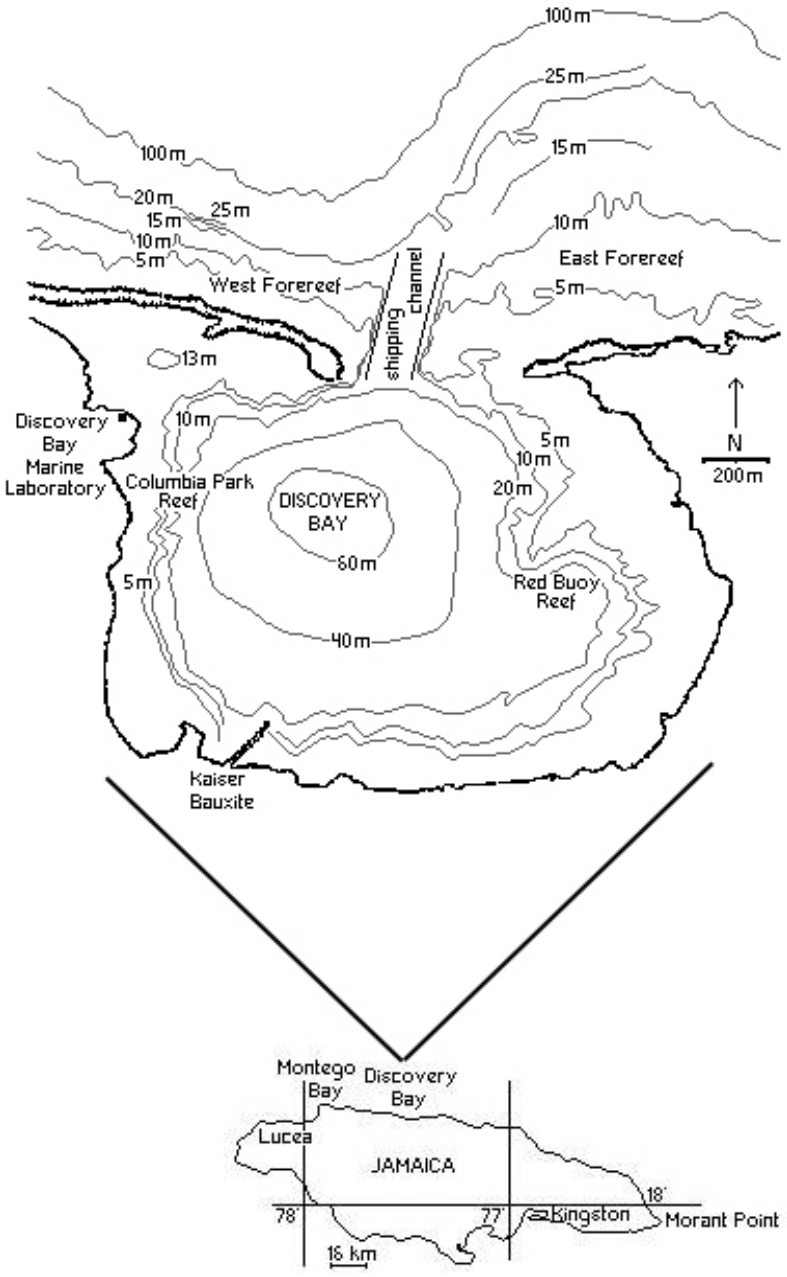

Figure 2.1. Schematic maps showing the position of Discovery Bay on the north coast of Jamaica and bathymetry of the bay.

2.2. Sample habitats

After intensive snorkelling, five soft-bottom benthic habitats within the study area were selected based on visual differences in sediment characteristics (Figure 2.2). All habitats were approximately 1.5 to 2.0 m deep, apart from habitat 5 which was approximately 4 m deep.

2.2.1. Habitat descriptions

2.2.1.1. Habitat 1

This habitat was situated landward of the eastern end of the west backreef crest, and was the nearest habitat to the shipping channel. Sediments were white in colour and contained small ripple marks perpendicular to the daily north easterly on shore current. The mean grain size of sediments was 217 µm, which corresponded to fine sands on the Wentworth scale. During the day there was often a gentle flow of water from an easterly direction over this habitat into the shallow western portion of the bay. At night, this flow ceased. No signs of mounds constructed by thalassinid shrimps were noticed here during field work. In this thesis this habitat is also referred to as ‘H1’.

2.2.1.2. Habitat 2

This habitat bordered the drop-off into the main bay. Sediments here appeared to be grey in colour and were noticeably darker than at habitat 1. The mean grain size of sediments was 353 µm, which corresponded to medium sands on the Wentworth scale. The ripple marks found at habitat 1 were not as obvious here, neither were there any signs of mounds constructed by thalassinid shrimps. There were, however, characteristic trails made by the Caribbean heart urchin, *Meoma*

ventricosa (Lamarck 1816). This species is a burrowing detritivorous spatangoid echinoid and actively bioturbates the upper sediment layers (Chesher, 1969). This species was only ever noticed in this habitat. Besides the trails left by this species, depressions approximately 10 - 15 cm deep and 1 m wide in diameter were regularly noticed around the sampling transect. These pits were presumed to be caused by the foraging activities of stingrays but were never noticed within the transect on any sampling occasion. In this thesis this habitat is also referred to as the 'H2'.

Figure 2.2. Overhead photograph showing the positions of the five sampling habitats within the shallow west lagoon. The numbers (1-5) represent the location of the habitats while the black lines represent the position and orientation of the 30 x 2 m sampling transects.

2.2.1.3. Habitat 3

This habitat ran parallel to the reef crest and is situated among small coral knolls bordering the back-reef and shallow lagoon. Being located just behind the reef crest this area is periodically subject to intense wave action as water surge flows over the reef crest. Sediments here were coarser than at habitats 1 or 2. Mean grain size was 534 µm, which corresponded to coarse sands on the Wentworth scale. In this thesis this habitat is also referred to as 'H3'.

2.2.1.4. Habitat 4

This habitat ran perpendicular to the reef crest and was densely populated by ghost shrimps (Decapoda: Order Thalassinidae). These macrofaunal ghost shrimps are bioturbators and actively burrow into the benthos forming sediment mounds which stand approximately 35 cm proud of the sea floor. Mean grain size was 351 µm, which corresponded to medium sands on the Wentworth scale. In this thesis this habitat is also referred to as 'H4'.

2.2.1.5. Habitat 5

This habitat ran perpendicular to the reef crest and was situated approximately 50 m away from habitat 5 but at a slightly deeper depth of 4 m. Like habitat 4 it was also densely populated by thalassinid shrimps but mean grain size was slightly smaller at 255 µm, which corresponded to medium sands on the Wentworth scale. In this thesis this habitat is also referred to as the 'H5'.

2.3. Sampling design

In order to assess spatial variation in the benthos a nested hierarchical sampling design (see Underwood, 1997) was employed (Figure 2.3). At each of the five underwater habitats four sites were nested at random, and within each site three plots were nested at random. Within each plot two replicate samples were obtained at random. Hence the three levels were as follows: habitat, sites nested within habitats, and plots nested within sites [i.e. H, S(H), P(S(H))]. Habitat was deemed a fixed factor since I was specifically concerned with differences between habitats. In contrast, site and plot were deemed random factors. Since no *apriori* information was available on the extent of spatial variation in benthos in this system, nested site and plot factors were necessary in the design in order to prevent results from being spatial confounded due to inadequate spatial replication (see Morrisey *et al.*, 1992a). Sampling for sediment granulometry and meiofauna was conducted on one occasion (see Chapters 3 and 4). The resulting linear model, under the null hypothesis that each variable is homogeneous across the considered spatial factors, is:

$$X_{ijkl} = \mu + Hi + S_j(H_i) + P_k(S_j(H_i) + Error_{ijkl}$$

Where:

Xijkl is each individual value of the dependent variable, μ is the overall mean, ***Hi*** is the fixed treatment effect of habitat, $S_j(H_i)$ is the effect of $Site_j$ nested within $Habitat_i$, $P_k(S_j(H_i)$ is the effect of $Plot_k$ nested within $Site_j$ nested within $Habitat_i$, and $Error_{ijkl}$ is the random error term.

The assessment of microphytobenthos incorporated an additional "Time" factor (random), and sampling was conducted approximately 3 weeks apart (see Chapter 3). The resulting linear model, under the null hypothesis that each variable is homogeneous across the considered spatial and temporal factors, is:

$$X_{ijklm} = \mu + T_i + H_j + T_iH_j + S_k(H_j) + T_iS_k(H_j) + P_l(S_k(H_j)) + T_iP_l(S_k(H_j)) + e_{ijklm}$$

Where:

X_{ijklm} is each individual value of the dependent variable, μ is the overall mean, T_i is the effect of Time, H_j is the fixed treatment effect of habitat, $S_k(H_j)$ is the effect of $Site_k$ nested within $Habitat_j$, $P_l(S_k(H_j))$ is the effect of $Plot_l$ nested within $Site_k$ nested within $Habitat_j$, and $Error_{ijklm}$ is the random error term.

2.4. Sampling layout

A 30 m transect line was attached to the benthos in the middle of each of the five habitats (Figure 2.3). The transect was marked at meter intervals allowing a 1 m^2 quadrat to be positioned at a defined place either side along the line. This created a potential of sixty discrete 1 m^2 sites, with 30 sites situated either side of the line.

Each 1 m^2 site (i.e. quadrat) was divided into sixteen plots measuring 25 cm by 25 cm. Each plot was further sub-divided into twenty-five 5- by 5 cm squares. Hence a 1 m^2 site contained a possible sixteen plots each of which contained twenty-five positions from which individual replicates could be obtained from. When sampling was undertaken, the exact positions of replicates within plots,

plots within sites, and sites within habitats were determined beforehand by random number tables, and replicate cores for sediment granulometry and microphytobenthos (Chapter 3) and meiofauna (Chapter 4 and 5) were obtained from the middle of each 5- by 5 cm square as best as possible.

This layout therefore incorporated a range of scales from which samples could be obtained, based on approximate nearest and furthest distances, as follows:

a) Between replicates nested within plots: 0.05 to 0.28 m
b) Between plots nested within sites: from 0.25 to 1.06 m
c) Between sites nested within habitats: from 1- to 29 m
d) Between habitats: 60- to 300 m

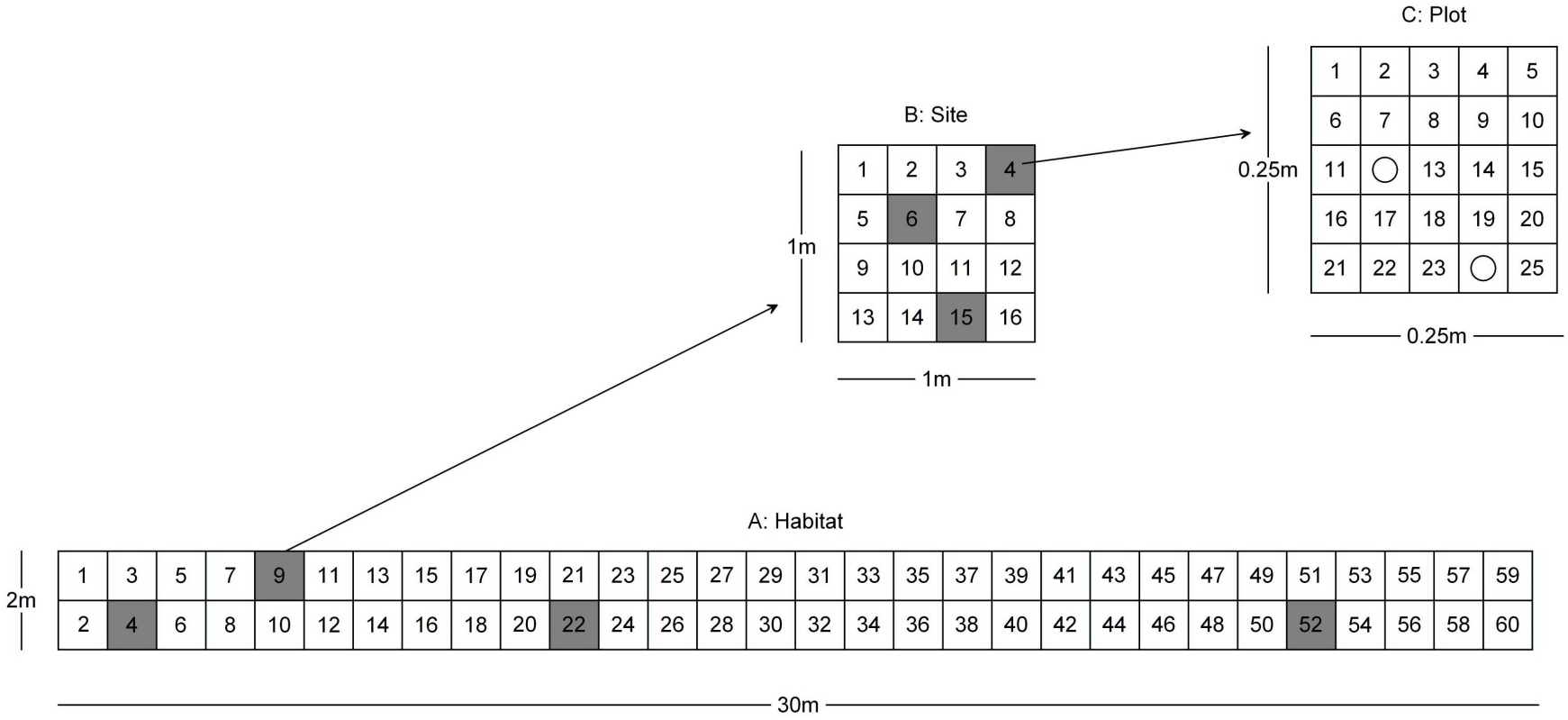

Figure 2.3. Schematic representation of sampling design showing A: one of the five sampling habitats containing four nested sites (in grey); B: a single site containing three nested plots (in grey); and C: a single plot from which two random replicate core samples were obtained (shown as circles at positions 12 and 24). Note scales.

2.5. Statistical analysis

Many statistical procedures were used to analyse the data obtained in this study ranging from basic descriptive and univariate statistical techniques, to more advanced multivariate methods which will be summarised below. The statistical packages used to carry out these procedures include “MINITAB version 14.2”, “STATGRAPHICS CENTURION version 15.2.05”, and “PRIMER (Plymouth Routines in Multivariate Ecological Research) version 6 beta”. All univariate data were tested for normality and homogeneity of variance before analysis using the Kolmogrov-Smirnov and Cochran’s C test (Underwood, 1997), respectively. If data did not conform to parametric statistical assumptions, suitable transformations were made before retesting. If after retesting data still did not conform, then non-parametric statistical methods were used. When significant ANOVA results were found, they were followed by unplanned multiple comparisons using Tukey’s honestly significant difference (Tukey HSD) test for comparison of means.

2.5.1. Non-metric Multi-Dimensional Scaling (MDS)

MDS is an ordination technique that attempts to plot the relationship between similarities in a multivariate data set as distances in multidimensional space. An ordination map is produced whereby similar samples are plotted at close distance to one another and dissimilar samples at further distances from one another. A stress value is calculated as a quantitative measure of how good the observed 2 (or 3) dimensional plot represents the ordination in multidimensional space. According to Clarke and Warwick (2001), stress values <0.05 give an excellent representation with no prospect of misinterpretation; values <0.1 correspond to a

good ordination with no real prospect of a misleading interpretation; values <0.2 give a potentially useful 2-dimensional picture although should not be solely relied upon and values >0.3 indicate that the points are close to being arbitrarily placed in 2-dimensional space.

2.5.2. Analysis of Similarities (ANOSIM)

ANOSIM is a non-parametric multivariate statistical procedure analogous to traditional Analysis of Variance. It is a permutation test based on rank (dis)similarities between two or more sampling groups. A test statistic, rho (*R*) is computed reflecting observed differences between groups (i.e. sites, times, treatments etc.) in the multivariate data set and is contrasted with differences among replicates within groups. *R* is scaled to lie within the range -1 to +1 with zero values representing the null hypothesis, i.e. similarities between and within sampling groups are the same. Conversely, values departing from zero reflect departure from the null hypothesis, i.e. a value of 1 denotes that all similarities within groups are less than any similarity between groups, and provide a comparative measure of the degree of separation of groups. Significance levels for each factor were calculated by referring the observed value of R to it's permutation distribution, created from 999 simulations. For more details see Clarke (1993) and Clarke and Gorley (2006).

2.5.3. Similarity Percentages (SIMPER)

SIMPER is a non-parametric procedure which decomposes average Bray-Curtis dissimilarities or Euclidean distances into percentage contributions in order to identify the species or variables primarily responsible for group-wise separation.

In other words, SIMPER can highlight species, taxa, or variables which can discriminate between groups of samples responsible for differences in the ANOSIM test. For more details see Clarke and Warwick (2001).

2.5.4. Principle Components Analysis (PCA)

PCA is an ordination technique used to reduce many variables in a multivariate dataset to a smaller number of new derived variables called principle scores (or components) which are uncorrelated. These scores can be plotted such that the first principle component axis accounts for as much of the variability in the dataset as possible, with the second axis accounting for as much of the remaining variability as possible. One of the main advantages of this technique is that it helps to reduce the dimensionality of a multidimensional data set to a more meaningful ordination enabling the major trends in the underlying variables to be easily seen.

3. MICROPHYTOBENTHOS AND SEDIMENT GRANULOMETRY

3.1. Introduction

Coral reef ecosystems (CREs) are among the most productive in the marine environment exhibiting high gross production in the order of 700 x 10^{12} g C per year (Crossland *et al.*, 1991). Due to their extensive areal coverage [~284,300 km^2 (Spalding *et al.*, 2001)] and high productivity rates, hermatypic corals and epilithic and macroalgal communities are generally regarded as the major primary producers within CREs (Larkum, 1983; Carpenter *et al.*, 1991; Hatcher, 1998). However, it is now firmly established that the microphytobenthos inhabiting coral reef sediments is ubiquitous, abundant and also highly productive (e.g. Clavier and Garrigue, 1999; Heil *et al.*, 2004; Rasheed *et al.*, 2004). Microphytobenthos refers to the photosynthetic unicellular eukaryotic algae, such as diatoms and dinoflagellates, as well as prokaryotic cyanobacteria that inhabit the surface layers of illuminated soft-bottom sediments (MacIntyre *et al.*, 1996). Since CREs contain large expanses of unconsolidated soft-bottom sediments (Furnas *et al.*, 1995; Clavier and Garrigue, 1999; Cochran *et al.*, 2007), which are extensively inhabited by microphytobenthos (e.g. Heil *et al.*, 2004), a significant contribution is made by these autotrophs towards total reef primary production (Sorokin, 1993; Clavier *et al.*, 2008; Werner *et al.*, 2008). On the Great Barrier Reef, for example, Uthicke and Klumpp (1998) estimated an annual net microphytobenthic production of 168 g C m^{-2} contributing up to 37% towards the total autotrophic production in the reef system. At the whole reef ecosystem scale, production by sediment-inhabiting microphytobenthos is even

considered equivalent to that of corals (Clavier and Garrigue, 1999), or at least within the same order of magnitude (Werner *et al.*, 2008).

For a number of reasons microphytobenthos is important to the dynamics of shallow water systems. As a significant and palatable primary producer, microphytobenthos is a readily available food resource consumed in large quantities by a wide variety of deposit-, epistrate- and filter-feeding organisms. These range in size from microscopic foraminifera (Austin *et al.*, 2005) and meiofauna (Montagna, 1984; Moens and Vincx, 1997; Buffan-Dubau and Carman, 2000) to larger macrofauna (Currin *et al.*, 1995; Stocks and Grassle, 2001; Yokoyama and Ishihi, 2003) and demersal fish (Mallin *et al.*, 1992; Takai *et al.*, 2002). Microphytobenthos therefore plays a central role in supporting secondary production. This is particularly so in unvegetated sediments devoid of macroalgae and/or seagrasses and in shallow water systems where the relative importance of phytoplanktonic production is decreased due to the shallow water column (McGlathery *et al.*, 2004). The secretion of carbohydrate-rich mucilages, by diatoms and cyanobacteria in particular (de Winder *et al.*, 1999; Smith and Underwood, 2000; Staats *et al.*, 2000), increases both the cohesive nature and erosion threshold of sediments thus limiting resuspension caused by water scour and tidal currents (Decho, 1990; Miller *et al.*, 1996; Lundkvist *et al.*, 2007). This helps to enhance sediment stability and prevent against coastal erosion (Austen *et al.*, 1999; Le Hir *et al.*, 2007; Lundkvist *et al.*, 2007).

Nutrient fluxes through the sediment-water interface are partly regulated by the photosynthetic activities of microphytobenthos. Production of oxygen and the

uptake of nutrients by benthic microalgae influences the rates and magnitude of sediment decomposition processes, as well as the regeneration of nutrients from sediment porewater to the water column (Rizzo *et al.*, 1992; Sundbäck *et al.*, 2000; Cibic *et al.*, 2007). This is particularly important within CREs, which exist within oligotrophic conditions, and therefore need efficient mechanisms for recycling within the system.

In shallow water systems the assessment of microphytobenthic biomass is a fundamental precursor to the many processes driven by benthic microalgal photosynthesis (Light and Beardall, 1998). Over the last decade and a half, the ecological significance of microphytobenthos from many different marine environments has received much attention (for example see reviews by MacIntyre *et al.*, 1996; Miller *et al.*, 1996; Cahoon, 1999; Underwood and Kromkamp, 1999). Studies have shown that the distribution of microphytobenthos is patchy over a range of spatial and temporal scales (Sundbäck, 1984; Plante *et al.*, 1986; Saburova *et al.*, 1995; Light and Beardall, 1998; Sandulli and Pinckney, 1999), due to many interacting and controlling factors (e.g. light, water motion, nutrients, grazing, bioturbation). While some studies report a negative relationship between microphytobenthic biomass and the proportion of fine grained sediments (Cahoon *et al.*, 1999), others have found that fine cohesive sediments support significantly higher concentrations of microphytobenthos than sites with sandy silts and sands (see review by Underwood and Kromkamp, 1999). Assessment of spatio-temporal variation in microphytobenthos across a range of differing scales, encompassing varied habitat types within a coral reef lagoon has, however, received limited attention

(for example see Hansen *et al.*, 1987, 1992; Boucher and Clavier, 1990; Garrigue, 1998; Clavier and Garrigue, 1999). Likewise, there is also a paucity of information on the distribution and ecology of microphytobenthos from tropical habitats (Underwood, 2002). What is apparent, however, is that microphytobenthos is highly variable within tropical lagoons. On the Great Barrier Reef, for example, values range from 8 to 1153 mg Chl *a* m^{-2}, upper values of which are some of the highest values ever recorded from marine sediments (see Roelfsema *et al.*, 2002; Heil *et al.*, 2004).

In the shallow lagoon at Discovery Bay the only study to have examined the abundance of microphytobenthos is by Bunt *et al.* (1972). Unfortunately this study did not detail where samples were obtained from (i.e. forereef, backreef, lagoon), although it was noted that they were taken at 16-, 30-, and 60 m depth. Therefore they were not taken within the shallow lagoon. There is also only one published study on the granulometry of sediments within the shallow west lagoon, and this study does not detail how many samples were obtained or exactly how they were taken (Aller and Dodge, 1974). Since variation in microphytobenthic biomass has important implications for both descriptive and experimental studies (Light and Beardall, 1998), and grain size statistical characteristics form the basis of schemes for classifying sedimentary environments (Alsharhan and El-Sammak, 2004), this research focuses on the distribution of microphytobenthos among five characteristic habitats within the shallow lagoon. In particular, the primary aim of this research is to document the sedimentary environment and to examine spatial and temporal variation in microphytobenthic biomass (as chlorophyll *a*) within the shallow west lagoon

using an experimental design which quantifies patchiness over a range of spatial scales.

3.2. Methods

3.2.1. Sample collection

120 samples for sediment granulometry and 360 samples for microphytobenthos were obtained according to the sampling design in Chapter 2. Sediment granulometry samples were obtained on the 14th of June 1999. Sampling for microphytobenthos took place on three occasions (26th to the 27th of May, 16th to the 17th of June, and the 9th to the 10th of July 1999) and was spread over two days per occasion due to logistical and processing constraints. In order to limit any bias occurring due to the need to sample over two days, microphytobenthic sampling was undertaken as follows: prior to sampling four random sites out of a possible sixty were determined for each habitat via computerised random numbers generation. The first two numbers generated were sampled on the first day and the second two on the second day. Sampling took place between 11am and 2pm each day. All samples were obtained whilst free diving.

3.2.1.1. Sediment granulometry

Sediment cores were obtained to a depth of 5 cm using a 2.6 cm inner diameter syringe with the Luer end cut off and a rubber bung cap. In the laboratory, cores were transferred to clean pre-weighed scintillation vials, and immediately re-weighed before being dried at 80 °C for 48 hours to a constant weight. Once dry, they were again weighed in order to calculate porosity before being sieved for 15 minutes using a mechanical shaker stacked with sieves ranging from 2 mm to

0.063 mm. GRADISTAT v5 (Blott and Pye, 2001) was subsequently used to compute sediment granulometry characteristic (SGC) statistics: mean sediment grain size, gravel (%), sand (%), silt/clay (%), sorting (σ_I), skewness (SK_1) and kurtosis (KG) following Folk and Ward (1957). Classification of sediment type followed Blott and Pye (2001) modified from Udden (1914) and Wentworth (1922). Sediment porosity was calculated as the difference between dry- and wet weight and expressed as a percentage. A derived measure of sediment heterogeneity was calculated according to Ward (1975), according to the following equation:

$$h = \frac{QD\phi}{Md\phi} \times \%silt$$

where *QDØ* is the sorting coefficient and *MdØ* is the median particle diameter [phi].

3.2.1.2. Microphytobenthos

Sediment cores for the analysis of microphytobenthos (as chlorophyll *a*) were obtained to a depth of 5 cm using a 1.4 cm inner diameter syringe with the Luer end cut off and a rubber bung cap. After samples had been cored and capped, they were immediately taken up to the surface and placed on ice in a sealed cool box on a moored boat. This cool box was kept out of the sunlight within a larger cool box in order to prevent any pigment degradation due to the high air temperatures. In the laboratory, samples were placed into 30 ml centrifuge tubes to which 16 ml of 100% acetone was added, making a final concentration of 80% with the interstitial water being taken into account (analysis of interstitial water content showed a mean of ~4 ml per sample core). Samples were then mixed

thoroughly on a vortex mixer, and extracted in the dark at 4 °C for 24 hours. After extraction samples were centrifuged at the highest setting (number 7) for 15 minutes in an International Clinical Centrifuge (Model CL, International Equipment Company, Needham, Massachusetts) before the supernatant was decanted and analysed in a Milton Roy Spectronic 'Genesys 2' spectrophotometer using the equations of Lorenzen (1967).

3.2.2. Statistical analysis

3.2.2.1. Sediment granulometry

Even after appropriate data transformations and subsequent retesting data did not conform to the assumptions of ANOVA. Consequently the Kruskal-Wallis non-parametric test was employed to test the null hypothesis that there was no difference in sediment granulometry characteristics (SGC: e.g. mean grain size; % gravel, % sand, % silt/clay; sorting coefficient; skewness; kurtosis; % porosity; sediment heterogeneity) between the five habitats. Significant results were further examined via the nonparametric 'Tukey-type' Nemenyi multiple comparison test according to Zar (1999).

Principal Components Analysis (PCA) was used to examine the relationships between the study habitats and the sediment particle size distribution (SPSD) and the sediment granulometry characteristics (SGC). Before analysis data were checked for multivariate normality by looking at draftmans plots. Gravel % was right skewed and sand % was left skewed and therefore $\log_{10}(V+1)$ and a $\log_{10}(100-V)$ transformations applied, respectively, according to Clarke and Gorley (2006). Formal significance tests examining the null hypothesis that there

were no differences in SPSD and SGC were performed using the Analysis of Similarities (ANOSIM) test (Clarke, 1993) on Euclidean dissimilarity matrices. SPSD data were standardised and then cumulated, while SGC data were normalised (Clarke and Gorley, 2006). Two-way nested ANOSIM tests were initially run on each habitat individually to assess whether there were differences at the plot and site scales in SPSD and SGC. Since no significant differences were found at the plot scale in any of the tests, it was justifiable to perform two-way nested ANOSIM over all habitats using site groups as samples (Clarke and Gorley, 2006).

3.2.2.2. Microphytobenthos

Hypotheses about the spatial and temporal variability in the biomass of microphytobenthos (as chlorophyll *a*) were tested by mixed-model nested ANOVA with four spatial scales (habitat, site[habitat], plot[site[habitat]], replicates) orthogonally sampled at three dates. Habitat was a fixed factor while date, site and plot were random factors. Normality of data and homogeneity of variances were checked using the Kolmogorov-Smirnov and Cochran's C test (Underwood, 1997), respectively. In order to meet the assumptions of ANOVA data were $\log_{10}$ transformed and retested, confirming assumptions before analysis. Significant results were followed by unplanned multiple comparisons using Tukey's honestly significant difference (Tukey HSD) test for comparison of means. Furthermore, spatial variability in microphytobenthos was tested for each individual date using nested three-factor ANOVA.

To quantify spatial variability among dates in the biomass of microphytobenthos coefficient of variation (CV = standard deviation / mean) was used (see Palmer *et al.*, 1997). For each habitat on each sampling occasion the CV was calculated firstly for plots (since there were $N = 2$ samples per plot, the "plot CVs" were calculated using 2 measurements) and then for each of the sites ($N = 6$ samples per site). Mean CV for each habitat was then calculated for the *within plot scale* based on 12 *within plot* CV's (since there were 12 plots per habitat) and for the within site scale based on 4 *within site* CV's (since there were 4 sites per habitat). At the habitat scale CV was calculated for each individual habitat from all 24 replicates and hence there is no mean value. As an additional graphical representation data have also been pooled by Date and Habitat in order to show the overall trend. Variance components derived from individual three-factor ANOVAs were also calculated as a second method by which to compare variation at the respective scales. However due to habitat being a fixed factor in the mixed ANOVA model, the results are only relative to the five habitats (Sokal and Rohlf, 1995) and are not respective of natural variation in the western lagoon as a whole.

3.3. Results

3.3.1. Sediment granulometry overview

A summary of the descriptive statistics of the different sediment granulometric characteristics is presented in Table 3.1. Relative grain size fractions are presented in Figure 3.1. Sediments ranged from fine to coarse sands, and were moderately to poorly sorted (Figure 3.2). Significant differences (Kruskal-Wallis test, $p<0.001$, df=4) in all individual sediment granulometry characteristics were found between the 5 study habitats (Figure 3.2, Table 3.2). Nemenyi multiple comparison tests comparing differences in the various characteristics between habitats did not reveal any clear-cut groups. However, out of the 9 measured sediment characteristics, only 3 of them were significantly different when habitats 1 and 2 were compared, and 4 of them significantly different when habitats 4 and 5 were compared.

3.3.1.1. Habitat 1

Habitat 1 sediments had the lowest average mean grain size of 217 μm (n=24, ± 18 SD) and all samples were classified as fine sand. This habitat had the highest mean percentage of sand and a low mean percentage of gravel. Sediments were in the main moderately sorted, coarse skewed and leptokurtic, and out of all the habitats exhibited the lowest index of sediment heterogeneity with the smallest range indicative of relatively homogeneous sediments.

3.3.1.2. Habitat 2

Habitat 2 sediments had a average mean grain size of 353 μm (n=24, ± 82 SD). Overall this habitat was considered a ‘medium sand habitat’; however 21

samples were classified as medium sand, 2 samples as coarse sand, and 1 sample as fine sand. Relative grain size fractions were similar to habitat 1, albeit an increase in the percentage gravel and silt/clay and a decrease in the percentage of sand was evident. Sediments were mostly symmetrically skewed but varied between moderately and poorly sorted, and between meso- and leptokurtic. Sediments were reasonably homogeneous albeit less so than at habitat 1.

3.3.1.3. Habitat 3

Habitat 3 sediments had the highest average mean grain size of 534 μm (*n*=24, ± 104 SD). Overall this habitat was considered a 'coarse sand habitat'; however 16 samples were classified as coarse sand and 8 samples as medium sand. Sediments were all poorly sorted, predominantly symmetrically skewed, and almost exclusively mesokurtic. This habitat had the highest percentage of gravel and the lowest percentage of sand and silt/clay, evidence of a high energy environment. Sediment heterogeneity was slightly higher than habitat 2.

3.3.1.4. Habitat 4

Habitat 4 sediments had a average mean grain size of 351 μm (*n*=24, ± 76 SD). Overall this habitat was considered a 'medium sand habitat'; however 22 samples were classified as medium sand, 1 sample as fine sand and 1 sample as coarse sand. The proportion of gravel was slightly raised compared to habitat 1, 2 and 5. Sediment samples were all poorly sorted, predominantly symmetrical, with kurtosis varying between meso- and platykurtic.

3.3.1.5. Habitat 5

Habitat 5 sediments had a average mean grain size of 255 μm (n=24, ± 24 SD) . Overall this habitat was considered a ‘medium sand habitat’; however 16 samples were classified as medium sand and 8 as fine sand. This habitat had the highest percentage of silt/clay and the lowest percentage of gravel. Sediments were all poorly sorted, predominantly coarse skewed, with kurtosis varying between predominantly meso- and platykurtic. Sediment heterogeneity was slightly lower than at habitat 4 and exhibited a slight decrease in range.

Table 3.1 Summary of granulometry statistics at each Habitat. Data are mean values with standard deviation in parentheses. (*n*=24).

Habitat	1	2	3	4	5
Sand Classification	fine	medium	coarse	medium	medium
Mean particle size (μm)	217 (18)	353 (82)	534 (104)	351 (76)	255 (24)
Median particle size (μm)	210 (17)	344 (78)	531 (113)	340 (90)	230 (26)
Percentage of gravel	0.9 (1.0)	1.2 (1.4)	5.9 (3.9)	2.0 (1.7)	0.4 (0.4)
Percentage of sand	97.1 (1.3)	96.7 (1.5)	92.9 (3.8)	94.9 (1.9)	95.6 (0.9)
Percentage of silt/clay	2.0 (0.8)	2.1 (0.8)	1.2 (0.5)	3.1 (1.3)	4.0 (0.8)
Sorting	0.8 (0.08)	1.0 (0.09)	1.2 (0.07)	1.3 (0.11)	1.3 (0.06)
Skewness	-0.14 (0.05)	-0.04 (0.06)	0.05 (0.10)	-0.04 (0.07)	-0.15 (0.042)
Kurtosis	1.28 (0.15)	1.12 (0.09)	0.93 (0.10)	0.92 (0.05)	0.95 (0.08)
Percentage porosity	34.3 (2.2)	33.2 (2.3)	36.5 (5.1)	34.8 (2.4)	37.0 (2.4)
Sediment heterogeneity	0.75 (0.3)	1.45 (0.7)	1.62 (0.7)	2.59 (0.9)	2.33 (0.5)

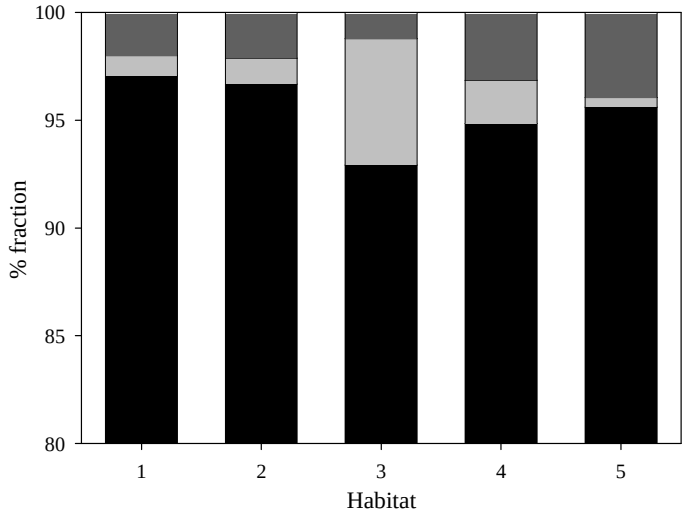

Figure 3.1. Relative grain size fractions at each habitat. Black bar = sand; light grey bar = gravel; dark grey bar = silt/clay. Note Y axis scale. (*n*=24).

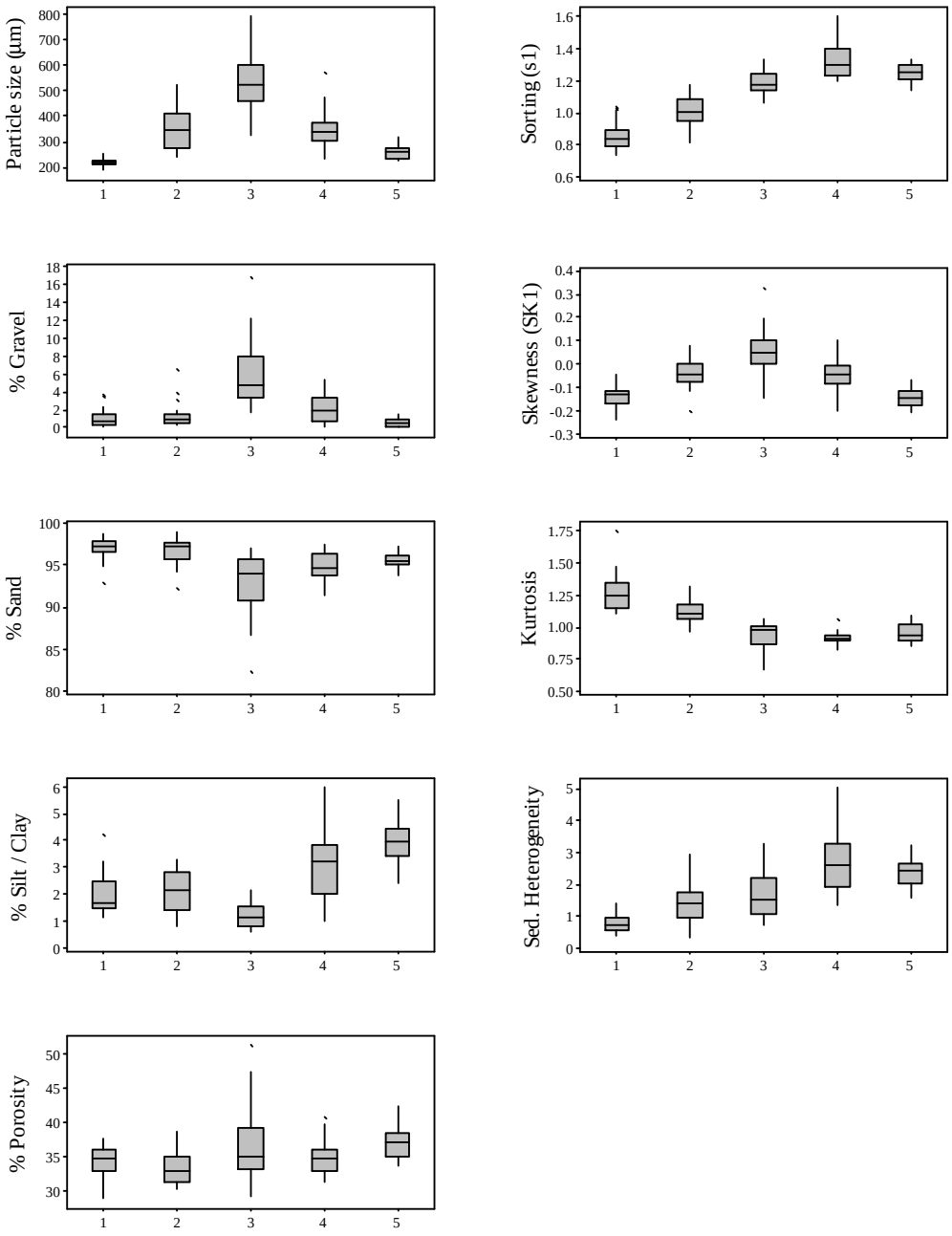

Figure 3.2. Box plots of sediment granulometry characteristics at the five lagoon habitats. Sed = Sediment. (*n*=24).

Table 3.2. Results of Kruskal-Wallis tests evaluating differences in the median of sediment granulometry characteristics between the five lagoon habitats. Differences between individual habitats were determined by *post-hoc* multiple comparisons using the Nemenyi test. (n=24).

Sediment Granulometry Characteristics	H	df	*p*	*Comparisons*
Mean particle size (μm)	94.12	4	<0.001	1=5, 4=2, 3
% Gravel	57.74	4	<0.001	1=2=4, 1=2=5, 3
% Sand	43.06	4	<0.001	1=2, 2=5, 3=4=5
% Silt / Clay	67.40	4	<0.001	1=2=3, 4=5, 2=4
Sorting (σ_I)	93.51	4	<0.001	1=2, 3=5, 4=5
Skewness (SK_1)	71.57	4	<0.001	2=3=4, 1=5
Kurtosis (KG)	83.29	4	<0.001	1=2, 3=4=5
% Porosity	23.36	4	<0.001	1=2, 1=3=4, 3=5
Sediment heterogeneity	68.82	4	<0.001	1, 2=3, 4=5

3.3.2. Ordination of sediment granulometry characteristics and particle size distributions

The principle component analysis on the abiotic sediment granulometry parameter data showed that the first two principal components explained 73.9 % of the total variance (Figure 3.3). The first PC was positively correlated with mean grain size (r = 0.42) and sand % (r = 0.42) and negatively correlated with kurtosis (r = -0.35). The second PC was positively correlated with silt / clay % (r = 0.62 and sediment heterogeneity (r = 0.45) and negatively correlated with skewness (r = -0.32). The ordination revealed that the degree of variability between replicate samples was least at habitat 1, where samples were grouped quite close together. At the other habitats variability was much greater, as revealed by the increase in distance between replicates on the ordination.

The principle component analysis on the sediment particle size data showed that the first two principal components explained 91.8% of the total variance (Figure 3.4). PC1 was positively correlated with particle size classes 0.710 to 0.500 μm (r = 0.341) and negatively correlated with particle sizes 0.180 to 0.125 μm (r = -0.551) and PC2 was positively correlated with particle sizes 0.355 to 0.250 μm (r = 0.654) and 0.125 to 0.090 mm (r = 0.320) and negatively correlated with particle sizes 1.000 to 0.710 mm (r = -0.380). A large degree of variability in particle size distributions occurred between replicate samples within each habitat, although compared to the SGC data, particle size is most homogeneous at habitat 5.

Results of the global ANOSIM tests (Table 3.3) confirmed that both sediment particle size distributions and sediment granulometry characteristics differed significantly among habitats (Global R = 0.801 and 0.756, respectively, P = 0.001 for both tests; Table 3.3). A significant site effect was also found, however R was low suggesting that the differences were between only a few sites (Global R = 0.273 and 0.256, respectively, P = 0.001 for both tests; Table 3.3). Results of pairwise tests showed that particle size distributions at all habitats were significantly different from each other. Sediment granulometry characteristics were also significantly different between all habitats except H2 and H4.

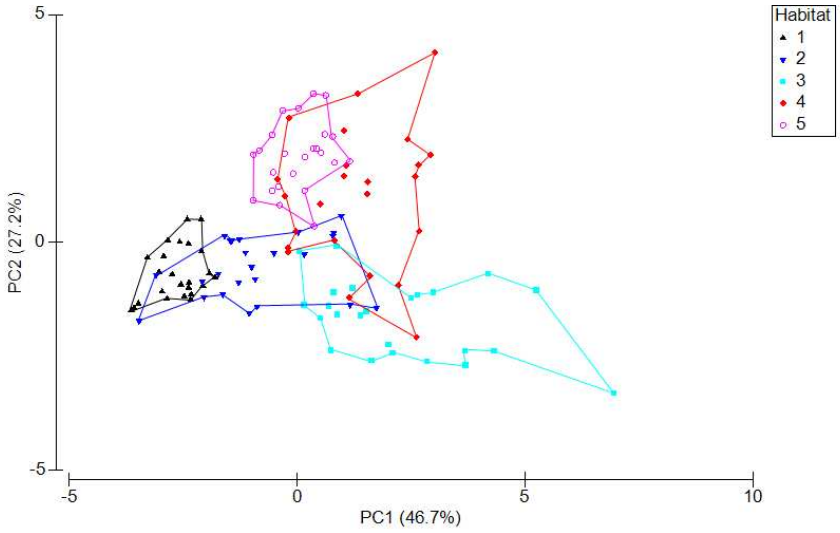

Figure 3.3. Principal component ordination of sediment granulometry characteristics from the five habitats in the shallow lagoon at Discovery Bay.

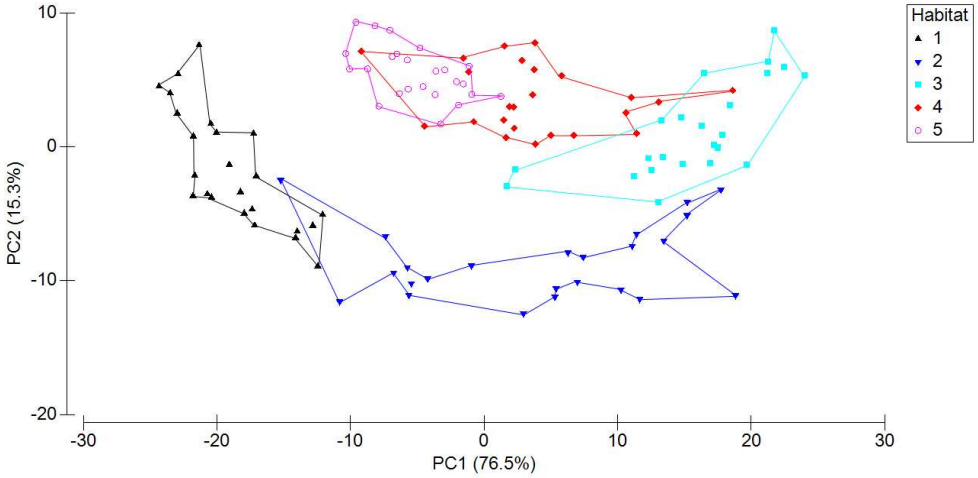

Figure 3.4. Principal component ordination of sediment particle size data from the five habitats in the shallow lagoon at Discovery Bay.

Table 3.3. *R*-statistic values and significance of pairwise two-way nested ANOSIM tests for differences in sediment conditions between the 5 lagoon habitats. All results are derived from Euclidean dissimilarity matrices. Before analysis sediment particle size distribution (SPSD) data were standardised to % fraction and then cumulated; sediment granulometry parameter (SGC) data were normalised (i.e. values for each variable have their mean subtracted and are then divided by their standard deviation).

Global Test	Habitat		Sites within Habitats	
	R	*P*	*R*	*P*
Sediment Particle Size Distribution	0.801	0.001	0.273	0.001
Sediment Granulometry Characteristics	0.756	0.001	0.256	0.001

Comparison	SPSD		SGC	
Habitats	*R*	*P*	*R*	*P*
1 vs. 2	0.76	0.029	0.711	0.029
1 vs. 3	1	0.029	0.992	0.029
1 vs. 4	1	0.029	0.880	0.029
1 vs. 5	0.99	0.029	0.860	0.029
2 vs. 3	0.573	0.029	0.490	0.029
2 vs. 4	0.531	0.029	0.290	0.057
2 vs. 5	0.698	0.029	0.628	0.029
3 vs. 4	0.833	0.029	0.531	0.029
3 vs. 5	1	0.029	0.952	0.029
4 vs. 5	0.771	0.029	0.468	0.029

3.3.3. Microphytobenthos

3.3.3.1. Spatio-temporal distribution

A total of 360 sediment cores from 3 dates and 5 hierarchically nested subtidal sampling habitats were analysed for microphytobenthos as benthic chlorophyll *a*. The biomass of microphytobenthos ranged more than fifteen-fold from 9- to 152 mg chl *a* m^{-2} (*N* = 360; mean = 41 mg m^{-2}; SE = 1.0; CV = 46.9%) over the 3 dates studied (Table 3.4; Figure 3.5, 1-3). No significant difference in biomass among dates or plots over all dates was detected, and no significant interaction between dates and habitats or between dates and sites nested within habitats was found (Table 3.5). There was, however, a highly significant date by plot(site(habitat)) interaction (Table 3.5), implying that at the smallest spatial scale (i.e. within plots / between replicates), variability in the spatial distribution of microphytobenthos changed among times of sampling.

Table 3.4. Summary of microphytobenthic biomass values (mg m^{-2}) at each habitat. SD = standard deviation. (*n*=72).

Habitat	Mean	SD	Minimum	Maximum
1	37.4	13.5	9.5	78.4
2	63.0	24.4	31.1	151.7
3	37.2	12.2	13.3	76.1
4	31.8	10.1	12.2	64.5
5	32.9	11.2	11.1	80.0

Due to the significant effect of habitat, three-factor nested ANOVAs were computed in order to more fully understand microphytobenthic spatial variability on individual

dates. Significant differences in mean microphytobenthic biomass between habitats were found on each date (Tables 3.6 – 3.8), with habitat 2 consistently having elevated levels of microphytobenthos relative to all other habitats (Figure 3.5). These differences were most significant for dates 1 (ANOVA $F_{4,15} = 10.55$, $P<0.001$) and 3 (ANOVA $F_{4,15} = 9.52$, $P<0.001$), although less so for date 2 (ANOVA $F_{4,15} = 3.52$, $P = 0.032$). Post-hoc Tukey HSD tests revealed that on dates 1 and 3 the mean biomass of microphytobenthos at habitat 2 was significantly higher than that occurring within any of the other habitats (Tukey HSD, $p<0.05$, Figure 3.5), whilst no significant differences in microphytobenthic biomass was detected between habitats 1, 3, 4 and 5 (Tukey HSD, $p>0.05$, Figure 3.5). On date 2 higher values of microphytobenthic biomass were again recorded at habitat 2; however on this occasion the only significant difference was between habitat 2 and 4 (Tukey HSD, $p<0.05$, Figure 3.5). Non significant variability among plots and sites was found on dates 2 and 3, respectively (Tables 3.6 – 3.8).

Table 3.5. Results of ANOVA used to investigate the spatial and temporal distribution of biomass of microphytobenthos.

Source of Variation	df	MS	*F*	p	Sig.	Error terms
Date	2	0.216	3.00	0.107	ns	Date x Hab.
Habitat*	4	1.007	8.37	0.002	**	[Date x Hab.+ Site(Hab.)] – Date x Site(Hab.)
Date x Habitat	8	0.072	2.11	0.066	ns	Date x Site(Hab)
Site (Hab)*	15	0.082	2.18	0.043	*	[Date x Site(Hab.) + Plot(Site(Hab))] - Date x Plot(Site(Hab))
Date x Site(Hab)	30	0.034	1.58	0.054	ns	Date x Plot(Site(Hab))
Plot(Site(Hab))	40	0.025	1.17	0.270	ns	Date x Plot(Site(Hab))
Date x Plot(Site(Hab))	80	0.021	1.70	0.002	**	Error
Error	180	0.013				

[1] Data transformed to $\text{Log}_{10}(x)$
ns = not significant; * $p<0.05$; ** $p<0.01$; *** $p<0.001$
* This was an approximate F-test due to the inability to assign exact error terms for the factor of interest.

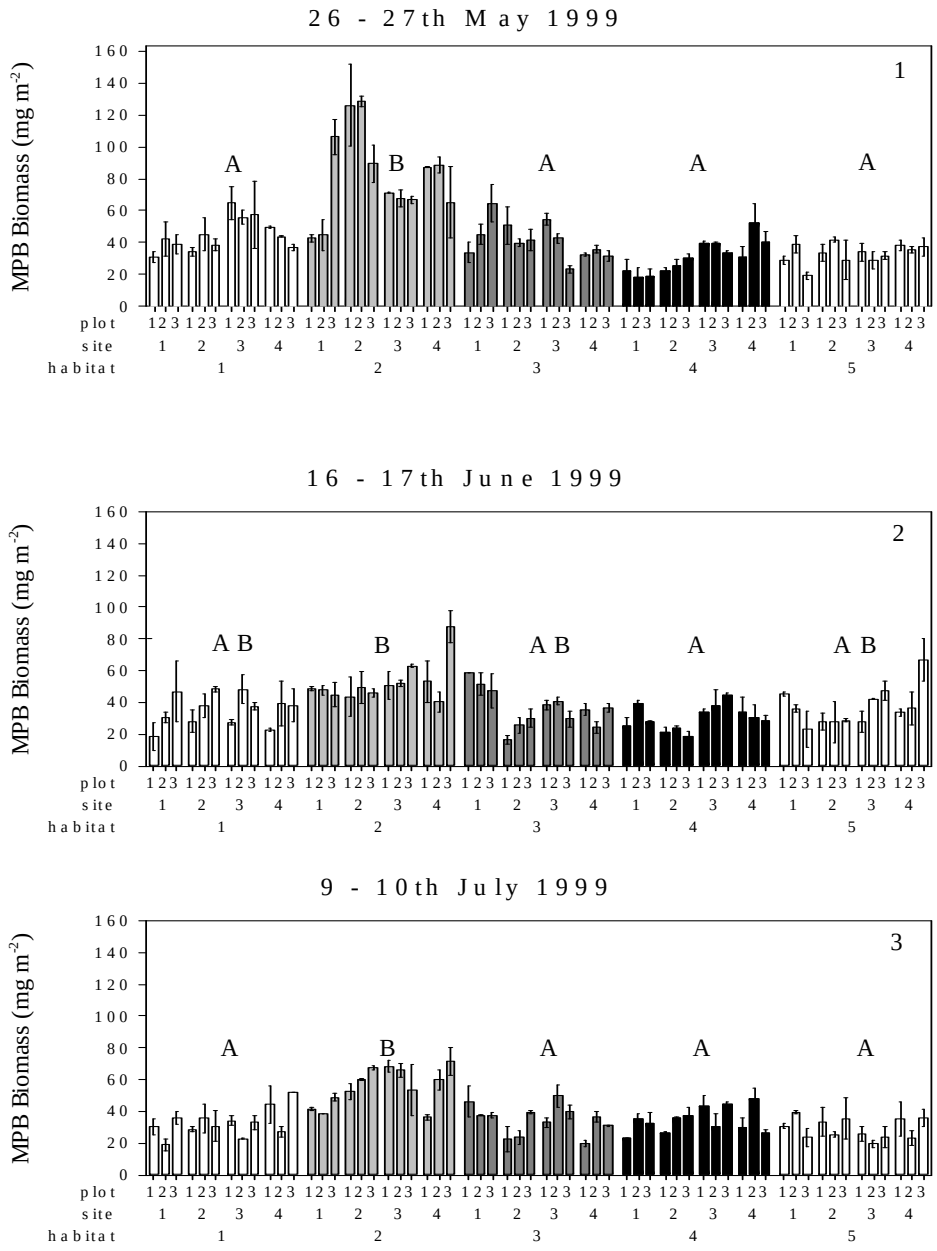

Figure 3.5. Mean (+/- 1SE) microphytobenthic biomass in each Plot for the 3 sampling dates, 1, 2, and 3. (*n*=2 replicate cores). Habitats with the same letter are not significantly different (Tukey's HSD test, α=0.05).

Table 3.6. Results of the three-factor nested ANOVA in the distribution of biomass of microphytobenthos at Date 1.

Source of Variation	df	MS	*F*	p	Sig.	Error terms
Habitat	4	0.658	10.55	0.000	***	Site (Hab)
Site (Hab)	15	0.062	3.15	0.002	**	Plot(Hab(Site))
Plot(Site(Hab))	40	0.020	1.87	0.014	*	Error
Error	60	0.011				

Data transformed to Log_{10} (x)
ns = not significant; * $p<0.05$; ** $p<0.01$; *** $p<0.001$

Table 3.7. Results of the three-factor nested ANOVA in the distribution of biomass of microphytobenthos at Date 2.

Source of Variation	df	MS	*F*	p	Sig.	Error terms
Habitat	4	0.203	3.52	0.032	*	Site (Hab)
Site (Hab)	15	0.058	2.17	0.026	*	Plot(Hab(Site))
Plot(Site(Hab))	40	0.027	1.58	0.053	ns	Error
Error	60	0.017				

Data transformed to Log_{10} (x)
ns = not significant; * $p<0.05$

Table 3.8. Results of the three-factor nested ANOVA in the distribution of biomass of microphytobenthos at Date 3.

Source of Variation	df	MS	*F*	p	Sig.	Error terms
Habitat	4	0.291	9.52	0.000	***	Site (Hab)
Site (Hab)	15	0.031	1.40	0.194	ns	Plot(Hab(Site))
Plot(Site(Hab))	40	0.022	2.08	0.005	**	Error
Error	60	0.010				

Data transformed to Log_{10} (x)
ns = not significant; * $p<0.05$; ** $p<0.01$; *** $p<0.001$

3.3.3.2. Spatio-temporal variation

Considerable spatial variation in the distribution of microphytobenthos was apparent at all spatial scales studied (Figures 3.5 to 3.7). To compare spatial variability in microphytobenthic biomass at the different scales both coefficients of variation (CV: Figures 3.6 & 3.7) and variance components (Table 3.9) were used. CV among replicate cores within plots over the three dates studied averaged 19.8% (n=180; SE = 1.14) suggesting that at the smallest spatial scale, i.e. within plots, the biomass of microphytobenthos tended towards a homogeneous distribution. However within plot CV ranged from 0 to 72.5% indicating that microphytobenthos exhibited homogenous distributions within some plots while in others the distribution was markedly patchy. Overall the CV was 47.0% (n=360), indicating a high degree of variability within the 5 habitats.

To establish the degree of variation in microphytobenthos at the different scales, the CV was plotted for each scale in each habitat for each date (Figure 3.6 a-c). In general CV increased with increasing spatial scale across all habitats, although at different degrees depending on habitat and sampling time. Most often the proportion of variation attributed to the plot scale was more than half of the total variation found within each habitat, as determined by the difference between the CV for the two respective scales. Moreover, it is apparent that the relative importance of each scale changes between habitats and dates. For example on date 1 variability at the plot and site scales at H4 are reasonably similar. However on date 3 a decrease in both the overall variability as well as small scale plot variability is apparent, although site scale variability remained relatively constant.

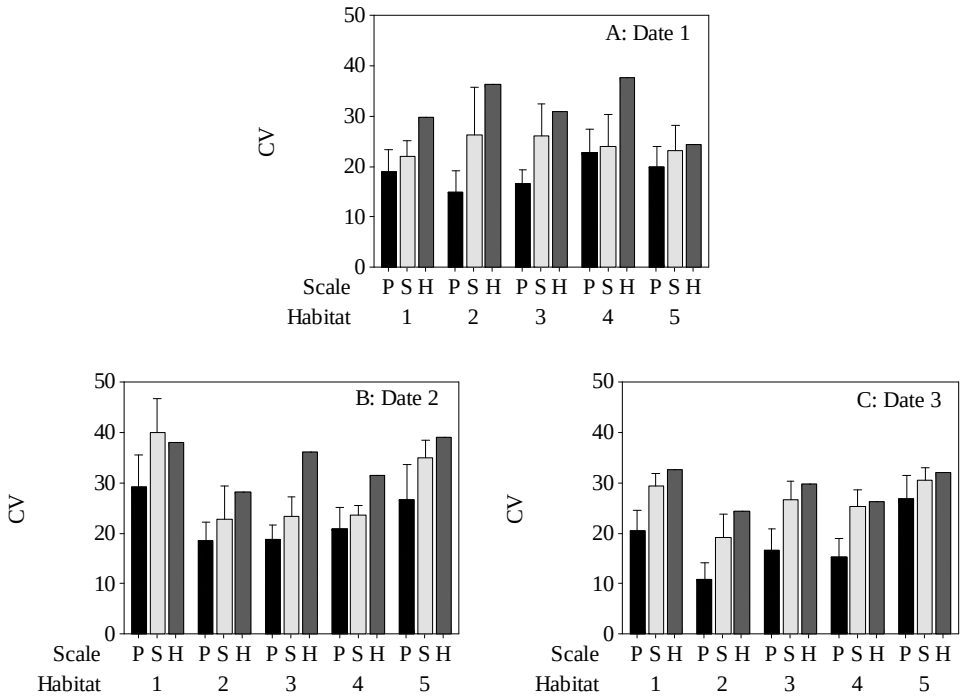

Figure 3.6. Mean coefficient of variation (+SE) in the biomass of microphytobenthos vs. scale for each habitat for the 3 sampling dates. P = plot; S = site; H = habitat. For each date and habitat mean CV is calculated from *n*=12 plots, *n*=4 sites, and *n*=1 habitat with 2, 6 and 24 replicates per scale, respectively.

To envisage the overall picture, CV was also plotted for each spatial scale pooled by date, and also by date itself for all replicates within the 3 sampling periods (Figure 3.7). A similar pattern appears with the plot scale contributing most of the variability (19.8%) towards microphytobenthic spatial variation in the five habitats. Further small increases in variability are apparent at the larger spatial scales, with contributions of 6.7- and 12.0% due to site and habitat scales, respectively. The role of temporal variability is however apparent, and contributed 23.7% more towards the overall variation in microalgal abundance than that found at the plot scale.

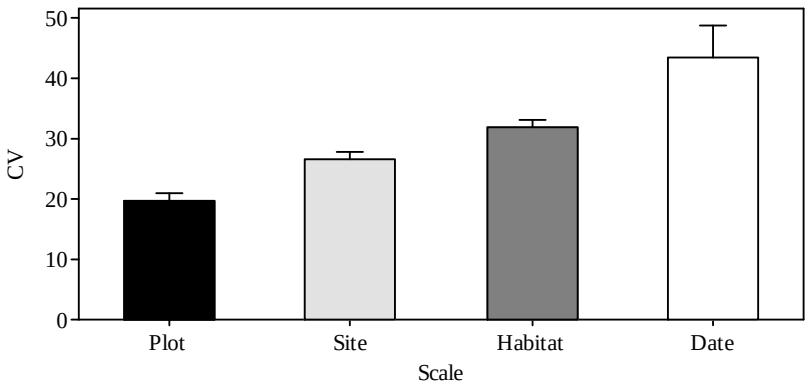

Figure 3.7. Overall pattern of variation in the biomass of microphytobenthos versus scale. Bars are mean coefficient of variation (+SE). Mean CV calculated from 180 plots (*n*=2 per plot); 60 sites (*n*=6 per site); 15 habitats (*n*=24 per habitat) and 3 dates (*n*=120 per Date).

Separate analysis of each date allows the variance components associated with the spatial scales site, plot and replicate to be partitioned. This permitted the determination of the percentage contribution of each scale to overall variation. Comparing the variance components for the 5 habitats revealed different patterns between the 3 dates (Table 3.9). Variation was highest for the smallest spatial scale, i.e. between replicates within plots, on all 3 dates. On dates 2 and 3 similar values and patterns were found and, as the spatial scale increased, the relative proportion of variation decreased. In contrast, a different pattern was found for date 1; on this date the importance of the site scale increased at the expense of the residual scale.

Table 3.9 Variance components estimates (%) of microphytobenthos. Data are derived from the mixed model nested analysis of variance using untransformed data (see Underwood, 1997).

	Date		
	1	2	3
Site	33.7	15.7	11.5
Plot	27.5	27.2	33.4
Residual	38.8	57.1	55.2

3.3.3.3. Relationship between microphytobenthos and sediment granulometry

A flaw of this research is that samples for sediment granulometry were not paired with samples for microphytobenthos. Consequently individual sediment characteristics cannot be correlated with the biomass of microphytobenthos, since beside the 'habitat' factor individual samples have nothing in common. As an alternative way of showing the relationship mean biomass of microphytobenthos was plotted against mean sediment grain size and the percentage of fines less than 125 μm for each habitat (Figure 3.8 and 3.9, respectively). These two sediment variables were chosen since they have previously been deemed to influence the distribution and biomass of microphytobenthos (Cahoon *et al.*, 1999). Nevertheless, the plots do not seem to reveal any specific relationships between these variables (Figure 3.9 and 3.10) and all correlations between the mean biomass of microphytobenthos and the mean of all sediment granulometry parameters at each habitat were insignificant (Pearson correlation coefficient, $p>0.05$, $n=5$).

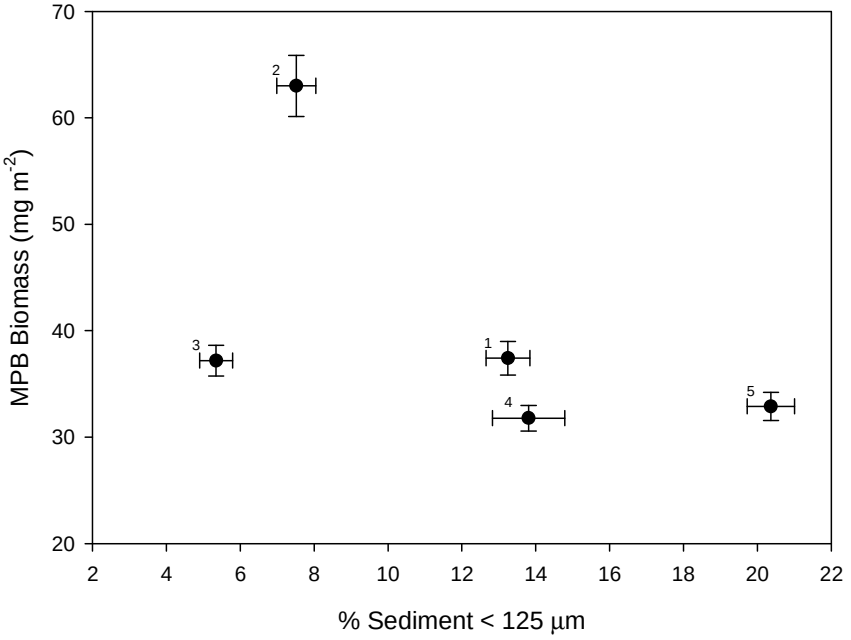

Figure 3.8. Relationship between mean biomass of microphytobenthos (*n*=72) and the proportion of sediments < 125 µm in grain size (*n*=24) at the 5 habitats.

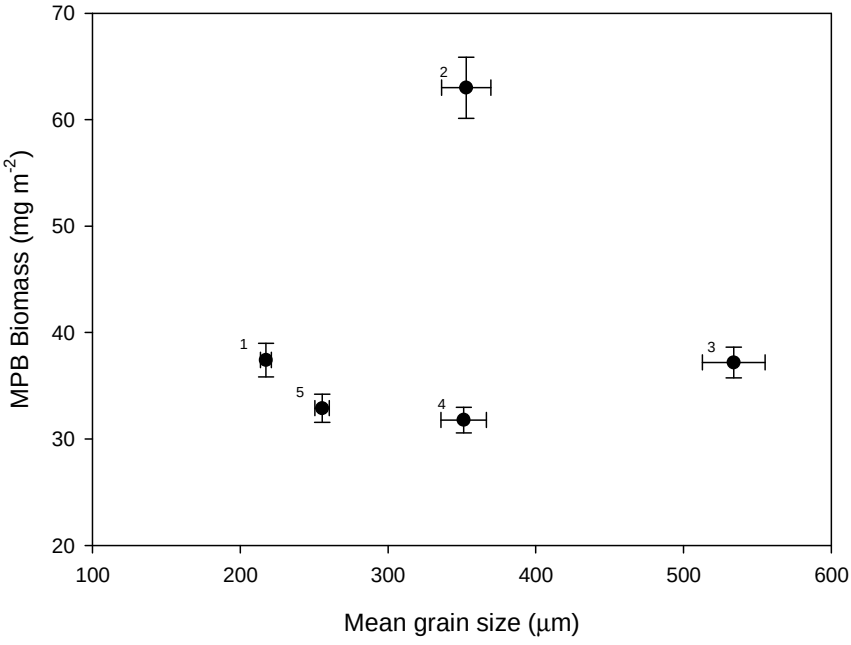

Figure 3.9. Relationship between mean biomass of microphytobenthos (*n*=72) and average mean grain size (*n*=24) at the 5 habitats.

3.4. Discussion

This study provides the first detailed description of the sediment granulometry and microphytobenthos within the shallow west lagoon at Discovery Bay and will enable comparison with other shallow tropical lagoon habitats.

3.4.1. Sediment granulometry

The results of this study confirmed that there were significant differences in sediment properties between the five visually discernible habitats within the shallow west lagoon. These habitats, which were chosen to represent contrasting bottom-types, were effectively separated into discrete habitats by the abiotic multivariate sediment plots. A considerable degree of variability in sediment properties within and between each habitat was confirmed by both uni- and multivariate plots, reflecting the many factors which govern the types and characteristics of deposits found, such as wave action, current velocity, roughness of the sediment, bioturbation and prevalence of conditions suitable for sedimentation (Gray, 1981).

As in most shallow water ecosystems, the sediments within coral reef lagoons are dynamic, heterogeneous habitats characterised by physicochemical conditions which vary over many spatial and temporal scales (Dudley, 2003). Based on the granulometry statistics, it is apparent that the habitats surveyed differ with respect to hydrodynamical conditions. While habitat 1 is shielded from wave exposure and exhibits moderately sorted fine sediments with low heterogeneity characteristic of a homogeneous and relatively stable environment, habitat 2 experiences an increase in current velocity reflected in a significant increase in mean particle size. The further increase in particle size and percentage of gravel at habitat 3 likely reflects both the

turbulent conditions and current surge that this habitat often experiences on a regular basis, due to swells from the offshore sea that pass over the reef crest into this area. This habitat is also located nearest the spur and groove forereef formations, where shallow thickets of the corals *Acropora cervicornis* and *A. palmata* once predominated. The effects of historical storm damage and consequent breakages and disintegration of detached forereef coral branches have undoubtedly left a sedimentary footprint here. When coring it was apparent that a shallow layer of coarse sand overlay a layer of larger coral fragments at deeper sediment depths. Compared to habitats 1, 2 and 3, the thalassinid habitats 4 and 5 which are situated in the more quiescent and depositional regions of the shallow western lagoon, exhibit an increase in the proportion of silt and clay, and generally have smaller particle sizes.

3.4.2. Distribution and biomass of microphytobenthos

The measured values of microphytobenthos found in this study ranged from 9- to 152 mg Chl *a* m^{-2}. These values are similar to the values recorded by Bunt *et al.* (1972) in the only other study conducted on the microphytobenthos at Discovery Bay (17- to 75 mg Chl *a* m^{-2}). This study was, however, conducted at deeper depths presumably around the main bay. The higher values recorded in the present study may partly be explained by the shallower habitat depths than in the study by Bunt *et al*. (1972), presumably resulting in an increase in light intensity at the benthos. Values reported here correspond well with the range of values recorded from many other similar tropical lagoon environments (e.g. Hansen *et al.*, 1987; Boucher and Clavier, 1990; Dizon *et al.*, 1994; Garrigue, 1998; Clavier *et al.*, 2008; Werner *et al.*, 2008). Maximum values were higher, however, than those recorded at Suva Lagoon in Fiji which ranged from 15 to 36 mg Chl *a* m^{-2} (Underwood, 2002), yet an order of

magnitude lower than the maximal values reported from the Great Barrier Reef which ranged between 23- and 1153 mg Chl *a* m^{-2} and are some of the highest values ever recorded from marine sediments (Roelfsema *et al.*, 2002).

In the present study highest values of microphytobenthos were consistently recorded in grey sands at habitat 2 over all three dates studied. This is consistent with the study by Boucher and Clavier (1990) which assessed microalgal biomass in white, grey and muddy sediments in the New-Caledonia lagoon and found grey and muddy sediments to support significantly higher biomasses of microphytobenthos than white sediments. In contrast, Clavier and Garrigue (1999) found no significant difference between grey and white sand bottoms in the south-west lagoon at New Caledonia, albeit grey sand bottoms were approximately 6 m deeper than white sand bottoms and presumably less illuminated which may partially explain the discrepancy since increases in water depth generally result in a decreased light intensity at the benthos (Light and Beardall, 1998). At Heron Reef in Australia Werner *et al.* (2008) found that sediment chlorophyll *a* content was lower at a deeper (5 m) station than at two nearby shallow (0.5 – 1 m) stations, although in the present study no significant differences were detected between the deeper H5 and the shallower H4 habitat.

In an attempt to explain the observed biomass of microphytobenthos among habitats one must consider possible factors that might have an influencing effect. As noted by Cahoon and Safi (2002) several factors interact to cause observed patterns in microphytobenthic biomass, including substrate characteristics, light intensity, physical disturbance, grazing and nutrient availability. Although some studies have found that coarse sands within CREs generally support higher microphytobenthic

biomasses (e.g. Johnstone *et al.*, 1990; Garrigue, 1998; Jones *et al.*, 1999), others have found the opposite (Underwood, 2002). With four out of the five habitats situated at the same water depth (i.e. habitats 1 to 4) it was assumed that light intensity at the benthos among these habitats would be roughly equal. Since habitat 5 was almost twice the depth of the other habitats it was hypothesised *apriori* that the biomass of microphytobenthos here would be lower than that found at habitat 4 located in close proximity. Surprisingly no significant difference was detected between habitats 4 and 5 suggesting the influence of other interacting factors. For example, the presence of subterranean freshwater springs and seeps in the vicinity of habitat 5, which supply nitrogen-rich groundwater to the system (D'Elia *et al.*, 1981; Greenaway and Gordon-Smith, 2006) may partly explain this discrepancy. While light availability is a key factor influencing microalgal production and biomass, it may not be the limiting factor in tropical clear-water sediment systems (Dizon and Yap, 2003) where nutrient supply is probably more important (Sorokin, 1981). Experiments by Dizon and Yap (1999) showed that coral reef sediments exposed to elevated levels of nitrate exhibited a rapid increase in chlorophyll *a* content, consistent with observations by Uthicke and Klumpp (1997) and Heil *et al.* (2004) which suggest that benthic microalgal biomass in tropical environments is nutrient limited. Thus the supply of nutrients in the vicinity of H5 may have positively enhanced biomass values of microphytobenthos, negating a possible decrease in biomass due to the lowered light levels at this deeper habitat. Hence the inability to detect a significant difference in microphytobenthic biomass between the shallow H4 habitat and the deeper nearby H5 habitat.

At Discovery Bay, nutrient concentrations away from ground water sources are generally low (0.2 to 1 µM nitrate, 0.02 to 0.04 µM phosphorous, and 0.02 to 0.04 µM ammonium (Greenaway and Gordon-Smith, 2006). In contrast, in shallow-water tropical marine sediments, pore water nutrient concentrations (50-100 µM DIN) can be over two orders of magnitude higher than in overlying seawater (Stimson and Larned, 2000). Microphytobenthos therefore obtain a large proportion of their nutrients from sediment sources rather than from the water column (Miyajima *et al.*, 2001). However in certain areas of the bay integrated water column nitrate values are enhanced (~1.4 to 1.9 µM, stations 7 to 10 in Webber *et al.*, 2005).

In order to account for the consistently elevated levels of microphytobenthos at habitat 2, some theories are presented. Firstly, the biomass of microphytobenthos at H2 is enhanced due to periodic upwelling of nutrient rich water which subsequently passes over this habitat. During the daytime water flow was almost exclusively in a north westerly direction perpendicular to the H2 transect. This is due to the summer north easterly trade winds creating a slow clockwise surface current within the bay (pers. obs., Gayle and Woodley, 2004). Water then travels towards the north west area of the shallow lagoon before finally exiting over the western reef crest (pers. obs., Gayle and Woodley, 2004). My own observations whilst diving suggest that the deep main bay acts as a sink for the deposition of detritus. On the forereefs communities have shifted from being coral-dominated to being dominated by macroalgae. In times of stormy weather a significant amount of macroalgal fragments and whole fronds are detached from the reef and transported into the bay (J. Woodley, former Director, D.B.M.L, pers. comm., and own observations). Much of this detritus settles out on to the benthos in the deeper main bay. Subsequent decomposition would release

nutrients into a body of water whose direction of travel would initially be over the shallow sediments at H2, due to the daily prevailing current direction. Integrated water column nutrient values determined by Webber *et al.* (2005) suggest that stations in the deeper westerly portion of the bay are richer in nitrate than stations in the eastern half of the bay or seaward of the shipping channel. These authors suggest that nutrient sources possibly arise from a lack of proper sewage treatment systems and the wide-spread use of soak-away pits by the local community and workers at a nearby bauxite loading port. However Webber *et al.* (2005) did not mention the possible influence of internal nutrient loading arising from *in situ* decomposition within the deeper bay. The findings of Webber *et al.* (2005) would tend to support the theory that the deep bay acts as a source of nutrients. It therefore seems feasible that the increase in biomass of microphytobenthos at H2 could be caused by the passage of nutrient rich water over this habitat, since H2 is located close to the drop-off into the main bay.

The second possible theory, is that the release of nutrients from sediments disturbed by the spatangoid heart urchin, *Meoma ventricosa* (Lamarck), supports enhanced production and biomass of microphytobenthos. *M. ventricosa* is a large surface-burrowing grazer / deposit feeder and was found in abundance only at habitat 2 (pers. obs.). Spatangoid echinoids are key bioturbators in unconsolidated marine sediments, and due to their burrowing activities increase the seawater-sediment exchange area, the transport of oxygen into sediments, and alter nutrient fluxes thereby improving conditions for production by microphytobenthos (Lohrer *et al.*, 2004, 2005; Vopel *et al.*, 2007). In experiments by Lohrer *et al.* (2004), which examined the effects of spatangoid urchins on sediment biogeochemistry in *in situ* chambers and at different

densities, there was a significant positive relationship between urchin density and primary production. Although no increase in chlorophyll *a* content in the surface sediments was found, these authors remark that grazing and bioturbation would tend to remove and subduct microphytobenthos from surficial sediment, thus negating any increase in microphytes driven by the increase in nutrient availability/quality. Excretion of ammonium by *M. ventricosa* would also supply microphytobenthos with a source of nutrients. Ammonium is an animal excretory by-product, and studies have shown that the productivity and biomass of microphytobenthos inhabiting coral reef sediments is enhanced by the release of ammonium from holothurians (Uthicke and Klumpp, 1997, 1998; Uthicke, 2001). It is possible, therefore, that excretion of ammonium by heart urchins would have a similar effect on the microphytobenthic community.

Within coral reef sediments excretion rates by meiofauna may be as high as 17.3 mg $N\ m^{-2}\ h^{-1}$ (Gray, 1985). As the proceeding chapter in this thesis has shown, the highest abundances of meiofauna were found in sediments at habitat 2. An important characteristic of CREs is the close coupling between benthic producers and consumers, with nutrients being tightly recycled within the benthos (Uthicke and Klumpp, 1998; Uthicke, 2001), due to being situated in oligotrophic waters. While meiofaunal grazing can control microalgal biomass under certain conditions (e.g. Sundbäck *et al.*, 1996; Carman *et al.*, 2000), the high biomass of microphytobenthos at habitat 2 could also be partly sustained by the close coupling between meiofauna and their food resources. Consumption of microphytobenthos by meiofauna, in particular by copepods and other crustacean herbivores, will lead to the production of

faeces and excretory by-products which, if retained within the sediments, could help to support production of new microphyte biomass.

Excluding habitat 2, no difference in microphytobenthic biomass was detected among the remaining habitats on any of the three dates, even though many sediment properties were found to differ between habitats. While several studies have found relationships, both positive and negative, between sediment grain size and benthic microalgal biomass (see Cahoon, 1999; Cahoon *et al.*, 1999; Underwood and Kromkamp, 1999), in this study, which encompassed habitats with sediments ranging from fine to coarse sands, no relationships were detected. Unfortunately, since replicates were not paired with one another, which was a flaw in the design of this study, correlations cannot be made between the full set of 120 abiotic sediment and the biotic microphytobenthic samples (see Chapman and Tolhurst, 2004). Therefore correlations of mean values for each habitat were made, yet none of the results were significant. Likewise, visual analysis of plots of mean grain size and proportion of fines against the complete set of microphytobenthos samples from all 3 dates did not reveal any relationships.

3.4.3. Spatial and temporal variation in microphytobenthos

In recent years the study of spatial and temporal variability in marine benthic populations and assemblages has received increasing amounts of attention (Ellis and Schneider, 2008, and references therein). It is now widely acknowledged that variability in soft-sediment communities is scale-dependent (Thrush, 1991; Azovsky, 2000), and therefore the change in abundance and/or composition of benthic assemblages may vary among times of sampling and/or from one place to another

(e.g. Norén and Lindegarth, 2005; Chapman and Underwood, 2008; Smale, 2008). In soft-sediments the biomass of microphytobenthos is well known to be patchy at a range of spatial and temporal scales (MacIntyre *et al.*, 1996), ranging from centimetres to kilometres, and from minutes to years, respectively (Azovsky *et al.*, 2004; Jesus *et al.*, 2005; Koh *et al.*, 2007; Pinckney and Lee, 2008). The causes of patchiness are many-fold. At small spatial scales biotic interactions may promote benthic microalgal patchiness. Grazing by copepods, for example, may deplete the biomass of microphytobenthos (Sundbäck *et al.*, 1996), while bioturbation can transport microalgae to deeper sediment layers. At larger spatial scales abiotic factors such as nutrient concentrations may be more important, although the release of nutrients from disturbed sediment by bioturbation (e.g. Lohrer *et al.*, 2004) may enhance microalgal production increasing variability at small spatial (and temporal) scales.

In this study, analysis of each individual date revealed significant variability in the biomass of microphytobenthos at the plot and site scales, and differences in mean biomass between habitats (see Bennington and Thayne, 1994). Considerable spatial variability among replicate samples within 0.25 m^2 plots was found, with CVs ranging from 0 to 72 %. This confirmed the patchy distribution of microphytobenthos within the study habitats, consistent with the findings of Garrigue (1998) for the tropical lagoon at New Caledonia, where CVs ranged from 8 to 92%. Nevertheless, average variability at the plot scale was generally low (19.8%), similar to the values recorded in a temperate sandy bay in Sweden of 12 to 13% by Sundbäck (1984) at the same spatial scale.

Comparing CV between spatial scales revealed a trend of increasing variability with increasing spatial scale, as has previously been noted by other authors (for example Sundbäck, 1984; Light and Beardall, 1998; Ni Longphuirt *et al.*, 2007). Yet on each date the CV at the plot scale was usually at least half of the total variability measured at the habitat scale, if not more, highlighting the predominance of small scale variation within the surveyed habitats. When comparing CV at specific scales across the different habitats and dates, it is apparent that variability is both spatially and temporally variable, thus changes in the biomass of microphytobenthos biomass differ among places from one time to another and at different magnitudes depending on scale. This interactive variability is a feature of soft-sediment habitats (Norén and Lindegarth, 2005), and was prevalent in this study as evidenced by the significant interaction between dates and plots. Considering the many factors that influence the abundance of benthic microalgae are themselves spatially and temporally variable, this result is not surprising.

At the scales of site and habitat, no significant temporal effect on microphytobenthic biomass was detected. However the coefficient of variation for each date ranged from 38 to 54 % indicating a reasonably high degree of temporal variability. It is of course possible that significant temporal variation in biomass occurred between the sampling dates approximately 3 weeks apart, yet was masked due to the lack of temporal replication at shorter time scales (e.g. Morrisey *et al.*, 1992b). Any future studies to assess temporal variations in the microphytobenthos in this system should therefore bear this in mind, and use a suitable sampling design to detect the scales of temporal variability.

3.5. Summary

This is the most comprehensive study on the microphytobenthos ever conducted at Discovery Bay. The data presented here show that while the characteristics of unconsolidated sediments differed markedly between the five separate habitats, the biomass of microphytobenthos was relatively homogeneous at this scale. Nevertheless, significant variability was observed within habitats, underling the need to use sampling designs that account for small scale variation. At habitat 2 consistently elevated levels of microphytobenthos were found, and it is hypothesised that this is due to upwelling of nutrient rich water from the deeper bay near to H2, as well as release of nutrients due to sediment disturbances by burrowing heart urchins. Furthermore, excretion of ammonium by these deposit feeders would also tend to increase the productivity and/or biomass of benthic microalgae.

4. DISTRIBUTION AND ABUNDANCE OF MEIOBENTHOS

4.1. Introduction

On average, marine soft-sediments contain 10^6 meiofauna per m^{-2} (Coull, 1988; Coull, 1999). Like the microphytobenthos (Chapter 3), the occurrence and abundance of meiofauna in marine soft-sediments is patchy (see reviews by Hicks and Coull, 1983; Heip *et al.*, 1985; Higgins and Thiel, 1988; Giere, 1993). Patchiness in meiofaunal populations and communities, i.e. the deviation in space from randomness in the direction of *aggregation* rather than *regularity* (see Diggle, 1983), exists at a range of spatial and temporal scales (Findlay, 1982; Phillips and Fleeger, 1985; Li *et al.*, 1997) and is caused by abiotic and biotic variables and interactions between them. Abiotic variables, such as salinity (Horn, 1978; Warwick, 1971), water motion (Palmer and Malloy, 1986; Gamenick and Giere, 1994), and sediment characteristics (Alongi, 1986; Ndaro and Ólafsson, 1999), as well as biotic variables including food quality and quantity (Decho and Castenholz, 1986; Decho and Fleeger, 1988; Blanchard, 1990; Pinckney and Sandulli, 1990), predation (Aarnio *et al.*, 1998; Danovaro *et al.*, 2007), dispersal (Bell and Sherman, 1980; Palmer, 1988; Armonies, 1994), biogenic structures (Warwick *et al.*, 1986; De Troch *et al.*, 2001; Gheerardyn *et al.*, 2008) and bioturbation (Branch and Pringle, 1987; Dittmann, 1996) are thought to regulate the distribution and abundance of benthic meiofauna.

Marine soft-sediment habitats are, however, complex systems. They exhibit several scales of temporal, spatial, and interactive variability in fauna, flora and sediment physico-chemical properties (Snelgrove and Butman, 1994; Norén and Lindegarth, 2005; Chapman and Tolhurst, 2007). At the microscopic level, benthic microalgae

and meiofaunal communities vary at short time scales and over small distances (Sandulli and Pinckney, 1999; Azovsky *et al.*, 2004). At the macroscopic level, seagrass beds and thalassinid shrimp ranges are generally more persistent in time and space unless subject to disturbance (Aller and Dodge, 1974; Hemminga and Duarte, 2000). Within a relatively small area (<0.25 km^2) in the shallow western lagoon at Discovery Bay several different habitats were observed, between which sediment granulometry and the degree of bioturbation varied (Chapter 3 this thesis; Aller and Dodge, 1974). While the distribution of macrofauna in this area has previously been documented (Aller and Dodge, 1974), there have been no studies on the infauna in for over 30 years and next to nothing is known about the meiofauna in this system (c.f. Gamenick and Giere, 1994).

Although macrofauna have most often been used to assess environmental change in marine benthos, it is widely acknowledged that the use of meiofauna has a number of distinct advantages (e.g. Moore and Bett, 1989; Kennedy and Jacoby, 1999; Somerfield *et al.*, 1995; Schratzberger *et al.*, 2001). Unlike the majority of macrofaunal species which have a planktonic life-stage, meiofauna are intrinsically tied to the sediment, exhibit direct benthic recruitment, have short generation times, are small in size, high in abundance, and exhibit asynchronous development (Higgins and Thiel, 1988; Coull and Chandler, 1992). This makes them suitable indicators of environmental change and benthic disturbance (Kennedy and Jacoby, 1999).

In recent decades the human population at Discovery Bay in Jamaica has increased several-fold (STATIN, cited by Greenaway and Gordon-Smith, 2006) and fish populations have been severely affected. During this time the local coral reefs have

undergone a phase-shift from coral- to algal-dominated communities, in part due to the release from grazing by herbivorous fish, but also due to the mass-mortality of *D. antillarum* as mentioned in Chapter 1. There has also been much debate on the relative importance of nutrient enrichment to the bay, and its effects on macroalgal growth and contribution to the phase-shift (e.g. Lapointe, 1997, 1999; Hughes *et al.*, 1999; Szmant, 2002). While there is no active terrigeneous sediment input into the bay from fluvial sources (Perry *et al.*, 2006), certain parts of the bay have been subject to inputs of iron-rich bauxite sediment from a local mining and shipping terminal for over 40 years (Perry *et al.*, 2006; Taylor *et al.*, 2007). Bauxite levels in the sediments within the marine reserve in the north west corner of the bay where this study took place are, however, below those reported to be toxic for biota (see Perry and Taylor, 2004).

As a first step to understanding the ecology of soft-sediment systems, knowledge of the patterns in the abundance and distribution of meiofauna is a valuable biological tool enabling environmental change to be detected and monitored (Gray, 1981; Coull and Chandler, 1992). Quantitative descriptions of patterns in organism distributions consequently help to identify processes structuring assemblages, while sampling designs which account for patchiness over a range of spatial scales, such as nested hierarchical sampling designs, enable unconfounded comparisons to be made among sampling sites (Morrisey *et al.*, 1992a; Underwood, 1997). Unfortunately, however, it is common for investigators comparing meiofaunal populations and communities between one place and another to take only a few samples at each sampling site (for example Guzmán *et al.*, 1987; Gomez Noguera and Hendrickx, 1997), and

appropriate experimental designs are not always employed (Li *et al.*, 1997; Fraschetti *et al.*, 2006).

The aim of this research is to examine, compare and contrast the meiofauna communities from the five selected habitats within the shallow western lagoon, using a sampling design which accounts for patchiness at a range of spatial scales.

4.2. Methods

4.2.1. Sample collection

One hundred and twenty sediment cores for the analysis of meiofauna were obtained on the 15th of June 1999, according to the nested hierarchical sampling design detailed in Chapter 2. Cores were taken to a depth of 5 cm using a 2.6 cm inner diameter syringe with the Luer end cut off and a rubber bung cap. In the laboratory, samples were transferred into plastic containers and a few drops of 4% formalin-buffered seawater were added whilst gently shaking the container. This step was taken in order to narcotize the meiofauna as slowly as possible in order to minimise any body shape distortion. Over a period of a few hours more drops were added until the containers were finally full. The 4% formalin solution was made from seawater which had been filtered through Whatman GF-F filter paper to exclude phytoplankton or any other microscopic pelagic organisms, and subsequently buffered with sodium tetraborate to a pH of 8.2. To help distinguish meiofauna during the sorting process a small amount of Rose Bengal was added to the fixative solution.

4.2.2. Sample processing

Sediment samples were washed through 500 and 63 μm mesh sieves. Organisms residing in the mixture retained on the 63 μm mesh sieve were then extracted from the sediment using the Ludox centrifugation method described by Burgess (2001). This is an isopycnic density separation method which relies on the difference in density between meiofauna and sediment to effect separation using Ludox, a colloidal silica gel, and has been shown to have an average extraction efficiency of 96.8 +/- 3.9 % over a range of sediment sizes from sand to silt-clay (Burgess, 2001). After extraction meiofaunal organisms were transferred to 70 % ethanol for storage before being counted and sorted to major taxa under a Nikon SMZ 1000 stereo microscope.

4.2.3. Statistical analysis

Three-way mixed model nested ANOVA was used to examine the null hypotheses that there was a) no significant difference in mean total meiofaunal density between habitats; b) no significant difference in mean density of individual taxa between habitats; c) no variability in the density of individual taxa between sites nested within habitats; and d), no variability in the density of individual taxa between plots nested within sites (see Bennington and Thayne, 1994). Data were either Log (x +1) or $(x + 1)^{0.5}$ transformed to satisfy parametric statistical assumptions. Meiofaunal communities were also analysed by multivariate methods using fourth root transformed data since certain taxa (such as nematodes) were consistently more abundant than others (Clarke and Warwick, 2001). This transformation reduces the effect of extremely abundant taxa whilst increasing the influence of less abundant taxa on the MDS ordination.

4.3. Results

4.3.1. Meiofaunal taxa

A total of 22 meiobenthic higher taxa were identified comprising 101,167 specimens. Of these, 7 taxa (nematodes, copepods, turbellarians, copepod nauplii, polychaetes, oligochaetes and ostracods) contributed more than 1% towards the total number of individuals and collectively accounted for 93% of all specimens (Figure 4.1; Table 4.1). In this research these taxa will be collectively referred to as 'common taxa'. Nematodes and copepods accounted for 81% of total meiofauna. Nematodes dominated all samples in all habitats with relative densities ranging from 52% at H3 to 69% at H2 (Figure 4.1). Copepods were the second most dominant taxon with relative densities ranging between 13% at H5 to 23% at H3 (Figure 4.1). Total meiofauna abundance ranged from 327.7 to 5518.9 individuals 10 cm^{-2} (Figures 4.2 – 4.4). Other taxa included, with total numbers found in the complete set of samples in parentheses: nemerteans (622), kinorynchs (387), gastropods (195), acari (155), bivalves (121), cumaceans (94), chironomids (77), priapulids (77), tanaids (62), cnidarians (37), amphipods (19), echinoderms (19), tardigrades (9), isopods (5), gnathostomulids (4) and sipunculids (3).

Excluding the oligochaetes, mean total abundance and mean abundance of individual common taxonomic groups varied significantly between habitats (Figures 4.2 to 4.4; Table 4.2 & 4.3). Mean total abundance and mean nematode abundance were both highest at H2, in the grey-coloured medium sands which contained the highest biomass of microphytobenthos (see Chapter 3), and lowest at H3 in the coarse sands behind the reef-crest subject to wave disturbance. Mean copepod and nauplii abundance were also highest at H2 but lowest in the medium-fine sands at H5, the

deep thalassinid habitat subject to intense bioturbation. The mean abundance of turbellarians was highest in the relatively undisturbed fine sands at H1, whereas lowest abundance also occurred in the coarse sands at H3. Mean polychaete abundance was lowest at H1 than at any of the other habitats. Mean ostracod abundance was highest at H3, and lowest in the medium-fine sands at H5.

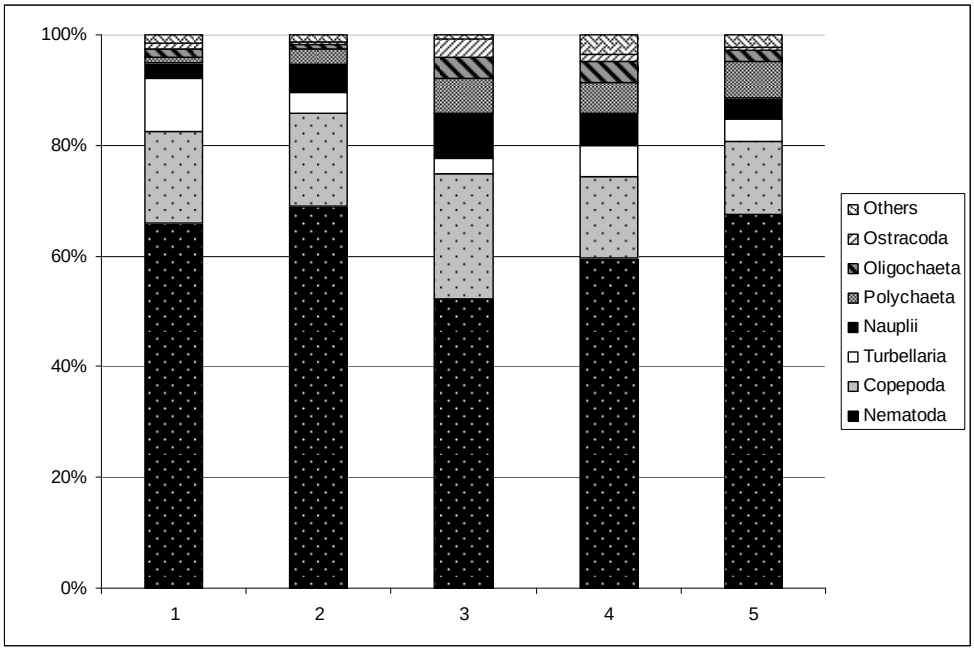

Figure 4.1. Relative abundance of meiofaunal taxa contributing more than 1% (i.e. common taxa) towards total abundance from the five habitats. Taxa contributing less than 1% to total abundance have been pooled into 'Others'.

Table 4.1 Mean density (individuals 10 cm^{-2}) and standard deviation (in parenthesis; *n*=24) of meiofaunal taxa from the five habitats, ranked in order of percentage of total meiofauna.

Taxa	H1	H2	H3	H4	H5	%
Total	1734 (718)	2333 (1043)	1056 (386)	1506 (523)	1311 (521)	
Nematoda	1146 (541)	1610 (883)	552 (237)	897 (351)	886 (366)	64.1
Copepoda	285 (84)	391 (172)	238 (121)	223 (106)	173 (75)	16.5
Turbellaria	166 (96)	88 (59)	30 (43)	83 (50)	52 (30)	5.3
Nauplii	49 (35)	123 (64)	87 (44)	89 (55)	50 (37)	5.0
Polychaeta	19 (14)	65 (49)	67 (47)	84 (52)	87 (79)	4.1
Oligochaeta	24 (20)	13 (18)	38 (69)	56 (58)	26 (32)	2.0
Ostracoda	19 (18)	13 (8)	37 (26)	21 (17)	8 (6)	1.2
Others	27 (22)	30 (27)	7 (6)	53 (38)	30 (15)	1.9

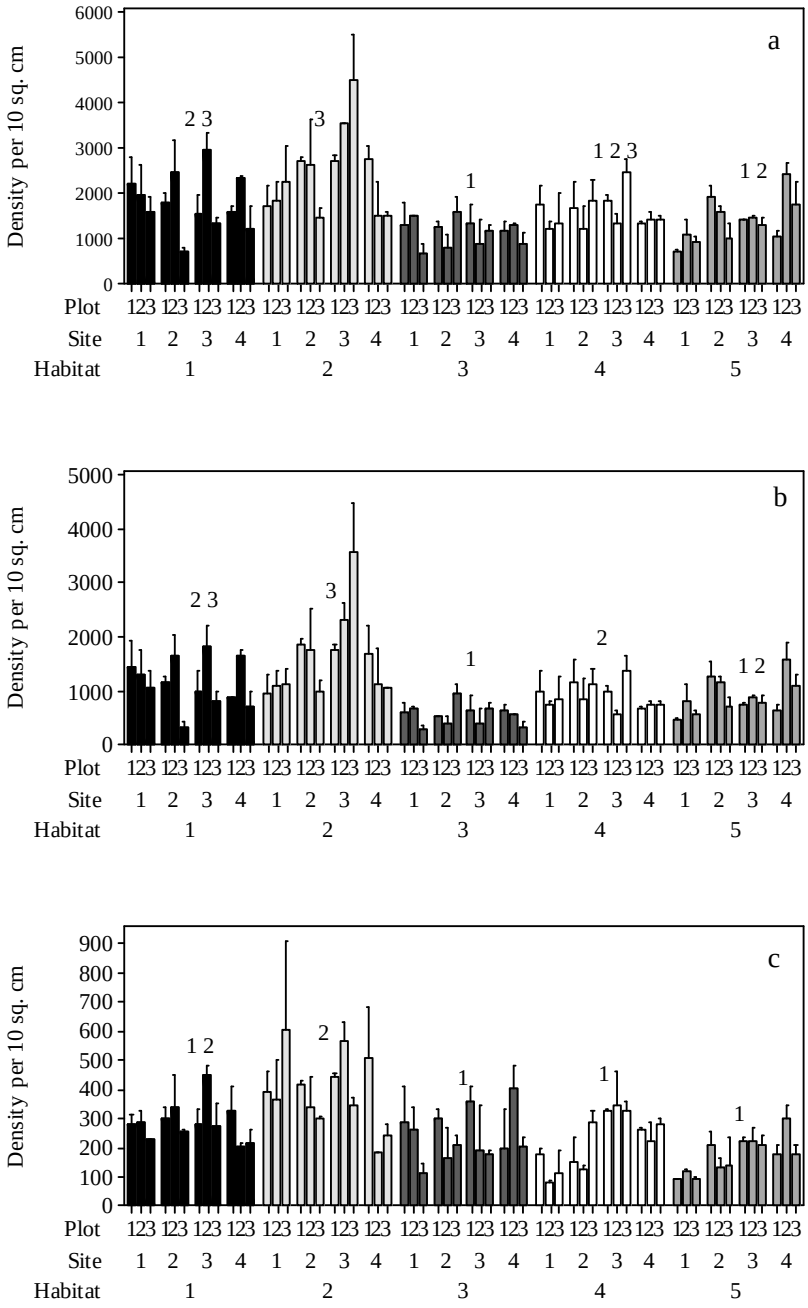

Figure 4.2. Mean density of (a) total meiofauna; (b) nematoda; and (c) copepoda. (*n*=2, +1SE). Habitats with the same number above the bars are not significantly different from one another (Tukey HSD, α=0.05, after data transformations as per Table 4.2).

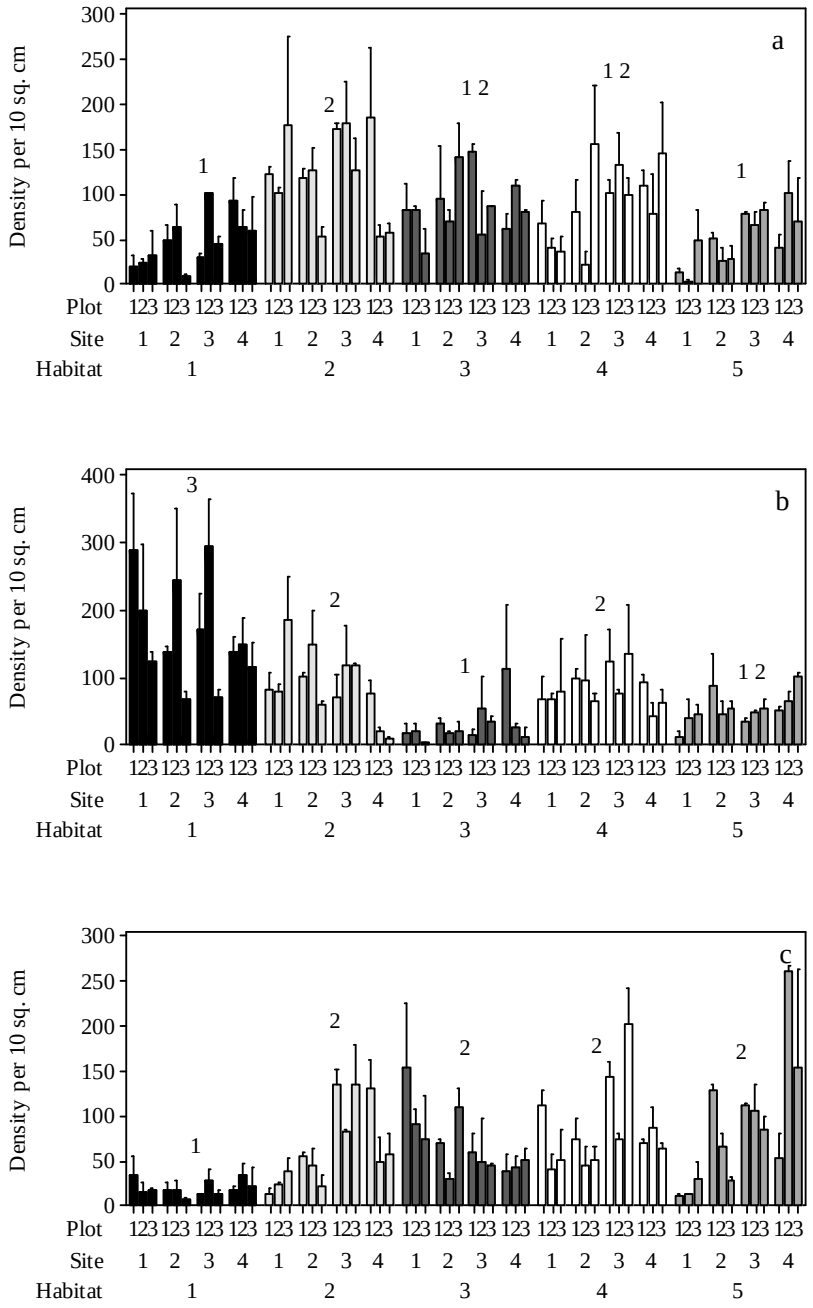

Figure 4.3. Mean density of (a) copepoda nauplii; (b) turbellaria; and (c) polychaeta. (*n*=2, +1SE). Habitats with the same number above the bars are not significantly different from one another (Tukey HSD, α=0.05, after data transformations as per Table 4.2).

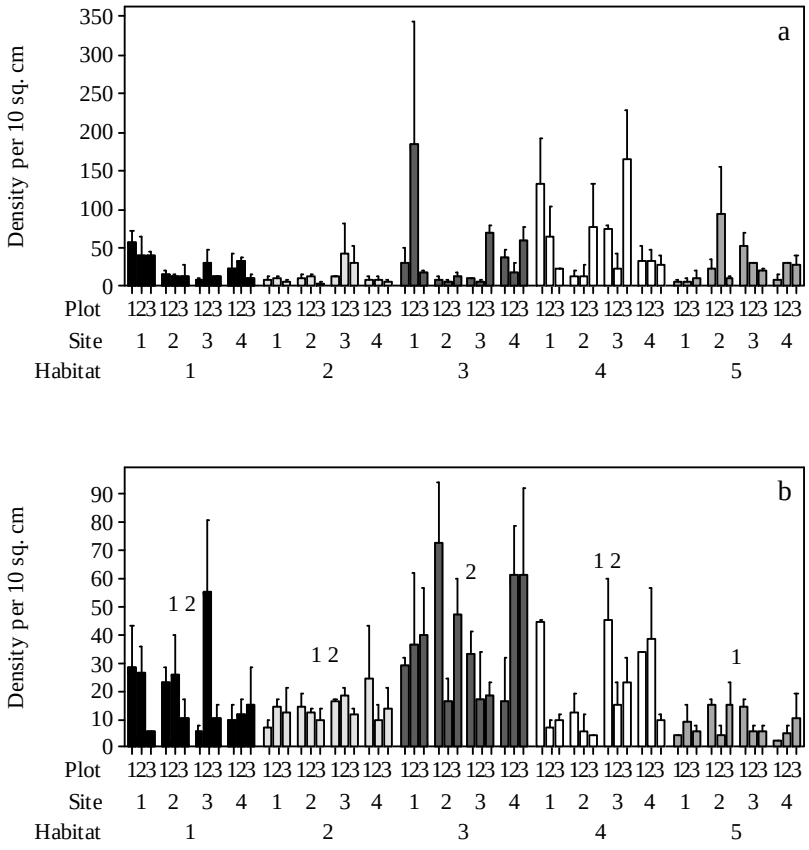

Figure 4.4. Mean density of (a); oligochaeta and (b) ostracoda (*n*=2, +1SE). Habitats with the same number above the bars are not significantly different from one another (Tukey HSD, α=0.05, data transformations as per Table 4.2). Note Tukey *post-hoc* test not carried out for the oligochaeta since ANOVA result not significant at Habitat level.

Table 4.2. Results of the three-factor nested ANOVAs examining the total number of individuals and selected taxa contributing more than 1% to total abundance.

	Total Abundance[1]				Nematodes[1]			
Source of Variation	df	Mean Sq.	F	*P*	df	Mean Sq.	F	*P*
Habitat H	4	0.335	7.150	0.002 **	4	0.646	10.84	0.000 ***
Site S(H)	15	0.047	1.150	0.350 ns	15	0.060	1.05	0.426 ns
Plot (S(H))	40	0.041	1.650	0.039 *	40	0.057	1.77	0.022 *
Residual	60	0.025			60			

	Copepods[2]				Copepod Nauplii[2]			
Source of Variation	df	Mean Sq.	F	*P*	df	Mean Sq.	F	*P*
Habitat H	4	148.885	5.99	0.004 **	4	77.974	4.97	0.009 **
Site S(H)	15	24.853	2.06	0.035 *	15	15.688	1.85	0.062 ns
Plot (S(H))	40	12.090	1.15	0.304 ns	40	8.492	1.57	0.055 ns
Residual	60	10.485			60	5.404		

	Turbellarians[2]				Polychaetes[1]			
Source of Variation	df	Mean Sq.	F	*P*	df	Mean Sq.	F	*P*
Habitat H	4	192.541	15.09	0.000 ***	4	1.556	4.02	0.021 *
Site S(H)	15	12.756	1.43	0.181 ns	15	0.387	3.85	0.000 ***
Plot (S(H))	40	8.929	1.22	0.245 ns	40	0.101	1.13	0.327 ns
Residual	60	7.327			60	0.089		

	Oligochaetes[1]				Ostracods[1]			
Source of Variation	df	Mean Sq.	F	*P*	df	Mean Sq.	F	*P*
Habitat H	4	1.067	2.270	0.110 ns	4	1.050	6.050	0.004 **
Site S(H)	15	0.470	1.970	0.044 *	15	0.174	1.000	0.470 ns
Plot (S(H))	40	0.239	1.270	0.199 ns	40	0.173	1.300	0.174 ns
Residual	60	0.188			60	0.133		

[1] Data transformed to Log (x +1) before analysis
[2] Data transformed to $(x + 1)^{0.5}$ before analysis
ns = not significant; * $p<0.05$; ** $p<0.01$; *** $p<0.001$

Table 4.3. Summary of mixed model 3-factor nested analysis of variance results for difference in mean density at the Habitat scale or significant variability at Site and Plots scales (see Bennington and Thayne, 1994). Dashed line = no significant difference; *p<0.05; **p<0.01; ***p<0.001.

Taxon	Spatial Scale		
	Habitat	Site	Plot
Total Abundance	**	-	*
Nematodes	***	-	*
Copepods	**	*	-
Copepod Nauplii	**	-	-
Turbellarians	***	-	-
Polychaetes	*	***	-
Oligochaetes	-	*	-
Ostracods	**	-	-

4.3.2. Spatial patterns

The results of the mixed model nested analysis of variance show that significant variability in the density of copepods, polychaetes and oligochaetes was detected at the site scale, i.e. variability within some sites nested within habitats was significantly different from others. Significant variability in the absolute density of meiofauna as well as the density of nematodes was also observed at the plot scale (Table 4.2 & 4.3). No significant variability in the density of copepods, copepod nauplii, turbellarians, polychaetes, oligochaetes or ostracods was detected at the plot spatial scale.

The contribution of site, plot and residual spatial scales towards the total variation within the 5 habitats was calculated for the total abundance of meiofauna as well as the 7 most common taxa (Table 4.4). The percentage of variation at each spatial scale was calculated as the component of variation at that scale divided by the total and multiplied by 100. Variance components were

only calculated for random factors and not for the habitat scale since it was a fixed factor (Sokal and Rohlf, 1995). The five habitats therefore represent the full population of sampling units at this spatial scale, rather than a random selection from all possible habitats within the shallow lagoon (see Underwood, 1997, for details). For total abundance and all common taxa, the proportion of variation was highest at the residual (i.e. within-plot) scale and varied between 60- and 82%. This indicates that there was large variation among replicates within plots, suggesting that patchiness exists at smaller spatial scales. As the sampling scale increased, the proportion of variation tended to decrease, indicating that the total density and density of individual taxa was more homogeneous at the plot and site scales (Table 4.4).

Table 4.4. Estimates of variance components of total numbers of individuals and selected taxa contributing more than 1% to total abundance. Data are derived from the mixed model nested analysis of variance using untransformed data (see Underwood, 1997). Total Abund. = total abundance; Nema = nematodes; Cope = copepods; Nauplii = copepod nauplii; Polych. = polychaetes; Turb. = turbellarians; Oligo. = oligochaetes; Ostra. = Ostracods; -: negative estimates.

Source of Variation	Total Abund.	Nema.	Cope.	Nauplii	Polych.	Turb.	Oligo.	Ostra.
Site	16.1	18.1	10.2	8.4	33.6	-	2.1	-
Plot	24.6	21.5	7.5	15.5	23.5	17.6	18.0	25.2
Residual	59.3	60.5	82.2	76.1	42.9	76.1	42.9	74.8

4.3.3. Multivariate taxonomic assemblage structure

The MDS ordination plot constructed from fourth-root transformed abundance data for all taxa reveals a slight clumping of samples by habitat, although it is difficult to discern any trends when all replicates are plotted (Figure 4.5). For this reason a second MDS plot is presented in which abundances from each site have been averaged. This enables community trend between habitats to be more easily distinguished (Figure 4.6). While it is important to obtain information on replicate variability in order to establish unequivocally that there are community differences between survey stations, by averaging samples the signal-to-noise ratio is increased and variability at each station reduced (Somerfield *et al.*, 1995). With the removal of within-site variability, the MDS plot shows a clearer pattern of variation; taxonomic community structure at H3 was evidently different from all other habitats, habitats 4 and 5 overlapped in community structure, whereas habitats 1 and 2 had only a small amount in common.

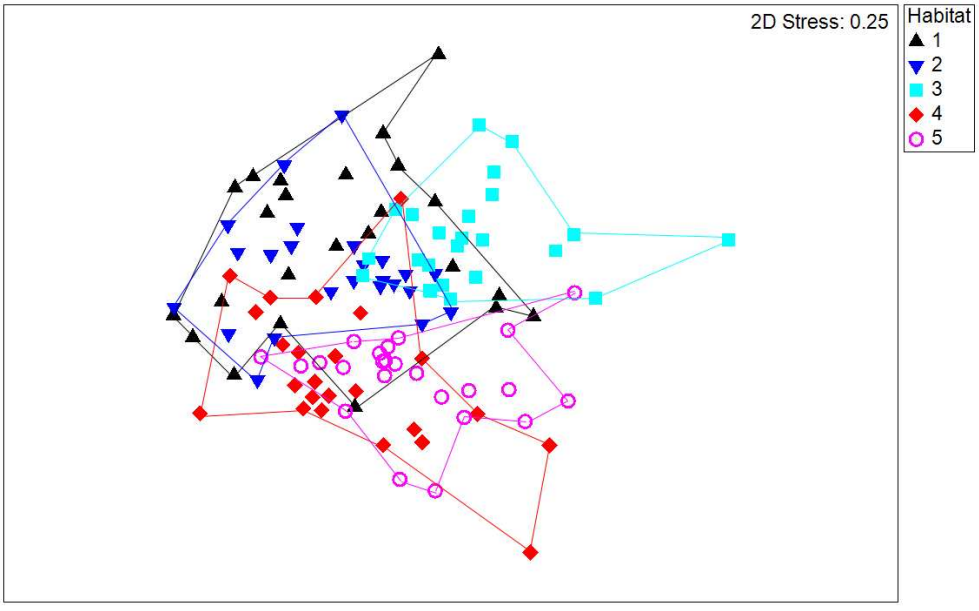

Figure 4.5. Multidimensional scaling (MDS) ordination of meiofaunal samples from the five lagoon habitats based on Bray-Curtis similarities calculated from fourth-root transformed data.

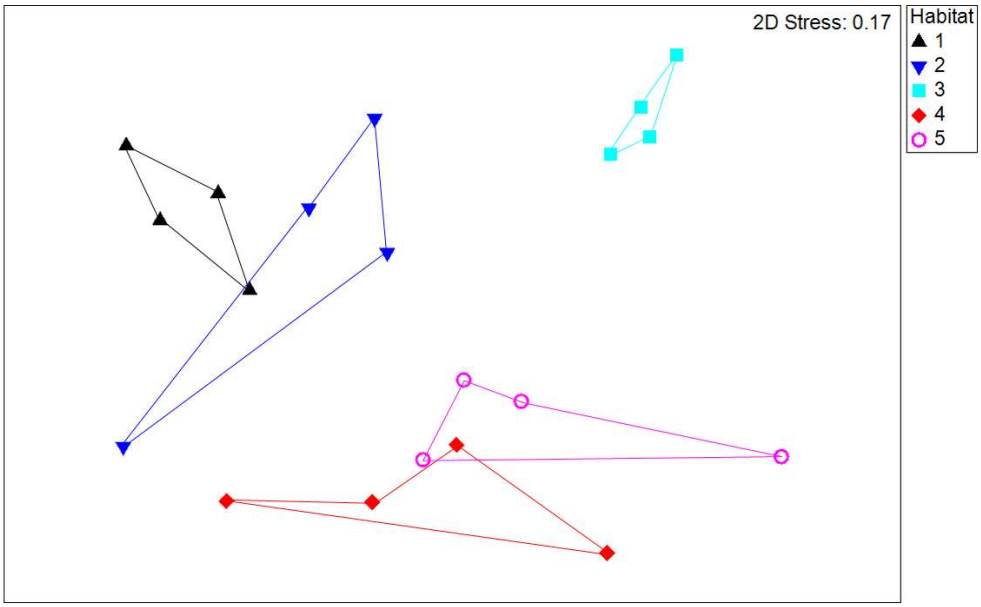

Figure 4.6. Multidimensional scaling (MDS) ordination of meiofaunal samples from the five lagoon habitats based on Bray-Curtis similarities calculated from fourth-root transformed data. Data have been averaged by site with 6 replicates per site for visual clarity.

Two-way nested ANOSIM tests of taxonomic assemblage structure (without averaging) on fourth root transformed data for each individual habitat revealed that there were no significant small scale differences between plots nested within sites. Therefore a two-way nested ANOSIM test using site groups as samples with 6 replicates per site was formulated for the full 5 habitat similarity matrix. Significant differences in meiofaunal taxonomic structure among sites within habitats and among habitats was detected (Table 4.5). Pair-wise tests revealed that meiofaunal taxonomic structure differed between every habitat combination, except between H4 and H5 (Table 4.5), statistically confirming the patterns observed in the MDS ordinations.

Table 4.5. *R*-statistic values and significance of two-way nested ANOSIM tests for differences in meiofaunal taxonomic structure between habitats and sites (using site groups as samples after checking for no significant area effect at the plot spatial scale). All results are derived from Bray-Curtis similarity matrices using fourth-root transformed data.

Global Test	R	*P*
Habitats	0.758	0.001
Sites within Habitats	0.151	0.001

Comparison		
Habitats	*R*	*P*
1 vs. 2	0.74	0.029
1 vs. 3	1	0.029
1 vs. 4	0.906	0.029
1 vs. 5	0.979	0.029
2 vs. 3	0.927	0.029
2 vs. 4	0.719	0.029
2 vs. 5	0.542	0.029
3 vs. 4	0.875	0.029
3 vs. 5	0.875	0.029
4 vs. 5	0.198	0.086

In order to determine the contribution of individual taxa towards the Bray-Curtis similarities within habitats, as well as dissimilarities between habitats, the Similarity Percentages (SIMPER) routine using fourth-root transformed data was utilised. Similarity between replicates within individual habitats ranged from 78.3 to 81.5 %. Nematodes and copepods were the most typical taxa within all habitats contributing between 36.6 to 42.1 % towards within habitat similarity. Between habitat dissimilarity ranged from 22.8% between H4 and H5, to 26.6 % between H1 and H3. The SIMPER analysis showed that the significant differences in taxonomic community structure between habitats, which was demonstrated by the ANOSIM tests, were due to changes in the relative abundance of many taxa, rather than differences in just a few. For each habitat comparison, no particular taxa dominated the dissimilarity. Cumulative

contributions from 4 taxa were needed before a 30% contribution towards average dissimilarity was reached, with no individual taxon contributing more than 13%.

4.3.4. Relationship between meiofauna, microphytobenthos and sediment properties

As mentioned in Chapter 3, samples for meiofauna, microphytobenthos and sediment properties were not paired with one another. This made it impossible to correlate individual taxonomic abundance to microphytobenthos or specific abiotic variables via univariate methods using the full data matrix of 120 samples per variable. Similarly, multivariate assemblage structure could not be linked to the environmental data via the BIOENV routine in PRIMER, since this routine explicitly requires that "The two matrices must unambiguously refer to a common set of samples otherwise no matching is possible" (see page 121, PRIMER User Manual / Tutorial in Clarke and Gorley, 2006)

Nevertheless, mean microphyte biomass has been plotted against mean meiofauna density at each habitat to envisage the relationship (Figure 4.7). This plot suggests that there could have been a possible positive relationship between these variables using all the data, although there is considerable variation around the relationship. Likewise, it appears there may have been a possible negative relationship between grain size and abundance, although again there is considerable variation around the relationship (Figure 4.8). Correlations between means of total abundance and individual common taxa groups with mean microphytobenthic biomass and the sediment granulometry variables for each

habitat were, however, not significant (Pearsons correlation coefficient, p>0.05, n=5).

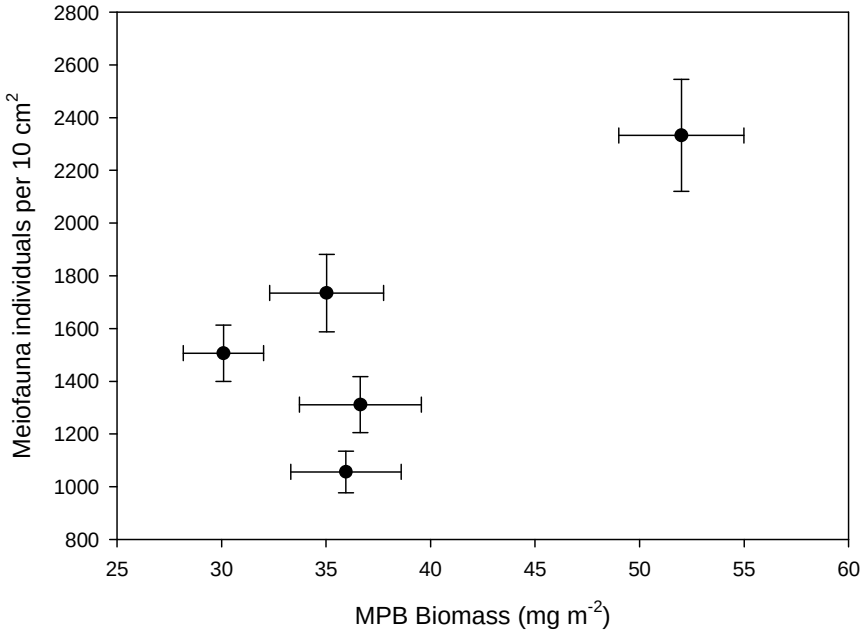

Figure 4.7. Relationship between mean density of meiofauna and mean biomass of microphytobenthos (date 2) at habitats 1 to 5 (n=24; +/- SE).

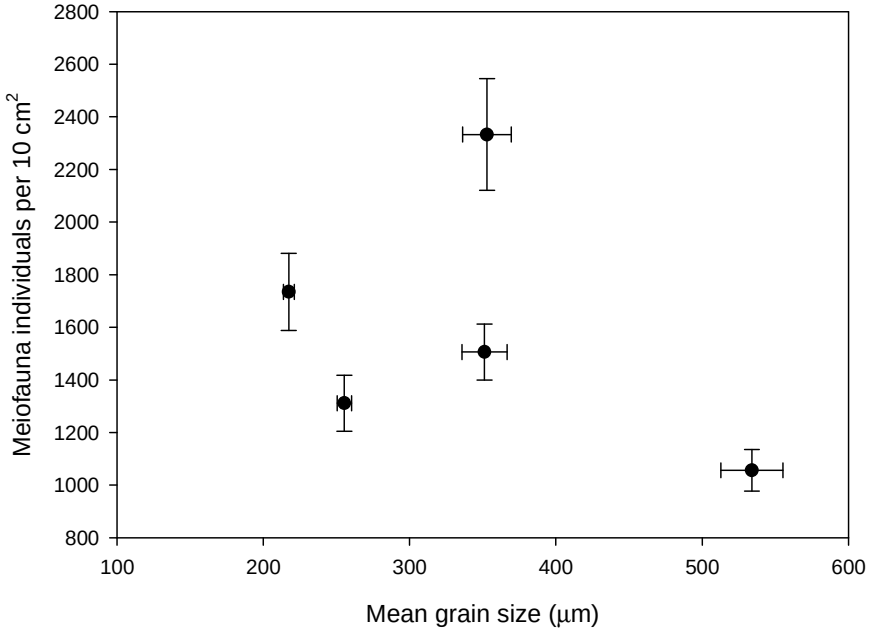

Figure 4.8. Relationship between mean grain size and mean density of meiofauna at habitats 1 to 5 (n=24; +/- SE).

In light of the data being un-paired, in order to show the extent of variation in the sediments and the structure of meiofaunal assemblages with increasing spatial scales, the average Euclidean distances (sediment) and Bray-Curtis dissimilarities (meiofauna) were calculated for all pairwise comparisons among replicates within plots, all plots within sites, and among all sites within each habitat (Figure 4.9). Since values are not independent (i.e. variation within plot includes variation among replicates, and variation within sites includes variation among plots) they were not formally analysed and thus do not have associated error bars (see Chapman and Tolhurst, 2007). Nevertheless, all habitats exhibited an increase in variability with increasing spatial scale for the sediments. Looking at the magnitude of change in Euclidean Distance between individual scales for the sediments, at H1 to H4 the greatest changes occurred from site to site within habitats. In contrast at H5 most of the change occurred from plot to plot within a site, with the site scale adding little additional variation (i.e. Euclidean Distance) to the overall pattern.

Comparing the patterns of changes in the magnitude of variation between scales in the sediments and in the benthos, a similar pattern is observed only at H2. At H2 there is a degree of matching between the scales at which the benthos and environment varied. For H1 and H3, variation in meiofaunal community structure among plots within sites exceeds that of variation among sites and does not match the pattern of change in the sediments. Similarly, at H4 variation in meiofaunal structure between replicates within plots is greater than among plots within sites, and there is also little matching in the pattern of variation at the different scales between sediment and benthos. At H5 the patterns are variable;

there was more change in the meiofauna among sites than there was for the sediment granulometry.

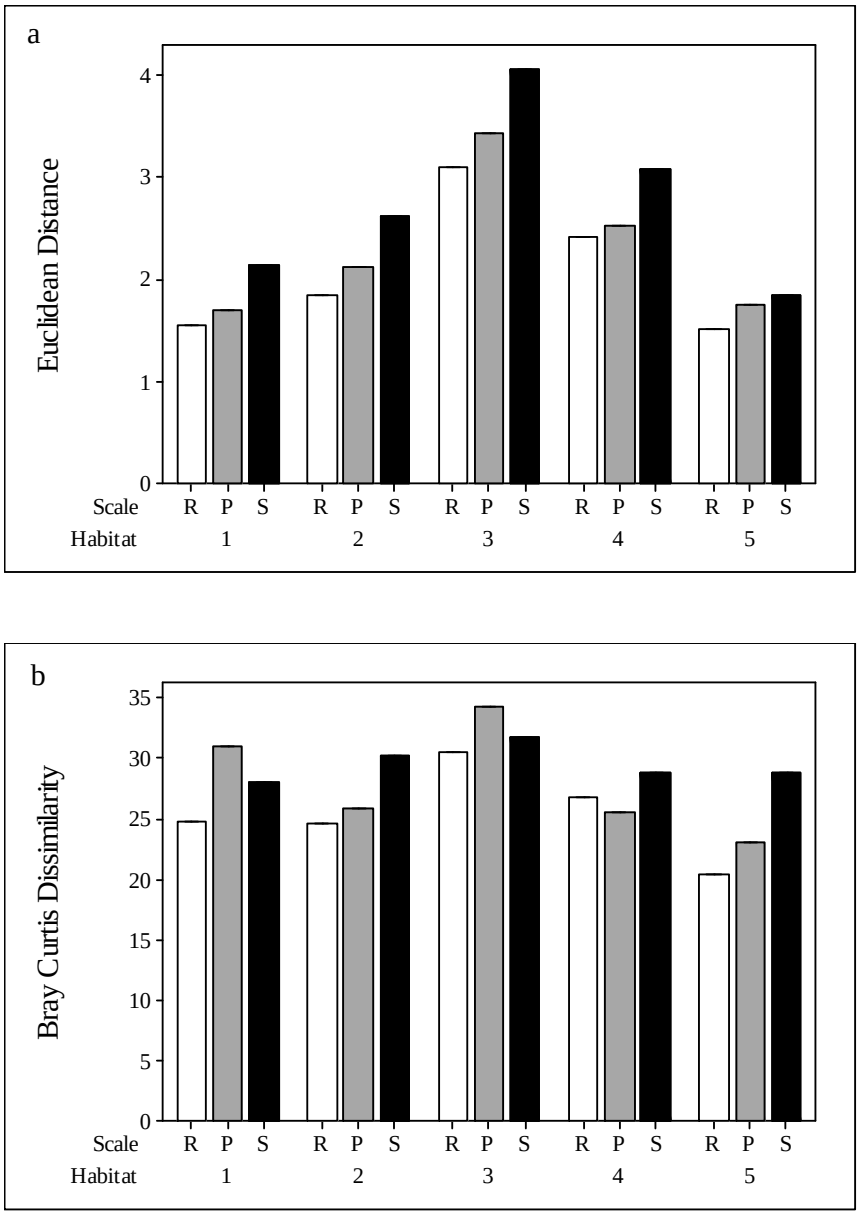

Figure 4.9. Mean Euclidian distances from normalised sediment granulometry parameter data (a) and Bray-Curtis dissimilarities from untransformed meiofauna data (b) for habitats 1-5 for all pairwise comparisons among replicates within plots (R, white bar), among plots within sites (P, grey bar), and among sites (S, black bar).

4.4. Discussion

This study is the first to extensively document the meiofauna from the west lagoon at Discovery Bay, and provides a general description of the spatial variability within five contrasting shallow habitats. These habitats were chosen on the basis of contrasting visual characteristics, in order to maximise the probability of detecting significant differences in biotic structure between habitats.

Meiofaunal abundance in the five habitats varied between 284 and 5344 individuals 10 cm^{-2}. These values correspond well with the ranges recorded from other tropical calcareous soft-bottom habitats, such as in the Gulf of Aqaba in the Red Sea (181 – 5007 ind. $10cm^{-2}$ Grelet, 1985), Cebu in the Philippines (744 – 8769 ind. $10cm^{-2}$ Faubel, 1984), the central Great Barrier Reef (220 – 1010 ind. $10cm^{-2}$ Hansen *et al.*, 1987), Rocas Atoll in north-east Brazil (278 – 4165 ind. $10cm^{-2}$ Netto *et al.*, 2003), Tuamotu in Polynesia (390 – 1293 ind. $10cm^{-2}$ Renaud-Morant *et al.*, 1971) and Zanzibar on the east African coast (219 – 3422 ind. $10cm^{-2}$ Ndaro and Ólafsson, 1999). Upper values found in this research, however, are roughly an order of magnitude higher than those from Massawa in the Red Sea (126 – 439 ind. $10cm^{-2}$ Arlt, 1995), southern Costa Rica (99 – 575 ind. $10cm^{-2}$ Guzmán *et al.*, 1987), and Moorea Island in French Polynesia (24 – 961 ind. $10cm^{-2}$ Thomassin *et al.*, 1982).

The dominant taxa in all samples from the five habitats at Discovery Bay were nematodes, followed by copepods, as has often been observed in soft-sediments of coral reef ecosystems (e.g. McIntyre, 1968; Coull, 1970; Renaud-Morant *et*

al., 1971; Rao and Misra, 1983; Villiers, 1988: Netto *et al.*, 1999). However this is not always the case. At Cebu in the Philippines (Faubel, 1984) as well as at Moorea Island in French Polynesia (Thomassin *et al.*, 1982) polychaetes dominated, whereas off the coast of Costa Rica foraminiferans were the main taxa (Guzmán *et al.*, 1987).

Although the distribution of meiofauna is controlled by many interacting abiotic and biotic factors, several studies have shown that spatial distributions are often related to sediment granulometry (see Fleeger and Decho, 1987; Giere, 1993; Coull, 1999). However numerous factors covary with sediment granulometry, which has been termed a 'community-controlling variable', due to the concomitant effects that sediment grain size has on many other biologically-meaningful variables (Gray, 1974). For example, while copepods are often reported to dominate exposed zones consisting of coarse sediments (Gourbault *et al.*, 1998), coarse sediments generally exhibit larger pore spaces, have higher advective pore water flow rates, higher oxygen concentrations and contain lower concentrations of organic matter. Conversely, nematodes often dominate sheltered zones where fine sediments prevail (Coull, 1970; Hicks and Coull, 1983; Heip *et al.*, 1985). However in finer sediments the concentration of organic matter is generally increased, pore space and advective pore water flow reduced and oxygen concentrations lowered (Gray, 1974). Indeed in their review on animal-sediment relations Snelgrove and Butman (1994) argue that the real reasons for observed sediment-species associations are most likely due to interactions between physical environmental properties which create a particular

sediment environment, rather than the sediment characteristics *per se* (i.e. grain size, organic content, porosity etc.).

In the present study there were clear differences in meiofaunal abundances between habitats, and the pattern of difference was taxon-specific. While the abundance of nematodes and turbellarians differed between habitats 1 and 3, the abundance of copepods, copepod nauplii and ostracods did not. Interestingly, both nematodes and copepods had highest densities in medium sands at habitat 2, which contained the highest biomass of microphytobenthos. In contrast, total meiofauna and nematode abundance was lowest in coarse sands subjected to wave disturbance at habitat 3, whereas at habitat 5, consisting of medium fine sands with an increase in silt content, copepod abundance declined. These results are probably partly due to intolerances of small nematodes (see Chapter 5) and other meiofauna to high pore water flow and sediment disturbance, and copepods to reduced oxygen supply (Giere, 1993) and are in general agreement with many other studies. For example, in an intertidal lagoon in Zanzibar the abundance of nematodes was significantly positively correlated with chlorophyll *a* and sediment granulometry (Ndaro and Ólafsson, 1999). In a transect across Davies Reef on the Great Barrier Reef, lowest nematode densities occurred in a habitat associated with intense wave action situated just behind the reef crest (Alongi, 1986). Kotta and Boucher (2001), comparing meiobenthic taxa from Miyako, New Caledonia and Moorea in the Pacific Ocean found that mean grain size and silt content of the sediment were important in explaining the structure of meiobenthic assemblages; nematode abundances were negatively correlated with mean grain size whereas the opposite held true for copepods. Thomassin *et al.*

(1982) and Rao and Misra (1983) also observed similar patterns whereby nematodes were most abundant in fine sands in sheltered zones and copepods dominated more exposed, coarser, cleaner sands. At a site in Bermuda, Coull (1970) showed that seasonal changes from fine to coarse sediments were accompanied by a change in dominance from nematodes to copepods.

The distribution and diversity of macrobenthos in the shallow lagoon at Discovery Bay has been related to gradients in sediment stability (Aller and Dodge, 1974). At H2 the high biomass of microphytobenthos would have tended to increase the cohesive nature of the sediments due to production of extracellular polymeric substances (EPS) thereby providing a more stable environment for interstitial organisms. Furthermore meiofauna, and nematodes in particular, produce EPS and pelletise sediment (Riemann and Schrage, 1978) promoting stability, although meiofaunal bioturbation and grazing on microphytobenthos can also act as a destabiliser (Admirral, 1984; Reichelt, 1991). Nevertheless, the important influence of microphytobenthos as a food resource for meiofaunal organisms (Pace and Carman, 1996; Moens and Vincx, 1997; Middleburg *et al.*, 2000; Nascimento *et al.*, 2008), either directly or indirectly, most likely played a large structuring role. Copepod abundance has been found to be highly correlated with microalgal abundance (Decho and Fleeger, 1988; Blanchard, 1990), and EPS produced by benthic microalgae can trap detritus and support high levels of bacteria, both of which are consumed by meiofauna (Hobbie and Lee, 1980; Meyer-Reil and Faubel, 1980; Montagna, 1984). In this study phaeopigment content was also measured at the same time as chlorophyll *a* using the method of Lorenzen (1967), and values were found to be

significantly higher at H2 than at other habitats (Kruskal-Wallis test, H=73.74, $p<0.001$, $n=72$). However Lorenzens's method, although accurate for the determination of chlorophyll *a*, has been shown to be inaccurate for the determination of phaeopigment (Louda and Monghkonsri, 2009) and hence values are not reported in Chapter 3. Nevertheless, the colouration of the sediments at habitat 2 were noticeably darker than those occurring in the other habitats, suggesting that they had higher concentrations of organic material / detritus and / or other pigments besides chlorophyll *a*.

In studying the nutrition of the echinoid *M. ventricosa* at Discovery Bay, Hammond (1983) concluded that half of the carbon assimilated was of detrital origin, whereas meiofauna were ingested only in small numbers and passed through the gut unassimilated and undigested. Out of hundreds of hours spent free-diving within the lagoon, *M. ventricosa* was only observed in the vicinity of habitat 2. It therefore appears that H2 was a detritally-enriched habitat, with enhanced biomass of microphytobenthos and breakdown products. This in turn seemed to positively influence the abundance of nematodes and copepods, which may have been a response to the diversity in the quality and quantity of suitable food resources, such as diatoms, detritus and/or bacteria, as well as an increase in sediment stability. Future studies on the meiofauna in relation to these potential factors would help to clarify the nature of the interaction between the meiobenthos, sediment stability, and food resources at habitat 2, and should be conducted.

In the shallow lagoon the density of total meiofauna, nematodes, copepods, nauplii and oligochaetes did not differ between habitats 1, 4, and 5, even though sediments at H1 were relatively undisturbed while those at H4 and H5 were densely occupied by thalassinid shrimps and subject to a high degree of bioturbation. In tropical lagoons burrowing thalassinid ghost shrimps actively bioturbate the sediment during burrow construction and feeding, causing changes in sediment properties and influencing the distribution and abundance of sediment infauna (Branch and Pringle, 1987; Murphy and Kremer, 1992). However the effects of bioturbation by thalassinid shrimps on meiofauna can be both positive or negative. At Davies Reef on the Great Barrier Reef, bioturbation and feeding activities of thalassinid shrimps negatively influenced meiofaunal communities (Alongi, 1986; Hansen *et al.*, 1987). In contrast, on a tropical tidal flat on the north east coast of Australia meiofauna densities were significantly higher in sediments with *Trypaea australiensis* than in sediments where shrimps had been experimentally excluded (Dittmann, 1996). This was explained by the positive effect of an extension in sediment oxygenation due to bioturbation, the trophic influence of shrimp fecal pellets on bacterial numbers, and the increase in chlorophyll *a* in deeper sediment layers due to sediment mixing. Similar results were also obtained in a separate *Callianassa spp*. exclusion study in South Africa (Branch and Pringle, 1987).

In the study by Hansen *et al.* (1987), although nematodes, copepods, polychaetes and ostracods exhibited lowered densities in shrimp burrow ranges at Davies Reef compared to other lagoon sites, the density of turbellaria did not seem to be affected. Similarly, in Dittmann's (1996) exclusion study the abundance of

nematodes and copepods declined significantly in caged areas without ghost shrimp, whereas differences in turbellarian densities were much less pronounced. In the present study turbellaria were heterogeneous across habitats with significantly higher densities in the undisturbed fine sands in H1 with limited bioturbation. In contrast, the density of meiofaunal polychaetes was lowest at H1, which could be due to predatory interactions between these two taxa. In an experimental manipulation study where the density of turbellarians was increased, Watzin (1983) found that the density of total macrofauna, spionid polychaetes and various other deposit feeders decreased and attributed the effect to predation pressure. In a study by Danovaro *et al.* (1993), the collapse of macrobenthic polychaete recruits coincided with an increase in abundance of predatory nematodes and turbellarians, suggesting that meiofauna may partly structure macrofaunal communities. It is therefore possible that the increased densities of turbellarians at H1 may have prevented the recruitment of temporary polychaetes to the benthos, or preyed upon them after recruitment.

Multivariate analyses revealed that taxonomic community structure was significantly different between all habitats except H4 and H5, situated within the thalassinid shrimp burrow-ranges. Similarly, univariate analyses were also unable to detect significant differences in the abundance of common taxa between H4 and H5. Nonetheless, sediment particle size distributions and sediment granulometry characteristics were significantly different between these habitats (see Chapter 3). This suggests that the biota were responding to other aspects of the environment which were perhaps similar between H4 and H5, rather than simply the physical characteristics of the sediment *per se*. Of course it

is feasibly possible that these habitats shared no common species; however this could only be inferred by identification of individuals to the species level of taxonomic resolution, rather than to higher taxa.

A main aim of this study was to examine meiofaunal communities between different habitats, using a sampling design that quantified organism patchiness and enabled variation at different spatial scales to be assessed. Calculation of components of variation for the random factors in the analysis of variance thus enabled the proportion of variability occurring between sites, plots, and replicates to be detected. For total meiofauna and all common taxa, most of the variability occurred at the smallest spatial scale, i.e. between replicates within plots. As the sampling scale increased, the proportion of variability subsequently decreased. This is a common feature of marine soft-sediments (Morrisey *et al.*, 1992a; Azovsky *et al.*, 2004; Chapman and Underwood, 2008), particularly for small organisms such as meiofauna which have rapid rates of reproduction and are intrinsically tied to the sediment. Patchy distributions of food resources (Decho and Fleeger, 1988; Blanchard, 1990; Pinckney and Sandulli, 1990), microscale gradients in sediment chemistry (Meyers *et al.*, 1987) and other interactions with the sediment microhabitat cause small scale patchiness. In contrast, physical factors which vary over large scales (e.g. current speed, salinity, anthropogenic disturbance) may be more important at generating large scale heterogeneity (Li *et al.*, 1997; Armenteros *et al.*, 2008).

Unfortunately it was not possible to directly relate the benthos to the sediment properties due to samples not being paired with one another. This is a major

critique of the way in which samples were collected. If attempts are to be made to match biological and environmental data, studies should do their best to make sure that data are collected from the same samples where possible, or at least immediately adjacent to one another if destructive sampling is planned (for example see Chapman and Tolhurst, 2007). Nonetheless, if the biota is responding to spatial variations in sediment granulometry then it should be expected that patterns in the variation of meiobenthos over the range of scales surveyed would be similar to those of the sediments. Yet patterns in mean Euclidean distance and Bray-Curtis dissimilarities for both sediments and meiobenthos appeared to match at habitat 2 only. For all other habitats spatial variation in the meiofaunal community was weakly matched to the spatial variation in the suite of sediment granulometry parameters, suggesting that the biota were not responding to the variation in the properties of the sediments alone.

4.5. Summary

This study has shown that the distribution of meiobenthos is heterogeneous within the shallow west lagoon at Discovery Bay. Although fauna were only examined at the higher taxon level, differences in the distribution of several taxa showed preferences for specific habitats. The high abundance of nematodes and copepods at habitat 2 attests to the role of microphytobenthos in structuring soft-sediment communities. Variance components attributed the bulk of spatial variation to the residual spatial scale, confirming the patchy nature of meiobenthos. Unfortunately since abiotic and biotic samples were not paired, it was difficult to establish correlative relationships, and attempts to match

community structure to the structure of the benthos suggested weak links. Nevertheless, this study has laid the ground work for further mensurative and manipulative studies on the meiofauna at Discovery Bay. These studies are urgently needed in order to increase our knowledge on the ecology of meiofauna from tropical marine systems, as well as to monitor and conserve near shore marine habitats.

5. NEMATODE FUNCTIONAL GROUPS, MORPHOMETRY, AND BIOMASS SIZE-SPECTRA

5.1. Introduction

Nematodes are the most abundant metazoans on the planet comprising four out of every five multicellular animals (Bongers and Ferris, 1999). In the marine environment, which covers 70% of the earth's surface, free-living nematodes exhibit high diversity, are ubiquitous in distribution, and are consistently found to be the dominant meiofaunal taxon (see review by Heip *et al.*, 1985). Although many studies have investigated the macrofauna inhabiting the soft-sediments of coral reef ecosystems, there have been far fewer studies on the smaller meiofauna component. Further still, only a few studies have specifically examined the meiofaunal nematodes (Grelet, 1985; Alongi, 1986; Boucher, 1997; Kotta and Boucher, 2001; Raes *et al.*, 2007; De Troch *et al.*, 2008).

Within coral reef sediments nematodes can be extremely abundant particularly in shallow lagoon habitats (Alongi, 1986; Gourbault and Renaud-Mornant, 1990; Ndaro and Ólafsson, 1999). They stimulate decomposition (Findlay and Tenore, 1982; Rieper-Kirchner, 1990; Alkemade *et al.*, 1992ab; but see De Mesel *et al.*, 2003, 2006), and increase sediment solute transport and pore water exchange (Reichelt, 1991; Aller and Aller, 1992;). They also channel energy from the microbial/detrital compartment up the food web to higher trophic levels including many species of macrofaunal invertebrates and fish (Colombini *et al.*, 1996; Danovaro *et al.*, 2007). Consequently, due to their enormous numbers and the varied roles that they play, nematodes are extremely important in marine ecosystem functioning.

While traditional methods in marine benthic ecological research generally rely on the collection of species abundance data to assess community structure and diversity, for a phylum as diverse and abundant as the Nematoda, the identification of animals to species can require considerable taxonomic expertise and time. Moreover, for the Caribbean region, there is a lack of identification keys to the species of major meiofaunal taxa (such as the nematodes). Therefore many species in the region are likely to be undescribed making their identification problematical (Richard Warwick, personal communication). In contrast, the classification of nematode communities by functional groups, morphometry, and size-based approaches simplifies the ecological analysis whilst offering additional insight into the structure of benthic communities beyond that of traditional species-based approaches (e.g. Tita *et al.*, 1999; Vanaverbeke *et al.*, 2003; Schratzberger *et al.*, 2007; Schratzberger *et al.*, 2008).

The functional group approach works by dividing communities into groups of taxa which share similar functional attributes. Organisms which are placed in the same group are believed or known to process the same resources and possess similarity in ecosystem function (Blondel, 2003). For marine nematodes, Wieser (1953) proposed a scheme containing four functional groups linking feeding ecology to the size of the buccal cavity. While many researchers have used Wieser's scheme (e.g. Netto *et al.*, 1999; Vanaverbeke *et al.*, 2007a; Liu *et al.*, 2008; Moreno *et al.*, 2008; Schratzberger *et al.*, 2008; Yodnarasri *et al.*, 2008), others have revised it depending on their own qualitative observations or to include additional trophic groups (Jensen, 1987; Romeyn and Bouwman, 1983; Moens and Vincx, 1997). However, since it is an impossible task to directly

study the feeding habits of the vast numbers of nematode species, Wieser's scheme was used in this study since Schratzberger *et al*. (2008) state that it remains the most feasible trophic classification of free-living marine nematodes from a variety of marine habitats.

The morphometric approach compares communities by analysis of their shape, which can be quantitatively assessed by non-destructive measurements of length and width (Vanaverbeke *et al.,* 2004). Typically most nematodes are long and slender and have a high length to maximal width (L/W) ratio. However some species, particularly those in the order Desmoscolecida (Soetaert *et al.*, 2002), are short and plump with a low L/W ratio. The prevalence of a plump morphotype has been recognised in a number of habitats, ranging from subtidal sediments in the English Channel (Ratsimbazafy *et al.,* 1994) and North Sea (Vanaverbeke *et al.,* 2004) to the hadal depths of the South Sandwich Trench in the Antarctic (Vanhove *et al.,* 2004).

The ecological advantages and disadvantages that affords either morphology have elicited several hypotheses. For example Tita *et al.* (1999) proposed a food-related hypothesis suggesting that nematode length [and therefore gut length (see Romeyn and Bouwman, 1983)] reflects adaptations to the quality of exploited food. Nematodes with long guts are suggested to have higher digestive efficiency making them better adapted to exploit lower quality foods, while in contrast those with short guts are adapted to feed on higher quality food. Soetaert *et al.* (2002) subsequently hypothesised that the different morphotypes represent ecological adaptations towards increased mobility (slender) or reduction in

predation (plump). Furthermore, it is suggested that the different morphotypes represent adaptations towards constraints posed by available oxygen levels (Soetaert *et al*., 2002). However the costs and benefits of either morphotype are not well understood, and comparisons of morphotype and L/W ratios between different habitats within a coral reef environment have not been assessed before.

Lastly, the sized-based approach plots organism biomass distribution over a sequence of logarithmically equal body size intervals as a biomass size-spectrum. Originally coined the Sheldon spectrum, after work on the size distribution of oceanic particles by Sheldon *et al.* (1972), biomass size spectra are useful ecological tools enabling communities to be compared by size (Schwinghamer, 1981). Given that body size influences many aspects of an organisms life, including metabolism, energy requirements, life history, production rate, physiological and behavioural functions as well as abiotic and biotic interactions, it is an important index of ecosystem organisation (Peters, 1983; Calder, 1984; Kerr and Dickie, 2001).

Initially Schwinghamer (1981) was the first to analyse the benthic biomass size spectra. He found that benthic organisms from a variety of intertidal habitats displayed trimodal biomass size spectra, the three modal biomass peaks (0.5 – 1 μm, 64 – 125 μm, and > 2 mm equivalent spherical diameter) corresponding to the sizes of micro-, meio-, and macrobenthos, respectively. Schwinghamer reasoned that pore space and grain size likely determine the upper and lower size limits for interstitial fauna, causing the characteristic biomass minima troughs that he found in the Sheldon spectrum. Further studies by Schwinghamer (1983,

1985) found similar trimodal spectra from habitats ranging from the upper intertidal to the abyssal plain, causing him to conclude that the trimodal distribution of biomass was a conservative and repeatable feature of marine soft-sediment benthos. Warwick (1984) however, looking at *species* size distributions of metazoans from 8 temperate sites of contrasting granulometry, salinity and depth, found that the shape of the spectrum was remarkably similar to the metazoan part of Schwinghamer's *biomass* size spectrum. He noticed that a species trough occurred at 45 μg, a size at which many life-history traits switch more or less abruptly (see table 4 Warwick, 1984), including type of development, mode of dispersal, generation time, reproduction, feeding mode, resource partitioning, growth cycle and mobility. This led Warwick to invoke evolutionary explanations (which do not contradict Schwinghamer's (1981) theory), that meiofaunal and macrofaunal life-history and feeding traits are optimised at particular body sizes and that departures from these optima limit the co-existence of similar sized species (Warwick, 1984).

Following these initial investigations a number of others have analysed the biomass size-spectra of metazoan benthic communities (e.g. Gerlach *et al.*, 1985; Drgas *et al.*, 1998; Duplisea and Drgas, 1999) and it has been shown that, unsurprisingly, nematodes generally dominate the meiofaunal fraction. Drgas *et al.* (1998), for example, showed that nematodes contributed from 46.2 to 96.4% of total biomass in the weight class 501 ng C to 1 μg C, yet in all other weight classes up to 500 ng the contribution was almost 100%. A similar pattern was also observed (Duplisea and Hargrave, 1996). Therefore, the construction of nematode biomass spectra (NBS) is suggested to reveal a similar pattern as if all

meiobenthic animals were measured (Vanhove *et al.*, 2004). Moreover, since meiofauna are suitable indicators of benthic disturbance (Kennedy and Jacoby, 1999), and nematodes are the dominant meiofaunal taxon, the use of NBS is potentially a very valuable and relatively easy tool to use in the assessment of environmental perturbation and natural changes. In particular, nematode biomass spectra have recently been used to understand the effects on the benthos of sand extraction at the Belgian continental shelf (Vanaverbeke *et al.*, 2007a; Vanaverbeke and Vincx, 2008), planktonic production cycles (Vanaverbeke *et al.*, 2003; Vanaverbeke *et al.*, 2004; Schratzberger *et al.*, 2008) and the impact of beam trawling (Schratzberger *et al.*, 2002) in the North Sea, as well as sea floor dredging on benthic colonisation of different types of sediment in an estuary in SE England (Schratzberger *et al.*, 2004). However, studies on nematode biomass and biomass spectra from tropical marine environments are lacking (although see Grelet, 1985). This study therefore intends to advance the general understanding of nematode communities in a coral reef ecosystem.

In the absence of taxonomic feasibility, the aim of this research is to examine nematode feeding groups, morphometry, and biomass size-spectra among habitats within the shallow lagoon at Discovery Bay. More specifically, this research aims to test hypotheses that a) different nematode feeding groups have affinities for particular benthic conditions, and b) that different nematode L/W relationships and biomass spectra will be found in habitats with contrasting sediment granulometry and subject to varying levels of natural benthic disturbance, such as wave swash and bioturbation.

5.2. Methods

5.2.1. Nematode sample processing

All nematodes from the meiofauna samples (Chapter 4) were evaporated to pure glycerol in a cavity block over a period of a few days before being mounted on to large wax-ringed slides able to contain a complete, whole sample (Darwin Initiative Marine Nematode Project, 2009). Each slide was then examined using a Zeiss Photomicroscope III compound microscope fitted with a combination of Plan and Planapochromatic optics and capable of oil immersion and Normarski Differential Interference Contrast image enhancement. This microscope was coupled to a JVC digital CCTV camera and linked to a computer allowing images of nematodes to be measured using the SigmaScan Pro (version 5) image analysis software package.

5.2.2. Nematode functional groups

From each sample, 50 nematodes were analysed for functional group according to Wieser's (1953) feeding group classification. These groups consist of (1A) selective deposit feeders with a small buccal cavity without armature which consume bacteria and small-sized organic particles; (1B) non-selective deposit feeders with large buccal cavities without armature feeding on organic deposits but targeting larger sized particles; (2A) epigrowth feeders with small buccal cavities and armature scraping food off surfaces or feeding on diatoms and microalgae; and (2B) predators feeding on nematodes and other small invertebrates with large buccal cavities with armature.

An index of trophic diversity (ITD) was also calculated following Heip *et al.*, (1985). This index is based on the relative proportions of each feeding type, and ranges from 0.25 (highest trophic diversity where the relative proportion of each feeding type is equal) to 1.0 (lowest trophic diversity consisting of only a single feeding type). ITD is calculated as:

$$ITD = \sum \theta^2$$

where θ is the relative proportion of feeding types after Wieser (1953).

5.2.3. Nematode morphometry

Each of the 50 nematodes analysed for feeding group were also measured for length (excluding filiform tails, if present) and mid-body widths.

5.2.4. Nematode biomass

Nematode biovolume was calculated from length and width measurements according to the formula by Andrassy (1956):

$$V = L \times W^2 / 1.6 \times 10^6$$

where V equals the biovolume, in nL; L and W equals nematode total length (excluding filiform tails, if present) and mid-body width, respectively, both in μm. Biovolume was then converted to wet mass assuming a specific gravity of 1.13 (Andrassy, 1956), and wet mass was converted to dry mass assuming a wet to dry ratio of 25% (Wieser, 1960; Feller and Warwick, 1988). Carbon content

was considered to be 40% of dry weight (Feller and Warwick, 1988). This is equivalent to 10% of wet weight according to Heip *et al.* (1985).

5.2.5. Data processing and analysis

5.2.5.1. Nematode functional groups

Differences in the relative abundance of nematode feeding groups within individual habitats were analysed via one-way ANOVA. Significant results were followed by Tukey's HSD test. The structure of nematode feeding groups among habitats was explored by MDS ordinations derived from Bray-Curtis matrices using untransformed relative abundance data. Formal significance tests examining the null hypothesis that there were no differences in feeding group structure between sites nested within habitats and between habitats using site groups as samples were performed using two-way nested ANOSIM on Bray-Curtis similarity matrices. Before analysis data were standardised to % contribution and analyses were performed on untransformed abundances so that no weighting was added to either feeding group. When significant differences were found, SIMPER analysis was undertaken to determine the contribution of specific feeding groups to the dissimilarity between habitats.

5.2.5.2. Nematode morphometry

Nematode lengths and maximum widths were analysed via nested ANOVA followed by Tukey HSD post-hoc multiple comparisons. Scatterplots of width versus length, as well as L/W frequency distributions were also plotted as per Soetaert *et al.* (2002). Differences in L/W frequency distributions were analysed using the Kolmogorov-Smirnov two-sample test. In addition, interquartile range

boxplots were constructed to allow easy visual depiction of the distribution of nematode lengths at each habitat.

5.2.5.3. Nematode biomass spectra

Regular nematode biomass spectra (RNBS) were constructed according to Vanaverbeke *et al.* (2003) using $\log_2$ groupings of nematode dry weight (μg) on the *x*-axis and total biomass per size class (dry weight, μg) on the *y*-axis. In other words, the dry weight (μg) of each nematode was assigned to a weight class on a $\log_2$ scale, and the magnitude of the class on the *y*-axis represented the sum of all organisms within that weight class. In this study, nematode biomass ranged from 0.0049- to 6.95 μg dry weight (dwt). Therefore $\log_2$ weight classes on the *x*-axis ranged from -8 (i.e. $\geq 2^{-8}$ to $< 2^{-7}$ [equal to ≥ 0.0039 to < 0.0078 μg dwt]) to 2 (i.e. $\geq 2^{2}$ to $<2^{3}$ [equal to ≥ 4 to < 8 μg dwt]). RNBS allows the magnitude of biomass per size class to easily be determined.

Cumulative nematode biomass spectra (CNBS) were also constructed as an alternative means of interpreting biomass spectra (Vanaverbeke *et al.*, 2003). CNBS plot the biomass as a running total and are helpful to visualise contributions of particular size classes to the complete spectrum. Cumulative size spectra were examined by ANOSIM. Formal significance tests examining the null hypothesis that there were no differences in size-spectra distributions between sites nested within habitats and between habitats (using site groups as samples) were performed on Euclidean distance matrices. Biomass data from each size class were first standardised to % contribution and then cumulated (Bob Clarke, Plymouth Marine Laboratory and PRIMER-E Ltd., personal

communication 2009). When significant differences were found, SIMPER analysis was undertaken to determine the contribution of specific size-classes to the dissimilarity between slopes.

5.3. Results

5.3.1. Nematode functional groups

The relative abundance of nematode functional (i.e. feeding) groups from the five different habitats in the shallow lagoon at Discovery Bay is shown in Figure 5.1. The proportion of selective deposit feeders was similar between habitats 1 to 4, but declined at habitat 5. Non-selective deposit feeders dominated habitats 1, 4 and 5, and their relative abundance was significantly higher than all other groups (Tukey's HSD; Table 5.1). A similar pattern of relative abundance occurred at habitats 1, 2 and 4, whereby non-selective deposit feeders had the highest relative abundance, followed by selective deposit feeders, then epigrowth browsers, and finally predators/omnivores; however these differences were not always significant (see Tukey post-hoc comparisons, Table 5.1). At habitat 3, proportions of non-selective deposit feeders were lowest. Proportions of epigrowth feeders were highest at habitat 3, and lowest at habitats 4 and 5. Highest proportions of predators/omnivores were recorded at habitats 3 and 5, but were lowest at habitats 1 and 4. Significant differences in relative abundance of feeding groups within habitats 1, 2, 4 and 5 occurred but no significant difference between feeding groups at H3 could be detected (Table 5.1). Trophic diversity (ITD) ranged from 0.286 at habitat 3 to 0.304 at habitat 4, however differences between habitats were not significant (One Way ANOVA, $F_{4,115}$ = 0.67, P = 0.615).

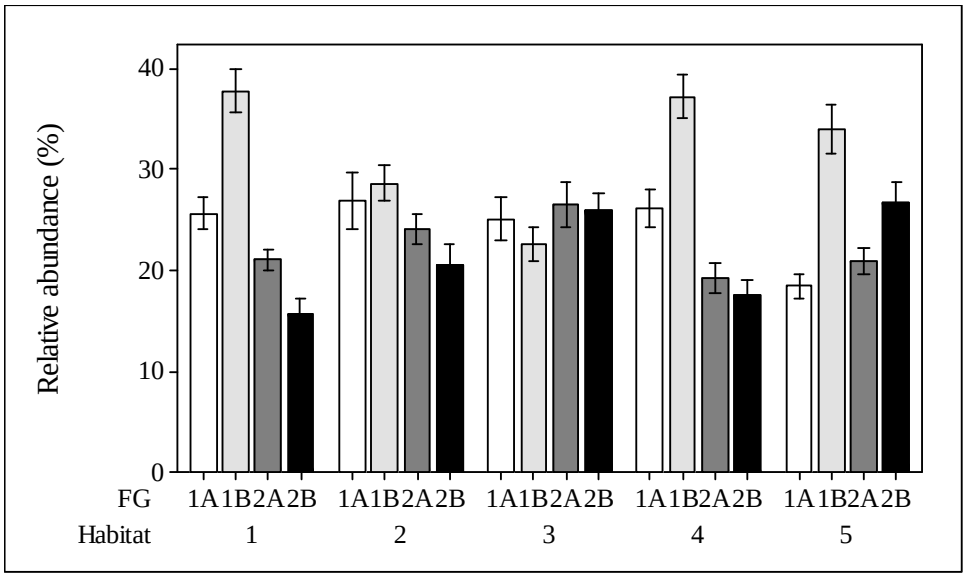

Figure 5.1. Mean (±SE) relative abundance (%) of nematode feeding groups from the 5 lagoon habitats at Discovery Bay (*n*=24, 1200 nematodes analysed per habitat).

Table 5.1. Results of One Way ANOVA and Tukey *post-hoc* comparisons (α=0.05) examining differences in the relative abundance (%) of nematode feeding groups within each of the 5 lagoon habitats at Discovery Bay.

Relative Abundance						
Source of Variation		df	MS	F	*P*	Tukey HSD
H1[1]	Feeding Group	3	0.235	33.82	0.000	1B>1A>2B, 1A=2A, 2A=2B
	Residual	92	0.007			
H2[1]	Feeding Group	3	0.033	2.74	0.048	1B>2B, 1B=1A=2A, 1A=2A=2B
	Residual	92	0.012			
H3	Feeding Group	3	74.8	0.81	0.490	No significant difference
	Residual	92	91.9			
H4	Feeding Group	3	1917.3	24.83	0.000	1B>1A>2A=2B
	Residual	92	77.2			
H5[1]	Feeding Group	3	0.129	14.17	0.000	1B>2B>1A, 2B=2A, 2A=1A
	Residual	92	0.009			

[1] Data arcsine transformed before analysis

MDS ordinations (Figure 5.2), based on the site-averaged proportions of nematode feeding groups for visual clarity, separated the trophic structure at habitats 1 and 4 from habitat 5. Habitats 2 and 3 revealed a large degree of variability in feeding group structure as evidenced by the distance between sites. Feeding group structure between sites within habitats 1, 4 and 5 was more similar than between sites within habitats 2 and 3. Global ANOSIM formal significance tests revealed significant site and habitat effects (Table 5.2); however R values, which are an absolute measure of the differences between groups (Clarke, 1993; Clarke and Gorley, 2006), were very low indicating that differences were limited. ANOSIM pairwise comparisons, on unaveraged Bray Curtis similarity data, showed that in 5 out of the 9 tests no significant differences in feeding group structure between habitats could be detected (Table 5.2). Pair-wise comparisons between habitats 1 and 4, as well as habitats 2 and 3 revealed negative *R* values, indicating that slightly more variability existed within habitats than between them.

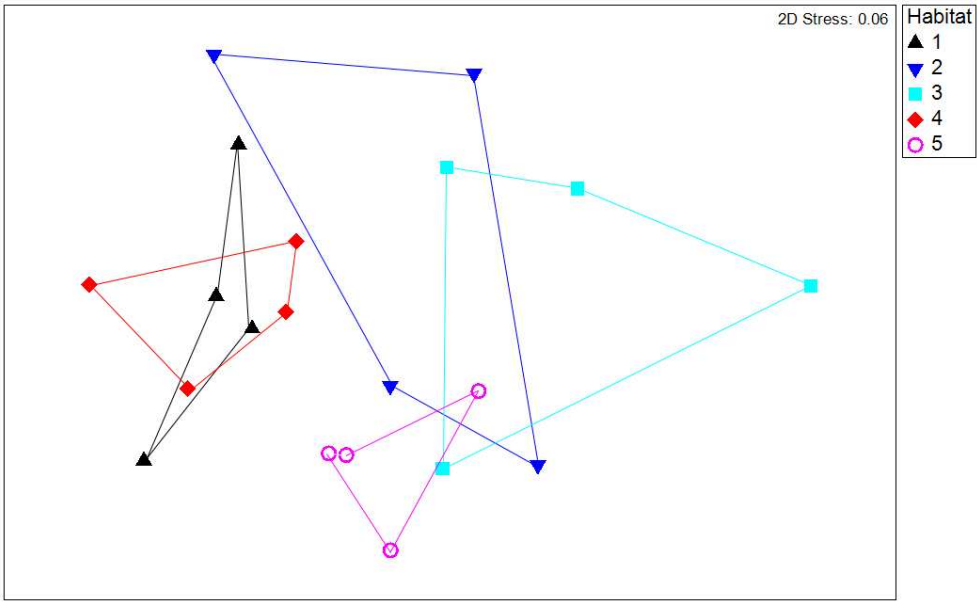

Figure 5.2. MDS ordinations of nematode feeding group relative abundance from the 5 lagoon habitats at Discovery Bay. Each point represents a single site.

Table 5.2. *R*-statistic values and significance of pairwise ANOSIM tests for differences in nematode feeding group structure between the 5 lagoon habitats at Discovery Bay.

Global Test	*R*	*P*
Difference between nested Sites across all Habitats	0.125	0.001
Difference between Habitats using Sites as samples	0.26	0.002

Habitat Comparisons	*R*	*P*
1 vs. 2	0.135	0.229
1 vs. 3	0.615	0.029
1 vs. 4	-0.146	1
1 vs. 5	0.438	0.029
2 vs. 3	-0.104	0.657
2 vs. 4	0.208	0.2
2 vs. 5	0.052	0.371
3 vs. 4	0.719	0.029
3 vs. 5	0.292	0.086
4 vs. 5	0.594	0.029

5.3.2. Nematode morphometry

In this study a total of 6000 nematodes were measured - 1200 from 24 samples taken from each of the five 30 x 2 m transects (i.e. habitats). A summary of nematode lengths, widths, individual and population biomasses are shown in Table 5.3. Nematode length spanned 3 orders of magnitude; the shortest nematode measured 88 μm and was found at habitat 2 while the longest nematode measured 4699 μm and occurred at habitat 3. Widths ranged between 9- and 120 μm, with the thinnest nematode found at habitat 1 and the fattest at habitat 3. Length and width frequency distributions were both positively skewed (not shown). Median lengths and widths from all measurements were 721- and 33 μm, respectively. Mean lengths and widths were 881- and 38 μm, respectively.

Mean nematode lengths and widths were significantly variable at the (small) plot scale but not at the (meso) site scale (Figures 5.3 and 5.4; Tables 5.5 and 5.6). Significant differences in mean lengths and widths were found between habitats (Tables 5.5 and 5.6). Mean nematode lengths at habitats 1 and 2 were significantly lower than at habitats 4 and 5 which were significantly lower than at habitat 3 (Tukey's HSD test; Figure 5.3; Table 5.5). Mean nematode width was significantly lower at habitat 2 than at habitat 3, however no significant differences were detected between the remaining habitats (Tukey's HSD test; Figure 5.4; Table 5.6).

Individual nematode biomass was highest at habitat 3 and lowest at habitat 1 (Table 5.3). Mean nematode population biomass, estimated from the product of

average abundance and mean individual biomass per habitat ranged from 237-398 μg dwt 10 cm^{-2}, equivalent to 95 to 159 μg C 10 cm^{-2} (Table 5.3). Considering all 6000 measurements, a rough figure for nematode biomass in the west lagoon is calculated at 113 μg C 10 cm^{-2} (0.113 g C m^{-2}). This figure is based on the average of five values from the five different habitats.

Table 5.3. Length, width and biomass characteristics of nematode assemblages from the 5 lagoon habitats at Discovery Bay. Numbers in brackets indicate 1 standard deviation (*n*=1200). Pop. Biomass = Population Biomass, estimated from the product of mean abundance and mean individual biomass per habitat. Dwt = dry weight. C = carbon.

	Length (μm)				Width (μm)				Ind. Biomass (μg dwt)				Pop. Biomass (μg 10 cm^{-2}).	
Hab.	Min.	Max.	Mean	Median	Min.	Max.	Mean	Median	Min.	Max.	Mean	Median	dwt	C
1	144	3723	728 (482)	616	9	112	38 (20.4)	32	0.004	5.571	0.210 (0.325)	0.125	241	96.4
2	88	4377	760 (594)	599	121	117	37 (17.8)	30	0.010	5.731	0.247 (0.455)	0.111	398	159.2
3	173	4699	1144 (635)	970	5	120	39 (15.3)	35	0.017	6.949	0.447 (0.672)	0.211	247	98.8
4	157	4584	946 (561)	767	14	9	38 (15.8)	34	0.013	4.036	0.319 (0.425)	0.168	286	114.4
5	141	3778	829 (491)	704	10	105	37 (15.8)	33	0.005	3.651	0.267 (0.400)	0.138	237	94.8

Table 5.4. Pearson correlation matrix between mean nematode abundance, mean length, mean width, mean L/W ratio, mean individual biomass, and nematode population biomass with mean chlorophyll *a* biomass, mean grain size, mean % porosity and mean % silt/clay for the 5 lagoon habitats at Discovery Bay.

	Chl *a* biomass	Grain size	Porosity	Silt/clay
Abundance	0.819	-0.461	-0.850	0.025
Length	-0.378	0.886*	0.571	-0.349
Width	-0.559	0.459	0.232	-0.537
L/W ratio	-0.504	0.803	0.596	-0.400
Mean ind. Biomass	-0.280	0.927*	0.540	-0.408
Population biomass	0.906*	0.106	-0.759	-0.146

* Indicates significant correlation, $p < 0.05$

Pearson correlation analyses between selected environmental variables and nematode abundance, lengths, widths, L/W ratios, individual biomass and population biomass and environmental parameters for the 5 habitats in the lagoon are shown in Table 5.4. Mean nematode length and mean individual biomass both exhibited significant positive correlations ($p < 0.05$) with mean grain size. Positive correlations between population biomass and mean chlorophyll *a* biomass were also significant ($p < 0.05$). Correlations for the remaining variables were not significant ($p > 0.05$).

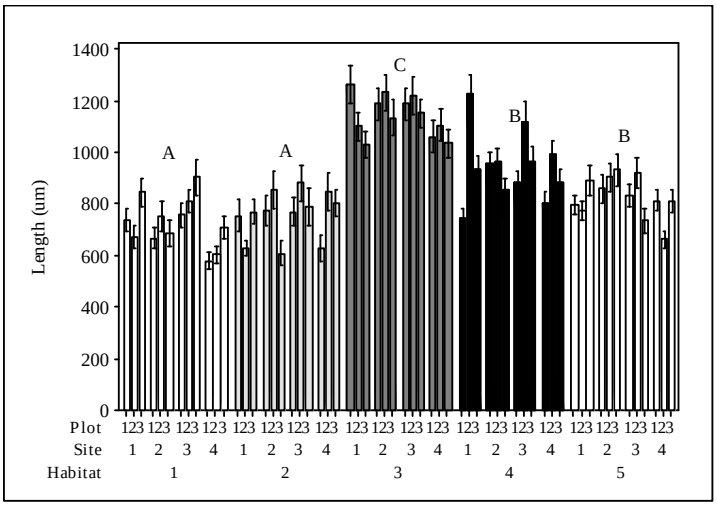

Figure 5.3. Mean lengths of nematodes from the 5 lagoon habitats at Discovery Bay (n=2, ±1SE). Habitats with the same letter are not significantly different from one another (Tukey's HSD test, α=0.05).

Table 5.5. Results of the three-factor nested ANOVA examining differences in mean nematode length from the 5 habitats within the shallow lagoon at Discovery Bay.

Source of Variation	df	MS	*F*	p	Sig.	Error terms
Habitat	4	9.99	53.81	0.000	***	Site (Hab)
Site (Hab)	15	0.186	1.06	0.423	ns	Plot(Hab(Site))
Plot(Site(Hab))	40	0.175	2.90	0.000	***	Error
Error	5940	0.060				

[1] Data transformed to $\text{Log}_{10}(x)$

ns = not significant; * p<0.05; ** p<0.01; *** p<0.001

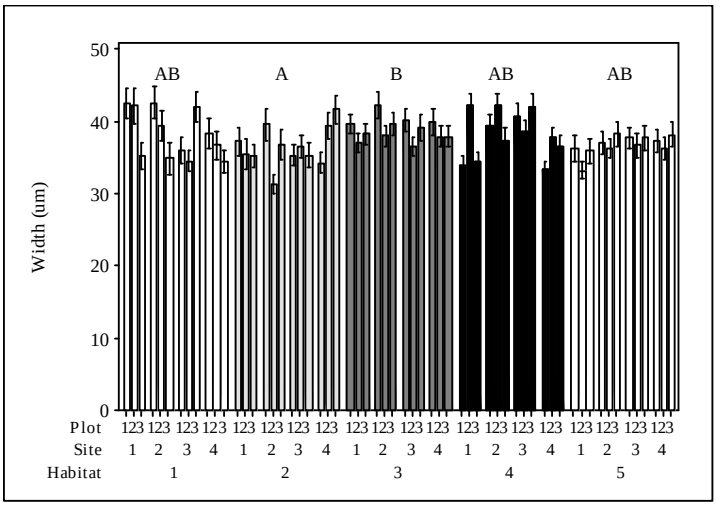

Figure 5.4. Mean widths of nematodes from the 5 lagoon habitats at Discovery Bay (n=2, ±1SE). Habitats with the same letter are not significantly different from one another (Tukey's HSD test, α=0.05).

Table 5.6. Results of the three-factor nested ANOVA examining differences in mean nematode width from the 5 habitats within the shallow lagoon at Discovery Bay.

Source of Variation	df	MS	*F*	p	Sig.	Error terms
Habitat	4	0.324	4.17	0.018	*	Site (Hab)
Site (Hab)	15	0.078	1.02	0.458	ns	Plot(Hab(Site))
Plot(Site(Hab))	40	0.076	2.53	0.000	***	Error
Error	5940	0.030				

[1] Data transformed to $\text{Log}_{10}(x)$

ns = not significant; * p<0.05; ** p<0.01; *** p<0.001

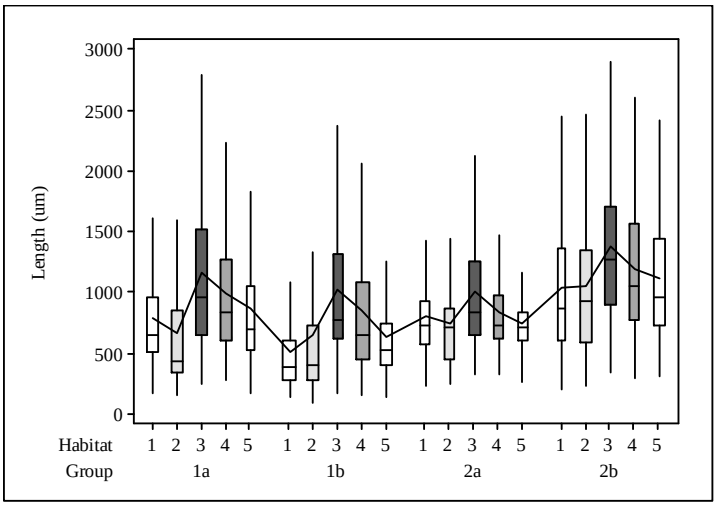

Figure 5.5. Boxplots of nematode length for each feeding group from each of the 5 lagoon habitats. Note that box width is proportional to the number of nematodes measured, which varied from 188 to 453 per habitat-group combination. The connecting line represents the mean of each feeding group.

Comparisons of nematode length for each feeding group across habitats revealed that the median length, first and third quartiles, upper whisker as well as mean length were all highest at habitat 3 (Figure 5.5).

Figures 5.6 and 5.7 show scatterplots of nematode body width versus length, and corresponding L/W frequency distributions for each habitat. Scatterplots and frequency distributions for all habitats pooled together are also shown. Body width versus length scatterplots confirm the presence of two morphotypes inhabiting habitats 1, 2, 4 and 5. These morphotypes show up in the scatterplots as two distinct clusters of points and in the frequency distributions as two distinct peaks, the first peak corresponding to the plump nematode morphotype at around a L/W ratio of 4, and the second peak corresponding to the typical slender morphotype at a L/W ratio of 22. In between these two peaks is a trough at a minimum L/W ratio of 10 to 12. However the actual position of the peaks and

troughs appears to vary slightly depending on habitat. At habitats 1 and 2 the plump nematode peak occurs at a L/W ratio of 4, whereas at habitats 4 and 5 the peak occurs at a higher L/W ratio of 8. These peaks are separated by troughs at a L/W ratio of 9 at habitats 1, 7 at habitat 2, and at 11 at habitats 4 and 5. At habitat 3, although a few plump nematodes exist, their numbers are vastly reduced with very few individuals having a L/W ratio less than 10. If the demarcation between plump and slender nematode morphotypes is set at a L/W ratio of 9, then 10.7- and 89.3 % of nematodes were of plump and slender morphotypes, respectively. Although nematodes were not identified, many of the plump nematodes (Figure 5.8) were of the genus *Richtersia* Steiner, 1916 (Pastor de Ward and Lo Russo, 2007). *Richtersia* spp. have large buccal cavities without armature and are non-selective deposit feeders (feeding type 1b). *Desmoscolex* spp. were also found in the plump nematode assemblage; these individuals are selective deposit feeders (feeding type 1a).

Frequency distributions of nematode L/W ratio were all right skewed and differed significantly between habitats (Kolmogorov-Smirnov Test, $p<0.05$). Only 28 nematodes had L/W ratios greater than 80. These were composed of all feeding groups, including 11 selective deposit feeders, 6 non-selective deposit feeders, 5 epigrowth browsers and 7 predators. The relationship between nematode body width and length and feeding group revealed two main clumps and many outliers (Figure 5.9). The main clump contains most of the nematodes and is composed of all feeding groups in the middle of the triangular area. Towards the line at the top edge there is a second clump consisting of plump nematodes which were predominantly non-selective deposit feeders.

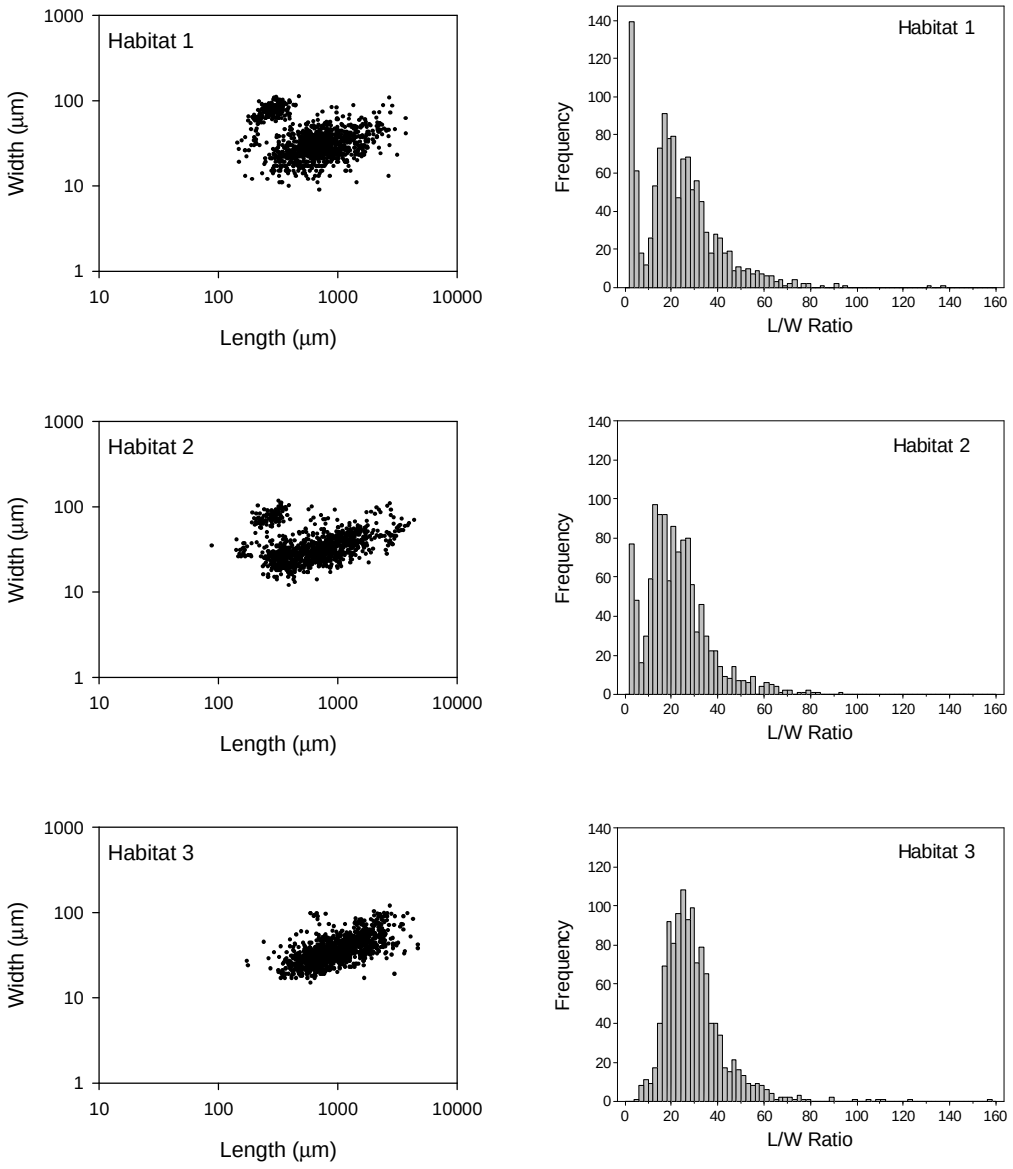

Figure 5.6. Scatterplots of body width versus length of nematodes from lagoon habitats 1 to 3 at Discovery Bay (left side), and corresponding frequency distributions of length/width ratios (right side). 1200 nematodes were measured per scatterplot / frequency distribution.

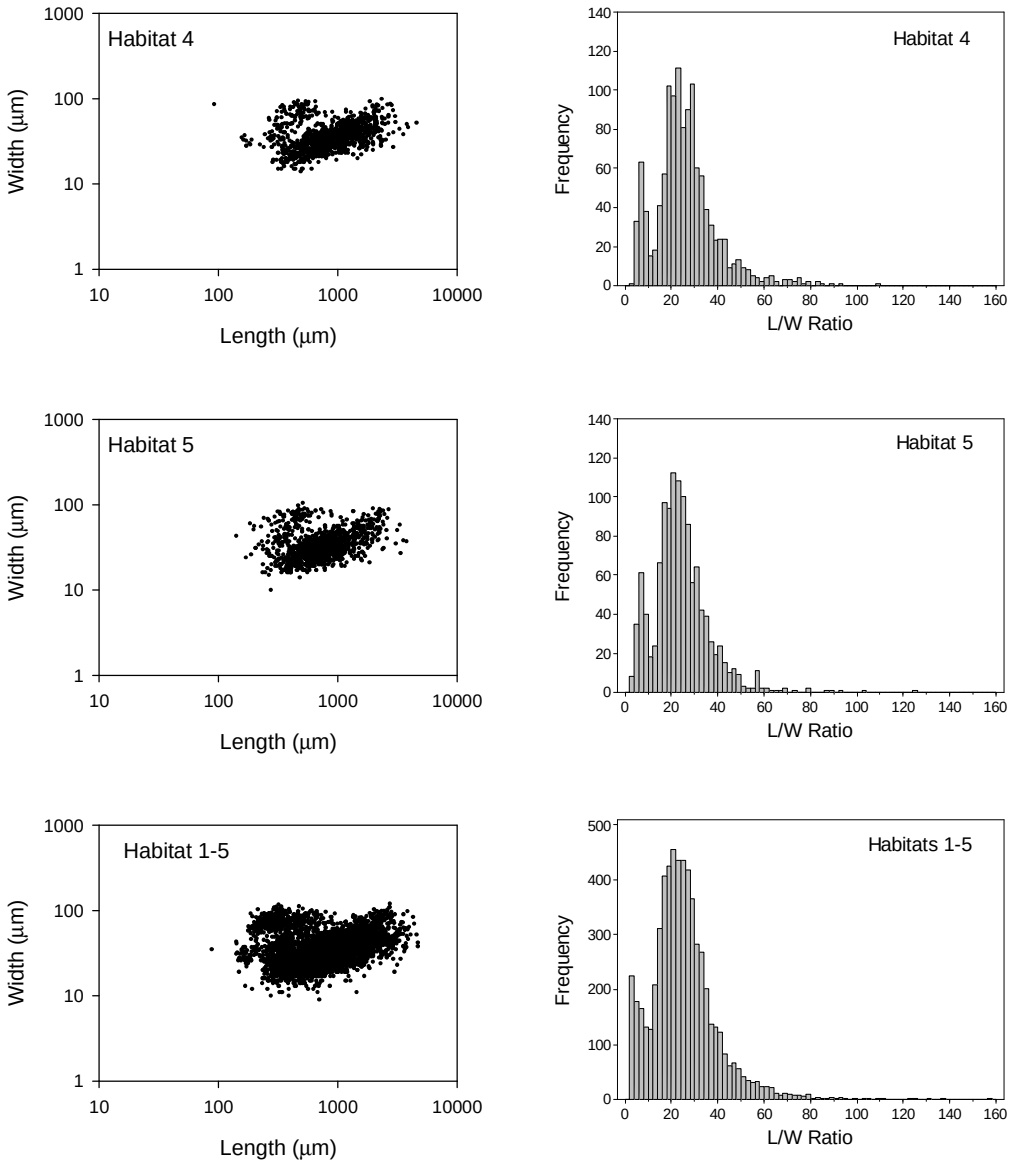

Figure 5.7. Scatterplots of body width versus length of nematodes from lagoon habitats 4, 5 and all habitats grouped together at Discovery Bay (left side), and corresponding frequency distributions of length/width ratios (right side). 1200 nematodes per scatterplot or frequency distribution were measured for individual habitats, and 6000 nematodes for all habitats grouped together.

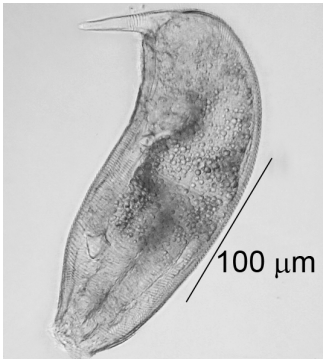

Figure 5.8. Plump nematode: *Richtersia* sp.

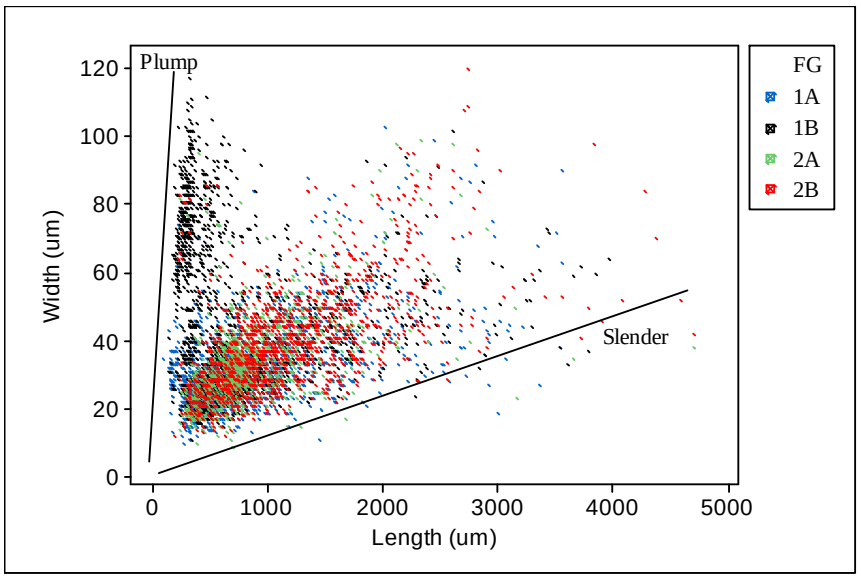

Figure 5.9. Relationship between nematode body width and length and feeding group. Plump nematodes are found nearer the top edge of the triangular area whereas slender nematodes are found nearer the bottom edge.

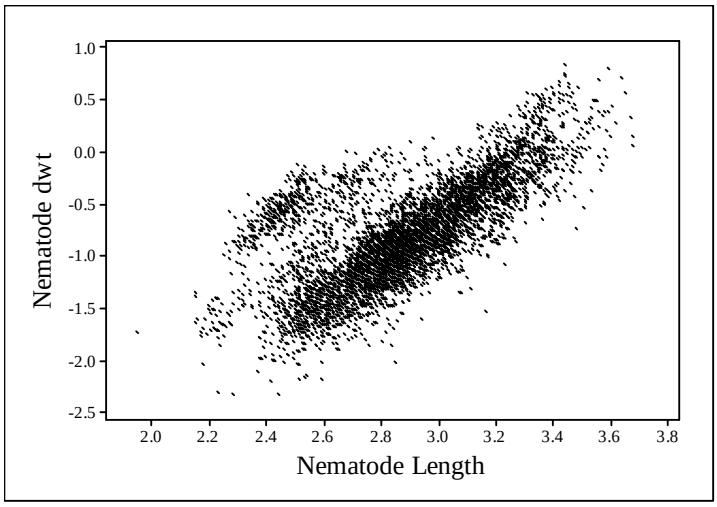

Figure 5.10. Relationship between nematode dry weight (dwt, μg) and length (μm). Scales are Log_{10}.

5.3.3. Nematode biomass and biomass spectra

Nematode biomass was significantly correlated with nematode length (Figure 5.10; Pearson's correlation coefficient, $r = 0.703$, $p < 0.001$, $n = 6000$). Individual nematode biomass was highest at habitat 3 and lowest at habitat 1 (Table 5.3). Mean nematode population biomass, calculated as the product of average densities at each habitat and average individual biomass ranged from 237 to 398 μg dwt 10 cm^{-2} (Table 5.3) equivalent to 95 to 159 μg C 10 cm^{-2}. Considering all the data, a crude mean figure of 113 μg C 10 cm^{-2} (0.113 g C m^{-2}) is calculated for the biomass of nematodes in the sediments in the west lagoon at Discovery Bay.

5.3.3.1. Regular biomass spectra

Regular nematode biomass spectra are shown in Figure 5.11. In general, spectra increased with increasing body size up to size classes -2 or -1 before decreasing in the larger size classes. For habitats 1 and 2, biomass peaked at size class -2 (0.25 –

to 0.5 μg dwt, equivalent to 0.1 to 0.2 μg C), whereas for habitats 3, 4 and 5, biomass peaked at size class -1 (0.5 to 1.0 μg dwt, equivalent to 0.2 – 0.4 μg C). Of note is that at H2 a second mode at size class 1 occurred due to a high predator and non-selective deposit feeder biomass. Visual inspections of the spectra show that total biomass at the peak size class differed between the habitats. At habitats 1, 2 and 5, total biomass at the peak size class varied between 70 and 80 μg dwt. At the coarse sand habitat H3 and the shallow thalassinid habitat H4 this value was much higher at ~130 and 100 μg dwt, respectively. While there was a rapid drop in biomass after the peak at size class 1 at habitat 4, this decrease is far less pronounced at habitat 3 and at size class 0 biomass is still above 110 μg dwt. Of note is that no nematodes within the smallest size classes 8 or 7 were found at habitat 3, or in size class 8 at habitat 2 or 4. Similarly no nematodes were found in the largest size class at habitat 5, even though the biomass at size class 1 for this habitat was still relatively high (38 μg dwt). While biomass was relatively low at the largest size class for habitats 1 and 4, at habitat 2 and 3 it was approximately 15- and 41 μg dwt, respectively.

5.3.3.2. Cumulative biomass spectra

Cumulative nematode biomass spectra are shown in Figure 5.12. These spectra show biomass per size class as a running total. All spectra appear relatively similar up to size class -3. At size class -2 spectra begin to depart from one another with differences in the rate of increase in biomass at larger size classes depending on habitat. The rate of increase in biomass at size classes larger than -2 is greatest for H3 and least for H1. Cumulative total biomass at H3 is more than twice the biomass at H1; other habitats were intermediate these two extremes. In

increasing order, cumulative total biomass for the remaining habitats was found at H2, H5, and H4, respectively. It should be pointed out that these biomass totals are based on the measurements of 1200 nematodes from each habitat.

Nested ANOSIM revealed that there were no significant differences in cumulative biomass spectra between sites nested within habitats, however significant differences between habitats were apparent (Table 5.7). Size spectra from the following habitats were significantly different from one another: 1 and 3, 1 and 4, 2 and 3, 3 and 4, and 3 and 5, with respective *R* values ranging from 0.427 to 1 (Table 5.7). Similarity percentages analysis (SIMPER) of total biomass per size class was used to determine the contribution of individual size classes to Euclidean dissimilarities between habitats. Information from SIMPER revealed that size classes -2 and -1, and to a lesser extent size class 0 contributed most to the dissimilarity between habitats. This is most easily seen in the regular nematode biomass spectra (Figure 5.11).

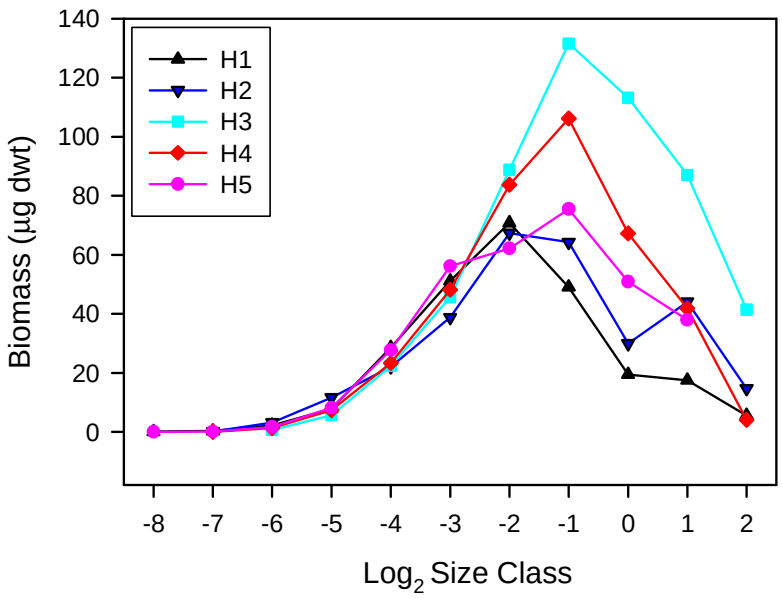

Figure 5.11. Regular nematode biomass spectra from each of the 5 lagoon habitats at Discovery Bay. Individual spectra represent data from 1200 nematodes.

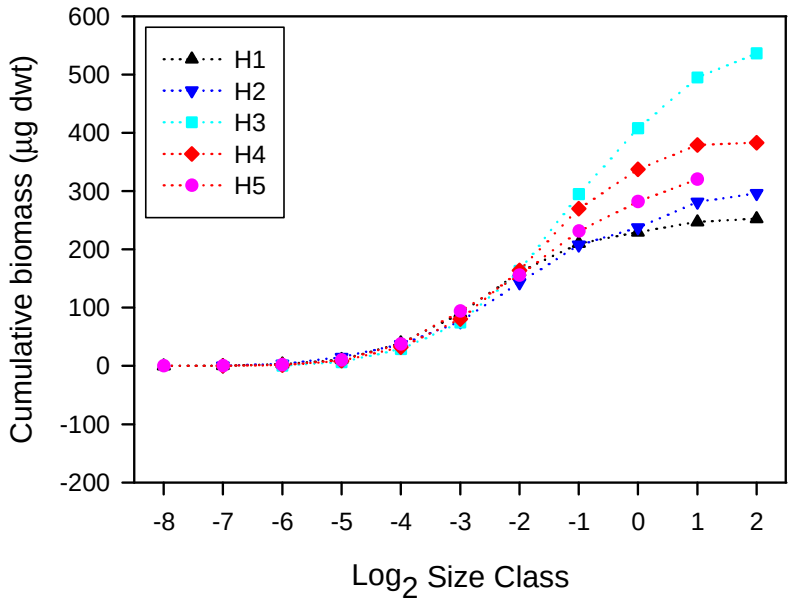

Figure 5.12. Cumulative nematode biomass spectra from each of the 5 lagoon habitats at Discovery Bay. Individual spectra represent data from 1200 nematodes.

Table 5.7. *R*-statistic values and significance of pairwise ANOSIM tests for differences in cumulative biomass spectra between the 5 lagoon habitats at Discovery Bay.

Global Test	*R*	*P*
Difference between nested Sites across all Habitats	0.05	0.07
Difference between Habitats using Sites as samples	0.458	0.001
Comparisons between Habitats	*R*	*P*
1 vs. 2	0.135	0.171
1 vs. 3	1	0.029
1 vs. 4	0.854	0.029
1 vs. 5	0.281	0.086
2 vs. 3	0.677	0.029
2 vs. 4	0.318	0.086
2 vs. 5	-0.01	0.40
3 vs. 4	0.427	0.029
3 vs. 5	0.573	0.029
4 vs. 5	-0.031	0.543

5.3.3.3. Abundance spectra

Nematode abundance spectra are shown in Figure 5.13. Peak abundance occurred at different size classes depending on habitat. Peak abundance occurred at size class -5 for habitat 2, at size class -4 for habitat 1, and at size class -3 for the remaining habitats. At habitats 1 and 2 abundances were higher in the smaller size classes (-8 to -6). At habitats 3 and 4 abundances were higher in the larger size classes (-2 to 0).

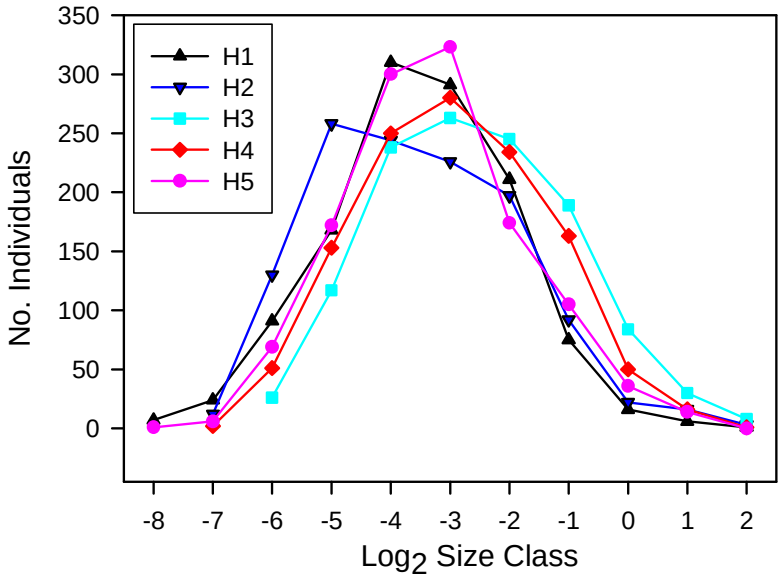

Figure 5.13. Nematode abundance spectra from each of the 5 lagoon habitats at Discovery Bay. Individual spectra represent data from 1200 nematodes.

5.4. Discussion

5.4.1. Nematode feeding groups

The study by Alongi (1986) was one of the first to examine the structure of nematode feeding groups within a coral reef environment. He found that different groups were associated with different functional zones of Davies Reef, on the Great Barrier Reef. At the reef crest and across the reef flat coarse to medium sands were inhabited primarily by predators/omnivores and epigrowth-feeding nematodes, while in fine to very fine sands in the lagoon non-selective and selective deposit feeders dominated. Gourbault and Renaud-Mornant (1990) also found that proportions of feeding groups differed between habitats in a Polynesian atoll, with non-selective deposit feeders dominating fine to medium clean sands and epigrowth browsers found in fine sands with a high silt content.

Like most lagoons, Discovery Bay is a heterogeneous environment, containing habitats which vary in sediment granulometry, biomass of microphytobenthos, extent of bioturbation and hydrodynamics. To a large extent the hydrography of any lagoon determines the characteristics of the sediments, with coarser particles dominating areas of wave swash and increased water motion, while finer particles are found in the more quiescent regions. Since nematodes are highly selective with regards to size, shape and quality of food offered (Wieser, 1953; Jensen, 1987), differences in the distribution of feeding types can give insight into the prevailing trophic conditions and food sources within a specific area. Although it is established that sediment organic content influences nematode distributions, rates of deposition of organic material exhibit high spatial and temporal heterogeneity within coral reef lagoons, as do sediment organic matter

concentrations (Sorokin, 1993; Alongi, 1998). While it is often expected that organic matter deposition should be higher in more quiescent areas, in coarse sediment reef zones deposition is not necessarily lower than in areas where finer sediments prevail. For example Koop and Larkum (1987) found highest deposition rates in the backreef area along a transect from the forereef to the lagoon. In contrast, due to large temporal variability Hansen *et al.* (1992) were unable to find any difference between a shallow site situated behind the reef crest and a deeper site in the main lagoon. Westrum and Meyers (1978), working at Discovery Bay measured carbon content of reef water in a transect running from the west forereef to the lagoon and detected an increase in TOC at a station situated just behind the reef crest. These authors concluded that "organic matter contributed at the crest is available as a resource to only a limited portion of the backreef community – that part located directly behind the reef crest". However this conclusion appears to be too simplistic. In times of adverse weather macroalgal detritus and organic particles, presumably sloughed off reefs on the seaward side of the reef crest and at the crest itself, are often observed wafting towards land within the water column. Furthermore, during algal blooms filamentous species such as *Chaetomorpha linum* are often deposited in the vicinity of habitats 4 and 5 (Pers. Com. Dr Jeremy Woodley, former Director of DBML, and own observations).

In the present study it was hypothesised that feeding groups would display particular affinities for certain habitats. In particular it was hypothesised that epigrowth-feeders, which use their teeth to scrape the surface of sand grains thereby grazing upon attached microalgae and bacterial mucilages (Wieser, 1953;

Giere, 1993) would dominate at habitat 2 where the biomass of microphytobenthos was highest. In contrast, non-selective deposit feeders were hypothesized to dominate the medium/fine sediments at habitats 4 and 5 (Aller and Dodge, 1974), situated in the quiescent region of the lagoon occupied by thalassinid shrimps, where the deposition and entrapment of particulate organic material between mounds was regularly observed.

While the data presented here indicate that nematode feeding group structure varied between habitats, some results were unexpected. Feeding group structure at habitat 2 was not dominated by epigrowth feeders, and therefore this hypothesis was rejected. In fact no particular group dominated at H2, although deposit feeders were most numerous. This may be because many selective and non-selective deposit feeders exhibit trophic plasticity and will consume diatoms and cyanophytes (Heip *et al.*, 1985; Moens and Vincx, 1997). Indeed Perkins (1958), who studied nematode feeding habits off the coast of Kent, concluded that Wieser's 1b group feed on diatoms and bacteria in equal measure. While microphytobenthos may be consumed, the formation of detritus from dead microalgae and leaching of extra polymeric substances can also enrich the sediment stimulating the microbial loop and providing a further food resource for deposit feeders (Uthicke and Klumpp, 1998). A number of studies have, however, shown that the relative abundance of epigrowth feeders can be highest in coarse grained coral reef sediments (Alongi, 1986; Boucher, 1997; Ndaro and Ólafsson, 1999; Netto *et al.*, 1999; Raes *et al.*, 2007). This is consistent with the results of the present study, although the difference in relative abundance between feeding groups in coarse sediments at H3 was not significant. Evidence that the biomass

of microphytobenthos in reef sediments is often highest in coarse grained sands (Johnstone *et al.*, 1990; Garrigue, 1998; Jones *et al.*, 1999) may nonetheless partly explain why epigrowth feeders have been found to dominate reef habitats of similar granulometry. In comparison, in muddy sediments in the North Sea, non-selective deposit feeders and epigrowth feeders dominated nematode trophic structure, which was largely explained by grain size and the total organic carbon content of the sediment (Schratzberger *et al.*, 2008).

Compared to temperate marine sediments, coral reef sands generally contain less organic material. Besides being highly permeable allowing for efficient advective exchange of particulate and dissolved materials with overlying waters, filtered organic material in coarse reef sands is rapidly mineralised by the microbial community (Rasheed *et al.*, 2003; Wild *et al.*, 2005; Sørensen *et al.*, 2007). The lower proportion of non-selective deposit feeders at H3 therefore likely reflects the oligotrophic nature of coarse reef sediments (Sorokin, 1993) and the removal of phytodetritus from the sediment surface due to strong hydrodynamic stress (Raes *et al.*, 2007). This results in the higher proportions of epigrowth-feeders and predators/omnivores, although nematode predation and top-down control of deposit feeders cannot be ruled out (Moens *et al.*, 2000). In addition physical disturbance may partly regulate nematode feeding group structure, since some diatom-feeding nematodes are more active than slow-moving bacterial feeders and are therefore less prone to physical disturbances (Schratzberger and Warwick, 1998). As will be discussed later, the length of nematodes at H3 was significantly greater than at other habitats, reflecting both the larger size of predators (and therefore the increased ability to consume smaller individuals), as well as a

possible adaptation to lower quality food resources resulting in species with longer gut lengths (Tita *et al.*, 1999).

At habitats 4 and 5 non-selective deposit feeders dominated the shrimp burrow habitats as hypothesized. This is probably because of an increase in the deposition of particulate detritus and associated bacteria in this part of the lagoon. On many occasions, particularly after adverse weather, both macroalgal and seagrass detritus were often seen accumulating within the dips between ghost shrimp mounds which appear to act as a catchment area for transient detritus. This matter would sometimes take from a few days to a week or more to fully decompose and would often be observed becoming overlaid with sediment.

Surprisingly feeding group structure was similar between habitats 1 and 4, an observation which was unexpected considering respective differences in sedimentary characteristics, although the biomass of microphytobenthos did not differ between the two habitats (Chapter 3). Ghost shrimps are deposit feeders and tend to be found in areas where there is increased deposition of detritus, resulting in sediments richer in organic matter which they feed on by removing it from around their mounds. This is suggested to slow bacterial growth rates (Hansen *et al.*, 1987). Although neither nematode densities nor feeding type are reported to differ depending on the top, side or bottom of the mound, Alongi (1986) found that nematode communities among ghost shrimp burrow ranges are almost exclusively dominated by non-selective deposit feeders. In contrast, in the Adriatic Sea, Koller *et al.* (2006) found that epistrate browsers dominated surface

sediments situated around mounds. The distribution of the macrobenthos within the Discovery Bay Lagoon has previously been related to a gradient in sediment stability; sediments in the western side of the lagoon, in the vicinity of habitat 4, were shown to be less stable due to high levels of biogenic reworking by ghost shrimps and contained a lowered diversity of macroinfauna compared to those on the eastern side (Aller and Dodge, 1974). Although these factors do not explain the similarity in nematode feeding group structure between such diverse habitats, they may offer further insight into the ecology of habitat 4 allowing future hypotheses about nematode feeding group structure between habitats 1 and 4 to be constructed.

5.4.2. Nematode morphometrics – lengths and widths

Nematode size-frequency distributions are typically right skewed with a long tail due to the high abundance of juveniles, a decrease in growth and increase in mortality with age (Soetaert *et al.*, 2002). In the lagoon at Discovery Bay the L/W size frequency distributions confirmed this generality of pattern. To my knowledge, the study by Grelet (1985) appears to be the only published study on the morphometry of nematodes from within a coral reef environment. Conducted along the coast of Jordan in the Red Sea, Grelet (1985) found that there was no difference in length between different habitats although he didn't offer any explanations for his findings.

In the present study nematode length was greatest in coarse sands, the L/W distribution shifting towards larger individuals at habitat 3. Longer nematodes,

besides having longer guts, are more mobile than smaller individuals providing them with a greater ability to seek accessible food (Soetaert *et al.*, 2002). As previously mentioned, the proportion of non-selective deposit feeders was much reduced at H3, possibly suggesting that the sediments had lower quantities of suitable food resources and/or that the quality of food was lower. Consequently, by having a longer gut the transit time of food within the body may be increased, resulting in a potential increase in absorption efficiency (Soetaert *et al.*, 2002). In a temporal study in the North Sea during and after a spring bloom event, decreases in the chlorophyll *a* concentration in bottom water after the bloom coincided with a decrease in small and corpulent species, and an increase in the abundance of larger adults (Vanaverbeke *et al.*, 2004). The findings of this temporal study seem synonymous with the differences between habitats in the present spatial investigation. In the more quiescent regions of the lagoon L/W histograms show an abundance of smaller, as well as plumper individuals. Yet at habitat 3 where deposition is limited and the substrate regularly disturbed by wave action, the histogram mode moves towards longer individuals. According to Tita *et al.* (1999), long guts are characteristic of animals exploiting low energy food. In their study, looking at nematode morphometry in the St Lawrence Estuary in Canada, they found that nematodes with small width-to-length ratios were characteristic of microvores, whereas greater ratios were typical of epigrowth-feeders and predators. Intermediate w/l ratios were found in ciliate-feeders, deposit-feeders and facultative predators. Tita *et al.* (1999) subsequently proposed a morphotype food-related hypothesis, whereby species morphotype reflects the quality of exploited food: nematodes with long guts such as microvores (i.e. small w/l ratio)

favour digestive efficiency, while those with short guts (i.e. larger w/l ratio), such as epigrowth-feeders and predators are adapted to high quality food.

Besides increased digestive efficiency, length may also convey advantages related to stability within the sediment, and hence the ability to prevent passive displacement into the water column, i.e. invertebrate drift (Palmer, 1988). At increased water velocities nematodes are more susceptible to being dislodged from sediments (Gamenick and Giere, 1994). Marine nematodes move through sediment interstices via a sinusoidal undulation of their longitudinal body musculature. Consequently, the minimum pore space through which they can move is primarily related to the length of the nematode, since the amplitude of undulation is proportional to body length (Kirchner *et al.*, 1980). Larger, longer nematodes, particularly those with long setae, are thought to be better adapted to hanging on to sediments in high energy environments (Warwick, 1971; Tietjen, 1976). Plus due to their length and wider girth they should also be better able to bridge sediment grains subjected to high advective pore water flow. Compared to finer sands and silts, coarse calcareous sands within reef systems are highly permeable and less cohesive, resulting in higher advective pore water flow rates (Rasheed *et al.*, 2003). Therefore, nematodes in coarse calcareous sands are potentially more likely to be subjected to higher erosive forces, than individuals of similar size in finer grained sediments where advective pore water flow rates are lower.

In a study on nematode morphometry from the shelf to the deep sea in European marine waters, longest average nematode lengths were found in sandbanks subjected to strong currents where food availability was extremely low (Vanaverbeke *et al.*, 2007b). As in this study, these authors hypothesised that the increased length probably prevents nematodes from being eroded. Increased nematode length may therefore be an ecological advantage helping to maintain occupancy within the sediment in habitats subjected to high levels of advective pore water flow or disturbance resulting in the suspension of individuals into the water column. This hypothesis is further backed by observations that the increased length of nematodes at H3 is independent of feeding group, i.e. the increased length is not simply due to the longer average length of predators/omnivores. Minimum and median nematode lengths were also highest at habitat 3.

It is nevertheless possible that shorter nematodes burrowed deeper into the sediment to avoid being swept away and were not adequately sampled in this study by the 5 cm deep sediment core. However *in situ* experiments conducted in sands of similar granulometry on the forereef seaward of H3 showed that nematodes did not increase in deeper sediment layers as current speed increased, to the point at which there was visible sediment disturbance (Gamenick and Giere, 1994). Furthermore, laboratory flume experiments found that as the speed of the water over the sediment increased, nematodes were entrained into the water column and their abundance in deeper sediment layers decreased (Gamenick and Giere, 1994). These observations therefore suggest that the larger lengths of nematodes at habitat 3 were not due to sampling artefacts. Lowest abundances of nematodes at habitat 3 (Chapter 4) further suggest that this habitat is less

hospitable to nematodes compared to the others surveyed within the lagoon. While nematodes were not identified to species, future studies should attempt to assess whether the increase in size at H3 is due to the community being composed of larger individuals of similar species as found in the rest of the lagoon, or alternatively whether there is a community shift towards different species that are longer and better adapted to the localised hydrodynamical disturbance.

5.4.3. Nematode morphometrics – plump and slender assemblages

Ratsimbazafy *et al.* (1994) were the first to confirm the existence of two distinct nematode morphotypes, consisting of a plump assemblage with low L/W ratios, and a slender assemblage with much higher L/W ratios. Further studies by other researchers have found these findings to be widespread (e.g. Soetaert *et al.*, 2002; Vanaverbeke *et al.*, 2004; Vanhove *et al.*, 2004). The results of the present study confirmed the existence of both plump and slender nematode morphotypes in the sediments of the coral reef lagoon at Discovery Bay. To my knowledge, this is the first time that both morphotypes have been documented from a coral reef environment. However, what is particularly interesting is that the plump morphotype was virtually absent in coarse sediments at habitat 3. In order to explain this finding, it is pertinent to discuss the theories that have been put forward regarding the adaptive advantages conveyed by being small and plump.

While slender nematodes comprise a large variety of nematode taxa, plump assemblages are typically composed of just a few, such as the desmoscolecids *Tricoma* spp., *Desmoscolex* spp., *and Richtersia* spp., as well as members of the

epsilonematids (Soetaert *et al.*, 2002; Vanaverbeke *et al.*, 2004). Since both morphotype groups include members from distantly related taxa, the duality in nematode design was hypothesized by Soetaert *et al.* (2002) to be an ecological adaptation conveying either greater mobility (i.e. slender/longer morphotype) or reduced vulnerability to predation (i.e. plump morphotype). This hypothesis was based on the fact that longer nematodes are more mobile and able to penetrate deeper into the sediment than shorter plump nematodes, whereas plump nematodes are heavily cuticularised with protective protrusions suggesting that these adaptations may be a defense mechanism against predation. Soetaert *et al.* (2002) further suggested that thin slender nematodes have a higher tolerance to lower oxygen levels than plump nematodes with increased body widths. Smaller nematode species likely have higher growth rates (e.g. Peters, 1983) and therefore the age at first breeding is reduced, since they reach adulthood faster than species that grow to a larger size. Consequently plump nematodes may be opportunists which take advantage of food supplies, but also quickly diminish in numbers when there are food shortages (see Vanaverbeke *et al.*, 2004).

So why were plump nematodes absent from habitat 3? At H3 sediment porosity was generally higher than at most other habitats (Chapter 3). Although porosity is of limited biological significance since it doesn't necessarily correspond to the pore volume available to animals (Giere, 1993), higher porosities and a low silt/clay fraction suggest larger interstitial spaces would be found at H3, thus not physically precluding fat plump nematodes. Moreover, minimum, maximum and mean nematode widths were all highest at H3, confirming that the size of the interstices were not a limiting factor for most individuals. It is possible that low

oxygen levels prevented plump nematodes from colonising sediments at H3, since compared to fine carbonate sediments oxygen consumption rates are greater in coarse carbonate sands (Rasheed *et al.*, 2003). This may partly explain why longer individuals and individuals with higher L/W ratios predominated, since they are better adapted to bridge gaps between oxic and anoxic layers in the sediment. If plump nematodes are more susceptible to low oxygen levels they would have been expected to reside within the top layers of the sediment, rather than being almost completely absent. This again rules out methodological artefacts caused by cores not being taken to a deep enough depth. Since plump nematodes were predominantly non-selective deposit feeders, perhaps their abundance was limited at H3 by the availability of suitable food resources? In sediments of the same median grain size but with different proportions of silt, Tita *et al.* (1999) found that nematodes with smaller L/W ratios were more abundant in sediments with increased organic matter, supporting their morphotype-food related hypothesis. Also, since plump nematodes are less mobile than the slender morphotype (Soetaert *et al.*, 2002), it is possible they are less adapted to hydrodynamic sediment disturbance and hence were unable to maintain contact with the benthos at higher friction velocities (a measure of shear stress or erosive force imparted by flowing water on bottom sediments and meiofauna (see Palmer, 1988)). It is therefore suggested that a combination of factors may be responsible for the absence of plump nematodes at H3. These include availability of oxygen, suitability of food resources, and the inability of individuals to resist dislodgement and erosion from sediments. In order to test this theory, as a first step laboratory flume experiments similar to those conducted by Gamenick and Giere (1994), but comparing nematode morphometry both in the water column and benthos

concurrently over a range of sediment particle sizes with different oxygen consumption rates should be conducted.

5.4.4. Nematode biomass and abundance / biomass spectra

The population biomass of nematodes varied between habitats within the lagoon but was highest at H2 which contained the highest biomass of microphytobenthos and abundance of nematodes (Chapters 3 and 4). A highly significant correlation between population biomass and microphytobenthos was found underlining the importance of this food resource, either directly via consumption or indirectly due to it's effect on sediment stability and the microbial web (Miller *et al.*, 1996; Moens *et al.*, 2002; van Oevelen *et al.*, 2006).

Average individual nematode biomass was highest at habitat 3 and was significantly positively correlated with grain size, corroborating the findings of Grelet (1985) for reef sediments in the Red Sea. In a study examining the relationship between nematode size and water depth from 120 locations around the world, mean nematode size was strongly correlated with median grain size over all depth ranges (Udalov *et al.*, 2005). Yet in contrast to the present study, when depth was removed from the model, the correlation between nematode size and grain size within the 0 to 10 m depth range became insignificant. However in the North Sea, average individual body size increased with decreasing grain size (Schratzberger *et al.*, 2008). Likewise, in the St Lawrence Estuary in Canada, mean individual nematode biomass was highest in muddy sediments compared to sandy sediments of similar median grain size (Tita *et al.*, 1999). This was because muddy sediments were mostly inhabited by large burrowing species. Above a

critical median grain size of about 200 μm most meiofauna are interstitial species (Wieser, 1959). For nematodes, however, the critical grain size is suggested to be even smaller (120- to 125 μm) due to their distinct slender morphology and sliding mode of transport which enables them to move through the slightest of spaces between sediment grains (Wieser, 1959; Coull, 1988). Since all sediment samples in the present study had median grain sizes > 182 μm, the majority of nematodes were presumed to be interstitial rather than burrowing species, hence the much higher abundance of the slender morphotype.

The range of nematode biomass (0.02- to 28 μg wet weight) found in this study is similar to the values found in other studies (e.g. Wieser, 1960; Gerlach *et al.*, 1985; Duplisea and Hargrave, 1996). Average nematode biomass figures of 0.3 g m^{-2} dwt and 0.113 g C m^{-2} for the west lagoon at Discovery Bay are calculated based on the product of average density and average biomass from all samples. These figures compare favourably to values found in the southern zone of the North Sea (0.5 g dwt m^{-2} Heip *et al.*, 1985) and lagoon sands in French Polynesia (~0.095 g C m^{-2}, calculated from Table 4 of Villiers, 1988), but are lower than in Helgoland Bight (0.6 g C m^{-2} Gerlach *et al.*, 1985) and tropical sediments in Gulf of Aqaba (1.06 g dwt m^{-2} Grelet *et al.*, 1987). Of course biomasses vary both spatially and temporally. Nevertheless these average values are the first obtained for this lagoon and should hopefully be of use in other studies, in particular trophic balance models such as ECOPATH (e.g. Polovina, 1984; Arias-Gonzalez, 1994; Rosado-Solorzano and Guzman Del Proo, 1998).

The present study is the first to examine nematode biomass spectra from a coral reef ecosystem. The results of the ANOSIM test demonstrated clearly that CNBS differed between habitats in the lagoon containing sediments ranging from fine to coarse sands. Consequently, the null hypothesis that there is no difference in nematode biomass spectra between habitats with contrasting sediment granulometry in the lagoon at Discovery Bay can be rejected. In coarse sands at H3 a shift towards higher biomasses in larger size classes (-1) was observed, while individuals were absent in the two smallest size classes (-8, -7). NBS from the remaining habitats were intermediate between H1 and H3, but shifted towards higher biomasses at larger size classes in the highly bioturbated medium to medium/fine sands at H4 and H5, respectively. Furthermore, average individual biomass in coarse sands at H3, where nematode abundance was lowest (Chapter 4), was more than double the amount found in undisturbed fine sands at H1.

While a number of studies have examined the entire biomass spectra of metazoan benthic organisms, Vanaverbeke *et al.* (2003) quoting (Edgar, 1990) mentioned that using different sampling gear and sieves with different mesh sizes (e.g. Gerlach *et al.*, 1985) can lead to the overestimation of biomass in the lower size classes. Vanaverbeke *et al.* (2003) further remarked that the use of different sampling gear could also introduce bias since a single type of gear is designed to effectively sample organisms within a specific size range. Hence these authors suggested that using a single type of sampling equipment and a single sieve mesh size to sample a single taxon such as the dominant meiofaunal taxon, i.e. the nematodes, could overcome some of these problems.

Unfortunately literature on nematode biomass spectra from sites of similar depth is not available; moreover there are no reports in the literature of benthic biomass spectra from tropical marine habitats. Nevertheless differences in biomass spectra have been suggested to be due to numerous factors, including sediment disturbance and food supply, For example, on the Belgian Continental Shelf the temporal effects of a phytoplankton bloom (food pulse) on NBS were examined (Vanaverbeke *et al.*, 2003). Concomitant with an increase in chlorophyll *a* in bottom waters, nematode biomass increased in the middle part of the regular nematode biomass spectra, due to an increase in the abundance of juveniles. This was attributed to the higher food availability in the months proceeding the bloom. In the present study a similar yet spatial effect was found. While it is only just evident in the regular biomass size spectra, the abundance size spectra clearly shows an increase in the number of individuals at habitat 2 in size classes -6 and -5. These nematodes were most likely juveniles and/or small opportunistic species possibly responding to the increased availability of microphytobenthos, breakdown products, or other related factors (i.e. extrapolymeric substances, bacteria, detritus, sediment stability). In organically enriched sediments, Duplisea and Hargrave (1996) showed that small meiofauna compose a larger fraction of the meiobenthos. Nonetheless, the slope of the upper half of the CNBS at habitat 2 was less steep than habitats 3, 4 and 5, suggesting that the increased biomass of microphytobenthos and relative increase in the number of individuals in smaller size classes had limited influence on the total cumulative biomass. Thus the consistent elevated levels of microphytobenthos at H2 over the study period did not seem to produce the same sort of effect on the biomass spectra as documented by Vanaverbeke *et al.* (2003). Of note though is the small second peak in the

RNBS at H2 at size class 1 which was due to a few large non-selective deposit feeders and predators/omnivores. The predators were possibly responding to the increase in abundance of smaller prey nematodes. Yet as noted by Schratzberger *et al.* (2008), community metrics can obscure strong responses of individual species, since increases in body size in response to food availability is highly species-specific (e.g. dos Santos *et al.*, 2008).

In the North Sea the effects of an annual phytoplankton production cycle on nematode community dynamics were followed (Schratzberger *et al.*, 2008). While most nematode species bred continuously throughout the sampling period, the epigrowth-feeding species *Spilophorella paradoxa* had increased growth following the deposition of the spring phytoplankton bloom. Body size distributions of this species varied spatially and temporally but were clearly related to differences in food resources in the sediment. High levels of both fresh and refractory material coincided with equal proportions of juveniles and adults in the population. However as carbon resources diminished over the winter months, smaller individuals increased and larger nematodes declined. Although the present study did not attempt to assess biomass spectra of individual species, it is interesting that the abundance spectra at H2, the most productive habitat, was dominated by smaller individuals yet with low biomass in the larger adult size classes. At several stations in the Bay of Fundy in Canada, causal analysis suggested meiofaunal biomass spectra were a function of fine sand and the abundance of microalgal biomass (Schwinghamer, 1983). Duplisea and Hargrave (1996), also working in the Bay of Fundy, were unable to detect differences between meiobenthic biomass spectra along a gradient of sediment organic

enrichment in the vicinity of a salmon aquaculture farm, suggesting that the additional organic material had limited effect. However in the deep sea, although nematode body size tends to decline with depth according to the body size miniaturisation hypothesis (Thiel, 1975), sites with increased food resources tend to have larger nematodes and higher biomasses in larger size classes than oligotrophic sites (Vanreusel *et al.*, 1995; Sommer and Pfannkuche, 2000; Udalov *et al.*, 2005; Kaariainen and Bett, 2006).

Besides the availability of food, nematode biomass spectra may also be affected by sediment disturbance caused by sand extraction and trawling. On the Kwintebank off the coast of Belgium, at a high sand extraction station biomass peaked earlier in the spectra relative to unexploited sandbanks and areas with low sand extraction, although differences in spectra between stations were not significant (Vanaverbeke *et al.*, 2003). These authors suggested the peak could be due to smaller species being more resilient to disturbances caused by sediment removal, resuspension and changes in overlying water currents, since smaller species show rapid growth and early reproduction and are often deemed 'colonisers'. Vanaverbeke *et al.* (2003) also found that biomass peaked at higher size classes at their Kwintebank gully station with limited extraction, and attributed this to the station having fine sediments with a median grain size of 171 µm. This is in contrast to the present study which found biomass peaked at lower size classes in fine sands at habitat 1, and higher size classes in disturbed sands at 3, 4 and 5. In the Baltic Sea, Duplisea and Drgas (1999) examined the complete metazoan size spectra across sites ranging from coarse sand to mud; however significant differences in spectra were found only over the smallest metazoan size

ranges corresponding to the meiofauna. In fine sediments biomass peaked at lower size classes than in the coarser sediments, in agreement with the results of the present study.

Where biomass spectra have been utilised to examine the effects of trawling disturbance on meiofauna communities, and nematodes in particular, Schratzberger *et al.* (2002) showed that there were no short- to medium term (1 – 392 days after trawling) impacts on nematode biomass or diversity, although community structure was slightly affected. These authors reasoned that nematodes, due to their small size, were likely resuspended by the benthic trawls and therefore suffered limited mortality; high turnover rates and short life cycles compensating for any short term negative effects. In contrast in the Aegean Sea, Lampadariou *et al.* (2005) found that 30 days after trawling most of the large nematodes were absent due to the disturbance at most sites studied. However this was not the case at their coarsest sediment site (median diameter 127 µm), a fact they could only relate to the size of the sediments.

Interestingly, when the magnitude of difference in average median grain size (µm) between any two habitats is less than 130 µm, the respective spectra are not significantly different (apart from habitat combination 1 vs. 4: 340 – 210 = 130 µm; see Chapter 3). This suggests that spectra from habitats with large differences in median grain size are more different to one another, whereas those with similar grain size are more similar. Nonetheless, while this study has shown that nematode biomass spectra from habitats of contrasting granulometry differed, the granulometry characteristics largely reflect the degree of exposure to currents and

waves. Despite the fact that grain size varied between habitats in this study, sediment disturbance caused by wave swash and bioturbation also varied. Although sediment disturbance was not quantified, sediment resuspension and bioturbation at a number of sites located close to the habitats in the present study have previously been evaluated by Aller and Dodge (1974). At their A5 station located in the vicinity of habitats 4 and 5, sediments were highly unstable due to intense bioturbation by *Callianassa* spp. and easily dispersed and resuspended by wave action (average 19 mg sediment cm^{-2} per day). In contrast, sediment resuspension was much lower at their B5 station (average 6 mg sediment cm^{-2} per day), which was located in close proximity to habitat 2. Furthermore, sediments at B5 were bound with benthic algae (supporting observations in Chapter 3), which helped to stabilise the sediments (Aller and Dodge, 1974; Miller *et al.*, 1996). According to Gray (1981), sediments composed largely of particles around 180 µm in size are the most stable of all, and occur where wave and current action are minimal. At habitat 1, average median grain size was 210 µm and there was limited bioturbation by epifauna and little sediment disturbance due to wave action. Therefore habitat 1 was deemed the most stable out of all habitats surveyed in the present study. Although it is acknowledged that grazing by spatangoid urchins and bioturbation by the abundant meiofauna community would tend to destabilise sediments at habitat 2, the high biomass of microphytobenthos would have an opposite, stabilising effect (Chapter 3 and Aller and Dodge, 1974; Miller *et al.*, 1996). Hence sediments at habitat 2 were also deemed relatively stable. Considering that habitat 3 was subject to intense wave swash, and that habitats 4 and 5 were intensely bioturbated, the differences in biomass spectra

could also possibly be explained by variations in natural disturbance at the various habitats.

In the marine environment disturbances due to wave motion and bioturbation are key factors which influence the structure and dynamics of soft-sediment benthic communities (see reviews by Hall *et al.*, 1994; Sousa, 2001). However NBS have not been specifically compared between habitats subjected to differing amounts of wave motion and bioturbation before. Yet since nematode biomass is significantly positively correlated with length, larger heavier (albeit only fractionally so) nematodes may be better adapted to withstand sediment instability in two ways: firstly they may be less delicate than smaller individuals and thus more able to withstand increased sediment movement, and secondly, due to their weight, it would take more energy to suspend them into the water column than lighter individuals. Obviously a key factor which small light benthic organisms have to contend with is living in sediments subjected to movement, resuspension and advective porewater flow. These factors would all tend to increase the passive incorporation of surface dwelling nematodes into the water column (see Palmer, 1988; Boeckner *et al.*, 2009).

As mentioned above, Vanaverbeke *et al.* (2007b) recently reported finding longest average nematode lengths in sandbanks subjected to strong currents and suggested that the increased length probably prevents them from being eroded. In highly dynamic sediments, large body size and long cephalic setae are also suggested to help provide anchorage (see Warwick, 1971). Therefore, while food availability and sediment disturbance influence nematode abundance and biomass size

spectra, it is also suggested that spectra in the shallow lagoon at Discovery Bay are also influenced by localised hydrodynamics. Moreover, it is hypothesized that water flow over and through the benthos selectively removes smaller individuals. Furthermore, it is suggested that this effect is greatest in sediments subjected to disturbances caused by high wave swash and bioturbation, which result in high advective porewater flow due to high pressure gradients (Precht and Huettel, 2003) and sediment resuspension (Aller and Dodge, 1974), respectively. Therefore, in order to more fully understand the causes of variation in nematode biomass spectra, the effect of hydrodynamics, bioturbation and sediment disturbance on nematode communities should be further studied.

5.5. Summary

Nematodes are increasingly being used to monitor the influence of natural and man-made disturbances on the marine environment. This study, conducted in a relatively pristine environment, revealed that different methodological approaches offer diverse insights into the relationships between the nematodes and the benthos. Differences in feeding groups, morphometry, and biomass spectra were found within the lagoon, however relationships with sediment characteristics and food resources were complex. Community metrics appeared to shift towards larger nematode lengths and higher biomasses at larger size classes as sediments shift from fine to coarse sand. While localised hydrodynamics largely cause observed grain size distributions, sediment stability and the potential for erosion of smaller individuals from sediments appears to be a plausible theory partly explaining the observed variations in morphometrics and size spectra within the lagoon. The observations in this study should therefore further enhance our

knowledge of the most abundant metazoan in the marine environment, while also allowing specific hypotheses to be constructed. The results presented can also provide baseline data from which to monitor natural change in nematode communities, as well as the effects of man-made disturbance on the benthos in the lagoon in the future.

6. SYNTHESIS AND CONCLUSIONS

The overall aim of this thesis is to understand the spatio-temporal patterns in the benthos within the shallow west lagoon at Discovery Bay, in order to gain further insight into the ecology of meiofauna and microphytobenthos. As one of the best studied coral reef ecosystems in the world, it is surprising that so few investigations have been conducted on the soft-sediment lagoon benthos. Since meiofauna are imperative to the structure and functioning of marine ecosystems, and microphytobenthos are at the base of soft-sediment food chains, this mensurative thesis aimed to investigate patterns in meiofauna and microphytobenthos in characteristic habitats within the shallow lagoon.

6.1. Aim 1: To characterise the sediment granulometry of five characteristic and visibly different habitats within the shallow lagoon

As a prerequisite to any benthic sampling campaign, the sediment characteristics of the study areas were assessed. These included sediment particle size distributions and derived granulometric statistics. Although sediments within seagrass beds were not examined, the habitats selected encompassed a range that were typical for the shallow lagoon. These included flat white fine sands in a sheltered area to coarse sands at a site bordering the backreef subject to wave break. Grey enriched medium sands of increased productivity midway between the reef crest and land were also surveyed, as were two topographically-complex thalassinid shrimp mound habitats, one shallow and the other slightly deeper both with increased proportions of fine particles.

Among the study sites there was a large degree of variation in the univariate physical characteristics of the benthos, yet the multivariate analyses effectively separated the stations into discrete habitats, confirming initial visual observations. Hence the first aim of this study was successfully completed.

6.2. Aim 2: To assess the spatial and temporal variation in microphytobenthos within the shallow lagoon

In soft-sediment habitats microphytobenthos is at the base of the food chain, stabilises sediments, and plays a large role in nutrient cycles. Assessment of microphytobenthos is therefore a fundamental precursor to the many processes driven by microphytobenthic primary production. However until the present study was conducted, microphytobenthos in the west lagoon had never been assessed before.

The biomass of microphytobenthos within the 5 habitats compared favourably with other tropical lagoon systems. In agreement with the literature, biomass was extremely patchy over small spatial distances, with most of the variation attributed to the plot scale. While average biomass was similar between most habitats, elevated levels were consistently found at habitat 2 over 3 sampling events during the study period. Between 1995 and 1996, surveys conducted within the main bay showed that sites in deeper waters and those situated around the south west of the bay were richer in nitrate, possibly due to a lack of proper sewage treatment systems and the wide-spread use of soak-away pits in the local vicinity (Webber *et al.*, 2005). While the influence of *in situ* decomposition was not mentioned, the

deep main bay acts as a sink for particulate detritus wafting in from reefs situated north east of the lagoon. It is therefore plausible that this area is also a source of recycled nutrients. Consequently, the elevated biomass at H2 was explained by the large body of water that travels over that habitat, supplying nutrients derived from both anthropogenic sources as well as the mineralisation of detritus deposited in the main bay.

Considering the abundance of meiofauna at H2, the elevated biomass of microphytobenthos almost certainly had an effect on the sediment communities. Furthermore, deposit feeding heart urchins were attracted to the area and consumed the rich sediment deposits. As heart urchins burrow they release trapped nutrients, enhance the flux of oxygen into the sediments further stimulating microbial decomposition and remineralisation, and provide a source of excretory ammonium (Lohrer *et al.*, 2004; Lohrer *et al.*, 2005; Vopel *et al.*, 2007). These factors combined further enhance microalgal production. High numbers of deposit- and epigrowth feeding nematodes, as well as presumably many grazing and bacteria-consuming copepods, were most likely sustained both directly by the microphytobenthos itself, and indirectly due to breakdown products, exudates and it's effect on the microbial web. Like the heart urchins, nitrogenous excretion by the high density of meiofauna (Gray, 1985) also enhances benthic primary production helping to maintain the high levels of benthic microphyte biomass over time at habitat 2.

6.3. Aim 3: Assess the spatial variation in meiobenthos within the shallow lagoon

Total meiofaunal abundance was in line with many other studies from similar habitats. Accordingly, nematodes dominated the meiofauna with copepods coming second. A total of 22 higher taxa were recorded, of which 6 (nematodes, copepods, turbellarians, polychaetes, oligochaetes and ostracods) contributed more than 1% to total abundance.

The distribution of common taxa was heterogeneous within the lagoon, and the structure of the communities clearly differed between habitats. As mentioned already, the high biomass of microphytobenthos at habitat 2 appeared to have a positive effect, either directly or indirectly, on the abundance of nematodes and copepods whose abundances were highest there. Variance components revealed that the proportion of variation was greatest at the smallest spatial scales, confirming the patchy nature of meiofauna communities.

Unfortunately biotic and abotic samples were not paired with one another at the time of sampling. Therefore attempts to correlate or match the patterns in faunal distributions to the benthos using the complete data matrix were prevented. Efforts were therefore made to indirectly match the variation in spatial patterns by plotting average Euclidean distances (sediment) and Bray-Curtis dissimilarities (meiofauna) for each spatial scale against one another. This was done to see if the fauna varied at similar spatial scales to that of the sediment granulometry parameters. However only habitat 2 showed a similar pattern of change in the

magnitude of the two indices at the different spatial scales. This suggests that, for the most part, the meiofauna were not responding directly to the variation in the measured sediment characteristics, and implies that other factors were most likely interacting to cause observed spatial distributions. This is not surprising considering the whole host of other factors besides sediment granulometry which influence patterns in the distribution of benthic organisms, such as predation, competition and sediment biogeochemical properties.

6.4. Aim 4: Examine nematode feeding groups among habitats in order to test hypotheses that different groups have affinities for certain benthic conditions

Based on visual observations of accumulated macroalgal and seagrass detritus at H4 and H5, as well as the fact that sediments in lagoons colonised by thalassinid shrimps are usually enriched with detritus and organic matter, it was hypothesized that non-selective deposit feeding nematodes would dominate at habitats 4 and 5. This was indeed correct and the relative abundance of this group was significantly higher than the rest. Non-selective deposit feeders also dominated at H1 in the fine clean sands perhaps due to it being a stable environment with high microbial resources. Additionally, epigrowth feeders were hypothesized to dominate where the biomass of microphytobenthos was highest. However this hypothesis was rejected since no particular group dominated at habitat 2. Deposit feeders, however, were most numerous, probably because of the varied range of sizes and types of food items that these two groups can consume. While it was apparent that different groups had affinities for particular habitats, the minimum relative proportion of any feeding group was ~ 15%, thus to some degree all groups were

represented at each habitat. This was confirmed by the high index of trophic diversity at each habitat.

6.5. Aim 5: Examine nematode body size and biomass spectra from communities subjected to different sediment conditions and forms of natural disturbance.

Differences in nematode lengths were found between habitats although widths were more homogeneous. Nematode lengths were shortest in the more stable habitats H1 and H2, longer in the bioturbated habitats H4 and H5, and longest at H3 in coarse sediments subject to wave swash. While these differences could have been due to variations in the age structure and species composition of the communities, it is argued that length conveys advantages towards stability within the sediment and erosion from it regardless. Frequency distributions of L/W ratios documented the shift in nematode size among the habitats, and revealed the disappearance of the plump morphotype group of nematodes at the wave disturbed habitat 3. Due to the high wave swash at H3, deposition of detritus is decreased there and high advective pore water flow likely removes much of the particulate organic matter and also many of the smaller nematode individuals from the sediments. Hence the longer size is possibly a two-fold response to erosive hydrodynamic forces and lowered food quantity and/or quality; nematodes from food poor environments being hypothesized to have increased L/W ratios in order to maximise assimilation efficiency of available food resources (Soetaert *et al.*, 2002; Tita *et al.*, 1999).

For the first time nematode abundance and biomass spectra were constructed for a coral reef environment, and significant differences in biomass spectra between habitats of contrasting sediment grain sizes were found. In disturbed sediments spectra shifted towards larger size classes and spectra peaks were recorded at higher biomasses. These results were in contrast to several published reports of disturbance due to trawling and sand extraction. The reasons for this are not entirely clear, but may suggest a differential response of nematode morphometrics to levels of natural compared to anthropogenically induced disturbances. Nevertheless, it is hypothesized that larger nematodes, which are also longer individuals, are better adapted to natural disturbance caused by waves and bioturbation. This may be due to being physically stronger, more able to resist erosion, or simply since they are heavier (although marginally so) and therefore not as likely to be entrained into the water column.

6.6. Discussion of methodology

Although this study showed that there were no temporal differences in the biomass of microphytobenthos between dates, variability in microphytobenthos over small times scales in the order of days is known. In order to show that there were indeed no significant differences (or significant differences, for that matter) between dates a few weeks apart, replication of the sampling unit, i.e. time, is needed (Underwood, 1997). Without this extra level of sampling the findings are, in effect, spatial ones since there is no temporal replication to unconfound variability at the 3 weekly time scale from that which could, and most likely, occurred at faster intervals (Underwood, 1997). In the present study replication of the temporal sampling unit was not undertaken due to the massive additional

amount of sampling effort that would have been needed, considering the high resolution of the spatial sampling design. This a possible criticism of the temporal sampling design used in this study.

Regarding the spatially nested sampling design, it should also be mentioned that the possibility arose for sites nested within habitats, as well as for plots within a site to be adjacent to one another. Although the positioning of sites within a habitat were never contiguous, it cannot be remembered if plots within a site ever were. If they had been, the assumption of independence of sampling units would have been violated. If so, it is recognised that variation at the residual scale would not have been able to be separated from variation at the plot scale in the proceeding nested Analysis of Variance (Underwood, 1997). In hindsight, replicates at all nested scales should have been assigned to positions within the relative habitat under the constraint that replicate units could not be contiguous. This would have alleviated the possibility of lack of independence in sampling units if plot samples had been contiguous to one another. Nevertheless, it is not possible to correct for this after the event and therefore the analysis was run as planned. The consequence of this is that, if plots had been assigned to contiguous positions depending on the random number generation sequence, residual variation would be confounded by variation at the scale of plots.

As discussed by Udalov *et al.* (2005), there are a number of sources of error, including preservation effects, weight calculations determined by different gravimetric and volumetric methodology, as well as conversion factors which one should be cautious of when making comparisons between biomasses of

meiofauna. In the present study a 40% conversion factor of dry weight to carbon biomass has been used in line with the majority of studies in the literature. Nonetheless, empirical determinations have suggested a dry mass to carbon conversion factor of 51.4% is more appropriate (Baguley *et al.*, 2004). This would tend to increase the figure calculated for carbon biomass of nematodes within the lagoon. Likewise, the 63 μm mesh aperture used for the separation of meiofauna from sediments would undoubtedly allow some of the smallest metazoans to pass through, thus underestimating the densities reported herein.

The number of measurements on nematodes from each habitat was equal (50 per sample, n=24, 1200 nematodes measured per habitat), yet absolute abundance among habitats varied. In order to obtain more accurate biomass spectra data, either all nematodes should be measured, or if this is not possible the number measured should be stratified so that the same proportion from each habitat is assessed.

6.7. Suggestions for further work

i) *Meoma ventricosa* are easily collected in the field, due to their size, tracks and surface burrowing lifestyle. *In situ* enclosure experiments could be conducted at habitat 2 to assess the effects of different densities of *M. ventricosa* on the biomass and production of microphytobenthos, the abundance and diversity of the meiofaunal community, and nematode feeding groups, morphometry and biomass spectra.

ii) Stable isotope analysis of flora, fauna and sediments would help to unravel the complicated interactions and trophic relationships between the different benthic compartments. In particular, the $\delta^{13}C$ and $\delta^{15}N$ isotopic compositions of selective nematode and copepod species could be used to assess the relative importance of different food sources.

iii) In order to test whether nematode length helps prevent against erosion from sediments, laboratory flume experiments could be conducted at different flow speeds and with natural sediments of varying median grain sizes (e.g. Gamenick and Giere, 1994). Morphometric analysis of organisms in sediments and the water column over a range of flow speeds would help to confirm the hypothesis that longer nematodes are better adapted to resist erosion from sediments. *In situ* experiments using suitable baffles to limit current speed and advective pore water flow, and cages to exclude thalassinid shrimps, would also help to understand the relationship between hydrodynamics, bioturbation and nematode morphometrics.

6.8. Concluding remarks

It is believed that this mensurative thesis has laid the groundwork for future studies on the benthic meiofauna and microphytobenthos in the shallow west lagoon at Discovery Bay. In light of the fact that shallow lagoon and bay ecosystems are currently under threat due to the effects of man, the observations and results contained within this thesis will surely be of help in the design of future monitoring protocols and ecological experiments.

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