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Ecological Monitoring of the Okura Estuary
Report 3: Final report for the year 2001-2002.

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Ecological Monitoring of the Okura Estuary Report 3: Final report for the year 2001-2002.

Dr M.J. Anderson
Dr R.B. Ford
Dr C. Honeywill
D.A. Feary

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Private Bag 92012
Auckland

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Department of Statistics and Leigh Marine Laboratory
University of Auckland

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Executive Summary

The Brief

The purpose of the monitoring programme in 2001-2002, reported here, was to document and compare levels of sedimentation among sites within the Okura Estuary and to examine the relationship between site characteristics, such as sedimentation, erosion and grain size data, with soft-sediment fauna. This work also provides information concerning current potential short-term effects of run-off within the estuary after periods of heavy rainfall. The study monitored sedimentation and benthic infauna at sites within the Okura estuary that were identified by previous studies (Cooper et al. 1999) as having "high", "medium" or "low" probabilities of sediment deposition. Although 16 sites (5 low, 7 high and 4 medium) were discussed by Cooper et al. (1999), 15 sites (5 low, 5 high and 5 medium) were chosen for the present study to achieve a balanced sampling design, 9 of which overlapped with sites monitored in last year's programme (Anderson et al. 2001b). The scientific classification of each of these sites into one of the three depositional probabilities was obtained directly as given from the map provided in Cooper et al. (1999, Fig. 3). Specifically, we addressed the question: Are the purportedly "high", "medium" and "low" depositional areas within the estuary actually different in terms of (i) the relative sediment load they receive after heavy rain and (ii) the extent of the impact on the fauna?

Primary Results

- Seventy-one percent of the multivariate variation in assemblages in the Okura estuary can be explained using the 16 physical variables measured.
- The strongest distinction among assemblages in the Okura estuary was that of spatial differences from site to site; all 15 sites were distinguishable from one another.
- Differences among sites were driven mainly by sediment characteristics, the existing ambient sediment grain sizes explained 46% of the variation in assemblages, and the short-term deposition of sediments explained an additional 12% of this variation.
- Assemblages in High depositional sites were very distinct from those in Low or Medium depositional sites.
- There was little difference between assemblages in Medium versus Low depositional environments.
- Seasonal effects on assemblages were also significant, although these were not as strong as the effects of Deposition.

- Although some effects of Precipitation (events of heavy rainfall) were detected, these varied seasonally and were much weaker than the effects of Site, Deposition or Season.

- Directional changes through time were detected in the assemblages at Okura within each of the three different depositional environments.

Recommendations

- Future sampling that incorporates additional estuaries should disregard sampling of chlorophyll *a* and sediment organics, as these did not aid models of ecological macrofaunal assemblages.

- In the future, two models should be developed for use across all estuaries in explaining biological variation:
    1. The physical characteristics of the sites (including distance from the mouth of the estuary, ambient sediment grain sizes and sediment deposition) should be used to create an overall physical gradient model of all sites, including those at Okura.
    2. These physical variables should also be used to classify sites in new estuaries into High, Medium and Low depositional environments.

- Future sampling for the Okura estuary should be combined with data from 2001-2002 to examine short-term and long-term patterns and directions of temporal change.

- To interpret the results from Okura in a wider regional context similar sampling designs should be employed in comparable estuaries.

- Data on existing sediment characteristics and ongoing sediment deposition are needed from Okura and other estuaries in the future to explicitly link biological changes with potential sediment influxes.

Introduction and Rationale

Background

Increased sedimentation caused by human activities has been shown to impact estuarine and coastal diversity over both large (100's km) and small (cm) scales (Edgar and Barret 2000; Benedetti-Cecchi et al. 2001). Macrofaunal species assemblages in soft-bottom intertidal areas are likely to be affected by a number of factors. Existing sediments at a site reflect long-term hydrodynamics and depositional history. The nature of these existing sediments will affect factors such as the amount of food available for deposit feeders. The hydrodynamics at a site will affect factors such as food availability to suspension feeders. The depositional environment is also likely to impact infauna through possible erosion, bed movement and the grain size of sediments. For example, organisms present in areas with high deposition may be adapted to higher levels of sedimentation than those in low depositional areas. These factors (and others, e.g., long term weather patterns, predation, parasitism, etc.) interact to determine how the ecological assemblages in an estuary vary both temporally and spatially.

Okura estuary is located near the Northern edge of the North Shore area of Auckland and is under increasing pressure from urbanisation This increasing pressure of development has raised concerns that potential associated increases in sedimentation will negatively impact the ecology of the estuary itself. Such concerns are particularly relevant given the status of the Okura estuary as a marine reserve.

Thus, considerable research has been done to date on various aspects of the estuary, by the National Institute of Water and Atmospheric Research (NIWA) and by scientists at the University of Auckland, including studies of:

- the biology and ecology of the soft-sediment benthic fauna (Hewitt *et al.* 1998; Norkko *et al.* 1999; Saunders and Creese 2000; Anderson *et al.* 2001a,b).
- the sedimentation and hydrological patterns/characteristics of the estuary (Green and Oldman 1999; Stroud *et al.* 1999)
- the potential impacts of urbanisation resulting from increased sedimentation (Cooper *et al.* 1999; Swales *et al.* 1999; Stroud and Cooper 2000).

From these studies, the outer reaches of the estuary were found to be predominantly sandy, with bivalves being the dominant macrobenthic species. Sampling of the inner reaches of the estuary revealed soft fine sediments with opportunistic polychaetes and burrowing crabs. Also, the number of taxa was found to peak in the mid-region of the estuary (Hewitt *et al.* 1998). These results taken collectively are strongly suggestive of an ecological gradient extending from the outer to the inner reaches of the estuary. The results of Norkko *et al.* (1999) serve as further confirmation of this pattern. Experimental laboratory work into the response of certain species to sediment deposition found several species to be affected by sufficient sediment volume and residence time. Specifically, fine sediment depths of greater than 2-3cm that resided for more than 7 days were sufficient to kill almost all of the organisms examined in experiments (Norkko *et al.* 1999).

Using information about the Okura catchment and the nature of its sediments (Green and Oldman 1999; Stroud *et al.* 1999), regions of the estuary were characterised by their probabilities of sediment deposition (Cooper *et al.* 1999). This resulted in the characterisation of different regions of the estuary into one of three depositional environments: High, Medium or Low. These depositional probability groups were then used by Cooper *et al* (1999) to predict possible differential impacts to different areas of the estuary under various development scenarios.

The pilot report of Anderson *et al.* (2001a) and subsequent annual report (Anderson *et al.* 2001b) further confirmed the influence of each of the 'gradient' and 'depositional' models on the ecological assemblages within different seasons. Specifically, assemblages were found to vary with patterns that were consistent with both depositional environment (High, Medium or Low) and the rank distance of sites from the mouth of the estuary. More specifically, bivalves and gastropods were found to be more abundant in the Medium/Low depositional areas compared to the High depositional areas, whereas the abundances of certain worms and crabs were found to be greatest in the High depositional areas. In contrast, there were no strong effects of sedimentation after specific rainfall events targeted during that study. There was, however, some evidence for important seasonal effects for certain species, including the cockle, *Austrovenus stutchburyi*, which appeared to recruit over the summer months. Recommendations were made for the continuation of monitoring both seasonally and before and after rainfall. Greater coverage of the estuary was recommended to increase the number of sites sampled in order to increase the power of the model and to detect effects on an estuary-wide basis, whilst decreasing within-site replication. It was also recommended that the sedimentation regime be quantified to allow a closer linkage between probable cause and effect due to sedimentation.

Models and Hypotheses for this Study

In order to test the consistency of the 'gradient' and 'depositional' models (Anderson *et al.* 2001b), we tested these models against the new ecological data collected in 2001-2002. Sampling was done more rigorously to assess potential short-term effects of heavy rainfall on assemblages. More particularly, sampling was done after periods of heavy rain and after dry periods within each of three different seasons and encompassed greater spatial replication at the site level than in the previous year, to allow more rigorous conclusions to be made. In addition, data collected in the Okura over the past year concerning actual deposition and bed movement of sediments was used to investigate whether these variables could improve previous models of the variation in macrofaunal assemblages present in Okura.

The characteristics of sediments (such as grain size) are recognised as influential in determining what organisms will be found in them (e.g. Gray 1974). In the estuarine environment a rough gradient of sediment types from coarse to fine is recognised running from the inner to the outer regions of the estuary. A gradient of sediment composition, and concomitant changes in species composition, have been shown for Okura (Hewitt *et al.* 1998, Norkko *et al.* 1999). Additionally, the hydrodynamics of an estuary dictate that sediment depositions will not be uniform, and the levels of this deposition will consequently influence species distributions. Therefore the spatial modelling proposed here for the benthic estuarine fauna includes factors for the different depositional probabilities (depositions), small-scale variation amongst sampling sites (sites), and the large-scale influence of distance to the mouth of the estuary (distance). In addition, variables characterising the short-term deposition of sediments and bed movement at each site were added to these models.

Sediment deposition is deemed to be temporally as well as spatially variable, largely because transportation of sediments is likely to be facilitated by spatially and temporally patchy rainfall events. This can be expected to have short-term influences on the benthic estuarine fauna, and precipitation itself displays strong small and large-scale temporal variability. Modelling of the temporal variability of the benthic estuarine fauna therefore requires short-term components relative to a specific rainfall event, and long-term components related to seasonality.

Impacts of sediment deposition on ecological communities are proposed to be manifest after events of heavy rainfall, and potentially the community structure will change further as either the sediment diminishes, or persists, after an initial influx of sediments. The timing of the sampling by reference to rainfall event has been chosen in order to examine impacts that are not expected to occur until at least 7 days after a rainfall event, as indicated by previous studies (e.g. fatal smothering of bivalve species, Hewitt *et al.* 1998, Norkko *et al.* 1999).

The questions addressed by the current study include:

1. Are the new data consistent with findings from previous studies, especially regarding the gradient and deposition models?
2. Do there appear to be large-scale temporal (i.e. seasonal) differences in the benthic assemblages between rainfall 'events'?
3. Do natural events of heavy rainfall significantly affect soft-sediment estuarine infauna, short-term or long-term?
4. Which taxa are most vulnerable to these rainfall events and which taxa recover after short periods of time?
5. Does information on short-term sediment deposition and its characteristics add to our understanding and ability to model the biology?

Note that 'depositional probability', 'depositional characterisation,' 'depositional area' and 'depositional environment' are being used throughout this report synonymously with the labelling of 'High', 'Medium' and 'Low' areas as shown in Figure 1 below (after Cooper *et al.* 1999).

Terminology/Abbreviations

In this report, we shall use the following terms and abbreviations:

Deposition (Dep) = characterisation of the site by depositional probability (i.e., High (H), Medium (M) or Low (L), after Cooper et al. 1999), indicating their relative likelihood of receiving sedimentation.

Sites (Si) = the 5 random sites within the estuary within each depositional environment (total = 15 sites). Six replicate cores were sampled from each site.

Precipitation (P) = characterisation of sampling times by previous precipitation history (Rain (R) or Dry (D)).

Rain (R) = a sampling time which had a rainfall of greater than 15mm in 24 hours 7 to 10 days prior to sampling.

Dry (D) = a sampling time without a rainfall greater than 15mm in 24 hours in the 10 days prior to sampling.

Season (Se) = characterisation of sampling times by time of year (Winter/Spring (W/S), Spring/Summer (S/S) or Late Summer (LS)).

Winter/Spring (W/S) is defined as August – October 2001,

Spring/Summer (S/S) is defined as November 2001 - January 2002,

Late Summer (LS) is defined as February - April 2002

AxB indicates an interaction term between factors A and B, and B(A) indicates that levels of factor B are nested within the levels of factor A.

The Present Report

The purposes of the present study were to test hypotheses regarding the relationship between ecological assemblages in Okura and:

1. the spatial effects of both the ecological gradient from the outer to inner reaches of the estuary and its areas of differential sediment deposition;
2. effects of rainfall events;
3. large-scale temporal changes between rainfall events (i.e. seasonal change);
4. environmental variables characterising short-term sediment deposition and longer-term bed characteristics at a site.

Results of the present study, particularly with regard to environmental sediment variables, will be used to characterise and model sites in other estuaries to compare with those in Okura for the expanded monitoring program design for 2002-2003.

Methods

Location of Sites and Sampling Methods

Selection of Sites

The sites chosen for sampling within the Okura estuary were chosen on the basis of three criteria. First, sites needed to cover the gradient from the mouth to the upper reaches of the estuary. Second, there needed to be several replicate sites in each of the High, Medium and Low depositional environments in order to obtain adequate measures of any spatial variation and to test the 'deposition' hypotheses. Also, we attempted to avoid confounding of the gradient with the depositional environment (e.g. it was important that not all sites with "High" probability of sediment deposition be located in the upper reaches of the estuary). This was important in order to distinguish the depositional from the gradient model.

We chose to retain the three replicate sites in each of High, Medium and Low sediment deposition areas as sampled in Anderson *et al.* (2001a, 2001b) and added six additional sites to increase the power of our analyses (Fig. 1). In total there were 15 sites, 5 each in the High, Medium and Low areas of sediment deposition. The High, Medium and Low sediment deposition areas were designated by reference to Fig. 3 of Cooper *et al.* (1999). For practical purposes in this report sites will be designated numbers 1-15, with site 1 being the outermost site (closest to the mouth of the estuary) and with site 15 being the innermost (Fig. 1). All sites were located in mid to low intertidal areas.

Timing of Sampling

Sampling occurred within 3 discrete 3-month blocks (hereafter referred to as seasons): August - October 2000 (Winter/Spring (W/S)), November 2000 - January 2001 (Spring/Summer (S/S)) and February - April 2001 (Late Summer (LS)). A 'Rain' and a 'Dry' sampling were taken within each period. A 'Rain' sampling was defined as a sampling that occurred 7-10 days after a rainfall event, defined as ≥ 15mm of rainfall in a 24-hour period. Examination of seventeen years of data from the Leigh Marine Laboratory meteorological records showed this to be a level of rainfall that should occur at least twice in every season. A 'Dry' sampling occurred when such a rainfall event had not occurred in ≥ 10 days. Sampling dates are summarised in Table 1.

Table 1. Sampling dates for 2001-2002.

Sampling Period	'Rain' Sampling	'Dry' Sampling
Winter/Spring 2001	7-9 Sept 2001	4-6 Oct 2001
Spring /Summer 2001-2002	17-19 Dec 2001	12-14 Nov 2001
Late Summer 2002	8-9 March 2002	7-8 Feb 2002

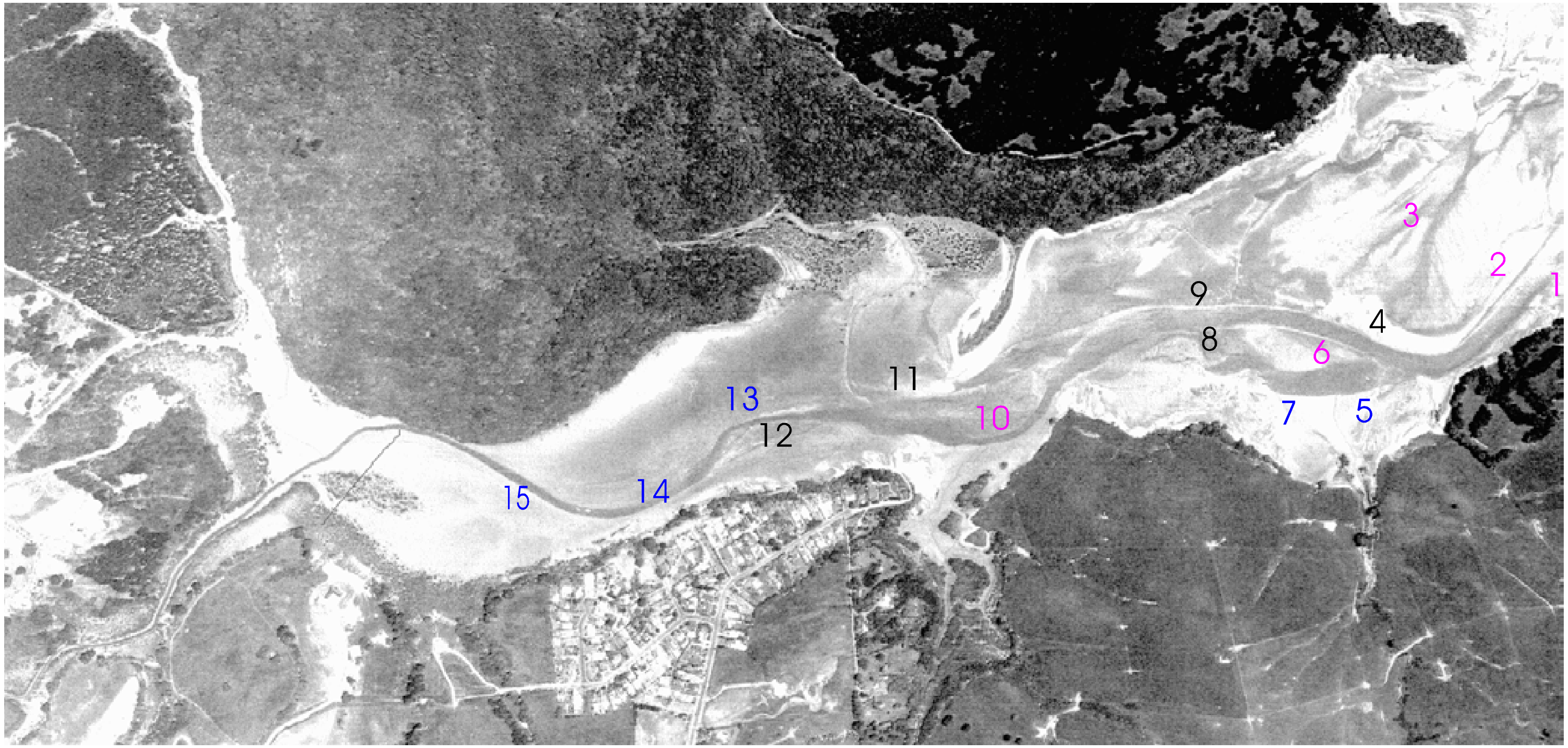


Fig. 1. Map of sampling sites within Okura estuary. Site numbers in pink are in Low depositional areas, site numbers in black are in Medium depositional areas and site numbers in blue are in High depositional areas (after Fig. 3 of Cooper *et al.* 1999 and Fig. 1 of Anderson *et al.* 2001b). The spatial extent of a site (50m x25m) is approximately as wide as the number 14 and half the height. Note that the numbering of sites is sequential from the outer to inner reaches of the estuary.

Field Sampling of Fauna

At each site the corner closest to the channel of an area measuring 50 m parallel to the shore (the x-axis) and 25 m perpendicular to the shore (the y-axis) was marked with a permanent flag. There were $n = 6$ cores obtained from random positions within each area by choosing a random number between 0 and 49 and between 0 and 24 for the x and y-axes, respectively. Cores were circular in shape, measuring 130 mm in diameter and 15 cm deep. Each core was sieved in the field using 0.5 mm mesh. Material retained on the sieve was brought back to the laboratory for sorting and taxonomic identification. All organisms retained were preserved in 10% formalin with 0.01% rose bengal and later transferred to 70% ethanol.

All organisms were identified to the lowest level of taxonomic resolution possible. This varied, depending on the particular group. For example, Oligochaete worms were grouped together, while Bivalves were identified to species. Some Polychaetes could be identified to species level, while others could only be identified to the genus or family level (see Appendix 2).

In addition to identification, size information was also recorded for three bivalve species: the cockle, *A. stutchburyi,* the wedge shell, *Macomona liliana* and the pipi, *Paphies australis.* For each of these species, individuals were classified as being either small (< 4 mm), medium (4-15 mm) or large (> 15 mm).

Field Sampling of Environmental Variables

One sample each for grain size, sediment organics and surface microalgae was also taken adjacent to each faunal core. Samples of grain size and sediment organics were obtained using a 38 mm diameter corer to a depth of 15 cm. Surface microalgae samples were taken by extracting a core using the same corer then slicing off the top 2-3 mm.

Samples of ambient grain sizes of sediments at each site were analysed from one time only (7-8 February 2002) using an unprocessed sub-sample sieved through 2 mm mesh, deflocculated then analysed using a Malvern Mastersizer-S laser particle size analyser. Sediment organic content and chlorophyll *a* were obtained at every sampling time. Sediment organic content was calculated from loss of weight on ignition of dried sediment samples at 550 °C for 6 hours. Microalgal abundance was estimated through chlorophyll *a* analysis. Chlorophyll *a* was extracted from all samples using Dimethylformamide, measured on a spectrophotometer and calculated using standard equations (Porra *et al.* 1989).

Measurement of Sedimentation and Rainfall

Following concerns raised in earlier work (Anderson *et al*, 2001a,b), measurement and characterisation of the level of sedimentation in each area throughout the study period was considered important. Sedimentation was characterised at each site by a combination of a sediment trap and a depth of disturbance rod. A sediment trap (36 mm diameter by 500 mm deep) was placed at the lowest point of each site so that the opening was 20-25 cm above the sediment surface. These traps collected sediment settling from the water column. Depth of disturbance rods (Clifton, 1969; Greenwood and Hale 1980) consisted of a reinforcing rod driven into the sediment ~ 1m from the sediment trap until exactly 20 cm protruded from the sediment surface. Measurements were then taken between the top of the rod and the ambient sediment surface at least once a month. The height of the rod above the sediment surface measured the net erosion or accretion at a site.

Sediment traps were deployed at each site in the field for a period of one week in every month (October-May). At deployment and collection, measurements were also taken of the depth of disturbance rods. Sediment never accumulated to a depth as great as 35 cm within the tube. This ensured the aspect ratio of the sediment traps was greater than 5:1, so resuspension did not occur (White 1990).

Sediment collected from traps was filtered (mesh size ~ 2 μm) dried and weighed at the laboratory. Three times for which all sediment traps were recovered were chosen for subsequent analysis: 12 October 2001, 19 April 2002 and 15 May 2002. These sediments were deflocculated (0.2% Calgon for 24 hours), then wet-sieved through 2000, 125 and 63 μm sieves. The fractions retained on the sieves were then dried and weighed to obtain the percentage weight of grain-size fractions 125-2000 μm, 63-125 μm and <63 μm diameter.

We note that the measures used do not allow us to distinguish between movement of sediments around the estuary and input from the surrounding catchment. However, terrigenous sediments are likely to be < 63 μm in diameter and we expect that sudden changes in sedimentation due to increased run-off would be manifest as increases in these fine sediments in traps over and above what is recorded from monitoring natural inputs over periods of time during the pre-development stages of monitoring. This is why we are endeavouring to characterise and model "natural" levels of sedimentation (from marine or terrestrial inputs) among sites in the estuary with the current monitoring programme.

Statistical Analyses

There were four factors in the experimental design for the sampling of the faunal data: Season (fixed with three levels, W/S, S/S and LS), Precipitation (fixed with two levels, Rain and Dry), Deposition (fixed with three levels, H, M and L), Site (random, 5 levels, nested in Deposition), with *n* = 6 replicate cores. There were a total of 540 observations (cores), from which a total of 73 taxa were recorded. In the reporting of results of any statistical analyses given in Tables, *P*-values given in bold indicate statistically significant effects (i.e. $P < 0.05$).

Multivariate analyses

The multivariate data were analysed for the full design, including all interaction terms (see Appendix 1), using non-parametric multivariate analysis of variance (NPMANOVA, Anderson 2001a). This method allows tests of significance for multivariate data on the basis of any distance or dissimilarity measure and uses permutation procedures to obtain *P*-values. Consequently, the assumption of multivariate normality is not required. Whenever there were not enough possible permutations to obtain a reasonable test, Monte Carlo *P*-values from the asymptotic permutation distribution were obtained (Anderson and Robinson, in review). For each term in the analysis, 4999 permutations (or Monte Carlo samples) were done to obtain *P*-values. All multivariate analyses were based on Bray-Curtis dissimilarities calculated among observations for data transformed to $y' = \ln(y+1)$. The Bray-Curtis dissimilarity measure is a useful and robust measure for community analysis (e.g. Clarke 1993) and the transformation ensured that very abundant taxa did not dominate the analysis, while ensuring that information concerning changes in relative abundances was not lost. NPMANOVAs were done using the computer programs NPMANOVA (Anderson, 2000) and DISTLM (Anderson, 2002b).

Terms that were found to be significant by NPMANOVA were then investigated more fully by doing multivariate pair-wise comparisons and by examining several ordinations to visualize patterns using (a) non-metric multi-dimensional scaling (MDS, an unconstrained ordination method, Kruskal and Wish 1978) and (b) canonical analysis of principal coordinates (CAP, a constrained ordination method, Anderson and Robinson, in review; Anderson and Willis, in press). These were done only for relevant combinations of the factors. For example, a significant Season x Deposition interaction would result in a logical investigation of (i) comparisons among Depositions for each Season and (ii) comparisons among Seasons for each Deposition. The constrained ordination (CAP) considers patterns in the multivariate data with respect to some *a priori* hypothesis, while the unconstrained method does not use the hypothesis in any way when drawing the diagram. See Appendix 1 for more details concerning these ordination techniques. All of these analyses were done on observations pooled at the site level (i.e. the $n = 6$ counts were summed for each variable to obtain a single observation for the site at that time, for a total of 90 observations). Non-metric MDS plots were done using the PRIMER computer package (courtesy of M.R. Carr and K.R. Clarke, Plymouth Marine Laboratory, United Kingdom). CAP plots were done using the CAP computer program (Anderson 2002a).

The relationship between the multivariate species data and the environmental variables (including depositional probabilities, distance variables, erosion/accretion variables, variables relating to sediment deposition, and variables relating to ambient conditions at sites) were analysed using nonparametric multivariate multiple regression (McArdle and Anderson 2001). Individual variables were analysed separately for their relationship with the multivariate species data (ignoring other variables), and variables were then subjected to a step-wise forward selection procedure to develop a model of the species data. This approach was also used to analyse natural sets or groups of variables (see Table 11). These analyses were also done on observations pooled at the level of sites. All tests were based on Bray-Curtis dissimilarities calculated among observations for data transformed to $y' = \ln(y+1)$. *P*-values for the marginal tests (examining a single variable or group of variables) were obtained using 4999 permutations of the raw data, while conditional tests (used for the forward selection procedure) were done using 4999 permutations of residuals under the reduced model (Anderson 2001b). All non-parametric multivariate multiple regressions were done using the computer program DISTLM (Anderson 2002b).

To visualize these multivariate patterns, a redundancy analysis (RDA) was done to compare the environmental variables to the species data. This analysis is a constrained ordination method (see Appendix 1): it constrains the ordination axes to be linear combinations of the environmental variables. It is the equivalent of a multivariate multiple regression followed by a PCA on the fitted values (Legendre and Legendre 1998). One can imagine an RDA to be a projection of the species data onto the environmental variables in a reduced space. However, traditional RDA implicitly preserves Euclidean distance, while in our case, the appropriate measure to use was Bray-Curtis. To base the RDA on Bray-Curtis dissimilarities, we first did a metric MDS (principal coordinate analysis) on a Bray-Curtis dissimilarity matrix (from $\ln(y+1)$-transformed species data), using correction method 1 to correct for negative eigenvalues (see Legendre and Anderson 1999 for details). This places the species data into a Euclidean space, which is fit for RDA, that preserves Bray-Curtis dissimilarities among points. The RDA of the environmental variables is therefore done on the complete set of PCO axes. The analysis was done using the program DistPCoA (Legendre and Anderson 1998), followed by the program CANOCO (ter Braak and Smilauer 1998).

Univariate Analyses

All individual taxa that were reasonably abundant across the entire design were analysed using univariate analysis of variance (ANOVA). ANOVAs were also done of several major groups (such as Polychaetes, Crustceans, Bivalves, etc.), of the total number of taxa (i.e. diversity or richness) and of the total number of individuals. ANOVAs were also done for several environmental sediment variables. In each case, Cochran's test was used to test the assumption of equal variances. Where the assumption of equal variances was violated ($P < 0.05$), data were transformed to $\ln(y+1)$, which generally resulted in more symmetric distributions (i.e. with less right-skewness, thus more normal), which also generally fulfilled the assumption of homogeneity. As a consequence, however, where this transformation was used, the ANOVA models are multiplicative in nature and results need to be interpreted in terms of medians, rather than arithmetic averages. In some cases, transforming the data did not result in homogeneous variances. In these cases, the analysis was done, relying on the robustness of ANOVA with such large overall sample sizes and balanced designs (Underwood 1981). These cases are noted in the results, however, and significant results from them need to be interpreted with some caution. For significant terms, the relevant pair-wise comparisons were done using Student-Newman-Keuls (SNK) tests. All ANOVAs were done using GMAV5 (courtesy of A.J. Underwood and M.G. Chapman, Centre for Research on Ecological Impacts of Coastal Cities, University of Sydney).

For organisms that were not abundant enough to analyse using ANOVA (i.e. < 2 per core), chi-squared tests were used to test for changes in their frequencies of occurrence across levels of each fixed factor in the design (i.e. Season, Deposition and Precipitation).

Analyses of Sediment Deposition

Five variables characterising sediment deposition were used to generate a model of short-term deposition at each site. These variables were: (1) change in bed height, averaged for each site from the 18 recording times and converted to $cm.day^{-1}$ ('BH'); (2) the standard deviation of change in bed height per site ('sdBH'), which was needed to characterise sites with low average bed height change over the year but with short time-scale bed-level fluctuations; (3) total sediment trapped at each site ('Sdep'), averaged from three separate samplings and converted to $g.cm^{-2}.day^{-1}$; (4) percentage of sediments trapped that were < 63 μm in diameter (i.e. fine sediments, referred to as '% fines') and (5) percentage of sediments trapped that were >125 μm in diameter (i.e. sands, referred to as 'gt125'). Fine sediments are probably of recent terrestrial origin, while sands are probably of recent marine origin.

Principal component analysis (PCA) and hierarchical agglomerative group-average clustering were used to generate a physical model of the sites (see Appendix 1 for details of these methods). For analysis by PCA, the 5 variables were first each standardised by dividing by their standard deviation (normalised). The cluster analysis was based on normalised Euclidean distance. Both of these analyses were done using the PRIMER computer package. Univariate ANOVAs were also done of the individual sediment variables.

Results

Sediment Deposition

Sediment deposition and bed height (erosion/accretion) measurements at the sites were highly variable, both temporally and spatially (Figs. 2, 3, 4, 5). In contrast to the characterisation of sites in terms of depositional probabilities (Cooper *et al.* 1999) these data showed that the greatest amount of sediment was actually collected in sediment traps at Medium depositional sites and the least at High depositional sites (Fig. 2). Site 8 (a Medium site) showed, on average, almost an order of magnitude more deposition than any other site (Fig. 3). Low depositional sites trapped sediments with the highest proportion of fine sediment (<63 µm), while Medium depositional sites trapped sediments with the highest proportion of coarse sediments (>125 µm) (Fig. 4). A significantly greater amount of coarse sediment was present in Medium sites compared to Low sites (Fig. 4). Erosion/accretion (both average and standard deviation) did not differ appreciably between depositional areas (Fig. 5). The average and standard deviation values for erosion/accretion were more variable when examined at the site level (Fig. 6). Site 10 showed the greatest average accretion and site 6 showed the greatest average erosion (Fig. 6). These 2 sites also showed the largest variability of erosion/accretion in the estuary (Fig. 6).

There were no clear separations or obvious groupings of the sites in either the cluster analysis dendrogram or the PCA of the sediment variables (Fig. 7, 8). Both analyses suggested gradual changes in these sediment variables across the 15 sites, i.e. a gradient in short-term characteristics of sedimentation. The first two PCA axes accounted for 73.7% of the total variance in the five variables (Fig. 8). The first PC axis (PC1) explained 51.8% of the variation and represented the contrast between total sediment deposition and percentage of fines. Thus, sites with high levels of total deposition tended also to have a greater proportion of coarse sediments. The second PC axis (PC2) explained 21.9% of the total variation and represented the contrast between the standard deviation of erosion/accretion and the average erosion/accretion (Table 2). For example site 8 (Fig. 8) has a high value for PC1 (x-axis) and an intermediate value for PC2 (y-axis), therefore it showed high total sediment and sand deposition, with intermediate values of bed height change. By contrast, site 6 (Fig. 8) showed low values on both axes so will be characterised by high deposition of fine sediments and a high level of average bed height change.

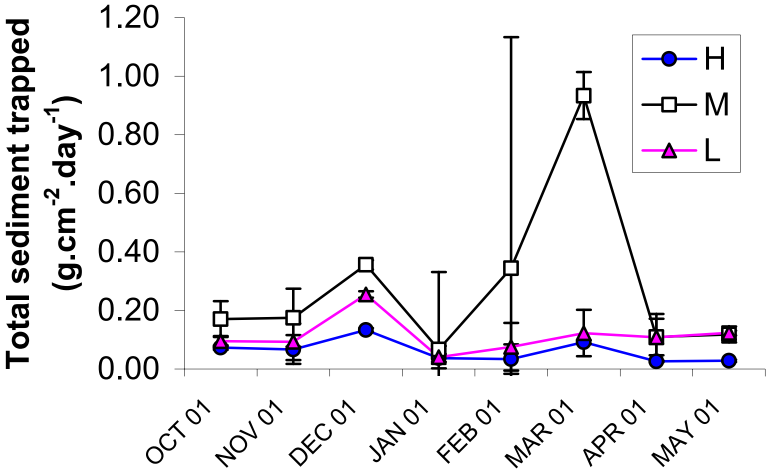


Fig. 2. Average (± 1SE) total weight of sediment trapped at eight different times, classified by depositional area (calculated from *n* = 5 sites).

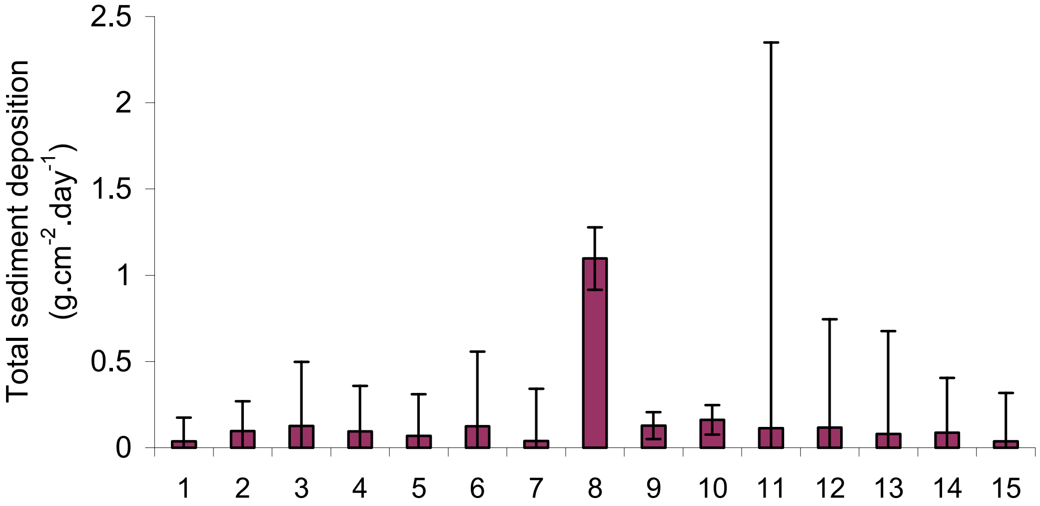


Fig. 3. Average (± 1SE) total weight of sediment trapped at eight different times, classified by site (calculated from *n* = 8 times).

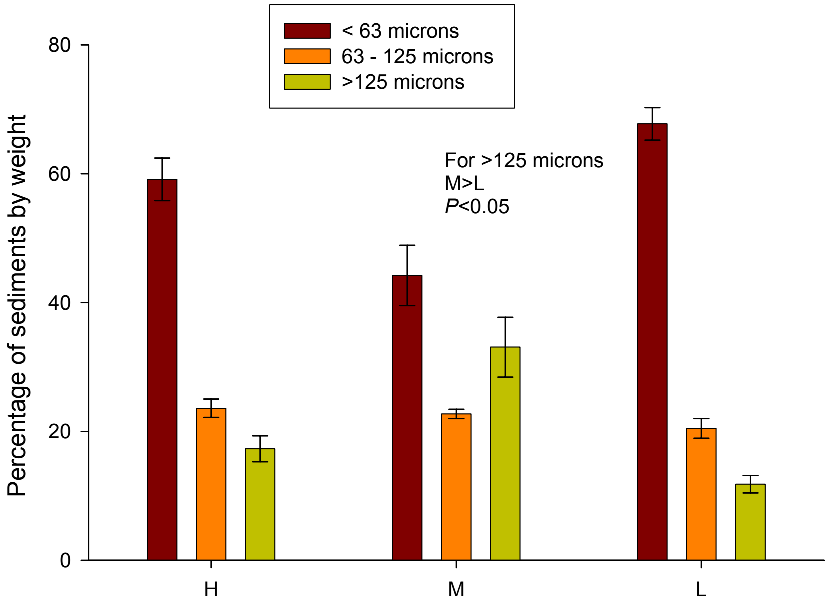


Fig. 4. Average (± 1SE) percentage of sediments of different grain sizes collected in traps in different depositional environments (calculated from *n* = 5 sites).

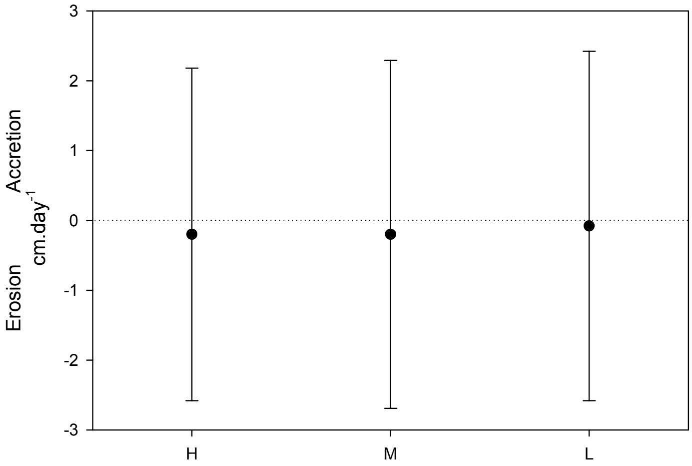


Fig. 5. Average (± 1sd) of erosion/accretion from August 2001 until May 2002 at each depositional area (calculated from *n* = 18 times). Dotted line indicates no average bed level change.

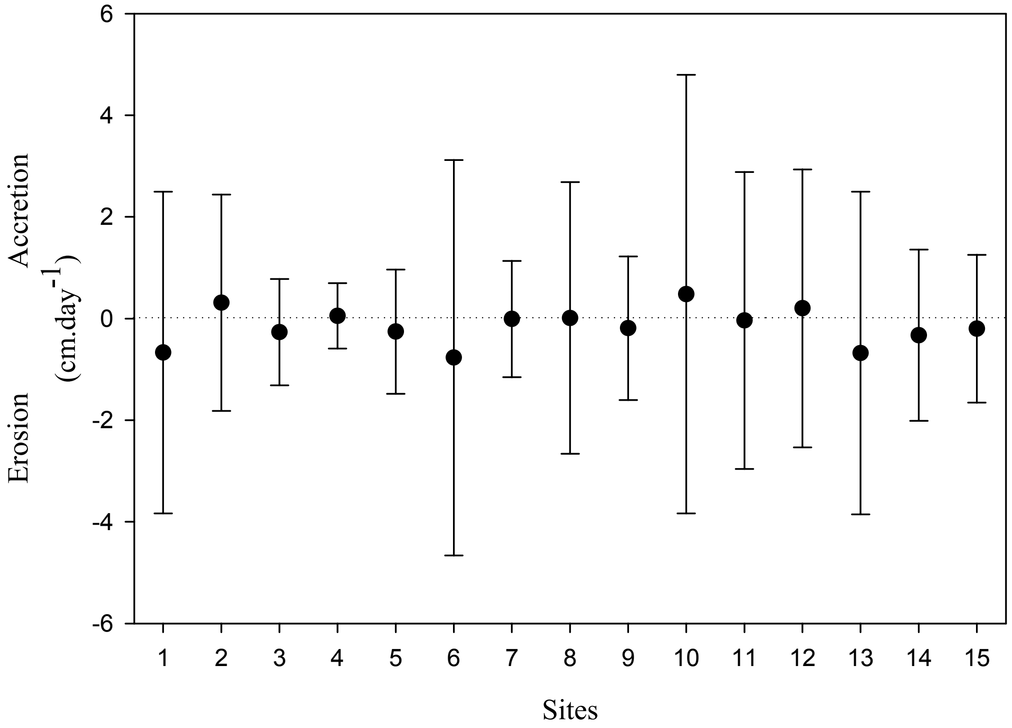


Fig. 6. Average (± 1sd) of erosion/deposition from August 2001 until May 2002 at each site (calculated from *n* = 18 times). Dotted line indicates no average bed level change.

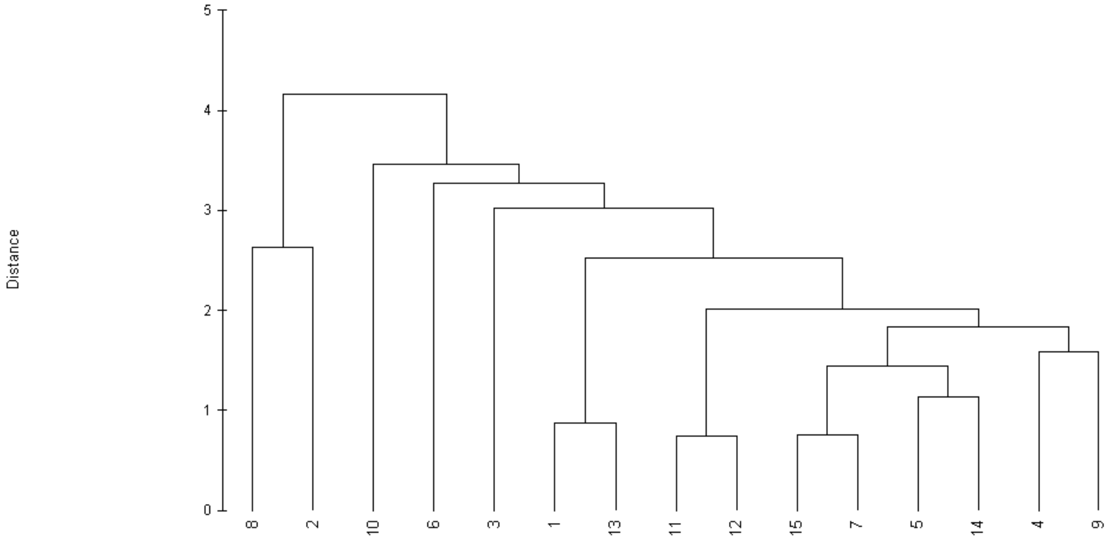


Fig. 7. Dendrogram based on hierarchical agglomerative group-average clustering of normalised Euclidean distances between sites using 5 sediment variables. Site numbers are on the x-axis.

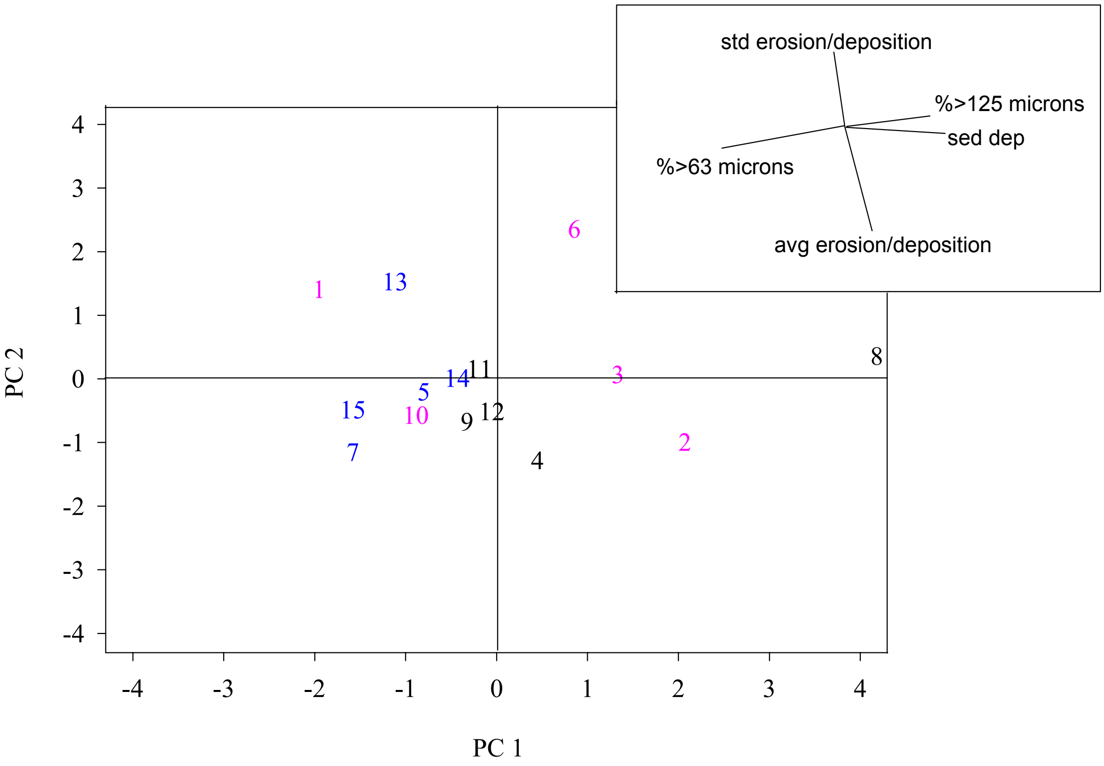


Fig. 8. PCA plot showing site similarities and eigenvectors, a greater distance between sites indicates greater dissimilarity. Sites located in the same direction as one or more of the variables will have high relative values of those variables. Numbers = sites, Pink = Low, Black = Medium and Blue = High depositional sites.

Table 2. Eigenvector weights from the PCA of 5 normalised sediment variables.

Variable	PC1	PC2
Average erosion/accretion (BH)	0.158	-0.773
Standard deviation of erosion/accretion (sdBH)	0.003	0.582
Total sediment deposition (Sdep)	0.534	-0.110
% > 125 µm (gt125)	0.585	0.099
% < 63 µm (% fines)	-0.590	-0.205

The PCA scores can be used to generate a model of relationships among sites on the basis of short-term sediment deposition. Therefore we may consider two possible sets of predictor variables to use as models of the short-term depositional environment to compare with the biological data: (1) the 5 original (standardised) sediment variables and (2) the PC scores (Table 3).

Each of these models showed a highly significant relationship with the composition and abundance of species at the sites (Table 4). This shows that the measured sediment deposition characteristics from the last year have a significant impact upon the biology. Of the 2 models, the 5 variables together explain the greatest amount of variation in the biological data (SS of raw sediment data/SS total x 100 = 30.8%). These 5 variables will therefore be considered in more detail, along with other environmental variables, in subsequent analyses and models of the faunal data.

Table 3. Values of sediment variables and PC scores for each of the 15 sites. BH = average change in bed height (erosion/accretion) in cm.day^{-1}, sdBH = standard deviation of change in bed height in cm.day^{-1}, Sdep = average total sediment deposition in g.cm^{-2}.day^{-1}, gt125 = average percentage of sediment greater than 125 μm in grain size, % fines = average percentage of sediment less than 63 μm in grain size.

Site	BH	sdBH	Sdep	gt125	% fines	PC 1	PC 2
1	-0.67	3.16	0.021	8.01	73.40	-1.951	1.410
2	-0.77	3.89	0.046	26.71	40.36	-0.889	-0.568
3	-0.19	1.41	0.052	11.29	68.06	-1.579	-0.482
4	0.48	4.32	0.037	7.16	72.74	-1.579	-1.147
5	-0.20	1.45	0.023	11.48	74.52	-0.053	-0.511
6	-0.01	1.14	0.028	7.30	76.96	-0.187	0.159
7	0.01	2.67	0.072	58.44	19.15	-0.435	0.013
8	-0.68	3.17	0.029	13.21	64.25	1.335	0.069
9	0.20	2.73	0.035	20.36	59.07	2.072	-0.991
10	-0.04	2.92	0.031	19.86	56.01	4.181	0.359
11	-0.33	1.68	0.038	13.20	58.40	-1.115	1.530
12	0.05	0.64	0.044	22.92	54.74	0.856	2.357
13	-0.26	1.22	0.023	17.53	59.05	-0.324	-0.673
14	-0.27	1.05	0.031	42.76	36.62	-0.783	-0.244
15	0.31	2.13	0.064	30.63	41.93	0.450	-1.282

Table 4. Nonparametric multivariate multiple regression of the relationship between each of these models of short-term sedimentation and the biological species data. The analyses were based on the Bray-Curtis dissimilarity measure calculated from *ln* (*y* + 1)-transformed species data. Observations were pooled at the site level. *P*-values were obtained using 4999 permutations.

Source	df	SS	MS	*F*	*P*
a) 5 sediment variables					
Regression	5	2.96928	0.59386	7.477	**0.0002**
Residual	84	6.67168	0.07942		
Total	89	9.64096			
b) Scores of sites along the first 2 PC axes					
Regression	2	1.63273	0.81636	8.869	**0.0002**
Residual	87	8.00823	0.09205		
Total	89	9.64096			

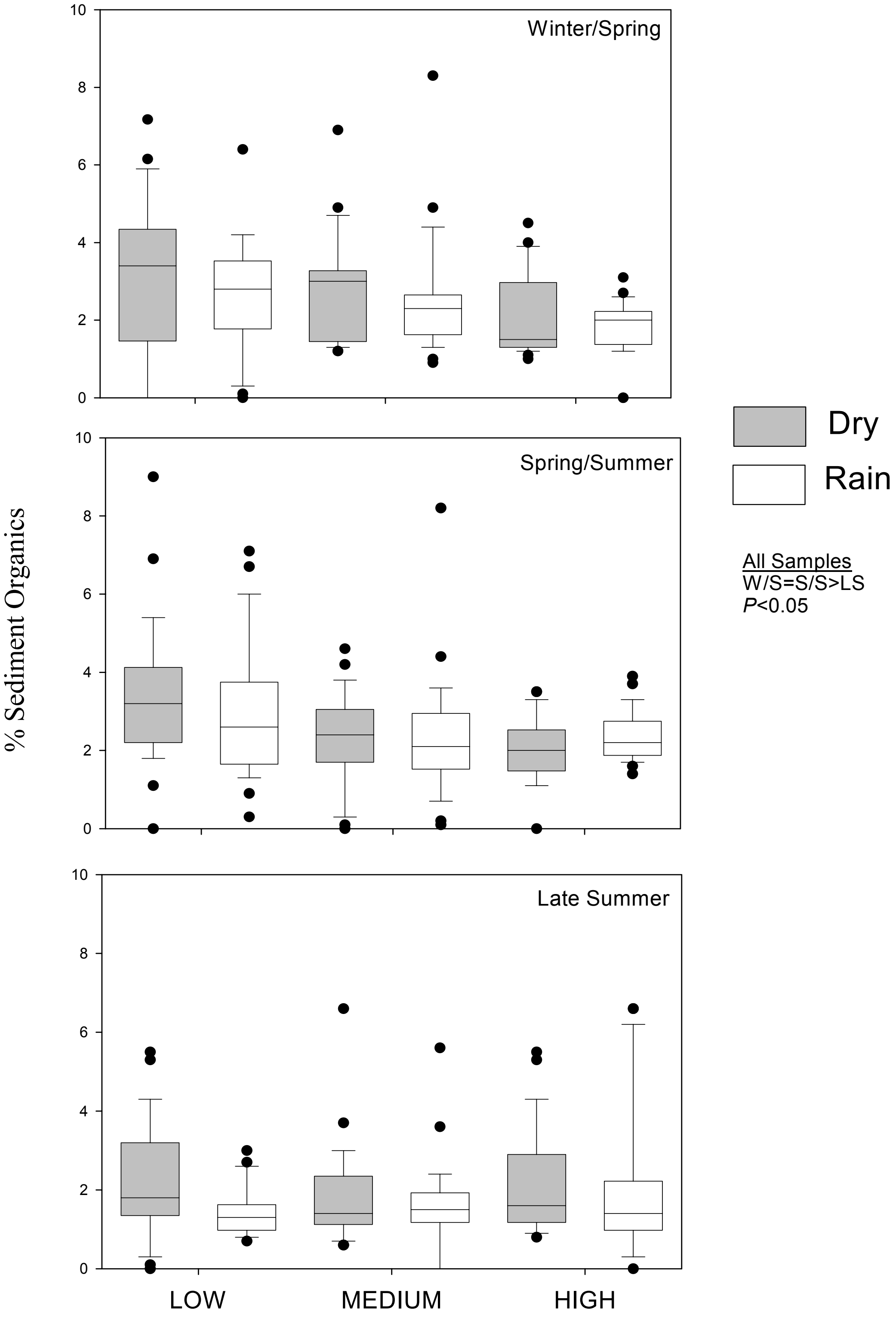
Ambient Sediment Variables

Sediment organics showed a significant effect of Season (Table 5). Late Summer showed significantly lower values (on average 0.8%) for sediment organics than the previous two seasons (Fig. 9). Chlorophyll *a* showed a significant interaction effect between Precipitation and Season (Table 5). For Dry samplings, Winter/Spring had significantly lower concentrations of Chlorophyll *a* than the other two seasons (Fig. 10). For Rain samplings, Summer/Spring showed the highest concentrations of Chlorophyll *a,* followed by Winter/Spring, then Late Summer (Fig. 10). In Late Summer the concentration of Chlorophyll *a* was significantly higher in the Dry sampling than in the Rain sampling. Sediment grain size showed significant effects of deposition. There was a trend for fine sediments (<63 µm) to increase and coarse sediments (>125 µm) to decrease from Low to High depositional areas (Fig. 11). There was a significantly greater percentage of fines at High depositional areas and a significantly greater percentage of coarse sediments at Low depositional areas (Table 6).

Table 5. ANOVA Results for Chlorophyll *a* and Sediment Organics. These two analyses were done on untransformed data, but in each case the assumption of homogeneity of variances was not fulfilled (Cochran's test, $P < 0.05$), so results need to be interpreted with some caution.

		Sediment Organics			**Chlorophyll *a***		
Source	**df**	**MS**	***F***	***P***	**MS**	***F***	***P***
Se	2	33.864	5.54	**.0133**	271.672	31.96	**0.0000**
P	1	1.912	0.30	.5946	412.434	13.06	**0.0036**
D	2	17.138	1.77	.2242	5.739	0.46	0.6449
Si(D)	9	9.664	7.31	**.0000**	12.610	5.65	**0.0000**
Se x P	2	0.534	0.19	.8250	169.354	17.17	**0.0000**
Se x D	4	4.248	0.70	.6049	18.098	2.13	0.1083
Se x Si(D)	18	6.108	4.62	**.0000**	8.499	3.81	**0.0000**
P x D	2	8.216	1.31	.3173	2.854	0.09	0.9142
P x Si (D)	9	6.283	4.76	**.0000**	31.529	14.15	**0.0000**
Se x P x D	4	1.870	0.68	.6141	3.536	0.36	0.8356
Se x P x Si(D)	18	2.746	2.08	**.0063**	9.836	4.42	**0.0000**
Res	345	1.321			2.322		
Total	539						

Organics



All Samples
W/S=S/S>LS
$P<0.05$

Fig. 9. Boxplots of the percentage of sediment organics for each combination of Season, Deposition and Precipitation.

Chlorophyll *a*

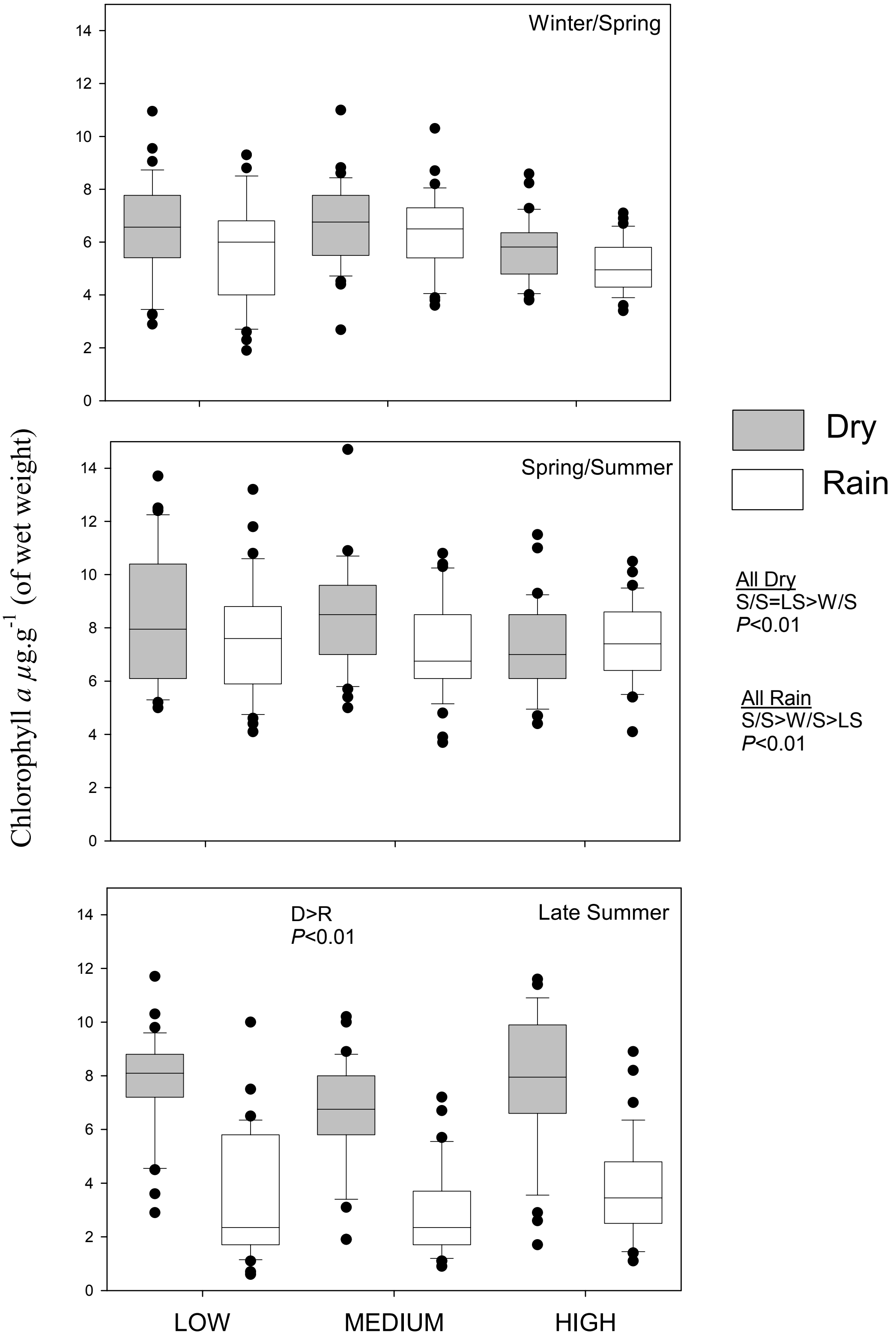


Fig. 10. Boxplots of Chlorophyll *a* concentration for each combination of Season, Deposition and Precipitation.

Table 6. ANOVA Results for ambient sediment grain size fractions. The two variables of < 63 µm and > 125 µm were transformed to ln(*y* + 1), while the variable 63-125 µm was left untransformed. However, in each case the assumption of homogeneity of variances was not fulfilled (Cochran's test, *P* < 0.05), so results need to be interpreted with some caution.

		< 63 microns			63-125 microns			>125 microns		
Source	**df**	**MS**	***F***	***P***	**MS**	***F***	***P***	**MS**	***F***	***P***
D	2	9.2715	11.88	**.0014**	796.1355	2.38	.1344	5.3750	8.14	**.0058**
Si(D)	12	0.7807	11.66	**.0000**	334.0139	33.11	**.0000**	0.6602	19.88	**.0000**
Res	75	0.0670			10.0888					

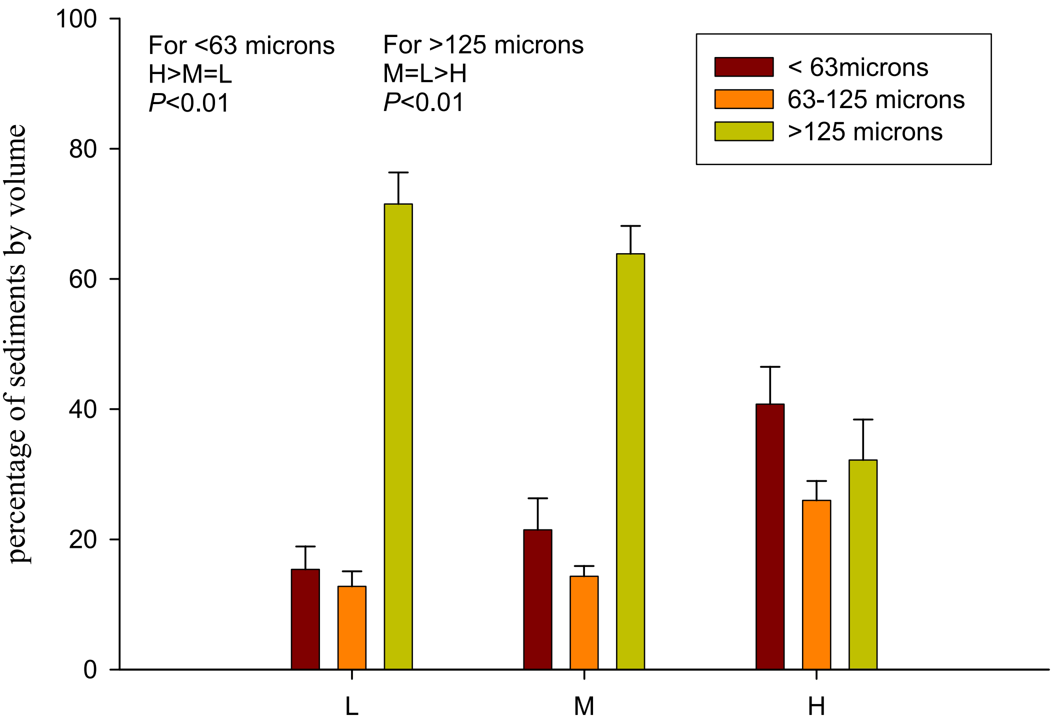


Fig. 11. Average (+ 1 SE) of ambient sediment grain size fractions within each depositional environment (calculated from 6 replicates x 5 sites = 30 observations).

Multivariate Analyses of Faunal Data

A list of all taxa recorded are given in Appendix 2. In addition, summaries of the faunal data by reference to the fixed main effects are given in Appendix 5.

There was important small-scale spatial variability in the soft-sediment assemblages (i.e. from site to site for each time of sampling), as evidenced by the significant 3-way interaction for Season by Precipitation by Site (i.e. $P < 0.01$ for SexPxSi(D), Table 7). The order in the strength of the effects, as suggested by the analysis (i.e. relative sizes of components of variation, estimated using the Mean squares in Table 7), is that Site effects within depositional environments were the strongest, followed by Depositional effects, then Seasonal effects and, finally, effects of Precipitation, which were the weakest.

Table 7. **Results of Non-parametric MANOVA investigating the effects of Season, Precipitation, Deposition and Site on macrofaunal species abundance and composition. The analysis was based on Bray-Curtis dissimilarities on data for 73 variables (taxa) transformed to ln(y + 1). *P*-values were obtained using 4999 permutations of units shown in the far right-hand column. Monte Carlo *P*-values (shown in italics) were used whenever the number of permutable units was too small to get a reasonable permutation test.**

Source	df	SS	MS	*F*	*P*	Denom MS	Permutable units
Season = Se	2	2.5200	1.2599	8.143	***0.0002***	SexSi(D)	45 SexSi(D) units
Precipitation = P	1	0.4878	0.4878	3.639	***0.0026***	PxSi(D)	30 PxSi(D) units
Deposition = D	2	24.0351	12.0176	5.224	***0.0002***	Si(D)	15 Si(D) units
Site(D) = Si(D)	12	27.6078	2.3007	25.726	**0.0002**	Res	540 raw data units
SexP	2	1.1608	0.5804	4.152	**0.0012**	SexPxSi(D)	90 SexSi(D) units
SexD	4	1.2232	0.3058	1.977	***0.0046***	SexSi(D)	45 SexSi(D) units
SexSi(D)	24	3.7133	0.1547	1.730	**0.0002**	Res	540 raw data units
PxD	2	0.3263	0.1632	1.217	*0.2558*	PxSi(D)	30 PxSi(D) units
PxSi(D)	12	1.6087	0.1341	1.499	**0.0028**	Res	540 raw data units
SexPxD	4	0.5957	0.1489	1.065	0.3772	SexPxSi(D)	90 SexSi(D) units
SexPxSi(D)	24	3.3553	0.1398	1.563	**0.0002**	Res	540 raw data units
Residual	450	40.2436	0.0894				
Total	539	106.8773					

This difference in the sizes of effects was also apparent visually in a metric MDS plot (= principal coordinate or PCO plot) of the entire data set (Fig. 12). Here, a single observation on the plot corresponds to the counts combined across 30 cores (6 cores in each of 5 sites). The first two PCO axes explain 72% of the total variation in this pooled data set. The first axis, explaining 61.1% of the variation, is largely the distinction of the High depositional assemblages from those in Medium and Low depositional sites (i.e. depositional effects). The second axis shows changes in assemblages through time (times 1-6 = two times of sampling within each of the three seasons), which essentially corresponds to seasonal effects. The precipitation effect within each season (R versus D) is extremely slight. For

Medium and Low depositional environments, the D's tend to be to the left of the R's within each season (Fig. 12), but this is not the case for the High depositional environments and thus no generalisations regarding effects of Precipitation seem possible.

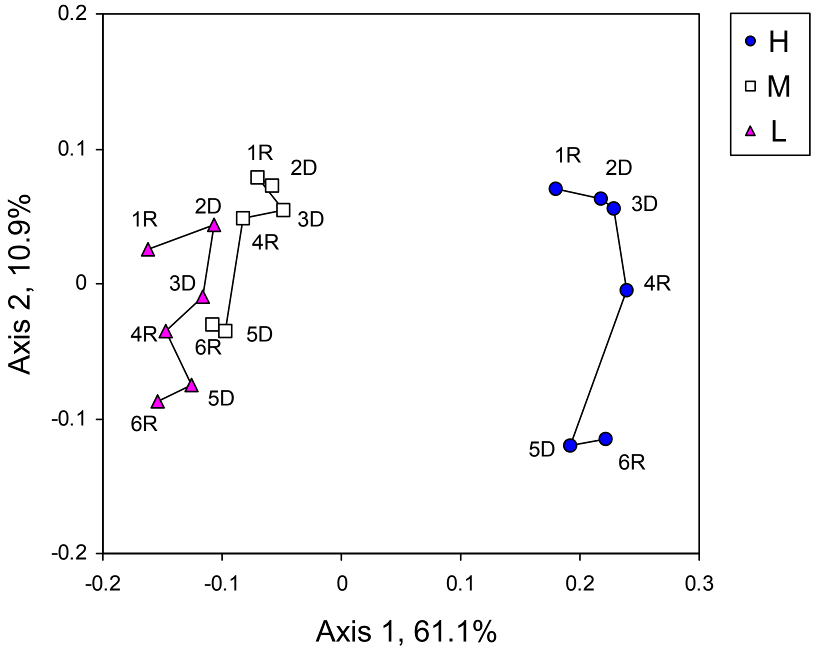


Fig. 12. Metric MDS plot of effects of Deposition (High, Medium or Low), Time (enumerated sequentially from 1 to 6, being 2 sampling times within each season) and Precipitation (Rain or Dry). Distances between points represent Bray-Curtis dissimilarities on summed abundances from the 6 cores x 5 sites for each combination of the above factors for 73 taxa, transformed to $\ln(y + 1)$.

Due to the significant site-to-site variation, the ensuing multivariate analyses were done on observations that were pooled at the site level (i.e. the numbers for each taxon were summed across the $n = 6$ individual cores). Effects of Deposition and effects of Precipitation both varied with Season (i.e. $P = 0.0046$ for SexD and $P = 0.0012$ for SexP, Table 7). Thus, in each case, effects needed to be considered separately within each season. Similarly, seasonal effects needed to be considered separately for each of the depositional environments. Although individual sites were variable, there were, however, consistent differences among assemblages in the three depositional environments (H, M and L) in samples from either Rain or Dry conditions (i.e. $P = 0.2558$ for PxD and $P = 0.3778$ for SexPxD, Table 7).

Effects of Deposition

Non-metric MDS plots and CAP plots showed very similar results for the three different seasons (Fig. 13). Assemblages in High depositional sites were very distinct from those in the Low or Medium sites, but these latter two did not appear to differ strongly from one another. The lack of strong differences between assemblages in Medium vs. Low sites was also shown by the small allocation success of the Low sites (i.e. in two of three seasons, only 30% of the Low sites were correctly allocated, which is no better than chance allocation in the case of three groups, see Table 8).

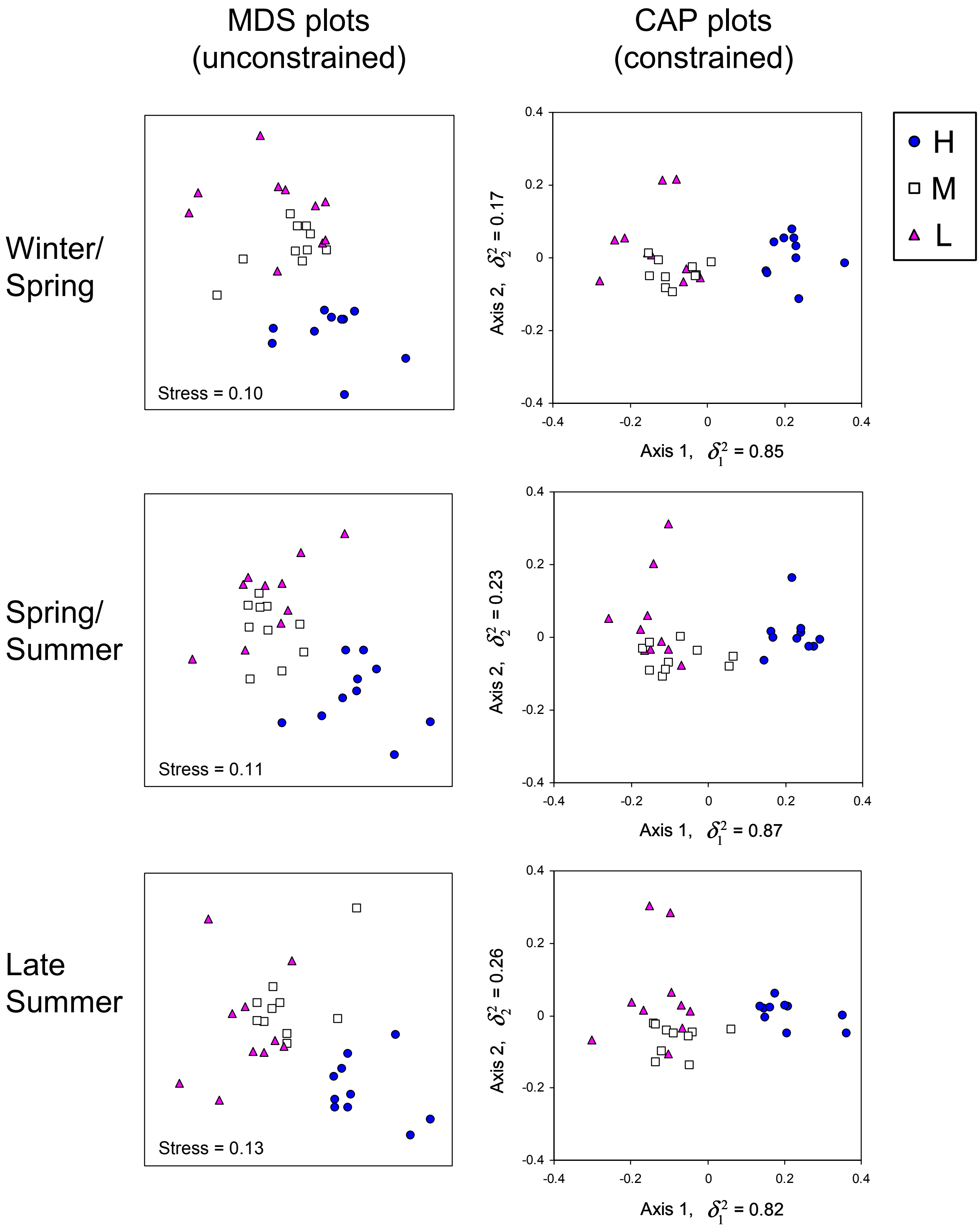


Fig. 13. Non-metric MDS plots (left-hand side) and CAP plots (right-hand side) showing the effects of Deposition in each of three Seasons. Analyses were based on Bray-Curtis dissimilarities of 73 variables that were transformed to ln(y + 1). Each point represents pooled information from n = 6 cores.

Pair-wise comparisons done separately for each season (with 4999 permutations each) showed that there were consistent strong and significant differences in assemblages in High vs. Medium and in High vs. Low depositional environments (*P* = 0.0002 for each of these tests, Fig. 13 and Table 8). The difference between assemblages in Medium vs. Low depositional environments was not as marked (Fig. 13), but was statistically significant in Spring-Summer and in Late Summer (*P* = 0.0228 and *P* = 0.0238, respectively), although not for the Winter-Spring season (*P* = 0.0666). Thus, despite a significant interaction with Season, effects of Deposition were overall quite consistent, with only slight differences in the sizes of effects.

Table 8. Results of CAP analyses examining effects of Deposition within each Season. *m* = the number of principal coordinate (PCO) axes used in the CAP procedure, %Var = the percentage of the total variation explained by the first *m* PCO axes, Allocation success = the percentage of points correctly allocated into each group, δ_1^2 and δ_2^2 are the first two squared canonical correlations. *P*-values were obtained using 999 random permutations.

			Allocation success (%)						
Season	***m***	**%Var**	**H**	**M**	**L**	**Total**	δ_1^2	δ_2^2	***P***
Winter/Spring	3	67.85	100	80	40	73.33	0.852	0.168	**0.001**
Spring/Summer	4	76.09	90	100	30	73.33	0.875	0.231	**0.001**
Late Summer	3	73.53	100	100	30	76.67	0.818	0.264	**0.001**

Correlations of individual taxa with the canonical axes are shown in Table A3.1 in Appendix 3. These suggested that *Austrovenus stutchburyi* (cockle), *Anthopleura* spp., *Elminius modestus* (barnacle), *Colorustylis lemurum* (Cumacean), *Notoacmaea helmsii* (gastropod), *Paphies australis* (pipi), *Sypharochiton pelliserpentis* (chiton), among others, were more abundant or frequent in Low and Medium depositional sites. In contrast, Nereids, crabs (*Helice* and *Macrophthalmus*), Glycerids and Oligochaetes appeared to be more highly correlatd with High depositional sites. More complete analyses of these and other relevant taxa are given in a later section.

Effects of Season

Effects of Season were not as strong as the effects of Deposition. This is clear because no strong separation of assemblages on the basis of their seasonal grouping could be seen in any of the non-metric MDS plots (Fig. 14, left-hand plots). However, the CAP plots did uncover significant seasonal effects for each depositional environment (Fig. 14, right-hand plots). The clearest separation was along CAP axis 1, which consistently separated out the assemblages from the Late Summer from those in Winter-Spring or Spring-Summer (Fig. 14).

Table 9. Results of CAP analyses examining effects of Season within each Depositional environment. m = the number of principal coordinate (PCO) axes used in the CAP procedure, %Var = the percentage of the total variation explained by the first m PCO axes, Allocation success = the percentage of points correctly allocated into each group, δ_1^2 and δ_2^2 are the first two squared canonical correlations. P-values were obtained using 999 random permutations.

			Allocation success (%)						
Deposition	***m***	**%Var**	**W/S**	**S/S**	**LS**	**Total**	δ_1^2	δ_2^2	***P***
High	8	89.94	100	80	100	93.33	0.914	0.681	0.001
Medium	10	93.63	60	70	20	50.00	0.772	0.413	0.002
Low	12	98.35	0	80	70	50.00	0.803	0.670	0.001

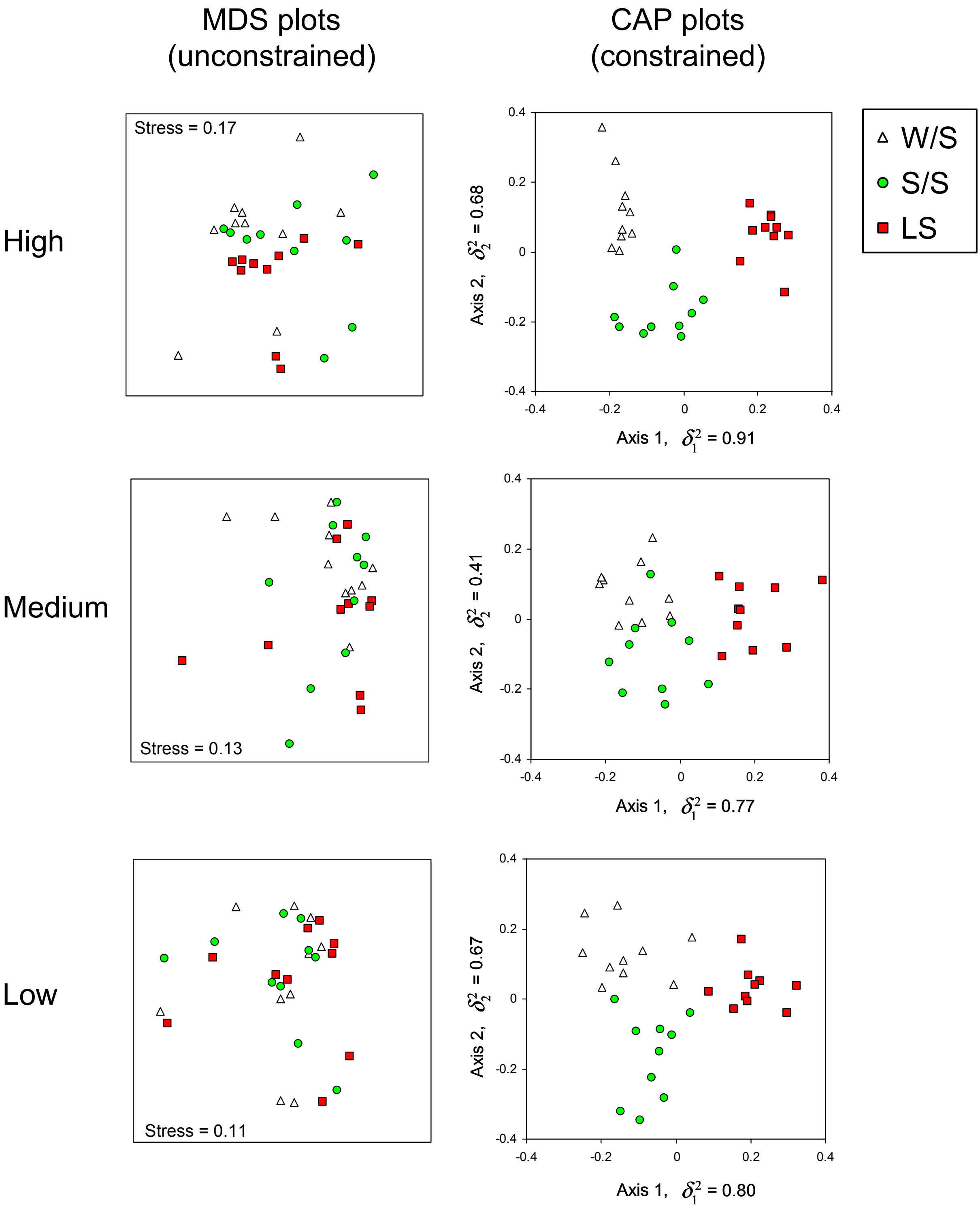


Fig. 14. Non-metric MDS plots (left-hand side) and CAP plots (right-hand side) showing the effects of Season in each of three Depositional environments. Analyses were based on Bray-Curtis dissimilarities of 73 variables that were transformed to ln(y + 1). Each point represents pooled information from n = 6 cores.

Pair-wise comparisons among seasons were done separately for each depositional environment. There were significant seasonal differences among assemblages for High depositional sites (*P* < 0.01 for all three comparisons among W/S, S/S and LS), while no seasonal differences were apparent in either Low or Medium depositional sites (*P* > 0.10 for all six of these comparisons). The lack of strong seasonal differences among assemblages for Medium and Low sites was also apparent in the small allocation success (only 50% overall, see Table 9).

Correlations of individual taxa with canonical axes suggested *Armandia* sp., Oligochaetes, *Psuedopolydora* sp. and *Colorustylis lemurum* were more abundant or frequent with the Late Summer Season, while *Helice/Macrophthalmus* (crabs), Crab zoea and Orbinids were more abundant or frequent in Winter/Spring (see Table A3.2, Appendix 3).

Effects of Precipitation

The effects of precipitation were weak compared to the spatial and seasonal effects and they varied significantly in different seasons (i.e. *P* = 0.0012 for SexP, Table 7). Assemblages from Rain vs. Dry conditions did differ significantly for each of the Winter/Spring and Spring/Summer seasons (Fig. 15, Table 10). However, there was no statistically significant effect of precipitation in Late Summer (Fig. 15, Table 10). Notice how the allocation success for Late Summer is only 50%, which is no better than chance allocation with 2 groups (Table 10). Note also how the CAP plot for Late Summer shows a nearly flat line (Fig. 15) and no significant correlation (δ_1^2 = 0.029, *P* = 0.708, Table 10).

Table 10. Results of CAP analyses examining effects of Precipitation within each Season. *m* = the number of principal coordinate (PCO) axes used in the CAP procedure, %Var = the percentage of the total variation explained by the first *m* PCO axes, Allocation success = the percentage of points correctly allocated into each group, δ_1^2 and δ_2^2 are the first two squared canonical correlations. *P*-values were obtained using 999 random permutations.

			Allocation success (%)				
Season	***m***	**%Var**	**Dry**	**Rain**	**Total**	δ_1^2	***P***
Winter/Spring	6	86.16	93.33	53.33	73.33	0.521	**0.005**
Spring/Summer	5	82.37	53.33	86.67	70.00	0.394	**0.021**
Late Summer	2	62.18	86.67	13.33	50.00	0.029	0.708

For assemblages sampled after Rain (R), there were no significant seasonal effects (*P* > 0.08 in all three comparisons of W/S, S/S and LS). However, slight seasonal effects were detected for assemblages sampled after Dry conditions (D), with Late Summer assemblages differing particularly from those sampled in Spring/Summer ($P = 0.0340$).

Correlations of individual taxa with canonical axes suggested that Oligochaetes, Copepods and Nemerteans were strongly associated with samples taken after Dry periods, while *Orbinia papillosa* was most strongly correlated with samples taken after Rain (see Table A3.3, Appendix 3).

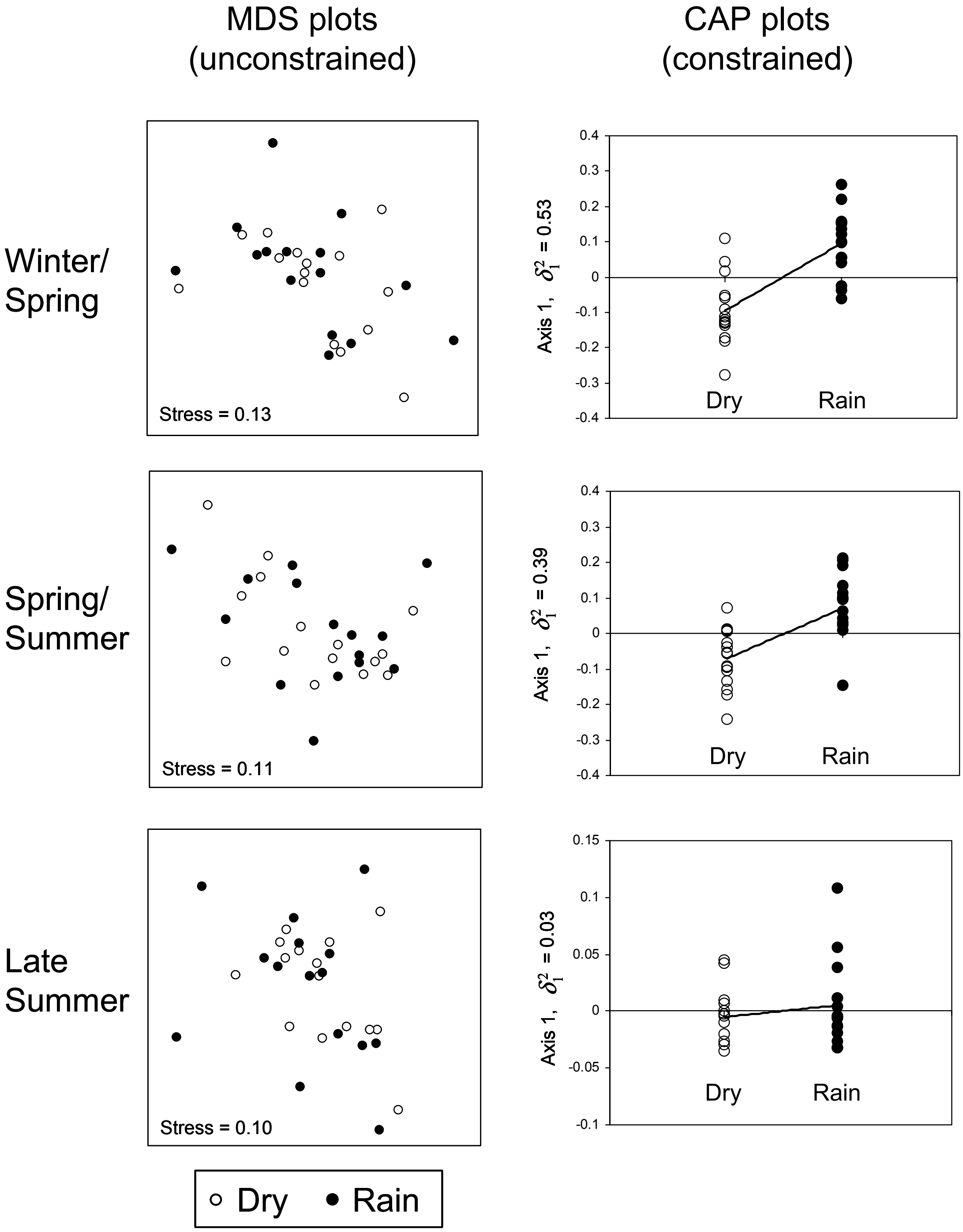


Fig. 15. Non-metric MDS plots (left-hand side) and CAP plots (right-hand side) showing the effects of Precipitation in each of three Seasons. Analyses were based on Bray-Curtis dissimilarities of 73 variables that were transformed to ln(y + 1). Each point represents pooled information from n = 6 cores.

Relationships of Fauna with Environmental Variables

There were several environmental variables that characterised individual sites and therefore could be used as a potential model of species data at the site level. These are listed in Table 11 and some combinations of the variables formed natural groupings, also shown in the Table. Two approaches were taken in the modeling. One was to relate the species data to individual environmental variables. The other was to relate the species data to groups of variables.

Table 11. List of environmental variables used in analyses.

Group	Variable Name	Description
Deposition (HML)	HvML	Contrast between High and Medium/Low sites
	MvL	Contrast between Medium and Low sites
Grain Size (GS)	GS1 – GS5	Five variables expressing percentage of grain sizes of ambient sediments falling into particular size classes:
	GS1	< 65.5 microns
	GS2	65.5 - 120.7 microns
	GS3	120.7 - 258.9 microns
	GS4	258.9 - 555.7 microns
	GS5	> 555.7 microns
Trapped	Sdep	Average total sediment deposition obtained in traps ($g.cm^{-1}.day^{-1}$)
	%fines	% of sediment in traps < 63 microns
	gt125	% of sediment in traps 63 - 125 microns
Erosion	BH	Average change in bed height (erosion/accretion) ($cm.day^{-1}$)
	sdBH	Standard deviation of change in bed height ($cm.day^{-1}$)
Distance	D	Rank distance of site from the mouth of the estuary (1-15)
	D2	Rank distance squared (D^2)
Organics	Org	Sediment organics (%)
Chlorophyll *a*	Chla	Chlorophyll *a* (in $\mu g.g^{-1}$ of wet weight)

As the modeling was done at the site level, there were 6 times of sampling for each of 15 sites, for a total of 90 observations. However, two of the observations did not have data for the variable of Organics, and so were omitted from analyses. Thus, there were 88 total observations included in the models of the 73 taxa.

Nonparametric multivariate regression (McArdle and Anderson, 2001) showed that all 16 variables together explained 71.40% of the variance in the species data, which was highly significant (F = 11.076, P = 0.0002). The variable that alone explained the greatest amount of variation was the contrast between High and Medium/Low depositional sites, (i.e. HvML, 31.8%), followed closely by ambient grain size variables (i.e. GS1-GS4 each considered independently explained over 20%, Table 12a). The following variables: Org, %fines, Sdep and Chla, did not have a significant relationship with the species data, when considered singly ($P > 0.05$ in each case, Table 12a).

When building a model, one must consider also the extent to which the variables overlap in what they explain of the species information. That is, the environmental variables are, themselves, correlated. Thus, a sequential model was built using forward selection, which produced the model shown in Table 12b. Note how the percentage of variation explained by, for example, the ambient grain size of particles (i.e. GS1-GS4) was dramatically reduced after taking into account the contrast of HvML (e.g. GS4 explained only 7.4% after removing effects due to HvML). Nevertheless, the sequential model shows that most of the variables do add significantly to our ability to explain variation in the species data, as evidenced by the P-values in the table of forward selection results (Table 12b). Only two variables, Chla and gt125, appeared to be unnecessary for the combined model ($P > 0.10$ in each case, Table 12b). Note that GS5 does not appear in Table 12b because it is redundant after fitting GS1-GS4 (i.e. because the five variables sum to 100%).

Table 12. Results of non-parametric multiple regression of individual environmental variables on the species data for (a) each variable taken individually (ignoring other variables) and (b) forward selection of variables, where the amounts explained by each variable added to the model takes into account the variability explained by variables already in the model (i.e. those variables listed above it). %Var = the percentage of the variance in the species data explained by that variable.

(a) Variables taken alone

Variable	%Var	*F*	*P*
HvML	31.77	40.038	**0.0002**
GS1	26.17	30.487	**0.0002**
GS2	24.98	28.636	**0.0002**
GS4	22.75	25.324	**0.0002**
GS3	22.13	24.434	**0.0002**
D2	16.58	17.097	**0.0002**
D	15.82	16.163	**0.0002**
BH	6.85	6.323	**0.0006**
GS5	5.91	5.405	**0.0010**
sdBH	4.68	4.224	**0.0014**
MvL	4.08	3.660	**0.0056**
gt125	2.84	2.518	**0.0326**
Org	2.15	1.888	0.0764
Perfin	2.13	1.872	0.0836
Sdep	1.77	1.547	0.1590
Chla	0.98	1.750	0.5020

(b) Variables fitted sequentially

Variable	%Var	*F*	*P*
HvML	31.77	40.038	**0.0002**
GS4	7.44	10.406	**0.0008**
GS3	5.89	9.019	**0.0012**
MvL	3.24	5.210	**0.0108**
Sdep	3.07	5.184	**0.0084**
GS2	2.72	4.807	**0.0078**
D2	3.15	5.892	**0.0034**
GS1	2.65	5.216	**0.0076**
BH	2.06	4.221	**0.0134**
sdBH	1.68	3.550	**0.0226**
Dist	2.02	4.472	**0.0094**
Org	1.20	2.720	**0.0478**
Chla	0.80	1.823	0.1300
gt125	0.70	1.614	0.1612
Perfin	2.20	5.389	**0.0024**

To visualize these multivariate patterns, a redundancy analysis was done to compare the environmental variables to the species data (Fig. 16). The first two RDA axes explained 22.4% of the variability in the species data and 54.5% of the relationship between the species and the environmental variables. Several important patterns emerge from the plot. First, the first axis corresponds to a strong separation between the High depositional sites (on the right-hand side) and the Medium and Low depositional sites (on the left-hand side). Second, the observations through time for the sites are so close together, that the 15 individual sites can be seen each as a cluster of 6 points on the diagram. These are so marked, that they have been labeled to identify them (in red). This suggests that the environmental variables go a long way to describe the distinctions between individual sites and do not seem to correlate at all with short or long-term temporal changes.

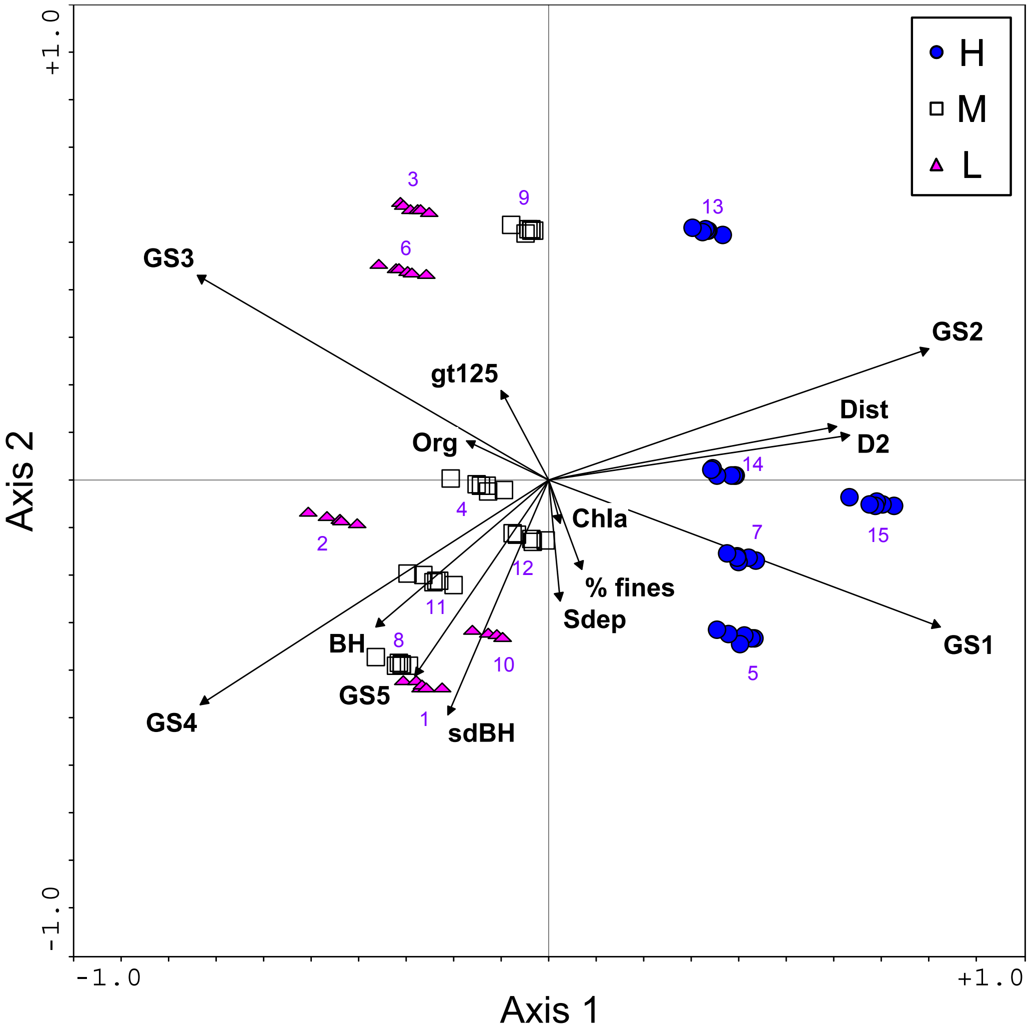


Fig. 16. Distance-based RDA ordination relating the environmental variables to the 73 taxonomic variables. The analysis was done on principal coordinate axes obtained from Bray-Curtis dissimilarities of $\ln(y + 1)$ transformed species counts, with correction method 1 for negative eigenvalues (see Legendre and Anderson 1999). Numbers in purple indicate site numbers for clusters of points. Names of variables are given in Table 11.

Furthermore, axis 1 is strongly positively correlated with rank distance (D), rank distance squared (D2), and the finer grain sizes of ambient sediments (GS1 and GS2), which are all indicative of High depositional sites. In addition, the first axis is negatively correlated with the larger grain sizes of ambient sediments (GS3 and GS4), which are indeed indicative of the Low and Medium depositional sites. The second axis is negatively associated with the Erosion variables (BH and sdBH) and the largest ambient grain size category (GS5). Certain sites (especially 1, 8, 10 and 11) are apparently associated with greater amounts of erosion and accretion, which also seems to occur where there are larger sediment particles. These results are consistent with what was found in the independent analyses of sediment information. The variables Sdep, % fines, Chla, Org and gt125 are all shown to be less important in their association with the species data (i.e. the lengths of their arrows in the diagram are not as long as for the other variables).

Also of interest was to consider a model on the basis of whole groups of variables. For example, we wished to know: is it necessary to measure all of these variables in the future to characterize sites and relate them to faunal composition?

Table 13. Results of non-parametric multiple regression of sets of environmental variables on the species data for (a) each set of variables taken individually (ignoring other sets) and (b) forward selection of sets of variables, where the amounts explained by each set added to the model takes into account the variability explained by sets of variables already in the model (i.e. those sets of variables listed above it). %Var = the percentage of the variance in the species data explained by that set of variables.

(a) Sets taken individually

Variable	%Var	*F*	*P*
GS	46.19	14.075	**0.0002**
HML	35.85	23.750	**0.0002**
Distance	19.74	10.454	**0.0002**
Trapped	12.58	4.031	**0.0002**
Erosion	12.29	5.956	**0.0002**
Org	2.15	1.888	0.0798
Chla	0.98	0.855	0.5020

(b) Sets fitted sequentially

Variable	%Var	*F*	*P*
GS	46.19	14.075	**0.0002**
Trapped	12.52	7.986	**0.0002**
HML	4.46	4.664	**0.0010**
Distance	4.62	5.384	**0.0006**
Erosion	2.05	2.487	**0.0104**
Org	0.98	2.407	**0.0336**
Chla	0.37	0.917	0.4178

The analyses of groups (whole sets) of variables are shown in Table 13. The set of variables with the greatest explanatory power was the set of ambient grain size variables, which alone (rather incredibly) explained 46.2% of the variation in the species data. Interestingly enough, once the grain size variables were fit, the next most important component was the information from trapped sediments (i.e. short-term sediment deposition information). There was almost no overlap between the ambient grain-size variables (GS) and short-term sediment deposition information (Trapped) in terms of the proportions of the species data explained (i.e., compare %Var for Trapped in Table 13a with its value in Table 13b). After fitting GS, Trapped explained an additional 12.5% of the variation in the species data (Table 13b). HML and Distance explained comparable amounts of the species' variation once GS and Trapped were included in the model, again with little overlap between them, so choosing one over the other in the sequential model made little difference. They each added about another 4.5% to the explained variation (Table 13b). Erosion variables and Organics, while only adding another 2 and 1% to the explained variation, respectively, were still statistically significant. Only Chlorophyll *a* appeared to be completely redundant in the model ($P > 0.4$, Table 13b).

Univariate Analyses of Faunal Data

It was found that all variables (counts of individual taxa) that were reasonably abundant and of interest for univariate analyses showed patterns of right skewness (see Appendix 1 for details) and were therefore transformed to $\ln(y + 1)$ before analysis. This was done to obtain more symmetric distributions and thus also to fulfill the assumption of normality required for ANOVA. In general, the use of this transformation also meant that variables had homogeneous variances across cells ($P > 0.05$, Cochran's tests). As a consequence of using such a transformation, however, all of the results must be reported in terms of effects on *median* (rather than *average*) abundances of organisms. The only variable which was not transformed prior to analysis was the total number of taxa, whose raw values already conformed to the assumptions of normality and homogeneity required for ANOVA.

Descriptive results are given for the more abundant taxa in the form of boxplots (see details in Appendix 1). In addition, the results of pair-wise comparisons (SNK tests) are given as text directly on the plots in order to aid interpretability. The pair-wise comparisons are reported in the plots as follows: levels of factors are given in order from largest to smallest. Inequalities mean a significant difference occurred (at either $P < 0.05$ or $P < 0.01$, as indicated in each case), while equal signs indicate no significant difference between levels. Also, pair-wise comparisons given directly on individual plots apply only to those plots, while those given to the right of the plots indicate comparisons that span the graphs.

Results for less abundant species (those having less than 2 individuals per core) are given in the form of chi-squared analyses on frequencies of occurrence, found in Appendix 4.

Effects of Deposition

High depositional sites contained significantly greater median numbers of *Notomastus* sp. polychaetes than did either Medium or Low depositional sites (Table 14, Fig. 17). Rarer taxa (<2 per core), such as the crustaceans *Helice/Macrophthalmus* complex, Crab zoea and the polychaetes Pectinarids, *Magelona dakini* and Other Orbinids, were all significantly more frequent in High than in Medium followed by Low depositional sites (see Table A4.1, Appendix 4).

There was a significantly higher median number of *Austrovenus stutchburyi* and of Bivalves in Low or Medium sites that in High sites (Table 14, Figs. 18 and 19). The effect of Deposition varied significantly in different Seasons for numbers of Crustaceans (Table 14, Fig. 20). However, pair-wise comparisons showed that there were significantly fewer Crustaceans in High sites than in either Medium or Low sites, for all seasons. The total number of individuals showed a significant three-way interaction (i.e. $P = 0.01$ for SexPxD, Table 14). Pair-wise comparisons showed that High depositional sites had a smaller median for total individuals than did Medium or Low sites for all times of sampling, except for that after a Dry period in Winter/Spring (Fig. 21). Less abundant taxa such as Oligochates, the polychaetes *Psuedopolydora* sp., *Boccardia* sp. and Other Spionids all showed significantly greater frequencies of occurrence in Low than in Medium, followed by High depositional sites (Table A4.1, Appendix 4).

Some effects of Deposition did not fit the pattern of either H>M>L or L>M>H. Significantly non-random distributions were observed for frequencies of occurrence of *Colorustylis lemurum* and of *Parakalliope* sp., in each case indicating L>H>M (Table A4.1). *Scoloplos cylindifer* also showed a significantly non-random distribution, but with its frequencies following the order H>L>M (Table A4.1).

Effects of Season

Significant Se x D interactions occurred for *Austrovenus stutchburyi,* and Crustaceans (Table 14). For High depositional sites only, it was found that the median number of *A. stutchburyi* was significantly greater in Late Summer compared to the other two seasons, and that the median number of Crustaceans was significantly greater in Winter/Spring than in the other two seasons (Figs. 18 and 19). Significant Se x P interactions occurred for Nemerteans, *Notomastus* sp., *Prionospio* complex, Crustaceans, Polychaetes and for the total number of taxa (Table 14). Results of pair-wise comparisons were highly variable, showing no clear or consistent patterns (Figs. 17, 20, 23, 24, 25 and 26). For example, at High depositional sites after Dry periods, the median total number of individuals was significantly smaller for Spring/Summer than for the other two seasons (Fig. 21). This pattern was reversed, however, at High depositional sites after Rain (Fig. 21).

Five of the less abundant taxa (*Helice/Macrophthalmus* complex, Other Orbinids, Other Anthozoa, *Magelona dakini* and *Phoxocephalid* sp.) showed significant seasonal changes that were consistent with a chronological decrease in their frequencies of occurrence over the seasons (Table A4.2). In contrast, Other Spionids showed a significant chronological increase in their frequencies over the seasons (Table A4.2). Six taxa (*Parakalliope* sp., *Halicarcinus* sp., *Boccardia* sp., Exogoninae, *Psuedopolydora* spp. and *Colorustylis lemurum*) showed significantly greater frequencies of occurrence in Late Spring, followed by Winter/Spring, the Spring/Summer. Two other species (*Scoloplos cylindifer* and *Aricidea* sp.) had significantly greater frequencies in Spring/Summer, while *Polydora* spp. had significantly greater frequencies in Winter/Spring.

Effects of Precipitation

The effect of Precipitation on the biology in Okura was variable when common taxa were examined. The abundance of *Nucula hartvigiana* showed the clearest influence of rain with significantly fewer organisms present after Rain compared to after Dry periods (Table 14, Fig. 22). The effect of Precipitation varied significantly with Season for Nemerteans, *Notomastus* sp., *Prionospio* complex, Crustaceans and the total number of taxa (Table 14, Figs. 17, 20, 23, 24 and 25). For all of these variables, median values were significantly greater after Rain than after Dry periods, except for *Notomastus* sp. in the Spring/Summer. In the Late Summer, samples taken after a Dry period had significantly higher median abundances of *Notomastus* sp. and Crustaceans than after Rain. This pattern was also the case for the total number of taxa. No other consistent differences were seen in the pair-wise comparisons. At High depositional sites, the median total number of individuals was significantly greater after Dry periods than after Rain, for both Winter/Spring and Late Summer (Fig. 21). However, for Spring/Summer, this pattern was reversed (Fig. 21).

Less abundant taxa were also variable in their response to Precipitation. Three crustacean taxa (*Hemigrapsus crenulatus, Waitangi* sp. and Unidentified Crustaceans) and one bivalve species (*Arthritica bifurcata*) showed significantly higher frequencies of occurrence after Rain than after Dry periods (Table A4.3, Appendix 4). Two crustacean (*Colorustylis lemurum* and Copepoda) and one polychaete (Exogoninae) showed significantly higher frequencies after Dry periods than after Rain (Table A4.3).

Size class information was collected for the three bivalves *Austrovenus stutchburyi, Paphies australis* and *Macomona liliana. A. stutchburyi* was the only species with large enough abundances to warrant an ANOVA on this information. The ANOVA showed that the different size classes were influenced by different factors (Table 15). Small *A. stutchburyi* showed a significant influence of Season (LS>W/S) and of Deposition (M=L>H, Fig. 27). Medium-sized *A. stutchburyi* showed an effect of Deposition where M=L>H (Fig. 27). Large *A. stutchburyi* showed a significant SexPxD interaction (Fig. 28). The effect of Deposition within this interaction showed L=M>H for the first three times of sampling (Rain and Dry for W/S and Dry for S/S) and M>L>H for the last three times of sampling (Rain for S/S and Rain and Dry for LS). No clear consistent effects of Precipitation or Season were shown for large *A. stutchburyi*.

All three size classes of *Paphies australis* showed significant effects of Deposition on their frequencies of occurrence (Table A4.4, Appendix 4), in each case with smaller frequencies in High compared to Low depositional environments, and greatest frequencies in Medium depositional sites. In contrast, only medium-sized *Macomona liliana* were affected by Deposition, with their frequencies showing a pattern of L>H>M (Table A4.4, Appendix 4).