

The macrobenthos of the Little Lagoon, Durban Bay.

by

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As the candidate's supervisor I have/have not approved this dissertation for
submission.

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Date:

Preface

The work described in this thesis was carried out in the School of Life and Environmental Sciences, University of Natal, Durban, from January 2001 to December 2002, under the supervision of Prof. A.T. Forbes.

This study represents original work by the author and has not otherwise been submitted in any form for any degree or diploma to any tertiary institution. Where use has been made of the work of others it is duly acknowledged in the text.

Deena Pillay
December 2002

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Abstract

The Little Lagoon is a shallow sandflat habitat situated in Durban Bay, which has been earmarked for removal, as part of the port expansion. In order to prevent the possible loss of such a significant habitat, it was proposed that this habitat be re-created elsewhere in the Bay. The aims of this project were therefore to provide a detailed assessment of the macrobenthic habitat of the Little Lagoon, and to identify the major determinants of the community structure. The ultimate goal was to provide essential background information to assess the success of the recreation of the Little Lagoon. Apart from seasonal changes in water temperature, no ecologically significant temporal fluctuations in the physical environment of the Little Lagoon were detected. This was directly translated into an extremely stable macrobenthic community, in which negligible seasonal changes to its composition were recorded. The polychaetes *Prionospio sexoculata*, *Glycera sp.*, the isopod *Leptanthura laevigata* and cumaceans dominated the community during every sampling season. From a spatial perspective, particle sizes and organic contents of surficial sediments were the major determinants of macrobenthic community structure. Densities of macrofauna were three to five times higher in organically rich sediments, and were dominated by surface and sub-surface deposit feeders such as the tanaid *Apeudes digitalis* and cirratulid polychaetes. In organically poor sediments, burrowing infauna such as *Prionospio sexoculata* and *Glycera sp.* dominated. Significantly though, biological interactions, specifically bioturbation by the sandprawn *Callianassa kraussi*, was an important determinant of community structure in the Little Lagoon. Two zones of high and low abundance of *C. kraussi* were recorded in the Little Lagoon. Abundance, species richness and diversity of macrofauna were significantly lower in the zone of high *C. kraussi* abundance. These parameters were significantly and negatively influenced by the abundance of *C. kraussi*, indicating that *C. kraussi* may act as a disturbance organism. Surface dwelling macrofauna were recorded in the zone of low *C. kraussi* abundance, but not in the zone of high *C. kraussi* abundance. It appeared that the bioturbative activity of *C. kraussi* of expelling sediment from burrows to the sediment surface resulted in the exclusion surface dwelling fauna, and played a major role in structuring the Little Lagoon macrobenthic community.

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1.1 Introduction

Durban Bay is situated on the east coast of Kwa-Zulu Natal between 29° 51' south and 31° 03' east, and is classified as an estuarine embayment (Begg 1978, Hay *et al.* 1993a, Whitfield 2000). The total area of the bay was estimated in 1978 to be 8 km², with a length of roughly 8 km and a width of approximately 3.3 km (Begg 1978). These dimensions and area are in agreement with estimates from current overhead photographs (Hay *et al.* 1993a). Two canalised rivers *viz.* the Umbilo and Mhlatuzana discharge into the southwest side of the bay, supplying a minimal amount of freshwater into the system (Forbes *et al.* 1994).

Throughout its history (from approximately 1892), there has been a strong theme of habitat destruction and deterioration associated with Durban Bay, as it has undergone numerous large-scale changes to the natural environment (Hay *et al.* 1993a). Prior to development, the bay probably functioned as typical estuarine habitat (Harris and Cyrus 1999), characterised by longitudinal salinity gradients. Currently, it operates as an embayment dominated by marine salinities (Begg 1978, Hay *et al.* 1993a) with little evidence of pronounced variations in salinity. This effect probably occurred due to the deepening and the removal of the sandbar at the entrance of the bay (Hay *et al.* 1993a), which had the effect of allowing seawater intrusion further into the bay, and thereby reducing the effects of the freshwater inputs.

The most obvious and perhaps the most ecologically significant of changes in the bay, were the reductions in the total areas of mangrove and shallow tidal sandflat habitats (Figs 1-3), (Hay *et al.* 1993a). The first record of mangrove swamp removals was made in 1888, when the mangrove swamps in the region between Albert Park and Congella (Fig 1) were cleared (Berjak *et al.* 1977). Such removal and clearance of mangrove areas continued periodically as harbour developments proceeded, and it is currently estimated from historical records that less than 10% of the original mangrove habitat survives (Fig 3). Similarly, much of the development of the harbour involved the deepening and dredging of channels, and the consequent removal of sandbanks, in order to facilitate entry and movement of ships into the bay. This has occurred at such a rate, that only 25% of the original shallow sandflat habitats currently exist in the harbour (Fig 3, Hay *et al.* 1993a). The destruction of these habitats had undoubtedly lead to the reduction in the overall diversity and species richness of the Bay, and was cited even as early as 1956, as being one of the major causes of “deterioration” and faunal “poverty” in the bay (Day and Morgans 1956).

The theme of habitat destruction associated with harbour developments in Durban Bay, is still currently prevalent. As one of the busiest shipping ports in Africa, and in order to maximise economic growth, there has been an urgent need to deal with the problem of increasing container traffic in Durban Bay. This function (i.e. container traffic) is presently the major cargo handling activity in the harbour. In recent years, traffic has steadily grown to approach the capacity of existing container terminal facilities. In order to maintain the economic competitiveness of the port, the harbour authorities have seen it necessary to increase the capacity of current container handling facilities by a westerly expansion of pier number two (Figs 5 & 6).

While this extension might prove to be essential in the overall economic and structural development of the harbour, there have been several concerns that this development might directly lead to the destruction and loss of ecologically significant sandbank habitats, and more particularly, the area commonly known as the Little Lagoon (Figs 5 & 6).

The Little Lagoon is located opposite pier number 2 (Figs 5 & 6), and is composed of a shallow subtidal habitat flanked on either side by intertidal sandbanks. At low spring tides, it is estimated that this habitat occupies an area of roughly 42 000m². A vestigial mangrove sanctuary is located approximately 300m south of pier number 2, which remains connected with the Little Lagoon during high tides. Much of the intertidal sandflats, and the shallow submerged habitats to a lesser degree, are inhabited by the burrowing sandprawn *Callianassa kraussi*. This organism is a major component of this habitat, both in terms of its numerical and gravimetric (biomass) dominance. Moreover, its burrowing activities have the potential to greatly alter sediment properties, as well as the structure of benthic communities (Cadee 2000, Flach and Tamaki 2000). The eastward shore of the Little Lagoon is utilised by burrowing soldier crabs, *Dotilla fenestrata*, which forage in sediments at low tides. The significance of the Little Lagoon habitat is that it is possibly one of the few remaining habitats along with Richards Bay that still support large populations of these organisms.

The ecological value of intertidal sandflat habitats is highlighted by the fact that at present, only three shallow sandbanks remain in Durban Harbour; one to the south of Pier 2, one centrally in the Bay, and one to the North of the central sandbank (Fig 3). These sandbanks constitute only 25% of the original sandflat habitat (Hay *et al.* 1993a), and are considered to be of extreme significance as habitats in the harbour, and also in the context of Kwazulu-Natal, because of their rarity in this province (Hay *et al.* 1993a).

On the basis of the possible loss of the above mentioned sandbank, it was proposed that the Little Lagoon habitat be re-created elsewhere in the harbour. For this to be successfully undertaken, there existed a need for a thorough investigation into the ecology of the Little Lagoon, since the last major ecological survey was undertaken in 1956 by Day and Morgans (1956). Based on this rationale, it was therefore the aim of the present study to carry out a detailed study of the macrobenthos of the Little Lagoon, and to characterise the benthic habitat and associated macrofaunal invertebrates of the Little Lagoon. A further aim was to identify the factors that influenced or regulated these macrofauna communities, with the ultimate goal being to provide the background ecological information and a benchmark to assess the success of the recreation of the Little Lagoon habitat elsewhere.

Apart from the management motivation for the study highlighted above, the fundamental scientific rationale was that the study offered the unique opportunity to investigate ecological processes in a tidal sandflat habitat, of which no knowledge exists in Kwa-Zulu Natal. On a similar note, the study also offered a broader opportunity to add to current knowledge of macrobenthic communities of estuarine habitats in Kwa-Zulu Natal, which in many cases are either extremely limited or outdated.

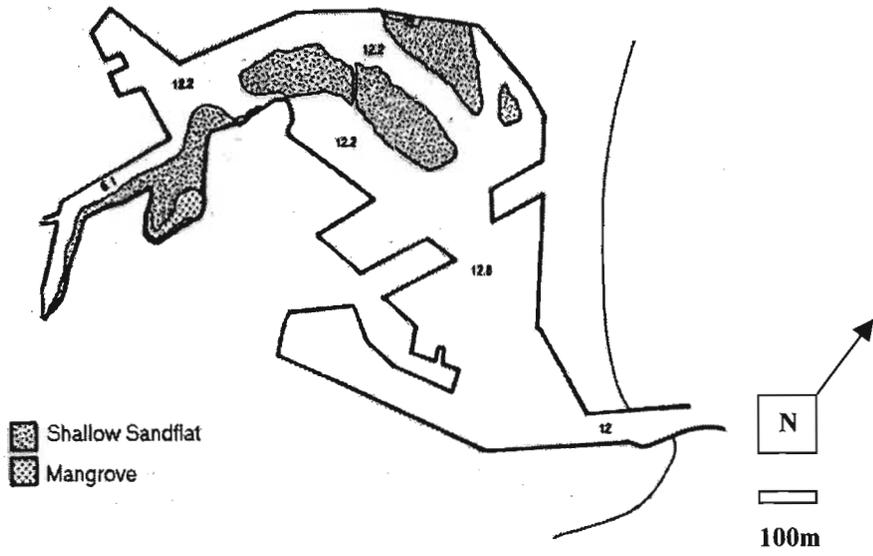


Fig 3: Areas of mangrove and shallow sandflat habitats in Durban Bay in 1991.

1.2 The Study Site

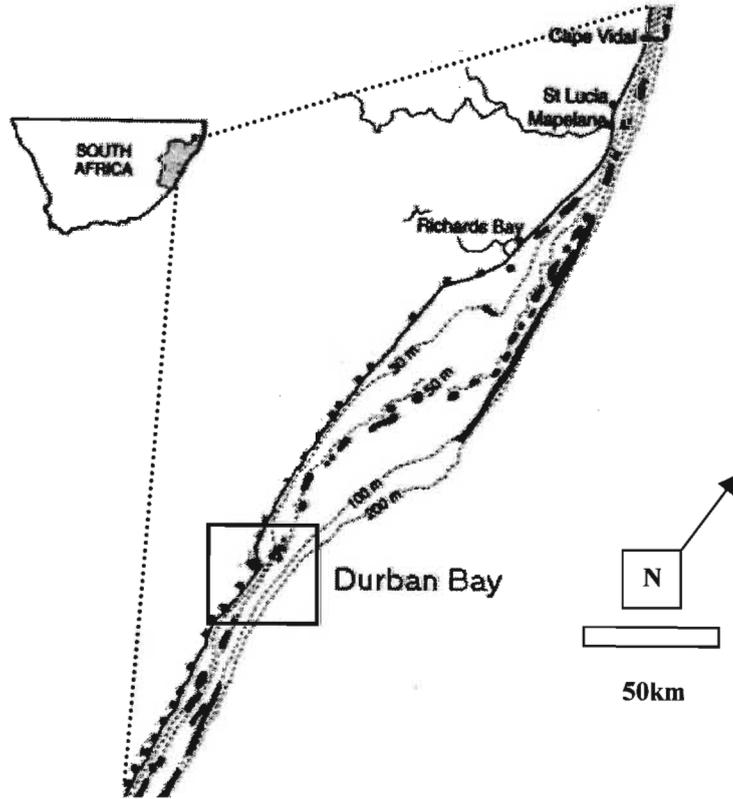


Fig 4: Geographical position of Durban Bay on the South African coastline.

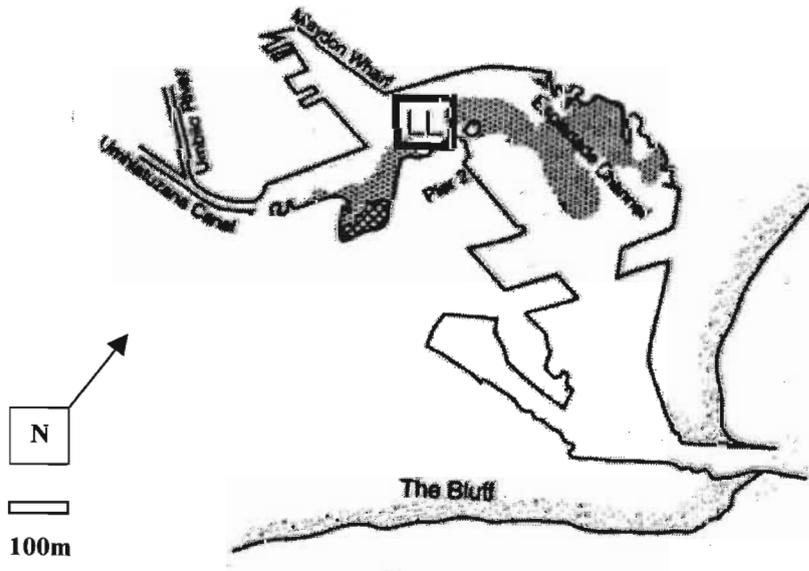


Fig 5: The location of Little Lagoon (LL) in Durban Bay.



Fig 6: Position of transects and sampling sites in the Little Lagoon.

1.3 Materials and Methods

Three transects were positioned across the Little Lagoon in a North-South direction, aligned parallel to each other, and positioned roughly 100 m apart. Each transect comprised four sampling stations, each being roughly 100 m apart (Fig 6). Sampling sites were positioned such that sites 1 and 4 of all transects were located on intertidal sandflats, and exposed at spring and neap low tides, whereas sites 2 and 3 were always sub-tidal. At high tides (both spring and neap), all sampling stations were submerged. The co-ordinates of sampling sites were determined using a Garmin 12 channel GPS (global positioning system) and were recorded for subsequent relocation. Sampling was undertaken in March, June, September and December 2001, and March and June 2002. In March and June 2001, grab samples were collected from a boat, but were collected on foot for the remaining four sampling seasons. The latter method allowed for a more precise relocation of sampling sites, whereas the former method was impractical due to drifting of the boat away from sampling sites.

1.3.1 Physico-chemical Measurements

Water temperature, salinity and dissolved oxygen were measured at each site, using a portable Horiba U-10 water sampler. These measurements were taken approximately 10 cm above the sediment surface, i.e. close to the sediment-water interface. Single sediment samples were collected from the upper 5 to 10 cm sediment layer (surface sediment) and from 1m deep (deep sediment), from which median particle sizes were determined according to methods described by Morgans (1956). For organic content determination, the sample was dried at 100°C and weighed, then heating to 600°C overnight, and weighed again. Organic content was expressed as the percentage loss of weight of the sample after incineration (Morgans 1956). Shell content of deep sediment was defined as fragments retained by 1 mm and 2 mm mesh size sieves (Morgans 1956). Deep sediment samples were collected using a prawn pump (Length=90 cm, diameter=5 cm Fig 7). Water depths were measured using a graduated shot-line at high and low tide during from which the on site tidal range was estimated.

1.3.2 Macrofauna samples

Two macrobenthic habitats were investigated in the Little Lagoon (Fig 7). In the first instance, the upper 20 cm sediment layer was sampled using a Zabalocki – type Eckman grab (area = 0.0236 m²), to target macrofauna that utilise the benthic habitat close to the sediment water

interface. The other habitat type investigated was the sediment layer up to a meter below the sediment surface, which was specifically intended to sample the endobenthic organism, *viz.* *Callianassa kraussi*, which burrows up 1 meter deep into sediments. Sediment cores from the endobenthos were collected using a stainless steel prawn pump (Length=90 cm, diameter=5 cm). Macrofauna from the upper 20 cm were retained in endobenthic sediment cores, together with *Callianassa kraussi* samples (Fig 7). From these cores, relationships between abundance of *Callianassa kraussi* and macrofaunal community structure were determined. Grab samples were collected at all sites, and endobenthic samples were collected from intertidal sites only (Sites 1 and 4), due to practical difficulties of sampling in deep, permanently sub-tidal regions. At each sampling site, three replicate samples (for both grab and endobenthic samples) were collected. Each grab sample replicate comprised three grabs, and endobenthic replicates consisted of five sediment cores. In total, nine grab and fifteen endobenthic samples were collected per sampling site.

Grab samples and endobenthic sediment cores were emptied into buckets to which water was added, and then stirred, thereby suspending benthic organisms. The supernatant was passed through a 0.50mm sieve to retain macrofauna. This procedure of stirring and sieving was repeated five times, and the contents of the sieve emptied into a plastic jar. The remaining sediments in the bucket were washed through a 2mm-mesh sieve, and the retained organisms emptied into the sample jar. Samples were preserved in a 4% formaldehyde solution and stained with Phloxine-B. In the laboratory, samples were sorted and organisms identified to species level where possible using a binocular microscope, and enumerated. The following references were used to identify macrobenthic organisms: (Branch and Branch 1981, Day 1967a, Day 1967b, 1969, Griffiths 1976, Kilburn and Rippey 1982). Individual specimens of *C. kraussi* from endobenthic cores, were sexed, and carapace lengths were measured, allowing for a spatial and temporal assessment of the population dynamics of this species in the Little Lagoon.

1.3.3 Statistical Analyses

All multivariate analyses were performed using the PRIMER (Plymouth Routines in Multivariate Ecological Research) statistical software package. Cluster analysis and non-metric multidimensional scaling (MDS) were used to visually assess spatial and temporal differences macrobenthic communities in the study site. The ANOSIM procedure was utilised to statistically test for significant differences between communities. MDS ordination and cluster plots were constructed from similarity matrices generated from Bray-Curtis similarities, after fourth root transformations ($\sqrt[4]{\sqrt{\cdot}}$) and row standardising of abundance data. The DIVERSE

procedure was used to calculate the following community parameters at sampling sites: Total Abundance (N), Species Richness, which was expressed as total number of species (S), and Shannon-Weiner diversity (H') to the base e. The SIMPER program was used to identify macrofaunal species that dominated and characterised specific sampling sites. Testing for spatial differences in macrofauna community parameters was performed using a Mann Whitney-U test in the case of two treatments. Where treatments exceeded two cases, a Kruskal-Wallis test was applied.

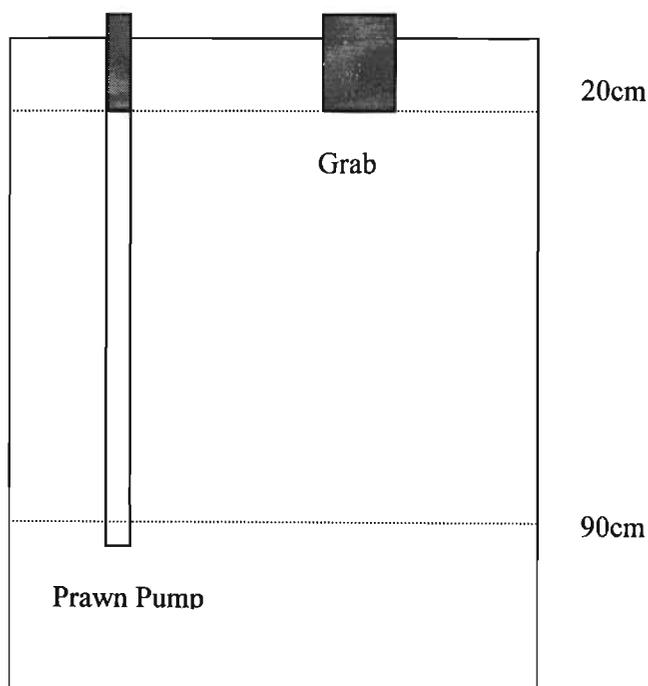


Fig 7: Schematic representation of a hypothetical 2-dimensional benthic habitat, indicating the two macrobenthic sampling techniques utilised.

The grab sampled the upper 20cm sediment layer. The prawn pump sampled *Callianassa kraussi* from sediments 90cm deep, as well as macrofauna in the upper 20cm sediment layer.

2. Results

2.1 The Physical Environment

2.1.1 Water Depth

Tidal range in the Little Lagoon was between 1 and 1.2m. Sites 1 and 4 of all transects were exposed at spring and neap low tides, but sites 2 and 3 on all transects were permanently submerged (Fig 8). Water depths at LWS were greatest at sites C2, A2 and C3, with depths of 1.25m, 0.9m and 0.85m, measured respectively (Appendix A).

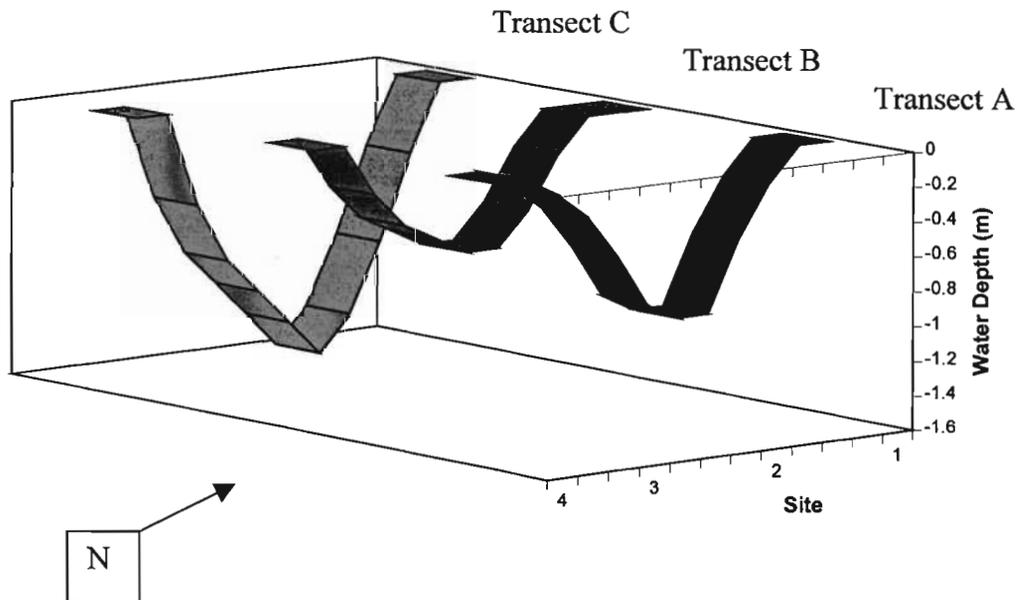


Fig 8: Cross-section of the Little Lagoon showing water depth at low water spring (LWS, n=2).

2.1.2 Water Temperature

There were pronounced seasonal differences in water temperatures in the Little Lagoon (Fig 9). Peak temperatures were recorded at the end of summer (March) of both years and ranged from 26.4 °C to 28.8 °C. Lowest temperatures were measured in June (range: 17.9 °C to 22.8 °C) and September (range: 20.5 °C to 22.8 °C). There was no evidence of spatial variations in water temperature in the Little Lagoon during the study (Appendix A).

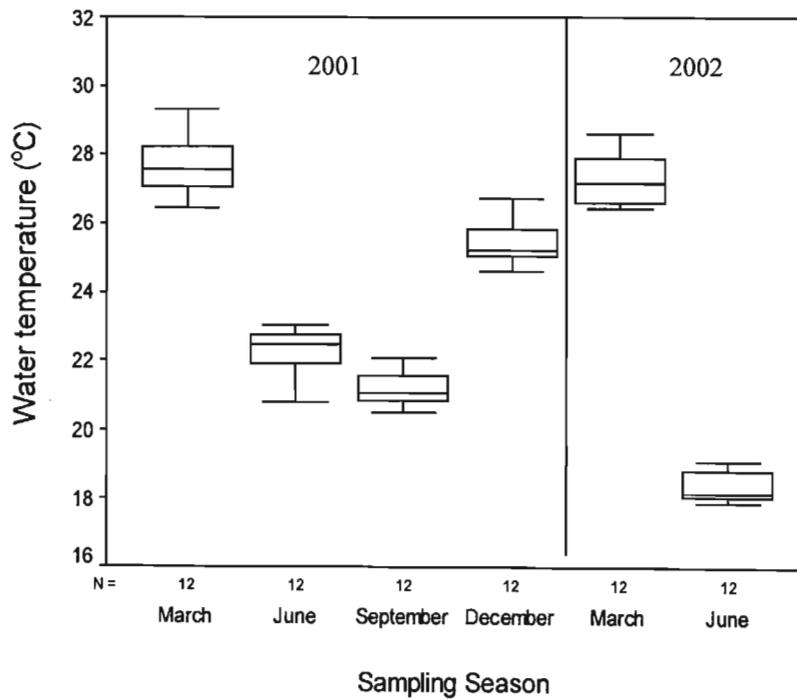


Fig 9: Temporal variations in water temperatures in the Little Lagoon (Boxes represent standard error, horizontal line across boxes indicates median values, vertical lines indicate maximum and minimum values, n = 12).

2.1.3 Salinity

Salinity of 20.4‰ was recorded on two occasions in March 2001 (Appendix A). Except for these outliers, salinities ranged from 27.1‰ to 37.6‰ during the six sampling periods (Fig 10), indicating a dominant influence of marine salinities. No evidence of spatial variations in salinity was detected.

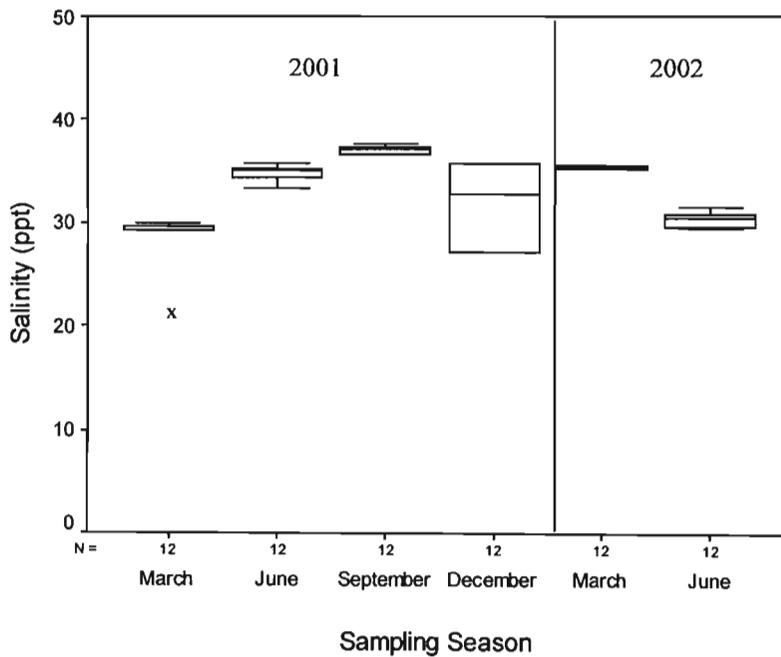


Fig 10: Seasonal variations in salinities in the Little Lagoon.

(Boxes represent standard error, horizontal line across boxes indicates median values, vertical lines indicate maximum and minimum values, n = 12. X=Outliers and extremes).

2.1.4 Dissolved Oxygen

There were no indications of ecologically significant spatial or temporal variations in concentrations of dissolved oxygen (DO) in the Little Lagoon during the study (Fig 11, Appendix A). Mean DO levels in the study area were never less than 6.09 mg/L, with the highest mean of 7.81 mg/L recorded in June 2002. The consistent DO levels recorded over the sampling period indicate that the Little Lagoon is well flushed.

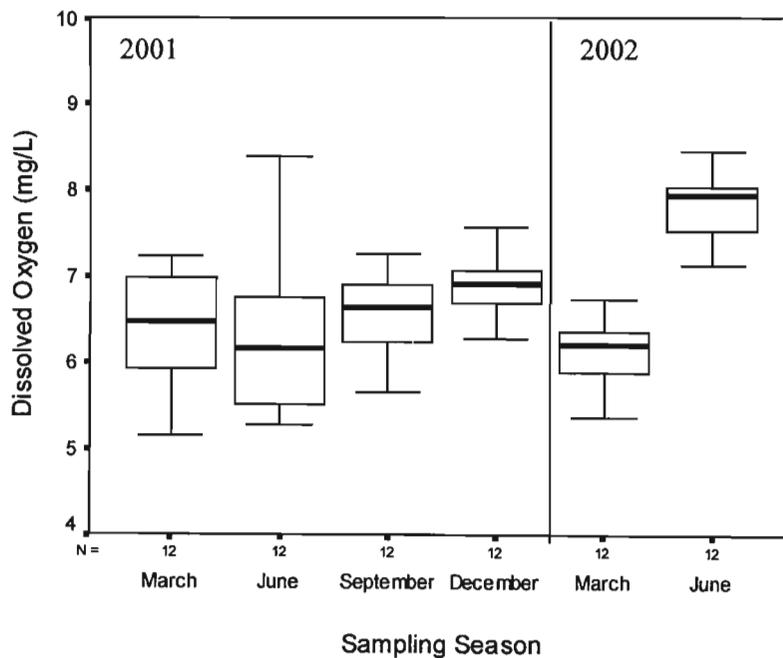


Fig 11: Temporal variations in concentration of dissolved oxygen in the Little Lagoon. (Boxes represent standard error, horizontal line across boxes indicates median values, vertical lines indicate maximum and minimum values, n = 12).

2.1.5 Sediment Properties

2.1.5.1 Surface Sediments

2.1.5.1.1 Particle Sizes

There were no significant seasonal differences in median sediment phi values ($p=0.9$) in the Little Lagoon during the study (Fig 13), which is indicative of a high degree of sediment stability in the study area. Consistent, spatial differences in particle sizes were however recorded (Figs 12 & 13). The majority of sediments in the Little Lagoon, were classified as fine sand (Morgans 1956), with median phi values ranging from 1.8 to 2.4 (Fig 13). Highest sediment median phi values were recorded at the two deepest sites *viz.* A2 and C2, and ranged from 3 to 3.2 and 2.7 to 3.1, and were classified as very fine sand. Lowest sediment phi values of 1.7 - 1.8 (medium sand) were recorded at site B2 (Figs 12 & 13).

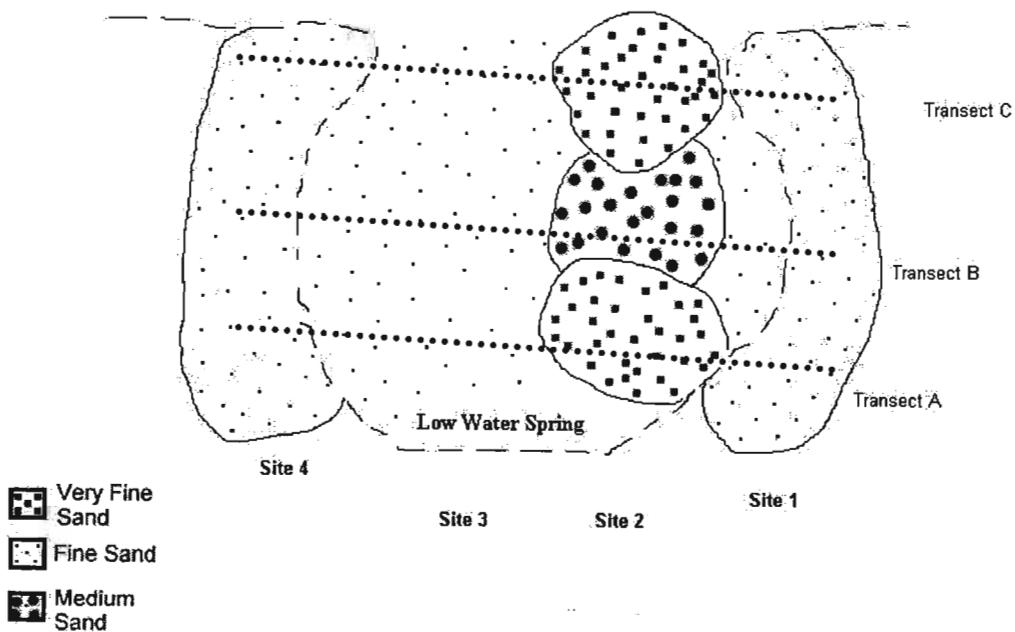


Fig 12: Sediment distribution in the Little Lagoon. Terms follow the Wentworth classification, Morgans (1956). The classification is based on mean sediment phi values determined per site, from 6 seasonal replicates.

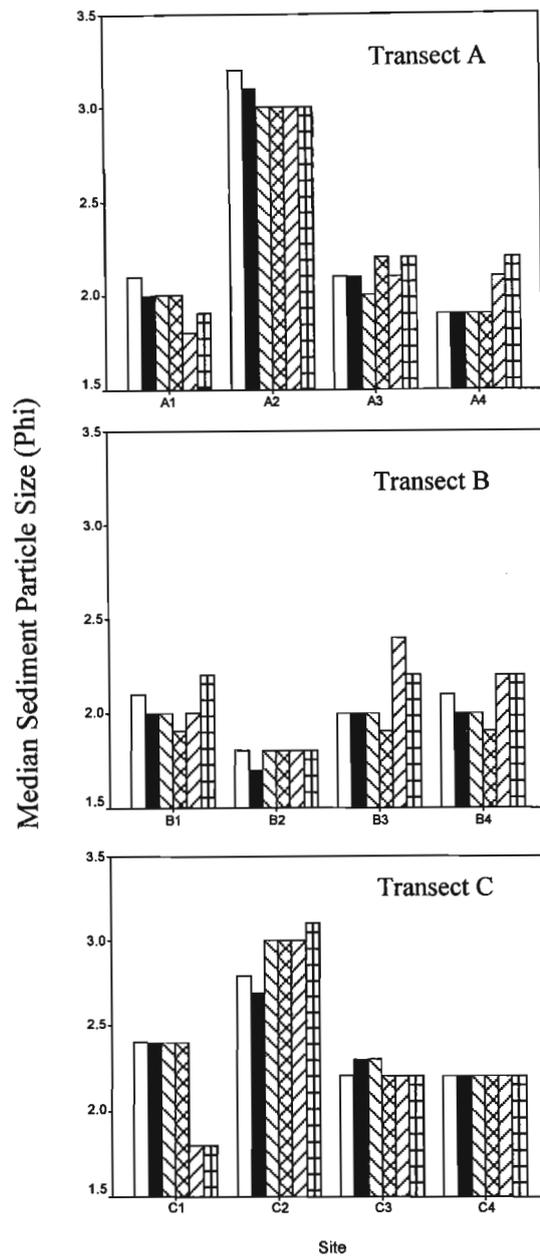


Fig 13: Temporal and spatial variations in sediment median phi values in the Little Lagoon on Transects A, B and C. Bars (from left to right of each transect) represent values obtained in March, June, September, December 2001, and March, June 2002.

2.1.5.1.2 Organic Contents

There were no significant seasonal changes in sediment organic contents in the Little Lagoon during the study ($p=0.1$, Appendix B), but obvious spatial differences were detected (Figs 14 & 15). Highest mean organic contents of 6.8% and 6.5% were recorded at sites A2 and C2 respectively, which were the deepest regions of the Little Lagoon, and in which very fine sand was present. In the remaining more shallow regions, organic contents were lower, and ranged from 1.8% to 3.3% (Fig 15). Increased organic content, and finer sediment types in the deeper regions of the Little Lagoon indicated that these areas act as deposition zones for organic material and submerged debris. Reduced organic contents and coarser sediment types in shallow zones imply that these regions act as erosional environments, characterised by relatively stronger wave action.

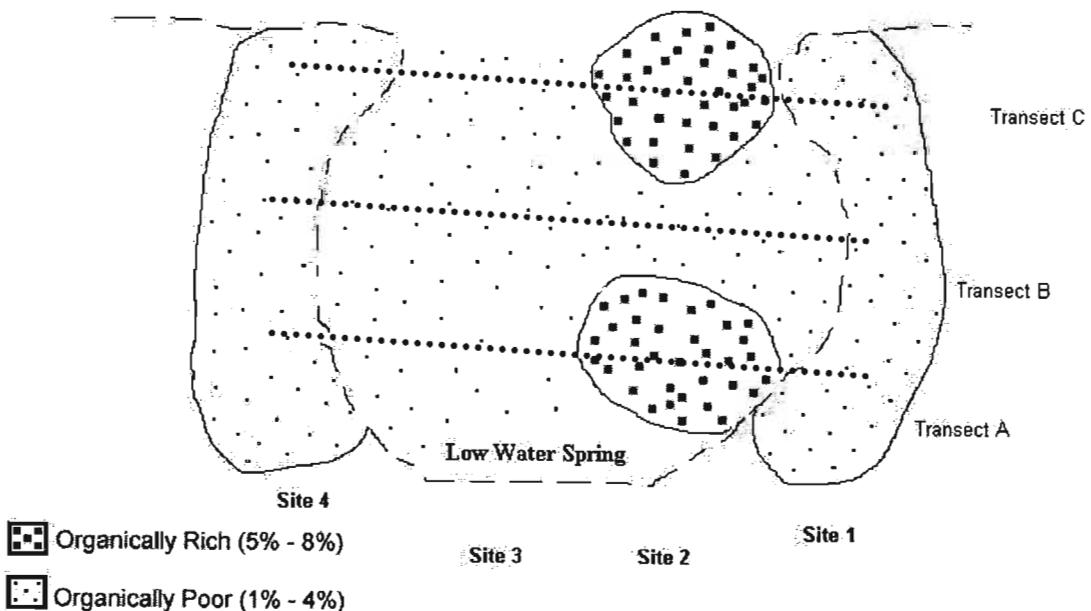


Fig 14: Location of organically rich sediment patches in the Little Lagoon.

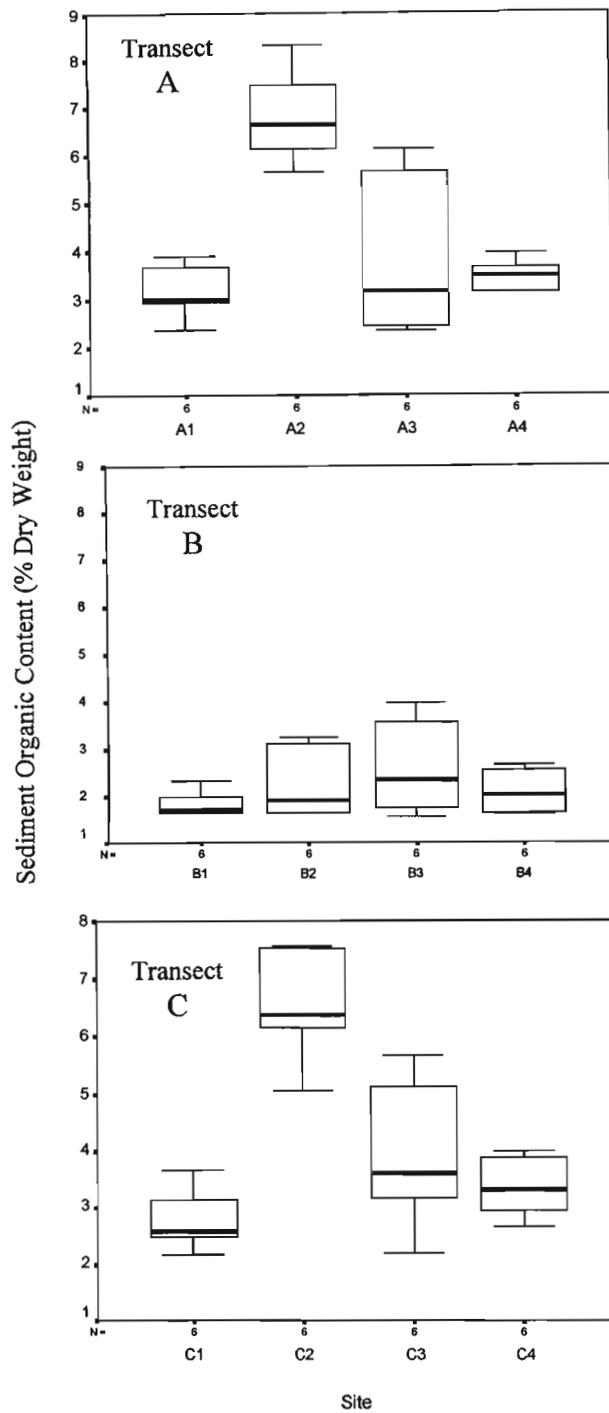


Fig 15: Spatial variations in sediment organic contents in the Little Lagoon on Transects A, B and C. (Boxes represent standard error, horizontal line across boxes indicates median values, vertical lines indicate maximum and minimum values, n = 6).

2.1.5.2 Deep Sediments

2.1.5.2.1 Sediment Particle Sizes

Deep sediments at sites A1, B1, C1, C4 were classed as fine sand, with phi values ranging from 2 to 2.5 (Fig 16). At sites A4 and B4, deep sediments were medium sand, with phi values ranging from 1.5 to 1.56.

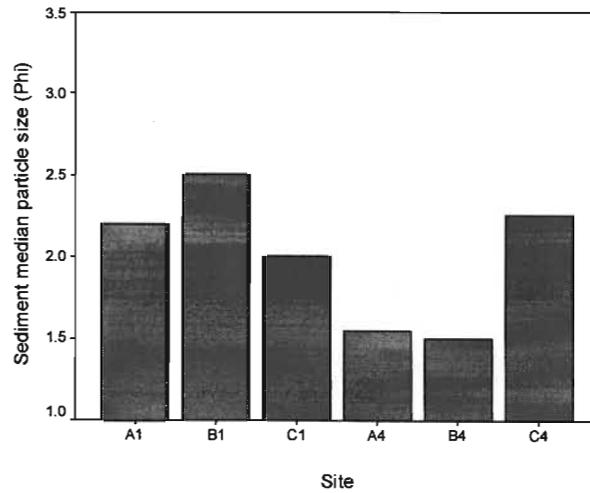


Fig 16: Particle sizes of deep sediment samples (n=1).

Greatest shell contents of 6% to 16% were recorded at sites A4 and B4 respectively. At the remaining sites, shell contents were lower, ranging from less than 1% to 3% (Figs 17 & 18).

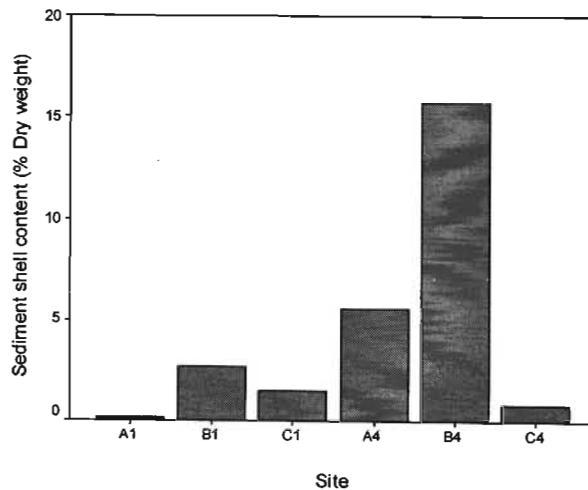


Fig 17: Shell contents in deep sediment samples (n=1).

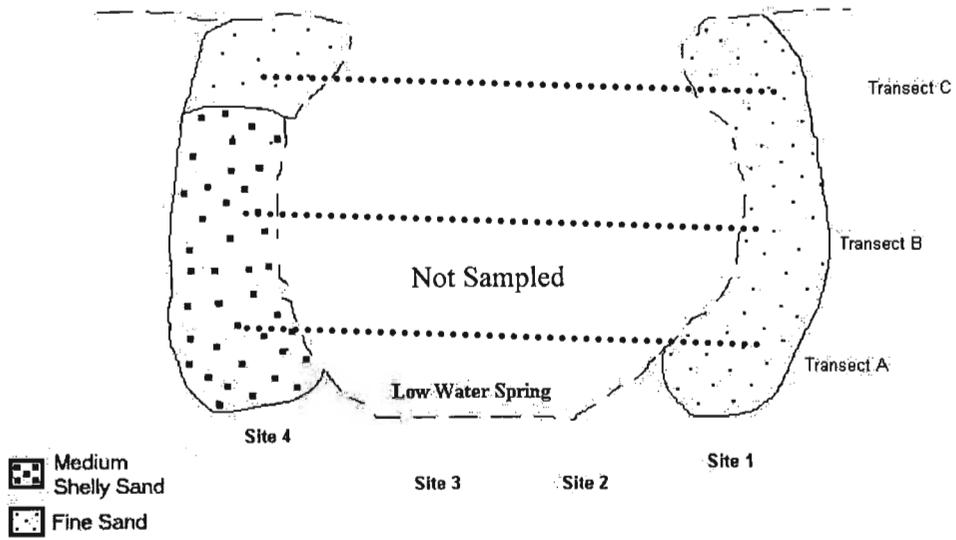


Fig 18: Deep sediment types in the Little Lagoon.

Organic contents were up to three times lower in deep sediment samples than in surface sediment samples, and ranged from 1.4% at C1 to 2.7% at A1 (Fig 19).

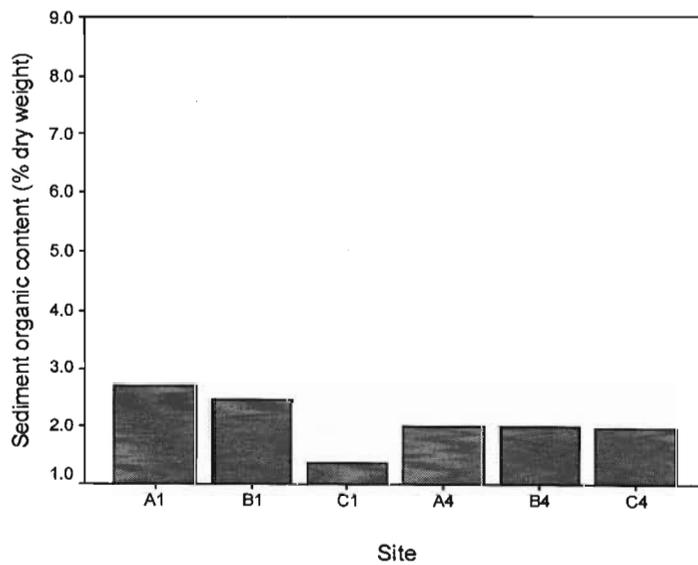


Fig 19: Organic contents in deep sediment samples (n = 1).

2.2 Macrofauna

A total of 38 macrobenthic species were recorded in the Little Lagoon during the study, with the Polychaeta, Crustacea and Mollusca being the major constituents. These taxa contributed 50%, 43% and 7% to the composition of the macrofauna community in the Little Lagoon (Table 1).

Table 1: Mean density (individuals/m²) of macrofauna at sampling sites in the Little Lagoon. Values are means of three site and six seasonal replicates (n=18). See Appendix C for seasonal specific species lists.

	A1	A2	A3	A4	B1	B2	B3	B4	C1	C2	C3	C4
Polychaeta												
Cirratulidae												
Unidentified Cirratulid polychaetes	1	1280	173	53	17	85	145	199	0	112	474	28
Phyllodocidae												
<i>Phyllodoce castanea</i>	0	7	1	2	1	0	0	4	0	5	1	0
Cossuridae												
<i>Cossura coasta</i>	0	228	2	0	2	73	5	0	0	406	39	0
Orbiniidae												
<i>Scoloplos johnstonei</i>	2	0	2	2	0	2	0	0	12	3	4	2
Spionidae												
<i>Prionospio sexoculata</i>	343	578	356	374	272	304	487	613	229	409	411	330
<i>Polydora sp</i>	0	0	0	0	0	2	1	0	1	0	0	0
<i>Scololepis squamata</i>	2	7	0	0	0	4	0	0	0	0	0	0
Nereidae												
<i>Ceratonereis erythroensis</i>	0	0	0	3	0	5	0	3	0	0	0	0
<i>Dendronereis arborifera</i>	6	5	7	42	3	0	22	64	0	1	0	10
Glyceridae												
<i>Glycera sp</i>	66	44	63	41	70	41	56	82	53	42	61	104
Capitellidae												
Unidentified capitellid polychaetes	73	17	2	1	5	3	0	2	16	28	10	0
Sabellidae												
<i>Megalomma sp</i>	0	2	0	0	0	0	0	0	0	0	0	0
<i>Desdemona ornate</i>	44	10	169	505	4	6	137	52	2	25	24	22
Maldanidae												
Unidentified Maldanid polychaetes	0	0	1	2	0	0	0	0	0	0	0	0
Eunicidae												
<i>Marphysa depressa</i>	0	1	0	0	0	0	0	0	0	0	0	0
Crustacea												
Anomura												
<i>Upogebia africana</i>	1	0	0	0	0	0	0	0	0	0	0	1

	A1	A2	A3	A4	B1	B2	B3	B4	C1	C2	C3	C4
<i>Callianassa kraussi</i>	36	0	0	5	31	46	0	8	16	5	61	22
Macrura												
<i>Betaeus jucundus</i>	0	0	0	0	0	0	0	0	0	0	1	0
Isopoda												
<i>Cyathura estuaria</i>	2	1	0	0	0	0	0	0	0	0	0	0
<i>Cirolana luciae</i>	10	0	0	0	6	5	0	0	0	36	2	1
<i>Leptanthura laevigata</i>	74	92	81	375	96	137	140	304	118	60	114	150
Amphipoda												
<i>Melita zeylanica</i>	2	0	0	2	0	0	0	1	0	0	0	0
<i>Corophium triaenonyx</i>	0	19	10	0	0	0	1	0	0	0	1	1
<i>Grandidierella bonnieroides</i>	5	2	20	13	3	2	0	7	5	0	5	20
Cumacea												
Cumacea	152	28	100	264	126	35	87	170	155	9	106	151
Brachyura												
<i>Thaumastoplax spiralis</i>	2	1	0	0	1	3	0	0	2	2	0	2
<i>Paratyloplax blephariskios</i>	0	24	0	0	0	38	0	0	0	14	0	1
<i>Hymenosoma orbiculare</i>	1	0	0	0	0	0	0	0	0	0	0	0
Tanaidacea												
<i>Apeudes digitalis</i>	0	3226	510	301	1	40	1037	13	0	5	124	3
Mollusca												
Gastropoda												
<i>Nassarius kraussianus</i>	2	58	103	25	2	49	84	57	2	53	24	32
<i>Acteocina fusiformis</i>	0	10	6	5	0	38	10	25	0	3	0	9
Bivalvia												
<i>Eumarcia paupercula</i>	12	20	55	13	10	14	54	53	6	10	9	24
<i>Solen cylindraceus</i>	0	4	1	2	1	2	5	2	0	1	0	0
<i>Dosinia hepatica</i>	13	26	77	33	22	46	67	37	10	15	22	23
<i>Brachidontes virgiliae</i>	0	35	24	0	0	0	22	11	1	0	0	2
<i>Fulvia papyracea</i>	0	0	2	0	0	1	0	0	0	0	2	0
<i>Tellina prismatica</i>	0	22	9	1	1	14	3	2	0	25	4	0
Sipunculida	2	0	0	0	0	0	0	0	0	0	0	0
Number of Species	22	26	23	22	20	25	18	21	15	22	21	21

2.2.1 The Macrobenthic community of the Little Lagoon

Four species dominated the macrofaunal community of the Little Lagoon (Table 2), and accounted for 75% of its community composition. These were the polychaete *Prionospio sexoculata*, which was the most numerically dominant (43%), followed by the isopod *Leptanthura laevigata* (13.4%), Cumacea (11.5%) and *Glycera sp.* (Polychaeta, 7.1%). The high contributions of these species, is a reflection of their occurrence at all sites in the Little Lagoon (Table 1). Cirratulid polychaetes (5.8%), the tanaid *Apseudes digitalis* (4.3%), the bivalve *Dosinia hepatica* (2.7%) and the polychaete *Desdemonia ornata* (2.5%) were less dominant in the Little Lagoon.

Table 2: The dominant macrofauna of the Little Lagoon, which accounted for 90% of the overall community composition. Values indicate percent contribution determined by the SIMPER routine.

Species	Contribution (%)	Cumulative %
<i>P.sexoculata</i>	43.4	43.4
<i>L.laevigata</i>	13.4	56.9
Cumacea	11.5	68.3
<i>Glycera sp.</i>	7.1	75.4
Cirratulid polychaetes	5.8	81.3
<i>A. digitalis</i>	4.3	85.6
<i>D. hepatica</i>	2.7	88.3
<i>D. ornata</i>	2.5	90

2.2.2 Temporal variations in the macrobenthic community of the Little Lagoon

There were no detectable seasonal changes in species composition of the macrobenthic community in the Little Lagoon during the study. The major species which accounted for 65% of the community composition such as *Prionospio sexoculata* (Polychaeta), *Leptanthura laevigata* (Isopoda) and *Glycera sp* (Polychaeta) and Cumacea to a lesser extent dominated communities during every season (Table 3).

Table 3: Seasonal changes in macrofauna of the Little Lagoon.

Species that accounted for 90% of the community composition are listed. Values represent percent contributions determined by the SIMPER routine.

Species	March 2001	June 2001	September 2001	December 2001	March 2002	June 2002
<i>Glycera sp</i>	25	18	11	13	7	7
<i>Prionospio sexoculata</i>	24	26	26	31	25	25
<i>Leptanthura laevigata</i>	18	18	20	7	12	16
Cirratulid polychaetes	8	5	3	6	6	6
<i>Nassarius kraussianus</i>	5	4	2	8	7	5
Cumacea	4	12	21	19	5	9
Capitellids	3					
<i>Eumarcia paupercula</i>	3	8		3	7	
<i>Dosinia hepatica</i>			5	5	13	10
<i>Callianassa kraussi</i>			3			5
<i>Apseudes digitalis</i>					6	
<i>Desdemona ornata</i>					5	8

2.2.3 Spatial organisation of assemblages in the Little Lagoon.

Within the macrobenthic community of the Little Lagoon as a whole, four specific spatially distinct macrobenthic assemblages were identified. ($p=0.001$, Figs 20 & 21). The spatial separation of these assemblages was associated with sediment type, and with the presence of the burrowing sandprawn *Callianassa kraussi*. Sediments in Zone D were classed as very fine, organically rich sand (Figs 13 & 14). Zone A was composed entirely of intertidal regions in which *C. kraussi* was abundant. Zone B comprised the intertidal sandflat region in which *C. kraussi* was rare (Ref. to Fig 30 for the distribution of *C. kraussi*), in combination with the subtidal region immediately adjacent to it (Fig 20). Sediments in Zone C were a combination of medium to very fine sand.

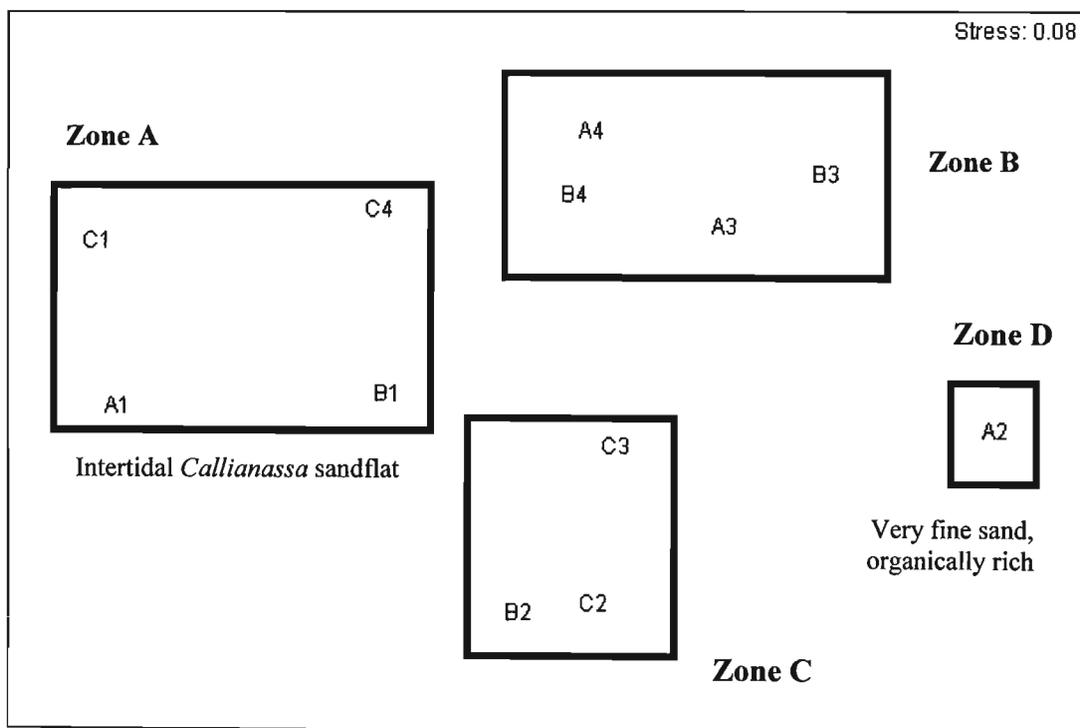


Fig 20: MDS ordination plot indicating spatially distinct macrobenthic assemblages in the Little Lagoon ($n=18$). Three replicates per site, and six replicates per season were averaged.

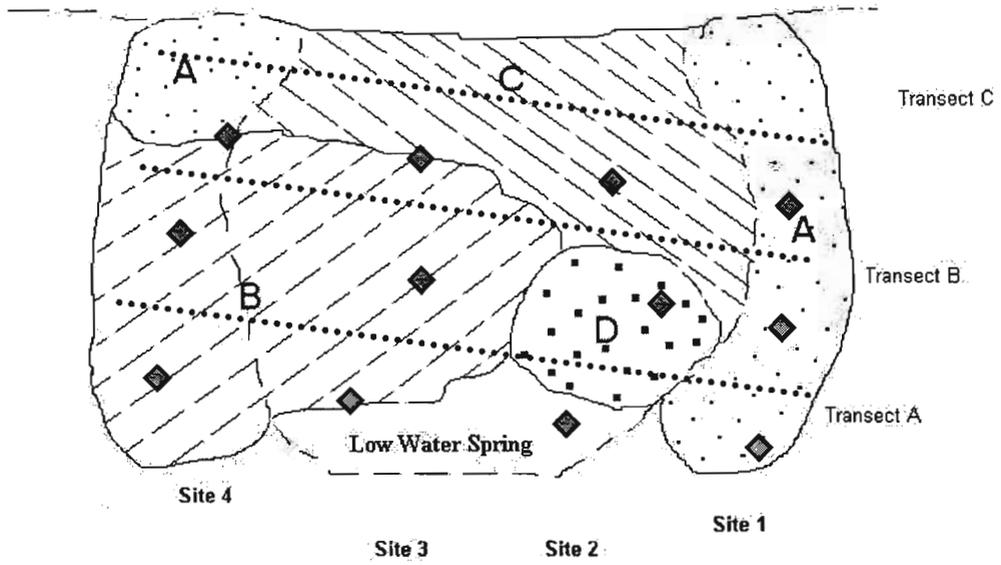


Fig 21: The positions of the four primary macrobenthic assemblages in the Little Lagoon (A=Intertidal *Callianassa* bed, B=intertidal sandflat (*Callianassa* absent) combined with adjacent subtidal zone, C=deep subtidal zone (medium to very fine sand) D=deep subtidal zone, (very fine sand, organically rich).
 ◆ = sampling site.

2.2.4 Species composition of macrofaunal assemblages.

The polychaetes *Prionospio sexoculata* and the isopod *Leptanthura laevigata* characterised all four zones (Table 4). The very fine, organically rich sediment of Zone D, was characterised by cirratulid polychaetes and the tanaid *Apseudes digitalis*. Mean densities of these organisms were 1280/m² and 3226/m² in this zone, which were six and three times higher than those recorded in other zones. The sandprawn *Callianassa kraussi* contributed only in zone A. Communities in Zone B, were characterised by the presence of the burrowing bivalves *Eumarcia paupercula*, and *Dosinia hepatica*, as well as the gastropod *Nassarius kraussianus*. The assemblage in Zone C was similar to that of zone B, except for the rarity of bivalves in Zone C.

Table 4: The numerically dominant macrofauna of four macrobenthic assemblages that accounted for 75% of the community composition. Values indicate percent contributions determined by the SIMPER routine.

Species	Assemblage			
	A	B	C	D
<i>P. sexoculata</i>	24	20	26	17
<i>L. laevigata</i>	17	12	14	8
Cumacea	14	11	12	
<i>Glycera sp</i>	13	12		9
<i>C. kraussi</i>	8			
Cirratulid polychaetes		8	11	20
<i>A. digitalis</i>				12
<i>N. kraussianus</i>		9	11	9
<i>D. hepatica</i>		8		
<i>E. paupercula</i>		5		

2.2.5 Species composition of intertidal and subtidal communities.

The polychaetes *P. sexoculata* and *Glycera sp.*, as well as the bivalve *E. paupercula* were recorded in subtidal and intertidal regions. Cirratulid polychaetes, the gastropod *N. kraussianus* and the tanaid *A. digitalis* were recorded in greater abundances in subtidal regions. The isopod *Leptanthura laevigata* and Cumacea were present in greater densities in intertidal zones (Table 5).

Table 5: The numerically dominant macrofauna of intertidal and subtidal regions that cumulatively accounted for 80% of the community composition. Values indicate percent contributions.

Species	Intertidal	Subtidal
<i>P. sexoculata</i>	24	21
<i>L. laevigata</i>	17	11
Cumacea	16	
<i>Glycera sp</i>	14	12
<i>E. paupercula</i>	6	7
Cirratulid polychaetes		13
<i>A. digitalis</i>		5
<i>N. kraussianus</i>		11

2.2.6 Spatial and temporal variations in macrofaunal density.

2.2.6.1 Temporal variations.

No consistent pattern of seasonal peaks and declines in macrofaunal densities were detected. (Fig 22). Lowest macrofaunal densities were recorded in March and June 2001, when grab samples were collected from a boat. Densities were higher during the remaining sampling season.

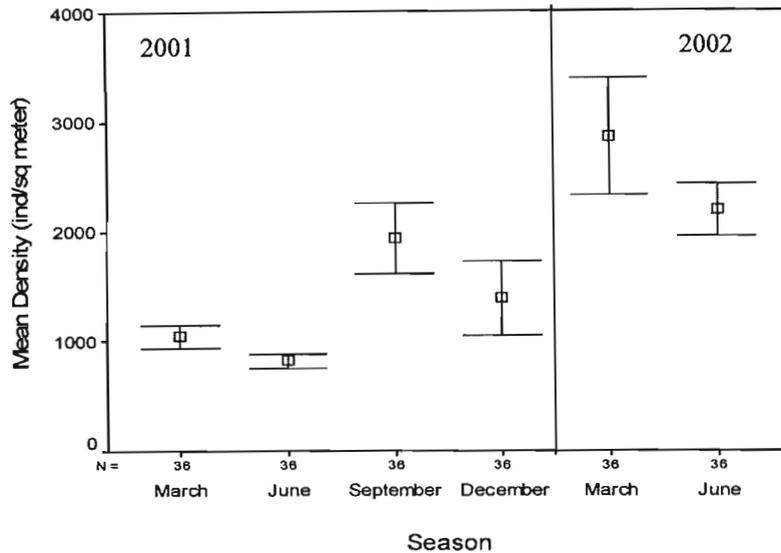


Fig 22: Temporal variations in macrofaunal densities in the Little Lagoon.

Squares indicate means, vertical bars represent standard error. Data from 12 sampling sites, and three replicates per site were pooled and averaged per season.

2.2.6.1 Spatial variations.

Densities of macrofauna were highest at site A2 (mean = 5743/m²) and ranged from 1129/ m² to 11779/ m² (Fig 23). The increased density recorded in this site is related to the very fine organically rich sediment of this region (Figs 13 & 14). At the remaining sites, mean densities were roughly three times lower than at A2, and ranged from 672/m² at site B1 to 2363/ m² at site B3. Densities of macrofauna were significantly higher in subtidal regions than in intertidal regions ($p < 0.05$), and ranged from $1120 \pm 82/\text{m}^2$ in intertidal regions, to $2268 \pm 242/\text{m}^2$ in subtidal regions.

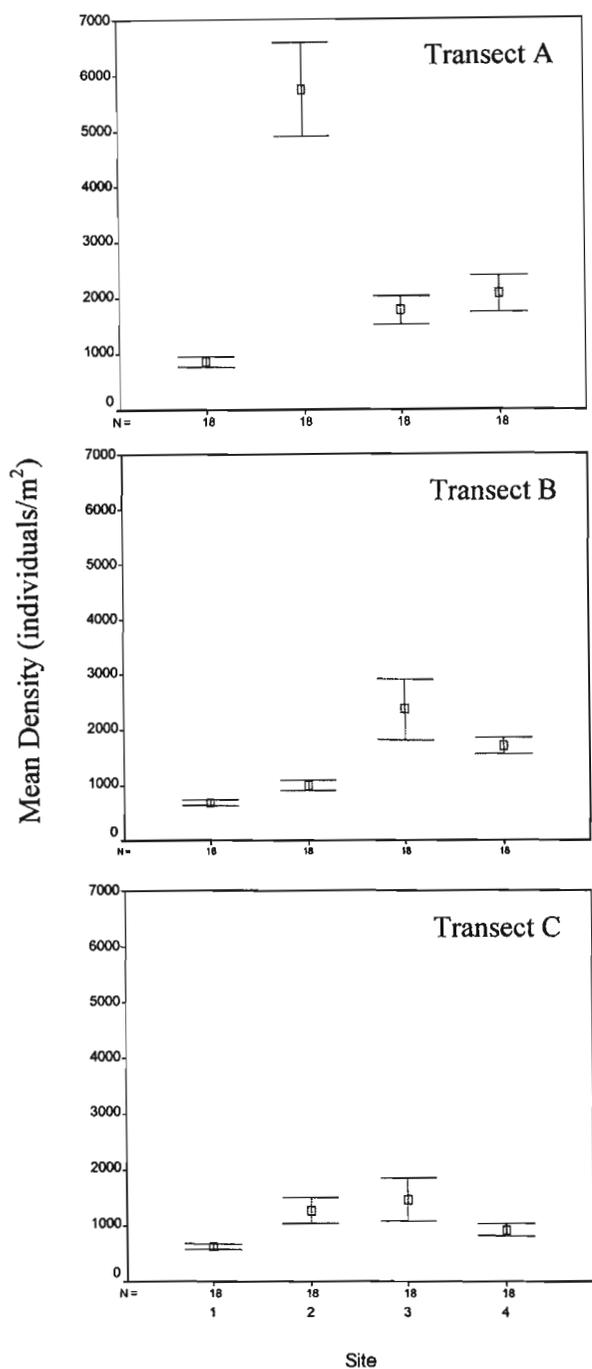


Fig 23: Mean density of macrofauna at sampling sites in the Little Lagoon. Squares indicate means, vertical lines represent standard error. Three site and six seasonal replicates were pooled and averaged per site.

2.2.7 Spatial and temporal variations in macrobenthic species richness.

2.2.7.1 Temporal variations.

Species richness of macrofauna ranged between seven and 10 species per three grabs in the Little Lagoon. No indications of temporal peaks and declines in species richness were detected (Fig 24).

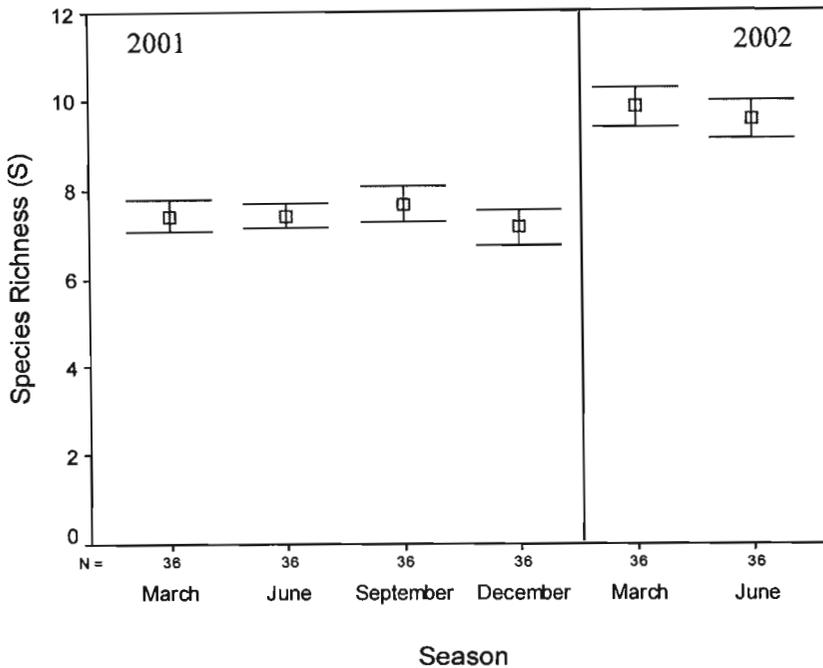


Fig 24: Seasonal variations in species richness (S) of macrofauna in the Little Lagoon.

(S = Total number of species collected in three grab samples). Squares indicate means, vertical bars represent standard error. Data from 12 sampling sites, and three replicates per site were pooled and averaged per season.

2.2.7.1 Spatial variations.

The highest mean species richness of 10.3 ± 0.5 per three grabs was recorded in the fine organically rich sediments of site A2 (Fig 25). At the remaining sites, richness varied from 5.6 ± 0.4 at site C1 to 9.7 ± 0.8 at site B4. Species richness was significantly higher in subtidal regions ($p < 0.05$; mean = 8.8 ± 0.2) than in intertidal regions (mean = 7.5 ± 0.2).

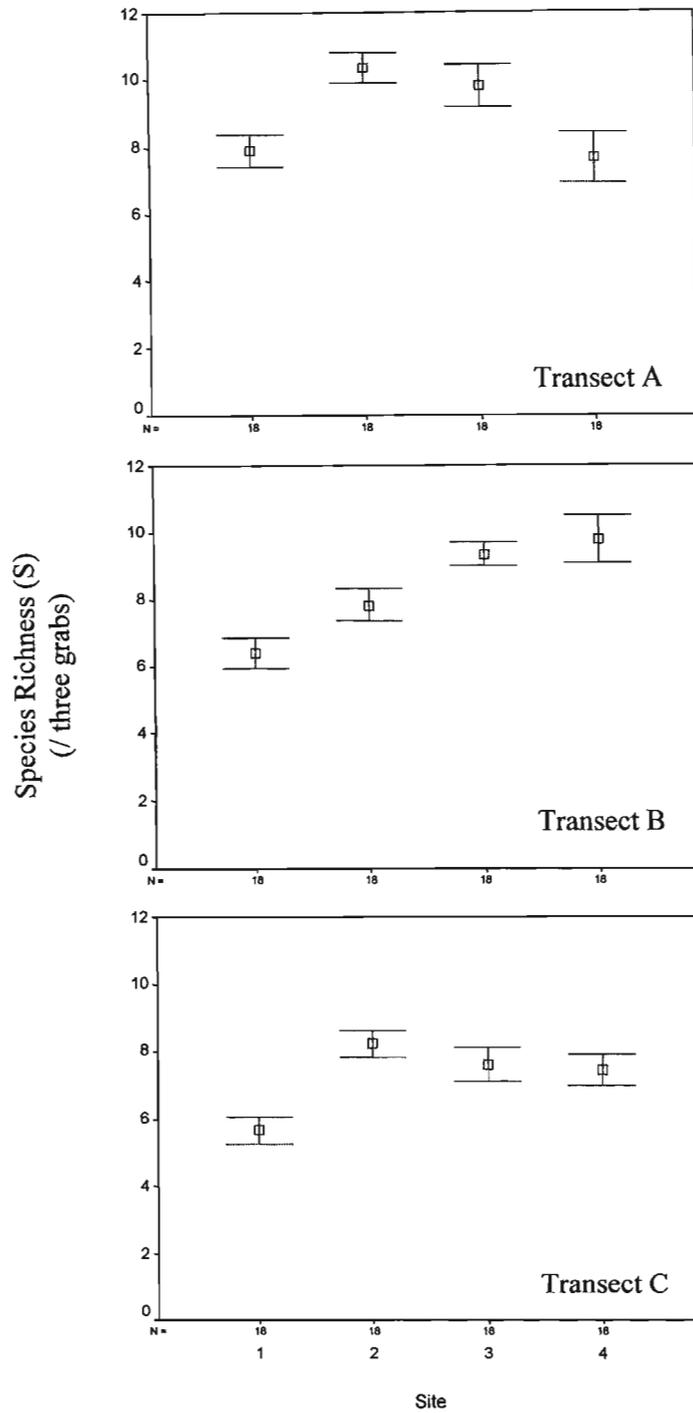


Fig 25: Species richness (S) of macrofauna at sampling sites in the Little Lagoon. S=Number of species collected in three grab samples. Squares indicate means, vertical lines represent standard error. Three site and six seasonal replicates were pooled and averaged per site.

2.2.8 Spatial and temporal variations in macrobenthic species diversity.

Species diversity (Shannon-Weiner) was low at site A2 (mean = 1.1 ± 0.08 ; Fig 26) although the highest species richness was also recorded at this site (Fig 25). The latter result reflects a strong numerical dominance by cirratulid polychaetes, *P. sexoculata*, and *A. digitalis*. At the remaining sites, diversity ranged from 1.2 ± 0.07 at C1 to 1.7 ± 0.06 .

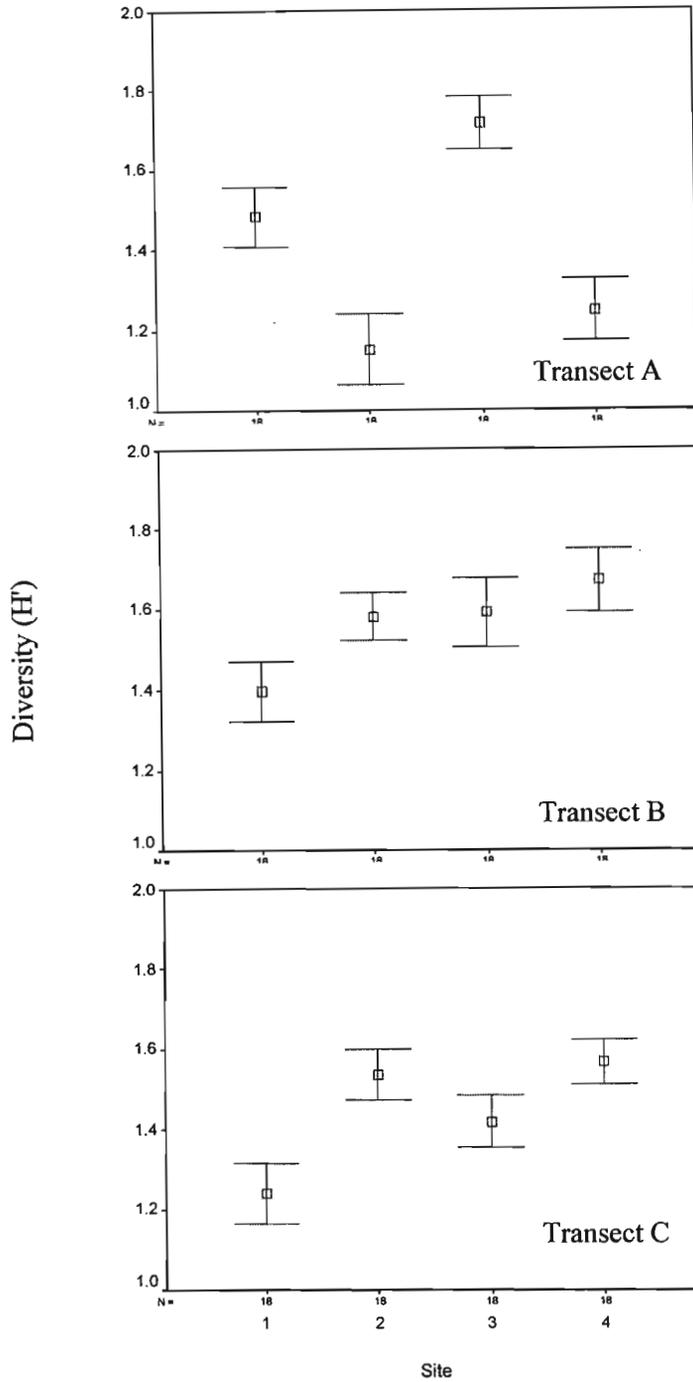


Fig 26: Species Diversity (H') of macrofauna at sampling sites in the Little Lagoon (Shannon-Weiner index, \log_e). Squares indicate means, vertical lines represent standard error. Three site and six seasonal replicates were pooled and averaged per site.

2.2.9 Feeding Modes of macrofauna in the Little Lagoon.

Suspension feeders such as the polychaete *Desdemonia ornata* were poorly represented in the Little Lagoon (Table 6), and contributed a maximum of 3%. Surface deposit feeders such as Cumacea and the isopod *Leptanthura laevigata*, together with infaunal deposit feeders such as *Prionospio sexoculata*, contributed most to the feeding modes of macrofauna in the Little Lagoon.

These feeding guilds were represented at all sites in the sampling area. Subsurface deposit feeders predominantly cirratulid polychaetes, contributed most in organically rich sediments of site A2 and C2 (33% and 25%). This group was scarce in organically poor sediments. Infaunal predators such as *Glycera sp.* contributed at all sampling sites, with contributions ranging from 8% to 25%.

Table 6: The feeding modes of the dominant macrofauna in the Little Lagoon.

Values represent percentage contributions determined by the SIMPER routine.

Contributions of dominant species contributing to 90% of the community composition are indicated.

Feeding Mode	A1	A2	A3	A4	B1	B2	B3	B4	C1	C2	C3	C4
Suspension/Filter (<i>Desdemonia ornata</i>)	3	0	0	3	0	0	0	0	0	0	0	0
Surface deposit (<i>L. laevigata</i> , Cumacea)	43	34	42	57	41	44	51	40	54	27	19	44
Subsurface deposit (Cirratulid polychaetes)	0	33	18	0	0	13	14	10	0	25	15	0
Infaunal deposit (<i>P. sexoculata</i>)	36	22	26	26	33	32	25	36	32	33	47	36
Predatory infauna (<i>Glycera sp.</i>)	17	9	14	12	25	10	8	14	13	15	19	20

2.3 The Endobenthos.

Results presented in the following subsection (from 2.3 till the end of results) are based on macrobenthic data obtained from sediment cores (depth 90cm), not grab samples.

2.3.1 Variations in size and abundance of *Callianassa kraussi*.

Mean abundance of *C. kraussi* peaked in September 2001 and June 2002 (Fig 27). Highest frequencies of individuals in the 0-2mm size class were recorded in June of both seasons (Fig 28). Both results indicate that recruitment of juveniles occurred over the winter and early spring period. During the periods prior to spawning (March), modal size classes peaked between the 4mm-8mm carapace lengths, indicating that the population consisted of larger adults.

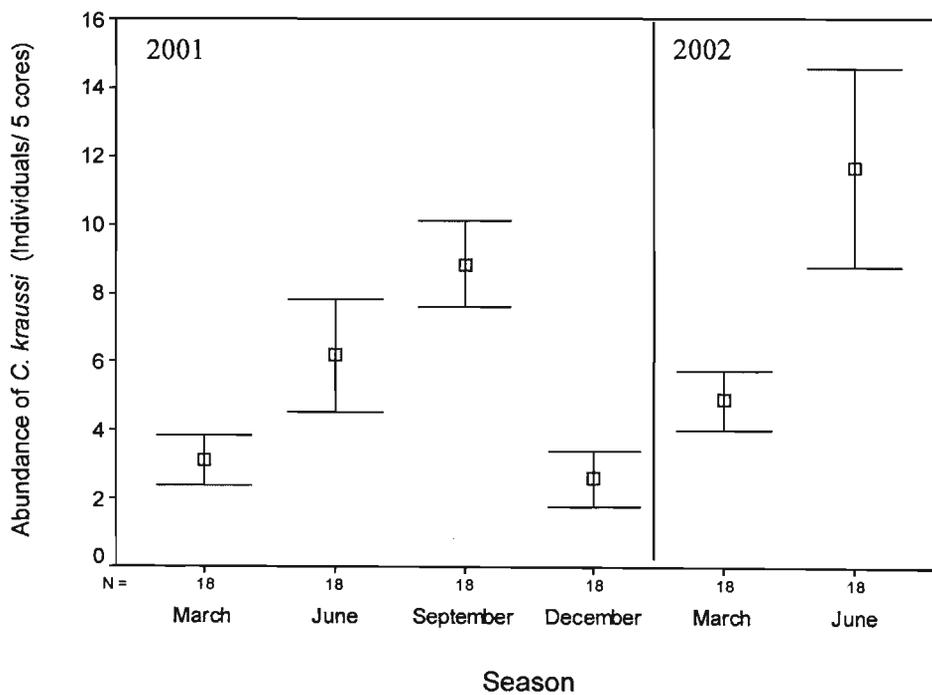


Fig 27: Temporal variations in abundance of *C. kraussi* in the Little Lagoon.

Squares indicate means, vertical lines represent standard error. Data were averaged from three site replicates and six seasonal replicates.

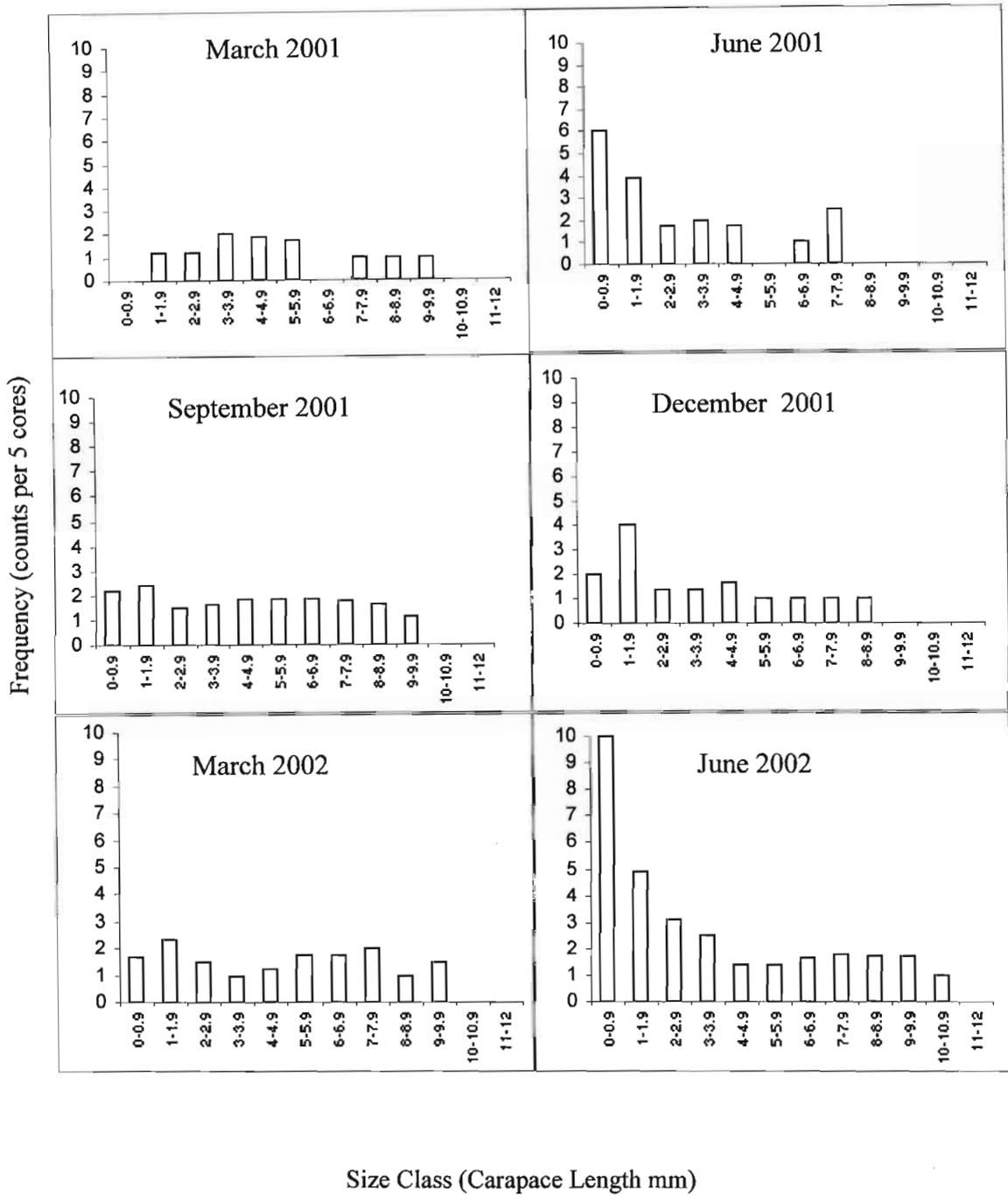


Fig 28: Seasonal trends in length-frequency histograms for *Callianassa kraussi*.
 Data from three site replicates and six seasonal replicates were pooled per season.

2.3.2 Spatial variations in abundance of *Callianassa kraussi*

There were two distinct zones of high and low *C. kraussi* abundance in the Little Lagoon (Fig 30). Abundance at sites B4 and A4, averaged less than 1 to 3 individuals per five cores respectively. Abundance was higher at the remaining sites, averaging between 5 and 13 individuals per five cores (Fig 29).

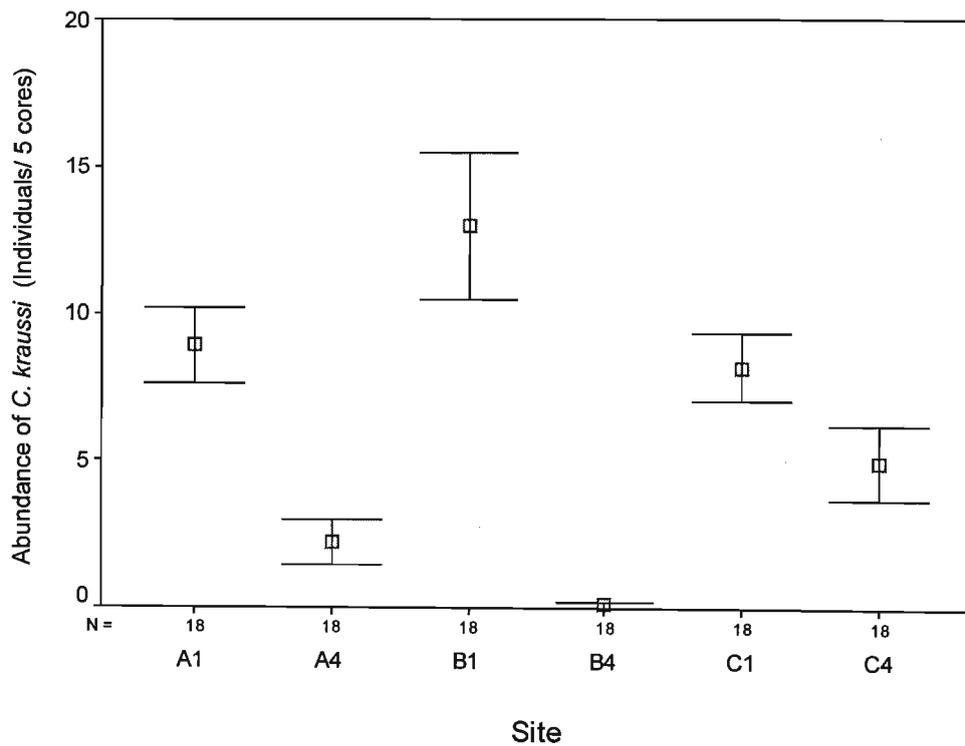


Fig 29: Spatial variations in abundance of *C. kraussi* in the Little Lagoon.

Squares indicate means, vertical lines represent standard error.

Data from three site replicates and six seasonal replicates were averaged.

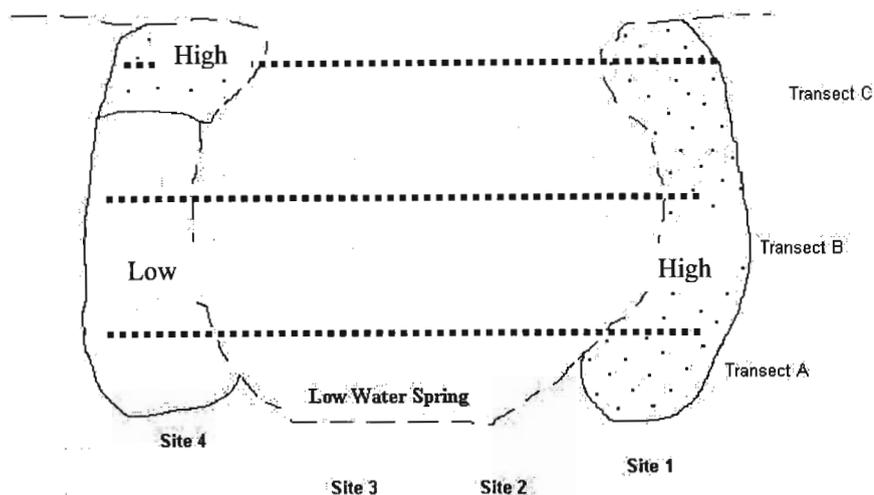


Fig 30: The two zones of high and low *C. kraussi* abundance in the Little Lagoon.

Surface sediment particle sizes ($p=0.076$, Fig 32) and organic contents ($p=0.67$, Fig 33) did not differ significantly between the zones of high and low *C. kraussi* abundance, but the shell content of deep sediments were up to five times higher in the zone of low *C. kraussi* abundance.

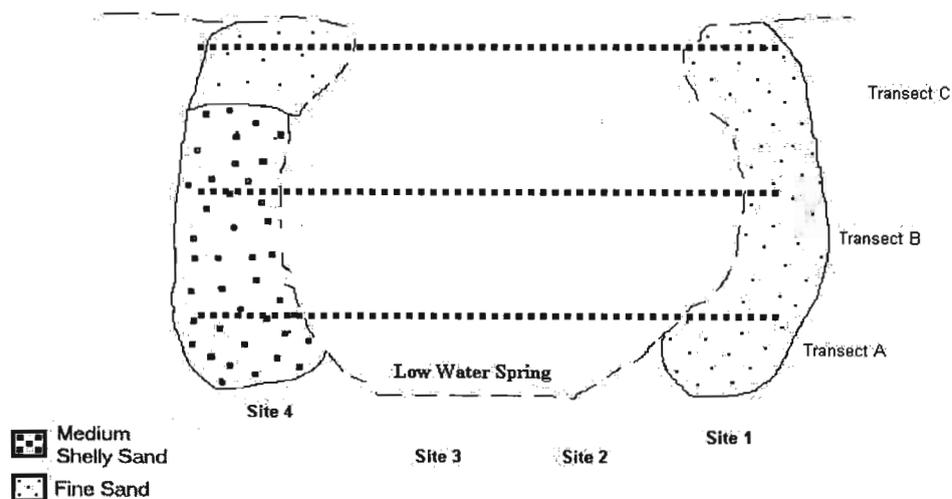


Fig 31: Deep sediment type in the Little Lagoon.

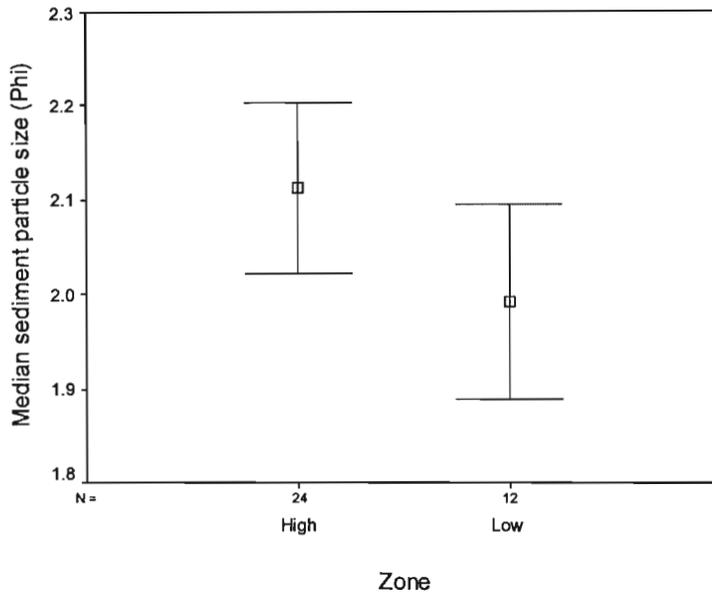


Fig 32: Phi values of surface sediments from the two zone of high and low *C. kraussi* abundance. Squares represent means, vertical lines indicate standard error.

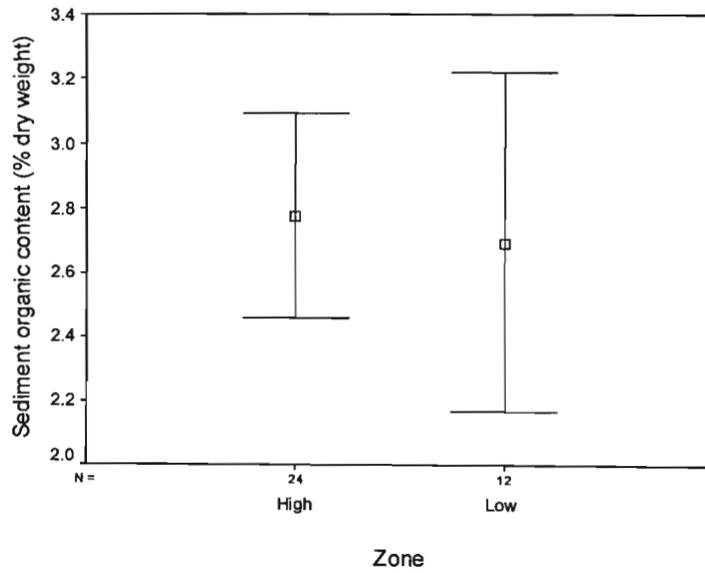


Fig 33: Organic contents of surface sediments from the two zones of high and low *C. kraussi* abundance. Squares represent means, vertical lines indicate standard error.

2.4 The role of *C. kraussi* in structuring macrobenthic communities.

MDS ordination indicated distinct spatial differences between macrobenthic communities associated with the zones of high and low *C. kraussi* abundance (Fig 34). The ANOSIM procedure indicated that the communities were significantly different from each other ($p=0.001$).

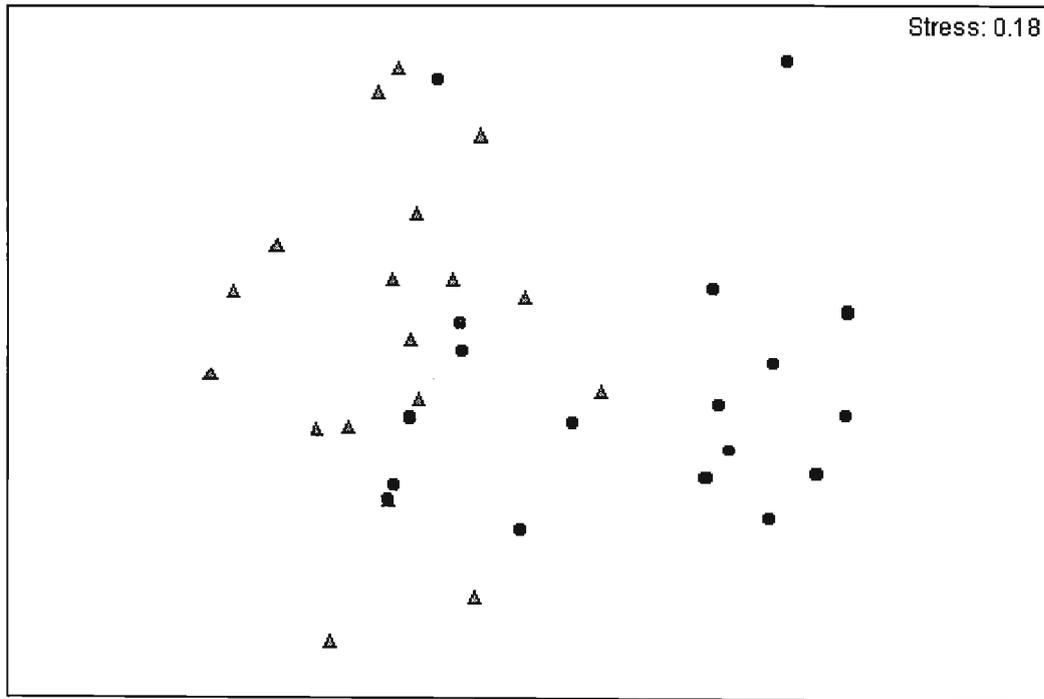


Fig 34: MDS ordination of macrofauna communities associated with the two zones of high (circles) and low (triangles) *C. kraussi* abundance. Each data point represents an individual site replicate (three replicates were collected per site), collected over six sampling seasons. Abundance data from sediment cores were utilised for the analysis.

2.4.1 Macrobenthic abundance, species richness and diversity in the zones of *C. kraussi* abundance.

Abundance, species richness and diversity of macrofauna differed significantly between the zones of high and low *C. kraussi* abundance. Macrofaunal abundance and species richness were at least two times greater in the zone of low *C. kraussi* abundance (Fig 35).

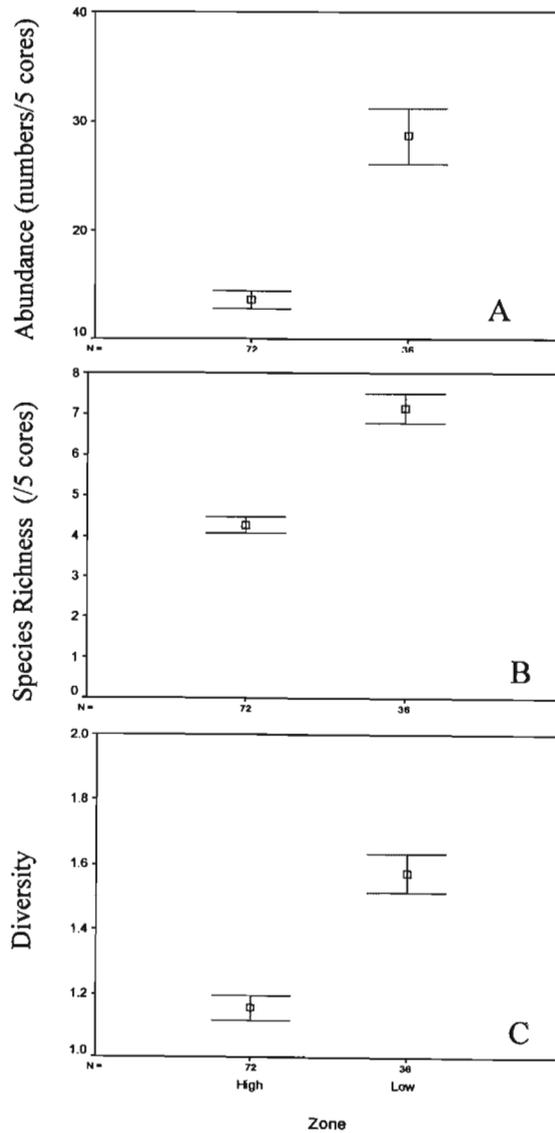


Fig 35: Abundance (A), species richness (B) and diversity (C) of macrofauna in the zones of high and low *C. kraussi* abundance. Squares represent means, vertical lines indicate standard error. Means were calculated from three site and six seasonal replicates.

2.4.2 The relationship between macrobenthic abundance, species richness, diversity and abundance of *C. kraussi*.

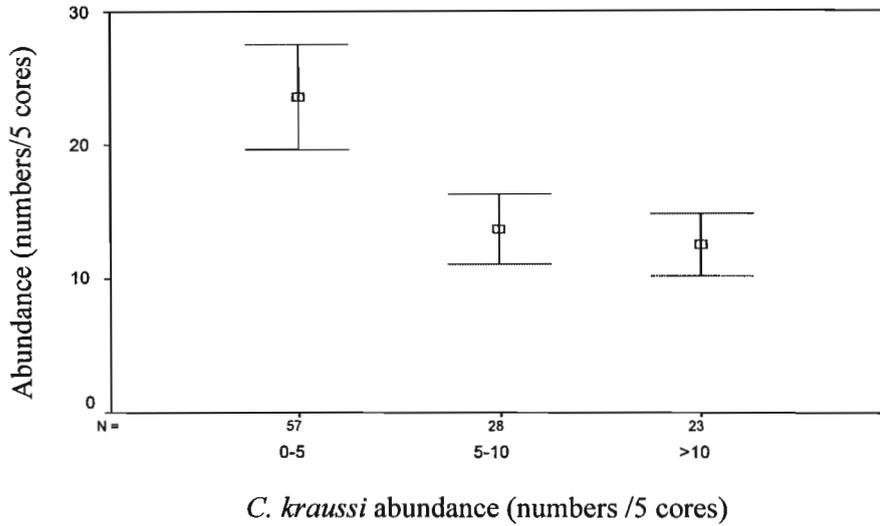


Fig 36: Relationship between abundance of *C. kraussi* and macrofauna abundance determined from core samples. Squares represent means, vertical lines indicate standard error.

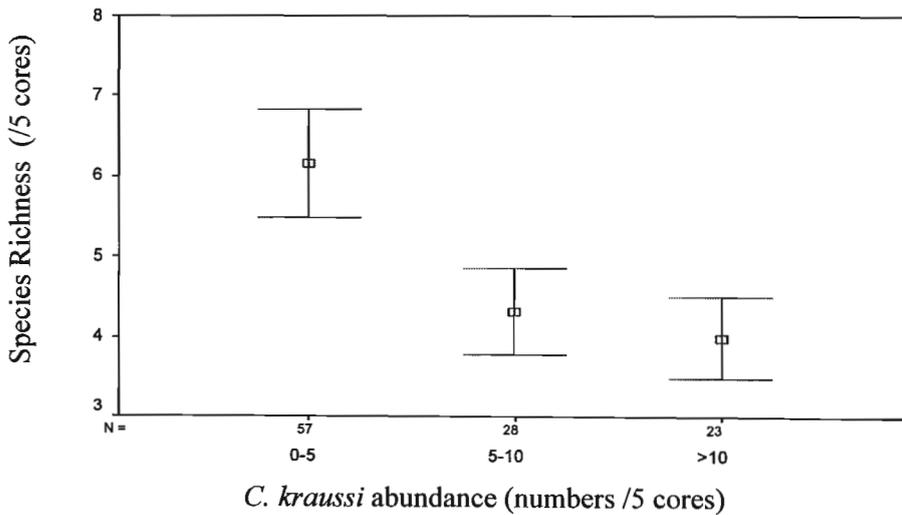


Fig 37: Relationship between abundance of *C. kraussi* and species richness of macrofauna determined from core samples. Squares represent means, vertical lines indicate standard error.

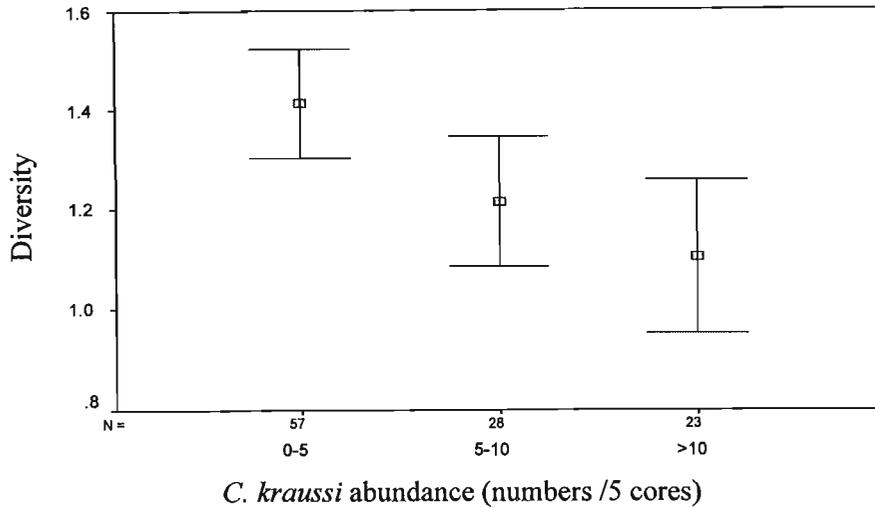


Fig 38: Relationship between abundance of *C. kraussi* and species diversity

(H' Shannon-Weiner; \log_e) of macrofauna determined from core samples. Squares represent means, vertical lines indicate standard error. Density classes on X-axes are: 0-5: low density, 5-10: intermediate density, >10: high density.

The abundance of *C. kraussi* had a significant effect on the abundance ($p < 0.001$), species richness ($p < 0.001$) and diversity ($p < 0.001$) of macrofauna (Figs 36-38). The negative association observed between macrobenthic community parameters and abundance of *C. kraussi* (Figs 36-38), implies that *C. kraussi* adversely impacts on these community parameters. Macrofaunal abundance, species richness and diversity did not differ significantly between intermediate and high *C. kraussi* densities. At low *C. kraussi* densities, abundance and species richness of macrofauna were significantly higher than at intermediate and high *C. kraussi* densities. Macrofaunal diversity differed significantly between low and high *C. kraussi* densities.

2.4.3. Macrobenthic community structure between zones of high and low *C. kraussi* abundance.

The zone of high *C. kraussi* abundance was dominated by the polychaetes *Prionospio sexoculata*, *Scoloplos johnstonei*, *Glycera sp* and an unidentified amphipod species (Table 7). These species were also recorded in the zone of low *C. kraussi* abundance, but the community was dominated by Cumacea, the isopod *Leptanthura laevigata* and cirratulid polychaetes (Table 8). Densities of burrowing bivalves, mainly *Dosinia hepatica* and *Eumarcia paupercula* were significantly higher in the zone of low *C. kraussi* abundance ($p < 0.0001$, Fig 39), and averaged roughly 2 individuals per five cores. In the zone of high *C. kraussi* abundance, densities were lower and averaged less than 0.5 individuals per five cores. Community differences are summarised in Fig 40.

Table 7: Macrobenthic species that cumulatively accounted for 90% of the community composition in the zone of high *C. kraussi* abundance determined by the SIMPER routine. Abundance = numbers/five sediment cores, n=18. Percentage contribution is indicated.

	Average abundance	Contribution (%)	Cumulative contribution (%)
<i>Scoloplos johnstonei</i>	3	32	32
Unidentified amphipod sp.	2.8	29	61
<i>Prionospio sexoculata</i>	2	16	77
<i>Glycera sp</i>	1.4	14	91

Table 8: Macrobenthic species that cumulatively accounted for 90% of the community composition in the zone of low *C. kraussi* abundance determined by the SIMPER routine. Abundance = numbers/five sediment cores, n=18. Percentage contribution is indicated.

	Average abundance	Contribution (%)	Cumulative contribution (%)
<i>Prionospio sexoculata</i>	7.5	32	32
Cumacea	1.6	12	44
<i>Leptanthura laevigata</i>	1.6	11	55
Cirratulid polychaetes	2.5	9	64
<i>Scoloplos johnstonei</i>	1.5	6	70
Unidentified amphipod sp.	1.8	6	76
<i>Glycera sp</i>	0.9	6	82
<i>Dendronereis arborifera</i>	2.4	5	87
<i>Eumarcia paupercula</i>	0.6	3	90

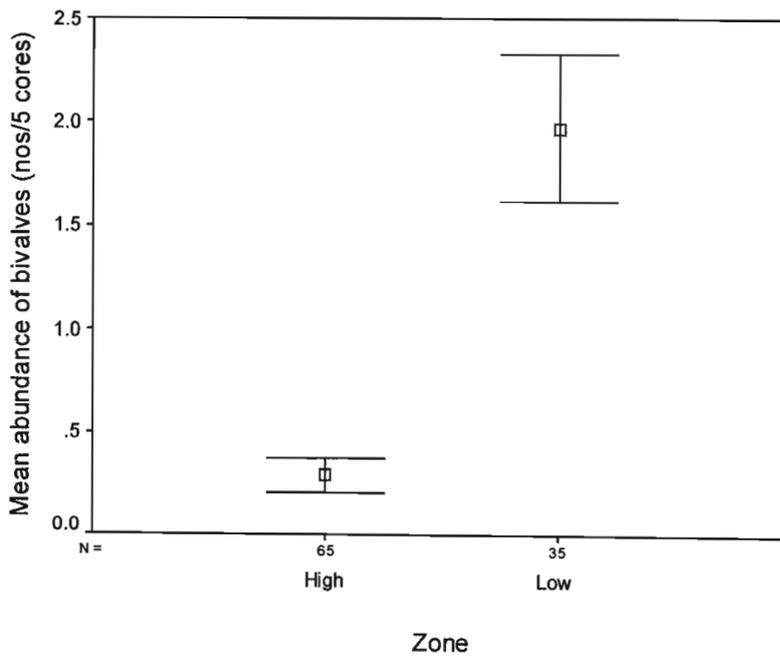


Fig 39: Abundance of burrowing bivalves (numbers/5 cores) between the zones of high and low *C. kraussi* abundance. Squares represent means, vertical lines indicate standard error.

2.4.4 Differences in feeding modes between zones of high and low *C. kraussi* abundance.

Table 9: Comparisons of feeding modes of the dominant macrofauna between the zones of high and low *C. kraussi* abundance. Values indicate percent contributions (Dominant macrofauna from Tables 7 & 8 were utilised in the analysis).

Feeding Mode	High	Low
Surface deposit	0	23
Subsurface deposit	0	10
Infaunal deposit	77	49
Predatory infauna	14	6

Burrowing infaunal deposit feeders such the polychaete *Prionospio sexoculata*, and predatory infauna such as *Glycera sp.* were recorded in the zones of high and low *C. kraussi* abundance. Surface deposit feeders such as Cumacea and *L. laevigata*, and subsurface deposit feeders predominantly cirratulid polychaetes, were recorded almost exclusively in the zone of low *C. kraussi* abundance, and not in the zone of low *C. kraussi* abundance (Table 9). Lifestyles and feeding modes are summarised in Fig 40.

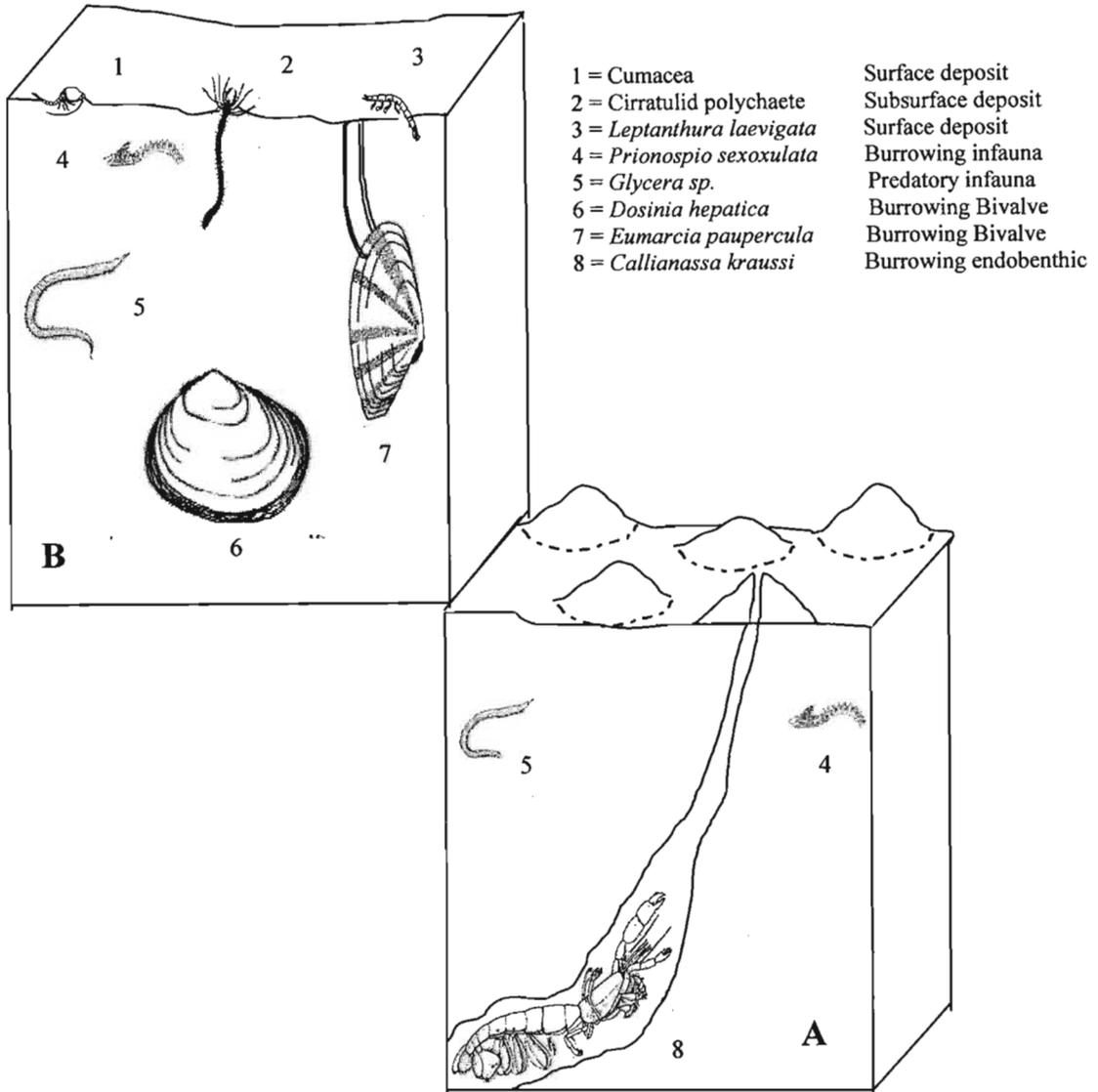


Fig 40: Schematic representation summarising differences in macrobenthic communities and lifestyles of organisms between zones of high (A) and low (B) *C. kraussi* abundance. Note the absence of surface and subsurface fauna in the zone of high *C. kraussi* abundance, and the irregular sediment surface.

3. Discussion

There were strong indications that the physical environment of the Little Lagoon was a relatively stable one, as negligible temporal variations in physico-chemical variables were recorded. This stability was detected in both the water column and in the sedimentary habitat.

Seasonal temperature fluctuations were the only pronounced source of temporal variations in the physical habitat of the Little Lagoon. Peak temperatures were recorded at the end of summer of both years, while lowest temperatures were measured at the end of winter (Fig 9). The remaining parameters such as salinity and concentrations of dissolved oxygen (DO) were generally uniform from a temporal perspective. Although salinities as low as 20.4‰ were recorded on two occasions (Appendix A), salinity in the Little Lagoon was essentially marine, and varied between 27.1‰ to 37.6‰ during the study, while concentrations of dissolved oxygen at all sampling sites were consistently between 6 mg/L and 7.8 mg/L. In both instances, no seasonal peaks and declines in either parameter were detected, and in instances where variations were detected, these were of little ecological significance. For example, the increase in concentrations of DO from 6 mg/L to 7.8 mg/L recorded between March and June 2002 (Fig 11), is statistically different, but appeared to be of little consequence to the macrobenthic community.

From a spatial perspective, differences in water temperature, salinity and DO were not detected in the Little Lagoon (Appendix A), indicating that the water column is a fairly homogenous environment. Pronounced spatial variations in sediment type and organic content of surficial sediments were however, a prominent feature of the benthic habitat in the Little Lagoon. (Figs 12-15). The two deepest regions of the Little Lagoon were sites A2 and C2 respectively (Fig 8). Surficial sediments in these regions were classed as very fine, organically rich sand, while those in the shallower regions of the Little Lagoon were classed as medium to fine organically poor sediments. Based on the relationship between water depth and sediment types, it can be deduced that deeper regions are sheltered, calm-water habitats, which act as deposition zones for submerged organic debris. The shallower regions on the other hand, are subjected to higher intensity wave action, and could be classed as erosional environments (Kennish 1990).

The macrofaunal community of the Little Lagoon as a whole, was composed of 38 species, with the Polychaeta, Crustacea and Mollusca being the major constituents of this assemblage (Table 1).

The macrobenthic community of the Little Lagoon could be visualised as being three tiered, or composed of three components, based on the relative abundance of organisms. The primary component of the assemblage is defined as comprising the dominant organisms, or those that cumulatively contribute to 75% of the overall community structure. The secondary component refers to organisms contributing between 75% and 90% to the community composition, followed by the third component comprising the remaining rare species.

The primary component of the macrobenthic community in the Little Lagoon was composed of four organisms viz. the polychaete *Prionospio sexoculata*, the isopod *Leptanthura laevigata*, Cumacea, and polychaetes of the genus *Glycera* (Table 2). These taxa were recorded at all sites in the Little Lagoon, indicating no spatial habitat preferences. In contrast the secondary component of the macrofaunal assemblage in the Little Lagoon, was composed of cirratulid polychaetes, the tanaid *Apseudes digitalis*, the bivalve *Dosinia hepatica* and the polychaete *Desdemona ornata* (Table 2). Species comprising the secondary component showed marked spatial habitat preferences (Table 1). The third component of rare species comprised 30 taxa, and of these, the polychaete *Cossura coasta*, and the crab *Paratyloidiplax blephariskios* were recorded almost exclusively in the organically rich sites A2 and C2.

The macrobenthos of the Little Lagoon was not a spatially homogenous sandflat community, as significant differences in community structure were recorded (Fig 20). These spatial differences in communities occurred in response to spatial heterogeneity in sediment particle sizes and organics contents of surficial sediments (Figs 12-15). In other words, sediment type and organic contents of surface sediments, in conjunction with water depths, were the most dominant physical determinants of macrobenthic community structure in the Little Lagoon.

In the fine, organically rich sediments of site A2, mean densities of macrobenthic organisms were roughly three to five time higher than in other regions of the Little Lagoon (Fig 23). Moreover, highest species richness was also recorded in this region (Fig 25). It therefore appeared that this site had a much higher carrying capacity than other sites in the Little Lagoon, due mainly to the relatively abundant food supply in the form of sediment organic contents in this site. This feature therefore favoured the development of communities in which organism were highly abundant and rich in species.

The community composition also differed substantially between very fine organically rich sediments and fine organically poor sediments. The organically rich sediments of site A2 for example was dominated by cirratulid polychaetes and the tanaid *Apseudes digitalis*. The abundance of both organisms were up to three times higher in site A2 than in any other site, with mean densities of 1280/m² and 3226/m² recorded respectively (Table 1). Cirratulid polychaetes are subsurface deposit feeders, which partially bury themselves in sediments and utilise tentacular filaments to feed on the sediment surface (Day 1969), while tanaids feed on detritus on the sediment surface (pers obs). Both species are specifically adapted to feeding in muddy, organically rich sediments, and are distributed preferentially in such sediments. In addition, the polychaete *Cossura coasta*, and the crab *Paratyloidiplax blephariskios* were also recorded almost exclusively in the organically rich, muddy sediments of sites A2 and C2, with the latter species known to prefer such sediments (Day 1969, Owen 1999).

High organic contents and very fine textures of surficial sediments seemed to "favour" the presence of subsurface deposit feeders (Table 6). Members of this feeding guild, predominantly cirratulid polychaetes, were recorded in highest abundances at the most organically rich sites of A2 and C2. At both sites, roughly 30% and 20% of feeding modes comprised sub-surface deposit feeders. In organically poor sediments, this feeding guild was poorly represented.

Much of the discussion presented above, in terms of stressing the roles of sediment organic contents and particle sizes as determinants of macrobenthic community structure, was highlighted by the pioneering study of Durban Bay by Day and Morgans in 1956. The distinction made between the "biota" of the Bay, was based on sediment types, which were either classed as "clean sand" or "muddy sand". The author pointed out that the lack of organic material and fine silt in clean sands, supported little animal life, and did not facilitate the construction of burrows. Muddy sands on the other hand fulfilled both criteria, and supported richer faunal assemblages (Day and Morgans 1956).

Macrobenthic community structure also differed substantially between subtidal and intertidal regions in the Little Lagoon. Intertidal regions were characterised by the isopod *Leptanthura laevigata* and Cumacea. These organisms are highly mobile surface fauna and could probably avoid desiccation and temperature stress during periods of low tides, i.e. when the sandflat was exposed, by migrating into subtidal regions. Subtidal regions were characterised by sedentary surface fauna such as the tanaid *Apseudes digitalis* and the gastropod snail *Nassarius kraussianus*. It appeared that the limited mobility of these organisms restricted them to subtidal

regions only. Cirratulid polychaetes were recorded in higher abundances in subtidal regions, but were also recorded in intertidal regions (Table 1). These organisms are sessile tube building subsurface feeders (Day 1967b), and it is suspected that during low tides, much of the body and tentacular filaments are withdrawn into its burrows, which protects the organism from temperature and desiccation stress.

From a temporal perspective, changes in macrobenthic community composition were negligible in the Little Lagoon (Table 3), implying that the community is quite a static or stable one, with no dramatic seasonal or temporal alterations to its composition. This is expected since drastic temporal variations in the physical habitat were not recorded. During every sampling season, the macrobenthic community of the Little Lagoon was dominated by four organisms *viz.* the polychaetes *Prionospio sexoculata*, *Glycera sp.*, the isopod *Leptanthura laevigata* and cumaceans (Table 2). In March and June 2001, densities of cirratulids and the tanaid *Apseudes digitalis* in site A2 were up to 3000 and 8000 times lower respectively than in remaining sampling seasons. If one considers that the organically rich sediments of site A2 occupy a patch of 3 – 5 m², and the practical difficulty in relocating sampling sites precisely by boat due to drifting, it is suspected that temporal differences in abundance of these organisms are due to inaccurate relocation of this site, and do not reflect seasonally induced changes to the community. Variations in abundance and sizes of *Callianassa kraussi* were the only source of temporally induced changes to the macrobenthic community in the Little Lagoon. Peaks in abundance of juveniles of *C. kraussi* were recorded in June of both seasons, indicating winter and early spring recruitment into the population (Figs 27 & 28).

In a highly dynamic system like the Mkomazi estuary for example, seasonal changes in estuarine flow rates, along with variation in salinity, sediment type and organic contents, acted as sources of natural disturbances, which in turn resulted in cascading modifications to the composition of macrobenthic communities (Waller 1998). During the summer periods, characterised by high rainfall and high flow rates, the macrofaunal assemblage of the Mkomazi estuary was essentially composed of a few capitellid polychaetes and chironomids. Under winter, low flow conditions, the community shifted to a *Desdemona ornata* (Polychaeta)-*Grandidierella lignorum* (Amphipoda) assemblage (Waller 1998). A similar pattern was recorded in the Mdloti estuary, which is a dynamic system, characterised by periodic opening and closure of the mouth (Jairam 2002). The macrobenthic assemblage during mouth open periods was dominated by the polychaete *Ceratonereis keiskama*, but shifted to one dominated

by the polychaetes *Desdemonia ornata* and *Prionospio steenstrupi* during periods of mouth closure (Jairam 2002).

Significant temporal differences in densities and species richness of macrofauna were also recorded in the Mkomazi estuary in response to seasonal changes in the physical environment highlighted above. During winter periods of low flow rates, densities of macrofauna were up to 15 times higher than during summer periods of high flow rates, but was also accompanied by a doubling of species richness (Waller 1998). Similarly, significant differences in abundance and species richness were recorded in the Mdloti and Mhlanga estuaries, associated with the opening and closing of the mouth (Jairam 2002).

In contrast to the systems highlighted above, there was no evidence of seasonally induced changes in the abundance and species richness of macrofauna in the Little Lagoon, as no obvious peaks and declines in these parameters were recorded (Figs 22 & 24).

In March and June 2001, abundance of macrofauna was two to three times lower than in remaining sampling seasons. If one takes into account that abundance of macrofauna were three to five times higher in site A2, and if one considers the problems previously mentioned associated with accurately relocating sites by boat, it is likely that reduced densities recorded in these seasons were because site A2 was inaccurately relocated, and was not a seasonally induced response.

The macrobenthic assemblage of the Little Lagoon was characterised by high densities and a diverse assemblage of large, long-lived organisms such as gastropod and bivalve molluscs (Table 1). From a benthic ecology perspective, these species are commonly referred to as *K*-selected organisms (Clarke and Warwick 1994, Chapman and Reiss 1997), and are generally not numerically dominant, but dominate the benthic biomass (Clarke and Warwick 1994). These *K*-selected organisms usually characterise stable environments, with little natural perturbations (Clarke and Warwick 1994). At the opposite end of the spectrum, i.e. where disturbances are common, communities are dominated by smaller, fast growing opportunistic species, which dominate numerically (Clarke and Warwick 1994). Six species of bivalve, and two species of gastropod molluscs were recorded in the Little Lagoon (Table 1), but in the dynamic systems of the Mkomazi (Waller 1998), Mdloti and Mhlanga (Jairam 2002), no such *K*-selected mollusc species were recorded.

Species richness of the macrobenthic community in the Little Lagoon was high, relative to other estuarine habitats in Kwa-Zulu Natal, and is directly related to the lack of fluctuations in the physical habitat. To put this into perspective, a total of 38 macrofaunal species were collected in the Little Lagoon during this study, while a macrobenthic survey of the St Lucia system in the early to middle 1990s yielded approximately 33 species (Weerts 1993), and 36 species from surveys of Richards Bay (Hay 1993b), both of which are generally considered to be relatively stable habitats. The area covered in the Little Lagoon was roughly 42 000m² (0.042km²), whereas those covered in the surveys of St Lucia and Richards Bay were roughly 325km² (Weerts 1993) and 425km² (Hay 1993) respectively. In other words, all three systems generally had similar species richness, but the Little Lagoon was 7000 to 10 000 times smaller than the St Lucia and Richards Bay systems, implying that the system is relatively rich in the context of Kwa-Zulu Natal.

While it is generally accepted that Durban Bay is a sheltered, stable estuarine habitat (Hay *et al.* 1993, Forbes *et al.* 1994) it is nevertheless worth highlighting for the following reason. In the absence of significant physical factors influencing and regulating macrobenthic communities, it is increasingly likely for such systems to be biologically regulated. In many estuarine habitats, it is likely that the variable nature of the physical habitat precludes the development of macrobenthic communities to climax states, as these communities are often in a state of transition (as shown by Waller 1998). In these transitional states, communities are generally not composed of large-bodied organisms (Clarke and Warwick 1994) that are able to exert influence on and structure communities. In such instances, the physical environment dictates structure and patterns of distribution of macrobenthic assemblages. In contrast, the sheltered nature of sandflat habitats such as in the Little Lagoon, encourages the development of macrobenthic communities. In such cases, large organisms such as bivalves and crustaceans will dominate the benthic biomass, with increased potential for these large organisms to influence communities (Kennish 1990). At this stage of development, biological processes such as competition, disturbance and predation can significantly structure macrobenthic communities (Flach and Tamaki 2001, Ditmann and Vargas 2001),

In the context of the Little Lagoon, the benthic biomass is dominated by the burrowing prawn *Callinassa kraussi*, and present in densities of up to 300 individuals/m² (from crude estimates of hole counts). A characteristic feature of the burrowing behaviour of this organism is its expulsion of sediment and deposition of mounds on the sediment surface. Underwater visual assessments of the habitats in which *C. kraussi* occurs, revealed an irregular bottom, dominated

by these sediment mounds. This process of biological reworking of sediments is referred to as bioturbation (Flach and Tamaki 2001) and the term encompasses sediment expulsion through burrow digging, egestion of faecal end-products, the mobilisation of sediment contaminants and organic particles, as well as ventilation activities i.e. water pumping activities (Flach and Tamaki 2001, Francois *et al.* 2001).

The distribution of *C. kraussi* in intertidal sediments of the Little Lagoon was uneven, as two distinct zones of high and low abundance were recorded (Fig 30). Sediment particle sizes and organic contents of surficial sediments, did not differ between these zones (Figs 32 & 33), but densities of shell fragments in deep sediments i.e. sediments between 0.8 m to 1 m deep, was up to three times higher than in the zone of high *C. kraussi* (Fig 31). It therefore appeared that shell fragments in deep sediments, which in many cases were large, whole bivalve shells, prevented the establishment of this organism, as these shells hindered burrowing activities.

Ordination plots indicated that there were two spatially distinct macrobenthic communities associated with the zones of high and low *C. kraussi* abundance (Fig 34), which were significantly different from each other ($p=0.001$). Total abundance of macrobenthic organisms also differed significantly between the two *C. kraussi* abundance zones. In sediments where *C. kraussi* was rare, the abundance of benthic macrofauna was up to three times higher than in sediments in which *C. kraussi* was abundant (Fig 35). These trends were also mirrored by species richness and diversity values, which also differed significantly between the zones of high and low *C. kraussi* abundance (Figs 35), with twice as many species recorded in sediments where *C. kraussi* was rare. In view of the absence of significant variations in sediment properties between the zones of high and low *C. kraussi* abundance, the interpretation of the latter results is that *C. kraussi* might directly be involved in structuring of macrobenthic communities in these intertidal regions.

Proving a causal relationship between *C. kraussi* and the structure of macrobenthic macrobenthic communities is difficult in the absence of experimental data, but several lines of indirect evidence point to this potential causality. Macrobenthic abundance, species richness and diversity were significantly and negatively influenced by the abundance of *C. kraussi* (Figs 36-38), implying that differences in community measures (abundance, species richness and diversity) observed between the zones highlighted above, are directly attributable to *C. kraussi*. The negative association between these macrobenthic community parameters and the abundance of *C. kraussi*, indicates that *C. kraussi* exerts some form of adverse impact on macrobenthic

communities, and is an indication that *C. kraussi* may be a "disturbance" organism. The only other possible interpretation of the negative association highlighted above, is that it may be a predatory response. This possibility is ruled out since thalassinid crustaceans such as *C. kraussi* are known to be deposit or filter feeders, or a combination of both (Coelho *et al.* 2000), but not predators.

There were also indications that the composition of macrobenthic communities differed substantially between zones in which *C. kraussi* was highly abundant and where it was rare. 90% of the composition of communities in sediments in which *C. kraussi* was highly abundant, was made up of four organisms *viz.* the polychaetes *Scoloplos johnstonei*, *Prionospio sexoculata*, *Glycera sp.*, and an unidentified amphipod.

In contrast, 90% of the community composition in the zone of low *C. kraussi* abundance, was made up by nine species (Table 8). In this zone, the macrobenthic assemblage that characterised the zone of high *C. kraussi* abundance was also present, but Cumaceans, the isopod *Leptanthura laevigata*, cirratulid polychaetes, *Dendronereis arborifera* and the bivalve *Eumarcia paupercula* were also recorded in high densities (Fig 40, Table 9). In addition, the abundance of burrowing bivalves, mainly *Eumarcia paupercula* and *Dosinia hepatica*, differed significantly between the zones of high and low *C. kraussi* abundance (Fig 39). In sediments where *C. kraussi* was rare, the abundance of these bivalves was up to four times higher than in sediments in which *C. kraussi* was highly abundant. Following on from the previous discussion concerning the requirement of environmental stability for communities to comprise abundant, large, *K*-selected species, the rarity of bivalves in regions of high *C. kraussi* abundance, can be interpreted as an indication of a stressful or highly disturbed habitat, which is induced by *C. kraussi*.

The macrofauna in the zone of high *C. kraussi* abundance was dominated by burrowing infaunal deposit feeders such as *Scoloplos johnstonei*, *Prionospio sexoculata*, *Glycera sp.*, with no surface feeders recorded (Table 9). In sediments in which *C. kraussi* was rare, these deposit feeders were still present, but surface deposit feeders such as Cumaceans, and the isopod *Leptanthura laevigata* together with sub-surface deposit feeding cirratulid polychaetes, were also present in high numbers (Table 9). Surface and sub-surface feeders were recorded only in the zone where *C. kraussi* was rare. The interpretation is that *C. kraussi* is somehow able to "exclude" surface and sub-surface feeding fauna (Fig 42). If one considers the range of biological activities associated with *C. kraussi*, then its bioturbative activity of expelling sediments from burrows to the sediment surface would be the only likely explanation for the

exclusion of surface fauna. It is hypothesised that the continual deposition of sediment through bioturbation by *C. kraussi*, and subsequent re-dispersion by wave action, creates a highly mobile sedimentary environment and an unstable benthic habitat on the sediment surface. The biological effect is that surface feeding fauna are "excluded" because the continual expulsion of sediment and resuspension by wave action, acts as a source of disturbance. General responses of macrofauna to increased levels of suspended sediments include a reduction in growth rates (Aller and Dodge 1974) and an increase in larval mortality (Loosanoff 1962 *loc cit.*). Bivalves are possibly "excluded" (Fig 39) because their siphons are clogged by sediments expelled from burrows of *C. kraussi*. Suspension feeders such as bivalves are known to be particularly susceptible to sediment disturbance induced by bioturbation, because increased levels of suspended sediments result in reduced filtration rates by these suspension feeders (Gerodette and Flechsig 1979, Rhoads and Young 1970). It is also possible that sediment expulsion can directly bury both adult and juvenile stages of benthic macrofauna (Rhoads and Young, 1970).

The first attempt to explain how bioturbators influence benthic communities was made by Rhoads and Young (1970), in order to explain the general trend of consistent spatial separation between suspension and deposit feeders. Suspension feeders in the study site were restricted to firm mud bottoms, whereas deposit feeders occurred in soft muddy bottoms. Much of this segregation was explained by the fact that extensive bioturbation by deposit feeders resulted in a "fluid" sediment surface, which upon re-suspension by wave action (even at low velocities), either clogged filtering apparatus, buried larvae, or prevented settlement of these suspension feeders. This mechanism or hypothesis was referred to as the trophic group amensalism hypothesis (Rhoads and Young 1970).

The next significant contribution to understanding the mechanism behind bioturbation and its role in structuring benthic communities was made by Brenchley (1981). From a combination of field and laboratory manipulations, it was proposed that bioturbators do not target a specific trophic group such as suspension feeders. Instead, the mobility of the organism and whether it lives on the sediment surface or burrows in sediments, are key to understanding the effects of bioturbators. In these experiments, tubicolous surface feeding amphipods were "excluded" at high bioturbation rates, but mobile suspension feeding gastropods and crustaceans, capable of burrowing, were not affected. Surface dwelling fauna with limited mobility, which were unable to "escape" the disturbance induced by increased suspended sediment loads, were excluded. Fauna that were mobile, could escape by burrowing (Brenchley, 1981).

Although both hypotheses differ slightly, they agree in that they recognise that the effect of bioturbation occurs principally at the sediment surface, thereby leading to the exclusion of surface fauna. These findings by Brenchley (1981) and Rhoads and Young (1970), concur with those recorded in the Little Lagoon, in which surface fauna were recorded in regions where *C. kraussi* was rare, but not where *C. kraussi* was abundant.

Much of the early research on bioturbation had focused on biogenic modifications to sediment properties (eg. Aller and Yingst 1985), but current research has tended to focus specifically on its effects on specific communities such as macrofauna (Widdicombe and Austen 1998, Widdicombe and Austen 1999, Widdicombe *et al.* 2000, Berkenbusch *et al.* 2000), meiofauna (Olafsson *et al.* 1993), seagrasses (Townsend and Fonseca 1998) and nematode communities (Schratzberger and Warwick 1999). Much of the interest shown for the above, is related to the realisation that bioturbation is a key process in structuring communities and setting and maintaining levels of diversity especially in stable physical habitats (Widdicombe *et al.* 1998).

A variety of organisms have been recognised as bioturbators, ranging from polychaetes and crabs to manatees and birds (Cadee 2001), but the burrowing callianassid crustaceans are considered to be the most influential of them in terms of sediment turnover rates i.e. the amount of sediment reworked over time, and because they can burrow up to 5m deep (Cadee 2001, Flach and Tamaki 2001). In addition, callianassids have the potential to expel a substantial amount of sediment from burrows. In some cases, sediment layers between 0.5 and 1m thick have reportedly been expelled annually, after subsequent leveling by wave action (Cadee 2001).

The most significant and well-known long-term study of changes in benthic invertebrate communities in relation to bioturbating callianassid shrimps, was made by Tamaki and co-workers, in the Ariake Sound Estuarine System in Japan. The benthic community in the study site underwent dramatic changes over the period between 1979 and 1998, the most significant of which was a ten-fold increase in densities of *Nihonotrypaea harmandi*, a callianassid sandprawn (Flach and Tamaki 2001). This increase in densities of *N. harmandi* was accompanied by the local extinction of the gastropod *Umbonium moniliferum*, from densities of 2000/m² in 1979 to 0 in 1986. The mechanism likely to account for such biologically induced extinction was that of larval burial and smothering arising from sediment reworking activities by *N. harmandi*. Following a decline in densities of *N. harmandi* in 1995, there was evidence of a recovery of the *U. moniliferum* population (Flach and Tamaki 2001).

Another modification of the benthic community in the Ariake Sound System, was that densities of the tube building polychaete *Pseudopolydora paucibranchiata*, which was up to the 1979 period the most dominant macrobenthic organism, had been reduced substantially following the expansion of *N. harmandi*. Similarly, densities of the surface deposit feeding opheliid polychaete *Armandia amakusaensis* decreased rapidly during 1979 and 1980, again in response to increased abundance of *N. harmandi*. In both cases, the sediment de-stabilising effect of bioturbation by *N. harmandi* has been identified as the mechanism driving such community changes (Flach and Tamaki 2001).

At the other end of the world, bioturbation by a New-Zealand sand prawn, *Callinassa filholi*, has also been recognized as a key process involved in structuring macrobenthic communities and influencing species richness of communities (Berkenbusch *et al.* 2000). The methods utilised by the author was that of a "natural experiment", by observing differences in macrobenthic communities and patches of high and low densities of the sand-prawn, and is similar to the approach utilised in the present study in the Little Lagoon. Significant differences in species composition were recorded between sites of high and low *C. filholi* density. Densities of a corophiid amphipod *Paracorophium excavatum* and a bivalve *Perrierina turneri* were significantly reduced in regions where *C. filholi* was highly abundant (Berkenbusch *et al.* 2000). The majority of corophiid amphipods are regarded as tubicolous surface fauna (Griffiths, 1976), and could therefore explain their absence in regions where *C. filholi* were abundant, based on the sediment disturbance created by the sandprawn. In addition, species richness and total numbers of macrobenthic organisms were significantly reduced in these regions (Berkenbusch *et al.* 2000). In the light of its impacts on macrobenthic community structure, and more importantly, its regulation of communities on a temporal level, the author considered *C. filholi* to be a keystone species (Berkenbusch *et al.* 2000), which implies that its removal leads to the "collapse" of such a community, and a drastic reduction in species richness (Chapman and Reiss 1997).

There are a few consistent patterns that emerge between the three case studies of *N. harmandi* (Japan), *C. filholi* (New Zealand), and *C. kraussi* (South Africa), and their respective impacts on macrobenthic communities. In the cases of *C. filholi* and *C. kraussi*, densities of bioturbators lead to low abundances of macrobenthic organisms, and communities with comparatively fewer species. In all three cases, surface fauna were excluded, as well as large *K*-selected organisms such as bivalves and gastropods. All of these impacts were a result of sediment deposition and de-stabilisation at the sediment surface.

The fact that these results have been replicated in three studies, and because it was done on a global scale, emphasises the previous point that bioturbation is a key process in sedimentary habitats, and no less so in the Little Lagoon. In the Little Lagoon, these results have been demonstrated for intertidal regions only, but there is no reason why bioturbation should not occur in sub-tidal regions, provided that *C. kraussi* is present. Crude underwater visual assessments indicated that *C. kraussi* was indeed present, as indicated by mounds of expelled sediment. Moreover, if one considers that bioturbation rates have been shown to be dependant on abundance and size of sandprawns (Berkenbusch and Rowden 1999), it is more than likely that *C. kraussi* may significantly influence the Little Lagoon macrobenthic community at a temporal level as well, in view of seasonal changes in sizes and abundance of this organism documented in this study (Figs 27 & 28). It therefore appears that bioturbation by *C. kraussi* is potentially by far the most influential process in the Little Lagoon, and over-rides any physical process as far as structuring macrobenthic communities at a spatio-temporal level is concerned.

4. Concluding Remarks

The study has demonstrated that the Little Lagoon habitat is essentially a sheltered, marine dominated system, in which fluctuations in the physical environment at a temporal level were negligible. These features had the effect of encouraging the development of highly stable macrobenthic communities which were rich in species, and in which the biomass was dominated by large *K*-selected species such as burrowing bivalves and sandprawns. More significantly though, the study has confirmed that a significant shift in thinking is required in understanding and predicting determinants of community structure in sandflat habitats such as the Little Lagoon. A large proportion of conventional research has focused on relating community structure of macrobenthic assemblages to physical and chemical parameters (Flach and Tamaki 2001), but the results of this study adds to the growing body of evidence indicating that biological interactions, specifically bioturbation in this case, are significant factors involved in structuring sandflat communities (Reise 1985).

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6. Appendix A

Table 1: Water depths (m) in the Little Lagoon recorded in March and December 2001. SE = Standard Error.

	March	December	Mean	SE
A1	0	0	0.0	0.0
A2	0.8	1	0.9	0.1
A3	1	0.4	0.7	0.3
A4	0	0	0.0	0.0
B1	0	0	0.0	0.0
B2	0.55	0.7	0.6	0.1
B3	0.1	0.4	0.3	0.2
B4	0	0	0.0	0.0
C1	0	0	0.0	0.0
C2	1.3	1.2	1.3	0.0
C3	0.7	1	0.9	0.2
C4	0	0	0.0	0.0

Table 2: Spatial and temporal temperature (°C) variations in the Little Lagoon. SE = Standard Error.

Season	2001				2002		Mean	SE
	March	June	September	December	March	June		
A1	28.0	22.5	21.0	25.7	26.6	17.9	23.6	1.6
A2	27.7	20.8	20.5	24.6	27.4	18.2	23.2	1.6
A3	27.6	22.4	20.6	25.2	27.4	18.2	23.6	1.6
A4	28.4	23.0	21.1	25.2	28.6	18.1	24.1	1.7
B1	27.1	22.5	22.1	26.7	26.6	17.9	23.8	1.5
B2	26.7	20.9	21.3	24.9	27.9	18.0	23.3	1.6
B3	28.8	22.8	20.7	25.1	26.9	18.3	23.8	1.6
B4	29.3	23.0	21.8	25.5	28.2	18.1	24.3	1.7
C1	26.4	22.7	22.8	25.9	27.9	18.8	24.1	1.4
C2	27.5	21.8	21.0	25.0	26.8	19.0	23.5	1.4
C3	27.3	22.1	21.1	25.1	26.5	18.9	23.5	1.4
C4	27.0	22.0	21.1	26.6	26.4	19.1	23.7	1.4

Table 3: Spatial and temporal salinity (ppt) variations in the Little Lagoon. Values in bold indicate outliers or extreme values. SE = Standard Error.

	2001				2002		Mean	SE
	March	June	September	December	March	June		
A1	29.3	34.6	37.2	27.1	35.2	30.0	32.2	1.6
A2	29.3	35.2	37.0	36.1	35.5	29.4	33.8	1.4
A3	30.0	34.7	36.7	35.3	35.4	30.4	33.8	1.2
A4	20.4	35.3	37.1	32.1	36.1	27.9	31.5	2.6
B1	29.8	35.2	37.3	27.2	35.2	30.0	32.5	1.6
B2	29.6	35.2	27.4	35.8	35.5	30.5	32.3	1.5
B3	29.8	33.2	36.6	35.5	35.4	30.8	33.6	1.1
B4	20.4	35.0	34.2	33.5	36.0	30.6	31.6	2.4
C1	29.6	35.3	36.9	28.9	29.2	30.8	31.8	1.4
C2	29.6	35.1	37.6	35.8	35.2	27.6	33.5	1.6
C3	29.5	35.7	37.6	35.8	35.3	31.3	34.2	1.3
C4	29.2	34.0	37.1	30.0	35.6	31.5	32.9	1.3

Table 4: Spatial and temporal variations in concentrations of dissolved oxygen (mg/L) in the Little Lagoon. SE = Standard Error.

	2001				2002		Mean	SE
	March	June	September	December	March	June		
A1	6.38	6.34	6.75	6.79	4.87	7.6	6.46	0.37
A2	5.95	6.79	5.66	7	6.21	8.1	6.62	0.36
A3	6.96	5.46	6.09	7.71	6.26	7.2	6.61	0.34
A4	6.74	8.4	7.26	6.91	7.11	8.08	7.42	0.27
B1	5.89	5.63	6.9	7.04	5.9	7.45	6.47	0.31
B2	6.58	6.4	5.75	6.57	6.48	7.98	6.63	0.30
B3	7.03	5.49	6.56	6.86	6.2	7.98	6.69	0.34
B4	8.76	8.7	6.48	7.11	6.74	7.13	7.49	0.41
C1	5.38	5.51	7.27	6.28	5.35	8.45	6.37	0.51
C2	5.16	6.75	6.38	6.62	5.9	7.95	6.46	0.38
C3	6.29	5.28	6.85	6.94	6.23	7.94	6.59	0.36
C4	7.24	6	6.91	7.57	5.86	7.9	6.91	0.34

Appendix B

Table 1: Spatial and temporal variations in median phi values of surface sediments in the Little Lagoon.

SE = Standard Error.

	2001				2002		Mean	SE
	March	June	September	December	March	June		
A1	2.1	2	2	2	1.8	1.9	1.97	0.04
A2	3.2	3.1	3	3	3	3	3.05	0.03
A3	2.1	2.1	2	2.2	2.1	2.2	2.12	0.03
A4	1.9	1.9	1.9	1.9	2.1	2.2	1.98	0.05
B1	2.1	2	2	1.9	2	2.2	2.03	0.04
B2	1.8	1.7	1.8	1.8	1.8	1.8	1.78	0.02
B3	2	2	2	1.9	2.4	2.2	2.08	0.07
B4	2.1	2	2	1.9	2.2	2.2	2.07	0.05
C1	2.4	2.4	2.4	2.4	1.8	1.8	2.20	0.13
C2	2.8	2.7	3	3	3	3.1	2.93	0.06
C3	2.2	2.3	2.3	2.2	2.2	2.2	2.23	0.02
C4	2.2	2.2	2.2	2.2	2.2	2.2	2.20	0.00

Table 2: Spatial and temporal variations in organic contents of surface sediments in the Little Lagoon.

SE = Standard Error.

	2001				2002		Mean	SE
	March	June	September	December	March	June		
A1	3.9	3.0	3.0	3.0	3.7	2.4	3.1	0.2
A2	7.5	6.2	5.7	7.0	8.3	6.3	6.8	0.4
A3	2.5	2.4	2.7	3.7	5.7	6.1	3.8	0.7
A4	3.4	3.7	3.6	3.2	4.0	2.1	3.3	0.3
B1	1.8	1.7	1.7	1.7	2.0	2.4	1.8	0.1
B2	1.9	1.7	1.7	2.0	3.3	3.1	2.3	0.3
B3	1.8	1.6	1.9	2.9	3.6	4.0	2.6	0.4
B4	1.6	1.7	1.9	2.7	2.1	2.6	2.1	0.2
C1	2.5	2.6	2.6	2.2	3.1	3.7	2.8	0.2
C2	5.1	6.2	7.5	6.2	6.6	7.6	6.5	0.4
C3	2.2	3.7	3.2	3.6	5.1	5.7	3.9	0.5
C4	3.0	3.0	2.7	3.7	4.0	3.9	3.4	0.2

Appendix C

Table 1: Mean density (individuals/m²) of macrofauna in the Little Lagoon recorded in March 2001.

Values are means of three site replicates.

	A1	A2	A3	A4	B1	B2	B3	B4	C1	C2	C3	C4
Polychaeta												
Cirratulidae												
Unidentified Cirratulid polychaetes	0	250	155	89	0	14	193	132	0	24	14	132
Phyllodoceidae												
<i>Phyllodoce castanea</i>	0	9	5	0	0	0	0	0	0	5	0	0
Cossuridae												
<i>Cossura coasta</i>	0	518	0	0	0	0	0	0	0	344	0	0
Orbiniidae												
<i>Scoloplos johnstonei</i>	0	0	14	5	0	5	0	0	38	5	9	5
Spionidae												
<i>Prionospio sexoculata</i>	193	730	334	702	325	38	612	593	169	377	52	452
<i>Polydora</i> SP.	0	0	0	0	0	0	0	0	0	0	0	0
<i>Scolelepis squamata</i>	9	0	0	0	0	0	0	0	0	0	0	0
Nereidae												
<i>Ceratonereis erythroensis</i>	0	0	0	0	0	0	0	0	0	0	0	0
<i>Dendronereis arborifera</i>	5	0	24	66	0	0	42	85	0	0	0	33
Glyceridae												
<i>Glycera</i> SP	188	33	108	99	122	141	132	188	132	66	151	137
Capitellidae												
Unidentified Capitellid polychaetes	113	104	14	5	33	19	0	14	94	0	61	0
Sabellidae												
<i>Megalomma</i> SP	0	0	0	0	0	0	0	0	0	0	0	0
<i>Desdemona ornata</i>	42	0	0	0	0	0	0	0	0	0	0	0
Maldanidae												
Unidentified Maldanid polychaetes	0	0	5	0	0	0	0	0	0	0	0	0
Eunicidae												
<i>Marphysa depressa</i>	0	0	0	0	0	0	0	0	0	0	0	0
Crustacea												
Anomura												
<i>Upogebia africana</i>	5	0	0	0	0	0	0	0	0	0	0	5
<i>Callinassa kraussi</i>	5	0	0	0	0	9	0	0	0	0	5	19
Macrura												
<i>Betaeus jucundus</i>	0	0	0	0	0	0	0	0	0	0	0	0
Isopoda												
<i>Cyathura estuaria</i>	0	5	0	0	0	0	0	0	0	0	0	0
<i>Cirolana luciae</i>	33	0	0	0	9	5	0	0	0	9	14	0
<i>Leptanthura laevigata</i>	160	56	0	612	151	146	61	104	52	38	71	75
Amphipoda												
<i>Melita zeylanica</i>	0	0	0	0	0	0	0	0	0	0	0	0
<i>Corophium triaenonyx</i>	0	0	0	0	0	0	0	0	0	0	0	0
<i>Grandidierella bonnieroides</i>	0	0	0	0	0	0	0	0	0	0	0	0
Cumacea												
Cumacea	108	0	0	66	56	0	19	28	61	0	0	0
Brachyura												
<i>Thaumastoplax spiralis</i>	5	5	0	0	0	0	0	0	5	0	0	9
<i>Paratylodiplax blephariskios</i>	0	127	0	0	0	0	0	0	0	14	0	0
<i>Hymenosoma orbiculare</i>	0	0	0	0	0	0	0	0	0	0	0	0
Tanaidacea												
<i>Apseudes digitalis</i>	0	71	0	570	0	0	47	19	0	0	5	19
Mollusca												
Gastropoda												
<i>Nassarius krausianus</i>	5	61	169	19	0	0	66	19	0	52	14	24
<i>Acteocina fusiformis</i>	0	0	0	0	0	0	0	0	0	0	0	0
Bivalvia												
<i>Eumarcia paupercula</i>	14	5	94	24	5	5	47	89	5	28	0	33
<i>Solen cylindraceus</i>	0	0	0	5	0	0	0	0	0	0	0	0
<i>Dosinia hepatica</i>	0	0	0	0	0	0	0	0	0	0	0	0
<i>Brachidontes virgiliae</i>	0	0	0	0	0	0	0	0	0	0	0	0
<i>Fulvia papyracea</i>	0	0	0	0	0	0	0	0	0	0	0	0
<i>Tellina prismatica</i>	0	0	0	0	0	0	0	0	0	0	0	0
Sipunculida												
	5	0	0	0	0	0	0	0	0	0	0	0

Table 2: Mean density (individuals/m²) of macrofauna in the Little Lagoon recorded in June 2001. Values are means of three site replicates.

	A1	A2	A3	A4	B1	B2	B3	B4	C1	C2	C3	C4
Polychaeta												
Cirratulidae												
Unidentified Cirratulid polychaetes	0	268	217	0	0	273	245	19	0	0	160	5
Phyllodoceidae												
<i>Phyllodoce castanea</i>	0	0	0	0	0	0	0	0	0	0	0	0
Cossuridae												
<i>Cossura coasta</i>	0	523	0	0	0	38	9	0	0	0	188	0
Orbiniidae												
<i>Scoloplos johnstonei</i>	9	0	0	5	0	0	0	0	14	14	0	0
Spionidae												
<i>Prionospio sexoculata</i>	188	424	297	99	85	424	339	250	61	80	292	47
<i>Polydora</i> sp.	0	0	0	0	0	0	0	0	5	0	0	0
<i>Scololepis squamata</i>	0	42	0	0	0	24	0	0	0	0	0	0
Nereidae												
<i>Ceratonereis erythroensis</i>	0	0	0	0	0	33	0	0	0	0	0	0
<i>Dendronereis arborifera</i>	9	5	9	0	14	0	9	94	0	0	0	0
Glyceridae												
<i>Glycera</i> sp.	52	66	85	42	122	5	89	99	85	71	47	71
Capitellidae												
Unidentified Capitellid polychaetes	0	0	0	0	0	0	0	0	0	0	0	0
Sabellidae												
<i>Megalomma</i> sp.	0	0	0	0	0	0	0	0	0	0	0	0
<i>Desdemona ornata</i>	0	5	0	0	0	0	0	0	0	0	0	0
Maldanidae												
Unidentified Maldanid polychaetes	0	0	0	0	0	0	0	0	0	0	0	0
Eunicidae												
<i>Marphysa depressa</i>	0	0	0	0	0	0	0	0	0	0	0	0
Crustacea												
Anomura												
<i>Upogebia africana</i>	0	0	0	0	0	0	0	0	0	0	0	0
<i>Callianassa kraussi</i>	71	0	0	19	38	0	0	0	5	28	0	56
Macrura												
<i>Betaeus jucundus</i>	0	0	0	0	0	0	0	0	0	0	5	0
Isopoda												
<i>Cyathura estuaria</i>	0	0	0	0	0	0	0	0	0	0	0	0
<i>Cirolana luciae</i>	0	0	0	0	19	0	0	0	0	146	0	5
<i>Leptanthura laevigata</i>	61	42	127	188	47	52	42	480	174	137	38	38
Amphipoda												
<i>Melita zeylanica</i>	0	0	0	0	0	0	0	0	0	0	0	0
<i>Corophium triaenonyx</i>	0	19	0	0	0	0	0	0	0	0	0	0
<i>Grandierella bonnieroides</i>	5	5	28	5	0	0	0	28	19	0	9	0
Cumacea												
Cumacea	179	9	99	108	99	0	113	137	292	28	0	19
Brachyura												
<i>Thaumastoplax spiralis</i>	0	0	0	0	0	19	0	0	0	9	0	0
<i>Paratylodiplax blephariskios</i>	0	9	0	0	0	141	0	0	0	0	0	0
<i>Hymenosoma orbitale</i>	5	0	0	0	0	0	0	0	0	0	0	0
Tanaidacea												
<i>Apseudes digitalis</i>	0	0	19	0	0	0	0	0	0	0	24	0
Mollusca												
Gastropoda												
<i>Nassarius kraustanus</i>	0	5	94	0	9	28	104	52	0	28	24	5
<i>Acteocina fusiformis</i>	0	0	0	0	0	0	0	0	0	0	0	0
Bivalvia												
<i>Eumarcia paupercula</i>	9	61	113	14	38	33	118	75	5	19	9	24
<i>Solen cylindraceus</i>	0	0	5	0	0	0	24	0	0	0	0	0
<i>Dosinia hepatica</i>	0	0	0	0	5	0	0	0	0	0	0	0
<i>Brachidontes virgiliae</i>	0	0	0	0	0	0	0	0	0	0	0	0
<i>Fulvia papyracea</i>	0	0	0	0	0	0	0	0	0	0	0	0
<i>Tellina prismatica</i>	0	0	0	0	0	0	0	0	0	0	0	0
Sipunculida												
Sipunculida	0	0	0	0	0	0	0	0	0	0	0	0

Table 3: Mean density (individuals/m²) of macrofauna in the Little Lagoon recorded in September 2001.

Values are means of three site replicates.

	A1	A2	A3	A4	B1	B2	B3	B4	C1	C2	C3	C4
Polychaeta												
Cirratulidae												
Unidentified Cirratulid polychaetes	0	895	169	0	0	141	75	0	0	99	0	5
Phyllodoceidae												
<i>Phyllodoce castanea</i>	0	0	0	0	0	0	0	0	0	0	0	0
Cossuridae												
<i>Cossura coasta</i>	0	245	9	0	0	395	24	0	0	1530	0	0
Orbiniidae												
<i>Scoloplos johnstonei</i>	5	0	0	0	0	0	0	0	5	0	5	0
Spionidae												
<i>Prionospio sexoculata</i>	325	584	282	127	348	292	377	702	306	584	179	471
<i>Polydora</i> SP.	0	0	0	0	0	9	5	0	0	0	0	0
<i>Scololepis squamata</i>	0	0	0	0	0	0	0	0	0	0	0	0
Nereidae												
<i>Ceratonereis erythroensis</i>	0	0	0	0	0	0	0	0	0	0	0	0
<i>Dendronereis arborifera</i>	0	5	5	0	0	0	5	33	0	0	0	0
Glyceridae												
<i>Glycera</i> SP	28	9	24	24	56	5	52	113	56	14	85	165
Capitellidae												
Unidentified Capitellid polychaetes	325	0	0	0	0	0	0	0	0	0	0	0
Sabellidae												
<i>Megalomma</i> SP	0	0	0	0	0	0	0	0	0	0	0	0
<i>Desdemona ornata</i>	5	5	9	5	5	0	9	0	0	14	0	0
Maldanidae												
Unidentified Maldanid polychaetes	0	0	0	0	0	0	0	0	0	0	0	0
Eunicidae												
<i>Marphysa depressa</i>	0	0	0	0	0	0	0	0	0	0	0	0
Crustacea												
Anomura												
<i>Upogebia africana</i>	0	0	0	0	0	0	0	0	0	0	0	0
<i>Callinassa kraussi</i>	42	0	0	5	19	0	0	47	9	0	75	14
Macrura												
<i>Betaeus jucundus</i>	0	0	0	0	0	0	0	0	0	0	0	0
Isopoda												
<i>Cyathura estuaria</i>	9	0	0	0	0	0	0	0	0	0	0	0
<i>Cirolana luciae</i>	0	0	0	0	0	0	0	0	0	0	0	0
<i>Leptanthura laevigata</i>	146	259	122	1040	198	56	99	970	155	19	137	146
Amphipoda												
<i>Melita zeylanica</i>	5	0	0	0	0	0	0	0	0	0	0	0
<i>Corophium triaenonyx</i>	0	33	19	0	0	0	0	0	0	0	5	0
<i>Grandidierella bonnieroides</i>	5	0	9	19	14	0	0	0	0	0	0	0
Cumacea												
Cumacea	348	99	372	956	250	0	207	650	311	5	273	438
Brachyura												
<i>Thaumastoplax spiralis</i>	0	0	0	0	0	0	0	0	5	0	0	0
<i>Paratyloidiplax blephariskios</i>	0	9	0	0	0	89	0	0	0	24	0	0
<i>Hymenosoma orbiculare</i>	0	0	0	0	0	0	0	0	0	0	0	0
Tanaidacea												
<i>Apseudes digitalis</i>	0	5315	66	0	0	0	0	0	0	0	0	0
Mollusca												
Gastropoda												
<i>Nassarius kraussianus</i>	5	66	33	0	0	38	85	0	5	52	0	0
<i>Actoecina fusiformis</i>	0	0	0	0	0	0	0	0	0	0	0	0
Bivalvia												
<i>Eumarcia paupercula</i>	9	19	24	0	0	14	42	5	0	0	14	0
<i>Solen cylindraceus</i>	0	0	0	0	0	0	0	0	0	0	0	0
<i>Dosinia hepatica</i>	33	24	52	5	9	19	99	9	0	14	9	9
<i>Brachidontes virgiliae</i>	0	0	0	0	0	0	0	0	0	0	0	0
<i>Fulvia papyracea</i>	0	0	0	0	0	0	0	0	0	0	0	0
<i>Tellina prismatica</i>	0	33	33	0	0	42	5	0	0	122	0	0
Sipunculida												
	0	0	0	0	0	0	0	0	0	0	0	0

Table 4: Mean density (individuals/m²) of macrofauna in the Little Lagoon recorded in December 2001.

Values are means of three site replicates.

	A1	A2	A3	A4	B1	B2	B3	B4	C1	C2	C3	C4
Polychaeta												
Cirratulidae												
Unidentified Cirratulid polychaetes	0	1022	132	0	0	33	56	626	0	89	85	0
Phyllodoceidae												
<i>Phyllodoce castanea</i>	0	5	0	0	5	0	0	0	0	24	0	0
Cossuridae												
<i>Cossura coasta</i>	0	80	0	0	0	0	0	0	0	99	42	0
Orbiniidae												
<i>Scoloplos johnstonei</i>	0	0	0	0	0	5	0	0	0	0	0	0
Spionidae												
<i>Prionospio sexoculata</i>	146	1158	443	108	169	334	381	471	38	240	504	457
<i>Polydora</i> sp.	0	0	0	0	0	0	0	0	0	0	0	0
<i>Scololepis squamata</i>	0	0	0	0	0	0	0	0	0	0	0	0
Nereidae												
<i>Ceratonereis erythroensis</i>	0	0	0	0	0	0	0	0	0	0	0	0
<i>Dendronereis arborifera</i>	0	5	5	0	0	0	0	0	0	0	0	0
Glyceridae												
<i>Glycera</i> sp	89	85	75	38	47	9	14	19	14	14	14	193
Capitellidae												
Unidentified Capitellid polychaetes	0	0	0	0	0	0	0	0	0	0	0	0
Sabellidae												
<i>Megalomma</i> sp	0	0	0	0	0	0	0	0	0	0	0	0
<i>Desdemona ornata</i>	0	0	28	0	0	0	5	174	0	5	9	0
Maldanidae												
Unidentified Maldanid polychaetes	0	0	0	0	0	0	0	0	0	0	0	0
Eunicidae												
<i>Marphysa depressa</i>	0	0	0	0	0	0	0	0	0	0	0	0
Crustacea												
Anomura												
<i>Upogebia africana</i>	0	0	0	0	0	0	0	0	0	0	0	0
<i>Callinassa kraussi</i>	0	0	0	0	0	0	0	0	19	0	0	0
Macrura												
<i>Betaeus jucundus</i>	0	0	0	0	0	0	0	0	0	0	0	0
Isopoda												
<i>Cyathura estuaria</i>	0	0	0	0	0	0	0	0	0	0	0	0
<i>Cirolana luciae</i>	14	0	0	0	0	5	0	0	0	0	0	0
<i>Leptanthura laevigata</i>	0	5	9	9	118	9	9	47	169	5	0	66
Amphipoda												
<i>Melita zeylanica</i>	5	0	0	14	0	0	0	0	0	0	0	0
<i>Corophium triaenonyx</i>	0	0	0	0	0	0	0	0	0	0	0	5
<i>Grandidierella bonnieroides</i>	5	0	0	19	0	0	0	5	0	0	0	85
Cumacea												
Cumacea	137	61	108	245	306	47	80	56	137	0	0	99
Brachyura												
<i>Thaumastoplax spiralis</i>	5	0	0	0	5	0	0	0	0	0	0	5
<i>Paratylodiplax blephariskios</i>	0	0	0	0	0	0	0	0	0	9	0	5
<i>Hymenosoma orbiculare</i>	0	0	0	0	0	0	0	0	0	0	0	0
Tanaidacea												
<i>Apeudes digitalis</i>	0	5254	433	0	0	0	5	0	0	5	28	0
Mollusca												
Gastropoda												
<i>Nassarius krausianus</i>	0	75	80	9	0	137	61	94	5	47	28	9
<i>Acteocina fusiformis</i>	0	19	19	0	0	160	33	42	0	9	0	0
Bivalvia												
<i>Eumarcia paupercula</i>	5	0	14	0	0	5	42	47	5	0	9	19
<i>Solen cylindraceus</i>	0	0	0	0	0	0	0	0	0	0	0	0
<i>Dosinia hepatica</i>	0	9	99	5	0	28	66	94	0	5	14	9
<i>Brachidontes virgiliae</i>	0	0	0	0	0	0	0	0	0	0	0	0
<i>Fulvia papyracea</i>	0	0	0	0	0	0	0	0	0	0	0	0
<i>Tellina prismatica</i>	0	89	9	0	0	19	9	0	0	28	9	0
Sipunculida												
	0	0	0	0	0	0	0	0	0	0	0	0

Table 5: Mean density (individuals/m²) of macrofauna in the Little Lagoon recorded in March 2002.

Values are means of three site replicates.

	A1	A2	A3	A4	B1	B2	B3	B4	C1	C2	C3	C4
Polychaeta												
Cirratulidae												
Unidentified Cirratulid polychaetes	5	1436	287	0	0	47	28	325	0	61	2580	28
Phyllodoceidae												
<i>Phyllodoce castanea</i>	0	28	0	0	0	0	0	24	0	0	5	0
Cossuridae												
<i>Cossura coasta</i>	0	0	0	0	9	5	0	0	0	0	5	0
Orbiniidae												
<i>Scoloplos johnstonei</i>	0	0	0	0	0	0	0	0	5	0	0	0
Spionidae												
<i>Prionospio sexoculata</i>	603	245	405	546	504	546	419	155	391	282	692	287
<i>Polydora</i> sp.	0	0	0	0	0	0	0	0	0	0	0	0
<i>Scololepis squamata</i>	0	0	0	0	0	0	0	0	0	0	0	0
Nereidae												
<i>Ceratonereis erythroensis</i>	0	0	0	19	0	0	0	14	0	0	0	0
<i>Dendronereis arborifera</i>	9	0	0	52	5	0	0	75	0	0	0	28
Glyceridae												
<i>Glycera</i> sp.	28	38	47	28	33	66	0	42	14	28	5	38
Capitellidae												
Unidentified Capitellid polychaetes	0	0	0	0	0	0	0	0	0	0	0	0
Sabellidae												
<i>Megalomma</i> sp.	0	5	0	0	0	0	0	0	0	0	0	0
<i>Desdemona ornata</i>	14	38	452	2806	19	5	504	28	0	9	38	122
Maldanidae												
Unidentified Maldanid polychaetes	0	0	0	14	0	0	0	0	0	0	0	0
Eunicidae												
<i>Marphysa depressa</i>	0	5	0	0	0	0	0	0	0	0	0	0
Crustacea												
Anomura												
<i>Upogebia africana</i>	0	0	0	0	0	0	0	0	0	0	0	0
<i>Callinassa kraussi</i>	9	0	0	0	5	0	0	0	0	5	0	0
Macrura												
<i>Betaeus jucundus</i>	0	0	0	0	0	0	0	0	0	0	0	0
Isopoda												
<i>Cyathura estuaria</i>	0	0	0	0	0	0	0	0	0	0	0	0
<i>Cirolana luciae</i>	0	0	0	0	9	0	0	0	0	61	0	0
<i>Leptanthura laevigata</i>	14	52	24	47	14	122	268	56	38	137	61	395
Amphipoda												
<i>Melita zeylanica</i>	0	0	0	0	0	0	0	5	0	0	0	0
<i>Corophium triaenonyx</i>	0	61	9	0	0	0	5	0	0	0	0	0
<i>Grandidierella bonnieroides</i>	5	0	66	9	0	0	0	5	0	0	0	14
Cumacea												
Cumacea	66	0	9	85	42	9	24	9	71	0	0	38
Brachyura												
<i>Thaumastoplax spiralis</i>	0	0	0	0	0	0	0	0	0	0	0	0
<i>Paratyloplax blephariskios</i>	0	0	0	0	0	0	0	0	0	0	0	0
<i>Hymenosoma orbiculare</i>	0	0	0	0	0	0	0	0	0	0	0	0
Tanaidacea												
<i>Apseudes digitalis</i>	0	8639	466	0	0	240	4774	28	0	0	683	0
Mollusca												
Gastropoda												
<i>Nassarius kraussianus</i>	0	85	104	52	5	71	113	127	0	71	66	146
<i>Actoecina fusiformis</i>	0	0	9	19	0	71	28	108	0	9	0	56
Bivalvia												
<i>Eumarcia paupercula</i>	9	28	56	28	19	28	52	85	19	14	19	66
<i>Solen cylindraceus</i>	0	5	0	5	5	5	5	0	0	0	0	0
<i>Dosinia hepatica</i>	42	75	80	61	99	137	127	75	24	38	28	85
<i>Brachidontes virgiliae</i>	0	207	89	0	0	0	132	61	0	0	0	14
<i>Fulvia papyracea</i>	0	0	9	0	0	5	0	0	0	0	9	0
<i>Tellina prismatica</i>	0	9	0	5	0	24	5	0	0	0	14	0
Sipunculida												
	5	0	0	0	0	0	0	0	0	0	0	0

Table 6: Mean density (individuals/m²) of macrofauna in the Little Lagoon recorded in June 2002.

Values are means of three site replicates.

	A1	A2	A3	A4	B1	B2	B3	B4	C1	C2	C3	C4
Polychaeta												
Cirratulidae												
Unidentified Cirratulid polychaetes	0	3809	75	226	104	0	273	94	0	400	5	0
Phyllodoceidae												
<i>Phyllodoce castanea</i>	0	0	0	9	0	0	0	0	0	0	0	0
Cossuridae												
<i>Cossura coasta</i>	0	0	0	0	0	0	0	0	0	461	0	0
Orbiniidae												
<i>Scoloplos johnstonei</i>	0	0	0	0	0	0	0	0	9	0	9	5
Spionidae												
<i>Prionospio sexoculata</i>	603	325	377	659	198	188	791	1507	410	890	749	264
<i>Polydora</i> sp.	0	0	0	0	0	0	0	0	0	0	0	0
<i>Scololepis squamata</i>	0	0	0	0	0	0	0	0	0	0	0	0
Nereidae												
<i>Ceratonereis erythroensis</i>	0	0	0	0	0	0	0	5	0	0	0	0
<i>Dendronereis arborifera</i>	14	14	0	137	0	0	75	99	0	5	0	0
Glyceridae												
<i>Glyceria</i> sp.	9	33	38	14	38	19	47	33	14	56	66	19
Capitellidae												
Unidentified Capitellid polychaetes	0	0	0	0	0	0	0	0	0	169	0	0
Sabellidae												
<i>Megalomma</i> sp.	0	5	0	0	0	0	0	0	0	0	0	0
<i>Desdemona ornata</i>	202	14	523	221	0	33	301	108	14	122	94	9
Maldanidae												
Unidentified Maldanid polychaetes	0	0	0	0	0	0	0	0	0	0	0	0
Eunicidae												
<i>Marphysa depressa</i>	0	0	0	0	0	0	0	0	0	0	0	0
Crustacea												
Anomura												
<i>Upogebia africana</i>	0	0	0	0	0	0	0	0	0	0	0	0
<i>Callinassa kraussi</i>	89	0	0	5	122	264	0	0	66	0	104	42
Macrura												
<i>Betaeus jucundus</i>	0	0	0	0	0	0	0	0	0	0	0	0
Isopoda												
<i>Cyathura estuaria</i>	0	0	0	0	0	0	0	0	0	0	0	0
<i>Cirolana luciae</i>	14	0	0	0	0	24	0	0	0	0	0	0
<i>Leptanthura laevigata</i>	61	137	202	353	47	433	358	169	122	28	377	179
Amphipoda												
<i>Melita zeylanica</i>	0	0	0	0	0	0	0	0	0	0	0	0
<i>Corophium triaenonyx</i>	0	0	33	0	0	0	0	0	0	0	0	0
<i>Grandidierella bonnieroides</i>	14	5	14	24	5	9	0	5	9	0	19	19
Cumacea												
Cumacea	75	0	14	127	0	151	80	141	61	24	363	311
Brachyura												
<i>Thaumastoplax spiralis</i>	5	0	0	0	0	0	0	0	0	5	0	0
<i>Paratylodiplax blephariskios</i>	0	0	0	0	0	0	0	0	0	38	0	0
<i>Hymenosoma orbiculare</i>	0	0	0	0	0	0	0	0	0	0	0	0
Tanaidacea												
<i>Apseudes digitalis</i>	0	75	2076	1234	5	0	1398	28	0	28	5	0
Mollusca												
Gastropoda												
<i>Nassarius krausianus</i>	5	56	137	71	0	19	75	52	0	66	14	9
<i>Acteocina fusiformis</i>	0	42	9	9	0	0	0	0	0	0	0	0
Bivalvia												
<i>Eumarcia paupercula</i>	24	5	28	9	0	0	24	19	5	0	5	0
<i>Solen cylindraceus</i>	0	19	0	0	0	5	0	14	0	5	0	0
<i>Dosinia hepatica</i>	0	47	231	127	19	89	113	42	38	33	80	33
<i>Brachidontes virgiliae</i>	0	0	52	0	0	0	0	5	5	0	0	0
<i>Fulvia papyracea</i>	0	0	0	0	0	0	0	0	0	0	0	0
<i>Tellina prismatica</i>	0	0	9	0	5	0	0	9	0	0	0	0
Sipunculida												
	0	0	0	0	0	0	0	0	0	0	0	0