PREDATION/DISTURBANCE EFFECTS OF GREATER FLAMINGOS (*PHOENICOPTERUS RUBER*) ON THE BENTHIC COMMUNITIES OF TWO SOUTHERN AFRICAN LAGOONS.

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by

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Thesis submitted to the faculty of science, University of Cape Town for the degree of Master of Science.

July 1992

CONTENTS.

ABSTRACT

Greater Flamingos, *Phoenicopterus ruber*, were excluded from intertidal areas of two lagoons and subtidal areas of one of these on the Namibian coastline. Macrofaunal and meiofaunal numbers increased at all exclusion sites, but taxon-specific responses were variable. Both intertidal sites were polychaete dominated; subtidally amphipods formed dense tube mats that covered the substrate. All except one macrofaunal species showed significant response to caging. Relative to controls, macrofaunal numbers increased approximately three times inside subtidal exclosures, and one and a half times intertidally, but diversity indices were similar between treatments. There was some evidence that amensalistic interactions developed between macrofauna within exclosures. Intertidally at Walvis Bay meiofauna showed little response to flamingo exclusion, but subtidally all groups showed statistically significant responses to treatments. At Sandwich Harbour, foraminifera and ostracod abundance changed significantly. Bacterial counts were lower in exclusions at all sites, but significantly so only at Sandwich Harbour, which was the only site where chlorophyll concentrations did not change significantly. Sediment particle size composition was unaffected at all sites. Eh and organic content of sediments changed least subtidally; pH was affected by the treatment at both Walvis Bay sites, but not at Sandwich Harbour. Partial cages, used as cage controls, indicated that results were not artefacts caused by caging.

Overall, it was clear that *P. ruber* was important in structuring communities in the areas studied. In the absence of *P. ruber*, physical disturbance may be the most important force structuring benthic communities.

INTRODUCTION

A long-held aim of ecological and evolutionary studies has been to gain understanding of the biological and physical forces controlling interactions within and between species, and between organisms and their abiotic environment. Comprehension of these forces would provide insight into the organisation, functioning and persistence of species assemblages and communities, and may cast light on the mechanisms of their evolution.

Peterson (1977) stated 'a major goal in the study of any ecological community is to achieve an appreciation for the dominant force or forces involved in community organisation'. Much of the literature on the benthos of both hard and soft marine substrates reflects this goal (e.g. Bell 1980, Van Blaricom 1982, Alongi 1985, Brey 1991). Workers on rocky marine communities have had considerable sucess in elucidating such forces - rocky shore communities are organised largely by intense competition for space, with one or few species tending to dominate any area. This competition may be mediated by biological or physical disturbance, including predation (Paine 1974, Peterson 1979). However, problems associated working in soft substrates, particularly in estuaries and lagoons, have hindered similar progress in the study of soft-sediment communities (Dayton 1984). While competition has often been cited as being important, and sometimes demonstrated as a structuring force in marine soft bottom communities (Woodin 1974, Peterson 1977), it clearly does not account adequately for community structure in the majority of cases (Black & Peterson 1988). The prevalence of infauna in soft substrates results in a de facto three-dimensional environment. This reduces competition for space, in part because vertical as well as horizontal spatial zonation can occur (e.g. Peterson & Andre 1980). The instability of soft sediments render them largely unsuitable for colonial organisms (Peterson 1979), and the predominantly infaunal benthic fauna does not provide secondary surfaces for larval settlement, a common phenomenon on rocky shores These factors make interference competition by means of overgrowth unlikely. Indirect interference effects may operate, such as trophic amensalism between deposit and filter feeders (Rhoads and Young 1970) or the effects of tube-building fauna on burrowing species (Brenchley 1982). However direct interference competition, the form of competition most often resulting in monopolization of the substrate by a single species or guild of species on rocky shores, is of reduced importance in soft sediment communities. While some competition-based models for soft-sediment community organisation have been proposed (e.g. Grassle & Sanders 1973), the relative importance of competition is still a matter of debate. Following Johnson's (1970) model viewing the benthos as a mosaic of disturbance-induced patches at different stages of competition, Grassle & Sanders (1973) proposed that each patch will initially be colonised by opportunistic species, due to resources being freely available in the absence of competitors. This will be followed by a succession of increasingly more efficient resource competitors. The persistence of less efficient competitors in the community is due to the continual presence of patches at different stages of succession. However, field evidence reviewed by Thistle (1981), indicates that colonising species may be responding to stimuli other than competitive release. Thistle suggests that the succession may be generated by changes in the nature of the resource base caused by the organisms themselves, and is therefore not driven by competitive interactions. Virnstein (1977) demonstrated that in the absence of predation an opportunistic, colonising species (the bivalve *Mulinia lateralis*) could persist at high densities and even exclude other species, although the mechanism of such exclusion may have been incidental predation on settling larvae or an amensalistic interaction rather than competition. He suggested that some species may be excluded because they are poor 'predation avoiders', rather than poor resource competitors. In a review of studies of predator exclusion in soft sediments, Peterson (1979) failed to find any cases in which the community tended toward competitive dominance by single species. Apart from reasons cited above, Peterson (1979) proposed that negative adult-larval interactions in soft sediments may prevent populations from reaching densities at which intense competition occurs, although later evidence suggests that consumption by filter-feeding adults may not significantly affect the abundance of settling larvae (Black & Peterson 1988). Other authors (eg Virnstein 1978, Quammen 1984) who have conducted predator exclusion experiments, similarly reported an absence of competitive exclusion, even where infauna occurred at high densities. Wilson (1983) found that intra- rather than interspecific competition was the major determinant of community structure in an infaunal community dominated by two species of spionid polychaete. Wilson (1984) demonstrated that the non-overlapping distribution of three species of spionid polychaetes in a lagoon was determined by habitat alone. Survivorship of animals in transplant experiments was unaffected by the densities of other species. Hence, while some examples of competition in soft sediments have been demonstrated, there is no indication that it occupies the central role with which it has been credited on rocky shores.

Apart from competition, disturbance (including predation) is the force most often presumed to affect community structure in soft sediments (Brey 1991). For example Wilson (1989) found that predation mediated intraspecific competition between adult and juvenile amphipods (*Corophium volutator*), and that abundance of *C. volutator* decreased in the absence of predators, due to reduced juvenile survival.

A feature of soft sediments is that any epibenthic predator feeding on the infauna is almost bound to cause a significant disturbance to the substrate. The two effects are therefore often difficult to distinguish, and most studies treat them as one (e.g. Oliver et al. 1985, Thrush 1986, Hall et al. 1990a, Thrush et al. 1991, Webb & Parsons 1991). Predation can be an important organising force of soft-sediment communities (Bell 1980), but unlike the situation on rocky shores, its main effect is not in mediating interspecific competition (Dayton 1984). Nevertheless, it is apparent that both physical and biologically-caused disturbances are integral to the organisation of marine soft bottom communities (Reidenauer & Thistle 1981). The scale of disturbances may range from the microscopic (e.g. Reidenauer 1989) to the catastrophic, and disturbances affect fauna from bacteria (Grossman & Reichardt 1991) to large, mobile animals. Effects attributed to disturbance range from local changes in abundance of fauna (e.g. Branch & Pringle 1987) to large-scale evolutionary trends (Thayer 1979, Sousa 1984).

The mechanisms by which disturbances act on marine communities is uncertain, but may include the freeing of space for larval recruitment, reduction of competition, or alteration of resources to allow colonisation by opportunist species (Thistle 1981). Hydrodynamically-caused disturbances are the main source of large-scale physical disturbance, while biologically-induced disturbances are generally important on smaller scales (Probert 1984, Brey 1991). Almost all studies of disturbance or predation effects on community structure use some form of exclosures to exclude a particular predator or group of predators, or to manipulate the densities of predators or competitors. Quammen (1981) refined this method, using cages with floating sides to separate predation effects of fish and birds. Exceptions to the above method are those studies which monitor recovery after natural biotic disturbances. (e.g. Oliver et al. 1985). While the former method has been used successfully on rocky shores, the compostition of soft sediments may be altered by physical structures making the results of such experiments more difficult to interpret on soft substrates.

One problem is that unlike the situation on rocky shores, non-destructive sampling of soft sediment fauna is almost impossible, and sampling disturbance is always a factor. Structures on the sediment surface, such as exclosures, are likely to trap drifting algae and to attract fauna in much the same way as a reef would. Trapped algae may decay, causing anoxic conditions inside exclosures (Arntz 1977). The presence of structures is less of a problem on the more heterogeneous topography of rocky substrates. Currents within cages are likely to differ from those outside, and this may lead to either sedimentation or scouring (Virnstein 1978), modifying the potential settling of planktonic larvae. Predators entering the cage as larvae or juveniles may confound the results of the experiment. Finally, it may be difficult to prevent predators from gaining access because they may burrow under the edge of a cage. Baird et al. (1985) have criticised caging manipulations on the additional grounds that emigraton from exclosures may occur to avoid intraspecific competition as densities within exclosures increase. Further, growth of animals over the duration of the experiment may mean that some individuals which were not retained in sieves at the beginning of the experiment may be retained toward the end. Either of these occurrences would lead to the underestimation of losses to predation. As a result, Baird et al (1985) argue that direct measurement of consumption by predators, or estimation of their daily energy requirements are more accurate means of estimating predation impacts on benthic communities. In contrast, Hall et al. (1990b) point out that energy flow in a predator-prey interaction may bear little on the functional importance of that relationship to the community, and that in the absence of predation, similar mortalities may be caused by other density dependent effects. They conclude that energetics studies may be of little value in estimating predator effects, and that field experiments are the least equivocal way of measuring such effects. Finally, it is difficult to see how energetics studies could account for losses due to disturbance of the sediment, independent of actual prey removal.

Thus despite potential problems, caging manipulations remain the most viable method for studying soft sediment communities, and with the prudent use of controls, it is generally possible to make useful interpretations of the data.

Several workers have studied the effects of shorebird predation or disturbance on the benthic communities of soft sediments. Among these, results differ considerably. Reise (1978) and Raffaelli & Milne (1987) found that large epibenhic predators, including shorebirds have little effect on prey abundance compared to the effects smaller invertebrate predators. Similarly, Kalejta (1991) investigated the effect of waders on two species of nereid worm. Although observations suggested that waders were removing up to 36% of *Ceratonereis keiskama* per month from control areas, exclusion experiments failed to detect significant treatment effects. This failure was attributed to biological interactions within cages. However, Hall et al. (1990b) showed that experiments may not have the power to show effects of similar magnitude, and Kalejta (1991) did not show tests for the power of the experiments conducted.

In contrast, Bengtson (1976) showed that shorebirds considerably reduced densities of prey species. Quammen (1981, 1984) found that shorebirds could affect abundances of invertebrate fauna in muddy substrates, although the effect was seasonal because shorebirds generally migrate annually.

An exception to this generality is the Greater Flamingo *Phoenicopteris ruber*. Flamingos occur in high densities, and are often resident in one area all year round. Their large size relative to most shorebirds implies proportionately greater impacts on prey species, and because of their ability to feed in water of considerable depth, they are potentially the only waders which may substantially affect subtidal as well as intertidal benthic communities. Greater Flamingos filter-feed on small invertebrates in shallow water, either by sweeping their beaks in an arc as they walk, or more commonly by using a circular jogging motion to suspend sediment while remaining in one spot ("walk feeding" and "stamp feeding" respectively, in the terminology of Bildstein et al. 1991). When the latter method of feeding is employed, large circular depressions (approx. 1m diameter) are left in the sediment. In areas where high numbers of flamingos occur, the entire topography of large areas of the sediment can be altered (Plate 1). Resident flocks of flamingos can continually disrupt the sediment by their feeding. Given the frequency and intensity of disturbance, it is logical to postulate that the disturbance/predation effects of these birds may be considerable, and may overshadow other biological interactions in areas of high flamingo density. It is therefore surprising that I could find no report of previous investigations of the effects of *P. ruber* on marine benthic communities, although Hurlbert & Chang (1983) did investigate the grazing effect of *Phoenicoparrus andinus* on the microbenthos of a lake.

At two lagoons on the coastline of Namibia, Walvis Bay and Sandwich Harbour (Fig 1), flocks of Greater (*P. ruber*) and Lesser (*P. minor*) Flamingos are resident, leaving only at irregular intervals to breed inland. When this occurs, they are absent from approximately January to April, after which they return with their young. At both sites, the birds feed subtidally and in unvegetated intertidal areas. Where the flamingos feed, their trade-mark 'wheelies' are a prominent and persistent feature of the mud-flats.

The two lagoons provided interesting comparative study sites for a number of reasons. They are close to each other, separated by no more than 50km. Neither lagoon has any significant freshwater inflow. Walvis Bay adjoins a

Plate 1: Depressions, caused by foraging of Greater Flamingos at Walvis Bay, cover large areas of the sediment.

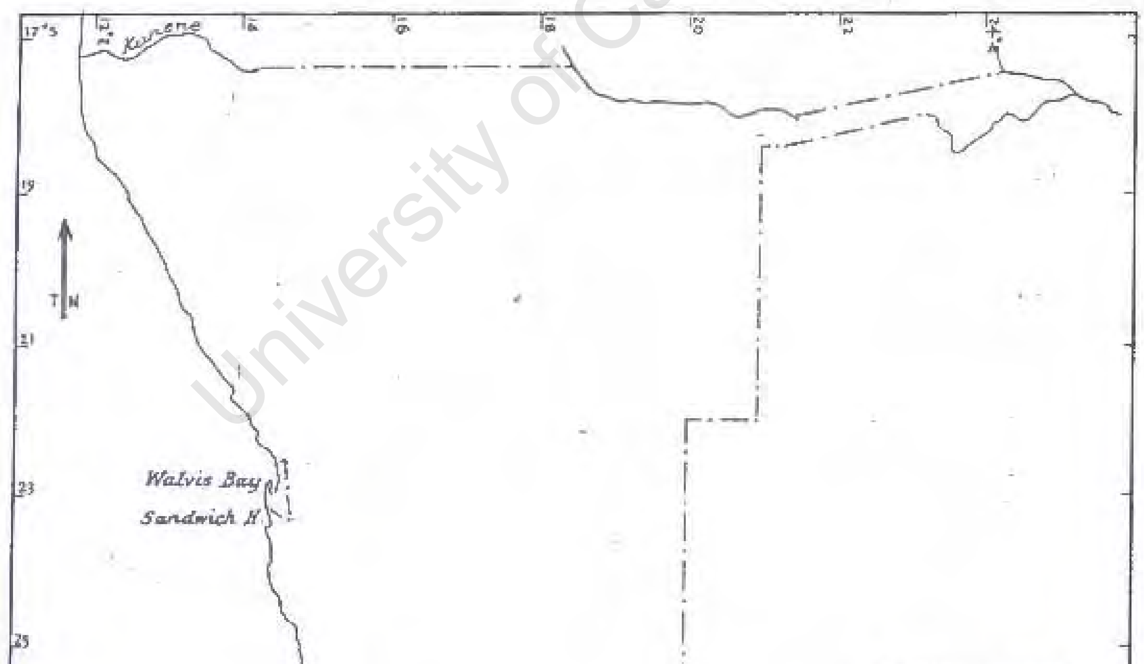

Fig. 1: Map showing the position of the study sites on the Namibian coastline. Inset shows Namibia (shaded) in perspective in southern Africa.

major harbour, and is surrounded by industrial salt pans. No vegetation occurs in the area of the lagoon. The lagoon is also a tourist attraction, and visitors, residents and trucks from the saltworks provide an almost constant stream of traffic around the lagoon. Despite this, Walvis Bay remains one of the premier sites for waders on the southern African coastline (Hockey & Bosman 1983).

Sandwich Harbour, although the site of a meat packing industry at the turn of the century, is now in almost pristine condition. It is a nature reserve, accessible to the public only on a daily walk-in basis. Only the narrow, northern end is easily accessible; the extensive mudflats of the southern end can be reached only by boat. The northern end of the lagoon is vegetated with reeds and spartina beds, but the channels of water flow are bordered by unvegetated mud, where the flamingos feed.

During the study undertaken, approximately 30 000 flamingos were resident at Walvis Bay, of which an estimated 12 000 were Greater Flamingos. In 1983, 32% of the South African coastal population of greater flamingos were resident at Walvis Bay (Hockey & Bosman 1983). At Sandwich Harbour, the number of flamingos varied during the study, but never exceeded 500 greater flamingos.

The present study was designed to quantify the disturbance/predation effects of Greater Flamingos on the benthic communities of these two lagoons, using caging manipulations. Unlike most other studies, which have investigated disturbance effects on a particular species or faunal level or on a particular interaction, I attempted to quantify the effects of flamingo exclusion on all the major biotic constituents of the community (bacteria, benthic diatoms, meiofauna and macrofauna). Since the two lagoons had differing numbers of flamingos, it was hoped that insight would also be gained regarding the effect of predator density on community structure. At Walvis Bay the effects of flamingos were investigated subtidally and intertidally, but at Sandwich Harbour caging manipulations were confined to the intertidal zone.

While the proximity of the two lagoons allowed easy comparison, the differences between them gave rise to interesting questions. It was expected that

Sandwich Harbour would have higher densities of organisms and greater species richness, in part because it is less disturbed or polluted by human activity, but also because the vegetation provides greater heterogeneity to the benthic habitat.

METHODS

Three sets of four exclosures each were erected. At Walvis Bay, one set of cages was established intertidally and one subtidally. At Sandwich Harbour, only intertidal cages were built.

Each exclosure measured 3,5 X 3,5m, and consisted of eight upright stakes, with two strands of rope stretched tautly between them. Due to the size of the predator being excluded, mesh was unnecessary, avoiding most problems normally encountered in caging manipulations, such as shading, interference with water flow, entrapment of floating debris and attraction of other fauna to a solid structure. The design excluded only flamingos, while allowing access to smaller animals such as waders and fish. While Lesser Flamingos were also inevitably excluded, they are water-column feeders (Jenkin 1957), eat mostly algae (Brown 1959) and cause little disturbance to the sediment. It was therefore deemed unlikely that their exclusion would have a major effect on the results of the experiment. The poles of the cages were hammered into the sediment to a depth of 40cm and stood 140cm proud of the surface. Flat plastic discs with holes in the centre were placed over each pole and pressed firmly into the sediment, helping to prevent erosion from around the poles. In order to minimize the possibility of bias due to edge effects or to nutrient enrichment due to guano from birds perching on the cages, a margin of 0.5m was left unsampled around the inside edge of the exclosures. On each occasion, samples were taken from a different position within the cages. Care was taken to avoid sampling areas that might have been disturbed by trampling during previous sampling.

There were four replicate control areas for each set of cages. Control areas were unmarked, but alternated with cages and were positioned at the same tidal level. This method of choosing control areas was used because it was felt that interspersion of treatments was more important than their random assignment for this type of experiment. The three sub-samples for each control plot were randomly taken within an area approximating that of the cages. No effort was made to specifically avoid or sample humps or pits in disturbed areas, and any preference of fauna for these microhabitats should not therefore have biased the results.

No separate structures were erected to control for cage effects (i.e. cage controls). Rather, half the cages were partially dismantled at each site on the penultimate sampling date, resampled on the last date and the data compared with both full cages and controls. Intertidally at Walvis Bay, the remaining cages disappeared between these two dates. This meant that no data were obtained for cage controls for this site.

The first set of cages was erected intertidally at Walvis Bay in April 1989. Samples were taken immediately after the cages were erected, one week later and two weeks after that, when the subtidal cages were established. Further samples were taken in July 1989, then at three-monthly intervals until the experiment was terminated in July 1990. The subtidal exclosures were erected in May 1989, coinciding with the third set of intertidal samples collected, and subsequent samples were taken at the same times as intertidally. Sandwich Harbour is a nature reserve. and the caging manipulations at Sandwich Harbour could only be initiated in October 1989 when a permit was issued.

Three subsamples were collected at each sampling date for each cage and each control. For analysis of sediment properties, subsamples were pooled. For all other samples, subsamples were analysed separately

SEDIMENT

1. Organic content of sediment

Sediment was sampled to a depth of 20cm using a core of diameter 21mm. Since no adequate facilities for freezing samples were available, they were either fixed with formalin or sun dried until they could be frozen. Organic content of the sediment was determined by placing oven dried, pre-weighed samples in a muffle furnace at 450°C for four hours to burn off all organic matter, and reweighing them. Organic content, calculated by subtracting the latter weight from the former,is expressed as $mg.g^{-1}$ sediment.

2. Sediment Particle Size.

Dry sediment samples were sifted through nested sieves of mesh sizes 710μm, 500μm, 300μm, 150μm, 106μm and 63μm. The weight of each fraction was calculated as a percentage of the total mass. Sieve mesh sizes were converted to ϕ units for presentation and analysis.

3. Chemical properties.

In January 1989, pH and redox potential were measured in the field using a portable crison pH meter

MICROALGAL STANDING STOCKS

Approximately 1g sediment was collected from the sediment surface, wrapped in aluminium foil and frozen until processed. Samples were weighed and placed into stainless steel tubes with a pinch of $MgCO_3$ and 10ml acetone, ground for three minutes and stored in the dark at 4°C for 48hrs. They were then centrifuged, and the supernatant extracted. Total chlorophyll was determined by reading optical densities at 750, 664, 647 and 630nm. After subtracting the reading obtained for 750nm from each of the others, to correct for turbidity, chlorophyll concentrations, (μg chlorophyll.g^{-1} sediment) were calculated using the formula from Branch and Pringle (1987):

$$\mu g\ chlorophyll = 21.78(OD_{630}) + 11.89(OD_{647}) + 4.75(OD_{664})$$

BACTERIA

5ml samples were taken from the sediment surface using a cylindrical corer and fixed in 4% formalin in 0.2μ filtered seawater. All samples were stored in the dark at 4°C until counted.

Bacterial numbers were determined by direct count under flourescent microscopy after being stained with DAPI. Bacteria were separated from sediment particles by addition of tetrasodiumpyrophosphate followed by sonication for 5 minutes (Velji & Albright 1986). Samples were then stained with DAPI at 5μg.ml^{-1} and incubated in the dark for twenty minutes; 2ml samples were then filtered at 178mm Hg onto 0.2μ nucleopore filters that had been pre-stained with irgalan black. One ml of a detergent (photo-flow) was filtered prior to the sample, to ensure even distribution of bacteria on the filter. At least 20 fields or 400 bacteria were counted for each sample. Due to logistical constraints, bacterial samples were counted only for the beginning and end of the experiment at each site.

MEIOFAUNA

All meiofaunal samples were taken with a core of area $6.3cm^2$. Samples were fixed in 7% formalin in filtered seawater. Meiofauna were extracted by washing the sample at least four times through a 63μ sieve. This method attained an extraction rate of approximately 90% (pers. obs.), but may exclude hard bodied meiofauna such as bivalves (Wynberg 1991). Extracted meiofauna were stained with Rose Bengal, identified to the level of major groups, and counted.

MACROFAUNA

Intertidal samples were taken by marking an area of $0.1m^2$, removing the sediment to a depth of 20cm and sieving it through 1mm mesh. Small, separate core samples (35mm diameter) were taken to count the polychaete *Capitella capitata*, since it was difficult to remove from the mesh. Subtidally, a core of 13cm diameter was used for all macrofauna. Animals were either sorted by hand, or were `floated' out. The latter method is less desirable, as it may underestimate bivalves, but was necessary when large numbers of amphipod tubes made hand-sorting impractical.

Macrofauna were identified to species level where possible and counted. Because doubt existed regarding the efficacy of the above methods for sampling the large polychaete *Diopatra neapolitana*, counts were made of their tubes before sampling and compared with actual numbers of worms collected.

STATISTICS

All statistics except the Shannon-Wiener indices were done using the PC version of SAS. Following Underwood (1981), it was decided to nest data rather than pooling subsamples as recommended by Hurlbert (1984). Samples for sediment particle size were an exception. All tests for treatment effects were done using nested anovas in the generalised linear modelling (GLM) procedure, which is designed to handle unbalanced data sets. Since most of the data deviated from normality, data were ranked before doing the anova, giving the equivalent of a Kruskal-Wallis test. Where relevant, Contrast was used in preference to multiple comparison tests. This allows specific hypotheses to be tested, and can be performed on nested data.

All error bars on the figures represent the calculated standard error of the data. At Walvis Bay intertidal the term 'initial' on the graphs indicates samples that were taken immediately after erection of the exclosures.

Shannon-Wiener diversity indices were calculated for macrofauna at all sites, and compared between treatments and controls using appropriate t-tests (Zar 1984).

RESULTS

Changes to the sediment were visible within three months of initiating the experiments. Intertidally, the sediment inside exclosures became smooth and uniformly tan. There was no sign of flamingo feeding, but wader tracks were common. Outside exclosures, perturbations caused by flamingos were still clearly visible (Plate 2). Subtidally at Walvis Bay, the sediment inside caged areas became dominated by dense tube mats, built mainly by ampeliscid amphipods. Tubes of the polychaete *Capitella capitata* were also present. In two of the cages, these mats were so dense that the sediment surface was raised above the water surface at low tides (Plates 3 & 4).

Direct observation using snorkeling gear at high tide confirmed that fish were feeding within exclosures. The exclosures were thus successful in excluding flamingos while allowing access to other species.

PHYSICAL CHARACTERISTICS OF SEDIMENTS

Particle size analyses showed little difference between treatments at any site (Fig. 2). All three sites had median particle sizes of between 1-1.5Φ for treatments and controls. QdΦ and SkqΦ were also similar between treatments and controls (Table 1).

Table 1: Median particle size (MDΦ), phi quartile deviation (QDΦ) and phi quartile skewness (SkqΦ) for all sites. EXCL = exclusion, CON = control. INTER. = intertidal, SUB. = subtidal.

	MDΦ		QDΦ		SkqΦ	
	EXCL	CON	EXCL	CON	EXCL	CON
W. BAY INTER.	1.25	1.40	0.30	0.30	-0.15	0
W. BAY SUB.	1.40	1.40	0.30	0.30	-0.10	-0.10
S. HARB. INTER.	1.50	1.30	0.68	0.50	0.03	-0.05

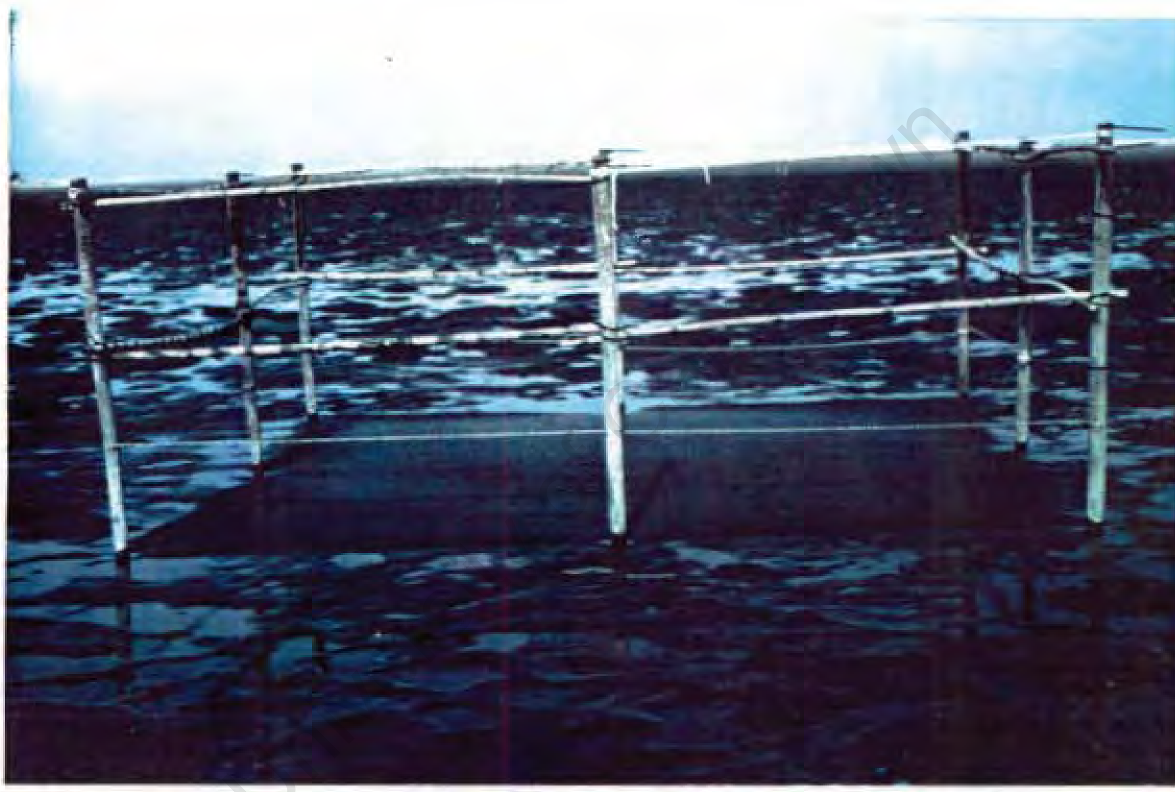

Plate 2: Intertidal exclosure at Walvis bay, showing the undisturbed sediment within.

Plate 3: Subtidal exclosure at Walvis Bay with the amphipod-tube mat protruding above the surface.

Plate 4: Section of a sub-tidal core-sample, showing the density and height of the tubes.

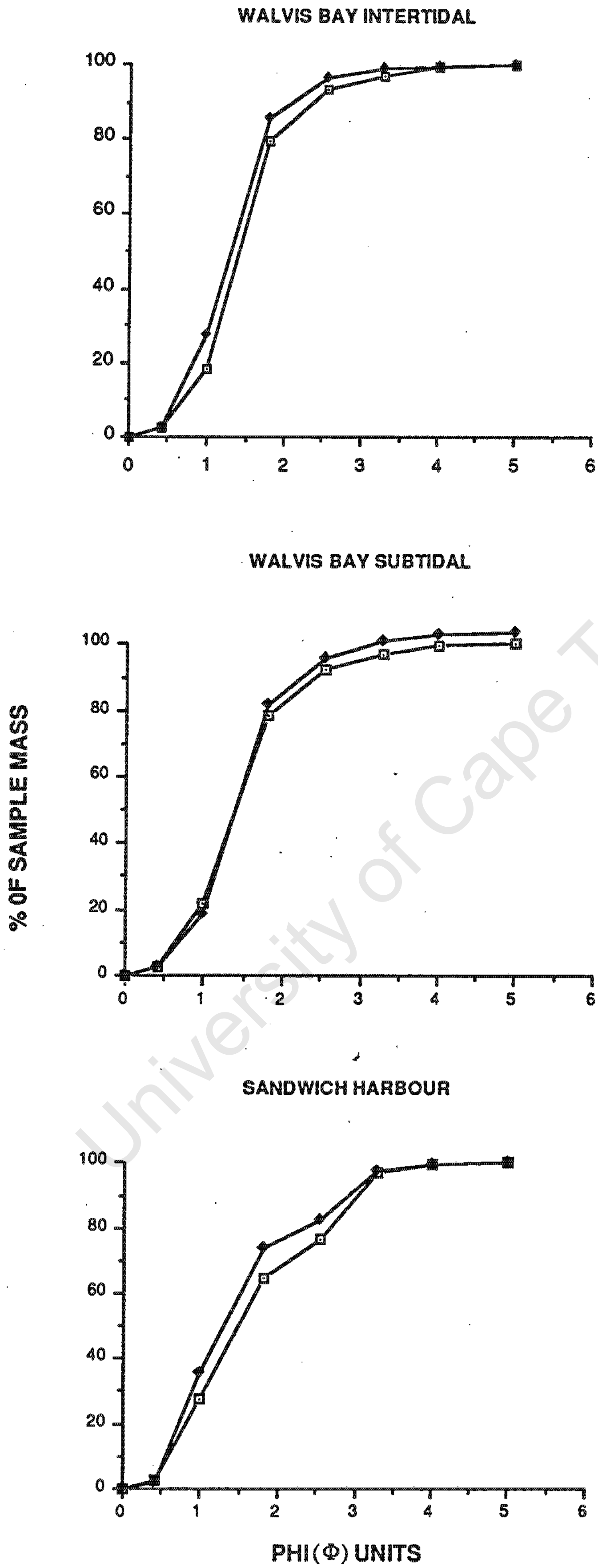

FIG. 2: Mean sediment particle size, expressed as a cumulative percentage of sample mass. —□— = exclusion —◆— = control.

Organic content of the sediments (Fig. 3) showed differences between treatments at all three sites, with both intertidal areas being significantly different from controls at the 0,05 level. Subtidally at Walvis bay, the difference was less pronounced, but still significant at the 0.1 level. Exclusion plots had lower organic content than the controls at Walvis Bay intertidal, but the reverse occurred at the other two sites.

Redox potential and pH differences between treatments and controls (Fig. 3) were largely overshadowed by gradients in sample number regardless of treatment. This is always a risk when placing experimental plots in a straight line, but was an inevitable consequence of needing to place the exclosures at similar tidal levels. Nevertheless, pH showed significant treatment effects subtidally at Walvis Bay (W Bay S), while redox potential, indicative of oxygen content of the sediment differed between caged and control areas intertidally at Walvis Bay (W. Bay I) ($P<0.1$) and at Sandwich Harbour (S. Harb.) ($P<0.1$). As with the organic content, the subtidal site showed least difference. At all three sites, the redox potential was negative, indicating hypoxic or anoxic sediments.

MICROALGAL STANDING STOCKS

Chlorophyll concentrations (Fig. 4) were significantly different between treatments and controls at both Walvis Bay sites ($P<0.05$), but not at Sandwich Harbour, which also had the least temporal variation in chlorophyll concentration. At Walvis Bay subtidal, the chlorophyll concentration increased consistently within exclosures, resulting in an apparently greater treatment effect at each successive sampling date. This did not occur at either intertidal site. Concentrations in the cage controls for July 1990 were lower at both sites than in either caged or control areas, but were always closer to concentrations in control areas than in cages.

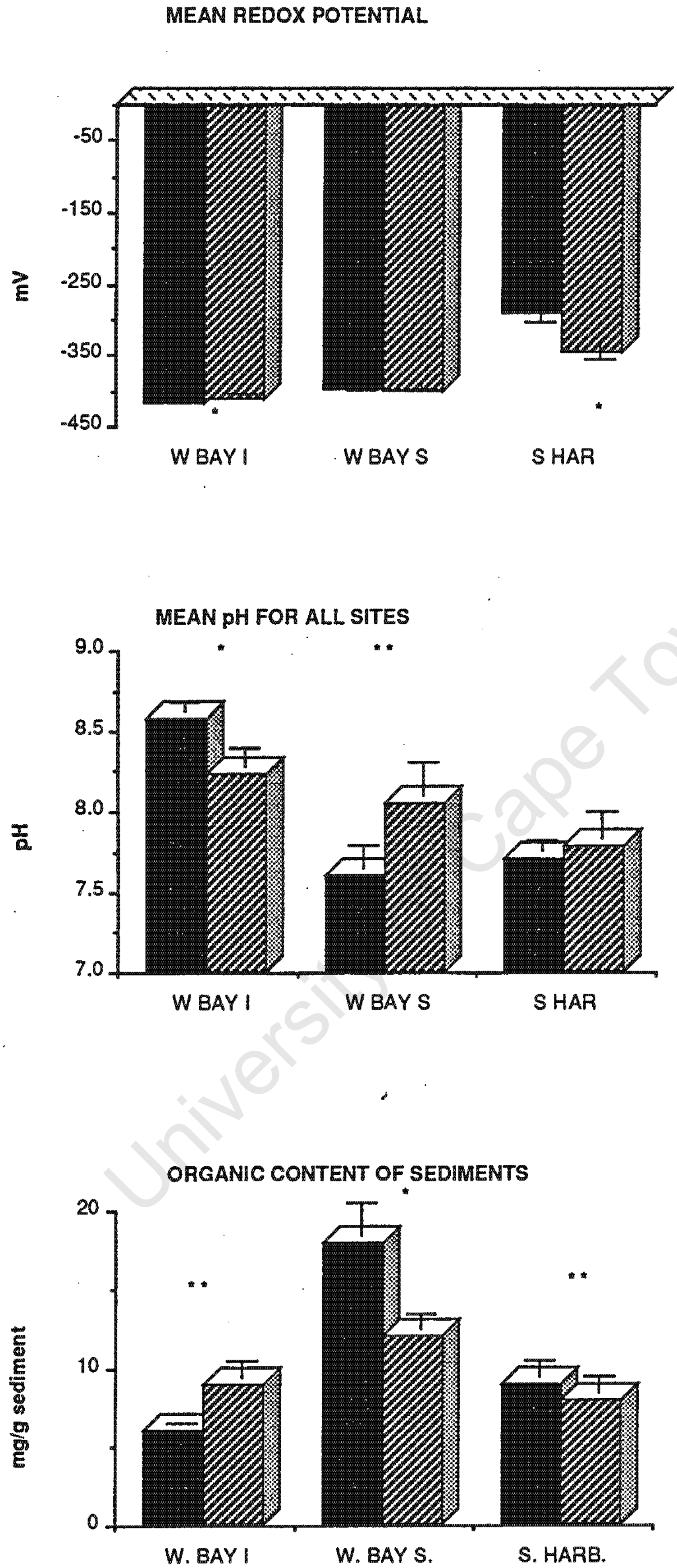

Fig. 3: Physical properties of sediments. W Bay I = Walvis Bay intertidal, W Bay S = Walvis Bay subtidal and S Harb = Sandwich Harbour intertidal. ■ = exclusion, ▨= control. *, ** indicate significance at 0.1 and 0.05 levels respectively.

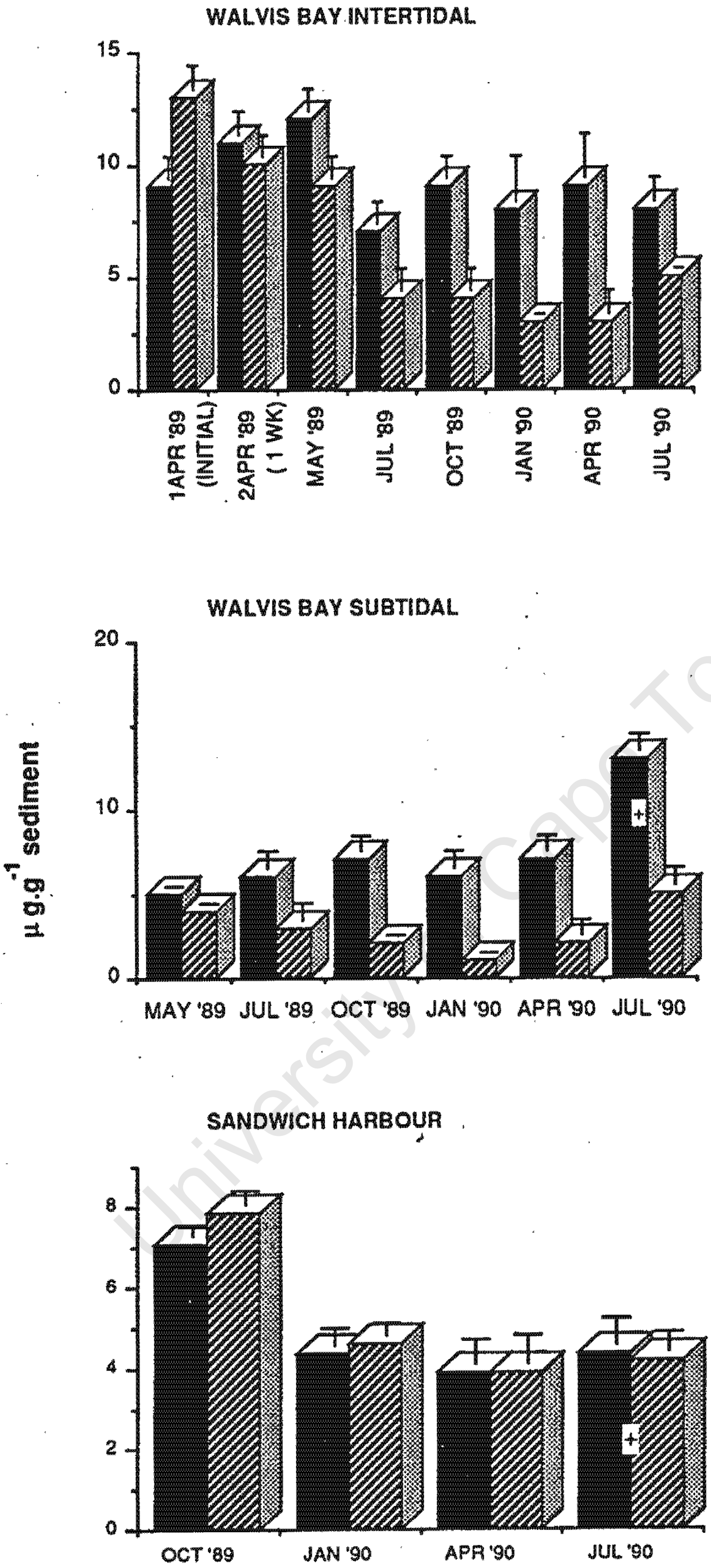

Fig. 4: Chlorophyll concentrations ($\mu g.g^{-1}$ sediment)
■ = exclusion, ▨ = control, + = cage control.

BACTERIA

Bacterial numbers (Fig. 5) were compared at the beginning and end of the experiment at each site. By the end of the study, numbers of bacteria in control areas were substantially higher than in exclusion areas at all sites. Only at Sandwich Harbour, however, was the difference statistically significant ($P < 0.05$). Bacterial counts compared favourably with estimates by Tibbles (1991) for Walvis Bay.

MEIOFAUNA

Table 2 summarises mean meiofaunal numbers, and the effects of date and treatment. Meiofauna at Walvis Bay intertidal showed the least response to caging, with only ostracods showing significant treatment effects. By contrast, subtidally all groups were significantly affected by the treatment, as was the total meiofaunal density. At Sandwich Harbour, densities of foraminifera and ostracods were statistically different between treatments and controls. While the norm seemed to be increased density inside exclosures, copepods at Walvis Bay subtidal and foraminifera and ostracods at Sandwich Harbour were significantly lower in exclusion areas. Total meiofaunal density was higher inside the exclosures at all sites, although significantly so only at Walvis Bay subtidal.

As might be expected, time of year (date) significantly influenced densities of all bar two meiofaunal groups. However in most cases, this seemed to have little influence on treatment effects.

Figures 6-9 show results for meiofaunal groups at each sampling date. Nematodes at Walvis Bay intertidal (Fig. 6) showed an erratic response to flamingo exclusion with abundances inside exlosures ranging above and below those of control areas. In the subtidal zone at Walvis Bay, nematodes increased significantly inside the cages, but this response was largely contingent on the

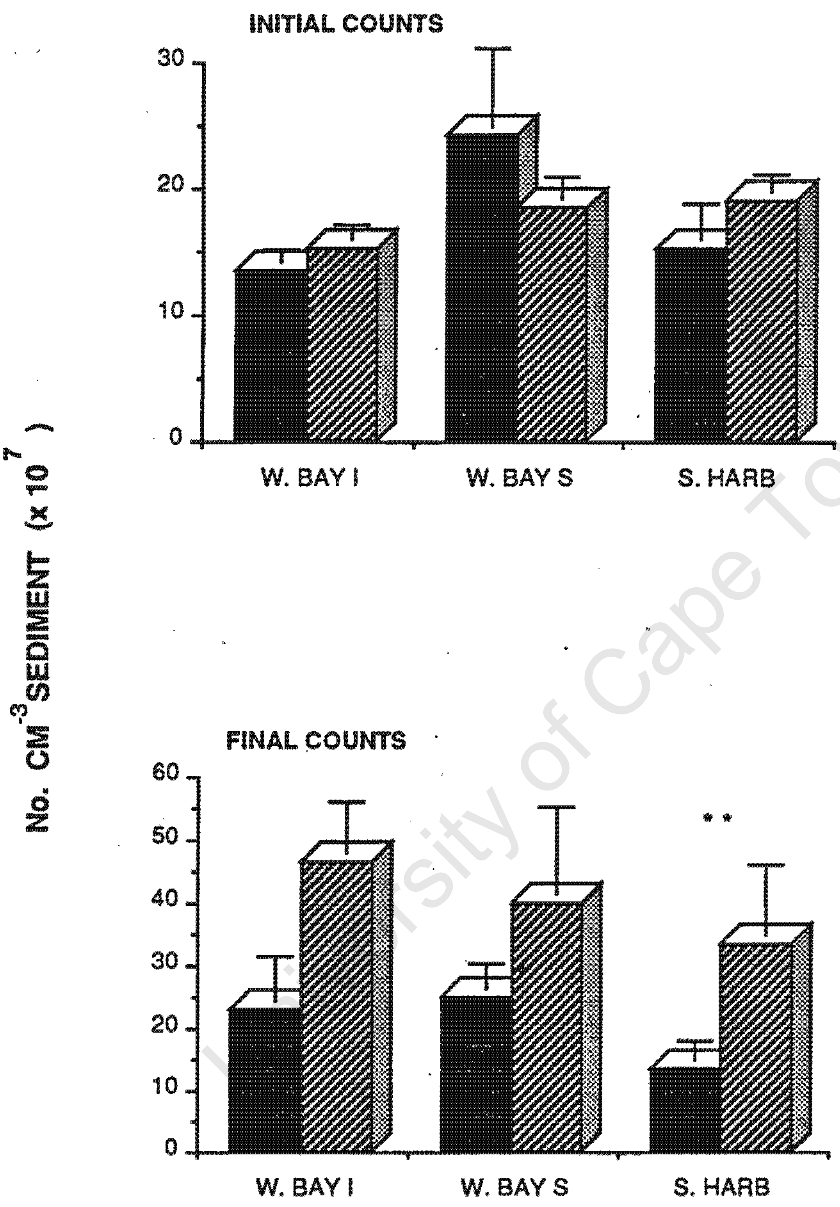

Fig. 5: Bacterial numbers at the beginning and end of the study. ■ = exclusion, ▨ = control. W Bay I = Walvis Bay intertidal, W Bay S = Walvis Bay subtidal, S Harb = Sandwich Harbour. ** indicates significance at 0.05 level.

Table 2: Mean meiofaunal numbers (cm^{-3} sediment) for the entire time of the experiment excluding the initial sampling date. EXCL=exclusion, CON=control. For the ranked anova, NS=not significant. *, ** and *** indicate significant differences at $P < 0.1$, 0.05 and 0.005 respectively. D and T are date and treatment differences. Underlining indicates a significant interaction term between date and treatment.

	WALVIS BAY INTERTIDAL				WALVIS BAY SUBTIDAL				SANDWICH HARBOUR			
	EXCL	CON	ANOVA D	ANOVA T	EXCL	CON	ANOVA D	ANOVA T	EXCL	CON	ANOVA D	ANOVA T
Nematodes	46.77	45.37	***	NS	18.87	15.20	***	**	19.65	18.15	**	NS
Foraminifera	0.65	0.50	**	NS	1.37	1.26	**	**	9.82	12.92	***	*
Copepods	10.09	10.94	***	NS	5.11	5.59	***	**	2.62	0.79	NS	NS
Ostracods	1.23	0.77	**	*	1.16	0.65	NS	*	12.38	15.79	***	**
Total meiofauna	58.54	56.82	***	NS	26.50	22.75	***	**	44.29	47.72	***	NS

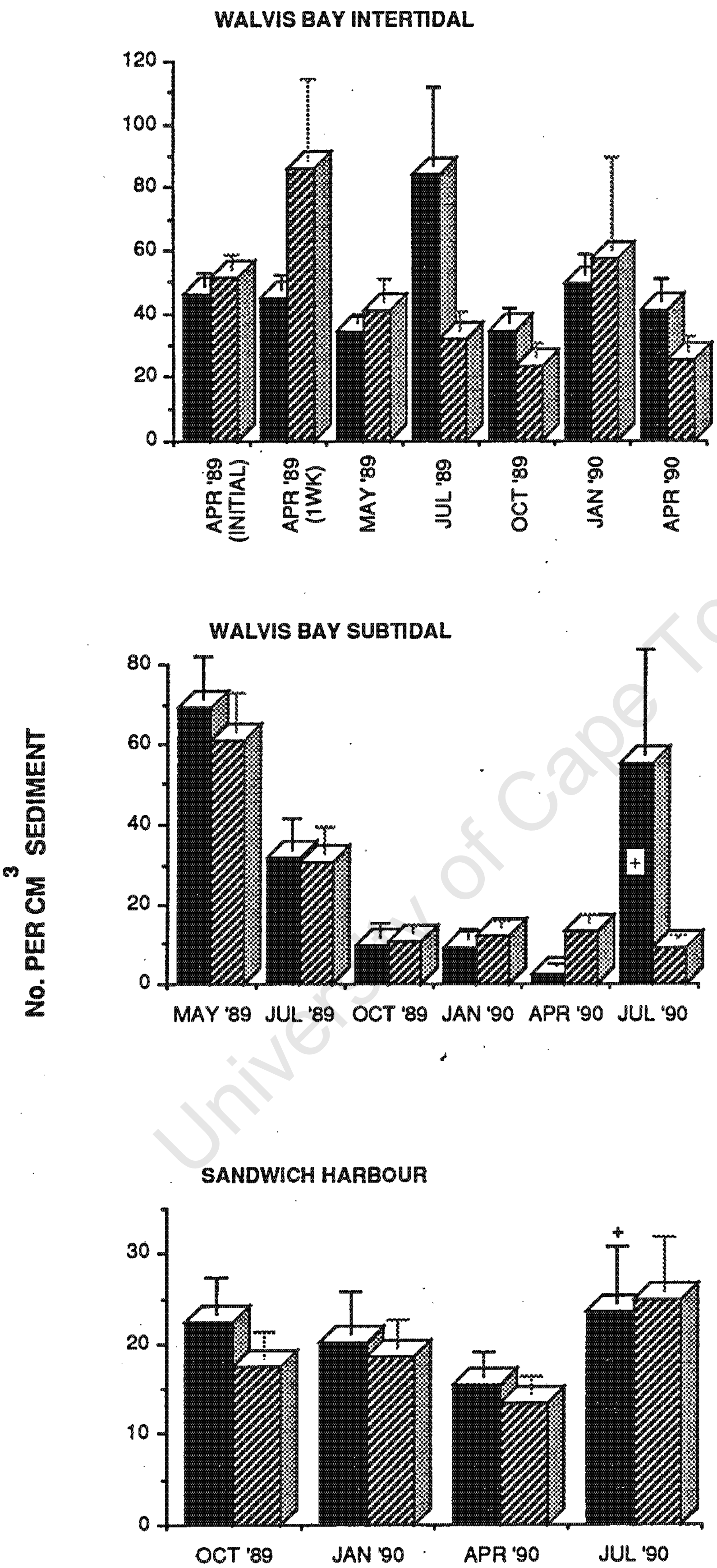

Fig. 6: Density of nematodes over time at each site.
■ = exclusion, ▨ = control, + = cage control

treatment effects on a single sampling date, July 1990. No clear pattern was apparent on other dates and it is doubtful that the statistical significance obtained is representative of an overall long term pattern. At Sandwich Harbour, nematodes were generally more abundant inside cages, but not significantly so.

Foraminiferans (Fig. 7) displayed a more consistent response at Walvis Bay Intertidal, being consistently more abundant inside cages, between May 1989 and April 1990 . At the subtidal site densities were higher inside the cages, but again, this response was only clearly evident on the last sampling date. No significant responses were recorded at Sandwich Harbour.

Copepods, (Fig. 8) displayed responses similar to those of foraminiferans at both Walvis Bay sites but were consistently, although not significantly, more common inside cages at Sandwich Harbour.

Ostracods (Fig. 9) were the only group to respond significantly to caging at all three sites, but this response was positive at the two Walvis Bay sites, and negative at Sandwich Harbour.

Patterns displayed by the total meiofauna (Fig. 10) closely followed those displayed by the nematodes. Densities were lower inside the cages at Sandwich Harbour, but higher at the other two sites. As was the case with all individual meiofaunal taxa, the significant increases recorded in cages at the Walvis Bay subtidal site could be attributed to the spectacular increases on the last sampling date.

Overall the responses of the meiofauna to flamingo exclusion were both site- and taxon-specific Of the eight significant responses recorded in Table 2, five showed increases and three decreases inside the cages.

Both Walvis Bay sites were largely nematode dominated (Fig. 11). At Sandwich Harbour, nematodes still constituted the largest group, but made up a considerably smaller proportion of the total. Ostracods contributed a surprisingly large proportion of the meiofauna at Sandwich Harbour. Copepods, the second largest group at Walvis Bay, comprised the smallest proportion of meiofauna at Sandwich Harbour. Further, the relative abundance of copepods decreased in the control at Sandwich Harbour, while marginally increasing at Walvis Bay. At Sandwich Harbour, the abundance of ostracods increased within

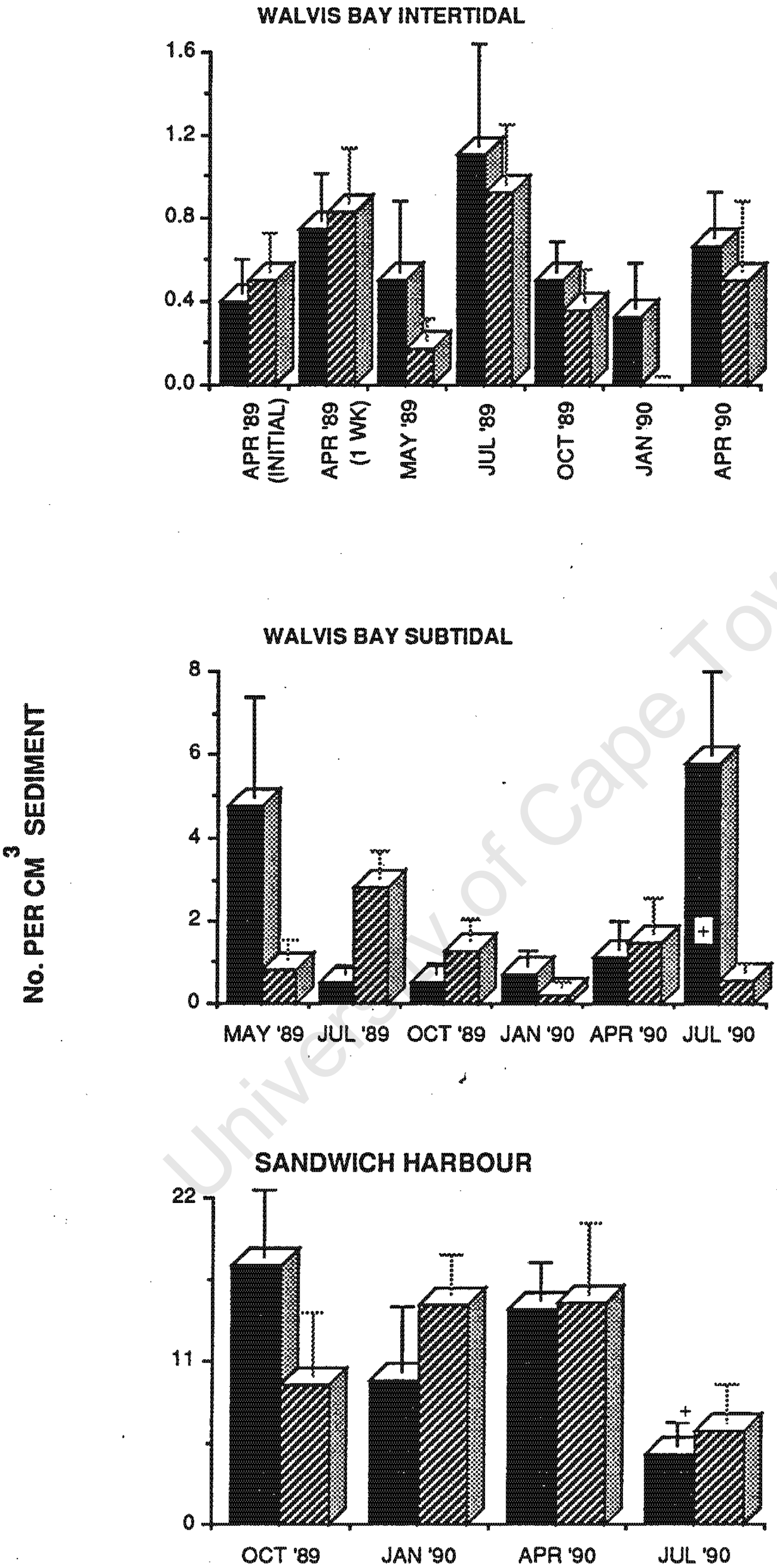

Fig. 7: Density of foraminifera over the time of the experiment.
■ = exclusion, ▨ = control, + = cage control.

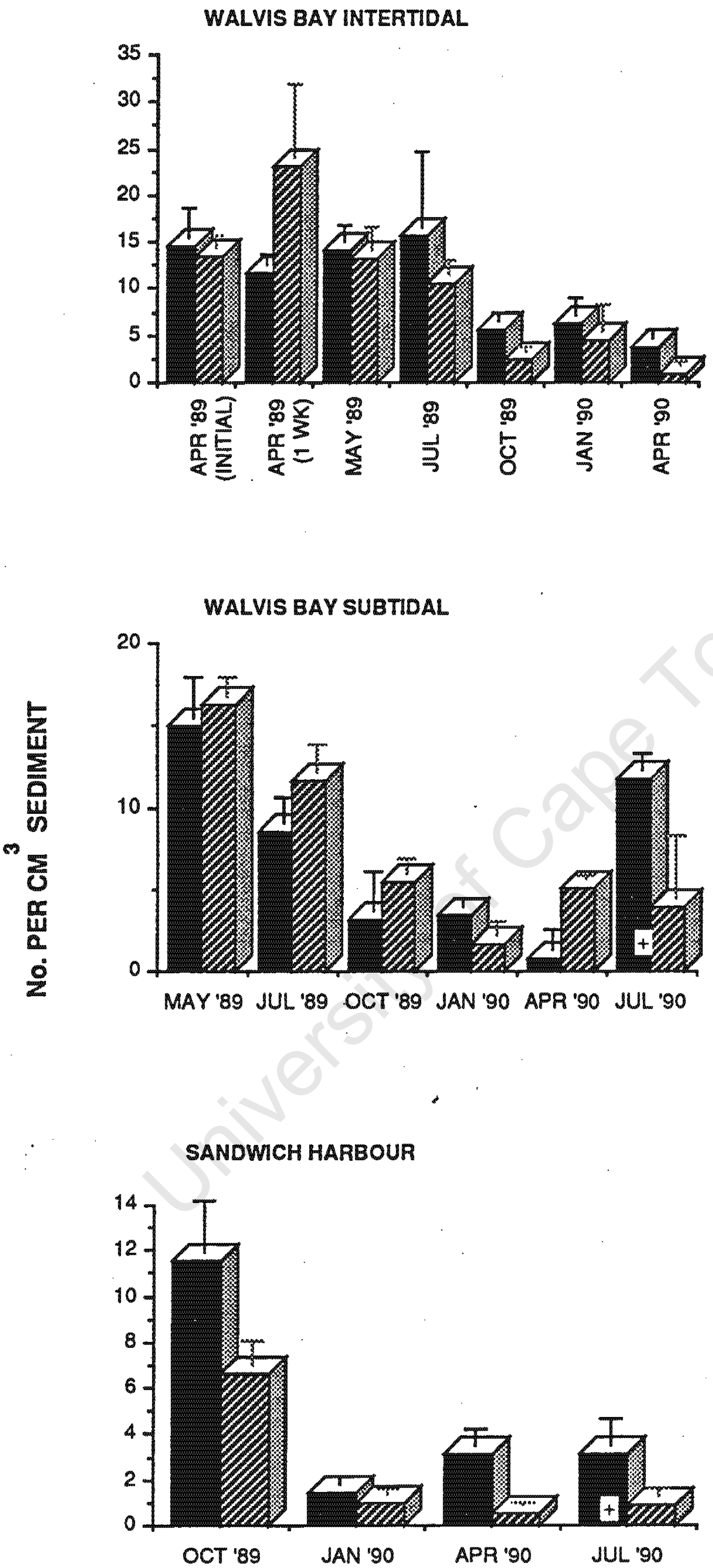

Fig. 8: Density of copepods, including nauplii over the time of the study. ■ = exclusion, ▨ = control, + = cage control.

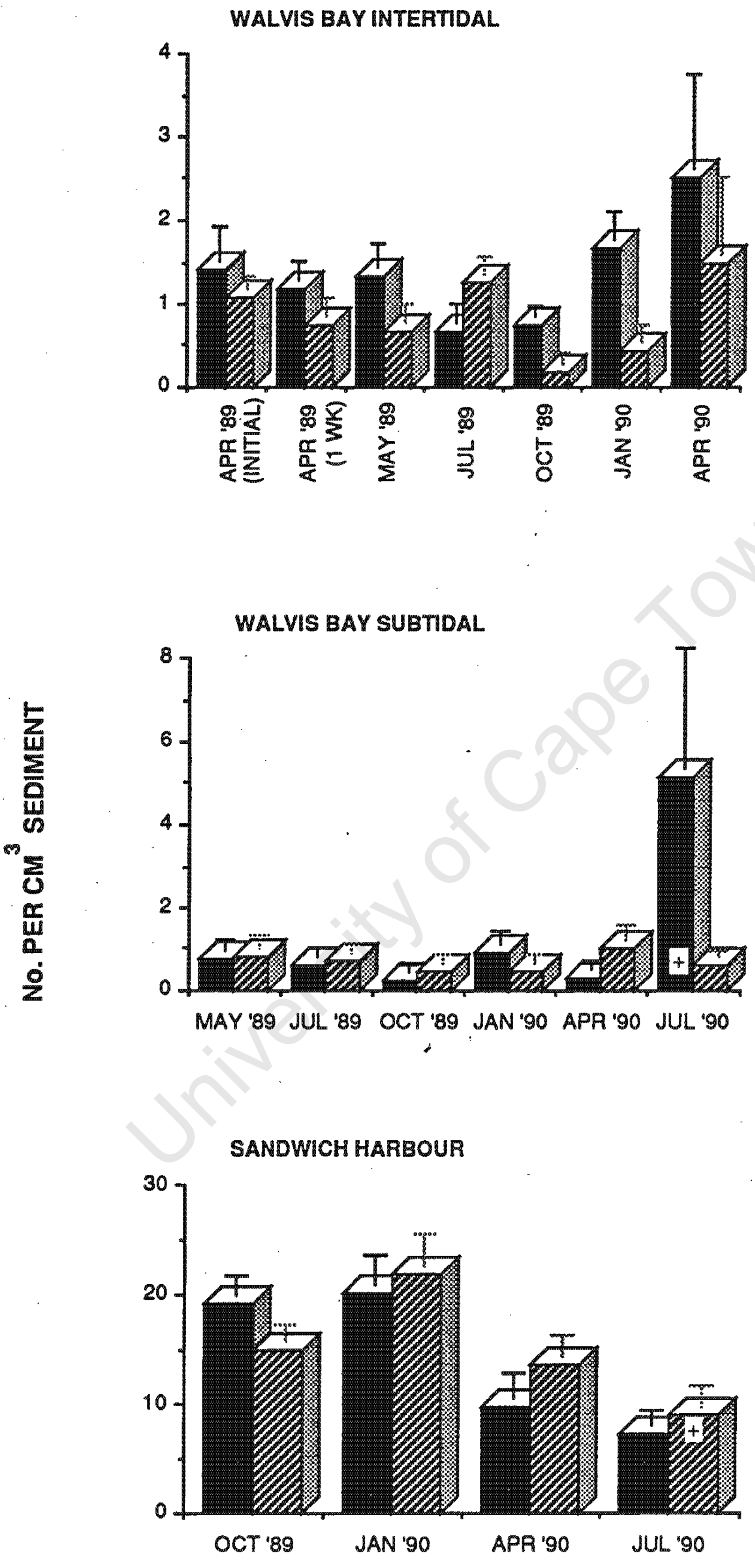

Fig. 9: Denstiy of ostracods over the time of the study.
■ = exclusion, ▨ = control, + = cage control.

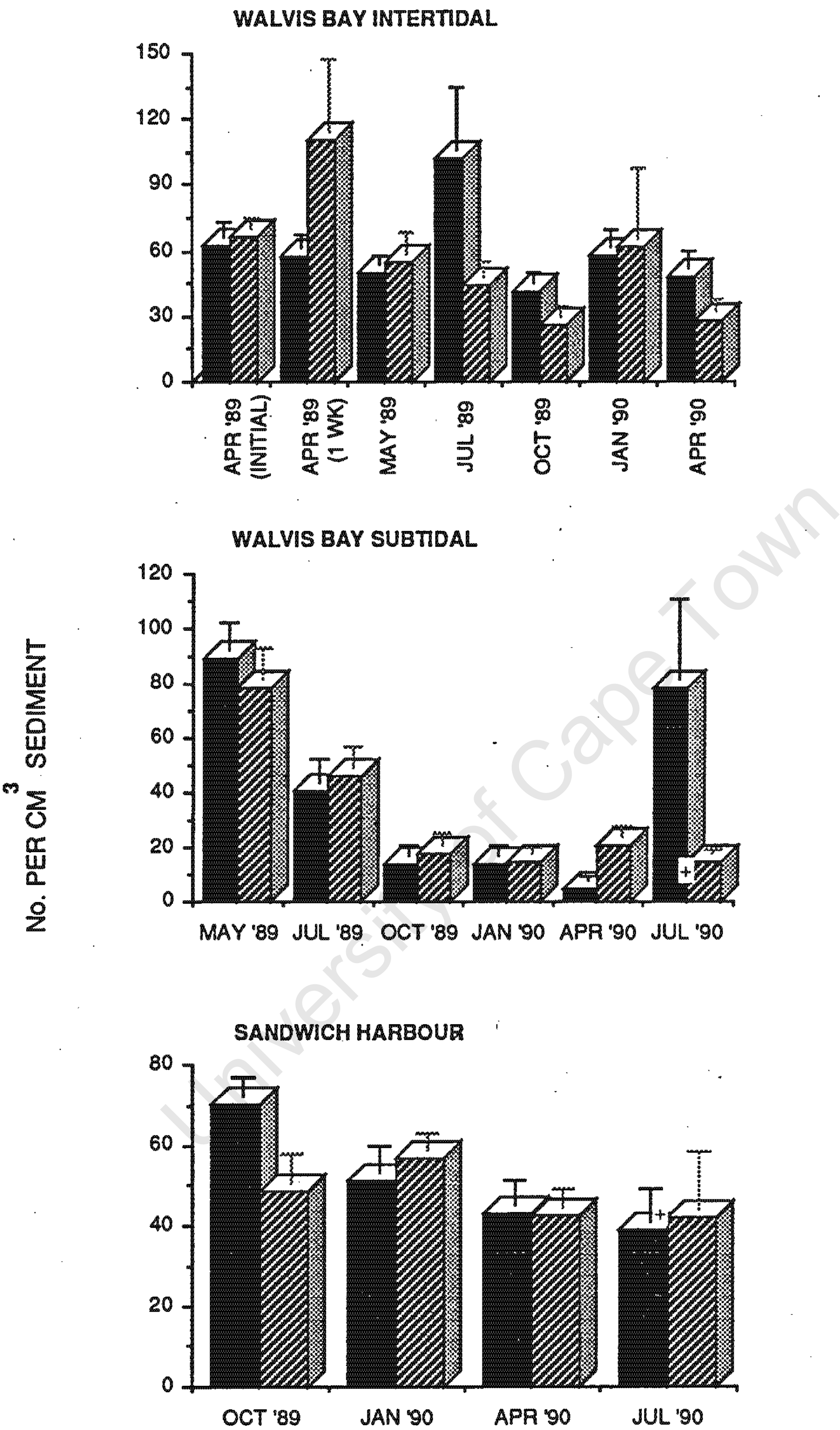

Fig. 10: Total meiofauna for the duration of the study.
■ = exclusion, ▨ = control, + = cage control.

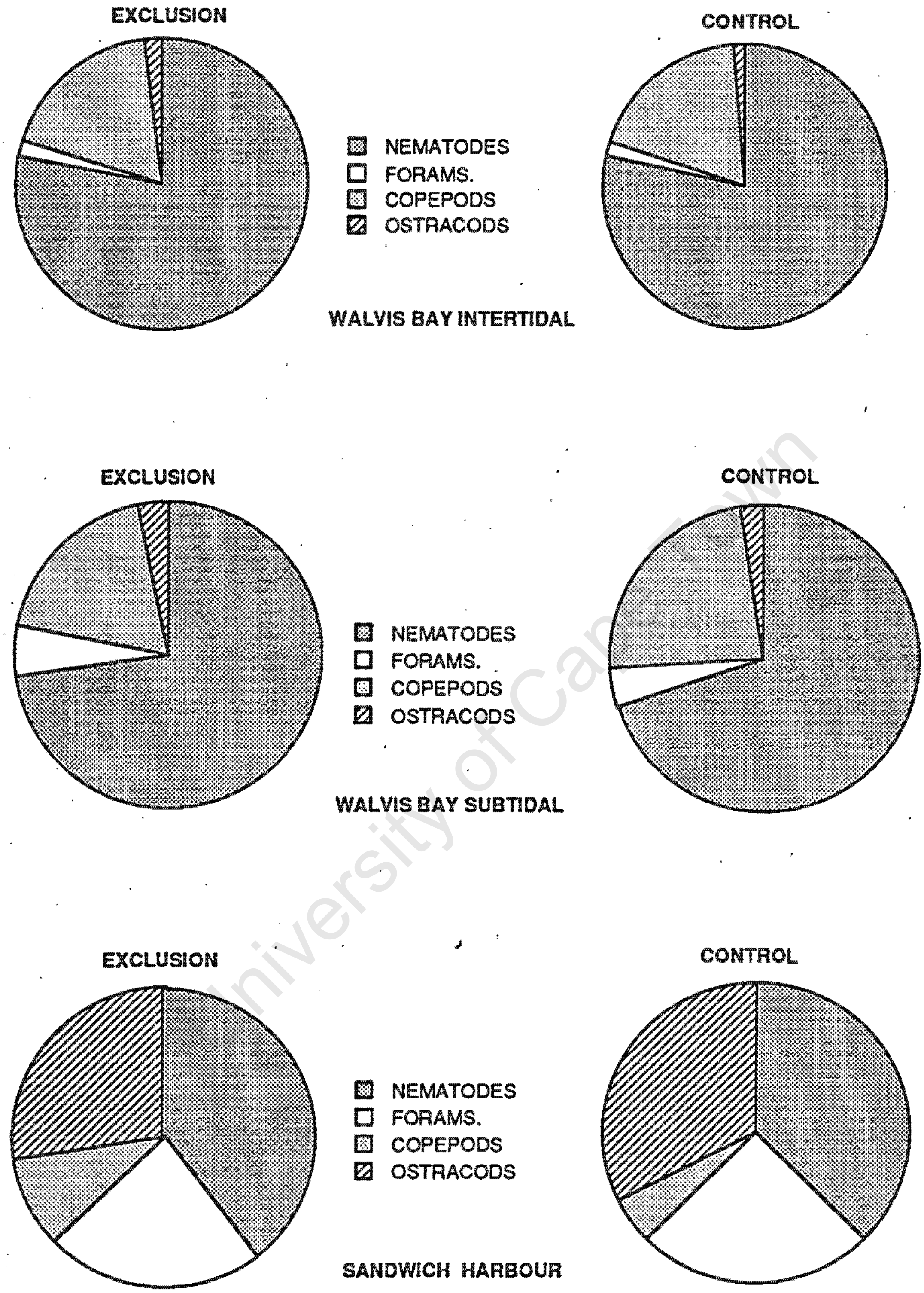

Fig. 11: Proportion of meiofaunal groups for each site and treatment for the duration of the experiment.

controls. Overall, however, changes in density seemed to have little effect on relative proportions of meiofaunal groups.

MACROFAUNA

Eighteen species were collected between the three sites. Of these, fifteen occur at Sandwich Harbour, thirteen at Walvis Bay subtidal and ten at Walvis Bay intertidal. With the exception of *Ampelisca brevicornis* at Sandwich Harbour, all macrofaunal species for which statistics were done were significantly affected by treatment, as was total macrofaunal density (Table 3). While most species increased in density within exclosures, some were negatively affected, notably both bivalves (*Dosinia lupinus* and an unidentified species) at Sandwich Harbour, and the polychaetes *Diopatra neapolitana* at Walvis Bay subtidal and *Prionospio sexoculata* at Walvis Bay intertidal. All other polychaete species increased in exclusion areas. The nemertean *Cerebratulus fuscus* decreased in density inside exclosures at Wavis Bay subtidal, but increased in them at Sandwich Harbour. All amphipods increased in exclosures relative to control areas except for *Lemboides* at Sandwich Harbour. Total macrofaunal density increased within exclosures at all sites.

Figures 12-24 show the results for individual species at each sampling date.

Capitella capitata (Fig. 12) was the most abundant polychaete at all sites. Its numbers were consistently higher in cages than in controls, and this difference tended to become more pronounced with time. *Prionospio sexoculata* (Fig. 13) and *Desdemona ornata* (Fig. 14) were common at Walvis Bay, but were replaced by *Boccardia polybranchia* (Fig. 15) at Sandwich Harbour. With the exception of *P. sexoculata* at Walvis Bay intertidal, all three increased abundances inside exclosures. As with *Capitella capitata*, the difference between caged and control areas increased over time for *B. polybranchia* and *D.ornata*. The large tube-building polychaete, *Diopatra neapolitana* (Fig. 16) occurred at all sites, but was abundant only subtidally, where caging had a consistently negative effect on its abundance.

Table 3: Species list of macrofauna for all three sites. Means (no.m^{-2}) are for the entire time of the experiment. Anovas of ranked data were done for date and treatment effects for all species with mean.s > 1 animal.m^{-2}. A=species absent from site. NS= not significant. * indicates $p<0.1$, ** indicates $p<0.05$ and *** indicates $p<0.005$. D and T indicate effects of date and treatment respectively. Underlining denotes a significant interaction between date and treatment.

	WALVIS BAY INTERTIDAL			WALVIS BAY SUBTIDAL			SANDWICH HARBOUR		
	EXCL	CON	ANOVA D T	EXCL	CON	ANOVA D T	EXCL	CON	ANOVA D T
POLYCHAETA									
Prionospio sexoculata	28	30	*** ***	884	217	*** ***	A	A	-- --
Capitella capitata	2206	1426	*** *	11013	4137	*** ***	1320	807	*** **
Desdemona ornata	11	3	*** ***	1914	124	NS **	A	A	-- --
Boccardia polybranchia	A	A	-- --	A	A	-- --	238	78	*** ***
Diopatra neapolitana	<1	<1	-- --	15	89	NS ***	<1	<1	-- --
Nereis falsa	A	A	-- --	A	A	-- --	<1	<1	-- --
Nereis succinea	A	A	-- --	A	A	-- --	<1	<1	-- --
NEMERTEA									
Cerebratulus fuscus	A	A	-- --	21	36	NS *	27	15	*** **
OLIGOCHAETA	<1	<1	-- --	<1	<1	-- --	139	53	*** ***
PHORONIDA	A	A	-- --	A	A	-- --	<1	<1	-- --
MOLLUSCA									
Dosinia lupinus	A	A	-- --	A	A	-- --	9	11	NS **
Small unid. bivalve	82	45	*** ***	18	2	NS ***	143	147	*** **
CRUSTACEA									
Hymenosoma orbiculare	3	1	*** ***	11	6	** ***	<1	<1	-- --
Ampelisca brevicornis	12	6	*** ***	11624	4602	*** ***	12	8	*** NS
Ampelisca palmata	95	29	*** ***	18820	5077	** ***	25	19	*
Lemboides spp.	<1	<1	-- --	1262	469	*** ***	1	2	*** **
Paridotea ungulata	A	A	-- --	<1	<1	-- --	A	A	-- --
PISCES									
Ophisurus serpens	A	A	-- --	<1	<1	-- --	<1	<1	-- --
Total macrofauna	2437	1542	*** ***	45594	14772	*** ***	1914	1141	*** **

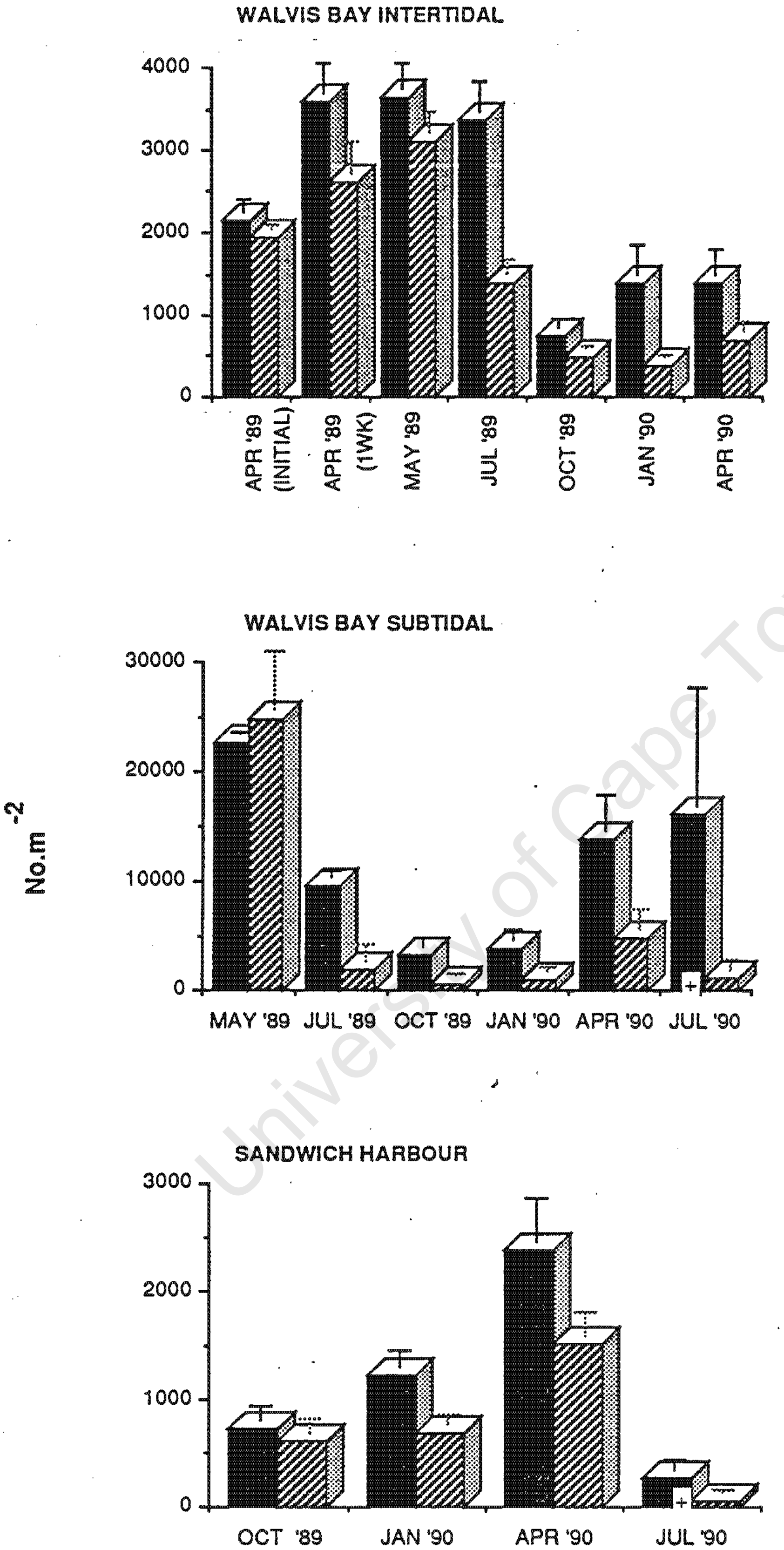

Fig. 12: Density of *Capitella capitata* at all sites.
■ = exclusion, ▨= control, + = cage control.

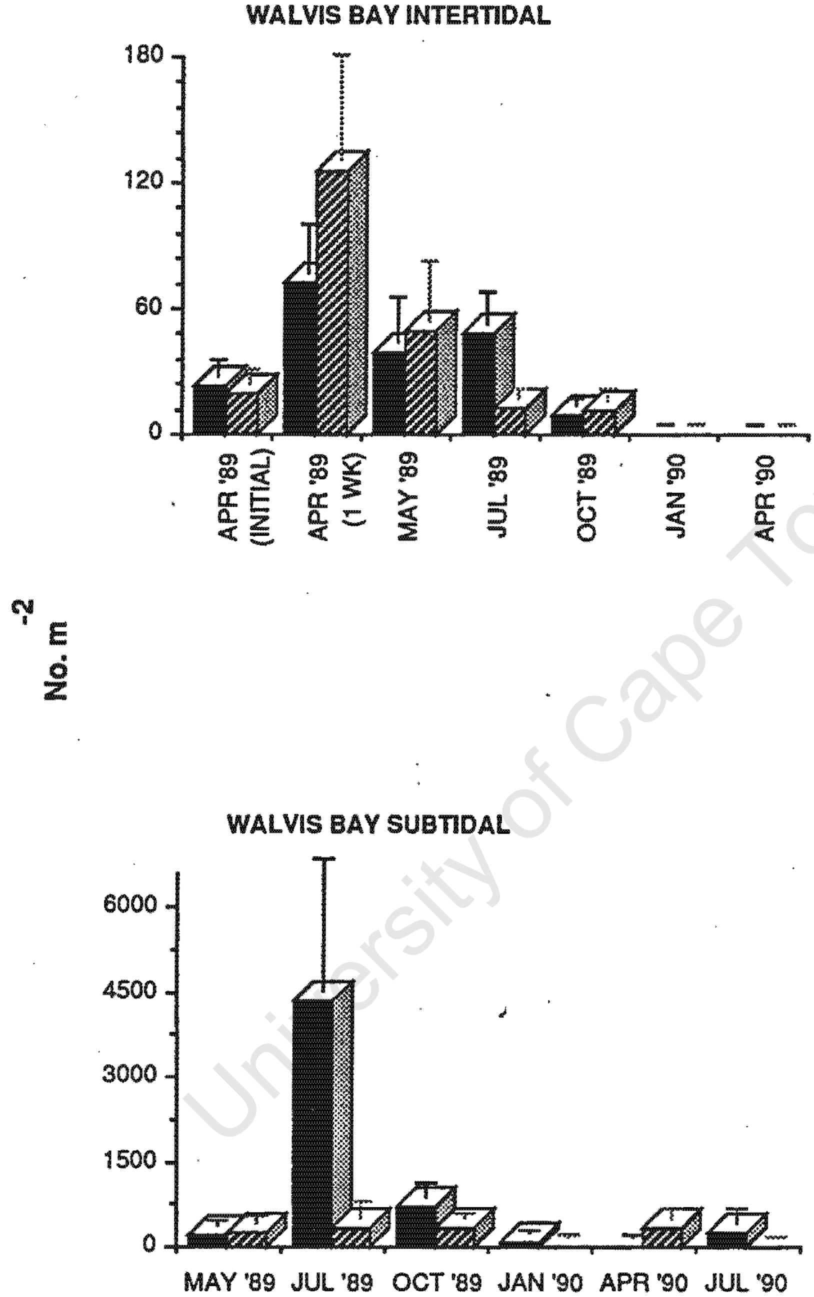

Fig. 13: Density of *Prionospio sexoculata* at Walvis Bay.
■ = exclusion, ▨ = control, + = cage control.

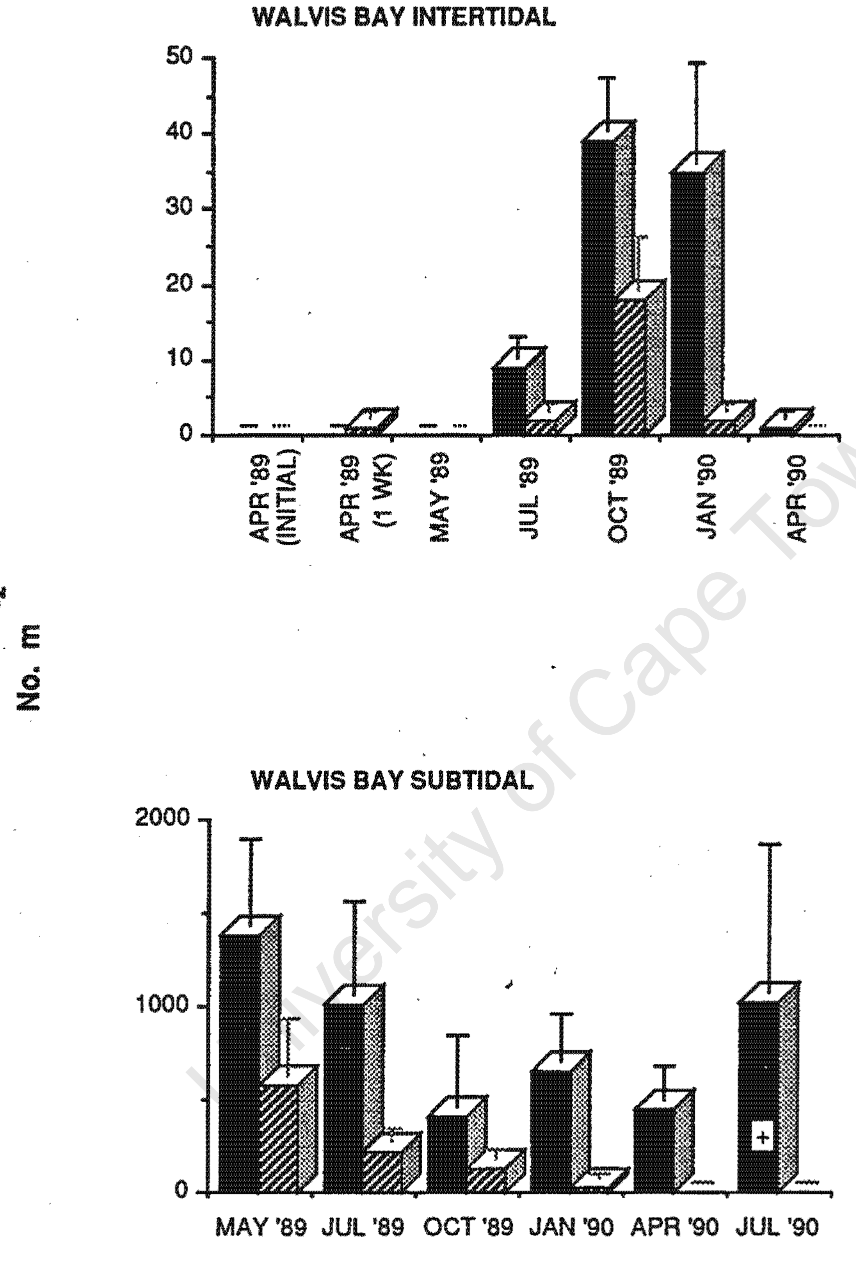

Fig. 14: Density of *Desdemona ornata* at Walvis Bay.
■ = exclusion, ▨ = control, + = cage control.

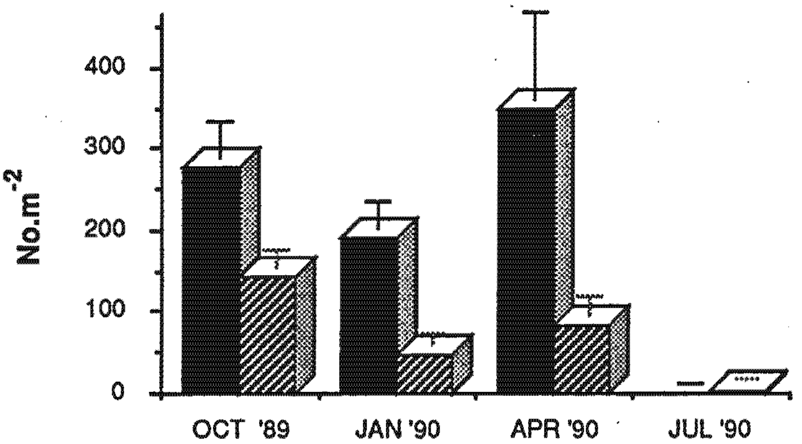

Fig. 15: Density of *Boccardia polybranchia* at Sandwich Harbour. ■= exclusion, ▨= control.

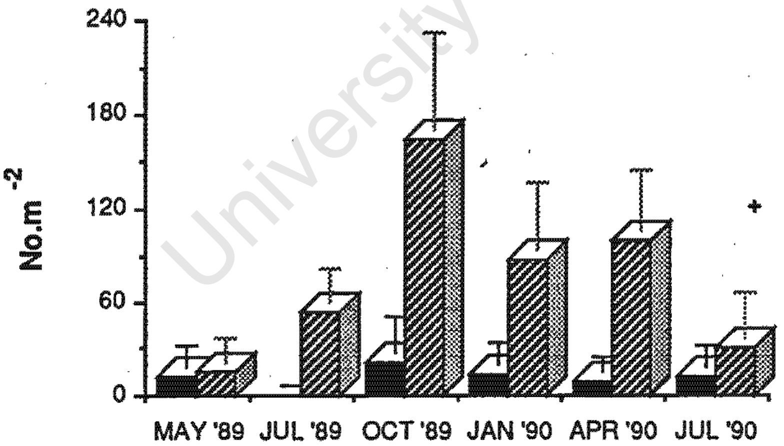

Fig. 16: Density of *Diopatra neapolitana* subtidally at Walvis Bay. ■= exclusion, ▨= control, + = cage control.

An unidentified oligochaete (Fig. 17), common at Sandwich, was rare at the other two sites. The nemertean worm, *Cerebratulus fuscus* (Fig. 18), by contrast, occurred at Sandwich Harbour and subtidally at Walvis Bay, but was entirely absent intertidally at Walvis. Both species increased in abundance in cages relative to controls, but this was least apparent for *C. fuscus* at Walvis Bay subtidal.

Two species of bivalve were collected. The first, a small (1-2mm) white bivalve, apparently similar to that found by Wynberg (1991) at Langebaan lagoon, was common at all three sites, but could not be accurately quantified on the dates when fauna was sorted by floating. For this reason, data were not available for this species on all dates (Fig. 19). The second, *Dosinia lupinus* (Fig. 20) was found only at Sandwich, reaching a density of c. 10 m^{-2} The unidentified species increased rapidly inside exclosures at Walvis Bay intertidal, during the early phase of the experiment, but could not be counted thereafter. No clear patterns were apparent for either species at Sandwich Harbour.

The crustacean fauna comprised three species of amphipod (Figs. 21-23), and one crab. The crab, *Hymenosoma orbiculare* was commonly found at both sites at Sandwich Harbour, but rarely at Sandwich Harbour. All *H. orbiculare* found were juveniles (3-10mm carapace width). The adults prefer sandier substrate, and are therefore not found in the muddier areas where flamingos forage. All three amphipod species occurred at all sites, although the *Lemboides* sp. occurred at very low density intertidally at Walvis Bay. At all sites, *Ampelisca palmata* was the most common amphipod, and the *Lemboides* sp. the rarest. Both species of *Ampelisca* showed decisive increases in numbers in exclosures at all sites, but this was most obvious at Walvis Bay subtidal, where they were extremely abundant, the substrate becoming completely dominated by amphipod and polychaete tubes (Plate 3).

Total macrofaunal density (Fig. 24) was consistently higher in exclosures than in control areas at all sites.

A notable feature of many macrofaunal species was their decrease over time during the study, regardless of treatment. Almost all the amphipods showed this

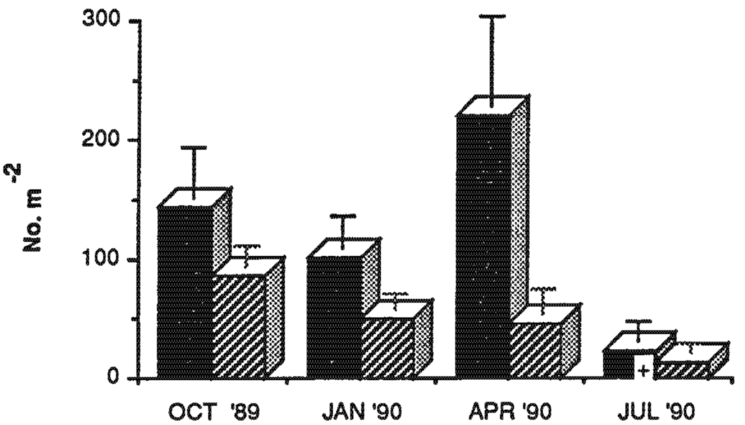

Fig . 17: Density of an unidentified oligochaete at Sandwich Harbour. ■ = exclusion, ▨ = control, + = cage control.

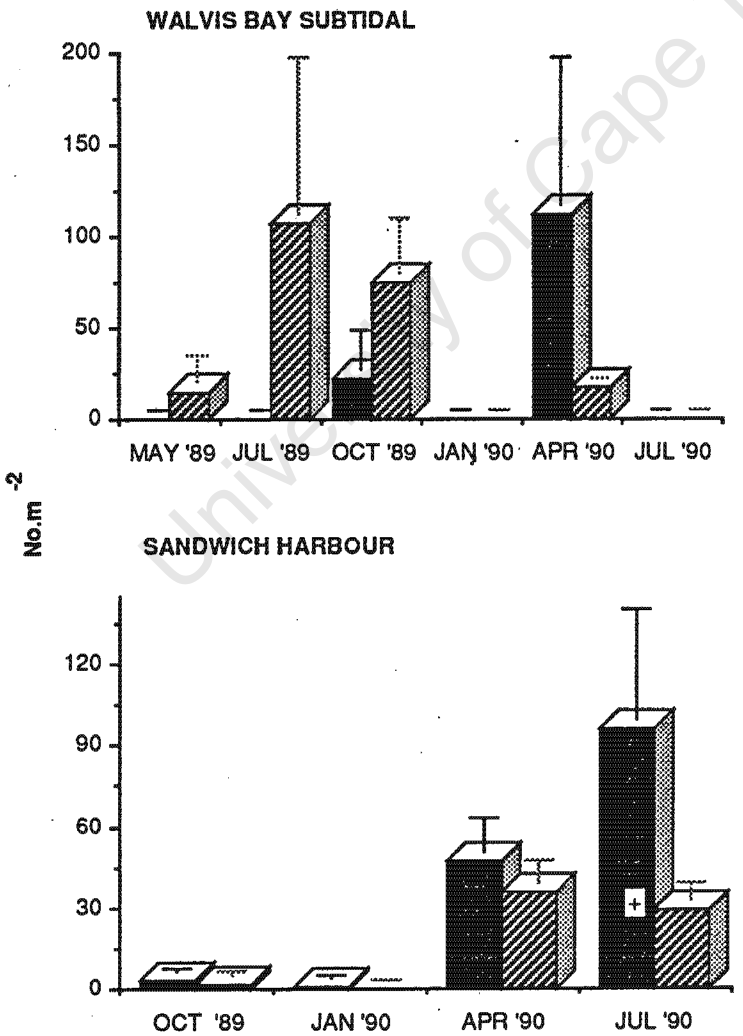

Fig. 18: Density of *Cerebratulus fuscus* at two sites. ■ = exclusion, ▨ = control, + = cage control.

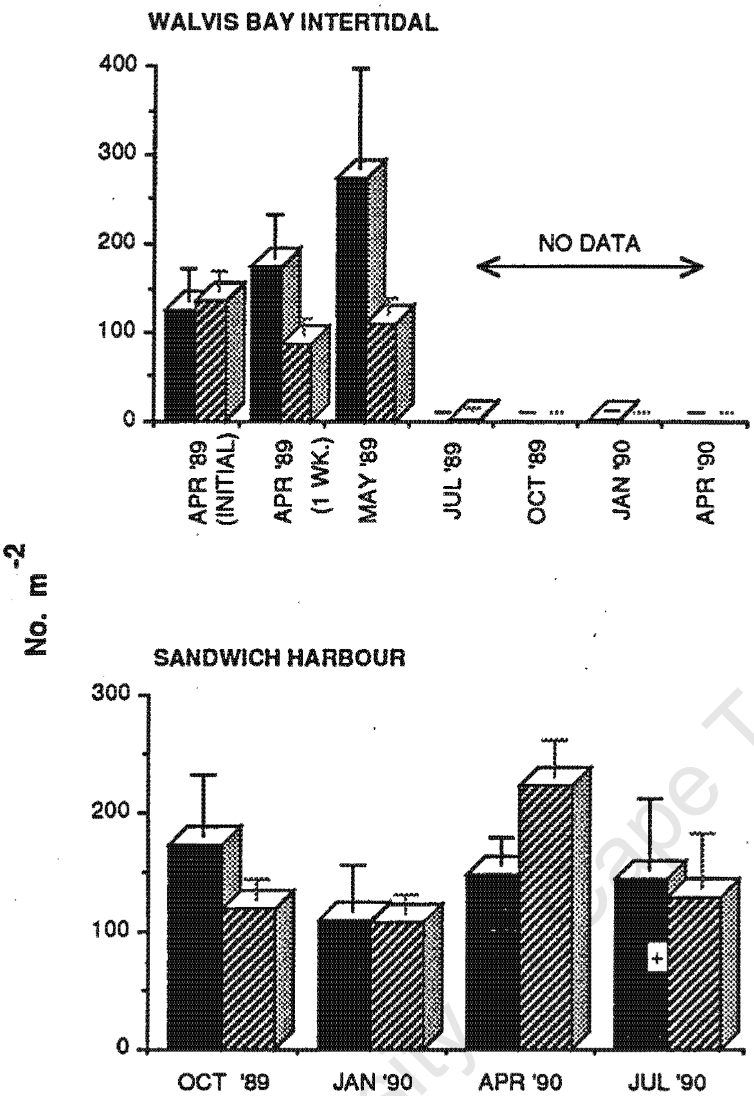

Fig. 19: Density of an unidentified bivalve. Data for Walvis Bay subtidal was not available. ■ = exclusion, ▨ = control, + = cage control.

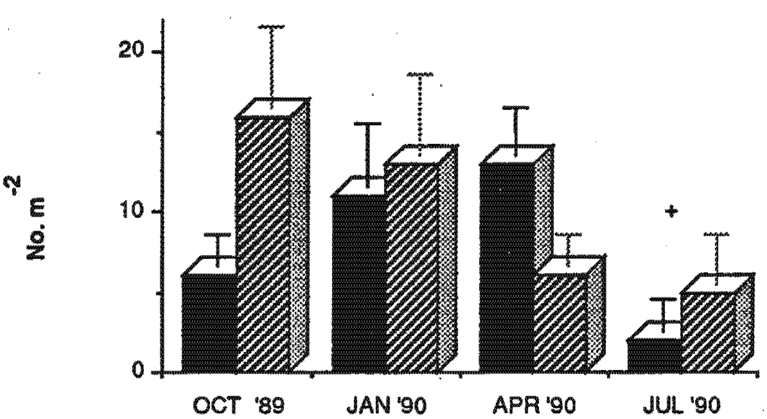

Fig. 20: Density of *Dosinia lupinus* at Sandwich Harbour. ■ = exclusion, ▨ = control, + = cage control.

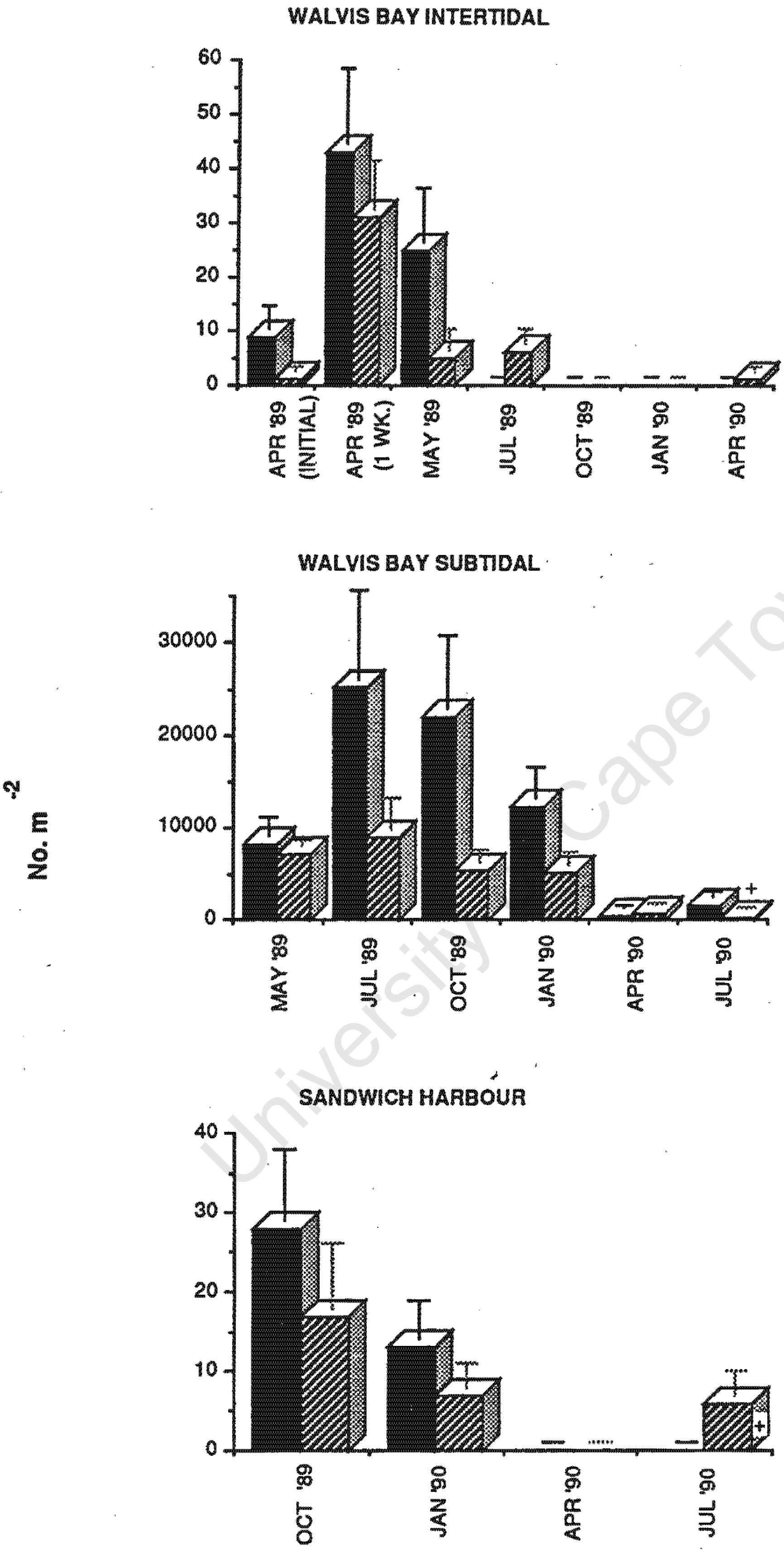

Fig. 21: Density of *Ampelisca brevicornis* at all three sites. ■ = exclusion, ▨ = control, + = cage control.

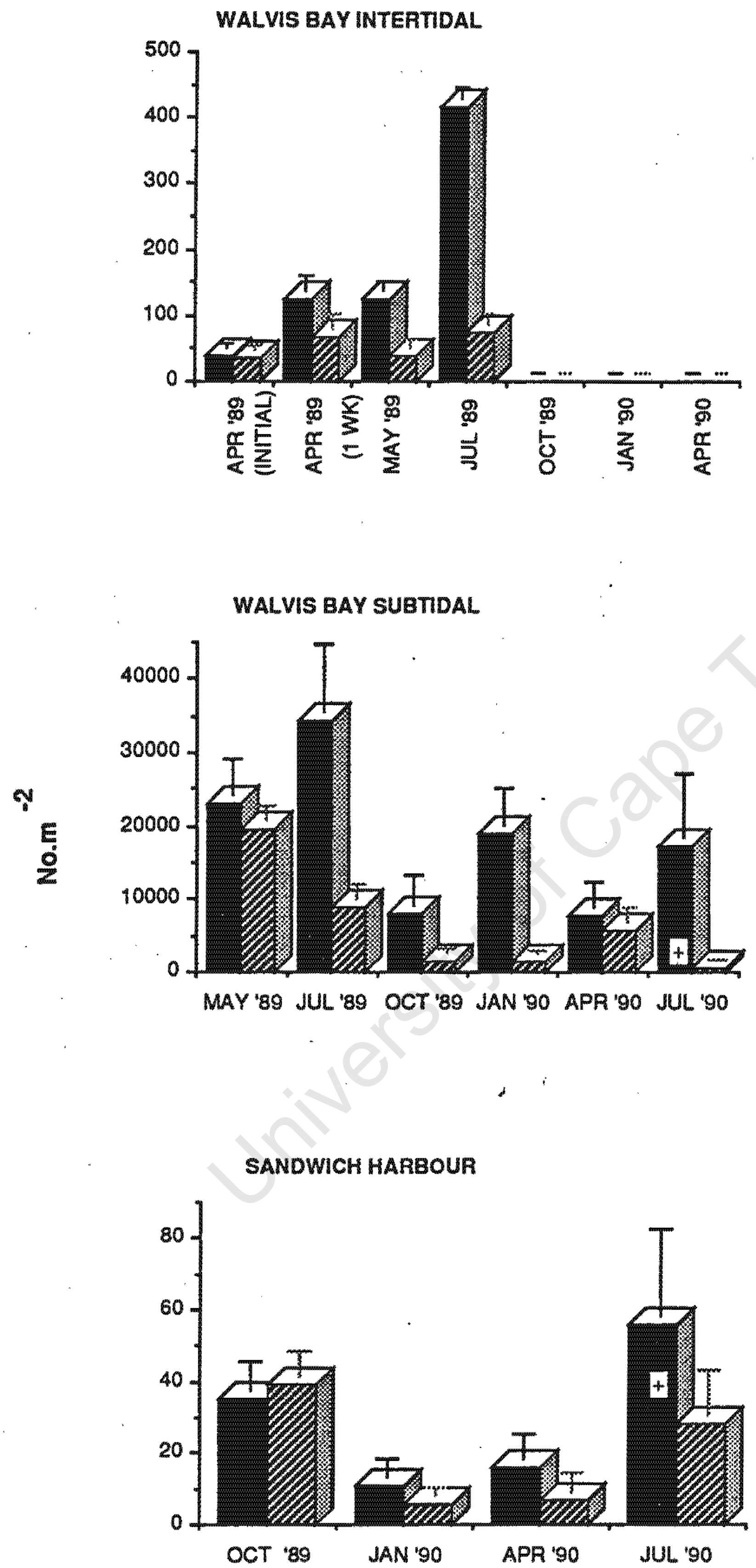

Fig. 22: Density of *Ampelisca palmata* at all three sites during the experiment. ■ = exclusion, ▨ = control, + = cage control.

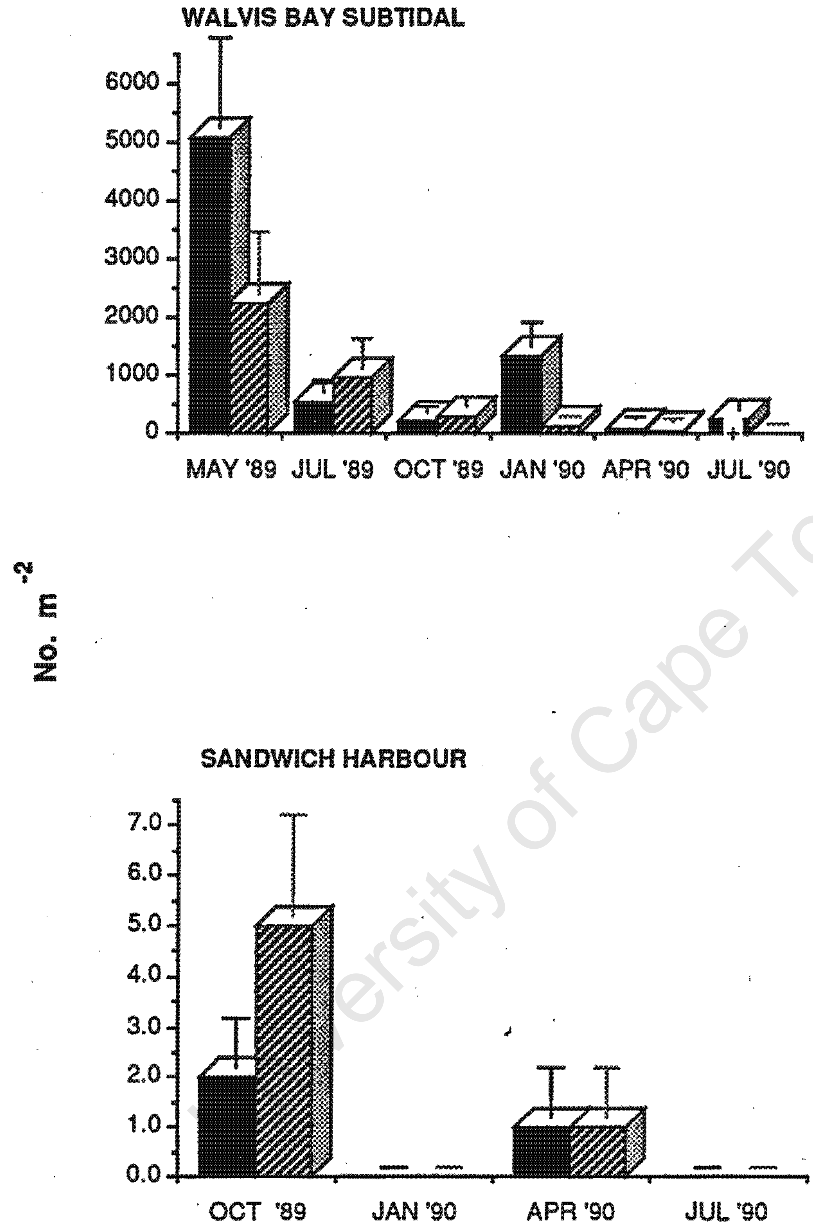

Fig. 23: Density of *Lemboides* sp. at two of the study sites. ■ = exclusion, ▨ = control, + = cage control.

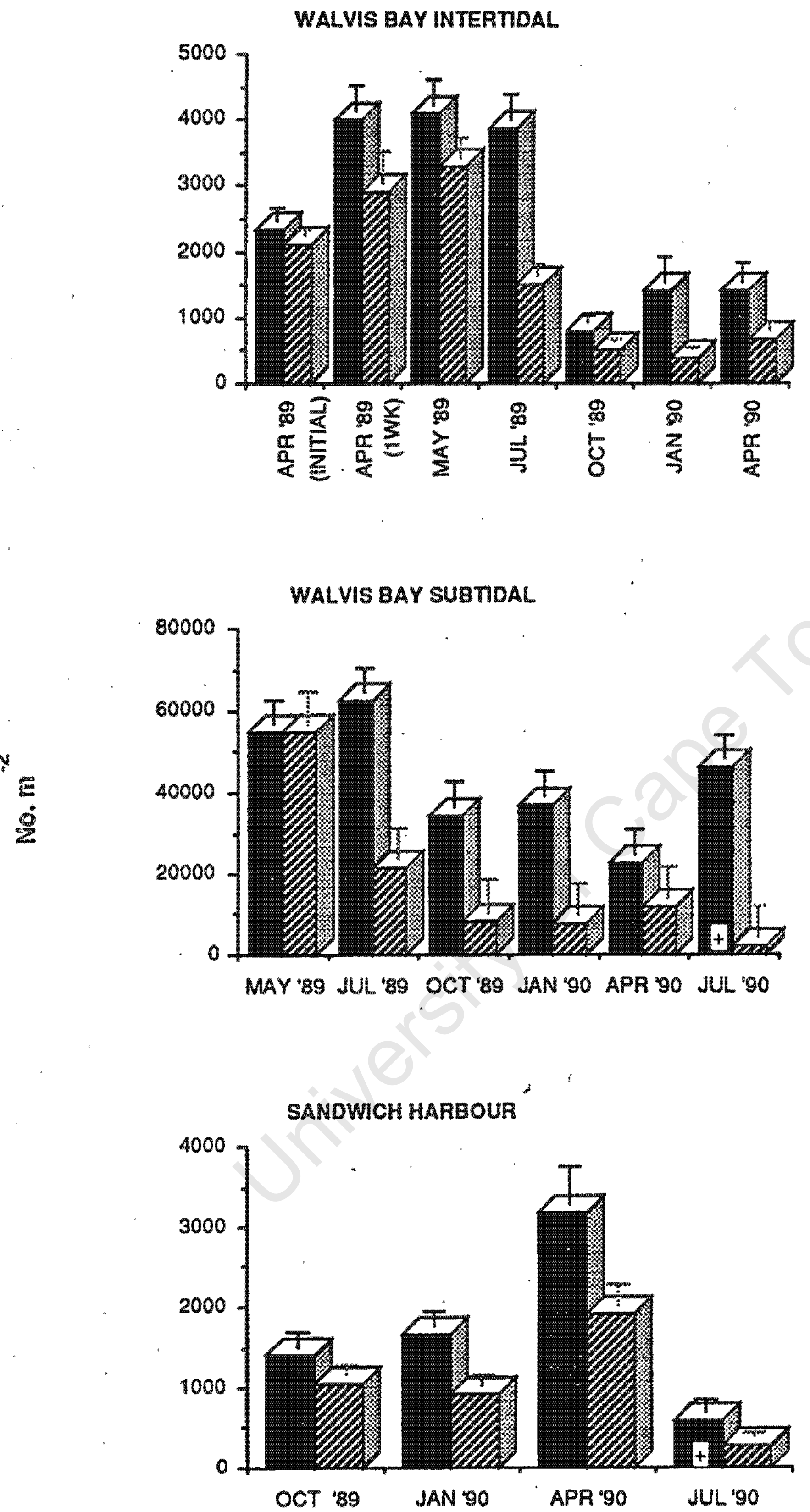

Fig. 24: Total macrofaunal density throughout the study.
■ = exclusion, ▨ = control, + = cage control.

tendency (Figs. 21-23) with almost no amphipods recorded at Walvis Bay intertidal after October 1989. The same trend was apparent with some of the polychaete species (Fig. 13) and is reflected in the change in total macrofaunal density over time, particularly at Walvis Bay intertidal (Fig. 24).

Both the intertidal sites were polychaete-dominated, with *C. capitata* comprising 70-80% of the faunal density at these sites (Fig. 25). At both sites, the relative abundance of *C capitata* decreased slightly in exclusion areas. Walvis Bay subtidal was dominated by amphipods rather than polychaetes, with *A. palmata* constituting c. 40% of the fauna in exclosures. The proportions of *A. brevicornis* and *C. capitata* decreased slightly in exclosures compared to control areas. As with the meiofauna, however, no major changes in species composition resulted from the exclusion of flamingos, and indices of diversity and evenness showed no difference between treatments and controls at any site (Table 4).

Table 4: Comparison of Shannon-Wiener diversity indices (H') and evenness (E) between treatments and controls for all sites. t tests for diversity indices (Zar 1984) were used. H' was calculated for all dates excluding first sampling date at each site.

	EXCLUSION		CONTROL		t	P
	H'	E	H'	E		
W. BAY INTERTIDAL	0.440	0.176	0.443	0.196	t=0.008	1>P>0.5
W. BAY SUBTIDAL	1.455	0.492	1.659	0.522	t=0.3609	1>P>0.5
S. HAR. INTERTIDAL	1.540	0.549	1.542	0.524	t=0.0022	1>P>0.5

CAGE CONTROLS

In July 1990, chlorophyll levels, and abundances of meiofaunal groups and macrofaunal species were compared between cage controls, full cages and control areas, using CONTRAST. In part due to a decrease in overall macrofaunal numbers at Walvis Bay, many differences may have been hidden, and 14 taxa showed no difference between treatments for that date (table 5). Where differences were apparent, cage controls and controls grouped together

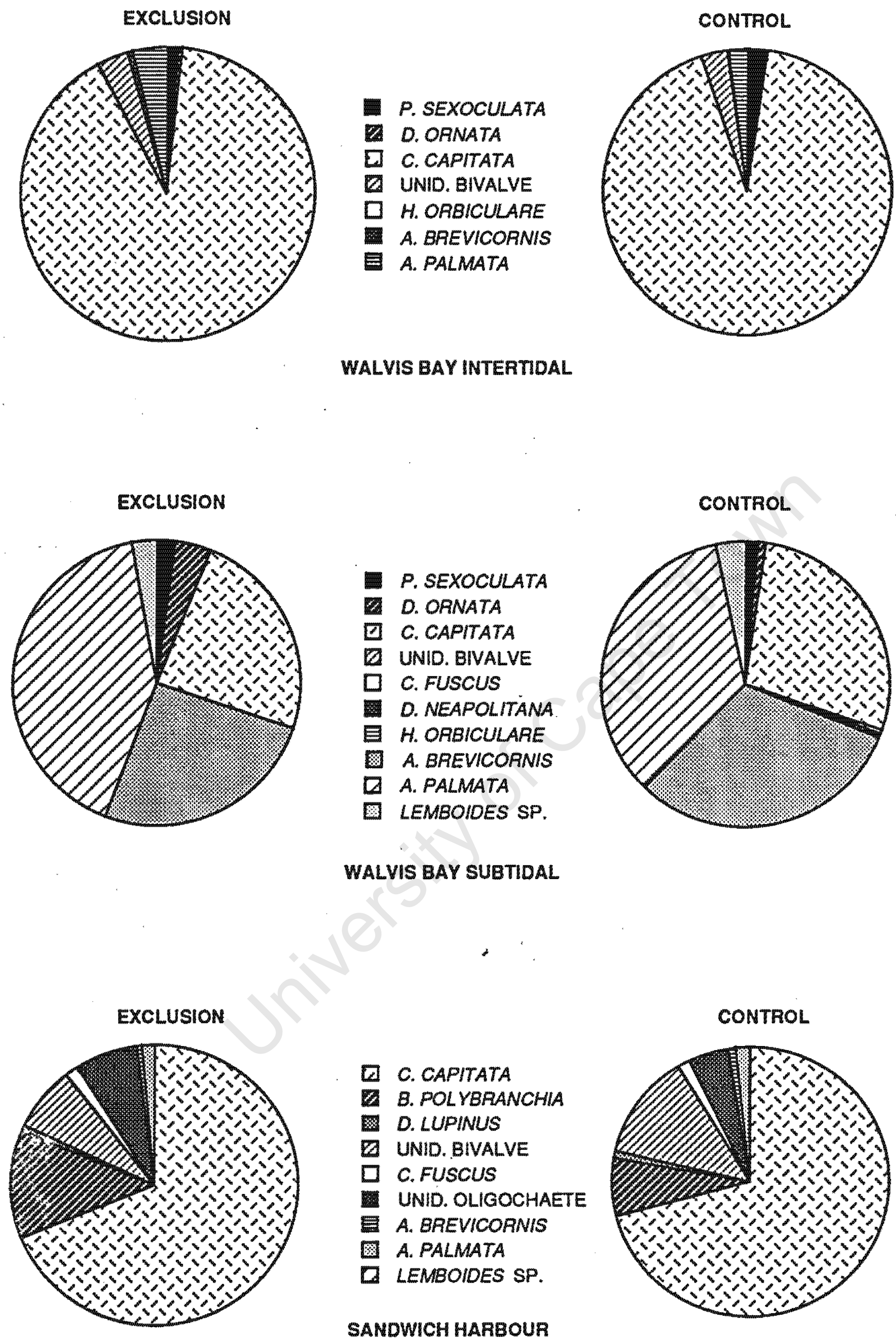

Fig. 25: Relative abundance of macrofaunal species over the duration of the study.

and were different from exclusion areas in ten of sixteen cases. In only two instances (*A. brevicornis* at Walvis Bay subtidal and chlorophyll at Walvis Bay subtidal) were exclusion and cage control values unequivocally grouped. In the remaining cases, cage control was either less similar to either of the other treatments than they were to each other, or the cage control value fell between the other two, and did not differ from either.

Table 5: Results of contrast for July 1990. E=exclusion, C=control, CC=cage control, N/A=not applicable. All differences are defined as $P<0.05$.

	WALVIS BAY SUBTIDAL	SANDWICH HARBOUR
<u>CHLOROPHYLL</u> $\mu g.g^{-1}$	$(E=CC)\neq C$	$(C=CC)\neq E$[a]
<u>MEIOFAUNA</u>		
Nematodes	$E=C=CC$	$E=C=CC$
Foraminifera	$(C=CC)\neq E$	$E=C=CC$
Copepods	$(C=CC)\neq E$	$E=C=CC$
Ostracods	$(C=CC)\neq E$	$(E\neq C)=CC$
Total meiofauna	$(C=CC)\neq E$	$E=C=CC$
<u>MACROFAUNA</u>		
P. sexoculata	$(E\neq C)=CC$	N/A
C. capitata	$(C=CC)\neq E$	$(E\neq C)=CC$
D. ornata	$(C=CC)\neq E$	N/A
B. polybranchia	N/A	$E=C=CC$
D. neapolitana	$E=C=CC$	N/A
C. fuscus	$E=C=CC$	$(C=CC)\neq E$
Oligochaete	N/A	$E=C=CC$
D. lupinus	N/A	$(C=CC)\neq E$[a]
Small unid. bivalve	N/A	$E=C=CC$
A. brevicornis	$(E=CC)\neq C$	$E=C=CC$
A. palmata	$(C=CC)\neq E$	$E=C=CC$
Lemboides	$E=C=CC$	$E=C=CC$
Total macrofauna	$(C=CC)\neq E$	$(C=CC)\neq E$[a]

$E=C=CC$: No difference between treatments - 14 cases.

$(C=CC)\neq E$: Cage control equal to control, and both different to exclusion - 12 cases.
[a] - C=E in these cases (3 of these).

$(E\neq C)=CC$: Control and exclusion differ, but neither differ from cage control - 3 cases.

$(E=CC)\neq C$: Exclusion equal to cage control, and both differ from control - 2 cases.

DISCUSSION

PHYSICAL PROPERTIES OF SEDIMENTS.

With the exception of sediment particle size distribution, the results showed a certain degree of change in all the properties of sediments measured. Redox potential was affected by treatment at both intertidal sites. pH changed within exclosures at both Walvis Bay sites, but not at Sandwich Harbour. All three sites were affected by caging with regard to sediment organic content, but this was least pronounced at Walvis Bay subtidal.

Many of the physical properties of sediments are interdependent. For example, Plante et al (1989) found links between sediment grain size, organic content and redox potential, and Reiŝe (1985) correlated time of day and tidal level with Eh. In my study, Eh, pH and organic content were all lowest at Sandwich Harbour, which also had slightly finer sediment than the other two sites. Nevertheless, all sites had strongly reducing sediments, (Eh values -330 to -420 mV: see Fig. 3) even although readings were taken near to the surface and at times when Eh should have been highest. Under similar conditions, positive REDOX values were obtained at Bogue inlet in North Carolina (Ott & Machan, 1971 cited in Reise 1985), and at Langebaan lagoon, on the South African west coast, Tibbles (pers. comm) obtained minimum Eh readings of c. -190mV.

Of the three sites, only Sandwich Harbour showed significant treatment effects for Eh (Fig. 3). None of the expected associated changes in physical properties of the sediment were observed.

Organic content of the sediment was different between treatments and controls at all sites. Higher organic content is normally associated with lower Eh, but the reverse was true at Sandwich Harbour. At Walvis Bay subtidal and Sandwich Harbour organic contents of sediments were higher inside exclosures than in controls, but differed at Walvis Bay intertidal by being higher in control areas. Total macrofauna and meiofauna were higher inside exclosures, and may have contributed to the elevation of organic content at two sites.

In general, changes of sediment properties were limited and inconsistent between sites, and no obvious patterns emerged which could have explained the observed changes in the biota.

CHLOROPHYLL

Since the chlorophyll samples were taken from the sediment surface, it was expected that the less disturbed sediment inside the exclosures would have higher chlorophyll content, despite the presence of higher numbers of nematodes and copepods which feed on microalgae (Blanchard 1991). Ampeliscid amphipods also feed on microalgae (Mills 1966), and this was expected to influence results, particularly subtidally at Walvis Bay. At both Walvis Bay sites, but not at Sandwich Harbour, chlorophyll concentrations in exclosures increased relative to controls as expected. At Walvis Bay subtidal the treatment effect may have been exaggerated by the fact that the sediment surface was elevated above that of surrounding areas, due to the development of dense mats of ampeliscid tubes. This meant that caged areas became exposed at spring low tides (Plate 3) when much of the sampling was done. Because the sediment surface became exposed, this could also have led to increased productivity and accounted for the increase in chlorophyll concentration in the exclosures (Fig. 4). All chlorophyll samples were taken from the sediment surface. Branch and Pringle (1987) demonstrated that sediment disturbance by the sand prawn *Callianassa kraussi* could bury viable microalgal cells to depths of 15-25cm. This implies that a substantial number of cells may have been buried, particularly in control areas. Since I sampled only surface microalgae, total chlorophyll concentrations may have been underestimated in control areas, where disturbance by flamingoes would have buried a proportion of the benthic diatoms. At Sandwich Harbour, there was less visible sign of sediment turnover by flamingoes, and the lack of treatment effects on chlorophyll concentration may reflect this.

BACTERIA.

By the end of the experiment, numbers of bacteria were lower inside exclosures at all sites than outside (Fig. 5). This is somewhat anomalous, since organic content was higher inside exclosures than in control areas at two sites. Since organic materials are needed for bacterial metabolism it would be expected that bacterial numbers and organic content of sediment should be positively correlated (Mazure & Branch 1979). This was true only of Walvis Bay intertidal. However organic content and particle size may be poor predictors of bacterial abundance within particular sediments (Cammen 1982). Cammen and Walker (1986) found that fluctuations in bacterial abundance were positively correlated with changes in microalgal density in the Bay of Fundy. In the present study, microalgal abundance was higher inside exclosures at two sites, but bacterial density remained higher in control areas. A tenable hypothesis for the depression of bacterial numbers inside cages is that higher grazing pressure inside exclosures is responsible: since it is unlikely that bacteria are grazed directly by flamingos, the lower number of bacteria inside exclosures may have been an effect of the higher density of bacterivores inside the cages.

Branch and Pringle (1987) showed that bacterial abundance increases in the presence of the sand prawn *Callianassa kraussi*, which is an important bioturbator of the sediment in areas where it is abundant. However, many of the bacteria were concentrated around the burrows of *C. kraussi*, and bioturbation alone may not cause increases in bacterial abundance. Nevertheless, the poosibility exists that exclusion of flamingoes led to declines in bacteria because bioturbation was reduced inside cages.

MEIOFAUNA

At Walvis Bay, almost no treatment effect on meiofaunal density could be seen in the intertidal zone. This contrasted markedly with the subtidal area and with Sandwich Harbour, where most of the meiofaunal groups responded positively to the exclusion of flamingoes, increasing inside cages relative to controls by the end of the experiment (Figs. 6-10).

Bell (1980) demonstrated that exclusion of macroepifauna could significantly increase meiofaunal abundance. However, Reise (1979) considered that infaunal macrofauna, although preying on meiofauna, rarely obtain the majority of their nutritional requirements from this source, and that macrofaunal predation alone is unlikely to significantly reduce meiofaunal populations. Results of macroepifaunal predation experiments on copepods (Webb & Parsons 1991) support this conclusion. Reise (1979) pointed out that predation within the meiofauna, or physical factors such as sediment reworking by macrofauna, could additionally influence meiofaunal abundance. He concluded that "a sole overriding master factor seems rather unlikely" (for controlling meiofauna). In my study, top meiofaunal predators such as turbellaria were absent. Since other meiofauna, such as nematodes were not identified to species level, it is not possible to estimate the proportion of predators amongst the meiofauna and hence the effect of internal predation. Furthermore, other negative or amensalistic effects between meiofaunal species have been demonstrated (Chandler 1989). Sediment turnover rates were visibly less inside exclosures than outside, and this may have partly accounted for treatment differences. However it is difficult to reconcile this explanation with the lack of significant responses at Walvis Bay intertidal, which was disturbed at a high frequency and intensity by the flamingos.

Bell (1980) found that exclusion of macroepifauna in a salt marsh could affect meiofaunal densities, but that these effects differed between taxa and were subject to seasonal variation. Reidenauer (1989) also found taxon-specific reactions to sediment disturbance. My results bear out this assertion, but indicate that meiofaunal reactions to disturbance may be site-specific as well, since taxa responded differently to flamingo exclusion at different sites; however this was not positively ascertained, because disturbance intensity also differed between sites. For example, density of copepods decreased inside exclosures at both Walvis Bay sites, but increased at Sandwich Harbour. In contrast, foraminifera and ostracods increased at both Walvis Bay sites, but decreased at

Sandwich, although the latter effect was not statistically significant (Table 1). Nematodes were the only group that increased within the exclosures at all sites, although this was not significant at Walvis Bay subtidal. Fluctuations in density between treatments was common, and this could not consistently be attributed to seasonal changes.

Meiofauna are susceptible to disturbances that alter the oxygen content of the sediment, even if they are not directly preyed upon by the bioturbator (Sherman & Coull 1980). However, meiofaunal communities are resilient (Alongi 1985), and recolonisation of such areas, particularly after single disturbances, may be rapid (Sherman & Coull 1980, Billheimer & Coull 1988). Meiofauna are adversely affected by high densities of *Capitella capitata* and other tubiculous colonisers (Alongi & Tenore 1985), although this could not be demonstrated to be due to disturbance of surface sediments alone (Alongi 1985). Of my three study areas two were dominated by *C. capitata*, and the third by tube-building amphipods and *C. capitata*. All these species increased significantly in exclosures, and may to some extent have offset the expected effects of flamingo exclusion on meiofauna abundance. Finally, the flamingos fed intermittantly at the experimental sites, with periods of up to several days lapsing between feeding events and these time lapses could not be accurately ascertained at the time of sampling. Continuous disturbance of sediments by calianassid prawns results in depression of meiofaunal numbers over long time periods (Branch & Pringle 1987), but meiofaunal recolonisation of intermittantly disturbed patches has been shown to occur within one tidal cycle or less (Sherman & Coull 1980). Thus it is possible that control areas had been recolonised between the time they were disturbed by flamingoes and the time of sampling. Furthermore, because of the manner in which they feed, flamingoes which were active in the control areas may have suspended meiofauna which could then have been deposited inside the exclusion cages. These phenomena could partly explain fluctuations in relative meiofaunal abundance between treatments. Hence, although there was apparently a long-term effect caused by flamingo exclusion for at least two sites, the mechanisms of this effect are uncertain, and other, uncontrolled factors could have been important.

MACROFAUNA

Of all the results, those of the macrofauna were the most unequivocal. All species tested at all sites were affected by caging, and of twenty-nine tests (including total macrofauna), twenty-six were significant at the 0.05 level or more. Compared to the meiofauna, responses of macrofauna were more uniform. With few exceptions, macrofauna were more abundant inside exclosures. While effects of time did influence the treatment effects in some cases (Table 2), there was never the degree of fluctuation evident in meiofaunal responses. In only two cases, *Dosinia lupinus* at Sandwich Harbour (Fig. 20) and *Cerebratulus fuscus* at Walvis Bay subtidal (Fig. 18), were the results of caging ambiguous. The reasons for the overall stability of macrofaunal compared to meiofaunal responses are probably two-fold. Macrofauna generally have longer generation times than meiofauna, and are slower colonisers of new patches. Secondly, macrofauna are higher up the `cascade' and are less likely to be subject to indirect effects caused by changes in the abundance of other species. This makes it less likely that slight changes in the environment would be reflected by corresponding changes in abundance.

A notable phenomenon in the study was the apparent decline in abundance of some species over time, regardless of treatment. Particularly affected were amphipods (Figs. 21-23) and the polychaete *Prionospio sexoculata* at Walvis Bay (Fig. 13). Some of these species were totally absent from samples taken in April and July 1990. This did not seem to be a seasonal occurrence, since these species were present at similar times the previous year, and increased predation pressure or density-dependent mortalities can be ruled out because the event was not treatment-specific. Further, marine invertebrates are able to survive at high densities due to developmental plasticity (Peterson 1979), decreasing the likelihood of density-dependent mortality. The Namibian coastline is periodically subjected to sandstorms resulting from easterly Berg winds which pick up large quantities of sand as they cross the desert. Much of this load, which is rich in mica, is deposited at the coast. Although these winds contribute little to the annual aeolian sediment deposition in the lagoon (CSIR report 1989), they deposit large loads over short periods during autumn and winter (usually between April and July). This can reputedly cause anoxic sediment conditions that result in mass mortalities (De Witt, pers comm). Whether the decline in abundance of some macrofauna can be attributed to such an event, is a matter of speculation. Nevertheless it may provide an example of episodic physical disturbance profoundly influencing the biota of a lagoon, and invites further investigation.

Despite the decrease in macrofaunal density, the dense mats of amphipod tubes persisted in subtidal exclosures until the end of the experiment. These mats were drastically reduced in partially dismantled cages however, suggesting that sediment disturbance during flamingo foraging was responsible for their reduction in partial cages. Flamingo foraging could adversely affect tube-building amphipods and polychaetes by exposing them to predation by other species (such as the snake eel *Ophisuris serpens*), or due to increased energy expenditure needed to rebuild tubes. These effects could be manifest as changes in growth rate or size structure rather than changes in abundance, and more detailed studies of population structure, along the lines of that done by Wilson (1989) on the amphipod *Corophium volutator* would be necessary to elucidate them.

In a review of caging experiments, Peterson (1979) found that the most common effect of excluding large predators from intertidal areas was that macroinfaunal density increased two to three times over their previous abundance. Of my three sites, only Walvis Bay subtidal conformed closely to this pattern. Both intertidal sites showed significant treatment effects on macrofauna, but of lesser magnitude. Virnstein (1977) suggested that predation might be more significant subtidally than intertidally, following a similar gradient to that hypothesized for most rocky shores by Connell (1972) who proposed that predation decreases in importance with tidal height. My results support this thesis. Why this should be so is unclear. One possibility is that predation is heavier subtidally, since predators have constant access to this area.

At both the lagoons studied in this project, the water was shallow enough for flamingos to forage around the subtidal cages for the majority of the time, while the opportunity to forage intertidally was limited to high tides. It is also possible that flamingos selectively forage in subtidal areas, since macrofaunal densities are higher subtidally.

In a few cases, exclusion of flamingos led to densities of macrofauna decreasing. Most notable were the nemertine worm *Cerebratulus fuscus* (Fig. 18) and the large bivalve *Dosinia lupinus* (Fig. 20) at Sandwich Harbour. Density of the large polychaete *Diopatra neapolitana* at Walvis Bay subtidal was also higher in control areas. Figure 16 shows that this is due to increased abundance in control areas rather than declining abundance in exclosures. Reise (1978, 1985) found that excluding fish and birds from areas of tidal flats of Königshafen led to size-specific changes in abundance of fauna, with smaller macrofauna decreasing inside exclosures and larger fauna increasing. My results were not as size-specific, but the fact that the three largest species in the area all decreased inside exclosures is in direct contrast to the results of Reise (1985), and illustrates the varying effects of excluding different predators. Reise (1985) attributed the patterns he found to preferential predation on large prey. In the present case, flamingos are limited to smaller prey. Larger organisms are therefore not predated on, and are seemingly unaffected by the sediment disturbance. However, they may be adversely affected by increased densities of other infauna, either because of competition for space, or due to the altered nature of the sediment surface, particularly subtidally. Increased density of deposit-feeding organisms has been shown to affect suspension feeders negatively (Rhoads & Young 1970). Both species of ampeliscid amphipod found in the present study are deposit feeders (Enequist 1950, Mills 1966), as is *C. capitata* (Day 1967), and in this light the decrease of *Dosinia lupinus* is expected. However densities of the unidentified small bivalve increased within exclosures at two sites as did the small suspension feeding polychaete *Desdemona ornata*, indicating some specificity in this type of interaction. More puzzling is the decreased density of *C. fuscus* inside exclosures at Walvis Bay subtidal. Since nemertea are carnivorous (Day 1974), and with little apparent competition, *C. fuscus* should have increased due to increased prey availability. Tube-building organisms are known to have adverse effects on burrowers in some cases (Woodin 1974, Hulberg & Oliver 1980) and the sediment surface within subtidal exclosures was densely tubiculous. Roots and other plant matter can have a similar effect (Brenchley 1982). Both roots and tubes are more inhibitory to large species than to smaller, morphologically similar ones. This may account for the decreased abundance of *C. fuscus* at Walvis Bay and bears out the pattern observed between small and large bivalves. At Sandwich Harbour the sediment never became dominated by tubes; there were buried roots and grasses, but these were not treatment-specific, and would not have influenced the results. Accordingly, *C. fuscus* increased inside cages at Sandwich Harbour.

In a survey of Walvis Bay lagoon, Hockey and Bosman (1983) reported *Prionospio sexoculata* densities of 5250 m^{-2} in an area close to my exclosures, but found no *Capitella*. This contrasts strongly with my results, which showed *C. capitata* to be the numerically dominant species in the intertidal zone. Whether this was a case of misidentification, or is indicative of changes in the benthic community of Walvis Bay, is uncertain. However, the two species are unlikely to be confused, and since *P. sexoculata* may dominate polluted areas (Christie & Moldan 1977), this could reflect recovery of a previously degraded habitat. Unfortunately, little work has been done at Walvis Bay, and data are scarce, making this difficult to confirm.

In summary, various components of benthic community structure are known to be interdependent. Guilds of macrofauna may affect each other, and macrofauna-meiofauna interactions are well documented. Cammen and Walker (1986) showed the relationship between bacterial abundance and microalgal production. It is thus logical that a single disturbance could produce a ripple effect that would affect all levels of the benthic community. In this study, the use of cages to prevent disturbance associated with a single large predator, the Greater Flamingo, resulted in changes in macro- and meiofaunal abundance, microflora density and primary production. Physical sediment characteristics were relatively unaffected, but some changes in organic content were evidenced.

Many of the effects were similar at three varied sites, suggesting that flamingos are important predators in a variety of habitats. The potential of Greater Flamingos to influence community structure was emphasised by the significant effects observed, even when the birds occurred in low numbers, as at Sandwich Harbour.

The results were most pronounced for macrofauna, less so for meiofauna, and least of all for physical characteristics of the sediment. It is not clear whether effects at all levels were directly due to removal of flamingo-induced disturbance, or whether a type of `cascade' was operating whereby each level of the community was affected by changes in the fauna one level higher. If the latter case is true, the lack of definite patterns at all sites for chemical and physical sediment data indicate that the commmunity structure is biologically controlled.

A COMMENT ON CAGE CONTROLS

Adequate controls for exclusion experiments on soft sediments have long been problematic (Peterson 1979). The conventional way of approaching this problem is by erecting sets of partial cages which ostensibly mimic cage effects, but don't exclude the species being manipulated (e.g. Quammen 1984, Frid & James 1988). Another approach (e.g. Bell 1980) is to monitor areas after partially dismantling existing exclosures. If any effects seen during an experiment were actual effects of predator exclusion, rather than artefacts of caging, then faunal densities within partially dismantled structures should return to background (control) levels. The validity of both the above methods of control is contingent on the assumption that the species being excluded will not react adversely to the presence of partial cages, and that their feeding behaviour will be similar in the presence or absence of the cage controls. While this assumption may hold for invertebrate predators, the same is not necessarily true for birds. Frid & James (1988) argued that their cage controls inhibited feeding by large epibenthic predators. I could not be sure that flamingos fed at the same intensity within partial cages as in completely open control areas. Conversely, cage controls may be ineffective because mobile predators may be attracted to the structures (Peterson 1979).

As previously discussed, I had reason to believe that the design of the exclosures themselves would minimise cage effects. This assumption was borne out during the experiment. No signs of scouring or siltation were evident in the cages and no weed or other organic matter clogged the ropes due to the distance between the strands. To test for potential caging effects, I dismantled two sides of two cages at each site to allow flamingoes access to the previously caged areas. Between April and July, the cages disappeared from the intertidal zone at Walvis Bay, preventing assessment of cage effects at that site. At the other two sites, results were fairly taxon-specific (Table 5). In a few cases, cage control values lay between control and exclusion values. In two cases, (*A. brevicornis* and chlorophyll levels at Walvis Bay subtidal), the cage control was unequivocally more similar to caged densities than to control densities. However, in the bulk of cases (81%) either there were no differences between all three treatments, or the cage controls were highly similar to the controls and both differed from the exclusion treatments (Table 5). Hence, the method used to control for caging effects (partial removal of cages) strongly indicated that there were no discernable caging effects which could have invalidated the experimental manipulations. This conclusion is robust: if the flamingos did feed less in cage controls than in open areas, this could only have incorrectly inferred a caging effect.

PREDATION, DISTURBANCE AND COMMUNITY STRUCTURE.

The three most commonly cited influences on community structure in soft sediments are competition, predation and disturbance. Amensalistic interactions are also common. All have been shown to be important in various systems, but none have individually proven pivotal, and a generalised paradigm for soft-sediment community structure has not been successfully formulated. This study attempted to examine the effect of a predator on benthic community structure. Rather than focusing on a particular interaction or group of fauna, I chose to try and follow the effect through the trophic levels. To my knowledge, few other studies have done this, exceptions being Branch & Pringle (1987) and Wynberg (1991). In my study, the disturbance associated with flamingo feeding clearly affected all levels of the benthic biota, but to varying degrees. The most apparent and dramatic response to removal of the disturbance was among the macrofauna, which were most directly affected by predation and disturbance. Other taxa were apparently subjected to secondary effects of disturbance. Only the bacteria seemed uniformly negatively affected by the absence of flamingos, although even in this case the response was not always significant. Densities of macrofauna and meiofauna increased overall without radically changing the taxonomic composition, richness or evenness of any site. Nonetheless, some points concerning soft-sediment community structure emerge.

Thistle (1981) stated that a criterion for the disturbance model of soft bottom community structure was that colonisers would exploit the early phase of recovery of a disturbed patch and ought to become disproportionately abundant. To utilise this criterion, it is necessary to have a known undisturbed patch by which background abundance can be determined. This condition is most likely to be met in studies of recovery after single or simulated disturbances. I had no comparable area that I was certain was undisturbed and could therefore not ascertain what "normal" abundances might be in undisturbed patches. The earliest samples I collected were at Walvis Bay intertidal, one week after the exclosures were erected. Although differences in abundance were already apparent between treatments for some macrofaunal species, no species declined drastically in exclosures at a later stage to indicate a process of competitive exclusion during succession. Meiofauna were not identified to species level and variations in abundance of individual species could not be monitored, but the magnitude of response of meiofaunal groups was generally small.

No macrofaunal species became locally extinct within exclosures, except when a similar decline was evident in control areas, indicating causes other than treatment. Such local extinction is postulated by Thistle (1981) as the second criterion for accepting that communities are organised by disturbance, as proposed by Grassle & Sanders (1973). While disturbance by flamingos did affect the benthic community, it seems unlikely that any species or guild of species was dependent on these disturbances for survival in the systems studied. *Capitella capitata* in particular is well documented as a rapid opportunistic coloniser of disturbed sediments (e.g Arntz 1977). In this light, its persistence and increased abundance inside the exclosures was surprising. Clearly there was no tendency towards exclusion of this species from caged areas by other species. There are three possible explanations for this. Although flamingos were clearly a major source of disturbance in the experimental area, it is possible that in their absence, other forms of disturbance were adequate for *C. capitata* to persist even within the exclosures. The sand shark, *Rhinobatos annulatus*, has been shown to be an important predator and bioturbator in other lagoon systems (Harris et al 1988). *R. annulatus* was seasonally abundant in both the lagoons in this study. At Sandwich Harbour, the diamond-shaped depressions left by sand sharks were frequently visible. At Walvis Bay, this was not as apparent, possibly because more intense disturbance by flamingos obscured signs of sandshark feeding pits. Depressions, possibly indicative of sandshark feeding, were frequently visible in the tube mats in the subtidal exclosures. *Rhinobatos* feeds mostly on crustaceans, selectively avoids polychaetes (Harris et al 1988). Predation by this and other species could have facilitated the persistence of *C. capitata* in the cages.

A second possibility is that *C. capitata*, despite being a coloniser, is able to compete successfully with other benthic fauna and can persist in patches after disturbance has ceased. This is particularly possible since the sediment at both sites had low oxygen content, and Arntz (1977) has shown that *C. capitata* can thrive under these conditions, although *C. capitata* populations in his exclosures only rose after most other fauna died, confirming their status as opportunists.

Finally it is possible that competition is not a strong organising force in the benthos of these lagoons, and species which might be excluded from patches in systems where competition is more important are not affected at Walvis Bay or Sandwich Harbour.

Competition is commonly held to be most intense between closely related species or between those species which utilise resources in similar ways, although this does not necessarily apply to competition for space (e.g. Virnstein 1977). Accordingly, any changes in community structure due to competition should be most obviously manifested among such species and most studies of competition concentrate on these species. In the present experiment, two species of congeneric tube building amphipod co-occurred at all three sites. Contrary to what competition theory would predict, the density of both species increased at all sites within exclosures. Additionally, *Capitella capitata*, a tube-building polychaete, was also found in higher densities inside exclosures than in control areas. The tubes of all these species were apparently interspersed, since they were commonly found in the same samples; however the samples were not examined for potential small-scale separation between species, as described by the spacing hypothesis of Wilson (1983). There was also an overall decline in macrofaunal abundance towards the end of the experiment, which may have obscured competitive interactions that might have become evident if high faunal densities had been maintained for longer. Peterson (1979), after reviewing caging experiments, concluded the lack of competitive exclusion in soft-sediment studies was not an artifact of the short duration of the experiments, although some of them lasted only three to six months. At Walvis Bay subtidal, where macrofaunal densities were highest, exclosures were maintained for fourteen months. Densities of macrofauna remained high for approximately eight months before declining in all treatments. In this light, it is unlikely that the potential for competitive exclusion was not realised purely because populations were not maintained at high densities for long enough.

Another feature often associated with competition is the habitat separation of related species. In my experiments, two species of spionid polychaete, *Prionospio sexoculata* and *Boccardia polybranchia* were found. *P. sexoculata* occurred at Walvis Bay, but not at Sandwich Harbour, and the reverse was true of *B. polybranchia.* While this could be interpreted as the result of resource partitioning, Wilson (1984), working in False Bay (Washington State) has demonstrated non-overlapping distributions of spionid polychaetes to be based on habitat selection regardless of the occurrence of potential competitors. Since *P. sexoculata* is known to dominate degraded sediments, and Walvis Bay is known to be degraded, habitat preference is again the more likely explanation here.

Peterson (1979) has postulated that one reason for the absence of competitive exclusion in soft sediments is that soft sediments offer reduced opportunities for interference competition; however he considered primarily the mechanisms of interference that are common to rocky shores, such as overgrowth of one species by another. Infaunal organisms have the potential to substantially alter the character of the sediment, particularly at the surface. Negative interactions between species have been documented several times on this basis. Among these are trophic group amensalism (Rhoads & Young 1970), and negative effects between burrowers and tube-builders (Woodin 1974, Hulberg & Oliver 1980). Although these interactions are likely to be amensalistic rather than competitive (since there is no identifiable resource being competed for), they are a result of interference mechanisms. During this study, species that were negatively affected by exclosures included a large suspension feeder, *Dosinia lupinus*, and a large, burrowing carnivore, *Cerebratulus fuscus*. Hence both forms of amensalism discussed above could have been operating in this experiment. Two small suspension feeders, the unidentified bivalve and the sabellid polychaete *Desdemona ornata*, increased abundance inside exclosures at two sites, suggesting a size-specific component to these interactions. While interference interactions can affect soft-sediment benthic communities, they are likely to be amensalistic rather than competitive, and will affect relatively few species. There was no tendency toward exclusion of any species within cages.

As expected, abundance of macrofauna was much higher subtidally at Walvis Bay than at either intertidal site and the difference in tidal levels overshadowed differences attributable to other properties of the sites. With regard to the intertidal sites, Walvis Bay had slightly higher densities of macrofauna in both control and exclusion areas than Sandwich Harbour. However the former site had a higher proportion of *Capitella capitata* than the latter and this species can thrive in disturbed sediments. In the intertidal zone, species richness was highest at Sandwich Harbour as predicted, but diversity

(H') was marginally higher in control areas at Walvis Bay subtidal than in the control sites at Sandwich Harbour. Walvis Bay intertidal had the lowest species richness, diversity and evenness (Table 4). Predictions of higher diversity and richness at Sandwich Harbour were thus supported with regard to the two intertidal sites, but the difference between inter- and subtidal areas at Walvis Bay were just as striking.

CONCLUSION

From changes in the abundance of macrofauna, meiofauna, bacteria and chlorophyll concentrations after exclusion of flamingos, it is clear that flamingos profoundly influenced the benthos of both lagoons studied. Since some of the species affected were not prey items of flamingos, and these effects were not all accounted for by other biological interactions, some part of this effect can be attributed to disturbance of the sediment independent of removal of prey by the flamingos.

It seems unlikely that any single factor controls community structure in the absence of this predation and disturbance. There was no evidence that competition was a factor; nor was there reason to believe that a mosaic of patches of the type proposed by Grassle and Sanders (1973) was responsible for patterns observed, although recolonisation of completely defaunated patches was not investigated. Amensalistic interactions were apparent, and these followed patterns predicted by Rhoads and Young (1970) and Hulberg and Oliver (1980). These interactions affected few species, however, eliminated none and did not have a major effect on the benthos as a whole. Sediment properties were mildly altered in exclosures, but this was more likely the result of changes in the biotic community than the cause of them. Since physical sediment properties were not substantially altered in exclosures and changes in chemical properties were not associated with expected changes in bacteria and chlorophyll concentrations, I suggest that the patterns observed are more parsimoniously interpreted as having resulted from changes in the macro- and meiofauna. All sites became dominated by tube-building, deposit-feeding animals, and amensalistic interactions would have been likely at the high densities achieved, particularly in the subtidal zone at Walvis Bay, where macrofaunal densities exceeded 50 000 individuals m^{-2}.

The decline in abundance of macrofaunal species toward the end of the experiment was independent of experimental treatments and was probably the result of physical processes. Apart from predation, physical disturbance, primarily due to wind-blown sediment, may be one of the major factors controlling community structure.

I conclude that predation-disturbance by flamingos is a major determinant of community structure intertidally and subtidally in the areas investigated. Differences in community structure in other parts of the lagoons may change the pattern of the response to flamingo predation, but its nature and magnitude of the response is likely to be similar. More generally, predation is the predominant biological interaction in the two systems studied. Since no other significant biological interactions were apparent, I propose that in the absence of predation-disturbance, physical disturbance would determine community strucure in these areas. Community structure in all areas studied is thus driven by disturbance in one form or another.

ACKNOWLEDGEMENTS

The assistance of all the following, without whom the project could not have been successful, is gratefully acknowledged.

To Dr. A. J. Williams and the staff of Walvis Bay Nature Conservation, who willingly gave of their time to help me find my way in Walvis Bay, and for use of lab space. The logistics of the project would have become impossible without them. A special mention is due to Mr. S. De Witt for freely sharing his considerable knowledge of the area with me.

Namibian Nature Conservation for allowing me the privilege of staying and working at Sandwich Harbour, surely one of the most spectacular places one could hope to see. Mr. P. Tarr was always helpful with advice regarding all aspects of my trips to Sandwich Harbour, and I am particularly grateful to him.

Field assistants proverbially have a difficult time on such projects, and those who helped me were no exception. A special mention is due to Des Kruger who manfully sieved a fair proportion of Sandwich Harbour with a fractured rib, after falling off a landrover which he had just single handedly freed from the sand. Other field assistants, too numerous to name, provided prodigious physical power as well as ideas, criticism and great company.

My supervisor, Prof. G. Branch, who formulated the project, and gave me invaluable advice and assistance throughout, was also largely responsible for identifying cryptic species.

Carlos Villacastin-Herrero, Bruce Emanuel and Geoff Hoy helped with computer-related problems. Rene Navarro gave much-needed statistical advice. The technical staff of the zoology dept, U.C.T. were always availble to give logistical support.

The project was funded by an FRD grant, as well as by an extremely generous donation from Walvis Bay Salt Refineries.

Special thanks are due to Carol McPherson, who bore the brunt of my frustrations when things went wrong, for unstinting support.

REFERENCES

Alongi, D.M. 1985. The effect of physical disturbance on population dynamics and trophic interactions among microbes and meiofauna. *J. Mar. Res.*, 43: 351-364

Alongi, D.M. & Tenore, K.R. 1985. The effect of detritus supply on trophic relationships within experimental benthic food webs. 1 meiofauna-polychaete (*Capitella capitata* (Type 1) Fabricus) interactions. *J. Exp. Biol. Ecol.*, 88: 153-164.

Arntz, W.E. 1977. Results and problems of an "unsuccessful" benthos cage predation experiment (Western Baltic), In: *Biology of Benthic Organisms*, edited by B.F. Keegan, P.O. Ceidigh & P.J.S. Boaden, 31-44, Pergamon Press, New York.

Anonymous 1989. A study of some of the physical and biotic processes affecting dredging within the Walvis Bay lagoon. CSIR report.

Baird, D., Evans, P.R., Milne, H. & Pienkowski, M. W. 1985. Utilization by shorebirds of benthic invertebrate production in intertidal areas. *Oceanogr. Mar. Biol. Ann. Rev.*, 23: 573-597.

Bell, S.S. 1980. Meiofauna-macrofauna interactions in a high salt marsh habitat. *Ecol. Monogr.*, 50(4): 487-505.

Bengtson, S.A. 1976. Effect of bird predation on lumbricid populations. *Oikos*, 27: 9-12.

Bildstein, K.L., Frederick, P.C. & Spalding, M.G. 1991. Feeding patterns and agressive behaviour in juvenile and adult American flamingos. *The Condor*, 93: 916-925.

Billheimer, L.E. & Coull, B.C. 1988. Bioturbation and recolonization of meiobenthos in juvenile spot (Pisces) feedng pits. *Est. Coast. Shelf. Sci.*, 27: 335-340.

Black, R. & Peterson C.H. 1988. Absence of preemption and interference competition for space between large suspension-feeding bivalves and smaller infaunal invertebrates. *J. Exp. Biol. Ecol.*, 120: 183-198.

Blanchard, G.F. 1991. Measurement of meiofauna grazing rates on microphytobenthos: is primary production a limiting factor? *J. Mar. Biol. Ecol.*, 147: 37-46.

Branch, G.M. & Pringle, A. 1987. The impact of the sand prawn *Callianassa kraussi* Stebbing on sediment turnover and on bacteria, meiofauna and benthic microflora. *J. Exp. Mar. Biol Ecol.*, 107: 219-235.

Brenchley, G.A. 1982. Mechanisms of spatial competition in marine soft-bottom communities. *J. Exp. Mar. Biol. Ecol.*, 60: 17-33.

Brey, T. 1991. The relative importance of biological and physical disturbance: an example from intertidal and subtidal sandy bottom communities. *Est. Coast. Shelf. Sci.*, 33: 339-360.

Brown, L. 1959. *The Mystery of the Flamingos* Country Life Ltd., London.

Cammen, L.M. 1982. Effect of particle size on organic content and microbial abundance within four marine sediments. *Mar. Ecol. Prog. Ser.*, 9: 273-280.

Cammen, L.M. & Walker, J.A. 1986. The relationship between bacteria and micro-algae in the sediment of a Bay of Fundy mudflat. *Est. Coast. Shelf. Sci.*, 22: 91-99.

Chandler, G.T. 1989. Foraminifera may structure meiobenthic communities. *Oecol.*, 81: 354-360.

Christie, N.D. & Moldan, A. 1977. Distribution of macrofauna in Langebaan Lagoon. *Trans. Roy. Soc. S. Afr.*, 42(3,4): 273-284.

Connell, J. H. 1972. Community interactionson marine rocky intertidal shores. *Ann. Rev. Ecol. Syst.*, 3: 169-192.

Day, J.H. 1967. *Polychaeta of southern Africa*, Parts 1 & 2. Trustees of the British Museum (Natural History), London.

Day, J.H. 1974. *A guide to marine life on South African shores*. 2d. ed. A.A. Balkema, Cape Town.

Dayton, P.K. 1984. Processes structuring some marine communities: are they general? In: *Ecological communities: conceptual issues and the evidence.* Edited by D.R. Strong, L.G.A. Simberloff & A.B. Thistle. Princeton University Press, Princeton, New Jersey.

Enequist, P. 1950. Studies on the soft-bottom amphipods of the Skagerak. *Zool. Bid. Från Upps.*, 28: 297-492.

Frid, C.L.J. & James, R. 1988. The role of epibenthic predators in structuring the marine invertebrate community of a British coastal salt marsh. *Neth. J. Sea. Res.*, 23(3): 307-314.

Grassle, J.F. & Sanders, H.L. 1973. Life Histories and the role of disturbance. *Deep-Sea Res.*, 20: 643-659.

Grossmann, S & Reichardt, W. 1991. Impact of *Arenicola marina* on bacteria in intertidal sediments. *Mar. Ecol. Prog. Ser.*, 77: 85-93.

Hall, S.J., Raffaelli, D.J., Basford, D.J. & Robertson, M.R., 1990.(a) The importance of flatfish predation and disturbance on marine benthos: an experiment with dab *Limanda limanda* (L). *J. Exp. Mar. Biol. Ecol.*, 136

Hall, S.J., Raffaelli, D. & Turrell, W.R. 1990. (b) Predator-caging experiments in marine systems: a reexamination of their value. *Am. Nat.*, 136(5): 657-672.

Harris, S.A., Bennett, B.A., & Branch, G.M. 1988. An assessment of the sand shark *Rhinobatus annulatus* as a predator in Langebaan lagoon. *S. Afr. J. Mar. Sci.*, 7: 153-159.

Hockey, P.A.R. & Bosman, A.L. 1983. Conservation-management of the Walvis Bay lagoon with special reference to its importance as a bird habitat. Report submitted to the Association of Round Tables of South Africa, Walvis Bay section.

Hulberg, L.W., & Oliver, J. 1980. Caging manipulations in marine soft-bottom communities - Importance of animal interactions on sedimentary habitat modifications. *Can. J. Fish. Aquat. Sci.*, 37

Hurlbert, S.H. 1984. Pseudoreplication and the design of ecological field experiments. *Ecol. Monogr.*, 54(2)

Hurlbert, S.H. & Chang, C.C.Y. 1983. Effects of grazing by the Andean flamingo (*Phoenicoparrus andinus*). *Proc. Natl. Acad. Sci. U.S.A.*, 80: 4766-4769.

Jenkin, P.M. 1957. Filter feeding of flamingoes. *Phil. Trans. Roy. Soc. London*, B240: 406-493.

Johnson, R.G. 1970. Variations in diversity within benthic marine communities. *Am. Nat.*, 104: 285-300.

Kalejta, B. 1991. Aspects of the ecology of migrant shorebirds (Aves: charadrii) at the Berg River estuary, South Africa. Phd thesis, University of Cape Town.

Mazure, H.G.F. & Branch, G.M. 1979. A preliminary analysis of bacterial numbers and biomass in Langebaan lagoon. *Trans. Roy. Soc. S. Afr.*, 44(1): 43-54.

Mills, E.D. 1966. The biology of an Ampeliscid amphipod crustacean sibling species pair. *J. Fish. Res. Brd. Can.*, 24(2): 305-355.

Oliver, J.S., Kvitek, R.G. & Slattery, P.N. 1985. Walrus feeding Disturbance: scavenging habits and recolonisation of the Bering Sea benthos. *J. Exp. Mar. Biol. Ecol.*, 91:233-246.

Paine, R.T. 1974. Intertidal community structure: experimental studies on the relationship between a dominant competitor and its principal predator. *Oecol.*, 41: 245-272.

Peterson, C.H. 1977. Competitive organization of the soft-bottom macrobenthic communities of southern California lagoons. *Mar. Biol.*, 43: 343-359.

Peterson, C.H. 1979. Predation, competitive exclusion and diversity in the soft-sediment benthic communities of estuaries and lagoons. In: *Ecological processes in coastal and marine systems.* Edited by R.J. Livingston, Plenum Publishing.

Peterson, C.H. 1980 Approaches to the study of competition in benthic communities in soft sediments. *in Estuarine perspectives* Acad. Press inc.

Peterson, C.H. & Andre, S.V. 1980. An experimental analysis of interspecific competition among marine filter feeders in a soft-sediment environment. *Ecol.*, 61(1): 129-139.

Plante, R., Alcclado, P.M., Martinez-Iglesias, J.C.& Ibarzabal, D. 1989. Redox potential in water and sediments of the Gulf of Batabanó, Cuba. *Est. Coast. Shelf Sci.*, 28: 173-184.

Probert, P.K. 1984. Disturbance, sediment stability and trophic structure of soft bottom communities. *J. Mar. Res.*, 42: 893-921.

Quammen, M.L. 1981. Use of exclosures in studies of predation by shorebirds on intertidal mudflats. *The Auk*, 98: 812-817.

Quammen, M.L. 1984. Predation by shorebirds, fish and crabs on invertebrates in intertidal mudflats: an experimental test. *Ecol.*, 65(2): 529-537.

Raffaelli, D. & Milne, H. 1987. An experimental investigation of the effects of shorebird and flatfish predation on estuarine invertebrates. *Est. Coast. Shelf Sci.*, 24: 1-13.

Reidenauer, J.A. 1989. Sand dollar *Mellita quinquiesperforata* burrow trails: sites of harpacticoid disturbance and nematode attraction. *J. Exp. Mar. Biol. Ecol.*, 130: 223-235.

Reidenauer, J.A. & Thistle, D. 1981. Response of a soft-bottom harpacticoid community to stingray *(Dasyatis sabina)* disturbance. *Mar. Biol.*, 65: 261-267.

Reise, K. 1978. Experiments on epibenthic predation in the Wadden Sea. *Helg. W. Meer.*, 30: 263-271.

Reise, K. 1979. Moderate predation on meiofauna by the macrobenthos of the Wadden sea. *Helg. W. Meer.*, 32: 453-465.

Reise, K. 1985. *Tidal Flat Ecology*. Springer-Verlag, Berlin Heidelberg, Germany

Rhoads, D.C. & Young, D.K. 1970. The influence of deposit feeding organisms on sediment stability and community trophic structure. *J. Mar. Res.*, 28(2): 150-178.

Sherman, K.M. & Coull, B.C. 1980. The response of meiofauna to sediment disturbance. *J. Exp. Mar. Biol. Ecol.*, 46: 59-71.

Sousa, W.P. 1984. The role of disturbance in natural communities. *Ann. Rev. Ecol. Syst.*, 15: 353-391.

Thayer, C.W. 1979. Biological bulldozers and the evolution of marine benthic communities. *Science*, 203:

Thistle, D. 1981. Natural physical disturbances and communities. *Mar. Ecol. Prog. Ser.*, 6: 223-228.

Thrush, S.F. 1986. Community structure on the floor of a sea lough: are large epibenthic predators important? *J. Exp. Mar Biol. Ecol.*, 104: 171-183.

Thrush, S.F., Pridmore, J.E., Hewitt, J.E. & Cummings, V.J. 1991. Impact of ray feeding disturbances on sandflat macrobenthos: do communities dominated by polychaetes or shellfish respond differently? *Mar. Ecol. Prog. Ser.*, 69: 245-292.

Tibbles, B.J. 1991. Estimates of bacterial productivity in Walvis Bay lagoon sediments. Report submitted to Ematek, CSIR.

Underwood, A.J. 1981. Techniques of analysis of variance in experimental marine biology and ecology. *Oceanogr. Mar. Biol., Ann. Rev.*, 19: 513-605.

VanBlaricom, G.R. 1982. Experimental analyses of structural regulation in a marine sand community exposed to oceanic swell. *Ecol. Monogr.*, 52(3): 283-305.

Velji, M.I. & Albright, L.J. 1985. Microscopic enumeration of attached marine bacteria of seawater, sediment, fecal matter and kelp blade samples following pyrophosphate and ultrasound treatment. *Can. J. Micro.*, 32: 121-126.

Virnstein, R.W. 1977. The importance of predation by crabs and fishes on benthic infauna in Chesapeake Bay. *Ecol.*, 58: 1199-1217.

Virnstein, R.W. 1978. Predator caging experiments in soft sediments: caution advised. *Est. Inter.*

Webb, D.G. & Parsons, T.R. 1991. Impact of predation-disturbance by large epifauna on sediment-dwelling harpacticoid copepods: field experiments in a subtidal seagrass bed. *Mar. Biol.*, 109: 485-491.

Wilson, H.W., Jr. 1983. The role of density dependence in a marine infaunal community. *Ecol.*, 64(2): 295-306.

Wilson, H.W., Jr. 1984. Non-overlapping distributions of spionid polychaetes: the relative importance of habitat and competition. *J. Exp. Mar. Biol. Ecol.*, 75: 119-127.

Wilson, H.W., Jr. 1989. Predation and the mediation of intraspecific competition in an infaunal community in the Bay of Fundy. *J. Exp. Mar. Biol. Ecol.*, 132: 221-245.

Woodin, S.A. 1974. Polychaete abundance patterns in a marine soft-sediment environment: the importance of biological interactions. *Ecol. Monogr.*, 44: 171-187.

Wynberg, R.P. 1991. The ecological effects of collecting *Callianassa kraussi* Stebbing and *Upogebia Africana* (Ortmann) for bait: impacts on the biota of an intertidal sandflat. MSc. thesis, University of Cape Town.

Zar, J.H. 1984. *Biostatistical Analysis*, second edition, Prentice-Hall inc., Englewood Cliffs, New Jersey.