

Original article

Evaluating the importance of predation on subtidal benthic assemblages in sandy habitats around rocky reefs

Francisco Barros^{a,b,*}

^a CREICC, Marine Ecology Laboratories, Old Geology Building, A11, University of Sydney, NSW, 2006, Australia

^b Programa de Pós-Graduação em Ecologia e Biomonitoramento, LAMEB, Instituto de Biologia, UFBA, R. Barão de Geremoabo s/n, Campus Ondina, CEP 40170 000, Salvador, BA, Brazil

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Abstract

It was proposed that predation could explain differences in the structure of the benthic macrofaunal assemblages in subtidal sandy sediments close to compared with those far from rocky reefs. This hypothesis was tested using experimental exclusion cages and partial cages at two sites at two distances at two different rocky reefs. Undisturbed uncaged assemblages of macrofauna close to the rocky reefs were generally different from those in the partial cages and full cages. However, caging artifacts could not be detected and there were no strong correlations between the macrofauna and the proportions of different grain size and organic content. The structure of the macrofaunal assemblages close to the rocky reefs was, nevertheless, different from those far from the reefs and the sediments were finer far from than close to the rocky reefs. The results indicated that factors other than predation or grain size caused the differences in the macrofauna. For the spatial and temporal scales used in this study, it was clear that, although predation maybe intense, on its own it cannot explain the differences in the structure of the assemblages close and far from rocky reefs. The importance of adequate replication on caging experiments is discussed and it is suggested that alternative ways need to be found to test predictions about the influence of predation on soft sediment benthic assemblages.

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1. Introduction

Natural and artificial subtidal rocky reefs provide habitats for diverse assemblages of marine organisms. Many studies have focussed on recruitment, productivity, and behaviour of assemblages of fish and benthic animals in these systems (Wenner et al., 1983; Bohnsack and Sutherland, 1985; Parrish, 1989).

There is general agreement that artificial or natural rocky reefs influence the structure of benthic macrofaunal assemblages inhabiting nearby soft-sediments (Davis et al., 1982; Ambrose and Anderson, 1990; Posey and Ambrose Jr., 1994; Barros et al., 2001). The above studies suggested that modifications of these assemblages might be caused by changes in the intensity of movement of water, direction of currents, rates of erosion or sedimentation, organic content of sediments, and in numbers or types of predators.

It is well known that rocky reefs attract fish (e.g., Bohnsack and Sutherland, 1985). Many reef-associated fish and crustaceans forage extensively over adjacent sandy substrata (Ogden and Buckman, 1973; Alongi, 1989; Frazer et al., 1991), implying that soft-sediment assemblages can subsidise populations of these fishes associated with rocky reefs (Lindquist et al., 1994). Nevertheless, few studies have tested whether reef-associated predators really do alter the adjacent biological environment by eating infauna.

Predation is recognised as an important process in ecological systems (e.g., Wilson, 1991). It involves transfer of energy between species, influencing the structure of assemblages. It can be affected by changes in habitat (e.g., Thrush, 1999) and has been suggested as a major factor affecting benthic populations in soft-sediments (Wenner et al., 1983). It has been argued that the effects of predation may be most drastic in physically controlled environments, because the prey organisms must give adaptative priority to the physical regime, rather than to refinement of biological interactions (Sanders,

* Corresponding author. Tel.: +51-71-2357487.

E-mail address: barrosf@ufba.br (F. Barros).

1968). Alternatively, it has been suggested that predation intensity is more important in benign than in harsh soft-sediment habitats (Peterson, 1991). Such debate is extensively discussed in ecological studies, particularly in intertidal rocky shores (e.g., Connell, 1972; Menge and Sutherland, 1976; Menge, 1978; Underwood and Denley, 1984). Nevertheless, there is no doubt that predation at environments subject to different levels of harshness with their different consequences on populations of preys is an important issue in ecology (e.g., Sih et al., 1985).

Field experiments involving manipulations of densities of predators are an important tool for studying the role of predation in natural assemblages (Englund and Olsson, 1996; Englund, 1997). Among the most common manipulations in marine ecology are caging experiments. They have been done in many different habitats, such as salt marshes (e.g., Kneib, 1988; Sarda et al., 1998), intertidal flats (e.g., Quammen, 1984; Raffaelli and Milne, 1987; Raffaelli et al., 1989; Fernandes et al., 1999; Richards et al., 1999; Thrush, 1999), seagrass beds (e.g., Fishman and Orth, 1996; Macia, 2000; Spitzer et al., 2000; Hindell et al., 2002), kelp beds (e.g., Kennelly, 1991; Sala, 1997), coastal lagoons (e.g., Irlandi and Mehlich, 1996; McArthur, 1998), mangroves (e.g., Schrijvers et al., 1998), coral reefs (e.g., Russ, 1987; Connell, 1997), artificial structures (e.g., Connell, 2001) and on subtidal mud-bottoms (e.g., Hines et al., 1990). There have been, however, few studies on subtidal sandy bottoms, possibly due to logistical difficulties involved in the construction and maintenance of the cages in such an exposed habitat. Furthermore, destruction of cages by wave-action, fishing gear and/or boat anchors is a major problem in such experiments (e.g., Arntz, 1977; Virnstein, 1978; Hulberg and Oliver, 1980; VanBlaricom, 1982; Posey and Ambrose Jr., 1994).

Caging often causes effects other than the exclusion of predators (e.g., reductions in water-flow and/or light, changes in sediment characteristics; Dayton and Oliver, 1980; Gray, 1981; Kennelly, 1983; Underwood and Denley, 1984; Dayton, 1994; Olafsson et al., 1994). These are known as caging artifacts and many studies have neglected such effects. The usual way that these effects have been examined is by including a partial cage treatment in experiments, where predators can enter cages, but part of the structure of the cage is present. Alternatively, Kennelly (1983, 1991) proposed a different approach to test for caging artefacts (also used by Russ, 1987).

Previous work in subtidal soft-sediments around Sydney, Australia, has shown that the structure of the macrofaunal benthic assemblages inhabiting sediments near (within 1 m) reefs were frequently more variable than those living away from (> 5 m) rocky reefs (Barros et al., 2001). This previous study also found differences in the spatial variability, diversity, and in the abundance of specific taxa. In the above experiment, it was observed that different animals (e.g., goatfish, flathead, stingrays, and crabs) disturbed the sediment to eat buried macrofauna, particularly close to rocky reefs. It was proposed that predation is an important process shaping the structure of the benthic macrofaunal assemblages in sandy

bottoms close and far from rocky reefs. The hypotheses were: (H1) predators (fishes and large crustaceans) associated with rocky reefs forage over nearby soft sediments, influencing the structure of macrofaunal assemblages close to rocky reefs; (H2) alternatively, predation on soft bottoms far from rocky reefs is an important process that influences the structure of the macrofaunal assemblages inhabiting sediments far from rocky reefs (for example, by predators eating macrofauna during the night) and (H3) a combination of the above two predictions, predation is an important process close to and far from the reef, although it differs between these two habitats (e.g., different predators eating different prey in each habitat).

2. Material and methods

2.1. The study sites

The above hypotheses were tested adjacent to two shallow rocky reefs in Botany Bay, New South Wales, Australia. These rocky reefs, one natural (Yarra) and one artificial (Break-wall), were about 500 m apart. Two sites, approximately 20 m apart, were haphazardly established perpendicular to each reef in depths of 3.5 to 4.0 m at low tide. Along each site, two distances were selected, close to the reef (within 2 m from the reef) and far from the reef (about 10–13 m from the reef). The rationale for these distances was that previous studies indicated that the structure of these assemblages were different at these distances from rocky reef (Barros et al., 2001).

2.2. The experimental treatments

Three pilot studies were done to test if the material used to construct cages were resistant to waves, if the cages were efficient at excluding predators and for edge effects (Barros, 2002). Some types of cages did not adequately excluded predators, others were washed away by waves. Therefore, the following procedure was the most adequate in terms of excluding predators, resistance to wave-action, and logistics (i.e., could be constructed efficiently). These pilot studies also showed that the sample size and number of cores were appropriate to detect differences in the structure of the macrofauna.

At each distance at each site, six cages were constructed. Two of these cages were complete cages and four were partial cages, used to test for caging artifacts (two only with sides, allowing access through the roof, and two only with roof, hereafter called top, allowing access through the sides). Furthermore, there was the uncaged treatment (undisturbed sandy bottom). Each cage was made of plastic oyster mesh (17 mm aperture), which was 40 × 40 cm and 25 cm high. To attach these cages to the sandy bottom, iron star pickets 135 cm high were driven into the sand and each corner of each cage was attached to the pickets using plastic cable ties. To avoid gap forming between the cages and the bottom (previously

observed in pilot studies), 40 cm long aluminium rods were driven through an additional strip of plastic mesh that was left between the corners of the cages. The construction of the complete cages and partial cages (sides and tops) was done in a diamond configuration (i.e., they were constructed with one iron picket in common) and each of these two connected structures is hereafter referred as a unit (Fig. 1). Additionally, undisturbed sandy bottom were also sampled following the same spatial configuration of the other treatments. There were two reasons for this diamond configuration. First, was the time and effort involved in setting up the experiment. Second, it was an alternative attempt to control for caging artifacts (Kennelly 1983, 1991). However, this attempt did not work, due to the harshness of the habitat, and was abandoned in favour of traditional controls (i.e., partial cages).

The experiment was checked weekly to fix possible damages and to make sure that there were no predators inside the cages. No a priori decision about which predators to manipulate or which prey to monitor was made. All predators larger than 17 mm (aperture of the plastic mesh) were excluded. The most common predators sighted in the area were goatfish (*Upeneichthys lineatus*, *Parupeneus signatus*), flathead (*Platycephalus marmoratus*, *P. longispinis*, *P. arenarius*) stingrays (*Urolophus sufflavus*, *Tyrgonoptera testacea*), crabs (*Portunus pelagicus*, *Thalamita admete*). Unfortunately, there is little ecological information on these species other than their geographical distribution and notes on taxonomy, maximum sizes, and habitats in which they occur (Kuiter, 1993; Edgar, 2000).

2.3. Sampling

To examine the test for consistency among times of the differences in the structure of the macrofaunal assemblages close to and far from reefs, two replicate cores (10 cm diameter \times 10 cm depth) were collected at each distance, at each site at each reef ($n = 32$), 4 days after the set up of the experiment. These cores, hereafter called uncaged, were sampled in accordance with the spatial sampling strategy of the experiment (e.g., each pair of cores was sampled within an area of 40×40 cm, using metal frames to delimit the area of each unit). These uncaged cores, sampled at the start of the experiment, were then compared with different uncaged cores sampled at the end of the experiment.

The experiment was set up over 3 days in July 2000. After 101 days, two replicate cores (10 cm diameter \times 10 cm deep) were haphazardly collected, by SCUBA, in the middle of each unit of each treatment (cage, side, top and uncaged), at each

distance, at each site, in each reef ($n = 128$) as biological samples. In each unit, two replicate cores (5 cm diameter \times 10 cm deep) were also collected for sediment analysis, to test for differences in grain size with distance from the rocky reefs and to test for caging artifacts (i.e., differences in grain size and organic content). The size of the sampling area and the number of cores were investigated by pilot studies (Barros, 2002). These pilot studies also suggested potential edge effects. Therefore, cores were sampled in the middle of each treatment to avoid such effects.

2.4. The general laboratory methods

Samples of sediment containing macrofauna were placed in plastic bags, immediately transported to the laboratory, maintained in a fridge for <24 h and fixed in 7% buffered formaldehyde in seawater. Samples were elutriated 10 times, using a 5 l jar, into a sieve of mesh size of 0.5 mm. The contents of the sieve were sorted under a dissecting microscope and preserved in 70% ethanol.

The animals were identified to intermediate taxonomic levels, usually family. Considering that, not only the biology and ecology, but also the taxonomic knowledge of the benthic fauna in Australia is limited, the above procedure minimised the time taken to sort (James et al., 1995). Moreover, several studies have shown that identification to species level is not necessary for the detection of patterns of spatial and temporal variability in macrofaunal assemblages (e.g., Gray et al., 1990; Clarke and Warwick, 1994; Chapman, 1998; Barros et al., 2001; Lindegarth, 2001).

Replicate samples of sediment were collected to encompass potential spatial variability in the grain-size distributions (Wheatcroft and Butman, 1997). Samples were placed in plastic bags, transported to the laboratory, and frozen. Approximately 120 g of sediment from each sample was thoroughly mixed and dried, to a constant weight, in an oven at 60°C (Folk, 1980; Gray, 1981). Dried sediment was sieved, using a mechanical shaker, for 10 min in a column containing sieves of mesh sizes 4 (hereafter called pebble > 4.00 mm), 2, 1, 0.5, 0.25, 0.125, and 0.063 mm. About 15 g of sediment was dried at 60°C in porcelain crucibles and combusted at 550°C for 1 h, to determine organic content and at 1000°C for one additional hour, to determine carbonates (Dean, 1974).

2.5. The analyses of data

First, to test for consistent differences between undisturbed benthic macrofaunal assemblages close to and far from

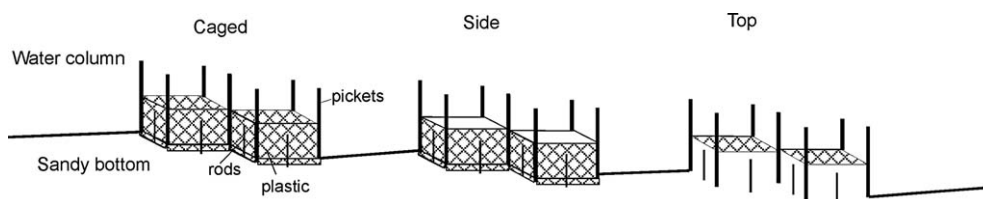


Fig. 1. Scheme of two units of cages and partial cages (sides and tops).

the rocky reefs, non-metric multivariate analyses of variance (NP-MANOVA, [Anderson, 2001](#)) were done using those samples collected in undisturbed areas (uncaged) at the start and at the end of the experiment, separately. Reef (Re; 2 levels) was random, and Distance (Di; 2 levels, fixed) was orthogonal to Re. There were two replicates (i.e., the cores from replicate site were pooled; $n = 8$). The Bray–Curtis dissimilarities and a posteriori tests for significant interactions (reef \times distance) were also calculated.

Second, if any hypotheses about the importance of predators was to be supported (i.e., predation is an important process close to (H1), far from (H2) or close to and far from the rocky reefs, (H3)), then a statistical interaction should be detected (i.e., distance \times treatment) where differences between caged treatments and the other treatments is significant only close to (H1), only far from (H2) or if predation has a different effect close to and far from (H3) the rocky reefs. Therefore, changes in the macrofaunal assemblages and in the total number of individuals, number of taxa, abundances of polychaetes, crustaceans, and the most abundant taxa (i.e., those that contribute 90% for the total number of individuals and that were present in more than 20% of the samples) were analysed using 2-factor mixed model of non-parametric MANOVA ([Anderson, 2001](#)) and ANOVA ([Underwood, 1997](#)), respectively. Distance (Di; 2 levels) was fixed, and treatments (Tr; 4 levels, fixed) were orthogonal to Di. There were two replicates (cores from each unit of similar treatment in each distance at each site were summed; $n = 4$). Non-metric multidimensional scaling (nMDS), performed on untransformed abundances and Bray–Curtis measures of dissimilarities ([Field et al., 1982](#); [Clarke, 1993](#); [Clarke and Warwick, 1994](#)), were used to plot the differences between different distances and among treatments in assemblages.

Changes among treatments in the percentages of different fractions, organic content, and carbonates of the sediments were analysed using 2-factor mixed model ANOVA. The analyses were done at each reef, separately. Distance (Di; 2 levels) was fixed, and treatments (Tr; 4 levels fixed) were orthogonal to Di. There were two replicates (i.e., replicate cores from different units were pooled, $n = 4$).

Preliminary analyses showed that there were substantial differences between units (10s of centimetres apart), sites (10s of metres apart) and reefs (100s of metres apart) indicating that there is a large spatial variability in these assemblages. These differences, however, were complex and not consistent within treatments (e.g., one treatment did not show consistent differences at one distance in both sites of either reef). Furthermore, these results are not relevant to the hypotheses being examined.

Multiple comparisons among the means were done with the Student–Newman–Keuls (SNK) test. Cochran's test was used to test for homogeneity of variances. If variances were heterogeneous, data were transformed ([Underwood, 1981](#)). For some taxa, transformation did not remove heterogeneity, so untransformed data were used. Interpretations were made cautiously, noting the robustness of analyses where balanced samples are used ([Underwood, 1997](#)).

Analyses were done using the BIOENV procedure ([Clarke and Ainsworth, 1993](#); [Clarke and Warwick, 1994](#)) to examine relationships of differences in the macrofauna to the different characteristics of the sediments (grain size fractions, organic content, and carbonates).

3. Results

3.1. Patterns in macrofaunal assemblages

3.1.1. Patterns of undisturbed assemblages

NP-MANOVA showed a significant interaction between reef and distance at the start ([Table 1a](#)) and at the end ([Table 1b](#)) of the experiment. At Yarra, there were significant differences in the structure of the undisturbed macrofaunal assemblages close to and far from the reef at the end of the experiment ([Table 1d](#)). At Breakwall, these differences were significant at the start and at the end of the experiment ([Table 1d](#)). Such differences essentially conform to previous work ([Barros et al., 2001](#)), where it was found that assemblages near rocky reefs were generally different from those

Table 1

NP-MANOVA testing for differences in the structure of the undisturbed macrofaunal assemblages between reefs and distances (close and far); (a) at the start of the experiment and (b) at the end of the experiment; and Bray–Curtis dissimilarities at different distances from each rocky reef and results of the a posteriori tests from NP-MANOVA for the start and end of the experiment: (c) Within = dissimilarities among replicates, (d) Between Distances = dissimilarities between distances from the rocky reefs

NP-MANOVA		(a) Start			(b) End		
Source of variation	Df	MS	<i>F</i>	<i>P</i>	MS	<i>F</i>	<i>P</i>
Reef = Re	1	22833	18.89	***	22339	17.54	***
Distance = Di	1	7953	0.834	NS	10621	0.835	NS
Re × Di	1	9554	7.907	***	12722	9.992	***
Residual	28	1208			1273		
Bray–Curtis dissimilarities			(c) Within		(d) Between Distances		
			Close	Far	Close vs. far		<i>P</i>
Yarra	Start		46	38	43		NS
	End		35	45	49		***
Breakwall	Start		61	43	81		***
	End		55	55	87		***

Note that sites were pooled ($n = 8$; NS = $P > 0.05$, *** = $P < 0.001$).

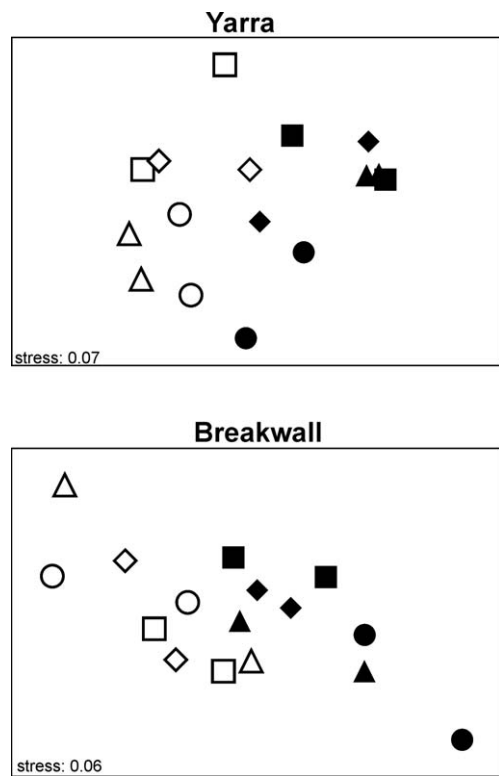


Fig. 2. nMDS ordinations comparing assemblages at each distance for each rocky reef. Different symbols are different treatments (cage = squares, side = diamonds, top = triangles, uncage = circles) and different colours are different distances (black = close, white = far). Cores from each unit of similar treatment in each distance at each site were summed ($n=4$).

further away. Nevertheless, only at the start of the experiment was the variability of the structure of the macrofaunal assemblages as expected (i.e., greater variability among replicates sampled close to than among replicates sampled far from the reef; Table 1c).

Table 2

NP-MANOVA testing for differences in the structure of macrofaunal assemblages between distances (close and far) from rocky reefs; (a) among treatments at the rocky reef Yarra and (b) at the rocky reef Breakwall; (c) Mean Bray–Curtis dissimilarities among replicates and between the different treatments (cage = Cg, side = Si, top = To, uncaged = Un)

NP-MANOVA		(a) Yarra				(b) Breakwall			
Source of Variation	Df	MS	F	P	MS	F	P		
Distance = Di	1	6348	9.92	***	8375	5.38	***		
Treatment = Tr	3	1301	2.03	*	1446	0.93	NS		
Di x Tr	3	842	1.31	NS	1773	1.14	NS		
Residual	8	640			1558				

(c) Dissimilarities									
Yarra	Close					Far			
		Cg	Si	To	Un	Cg	Si	To	Un
	Cg	46				42			
	Si	49	50			44	43		
	To	45	46	41		45	42	37	
	Un	53	50	52	37	47	42	39	40

Breakwall	Close					Far			
		Cg	Si	To	Un	Cg	Si	To	Un
	Cg	42				34			
	Si	41	35			41	44		
	To	37	36	31		50	53	61	
	Un	41	43	32	23	43	47	55	47

($n=2$, * = $P < 0.05$, *** = $P < 0.001$).

3.1.2. Caging experiment

3.1.2.1. Multivariate results. For each reef, comparisons of treatments at the same distance were complex (Fig. 2). NP-MANOVA showed significant differences between distances at each reef and, between treatments only at Yarra (Table 2a,b). Nevertheless, a posteriori tests fail to detect consistent differences between treatments at this reef. Close to each reef, the dissimilarities among replicates from uncaged plots were smaller than those from the other treatments (Table 2c).

The n-MDS plot indicated that assemblages were not different between treatments. This ordination did also, however, show that reefs were separated (Fig. 3).

3.1.2.2. Univariate results. Close to each rocky reef, there was greater numbers of individuals in uncaged treatments than at any other treatment (Fig. 4a), and there were significant differences between treatments at Yarra (Table 3). However, the SNK tests fail to detect consistent differences between treatments at this reef. Crustaceans showed the same pattern (Fig. 4d) however, this pattern was not significant. Close to Breakwall, Molluscs showed a similar pattern, but not significant (Fig. 4e). The numbers of taxa and polychaetes (Fig. 4b,c) did not show any significant differences.

Taxa that were abundant and/or frequent in the samples were the polychaete families Syllidae (13% of the total number of individuals and present in 98% of the samples), Capitellidae (1% and 39%), Pisionidae (7% and 66%) and Eunicidae (4% and 66%); the amphipods Phoxocephalidae (14% and 91%), one unidentified Gammaridae (17% and 84%), Dexaminidae (8% and 31%), Caprellidae (2% and 38%); the isopods from the families Cirolanidae (3% and 23%) and

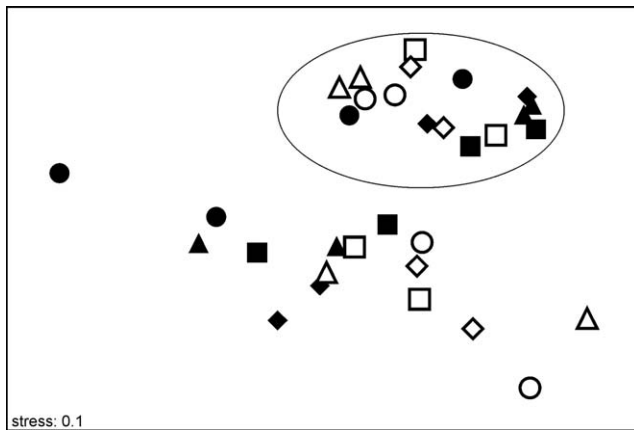


Fig. 3. nMDS ordination comparing assemblages in each treatment (caged = squares, side = diamonds, top = triangles, uncaged = circles) at each distance (black = close to the reefs, white = far from the reefs) at each rocky reef (Yarra = symbols inside the ellipse, Breakwall = symbols outside the ellipse). For each rocky reef, cores from each unit of similar treatment in each distance at each site were summed ($n = 4$).

Sphaeromatidae (9% and 33%); a micro-bivalve from the family Veneridae (8% and 48%) and oligochaetes (4% and 49%).

Most of these taxa showed no consistent differences between treatments (Figs. 5 and 6, Table 3). Veneridae showed significant greater numbers in uncaged treatments than at any other treatment close to the Breakwall (Fig. 6a, Table 3, SNK: $p < 0.05$). Far from Yarra, Gammaridae were significantly more abundant in top and uncaged than in caged and side treatments (Fig. 5d, Table 3, SNK: $p < 0.05$). Phoxocephalidae were more abundant in uncaged treatments at Yarra (Fig. 5b, Table 3, SNK: $p < 0.05$).

Few taxa showed significant differences at different distances from the reefs. Phoxocephalidae and Dexaminidae showed significant greater numbers close to than far from Yarra (Fig. 5b and Fig. 6e, respectively; Table 3; SNK: $p < 0.05$) and Gammaridae, Cirolanidae, and Sphaeromatidae showed similar pattern at Breakwall (Figs. 5d,f and 6d, respectively; Table 3; SNK: $p < 0.05$). The opposite pattern (i.e., significant more abundant far from than close to the reef) was observed for Oligochaetes and Capitellidae at Breakwall (Fig. 5c and Fig. 6b, respectively; Table 3; SNK: $p < 0.05$), and Caprellidae and Veneridae at Yarra (Fig. 5e and Fig. 6a, respectively; Table 3; SNK: $p < 0.05$).

3.2. Sediments

The organic content of the sediments were very low, never exceeding 3%, as expected for sandy bottoms. The sediments were composed mainly of medium sand (0.250–0.500 mm; $53.2\% \pm 1.3$; mean \pm S.E.) followed by pebble (mostly shell debris >4 mm; $16.4\% \pm 1.1$; mean \pm S.E.).

Some sediment fractions, together with organic content, showed significant differences among distances (Table 4). The percentages of organic content, carbonates, pebble, and very coarse sand were significantly greater close to than far from Breakwall (Table 4; SNK: $p < 0.05$). At Yarra the percentage

of pebble showed similar trend, but was not statistically significant, and the percentage of very coarse sand showed the opposite pattern (i.e., far $>$ close; Table 4; SNK: $p < 0.05$). The percentage of medium sand was significantly greater close to Yarra and smaller close to Breakwall (Table 4; SNK: $p < 0.05$). The percentage of fine sand was significantly smaller close to than far from both reefs (Table 4; SNK: $p < 0.05$). Very fine sand was significantly more abundant far from than close to Yarra (Table 4; SNK: $p < 0.05$).

4. Discussion

Some of the most common models employed to explain differences between the structure of macrofaunal assemblages close to and far from rocky reefs are differences in sediment grain size and predation by reef-associated fish. Several studies suggest predation as an important factor in shaping the structure of subtidal sandy-bottom benthic macrofaunal assemblages (e.g., Arntz, 1977; Virnstein, 1978; Hulberg and Oliver, 1980; VanBlaricom, 1982; Posey and Ambrose Jr., 1994). These studies were, however, poorly replicated or unbalanced, and may have confounded the interpretation of the results. For example, VanBlaricom (1982) suggested that manipulating high density populations of a species of crab (*Portunus xantusii*) have important negative effects on some infaunal populations. Nevertheless, he used much higher densities of crabs inside cages than those naturally encountered in the natural habitat and did the experiment at a single site. Posey and Ambrose Jr. (1994) suggested that predation is important in determining the patterns of abundance of benthic macrofauna in sediments around an offshore hard bottom reef. Due to loss of cages, however, their exclusion experiment had little replication. Virnstein (1977) observed an increase in abundance of macrofauna inside cages and suggested that infaunal population sizes are limited by predation. Nevertheless, his results are confounded by the use of an unbalanced experimental design (i.e. several types of cages and controls in different places at different times). If the experimental design of the present study had been done only at two sites far from the Breakwall, it would show a strong influence of predation over pisionids. At multiple locations and distances, however, these patterns were not consistent.

Few studies have suggested a weak effect of predation on macrofaunal assemblages in subtidal sands. Hall et al. (1990a), based on the results of inclusion experiments, suggested that neither predation nor disturbances by dabs (*Limanda limanda*) are likely to be important for populations of prey. They also had problems associated with caging. For example, some of the fish escaped from the enclosures and consequently decreased initial replication. In another experimental inclusion, Hall et al. (1990b) found little evidence that predation by a crab (*Liocarcinus depurator*) had any significant effect on the abundance of benthic species. Nevertheless, they also had several problems (e.g., some cages were unsuccessful in maintaining densities of crabs at the chosen levels). These

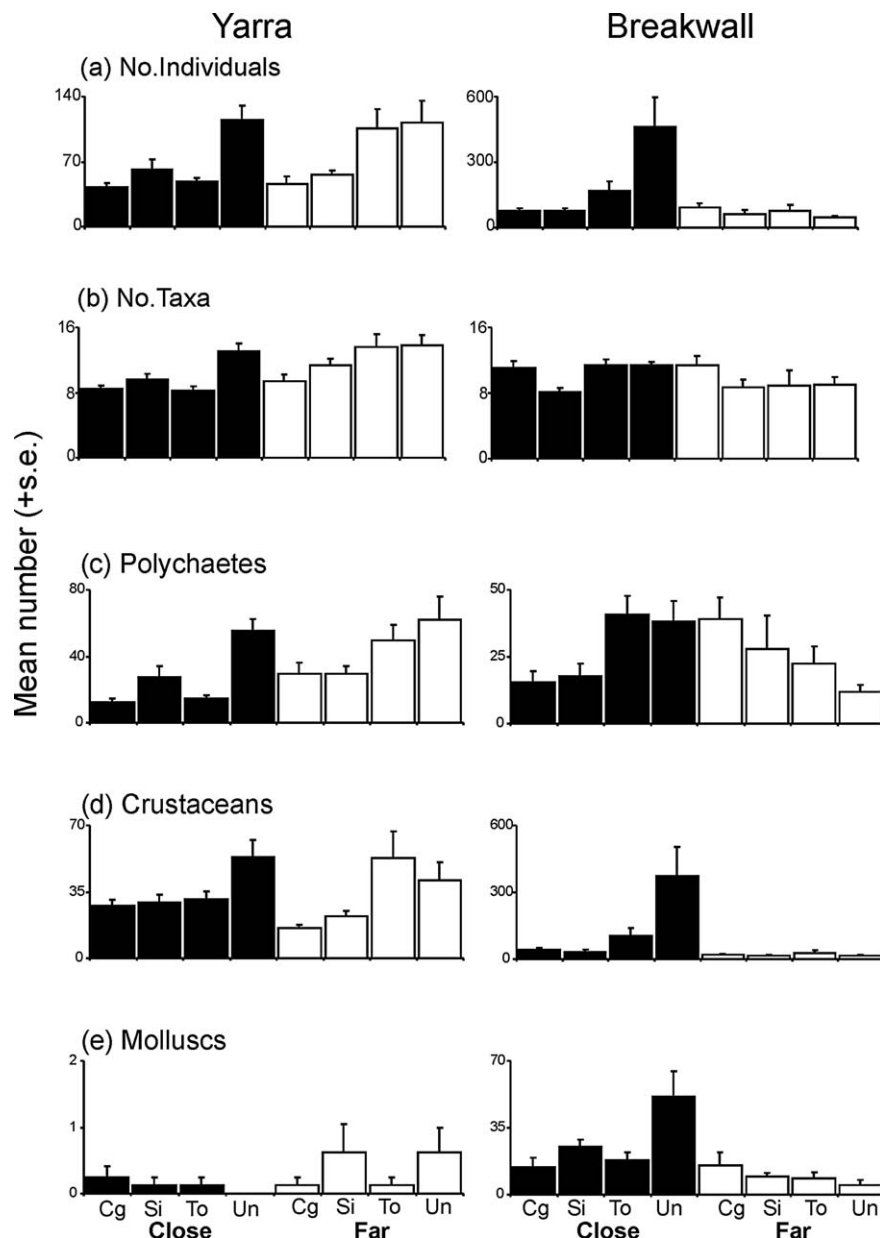


Fig. 4. Mean (+SE) number of individuals (a), taxa (b), polychaetes (c), crustaceans (d) and molluscs (e) in each treatment (Cg = caged, Si = side, To = top, Un = Uncaged) at each distance (black = close, white = far) at each rocky reef. Note that the two sites were combined ($n=8$).

authors recognised that the interpretation of experiments where there are no significant effects is problematic; the lack of effect may be real, or the experimental design may be inadequate for detecting the effect using inferential statistics.

Predicting the impact and importance of predators in subtidal benthic systems is difficult because we know relatively little about the behaviour and natural history of most of the species in these assemblages (Hall et al., 1990c). For example, prey movements can cause the effects found in small-scale experiments to be severely biased estimates of the population effects of predation on prey populations (Englund and Olsson, 1996). Thrush (1999) emphasised a number of important factors that can modify the way predation influences macrobenthic assemblages. He suggested that, to evaluate the effects of predation in soft-sediment assemblages, it is nec-

essary to know more about the biology of predators and prey, particularly in relation to different scales of heterogeneity within sediments.

In the present study, the multivariate analyses showed that, close to each rocky reef, there was less variability at the uncaged than at the other treatments, potentially indicating a caging artifact. Concomitantly, the univariate analyses showed that the partial and full cages occasionally influenced negatively the abundance of invertebrates (i.e., invertebrates in cage, side and top treatments showed smaller numbers than in uncaged treatments). For example, this was a significant pattern showed by Veneridae close to the Breakwall and by Phoxocephalidae at Yarra at both distances.

It is possible that the partial and full cages could have had some influence on the movement of the sediment (i.e., bed-

Table 3

Summary of significant results from two factor ANOVA comparing numbers of benthic invertebrates in four treatments (Tr, fixed: cage, side, top, uncaged), at two distances (Di, fixed: close, far) in two rocky reefs (Yarra and Breakwall)

		Yarra				Breakwall		
		Di	Tr	Di × Tr		Di	Tr	Di × Tr
Individuals		NS	*	NS	¹	NS	NS	NS
Phoxocephalidae		*	**	NS		NS	NS	NS
Oligochaetes		NS	NS	NS	¹	**	NS	NS
Gammaridae		–	–	**	¹	***	NS	NS
Caprellidae		*	NS	NS		–	–	*
Cirolanidae	²	NS	NS	NS	¹	*	NS	NS
Veneridae	¹	**	NS	NS		–	–	*
Capitellidae		NS	NS	NS		**	NS	NS
Pisionidae	¹	NS	NS	NS		–	–	*
Sphaeromatidae		NS	NS	NS	¹	*	NS	NS
Dexaminidae	¹	*	NS	NS	¹	NS	NS	NS

($n=2$, NS = $P > 0.05$, * = $P < 0.05$, ** = $P < 0.01$, ¹ Ln ($x + 1$) transformed, ² Cochran's test was significant, – appear when interaction is significant and consequently the main factors are irrelevant).

load movement). Thus, sediment transport was probably different between the partial and full cages compared to undisturbed areas (uncaged) and negatively affected the abundance of the invertebrates. It would, however, be very unlikely that this alteration would not cause changes in characteristics and/or composition of the sediments. Additionally, during the experiment there were a few storm events. Potentially, these storms might also have affected the macrofaunal assemblages, defaunating the sediments. Thus, would be possible that the recruitment would have been different in uncaged than in the partial and full cages.

The physical disturbance caused by the construction of the cages, could potentially also influence the structure of the benthic assemblages. The physical disruption of the sediments has been shown to affect the structure of benthic assemblages in soft-sediments (Skilleter, 1996). There are no data to test such disturbance, however, considering that natural disturbances by wave-action are fairly common at the sites studied, it is very unlikely that the disturbance caused by the construction of the cages would had an affected on the structure of the macrofauna after 3 months. Moreover, there is evidence that benthic assemblages in soft sediments can rapidly recover from small disturbances (e.g., VanBlaricom, 1982; Thrush, 1999).

The attraction of predators to cages structures could, on the other hand, affect the results of the experiment. It could be suggested that all predators were excluded by the full cage treatment, some were not excluded by the side treatments, and others not excluded by the top treatments. However, such attraction was not observed during the course of the experiment (i.e., fish counts were made and there were no greater numbers of fish close to any treatment).

The results of this experiment showed no evidence for effects of predation. Nor could differences in sediments explain the observed patterns. The structure of the macrofaunal assemblages close to reefs was, nevertheless, different from those far from the rocky reefs. Artificial and natural rocky reefs may affect nearby macrofaunal assemblages in several ways. For example, the movement of water near rocky

reefs could modify the nearby soft sediments, affecting the abundance and type of suspended particles, the stability of the substratum and availability of food (Ambrose and Anderson, 1990). Additionally, because composition of species and abundances are influenced by the presence of larvae in given localities, natural variations in larval dispersion and recruitment caused by reefs may also contribute to explain these differences.

Another model that could explain differences between assemblages close to and far from the rocky reefs is dissimilarities in the heterogeneity of the sandy bottom close to and far from the reefs. For example, it has been shown that, as the amount and complexity of physical structure in a habitat increases, the diversity and abundance of associated organisms also generally increase (MacArthur and MacArthur, 1961; Kohn and Leviten, 1976; Stoner, 1980; Beck, 2000). Furthermore, spatial heterogeneity can alter the effects of predation by lessening its impact on the benthos, through the provision of a spatial refuge and by decreasing foraging efficiency of predators (Gilinsky, 1984; Sih et al., 1985; Skilleter, 1994).

The results showed that sediments far from the reef had finer sands than those close to the reefs, concordant with results obtained from other reefs in the same area (Barros et al., 2001). An increase in coarser fractions close to the reef could lead to an increase in the spatial heterogeneity of the sediments when compared with those far from the reef (which are more homogeneous, composed of fine sand).

Another issue that should be considered here are potential differences between ripple marks close to and far from the reefs. During the experiment, there appeared to be no differences in the pattern of ripple marks due to the construction of the cages and partial cages (personal observations) and, for the purposes of this study, the samples were randomly allocated between crests and troughs. This potential influence of microtopography was studied by Barros et al. (2004), although, needs further investigation.

It has been argued that the effects of predation may be most drastic in physically controlled environments (Sanders,

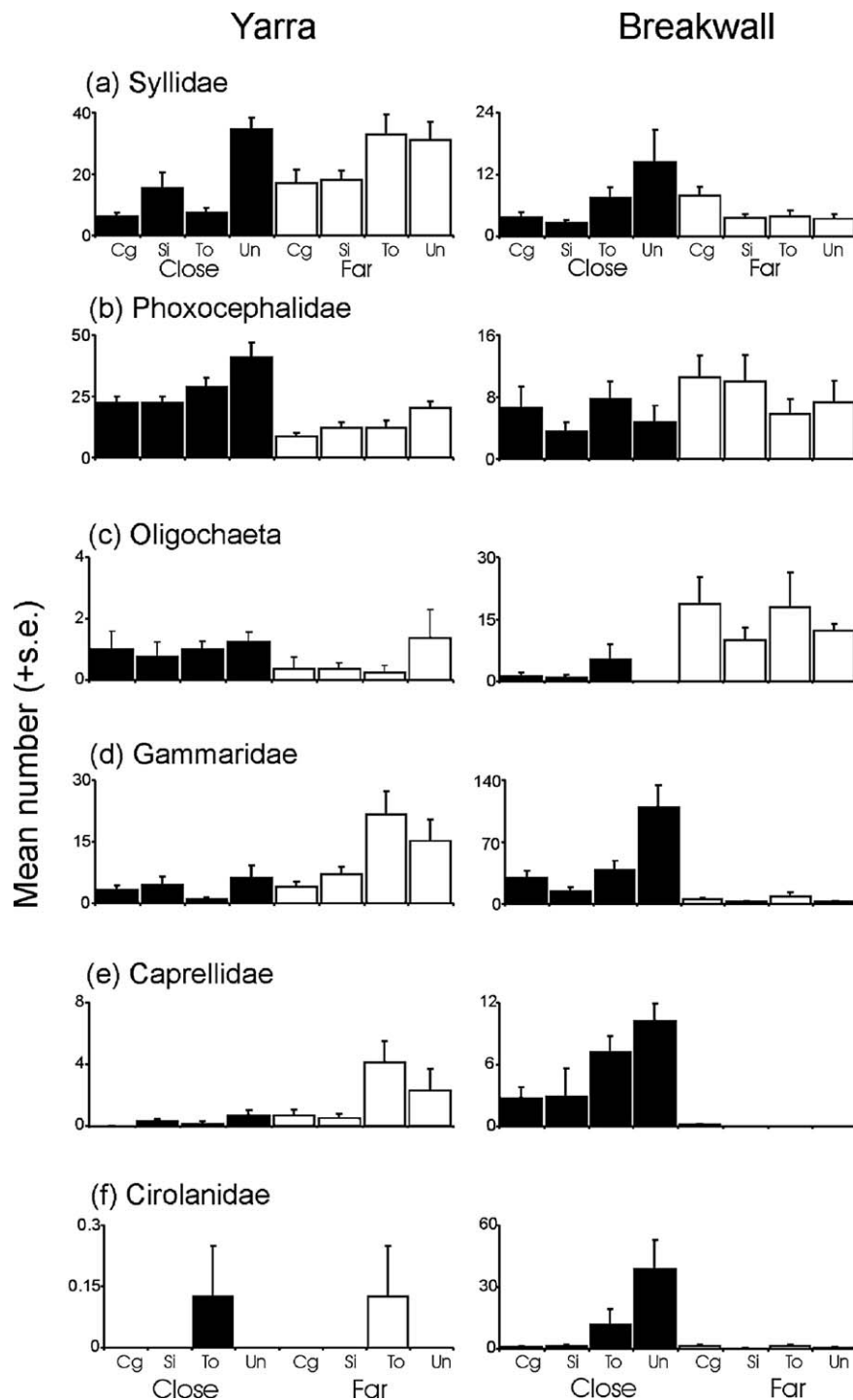


Fig. 5. Mean (+SE) number of Syllidae (a), Phoxocephalidae (b), Oligochaeta (c), Gammaridae (d), Caprellidae (e) and Cirolanidae (f) in each treatment (Cg = caged, Si = side, To = top, Un = Uncaged) at each distance (black = close, white = far) at each rocky reef. Note that the two sites were combined ($n=8$).

1968) and, alternatively, that predation intensity is more important in benign than in harsh soft-sediment habitats (Peterson, 1991). In the present study, it seems that factors other than predation or grain size, caused the observed differences in the structure of the benthic macrofaunal assemblages close to and far from rocky reefs. More likely, it is a combination of several factors acting together. In this case, results of experiments testing one or two processes separately may lead to an erroneous conclusion of lack of impor-

tance in explaining the observed patterns. For the spatial and temporal scales used in this study, it was, however, clear that, although predation maybe intense, on its own it cannot explain the differences in the structure of the benthic assemblages. Additional experiments at different spatial and temporal scales might assist to understand if predation can really affect these assemblages.

Nevertheless, based on this study and a number of others that had problems associated with caging experiments, it is

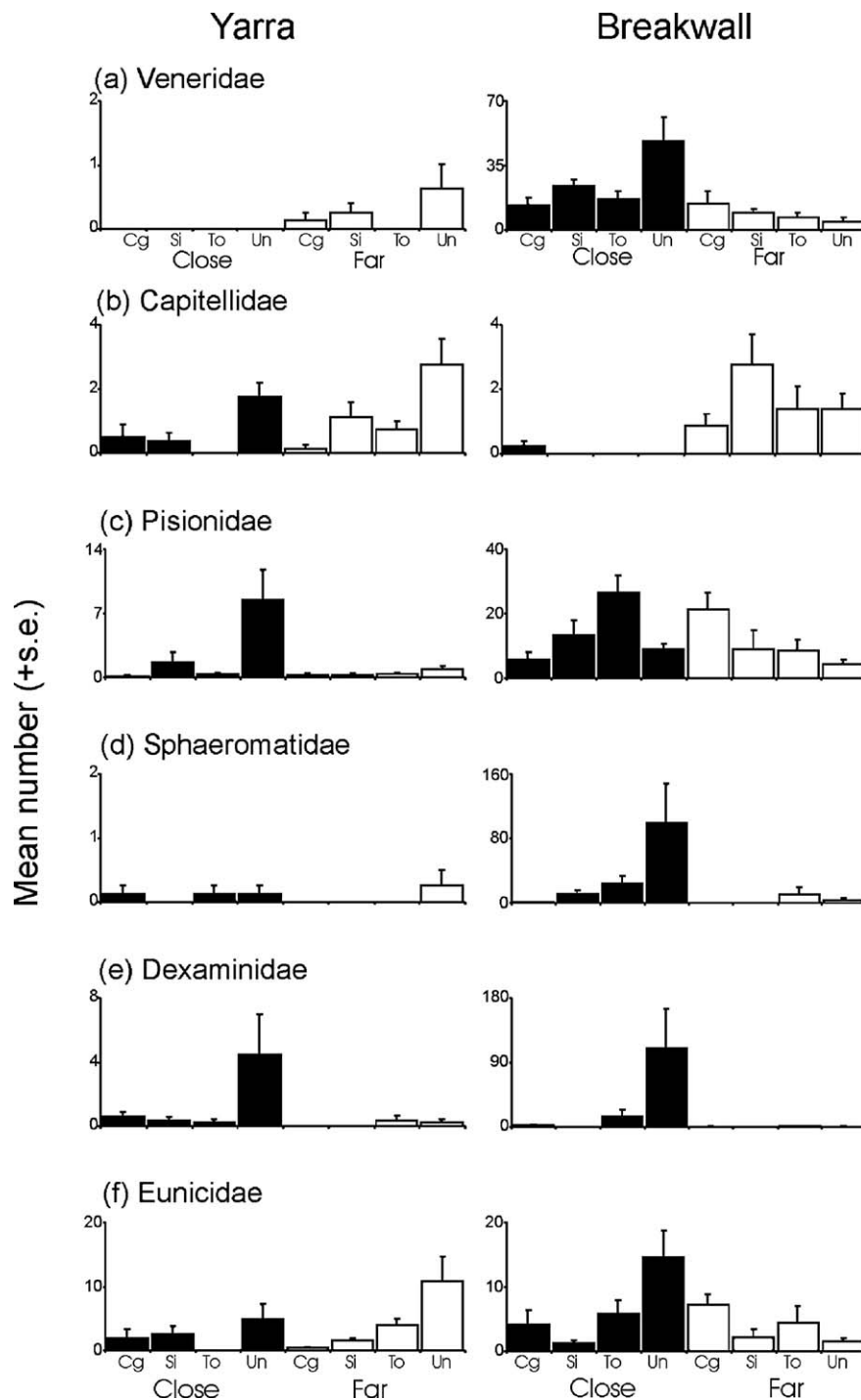


Fig. 6. Mean (+SE) number of Veneridae (a), Capitellidae (b), Pisionidae (c), Sphaeromatidae (d), Dexaminidae (e) and Eunicidae (f) in each treatment at each distance (Cg = caged, Si = side, To = top, Un = Uncaged) at each distance (black = close, white = far) at each rocky reef. Note that the two sites were combined ($n=8$).

remarkable the logistical difficulties in caging experiments in subtidal habitats, and it is suggested that we need to think carefully how to control artifacts. Possibly, alternative ways need to be found to test predictions about the influence of predation on the structure of macrofaunal assemblages inhabiting sandy bottoms. Finally, it is necessary to acknowledge that experimental treatments can give distinct results at dif-

ferent sites. Thus, manipulative studies should encompass different spatial scales.

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Table 4

Summary of results from two factor ANOVA and SNK tests (in italics) comparing percentages of organic content, carbonates and different fractions of sediment in four treatments (Tr, fixed: Cg = cage, Si = side, To = top, Un = uncaged), at two distances (Di, fixed: clo = close and far = far) in two rocky reefs (Yarra and Breakwall

	Yarra			Breakwall		
	Di	Tr	Di × Tr	Di	Tr	Di × Tr
Organic Content	NS	NS	NS	*	NS	NS
Carbonates	NS	NS	NS	*	NS	NS
Pebble (>4 mm)	NS	NS	NS	*	NS	NS
Granule (2–4 mm)	**	NS	NS	NS	NS	NS
Very coarse sand (1–2 mm)	***	NS	NS	**	NS	NS
Coarse sand (0.5–1 mm)	NS	NS	NS	NS	NS	NS
Medium sand (0.25–0.5 mm)	***	NS	NS	**	NS	NS
Fine sand (0.125–0.25 mm)	***	NS	NS	***	NS	NS
Very fine sand (0.063–0.125 mm)	**	NS	NS	NS	NS	NS

($n=2$, NS = $P > 0.05$, * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$).

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