



Effects of habitat modification in mangroves on the structure of mollusc and crab assemblages

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Abstract

The abundance and species richness of mollusc and crab assemblages were examined in a subtropical mangrove forest in Moreton Bay, Queensland, Australia, which has been disturbed and damaged by the construction of a wooden boardwalk and a path. Sections of the forest immediately adjacent to the boardwalk and path were compared with reference areas to determine whether changes to the small-scale structural complexity within the forest affected the benthic fauna. The disturbed area was characterised by having 65–80% fewer pneumatophores, significantly fewer species and individuals of molluscs, but significantly more species and individuals of crabs than the reference areas.

The abundance of mangrove pneumatophores and the attached epiphytic algae were manipulated at two sites to determine whether observed differences in these features could account for the differences in the assemblage of molluscs in the disturbed area of the forest compared with reference areas. Five experimental treatments were used: undisturbed controls, pneumatophore removals (abundance reduced by ca. 65%), epiphytic algal removals (algae removed from ca. 65% of pneumatophores), pneumatophore disturbance controls and algal disturbance controls. The experimental reduction of the abundance of mangrove pneumatophores and the associated epiphytic algae led to significant declines (by as much as 83%) in the number of molluscs utilising the substratum in the modified plots. There was no significant difference in the abundance of molluscs in the pneumatophore and algal removal plots suggesting any effect was primarily related to removal of the epiphytic algae from the surface of the pneumatophores.

The responses by the biota to the changes in the physical environment demonstrate that even relatively small-scale modifications to the physical structure of subtropical mangrove forests can lead to significant effects on the diversity and abundance of macrobenthic organisms in these habitats. Such modifications have the potential to cause cascading effects at higher trophic levels with a deterioration in the value of these habitats as nursery and feeding grounds. Future efforts at conservation of these estuarine environments must focus on the prevention or reduction of modifications to the physical structure and integrity of the system, rather than just on the prevention of loss of entire patches of habitat. © 2000 Elsevier Science B.V. All rights reserved.

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1. Introduction

Much attention has been focused on the effects of loss of habitat on the diversity and abundance of organisms in aquatic environments (e.g. freshwater submerged aquatic vegetation — Kelso et al., 1996; subtidal kelp forests — Foster and Schiel, 1985; Fielding et al., 1994; mangroves and seagrasses — Hatcher et al., 1989). Declines in the world-wide distribution of vegetated estuarine habitats such as mangroves, saltmarshes and seagrass beds (Saenger et al., 1983; Hatcher et al., 1989) have also been linked to reductions in the secondary production of coastal and nearshore fisheries (e.g. Robertson and Duke, 1987). Reduced secondary production in coastal fisheries could be mediated through reductions in primary production and subsequent export of nutrients and carbon from mangroves to nearshore area ecosystems (e.g. Lugo and Snedaker, 1974; Odum and Heald, 1975; Conacher et al., 1996), or through a reduced value of the habitat in providing protection from predators and/or an abundant food source for juvenile fishes and crustaceans (Robertson, 1988; Hatcher et al., 1989; Robertson and Blaber, 1992).

The complex system of prop-roots and pneumatophores in mangrove forests, in conjunction with an often dense layer of leaf litter and detritus on the substratum, provides ample cover from predators for small invertebrates and juvenile fish (Odum and Heald, 1972; Thayer et al., 1987; Hatcher et al., 1989). Accumulations of detritus and leaf material in mangroves might also provide an enhanced food source for animals such as small crustaceans and polychaetes (e.g. Daniel and Robertson, 1990). Some studies have examined effects of mangrove loss on benthic and epibenthic animals (e.g. Levings et al., 1994) but few studies have examined how smaller-scale modification of habitat complexity affects the biodiversity and abundance of mangrove-associated fauna (reviewed by Hatcher et al., 1989). Of those studies that have looked at the impact of modification within mangroves, one reduced the abundance of oysters which provide hard substrata for littorinid snails in mangrove forests (Underwood and Barrett, 1990) and found the density of snails decreased substantially. Another found that the ocypodid crab, *Heloecius cordiformis* (H. Milne-Edwards, 1837), did not respond to changes in the density of pneumatophores, the abundance of epiphytic algae or the density of roots in the substratum but did respond to the presence of softer mud in which to burrow (Kelaher et al., 1998b). A third study (McGuinness, 1992), found the abundance of the snail, *Cerithidea anticipata*, varied among sections of mangroves subjected to different levels of disturbance.

This study examined the structure of crab and mollusc assemblages in a subtropical mangrove forest where the physical structure of the habitat has been modified by the construction of a boardwalk and path to allow public access into the habitat. This allowed us to test the general hypothesis that habitat modification and changes to the structural complexity would significantly affect the diversity and abundance of macrobenthic organisms in a mangrove system. Conservation efforts for these systems often focus on the preservation of entire patches of habitat, rather than reducing smaller-scale

modifications to the system, yet if such modifications impact significantly on the resident biota, there is a great potential for cascading effects through higher trophic levels.

2. Materials and methods

2.1. Study sites

This study was done along the western shore of Moreton Bay, Queensland, in the Boondall Wetlands Reserve, north of Brisbane (Fig. 1). Moreton Bay is a large subtropical estuarine embayment on the east coast of Australia (lat. 27° 20' S, long. 155° 55' E), enclosed by the mainland in the west and sand barrier islands in the east. The Boondall Wetlands Reserve provides protection for grasslands, *Melaleuca*-dominated woodlands, saltmarshes, mangrove forests and mudflats along the southern shoreline of Bramble Bay (Shilton, 1993). The mangrove forests within the Reserve cover ~10 km² in area and are dominated by the grey mangrove *Avicennia marina* (Forsk.) Vierh., with occasional single mature trees of *Rhizophora stylosa* (Griff.), *Ceriops tagal* (C.T. White) and *Aegiceras corniculatum* (L.). Two creeks, Nundah and Nudgee, meander through the Reserve, dissecting the mangrove forest into three individual stands, two of which were chosen as study areas (0.5 km² and 3.0 km² in area; Fig. 1).

A wooden boardwalk through part of the mangrove forest was constructed in October 1994 to facilitate public access through the wetland habitats, while limiting direct damage to plants and animals from trampling and other forms of disturbance. The boardwalk starts at the terrestrial edge of the Reserve and runs parallel with Nudgee Creek. It stands ~1 m above the substratum with support pilings constructed of pine logs buried in concrete. At the end of the boardwalk, access through the wetlands is an unpaved pathway, ~25–100 cm in width, created by continual trampling and compaction of the substratum. During construction of the boardwalk, branches and some trees were removed creating gaps in the overhead canopy, but there were still abundant mangrove saplings and accumulations of leaf litter in the immediate vicinity of the boardwalk and path (see Section 3).

2.2. Sampling design

To determine whether the abundance of crabs and molluscs in the mangroves varied in relation to the presence of the boardwalk and path, the different assemblages around the boardwalk/path and at two reference locations were sampled. The sampling design was based on Underwood's Beyond-BACI asymmetrical analyses of variance (e.g. Underwood, 1993), where a single putatively impacted location (containing the boardwalk and path) was compared with the average of two reference locations. The Beyond-BACI designs have been modified here to take into account that data were only collected after the construction and development of the boardwalk and path (e.g. Glasby, 1997).

The two reference locations were separated from each other by 700 m and from the boardwalk/path location by Nudgee Creek (Fig. 1), which limited human access to

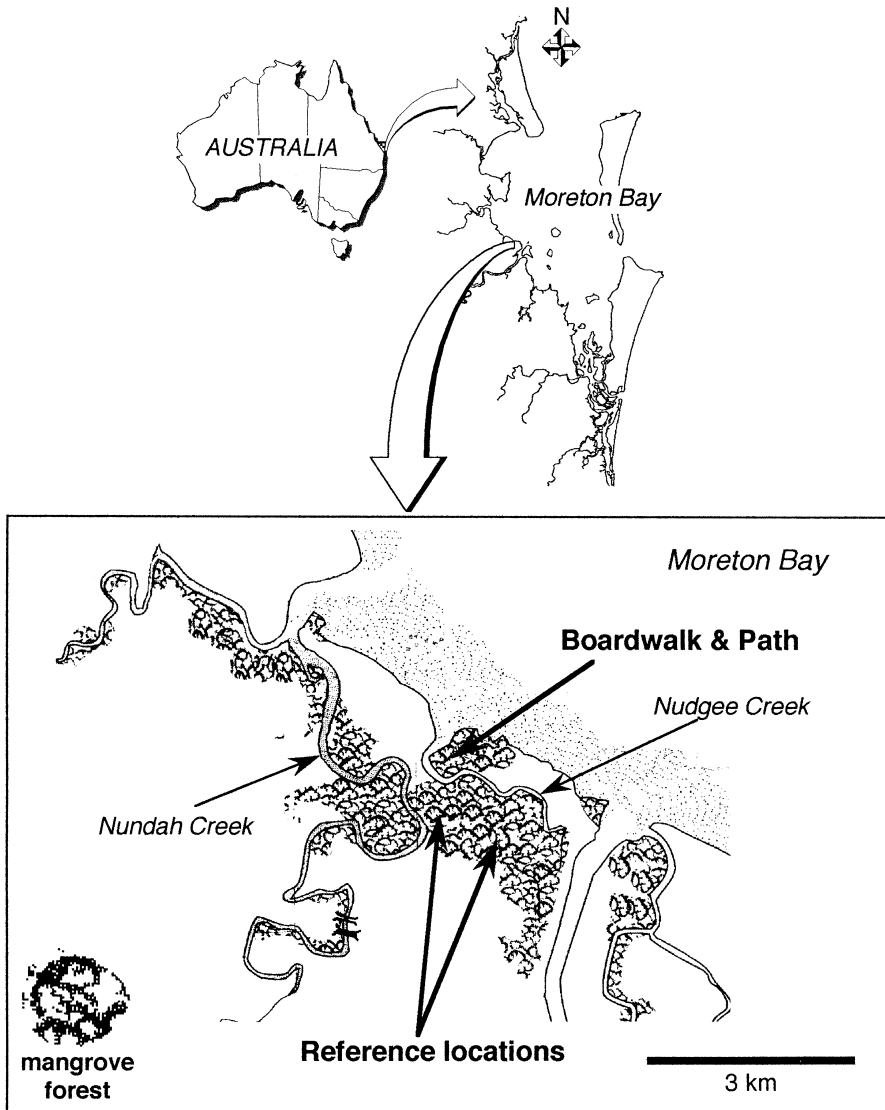


Fig. 1. Map of Australia showing the location of Moreton Bay, in SE Queensland and an expanded map of the Boondall Wetlands Reserve north of Brisbane showing the disturbed area and the two control areas used in this study.

these. There were few obvious signs of human damage in either of the reference locations (e.g. Skilleter, 1996b).

Samples were collected in two different habitats within the mangrove forest to take account of the fact that the boardwalk passed along the edge of the mangrove–terrestrial interface in several areas, while along the rest of its length it was completely surrounded

by mangrove trees. The proximity to alternative types of habitat has been shown to have important influences on the abundance and diversity of animals in other estuarine systems (e.g. Irlandi and Crawford, 1997).

The mangrove–terrestrial interface (hereafter referred to as the ‘edge’ habitat) was characterised by nearby (10–15 m away) *Casuarina* and *Melaleuca* trees, and the mangrove trees were less abundant than in other sections of the mangrove forest (hereafter referred to as the ‘forest’ habitat). The path only passed through the forest habitat, so comparisons between this section of the putatively impacted location and the reference locations were only made for a single habitat (see Section 2.5). The sections along the boardwalk sampled in edge and forest habitat were ~150 m apart. Within each habitat × location combination, samples were collected from three randomly selected sites, each ~40 m apart and 1–5 m from the boardwalk or path (in the impacted location), well within the area where there was visible signs of modification to the surrounding environment.

2.3. Mollusc assemblage

Four randomly selected 0.1 m² (~0.32 × 0.32 m) quadrats were sampled to determine the abundance and species richness of molluscs at each site within each habitat × location combination. In each quadrat, the numbers of pneumatophores and mangrove saplings were counted and the leaf litter and debris were removed and placed into a labelled plastic bag. A spoon was then used to scoop off the upper 3–4 mm of sediment, above the mangrove nutritive root layer, into a bag. Molluscs were rarely found within the root mat, but were present in the thin overlying layer of sediment (see also Skilleter, 1996b).

In the laboratory, the contents of the bags were washed over a 0.75-mm sieve and fixed in 70% ethanol within 6 h of collection. The contents of each sample were sorted under a magnifying lamp to remove all molluscs. The material left after removal of the molluscs was then washed over a 2-mm sieve, excess water removed by blotting and placed in preweighed paper bags, dried at 70°C for 4 days and weighed.

2.4. Crab assemblage

The abundance of mangrove crabs in the boardwalk/path location and the two reference locations was determined using pitfall traps. Pilot studies were used to compare estimates of abundance obtained from visual counts (e.g. Warren, 1990), destructive excavation of the burrows (e.g. Sasekumar, 1974) and pitfall traps (e.g. Salmon and Hyatt, 1983). Visual counts were ineffective in the reference locations because the accumulation of leaf litter and density of mangrove saplings made the crabs difficult to identify and count; few species were recorded by this method. Destructive sampling and pitfall traps sampled the same subset of species (unpublished data), but the latter method was less time-consuming and damaging to the mangrove habitat and was chosen for use here.

Each pitfall trap consisted of a 2-l plastic container with 3-mm holes drilled into the side and base to allow drainage of water from the trap at low tide. The traps were closed

with a tight-fitting lid which had a 5-cm funnel attached to the underside, directed downwards. Each trap was baited with a piece of pre-frozen sardine secured to the inside base of the trap. The traps were dug into the substratum so the lid was flush with the surface of the sediment. Any gaps around the edges of the trap were packed with mud to reduce the risk of the traps floating away on a rising tide. Five replicate traps were haphazardly deployed at each site on 14–16 May 1996, and again on 28 June 1996. After 24 h, the traps were removed from the substratum, the plug of sediment originally removed from the hole was replaced, and all crabs from each trap were fixed in 70% ethanol/seawater for later counting and identification.

2.5. Statistical analyses of sampling data

Several different asymmetrical analyses of variance were used to analyse the data on abundances and species richness of crabs, molluscs and the abundance of litter, pneumatophores and saplings. Firstly, the boardwalk location was compared with the two reference locations, incorporating data from each of the two habitats (edge versus forest) as a fixed factor and ‘sites’ as a random nested factor. Secondly, the path location was compared with the two reference locations using only data from the forest habitat because the edge habitat did not occur anywhere along the length of the path. Data on abundances of molluscs were only collected on a single occasion. Analyses on abundances and species richness of crabs also included a factor ‘time’, incorporating data from both sampling dates. Construction of mean square estimates was done using the principles described in Underwood (1993). Post-hoc pooling of mean square estimates was done at $\alpha \geq 0.25$ (Winer et al., 1991). Significance was assessed at the $P < 0.05$ level, although a precautionary approach to interpretation of results has been taken (e.g. Gray, 1996) so where effects were significant at $P < 0.10$ this is also indicated (e.g. Mapstone, 1995).

Differences in the taxonomic composition of the assemblage of molluscs in the boardwalk/path location compared with the two reference locations were determined by non-metric multidimensional scaling (nMDS) on unstandardised fourth root transformed data, using the Bray–Curtis similarity measure (Clarke, 1993). The statistical significance of differences among locations was assessed using analysis of similarities (ANOSIM), a non-parametric method based on randomisation of rank-similarities among all samples (Clarke, 1993). There were insufficient data available to allow similar multivariate analyses to be done for the crab assemblage.

We used the BIO-ENV routine (Clarke and Ainsworth, 1993) to compare the rank-similarity matrices for the faunal data with the matrices created using environmental data based around structural features of the habitats (i.e. numbers of pneumatophores and saplings and the biomass of leaf litter on the substratum). The BIO-ENV procedure compares the two rank-similarity matrices to determine the optimal combination of environmental variables which may help explain the patterns in community structure among samples, as portrayed by nMDS and analysed using ANOSIM (Clarke and Ainsworth, 1993). Data on numbers of pneumatophores were log-transformed to improve the appropriateness of Euclidean distance as a measure of the among-sample dissimilarity for the physical data (Clarke and Ainsworth, 1993).

2.6. Experimental manipulation of habitat

We manipulated the abundance of mangrove pneumatophores and the epiphytic algae covering these pneumatophores to determine whether observed differences in these features could account for the differences in the abundance and species richness of crabs and molluscs between the boardwalk/path location and the average of the two reference locations (see Section 3). The experiment was set up on 26–30 August 1996 at two randomly selected sites in the forest habitat at one of the reference locations.

Five experimental treatments (see below) were required to determine the effects of reducing the abundance of pneumatophores and/or epiphytic algae on the crab and molluscan assemblages. At each of the two sites, $20 \times 0.5 \text{ m}^2$ ($\sim 70.7 \times 70.7 \text{ cm}$) plots were randomly selected on the forest floor and marked on one diagonal with 30 cm lengths of dowel pushed 15 cm into the substratum. Four of these plots were assigned at random to each of the five treatments.

The experimental design was as follows.

Treatment 1: undisturbed controls — plots which were marked in the corners but otherwise undisturbed in any way.

Treatment 2: pneumatophore removals — the density of pneumatophores was reduced by $\sim 65\%$ to 230 m^{-2} , a reduction equivalent to the difference in density between the boardwalk/path location and the reference locations. The pneumatophores were cut with garden shears flush with the substratum and removed.

Treatment 3: epiphytic algal removals — the epiphytic algae were removed from 65% of the pneumatophores leaving the remainder of the pneumatophores undisturbed. The algae were removed by hand until there was no obvious plant material left adhering to the pneumatophores.

Treatment 4: pneumatophore disturbance controls — this treatment controlled for any artifacts associated with the removal of the pneumatophores, such as disturbance to the substratum when pneumatophores were being cut, material leaking from the damaged pneumatophores, etc. To mimic any such effects, 65% of the pneumatophores in the plots were nicked with garden shears at a point flush with the substratum. The cuts in the pneumatophores were only superficial but enough to expose the underlying material.

Treatment 5: algal disturbance controls — this treatment controlled for any artifacts associated with the removal of the epiphytic algae from the surface of the pneumatophores. The algal mat on the pneumatophores was agitated and gently shaken to simulate the effects the disturbance caused while removing the algae (Treatment 3).

One month later, at the end of September 1996, each experimental plot was sampled with a 0.1-m^2 quadrat positioned in the centre of the plot and using the same methods as described above for molluscs. The abundance data from this experiment were analysed using two-factor (treatment-fixed; sites-random), mixed-model analyses of variance and a posteriori Student–Newman–Keuls (SNK) multiple comparison tests. Differences in the taxonomic composition of the molluscan assemblage among the treatments were

determined by non-metric multidimensional scaling (nMDS) on unstandardised fourth root transformed data, using the Bray–Curtis similarity measure. The statistical significance of differences among locations was assessed using analysis of similarities (ANOSIM).

3. Results

3.1. Structure of the habitat

The area around the boardwalk and the path supported 65–80% fewer mangrove pneumatophores than found in the control locations (Table 1; Fig. 2A). There were no significant differences in the number of pneumatophores between the forest and edge habitats, nor were any of the interactions involving habitat significant (Table 1). There was very little variation in the number of pneumatophores between the two control locations (Table 1; Fig. 2A), but there was significant variation at the spatial scales of sites within the boardwalk/path location and the controls.

Although there were fewer saplings found in the proximity of the boardwalk and path than in the controls, these differences were not detected as being significant (Tables 2 and 3). There was substantial variation in the number of saplings at the spatial scale of sites within locations, and also among the control locations (Fig. 2B). The biomass of leaf litter on the substratum near the boardwalk and the path was very similar to the controls (Fig. 2Ci, ii). Again, there was substantial variation in the biomass of leaf litter at the spatial scales of sites and among control locations (Tables 2 and 3).

Table 1

Example of asymmetrical analysis of variance of the number of pneumatophores in 0.1-m² quadrats from two control locations and the boardwalk location. The complete analysis is shown here to illustrate the full design for the sampling programme. Data were untransformed; $n = 4$ quadrats in each site. There were three independent sites sampled in each combination of habitat (forest versus edge) and location (boardwalk versus controls)

Source of variation	df	SS	MS	<i>F</i> -ratio	Sign.	<i>F</i> (df)
Habitat	1	760.50	760.50	0.50	0.55	(1,2)
Locations	2	31 077.03	15 538.51			
B/walk vs. among controls	1		30 829.51	30 829.51	28.36	0.0005 (1,9) ^b
Among controls	1		247.52	247.52	0.21	0.66 (1,12)
Habitat × locations	2	3055.08	1527.54			
H × (b/walk vs. am. cont.)	1		3052.56	3052.56	2.88	0.12 (1,9) ^a
H × among controls	1		2.52	2.52	0.00	0.96 (1,8)
Sites (H × locations)	12	11 937.33	994.78			
Sites (H × b/walk)	4		2400.17	600.04	3.67	0.01 (4,54)
Sites (H × among controls)	8		9537.17	1192.15	7.30	0.00 (8,54)
Residual	54	8820.50	163.34			

^a Tested against pooled term: [habitat × (among controls)] + [sites (habitat × (among controls))] $df = 9$, $SS = 9539.69$, $MS = 1059.97$.

^b Tested against pooled term: [among controls] + [sites (habitat × (among controls))] $df = 9$, $SS = 9784.69$, $MS = 1087.19$.

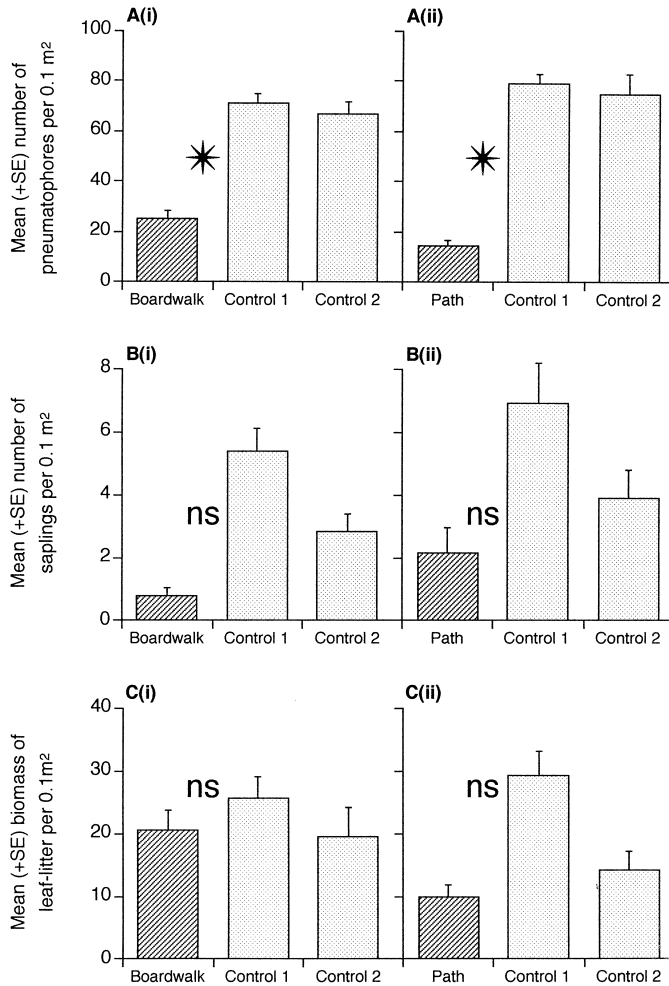


Fig. 2. Mean (+S.E.) number of pneumatophores, saplings, and the biomass of leaf-litter at the boardwalk and path locations and the two control locations. Asterisks indicate significant differences between disturbed location and the average of the controls ($P < 0.05$), ns indicates no significant difference ($P > 0.05$). ($N = 24$ quadrats, pooled across three sites and two habitats for comparisons with the boardwalk location; $N = 12$ quadrats, pooled across three sites for comparisons with the path location).

3.2. Mollusc assemblage

Significantly fewer species of molluscs and individuals (total) were found in the sediments near the boardwalk and path than in the control locations (Tables 2 and 3; Fig. 3A and B). Of the species of molluscs which were sufficiently abundant to analyse separately, *Salinator solida* (von Martens, 1878) was significantly less abundant near the boardwalk but not the path, compared with the controls (Tables 2 and 3; Fig. 3Ci), while the reverse was true for *Melosidula zonata* (H. and A. Adams, 1855) (Tables 2 and 3;

Table 2

Summaries of asymmetrical analyses of variance on the number of saplings and biomass of leaf litter, and the number of species of molluscs, total number of individuals, number of *Modiolus peronianus*, *Melosidula zonata* and *Salinator solida* in 0.1-m² quadrats from two control locations and the boardwalk location. Data for total number of individuals were transformed to $\log_e(x)$. Other details as in Table 1

Source of variation	Saplings	Biomass	Species	Individuals	<i>Modiolus</i>	<i>Melosidula</i>	<i>Salinator</i>
Habitat	$P > 0.355$	$P > 0.515$	$P > 0.990$	$P > 0.468$	$P > 0.376$	$P > 0.390$	$P > 0.817$
Locations							
B/walk vs. among controls	$P > 0.373$	$P > 0.770$	$P < 0.004$	$P < 0.001^a$	$P > 0.452$	$P > 0.172$	$P < 0.053$
Among controls	$P < 0.069$	$P > 0.136$	$P > 0.310$	$P > 0.507$	$P > 0.150$	$P > 0.812$	$P > 0.403$
Habitat × locations							
H × (b/walk vs. am. cont.)	$P > 0.124$	$P > 0.647$	$P > 0.592$	$P > 0.942$	$P > 0.208$	$P > 0.401$	$P > 0.466$
H × among controls	$P > 0.727$	$P < 0.056$	$P > 0.366$	$P < 0.036$	$P > 0.529$	$P > 0.771$	$P > 0.325$
Sites (H × loc)							
Sites (H × b/walk)	$P > 0.773$	$P < 0.001$	$P < 0.003$	$P < 0.001$	$P > 0.875$	$P < 0.061$	$P > 0.724$
Sites (H × am. controls)	$P < 0.001$	$P > 0.117$	$P < 0.003$	$P < 0.044$	$P < 0.004$	$P > 0.1245$	$P < 0.014$
Residual							

^a Tested against pooled term: [among controls] + [sites (habitat × (among controls))]

Fig. 3Cii). There were no significant differences in the abundance of the mytilid bivalve, *Modiolus peronianus* (Laserson, 1956), between the boardwalk and the controls (Tables 2 and 3).

The composition of the molluscan assemblage in the forest habitat near the boardwalk and the path was significantly different from the control locations, with the latter not being different from each other (ANOSIM: boardwalk vs. controls $P < 0.001$; path vs. controls $P < 0.0001$; Fig. 4A and C). The composition of the molluscan assemblage in the edge habitat near the boardwalk was different from each of the controls, but the two control locations also differed from each other (ANOSIM: $P < 0.0001$; Fig. 4B), suggesting these differences are not correlated with the presence of the boardwalk through the edge habitat.

In all cases, the abundance of the pneumatophores alone provided the optimal

Table 3

Summaries of asymmetrical analyses of variance on the number of saplings and biomass of leaf litter, and the number of species of molluscs, total number of individuals, number of *Modiolus peronianus* and *Melosidula zonata* in 0.1-m² quadrats from two control locations and the path location. Data were untransformed; $n = 4$ quadrats in each site. There were three independent sites sampled in each location (path versus controls). Only the forest habitat was sampled (see text for further details)

Source of variation	Pneumat.	Saplings	Biomass	Species	Individuals	<i>Modiolus</i>	<i>Melosidula</i>
Locations							
Path vs. among controls	$P < 0.008$	$P > 0.187$	$P > 0.534$	$P < 0.005$	$P < 0.077$	$P > 0.129$	$P < 0.001$
Among controls	$P > 0.837$	$P > 0.262$	$P < 0.059$	$P > 0.906$	$P > 0.313$	$P > 0.272$	$P > 0.255$
Sites (H × loc.)							
Sites (H × path)	$P > 0.161$	$P > 0.122$	$P > 0.182$	$P < 0.005$	$P > 0.839$	$P > 0.978$	$P > 0.901$
Sites (H × am. controls)	$P < 0.001$	$P < 0.019$	$P < 0.085$	$P < 0.061$	$P < 0.034$	$P < 0.005$	$P > 0.537$
Residual							

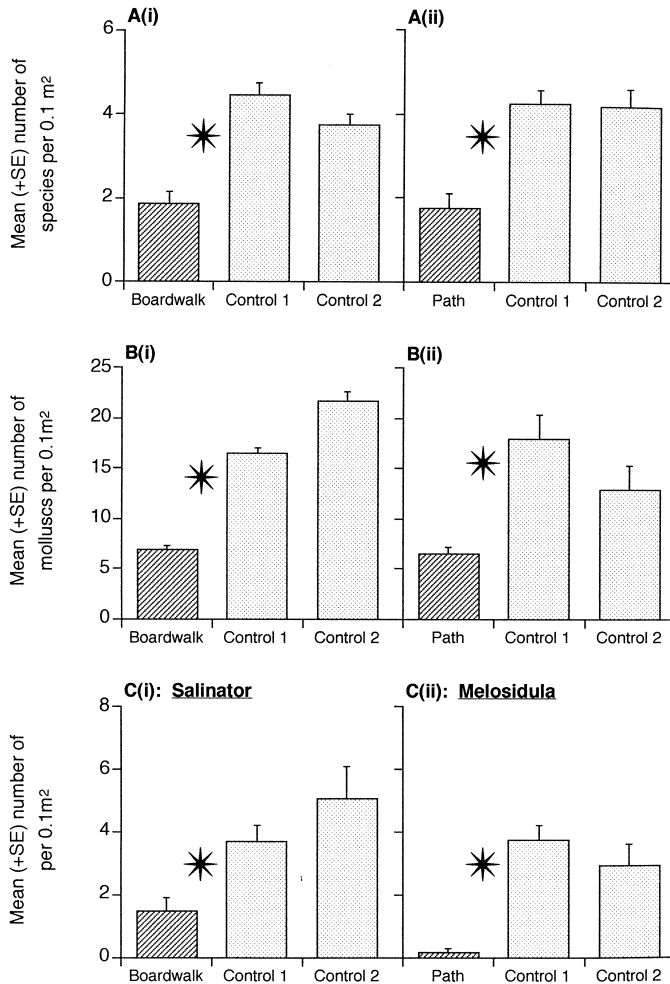


Fig. 3. Mean (+ S.E.) number of species of mollusc, individual molluscs, *Salinator solida* and *Melosidula zonata* at the boardwalk and/or path locations and the two control locations. Other details as in Fig. 2.

correlation between the environmental data (i.e. numbers of saplings and pneumatophores and biomass of litter) and the rank similarities underlying the nMDS based on the molluscan assemblage (BIOENV: $\rho_w = 0.49$ — forest habitat, boardwalk vs. controls; $\rho_w = 0.26$ — edge habitat, boardwalk vs. controls; $\rho_w = 0.38$ — forest habitat, path vs. controls). These results suggest the model that the significant differences in the number of pneumatophores between the boardwalk/path location and the controls was responsible for the observed differences in the abundance and structure of the molluscan assemblage between the treatments. This was examined in the manipulative experiment described below (Section 3.4).

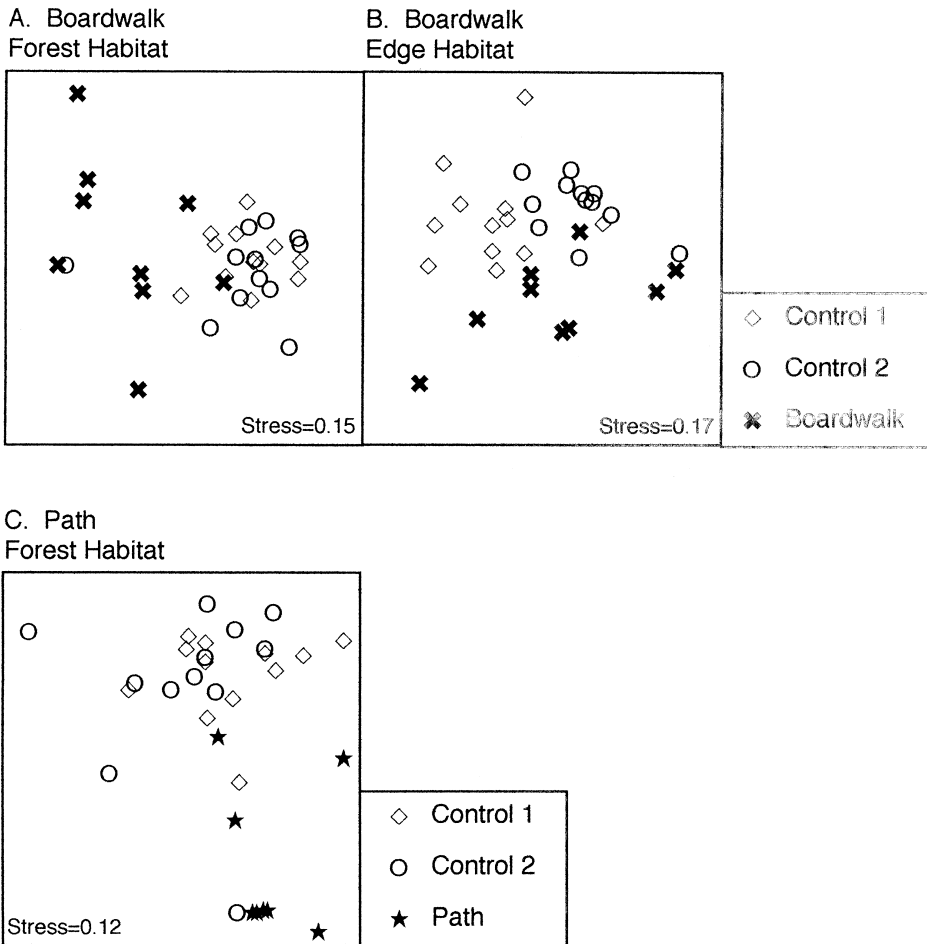


Fig. 4. nMDS ordinations on fourth root transformed species abundance data from quadrats sampled at either the boardwalk or path locations and the two control locations. There were $n = 4$ replicates from each of three sites in the forest and edge habitats (boardwalk comparisons) or forest habitat (path comparisons).

3.3. Crab assemblage

There were significantly more crabs caught per trap (per 24 h trapping period) near the boardwalk than in the control locations (Table 4), although the number of crabs caught near the boardwalk was generally small (Fig. 5A). The number of crabs varied significantly between the forest and edge habitats and between the two times of sampling, but there were no significant interactions between habitat nor time and the comparison of interest, the boardwalk versus the average of the controls (Table 4).

Parasesarma erythroductyla (Hess, 1865) and *Helograpsus haswellianus* were the most abundant of the species caught in the traps, comprising 24% and 52% of the total number of individuals, respectively. No significant treatment effects (i.e. boardwalk vs.

Table 4

Example of asymmetrical analysis of variance of the number of crabs in pitfall traps per 24-h period from two control locations and the boardwalk location on two separate occasions. The complete analysis is shown here to illustrate the full design for the sampling programme. Data were untransformed; $n = 5$ traps in each site. There were three independent sites sampled in each combination of habitat (forest versus edge) and location (boardwalk versus controls)

Source of variation	df	SS	MS	F-ratio	Sign.	F (df)
Time	1	53.35	53.36	22.18	0.042	(1,2)
Habitat	1	37.36	37.36	3.99	0.057	(1,24)
Locations	2	60.08	30.04			
B/walk vs. among controls	1	54.445	54.45	5.17	0.036	(1,1) ^b
Among controls	1	5.633	5.63	0.52	0.481	(1,16)
Time × habitat	1	5.69	5.69	1.61	0.333	(1,2)
Time × locations	2	4.81	2.41			
Time × (b/walk vs. am. cont.)	1	0.01	0.01	0.00	0.974	(1,17) ^a
Time × (among cont.)	1	4.80	4.80	0.44	0.515	(1,16)
Habitat × locations	2	59.81	29.91			
H × (b/walk vs. am. cont.)	1	27.78	27.78	0.87	0.523	(1,1)
H × among controls	1	32.03	32.03	2.95	0.105	(1,16)
Time × habitat × locations	2	7.08	3.54			
Tm × H × (b/walk vs. am. cont.)	1	5.88	5.88	0.57	0.460	(1,17) ^a
Tm × H × (among controls)	1	1.20	1.20	0.11	0.744	(1,16)
Sites (Tm.H.L)	24	224.67	9.36	2.79	0.0001	(24,144)
Sites (Tm.H.L(b/walk))	8	51.20	6.40	1.91	0.063	(8,144)
Sites (Tm.H.L(am. cont.))	16	173.47	10.84	3.23	0.0001	(16,144)
Residual	144	482.80	3.35			

^a Tested against pooled term: [Tm × H × (among controls)] + [sites (Tm × H × (among controls))] df = 17, SS = 174.667, MS = 10.275.

^b Tested against pooled term: [among controls] + [sites (Tm × habitat × (among controls))] df = 17, SS = 179.100, MS = 10.535.

among controls, or associated interactions) were detected for *P. erythroductyla* (Tables 5 and 6). There was a significant time × habitat × treatment interaction detected for *H. haswellianus* (Tm × H × (b/walk vs. am. controls); Tables 5 and 6), resulting from significantly more crabs being caught near the boardwalk than the controls in the edge habitat but not in the forest habitat at time 1, and no differences between treatments at time 2 (Fig. 5B).

There were significantly more species of crabs caught near the path than in the controls at time 1, but the reverse was true for time 2 (time × (path vs. am. controls); Table 6; Fig. 6A). There were substantially more individuals caught near the path than in the controls at time 1 (Fig. 6B) but there was no difference between the treatments at time 2 (Fig. 6B), explaining the significant interaction (time × (path vs. among controls); Table 6). An identical result was obtained for *Helograpsus haswellianus* (Whitelegg, 1889) (Table 6), which comprised 86% of the individuals caught near the path.

3.4. Experimental manipulation of habitat

As expected, the number of pneumatophores was significantly less in the pneumatophore removal plots, compared with all other treatments, but reduction of the

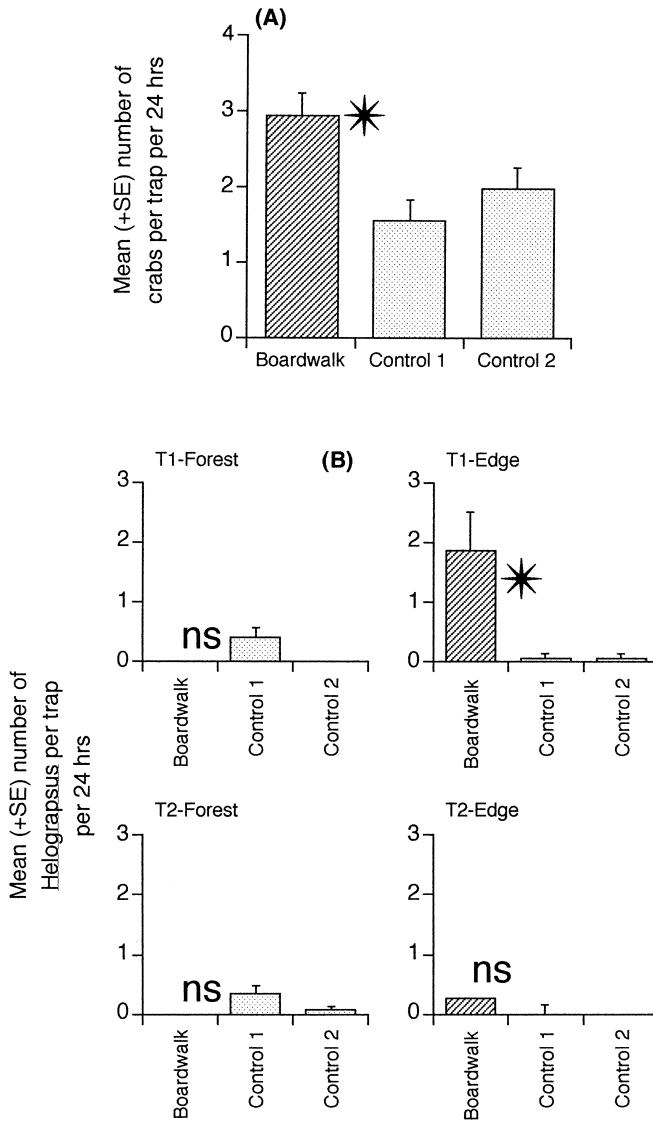


Fig. 5. (A) Mean (+ S.E.) number of crabs at the boardwalk and control locations. ($N = 60$ traps, pooled across two times, three sites and two habitats). (B) Mean (+ S.E.) number of *Helograpsus haswellianus* in the forest and edge habitats at the boardwalk and control locations on two different occasions ($N = 15$ traps, pooled across three sites). Other details as in Fig. 2.

abundance of pneumatophores and the attached epiphytic algae had no effect on the biomass of leaf litter within the plots. Visual inspection confirmed that the algae had not recolonised the cleared pneumatophores by the end of the experiment.

There were ~83% fewer molluscs in the pneumatophore and algal removal plots than

Table 5

Summaries of asymmetrical analyses of variance of the number of species of crabs, total number of individuals and numbers of *Parasesarma erythroactyla* and *Helograpsus haswellianus* in pitfall traps per 24 h period from two control locations and the boardwalk location on two separate occasions. Other details as in Table 4

Source of variation	Species	<i>Parasesarma</i>	<i>Helograpsus</i>
Time	$P < 0.061$	$P > 0.258$	$P > 0.377$
Habitat	$P < 0.077$	$P < 0.068$	$P > 0.166$
Locations			
B/walk vs. among controls	$P > 0.425$	$P > 0.154$	$P > 0.212$
Among controls	$P < 0.035$	$P > 0.832$	$P > 0.193$
Time × habitat	$P < 0.026$	$P > 0.755$	$P > 0.377$
Time × locations			
Time × (b/walk vs. am. cont.)	$P > 0.331$	$P > 0.675$	$P < 0.001$
Time × (among cont.)	$P > 0.652$	$P > 0.330$	$P > 0.795$
Habitat × locations			
H × (b/walk vs. am. cont.)	$P > 0.454$	$P > 0.546$	$P > 0.146$
H × among controls	$P < 0.084$	$P > 0.171$	$P > 0.193$
Time × habitat × locations			
Tm × H × (b/walk vs. am. cont.)	$P > 0.990$	$P > 0.587$	$P < 0.001$
Tm × H × (among controls)	$P > 0.763$	$P > 0.832$	$P > 0.795$
Sites (Tm.H.L)			
Sites (Tm.H.L(b/walk))	$P > 0.165$	$P < 0.001$	$P < 0.001$
Sites (Tm.H.L(am. cont.))	$P < 0.001$	$P < 0.022$	$P > 0.981$
Residual			

in the control plots (Fig. 7), indicating a marked response by the molluscs to the alterations in the physical structure of the mangrove forest. There was a slight, but not significant, decline in the number of individuals in the ‘pneumatophore disturbance’ and ‘algal disturbance control’ plots compared with the ‘undisturbed control’ plots (Table 7; SNK tests, Fig. 7). There was no significant difference in the abundance of molluscs in the pneumatophore and algal removal plots suggesting any effect on the molluscs was

Table 6

Summaries of asymmetrical analyses of variance of the number of species of crabs, total number of individuals and numbers of *Parasesarma erythroactyla* and *Helograpsus haswellianus* in pitfall traps per 24-h period from two control locations and the path location on two separate occasions. Other details as in Table 4

Source of variation	Species	Individuals	<i>Parasesarma</i>	<i>Helograpsus</i>
Time	$P > 0.322$	$P > 0.382$	$P > 0.239$	$P > 0.423$
Locations				
Path vs. among controls	$P > 0.238$	$P < 0.001$	$P > 0.179$	$P < 0.001$
Among controls	$P > 0.990$	$P > 0.990$	$P > 0.990$	$P > 0.990$
Time × locations				
Time × (path vs. am. cont.)	$P < 0.012$	$P < 0.001$	$P < 0.073$	$P < 0.001$
Time × (among cont.)	$P > 0.919$	$P > 0.916$	$P > 0.552$	$P > 0.968$
Sites (Tm.L)				
Sites (Tm.L(path))	$P < 0.038$	$P < 0.069$	$P > 0.263$	$P > 0.167$
Sites (Tm.L(am. cont.))	$P < 0.003$	$P > 0.982$	$P < 0.004$	$P > 0.990$
Residual				

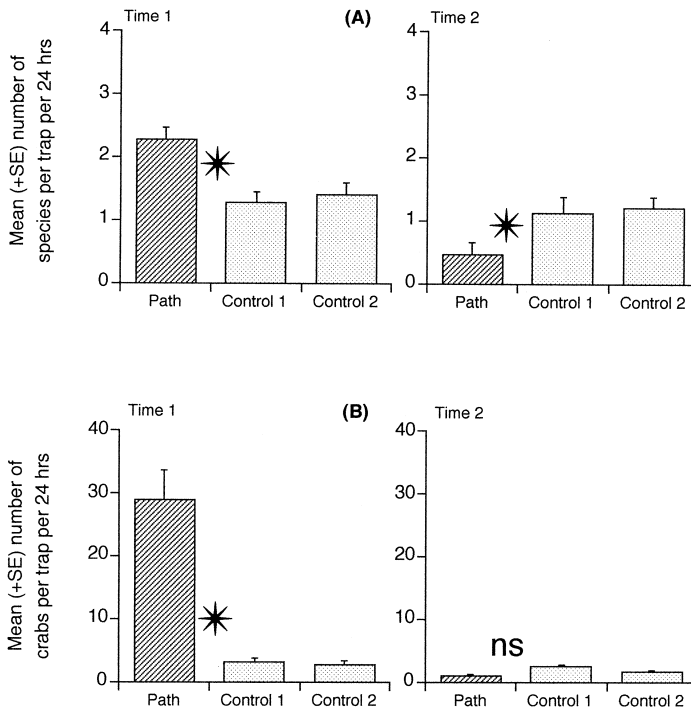


Fig. 6. Mean (+S.E.) number of species of crab and number of individual crabs at the path and control locations on two different occasions. ($N = 15$ traps, pooled across three sites.) Other details as in Fig. 2.

primarily related to removal of the epiphytic algae from the surface of the pneumatophores.

These results were generally repeated when considering most of the individual taxa sufficiently abundant for univariate analysis. The numbers of *Salinator solida*, *Assiminea tasmanica* (Tenison-Woods, 1876) and *Modiolus peronianus* were all significantly reduced in the pneumatophore and algal removal plots compared with the undisturbed control plots, but there was no significant difference in the abundance of these species between the two types of removals (Fig. 7; Table 7). Again, there was some indication of a small, experimental artifact arising from manipulations to the experimental plots. In the case of the mussel, *Modiolus peronianus*, there was a significant artifact associated with the algal disturbance control (Fig. 7). There was a significant treatment \times site interaction detected for the snail, *Melosidula zonata*, arising because of the pronounced and significant experimental artifacts detected at one of the two sites but not the other (Fig. 7; Table 7). The second of the two sites showed an identical pattern of decline in the removal treatments as described for the other species.

The effects of the manipulations were less clear when examining the structure of the entire molluscan assemblage using nMDS and ANOSIM analyses. Although some of the treatments were significantly different from each other ($P < 0.03$ — ANOSIM; nMDS;

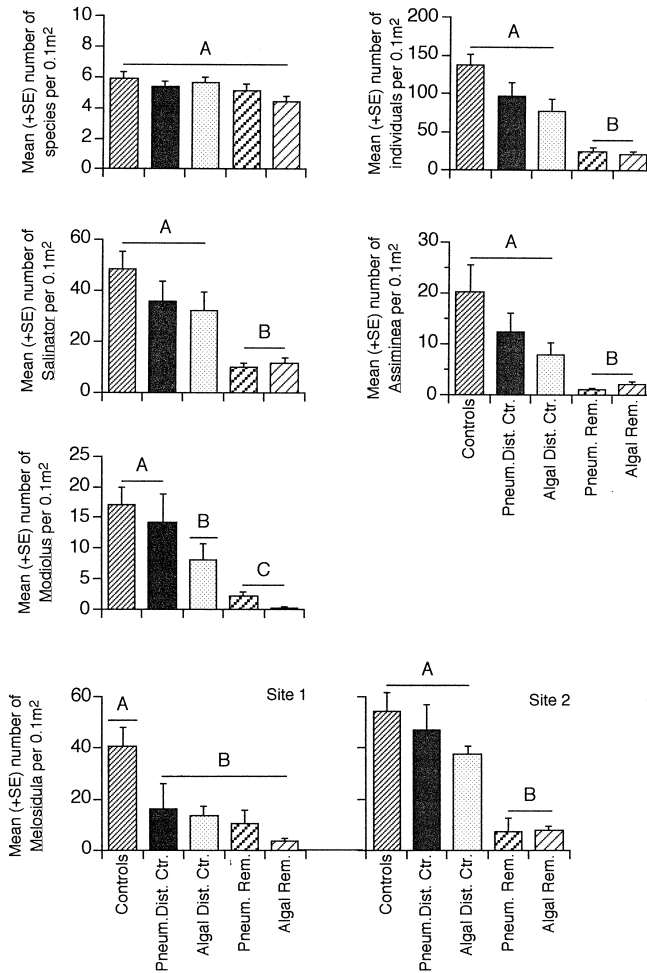


Fig. 7. Mean (+S.E.) number of species of mollusc, individual molluscs, *Salinator solida*, *Assimineea tasmanica*, *Modiolus peronianus* and *Melosidula zonata* in each of five different experimental treatments (unmanipulated controls, pneumatophore disturbance controls, algal disturbance controls, pneumatophore removals and algal removals). ($N = 8$ plots, pooled across two sites, except for *Melosidula zonata* where $N = 4$ plots at each site.) Letters above the histograms indicate groups of means identified as significantly different ($P < 0.05$) by SNK tests; treatments with the same letter were not significantly different ($P > 0.05$).

Fig. 8), the overall pattern suggested that any effects were primarily due to artifacts arising from the experimental manipulations of the pneumatophores and epiphytic algae.

4. Discussion

The differences in the physical structure of the mangrove forest included fewer

Table 7

Summaries of analyses of variance on the number of species of molluscs, total number of individuals and numbers of *Salinator solida*, *Assimineea tasmanica*, *Melosidula zonata* and *Modiolus peronianus* in 0.1-m² quadrats from five treatments (undisturbed control, pneumatophore disturbance control, algal disturbance control, pneumatophore removal and algal removal) established at each of two sites ($n = 4$ replicates). Data were untransformed except for *Salinator solida* where a $\log_e(x + 1)$ transform was used to stabilise variances

Source variation	Biomass	Pneumat.	Saplings	Species	Individ.	<i>Salinator</i>	<i>Assimineea</i>	<i>Melosidula</i>	<i>Modiolus</i>
Treatment	$P > 0.366$	$P < 0.004$	$P > 0.260$	$P > 0.368$	$P < 0.025$	$P < 0.027$	$P < 0.004$	$P < 0.054$	$P < 0.004$
Site	$P > 0.200$	$P < 0.005$	$P < 0.002$	$P > 0.675$	$P < 0.002$	$P < 0.001$	$P > 0.602$	$P < 0.002$	$P > 0.258$
Treatment \times site	$P > 0.507$	$P > 0.195$	$P > 0.276$	$P > 0.235$	$P > 0.111$	$P > 0.504$	$P > 0.270$	$P < 0.017$	$P > 0.911$

pneumatophores and less of the associated epiphytic algae in the disturbed areas of the mangrove forest, with associated significant reductions in the abundance and diversity of molluscs, but significantly greater abundance and diversity of crabs, compared with reference areas. This is the same pattern as previously described by Kelaher et al. (1998a,b) for the abundance and diversity of crabs and molluscs in relation to a reduced abundance of pneumatophores, associated epiphytic algae and leaf litter in disturbed areas of temperate mangrove forests in Sydney (Australia).

The experimental reduction of the abundance of *Avicennia marina* pneumatophores and the associated epiphytic algae in the forest habitat led to significant declines (by as much as 83%) in the number of molluscs utilising the substratum within the modified

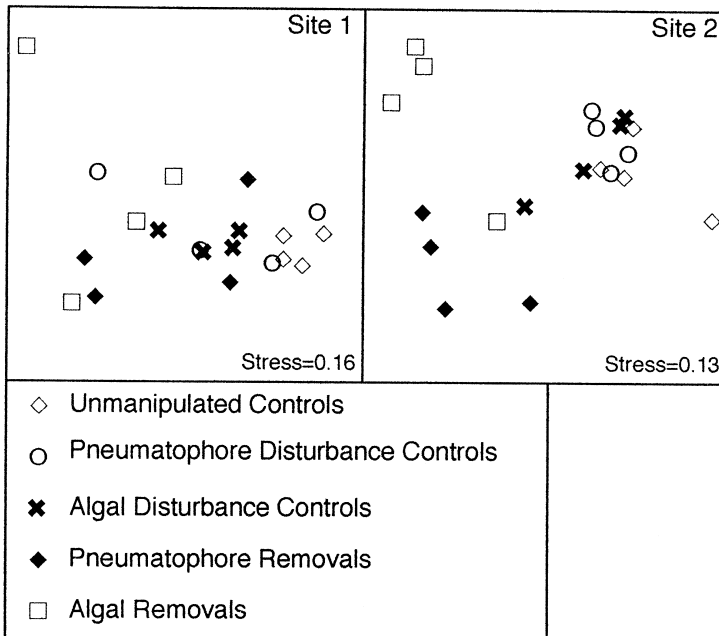


Fig. 8. nMDS ordinations on fourth root transformed species abundance data from quadrats in each of five different experimental treatments. There were $n = 4$ replicates from each of two sites.

plots. These results support the hypothesis that differences in the abundance and diversity of molluscs between the disturbed and reference areas were, in fact, caused by the differences in the abundance of pneumatophores and algae. The effect of removal of the epiphytic algae from the surface of the pneumatophores was as great as the removal of the entire pneumatophore (with attached algae) suggesting the molluscs may be responding primarily to some aspect relating to the presence of the algae. Very few of the molluscs were ever found specifically associated with the epiphytic algae, nor were they found on the surface of the pneumatophores. Most were found living underneath the layer of accumulated leaf litter, or buried a few millimetres below the surface of the substratum (but above the nutritive root layer). A reduction in available surface area for attachment on the pneumatophores, or among the algae, is therefore unlikely to be the primary reason for the observed responses by the molluscs to the modifications of the physical environment.

The most abundant gastropods in our study, such as *Salinator solida* and *Assiminea tasmanica*, are primarily grazers and deposit-feeders (Hutchings and Recher, 1982; and see Berman and Carlton, 1991; Yu et al., 1997 for related species) and may have responded to a reduction in available microbial food and detritus trapped among the pneumatophores and the algae. The presence of emergent structures, such as pneumatophores, can cause localised deposition of fine particles including sediments, detritus and other organic material onto the substratum (e.g. Eckman, 1979, 1983), due to modifications to the benthic boundary layer currents (Butman, 1987; Abelson and Denny, 1997). A reduction in the density of pneumatophores and the mass of attached algae would lead to increases in near-bottom flow rates, with a concomitant reduction in deposition of material suitable as food for deposit-feeders. Our experimental manipulations of the pneumatophores and algae had no detectable effect on the biomass of leaf litter in the different treatment plots, but simple measures of biomass may not provide a reliable measure of the available food for deposit-feeders and grazers, which can include microalgae, bacteria and detritus (e.g. Levinton, 1979; Lopez and Levinton, 1987). More detailed analysis of the microbial community would be necessary to determine whether the molluscs were responding to changes in food supply caused by alterations to the physical heterogeneity of the habitat.

Almost all of the macroalgal material in the experimental plots and in the disturbed areas was attached to the surface of the pneumatophores, forming a dense canopy, often completely obscuring the sediment/leaf litter on the substratum. The presence of this dense mat of algal material in undisturbed areas may have provided protection and cover for the molluscs from predators such as toadfish (*Tetractenos hamiltoni*) which are locally common and are known predators of epibenthic crabs and gastropods in mangrove systems (Hughes, 1984; Warren, 1990). The presence of material on or below the surface of the substratum is known to provide important refuges from predation for macrobenthic invertebrates in estuarine systems (e.g. Dauer et al., 1982; Harmon et al., 1986; Skilleter, 1994) and the dense mat of epiphytic algae may be sufficient to reduce rates of predator-induced mortality within the mangrove forest. Experimental manipulations of the abundance of predators, in conjunction with modifications to the structural heterogeneity of the habitat, would be needed to test this model further.

Kelahr et al. (1998b) manipulated the abundance of pneumatophores and algae in

temperate mangrove forests but found that neither was important in determining the abundance of the ocypodid crab, *Heloecius cordiformis* (Milne-Edwards). Experimental manipulations of the substratum demonstrated that the factor which could best account for the increased abundance of crabs near the boardwalks in their study was the hardness of the substratum, which presumably affected the capacity of the crabs to form and occupy burrows. The dominant species of crabs in our study, *Parasesarma erythro-dactyla* and *Helograpsus haswellianus* (Family Grapsidae), both burrow into the substratum and are therefore likely to show similar responses to *Heloecius cordiformis* in relation to the ease of burrowing into the substratum in disturbed areas.

Localised increases in the abundance of crabs in areas where there is reduced physical heterogeneity may have important implications for other components of mangrove systems. Mangrove crabs, including sesarmids such as *Parasesarma erythro-dactyla*, are important seed-predators, especially in tropical systems (Smith, 1987; Camilleri, 1992), so increases in their abundance may influence the recruitment of mangrove seedlings and their capacity to recolonise areas after disturbance. Mangrove crabs are also important in determining the rates of accumulation of decaying leaf litter (Robertson and Daniel, 1989), and hence have the potential to influence the biomass of material available for export to nearshore coastal systems (e.g. Flores-Verdugo et al., 1987). Crabs may also influence the abundance of meiofauna, both directly (e.g. Hoffman et al., 1984; Olafsson and Ndaru, 1997) or mediated through the relationships between litter accumulation and the meiofaunal community (Gee and Somerfield, 1997).

In a previous study (Skilleter, 1996b), there was a strong positive correlation between the amount of physical damage in six different mangrove forests near Sydney, Australia and the density of *Avicennia marina* pneumatophores. In that study, the main types of degradation within the wetlands were associated with compaction of the sediments from trampling and the formation of pools and puddles which retained stagnant water after rainfall. Mangrove genera such as *Avicennia* are thought to increase the number of aerial roots per unit area as a response to stresses from waterlogging and reduced oxygen content in the soil (Hutchings and Saenger, 1987).

In the present study, there were 65–80% fewer pneumatophores in the disturbed areas, compared with control sections of forest, suggesting the sediment in the disturbed areas was not compacted sufficiently to cause *Avicennia* to increase the density of aerial roots, or the increased burrowing of the crabs led to significant increases in aeration within the sediment. This supports the findings by Kelaher et al. (1998b) who found that the substratum adjacent to three different boardwalks was less compact than that several metres away.

There was some evidence that artifacts arising from the experimental manipulation of the habitat could account for a small proportion of the effects on the molluscs, but in most cases, the effects of removal of the pneumatophores and algae were greater than any effects which could be attributed to these artifacts. Certainly, the molluscs showed some responses to small-scale physical disturbance of the structure provided by the peg-roots and the algae. There is a great potential for experimental artifacts in soft-sediment systems because virtually all activities lead to some disruption of the substratum, with subsequent effects on the biota (Skilleter, 1996a).

In summary, this study has shown that even relatively small-scale modifications to the

physical structure of subtropical mangrove forests can lead to significant effects on the diversity and abundance of macrobenthic organisms in these habitats. Future efforts at conservation of these estuarine environments must focus not only on the prevention of loss of entire patches of habitat, but should aim to prevent or reduce modifications to the physical structure and integrity of the system. Reductions in the physical heterogeneity within forests can arise before complete loss of habitat begins, or is noticed, with subsequent effects on the abundance and diversity of macrobenthic invertebrates and, possibly, other animals.

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