Effects of pruning a temperate mangrove forest on the associated assemblages of

macroinvertebrates[1]

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Abstract. Mangrove forests around the world are being impacted by development in adjacent land and water areas. We undertook an After-Control-Impact study to assess the effects of mangrove forest pruning on the associated benthic macroinvertebrate fauna. Pruning, undertaken 5 years before our sampling period, reduced the height of the forest canopy from 5 m to 1 m. Macrobenthic assemblages were sampled in September 2000 and January 2001 from two randomly selected sites within the pruned section of forest and two sites in each of two control locations in the same forest. Assemblage composition in the pruned and undisturbed mangrove forests was not significantly nor were there significant differences in variability between the two areas. Similarity matrices for assemblages based on higher taxonomic groups and molluscs were highly correlated with similarity matrices for all taxa, indicating the utility of more rapid forms of assessment in this habitat. The results suggest that although short-term impacts may have occurred, no impact on macroinvertebrate assemblages was evident five years after the pruning.

Introduction

Mangrove ecosystems have a high value for conservation. In addition to contributing a unique form of aquatic vegetation and biodiversity habitat, they provide many benefits to humans. These benefits include physical protection of shorelines, support for juveniles of many commercially important species, nutrient absorption and sediment filtration (Robertson and Alongi 1995). The structure of mangrove forests modifies many ecological processes occurring within these ecosystems. Wolanski *et al*. (1992) constructed an explanatory model that linked the structural features of mangroves, the dynamic physical processes they influenced, and their environmental consequences. In particular, they hypothesized that canopy structure influenced wind strength and shading, both of which influenced the degree of stagnation of bottom water and rates of evapotranspiration. These physical processes were linked to the release of nutrients from the mud and changes in the concentrations of materials (Wolanski *et al*. 1992).

The model of Wolanski *et al*. (1992) suggests that natural and anthropogenic disturbances to the structure of mangrove forests are likely to cause impacts to important physical processes occurring within mangrove forests and to associated assemblages of animals and plants. Creation of canopy gaps by natural processes leads to a change in soil characteristics (Clarke and Kerrigan 2000) and increases in density and growth rates of saplings (Sherman *et al*. 2000). Anthropogenic disturbances to the structure of mangrove forests produce impacts on associated assemblages of animals and plants (Hutchings and Recher 1983; Liddle 1991; Schrijvers *et al*. 1995; Skilleter 1996; Kelaher *et al*. 1998a,b; Skilleter and Warren 2000). Increasing levels of damage to urban mangrove forests are

correlated with changes in abundance of taxa and overall changes in composition of molluscan assemblages (Skilleter 1996).

Indicators of human impacts on assemblages of benthic macroinvertebrates include changes in relative abundance of species, loss of 'sensitive' species, and additions of 'tolerant' species (e.g. Clarke 1993; Roberts 1996; Roberts *et al.* 1998). Warwick and Clarke (1993) also found that assemblages impacted by human activities became more variable than assemblages under natural conditions. Their results relating to increased variability were based on studies of nutrient enrichment and meiobenthos, oil field pollution and macrobenthos, El Nino and corals, and fishes and coral mining. However, other studies (Chapman *et al*. 1995; Kelaher *et al*. 1998b) have not found a relationship between anthropogenic disturbance and increased assemblage variability.

Monitoring and assessment of assemblages of benthic macroinvertebrates are time-consuming and require taxonomic and ecological knowledge that is limited for many invertebrate groups in Australia (Underwood and Chapman 1999). A possible solution is to use an alternative measure that is more efficient to measure, such as a single 'indicator' group that responds varies in the same way as the complete faunal assemblage. For example, molluscs are often the only group counted in surveys of mangroves because their taxonomy is well known and they are easily counted (e.g. Skilleter 1996). Alternatively, spatial and temporal variations in entire macroinvertebrate assemblages can be as clearly represented by data aggregated to genus, family or class as data sets based on species identification (Ferraro and Cole 1990; Warwick *et al*. 1990; James *et al*. 1995; Somerfield and Clarke 1995; Olsgard *et al*. 1997). There are, however, few studies of the value of these alternative

measures in habitats other than sub-littoral soft sediments in the northern hemisphere and for disturbances other than organic enrichment.

This study investigated a unique form of disturbance to the structure of mangrove forests: pruning to improve water views of an estuary. The pruning did not cause the death of the mangrove trees but reduced their height and altered the structure of a section of the mangrove forest. There appear to be no published studies into the impacts of pruning on mangroves and their associated faunal assemblages. The possibility of this type of impact occurring again may increase as population growth on urban coastlines forces housing developments closer to mangrove forests. The pruning reported in this paper occurred without prior warning and it was therefore not possible to gather data on the composition of assemblages before the event. Information on the long-term consequences of anthropogenic impacts in critical habitats, including mangrove forests, is limited (McGuinness 1990; Levings *et al*. 1994; Robertson and Alongi 1995; Kelaher *et al*. 1998b).

This study tested the hypotheses that five years after a pruning event altered the structure of a mangrove forest, benthic assemblages in the pruned section of forest differed from assemblages in nearby unpruned mangrove forests; and assemblages in the pruned location were more variable than assemblages in control locations. This study also tested the hypothesis that assemblages based on either all taxa, a group of easily identifiable higher taxa, or molluscs showed the same pattern of differences between the pruned and control locations.

Materials and methods

Study Site

This study was done in an estuarine forest of *Avicennia marina* mangroves approximately 100 km north of Sydney, New South Wales, Australia (Fig. 1). The forest formed part of a mangrove stand on the western side of Kincumber Broadwater, a lagoon forming part of a larger estuary (Brisbane Water). In 1996, a 70 m stretch of this mangrove forest was pruned, reducing the height of the canopy top from approximately 4-5 m to about 1 m (determined from the height of the tree stumps). This study was undertaken in the pruned area of the forest and two sections of unpruned forest on either side of the impacted area. At the time of this study there had been considerable re-growth of the pruned mangroves in the form of extensive shooting and leaf growth, and the highest were approximately 2 m in height. The extensive shooting and leaf growth occurred almost to ground level, making it difficult to gain access to the sampling sites. In contrast, the unpruned areas of forest had an open understorey with all leaf growth concentrated in the canopy.

Sampling Design

No sampling had been conducted before or immediately after the pruning event and so this study is an After/Control/Impact study (Chapman *et al*. 1995; Roberts 1996), with sampling spatially and temporally replicated at control and impact locations. An asymmetrical sampling design with one disturbed and two control locations was used. Locations were approximately 100 m apart, with control 1 situated north of the pruned location and control 2 situated south of the pruned location. Two replicate sites (10 m x 10 m) within each

location, approximately 50 m apart, were randomly selected for sampling in September 2000 and January 2001. Four replicate 0.1 m^2 quadrats were haphazardly placed about 5 m apart in each site. All sediment and leaf litter were removed to the nutritive root layer (from 1-2 cm depth), placed in a plastic bag, preserved in 5-7% formalin, and taken to the laboratory for sorting of infauna. Sediments were sieved in the laboratory through 1 mm and 500 μm mesh sieves and both fractions were retained; however, the results only from the 1 mm sieving are reported here. Samples were sorted under magnifying lamp and dissecting microscope and specimens were identified to a range of taxonomic levels (depending on expertise and availability of suitable keys) or to morphospecies. Molluscs were identified to species level with the exception of two morphospecies that could not be positively identified; amphipods, isopods and insect larvae were identified to morphospecies; polychaetes were identified to one family and to morphospecies; one crab was able to be identified to genus or to family; nematodes and oligochaetes were identified to morphospecies.

Statistical Analyses

Multivariate analysis was undertaken with PRIMER (ver 5) software (Clarke and Warwick 2001). Analyses were undertaken on three groups of data: (1) all taxa, consisting of the complete matrix of all taxa and their abundances; (2) data aggregated to the following groups (representing easily identifiable separations of taxa): Amphipoda, Isopoda, Gastropoda, Bivalvia, Decapoda, Polychaeta, Oligochaeta, Nematoda, Insecta; and (3) molluscs. Abundances of different taxa within the same sample varied from one to more than 1,000 individuals and therefore raw abundance data for each taxon were fourth-root transformed prior to analysis. This transformation reduces the dominance of abundant taxa and increases the importance of taxa with low numbers (Clarke 1993). Non-metric multidimensional

scaling (nMDS), based on a Bray-Curtis similarity matrix, was used to produce two-dimensional ordination plots of assemblages in each location. Stress values are indicative of the adequacy of the ordination in representing the structure of the group of samples, with values < 0.15 being regarded as reliable (Clarke 1993).

The significance of differences between assemblages in the control and pruned locations was examined by analysis of similarities (ANOSIM) in PRIMER. The design of this study (one putatively impacted and two control locations with replicate sites nested within each location) potentially allows the difference between locations to be tested by a two-way nested ANOSIM. However, this number of replicate sites within each location led to a small number of permutations available for a powerful test of the differences amongst locations. Pooling of sites within locations to increase the maximum number of permutations was not warranted because of significant differences between sites in at least one location at each time. The difference between the putatively impacted and control locations was therefore tested by one-way ANOSIM involving pair-wise comparisons between all sites. The identity of taxa responsible for differences in assemblage composition between the putatively impacted and control locations was determined by the similarity percentages (SIMPER) routine in PRIMER.

The hypothesis that assemblages at the pruned location were more variable than assemblages at the control locations and this difference was consistent through time was tested by asymmetrical analysis of variance (Underwood 1993; Glasby 1997) of Bray-Curtis similarity values between replicates within each site, based on a similar test by Kelaher *et al*. (1998b). To avoid problems with independence only two Bray-Curtis similarity values were possible in each site: between randomly selected pairs of quadrats (i.e. N = 2 replicates).

The single pruned location was compared to the two control locations, with site analysed as a random factor nested in location. An impact was considered to be present if the F-value based on the mean squares for the pruned location divided by the mean squares for the control locations was significant. However, this test was only done if the interaction between time and putatively impacted location (T x I) was non-significant at $P > 0.25$. Cochran's test was used to test for homogeneity of variances and the Ln $(x + 1)$ transformation used where necessary to eliminate heterogeneity (Underwood 1997).

Similarities in spatial patterns of assemblages based on all taxa and assemblages based on higher groups and molluscs were tested separately using the RELATE routine in PRIMER, which calculates Spearman rank correlation coefficients between the entries in each pair of Bray-Curtis similarity matrices (Somerfield and Clarke 1995; Clarke and Warwick 2001). Significance of the correlation coefficients was determined by a permutation procedure (in RELATE) because the data sets being compared were not independent.

Results

Overall, 42 taxa of invertebrates were found in the sediments and among leaf litter, with 8 species of gastropods, 4 species of bivalves, 4 species of amphipods, 3 species of isopods, 2 species of crabs, and 4 species of polychaetes. A number of taxa were also identified to morphospecies and kept for future taxonomical identification, including: insect larvae (9 morphospecies), oligochaetes (5 morphospecies), nematodes (2 morphospecies) and platyhelminthes (1 morphospecies).

In September 2000 assemblages from the pruned and control 2 locations overlapped and were separated from the control 1 location, for assemblages based on all taxa, higher groups and molluscs (Fig. 2). Replicates from all locations overlapped in January 2001 and locations were not clearly separated on the nMDS ordinations.

nMDS ordinations of assemblage composition suggest that distances between replicate samples within impacted sites were similar to the distances between replicate samples within control sites (Fig. 2). Asymmetrical ANOVA confirmed that variability in assemblage composition between replicate quadrats in the pruned location was not significantly different from variability in the control locations ($F_{1,6} = 0.003$, $P > 0.25$, based on pooled non-significant terms).

Pair-wise ANOSIM tests revealed no consistent differences between the pruned and control locations in either September 2000 or January 2001 for each assemblage (Table 1). In September 2000 the differences between the two control locations were as great, or greater than, the differences between the pruned location and both control locations (based on relative sizes of pairwise R-values). There was no difference between sites within the control 2 and pruned locations. In contrast, sites within control 1 location were as different from one another as they each were from sites in the control 2 and impact locations. In January 2001 the magnitude of difference for most pair-wise comparisons was less than it was in September 2000. This reflected the absence of any clear separation between locations in the nMDS ordinations for January 2001.

The previous tests revealed no consistent differences in assemblages occurring at the pruned and control locations. The SIMPER routine was therefore used to characterize the taxa occurring in each location and to confirm that no consistent differences occurred in the suite of taxa characterizing each treatment. The pruned and control 2 locations were characterized by a similar suite of taxa in September 2000 for each of the assemblages, and the suite of taxa characterizing assemblages at the control 1 location differed from both the control 2 and pruned location (Table 2). The two gastropods *Tatea huonensis* and *Ophicardelus sulcatus* contributed 50.5% of the similarity of samples within control 2 location and 43.2% of the similarity of samples within the pruned location. The higher groups contributing most to similarity of assemblages in both the control 2 and pruned locations were gastropods, amphipods and insect larvae (contributing 78.1% and 81.2% respectively). Control 2 and pruned locations were also characterized by a similar suite of molluscs in September 2000 (Table 2).

Taxa contributing the greatest amount to similarity of samples differed between the three locations in January 2001 for each of the assemblages and there were no consistent differences between pruned and control locations and no consistent similarities between the two control locations (Table 2). Taxa and groups contributing the greatest amounts to similarity of samples changed between September 2000 and January 2001 at the control locations but not at the pruned location. For the all taxa assemblage the importance of amphipods declined at control 1 location and the importance of *Tatea huonensis* declined at control 2 location. There was no change in the identity of the three taxa, or the three groups, contributing the highest amounts to similarity of samples within the pruned location between September 2000 and January 2001.

The underlying Bray-Curtis similarity matrices for all taxa and higher group assemblages were highly correlated in both September 2000 ($\rho = 0.73$, $P = 0.001$ and for all of the following correlations) and January 2001 ($\rho = 0.75$). Bray-Curtis similarity matrices for all taxa and molluscs were highly correlated in September 2000 ($\rho = 0.87$) but the correlation decreased in January 2001 ($\rho = 0.67$). These results confirm that variations in assemblage composition that existed among the three locations were similarly described by each assemblage type.

Discussion

Five years after a drastic change in mangrove forest structure the associated assemblages of benthic macrofauna were not different from assemblages in adjacent, unpruned sections of mangrove forests. In September 2000 differences in assemblage structure between control and pruned locations were no greater than differences between control locations and, in some pair-wise comparisons, were similar to the differences between control sites. No clear patterns were evident in January 2001 data and for some comparisons a pruned site was more similar to one of the control sites than to the other impact site. The only apparent difference between control and pruned sites appeared in their patterns of change over time. Assemblages based on all taxa changed between September 2000 and January 2001 in one site in each control location. In contrast, no pruned site changed significantly over the same time period. Assemblage variability did not differ between the pruned and control locations, although the test used in the present study had low power. Increased variability in assemblage structure has been hypothesized to be an indicator of disturbance to benthic

macrofauna (Clarke 1993; Warwick and Clarke 1993); however, other studies of mangrove benthic assemblages do not support this (Kelaher *et al*. 1998b).

No consistent differences were evident between pruned and control locations in the taxa characterizing assemblages. The pruned and control 2 locations were characterized by similar sets of taxa in September 2000 for assemblages based on all taxa, higher groups and molluscs. All locations differed in their characteristic taxa, for each assemblage type, in January 2001.

The present results differ from other studies in which structural impacts to mangroves were shown to cause significant changes in benthic assemblages. Skilleter and Warren (2000) found that molluscan assemblages adjacent to boardwalks and walking trails were significantly different to assemblages in control locations, and experimentally verified that this was due to reduced abundance of pneumatophores and associated reduction in coverage of epiphytic algae. In another study of the impacts of boardwalks, Kelaher *et al*. (1998b) found localised (i.e. within 1-3 m) changes in benthic assemblages in three different mangrove forests. Skilleter (1996) surveyed the near-shore habitat in urban mangrove forests with varying degrees of damage from a range of anthropogenic sources and found clear separation of molluscan assemblages in each location according to the degree of damage.

Studies by Skilleter (1996), Kelaher *et al*. (1998b) and Skilleter and Warren (2000) assessed impacts arising from a continuing source of structural disturbance within mangrove forests. The present study assessed the impact of a single unique change in forest structure that occurred five years prior to this study. Forest structure in the pruned location differed

dramatically from both control locations at the time of this study, with a lower canopy and increased leaf density closer to the ground. If benthic assemblages within the pruned area were still affected by the disturbance at the time of this study, the present results suggest the magnitude of this impact was within the range of natural variation in benthic assemblage structure. Alternatively, the absence of any consistent difference of assemblage structure in the pruned location could be a result of disturbances from pruning extending beyond the pruned forest and into the so-called control locations through, for example, increases in light penetration, altered air and water movements and changed temperature regimes. Unfortunately, the impact of this event was not assessed earlier and it is possible that changes in assemblage structure occurred soon after the pruning. This underscores the difficulty in predicting the occurrence of such events and the importance of assessing the impacts of unpredictable, novel events as soon as possible.

The present study provides support for the use of higher groups or molluscs only in this habitat as an alternative to a more detailed identification of all taxa. Similar trends were evident for each assemblage type in pair-wise tests of sites between the pruned and control locations in both September 2000 and January 2001 surveys. Bray-Curtis similarity matrices for assemblages based on higher groups or molluscs were both highly correlated with the similarity matrices for assemblages based on all taxa. However, the strength of the correlation between the Bray-Curtis similarity matrices for all taxa and molluscs declined between September 2000 and January 2001 (unlike the correlation with higher groups). There has been considerable interest in recent years in potential short-cuts to biodiversity assessments (Ward *et al*. 1999; Gladstone 2002). Aggregation of data to genus or family, and in some cases to phylum, results in no loss of information about trends in community structure (e.g. Ferraro and Cole 1990, 1995; James *et al*. 1995; Somerfield and Clarke 1995;

Vanderklift *et al*. 1996; Olsgard *et al*., 1997). In a recent study also undertaken on benthic macroinvertebrate assemblages of mangroves, Chapman (1998) found that patterns of differences between assemblages (at a range of spatial scales) were retained following aggregation of 93 taxa to 9 easily identifiable groups.

In conclusion, the results of this study indicate that no impact was detectable on assemblages of benthic macroinvertebrates five years after a mangrove forest had been pruned. However, the absence of data collected both before and immediately after the pruning means the existence of short-term impacts cannot be ruled out. The present results also support conclusions from other workers (e.g. Chapman 1998) that studies undertaken in similar mangrove habitats will benefit more by allocating limited resources to the collection of additional replicate samples rather than to the identification of specimens to the lowest possible taxonomic level. In the case of the habitat studied here, given the consistently high correlation with all taxa in both time periods further studies would benefit from the use of data aggregated to higher groups.

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References

Chapman, M.G. (1998). Relationships between spatial patterns of benthic assemblages in a
mangrove forest using different levels of taxonomic resolution. *Marine Ecology
Progress Series* **162**, 71-78.

Chapman, M.G., Underwood, A.J., and Skilleter, G.A. (1995). Variability at different spatial
scales between a subtidal assemblage exposed to the discharge of sewage and two
control assemblages. *Journal of Experimental Marine Biology and Ecology* **189**, 103-
122

Clarke, K.R. (1993). Non-parametric multivariate analyses of changes in community
structure. *Australian Journal of Ecology* **18**, 117-143.

Clarke, K.R., and Warwick, R.M. (2001). 'Change in Marine Communities: An Approach to
Statistical Analysis and Interpretation.' 2nd ed (Plymouth Marine Laboratory: UK).

Clarke, P.J., and Kerrigan, R.A. (2000). Do forest gaps influence the population structure
and species composition of mangrove stands in northern Australia? *Biotropica* **32**, 642-
652.

Ferraro, S.P., and Cole, F.A. (1990). Taxonomic level and sample size sufficient for assessing pollution impacts on the Southern California Bight macrobenthos. *Marine Ecology Progress Series* **67**, 251-262.

Ferraro, S.P., and Cole, F.A. (1995). Taxonomic level sufficient for assessing pollution impacts on the Southern California Bight macrobenthos – revisited. *Environmental Toxicology and Chemistry* **14**, 1031-1040.

Gladstone, W. (2002). The potential value of indicator groups in the selection of marine reserves. *Biological Conservation* **104**, 211-220.

Glasby, T.M. (1997). Analysing data from post-impact studies using asymmetrical analysis of variance. *Australian Journal of Ecology* **22**, 448-459.

Hutchings, P.A., and Recher, H.F. (1982). The fauna of Australian mangroves. *Proceedings of the Linnean Society of NSW* **106**, 83-121.

James, R.J., Lincoln Smith, M.P., and Fairweather, P.G. (1995). Sieve mesh-size and taxonomic resolution needed to describe natural spatial variation of marine macrofauna. *Marine Ecology Progress Series* **118**, 187-198.

Kelaher, B.P., Underwood, A.J., and Chapman, M.G. (1998a). Effect of boardwalks on the semaphore crab *Heloecius cordiformis* in temperate urban mangrove forests. *Journal of Experimental Marine Biology and Ecology* **227**, 281-300.

Kelaher, B.P., Chapman, M.G., and Underwood, A.J. (1998b). Changes in benthic assemblages near boardwalks in temperate urban mangrove forests. *Journal of Experimental Marine Biology and Ecology* **228**, 291-307.

Levings, S.C., Garrity, S.D., and Burns, K.A. (1994). The Galeta oil spill. III. Chronic reoiling, long-term toxicity of hydrocarbon residues and effects on epibiota in the mangrove fringe. *Estuarine Shelf and Coastal Science* **38**, 365-395.

Liddle, M.J. (1991). Recreation ecology: effects of trampling on plants and corals. *Trends in Ecology and Evolution* **6**, 13-17.

McGuinness, K.A. (1990). Effects of oil spills on macroinvertebrates of salt marshes and mangrove forests in Botany Bay, New South Wales, Australia. *Journal of Experimental Marine Biology and Ecology* **142**, 121-135.

Olsgard, F., Somerfield, P.J., and Carr, M.R. (1997). Relationships between taxonomic resolution and data transformations in analyses of a macrobenthic community along an established pollution gradient. *Marine Ecology Progress Series* **149**, 173-181.

Roberts, D.E. (1996). Patterns of subtidal marine assemblages associated with deep water sewage outfall. *Marine and Freshwater Research* **47**, 1-9.

Roberts, D.E., Smith, A., Ajani, P., and Davis, A.R. (1998). Rapid changes in encrusting marine assemblages exposed to anthropogenic point-source pollution: a 'Beyond BACI' approach. *Marine Ecology Progress Series* **163**, 213-224.

Robertson, A.I., and Alongi, D.M. (1995). Mangrove systems in Australia: structure, function and status. In 'The State of the Marine Environment Report for Australia Technical Annex: 1 The Marine Environment.' (Eds L.P. Zann and P. Kailola) pp 119 – 133. (Great Barrier Reef Marine Park Authority: Townsville).

Schrijvers, J., Van Gansbeke, D., and Vincx, M. (1995). Macrobenthic infauna of mangroves and surrounding beaches at Gazi Bay, Kenya. *Hydrobiologia* **306**, 53-56.

Sherman, R.E., Fahey, T.J., and Battles, J.J. (2000). Small-scale disturbance and regeneration dynamics in a neotropical mangrove forest. *Journal of Ecology* **88**, 165-178.

Skilleter, G.A. (1996). Validation of rapid assessment of damage in urban mangrove forests and relationships with molluscan assemblages. *Journal of the Marine Biological Association of United Kingdom* **76**, 701-716.

Skilleter, G.A., and Warren, S. (2000). Effects of habitat modification in mangroves on the structure of mollusc and crab assemblages. *Journal of Experimental Marine Biology and Ecology* **244**, 107-129.

Somerfield, P.J., and Clarke, K.R. (1995). Taxonomic levels, in marine community studies, revisited. *Marine Ecology Progress Series* **127**, 113-119.

Underwood, A.J. (1993). The mechanics of spatially replicated sampling programmes to

    detect environmental impacts in a variable world. *Australian Journal of Ecology* **18**,

    99-116.

Underwood, A.J. (1997). 'Ecological Experiments: Their Logical Design and Interpretation

    Using Analysis of Variance' (Cambridge University Press: Cambridge).

Underwood, A.J., and Chapman, M.G. (1999). Problems and practical solutions for

    quantitative assessment of biodiversity of invertebrates in coastal habitats. In 'The

    Other 99%: The Conservation and Biodiversity of Invertebrates.' pp 19-25. (Eds: W

    Ponder, D Lunney) (Royal Zoological Society of NSW: Sydney).

Vanderklift, M.A., Ward, T.J., and Jacoby, C.A. (1996). Effect of reducing taxonomic

    resolution on ordinations to detect pollution-induced gradients in macrobenthic

    infaunal assemblages. *Marine Ecology Progress Series* **136**, 137-145.

Ward, T., Vanderklift, M.A., Nicholls, A.O., Kenchington, R.A. (1999). Selecting marine

    reserves using habitats and species assemblages as surrogates for biological diversity.

    Ecological Applications **9**, 691-698.

Warwick, R.M., and Clarke, K.R. (1993). Increased variability as a symptom of stress in

    marine communities. *Journal of Experimental Marine Biology and Ecology* **172**, 215-

    226.

Warwick, R.M., Platt, H.M., Clarke, K.R., Agard, J., and Gobin, J. (1990). Analysis of macrobenthic and meiobenthic community structure in relation to pollution and disturbance in Hamilton Harbour, Bermuda. *Journal of Experimental Marine Biology and Ecology* **138**, 119-142.

Wolanski, E., Mazda, Y., Ridd, P. (1992). Mangrove hydrodynamics. In 'Tropical Mangrove Ecosystems.' (Eds A.I. Robertson and D.M. Alongi.) pp 43-62. (AGU Press: Washington).

FIGURE CAPTIONS

Fig 1. Position of study location (●).

Fig 2. Non-metric multidimensional scaling (nMDS) ordinations comparing

macroinvertebrate assemblages based on all taxa in (a) September 2000 and (b) January

2001. Solid and open symbols depict replicate sites within control 1 (Δ), control 2 (□) and

pruned (O) locations.

Tasman
Sea

0   1.5   3
Kilometres

(a)

Stress: 0.16

(b)

Stress: 0.2
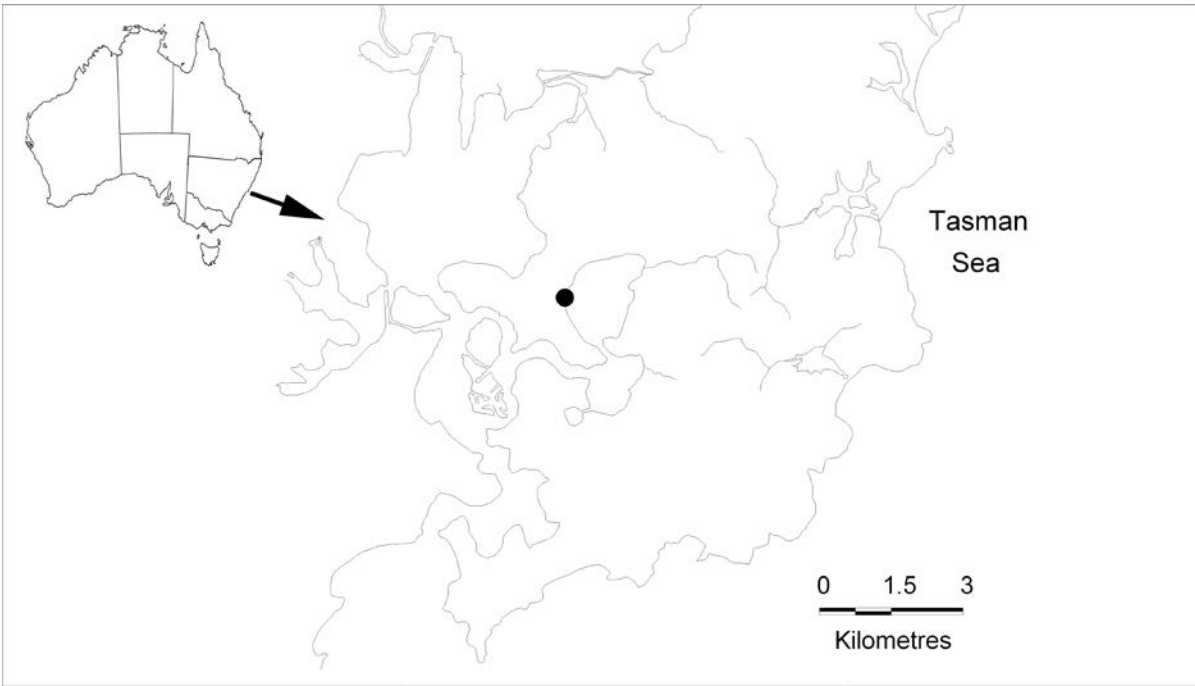
Table 1. Summary of one-way ANOSIM tests comparing assemblages in each site of the pruned location (P) with each site in each of two control locations (C1 and C2). Values shown are R values for pair-wise comparisons between sites and their significance level (* $P < 0.05$, ** $P < 0.01$, NS $P > 0.05$). C1-1 = control location 1, site 1 etc.

All Taxa

Sept 2000 — Global $R = 0.65$ **

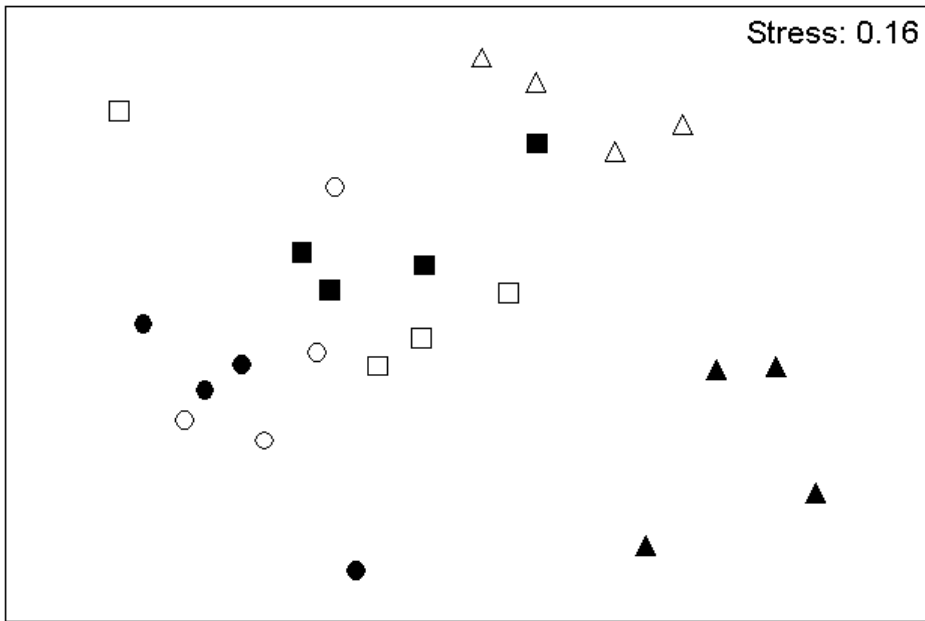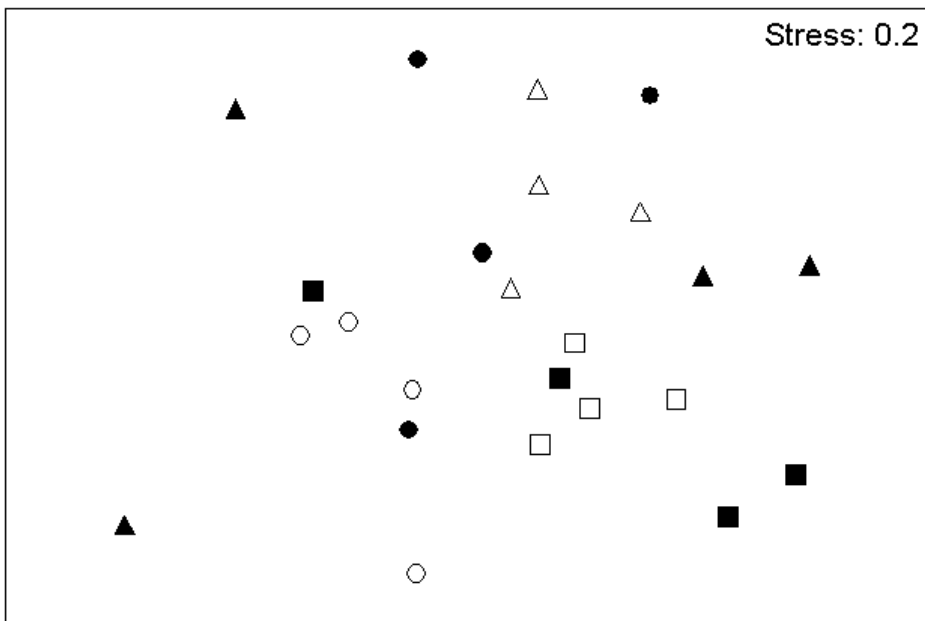|	C1-1	C1-2	C2-1	C2-2	P1
C1-2	0.93*				
C2-1	0.95*	0.82*			
C2-2	0.77*	0.94*	0.03 NS		
P1	1.00*	0.98*	0.36*	0.47 NS	
P2	0.99*	1.00*	0.33 NS	0.46 NS	-0.19 NS

Jan 2001 — Global $R = 0.39$ **

	C1-1	C1-2	C2-1	C2-2	P1
C1-2	0.40*				
C2-1	0.20 NS	0.43 NS			
C2-2	0.45*	0.56*	0.16 NS		
P1	0.41*	0.10 NS	0.24 NS	0.57*	
P2	0.48*	0.78*	0.25 NS	0.77*	0.43*

Higher Groups

Sept 2000 — Global $R = 0.55$ **

	C1-1	C1-2	C2-1	C2-2	P1
C1-2	0.92*				
C2-1	0.61*	0.75*			
C2-2	0.25 NS	0.87*	0.11 NS		
P1	0.68*	0.75*	0.21 NS	0.27 NS	
P2	0.90*	0.94*	0.44*	0.31 NS	-0.08 NS

Jan 2001 — Global $R = 0.39$ **

	C1-1	C1-2	C2-1	C2-2	P1
C1-2	0.37 NS				
C2-1	0.32 NS	0.37 NS			
C2-2	0.48*	0.45*	0.13 NS		
P1	0.46 NS	0.17 NS	0.27 NS	0.48*	
P2	0.20 NS	0.60*	0.42 NS	0.75*	0.3 NS

Molluscs

Sept 2000 — Global $R = 0.51$ **

	C1-1	C1-2	C2-1	C2-2	P1
C1-2	0.59*				
C2-1	0.61*	0.60*			
C2-2	0.66*	0.92*	0.09 NS		
P1	0.68*	1.00*	0.44*	0.56*	
P2	0.69*	0.95*	0.20 NS	0.47 NS	-0.20 NS

Jan 2001 — Global $R = 0.29$ **

	C1-1	C1-2	C2-1	C2-2	P1
C1-2	0.36 NS				
C2-1	0.10 NS	0.30 NS			
C2-2	0.40 NS	0.23 NS	0.02 NS		
P1	0.14 NS	-0.08 NS	0.13 NS	0.30 NS	
P2	0.58*	0.80*	0.32 NS	0.60*	0.18 NS

Table 2. Taxa ranked (1 = highest) in order of their contribution to similarity of samples for assemblages based on all taxa, higher groups, and molluscs.

All taxa

Taxa	September 2000			January 2001		
	Control 1	Control 2	Pruned	Control 1	Control 2	Pruned
Amphipoda	1	3	5	6	1	3
Arthritica helmsi	3	6		4	7	
Assiminea sp.			4	1		2
Hymenosomoatidae						7
Insect larvae 1					2	
Insect larvae 6	2	5	8	5	5	6
Nematode #9				8		10
Nereidae					4	
Oligochaete #8				2	6	9
Ophicardelus ornatus		4	2		8	5
Ophicardelus sulcatus		2	3	7		4
Paragrapsus sp.		8	7			8
Salinator solida	4	7	6	3		
Tatea huonensis		1	1		3	1

Higher groups

Group	September 2000			January 2001		
	Control 1	Control 2	Pruned	Control 1	Control 2	Pruned
Amphipoda	1	2	2	5	2	2
Bivalvia	3	5		2	4	
Decapoda		4	4		6	5
Gastropoda	4	1	1	1	3	1
Insecta	2	3	3	4	1	3
Isopoda						6
Oligochaeta				3		
Polychaeta			5		5	4

Table 2 cont'd

Molluscs

Taxa	September 2000			January 2001		
	Control 1	Control 2	Pruned	Control 1	Control 2	Pruned
Arthritica helmsi	1	4	4	2	2	
Assiminea sp.				1	4	2
Ophicardelus ornatus	4	3	2		3	4
Ophicardelus sulcatus		2	3	4	5	3
Salinator solida	2			3		
Solitellina sp.			5		6	
Tatea huonensis		1	1		1	1
Xenostrobus sp.	3					