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Ecological response to MPA zoning following cessation of bait harvesting in an estuarine tidal flat

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Abstract

Research in marine protected areas (MPAs) needs to focus beyond targeted species to the functional value of MPAs in maintaining ecosystem services and ecological diversity. Estuarine tidal flats are speciose and provide vital ecosystem services but are largely neglected in MPA research. Here, the ecological effect of an MPA on an estuarine tidal flat was determined by quantifying patterns in macroinvertebrate assemblages and sediment variables over a 3 yr period: 1 yr prior to and 2 yr following MPA zoning. An asymmetrical beyond BACI (before after control impact) design was used with 1 protected and 2 reference tidal flats. Following the exclusion of humans targeting callinassid crustaceans for bait, significant changes in the assemblages were observed in the no-take zone compared to reference locations. These shifts were maintained for the 2 yr of sampling following zoning. Relatively immobile, suspension- and deposit-feeding species increased up to 6-fold in abundance, especially juvenile bivalves (e.g. *Eumarcia fumigata* and *Soletellina alba*) and small polychaetes. In contrast, there was a reduction in some of the highly mobile, predatory and scavenging species (e.g. the amphipod *Urohaustorius metungi* and the polychaete *Sigalion ovigerum*). We observed an increase in spatial homogeneity in the assemblage as well as increases in the silt and clay content at the protected flat, while patchiness was maintained at the reference sites. Importantly, these results add to the growing body of evidence that MPAs also significantly affect non-target fauna and produce shifts in beta-diversity. Our findings imply that MPAs are an effective tool for conservation management.

Keywords

Soft sediment, estuary, invertebrates, beta-diversity, marine protected areas

Disciplines

Medicine and Health Sciences | Social and Behavioral Sciences

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**Ecological response to MPA zoning following cessation of bait harvesting in an
estuarine tidal flat**

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ABSTRACT

Research in Marine Protected Areas (MPAs) needs to focus beyond targeted species to the functional value of MPAs in maintaining ecosystem services and ecological diversity. Estuarine tidal flats are speciose and provide vital ecosystem services, but are largely neglected in MPA research. Here, the ecological effect of an MPA on an estuarine tidal flat was determined by quantifying patterns in macroinvertebrate assemblages and sediment variables over a three year period; one year prior to and two years following MPA zoning. A spatially and temporally replicated asymmetrical Beyond BACI design was used with one protected and two reference tidal flats. Following the exclusion of humans targeting callinastid crustaceans for bait, significant changes in the assemblages were observed in the no-take zone compared to reference locations. These shifts were maintained for the two years of sampling following zoning. Relatively immobile, suspension and deposit-feeding species increased up to six-fold in abundance; especially juvenile bivalves (e.g. *Eumarcia fumigata* and *Soletellina alba*) and small polychaetes. In contrast, there was a reduction in some of the highly mobile, predatory and scavenging species (e.g. the amphipod *Urohaustorius metungi* and polychaete *Sigalion ovigerum*). We observed an increase in spatial homogeneity in the assemblage as well as increases in the silt and clay content at the protected flat, while patchiness was maintained at the reference sites. Importantly, these results add to the growing body of evidence that MPAs significantly affect non-target fauna and produce shifts in beta-diversity. Our findings imply that MPAs are an effective tool for conservation management.

Keywords: soft-sediment; estuary; invertebrates; beta-diversity; marine protected areas

INTRODUCTION

Marine Protected Areas (MPAs) are playing an increasingly important role in the conservation of marine habitats (Halpern & Warner 2002, Lubchenco et al 2003, Gaston et al 2006) and the management of fisheries (Hastings & Botsford 2003; Tetreault & Ambrose 2007, White & Kendall 2007, Kelaher et al 2014). In light of the expanding global network of Marine Protected Areas and the need to better incorporate scientific knowledge into the MPA decision making processes, there is a need to assess their efficacy across a range of habitats. In addition, we need to determine the effects of MPAs on ecosystem function and the provision of ecosystem services (Sutherland et al 2006, Claudet & Guidetti 2010, Granek et al 2010).

Habitat diversity differs dramatically across the breadth of climatic zones, bioregions and at a variety of spatial scales for each habitat type within these regions. Consequently, management must be informed by research from a variety of habitats at a range of spatial and temporal scales. To date, research relating to Marine Protected Areas has been dominated by studies in tropical climates, reef ecosystems or has focused on target species or those with iconic status (Russ & Alcala 2003, Willis et al 2003, Shears et al 2006). In a literature search of peer-reviewed papers on Marine Protected Areas in the last decade (2000-2011), coral habitat was represented by 40% of the literature, reefs by 47.5% and soft-sediments by 12.5% of the peer-reviewed papers. Further, only 6% of publications addressed soft sediment invertebrates (Figure 1). This research bias is understandable in light of justifying the impact and benefits of MPAs to society and the socio-economic interest in fisheries resources. However, considering that soft sediments comprise arguably the largest habitat on earth with a considerable portion of the earth's biological diversity (Snelgrove 1997, Zajac 2008), such a skewed research effort risks

undermining the objective of MPAs. That is, to comprehensively represent the full suite of ecological diversity (Worm et al 2006, Granek et al 2010).

In addition to the diversity they support and their ecological significance, one soft sediment habitat type in particular, estuarine tidal flats, is under considerable anthropogenic pressure given coastal development and human activities. Further, tidal flats provide life-stage specific habitat and feeding grounds for commercially and recreationally important fish resources (Robertson 1984, Loneragan & Bunn 1999, van der Veer et al 2001) and many migratory bird species (Shepherd & Boates 1999). Hence, changes to the ecological diversity of tidal flat habitat imply impacts on ecosystem functioning (Hooper et al 2005).

Although there is a considerable body of literature relating to the ecology of tidal flats, only a small number test the impact of human activity (but see Wynberg & Branch 1994, Kaiser et al 2001, Skilleter et al 2005, Rossi et al 2007). Fewer still seek to relate such knowledge to management initiatives, or to demonstrate responses at large scales as a consequence of management. Thus management of tidal flat habitat in MPAs is based on scant empirical data, protection is difficult to justify and representation in MPAs is relatively low.

A large bioturbating ghost shrimp or nipper, *Trypaea australiensis* (callianassidae) dominates tidal sediment flats in eastern Australia (Hailstone and Stephenson 1961). Recreational fishers heavily exploit this crustacean for bait with a bag limit of 100 individuals per fisher (Anon 2014). Animals are removed from their burrows with a ‘nipper pump’ disturbing the sediment and associated fauna in the process. An experimental study of disturbance associated with bait harvesting of shrimps on South Africa tidal flats concluded there were lasting impacts on sand flat macrofauna (Wynberg and Branch 1994). The objectives of the present study were to assess change in the

structure of a tidal flat macrofaunal invertebrate assemblage and associated sediments over the course of three years; one year prior to and two years following no-take zoning. The no-take tidal flat within Jervis Bay Marine Park (JBMP) was compared to two similar reference tidal flats outside the Marine Park, where recreational fishers regularly pump ghost shrimp for use as bait. No-take zoning meant that bait pumping and trampling by bait collectors ceased across the protected tidal flat.

METHODS

Study Locations

A spatially and temporally replicated hierarchical sampling design was used to sample macrofaunal assemblages across a whole tidal flat within each of three estuaries (Currumbene Creek - Jervis Bay Marine Park (35° 01' S, 150° 40' E), Sussex Inlet (35° 10' S, 150° 35' E), Narrawallee Inlet (35° 18' S, 150° 28' E)) on the south coast of New South Wales, Australia (Winberg et al 2007). The estuaries were separated by ≈ 30 km and the tidal flats were within 1 km upstream of the permanently open mouths of the estuaries. Currumbene Creek was gazetted as a no-take MPA in the Jervis Bay Marine Park in November 2002. Recreational bait pumping practices continued on a regular basis in the reference tidal flats at Sussex Inlet (S) and Narrawallee Inlet (N) throughout the study, while nipper pumping activity virtually ceased within the no-take MPA, with compliance in the heavily-patrolled Currumbene Creek close to fully effective. An average of 1.8 ± 1.5 (standard deviation) infringement notices were issued annually from 2007-2012 for nipper pumping within this sanctuary zone and none have been issued in the last 27 months (Mark Fackerell, JBMP compliance pers. comm.).

Sampling design

The experimental design of the sampling followed the logic of asymmetrical Beyond BACI (Before After Control Impact) sampling designs, as described by Underwood (1992). Each of the three tidal flats was sampled on one day within each of two time periods between June and October; prior to no-take zoning of Currumbene Creek. We employed a spatially hierarchical sampling design; in each time period, three sites were haphazardly selected at least 100m from each other within each tidal flat. At each site, three 2m² plots were randomly selected approximately 20m from each other, and sampled with three replicate sediment cores per plot (see Fig. 1 in Winberg et al 2007). The sites within each tidal flat were resampled, during the same months, one year and two years later; thus a total of 6 sites were sampled in each tidal flat each year. In total, 54 cores were taken per tidal flat per year (27 cores on two occasions per year) with a total of 486 cores over the 3 years of sampling. Previous studies have shown that the greatest spatial variation in estuarine tidal flats can occur at scales of 100s of meters (Edgar & Barrett 2002, Winberg et al 2007). Therefore the same sites were revisited throughout the study to minimize spatial variation. With 6 months intervening between periods of sampling on each tidal flat we considered our replicate cores to be independent.

Cores (15 cm wide x 25 cm deep) were inserted into the sediment and levered out with a shovel. Sediment was sieved *in situ* through 1.2 mm mesh bags. Sediment samples for grain size and organic content analyses were also taken at each plot using a smaller 4cm diameter corer to a depth of 5cm, and placed in sealed plastic bags and frozen. Faunal samples were transferred into finer 0.5 mm mesh bags and frozen on return to the laboratory. Samples were later defrosted then stained within the mesh bag (Biebrich Scarlet in 5% formol) for at least two days to aid enumeration. Samples were then preserved in 70% alcohol until they were quantified. Taxa were identified to the lowest

taxonomic level possible, usually species, using a dissecting microscope. Rarer, juvenile or difficult taxa were identified to the genus or family level. Sediment samples were defrosted for grain size analysis using the Malvern Mastersizer laser analyzer.

Detecting patterns of change

Using multivariate data, we generated Bray-Curtis similarity matrices for both untransformed and presence/absence data at the highest taxonomic resolution (mostly to species level). Untransformed data provided the clearest multivariate measure of relative change in abundance, while presence absence data was used to explore changes in species composition. To visualize changes in whole assemblages on the tidal flats in each of the years, we used MDS plots. The data were pooled at the scale of sites prior to Bray-Curtis similarity matrices being calculated as recommended by Clarke (pers. comm.), as this was previously shown to be the scale of most variation (Winberg et al 2007). The Bray-Curtis similarity matrices for each tidal flat and year were again compared in a Second-Stage matrix of Spearman rank correlations (Clarke & Gorley 2006, Terlizzi et al 2009).

We used the PERMANOVA extensions to the PRIMER 6+ software package (beta version 17) to accommodate the full nested hierarchical design and spatial asymmetry of the data set. Monte Carlo probability values were used as recommended by Anderson (2005) where the smallest scale of replication was $n = 3$ (cores within plots). Further multivariate pair-wise a posteriori tests were used to identify effects of protection within the factors of interest.

SIMPER analysis of the untransformed data, pooled at the scale of sites, was used to determine which taxa contributed most to differences in the Currumbene Creek tidal flat before and after no-take zoning. Those taxa contributing to more than 80%

(cumulative) of differences between the assemblages at the impacted tidal flat were selected for further univariate analysis. Additional SIMPER analysis with presence absence data was used to determine if there were compositional changes, or changes to compositional homogeneity between sites.

Univariate analyses were done for selected taxa (outlined above), as well as a range of diversity measures (species richness, abundance, Shannon H' diversity and J' Pielou's evenness). Diversity measures were calculated from the entire data set. Species belonging to the 2 common families of polychaetes, spionidae and capitellidae, were considered functionally uniform (Read 2004) and to reduce any effects of taxonomic uncertainty, species were not distinguished for the univariate analyses. Finally, changes in the abundance of the species targeted by recreational fishers, *Trypea australiensis*, was also analyzed, as were changes in the percentage silt and clay in sediments over the course of the sampling.

Prior to the calculation of the asymmetrical ANOVA, the overall sources of variation across sample scales and time were established in a fully symmetrical four factor ANOVA (for methods see Underwood (1994) or Terlizzi et al (2005)) (Estuaries, Time, Sites and Plots) for biological variables and three factors for silt and clay (Estuaries, Time and Sites). Assumptions of ANOVA were tested; normality was assessed visually in plots of means against variances (Quinn & Keough 2002), and Cochran's C was used to test for homogeneity of variance. Data were transformed to achieve homogeneity where necessary. For a number of variables, Time was not significant ($p > 0.25$) and data were pooled at that level to increase the power of the test (Underwood 1993, Terlizzi et al 2005). ANOVAs were done with GMAV 5 software (University of Sydney, Australia).

We extended the asymmetrical analysis of one Impact (protected) site and two Control (reference) sites to include temporal asymmetry (1 Year before protection and 2 Years

after) by calculating further sums of squares from After and After/Control data set ANOVA. Particular to this model, the factor time was nested in locations as 3 of the 6 sites within locations were sampled on unique days. However the temporal Before and After effects were orthogonal to spatial scales.

RESULTS

Over 80 macrofaunal species were identified over the three year period, with 59 occurring in Currumbene Creek, 45 in Sussex Inlet and 53 in Narrawallee Inlet. The three tidal flats were compositionally very similar, with the assemblage being dominated by polychaetes (38-45%), molluscs (27-31%) and crustaceans (15-25%). Although polychaetes were the most diverse phylum with 31 taxa, 80% of the total abundance in each tidal flat was attributed to just four species; the bivalves (*Mysella vitrea* and *Eumarcia fumigata*) and crustaceans (*Urohaustorius metungi* and *Mictyris* sp.). There were, however clear differences in total abundance between the different tidal flats, which is further described in Winberg et al (2007).

The closure of Currumbene Creek tidal flat to bait collection produced major shifts in the structure of this assemblage. The shift represented a change in relative abundance, but not composition, of species in the protected tidal flat compared to the reference locations (Fig. 2a.b.). The MDS output was supported by spearman rank correlation coefficients comparing the year prior to protection with each of the subsequent years. Species dominance curves (not presented, see Fig. 3-2 in Winberg 2008) indicated a decrease in the dominance of taxa following protection at Currumbene Creek which was not observed at the reference locations.

PERMANOVA confirmed that the changes apparent in the MDS plots were significant, with differences in the interaction across years between the reference (unprotected) and impact (protected) tidal flats at the scale of sites ($p(\text{MC}) = 0.02$) (Table 1). Secondary pairwise tests confirmed that 75% of site comparisons in the protected tidal flat changed significantly from before to after protection, while site assemblage change was seen in only 29% of comparisons in the reference tidal flats and was not significant across all sites. SIMPER analysis identified 7 taxa that contributed significantly to over 80% of the dissimilarity between assemblages sampled on the Currumbene tidal flat before and after protection (Table 2), including five taxa increasing and three decreasing significantly in abundance (Fig. 3). The abundance of *Eumarcia fumigata* increased nearly six-fold consistently across the tidal flat. The increase in the numbers of the naticidae was driven by heavy recruitment at a single site (C3) during both years following protection and are not reliably linked to any effect of zoning. The remaining two taxa, the juvenile bivalves *Soletellina alba* and capitellid polychaetes, both increased in abundance consistently across the tidal flat with significant effects at the smaller scales of plots and sites respectively.

Of the five taxa that increased in abundance (Fig. 3), four also showed an increase in homogeneity (H) across the tidal flat as they occurred in more samples (SIMPER presence/absence data) than prior to protection (Table 2). This reduction in patchiness was further supported by a significant increase in the measure of J' Pielou's evenness (Table 2). None of the other diversity measures provided any evidence of change due to MPA zoning.

Three species showed significant reductions in abundance (Fig. 3) and concurrent increasing patchiness (Table 2); including the targeted callianassid *Trypaea australiensis*. *T. australiensis* numbers however were low as the sampling technique was not optimal to

estimate abundance of this species. Decreases in the abundance of the amphipod *Urohaustorius metungi* were dramatic and consistent across the Currumbene flat, falling almost 60%, while densities of the polychaete *Sigalion ovigerum* fell almost 70%, showing a consistent trend at 4 sites. All shifts in abundance of the seven species were generally evident from the year following protection, and maintained for the two years that sampling occurred. Paralleling these biological changes, silt and clay content increased significantly at the Currumbene Creek no-take location in the two years following MPA zoning. No such change was seen at the Narrawallee reference location (Figure 4), while Sussex Inlet lacked silt or clay.

DISCUSSION

The zoning of the Currumbene Creek tidal flat within a no-take Marine Protected Area was associated with a range of measurable changes to soft-sediment macrofaunal assemblages. Following closure of the Currumbene tidal flat to bait harvesting, responses were rapid and included large shifts in the abundance of non-target species, as well as modification of the fine sediment fraction. Collectively, the changes in the assemblages were indicative of a functional shift from more mobile taxa, predominantly scavengers or predators, to less mobile, smaller, suspension or deposit feeding species. These changes were not reflected at the two reference locations and were maintained for the two years of sampling after enforcement, supporting our contention that a reduction in sediment disturbance and/or trampling, associated with bait harvesting activities, was a key driver of these shifts. We cannot assess changes in the abundance in the targeted ghost shrimp *Trypaea australiensis* as our coring methodology was directed at associated macrofauna and could not adequately sample the deep-burrowing ghost shrimp.

While evidence of a response in soft sediment habitat to the removal of disturbance is scant, a growing number of observational and experimental studies in this habitat report that small, relatively immobile filter feeding species are negatively impacted by sediment disturbance. This occurs through processes including smothering, blockage of filtering organs, sediment compaction, exposure to predators, aerial exposure or physical damage. A common feature of studies demonstrating impacts from trampling or heavy compression of sediments (Chandrasekara & Frid 1996, Casu et al 2006, Rossi et al 2007, Schlacher et al 2007), raking or similar disturbance (Ferns et al 2000, Kaiser et al 2001, Pillay et al 2007), dredging (Morello et al 2005), bait pumping (Skilleter et al 2005) and boat wash (Bishop & Chapman 2004), is a decrease in detritivore or filter feeding polychaetes (e.g. capitellidae, spionidae and orbinidae), as well as small or juvenile molluscs. In contrast, highly mobile, scavenging and predatory taxa are less sensitive and are among the first to benefit following disturbance (Reise 1982, Britton & Morton 1994, Morello et al 2005). These outcomes are consistent with our findings.

We contend that the changes observed in the tidal flat assemblage are linked to harvesting activities based on the following reasoning. First, experimental harvesting of shrimps, including callinassids, in the same habitat overseas reveal long term impacts on tidal flat macrofauna (Wynberg and Branch 1994). Second, anecdotal observations of bait harvesters confirms that the heavily-patrolled no-take Currambene Creek tidal flat is no longer fished, while high levels of recreational bait pumping continue to occur at the reference locations. Third, a recent experimental study seeking to disentangle the effects of trampling and bait harvesting accorded closely with our findings. This study is currently being prepared for publication (N Knott, pers. comm.).

It is likely that the changes we have observed will have important trophic implications for the fauna on the tidal flat (Roth & Wilson 1998), their competitive interactions (Thrush et al 1997, Holt et al 2004) as well as shifts in chemical processes (Bird et al 2000, Webb & Eyre 2004). Evidence for trophic cascade responses following cessation of targeted fishing activities in MPAs has been documented across numerous shallow reef habitats (Pinnegar et al 2000, Shears and Babcock 2003, Barret et al 2009). The rate of change that we have observed for indirect effects on non-target taxa is more rapid than previous MPA studies (Babcock et al 2010). While we observed marked shifts in abundance over a single year, Babcock and co-workers (2010) report that indirect effects on non-target taxa are usually only observed after a substantial time lag exceeding a decade.

Tidal flats in southeastern Australia experience very high levels of bioturbation and biogenic disturbance from the foraging of teleosts and elasmobranchs (Authors pers. obs.). However, we observed a clear trend towards increased homogeneity at the protected tidal flat as judged by Pielou's measure of evenness and multivariate SIMPER analyses. Again this mirrors evidence from disturbance studies where increases in spatial heterogeneity have been observed as a result of bait-pumping and hand-raking (Kaiser et al 2001, Skilleter et al 2005).

An emerging criterion in detecting shifts of functional assemblages evident in this and only a few other studies, is the importance of an understanding the scales of spatial pattern and linking these to multivariate measures of biodiversity (Quintino et al 2006, Winberg et al 2007, Terlizzi et al 2009). This is essentially a measure of impacts on and changes to beta-diversity, and in contrast to univariate measures that were also applied here, is necessary to detect and interpret change. Despite numerous common species, there were clearly different assemblages across the tidal flat at the scale of sites ($\geq 100\text{m}$)

(Winberg et al 2007), and therefore species shifts were most evident at this scale. Only two taxa, the bivalve *Eumarcia fumigata* and amphipod *Urohaustorius metungi*, changed in abundance consistently at the scale of the whole tidal flat.

Our findings relate directly to the management of MPAs and deliver on what Claudet & Guidetti (2010) identified as critical considerations in evaluating the effects of MPAs. This medium term (3 year) case study provides evidence of ecological change in beta-diversity, assemblage homogeneity and sediment characteristics in response to Marine Protected Area zoning and removal of anthropogenic disturbance. Our findings were consistent with the predictions developed at the experimental scale by Skilleter et al (2005) for similar habitats in temperate Australia. Such ecological shifts are predicted to have consequences for a range of ecosystem services including nutrient processes, trophic energy flow, inter and intraspecific interactions, as well as recruitment of vertebrate and invertebrate fauna (Austen et al 2002).

Our study highlights the need for a focus on additional habitat types, and the critical need for the use BACI designs. A simplistic focus on targeted-species with univariate data risks failing to detect subtle but important ecosystem changes; the evidence of and support for the benefits of MPAs in what is still a political and contentious issue in many countries. Our findings also point to increased resilience in no-take MPA habitats (Bevilacqua et al 2006) and imply that no-take tidal flats in Marine Protected Areas are an effective tool for conservation management.

The closure of areas to fishing activities represents a large-scale manipulative experiment that provides insight into ecosystem function. While it is beneficial for scientists to grasp the opportunity to use management decisions to do large scale experiments, it is also necessary for natural resource managers to engage scientists in a meaningful way for well-informed conservation management. These ideas are not new

(Underwood 1995, Bishop & Chapman 2004); however there remains broad potential for this mutually beneficial approach to be explored. After all, the justification for most conservation research is that it will lead to better and justifiable management of natural resources.

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Table 1: PERMANOVA table of results indicating significant interactions in bold, and pairwise tests between before and after zoning for each of the tidal flats. Year Ye, Estuary Es, Before B, After A, Control C, Impact I, Time Ti, Site Si, Plot Pl, Residual R. Currambene Creek CC, Sussex Inlet SI, Narrawallee Inlet, NI.

Source	df	SS	MS	Pseudo-F	P(MC)
YexEs	4	5.27E+10	1.32E+10	3.1975	0.037
BvsA x Es	2	9.01E+10	4.50E+10	3.4371	0.086
Ye x Cvl	2	3.03E+10	1.51E+10	2.7737	0.116
Ye x Ti(Es)	6	2.47E+10	4.12E+09	1.5344	0.161
BvA x Ti(Es)	3	3.93E+10	1.31E+10	2.5584	0.059
YexTi(Cvl)	4	2.00E+10	4.99E+09	1.8811	0.109
YexSi(Ti(Es))	24	6.44E+10	2.69E+09	1.7826	0.009
BvAxSi(Ti(Es))	12	6.15E+10	5.12E+09	2.7401	0.001
YexSi(Ti(Cvl))	16	4.25E+10	2.65E+09	1.7817	0.021
YexPl(Si(Ti(Es)))	72	1.08E+11	1.51E+09	0.65479	0.998
BvAxPl(Si(Ti(Es)))	36	6.73E+10	1.87E+09	0.93464	0.598
YexPl(Si(Ti(Cvl)))	48	7.15E+10	1.49E+09	0.64529	0.994
Res	379	8.72E+11	2.30E+09		
Total	485	1.12E+12			
Pairwise				t	P(MC)
CC BvsA year 1				1.8407	0.052
CC BvsA year 2				1.9176	0.048
CC After year 1-year 2				1.4193	0.173
SI BvsA year 1				1.3364	0.236
SI BvsA year 2				1.0258	0.517
SI After year 1-year 2				0.77832	0.726
NI BvsA year 1				1.1336	0.361
NI BvsA year 2				0.98832	0.526
NI After year 1-year 2				1.3513	0.210

Table 2: Taxa that contribute to consistent and significant dissimilarities in abundance Before and After Marine Park zoning at the protected (Impact) tidal flat and in contrast to unprotected (Control) sites (A= abundance H= heterogeneity, increase (+) or decrease (-)).

Species	A	H	F	p	factor	F vs.
<i>Urohaustorius metungi</i>	-	-	13.13	0.001	Bvs.A x Cvs.I	years x sites(T(estuaries))
			19.05	<0.001	Bvs.A x time(Impact)	residual (Impact)
<i>Eumarcia fumigata</i>	+	+	<0.001	<0.001	Bvs.A x time(Impact)	After x time(Impact)
			26.21	<0.01	Bvs.A x sites(Impact)	After x sites(T(Impact))
			0.14	<0.001	Bvs.A x plots(S(Impact))	Bvs.A x plots(S(Control))
Spionidae	+	-	112.77	<0.001	Bvs.A x sites(Impact)	Bvs.A x sites(Control)
Naticidae juv sp.	+	+	13.60	<0.001	Bvs.A x sites(Impact)	years x plots(S(Impact))
			6.96	<0.001	Bvs.A x plots(S(Impact))	Bvs.A x plots(S(Control))
<i>Soletellina alba</i>	+	+	16.24	<0.001	Bvs.A x Cvs.I	years x plots(S(estuaries))
			3.83	0.06	Bvs.A x sites(Impact)	Bvs.A x sites(Control)
			8.34	<0.001	Bvs.A x plots(S(Impact))	Bvs.A x plots(S(Control))
Capitellidae	+	+	164.00	0.100	Bvs.A x Cvs.I	Bvs.A x Control
			5.86	0.020	Bvs.A x sites(Impact)	Bvs.A x sites(Control)
<i>Sigalion ovigerum</i>	-	-	7.42	<0.001	Bvs.A x sites(Impact)	Residual (Impact)
			3.43	0.001	Bvs.A x plots(S(Impact))	Bvs.A x plots(S(Controls))
<i>Trypaea australiensis</i>	-	-	5.92	0.001	Bvs.A x sites(Impact)	years x plots(Impact)
			6.74	<0.001	Bvs.A x plots(S(Impact))	Bvs.A x plots(S(Controls))
Diversity measures			F	p	factor	F vs.
J' Pielou's evenness	+		8.31	<0.001	Bvs.A x sites(Impact)	Year x plots(S(Impact))
Sediment characteristics			F	p	factor	F vs.
% silt and clay	+		5.40	0.040	Bvs.A x Cvs.I	Year x sites(estuaries)

Fig. 1: Percentage of the 2283 peer reviewed publications in marine protected area research that focus on invertebrates in soft sediments; searched in Scopus between 2000 and 2011.

Fig. 2: Second stage MDS of resemblance matrices and corresponding composition and abundance (a), and composition only (b), correlations (Spearman) between data collected before and for each year after (prior-year 1 after and prior-year 2 after) in each of the three tidal flats, Currumbene Creek (C), Sussex Inlet (S) and Narrawallee Inlet (N).

Fig. 3: Five taxa that increased and three taxa that decreased in average abundance per core in the protected tidal flat (C = Currumbene Creek) versus the two reference tidal flats (S = Sussex Inlet and N = Narrawallee Inlet) (n=9). *Trypaea australiensis* was targeted by recreational bait collectors while the remaining species were not targeted.

Fig. 4. Percentage silt and clay content of sediments in (a) each of the tidal flats (C = Currumbene Creek, N = Narrawallee Inlet) before (dark grey) and after (light grey) no-take protection of Currumbene Creek. Note that Sussex Inlet lacked silt or clay.

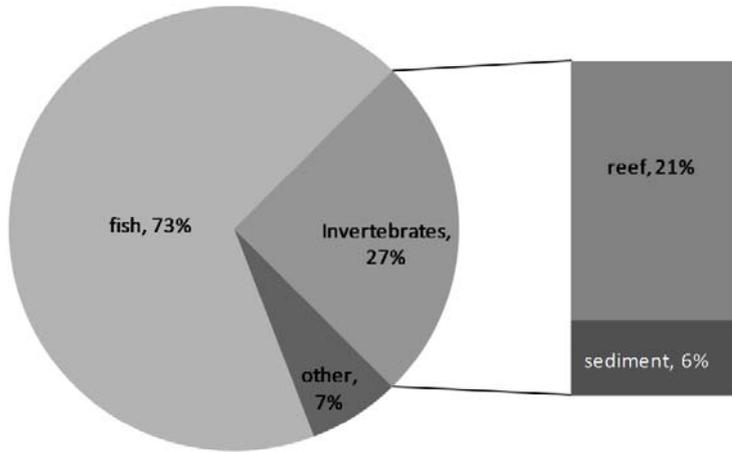


Fig. 1.

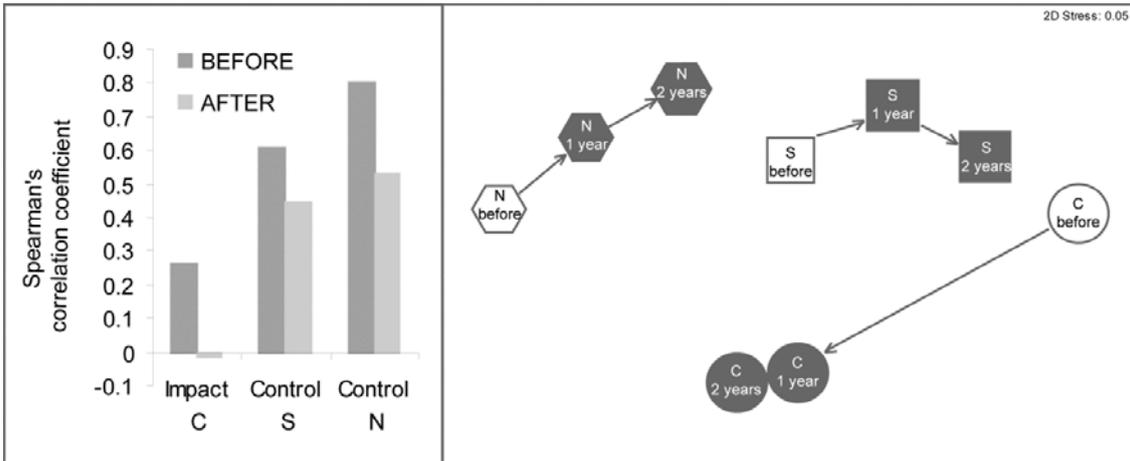


Fig. 2a.

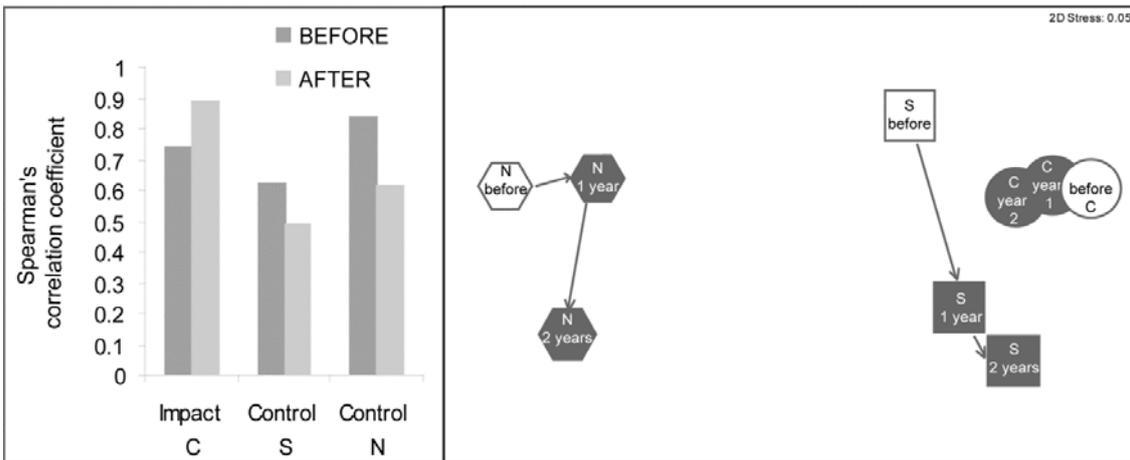


Fig. 2b.

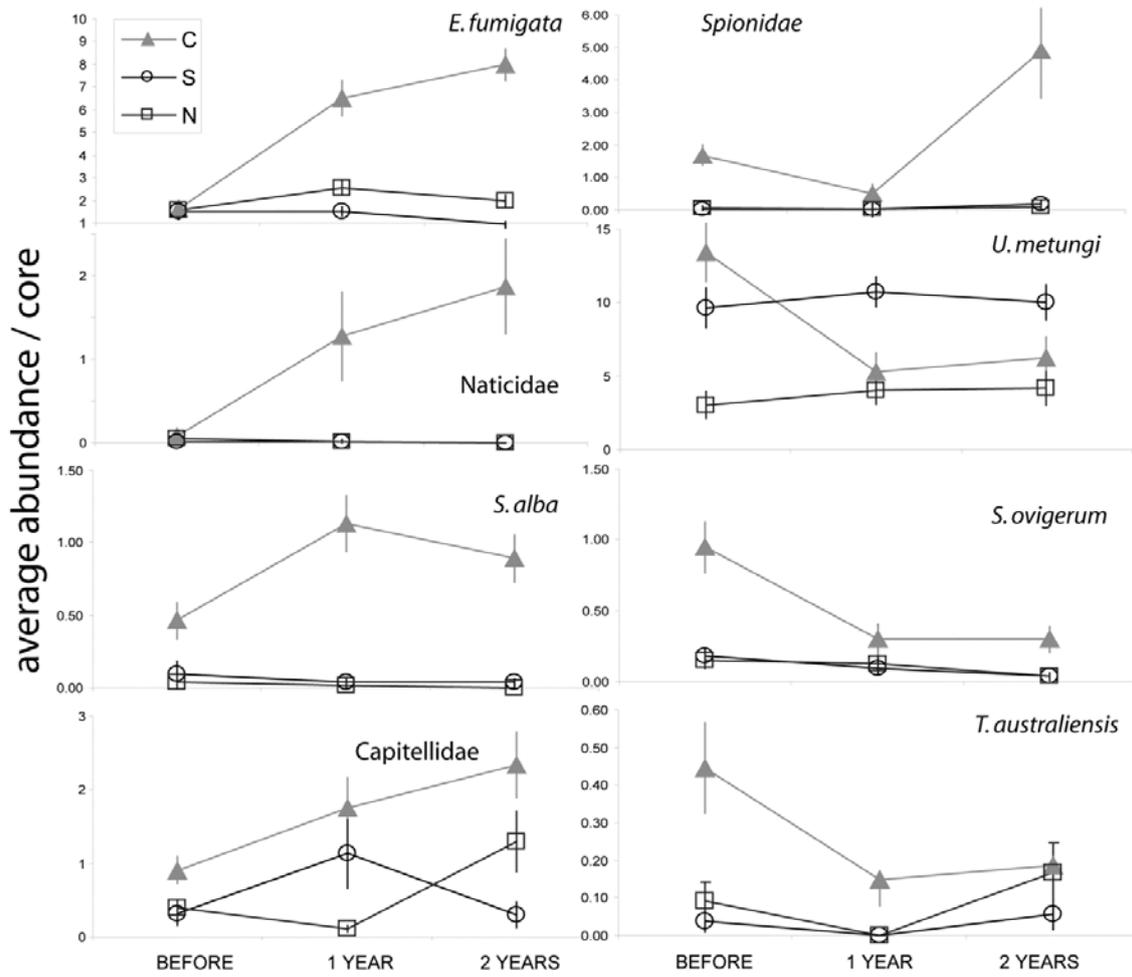


Fig. 3.

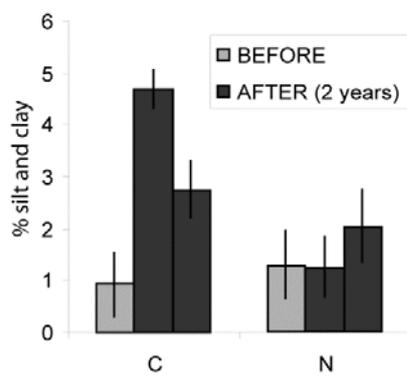


Fig. 4.