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 callianasid 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.

KEY WORDS: Soft sediment · Estuary · Invertebrates · Beta-diversity · Marine protected areas

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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 MPAs 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 provi-

sion 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 MPAs 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 MPAs 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%. Further, only 6% of publications addressed soft-sediment invertebrates (Fig. 1). This research bias is understandable in light of justifying the impact and benefits of MPAs to society and the socioeconomic 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 of studies have tested 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

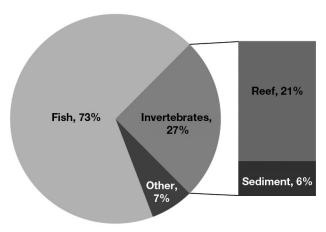


Fig. 1. Percentage of the 2283 peer-reviewed publications in marine protected area research that focus on invertebrates in soft sediments; searched in Scopus between 2000 and

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 & Stephenson 1961). Recreational fishers heavily exploit this crustacean for bait with a bag limit of 100 individuals per fisher (NSWDPI 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 & 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 3 yr, 1 yr prior to and 2 yr following no-take zoning. The no-take tidal flat within Jervis Bay Marine Park, Australia, was compared to 2 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.

MATERIALS AND 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 3 estuaries (Currambene Creek, Jervis Bay Marine Park, 35°01'S, 150°40'E; Sussex Inlet, 35°10'S, 150° 35′ E; and 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. Currambene 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 and Narrawallee Inlet throughout the study, while nipper pumping activity virtually ceased within the no-take MPA, with compliance in the heavily patrolled Currambene Creek close to fully effective. A mean (\pm SD) of 1.8 \pm 1.5 infringement notices were issued annually from 2007-2012 for nipper pumping within this sanctuary zone, and none have been issued 27 mo post 2012 (M. Fackerell, Jervis Bay Marine Park 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 3 tidal flats was sampled on one day within each of 2 time periods between June and October, prior to no-take zoning of Currambene Creek. We employed a spatially hierarchical sampling design; in each time period, 3 sites were haphazardly selected at least 100 m from each other within each tidal flat. At each site, three 2 m² plots were randomly selected approximately 20 m from each other and sampled with 3 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 1 yr and 2 yr 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 2 occasions per year) with a total of 486 cores over the 3 yr 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 mo intervening between periods of sampling on each tidal flat, we considered our replicate cores to be independent.

Cores (15 cm wide \times 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 4 cm diameter corer to a depth of 5 cm 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 2 d 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. Rare, 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 multidimensional scaling (MDS) plots. The data were pooled at the scale of sites prior to Bray-Curtis similarity matrices being calculated as recommended by K. R. 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's 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 pairwise *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 Currambene 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 whether there were compositional changes, or changes to compositional homogeneity between sites.

Univariate analyses were performed for selected taxa (outlined above), as well as a range of diversity measures (species richness, abundance, Shannon diversity [H'] and Pielou's evenness [J']). 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, $Trypea\ australiensis$, were 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 4-factor ANOVA (estuary, time, site and plot) (for methods, see Underwood 1994 or Terlizzi et al. 2005) for biological variables and 3 factors for silt and clay (estuary, time and site). 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 performed with GMAV 5 software (University of Sydney, Australia).

We extended the asymmetrical analysis of 1 impact (protected) site and 2 control (reference) sites to include temporal asymmetry (1 yr before protection and 2 yr after) by calculating further sums of squares from the ANOVA on the after and after/control data sets. Particular to this model, the factor time was nested in location 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 3 yr period, with 59 occurring in Currambene Creek, 45 in Sussex Inlet and 53 in Narrawallee Inlet. The 3 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 4 species: the bivalves *Mysella vitrea* and *Eumarcia fumigata* and the 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 Currambene 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. 2). The MDS output was supported by Spearman's 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 protec-

tion at Currambene 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 (Monte Carlo probability value p(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 Currambene Creek tidal flat before and after protection (Table 2), including 5 taxa increasing and 3 decreasing significantly in abundance (Fig. 3). The abundance of *E. fumigata* increased nearly 6-fold consistently across the tidal flat. The increase in the number of the Naticidae was driven by heavy recruitment at a single site (C3) during both years following protection and is not reliably linked to any effect of zoning. The remaining 2 taxa, the juvenile bivalve Soletellina alba and capitellid polychaetes, both increased in abundance consistently across the tidal flat with significant effects at the smaller scales of plot and site, respectively.

Of the 5 taxa that increased in abundance (Fig. 3), 4 also showed an increase in homogeneity 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' (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. However, T. australiensis abundance was low as the sampling technique was not optimal to estimate abundance of this species. Decreases in the abundance of the amphipod *U. metun*gi were dramatic and consistent across the Currambene Creek tidal flat, falling by almost 60%, while densities of the polychaete Sigalion ovigerum fell by almost 70%, showing a consistent trend at 4 sites. All shifts in abundance of the 7 species were generally evident from the year following protection, and maintained for the 2 yr that sampling occurred. Paralleling these biological changes, silt and clay content increased significantly at the Currambene Creek

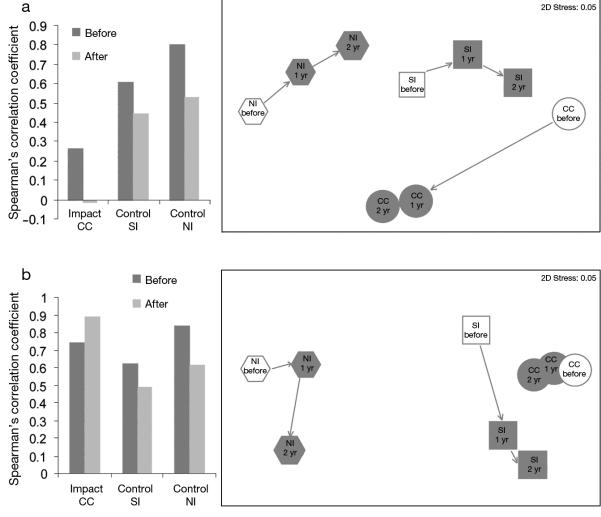


Fig. 2. Second-stage multidimensional scaling of (MDS) resemblance matrices and corresponding (a) composition and abundance and (b) composition-only correlations (Spearman) between data collected before and for each year after (prior–1 yr after and prior–2 yr after) in each of the 3 tidal flats, Currambene Creek (CC), Sussex Inlet (SI) and Narrawallee Inlet (NI)

no-take location in the 2 yr following MPA zoning. No such change was seen at the Narrawallee Inlet reference location (Fig. 4), while Sussex Inlet lacked silt or clay.

DISCUSSION

The zoning of the Currambene Creek tidal flat within a no-take MPA was associated with a range of measurable changes to soft-sediment macrofaunal assemblages. Following closure of the Currambene Creek 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 2 reference locations and were maintained for the 2 yr 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. Although we assessed changes in the abundance of the targeted ghost shrimp *Trypaea australiensis*, our coring methodology was directed at associated macrofauna and may underestimate densities of 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

Table 1. PERMANOVA table of results for invertebrate diversity and abundance on estuarine tidal flats (1 treatment and 2 reference flats) before and after marine protected area establishment. Pairwise tests are also given before and after zoning for each of the tidal flats. Significant interactions are depicted in **bold**. Ye: year; Es: estuary; B: before; A: after; C: control; I: impact; Ti: time; Si: site; Pl: plot; Res: residual. CC: Currambene Creek; SI: Sussex Inlet; NI: Narrawallee Inlet. p(MC): Monte Carlo probability value

Source df		SS	MS	Pseudo- F	p(MC)
Ye × Es	4	5.27×10^{10}	1.32×10^{10}	3.1975	0.037
B vs. $A \times Es$	2	9.01×10^{10}	4.50×10^{10}	3.4371	0.086
Ye × C vs. I	2	3.03×10^{10}	1.51×10^{10}	2.7737	0.116
$Ye \times Ti(Es)$	6	2.47×10^{10}	4.12×10^{9}	1.5344	0.161
B vs. $A \times Ti(Es)$	3	3.93×10^{10}	1.31×10^{10}	2.5584	0.059
$Ye \times Ti(C \text{ vs. I})$	4	2.00×10^{10}	4.99×10^{9}	1.8811	0.109
$Ye \times Si(Ti(Es))$	24	6.44×10^{10}	2.69×10^{9}	1.7826	0.009
B vs. $A \times Si(Ti(Es))$	12	6.15×10^{10}	5.12×10^9	2.7401	0.001
$Ye \times Si(Ti(C vs. I))$	16	4.25×10^{10}	2.65×10^{9}	1.7817	0.021
$Ye \times Pl(Si(Ti(Es)))$	72	1.08×10^{11}	1.51×10^{9}	0.65479	0.998
B vs. $A \times Pl(Si(Ti(Es)))$	36	6.73×10^{10}	1.87×10^{9}	0.93464	0.598
$Ye \times Pl(Si(Ti(C vs. I)))$	48	7.15×10^{10}	1.49×10^{9}	0.64529	0.994
Res	379	8.72×10^{11}	2.30×10^{9}		
Total	485	1.12×10^{12}			
Pairwise				t	p(MC)
CC B vs. A Year 1				1.8407	0.052
CC B vs. A Year 2				1.9176	0.048
CC A Year 1-Year 2				1.4193	0.173
SI B vs. A Year 1				1.3364	0.236
SI B vs. A Year 2				1.0258	0.517
SI A Year 1-Year 2				0.77832	0.726
NI B vs. A Year 1				1.1336	0.361
NI B vs. A Year 2				0.98832	0.526
NI A Year 1-Year 2				1.3513	0.210

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 Orbiniidae), 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 callianassids, in the same habitat overseas reveal long-term impacts on tidal flat macrofauna (Wynberg & 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 (N. Knott, pers. comm.). This study is currently being prepared for publication.

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 & Babcock 2003, Barrett et al. 2009). The rate of change that we have observed for indirect effects on non-target taxa is more rapid than observed in previous MPA studies (Babcock et al. 2010). While we observed marked shifts in abundance over a single year, Babcock et al. (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).

Table 2. Taxa that contribute to consistent and significant dissimilarities in abundance, as well as measures of diversity and sediment characteristics, before and after marine park zoning at the protected (impact) tidal flat and in contrast to unprotected (control) sites. Significant interactions are depicted in **bold**. +: increase; -: decrease. Abbreviations as in Table 1

_	Abundance	Heterogeneity	F	p	Factor	F vs.
Species						
Urohaustorius metungi	_	_	13.13	0.001	B vs. $A \times C$ vs. I	$Ye \times Si(T(Es))$
			19.05	< 0.001	B vs. $A \times Ti(I)$	Res (I)
Eumarcia fumigata	+	+	< 0.001	< 0.001	B vs. $A \times Ti(I)$	$A \times Ti(I)$
			26.21	< 0.01	B vs. $A \times Si(I)$	$A \times Si(T(I))$
			0.14	< 0.001	B vs. $A \times Pl(Si(I))$	B vs. $A \times Pl(Si(C))$
Spionidae	+	_	112.77	< 0.001	B vs. $A \times Si(I)$	B vs. $A \times Si(C)$
Juvenile Naticidae sp.	+	+	13.60	< 0.001	B vs. A x Si(I)	$Ye \times Pl(Si(I))$
			6.96	< 0.001	B vs. $A \times Pl(Si(I))$	B vs. $A \times Pl(Si(C))$
Soletellina alba	+	+	16.24	< 0.001	B vs. $A \times C$ vs. I	$Ye \times Pl(Si(Es))$
			3.83	0.06	B vs. $A \times Si(I)$	B vs. $A \times Si(C)$
			8.34	< 0.001	B vs. $A \times Pl(Si(I))$	B vs. $A \times Pl(Si(C))$
Capitellidae	+	+	164.00	0.100	B vs. $A \times C$ vs. I	B vs. $A \times C$
			5.86	0.020	B vs. $A \times Si(I)$	B vs. $A \times Si(C)$
Sigalion ovigerum	_	_	7.42	< 0.001	B vs. $A \times Si(I)$	Res (I)
			3.43	0.001	B vs. $A \times Pl(Si(I))$	B vs. $A \times Pl(Si(C))$
Trypaea australiensis	_	_	5.92	0.001	B vs. $A \times Si(I)$	$Ye \times Pl(I)$
			6.74	< 0.001	B vs. $A \times Pl(Si(I))$	B vs. $A \times Pl(Si(C))$
Diversity measures						
J' (Pielou's evenness)	+		8.31	< 0.001	B vs. $A \times Si(I)$	$\mathrm{Ye} \times \mathrm{Pl}(\mathrm{Si}(\mathrm{I}))$
Sediment characteristics						
Silt and clay (%)	+		5.40	0.040	B vs. $A \times C$ vs. I	$Ye \times Si(Es)$

An emerging criterion in detecting shifts of functional assemblages evident in this and only a few other studies is the importance of an understanding of 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 (≥100 m) (Winberg et al. 2007), and therefore species shifts were most evident at this scale. Only 2 taxa, the bivalve Eumarcia fumigata and the 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. Our medium-term (3 yr) case study provides evidence of ecological change in beta-diversity, assemblage homogeneity and sediment characteristics in response to MPA 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, interspecific 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 of 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 notake MPA habitats (Bevilacqua et al. 2006) and imply that no-take tidal flats in MPAs 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 perform large-scale experiments, it is also necessary for natural resource managers to

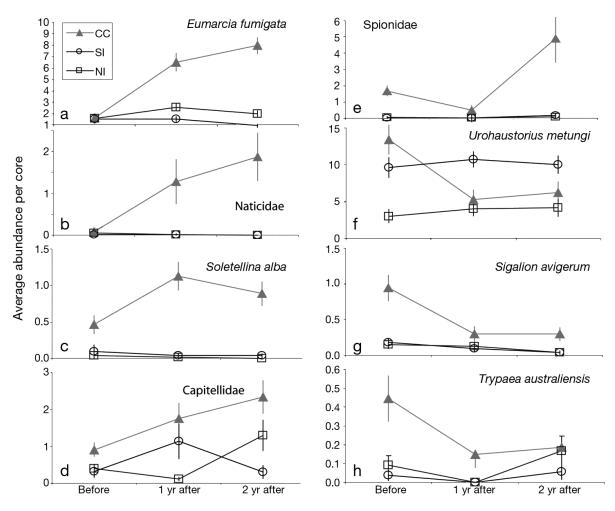


Fig. 3. (a-e) Five taxa that increased and (f-h) 3 taxa that decreased in average abundance per core in the protected tidal flat (CC: Currambene Creek) versus the 2 reference tidal flats (SI: Sussex Inlet; NI: Narrawallee Inlet) (n = 9). Trypaea australiensis was targeted by recreational bait collectors while the remaining species were not targeted

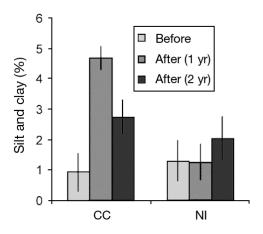


Fig. 4. Percentage silt and clay content of sediments in each of the tidal flats (CC: Currambene Creek; NI: Narrawallee Inlet) before (light grey) and after (1 yr, medium grey; 2 year, dark grey) no-take protection of Currambene Creek. Note that Sussex Inlet lacked silt or clay. Data are means \pm SE

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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LITERATURE CITED

- Anderson MJ (2005) PERMANOVA: a FORTRAN computer program for permutational multivariate analysis of variance. Department of Statistics, University of Auckland
- Austen MC, Lambshead PJD, Hutchings PA, Boucher G and others (2002) Biodiversity links above and below the marine sediment—water interface that may influence community stability. Biodivers Conserv 11:113–136
- Babcock RC, Shears NT, Alcala AC, Barrett NS and others (2010) Decadal trends in marine reserves reveal differential rates of changes in direct and indirect effects. Proc Natl Acad Sci USA 107:18256–18261
- Barrett NS, Buxton CD, Edgar GJ (2009) Changes in invertebrate and macroalgal populations in Tasmanian marine reserves. J Exp Mar Biol Ecol 370:104–119
- Bevilacqua S, Terlizzi A, Fraschetti S, Russo GF, Boero F (2006) Mitigating human disturbance: Can protection influence trajectories of recovery in benthic assemblages? J Anim Ecol 75:908–920
- Bird FL, Boon PI, Nichols PD (2000) Physicochemical and microbial properties of burrows of the deposit-feeding thalassinidean ghost shrimp *Biffarius arenosus* (Decapoda: Callianassidae). Estuar Coast Shelf Sci 51:279–291
- Bishop MJ, Chapman MG (2004) Managerial decisions as experiments: an opportunity to determine the ecological impact of boat-generated waves on macrobenthic infauna. Estuar Coast Shelf Sci 61:613–622
- Britton JC, Morton B (1994) Marine carrion and scavengers. Oceanogr Mar Biol Annu Rev 32:369–434
- Casu D, Ceccherelli G, Castelli A (2006) Immediate effects of experimental human trampling on mid-upper intertidal benthic invertebrates at the Asinara Island MPA (NW Mediterranean). Hydrobiologia 555:271–279
- Chandrasekara WU, Frid CLJ (1996) Effects of human trampling on tidal flat infauna. Aquat Conserv 6:299–311
- Clarke KR, Gorley RN (2006) PRIMER V6: user manual/tutorial. PRIMER-E Ltd, Plymouth
- Claudet J, Guidetti P (2010) Improving assessments of marine protected areas. Aquat Conserv 20:239–242
- Edgar GJ, Barrett NS (2002) Benthic macrofauna in Tasmanian estuaries: scales of distribution and relationships with environmental variables. J Exp Mar Biol Ecol 270:1–24
- Ferns PN, Rostron DM, Siman HY (2000) Effects of mechanical cockle harvesting on intertidal communities. J Appl Ecol 37:464–474
- Gaston KJ, Charman K, Jackson SF, Armsworth PR and others (2006) The ecological effectiveness of protected areas: the United Kingdom. Biol Conserv 132:76–87
- Granek EF, Polasky S, Kappel CV, Reed DJ and others (2010) Ecosystem services as a common language for coastal ecosystem-based management. Conserv Biol 24: 207-216
- Hailstone TS, Stephenson W (1961) The biology of *Callianassa* (*Trypaea*) australiensis Dana 1852 (Crustacea, Thalassinidea). Univ Queensland Pap 1:261–282
- Halpern BS, Warner RR (2002) Marine reserves have rapid and lasting effects. Ecol Lett 5:361–366
- Hastings A, Botsford LW (2003) Comparing designs of marine reserves for fisheries and for biodiversity. Ecol Appl 13:65–70
- Holt AR, Warren PH, Gaston KJ (2004) The importance of habitat heterogeneity, biotic interactions and dispersal in abundance-occupancy relationships. J Anim Ecol 73: 841–851

- Hooper DU, Chapin III FS, Ewel JJ, Hector A and others (2005) Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. Ecol Monogr 75:3–35
- Kaiser MJ, Broad G, Hall SJ (2001) Disturbance of intertidal soft-sediment benthic communities by cockle hand raking. J Sea Res 45:119–130
- Kelaher BP, Coleman MA, Broad A, Rees MJ, Jordan A, Davis AR (2014) Changes in fish assemblages following the establishment of a network of no-take marine reserves and partially-protected areas. PLoS ONE 9: e85825
- Loneragan NR, Bunn SE (1999) River flows and estuarine ecosystems: implications for coastal fisheries from a review and a case study of the Logan River, southeast Queensland. Aust J Ecol 24:431–440
- Lubchenco J, Palumbi SR, Gaines SD, Andelman S (2003) Plugging a hole in the ocean: the emerging science of marine reserves. Ecol Appl 13:3–7
- Morello EB, Froglia C, Atkinson RJA, Moore PG (2005) Impacts of hydraulic dredging on a macrobenthic community of the Adriatic Sea, Italy. Can J Fish Aquat Sci 62: 2076–2087
- NSWDPI (2014) Recreational fishing: bag and size limits—saltwater. Available at www.dpi.nsw.gov.au/fisheries/recreational/regulations/sw/sw-bag-and-size (accessed 15 June 2014)
- Pillay D, Branch GM, Forbes AT (2007) The influence of bioturbation by the sandprawn *Callianassa kraussi* on feeding and survival of the bivalve *Eumarcia paupercula* and the gastropod *Nassarius kraussianus*. J Exp Mar Biol Ecol 344:1–9
- Pinnegar JK, Polunin NVC, Francour P, Badalamenti F and others (2000) Trophic cascades in benthic marine ecosystems: lessons for fisheries and protected-area management. Environ Conserv 27:179–200
- Quinn GP, Keough MJ (2002) Experimental design and data analysis for biologists. Cambridge University Press, Cambridge
- Quintino V, Elliott M, Rodrigues AM (2006) The derivation, performance and role of univariate and multivariate indicators of benthic change: case studies at differing spatial scales. J Exp Mar Biol Ecol 330:368–382
- Read GB (2004) Guide to New Zealand shore polychaetes. NZ Coastal Marine Invertebrates Guide. Available at www.annelida.net/nz/Polychaeta/ShorePoly/NZShore-Polychaeta_begin.htm (accessed 8 January 2014)
- Reise K (1982) Long-term changes in the macrobenthic invertebrate fauna of the Wadden Sea: Are polychaetes about to take over? Neth J Sea Res 16:29–36
- Robertson AI (1984) Trophic Interactions between the fish fauna and macrobenthos of an eelgrass community in Western Port, Victoria. Aquat Bot 18:135–153
- Rossi F, Forster R, Montserrat F, Ponti M, Terlizzi A, Ysebaert T, Middelburg J (2007) Human trampling as short-term disturbance on intertidal mudflats: effects on macrofauna biodiversity and population dynamics of bivalves. Mar Biol 151:2077–2090
- Roth S, Wilson JG (1998) Functional analysis by trophic guilds of macrobenthic community structure in Dublin Bay, Ireland. J Exp Mar Biol Ecol 222:195–217
- Russ GR, Alcala AC (2003) Marine reserves: rates and patterns of recovery and decline of predatory fish, 1983–2000. Ecol Appl 13:1553–1565
- Schlacher TA, Thompson L, Price S (2007) Vehicles versus conservation of invertebrates on sandy beaches: mortali-

- ties inflicted by off-road vehicles on ghost crabs. Mar Ecol 28:354–367
- Shears NT, Babcock RC (2003) Continuing trophic cascade effects after 25 years of no-take marine reserve protection. Mar Ecol Prog Ser 246:1–16
- Shears NT, Grace RV, Usmar NR, Kerr V, Babcock RC (2006) Long-term trends in lobster populations in a partially protected vs. no-take marine park. Biol Conserv 132: 222–231
- Shepherd PCF, Boates JS (1999) Effects of a commercial baitworm harvest on semipalmated sandpipers and their prey in the Bay of Fundy Hemispheric Shorebird Reserve. Conserv Biol 13:347–356
- Skilleter GA, Zharikov Y, Cameron B, McPhee DP (2005) Effects of harvesting callianassid (ghost) shrimps on subtropical benthic communities. J Exp Mar Biol Ecol 320: 133–158
- Snelgrove PVR (1997) The importance of marine sediment biodiversity in ecosystem processes. Ambio 26:578–583
- Sutherland WJ, Armstrong-Brown S, Armsworth PR, Tom B and others (2006) The identification of 100 ecological questions of high policy relevance in the UK. J Appl Ecol 43:617–627
- Terlizzi A, Benedetti-Cecchi L, Bevilacqua S, Fraschetti S, Guidetti P, Anderson MJ (2005) Multivariate and univariate asymmetrical analyses in environmental impact assessment: a case study of Mediterranean subtidal sessile assemblages. Mar Ecol Prog Ser 289:27–42
- Terlizzi A, Anderson MJ, Bevilacqua S, Fraschetti S, Włodarska-Kowalczuk M, Ellingsen KE (2009) Beta diversity and taxonomic sufficiency: Do higher-level taxa reflect heterogeneity in species composition? Divers Distrib 15:450–458
- Tetreault I, Ambrose RF (2007) Temperate marine reserves enhance targeted but not untargeted fishes in multiple no-take MPAs. Ecol Appl 17:2251–2267
- Thrush SE, Cummings VJ, Dayton PK, Ford R and others (1997) Matching the outcome of small-scale density manipulation experiments with larger scale patterns an example of bivalve adult/juvenile interactions. J Exp Mar Biol Ecol 216:153–169
- Underwood AJ (1992) Beyond BACI: the detection of envi-

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- ronmental impacts on populations in the real, but variable, world. J Exp Mar Biol Ecol 161:145–178
- Underwood AJ (1993) The mechanics of spatially replicated sampling programmes to detect environmental impacts in a variable world. Aust J Ecol 18:99–116
- Underwood AJ (1994) On Beyond BACI: sampling designs that might reliably detect environmental disturbances. Ecol Appl 4:3–15
- Underwood AJ (1995) Ecological research and (and research into) environmental management. Ecol Appl 5:232–247
- van der Veer HW, Dapper R, Witte JI (2001) The nursery function of the intertidal areas in the western Wadden Sea for 0-group sole *Solea solea* (L.). J Sea Res 45:271–279
- Webb AP, Eyre BD (2004) The effect of natural populations of the burrowing and grazing soldier crab (*Mictyris longicarpus*) on sediment irrigation, benthic metabolism and nitrogen fluxes. J Exp Mar Biol Ecol 309:1–19
- White C, Kendall BE (2007) A reassessment of equivalence in yield from marine reserves and traditional fisheries management. Oikos 116:2039–2043
- Willis TJ, Millar RB, Babcock RC (2003) Protection of exploited fish in temperate regions: high density and biomass of snapper *Pagrus auratus* (Sparidae) in northern New Zealand marine reserves. J Appl Ecol 40:214–227
- Winberg PC (2008) Confronting the challenges of tidal flat conservation: spatial patterns and human impacts in a Marine Protected Area in southern NSW, Australia. PhD dissertation, Institute for Conservation Biology and Management, University of Wollongong
- Winberg PC, Lynch TP, Murray A, Jones AR, Davis AR (2007) The importance of spatial scale for the conservation of tidal flat macrobenthos: an example from New South Wales, Australia. Biol Conserv 134:310–320
- Worm B, Barbier EB, Beaumont N, Duffy JE and others (2006) Impacts of biodiversity loss on ocean ecosystem services. Science 314:787–790
- Wynberg RP, Branch GM (1994) Disturbance associated with bait collection for sandprawns (*Callianassa kraussi*) and mudprawns (*Upogebia africana*): long-term effects on the biota of intertidal sandflats. J Mar Res 52:523–558
- Zajac R (2008) Challenges in marine, soft-sediment benthoscape ecology. Landscape Ecol 23:7–18

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