

Functional traits reveal early responses in marine reserves following protection from fishing

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ABSTRACT

Aim Evaluating the effectiveness of marine reserves in achieving conservation goals is challenged by the decadal scales over which biological systems respond following protection. Given that trophic interactions underpin community responses following protection and that complex ecological interactions make responses difficult to identify, quantifying changes in species traits may provide detail missed by traditional diversity measures, including information relevant to ecosystem functioning. We determine whether this is the case by comparing community metrics based on functional traits to taxonomic diversity measures associated with ‘no take’ marine reserves and partially protected, fished areas along eight degrees of latitude.

Location Eighteen ‘no take’ marine reserves and 14 partially protected, fished areas along the east coast of Australia.

Method We use two independent datasets from shallow and deep coastal rocky reefs to analyse trait-based metrics and taxonomic diversity from sites inside reserves to sites in partially protected, fished areas.

Results Taxonomic diversity (species diversity and richness) and trait-based multimetrics (functional richness and dispersion) showed no difference with level of protection. Total fish abundance responded positively to protection, but only on shallow reefs. Comparing values of individual functional traits implied a return of larger bodied species of fish in protected areas and an increase in trophic level. The latter was significant on deeper reefs and was strongly correlated with age of protected area. Thus, recovery responses were largely associated with community mean functional trait values, highlighting the value of trait-based approaches for detecting change, when no differences in traditional taxonomic diversity measures were apparent.

Main conclusions We empirically demonstrate that functional traits can elucidate early conservation outcomes, when traditional multimetric diversity indices do not distinguish protected and fished communities. Ecologically relevant but sensitive metrics are fundamental to allow information to be incorporated into adaptive management strategies, which often occur on political rather than biological time-scales.

Keywords

Conservation, effectiveness, fish, marine reserve, protected areas.

INTRODUCTION

Reliable detection of meaningful changes in protected areas underpins adaptive management for optimizing and improving

reserve network design. Evaluating change in protected areas traditionally relies on comparisons of species diversity, abundance, biomass or organism size among areas afforded different levels of protection or before versus after reserve

designation (e.g. Lester *et al.*, 2009). Detecting change in such metrics relies on biological processes including species dispersal, growth or fecundity, processes which may take decades to manifest (e.g. Edgar *et al.*, 2009; Babcock *et al.*, 2010). For example, change in marine-protected areas is generally slow, with direct changes in species abundance or biomass taking 5–20 years and indirect, community-level effects taking even longer to manifest (e.g. Edgar *et al.*, 2009; Babcock *et al.*, 2010). A lack of change in traditional metrics within marine reserves could, in fact, be due to the inability of these metrics to detect earlier or subtle community-level changes, rather than a failure to meet conservation goals. The goal of many protected areas is to protect not only biological diversity but also ecosystem processes (Jones, 1994; Halpern & Warner, 2003). Traditional metrics alone do not encompass the broader range of changes that may occur following protection, many of which may have a bearing on ecosystem functioning.

Ecological and biological changes associated with protection are often trophically or functionally driven (e.g. Myers & Worm, 2003; Babcock *et al.*, 2010). Foremost, reserves commonly protect species from extractive activities (fishing, hunting and collecting), thereby releasing targeted and by-catch species from human pressure, resulting in an increase in abundance or return of these species to protected areas. In addition, given that such species are often large bodied, higher order predatory species (e.g. sharks, snappers, Myers & Worm, 2003), which play a fundamental role in structuring biological communities, trophic cascades often result in a host of indirect effects on associated communities. Early changes in protected areas may therefore manifest in subtle trophic and functional complexities of communities (Claudet *et al.*, 2010), which may be missed by traditional comparison of variation in the abundance and size of individual species. Metrics incorporating trophic or functional information may thus allow the detection of early or subtle change (Mouillot *et al.*, 2013) or where there exists great heterogeneity in responses to protection (Claudet *et al.*, 2010). Importantly, these metrics can also provide unique perspectives of biodiversity (Stuart-Smith *et al.*, 2013), as well as signify changes in key ecosystem processes (Mouillot *et al.*, 2013) and climate change resilience (Bates *et al.*, 2014), which are common but often unquantified conservation goals. Additionally, these metrics may be effectively comparable across broader spatial scales and regions of greatly differing species composition.

Here, we compare traditional, functional and trophic metrics of fish communities from 18 'no take' marine reserves to partially protected, fished areas across eight degrees of latitude and three bioregions in temperate Australia to test whether functional metrics outperform traditional metrics in detecting early change in marine reserves. We also examine relationships between these traits and reserve age to test whether changes in functional and traditional metrics are correlated with the time an area has been protected. We use two independent datasets to provide a robust assessment of

the usefulness of functional and trophic traits in detecting change in these marine reserves: (1) data from baited remote underwater video (BRUV) surveys on deeper reefs (*c.* 30 m depth) and (2) data from visual scuba censuses (Reef Life Survey, RLS, Edgar & Stuart-Smith, 2014) of shallow reefs (< 18 m depth).

METHODS

Data on fish communities (including elasmobranchs) were collected from up to 18 individual marine reserves spanning five networks of marine-protected areas (hereafter called marine parks) across eight degrees of latitude (Fig. 1). From north to south (and age as of 2011), these marine parks were Cape Byron Marine Park (CBMP: 5 years old), Solitary Island Marine Park (SIMP: 9 years old), Port Stephens-Great Lakes Marine Park (PSGLMP: 4 years old), Jervis Bay Marine Park (JBMP: 9 years old) and Batemans Marine Park (BMP: 4 years old). The length of time the entire reserve networks were actively protected with enforcement and compliance ranged from 4 to 9 years, although some individual reserves within SIMP (not sampled here) and JB had been protected for longer (13–20 years). We use age of protection with active enforcement and compliance at the time of sampling for analyses (see details of data sets). The broad conservation goals of these marine parks are to protect biological diversity and ecological processes (NSW MPA, 2001).

Individual reserves within each marine park were all of different sizes, different distances from the mainland and population centres, and varied in the extent they were connected to terrestrial protected areas. Sampling was spatially separated in marine reserves [hereafter called Sanctuary zones (SZ), $n = 18$ and 12 for BRUV and RLS data, respectively] and partially protected areas [hereafter called Habitat Protection zones (HPZ), $n = 14$ and 9 for BRUV and RLS data, respectively] within each marine park. The SZs and HPZs included in the RLS data were a subset of those sampled for BRUV, i.e., were located in the same places (albeit in different depths). These zones are representatively distributed (NSW MPA, 2001) in a mosaic throughout each marine park, creating networks of marine reserves (SZ) and partially protected areas (HPZ). In all marine parks, SZs are strict *no take* marine reserves that allow for non-extractive activities (i.e. scuba diving), while HPZ's are partially protected areas where the species that can be harvested and the fishing methods that can be used are prescribed by legislation. For example, lawful recreational fishing is generally allowed in HPZ's, but commercial trawling is not permitted. More specific details about prohibited activities in HPZ can be found in the Marine Estate Management Act 2014 No 72 (<http://www.legislation.nsw.gov.au/viewtop/inforce/act+72+2014+cd+0+N>) and Read & West (2010). Little information is available on the relative intensity of recreational fishing among HPZ areas, except within SIMP, where aerial surveys revealed similar fishing intensity among HPZ throughout the marine park (NSW MPA, 2009). High-resolution mapping

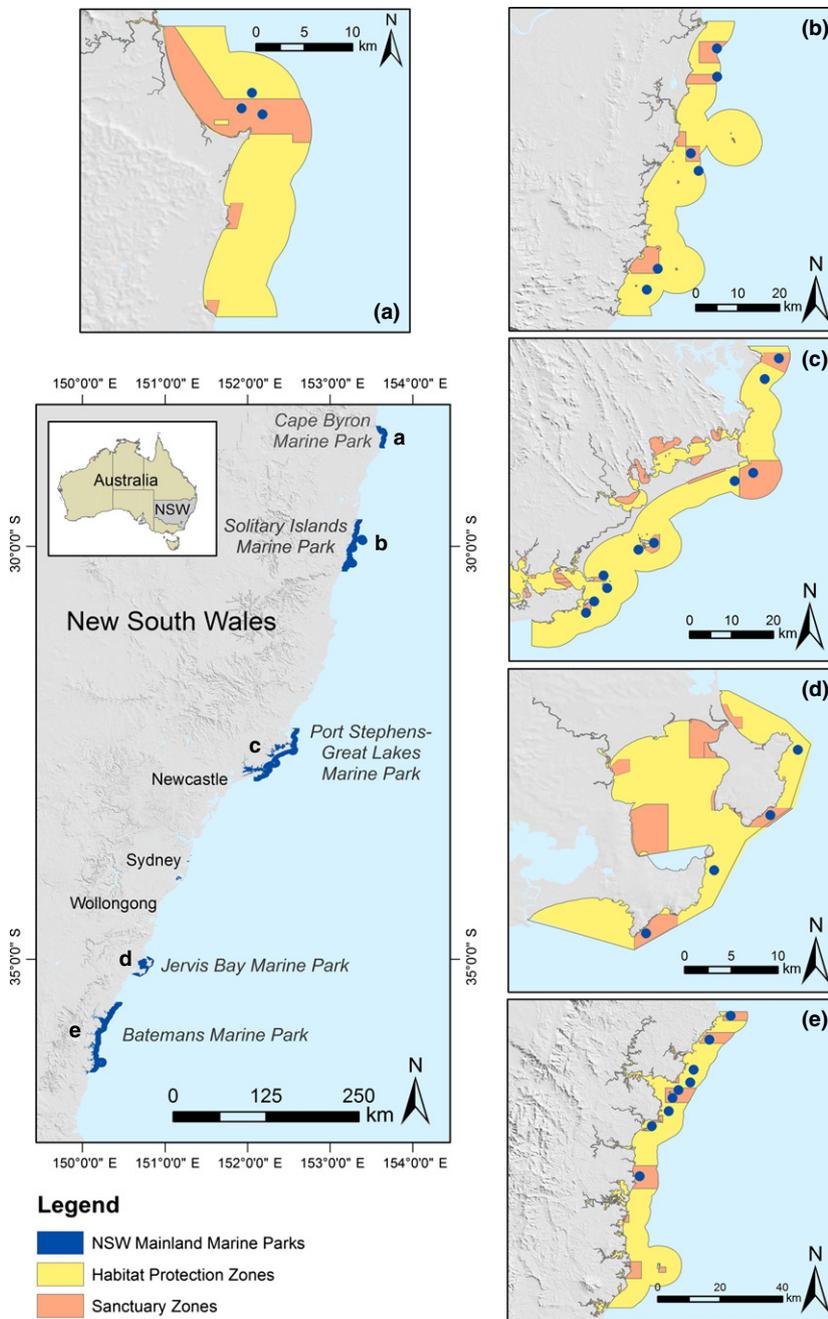


Figure 1 Map showing the five marine parks sampled and arrangement of sanctuary (SZ; pink) and habitat protection (HPZ; yellow) zones that were sampled within each marine park. Each dot indicates the zones that were sampled for baited remote underwater video. (a) Cape Byron Marine Park, (b) Solitary Islands Marine Park, (c) Port Stephens-Great Lakes Marine Park, (d) Jervis Bay Marine Park and (e) Batemans Marine Park.

conducted at the majority of survey locations (Jordan *et al.*, 2010) indicates few systematic differences in habitat structure or benthic topography. Moreover, no *a priori* differences in fish assemblages between zones are known. All zones within marine parks were chosen to be representative of the variety of habitats in the region and, when established, there was generally little available information on reef fish or habitat structure.

Datasets

We use two large, independent datasets [BRUV and RLS] to robustly determine the utility of functional metrics to detect

changes across rocky reef habitats at different depths [defined here as shallow (RLS) and deep (BRUV)] methods.

For the BRUV dataset, fish communities on rocky reefs at depths of *c.* 30 m reefs were sampled in the austral winter in 2011, as described in Kelaher *et al.* (2014). Briefly, at each site (chosen as representative rocky reef within the appropriate depth range), four BRUV units baited with *c.* 500 g of chopped pilchards (*Sardinops neopilchardus*) were deployed on the seafloor a minimum distance of 200 m apart and left for a minimum of 30 min. There were two sites separated by 1–3 km per zone per park. In each marine park, the number of zones sampled varied due to differences in the size of each park and availability of suitable rocky reef; CBMP ($n = 2$ SZ

and 1 HPZ), SIMP ($n = 3$ of each zone), PSGLMP ($n = 5$ of each zone), JBMP ($n = 2$ of each zone) and BMP ($n = 6$ SZ and 3 HPZ). Each BRUV unit was constructed as per Malcolm *et al.* (2007), which included a galvanized metal frame containing a video camera (mini DV SONY or digital Canon HG21) pointed at a bait bag mounted horizontally at the end of a 1.5-m-long bait arm. Cameras were housed within high-pressure polyvinyl chloride pipe with flat acrylic end-ports yielding a field of view of 110° .

Videos of 30-min duration were analysed in the laboratory using a field of view 2 m behind the bait bag, which represented a standardized area of 9.4 m^3 (Malcolm *et al.*, 2007). For each replicate BRUV deployment, we determined species richness, total max n and max n of each fish species. Max n for a species was the maximum number of individuals in any frame at any point in time and total max N was the sum of max n for each species (Cappo *et al.*, 2004). Both are estimates of relative abundance that are considered appropriate for BRUV video analyses because they avoid problems associated with counting the same individual fish more than once and correlate well with fish abundances measured via other methods (Willis *et al.*, 2000).

Shallower reefs at depths of $< 18 \text{ m}$ were surveyed between 2008 and 2013 (age of zones therefore ranged from 2 to 13 years of protection) by scuba divers using standard RLS visual census techniques as described in Edgar & Stuart-Smith (2014) and in the RLS methods manual (http://reeflife-survey.com/files/2008/09/NEW-Methods-Manual_15042013.pdf), and as used in a recent global assessment of marine reserves (Edgar *et al.*, 2014). Most of these surveys (*c.* 70%) were undertaken over the warmer period between November and May, although some data from the winter months were included. Surveys involved divers recording the identities and abundance of all fishes observed within 5 m either side of a 50-m transect line, which was laid along a depth contour. Multiple transects were surveyed at each site included in this study (mean per site 3.4 ± 0.3 transects SE, min = 1, max = 8, mean depth $9.1 \pm 3.8 \text{ m}$, min = 3 m, max = 18 m). Abundance estimates were made by counting all individuals of most species and estimating the number of the few highly abundant species. The majority of fishes were recorded to species level, but unidentified fishes (0.01% of records) were classified at the finest taxonomic resolution possible. Species richness and abundance were calculated as the total number of species and total number of individuals per transect (500 m^2) at each site, respectively.

Functional traits

For both datasets, eight functional traits were allocated for each species from the global reef fishes trait database used in Stuart-Smith *et al.* (2013) (Table 1). These include traits related to body size, trophic position, behaviour (some specifically related to habitat use) and physiology. They cover species attributes relevant to various aspects of spatial variation and types of resource use and potential strength of

Table 1 Traits used to calculate functional richness and dispersion. Maximum length (LMax) and trophic level (TL) are sourced from Fishbase and the other traits from authors knowledge and literature. See Stuart-Smith *et al.* (2013) for further detail.

Functional trait	Category	Units
LMax	Body size	Total length (cm), continuous
TL	Trophic	Index, continuous, range 2–4.7
Gregariousness	Behaviour	Index from 1 to 3 indicating solitary, found in pairs or sometimes aggregating and schooling species
Water column position	Behaviour	Benthic, demersal, site-attached pelagic, roaming pelagic
Diel activity pattern	Behaviour	Diurnal, nocturnal
Preferred substrate	Habitat use	Hard substrate, soft sediment
Complexity preference	Habitat use	Typically associated with habitats of low (e.g. urchin barrens), medium, high (e.g. kelp or branching coral-dominated) structural complexity
Thermal affinity	Physiology	95th percentile of the upper occupied temperature distribution, $^\circ\text{C}$

interactions. In combination, they allow fine partitioning of species' functional similarities. While all traits were used to generate functional similarities and were thus included in functional richness and dispersion metrics, we also explored patterns in individual traits separately. The maximum length (LMax) for each species used in this study represents the theoretical maximum size of a given species based on its growth curve, rather than being based on a measure of individual body size taken from survey data, as usually used. Trophic level (TL) is a continuous index representing the position of each species in the food chain and was obtained for each species from Fishbase (Froese & Pauly, 2014). We expected values of LMax and TL across the assemblage to increase in SZ relative to HPZ. We also tested for difference in the thermal affinity of species, a physiological trait based on combined distribution and spatial sea surface temperature information (Bates *et al.*, 2014), as well as categorical traits relating to gregariousness, water column position, diel activity pattern, preferred substrate type and associations with complex habitats. Although the realised values of some traits may be spatially and temporally variable, there is no reason to expect that such variation may be related to protection from fishing in a consistent manner.

Statistical analyses

For traditional metrics, we calculated species diversity as the inverse Simpson index as well as analysing max *n* and species richness. For functional and trophic traits, we calculated functional dispersion (FD_{is}) and functional richness as the convex hull volume (FRic) with the package 'FD' using the function *dpFD* (Laliberté & Shipley, 2011). Responses in individual traits were tested using community-weighted means (CWMs) of each trait. CWM values were calculated using both presence–absence and abundance data, with results representing the average value of the trait among species or among individuals in a given survey, respectively. For categorical traits, values represent the proportion of species or individuals that fall within a particular category of the trait. Results were identical irrespective of whether we used presence–absence or abundance data for CWMs, and thus, only the presence–absence CWM results (i.e. average trait values of species present) are presented in plots for ease of interpretation. The exception to this was the TL CWM, for which significant trends with presence–absence data were not significant using abundance data.

The BRUV and RLS datasets use fundamentally different methods, as described earlier, and target rocky reef habitats at different depths and therefore different taxa. For this reason, we did not attempt to directly compare results from the different methods, but instead we focus on the interactions between method/depth and zone type [*data.setrls:ZoneSZ*], rather than a main effect comparing the two methods '*data.setrls*', which is confounded by depth/method.

To gain a qualitative understanding of the types of species contributing to significant differences in functional metrics, we compared species contributing at least 2% of multivariate Bray–Curtis dissimilarity (SIMPER, PRIMER Clarke, 1993) using both abundance and presence–absence transformed data, to the ranked values of traits for each species. Abundance data were used to gain an understanding of the combined contribution of species abundances and identity to fish assemblage differences between zones based on analyses using individual-weighted data. Presence–absence data were then used to gain an understanding of the influence of species identity only on differences between zones from trait analyses based on presence–absence data. This was done for each dataset and each marine park separately. For LMax, species were considered 'large' if they had LMax > 30 cm (Edgar *et al.*, 2014). Species were considered to have a 'high' TL if TL was > 3.5 for RLS data and 3.6 for BRUV data. These values mostly represented piscivorous (and some invertivorous) and predatory species and accounted for approximately 40% of species present in each dataset. Variation in TL and LMax between datasets occurred because BRUV preferentially targets a suite of higher TL species due to bait attraction (Watson *et al.*, 2010).

For traits that showed significant differences between marine park zones, we determined whether age and distance from nearest town and boat ramp (fishing access point)

influenced these patterns by conducting Pearson correlations overall and within protected areas only (SZ) for each dataset. Data were normally distributed. Age was calculated as the period a zone has been actively enforced with patrolling and compliance when sampled. It varied slightly between datasets due to slight temporal differences in sampling.

Statistical modelling

We used mixed-effects models fitted using maximum likelihood (ML) and the package 'nlme' (Pinheiro *et al.*, 2014). To account for the random effects on the model intercept due to non-random sampling within each of the different parks, we included the random effects of location (categorical variable) nested in park. In all cases, including the nested random effects of site in location reduced the model Akaike information criterion (AICc) and explained more than 1% of the variance.

In our global models, we included a zone factor (HPZ versus SZ) to test for a general zone-related difference in response variables: species richness, species diversity, functional richness, FD, abundance (log transformed) and individual trait CWMs. Our global model included Park (CBMP, SIMP, PSGLMP, JBMP or BMP), Dataset (BRUV or RLS) and the interaction between both Zone and Park within Dataset as fixed effects. In all cases, the model fit and residual structure were visually inspected to ensure that the test assumptions were met (graphical residual analysis, Crawley, 2012), and the error structure of park-level variance was applied to normalize the residuals using the function *varIdent*.

To include model selection uncertainty (i.e. models with different fixed effects can have similar AICc scores) in the estimate precision of the parameters, we used a model averaging approach. Multimodel inference produced model-averaged (based on AICc) ML parameter estimates and unconditional standard errors (Adjusted SE, Tables 2 and 3) using the package 'MuMIn' and the function *model.avg* with missing coefficients set to zero (Barton, 2013). The confidence model set was the subset of models that contributed 90% of the cumulative Akaike weights from among all possible candidate models to represent the various possible combinations of fixed effects included in the global model. Contrast coefficients estimates for fixed effects that were included in the confidence model set are reported as treatment contrasts (type I sum of squares, which is preferred for unbalanced sampling designs) in the model results summary tables. Component model sets are shown in Table S1 in Supporting Information.

RESULTS

Species diversity and richness showed no differences between SZ and HPZ (Table 2, Fig. 2). There were also no differences in functional richness or dispersion between SZ and HPZ, and this result was consistent across the two datasets and among marine parks (Table 2, Fig. 2).

Table 2 Multimodel inference produced model-averaged (based on AICc) ML parameter estimates and unconditional standard errors (adjusted SE) for multivariate community metrics. Parameters included in the full model were park (BMP, CBMP, JBMP, PSGLMP, SIMP) and dataset (BRUV and RLS) and the interaction of each with zone (HPZ and SZ). Only those terms that were included in the confidence model set for each response of interest are reported. Coefficient estimates are treatment contrasts where the ‘intercept’ represents the reference: BRUV data from the HPZ, and the marine park, BMP. Treatments that were significantly different from the reference are bolded. The upper and lower confidence interval limits represent the 95% confidence window. The component models are in Table S2.

Species diversity	Estimate	SE	Adjusted SE	Lower CI	Upper CI	P
Intercept	5.41	0.34	0.34	4.74	6.08	0.000
data.setrls	-2.47	0.29	0.30	-3.05	-1.88	0.000
ParkCBMP	1.34	1.77	1.80	-2.20	4.88	0.458
ParkJBMP	1.08	0.76	0.79	-0.47	2.63	0.173
ParkPSGLMP	0.68	0.41	0.43	-0.16	1.52	0.115
ParkSIMP	1.60	0.49	0.512	0.59	2.61	0.002
ZoneSZ	0.14	0.43	0.43	-0.72	0.99	0.761
ParkCBMP:ZoneSZ	-4.79	1.68	1.77	-8.25	-1.33	0.007
ParkJBMP:ZoneSZ	1.13	1.19	1.25	-1.33	3.59	0.368
ParkPSGLMP:ZoneSZ	-0.65	0.65	0.66	-1.934	0.64	0.321
ParkSIMP:ZoneSZ	-0.33	0.81	0.85	-2.00	1.35	0.703
Species richness						
Intercept	10.59	0.89	0.89	8.85	12.33	0.000
data.setrls	5.12	1.19	1.20	2.76	7.47	0.000
ParkCBMP	5.78	1.84	1.93	2.00	9.55	0.003
ParkJBMP	4.35	1.37	1.44	1.53	7.16	0.003
ParkPSGLMP	7.70	0.93	0.97	5.80	9.61	0.000
ParkSIMP	2.72	1.08	1.13	0.51	4.93	0.016
ZoneSZ	0.95	0.83	0.84	-0.70	2.59	0.261
data.setrls:ZoneSZ	2.61	1.33	1.35	-0.04	5.26	0.054
Functional richness						
Intercept	0.42	0.02	0.02	0.38	0.46	0.000
data.typerls	-0.37	0.02	0.02	-0.40	-0.34	0.000
ParkCBMP	0.11	0.04	0.04	0.02	0.20	0.012
ParkJBMP	0.21	0.03	0.04	0.14	0.29	0.000
ParkPSGLMP	0.17	0.02	0.02	0.12	0.21	0.000
ParkSIMP	0.11	0.02	0.03	0.06	0.16	0.000
ZoneSZ	0.02	0.02	0.02	-0.02	0.05	0.300
Functional dispersion						
Intercept	0.16	0.00	0.00	0.16	0.17	0.000
data.setrls	-0.03	0.01	0.01	-0.04	-0.02	0.000
ZoneSZ	-0.01	0.01	0.01	-0.01	0.01	0.384
data.setrls:ZoneSZ	-0.01	0.01	0.01	-0.03	0.01	0.210
ParkCBMP	0.01	0.01	0.01	-0.02	0.03	0.604
ParkJBMP	0.02	0.01	0.01	0.00	0.04	0.044
ParkPSGLMP	0.01	0.01	0.01	-0.01	0.02	0.351
ParkSIMP	0.01	0.01	0.01	-0.00	0.03	0.071

AICc, Akaike information criterion; BMP, Batemans Marine Park; JBMP, Jervis Bay Marine Park; BRUV, baited remote underwater video; HPZ, Habitat Protection zones; ML, maximum likelihood; PSGLMP, Port Stephens-Great Lakes Marine Park; RLS, Reef Life Survey; SIMP, Solitary Island Marine Park; SZ, Sanctuary zones.

Linear Mixed-Effects Full Model Structure: Response.of.interest~ data.set+Zone:dataset+Park+Zone:Park,weights=varIdent(form=~1|dataset/Park), random=~1|Location/Site,method='ML'.

Total abundance (or Total Max *N* for BRUV) was higher in SZ than in HPZ in both datasets, but only significantly so in shallow sites surveyed by RLS (Fig. 3). The average maximum length of species (LMax CWM) was consistently higher in SZ across both datasets. Not all parks responded to the same degree, however, and differences were stronger in the

lower latitude parks (Table 3, Fig. 3). Fishes typically associated with structurally simple habitats (classified as ‘low’ in the trait describing association with complex habitats such as coral and kelp beds) were more frequent in SZ than HPZ, and this pattern was consistent in both datasets (Table 3, Fig. 3).

Table 3 Multimodel inference produced model-averaged (based on AICc) ML parameter estimates and unconditional standard errors (adjusted SE) for univariate community metrics. Parameters included in the full model were park (BMP, CBMP, JBMP, PSGLMP, SIMP) and dataset (BRUV and RLS) and the interaction of each with zone (HPZ and SZ). Only those terms that were included in the confidence model set for each response of interest are reported. Coefficient estimates are treatment contrasts where the ‘intercept’ represents the reference: BRUV data from the HPZ, and the marine park, BMP. Treatments that were significantly different from the reference are bolded. The upper and lower confidence interval limits represent the 95% confidence window. The component models are in Table S2.

log(Total max <i>N</i>)	Estimate	SE	Adjusted SE	Lower CI	Upper CI	<i>P</i>
Intercept	1.48	0.06	0.06	1.36	1.59	0.000
data.setrls	1.20	0.08	0.08	1.04	1.35	0.000
ParkCBMP	0.29	0.11	0.12	0.06	0.52	0.012
ParkJBMP	0.08	0.09	0.09	-0.10	0.26	0.382
ParkPSGLMP	0.32	0.07	0.07	0.19	0.46	0.000
ParkSIMP	-0.07	0.07	0.07	-0.21	0.07	0.348
ZoneSZ	0.07	0.06	0.06	-0.05	0.19	0.251
data.setrls:ZoneSZ	0.18	0.09	0.09	0.01	0.35	0.043
ParkCBMP:ZoneSZ	0.16	0.19	0.20	-0.23	0.54	0.425
ParkJBMP:ZoneSZ	-0.22	0.14	0.14	-0.50	0.06	0.121
ParkPSGLMP:ZoneSZ	-0.15	0.10	0.10	-0.35	0.05	0.145
ParkSIMP:ZoneSZ	-0.03	0.12	0.12	-0.27	0.21	0.788
Maximum length						
Intercept	50.35	2.04	2.05	46.34	54.36	0.000
data.setrls	-16.02	1.92	1.95	-19.84	-12.21	0.000
ParkCBMP	11.82	9.81	10.03	-7.84	31.49	0.239
ParkJBMP	9.76	4.20	4.40	1.14	18.38	0.000
ParkPSGLMP	9.48	2.28	2.39	4.79	14.16	0.093
ParkSIMP	4.50	3.38	3.49	-2.34	11.33	0.192
ZoneSZ	4.48	2.22	2.25	0.06	8.90	0.047
ParkCBMP:ZoneSZ	22.75	10.24	10.76	1.65	43.84	0.035
ParkJBMP:ZoneSZ	-1.40	6.86	7.21	-15.54	12.74	0.846
ParkPSGLMP:ZoneSZ	0.60	3.68	3.74	-6.72	7.92	0.873
ParkSIMP:ZoneSZ	-6.61	4.36	4.58	-15.59	2.37	0.149
data.setrls:ZoneSZ	-2.79	3.17	3.22	-9.11	3.52	0.386
TL						
Intercept (BMP/HPZ/BRUV)	3.27	0.02	0.02	3.23	3.31	0.000
data.set(rls)	-0.04	0.02	0.02	-0.09	0.01	0.083
Park(CBMP)	0.18	0.03	0.03	0.12	0.25	0.000
Park(JBMP)	0.06	0.03	0.03	-0.00	0.11	0.056
Park(PSGLMP)	0.06	0.02	0.02	0.03	0.10	0.000
Park(SIMP)	0.12	0.02	0.02	0.08	0.16	0.000
Zone(SZ)	0.03	0.02	0.02	0.00	0.07	0.044
data.set(rls)*Zone(SZ)	-0.08	0.03	0.03	-0.13	-0.03	0.003
Complexity						
Intercept	0.15	0.01	0.01	0.13	0.18	0.000
ParkCBMP	-0.01	0.03	0.03	-0.06	0.05	0.797
ParkJBMP	0.01	0.02	0.02	-0.03	0.05	0.738
ParkPSGLMP	-0.04	0.01	0.01	-0.06	-0.01	0.007
ParkSIMP	-0.01	0.01	0.01	-0.04	0.02	0.405
ZoneSZ	-0.04	0.01	0.01	-0.06	-0.01	0.003
data.setrls	0.01	0.01	0.01	-0.01	0.02	0.534
ParkCBMP:ZoneSZ	-0.05	0.04	0.04	-0.13	0.03	0.199
ParkJBMP:ZoneSZ	0.02	0.03	0.03	-0.04	0.09	0.478
ParkPSGLMP:ZoneSZ	0.04	0.02	0.02	-0.00	0.07	0.063
ParkSIMP:ZoneSZ	0.02	0.02	0.02	-0.02	0.07	0.323

AICc, Akaike information criterion; BMP, Batemans Marine Park; JBMP, Jervis Bay Marine Park; BRUV, baited remote underwater video; HPZ, Habitat Protection zones; ML, maximum likelihood; PSGLMP, Port Stephens-Great Lakes Marine Park; RLS, Reef Life Survey; SIMP, Solitary Island Marine Park; SZ, Sanctuary zones; TL, trophic level.

Linear Mixed-Effects Full Model Structure: Response.of.interest~ data.set+Zone:dataset+Park+Zone:Park,weights=varIdent(form=~1|dataset/Park), random=~1|Location/Site,method='ML').

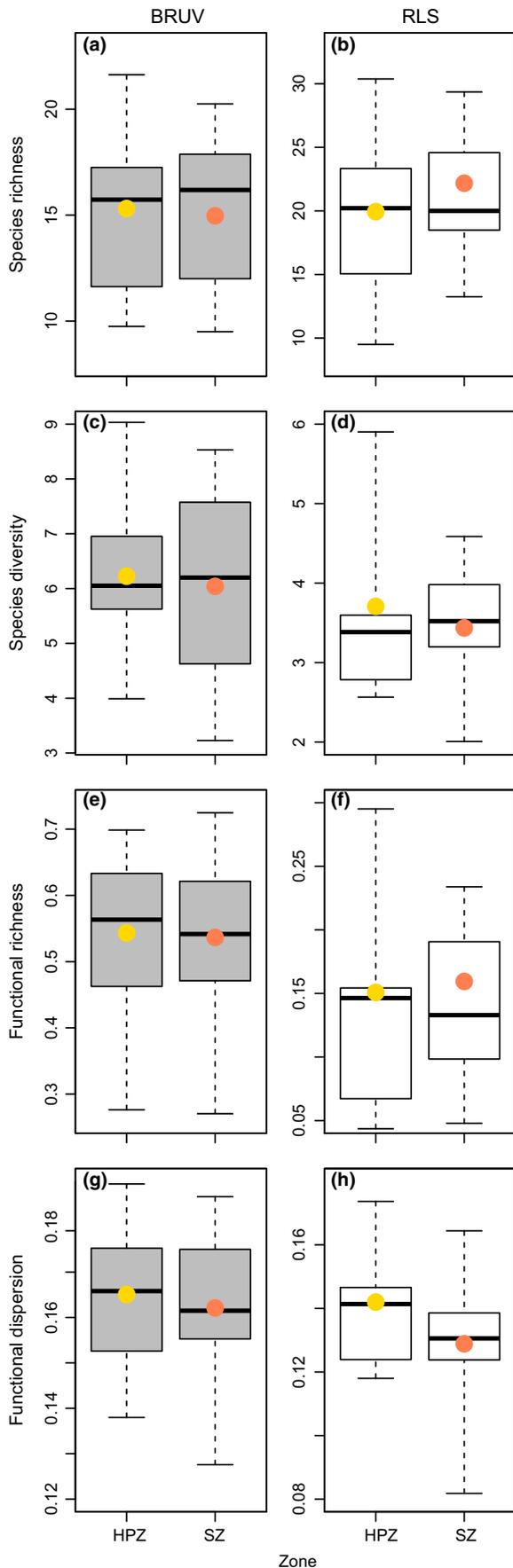


Figure 2 Box plots showing species richness (a, b), species diversity (c, d), functional richness (e, f) and functional dispersion (g, h) between sanctuary (SZ; pink) and habitat protection (HPZ; yellow) zones for the two independent datasets.

Greater LMax in SZ was driven by a combination of greater occurrence and abundance of larger bodied species in SZ samples relative to HPZ. For BRUV data, the widely distributed and targeted species snapper (*Chrysophrys auratus*, Forster, 1801; top 7–12% of species for LMax) was seen more frequently in SZ samples in all marine parks (Fig. 4) and was more abundant in SZ in all parks. Abundances of *C. auratus* in SZ were 12 times greater in CBMP, five times greater in BMP and two times greater in PSGLMP and SIMP. Similarly, the large, targeted silver trevally (*Pseudocaranx georgianus*, Bloch & Schneider, 1801) was more abundant (up to 2.6 times) in SZ in the four parks in which it occurred. Other species that contributed to greater LMax in SZ varied among marine parks due to different species compositions, but were a combination of both targeted and non-targeted species.

The average TL of fish communities differed in the SZ compared to HPZ. TL was significantly higher in SZ for BRUV data (Table 3, Fig. 3g). For BRUV data, the percentage of high-TL species that contributed at least 2% of multivariate dissimilarity between zones and were seen more frequently in SZ samples was between 50% (PSGLMP) and 83% (BMP). Again, species contributing to differences between zones were a mix of targeted and non-targeted species and varied among marine parks.

Positive associations were evident between age of marine park and TL for BRUV data overall (1, 30 d.f., $r = 0.46$, $P < 0.05$), and this relationship became stronger when SZ were analysed separately (1, 16 d.f., $r = 0.505$, $P < 0.05$ and $r = 0.747$, $P < 0.01$ for species- and abundance-weighted TL CWM, respectively). No significant correlations were found between LMax and marine park age (d.f. = 1, 17 $r = -0.44$ and d.f. = 1, 30, $r = 0.212$, $P > 0.05$, for RLS and BRUV data, respectively) or between total abundance/total Max N and age (d.f. = 1, 17 $r = -0.186$ and d.f. = 1, 30 $r = -0.31$, $P > 0.05$, for RLS and BRUV data, respectively). There were also no significant correlations ($P > 0.05$) between distance from nearest town or boat ramp (fishing access point) and any metric, either overall or within SZ. There were no differences in fish thermal affinity, gregariousness, water column position, diel activity pattern or preferred substrate between zones (see Table S2).

DISCUSSION

Early detection of biological change in protected areas (where change has occurred) is critical to assess conservation goals, particularly those related to the maintenance of natural ecological processes. Relative to change in traditional diversity measures, which may take decades to manifest (Babcock

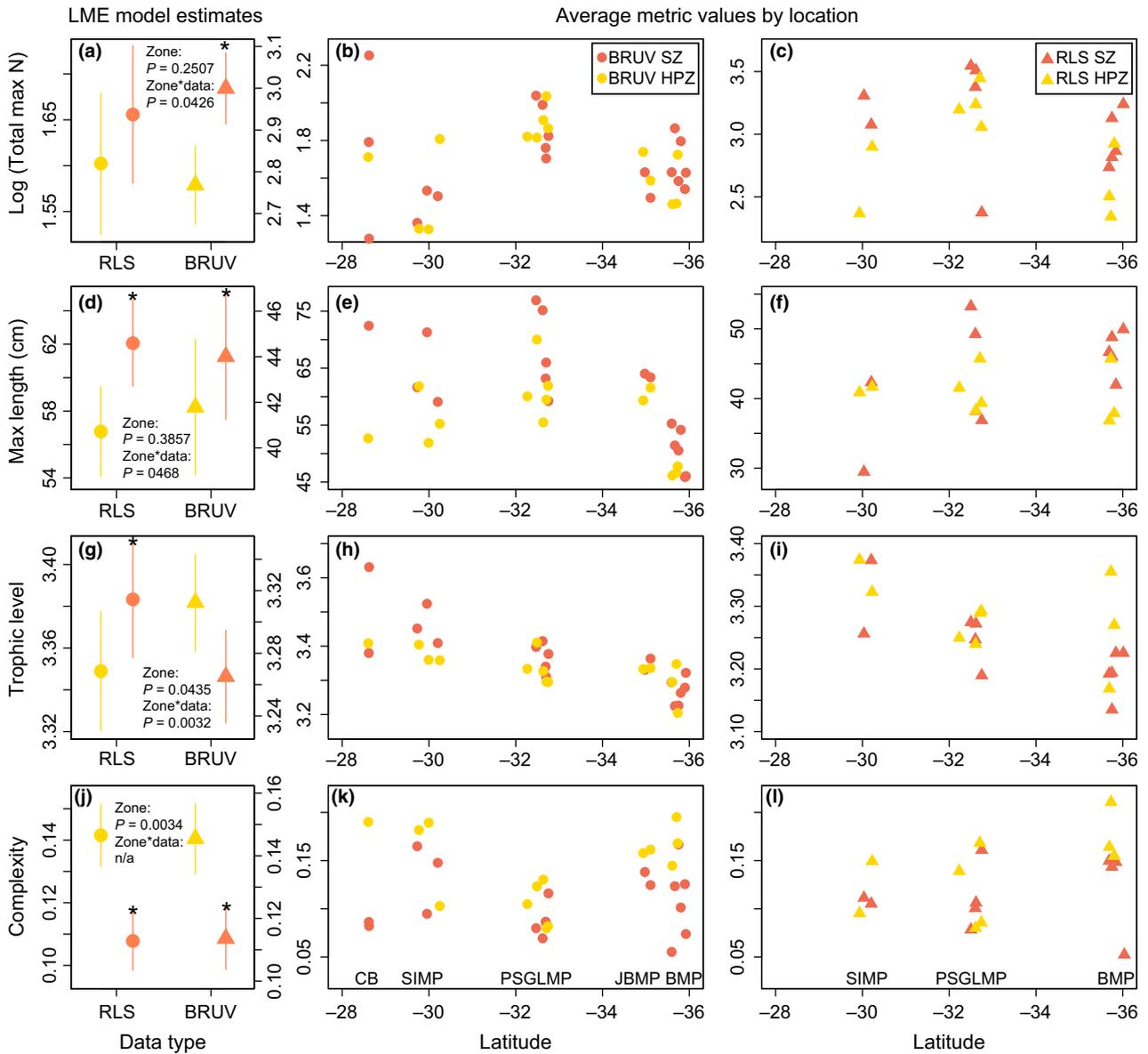


Figure 3 Differences in log total Max N [or total abundance for Reef Life Survey (RLS) data], LMax, trophic level (TL) and complexity between sanctuary (SZ; pink) and habitat protection (HPZ; yellow) zones and across latitudes/parks for the two independent datasets predicted from linear mixed effects (LME) models (a, d, g, j). An asterisk indicates a significant difference in the SZ versus Habitat Protection zones. The average values for each location sampled in each park, for each dataset (baited remote underwater video: b, e, h, k and RLS: c, f, i, l).

et al., 2010; Edgar *et al.*, 2014), functional or trophic traits of communities may allow for early or more subtle community-level changes to be detected, particularly those associated with change in ecological processes (e.g. Mouillot *et al.*, 2013; Bates *et al.*, 2014). Indeed, we identified change in the mean values of individual traits between areas afforded different levels of protection, when traditional diversity metrics and metrics based on multiple functional traits showed little or no response, and these differences were apparent in reserves as young as 4 years old. Importantly, we demonstrate the utility and robustness of some traits for detecting early change across two large independent datasets from different depths and using different methods.

The strongest and most consistent result across five networks of marine reserves and two datasets was greater LMax in SZ relative to HPZ, and this result was independent of zone age. Noting that LMax is not a measure accounting for the size of individuals observed in surveys, but is a species-level characteristic representing maximum attainable size, this result represents a greater frequency and abundance of larger species in surveys in SZ. Increases in the mean size, biomass or abundance of fishes are a common result of MPA studies (e.g. Lester *et al.*, 2009; and this study for abundance) and are commensurate with cessation of fishing (which tends to target larger individuals). In contrast, our results also indicate a significant shift in species composition towards

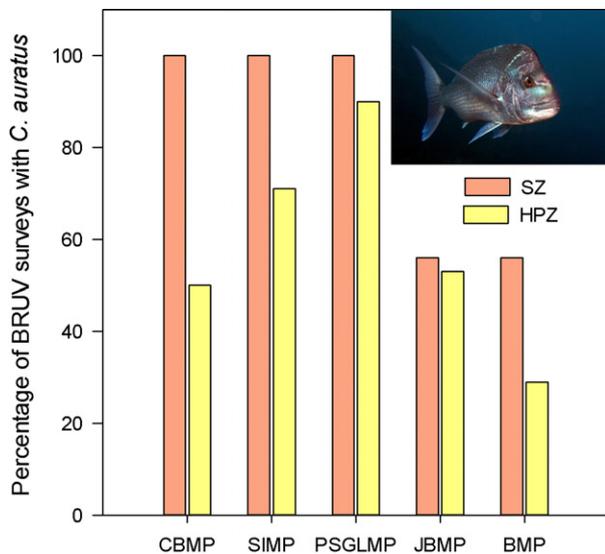


Figure 4 The percentage of baited remote underwater video samples in which snapper (*Chrysophrys auratus*, Forster, 1801) was present within sanctuary (SZ; pink) and habitat protection (HPZ; yellow) zones of each marine park.

increased presence and abundance of larger bodied species (rather than representing growth of protected individuals) in marine reserves (see also Claudet *et al.*, 2010). Although this may be in part due to greater abundances and densities of large species in SZ leading to more sightings in more SZ samples, it is also due to different species of larger bodied fish occurring in SZ that are often not observed or encountered less frequently in fished areas. Such a change can occur over a very short time-scale if such species are removed from coastal reefs by fishing very quickly after recruiting to this habitat.

The average TL of fish communities was greater in SZ relative to fished areas for BRUV data, and this pattern was strongly related to length of protection. This is perhaps not surprising given that larger fishes (greater LMax) tend to belong to higher TL (Pauly *et al.*, 2001) and are often among the most heavily targeted species on reefs (Myers & Worm, 2003). One of the key long-term benefits of marine reserves is their capacity to reverse the trophic downgrading prevalent in marine systems around the world (Estes *et al.*, 2011). Certainly, the restoration of size structure and top-down forcing via trophic cascades in marine reserves has been shown to have predictable positive influences on key habitat-forming species, such as large macroalgae (Babcock *et al.*, 2010) and the cover of coral (Selig & Bruno, 2010). The unanticipated and diverse impacts of restoring trophic and size structure in ecosystems may be equally important (Estes *et al.*, 2011). For example, the establishment of marine reserves in the Channel Islands of southern California facilitated greater localized abundances of predatory spiny lobsters (*Panulirus interruptus*), which led to reduced abundances of urchins. Low densities of urchins reduced disease transmission and

the frequency of urchin wasting disease in reserves (Lafferty, 2004). Given the pervasive influence of top-down forcing on community structure and ecosystem function (Estes *et al.*, 2011), the detection of increased TL and LMax in reserves may provide an early indicator of the onset of long-term changes associated with restoration of trophic cascades (Babcock *et al.*, 2010).

Both targeted and non-targeted species of fish contributed to differences in LMax and TL between zones, suggesting that some changes are indirect rather than a direct result of cessation of fishing in protected areas. Trophic cascades involving predatory fishes, urchins and macroalgae following protection in temperate marine reserves are well documented (e.g. Shears & Babcock, 2003), but more subtle trophic or non-consumptive (competitive or behavioural) interactions among fish are poorly understood. Certainly, an increase in predatory fish abundances in protected areas has been shown to decrease the abundance of prey fish species relative to fished areas (Graham *et al.*, 2003; Harasti *et al.*, 2014). Moreover, the presence of large, predatory species (sharks) has been shown to have non-consumptive effects, decreasing the diversity and abundance of other fish species (Klages *et al.*, 2013). The age of the marine parks studied here (up to 9 years) is likely the minimum time one might expect to detect indirect trophic effects (Babcock *et al.*, 2010). Behavioural or competitive interactions among fishes, however, may manifest on much shorter time-scales.

The 'complexity' trait we used indicates species' associations with or dependencies on complex habitats such as kelp beds. The rationale for this trait being used in studies of MPAs includes its potential as an indirect measure to capture changes in available habitat through higher order trophic effects (e.g. the recovery of kelp beds mentioned above) and/or changes in habitat use of species, as well as having relevance to shifting concentration of ecological interactions, when interpreted with other traits. Changes in either the extent of habitat types or habitat use of species may occur following protection, but the former is expected to be a long-term response, while the latter could occur over shorter time frames. Our result of higher frequencies of species associated with simple habitats in SZs is unlikely to have resulted from habitat change occurring through cascading trophic interactions, given the short time frame and that such a result would imply a loss of kelp beds and corals has occurred in SZs relative to HPZs, for which there is no evidence. It is also possible that our result relates to the shift to larger bodied and higher TL species because such species are less likely to be associated with complex habitats for shelter or prey (compared with small-bodied species at intermediate TLs). Alternatively, the result of higher frequencies of species associated with simple habitats in SZs could also arise if SZs were originally placed in areas with lower kelp or coral cover than nearby HPZs but this is unlikely (see Methods).

We found no overall differences in traditional or multi-metric diversity estimates (species diversity, species richness

and functional group richness, and dispersion) between SZ and HPZ. This result was also found in Bates *et al.* (2014) for a single, 20-year old reserve known to be effective and indicates that protection from fishing does not always result in net loss or net gain in the variety of species or functional groups. Rather, protection appears to lead to subtle shifts in the types of species and functional groups that predominate between areas with different levels of protection. This result is not surprising given that complex trophic interactions that are spatially and temporally heterogeneous are likely to result in variable directional change in diversity estimates.

Indeed, relative to HPZ, we found a trend for estimates of diversity and richness to often have greater variation among replicate SZ reserves within each marine park (see Fig. 3), a trend consistent with patterns observed in Tasmanian MPAs that were attributed to landscape-level habitat heterogeneity (Edgar *et al.*, 2009). Despite this, the highest values of diversity were often found within SZ. This suggests that individual reserves respond differently to protection, but that protection may still lead to an increase in diversity in comparison to fished areas (Kelaher *et al.*, 2014). Greater species and functional diversity is thought to confer community resilience to stressors (e.g. invasion, climate change) including within MPAs (Bates *et al.*, 2014). Despite no overall change in diversity estimates across marine parks, identification of individual reserves with particularly high species or functional diversity may allow prioritization of such areas in adaptive management and compliance programs with the aim that these areas may be more resilient in a future of increasing anthropogenic stress.

Early detection of change (or lack thereof) in protected areas is critical to allow biological information to be incorporated into adaptive management strategies, which often occur on political rather than biological time-scales. Political change can occur as frequently as every 3–4 years; legislation requires that the MPAs studied here in NSW, Australia, are reviewed initially after 5 years (Kelaher *et al.*, 2014). These time-scales are at the lower end of expectations of detection of direct change in marine reserves (Babcock *et al.*, 2010; Edgar *et al.*, 2014). Certainly, previous studies conducted in young temperate reserves (e.g. 5 years) have demonstrated limited change in traditional metrics (Edgar & Barrett, 2012; Coleman *et al.*, 2013), suggesting that this time-scale is often too short to allow scientific studies to detect biological change (but see RLS results for total abundance here). As such, robust information may often not be available over subdecadal scales to facilitate evidence-based, adaptive management to enhance biodiversity conservation (Kelaher *et al.*, 2014). Ecologically relevant but sensitive trait-based metrics provide a potential solution to this problem as they can outperform some traditional metrics and provide a useful addition for distinguishing early conservation outcomes. Given immense public pressure to demonstrate the efficacy of new marine-protected areas, early detection of change where it occurs can enhance support for marine reserves and contribute greatly to their overall success.

ACKNOWLEDGEMENTS

We thank RLS volunteers and staff of all marine parks. Support to GJE and RSS from an ARC Linkage Grant, and to RSS through the Marine Biodiversity Hub. We appreciate comments of four referees.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Table S1 Details of component model sets.

Table S2 Results from statistical analyses of non significant numeric and categorical traits.

BIOSKETCH

This paper is a collaboration between colleagues working in marine conservation on the east coast of Australia and represents a strong partnership between industry (MAC, HM, DH, AJ, NK) and academic (AB, RSS, GE, BPK) researchers.

Author contributions: B.P.K. and R.S.S. conceived the idea; all authors collected the data; A.B. and M.A.C. conducted analyses; M.A.C. and A.B. led the writing.

Editor: David Schoeman