



Community-wide effects of protection reveal insights into marine protected area effectiveness for reef fish

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ABSTRACT: Marine protected areas (MPAs) are not designed the same, nor are they equally effective. Efficacy of MPAs is frequently gauged by measuring the direct ecological responses of fish communities. However measuring the indirect, or knock-on effects from protection can provide additional insight into MPA effectiveness at the community level. Here we applied trait-based and community analyses to investigate MPA effectiveness by evaluating both direct and indirect effects of protection on fish assemblages using baited remote underwater stereo-video data from inside and outside 5 no-take MPAs along the South African coastline. The trait-based analyses indicated the presence of a significant overall direct effect (increased abundance of mature individuals targeted by fisheries) and indirect effects (reduction of the abundance of species not targeted by fisheries) inside MPAs, and highlighted that fish maturity is an essential trait to incorporate when assessing direct effects of protection. However, investigation of the species data of the individual MPAs showed positive reserve effects at the community level (both direct and indirect effects) in only 3 MPAs. For the most part these results conform with current theories on the factors that contribute to MPA effectiveness. Yet, one old, large and isolated no-take MPA showed no direct effects of protection, which is attributed to the lack of adequate offshore reef habitat throughout this MPA. While these results support the value of MPAs as ecosystem management tools, they highlight the need for appropriate site selection when designing MPAs.

KEY WORDS: MPA effectiveness · NEOLI · Stereo-BRUVs · Functional entities · Life-stage · Ecological isolation

1. INTRODUCTION

Due to rapidly changing ecosystems, the urgency to establish effective marine protected areas (MPAs) is now greater than ever (Edgar 2017). Effective MPAs increase diversity, local abundance and biomass and support the recovery of depleted stocks

within their boundaries (Gell & Roberts 2003, Worm et al. 2006, Lester et al. 2009). However, many MPAs are ineffective and fail to achieve biodiversity and fisheries management goals (Edgar et al. 2014, Gill et al. 2017). Therefore, it is not surprising that MPA implementation, especially as a fisheries management tool, has been under much scrutiny (Agardy et al.

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2003, Hilborn et al. 2004, Jones 2007, Rice et al. 2012). Nonetheless, MPAs are still a popular management tool which aims to conserve biodiversity and mitigate the anthropogenic impacts associated with fishing (Pikitch et al. 2004, Fletcher et al. 2010). To ensure MPAs are effective and beneficial, more reliable primary research and in-depth synthesis of current knowledge is needed to provide a solid basis for management and policy implementation (Halpern 2014, Woodcock et al. 2017).

Fishing typically targets larger-bodied species and individuals, due to both fishing regulations and angler/consumer preference (Pauly et al. 2002, Gwinn et al. 2015). Fishing thus reduces the abundance and biomass of target species, truncates size distributions and reduces spawner biomass of affected populations (Jennings & Kaiser 1998, Myers & Worm 2003). Recoveries of spawner biomass and exploited populations are therefore considered direct effects of protection. Such direct effects are well documented (Cowley et al. 2002, Halpern 2003, Russ & Alcalá 2003, Aburto-Oropeza et al. 2011) and commonly identified by comparing target fish abundance and biomass between protected and exploited sites (Halpern 2003, Micheli et al. 2004, Willis & Millar 2005, Maggs et al. 2013, Soler et al. 2015). Larger fish species are usually predators and thus important in the regulation of prey populations (Jennings & Kaiser 1998), or can be superior competitors that affect species interactions. Selective removal of larger, higher trophic level species can therefore lead to alterations in the structure of a fish community (Babcock et al. 1999, Jennings et al. 1999, Pinnegar et al. 2000) due to ecological release, from both predators (prey release) and interspecific competition (Chase et al. 2002). Such community-wide changes are considered indirect effects of fishing, and are expected to manifest in higher abundances of species that are prey, occupy lower trophic levels, are less competitive, or are less desirable from an angling perspective (non-target species). In the context of MPA effectiveness, indirect or community-wide effects of protection will only be detected once target populations have recovered to the point where they influence the abundance of non-target species (Babcock et al. 2010). Consequently, we can gauge the efficacy of an MPA by monitoring non-target species abundances in concert with the biomass of target species. As such, investigation of both direct and indirect effects can provide a more complete assessment of MPA effectiveness, and give greater insight into the factors that maximise their conservation value. Importantly, although indirect effects might in certain instances

be an undesirable outcome, they nonetheless represent the restoration to the natural state, and should be viewed as indicative of an MPA which managed to restore and maintain ecosystem functioning.

The direction and strength of direct and indirect effects arising from MPAs can be attributed to ecological processes and/or management criteria. From an ecological perspective, the species diversity and level of omnivory in an ecosystem, habitat complexity (Salomon et al. 2010) and the trophic groups considered (Babcock et al. 2010) are all thought to affect the extent of indirect effects from fishing. From a management and planning point of view, reserve characteristics such as no-take zonation, enforcement, old age, large size and ecological isolation (the NEOLI criteria, see Edgar et al. 2014), as well as governance, buffer size and budget, influence MPA effectiveness (Edgar et al. 2014, Gill et al. 2017, Woodcock et al. 2017).

To obtain a more holistic understanding of MPA effectiveness, standardised and comparable data from inside and outside multiple replicate MPAs need to be collected. However, because MPAs are typically widely spaced along a coastline, environmental filtering by changes in conditions, competitive exclusion and stochastic processes can lead to high turnover in fish assemblage structure (Lamanna et al. 2014). Consequently, such fish communities are not often comparable, as there is no broad-scale consistency in the species, making it difficult to identify general patterns (Keddy 1992, Hockey & Branch 1997, Day & Roff 2000). Functional trait-based analysis is a possible solution, as species from all locations are grouped according to a set of generic functional traits, thereby removing local variation in species identity and facilitating broad-scale analyses (Weiher & Keddy 1995, Violette et al. 2014). In addition, trait-based analyses can provide insights into the biological traits that are most sensitive to direct or indirect effects of protection (Thrush & Dayton 2010, Mouillot et al. 2013, 2014, Coleman et al. 2015, Villéger et al. 2017).

Here, we quantified the direct and indirect effects of protection by examining the abundance and biomass of target and non-target fish species collected between 2013 and 2016, inside and outside 5 no-take MPAs from the warm-temperate and subtropical ecoregions of southern Africa. We first established if direct effects of protection were evident before investigating any secondary or indirect effects. Direct effects were expected to manifest as a significant increase in the average biomass of target species inside MPAs due to absence of selective targeting of larger individuals by fishing, and were considered a positive

reserve effect at the resource level (target species). In contrast, indirect effects were expected to manifest as a significant decrease in the abundance of non-target species inside MPAs due to either predation or competition from the recovered populations of target species (Götz et al. 2009). The presence of both direct and indirect effects of protection was considered to be a strong positive reserve effect at the community level (i.e. predators and highly competitive species have recovered to the point that they significantly affect the abundances of prey or interspecific competitors). Analyses were based on multivariate response data. Due to differences in fish species sampled from different MPAs, we first took a functional trait-based approach to establish if there was an overall effect of protection on target species and non-target species. Next, we investigated the protection effect at each MPA using species data.

2. MATERIALS AND METHODS

2.1. Study region

Data were collected from inside and outside 5 MPAs from the south-west to central north-east coast of South Africa (Fig. 1). Moving west to east, the 5 MPAs investigated were De Hoop, Tsitsikamma National Park, Bird Island, Amathole, and Pondoland (Fig. 1). Within the study region, there is a gradual increase in sea water temperature from the west to the east, which is associated with a similarly gradual turnover in species composition along the coastline (Table 1). The data set thus spans a diverse array of ecosystems in the warm-temperate ecoregion of southern Africa, with Pondoland being the only subtropical representative (Fig. 1; see Sink et al. 2012).

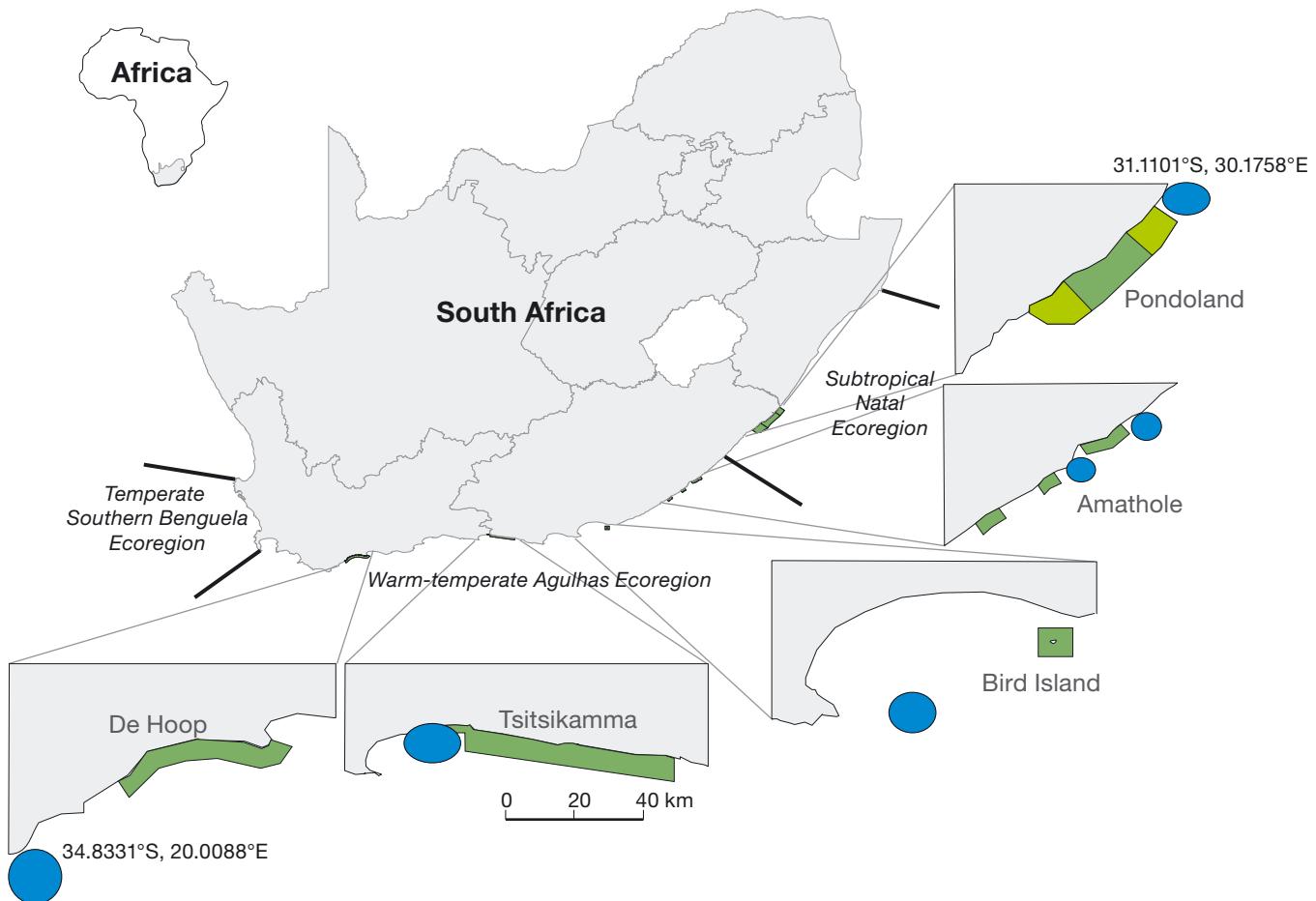


Fig. 1. Locations of the 5 studied marine protected areas (MPAs) along the south-east coast of South Africa. Dark lines demarcate the different marine ecoregions (*in italics*) along the South African coastline. Green represent no-take zones within the studied MPAs and blue circles represent the fished sites

Table 1. Information on the sampling locations (marine protected areas [MPAs] and adjacent fished sites). The information provided includes the factors identified by Edgar et al. (2014) that contribute towards MPA effectiveness. The corresponding abbreviation associated with the MPAs represent the no-take (N), enforced (E), old (O), large (L) and isolated (I) criteria met by each MPA (NEOLI criteria; see Edgar et al. 2014). Values in parentheses are explained in the heading of the relevant category

Location	Water Dist. from shore temp (°C; mean ± SD)	Sampling trip (yyyy-mm)	Sites	Sample size	Established (yr until survey)	Size (size no-take area) (km ²)	Enforcement	Isolation	Permitted fishing pressure in no-take zone	Offshore habitat
De Hoop – NOLI										
Coastal	11.1 ± 1.1	2015-03	De Hoop MPA	22	1985 (30)	288 (288)	Medium	High Low	None High	Sand with sporadic reef patches Reef with sporadic sand patches
Tsitsikamma – NEOL	12.5 ± 3.2	2013-02	Tsitsikamma MPA	55	1964 (49)	360 (360)	High	Medium Medium	None Medium	Reef with sporadic sand patches Reef with sporadic sand patches
Bird Island – Algoa Bay (NI)	15.9 ± 2.5	2014-03	Bird Island MPA	18	2004 (10)	7 (7)	Medium	High High	None High	Mostly reef Mostly reef
Amathole – NOL	14.7 ± 1.8	2015-05	Amathole MPA	39	Community 1981 (34) Officially 2011 ^a (4)	247 (247)	Medium	Low	None	Reef with sporadic sand patches
Pondoland – NELI	19.5 ± 2.5	2014-01	Pondoland MPA	25	2004 (10)	1380 (643)	High	High Low	None High	Reef with sporadic sand patches Reef with sporadic sand patches
		2015-05	Pondoland adjacent	25						

^aAlthough the Amathole MPA was not officially proclaimed as a no-take MPA until September 2011, voluntary sanctuaries were established by the Border Deepsea Angling Association in 1981 (and later gazetted as closed fishing areas). Stewardship of this MPA ensured that the sanctuaries were well policed prior to official establishment

2.2. Sampling strategy and technique

At each of the 5 locations (which herein refers to both the MPA and adjacent fished site) reef fish assemblage data were collected within the MPA and at nearby unprotected zones, where fishing is known to occur (Table 1). Sampling took place from February 2013 to March 2016. All data collected within the MPAs were collected from the no-take zones, where no extractive activity is allowed. Samples of the reef fish assemblages were collected from reefs between 10 and 60 m depth at randomly selected sampling stations with a minimum distance of 300 m between adjacent stations. The minimum separation of 300 m was selected to avoid spatial autocorrelation and the confounding effects of the bait plume (Taylor et al. 2013).

Reef fish assemblages were sampled with baited remote underwater stereo-video systems (stereo-BRUVs), which constitute a standardised fisheries-independent method that allows for the estimation of relative abundances and accurate size measurements (Harvey & Shortis 1996, Harvey et al. 2001, Watson et al. 2005). Stereo-BRUVs were employed in this study as they are currently the only non-destructive method that is able to sample the depth range of the MPAs, including the depths at which fishing predominantly occurs in South Africa. At each sampling station, a single stereo-BRUVs was deployed from a boat and left on the seabed to record for a 60 min period (Watson et al. 2005, Langlois et al. 2012a,b, Bernard et al. 2014). The stereo-BRUVs design was simi-

lar to that described in Bernard et al. (2014) and consisted of a stainless steel frame with 2 high-definition digital cameras mounted 70 cm apart converging inwards at an angle of 8°, baited with approximately 800 g of crushed sardine *Sardinops sagax*.

2.3. Video analysis

Video samples were processed in EventMeasure (Stereo) software (www.seagis.com.au). Abundance was estimated as the maximum number of individuals of a species recorded in one video frame over the 60 min analysis period (MaxN; Willis & Babcock 2000). Where possible, the fork or total length, as appropriate for the species, was measured for each fish counted in the MaxN frame. Biomass was estimated using the Bayesian length-weight relationships obtained from FishBase (Froese & Pauly 2014) and averaged for each species per stereo-BRUVs sample. To ensure accurate length measurements were obtained in EventMeasure, camera sets were calibrated before and after each field trip with the CAL v1.32 software (www.seagis.com.au), following Harvey & Shortis (1996, 1998).

2.4. Target and non-target fish species

This study focussed on 2 main groups of reef fish: those reef fish species considered to be primary targets of the local commercial and recreational fisheries (i.e. those that are preferentially captured due to angler preferences and economic value) and fish species that are not targeted (non-targets) and typically not kept (Table S1 in the Supplement at www.int-res.com/articles/suppl/m620p099_supp.pdf). Species were categorised according to information obtained from Mann (2013) and expert opinion (Table S1). Primary target species were included, as they are expected to demonstrate the strongest effect of fishing, and they are often superior competitors. Non-target species were included as variations in their populations can be assumed to be independent of the direct effects of fishing. Fish species of minor importance to fisheries (i.e. those that are less desirable, but kept when caught for bait or subsistence) were excluded from the analyses as their populations are likely to be influenced by both fishing pressure and top-down effects of biotic interactions. Analyses also excluded pelagic or migratory species whose movement behaviour makes them susceptible to fishing outside of MPAs.

2.5. Trait classification

The gradual turnover of fish species, moving from the colder southwest coast to the warmer northeast coast of South Africa, resulted in unique fish assemblages at each location (especially apparent between Pondoland and the locations to the west). Consequently, a trait-based approach was taken to test the overall hypothesis that fishing affected the functional structure of the fish community. The traits were based on Mouillot et al. (2014) with slight modifications to suit our specific questions. Our traits included maximum body size, diet preference, preferred position in the water column, mobility and shoaling behaviour, which were applied at the species level; and life-stage (an estimate of individual maturity, using the length measurements obtained from the stereo-BRUVs; Table S2). These traits were selected as they represent functional characteristics of fish species that influence biotic interactions and influence their vulnerability to fishing pressures. The trait-based analyses were in 2 forms; the first focused only on species-level functional traits, where fish were grouped to create 'species level functional entities' (SFEs), and the second included the individual-level functional trait of life-stage together with the species-level functional traits, where fish were grouped to create 'individual and species level functional entities' (ISFEs; Table S2).

Life-stage was assigned by taking the individual size measurement of each fish sample and classifying it as either adult or juvenile based on the size at 50% maturity, which was obtained from FishBase (Froese & Pauly 2014). Where no published maturity data were available, the size at 50% maturity was predicted based on the relationship between maturity and maximum attainable size of other species in the same fish family (Table S3; Figs. S1 & S2 in the Supplement). Where there were insufficient data to model the relationship between maturity and maximum attainable size for a specific fish family, the species were assigned the average proportion of size at maturity/maximum size for their type (bony fish or elasmobranchs).

2.6. Explanatory variables of secondary interest

To differentiate between habitat and MPA effects we included quantitative and categorical explanatory variables to control for variation in the data, which were not attributable to variables of primary interest (Miller & Russ 2014). The explanatory vari-

ables recorded for each stereo-BRUVs sample were field of view (visibility and percent visible water column), temperature (°C), depth (m) and bottom type. Visibility (m) for each stereo-BRUVs sample was estimated in EventMeasure by creating a 3D point at the furthest distance at which an object could easily be identified. Percent visible water column was calculated in the Vidana software (Hedley 2003) by quantifying the amount of visible water column in relation to visible reef. Average water temperature for the duration of each stereo-BRUVs deployment was obtained from temperature loggers (HOBO Pro v2, Onset) attached to the stereo-BRUVs systems. Sample depth was recorded from the boat's echo sounder, and bottom types were classified into one of 5 categories from images of the seafloor taken from each stereo-BRUVs samples. The 5 bottom types were sand-inundated reef (reef covered in a thin layer of sand, with small patches of reef or erect macrobenthos breaking through), patch-reef low (mosaic of sand and reef, visible reef varying by <1 m in height), patch-reef high (mosaic of sand and reef, visible reef varying by >1 m in height), reef low (100% reef varying by <1 m in height) and reef high (100% reef varying by >1 m in height). Samples with 100% sand were excluded from the analyses.

2.7. Statistical analyses

Multivariate (permutational multivariate analysis of variance; PERMANOVA) and univariate (permutational analysis of variance; permutational ANOVA) analyses were conducted in PRIMER v7 with PERMANOVA+ add-on (Anderson et al. 2008, Clarke & Gorley 2015) and based on 3 model designs. (1) The first model design was to test the hypothesis that protection affects trait combinations (SFEs and ISFEs) of the fish assemblages, with 'location' (De Hoop, Tsitsikamma, Bird Island, Amathole, Pondoland) as a random factor and 'status' (protected or exploited) as a fixed factor, with an interaction between location and status. (2) The second model design tested the impact of protection on fish at the species-level in terms of abundance and biomass data by considering the main effects and interaction effect between 'status' and 'location'. (3) The third model tested if the univariate summed MaxN and the average biomass differed between exploited and protected sites separately for each location thus only including 'status' as a fixed factor.

To account for variability in the data due to differences in sample-specific environmental variables,

the estimated covariates (e.g. visibility, depth) were added before the terms (e.g. location, status) in the models. Thus all models were first fitted with the continuous covariates in the following order: 'visibility', 'percent water column', 'temperature', 'depth' and the categorical covariate 'bottom type' (random effect). These covariates were then followed by 'location', (model 1: random effect, model 2: fixed effect) and 'status' (fixed effect), in a sequential PERMANOVA. All analyses were done separately for the target and non-target species to help determine the direction of change for each of the groups. Because of the unbalanced nature of the sampling design, analysis was based on type I sum of squares using 9999 permutations under a reduced model (Anderson et al. 2005, 2008). Pairwise analyses were conducted where significant results were observed.

Trait-based analyses were performed on a fourth-root transformed, adjusted Bray-Curtis resemblance measure (to accommodate samples where no fish were recorded) and univariate analysis on untransformed adjusted Euclidean distances. Analysis of species data (abundance and average biomass) were based on the adjusted Modified Gower log base 5 distance measure. Modified Gower accounts for highly abundant species, as it places greater emphasis on the compositional change of a community rather than actual MaxN or average biomass values (Anderson et al. 2006). Here we also applied Modified Gower to the biomass data, since relative abundances of organisms measured by continuous biomass values behave, statistically, in a very similar way to relative abundances recorded as integer counts (variance is a function of the mean, over-dispersed, bounded at zero, right-skewed). When Modified Gower is applied to biomass values, the resulting dissimilarity value is interpreted as the average log-difference in biomass per species (Anderson et al. 2006). We chose to use a log base of 5, so that one unit in Modified Gower space corresponds to a 5-fold difference in biomass. The species abundance and biomass data of each location (MPA and adjacent fished area) were visualised in PRIMER v7 using metric multidimensional scaling (mMDS), which compared to the more traditional principal coordinate analysis, is more robust and provides greater reduction of dimensionality to visualise important patterns (Clarke & Gorley 2015). Finally, similarity percentages (SIMPER) were estimated to identify the trait combinations / fish species that together contributed to 70% of the dissimilarity between exploited and MPA sites at each location (Clarke & Gorley 2015).

3. RESULTS

3.1. Trait-based analyses

3.1.1. Abundance

(species level functional entities; SFEs)

According to the trait-based analyses, no overall effect of protection was observed in the abundances of the SFEs within the target species group (pseudo-

$F_1 = 1.12$; $p = 0.404$; Table S4a). However, there was a significant interaction effect between 'location' and 'status' (pseudo- $F_4 = 8.31$; $p < 0.001$; Table S4a), with the pairwise analyses indicating that 'status' (protection) significantly affected the SFEs of the target species at all locations (Table S5a), but that the direction of impact was inconsistent. This was also illustrated in the SIMPER results, where the effect of protection on the average abundances of the target SFEs varied between locations and different SFE groups (Fig. 2a;

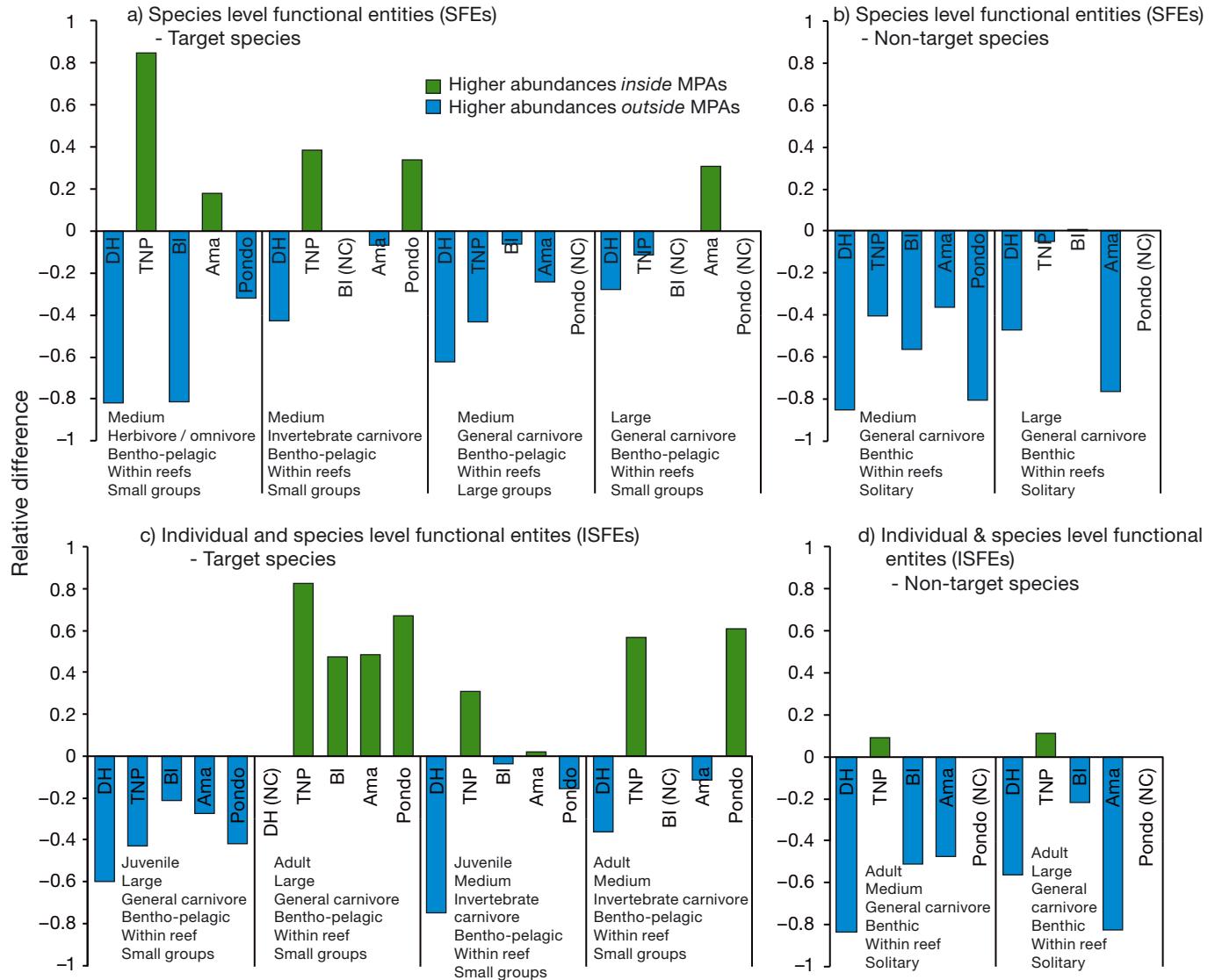


Fig. 2. Results from the similarity percentages (SIMPER) of the species level functional entities (SFEs; abundance) of (a) target species and (b) non-target species. Individual and species-level functional entities (ISFEs; length) of (c) target species and (d) non-target species. Data are the average abundances calculated from the fourth root transformed Bray-Curtis resemblances. The SIMPER results are expressed as the relative difference in abundance between protected and exploited sites where zero = no difference and 1 or $-1 = 100\%$ different. Functional entities with higher values inside the marine protected area (MPA) are plotted on the positive scale (green) and functional entities with higher values outside the MPA on the negative scale (blue). DH: De Hoop, TNP: Tsitsikamma, BI: Bird Island, Ama: Amathole, Pondo: Pondoland. (NC) = no contribution, indicating that the functional entity did not contribute to the 70 % dissimilarity between protected and exploited sites at the specific location.

For full SIMPER results and species represented by each functional entity see Tables S6 & S8 in the Supplement

Table S6). The abundances of non-target SFEs was significantly affected by protection (pseudo- $F_1 = 12.15$; $p = 0.014$; Table S4b), with pairwise analyses indicating a significant effect at all locations, except for Bird Island (Table S5b). In contrast to the target species, the direction of impact was consistent for all functional entities of the non-target groups, with higher average abundances at exploited compared to protected locations (Fig. 2b; Table S6).

3.1.2. Length (individual and species level functional entities; ISFEs)

In contrast to the results from the SFEs, which did not take into account the individual size of the fish observed, protection significantly affected the ISFEs within the target group (pseudo- $F_1 = 4.2$; $p = 0.027$; Table S7a), with pairwise analyses indicating a significant protection effect at all locations, Table S5c). The SIMPER results of the target group revealed a fairly consistent pattern for the ISFEs, with higher average abundances of adult fishes in protected compared to exploited locations (Fig. 2c; Table S8a). However, while no main effect of protection was observed for the non-target group (pseudo- $F_1 = 4.48$; $p = 0.062$; Table S7b), the interaction revealed a significant effect of protection at De Hoop, Tsitsikamma and Pondoland (Table S5d). For the non-target ISFEs, adult fishes were also most consistently affected, with higher average abundances outside most of the MPAs, except Tsitsikamma (Fig. 2d; Table S8b).

3.2. Multivariate analysis on species data

3.2.1. Target species

Examination of the multivariate species data revealed that the abundance and biomass of target species assemblages were significantly affected by protection at all locations (abundance: pseudo- $F_1 = 9.1$; $p < 0.001$; biomass: pseudo- $F_1 = 6.84$; $p < 0.001$; Tables S9a & S10a). Although pairwise analyses supported this finding (Table S11a,c), the mMDS, SIMPER and univariate outputs revealed that the direction of change differed among locations (Figs. 3–7a,b).

3.2.2. Non-target species

Similar to the target species, the abundance and biomass of non-target species assemblages were

significantly influenced by protection (abundance: pseudo- $F_1 = 9.1$; $p < 0.001$; biomass: pseudo- $F_1 = 6.84$; $p < 0.001$; Tables S9b & S10b). Pairwise comparisons indicated that protection significantly affected the abundance of non-targets at all locations. On the other hand, there was no effect of protection on the biomass of non-target species at the Amathole and Pondoland locations (Table S11d).

3.2.3. De Hoop Marine Protected Area

Fish assemblages (abundance and biomass) of target and non-target species differed between MPA and fished areas (Fig. 3), with higher abundance and biomass of reef-associated species outside the MPA, in comparison to inside the MPA (Fig. 3). The exception was *Mustelus mustelus*, for which higher abundance and biomass estimates were observed inside the MPA, in comparison to outside (Fig. 3e,f). The pattern observed for the non-target species at the De Hoop MPA was similar to the target species with higher abundance and biomass values outside the MPA (Fig. 3c–f). Univariate analyses of the summed MaxN and average biomass revealed no difference between the exploited and protected sites for any of the response variables considered (target abundance: pseudo- $F_1 = 6.81$; $p = 0.086$, target biomass: pseudo- $F_1 = 1.4$; $p = 0.337$, non-target abundance: pseudo- $F_1 = 5.2$; $p = 0.091$ and non-target biomass: pseudo- $F_1 = 5.07$; $p = 0.12$).

3.2.4. Tsitsikamma National Park Marine Protected Area

The target and non-target fish assemblages at the Tsitsikamma MPA differed significantly in terms of abundance and biomass (Fig. 4a–d). Results from the mMDS and the SIMPER analysis suggest that both abundance and biomass values of the target species were higher inside compared to outside the MPA (Fig. 4a,b,e,f). However, not all target species were recorded at higher abundances inside the MPA, with *Argyrozon argyrozon*, *Pterogymnus laniarius* and *Rhabdosargus globiceps* being more abundant at exploited sites (Fig. 4e). This variable pattern in the abundance of target species was supported by the absence of a significant protection effect in the univariate analysis of summed target species MaxN (pseudo- $F_1 = 0.22$; $p = 0.695$). Higher average biomass values (mean \pm SD) were recorded inside the

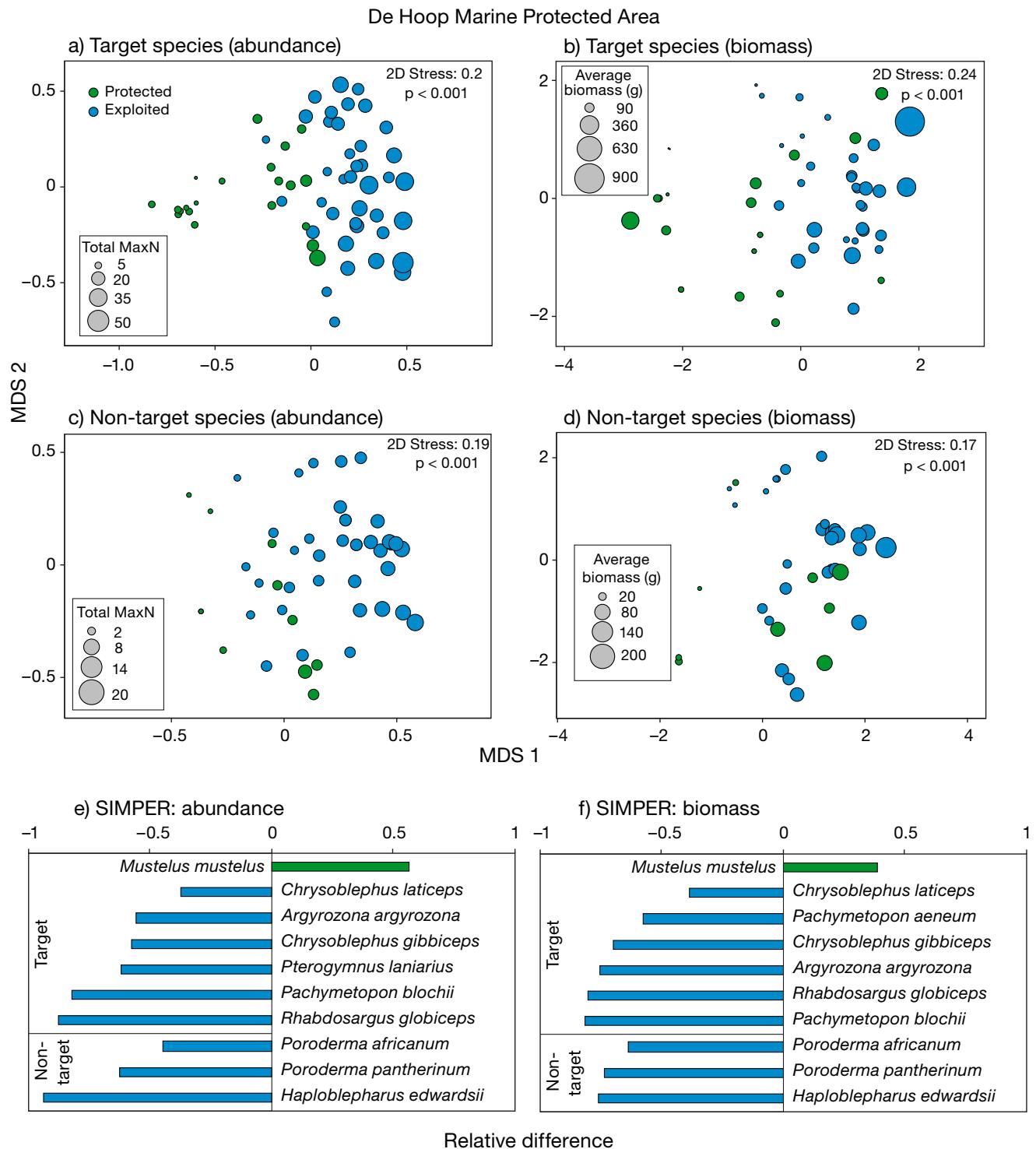


Fig. 3. Metric multi-dimensional scaling (MDS) of the abundance (MaxN) and biomass (average) values recorded for (a,b) target and (c,d) non-target species at the De Hoop Marine Protected Area. Bubble sizes represent the total MaxN of each stereo-BRUVs sample for the abundance plots, and averaged biomass for the biomass plots. (e,f) Bar graphs show the similarity percentage (SIMPER) results of the average abundance and biomass calculated from fourth root transformed Bray-Curtis resemblances. The SIMPER results are expressed as the relative difference in abundance/biomass between protected and exploited sites where zero = no difference and 1 or -1 = 100 % different. Fish with higher values inside the MPA are plotted on the positive scale (green) and fish with higher values outside the MPA on the negative scale (blue). p-values represent pairwise results (Table S11)

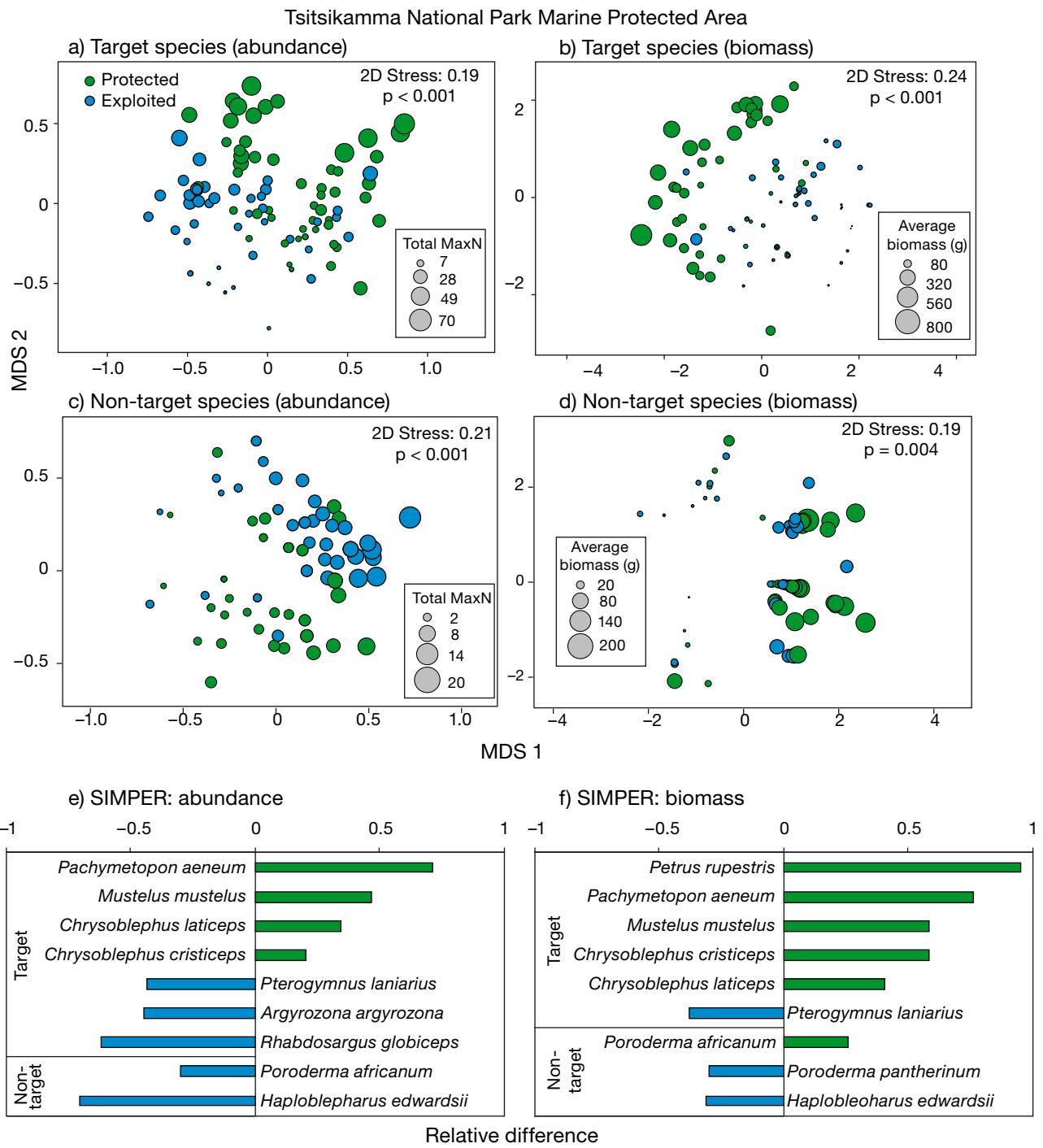


Fig. 4. As in Fig. 3, but for the Tsitsikamma National Park Marine Protected Area

Tsitsikamma MPA for target species (protected: 175.2 ± 153.6 ; exploited: 36.6 ± 40.4 g; pseudo- $F_1 = 48.7$; p = 0.003; Fig. 4b) and the results from the SIMPER analyses revealed that the biomass of all the highest contributing species, except *P. laniarius*, were higher inside the MPA compared to outside. The abundances of non-target species were signifi-

cantly higher outside the Tsitsikamma MPA (mMDS; Fig. 4c) as indicated by the SIMPER results (Fig. 4e) and the univariate analysis of the summed MaxN (protected: 2.9 ± 2.1 ; exploited: 4.7 ± 3.1 ; pseudo- $F_1 = 108.58$; p < 0.001). There was no effect of protection on the average biomass of non-target species (pseudo- $F_1 = 1.47$; p = 0.286; Fig. 4d,f).

3.2.5. Bird Island Marine Protected Area

Multivariate analyses of the target and non-target abundance and biomass data revealed a significant protection effect on the Bird Island fish assemblages (Fig. 5a–d). Although protection affected the assemblage structure of the target species abundances, no obvious difference was evident in the mMDS or univariate analysis (Fig. 5a; pseudo- $F_1 = 2.43$; $p = 0.225$). Yet the SIMPER analysis suggested higher abundances of most target species inside the Bird Island MPA (Fig. 5e). Target species had higher average biomass inside the Bird Island MPA (mean \pm SD; Fig. 5b,f; protected: 195.6 ± 127.6 ; exploited: 121.1 ± 57.5 g; pseudo- $F_1 = 28.8$; $p = 0.021$). Abundances of non-target species tended to be higher outside the Bird Island MPA (Fig. 5c,e), which was supported by the significant protection effect in the univariate analysis (protected: 2.6 ± 1.7 ; exploited: 4.3 ± 2.5 ; pseudo- $F_1 = 34.61$; $p = 0.014$). The SIMPER and the mMDS analysis run on the biomass data of non-target species showed higher overall biomass outside the Bird Island MPA, however, this pattern was not supported by the univariate analysis (Fig. 5d,f; pseudo- $F_1 = 1.12$; $p = 0.377$).

3.2.6. Amathole Marine Protected Area

Multivariate analyses of the target species abundance and biomass data indicated significantly different fish assemblages in the exploited compared to protected sites of the Amathole MPA (Fig. 6a,b). The mMDS output of the abundance values of the target species suggests similar abundance values between the exploited and protected sites of Amathole (Fig. 6a). The univariate (pseudo- $F_1 = 0.61$; $p = 0.501$) and SIMPER analyses supported this pattern, and the highest contributing species reacted differently to protection (Fig. 6e). In contrast to the abundances of the target species, higher biomass of target species were observed inside the Amathole MPA (Fig. 6b). This result was further supported by the univariate (mean \pm SD; protected: 260.4 ± 270.1 g, exploited: 66.9 ± 44.3 g, pseudo- $F_1 = 19.8$; $p = 0.009$) and SIMPER analyses (Fig. 6f). Generally, low abundance and biomass values were recorded for the non-target species of the Amathole MPA. The non-target fish assemblage composition differed between the Amathole MPA and adjacent fished sites, and according to the mMDS and SIMPER results, higher abundances were recorded outside the Amathole MPA (Fig. 6c,e). However, this pattern of greater abundances of non-

target species outside the Amathole MPA was not supported by the univariate analysis (pseudo- $F_1 = 3.2$; $p = 0.103$). No difference in the multivariate analysis of the non-target biomass data were observed (Fig. 6d), a result which was supported by the univariate analysis (pseudo- $F_1 = 0.79$; $p = 0.495$).

3.2.7. Pondoland Marine Protected Area

Multivariate analyses of the Pondoland fish assemblages revealed that protection significantly changed the abundance and biomass of the target species, and the abundances (but not biomass) of the non-target species (Fig. 7a–c). Although protection significantly affected the assemblage structure of the target species abundances, no clear trend was observed for this group, and the mMDS and the SIMPER analyses suggest similar abundances inside and outside the Pondoland MPA. This result was supported by the univariate analysis (pseudo- $F_1 = 2.36$; $p = 0.169$). In contrast, the mMDS, SIMPER and univariate results all revealed higher biomass values of target species inside the Pondoland MPA (mean \pm SD; protected: 286.1 ± 193.9 g, exploited: 97.9 ± 50.2 g, pseudo- $F_1 = 14.93$; $p = 0.017$; Fig. 7b,f). The analysis of the non-target species assemblages indicated that they occurred at higher abundances outside the MPA (protected: 3.4 ± 3.2 , exploited: 6.2 ± 5 , pseudo- $F_1 = 11.18$; $p = 0.029$; Fig. 7c,e). This pattern was not reflected in the non-target biomass analyses, where no clear trend was evident (pseudo- $F_1 = 2.5$; $p = 0.177$; Fig. 7d,f).

4. DISCUSSION

The aim of this study was to investigate direct and indirect effects of protection on reef fish at the community level in an attempt to better understand MPA effectiveness. In theory, indirect effects (i.e. those stemming from a knock-on effect initiated by target fish recovery) can only be assumed if direct effects have been detected. Here, significantly higher biomass or greater abundance of sexually mature target species inside MPAs in combination with a reduced abundance of non-target species inside MPAs was considered a clear positive reserve effect at the community level. Based on the trait-based analyses, the general pattern is that the 5 South African MPAs have had community-wide impacts on reef fishes, which suggests that the MPAs are effective. However, closer inspection of

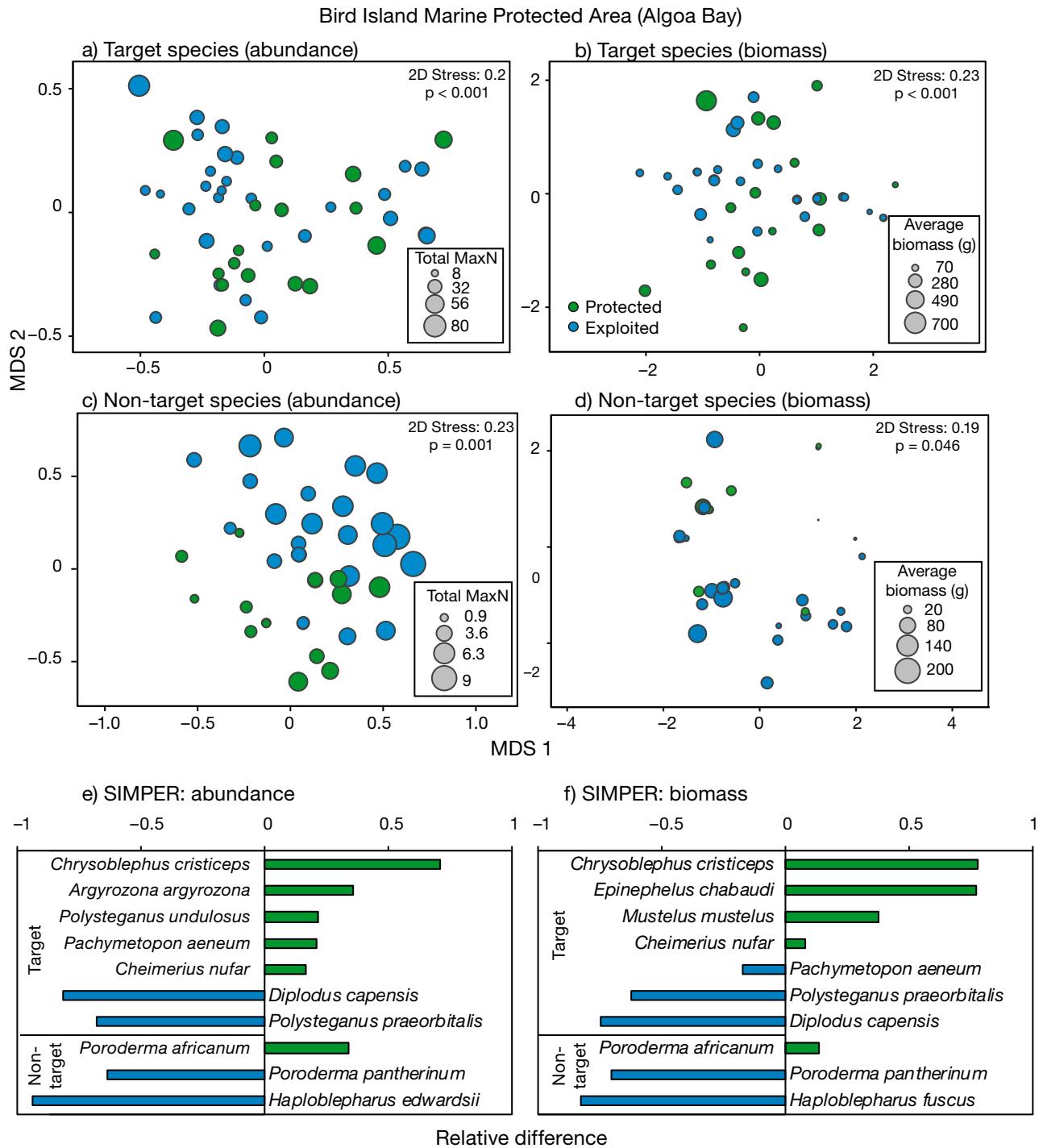


Fig. 5. As in Fig. 3, but for the Bird Island Marine Protected Area

the multivariate species data indicates that despite a significant difference in the fish assemblages between protected and exploited sites at most locations, the direction of change was not consistent, and only 3 of the MPAs show clear positive reserve effects at the community level.

4.1. Trait-based analyses

It seems that accounting for traits at the individual level (ISFEs) is especially important for the detection of the direct effects of protection. Here, we incorporated the size of fish as an individual trait, since it

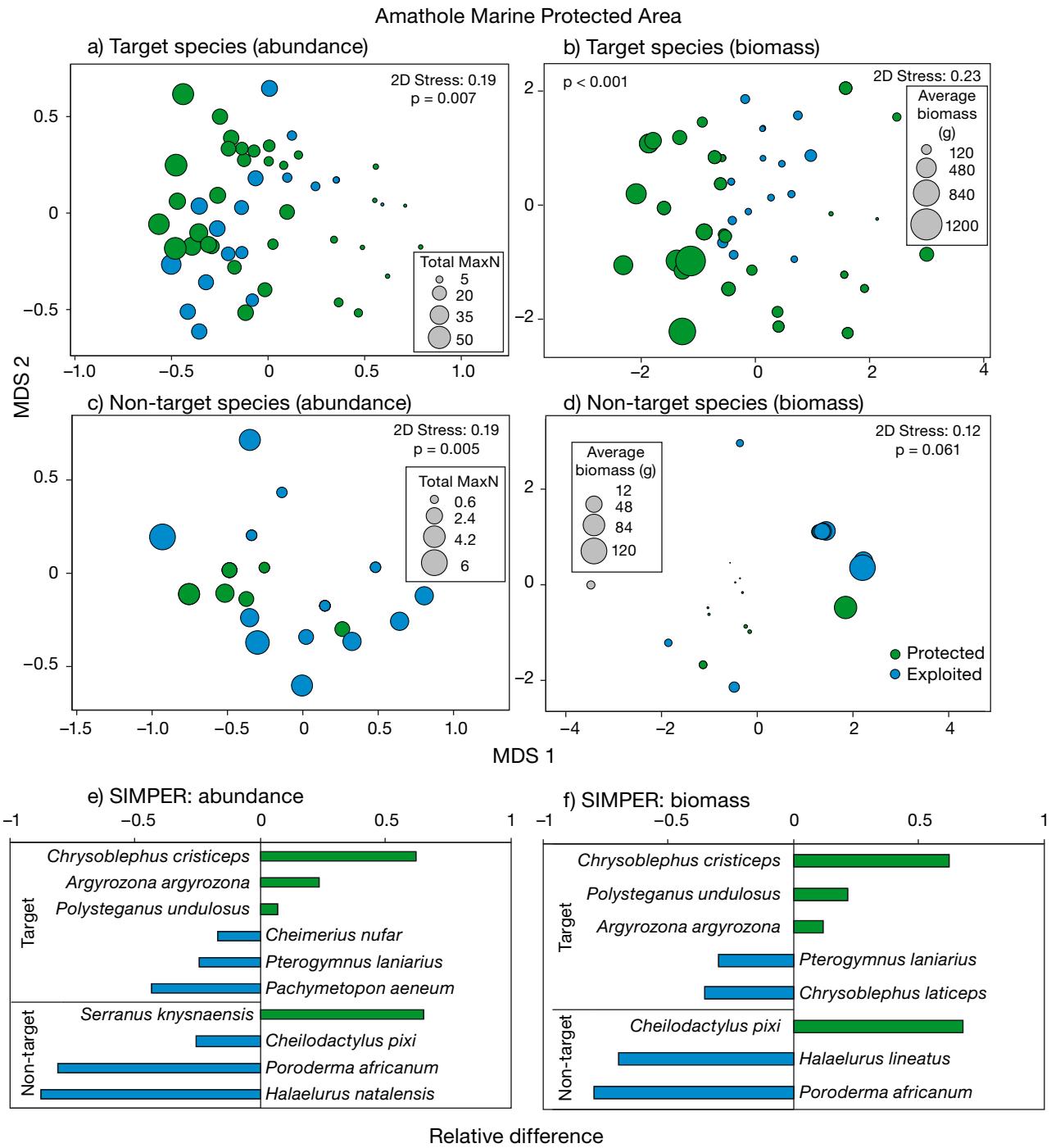


Fig. 6. As in Fig. 3, but for the Amathole Marine Protected Area

changes with age, correlates with life history parameters (Blueweiss et al. 1978), is important in species interactions (Cohen et al. 1993), and is essential when considering fishing effects (Rochet & Trenkel 2003, Graham et al. 2005). Ignoring important changes in function that occur throughout ontogeny

results in an inadequate description of a fish community (Rudolf & Rasmussen 2013, Mindel et al. 2016), as is evident in the target SFEs analyses presented here. Protection mostly affected the age structure of the functional entities within the target group (demonstrated in the analysis of the ISFEs) and the

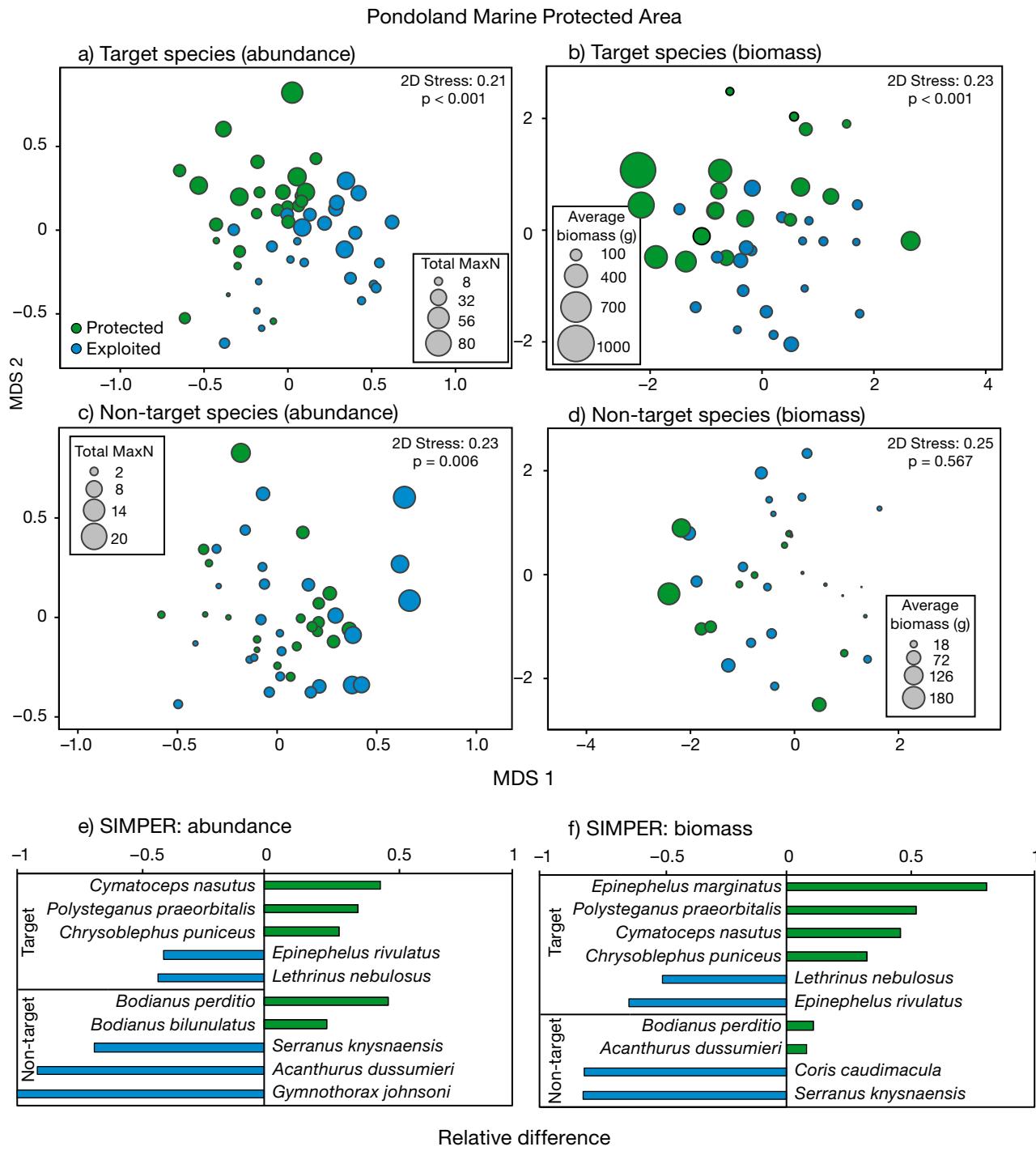


Fig. 7. As in Fig. 3, but for the Pondoland Marine Protected Area

abundance of functional entities in the non-target groups (demonstrated in the analysis SFEs; Tables S4 & S5). Here, protection increased the abundance of adult target species and decreased the abundance of non-target species inside MPAs (Fig. 2b,c) suggesting a positive overall reserve effect, and that the 5

South African MPAs investigated here are generally successful.

The positive reserve effect appeared to be strongest for the adult life-stage of large (60–120 cm), general carnivore, benthic-pelagic species that typically move within reef complexes and occur in small

groups (Fig. 2c). This implies that, in the geographical context of this research, these types of species benefit most from protection, and are potentially the most vulnerable to fishing impacts. Interestingly, the opposite was true for juveniles of this functional group, which were more abundant outside the MPAs, and might suggest that the presence of adults may influence the recruitment, survival or detectability of juveniles.

4.2. Location-specific analyses based on species assemblages

While 'status' had a significant effect in the full analysis, the location-specific analysis showed that not all of the MPAs are fulfilling their ecological potential (Table 2). Three of the MPAs (Tsitsikamma, Bird Island and Pondoland) clearly demonstrated both direct and indirect effects of protection (Table 2), suggesting that the fish assemblages within these MPAs may have returned towards some previous state prior to intense exploitation (Babcock et al. 2010). The Amathole MPA demonstrated clear direct effects, but the indirect effects were not recorded in all analyses. On the other hand, no direct effects were recorded in the De Hoop MPA, and indirect effects were only evident in the multivariate response data; it is unlikely that these were related to the presence of the MPA (Table 2).

Within the Agulhas ecoregion (see Fig. 1), the recovery of target species (e.g. *Chrysoblephus laticeps*, *C. cristiceps*, *Argyrozonza argyrozonza*) appeared to

indirectly effect non-target species primarily from the Scyliorhinidae family (e.g. *Poroderma africanum*, *P. pantherium*). These non-target species occupy a similar trophic position to the target species, and would not be considered their prey (Mann 2013). As such, the indirect effects identified in this research are likely driven by competition rather than predation. Many of the Scyliorhinidae species are nocturnally active (Mann 2013), and it is possible that higher abundances of large competitors inside MPAs promotes nocturnal activity, while the lack of competition outside MPAs allows them to be more active during daytime. In the Pondoland MPA, which is situated in the sub-tropical ecoregion of southern Africa, species within the target group that showed a strong recovery, included both potential predators (*Epinephelus marginatus* and *Polysteganus praeorbitalis*) and competitors (*Cymatoceps nasutus* and *Chrysoblephus puniceus*) of the non-target species, suggesting that multiple factors may be driving the indirect effects detected here.

In a recent study, Edgar et al. (2014) showed that the ecological conservation benefits associated with MPAs were highly dependent on the degree to which fishing is allowed within MPAs; level of enforcement; MPA age; MPA size and degree of ecological isolation (habitat disruption inhibiting movement of fish across MPA boundaries). Accumulation of these 5 key features, namely that a MPA is considered no-take, enforced, old, large and isolated (NEOLI), exponentially increased the positive ecological response to protection (Edgar et al. 2014). Here we summarise the main findings of the analyses for each

Table 2. Summary of the location-specific results. Locations were ranked according to the NEOLI criteria (abbreviations as in Table 1; see Edgar et al. 2014), with Tsitsikamma scoring the highest and Bird Island the lowest (see Table 1 for the classification of each location). Values in **bold** represent a significant effect

MPA	Measure	Fisheries group	Overall trend		Uni-variate	Abundance or biomass (mean ± SD)	
			Multi-variate	Bubbles		Protected	Exploited
Tsitsikamma (NEOL)	Biomass	Target	<0.001	Higher inside	Higher inside	0.003	175.2 ± 153.6
	Abundance	Non-target	<0.001	No clear pattern	Higher outside	<0.001	2.9 ± 2.1
De Hoop (NOLI)	Biomass	Target	<0.001	Higher outside	Higher outside	0.337	72.1 ± 71.8
	Abundance	Non-target	<0.001	Higher outside	Higher outside	0.091	1.9 ± 2.3
Pondoland (NELI)	Biomass	Target	<0.001	Higher inside	Higher inside	0.018	286.1 ± 193.9
	Abundance	Non-target	0.0061	Higher outside	Higher outside	0.028	3.4 ± 3.2
Amathole (NOL)	Biomass	Target	<0.001	Higher inside	Higher inside	0.009	260.4 ± 270.1
	Abundance	Non-target	0.005	Higher outside	Higher outside	0.103	0.8 ± 1.2
Bird Island (NI)	Biomass	Target	<0.001	Higher inside	Higher inside for	0.021	195.6 ± 127.6
	Abundance	Non-target	0.001	Higher outside	Higher outside	0.014	2.6 ± 1.7

MPA, with the MPAs arranged according to their theoretical effectiveness derived from the NEOLI criteria (Table 2). Three of the MPAs investigated here (Tsitsikamma, De Hoop and Pondoland) scored 4 out of the 5 NEOLI features (Table S12). While the results from Pondoland and Tsitsikamma conform to the level of effectiveness predicted by Edgar et al. (2014), De Hoop did not demonstrate a reserve effect, and abundance and biomass of target species tended to be higher outside, rather than inside the MPA (Fig. 3).

The lack of reserve effect at De Hoop is most likely due to the absence of suitable offshore habitat for reef fish species (Table 1). According to a recent mapping report (Coetzee et al. 2017), reef habitat was almost non-existent within the De Hoop MPA, with most of the habitat classified as reef restricted to the shoreline. Indeed, previous research has demonstrated that the De Hoop MPA has had a positive effect on the fish communities that occupy the reefs of this narrow coastal belt (Bennett & Attwood 1991). Outside the MPA there are large expanses of offshore reef that support important hook and line fisheries. In the analyses we controlled for habitat by excluding samples collected on sand and including bottom type as a random effect. Consequently, the absence of a reserve effect at De Hoop suggests that the observed results are not due to sample-specific habitat differences, but could rather be related to the area of available habitat at the reserve level. Several studies have shown that predator biomass scales with habitat size, and larger habitats (reefs) support higher biomass of predatory and larger fish species (Bohnsack et al. 1994, McIntosh et al. 2018). Therefore, despite the increased vulnerability of target species outside the reserve, access to more suitable habitat plays a more important role than fishing in structuring fish populations. While the De Hoop MPA may provide little benefit to offshore reef fish, the protection of sand habitat may benefit other target fish species (e.g. the sand associated *Mustelus mustelus*; Fig. 3e,f), and gives further support to the predominance of sand habitat in this reserve. Ensuring that an adequate quantity of the correct habitat is afforded protection within MPAs is an essential planning feature prior to MPA establishment (Foley et al. 2010). The concept of essential fish habitat (Rosenberg et al. 2000) is crucial in an ecosystem approach to fisheries management, as protecting the correct habitat ensures fisheries and conservation benefits, thereby avoiding the establishment of 'paper parks' (Edgar 2017).

High scoring MPAs (those with at least 4 out of 5 features) were most effective according to Edgar et al. (2014). For the most part, our results provide sup-

port for the NEOLI criteria in predicting MPA effectiveness, with Tsitsikamma and Pondoland (scoring 4 out of 5 NEOLI features; Table S12 & S13) demonstrating strong positive reserve effects at the resource (target fish species) and community level (Table 2). Established in 1964, Tsitsikamma is an old no-take MPA and the only NEOLI feature it was lacking is isolation, as there is a degree of connectivity between the coastal reefs in the region (Table S12). Pondoland, is relatively young (10 yr old when the data were collected), but it has a very large no-take zone and is situated in a relatively inaccessible region with low population densities and limited access to the offshore marine environment.

Isolation was considered by both Edgar et al. (2014) and the follow-up analysis by Rudd (2015), to disproportionately improve the positive ecological response to protection, and demonstrated the strongest influence on richness and biomass. The importance of this NEOLI category seems to further explain the success of the relatively young Pondoland MPA (Maggs et al. 2013) and the small and young Bird Island MPA, which only scored 2 of the 5 NEOLI criteria (no-take and isolation; Tables 1, S12 & S13). Bird Island is an offshore MPA consisting predominantly of reef which is isolated from the mainland and adjacent reefs by expanses of sand habitat. The island is also home to large colonies of sea birds and seals, and is likely to be a highly productive ecosystem (Chadwick et al. 2014). It is possible that isolation, together with suitable habitat and high productivity combine to enhance the effectiveness of this small MPA. The proposed inclusion of the Bird Island into the substantially larger Addo MPA (Government Gazette No. 39646) will likely further enhance the value of this protected area.

Indirect effects were apparent in the Amathole MPA, but unlike those seen in Pondoland, Bird Island and Tsitsikamma (which demonstrated indirect effects in the multivariate response and the total abundance data), the total abundance of non-target species in the Amathole MPA was not significantly affected (Table 2). The high connectivity (or lack of isolation) of reef habitat inside and outside of the Amathole MPA may explain the absence of clear indirect effects at this site. The Amathole MPA is characterised by 3 of the 5 NEOLI criteria (no-take, old and large). While the MPA is large, it consists of 3 no-take zones (areas: 62, 61 and 123 km²) that are separated by approximately 20 km of coastline where intense fishing occurs. The reef habitat within the no-take zones is patchy, and where there are notable reef complexes, these straddle the MPA

boundaries. It is possible that the limited habitat and high degree of connectivity between protected and exploited habitats have precluded the emergence of strong indirect effects on the assemblage of non-target species. More informed spatial planning is thus required for the establishment of no-take areas in the recently proposed extension of the Amathole MPA (Government Gazette No. 39646).

The results of the present study suggest that it may be inappropriate to consider only species-level functional traits when attempting to assess the direct effects of protection. The size of individual fish is non-randomly influenced by fishers, and plays an important role in both population and community ecology. Our results highlight the value of including size to capture a portion of the individual-level variation within functional trait-based analyses that aim to investigate fishing effects. Furthermore, many, if not most, species-level functional traits (e.g. diet, habitat and depth preferences) change according to the age and size of the fish, and this should be incorporated within the classification of functional entities. The positive ecological response at the resource level for most of the South African MPAs examined indicates that no-take MPAs support greater biomass of target species within their boundaries. Indirect effects are evident as the emergent effects on non-target species populations when large individuals of species targeted by fisheries are present or increase in abundance. However, indirect effects were not consistently recorded at all locations, and it is possible that this can be attributed to shortcomings in individual MPA design. While the NEOLI criteria are useful predictors of MPA effectiveness, our results demonstrate the importance of not only protecting the correct habitat, but also including adequate quantities of suitable habitat when designing MPAs. Further research should be directed into measuring the effect of habitat area, at the landscape or reserve level, on reef ecosystem productivity and MPA effectiveness.

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