frontiers | Frontiers in Marine Science

TYPE Original Research
PUBLISHED 16 December 2022
DOI 10.3389/fmars.2022.893260

OPEN ACCESS

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SPECIALTY SECTION
This article was submitted to
Marine Conservation and
Sustainability,
a section of the journal
Frontiers in Marine Science

RECEIVED 10 March 2022
ACCEPTED 28 November 2022
PUBLISHED 16 December 2022

CITATION
Baliwe NG, Pfaff MC and Branch GM
(2022) Assessing the effects of no-take
zones in a marine protected area
spanning two ecoregions and rock
substrate types.
Front. Mar. Sci. 9:893260.
doi: 10.3389/fmars.2022.893260

Assessing the effects of no-take zones in a marine protected area spanning two ecoregions and rock substrate types

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This study assessed the effectiveness of no-take areas in the Table Mountain National Park MPA in protecting the biodiversity of intertidal rocky shores from impacts of harvesting. Surveys were conducted in areas of controlled harvesting and in no-take areas to compare the densities and sizes of exploited species and the community composition between shores experiencing these two levels of protection, in two ecoregions and on two types of rock substrate. Clear patterns emerged. Firstly, no-take areas had significantly greater densities of the exploited limpets *Cymbula granatina*, *C. oculus* and *Scutellastra argenvillei*, particularly on sandstone shores, relative to their abundance in harvested areas. Conversely, densities of the rarely harvested limpets *S. cochlear*, *S. longicosta* and *S. granularis* did not differ in any manner consistent with protection levels. Secondly, *C. granatina* and *S. argenvillei* were significantly larger in no-take areas, although *C. oculus* displayed the opposite pattern. None of the rarely harvested limpets showed consistent differences in sizes between protection levels. Thirdly, community composition differed between protection levels, particularly on sandstone shores and in the lower intertidal zones where limpets are common. No-take areas were distinguished by greater abundances of harvested limpets and mussels, while harvested areas were dominated by ephemeral and corticated algae, which flourished under reduced grazing pressure by limpets. Our study provides congruent evidence that no-take areas within this MPA are effective in maintaining a natural rocky-shore community composition, and natural densities and size structures of exploited species, testifying to the management success of no-take areas in the Table Mountain National Park, especially on sandstone shores of the Southern Benguela, where densities of harvested species are high, and harvesting is concentrated.

KEYWORDS

algae, ecosystem effects of fishing, harvesting, limpets, MPA, Table Mountain National Park

1 Introduction

Harvesting is a major threat to rocky shore biodiversity worldwide. Stocks of many species have been depleted and some face extinction due to overexploitation (Lasiak, 1991a; Espinosa et al., 2006; Espinosa et al., 2009; Coppa et al., 2012; Espinosa et al., 2014; Coppa et al., 2015). To reduce harvesting pressure and allow recovery of overexploited species, Marine Protected Areas (MPAs) have been established and efforts to develop more MPAs have intensified, to the extent that over 6800 MPAs exist worldwide (López et al., 2012; Bennett and Dearden, 2014; Marra et al., 2017). As of 2000, 19 MPAs had been proclaimed on the coast of South Africa (Chadwick et al., 2014); but an additional 21 Offshore Marine Protected Areas were proposed in 2018 (Sink, 2016) and gazetted in 2019 (Findlay, 2020), bringing the total area inside MPAs up to 5% of the Exclusive Economic Zone of South Africa.

As a result of growing numbers of MPAs, questions have been asked worldwide about their effectiveness in mitigating anthropogenic impacts and allowing recovery of depleted populations (Benedetti-Cecchi et al., 2003; García-Charton et al., 2008; Abecasis et al., 2015; Coppa et al., 2015). In South Africa, critical examination of the performance of MPAs has often focused on particular species and specific reserves, such as Langebaan Lagoon in the West Coast National Park (Kerwath et al., 2009), Dwesa-Cwebe Nature Reserve (Lasiak, 1993a; Lasiak, 1993b; Lasiak, 1998, Lasiak, 2006, Branch and Odendaal, 2003; Nakin et al., 2012; Nakin and McQuaid, 2014; Nakin and McQuaid, 2016), Tsitsikamma (Buxton and Smale, 1989; Buxton, 1993; Cowley et al., 2002; Brouwer et al., 2003), de Hoop (Bennett and Attwood, 1991; Bennett and Attwood, 1993; Attwood and Bennett, 1994; Attwood and Bennett, 1995), Goukamma (Kerwath et al., 2008; Götz et al., 2009a; Götz et al., 2009b; Kerwath et al., 2013), Pondoland (Maggs et al., 2013; Mann et al., 2016) and Maputaland (Currie et al., 2012; Floros et al., 2012; Floros et al., 2013; Nel et al., 2013). In addition, two recent overviews of the effectiveness of all South African MPAs in terms of their ecological and socio-economic performances have been undertaken (Kirkman et al., 2021; Mann-Lang et al., 2021). Relatively little attention has been paid to the Table Mountain National Park (TMNP), although Lechanteur (1999) and Lechanteur and Griffiths (2002) demonstrated that reef fish were more abundant inside the Castle Rocks Reserve no-take section than outside, despite this reserve being quite small.

Such evaluations are important for adaptive management of MPAs, particularly as authorities are increasingly moving to an ecosystem-based approach (Crowder and Norse, 2008) and rely on scientific evidence from community-level surveys rather than focusing on individual species alone (Benedetti-Cecchi et al., 2003; García-Charton et al., 2008; Abecasis et al., 2015; Coppa et al., 2015).

Harvesting has direct and indirect impacts on rocky shore organisms. Humans tend to selectively remove preferred species and larger individuals, reducing densities, average sizes, and ages of target species (Durán and Castilla, 1989; Branch and Odendaal, 2003; Micheli et al., 2005; Coppa et al., 2012), altering genetic composition (Fenberg and Roy, 2008), and driving some species to the point of extinction (Espinosa and Rivera-Ingraham, 2017, Carballo et al., 2019). As a result, greater densities and larger sizes of frequently harvested organisms are commonly recorded inside no-take MPAs compared to outside. Examples of the effects of protection include the kelp *Durvillaea antarctica* (Castilla and Bustamante, 1989), the limpets *Helcion concolor* (Branch, 1975), *Cymbula oculus* (Branch and Odendaal, 2003), *Fissurella crassa*, *F. limbata* (Godoy and Moreno, 1989; Durán and Castilla, 1989), *Lottia gigantea* (Sagarin et al., 2007; Fenberg and Roy, 2012), several European species of *Patella* (Espinosa et al., 2009; López et al., 2012; Zarrouk et al., 2016; Marra et al., 2017), the mussel *Perna perna* (Lasiak, 1998; Rius et al., 2006) and the urchins *Strongylocentrotus franciscanus* (Tuya et al., 2000) and *Paracentrotus lividus* (Bertocci et al., 2014).

However, the establishment of MPAs can also be associated with declines in the densities of some species through the indirect effects of protecting their predators or competitors (McClanahan and Muthiga, 1988; McClanahan and Arthur, 2001; Guidetti, 2006; Giakoumi and Pey, 2017). This can neutralize or even reverse protection effects for some species: as their predators or competitors increase in abundance, subordinate competitors or prey become depleted and fail to respond positively to protection. For example, Nakin and McQuaid (2014) recorded similar densities for *Helcion concolor* and *Scutellastra longicosta* inside and outside Dwesa-Cwebe Nature Reserve on the east coast of South Africa, despite both species being harvested in that region. Similarly, community composition did not differ in different zones of the Tuscan Archipelago National Park (Benedetti-Cecchi et al., 2003) or in Torre Guaceto MPA in the Mediterranean (Fraschetti et al., 2005). Therefore, the effects of MPAs can be area-specific and species-specific, or reflect the efficiency of enforcement, thus indicating a need for evaluation on a case-by-case basis (Benedetti-Cecchi et al., 2003; Nakin et al., 2012).

Reduction in the abundance of large individuals of herbivorous species caused by harvesting can alter ecosystem functioning by weakening their effects on other species (Underwood and Jernakoff, 1984; Lasiak and Field, 1995; Lasiak, 1998; Benedetti-Cecchi et al., 2003; Fraschetti et al., 2005; Sagarin et al., 2007). Conversely, such interactions among species may be strengthened when target species that are protected inside MPAs increase in abundance, leading to changes in community composition as prey or competitors are driven to lower levels (Durán and Castilla, 1989; Lasiak and Field, 1995; Lasiak, 1998; Benedetti-Cecchi et al., 2003; Fraschetti et al., 2005; Rius et al., 2006; Martins et al., 2008). Consequently, the community composition of harvested and no-take areas often differ, as reflected by the prevalence of species such as limpets, abalone and mussels in the absence of harvesting in protected areas, whereas harvested areas tend to be dominated by algae as a result of the removal of grazers or species that compete with algae for space (Hockey and Bosman, 1986; Lasiak and Field, 1995; Martins et al., 2008). For example, depletion of the keystone predator *Concholepas concholepas* on exploited rocky shores in Chile has led to a domination by its prey, the mussel *Perumytilus purpuratus* (Durán and Castilla, 1989). In the light of these direct and indirect effects of protection it is important to evaluate the effectiveness of MPAs in conserving the community composition of ecosystems as a whole, as well as in preserving the demographics and dynamics of individual populations (Henriques et al., 2017).

Our study examines the effects of the Table Mountain National Park (TMNP) MPA on, firstly, densities and sizes of key intertidal limpets and, secondly, rocky-shore community composition, taking into account differences between the two ecoregions that our study spanned, and between rocky substrate types that are present in the park. Our primary comparisons were between the densities and sizes of targeted species, and the community compositions, of sites that are fully protected (i.e., ‘restricted’ or ‘no-take’ areas) versus corresponding areas where harvesting is permitted but controlled (termed ‘controlled’ or ‘harvested’ areas). However, we sampled a sufficient number of replicate sites also to be able to examine the effects of biogeography and rock type. These are novel steps, for few studies of the efficacy of MPAs take into account the complicating effects of biogeography and rock type (see, for example, Barrett et al., 2009; Coppa et al., 2015; Dimitriadis et al., 2018). Bertocci et al. (2012) have demonstrated the difficulties of detecting protection effects in the face of natural spatial and temporal variability of populations.

The following hypotheses were tested: (1) There is a selective removal of large individuals of the targeted limpets *Cymbula granatina* and *Scutellatra argenvillei* in areas where harvesting takes place. (2) *In situ* Densities and average sizes of the frequently harvested limpets *C. granatina*, *C. oculus* and *Scutellastra argenvillei* will be greater in no-take areas than in harvested areas. (3) For limpets that are rarely harvested, i.e., *Scutellastra cochlear*, *S. longicosta* and *S. granularis*, protection will not have an effect: their densities and sizes will not differ consistently between no-take and harvested areas. (4) Differences will exist in community composition between no-take and harvested areas, with functional groups that are susceptible to harvesting being more abundant in no-take than harvested areas. (5) Functional groups that are not harvested may proliferate in exploited areas due to the removal of groups that normally control their abundance. (6) Protection effects will differ between ecoregions and rock types, as species assemblages differ between the ecoregions, and the abundances of some species are influenced by rock type.

2 Materials and methods

2.1 Study design and sites

The TMNP MPA was established in 2004 and occupies a transition between the Agulhas and Southern Benguela ecoregions, with Cape Point constituting a well-known coastal biogeographic break (Emanuel et al., 1992; Sink et al., 2019), across which gene flow is reduced (Von der Heyden, 2009; Wright et al., 2015). We surveyed shores on both the east and west sides of the Cape Peninsula, thus covering both ecoregions. Diverse rock types are present, but Cape Granite and Table Mountain Sandstone (TMS) predominate (McQuaid and Branch, 1985; Pfaff et al., 2019). Both rock types are represented in no-take ‘restricted’ areas and in harvested ‘controlled’ areas (Figure 1). Site names, protection level, rock type, ecoregion and GPS coordinates are recorded in Supplementary Table A1.

Sixteen sites were selected for study, representing two protection levels, two ecoregions and two rock types, with two replicate sites for each combination. Site selection was spatially randomized by placing replicate sites in different no-take areas. Wave action was standardized by selecting sites that fell in the range defined as ‘semi-exposed’ to ‘exposed’ by Steffani and Branch (2003), thus avoiding ‘sheltered’ or ‘extremely exposed’ shores.

2.2 Sampling procedure

Surveys of community composition were conducted at all 16 sites. Sampling was undertaken under permits issued by the Department of Forestry Fisheries and Environment and SANParks. For each site, four intertidal zones were identified based on their relative level and biotic indicators, termed the low, mid, high and top shore, at respective heights of approximately +0.2, +0.8, +1.2 and +1.5 m above low water spring tide (mean spring tidal range being 1.87 m). In each zone, 15 replicate 50×50-cm quadrats (divided into 25 cells of 4% cover each) were randomly placed and visually non-destructively sampled. All macro-organisms were identified and quantified as percentage cover for sessile organisms and as counts for mobile fauna (Bustamante and Branch, 1996; Blamey and Branch, 2009). To standardize, counts were later converted to percentage cover (Wieters et al., 2009).

Densities and sizes (shell lengths) of three limpet species commonly harvested in the region, *Cymbula granatina*, *C. oculus* and *Scutellastra argenvillei* (Eekhout et al., 1992; Bustamante et al., 1995; Branch and Odendaal, 2003), and

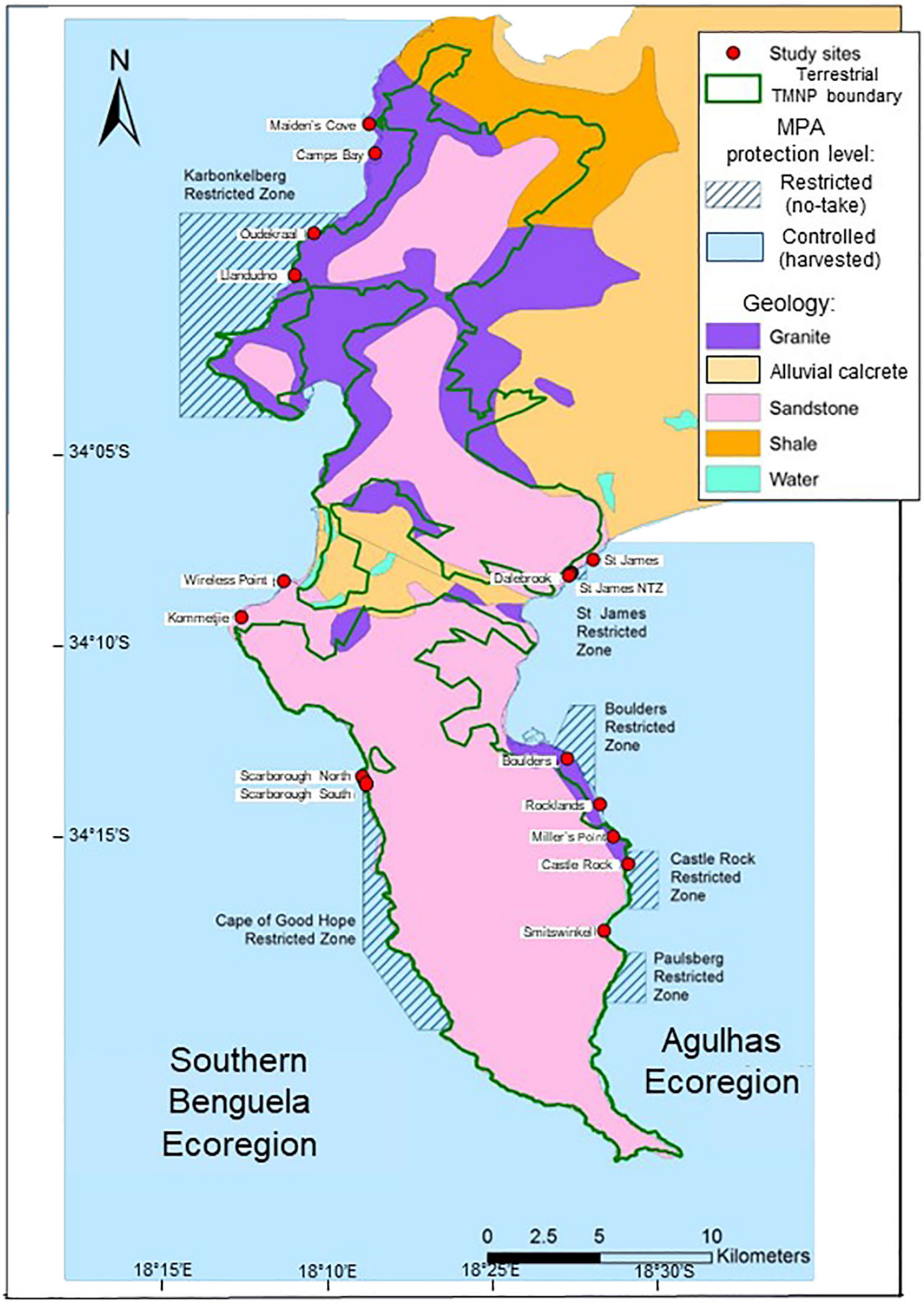

FIGURE 1
Map of the Cape Peninsula showing the Table Mountain National Park Marine Protected Area (TMNP MPA), with Controlled zones where harvesting is permitted (blue unmarked areas) and Restricted 'no-take' zones (blue hatched areas). Study sites are marked with red dots, and colour coding of the land indicates different geological formations.

three species of limpet rarely harvested there, *S. cochlear*, *S. granularis* and *S. longicosta*, were compared between harvested and no-take areas. Classification of species as 'commonly harvested' or 'rarely harvested' was based on our own observations, as reported in the results, and those of Lasiak (1991b) and Nakin and McQuaid (2014). These authors did report *Scutellastra longicosta* as being harvested on the south-east coast of South Africa, but there was no evidence of this in our study area. Measurements of densities and sizes were made separately in all four intertidal zones within the 15 replicate quadrats, with a minimum of 50 individuals being measured per species per zone per site.

Data for the shell lengths (measured with calipers to 0.1 mm accuracy) and relative abundances of shellfish (from counts of material that had been harvested) were obtained from South African National Parks field rangers' records, and opportunistically from confiscated material and discarded shucked shells. These data allowed assessment of which species are most often harvested, and whether harvesters are selectively collecting larger individuals relative to the size spectrum available. The latter comparisons were restricted to *C. granatina* at two sites, and *S. argenvillei* at one site, as it was only there that sample sizes of harvested limpets were large enough for rigorous statistical comparisons.

2.3 Data analyses

To compare the mean sizes of *Cymbula granatina*, individuals collected by harvesters at Wireless Point and Kommetjie with those present on the shore at these respective sites and, likewise, for *Scutellastra argenvillei* at Wireless Island, Student's t-tests were used. If assumptions of normality and equality of variance were not met, Mann-Whitney U tests were applied.

Univariate GLMs were employed to test for harvesting effects on densities and sizes (i.e., shell lengths) of individual limpet species. Not all species were present in both ecoregions or for some ecoregion-rock type combinations, therefore the data were analyzed separately per ecoregion and rock type. Individual GLMs included factors Protection level (as proxy for harvesting effects) and Site nested within Protection level. Significance levels were Bonferroni-adjusted to account for type-I error inflation associated with multiple tests of a variable.

Multivariate analyses to determine harvesting effects on the entire rocky shore community were conducted separately for each intertidal zone representing a unique biotope, i.e. low, mid, high and top zones. To meaningfully compare community composition between the two ecoregions comprising different species but comparable functional groups, species within each quadrat were grouped into functional groups based on criteria specified below (Supplementary Table A2). Grouping may obscure the effects for rare species, but reduces statistical challenges associated with numerous dependent variables (Warton et al., 2012; Warton et al., 2015). Algal grouping was based on morphology, productivity and susceptibility to herbivory (Steneck and Dethier, 1994). Invertebrates were grouped by trophic category and foraging strategy (Wieters et al., 2009). Herbivores were divided into 'grazers' that crop algae, 'trappers' snaring drift algae or fronds (individuals of the limpets *Cymbula granatina* > 30 *mm* and *Scutellastra argenvillei* > 40 *mm*), and 'gardeners' cultivating patches of algae.

Percentage cover data of functional groups were analyzed with four-way multivariate GLMs using the mvabund package in R (Wang et al., 2012). The factors included in the models were Ecoregion, Rock Type, Protection (all fixed and crossed) and Site (random, nested in Rock Type). The nature of any significant differences was statistically explored using *post-hoc* pairwise multivariate comparisons included in the PERMANOVA toolbox in PRIMER; multidimensional scaling (MDS) ordination plots were used to visualize and interpret the community patterns. SIMPER analyses explored which functional groups were responsible for observed differences between harvested and no-take areas of the MPA.

Statistical analyses were performed in R (R Core Team, 2019), using the car package (Fox and Weisberg, 2019) and mvabund package (Wang et al., 2012). Pairwise PERMANOVA, MDS and SIMPER analyses were conducted with PRIMER V7 (Clarke and Gorley, 2015).

3 Results

3.1 Abundances and sizes of limpets collected by harvesters

Harvesters at Kommetjie, Wireless Point and Wireless Island targeted three species of limpets, together with the mussels *Choromytilus meridionalis* and *Mytilus galloprovincialis* (pooled as 'mussels' as rangers' records treated them as a group) (Table 1). *Cymbula granatina* was the most harvested limpet, followed by *C. oculus*. *Scutellastra argenvillei* was collected at Wireless Island only, while *S. cochlear* and *S. granularis* were never taken.

Harvesters focused on large individuals of *C. granatina* at both sites examined, with the difference between the mean sizes of harvested individuals and those in the natural populations being significant (Mann Whitney U test, $p \leq 0.001$ in both cases; Figures 2A, B). The smallest harvested individuals were respectively 40-45 mm and 60 mm, whereas natural populations had individuals as small as 5-20 mm. Although a similar pattern emerged for *S. argenvillei*, with harvested individuals falling in the range 60–100 mm and the natural population spanning 5–100 mm, the difference in mean sizes was in this case not significant (Figure 2C; Mann Whitney U test, $p = 0.3094$).

3,2 Densities of limpets

On sandstone (TMS), all three commonly harvested limpets *Cymbula granatina*, *C. oculus* and *Scutellastra argenvillei* had significantly lower densities in harvested areas than in no-take areas. Harvesting effects were significant despite significant variability between replicate sites in most cases and the reduced power of Bonferroni-adjusted analyses. Densities on granite were low regardless of the level of protection and showed no harvesting effects or - in the case of *C. oculus* - greater

TABLE 1 Number of individuals harvested for seven species of commonly harvested (*) and rarely harvested ($^{\#}$) species at Ko, Kommetjie, WI, Wireless Island and WP, Wireless Point, the three most heavily harvested sites.

Date	Site	*C. granatina**	*C. oculus**	*S. barbara*$^{\#}$	*S. argenvillei**	Mussels*	*S. cochlear*$^{\#}$	*S. granularis*$^{\#}$
23/10/1985	WI	42	5	0	40		0	0
23/10/1985	WP	42	11	1		12	0	0
14/8/2005	WP	300	40	4			0	0
21/12/2014	WP	19	3	1		125	0	0
23/11/2014	WP	19	3	1		45	0	0
25/04/2017	Ko	280	47	0			0	0
1/05/2019	Ko	432	83	4	7	142	0	0
TOTALS		1134	192	11	47	324	0	0

densities in Agulhas harvested areas (Supplementary Table A3 *post-hoc* ; Figures 3A–C).

In contrast, densities of the rarely harvested limpets showed inconsistent or no effects of protection. *Scutellastra longicosta* densities did not differ significantly between levels of protection on either rock type (Figure 3D). *Scutellastra cochlear* densities were lower in harvested areas on TMS in both ecoregions, while no or reversed protection effects existed on granite (Figure 3E). *Scutellastra granularis* also showed inconsistent harvesting effects, with greater densities in protected than harvested sites on granite in the Southern Benguela, whereas no significant or negative effects of protection were evident at the other three combinations of ecoregion and rock type (Figure 3F).

3.3 Sizes of limpets

Of the commonly harvested limpets, Cymbula *granatina* was significantly larger inside the no-take than the harvested areas, regardless of rock type (Supplementary Table A4; Figure 4A). *Cymbula oculus* was counterintuitively larger in the harvested areas, but only on sandstone shores (Figure 4B). For *Scutellastra argenvillei*, *post-hoc* sizes were larger in the no-take than harvested areas, but on sandstone shores only; protection had no effect on granite, where its densities were low (Figure 4C).

Of the rarely or never harvested limpets (Supplementary Table A4), the size of *S. longicosta*, was not affected by either protection level or rock type (Figure 4D). For *S. cochlear*, sizes were greater in harvested than no-take areas in the Agulhas ecoregion on granite, but protection had no effect elsewhere (Figure 4E). For *S. granularis*, sizes were significantly larger in harvested areas in the Benguela on both TMS and granite and on Agulhas TMS, but not significantly different on Agulhas sandstone (Figure 4F).

3.4 Community effects

MDS plots of the four zones on the shore exhibited a clear biogeographic distinction between the Southern Benguela and Agulhas ecoregions (Figure 5). Differences also existed between replicate sites (Supplementary Table A5). The distinctions between protection levels and sites emerged more clearly when the data were disaggregated to separate the ecoregions and rock types and bring to the fore the protection and site effects (Supplementary Figure A1). Over and above the regional differences, clear harvesting effects existed, but they differed among intertidal zones, ecoregions and rock types. In the low

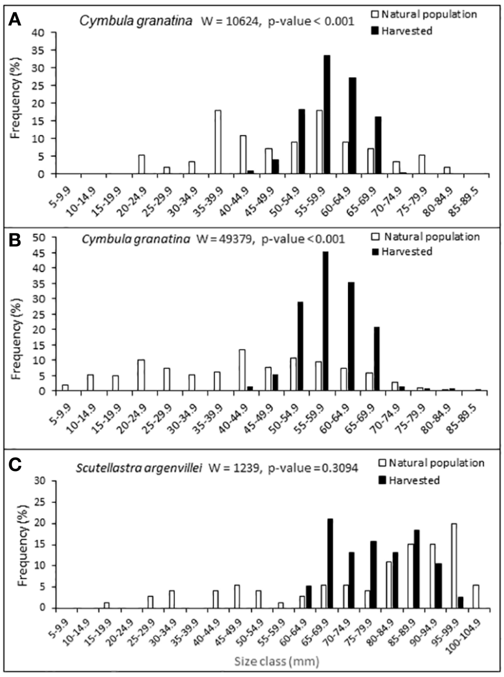

FIGURE 2

Comparisons of shell lengths of harvested individuals and those in natural populations, for **(A)** *C granatina* at Kommetjie, **(B)** *C granatina* at Wireless Point and **(C)** *S. argenvillei* at Wireless Island. Mann Whitney U tests (W) and probabilities of differences between sizes of harvested and natural samples are shown. Sample sizes for respectively harvested and natural samples were n=280 and n=56 for Kommetjie, n=298 and n=209 for Wireless Point, n=38 and n=72 for Wireless Island.

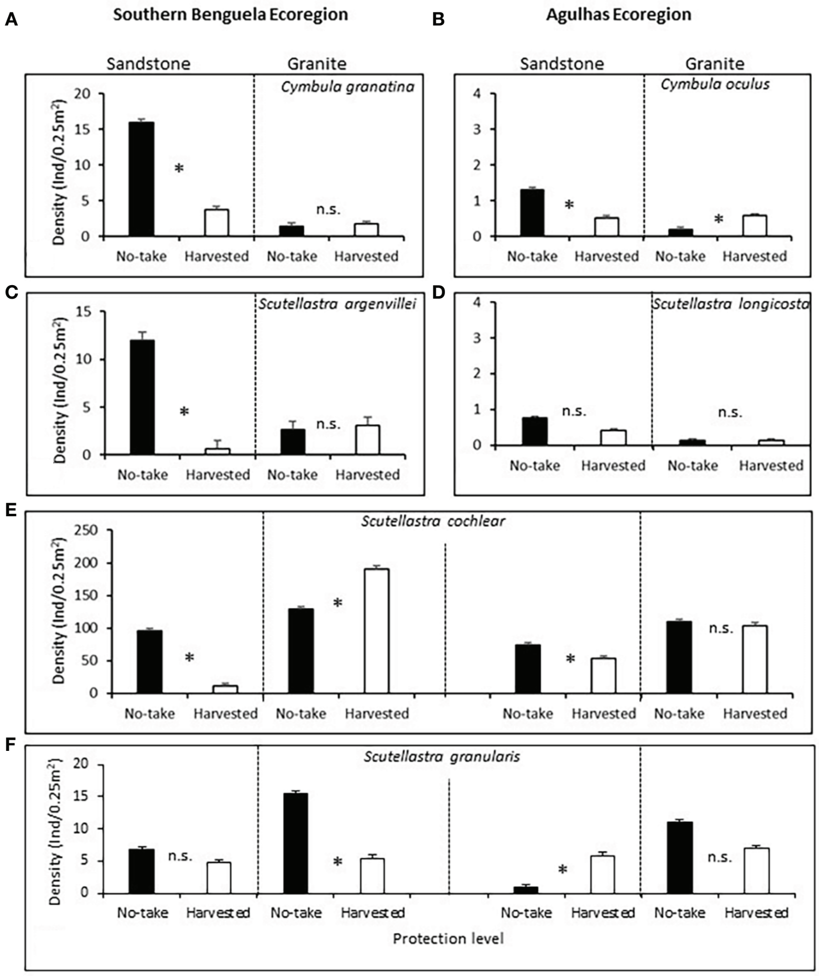

FIGURE 3
Mean densities (+1SE) of the frequently harvested limpets **(A)** *Cymbula granatina*, **(B)** *C oculus* and **(C)** *Scutellastra argenvillei*, and the rarely harvested limpets **(D)** *S. longicosta*, **(E)** *S. cochlear* and **(F)** *S. granularis*, with regard to protection level and rock type. The first four species **(A-D)** occur predominantly in only one ecoregion, so this factor was not included for their analyses, but was included in the analyses for the fifth and sixth species), which occur in both ecoregions. Ind, individuals. Asterisks between bars, Bonferroni-corrected significant differences; n.s., non significant.

intertidal zone (Supplementary Figure A1A), dissimilarities between harvested and no-take areas existed for TMS but not granite ledges where site differences dominated; and were more pronounced in the Southern Benguela than the Agulhas ecoregion. Similarly, in the mid intertidal zone (Supplementary Figure A1B) harvesting effects existed only for TMS and not granite shores, in both ecoregions (Supplementary Figure A1B). In the high intertidal zone, harvesting effects were most prominent on Southern Benguela TMS, while site differences overrode harvesting differences in all other cases (Supplementary Figure A1C). On the top intertidal zone, site differences were pronounced, overriding harvesting effects in all cases (Supplementary Figure A1D).

3.5 Functional groups distinguishing between harvested and no-take areas

SIMPER analyses (Figures 6–9), coupled with the MDS ordinations discussed above, indicated that marked dissimilarities existed between no-take and harvested areas, but varied among ecoregions, rock types and intertidal zones. On the low shore (Figure 6), ephemeral algae were consistently more abundant on harvested shores, most obviously in the Southern Benguela ecoregion. Corticated algae followed suit and distinguished harvested sites in all cases except Southern Benguela granite. Algal crusts were more prevalent on harvested shores on granite in both ecoregions, but on sandstone the

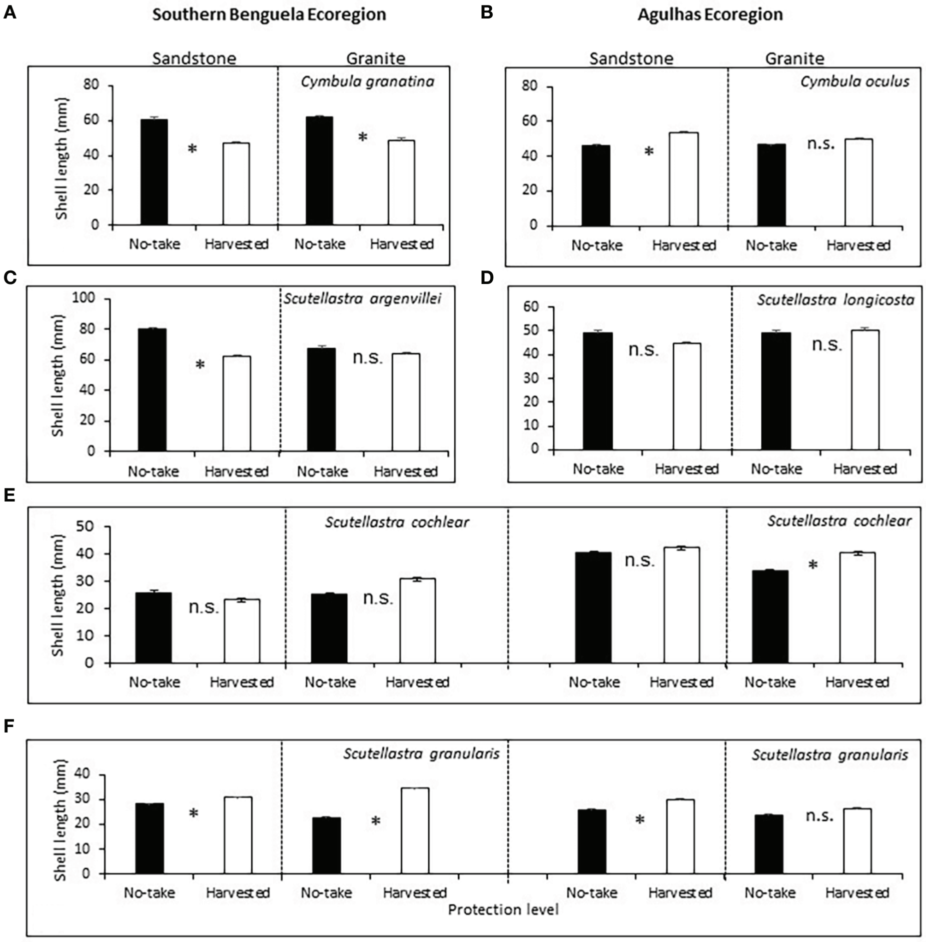

FIGURE 4
Mean shell lengths (+SE) of limpets, in relation to protection levels, rock types and ecoregions (in the case of species that occurred in both ecoregions). Asterisks between bars indicate Bonferroni-corrected significant differences. For further details see caption to Figure 3.

reverse was true. Herbivores (particularly trappers and gardeners) were more abundant at no-take sites.

Within the mid intertidal zone (Figure 7), corticated algae were more abundant on harvested shores (with the exception of Southern Benguela granite), and harvested sites housed larger amounts of ephemeral algae than no-take sites in the Southern Benguela ecoregion. Algal crusts were, contrary to the low-shore pattern, more abundant on no-take shores, being distinguishing members of no-take shores in three cases. Filter feeders also distinguished no-take sites in three of the four comparisons.

In the high shore (Figure 8), ephemeral algae were prevalent at the majority of harvested sites, distinguishing these shores in three of four cases. Corticated algae, however, reversed the trend evident lower on the shore and were more abundant at, and distinguished, no-take sites in two instances. Of the herbivores, trappers yielded no consistent results with respect to protection level, but greater grazer abundances were found on protected shores in three cases, two of which diagnostic of no-take shores. Filter feeders yielded mixed results, being more abundant on no-take shores in two cases, but less abundant there in the other two cases.

On the top shore (Figure 9) ephemeral algae were more abundant in no-take areas, with one exception. Corticated algae remained more common in harvested sites in three out of four cases. Grazers– dominated by the rarely harvested limpet *S. granularis* - attained greater densities on harvested shore in all cases bar Southern Benguela granite. In three of four instances, filter feeders distinguished and achieved greater abundance in no-take areas.

3.6 Functional groups distinguishing between ecoregions

SIMPER identified groups that distinguished ecoregions (Figure 10). Most differences were zone-specific, but

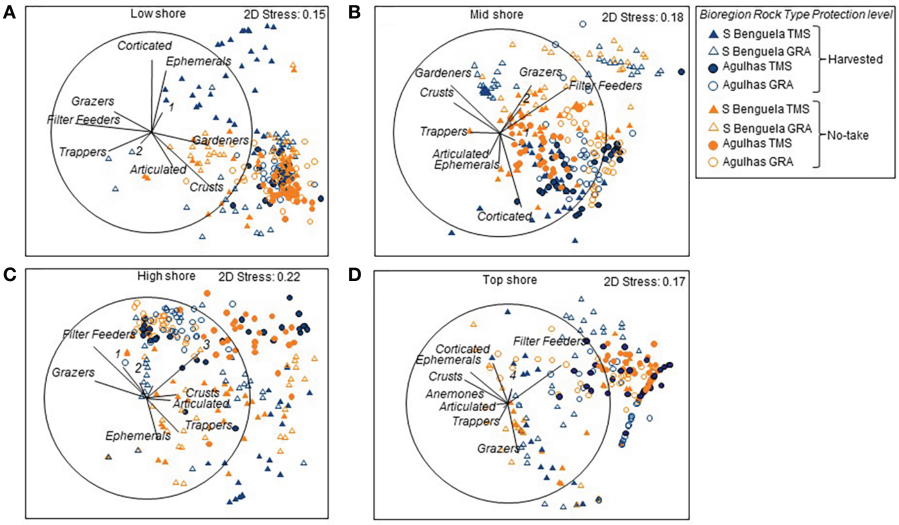

FIGURE 5
MDS plots showing differences in community composition among quadrats reflecting the effects of Protection, Ecoregion and Rock type for **(A)** low, **(B)** mid, **(C)** high and **(D)** top zones of 16 sites within the Table Mountain national `park MPA, which spans the Southern Benguela (S Benguela) and Agulhas ecoregions and features Table Mountain sandstone (TMS) and granite (GRA) For clarity some functional groups are numbered: 1 – Predators ad scavengers; 2 = anemones; 3 = Corticated alage; 4 – Gardeners.

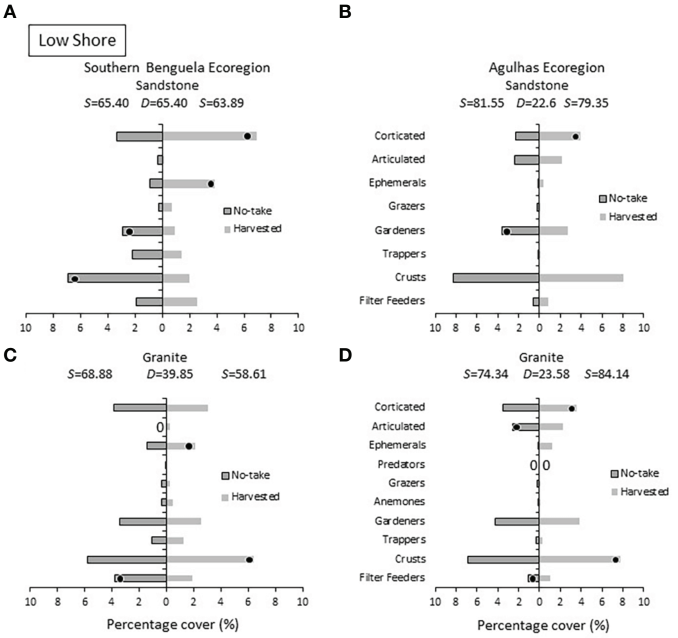

FIGURE 6
Low shore: Percentage cover of groups responsible for the similarities (*S*) within harvested or no-take areas and the dissimilarities (*D*) between them, on sandstone in **(A)** the Southern Benguela and **(B)** in the Agulhas Ecoregion, and on granite in **(C)** the southern Benguela and **(D)** Agulhas. Black dots identify groups distinguishing between harvesting and no-take zones and are placed in the zone with the greatest abundance; 0 = absence.

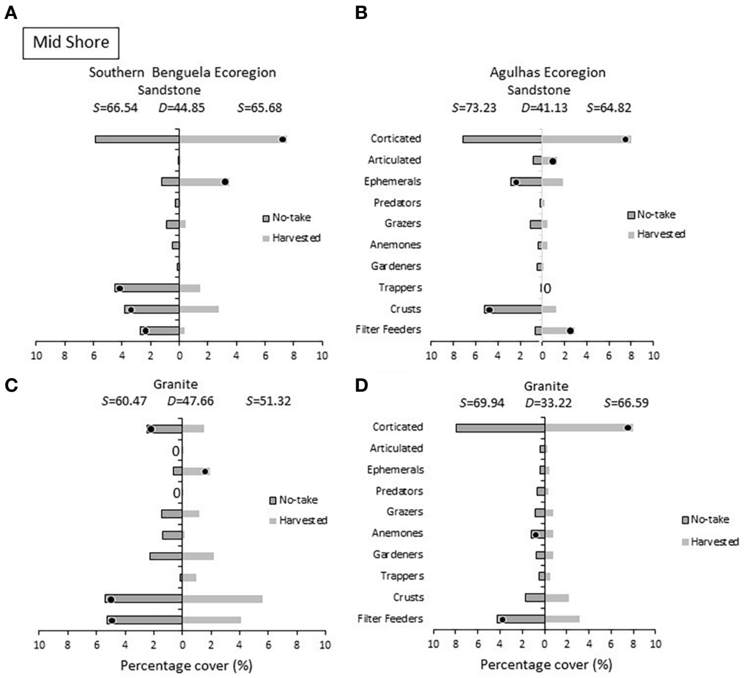

FIGURE 7
Mid shore: Percentage cover of groups responsible for similarities (*S*) within harvested or no-take areas and dissimilarities (*D*) between them, on **(A)** sandstone in the Southern Benguela and **(B)** in the Agulhas ecoregions, and on granite in **(C)** the southern Benguela and **(D)** Agulhas. See caption for Figure 6 for further interpretation.

ephemeral algae consistently distinguished the Southern Benguela, as did crustose algae in all zones bar the low shore, where they distinguished the Agulhas ecoregion, associated with a greater abundance of gardening limpets in that zone and region. Grazers were abundant in only the high and top zones, where they distinguished the Southern Benguela. Articulated coralline algae were abundant only in the low shore, where they distinguished the Agulhas. Corticated algae distinguished the Agulhas in the mid and high shore where their abundance was greatest but distinguished the Southern Benguela in the low and top zones. Filter feeders distinguished the Agulhas in the high and top zones where they were most abundant, but the Southern Benguela in the low and mid zones.

4 Discussion

Exploitation is a major factor driving communities on intertidal rocky shores, but its impacts vary among rock types and ecoregions (Hockey et al., 1988; Lasiak and Field, 1995; Lasiak, 1999; Airoldi et al., 2005; Jimenez et al., 2011; Jimenez et al., 2015; Jimenez et al., 2016). The key findings of our study supported our hypotheses that (1) shellfish gatherers selectively harvest large individuals of limpets, (2) reducing the densities and usually the mean sizes of frequently harvested species, but (3) not those of rarely harvested species. (4) Protection influenced the community composition of rocky shores; but the magnitude of its effects was specific to functional groups and depended on ecoregion, rock type and zone. (5) Functional groups that are not harvested did proliferate in harvested areas where species normally controlling them were depleted. (6) Protection effects did differ between ecoregions and rock types. Overall, these outcomes confirmed that (a) protection inside no-take areas in the Table Mountain National Park MPA has significant beneficial effects on commonly harvested invertebrates, but less influence (or none at all) on rarely harvested ones and (b) community composition did respond to protection.

4.1 Selection of species and sizes by harvesters

Previous studies have demonstrated that shellfish gatherers have preferences for particular species (Durán et al., 1987; Airoldi et al., 2005; Nakin and McQuaid, 2014). This leads to a small number of species dominating the catches (Hockey and Bosman, 1986; Lasiak, 1991b; Lasiak, 1993b; García-Escárzaga et al., 2017). For example, Durán et al. (1987) showed that in Chile shellfish gatherers concentrate their harvest on

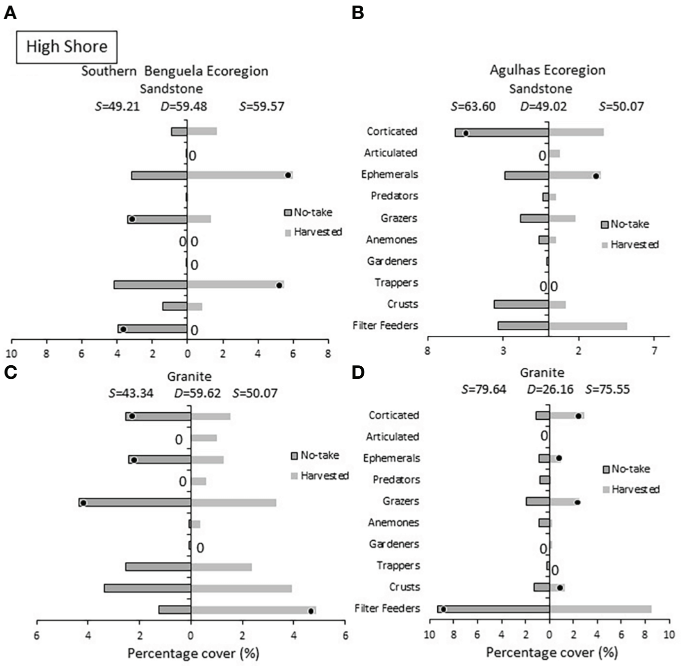

FIGURE 8
High shore: Percentage cover of groups responsible for similarities (*S*) within harvested or no-take areas and dissimilarities (*D*) between them, on **(A)** sandstone in the Southern Benguela and **(B)** Agulhas ecoregions, and on granite in **(C)** the southern Benguela and **(D)** Agulhas. See caption for Figure 6 for further interpretation.

Concholepas concholepas and *Fissurella crassa*. Our study revealed that, unlike the east coast of South Africa where the mussel *Perna perna* dominates catches by shellfish gatherers (Hockey and Bosman, 1986; Hockey et al., 1988; Lasiak, 1991a; Lasiak, 1992), the limpet *Cymbula granatina* was the most exploited intertidal shellfish in Table Mountain National Park. This could be attributed to its large size, high densities, accessibility on relatively sheltered shores (Eekhout et al., 1992; Bustamante et al., 1995; Blamey and Branch, 2009), and comparatively low strength of attachment (Branch and Marsh, 1978). All these characteristics lead to easy harvesting of this species on rocky shores, making it vulnerable to overfishing (Lasiak, 1991b). Indeed, there is a long history of exploitation of species such as this in southern Africa, extending back at least 100 000 years in the archaeological record (Jerardino et al., 2008; Parkington et al., 2013; Will et al., 2016; Jerardino, 2021). *Cymbula oculus* was also harvested at three Southern Benguela sites, but in smaller amounts, reflecting the fact that its densities there are lower than those of *C. granatina*, reflecting its prevalence in the warmer waters of the Agulhas Ecoregion (Branch, 1971). By contrast, *Scutellastra argenvillei*, which inhabits semi-exposed to exposed areas (Branch and Steffani, 2004), was recorded as being harvested at only one site in any numbers. The absence of *S. longicosta*, *S. cochlear* and *S. granularis* from any catch records supports the view that they are rarely harvested in the region we investigated, although *S. longicosta* is harvested on the more easterly shores of South Africa (Hockey et al., 1988; Nakin et al., 2012; Nakin and McQuaid, 2014; Nakin and McQuaid, 2016).

The selection of larger individuals of *C. granatina* by shellfish gatherers upholds our first hypothesis to this effect and supports other findings that shellfish gatherers target large individuals (Durán et al., 1987; Lasiak, 1991a; Lasiak, 1992; Jimenez et al., 2011; Alexander and Gladstone, 2012). This usually leads to reductions in the mean sizes of the individuals in the natural populations (Eekhout et al., 1992; Jimenez et al., 2011), with profound effects on reproductive output (Branch, 1975; Branch and Odendaal, 2003).

4.2 Densities of key species

Exclusion of shellfish gatherers from MPAs often leads to greater densities of commonly harvested species inside no-take areas relative to harvested areas (Moreno et al., 1984; Hockey and Bosman, 1986; Moreno et al., 1986; Hockey et al., 1988; Edgar and Barrett, 1999; Alexander and Gladstone, 2012; Bednar and Trulio, 2017). For example, higher densities of the limpet *Cellana tramoserica* were found in the Bouddi National Park Marine Extension relative to unprotected shores (Alexander and

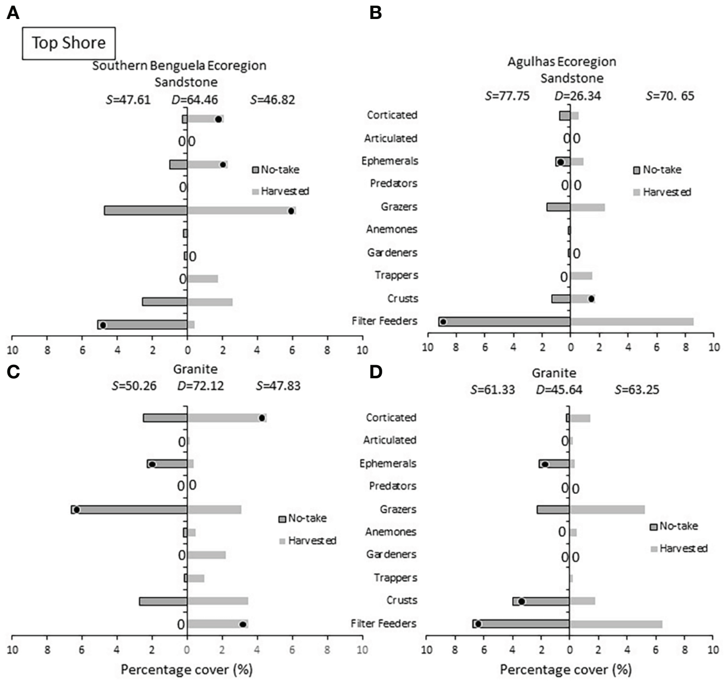

FIGURE 9
Top shore: Percentage cover of groups responsible for similarities (*S*) within harvested or no-take areas and dissimilarities (*D*) between them, on **(A)** sandstone in the Southern Benguela and **(B)** Agulhas ecoregions, and on granite in **(C)** the southern Benguela and **(D)** Agulhas. See caption for Figure 6 for further interpretation.

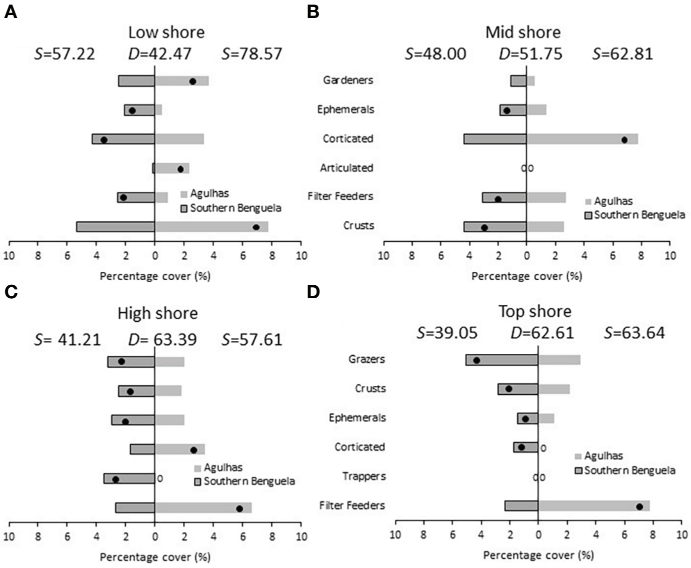

FIGURE 10
Percentage cover of groups responsible for the similarities (*S*) within ecoregions and the dissimilarities (*D*) between ecoregions at the four intertidal zones: Low shore, mid shore, high shore and top shore **(A–D)**. Black dots identify groups distinguishing between ecoregions, and are placed in the ecoregion with the greatest abundance; 0 = absence.

Gladstone, 2012). The same was true for *Patella ulyssiponensis* in La Palma MPA (López et al., 2012), for *Cymbula oculus* in Dwesa Nature Reserve in South Africa (Branch and Odendaal, 2003), and for *Fissurella picta* and *Fissurella limbata* in the Marine Reserve of Mehuin in Chile (Duarte et al., 1996). These increased densities were all attributed to protection. Our results produced similar patterns for the commonly harvested limpets *C. granatina*, *C. oculus* and *S. argenvillei*, particularly on sandstone where these species are most abundant.

The conclusion that protection is responsible for increased densities of harvested species is strengthened by the fact that the rarely harvested limpets *S. granularis*, *S. longicosta* and *S. cochlear* had equivalent densities at both protection levels in most instances (six out of ten comparisons). This difference is what would be expected if it is harvesting, rather than any other factors, that accounts for the decline in harvested species in sites that are not protected. Of the species that are not harvested, in the case of *S. longicosta*, no differences in density existed inside and outside no-take areas. For the other two species that are not harvested, there were, however, departures from this pattern, but they still amounted to an absence of any protection effect, or at least inconsistencies in its effects. For *S. cochlear*, densities inside and outside no-take MPAs were the same in two cases, greater in no-take areas in one case, and greater in harvested areas in one case. *Scutellastra granularis* attained high densities inside no-take areas in only one instance. It is possible that that its abundance is influenced more by the arrival of the alien mussel *M. galloprovincialis* (Griffiths et al., 1992; Branch et al., 2008; Branch et al., 2010) than any other factor, as this mussel greatly boosts this limpet's recruitment (Van Erkom Schurink and Griffiths, 1990). In the Agulhas Ecoregion, *S. granularis* density is also often restricted by barnacles such as *Tetraclita serrata* and *Chthamalus dentatus* (Branch, 1976; Nakin and McQuaid, 2014), which are substantially less abundant in the Southern Benguela than the Agulhas (Boland, 1997). There were significant and complex interactions among ecoregion, rock types and protection level for *S. granularis* and *S. cochlear* as a result of these variable outcomes, which was not unexpected in the absence of any likely direct effect of protection. The absence or inconsistent outcomes of any protection effect observed for rarely harvested species also concurs with previous studies. For example, another rarely harvested species, *Cellana capensis*, had higher densities in harvested than no-take areas on the southeast coast of South Africa (Lasiak, 1993a).

Protection of even harvested species by way of no-take areas is, however, not always effective. An absence of any protection effect was reported by Nakin and McQuaid (2014) for limpets in Dwesa Nature Reserve, attributable to illegal harvesting in the reserve and differences in the intensity of harvesting outside the reserve. Similarly, Coppa et al. (2012; 2015) associated the decline of *Patella ferruginea* in Italy's Mal di Ventre MPA with ineffective enforcement of regulations. Although *C. oculus* had high densities inside sandstone no-take areas, its overall abundance appears to have dramatically decreased in the TMNP MPA over the past 11 years, from 12.35 m^{-2} to 8 m^{-2} (Maneveldt et al., 2009). The lack of protection effect on the granite rocky shore might be due to higher mortality associated with dislodgement of limpets from granite rocks, as it has been suggested that they cannot attach as firmly to this rock type (McQuaid et al., 1985). Thus, low densities of *C. oculus* on granite rocky shores may not reflect a failure of protection inside no-take areas of the MPA, but rather an influence of habitat type on the density of the species.

We had anticipated that there would be differences in the abundances of limpets between the two ecoregions spanned by our study. This manifested itself in two ways. First, some species were either confined to, or substantially more abundant, in one of the two ecoregions. That was the case for *C. granatina* and *S. argenvillei* (predominantly Southern Benguela), and *C. oculus* and *S. longicosta* (predominantly Agulhas). For those species that occurred in both ecoregions, we had expected that there might be greater abundances in the Southern Benguela than the Agulhas Ecoregion because of the greater productivity on the west coast and the fact that greater biomasses of grazers have been recorded there (Bustamante et al., 1995). That was, however, not the case. There were no obvious differences in abundances of either *S. granularis* or *S. cochlear* between ecoregions.

The densities of *S. longicosta* that we recorded were magnitudes less than those recorded in Dwesa Nature Reserve (Nakin and McQuaid, 2014). This might reflect that the species is reaching the western limit of its distribution range in the TMNP, resulting in low densities (Hidas et al., 2010).

4.3 Sizes of key species

Shellfish gatherers generally target large individuals, as noted above for *Cymbula granatina* and *Scutellastra argenvillei*. This can truncate the size distribution of populations in harvested areas (Sagarin et al., 2007; Jimenez et al., 2011; Alexander and Gladstone, 2012; Coppa et al., 2012; Fenberg et al., 2012; Coppa et al., 2015; Bednar and Trulio, 2017), as has been reported for *Cymbula oculus* (Branch and Odendaal, 2003), *Cellana capensis* (Lasiak, 1993a), *Lottia gigantea* (Sagarin et al., 2007; Lucas and Smith, 2016), and many other species, including fish (Marra et al., 2017; Heyns-Veale et al., 2019).

In our results, harvesting had variable effects on the sizes of key species. The most frequently harvested species, *C. granatina*, consistently had larger sizes inside protected vs. harvested areas, on both sandstone and granite rocks. The second frequently harvested species, *Scutellastra argenvillei*, yielded the same outcome on sandstone, but not on granite, possibly because densities there were much lower, and no harvesting of this species was recorded at sites with granite rocks. However, *C. oculus*, which is also harvested, displayed a weak effect of protection on size, being larger outside no-take areas than inside on sandstone, and not significantly different on granite. Effects of protection may thus be species-specific, habitat-specific and region-specific (Nakin and McQuaid, 2014). The existence of larger individuals in protected areas enhances reproductive output because of their greater fecundity (Branch, 1975; Branch and Odendaal, 2003; Orozco et al., 2013; Zarrouk et al., 2016). For species like *C. oculus* that are protandric hermaphrodites and change sex from male to female at an intermediate size, a reduction of mean size will also affect population reproductive output as it will skew sex ratios in favor of males (Branch and Odendaal, 2003).

In contrast to the three harvested species of limpets, all three rarely harvested species, *S. longicosta*, *S. granularis* and *S. cochlear*, conformed to expectation and showed either no effects or no consistent effects of protection on their mean sizes. The size of *S. longicosta* was not related to the level of harvesting, and the same was true in three of the four comparisons possible for *S. cochlear*. For *S. granularis*, size was larger at harvested sites – significantly so in three of the four cases.

Similar findings were reported for *S. granularis* at Dwesa Nature Reserve, with larger sizes outside than inside the reserve (Nakin and McQuaid, 2014). The occurrence of larger individuals in harvested areas may reflect reduced competition due to the removal of harvested competitors, although that has not yet been demonstrated empirically. Lasiak and White (1993) have, however, shown that high densities of the limpet *Cellana capensis* reduce microalgal availability, with implied competitive effects for other species.

The sizes and densities of key limpet species were forecast to be greater in the Southern Benguela than the Agulhas Ecoregion because of greater productivity there as a result of upwelling (Bustamante et al., 1995). This was, however, not the case.

4.4 Community composition

There were considerable differences in community composition between the harvested and no-take areas, with relatively greater abundances of filter feeders, grazers and trappers inside no-take areas. Reductions of these groups in harvested areas have frequently been reported (Moreno et al., 1984; Hockey and Bosman, 1986; Lasiak and Field, 1995; Sharpe and Keough, 1998; Lasiak, 1998; Lasiak, 1999; Ceccherelli et al., 2005; Sink et al., 2010; Ceccherelli et al., 2011; Barbiero et al., 2011). Their depletion at harvested sites was likely responsible for the increased abundances of algae due to diminished grazing and/or competition for space. Similar findings have been reported for Dwesa-Cwebe, Hluleka and Mkambati Nature Reserves, and in Tsitsikamma MPA, on the east and south coasts of South Africa respectively, where community composition inside these protected areas is dominated by commonly harvested species such as *Perna perna*, *Haliotis spadicea*, *Scutellastra barbara*, *Cymbula oculus* and *Cymbula miniata* (Hockey and Bosman, 1986; Lasiak and Field, 1995; Dye, 1998; Lasiak, 1998; Lasiak, 1999; Hanekom, 2011). Comparable outcomes have been noted worldwide: the commonly harvested urchin *Heliocidaris erythrogramma* is a characteristic and distinguishing taxon for no-take areas in Tasmanian marine reserves (Barrett et al., 2009). Three other harvested taxa, *Tridacna* spp., *Trochus niloticus* and *Turbo* spp., are the major groups distinguishing between protected and no-take areas in New Caledonia (Jimenez et al., 2015; Jimenez et al., 2016). The fact that harvested filter feeders, grazers and trappers were the major functional groups distinguishing between harvested and no-take areas in our data strengthens our conclusion that protection influenced the community composition, as reflected in other studies (Lasiak and Field, 1995; Lasiak, 1998; Lasiak, 1999). Protection in no-take areas often results in a mosaic of communities, with patches of filter feeders, grazers and trappers, while adjacent harvested areas tend to have extensive uniform mats of algae, as described for Dwesa-Cwebe and Hluleka Nature Reserves and Tsitsikamma MPA (Hockey and Bosman, 1986; Lasiak and Field, 1995; Dye, 1998; Lasiak, 1998; Hanekom, 2011).

Whilst not the primary focus of this study, community composition also differed in a consistent and significant manner between ecoregions, which led to frequent interaction effects between protection and ecoregion. Our results agree with the biogeographic findings of Bustamante et al. (1995) and Bustamante and Branch (1996) that community composition is markedly different between the Agulhas and Southern Benguela ecoregions, which is the most clear-cut biogeographic break along the coast of southern Africa (Emanuel et al., 1992). This is associated with greater nutrient availability and lower temperatures in the Southern Benguela (McQuaid et al., 1985; Emanuel et al., 1992; Bustamante et al., 1995). In our results, the Southern Benguela displayed higher abundances of ephemeral algae, grazers and trappers, probably as a result of upwelling boosting nutrient availability and primary productivity (Bustamante et al., 1995; Bustamante and Branch, 1996).

The presence of larger quantities of algal crusts inside some of the no-take areas probably reflects trophic cascades and competitive interactions among functional groups, since this group has been shown to positively related to the abundance of grazers, which deplete macroalgae (Blamey and Branch, 2009) that would otherwise overgrow crusts. Harvested areas frequently had the highest percentage cover of corticated and ephemeral algae, which signals an altered community composition associated with lower densities of grazers (Bustamante et al., 1997; Lasiak, 1998; Barbiero et al., 2011).

The average levels of similarity (70.9%) in the Agulhas Ecoregion were equivalent to those considered to be converged communities (Sink et al., 2010; Jimenez et al., 2012). In addition, both protection levels were characterized by similar functional groups and dominated by algae, which are usually typical of areas experiencing high harvesting pressure (Hockey and Bosman, 1986; Lasiak and Field, 1995; Lasiak, 1998; Barrett et al., 2009; Sink et al., 2010). Thus, the dominance of some groups of algae in no-take areas in the Agulhas Ecoregion contradicts early findings in other MPAs along the south and east coasts of South Africa, such as Dwesa, Hluleka and Mkambati Nature Reserves (Hockey and Bosman, 1986; Lasiak and Field, 1995; Lasiak, 1998) and Tsitsikamma MPA (Hanekom, 2011), where commonly harvested consumers dominate and characterize no-take areas, with algae being less abundant (Lasiak and Field, 1995; Lasiak, 1998; Hanekom, 2011). This may, however, reflect the influence of upwelling in the Table Mountain National Park MPA, which supplies nutrients and thus facilitates algal growth and productivity, while the contrary findings were from more oligotrophic regions of the country, where grazing may have a more severe effect on algal abundances.

In the Southern Benguela Ecoregion, differences between harvested and no-take areas were more obvious (D = 39.85–72.12%), reflecting greater divergence (Sink et al., 2010; Jimenez et al., 2012) than in the Agulhas Ecoregion. There, communities reflected conventional expectations to a much greater degree, especially on sandstone shores, where corticated and ephemeral algae were prevalent in harvested situations, associated with the depletion of herbivores.

In terms of individual species, one striking absentee from the list of characteristic species of the Agulhas Ecoregion was the indigenous brown mussel *Perna perna*, which was abundant in False Bay at the southeast limits of the Agulhas Ecoregion in the 1980s but had diminished by 2011 (Griffiths and Mead, 2011; Reimers et al., 2014), and was never recorded in our study. Changes in its abundance and presence in this region are likely associated with cooling of the waters and a southeasterly contraction of this species' range (Pfaff et al., 2019). Replacing it, the alien Mediterranean mussel *Mytilus galloprovincialis* has become a dominant element of all the shores studied.

5 Conclusions

Our study was both enriched and complicated by the fact that our comparisons of the effects of protection spanned two ecoregions and two rock types. Had we confined analyses to the Southern Benguela, where harvesting is most intense, and to sandstone, where the limpets we examined are most abundant, the effects of protection would have been unambiguous: protection increases the abundance of grazers and mussels, but the abundance of algae is decreased due to greater grazing and competition for space. However, expanding the study to cross ecoregional boundaries and rock types yielded a much richer understanding . Ecoregions differed in ways we had not expected, and rock type introduced interactions that muted the effects of protection on granite where many of the harvested species were less abundant.

In summary, shellfish gatherers collected mainly the limpets *C. granatina*, *C. oculus* and *S. argenvillei* and mussels, and targeted large individuals, supporting our first hypothesis. Our second hypothesis, that protection would result in greater densities and sizes of harvested limpets, was supported on sandstone shores, but not on granite rocky shores where their densities were uniformly low. Our third hypothesis, that rarely harvested species would show no differences in densities and sizes attributable to protection gained partial support: *S. longicosta* conformed to the hypothesis, whereas *S. granularis* provided only partial support, being larger in harvested areas in three out of four cases, and only once having greater densities in no-take zones; *S. cochlear* yielded sizes that were larger in harvested than no-take areas in one instance, and its densities were ambivalent with respect to protection level.

Differences in protection did affect rocky shore community composition, supporting our fourth hypothesis. The depletion of limpets and filter feeders was associated with dramatic increases in algal domination in the harvested areas of Southern Benguela sandstone shores, upholding our fifth hypothesis. Effects of harvesting on community composition were thus specific to region, zone and rock type, supporting our sixth hypothesis.

Likely causes of these differences include (a) differences in the intensity of harvesting in different areas; (b) targeting of different species; (c) effectiveness of enforcement of protection, (d) differences in abundance between rock types, and (e) differences in the abundances of alien species, particularly *Mytilus galloprovincialis*. Influences of protection were most clear for sandstone rocks in the Southern Benguela, where harvesting was concentrated and target species most abundant.

Due to their accessibility or vicinity to coastal communities, some sites are harvested more intensely than others. In addition, the effectiveness of law enforcement varies among the sites. The management of TMNP MPA would benefit from data of actual harvesting levels and measures of compliance, as well as experimental tests of the impacts of different harvesting intensities on rocky shore biodiversity. We would urge all three measures to be pursued.

Overall, this study supports the effectiveness of no-take areas in the TMNP MPA in maintaining densities and average sizes of harvested limpets. With the removal of these keystone grazers, communities will transform towards algal-dominated systems, which demonstrates the ecosystem effects of the MPA's conservation measures.

Data availability statement

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

Author contributions

All authors contributed remarkable in the production of this manuscript from conceptualization, data collection, data analysis and writing.

Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2022.893260/full#supplementary-material

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