Evaluating the evidence for ecological effectiveness of South Africa’s marine protected areas

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We reviewed 140 papers to assess the ecological effectiveness of South Africa’s marine protected areas (MPAs). Evidence was assessed for coverage and representativity, protection of important biodiversity areas, other recognised elements of effectiveness, connectivity, and ecological effects—from the scale of individual MPAs to the MPA network scale. We conducted complementary novel analyses to supplement the review and to objectively determine where and how the MPA network can be improved. Evidence shows that South Africa’s MPAs now provide some protection to all ecoregions and 87% of ecosystem types but to less than 50% of assessed species groups. MPAs are generally well-sited, but gaps were revealed on the west coast and in estuaries, the deep sea, and two ecologically and biologically significant areas. Enforcement emerged as a key concern, and many MPAs could be improved through expansion or by increasing no-take areas. The majority of relevant papers recorded beneficial ecological effects, detectable as increases in parameters such as the abundance, biomass, sizes or reproductive output of species. Few papers examined whether ecological benefits translate into adjacent fisheries benefits, but all those that did recorded positive effects. Full protection was more effective than partial protection, with effectiveness most clearly demonstrated for vulnerable target taxa. Further research and monitoring to achieve evaluations of effectiveness are recommended, with greater focus on neglected MPAs and species. Understanding the ecological connectivity between MPAs, an important dimension for climate-change adaptation and hence for the persistence and resilience of South Africa’s marine biodiversity, is identified as a key area for future research and inclusion in MPA planning.

Keywords: biodiversity protection, connectivity, conservation, EBSA criteria, fish, fishing, invertebrates, NEOLI features, protected area network, spillover

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Introduction

The biodiversity and ecological integrity of many marine ecosystems are being threatened (Worm et al. 2006; O’Hara et al. 2019). For this reason, many marine habitats, species and ecosystem functions have been granted protection from human pressures in marine protected areas (MPAs), a tool that is increasingly favoured as a response to declines in marine biodiversity (Beaugrand et al. 2015; McCauley et al. 2015). The Convention on Biological Diversity’s (CBD’s) definition of a marine and coastal protected area is “any confined area within or adjacent to the marine environment, together with its overlying waters and associated flora, fauna, and historical and cultural features, which has been reserved by legislation or other effective means, including custom, with the effect that its marine and/or coastal biodiversity enjoys a higher level of protection than its surroundings” (CBD 2004, p 2). Many
countries have declared MPAs towards meeting their obligations as signatories to international agreements, notably to achieve the CBD’s Aichi Biodiversity Target 11: to protect 10% of coastal and marine areas by 2020 (CBD 2010), which is also echoed in the CBD Sustainable Development Goal (SDG) 14.5 (UN General Assembly 2015).

South Africa has an unusually high proportion of endemic marine species, averaging 28% across all taxa, which accentuates the national responsibility for conservation (Griffiths and Robinson 2016). In addition to conserving natural marine ecosystems and biodiversity, MPAs are advocated as a means to rebuild depleted fish stocks, improve fishery yields and provide insurance against stock collapse (Atwood et al. 1997; Roberts et al. 2003b; Shanks et al. 2003; Halpern et al. 2006; Horigue Gaines et al. 2003; Palumbi 2003; Roberts et al. 2003a, 2003b; Shanks et al. 2003; Palumbi 2003; Roberts et al. 2003a, 2003b; Shanks et al. 2003; Palumbi 2003; Roberts et al. 2003a, 2003b; Shanks et al. 2003; Palumbi 2003; Roberts et al. 2003a, 2003b; Shanks et al. 2003; Palumbi 2003; Roberts et al. 2003a, 2003b; Shanks et al. 2003; Palumbi 2003; Roberts et al. 2003a, 2003b; Shanks et al. 2003; Palumbi 2003; Roberts et al. 2003a, 2003b; Shanks et al. 2003; Palumbi 2003; Roberts et al. 2003a, 2003b; Shanks et al. 2003; Palumbi 2003; Roberts et al. 2003a, 2003b; Shanks et al. 2003; Palumbi 2003; Roberts et al. 2003a, 2003b; Shanks et al. 2003; Palumbi 2003; Roberts et al. 2003a, 2003b; Shanks et al. 2003; Palumbi 2003; Roberts et al. 2003a, 2003b; Shanks et al. 2003; Palumbi 2003; Roberts et al. 2003a, 2003b; Shanks et al. 2003; Palumbi 2003; Roberts et al. 2003a, 2003b; Shanks et al. 2003; Palumbi 2003; Roberts et al. 2003a, 2003b; Shanks et al. 2003; Palumbi 2003; Roberts et al. 2003a, 2003b; Shanks et al. 2003; Palumbi 2003; Roberts et al. 2003a, 2003b; Shanks et al. 2003; Palumbi 2003; Roberts et al. 2003a, 2003b; Shanks et al. 2003; Palumbi 2003; Roberts et al. 2003a, 2003b; Shanks et al. 2003; Palumbi 2003; Roberts et al. 2003a, 2003b; Shanks et al. 2003; Palumbi 2003; Roberts et al. 2003a, 2003b; Shanks et al. 2003; Palumbi 2003; Roberts et al. 2003a, 2003b; Shanks et al. 2003; Palumbi 2003; Roberts et al. 2003a, 2003b; Shanks et al. 2003; Palumbi 2003; Roberts et al. 2003a, 2003b; Shanks et al. 2003; Palumbi 2003; Roberts et al. 2003a, 2003b; Shanks et al. 2003; Palumbi 2003; Roberts et al. 2003a, 2003b; Shanks et al. 2003; Palumbi 2003; Roberts et al. 2003a, 2003b; Shanks et al. 2003; Palumbi 2003; Roberts et al. 2003a, 2003b; Shanks et al. 2003; Palumbi 2003; Roberts et al. 2003a, 2003b; Shanks et al. 2003; Palumbi 2003; Roberts et al. 2003a, 2003b; Shanks et al. 2003; Palumbi 2003; Roberts et al. 2003a, 2003b; Shanks et al. 2003; Palumbi 2003; Roberts et al. 2003a, 2003b; Shanks et al. 2003; Palumbi 2003; Roberts et al. 2003a, 2003b; Shanks et al. 2003; Palumbi 2003; Roberts et al. 2003a, 2003b; Shanks et al. 2003; Palumbi 2003; Roberts et al. 2003a, 2003b; Shanks et al. 2003; Palumbi 2003; Roberts et al. 2003a, 2 Kirkman, Mann, Sink, Adams, Livingstone, Mann-Lang, Pfaff, Samaai, van der Bank, Williams and Branch
et al. 2014; Fredston-Hermann et al. 2018). These principles include coverage of all ecosystem types in all biogeographic regions (ecological representivity), replication of ecological features in the network as an insurance against loss, connectivity, and protection of areas of particular importance for biodiversity and ecosystem services (CBD 2009a). Most are reflected in the CBD’s Aichi Biodiversity Target 11 on protection (CBD 2010), and all are relevant to assessing the design effectiveness of South Africa’s MPA network. This review deliberately excludes the contentious issue of MPA targets, both political targets that aim to stretch governments and stakeholders to advance protection, and also the large body of scientific literature that supports such targets, which is beyond the scope of this review.

The adequacy and viability of individual sites under protection are essential MPA design components, and in this regard features of MPAs that promote effective protection have been proposed (e.g. Claudet et al. 2008; McLeod et al. 2009; Gill et al. 2017). Several of these are contained in the NEOLI features put forward by Edgar et al. (2014). In their global assessment linking MPA features to proven outcomes for effective protection, they identified five key features that improve MPA effectiveness, specifying that an MPA should ideally meet at least four of them. The five features include that an MPA must be No-take, well Enforced, Old (>10 years), Large (>100 km²), and include reefs that are Isolated by deep water or sand (Edgar et al. 2014). A separate global meta-analysis of 324 reefs, including 41 protected areas, also provided strong empirical evidence for the positive effects of age, size and compliance on the effectiveness of MPAs in terms of the extent of recovery towards pristine conditions (McClanahan and Graham 2015). We therefore considered the NEOLI framework to be a useful one that we could adapt for the South African context, as an exercise to help identify where improvement can be made in the design and management of MPAs to achieve desired conservation goals.

Outcomes of MPA protection may be exemplified by changes in parameters such as the abundance and sizes of species inside MPAs (Polunin and Roberts 1993; Francis et al. 2002; Götz et al. 2008a; Richardson et al. 2011), or changes in catches in adjacent areas arising from the spillover of adults or enhancement of larval export (McClanahan and Mangi 2000; Russ et al. 2004; Halpern et al. 2009; Harrison et al. 2012; Kenwath et al. 2013). There have been multiple studies of such MPA effects conducted in South Africa, which are reviewed here.

We employ a dual approach to evaluate ecological effectiveness of MPAs in South Africa. First, all literature relevant to the different aspects of MPA ecological effectiveness is reviewed comprehensively. Second, novel analyses are used to complement the findings of the literature review, to assist with identifying patterns in the results, or to identify obvious gaps that emerged from the review. This gives rise to both review content and novel analyses and statistics being presented together in sections below, although we make it clear which components of our review constitute results from our analyses and which are derived from reviewed articles. Following this introduction, we outline the general methods adopted, and then structure the results and discussion under five main themes (spatial coverage and ecological representivity, areas of biodiversity importance, NEOLI features, connectivity, and ecological effects), and end with our conclusions and recommendations.

Methods

Through internet searching with appropriate key words using Google Scholar, we identified and reviewed relevant research papers, books, reports and theses containing evidence for the effectiveness (or lack thereof) of specific South African MPAs in terms of protecting marine biodiversity, enabling recovery of marine resources and providing benefits to fisheries. This included assessing ecological effects of MPAs as measured for individual species or species assemblages, and detectable in the form of quantifiable changes in parameters such as abundance, biomass, size or reproductive output of populations or communities, derived from comparisons made inside versus outside MPAs, or before and after proclamation. Where applicable, protection benefits of other sites such as fishery closures to benefit seabird foraging were included. The focus of this article is the marine territory of mainland South Africa, extending from the shore to the outer limit of the EEZ. Estuaries are briefly considered, but a comprehensive analysis of estuarine protection is reported in van Niekerk et al. (2019). The Prince Edward Islands (PEI) MPA in South Africa’s Southern Ocean territory is not included.

For the scale of the MPA network, we drew largely from the recent national biodiversity assessment (Sink et al. 2019) and made use of information from several systematic conservation plans (e.g. Clark and Lombard 2007; Sink et al. 2011; Chalmers 2012; Harris et al. 2012, 2019; Majiedt et al. 2013). The systematic conservation plans identified gaps in South Africa’s marine biodiversity protection and provided the basis for the recent expansion of the existing MPA network (DPME 2015), while national biodiversity assessments include regular appraisals of MPA coverage, including different ecoregions and ecosystem types (ecological representivity). A regional process to describe ecologically or biologically significant marine areas (EBSAs) (Harris et al. 2019; Kirkman et al. 2019) according to CBD guidelines (CBD 2009b) provided a useful indicator, through spatial overlay of EBSAs with MPAs, to assess whether MPAs are appropriately situated to ensure the persistence of marine biodiversity and associated ecosystem services.

We also scored each of South Africa’s MPAs according to the NEOLI features, namely protection level, enforcement, age, size, and isolation. In their original paper, Edgar et al. (2014) focused on effectiveness for the protection of reef-fish assemblages, and as such not all of their features are applicable to all South Africa’s MPAs, especially the last-named feature (isolation), which we rated in terms of isolation of the MPA from adverse human influences. We therefore modified the criteria for two of the features to make them more appropriate. Details of this and of how scoring was conducted in the South African context are provided in Supplementary Table S1.
Table 1: Overview of marine protected area (MPA) protection in South Africa since 2019, for the marine territories of the mainland and of the Prince Edward Islands (PEIs), and the combined marine territories: numbers of MPAs, MPA area coverage, and MPA no-take area coverage, in absolute terms and as a percentage of the marine territory. Pre-2019 values for the combined mainland and marine territory are given in parentheses.

| No. of MPAs | Marine territory area (km²) | MPA area (km²) | % MPA protection | MPA no-take area (km²) | % MPA no-take protection |
|-------------|-----------------------------|----------------|------------------|------------------------|-------------------------|
| Mainland (pre-2019) | 41 | 1 072 151 | 57 805 | 5.4 | 32 181 | 3.0 |
| PEIs | 25 | 474 897 | (6 436) | (0.5) | (1 623) | (0.17) |
| Total (pre-2019) | 62 | 1 547 048 | 227 898 | 14.7 | 60 675 | 3.9 |

For comparisons or calculations that required GIS, we used ESRI’s ArcMap 10.3.1, applying a modified Albers equal-area conic projection, specific to South Africa. These comparisons and calculations included determining replication of ecosystem types in multiple MPAs, and calculation of nearest-neighbour distances between MPAs for connectivity analyses. Shapefiles for MPAs were sourced from the South African Protected Areas Database (SAPAD), available at the Environmental GIS website (https://egis.environment.gov.za/) of South Africa’s Department of Forestry, Fisheries and the Environment (DFFE); shapefiles for EBSAs were sourced from the EBSA Portal (https://cmr.mandela.ac.za/EBSA-Portal) of Nelson Mandela University’s Institute for Marine and Coastal Research; and the map of South Africa’s marine ecosystem types from the Biodiversity GIS website (https://www.sanbi.org/link/bgis-biodiversity-gis/) of the South African National Biodiversity Institute (SANBI). Other sources of MPA information included relevant government acts and regulations (https://www.environment.gov.za/legislation/actsregulations), and MPA management plans and fact sheets obtainable at the MPA Forum website (http://mpanet.org.za/marine-protected-areas/#).

Results and discussion

Spatial coverage and ecological representivity

The declaration of 20 new or expanded MPAs in 2019 added 51 477 km² of protected area estate to South Africa’s mainland marine territory in MPAs to 5.4% (Table 1). The creation of the new MPAs met Operation Phakisa’s target of achieving 5% protection (DPME 2015) and took the country just over half way towards the 10% target of the CBD (CBD 2010) and a quarter of the way to the NPAES target (NPAES 2010). There are many types of management zones in the expanded MPA network, including multiple forms of ‘no-take’ zones (restricted, sanctuary and wilderness zones) and many iterations of ‘controlled’ zones where restrictions apply to benthic versus pelagic components of the environment, certain species or certain types of fishing, fishing gear, fishing sectors or practices (such as catch-and-release) (Figure 1; Supplementary Table S2).

In CBD terms (CBD 2009a), ecological representivity is adequately captured in a network when it protects an acceptable sample of all biodiversity. Lombard et al. (2004) assessed representivity of species in South Africa’s MPA network (at that stage encompassing coastal and nearshore areas only) in the early 2000s. Data for the species distribution ranges of more than 1 200 coastal fish species (Turpie et al. 2000), over 2 500 intertidal invertebrate species (Emanuel et al. 1992; Awad et al. 2002) and approximately 800 seaweed species (Bolton and Stegenga 2002; Bolton et al. 2004) were assigned into 50- or 100-km-long coastal strips. The analyses indicated that approximately 98% of the fish species and 90% of both shallow-water invertebrates and seaweeds occurred in coastal strips that included MPAs. Anderson et al. (2009) and Daru and le Roux (2015), respectively, also showed that several of the coastal MPAs are well-positioned for protection of seaweed and seagrass species.

A limitation of the approach of Lombard et al. (2004) was that several of the coastal MPAs do not occur within MPAs in that strip even if their actual presence in the MPA was sometimes uncertain. Solano-Fernandez et al. (2012) provided a more accurate estimate of the level of protection of fish communities by using point-location data. This included over 700 fish species caught in four different fisheries inclusive of offshore areas (trawling, boat-angling, shore-angling and estuarine seine-netting). The results were more pessimistic than those of Lombard et al. (2004), showing that only 49% of the taxa had actually been recorded in the 14 coastal MPAs that were sampled. Fishes that occurred in the offshore trawl grounds of the west and south coasts, the fishes of the uThukela Bank (caught by crustacean trawl fisheries), and fishes of the estuaries in southern and central KwaZulu-Natal Province were identified as most in need of protection.

Benefits to fish species that accrued from the 2019 expansion of the MPA network to offshore areas were estimated in a study by G Logan (University of Cape Town, unpublished data),1 while the proposed network was still in the negotiation phase. The study, which combined seven standardised fisheries datasets to evaluate the distribution of ichthyofaunal communities within MPAs of the Agulhas and Southern Benguela ecoregions, indicated that the proposed expansion would increase representation of fish species in the MPA network from 27% to 39%.

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1Logan G. 2018. Assessment of the effectiveness of South Africa’s future marine protected areas at representing ichthyofaunal diversity on the continental shelf. BSc Honours project, University of Cape Town, South Africa.
(Solano-Fernandez et al. 2012) to about 50%, and would increase representation of distinctive fish communities from 19% (Solano-Fernandez et al. 2012) to 35%. Purdon et al. (2020) used presence data of nine odontocete species to predict their occurrence in South African waters using ensemble modelling. They found that odontocete habitat was poorly protected by the MPA network pre-2019 (<2% of modelled occurrence habitat) but was more than doubled (>5%) in the expanded network.

Knowledge of the spatial distribution patterns of some other groups of marine species in South Africa, especially invertebrates, is much less complete (Awad et al. 2002). In particular, information on the diversity and distribution of taxa generally declines from the coast to offshore (Gibbons et al. 1999). Thus, there are considerable gaps in our understanding of marine biodiversity patterns. For this reason biogeographic units mapped on the basis of physical habitat conditions are typically used as surrogates for

Figure 1: South Africa’s marine protected area (MPA) boundaries and zones (excluding the Prince Edward Islands MPA), overlaying the six marine ecoregions (Sink et al. 2019) within the outer boundary of the exclusive economic zone. The three categories of protection shown are a simplification of multiple types of zones in the South African MPA network, including several forms of no-take zones (restricted, sanctuary and wilderness zones) and many iterations of controlled zones where restrictions apply to benthic versus pelagic components of the environment, certain species or certain types of fishing, fishing gear, fishing sectors or practices (such as catch-and-release). Also, fine-scale near-shore zonation of some coastal MPAs is not visible on the map. Greater detail on different management zones can be obtained from the South African Protected Areas Database (SAPAD), available at the Environmental GIS website (https://egis.environment.gov.za)
biodiversity in broad-scale marine biodiversity assessments in South Africa (e.g. Sink et al. 2012, 2019; Livingstone et al. 2018), an approach that has increasingly been employed globally (e.g. Lourie and Vincent 2004; Briggs and Bowen 2012). In the South African biodiversity assessments, the principal biogeographic units used are ecoregions mapped at the national scale, and ecosystem types based on biotic and abiotic factors, which are subsets of ecoregions in a hierarchical classification system (Sink et al. 2019).

Protection levels of the ecosystem types are determined as indicators for ecological representivity of the MPA network in South Africa’s periodically conducted national biodiversity assessment (Sink et al. 2012, 2019). Ecosystem types are categorised according to the proportions of each that overlap with protected areas, taking into account site-specific characteristics, namely the relative condition (intactness) of areas under protection and the degree of protection afforded by the MPAs (e.g. no-take versus partially protected areas where some extractive use is allowed). The protection-level categories are Well Protected (≥20% of an ecosystem type in good condition is protected), Moderately Protected (≥10 and <20% of ecosystem type is protected), Poorly Protected (≥0.2 and <10% of ecosystem type is protected) and Not Protected (<0.2% protected). The 20% target corresponds with the recommended level of coverage of distinct habitat (or ecosystem) types in MPA networks for adequate representation, considered by McLeod et al. (2009) to be 20–30%, and is in line with South Africa’s medium-term target for MPA protection of the mainland marine territory, which is 20% by 2028 (NPAES 2010).

In the most recent national biodiversity assessment (Sink et al. 2019), protection level was calculated for each of the 150 recognised marine ecosystem types, to compare protection levels before and after the expansion of the MPA network (Figure 2). Prior to the promulgation of new areas for protection, only 20% of marine ecosystem types were Well Protected by the 25 (mainly coastal) MPAs then in existence, while 47% of types were Not Protected. Of the 70 ecosystem types that were Not Protected, 51 received their first protection with the declaration of the new (predominantly offshore) MPAs, reducing the number of ecosystem types within the Not Protected category from 47% to 13%. Thirteen previously Not Protected and four Moderately Protected ecosystem types advanced to Well Protected, an improvement from 20% to 31% of ecosystem types now falling within the latter category, and 87% of the 150 ecosystem types now have at least some representation in the MPA network. However, with only 50% or less of taxa or communities that have been examined being represented in the MPA network (Purdon et al. 2020; G Logan, unpublished data), there is apparently a mismatch between species distributions and ecosystem types. Further research, especially of offshore areas, is needed to address such limitations and refine the ecosystem-classification mapping.

The expansion substantially increased representation of all ecoregions in the MPA network and addressed some of the gaps in protected area coverage, especially on the west coast and offshore (Figure 1). However, coastal protection is still skewed to the east coast, and most ecosystem types that are still Not Protected occur in the deep sea, particularly on the continental slope, with most of the slope and abyssal ecosystem types being still Poorly Protected (Sink et al. 2019). Van Niekerk et al. (2019) and Whitfield et al. (2020) have independently identified that South African estuarine ecosystems and species are underrepresented in MPAs. In addition to providing first protection for ecosystem types that are Not Protected, increasing the protection levels of Poorly Protected and Moderately Protected ecosystem types should be considered for future MPA expansion. Furthermore, only 28% of ecosystem types are represented in three or more MPAs. Three is the minimum number recommended to provide replication as insurance against loss of a habitat due to a single disturbance event and to permit replenishment after such a disturbance (Salm et al. 2006; Green et al. 2007; McLeod et al. 2009). Ensuring adequate replication and sufficient connectivity among habitats of a given type are therefore additional considerations for further MPA expansion.

Although most of South Africa’s MPAs provide some protection to the pelagic zone within their bounds, none are dedicated specifically to pelagic ecosystems. This reflects the global situation, and Game et al. (2009) regard pelagic ecosystems as a ‘missing dimension of ocean conservation’ because even though pelagic ecosystems occupy 99% of the ocean’s volume, there are fewer MPAs for pelagic ecosystems than for any other ecosystem. In South Africa, 12 of the 41 MPAs in fact permit fishing (either within all or part of the MPA) specifically directed at pelagic species, including ‘game fish’ or small pelagic shoaling fish, while protecting benthic species and communities. The rationale for this includes that pelagic fishing does not impact the
benthic habitat targeted for protection, and the assumption that many pelagic species are unlikely to benefit from MPAs because they are too mobile (Gell and Roberts 2003). The latter is one of the main criticisms of the concept of pelagic MPAs (Kaplan et al. 2010). However, some South African studies, in particular at the Langebaan Lagoon MPA (now incorporated into the West Coast National Park), have shown that even a small MPA can provide protection benefits to highly mobile fish or shark species (Attwood et al. 2008; Kerwath et al. 2008a; Hedger et al. 2010; da Silva et al. 2013) (see Supplementary Table S3). Game et al. (2010) countered the criticism of pelagic MPAs by arguing that they should not focus on the management of single stocks, but rather on important pelagic features such as spawning grounds or on areas experiencing frequent eddies and upwelling that benefit multiple species. Grantham et al. (2011) have gone as far as advocating areas that should be preferred for an integrated pelagic and benthic protected-area design, based on assessments of productivity, upwelling, eddies and filaments, retention, the abundances and variability of copepods, anchovy and sardine, and coastal foraging distances of birds.

**Areas of biodiversity importance**

Historically, MPAs in South Africa were situated predominantly as extensions of land-based reserves or were implemented to protect commercially important fish species or intertidal habitats (Attwood et al. 1997). Since then, numerous studies have described the biodiversity or biodiversity features that are currently protected by various MPAs (e.g. Bennett and Attwood 1993; Attwood et al. 1997; Hanekom et al. 1997; Götz 2005; Sink et al. 2005; Mann et al. 2006; Ceilier et al. 2007; Götz et al. 2009a, 2009b; Olbers et al. 2009; Hanekom 2011; Currie et al. 2012; Floros et al. 2012; Solano-Fernandes et al. 2012; Venter and Mann 2012; De Vos et al. 2014, 2015; Roberson et al. 2015; Attwood et al. 2016; Heyns et al. 2016; Tucker et al. 2017; Joshua et al. 2018; Osgood et al. 2019; Purdon et al. 2020). Some studies, especially of ‘iconic’ marine species that are listed as Threatened or Protected in South Africa (RSA 2017), further describe how species utilise the MPAs (e.g. Hughes 1973; Crawford et al. 2000; Elwen and Best 2004; Huisamen et al. 2011; Dicken et al. 2013; Conry 2017; Daly et al. 2018; Vargas-Fonseca et al. 2018). For the most part, however, these studies do not provide evidence of whether MPAs are ideally situated to protect areas of importance for biodiversity.

Consideration of MPA locations in relation to ecologically or biologically significant marine areas (EBSAs) can provide an indication of how appropriately MPAs are situated in relation to areas of importance for biodiversity. EBSAs were described for South Africa, as part of CBD regional processes, in 2012–2013 (Kirkman et al. 2019; https://cmr.mandela.ac.za/EBSA-Portal/South-Africa), and were endorsed by the CBD Conference of the Parties in 2014 (CBD 2014). Seven criteria whereby sites of potential EBSAs are evaluated include (among others) their importance for biological productivity or biodiversity, for the life-history stages of species, and for threatened, endangered or declining species and/or habitats (CBD 2009b). Thus, EBSAs include critical areas for the persistence of marine biodiversity such as nursery grounds, spawning aggregations and breeding and feeding areas for threatened species, and they have been defined as geographically or oceanographically discrete areas that provide important services to one or more species/populations or to the ecosystem as a whole when compared with surrounding areas or areas of similar ecological characteristics (CBD 2009b).

Our study showed that overlay of the 18 EBSAs in the mainland’s marine territory with the existing MPAs reveals that every MPA in the network occurs within, or overlaps with, EBSA boundaries (Figure 3). This would be expected for the MPAs recently declared (in 2019), given that EBSA status of areas contributed to their positioning and motivation. However, many of the MPAs established pre-2019 have been regarded as being designated with little planning or understanding of their potential protection benefits (Attwood et al. 1997; Lemm and Attwood 2003). The fact that they are all represented in the country’s revised EBSA network implies that from a national protection perspective they are actually well situated. New MPAs to protect the only two EBSAs not represented in the MPA network (i.e. Orange Cone EBSA and Mallory Escarpment and Trough EBSA) (Figure 3) are priorities for further MPA expansion.

**NEOLI features**

Scores that we determined for each of the 41 MPAs under consideration for the five NEOLI features are shown in Supplementary Table S2 and summarised in Figure 4. The MPAs that overall scored the highest against the features (four High scores and one Medium score) were all coastal, older, relatively large MPAs that are no-take or include considerable no-take areas, and that are relatively isolated from dense human settlements or detrimental human activities. These include the Tsitsikamma, De Hoop, Pondoland and iSimangaliso MPAs, the last of which was expanded in a new declaration in 2019. In contrast are some of the smaller ‘old’ MPAs that are not no-take (e.g. Rocherpan), are close to population centres or intensive human activities (e.g. Helderberg, Marcus Island) and scored low for enforcement (e.g. Helderberg and Rocherpan). New MPAs by default scored lowest for age and for enforcement, which has yet to be properly planned and implemented.

Considering the ‘no-take’ (N) component of NEOLI, of the 41 MPAs that currently exist within the marine territory of mainland South Africa, nine MPAs (22%) are entirely no-take, an equivalent percentage do not include any no-take zone, and the remaining MPAs have at least one no-take zone along with one or more controlled zones. The total no-take area is 32 181 km², which is only 3% of the mainland’s marine territory. Benefits of no-take areas for recovery and management of target species in South Africa have been pointed out by several authors (e.g. Attwood 2003; Cowley et al. 2008), and evidence for the ecological effects of no-take protection that we have derived from the literature is summarised in Supplementary Tables S3 and S4 and discussed below in the section ‘Ecological effects’. At the time of writing, re-zonation of three of the older MPAs in the Western Cape Province, namely Robberg MPA, Goukamma MPA and Betty’s Bay MPA, to introduce or increase no-take area, is under consideration following
gazetting of the proposals for public comment in 2017 (https://www.environment.gov.za/legislation/gazetted_notices).

Such re-zonation of existing MPAs, and advancing no-take protection under future MPA expansion, will improve MPA effectiveness in terms of conservation.

The ‘enforcement’ (E) component was based for the most part on self-scores of MPA managers, and as such was considered to be one of two features that were scored most subjectively (the other being Isolation). Nevertheless, this was the only feature for which there were no High scores, which is considered to be a realistic reflection of the state of enforcement in South Africa’s MPAs (Brill and Raemaekers 2013; Chadwick et al. 2014; Adams and Kowalski 2021).

Regarding MPA age (‘Old’), at least 10 years of protection is required for positive results from an MPA according to Edgar et al. (2014), although there are conflicting results from various studies on the relationship between the age of an MPA and the effectiveness of protection. Whereas some studies (e.g. Russ and Alcala 2004; Claudet et al. 2008) have shown that long-term protection is needed for positive results, others (e.g. Halpern and Warner 2002) found that biological responses inside marine reserves can develop quickly (within 1–3 years) and last through time. While scores for age (O) can only improve for the new MPAs, age can contribute to effectiveness only if adequate enforcement is implemented and upheld (McClenahan and Graham 2015).

Figure 3: South Africa’s marine protected area (MPA) network (excluding the Prince Edward Islands MPA), overlaying the updated network of described ecologically or biologically significant marine areas (EBSAs). The numbers on the map identify the MPAs, and the name labels are the EBSAs. ABNJ = areas beyond national jurisdiction.
With respect to MPA size (‘Large’), our results show that of the 41 MPAs in South Africa’s mainland EEZ, 28 (68%) are greater than 100 km$^2$ in area, thus meeting the recommended minimum size specified by Edgar et al. (2014), and five MPAs (12%) are less than 5 km$^2$ in area (Figure 5), indicating potential concern in terms of size recommendations. The appropriate size for MPAs is contentious and has been the subject of numerous theoretical and empirical studies. Underlying the debate are considerations about the minimum size required to protect biodiversity and ecological processes, and the greater costs and user conflict associated with increased size (McLeod et al. 2009). While there is no ideal size applicable to all MPAs, and size should be determined by the specific management objectives for each MPA and the species and habitats identified for protection (McLeod et al. 2009; Roberts et al. 2003a), there has been considerable debate over ‘single large or several small’ protected areas or ‘SLOSS’ (Atwood and Bennett 1995). It is often assumed that larger reserve sizes will always be ‘better’ (see Halpern 2003) because they have less edge effects, a larger core to retain mobile animals and can house larger populations, yet several small areas may dilute the risk of a local catastrophe and house a greater variety of species owing to differences in habitat among the areas. The ‘single large’ approach has been supported by some related empirical studies (e.g. Claudet et al. 2008) but not by all (e.g. Halpern 2003; Guidetti and Sala 2007). Taking into account findings on dispersal distances of organisms or genetic patterns of isolation by distance, Largier (2003), Palumbi (2003), Shanks (2009) and von der Heyden (2009) have advocated that networks of smaller, well-connected MPAs are preferable to large standalone MPAs, especially in coastal areas (Shanks et al. 2003; Wright et al. 2015). According to Hastings and Botsford (2003), fisheries goals of maximising adult spillover and larval export to areas outside MPAs—to augment fisheries yields there—require that reserves should be as small as practically possible. Even small no-take areas of MPAs such as Castle Rock in False Bay, with a maximum length of 3.25 km, effectively protect resident fish (Kenwath et al. 2007a, 2008b), although they are too small to provide much benefit in terms of spillover (Lechanteur 1999). Based on the finding that the majority of larvae of benthic organisms either exhibit short-distance (<1 km) or long-distance (>20 km) dispersal strategies, Shanks et al. (2003) recommended that, as a minimum, an MPA diameter of 4–6 km would be sufficient to contain larvae or propagules of short-distance dispersers, and that MPAs should be spaced 10–20 km apart to account for long-distance dispersal. Others have recommended minimum sizes of between 10 and 20 km diameter (Friedlander et al. 2003; Fernandes et al. 2005; Mora et al. 2006; McLeod et al. 2009), the 10-km diameter minimum
being similar to the 100-km² area threshold specified by Edgar et al. (2014).

The ‘Isolation’ feature (I), revised for the South African context, was perhaps the most abstract feature to score in our study, given the difficulty of contextualising the various pressures that are in the vicinity of different MPAs, their potential impacts, and how the risks depreciate with distance from the MPA. As could be expected, given the concentration of human numbers and activities in coastal areas, older (mostly coastal) MPAs generally scored lower than the recently declared MPAs, which are mainly offshore (Figure 4).

**Connectivity**

From the above it is clear that consideration of size should also take connectivity into account, which in the marine realm can be defined as the natural linkage between marine habitats (Shanks et al. 2003; Kerwath et al. 2013; Teske et al. 2015). Connectivity between MPAs is considered to be critical if they are to play an effective role in climate-change adaptation, by maintaining dispersal, gene flow and replenishment of local populations, genetic continuity and protection of the full spectrum of genetic diversity (von der Heyden 2009). However, although indicators have been developed to assess connectivity of terrestrial protected areas (e.g. the protected connected land [ProtConn] indicator: Saura et al. 2017, 2018), these have yet to be adapted for MPA connectivity (Bacon et al. 2019).

Generally, the concept of connectivity is less clearly defined for the marine than the terrestrial realm, including how to accommodate connectivity patterns under changing climate (Roberts et al. 2017). Oceans are fundamentally more connected than land because of water movements and a relative scarcity of barriers to movement. Marine life has adapted to this fluid environment in that the majority
of marine species have broadly dispersing larvae or propagules, or are nutritionally dependent on planktonic forms. In addition, whereas sites on land can usually be assigned only one or a few land-use categories (e.g. agriculture, mining), numerous activities may occur at the same place in the ocean (e.g. shipping, fishing, tourism, etc.) without necessarily precluding connectivity (Harris et al. 2020). It has thus been argued that accounting for connectivity in marine planning relates more to the sizing and spacing of MPAs in networks than to the existence of ecological corridors allowing exchanges among populations (Shanks et al. 2003; McLeod et al. 2009).

Our analysis of the combination of MPA size and nearest-neighbour distances between MPAs highlights those MPAs that are both very small and remote from other MPAs (Figure 5). Of the five smallest MPAs, Jutten, Malgas and Marcus islands are in very close proximity to each other in Saldanha Bay (Figure 1), Rocherpan is both extremely small and remote from the nearest MPA, while the small Helderberg MPA is 10–20 km from the nearest MPA. Other small MPAs such as Betty’s Bay and Stilbaai are even larger distances from their nearest neighbouring MPAs. All of these MPAs are on the south and west coasts of South Africa. Our analysis shows that the average distance between any one MPA and its nearest neighbour was estimated at 35 (SD 39.5) km. Distances of no more than 15–20 km between MPAs have been recommended (Shanks et al. 2003; Morá et al. 2006; Mann et al. 2016a) to ensure self-replenishment and transfer of larvae or propagules among MPAs for organisms with different modes of dispersal, based on estimates that exist for dispersal distances of the early stages of benthic organisms with various life histories and dispersal strategies. However, we found that only 41% of the 41 MPAs occur within a 20-km radius of each other, with 32% within a 10-km radius. Such a rule-of-thumb comparison for the distribution of MPAs from each other naturally generalises, and does not take into account factors such as the oceanographic conditions of the South African seascape, including the effects of advection and retention by currents on larval dispersal and the implications for MPA effectiveness (Gaines et al. 2003), or biogeographical barriers to genetic connectivity (von der Heyden 2009; Teske et al. 2011; Phair et al. 2021). However, it does underline challenges regarding MPA connectivity that have been previously highlighted (e.g. von der Heyden 2009), especially for coastal MPAs of the west and south coasts, as discussed below.

Based on mitochondrial DNA datasets for a phylogenetically diverse range of rocky-shore and reef-dwelling marine species, Wright et al. (2015) showed that the South African MPA network at the time was poorly connected from a genetic perspective. In particular, short generational dispersal distances (<10 km for most studied taxa) and biogeographical barriers to dispersal meant that the design of the (then coastal) MPA network may not be effective in protecting evolutionary processes. The authors recommended that MPAs should be more closely spaced to increase connectivity. At the time, average distance between MPAs was ~110 km (von der Heyden 2009). While our data show that this distance has decreased to nearly 40 km post-2019, it still exceeds that considered to be optimal for genetic connectivity, especially on the west and south coasts where only one new coastal MPA was declared in 2019 (Figure 1). Furthermore, for the west and south coasts, several sites have been identified as being in need of protection, based on genetic structure or diversity (von der Heyden 2009; Tolley et al. 2019). Protection of such sites could safeguard areas of evolutionary importance, and enhance genetic connectivity along the coastline. However, until now, genetic and genomic data have not been considered in MPA planning and design in South Africa (von der Heyden 2009; Sink et al. 2019).

The dispersal capabilities of different species are ultimately the most vital determinant of the optimal distance between MPAs that will allow connectivity between genetically related meta-populations while also providing protection to genetically distinct units. Many species that are sedentary as adults have wide larval dispersal abilities. For example, Reaugh (2006) estimated dispersal distances of barnacle and mussel larvae in iSimangaliso to be respectively 25 km and 36 km. However, dispersal capabilities differ widely among species. Generally, the expectation is that efficient dispersers will have populations that are genetically homogeneous, whereas those with short-distance (or non-existent) dispersal will be genetically differentiated among populations. Ridgway et al. (2008), for example, showed that populations of the coral Pocillopora verrucosa in MPAs in Mozambique form a separate genetic cluster from those in South Africa, implying weak genetic connectivity and the need for conservation of both sets of populations to protect this genetic diversity. Conversely, Teske et al. (2010) recorded genetic uniformity among populations of the seafloor Chrysoblephus laticeps among MPAs and exploited areas spanning the whole of the species’ core range in South Africa—despite limited adult movements and high fidelity to home reefs, implying larval dispersal is important in maintaining the genetic uniformity. Such genetic homogeneity indicates that representation of the species’ genetic diversity can be achieved in a small number of reserves, and that connectivity among existing coastal MPAs will be considerable.

Dispersal abilities thus have very important implications for both connectivity and protection of genetic diversity and, hence, the positioning and spacing of MPAs. However, direct measurements of mean larval dispersal are challenging for individual species and extremely difficult for entire communities. Therefore, combinations of genetic analyses, modelling and measurements of water movements have been advocated to elucidate larval dispersal and connectivity (Götz et al. 2013; Sink et al. 2019) and inform future MPA design and other spatial-management tools. For example, modelling water movements in the vicinity of the Goukamma MPA has indicated that larvae of Chrysoblephus laticeps will disperse at least 100 km from the MPA over a period of 4 days, leading not only to self-seeding within the MPA but also supplying the adjacent coast and ensuring connectivity with the Robberg MPA and Tsitsikamma MPA, respectively 50 km and 100 km to the east, and with Stilbaai MPA 100 km to the west (Götz et al. 2013).

The combination of genetic analyses with biophysical models to estimate dispersal paths and rates has also been applied to some common rocky-shore intertidal species in South Africa (Mertens et al. 2018). Of the five species...
Investigated, three were broadcast-spawners with planktonic larvae. Of these, two species (the limpet *Scutellastra granularis* and the winkle *Oxystele tigrina*) showed limited local retention of larvae (12–13%), whereas the third species (the urchin *Parechinus angulosus*) showed virtually no retention (<0.001%). One surprise was that the urchin, despite having the greatest dispersal capacity, had the highest genetic structuring; another was that two ‘non-dispersers’ (the klipvis *Clinus superciliosus* and the starfish *Parvulastra exigua*) spanned the highest and the lowest values of genetic diversity, respectively. This illustrates that although genetic studies show great potential for refining measures of connectivity (von der Heyden 2009), until a sufficient number of species have been analysed, optimal figures for MPA spacing will be species-specific and it will not be possible to generalise about the distances that will achieve optimal connectivity among MPAs. It is anticipated that such genetic research will inform future efforts to improve the ecological connectivity of MPAs (Pujolar et al. 2013; Jenkins and Stevens 2018; Sink et al. 2019; Tolley et al. 2019; Henriques et al. 2020), especially in combination with a comprehension of water movements (Patrick et al. 2013) and an understanding of propagule dispersal and adult movements (Pujolar et al. 2013; Magris et al. 2018; Reisinger et al. 2018; Sink et al. 2019; Hindell et al. 2020).

**Ecological effects**

Numerous studies have assessed the ecological benefits or effects of South Africa’s MPAs or other sites providing some form of protection, including areas closed to fishing, or terrestrial nature reserves providing coastal protection. These studies are considerably skewed towards species that are harvested commercially, recreationally or for subsistence, with most focusing on fish or shark species (46%) followed by invertebrates (26%), with the rest covering flora (12%), iconic species (turtles and penguins; 7%) or larval phases (4%) (Figure 6). These studies are summarised in Supplementary Table S3, which focuses on studies of individual species, and in Supplementary Table S4, which focuses on studies of species assemblages. The greatest number of studies have been conducted at Tsitsikamma (mainly linefish), Dwesa-Cwebe (mainly invertebrates), De Hoop, Goukamma and iSimangaliso (also mainly fish). Comparable studies at many of the smaller MPAs are lacking. The majority (60%) of papers that were reviewed focus on individual species or suites of species (Supplementary Table S3), and most of these (64%) record beneficial ecological effects. These were detectable in the form of changes in various parameters, such as abundance, size, biomass, density, reproductive output and others, between MPAs (or no-take areas) and unprotected areas, or over time since declaration. However, there were also cases where an MPA’s effects were neutral (31%) or even negative (5%). The latter were largely attributed to: (i) unsuitable habitat in the MPA; (ii) failure of compliance; (iii) examination of species that are not fished and therefore not depleted outside the MPAs; or (iv) increases in fishery-targeted species inside no-take MPAs that diminish other species by competition or predation. Very few papers took the step of determining whether ecological benefits translated into benefits for fisheries in adjacent areas, but those that did recorded positive effects. Measures of community or ecosystem status were less often addressed (40% of papers) and were more ambiguous in their outcomes. Changes or differences in community composition were often detected inside versus outside MPAs, and the changes were interpretable as beneficial (a return towards a pristine state) in 48% of cases, neutral in 28% or negative in 24%. These overall findings are expanded on and discussed below.

A number of studies have provided evidence of residency of reef-fish species in South Africa’s MPAs, inferring that such species will benefit from protection in MPAs (Buxton and Allen 1989; Attwood and Bennett 1994; Brouwer 2002; Cowley et al. 2002; Griffiths and Wilke 2002; Brouwer et al. 2003; Attwood and Cowley 2005; Kerwath et al. 2007b; Kerwath et al. 2013; Maggs et al. 2013a; Mann et al. 2016b; Bennett et al. 2017), and empirical observations and modelling indicate that this will be the case even for small MPAs (Kerwath et al. 2007a, 2008b). Maggs and Cowley (2016), summarising the Oceanographic Research Institute’s Cooperative Fish Tagging Project (ORI-CFTP) dataset of ~7 400 recaptures of nearly 80 000 fish tagged by researchers in the no-take zones of seven MPAs (including data for several studies that are summarised in Supplementary Table S3), showed that 62–96% of recaptures were within the no-take area where the individual fish was tagged. This could still allow for considerable potential spillover, given that the MPAs had substantially greater abundances of these species than surrounding areas. Some studies have also shown evidence of protection benefits to fish or shark species that are highly mobile or migratory, in particular at Langebaan Lagoon MPA (Attwood et al. 2008; Kerwath et al. 2008a; Hedger et al. 2010; da Silva et al. 2013).

Results from numerous South African studies (summarised in Supplementary Table S3 and Figure 7a) demonstrate multiple positive effects of MPAs, as evident in increases in abundance (density, catch rates, biomass or percentage cover) or mean body size (length or mass) of populations, mainly of fishery-targeted species (Buxton and Smale 1989; Bennett and Attwood 1991, 1993; Cowley et al. 2002; Brouwer et al. 2003; King 2005; Götz et al. 2013; Maggs et al. 2013a, Mann et al. 2016b). This is consistent with numerous comparable studies from around the world (e.g. Bell 1983; García-Rubies and Zabala 1990; Polunin and Roberts 1993). Fewer studies in South Africa have addressed other parameters such as age, growth rate, condition indices, fecundity or reproductive output, and survivorship, but most that have done so also provide evidence of positive MPA effects (e.g. Buxton 1993; Lasiak 1993; Branch and Odendaal 2003; Pelc et al. 2009). Duncan et al. (2019) demonstrated that high-performance aerobic-scope phenotypes of *Chrysoblephus laticeps* are reduced in populations that are exploited, as compared with those protected in MPAs, and argue that MPAs, by harbouring individuals that have a wider range of physiological traits, provide resilience to environmental variability, including climate change. An exception to the general pattern described above of protected areas producing positive effects was a study of west coast rock lobster *Jasus lalandii*, which included Betty’s Bay MPA and rock lobster sanctuaries.
on the west coast (Mayfield et al. 2005). While the MPA was found to have positive effects for rock lobsters in terms of abundance and size, the effects of the lobster sanctuaries were either neutral or even negative, likely because they were poorly situated and contained large areas of unsuitable substrate (i.e. poor lobster habitat).

Positive effects on abundance and size were also generally apparent in studies of groups or assemblages of species in South African MPAs (e.g. Hockey and Bosman 1994; Hanekom et al. 1997; Lasiak 1998; Heyns-Veale et al. 2019) (Figure 7b; Supplementary Table S4). For example, Currie et al. (2012) and Floros et al. (2012) found that abundance or biomass of reef fish assemblages in the iSimangaliso area increases with increasing protection, from open-access reefs to partly protected areas (allowing for limited fishing and/or diving) to fully protected no-take sanctuary areas. Zones that were partially protected, in which limited fishing and/or diving were allowed, were found to be far less effective than the sanctuary areas, although to some extent this may be related to reef size and the availability of suitable reef fish habitat (Dames et al. 2020). These studies have a bearing on the effectiveness of having only partial protection of reef-fish species. In four of the five coastal MPAs that they assessed, Heyns-Veale et al. (2019) showed significant positive reserve effects for several fishery-targeted reef fish, in terms of abundance or biomass of mature individuals in no-take versus nearby fished areas. This positive ‘direct’ effect of protection was strongest for target species described as being large, carnivorous, benthopelagic species that typically occur in small groups and move within reef complexes, and the interpretation by the authors was that these species are most vulnerable to fishing and thus benefit the most from protection (Supplementary Table S4). The relative dominance of such predatory fish in Tsitsikamma’s reef assemblages, with minimal change in species composition over time, was interpreted by James et al. (2012) to imply that the fish community of South Africa’s oldest MPA had recovered to a near-pristine condition as an outcome of protection.

Benefits of no-take areas to adjacent fisheries rely on the export of fish or spawning products beyond the no-take
area (Russ and Alcala 1996; Palumbi 2001; Zeller et al. 2003; Russ et al. 2008). Several studies in South Africa, based on tag-and-release or on acoustic telemetry, have provided evidence for movements of adult fish (or squid) from no-take areas to restock adjacent harvested areas (Attwood and Bennett 1994, 1995; Sauer 1995; Brouwer 2002; Brouwer et al. 2003; Attwood and Cowley 2005; Maggs et al. 2013b; Mann et al. 2015), and Maggs and Cowley (2016) also showed that between 4% and 39% of recaptures of fish tagged in MPAs were in harvested areas, providing evidence for ‘spillover,’ although they cautioned that there was no evidence that this was because of density dependence. Dispersal of juvenile phases (e.g. eggs, larvae, young recruits) from no-take areas is increasingly being considered in MPA designs globally, in terms of re-seeding harvested areas (Tremblay et al. 1994; Murawski et al. 2000; Harrison et al. 2012; Marshall et al. 2019), or with regard to subsequent recruitment within the no-take area through retention of juveniles produced in the MPA or the import of juveniles from spawning areas (Warner et al. 2000; Gaines et al. 2003). In South Africa, few studies have taken currents into account when assessing the potential for export of these phases from MPAs to unprotected areas, and most of those that have done so have focused on Tsitsikamma (Sauer 1995; Tilney et al. 1996; Attwood et al. 2002; Brouwer et al. 2003; Roberts and van den Berg 2005). These studies have shown that reef fishes and squid are likely to be exported beyond the boundaries of the MPA through transport of ichthyoplankton and squid paralarvae, where they may benefit fished populations and adjacent fisheries.

It is predicted that the spillover or emigration of adults across the borders, and the export of pelagic eggs and larvae from any increases in spawning stocks inside an MPA, will enhance adjacent stocks especially when stocks outside the MPA are over-exploited (Roberts and Polunin 1991; Keliner et al. 2007; López-Sanz et al. 2011; Kerwath et al. 2013). Internationally, several studies have reported this effect of MPAs for fish species and assemblages (e.g. Edgar and Barrett 1999; Harrison et al. 2012; Soler et al. 2015), and associated benefits to local fisheries such as higher catches and catch rates (e.g. Roberts et al. 2001; Russ et al. 2004, 2008; Halpern et al. 2009). These studies suggest that the benefits of MPAs outweigh the loss of fishing area, but several studies of this aspect of the effectiveness of MPAs have yielded ambiguous findings (e.g. Barrett et al. 2007; Jaworski et al. 2010) and some MPAs appear to be ineffective at providing the desired fisheries benefits (e.g. Edgar et al. 2014). In South Africa, some studies of fishes or intertidal invertebrates have shown increased abundance of target species close to the boundaries of MPAs compared with areas further way, demonstrating benefits for fishers or harvesters (King 2005; Pelc et al. 2009; Cole et al. 2011). A definitive study by Kerwath et al. (2013) provided evidence of a rapid increase in the catch rates of Chrysoblephus laticeps in the vicinity of the Goukamma MPA (which is closed to boat-angling) following its proclamation. This is in contrast to persistently low catch rates in areas elsewhere along the coast that are not in the vicinity of MPAs, and accords with the prediction that spillover benefits are most likely to be detected

Figure 7: Results from a literature review showing published MPA effects at the level of (a) individual species and (b) species assemblages. Details of the studies and their findings are provided in Supplementary Tables S3 and S4, respectively. Effects were categorised as positive (+), weak, neutral, insignificant or inconclusive (O), or negative (×). Number of cases for (a) represents the sum of species per MPA for which effects were tested, and for (b) represents the sum of species groups or assemblages per each MPA for which effects were tested, with a distinction between fishery-targeted species (TS) and rarely targeted or non-targeted species (R/NTS). The parameter Abundance is inclusive of abundance, density, catch rate, biomass or percentage cover; Size represents either length or mass; GR = growth rate; Fec. = fecundity; Mat. = maturity; Repr. = reproductive output.
where a fishery is depleted (Buxton et al. 2014) but where suitable habitat exists in the MPA vicinity. The increase at Goukamma continued after five years (the time-lag expected for larval export to become effective), doubling the pre-MPA CPUE after 10 years. This increase was attributed to a succession of spillover of adult fish from the MPA followed by a recruitment boost caused by increased larval dispersal. The study also found no evidence to suggest that a fisher’s profits were in any way affected by the MPA, as might have been expected through initially reduced catch rates or increased distances that fishers needed to travel, which are common economic arguments against the use of MPAs as fishery management tools (Sladek-Nowlis and Roberts 1990). By demonstrating a positive effect, this study should improve the acceptance of MPAs by fishers as a viable fishery-management option, but this will need to be communicated more widely.

While intertidal species that are targeted for harvesting provide for relatively straightforward comparisons between harvested and unharvested sites, the findings of such studies have not always been so straightforward in South Africa, with the reserve’s effects being weak or inconclusive in some cases, possibly related to ineffective compliance (e.g. Cole et al. 2011; Nakin et al. 2014, 2016). It has also proved difficult to generalise about reserve effects on the growth and mortality of different limpet species, as the responses appeared to be site-specific (Lasik 2006) or species-specific (Nakin et al. 2012), with species that are not harvested regularly showing no clear benefits of MPAs (Lasik 1993; Baliwe 2021). For the most part, however, abundances and sizes of targeted intertidal invertebrate species were greater in protected areas, with evidence of benefits to adjacent unprotected areas (e.g. Lasik 1993, 1998; Hockey and Bosman 1994; Lasik and Field 1995; Pelc et al. 2009; Cole et al. 2011; Ludford et al. 2012; Nel and Branch 2014). Comparisons of the limpet Cymbula oculus inside versus outside the Dweasa and Tsitaikamma MPAs (Branch and Odendaal 2003) revealed clear positive effects of the MPA on the species’ size, age and abundance. Sex ratios outside MPAs were strongly skewed towards males because the species is protandric and harvesting targets the larger (female) individuals. However, protection had a negative effect on recruitment, possibly because the greater abundance of adults in the MPAs decreases the survival of settlers. Also in relation to sex ratios, Garratt (1993) found the protogynous slinger seabream Chrysoblephus puniceus had a strongly female-biased sex ratio in heavily-harvested areas of KwaZulu-Natal (1:18.8) compared with the population in St Lucia Reserve (1:4.6)—and there are many other examples of sex ratios being distorted by fishing directed at the largest individuals of species that undergo sex change and, conversely, of MPAs maintaining more-balanced sex ratios (Buxton 1993; Kerwath et al. 2008b; Tunley et al. 2009). Sex change is thus among the factors that increase the vulnerability of a fish species to harvesting.

Negative effects of MPA protection in South Africa have been documented, especially for rarely targeted or non-fishery species, likely due to increased competition, predation or grazing arising from augmentation of protected targeted species in the no-take areas (Hockey and Bosman 1994; Lasik 1998; Götz et al. 2009a, 2009b). Such indirect effects of protection afforded to target species, including trophic cascades and apparent competition with negative impacts on non-target species, have also been documented elsewhere in the world, including frequent declines of urchins following increases in fish abundance inside MPAs (e.g. McClanahan and Muthiga 1988; McClanahan et al. 1999, 2001; Shears and Babcock 2003; Micheli et al. 2005; Babcock et al. 2010). This can even result in a decline in diversity as a result of protection (e.g. Hockey and Bosman 1994). In addition, some MPAs fail to improve the abundance of particular groups of species simply because the location lacks suitable habitat for those species, even though the habitat might be present in nearby unprotected areas, as was the case for reef fishes at De Hoop (Heyns-Veale et al. 2019) and chondrichthyans at Walker Bay Whale Sanctuary (Osgood et al. 2019).

Götz et al. (2013) developed a framework to assess the ecological benefits of MPAs, which is of relevance to the protection of linefishes and other harvested species. The framework consists of six steps that are described in the caption to Figure 8. The first step is to determine whether fishing intensity is less inside the MPA than outside: if it is not, the success of the MPA cannot be validly tested. While this step is not always quantified explicitly, there has been a tacit assumption in most studies that fishing is less inside than adjacent to an MPA. Our review of studies that address steps 2–6 provides ample quantitative evidence for the ecological effectiveness of MPAs in South Africa (Figure 8). However, these steps have been applied with declining frequency, and Goukamma, which was used as a case study for the framework of Götz et al. (2013), is the only MPA to which all the steps have been applied. More studies along the lines of Kerwath et al. (2013) (i.e. including step 6) are required to assess whether effects detected in steps 2 to 5 necessarily translate to benefits for the local communities or the users of the adjacent ocean space. The challenges of assessing larval and propagule dispersal and export of organisms from MPAs have been outlined in our study, and, together with an understanding of movement patterns of migratory species and gene flow, are vital areas for future research to improve knowledge about the ecological connectivity of MPAs and to inform further MPA expansions. This is a critical issue for MPAs to play an effective role in climate-change adaptation (von der Heyden 2009; Roberts et al. 2017) and hence contribute to the persistence and resilience of South Africa’s marine biodiversity.

There is also a shortage of evidence for effective protection of non-harvested species. A possible exception is the population of loggerhead turtles Caretta caretta that has benefitted strikingly from protection of its breeding habitat in the Maputaland and St Lucia MPAs (now both within iSimangaliso MPA) and the population of leatherback turtles Dermochelys coriacea that has also recovered, although to a lesser extent (Hughes 1996; Nel et al. 2013; Harris et al. 2015). Another example, involving the iconic African penguin Spheniscus demersus, concerns the effects of experimentally alternating purse-seine fishing with fishery closures around pairs of islands where the African penguin breeds—one pair of islands off the coast of the Eastern Cape Province (Bird and St Croix islands) and the other pair off the Western Cape coast (Dassen and Robben islands). Closures around these
islands were shown to reduce foraging effort for penguins (Pichegru et al. 2012). This did not always translate to improvements in adult or chick conditions or growth rates, yet a marked positive effect of fishery closures on chick survival was shown for the Western Cape islands (Pichegru et al. 2010, 2012; Sherley et al. 2015, 2018). Sherley et al. (2018) concluded that fishing closures can improve the population trends of some predators such as the endangered African penguin that are dependent on forage fish, but emphasised that detecting demographic gains for mobile marine predators from small no-take zones requires experimental time-frames and scales that will often exceed those desired by decision-makers. Robinson et al. (2015) consider that fishery effects are likely to influence penguin survival only when sardine biomass drops below 25% of the maximal level. Such complications likely contribute to the scarcity of evidence for effective protection of higher predators by fisheries exclusions.

Conclusions

Following the expansion of the protected areas network in 2019, South Africa now has an MPA network that: (i) is representative of all ecoregions and the majority (87%) of marine ecosystem types; (ii) has increased species representation for fishes and marine mammals; and (iii) includes parts of most of the areas of identified importance for biodiversity (16 of 18 EBSAs are now at least partially represented in the MPA network). The remaining ecosystem types that are Not Protected or Poorly Protected, and the remaining two EBSAs or parts of EBSAs that have no protected constituent, should be priorities for future MPA expansion. Key gaps exist on the west coast, in estuarine ecosystems and for the deep sea; all these warrant prioritisation for protection. Estimates of the proportion of species represented in MPAs range from 50% to 98%, depending on the approach adopted and the taxa examined, but all papers reviewed agree on the need for further expansion, improved national species-distribution data, and quantification of the relative abundances of species rather than just their presence or absence. An emphasis on fish is evident in the studies, and greater attention needs to be given to less-frequently studied groups such as invertebrates.

Shortcomings with respect to the ecological connectivity of South Africa’s MPAs have been noted by von der Heyden (2009) and Henriques et al. (2020), and are highlighted again in our study, in particular with regard to coastal MPAs on the west and south coasts of the country where some of the MPAs are both small and remote from other MPAs. Improving the features of MPAs that Edgar et al. (2014) have identified as being conducive to effective protection, such as increasing the size of smaller MPAs (especially those <5 km²) and increasing the amount of no-take areas in the MPA network, should also be implemented to improve the MPA network. However, it is also essential to maintain the effectiveness of MPAs that have scored highly in terms of NEOLI criteria and have provided evidence of ecological effectiveness. These include some of the older and larger coastal MPAs, such as Tsitsikamma, Pondoland, iSimangaliso and De Hoop. In the case of De Hoop, there is evidence that offshore expansion could greatly increase its effectiveness for reef-fish protection by securing reefs that currently fall outside the MPA’s boundary (Heyns-Veale et al. 2019).

Efforts and costs that are dedicated to further expansion of the MPA estate—to address gaps in the MPA network and the protection targets—should not be at the expense of ensuring effective management of the existing MPAs, including compliance. This particularly applies to the 20 new or extended MPAs declared in 2019, which are mostly offshore and subject to management and compliance issues that still need extensive consultation, planning and implementation. However, it also applies to the older coastal MPAs (i.e. those declared before 2019). In our evaluation of MPAs in terms of the NEOLI criteria, enforcement (compliance) was the feature that consistently scored the poorest, a finding that also has been emphasised in estuarine protection assessments. This is a serious concern, and addressing it will require deliberation of socio-economic issues in the areas affected by the MPAs, as discussed by Mann-Lang et al. (2021).

Our review of South African MPAs (see Supplementary Tables S3 and S4) highlights a shortage of studies on non-targeted species, including iconic taxa including cetaceans, seabirds and seals, as the majority of studies focus on the protection and recovery of fishery-targeted linefish species or harvested intertidal resources. Also, most of the relevant studies have been limited to a subset of the larger coastal MPAs, whereas most of the smaller MPAs, some of which are also deficient in terms of enforcement, have been largely neglected in terms of research and monitoring. However, for those MPAs that have been evaluated, our review has assembled a host of evidence that upholds the ecological effectiveness of MPAs in South Africa, manifested especially through increases inside the MPAs in the abundances and sizes of targeted species, as compared with the species’ status in unprotected areas or prior to the
proclamation of the MPAs. This definitively addresses the main objective of this study, which was to assess whether South Africa’s MPAs provide effective ecological protection for its marine species and species assemblages.

**Recommendations**

Six key recommendations emerge from this review:

(i) A better understanding of the ecological connectivity of MPAs is essential to inform further MPA expansion and to elucidate the role of MPAs in mitigating climate change; especially needed is additional research on larval and propagule dispersal, the movement patterns of migratory species, and gene flow. Connectivity information for marine and estuarine realms should be fed into integrated coastal and marine spatial biodiversity plans.

(ii) With highlighted gaps in representivity, connectivity and replication in mind, the west and south coasts, as well as the deep sea, unprotected EBSAs, and estuarine ecosystems need to be prioritised in future MPA expansions. Improving features of MPAs that are conducive to effective protection, such as increasing the amount of no-take area, increasing the size of smaller MPAs (especially those <5 km²), or expanding boundaries to incorporate key habitats in nearby unprotected areas, should also be considered.

(iii) Efforts and costs that are dedicated to further expansion of the MPA estate—to address gaps in the MPA network and protection targets—should not be at the expense of ensuring effective management and compliance in existing MPAs.

(iv) The capacity for existing legislated MPAs to protect biodiversity and associated human benefits, and maintain their demonstrated ecological effectiveness, should not be diminished by re-zonation unless compensatory areas are designated to offset any reduction in their effectiveness, so as to ensure that the net level of ecological effectiveness is maintained.

(v) Targeted research and monitoring for evaluation of the effectiveness and benefits to adjacent fisheries is required, with greater focus on the MPAs and taxa that have so far been inadequately studied.

(vi) An appropriate protocol that will assess the ecological, socio-economic and management efficacy of MPAs is needed, which will rigorously and defensibly determine whether they are meeting their specific ecological, social and management objectives. We will pursue this objective in a future article, and meanwhile will outline such a protocol and test it in workshops with MPA authorities, managers and users.

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