

Role of the Amathole Marine Protected Area in protecting vulnerable and threatened reef fish

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ABSTRACT

The Amathole Marine Protected Area (MPA) was first established on a voluntary basis in the 1980's by local ski-boat fishermen and comprised three small no-take areas near East London. In 2011, the areas received official recognition as the Amathole MPA and in 2019 an offshore extension was granted, increasing the area covered from 250 km² to over 4000 km². Though the inshore Amathole MPA has benefitted from decades longer of reprieve from fishing activity than the offshore MPA, it is limited in both its coastal and depth extent, placing in doubt its capacity to provide meaningful protection to several heavily threatened target species. Among the numerous endemic Sparids for which the Amathole region constitutes a vital portion of their distributional range are red steenbras (*Petrus rupestris*), seventyfour (*Polysteganus undulosus*), and dageraad (*Chrysoblephus cristiceps*). The stocks of all three species have collapsed and urgent intervention has been recommended to enable their recovery, including protection in strategically placed MPAs. The offshore Amathole MPA covers an extensive portion of prime habitat for these and other species, but no formal research has been carried out on fish assemblages in the region. As such, data to substantiate the benefits of the inshore Amathole MPA and to provide a baseline reference for the offshore MPA are lacking. This study made use of baited remote underwater stereo-video systems (stereo-BRUVS) to survey fish assemblages in the inshore Amathole MPA, adjacent inshore exploited areas, and exploited areas seaward of the inshore MPA. Sampling was carried out in 2015 and 2016, prior to the establishment of the offshore Amathole MPA. Fish assemblages from the inshore MPA were compared with those from adjacent exploited areas within the same depth range and from the offshore zone between 76 and 112 m depth. Within the inshore zone, biomass and abundance of target species were greater inside the MPA than in adjacent exploited areas, with vulnerable fisheries species showing the strongest response to protection. Offshore assemblages consisted of fewer species and fewer fish overall than those from the inshore zone but were dominated by larger individuals and those from higher trophic levels. The size of *C. cristiceps* was consistent across the sampled depth range but abundance of this species declined rapidly at depths of more than 60 m. Within the inshore zone, both abundance and size of *C. cristiceps* were greater in the MPA than in adjacent exploited areas. The size of *P. rupestris* was consistent across the sampled depth range and between protected and exploited areas, but this species was considerably more abundant offshore. Where *P. rupestris* was detected inshore it was almost exclusively in the MPA. No difference in the size or abundance of *P. undulosus* was found between the inshore MPA and inshore

exploited areas, but both measures were found to increase with depth, with reproductive-sized adults restricted to the offshore zone. Despite its limited benefits for larger species, the inshore Amathole MPA is a critical refuge for smaller and more resident species like *C. cristiceps*, demonstrating the possibilities for conservation and management of endangered species in small MPAs. Baseline abundance and size measures for *P. rupestris* and *P. undulosus* recorded here indicate that the offshore extension of the Amathole MPA is ideally situated to protect spawner stock of these species and potentially contribute to the recovery of their stocks across a wider distributional range.

Key words: MPA, Amathole, linefish, reef, management, depth, abundance, biomass, *Petrus rupestris*, *Polysteganus undulosus*, *Chrysoblephus cristiceps*

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The following thesis has not been submitted to any university other than Rhodes University, Grahamstown, South Africa. The work presented here is that of the author.

1 GENERAL INTRODUCTION

Fish stocks globally, and in South Africa, are declining past sustainable levels in response to overexploitation and degradation of the marine environment (DEAT 1997, Pauly et al. 1998, Griffiths 2000, Hoegh-Guldberg 2010, Halpern et al. 2015, DAFF 2016, FAO 2016). In South Africa, this prompted a surge in research into fisheries management and the introduction of more realistic catch restrictions based on species-specific information (DEAT 1997, Mann 2013). However, these restrictions were largely insufficient to halt the decline in stocks and research carried out in the 1990s revealed that many species, including those thought to have still been at sustainable levels, were in fact overexploited (Garratt 1996, Griffiths 2000, Mann 2013, Kerwath et al. 2019). Subsequent to the introduction of the Linefish Management Protocol in the late 1990s (Griffiths et al. 1999) a state of emergency in the South African linefishing sector was declared in 2000 (DAFF 2016).

The majority of South Africa's linefish stocks need assessment. Of those for which stock status is known, many are considered to be overexploited or collapsed (Chale-Matsau 2001, Mann 2013, Parker et al. 2016, Kerwath et al. 2019). Stock assessments conducted since the declaration of the state of emergency in 2000 indicate that some species, such as slinger (*Chrysoblephus puniceus*), hottentot (*Pachymetopon blochii*) and carpenter (*Argyrozona argyrozona*), have begun to recover, while others, such as silver kob (*Argyrosomus inodorus*), are still overfished (Winker et al. 2017a,b,c,d). Furthermore, despite extensive restrictions on the capture of red steenbras (*Petrus rupestris*), seventyfour (*Polysteganus undulosus*), and dageraad (*Chrysoblephus cristiceps*), these species are currently considered endangered, or in the case of the latter two, critically endangered (Mann et al. 2014, Mann et al. 2014b, Buxton et al. 2014). In such cases, recovery may depend on the protection of adult stock and juveniles, which might only be possible by means of temporal and spatial closures (Chale-Matsau et al. 2001, Roberts et al. 2005, Ballantine 2014).

Globally, the general failure of single-species restrictions to avert the collapse of commercial fish stocks led to the development of a more holistic ecosystem-based approach to fisheries management (EBFM; Jennings & Kaiser 1998). This approach takes into account interactions between fish, their environment, and humans as well as the uncertainties these interactions entail (Garcia et al. 2003). An integral component of EBFM is the use of Marine Protected Areas (MPAs) to conserve biodiversity and productivity in sensitive areas. The IUCN defines an MPA as "Any area of intertidal or subtidal terrain,

together with its overlying water and associated flora, fauna, historical and cultural features, which has been reserved by law or other effective means to protect part or all of the enclosed environment” (Kelleher 1999). MPAs can act as a safeguard against species management error where accurate ecosystem data are unavailable (Roberts et al. 2005, Ballantine 2014). This is particularly relevant in (i) areas where resources and governance to implement more specific restrictions are lacking, (ii) in multi-species fisheries, where unintentional bycatch and dumping of protected species counteracts the value of single-species restrictions, and (iii) for highly resident and endemic species which are susceptible to local overexploitation (Buxton 1993, Gell & Roberts 2003, Hilborn et al. 2004, Micheli et al. 2004, Sink 2016).

Appropriately designed and managed MPAs allow for the recovery of ecosystem components and functions, resulting in increased longevity and subsequent increase in the abundance and biomass of otherwise vulnerable species (Halpern & Warner 2002, Gell & Roberts 2003, Micheli et al. 2004, Russ et al. 2008, Lester et al. 2009, Edgar et al. 2014, Baskett & Barnett 2015). The maintenance of size and age structure of targeted fish populations in these areas sustains higher reproductive rates and serves as a buffer against evolutionary responses to selective fishing, while the retention of genetic diversity allows for more resilience in response to environmental variability (Berkeley et al. 2004, Reusch et al. 2005, Roberts et al. 2005, Micheli et al. 2012, Hixon et al. 2014, Baskett & Barnett 2015, Mellin et al. 2016). This proliferation within the borders of well enforced, no-take protected areas has been known to replenish stocks in adjacent exploited areas through spill-over of eggs and larvae and the migration of juvenile and adult organisms, thus allowing for sustainable harvesting in adjacent areas where fishing is permitted (Pauly et al. 2002, Abesamis & Russ 2005, Stobart et al. 2009, Goñi et al. 2010, Micheli et al. 2012, Kerwath et al. 2013, Buxton et al. 2014). By enabling the recovery of biodiversity, MPAs also serve as a vital source of reference information for research into healthy marine environments (Micheli et al. 2004, Ballantine 2014, Sink 2016).

To provide such benefits, MPAs need to meet several criteria, the importance of which varies according to the objectives of the MPA and nature of habitats and organisms of interest:

- The size of the protected area should be appropriate for the range and distribution of the species it is intended to protect (Gell & Roberts 2003, Agardy et al. 2011, Sink 2016).
- The length of time for which the MPA has been established is positively correlated to observed increases in abundance and biomass (Micheli et al. 2004, Claudet et al. 2008, Edgar et al. 2014).

- Isolation by natural barriers, such as unsuitable habitat or deep seas, further enhances conservation benefits since this limits the amount of migration to exploited areas (Edgar et al. 2014).
- The level of protection is important since no-take MPAs perform better than partially protected areas (Lester & Halpern 2008, Edgar et al. 2014).
- The participation and support of stakeholder groups, particularly local fishing communities, is vital for the successful implementation of MPAs (Claudet & Guidetti 2010, Di Franco et al. 2016).
- The objectives of the MPA should be well-defined and attainable since failure to meet objectives and demonstrate success can lead to stakeholder disillusionment and withdrawal of support (Turpie et al. 2000, Hilborn et al. 2004, Agardy et al. 2011, Rice et al. 2012, Agardy 2017).
- Sufficient governance, resources and manpower should be made available for effective enforcement, management, and monitoring (Guidetti et al. 2008, Edgar et al. 2014, Di Franco et al. 2016, Sink 2016, Gill et al. 2017, Agardy 2017).

The inshore Amathole MPA in the Eastern Cape comprises three separate reserves in the vicinity of East London at the Gxulu River mouth, Gonubie point and the Kei River mouth. The reserves together cover 44 km of coastline and extend three nautical miles out to sea, totalling just under 250 km² of protected ocean area and reaching depths of up to 80 m (WWF-SA 2018). The Amathole coast boasts a rich marine fauna and is central in the distribution of numerous endemic seabream (Family: *Sparidae*) species, including three of particular conservation interest – dageraad (*C. cristiceps*), seventyfour (*Polysteganus undulosus*) and red steenbras (*Petrus rupestris*) The three areas comprising the inshore Amathole MPA were originally proposed as areas closed to fishing by members of local ski-boat angling clubs in 1981, in a bid to protect inshore reefs from overfishing. Although the clubs successfully lobbied for government recognition of the areas, the declaration of the areas as “Closed Areas” rather than MPAs in 1984 meant that no official budget was provided for research or enforcement, and adherence to regulations was voluntary. The ski-boat fishermen who had proposed the MPAs actively discouraged poaching by self-policing the areas. The culture of compliance that this practice fostered is invaluable to MPA management (Bova et al. 2017) and in this instance may have been even more effective than more traditional management approaches. As fish stocks in the reserves began to recover, increasing numbers of anglers took advantage of the lack of enforcement, fishing in the closed areas (John Rance, BDSAA, pers. comm.). In 2011 the closed areas were officially gazetted as MPAs, thereby securing a budget for research, monitoring, and enforcement. The involvement and support of local fishermen in the creation

and enforcement of the inshore Amathole MPA has added decades to the amount of time fish stocks have had to recover in the protected areas, as well as fostering a sense of responsibility for the MPA in the fishermen which continues to contribute to their success.

In July 2014, the South African government initiated “Operation Phakisa”, a plan to fast-track mobilization of economic activity in South Africa’s oceanic territory by prioritising marine industries such as oil and gas, aquaculture, and maritime trade (Operation Phakisa 2018). Part of the planning process involves ensuring that such operations are carried out in an environmentally sustainable manner, without compromising ecosystem services and biodiversity in the marine environment (Harris et al. 2014). This in turn requires fast-tracking the protection of areas of particular importance to marine biodiversity and for the provision of essential ecosystem services. Amongst other measures, a network of MPAs covering at least 5 % of South Africa’s Exclusive Economic Zone (EEZ) was proposed, and detailed ecosystem surveys were carried out to identify potential sites that would maximise conservation benefits with minimal impact on stakeholders (Sink 2016). Included in the network and gazetted in May 2019 was an offshore expansion of the original inshore Amathole MPA (Harris et al. 2014, S.A. Government 2019). The offshore marine environment of the Amathole coast was identified as a priority area for conservation of several critically endangered habitats, all of which have remained well preserved there until now (ACEP 2017). The expansion, comprising two areas leading offshore from the protected areas at Gxulu and Kei Mouth, increases the area protected by 4000 km² and reaches depths of over 2000 m (S.A. Government 2019, MPASA 2020).

1.1 PROBLEM IDENTIFICATION

Since the inshore Amathole MPA was originally created by recreational fishermen, with limited ecological data and without input from other stakeholder groups, it is possible that the MPA is not achieving its intended ecological outcomes. For instance, neglecting to consider the needs of other stakeholders may result in lower levels of compliance among the broader stakeholder group (Agardy et al. 2011, Rice et al. 2012). Limited knowledge of the habitat within and adjacent to the MPA may mean that the MPA is inappropriately placed to protect the vulnerable biodiversity within the region (Agardy 2017). Furthermore, the fragmented design of the inshore MPA and the small individual size of the three areas increases the risk that fish will move out of the MPA and be captured in the adjacent exploited areas, limiting conservation benefits (Di Franco et al. 2018). Preliminary research carried out by Dr Malcolm Smale in 2004 with the assistance of local ski-boat fishermen in the inshore MPA indicated that

the abundance of several endemic seabream species had increased in the closed areas, but that consistent differences in size were not observed, suggesting that the reserves were not providing maximum conservation benefits at that time (Malcolm Smale, unpublished data). No detailed survey of fish assemblages in the inshore Amathole MPA and surrounds has been carried out since the research by Dr. Smale. As such, no data are available to substantiate the benefits of the inshore MPA to vulnerable and threatened reef fish species.

In contrast, the recent offshore extension of the Amathole MPA is supported by ecological surveys, which have identified unique ecosystems and confirmed the value of the area particularly for linefish conservation (ACEP 2017). Though this basis has been sufficient to secure the declaration of the area as an MPA, quantitative data on relevant species are required to support these assertions and provide a baseline reference for future comparisons.

1.2 AIMS

This study aimed to investigate to what extent the inshore Amathole MPA currently meets the conservation objective of providing a sanctuary for linefish species impacted by boat-based exploitation (DEA, 2011), and to describe differences between inshore and offshore fish assemblages, with consideration of implications for linefish conservation and of the recent offshore extension of the MPA.

To this end, the following research questions were addressed:

- Do fish assemblages within the inshore Amathole MPA differ significantly from those in adjacent exploited areas with similar habitat and depth range?
- How do fish assemblages respond to habitat variability (such as depth and availability of reef structure) in the area of the inshore Amathole MPA and is the inshore MPA appropriately designed to optimise this criterion for vulnerable and threatened reef fish species?
- Do fish assemblages within the depth range of the inshore Amathole MPA differ significantly from those further offshore?
- What depth range is best suited to maximise protection for three threatened endemic seabreams, *Chrysolephus cristiceps*, *Petrus rupestris* and *Polysteganus undulosus*?

2 STUDY AREA AND GENERAL METHODOLOGY

2.1 STUDY AREA

2.1.1 MARINE ECOSYSTEM

The Amathole district falls within the warm-temperate Agulhas Ecoregion on the south east coast of South Africa, as defined in the South African National Biodiversity Assessment (Figure 2.1; Sink et al. 2011, Sink et al. 2019). This ecoregion covers the area of continental shelf from Cape Point in the west to the Mbashe River in the east. The Agulhas Ecoregion is characterised by cooler waters than those of the south flowing warm water Agulhas Current, which flows at the edge of the widening continental shelf (Figure 2.1; Goschen & Schumann 2011). The force of the current veering away from shore draws deep waters to the surface, causing nutrient-rich upwellings which feed the exceptionally high diversity in the area (Schumann & Beekman 1984, Schumann 1987, Lutjeharms et al. 2000, Goschen & Schumann 2011). The 200 km of coastline of the Amathole district, between Fish River and Mbashe River, correspond to the eastern limit of the Agulhas Ecoregion, where the continental shelf tapers up towards KwaZulu-Natal. The shelf break in the vicinity of the Amathole MPAs occurs between 110 and 140 m depth, approximately 20 km from shore (Dlamini, 2017). The Agulhas Current still travels close enough to shore at this point that the inshore boundary, a region of intensive cyclonic shear between the current and the shelf waters, lies inshore of the shelf break, heavily influencing the inshore environment (Goschen & Schumann 2011). The Agulhas Current, in addition, conveys warm water and tropical species southward from the sub-tropical Natal Ecoregion (Schumann, 1987, Lutjeharms 2006).

Cold water upwellings, often experienced following strong north-easterly winds, regularly follow the shelf back up the coast as far as the Mbashe River, and occasionally beyond (Christensen 1980, Beckley & Van Ballegooyen 1992, Turpie et al. 2000, Lutjeharms 2006, Goschen & Schumann 2011, Sink et al. 2019). These, along with strong south-westerly winds, can result in sporadic counter-currents travelling back up the coast which can last for days at a time (Roberts et al. 2010, Goschen & Schumann 2011).

The geology of the Amathole coast is dominated by sandstone and conglomerate rock formations (Dlamini, 2017). The weathering of these structures over time gives rise to the intricate reef complexes that characterise the area, providing a wealth of habitats for marine life including numerous species of conservation and commercial value (Sink et al. 2019).

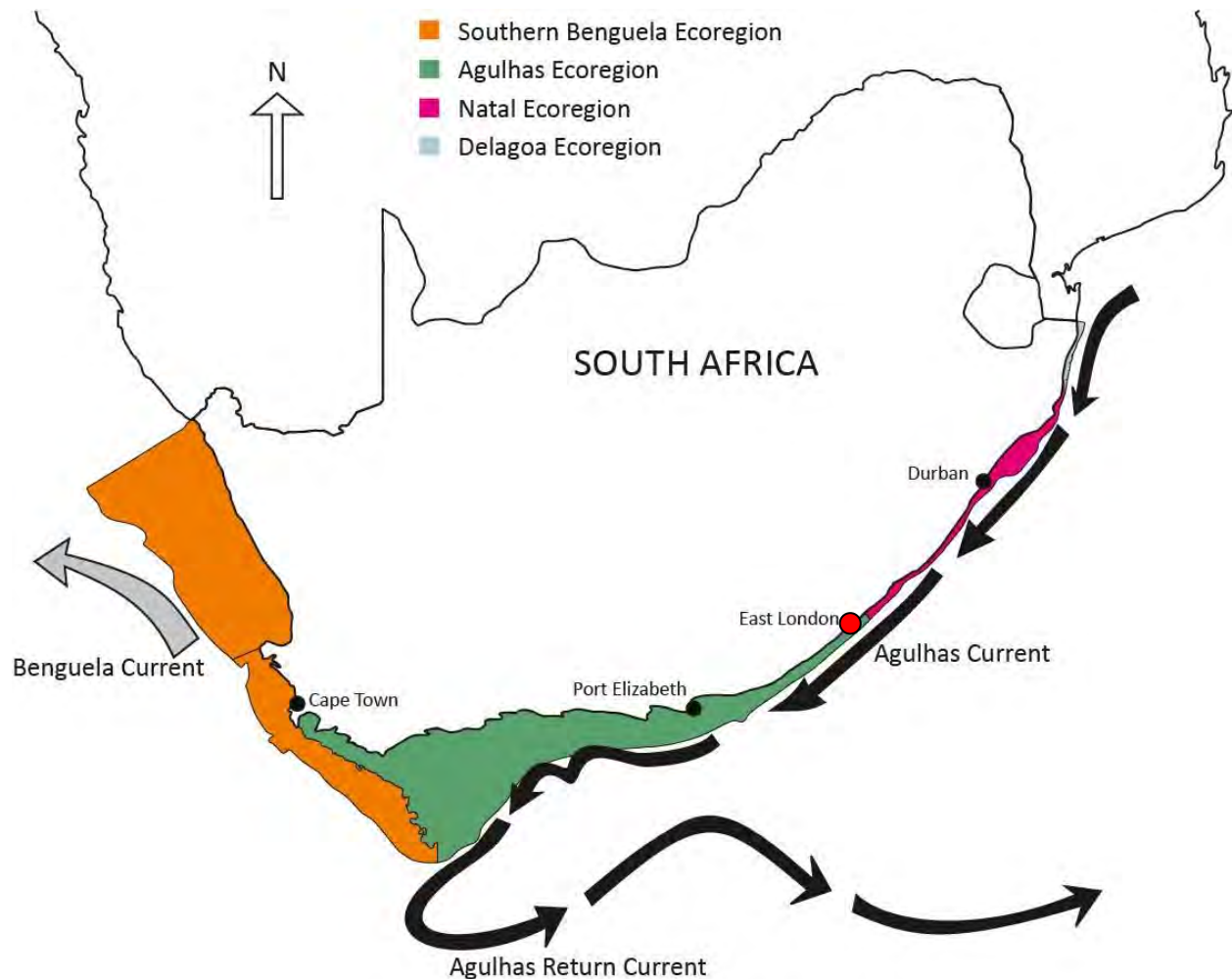


Figure 2.1: South Africa's four coastal marine ecoregions as per the South African National Biodiversity Assessment (SANBI 2018). The Amathole Marine Protected Area is situated near the northern border of the Agulhas Ecoregion with the Natal Ecoregion, in the vicinity of East London. Black arrows represent the Agulhas Current and the grey arrow represent the Benguela Current [modified from Lutjeharms (2006)]. Figure courtesy of Elodie Heyns-Veale.

Although the environmental characteristics defining the eastern boundary of the Agulhas Ecoregion are reasonably consistent over time, biological distributions, in particular those of fish, tend to be more blurred, with a gradual turnover of species along the coast (Turpie et al. 2000, Goschen & Schumann 2011). The east coast of South Africa is particularly rich in endemic seabreams (Family: *Sparidae*), with peak diversity of this family in southern KwaZulu-Natal (Turpie et al. 2000, Fennessy et al. 2003, Comeros-Raynal et al. 2016, Henriques et al. 2020). Inshore reefs in the Amathole region are dominated

by smaller shoaling species (Buxton & Smale 1984), while larger species, including several of notable conservation and commercial interest, occupy the deeper reefs (Fennessy et al. 2003, ACEP 2017, Mann 2013). The first recorded coelacanth (*Latimerius chalumnae*) was found off the Amathole coast and the canyons and terraces leading to the shelf break and slope are thought to be one of the few refuges for this species (ACEP 2017).

2.1.2 AMATHOLE MPAS

The three protected areas at Gxulu, Gonubie and Kei that comprise the inshore Amathole MPA extend three nautical miles (5.6 km) seaward from the high-water mark to depths of between 60 and 80 m (Figure 2.1). The Gxulu protected area runs approximately 12 km from Christmas Rock (33° 11' 33.6" S; 27° 38' 37.6" E) to the Gxulu River mouth (33° 07' 8.7" S; 27° 43' 53.6" E). The Gonubie protected area runs approximately 10 km from Nahoon Point (32° 59' 46.7" S; 27° 57' 5.8" E) to Gonubie Point (32° 56' 29.1" S; 28° 02' 7.2 E). The Kei protected area runs approximately 22 km from the Nyara River mouth (32° 47' S; 28° 10' 53" E) to the Kei River mouth (32° 40' 49" S; 28° 23' 11.6" E; (Figure 2.2; S.A. Government 2011).

The two extensions comprising the offshore Amathole MPA cover 4000 km² of ocean surface, extending beyond the shelf break to depths of up to 2200 m (MPASA 2020). The Kei offshore protected area extends from the north-eastern boundary of the inshore protected area at Kei Mouth (32° 42' 50.4" S; 28° 25' 15.6" E), and then runs sequentially to 32° 43' S; 28° 46' E, then to 33° 0' S; 28° 46' E, then 33° 0' S; 28° 11' E, then 32° 50' 43" S; 28° 11' 9.2" E before re-joining with the inshore protected area at its south-eastern border (32° 49' 27.8" S; 28° 12' 54" E; Figure 2.2; S.A. Government 2019).

The Gxulu offshore protected area extends from the north-eastern boundary of the inshore protected area at Gxulu river (33° 9' 30.8" S; 27° 45' 54.8" E), and then runs to 33° 12' 25.5" S; 27° 55' 4.8" E, then 33° 29' 5.5" S; 27° 55' 4.8" E, then 33° 45' S; 27° 32' 42" E, then 33° 45' S; 27° 10' 59.9" E, then 33° 35' S; 27° 10' 59.9" E and back to the south-eastern border of the inshore protected area (33° 14' 1.1" S; 27° 40' 25.3" E; Figure 2.2; S.A. Government 2019).

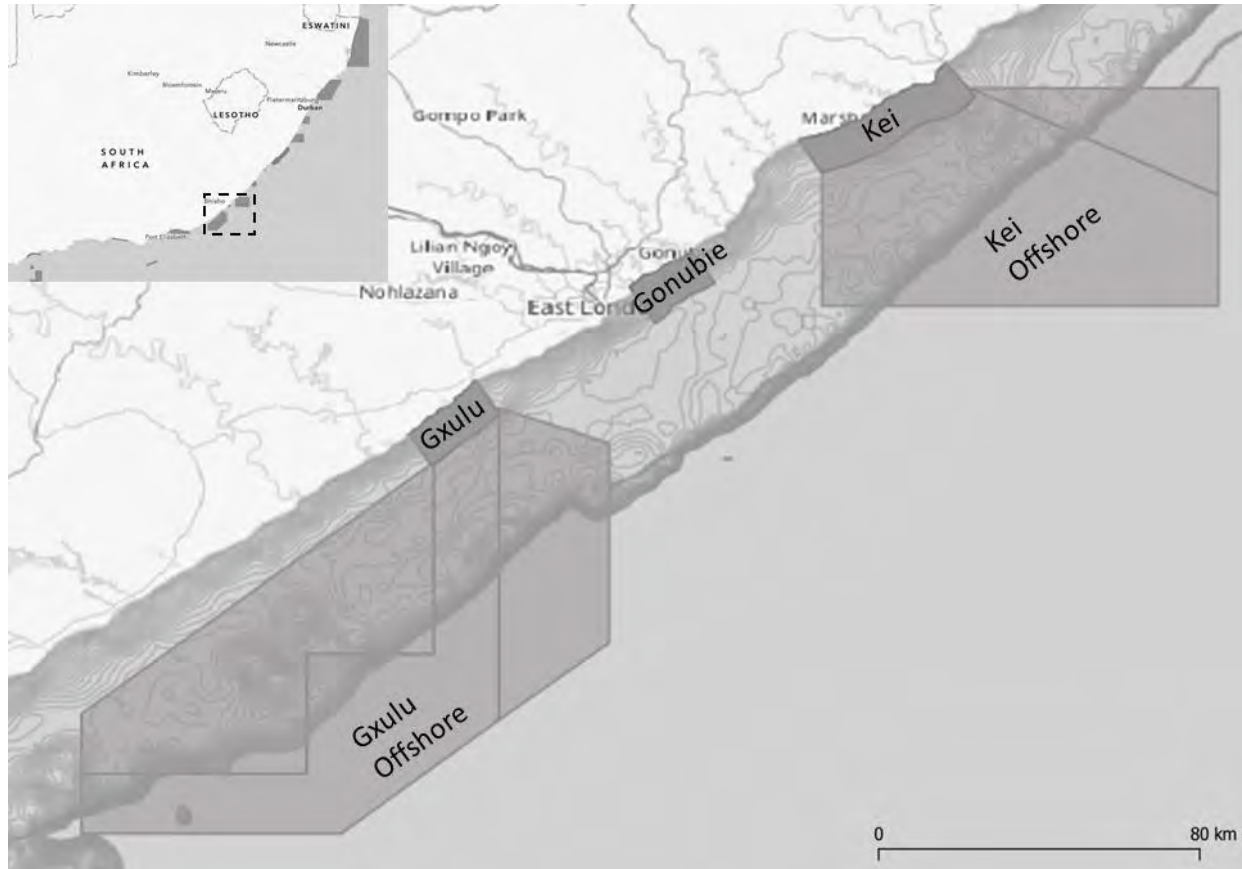


Figure 2.2: Arrangement of the three areas comprising the inshore Amathole Marine Protected Area at Gxulu, Gonubie, and Kei and of the two offshore extensions at Gxulu and Kei. The position relative to the South African coastline is shown in the inset boxed area. Bathymetry is shown to the shelf edge at the 200 m isobath.

2.1.3 TERRESTRIAL INFLUENCES AND PRESSURES

Freshwater input is one of the defining features of the Eastern Cape coast and sixty-three functional estuaries of variable size are found along the Amathole stretch (ADM 2016). The Kei River, on the north-eastern boundary of the inshore Amathole MPA, is one of the largest and most important drainage basins in the Eastern Cape, and the Kei mouth alluvial fan supports an array of unique habitats and ecosystems (ACEP 2017). Although freshwater input has minimal influence on salinity levels at a large scale (Goschen & Schumann 2011), water quality and sediment load can have transformative effects on local habitats (Momba et al. 2009, ACEP 2017). East London, centred around a port on the Buffalo River, is the most populous urban area along the Amathole coastline, with over 300 000 residents in the greater metropolitan area (ECSECC 2017). The port, a source of high levels of pollution and marine

traffic (Momba et al. 2009, Adeniji et al. 2017), lies between the Gxulu and Gonubie protected areas (Figure 2.2). The East London Harbour supports one of the larger recreational and commercial linefisheries on the South African coast (FAO 2001). In addition to the harbour, twenty-two public boat launching sites are registered along the Amathole coast (DEDEAT 2016), with six ski-boat fishing clubs based between Christmas Rock and Kei Mouth.

2.2 MATERIALS AND METHODS

2.2.1 DATA COLLECTION

Sampling entailed recording fish assemblages at selected deployment sites using baited remote underwater stereo-video systems (stereo-BRUVs) (Harvey & Shortis 1995, Bernard et al. 2014). The stereo-BRUVs consisted of a custom-built stainless-steel frame with two waterproof camera housings mounted horizontally 70 cm apart with an inward convergence angle of 8°. The housings contained identical high-definition (HD) cameras. The inward convergence angle insured that the cameras field of view converged towards a central bait container positioned 1.5 m in front of the stereo-BRUVs. The bait container is a removable, perforated PVC canister supported on a 1.5 m arm which extends out in front of the cameras (Bernard et al. 2014). The overlapping fields of view produced by the convergent cameras of the stereo-BRUVs permit estimation of the depth and size of objects recorded by both cameras at once calibrated (Harvey & Shortis 1995).

2.2.1.1 CALIBRATION

Prior calibration of the cameras, in position on the stereo-BRUVs frame, is required in order to account for the angle of orientation of each camera as well as camera characteristics such as focal length and lens distortion (Harvey & Shortis, 1998). Calibration is repeated after each field trip to allow for any in-field alterations to the position of the camera. Calibration was carried out in a swimming pool by training the cameras on a three-dimensional frame with clear markings on it, which is rotated at various angles to allow for automated calibration of the camera settings with the software package CAL (SeaGIS 2012).

2.2.1.2 DEPLOYMENT AND RETRIEVAL

Prior to each deployment, the bait container was filled with 0.8-1 kg of crushed sardines (*Sardinops sagax*), and the cameras were set to record and secured in the waterproof housings. The stereo-BRUVs were weighted to keep them stable on the sea floor and attached to a rope with marker buoys at the

surface to permit recovery. Once the boat was in position and stationary, the stereo-BRUVs were lowered to the seafloor with the aid of a capstan winch and swinging davit arm. GPS coordinates and depth data from the on-board echo-sounder were recorded for each sample once the system settled on the substrate. The use of up to four stereo-BRUVs at a time permitted the staggering of deployments, thereby maximising the number of samples possible. Once the first system had been deployed and the GPS coordinates for the site noted, the remaining systems were sequentially deployed before returning to retrieve the first. Retrieval was carried out after one hour with the use of a motorised capstan winch attached to a custom-built pulley arm. When back on deck, the video data were recovered and the stereo-BRUVs was prepared for the next deployment at a new sampling site. Deployment sites were separated by at least 300 metres to avoid cross-contamination of bait plumes and ensure independence of samples (Bernard & Götz 2012).

2.2.1.3 FOOTAGE ANALYSIS

Video recordings were analysed using the EventMeasure (Stereo) software (SeaGIS 2012). Analysis began from the point that the systems settled on the seafloor and continued for an hour from this point. This allows sufficient time to detect the majority of species present while keeping the amount of time necessary for analysis to a minimum (Bernard & Götz 2012, De Vos et al. 2014). Species were identified as they appeared in the footage using reference archives from previous studies, online resources (Froese & Pauly 2018) and published guides to South African fish (Smith 1949, van der Elst 1981, Compagno et al. 1989, Branch et al. 1994, Heemstra & Heemstra 2004). For each species identified, MaxN was recorded which is the maximum number of individuals of that species visible in the field of view of a single frame. Although MaxN is considered a conservative estimate of relative abundance (Cappo et al. 2004), it is preferable to overestimation of abundance as a result of repeatedly counting the same individuals (Cappo et al. 2006). Length data were obtained for as many of the fish counted in the MaxN frame as possible. Measurement of fork-length (FL) for individual fish was carried out by identifying the tail fork and anterior tip of the fish in both of the synchronised videos using the calibrated EventMeasure (Stereo) software (SeaGIS 2012). In the case of fish species having a square or rounded tail, total length (TL) was measured.

Samples with less than 1.5 m visibility, those with technical issues (such as equipment malfunction or truncated recordings), and those in which the cameras settled at obstructive angles (facing toward the sea floor or the surface) were considered unsuitable for analysis. In the event where only one camera

produced unsuitable results, rendering stereo length measurements impossible, MaxN analysis was still carried out using the video collected.

2.2.2 RESEARCH DESIGN

2.2.3 SAMPLE SITE SELECTION

Sampling was carried out within the protected areas at each of the three locations of the inshore Amathole MPA (Gxulu, Gonubie and Kei), and the corresponding inshore exploited areas to the North-East of each one (Figure 2.3). Further sampling was carried out at offshore exploited areas seaward of the Gxulu exploited area and off the Gonubie protected area (Figure 2.3). Note that at the time of sampling the offshore Amathole MPA had not yet been declared and all offshore samples were considered as exploited. For the comparison between the inshore MPA and inshore exploited areas (Chapter 3), samples were pooled according to management status (protected or exploited) and location (Gxulu, Gonubie or Kei). For the comparison between the inshore and offshore zones (Chapter 4), samples were pooled according to management status (protected or exploited) and zone (inshore or offshore). Sampling took place over four days in May 2015 and 12 days in March and April of 2016. Due to challenging sea conditions and logistical constraints, only one day of sampling was possible at the Kei exploited area resulting in only seven samples from this area.

Equipment malfunction prevented the completion of a detailed bathymetric survey of the study areas prior to scheduled stereo-BRUV sampling, meaning that sampling effort could not be efficiently stratified according to substrate type. In order to reduce time in the field spent locating suitable deployment sites, existing coarse-scale bathymetric maps of the area from previous studies (GEBCO 2014) were used as a guideline. Local anglers were also asked to mark on the maps of the areas where they thought reef complexes were present. This information was used to refine potential sampling sites within each study area. The localised bathymetry of these sites was assessed in the field with a high-resolution GPS linked echo-sounder (Garmin GPSMAP 8020XS fitted with AirMar TM150 chirp transducer) and the stereo-BRUVs were deployed when suitable substrate was detected. Since the vast majority of fish species targeted by boat-based fishing in the Amathole region are reef-dwelling species (Fennessy et al. 2003), considerable effort was made to ensure that sufficient samples were obtained from this habitat type for each experimental condition.

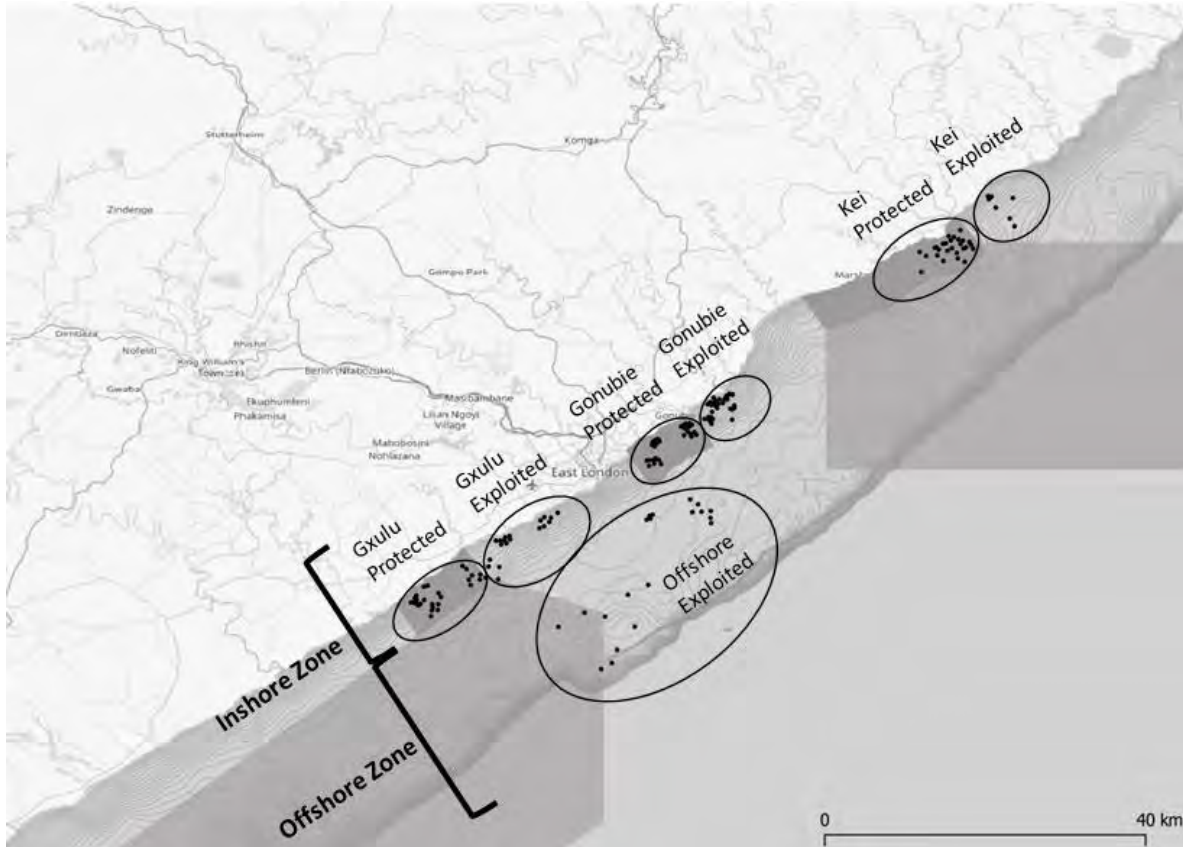


Figure 2.3: Distribution of sampling sites (black circles) in the three protected areas comprising the inshore Amathole MPA (dark grey boxes) and adjacent exploited areas within the same depth range to the north-east of each protected area (inshore zone), and at offshore exploited sites (offshore zone).

A strong signal return on the sonar image indicating the presence of irregular structure and a rapid change in bathymetric profile of over two metres was considered an indication of the likelihood of reef substrate at a potential sampling site. However, this method for detecting suitable reef substrate is susceptible to interference from swell which resulted in a high percentage of samples being deployed on sand with little or no reef formations. Although this was considered representative of the prevailing substrate greater efforts were made to locate reef areas to ensure adequate representation of reef assemblages. Although this approach ensured that sufficient data were collected to adequately represent both substrate categories in all of the study areas (i.e. sand and reef areas), it resulted in notable variation in the number of samples between locations within management groups.

Sampling sites for the inshore analysis were selected to represent the full depth range of the inshore MPAs. The selection of sampling sites in the offshore zone was opportunistic and based on GPS coordinates from local fishermen indicating the location of offshore reef complexes where they had fished. In the absence of suitable bathymetric data this was deemed the most appropriate approach to sample reef associated species.

2.2.4 DATA ANALYSIS

In order to evaluate the effectiveness of the Amathole MPA in conserving vulnerable and threatened reef fish species, the composition, abundance, and size structure of fish assemblages were assessed in response to a suite of explanatory and environmental variables. Multivariate statistical techniques were used to evaluate changes in fish assemblage structure, while univariate statistics were used to model responses at species and species-group level.

The analysis was two-part:

- The first part focused on the inshore zone (Figure 2.3) and compared fish assemblages in protected areas with those in adjacent exploited areas of similar depth and habitat type. This analysis aimed to investigate whether the inshore Amathole MPA has thus far benefitted vulnerable and threatened reef fish species in the area (Chapter 3).
- The second part focused on comparing the fish assemblages of the inshore and the offshore zones. This analysis aimed to explore the conservation value of the of the offshore Amathole MPA (Chapter 4).

2.2.4.1 EXPLANATORY VARIABLES AND COVARIATES

The response of fish assemblages to the following categorical variables was evaluated:

- Location (fixed, 3 levels: *Gxulu*, *Gonubie* and *Kei*)
- Management (fixed, 2 levels: *protected* and *exploited*)
- Zone (fixed, 3 levels: *inshore protected*, *inshore exploited*, and *offshore exploited*)
- Substrate (fixed, 2 levels: *reef* and *sand*)

The effects of the continuous environmental variables depth (m), temperature (°C), and visibility (m) were also taken into account, as were those of the experimental artefacts (i.e. percentage of the water column in the field of view and the percentage obstruction) Each of these is defined as follows:

Location: The three protected areas comprising the inshore Amathole MPA are distinct in size, extent of reef cover, and level of influence from estuaries and urban developments. Likewise, the exploited areas are subject to varying ease of access by fishing vessels. As such, it is possible that distinct fish assemblages exist in each protected area and that the response to protection varies between them. In order to account for this the three protected areas, Gxulu, Gonubie and Kei, and their corresponding exploited areas were considered separately for the inshore analysis.

Management: To evaluate whether the inshore Amathole MPA has been effective in meeting the objective of providing sanctuary to species impacted by boat-based exploitation, fish assemblages within the three protected areas were compared with those in adjacent exploited areas of equivalent depth and habitat type for the inshore analysis.

Zone: To evaluate whether the limited depth extent of the inshore Amathole MPA excludes critical habitat for species of conservation interest, samples from the inshore zone were compared with samples taken from the offshore zone. Since it is possible that fish assemblages differ between inshore exploited and protected areas, the two inshore assemblages (i.e. inshore protected and inshore exploited zones) were compared separately to the offshore exploited assemblages to ensure that differences detected between zones were independent of those resulting from management status. As the offshore Amathole MPA had not yet been approved at the time of sampling, all offshore samples were considered as exploited, although some sites now fall within the extended protected area (see Figure 2.3).

Substrate: Substrate is a critical determinant of habitat type and in turn, the fish assemblage found in a given area (Demestre et al. 2000, Harman et al. 2003, Chatfield et al. 2010, Heyns-Veale et al. 2016). In order to account for differences in prevalence of reef structure between locations, management (protected or exploited) and inshore and offshore zones, substrate type was included amongst the principal variables. Although reef substrate can be further divided according to profile and the associated macrobenthic assemblage, for this research substrate was simply defined as either sand (> 80% sand cover) or reef (>20% reef cover). This accounts for differences in fish assemblages based on substrate without further subdivision beyond the interest of the study aims. The nature of the substrate of each sample site was ascertained from the video footage obtained.

Depth: As with substrate, depth is acknowledged as a key determinant of habitat in marine species (Buxton & Smale 1989, Friedlander & Parrish 1998, Demestre et al. 2000, Fitzpatrick et al. 2012, Heyns-

Veale et al. 2016). For this reason, inshore samples were obtained from the greatest possible range of depths within each of the three inshore protected areas. Samples from the corresponding exploited areas were limited to the same depth range. Offshore samples were obtained from across the shelf to the shelf edge at the greatest depths possible within the limitations of the available equipment. Depth was measured by means of an on-board echo-sounder (Garmin GPSMAP 8020XS fitted with AirMar TM150 chirp transducer) at each point at which stereo-BRUVs were deployed.

Temperature: Many fish are strongly adapted to specific temperature ranges and as a result the presence or abundance of some species may vary in response to fluctuating temperatures (Coutant 1987, Smale 1988, Buxton & Smale 1989, Clarke & Johnston 1999). A temperature logger (Onset Hobo) was attached to the stereo-BRUVs to take temperature measurements every five minutes. The average temperature over a thirty-minute period starting fifteen minutes after the stereo-BRUVs reached the seafloor was taken as the temperature reading for each sample, thus giving ample time for the logger to adjust to the ambient temperature.

Visibility: Fish rely extensively on vision for feeding, predator evasion, intra-species interaction and navigation (Guthrie 1986). As such water turbidity (visibility) affects fish behaviour (Thetmeyer & Kils 1995, Utne-Palm 2002) which can influence their abundance at a particular site. Poor visibility, in addition, impairs the ability to detect, identify and estimate the size of individual fish in video recordings. Maximum visibility for each sample was determined by measuring the furthest distance from the stereo-BRUVs at which an individual fish could be identified. This was carried out using the EventMeasure (Stereo) software (SeaGIS 2012). Samples with visibility of less than 1.5 m were excluded from the analysis as it was considered that the majority of individuals present would be undetected or unidentifiable.

% Water Column: The percentage of water column in the field of view gives an indication of the angle at which the cameras recorded. Since a high-angled field of view includes less substrate in the recording, this can limit the ability to detect species that are closely associated with the reef or sand, while a low angle limits detection of more pelagic species (Bernard & Götz 2012). The percentage water column was calculated from a single frame image of each deployment recording using the Vidana software package (Hedley 2003). Samples where the stereo-BRUVs frame came to rest on its side rather than upright, resulting in a ventral view of the fish filmed, or where the camera aimed directly at the substrate, were discarded.

% Obstruction: The percentage of the field of view obscured by physical obstructions such as reef outcrops or algal fronds directly affects the ability to detect and measure individual fish. Obstructions in the field of view between the camera and the bait canister were calculated in the same manner as the percentage water column above.

2.2.4.2 RESPONSE VARIABLES

To determine the effect of protection and depth on fish assemblages in the Amathole MPA and surrounds, the response in MaxN of the entire fish assemblage was analysed using multivariate statistics. Species richness and the MaxN, Total Biomass, and Max Biomass of selected species groups (Primary and Vulnerable fisheries species) and of species of particular conservation interest (*Petrus rupestris*, *Polysteganus undulosus* and *Chrysolephus cristiceps*) were investigated using univariate statistics to better understand the observed patterns.

Species Groups

Reef-associated fisheries species were grouped for univariate analysis. Schooling and wide-ranging pelagics (*Atractoscion aequidens*, *Pomatomus saltatrix*, *Scomber japonicus* and *Trachurus trachurus*) were excluded from the univariate analysis of Primary and Vulnerable Fisheries Species analysis groups, as the grouping was intended to evaluate the effect of the spatial closure on target reef fish, and the sporadic occurrence of large passing schools of pelagics was found to obscure results.

Primary Fisheries Species: Species considered to be primary targets of commercial and recreational fishing in South Africa were based on the classification by Heyns-Veale et al. 2019 (Table 2.1).

Vulnerable Fisheries Species: Species classified by Heyns-Veale et al. (2019) as either primary or secondary fishery targets in South Africa and that are listed as Vulnerable, Endangered, or Critically Endangered on the Red List by the International Union for Conservation of Nature (IUCN) (IUCN 2018) or are categorized as red (do not purchase) by the South African Sustainable Seafood Initiative (SASSI; WWF-SASSI 2018) (Table 2.1). Of the 17 Vulnerable Fisheries Species detected, four, namely *Chrysolephus cristiceps*, *Chrysolephus gibbiceps*, *Petrus rupestris*, and *Polysteganus undulosus* are listed by the IUCN as Endangered, or in the case of *P. undulosus* and *C. cristiceps* Critically Endangered, while another, the Atlantic wreckfish (*Polyprion americanus*), though listed as data deficient, is widely considered as endangered in South African waters and is included with *P. undulosus* on the prohibited species list (S.A. Government 1998). As such, these species are of particular conservation interest.

Table 2.1: List of primary fisheries species and vulnerable primary and secondary fisheries species (as per the classification by Heyns-Veale et al. 2019) identified in samples from the inshore Amathole Marine Protected Area and surrounding exploited areas.

Species	Primary Fisheries Target	Vulnerable Fisheries Target
<i>Argyrozona argyrozona</i>	Yes	
<i>Cheimerius nufar</i>	Yes	
<i>Chelidonichthys kumu</i>	Yes	
<i>Chrysoblephus cristiceps</i>	Yes	Yes
<i>Chrysoblephus gibbiceps</i>	Yes	Yes
<i>Chrysoblephus laticeps</i>	Yes	
<i>Chrysoblephus puniceus</i>	Yes	
<i>Cymatoceps nasutus</i>	Yes	Yes
<i>Diplodus capensis</i>	Yes	Yes
<i>Diplodus hottentotus</i>		Yes
<i>Epinephelus andersoni</i>	Yes	
<i>Epinephelus chabaudi</i>	Yes	
<i>Epinephelus marginatus</i>	Yes	Yes
<i>Gymnocrotaphus curvidens</i>		Yes
<i>Mustelus mustelus</i>	Yes	
<i>Pachymetopon aeneum</i>	Yes	
<i>Pachymetopon grande</i>		Yes
<i>Petrus rupestris</i>	Yes	Yes
<i>Polyprion americanus</i>	Yes	Yes
<i>Polysteganus praeorbitalis</i>	Yes	Yes
<i>Polysteganus undulosus</i>	Yes	Yes
<i>Pterogymnus lanarius</i>	Yes	
<i>Rhabdosargus globiceps</i>	Yes	Yes
<i>Rhabdosargus holubi</i>		Yes
<i>Rhabdosargus sarba</i>		Yes
<i>Sarpa salpa</i>	Yes	
<i>Umbrina sp.</i>		Yes

Response Variables

The response variables designated to analyse the composition, abundance and size structure of fish assemblages were species richness, relative abundance (MaxN), total biomass and maximum biomass. These metrics are defined as follows:

Species richness: Defined here as the number of species observed in each sample. While an increase in species richness can be indicative of the recovery of biodiversity within a protected area (Cote et al. 2001, Halpern & Warner 2002, Lester et al. 2009), depending on the state of the ecosystem prior to protection, the recovery of higher trophic levels can drive a decrease in the abundance of smaller prey fish within protected areas resulting in higher species counts in exploited areas (Edgar & Stuart-Smith 2009, Stobart et al. 2009, Maggs 2011).

MaxN: This parameter describes the relative abundance of each species in each sample, calculated by counting the maximum number of individuals of a species visible in the field of view in a single frame over the duration of the 60-min video sample. For univariate analysis of species groups, the MaxN of all species pertaining to the relevant group were summed for each sample.

The density of many fish species increases within MPAs (Buxton & Smale 1989, Lester et al. 2009, Halpern & Warner 2002, Micheli et al. 2004). However, a number of species exhibit a negative response to protection (Micheli et al. 2004), which can conceal responses from other species when carrying out analysis at community level (Edgar & Stuart-Smith 2009, Lester et al. 2009). Often, as the density of higher trophic level, predatory species increases, that of lower trophic level, prey species decreases (Graham et al. 2003, Willis & Anderson 2003, Micheli et al. 2004, Götz et al. 2009, Heyns-Veale 2019).

Total Biomass: Measured lengths of individual fish were converted to biomass estimates using length-weight conversion equations obtained from literature and FishBase (Mann 2013, Froese & Pauly 2018). The estimated masses of all individuals measured at MaxN were summed to calculate the Total Biomass of each species in each sample. Total Biomass values for groups of species were calculated by summing the Total Biomass values of all species in the group for each sample. Total Biomass, like MaxN from which it is derived, is a relative measure, only taking into account those individuals visible at maximum abundance. Despite this limitation, Total Biomass was considered a reasonable approximation of community biomass, which has been shown to be a more consistent indicator of density responses at community level for reef fish than abundance measures (Nash & Graham 2016).

The biomass of fish has been shown to increase in MPAs compared to exploited communities (Buxton & Smale 1989, Halpern & Warner 2002, Micheli et al. 2004, Lester et al. 2009). An increase in total biomass within protected areas can take place within a relatively short space of time after their establishment (Halpern & Warner 2002), while over longer periods of time the proportion of biomass attributable to

larger, longer-lived species from higher trophic levels increases (Gell & Roberts 2003, Micheli et al. 2004).

Max Biomass: Max biomass corresponded to the estimated biomass of the largest individual of a given species measured at MaxN in each sample. This variable was used to evaluate the responses of individual species to protection and depth. While Total Biomass takes into consideration the full size range of the population, Max Biomass looks specifically at the largest individuals. Since fish size is associated with fecundity (Birkeland & Dayton 2005, Hixon et al. 2014), Max Biomass was considered a better indicator of the effect of protection for spawner biomass than Total Biomass. As with Total Biomass, this measure is limited by the size range of individuals visible at MaxN. Though it is possible that larger individuals than those observed at MaxN were detected during the one hour deployment, it was not feasible to measure large individuals throughout the footage for all species. Max Biomass was nonetheless considered representative of variability in size over depth range and more informative for the single species analysis than Total Biomass.

2.2.4.3 COMMUNITY STATISTICS

Multivariate analyses of the response by fish assemblages to explanatory and environmental variables were carried out using Primer-e v6 (Clarke & Gorley 2006) with PERMANOVA add on (Anderson et al. 2008). Permutational Multivariate Analysis of Variance (PERMANOVA) (McArdle & Anderson 2001, Anderson 2001) was used to determine significant patterns in fish assemblage structure in response to explanatory variables. This routine uses permutations to perform geometric partitioning of multivariate response data to a suite of explanatory variables and their interactions. Pseudo-F statistics were calculated for each variable as an estimate of the contribution to overall variation of the response data and p-values as an estimate of the significance of these contributions. An estimate of the component of variation (ECV) for each term was calculated using the estimated mean squares for that term based on the resemblance matrix. This permits comparison of the relative contributions of terms towards the overall variation in the response variable. Since the estimates are based on squared values, the percentage contribution of each component toward overall variability was calculated using the square root of each estimate. The PERMANOVA routine by default partitions data according to all terms stipulated in the experimental design and their interactions. In cases where the component of variation for a term or interaction was negative, or the p-value greater than 0.25, the term was “pooled” such

that the component of variation for the specified term is set to zero and those for the remaining terms recalculated. This was carried out sequentially for each term meeting the exclusion criteria, starting with the term with the lowest mean square (Anderson et al. 2008).

To account for differences in environmental variables and experimental artefacts between stereo-BRUVs samples, continuous covariates were fitted before testing for the main effects in a sequential PERMANOVA. Analyses were based on 999 permutations under reduced model and type I (sequential) sum of squares. Type I sum of squares also permits analysis of data in an unbalanced experimental design (Anderson et al. 2008). The resemblance matrix for the multivariate response data (MaxN, and Total Biomass) was generated using the modified-Gower resemblance measure, transformed to the log base 10. The log transformation of values prior to calculating resemblance places greater emphasis on presence-absence structure than straightforward count data. This provides insight into compositional changes in fish assemblage structure, essentially weighting the contributions of common and rare species for multivariate representations (Anderson et al. 2006). To further investigate significant interactions between variables, pairwise comparisons were performed (Anderson et al. 2008). The distributions of continuous covariates were examined by means of paired scatter plots and those found to display asymmetric distribution (depth, visibility and % obstruction) were square root transformed in order to make them appropriate for use in Euclidean distance measurements (Clarke & Warwick 2001).

The PERMDISP routine was used to test homogeneity of dispersions around the centroid for groups within each variable, based on the previously calculated modified-Gower resemblance matrices. Although PERMANOVA analysis makes the assumption that dispersions are relatively constant across groups (Anderson 2006), a non-significant result from the PERMDISP routine was not considered essential in order to continue with PERMANOVA analysis since PERMDISP is capable of detecting differences in dispersion that may not adversely affect the PERMANOVA results (Anderson et al. 2008, Anderson & Walsh 2013). Rather, the PERMDISP results were used to expose patterns in the variability among samples that might contribute towards statistical results.

Multidimensional scaling techniques were used to visualise potential differences between groups. These ordinations represent dissimilarities between points or samples in the modified-Gower resemblance matrices as Euclidean distances in a reduced number of dimensions (Kruskal 1964). Non-metric multidimensional scaling (nMDS) is an unconstrained ordination technique based on the rank order of dissimilarities between data points, which can reveal overall patterns in the data cloud as well as within-group variability (Anderson & Willis 2003, Anderson et al. 2008). How well the distances in the Euclidean

space represent the actual rank order of dissimilarities is reflected in the stress criterion (Anderson et al. 2008). Clarke (1993) suggested that stress values below 0.2 represent a fair fit, below 0.15 a good fit, and below 0.1 ideal. Canonical Analysis of Principal Coordinates (CAP) is a constrained ordination technique used to perform discriminant analysis, which finds the axes most correlated with *a priori* groups (Anderson & Willis 2003). This is particularly useful when significant differences between groups have been detected, but the direction of those differences is masked by the direction of the total greatest variation in the data cloud (Anderson & Willis 2003). The CAP routine provides a delta value (δ) indicative of the strength of association between the multivariate data cloud and the grouping, an estimation of the amount of total variability explained by the ordination axes, and cross-validation results, indicating to what extent the model was able to accurately distinguish between groups and where it was inaccurate (Anderson et al. 2008). Non-metric multidimensional scaling was used to examine general patterns in the variability between samples. Canonical Analysis of Principal Coordinates was carried out to further clarify the association between the ordination and the grouping variable, since the influence of substrate was at times so dominant as to obscure groupings defined by other variables, and in order to infer about the strength of the grouping variable. Ordination plots were overlaid with vectors representing linear relationships of species associated with ordination axes by a Spearman's correlation of 0.4 or above to gain insight into the species associated with different groupings (Anderson et al. 2008). Lastly, the SIMPER routine (similarity percentage breakdown) was used to analyse the contribution of individual species to differences between groups, based on Bray-Curtis similarity measures of log-transformed response data (Clarke 1993).

2.2.4.4 UNIVARIATE STATISTICS

The effects of explanatory variables on the univariate response variables were tested using generalised linear models (GLMs) in the R statistical environment (RStudio Team 2016, R Core Team 2017). Preparatory data exploration for selection of statistical models was carried out using established methods (Zuur et al. 2010, Zuur et al. 2013). Values of explanatory and response variables were inspected for outliers by means of boxplots and Cleveland dotplots. As all outlying values were determined to be due to natural variation in the data rather than experimental error, no samples were excluded from the analysis. A matrix of scatterplots pairing values of continuous covariates against one another was used along with variance inflation factors to check for possible collinearity between these, while collinearity between continuous and categorical covariates was assessed with boxplots. Where collinearity was found to have a detrimental effect on the model the covariate with the higher VIF was

eliminated. Effects of individual covariates on the response variable were assessed using boxplots and dotplots, and interaction between explanatory variables of main effects and covariates assessed using multi-panel scatterplots. Zero-inflation and sampling bias were also assessed before describing the full explanatory model. This exploratory analysis was used to inform the choice of model used and the terms included in the full models.

Optimisation of the model was carried out by sequential removal of terms according to the results of a likelihood-based ratio test (Drop1 routine), investigation of homogeneity and dispersion by means of diagnostic plots of residuals and selection of the model with the lowest Akaike Information Criterion (AIC) score (Akaike 1974). Variables were successively discarded from individual models as indicated by optimisation procedures to determine the best-fit reduced model, which differed according to the response variable and species or species group under consideration. Sequential likelihood ratio tests were carried out to compare the deviance explained by the optimised and saturated models.

For species richness and MaxN models a Poisson distribution was applied initially to the GLM and the dispersion statistic of the optimal model calculated. Where data was found to be over-dispersed a Negative-Binomial distribution was applied instead (Zuur et al. 2013). For Total Biomass models, a Tweedie distribution was applied in order to account for the high frequency of zeros, right-skewed data (Tweedie 1984, Winker et al. 2014). The index parameter (p) for each model was assigned by selection of the model with the lowest AIC score. The MaxN and Max Biomass of single species were modelled using Hurdle modelling (Cragg 1971, Mullahy 1986). This type of model addresses zero-inflation by modelling responses based only on data where the species in question was detected, predicting overall detection probability separately. The Hurdle model consisted of a binomial Generalized Linear Model (GLM) of presence-absence data to predict detection probability. Thereafter a Poisson or Negative-Binomial distribution was used to model MaxN where the species of interest was detected and Tweedie distribution for Max Biomass. An analysis of deviance was carried out on each model using sequential likelihood ratio tests, to determine whether variables made significant contributions to the overall variability explained by the model. The percentage of variability explained by the model was calculated as $1 - (\text{residual deviance} / \text{null deviance})$, and the percentage contribution of each term to the variability explained by the model was calculated as the deviance for that term divided by the total deviance explained by the model. Model summaries were used to detect the direction of variation attributed to each variable by means of coefficient estimates. To assist interpretation, predicted values of variables found to be significant in the analysis of deviance were plotted, based on the standard average value of

each one. Non-significant variables were excluded to ensure that the effects of explanatory variables were not distorted.

3 COMPARISON OF FISH ASSEMBLAGES IN THE INSHORE AMATHOLE MARINE PROTECTED AREA AND ADJACENT EXPLOITED AREAS

3.1 INTRODUCTION AND AIM

The inshore Amathole MPA meets several of the criteria thought to influence the success of a marine reserve in achieving conservation and fisheries objectives. Although only officially declared as an MPA in 2011, the historical voluntary enforcement of the no-take areas on the part of local ski-boat fishermen created a sense of responsibility and pride that no doubt continues to assist in the success of the inshore Amathole MPA. Where often generating stakeholder support for closed areas can be a major obstacle in their implementation (Ballantine 2014, Giakoumi et al. 2018), in the case of the inshore Amathole MPA, it was a key public stakeholder that advocated for their establishment. In addition, the voluntary enforcement of the no-take areas prior to proclamation of the MPA means that the area has benefitted from a respite from fishing pressure for decades longer than it has received official recognition or budget for enforcement. The duration of protection is paramount in allowing time for fish stocks to recover (Edgar et al. 2014, Russ & Alcala 2004), particularly so for large species, which can take longer to recover (Micheli et al. 2004). This extended enforcement of fishing closure in the inshore Amathole MPA may have provided valuable time needed for target species to recover.

On the other hand, the fact that that only one stakeholder group, the recreational ski-boat fishermen, participated in the original establishment of the MPA may have resulted in the omission of necessary diligence to ensure that maximum benefits could be obtained in terms of fisheries and conservation objectives. When planning MPAs objectives need to be realistic and clearly defined, such that careful design and planning of the protected area allows for a high probability of meeting them (Agardy 2017). In the case of the inshore Amathole MPA, the objective of the ski-boat fishermen in setting out the closed areas was to protect inshore reefs from over-fishing (John Rance, BDSAA, pers. comm.). The objectives defined in 2011 when the areas were set out as an MPA by the then Department of Environmental Affairs were amended to include conservation of the marine environment and marine biodiversity in the Amathole region, provision of sanctuary for species impacted by boat-based exploitation, provision of benchmark areas for scientific research and monitoring, and the reduction of habitat degradation in the area (DEA, 2011). However, no research was carried out at the time to

establish whether the three protected areas comprising the inshore Amathole MPA were appropriately designed to meet these new fisheries and biodiversity management objectives.

The size of a protected area significantly influences its ability to provide sanctuary to target species (Gell & Roberts 2003, Agardy et al. 2011). The inshore Amathole MPA covers 54 km of coastline and almost 250 km² of ocean surface (WWF SA 2018), but this area is split into three separate protected areas, isolated from one another by exploited areas larger than the protected areas cover individually. Previous studies suggest that the benefits of MPAs are stronger with greater degrees of isolation from similar habitats and exploited areas (Edgar et al. 2014), and that the fragmented distribution of the areas comprising the inshore Amathole MPA may lead to habitual movement of fish outside the boundaries of the reserve, exposing them to exploitation and diminishing the ability of stocks to recover in the protected areas (Malcolm Smale, unpublished data). However, the necessary size required for an MPA to provide refuge to vulnerable species is also dependent on the size and behaviour of the target species (Edgar et al. 2014, Lester et al. 2009). If the size of the protected area is in reasonable excess of the home range of target species it is possible that this will allow for recovery of stock within a limited area (Gell & Roberts 2003, Götz et al. 2009, Afonso et al. 2011, Di Franco et al. 2018). Likewise, if the protected area incorporates parts of the habitat of target species occupied during vulnerable life-stages, such as spawning aggregations, nursery areas or areas preferred by sexually mature individuals, it can still be consequential for the conservation of these species (Edgar et al. 2014, Gell & Roberts 2003).

A large proportion of species targeted by ski-boat fishermen in the Amathole region belong to the seabream or sparid family (*Sparidae*), many of which are known to be highly resident (Mann 2013). It is, therefore, plausible that although limited in their extent, the three areas making up the inshore Amathole MPA provide adequate area for recovery of some of these species. However, residency may limit the effects of enhanced recruitment in the protected areas if density-dependent interactions result in the movement of individuals outside of the borders of the reserve (Abesamis & Russ 2005, Götz et al. 2009, Baskett et al. 2011, Kerwath et al. 2013, Thorson et al. 2016). The Amathole region is central in the distribution of dageraad (*Chrysoblephus cristiceps*), seventyfour (*Polysteganus undulosus*) and red steenbras (*Petrus rupestris*). In particular, adults of *P. rupestris* are thought to make a once-off migration to the area where they remain for the rest of their reproductive lives (Hecht & Buxton 1993, Brouwer 2002). As such, the inshore Amathole MPA is ideally placed to protect spawner biomass of these endangered species.

Bathymetric data and anecdotal evidence from local ski-boat fishermen allude to irregular distribution of reef complexes in the inshore Amathole MPA and surrounding exploited areas, with corresponding irregularity in the presence of reef fish. Inopportune placement of the protected area would be counterproductive, since reef complexes suited to supporting species of interest are frequent and extensive in the area. The inclusion of large areas unsuitable to species of interest can skew estimations of the effectiveness of the protected areas while unnecessarily inconveniencing stakeholders (Agardy et al. 2011).

In order to assess the influence of the aforementioned factors on reef fish in the inshore Amathole MPA, several measures of the fish assemblage structure were compared between the protected areas and the adjacent exploited areas of comparable depth and habitat. This method of measuring the impact of MPAs on fish has been employed successfully in previous studies of a similar nature in South Africa (Buxton & Smale 1989, Götz et al. 2009, Maggs et al. 2013, Heyns-Veale et al. 2019) and further afield (Willis & Anderson 2003, Micheli et al. 2004, Watson et al. 2007). Fishing is known to have significant effects on the size and density of target species (Buxton & Smale 1989, Buxton 1993, Law 2000, Conover & Munch 2002, Götz et al. 2009) and as such these measures are often used as indications of the effectiveness of MPAs in providing sanctuary to these species (Côte et al. 2001, Halpern 2003, Lester et al. 2009).

Therefore, considering the small and fragmented design of the inshore Amathole MPA and the lack of supporting data at the time of its designation, the aim of this research chapter was to determine whether the inshore Amathole MPA supports greater diversity of reef fishes and higher abundances and biomass of target species, with consideration of the distribution of suitable habitat as a determining factor in meeting this objective. In particular, the objectives were

- i) to determine the effect of protection on the abundance (MaxN) of the entire fish assemblage by comparing the multivariate response of the fish assemblage data between the protected and exploited areas at each of the three locations of the inshore Amathole MPA.
- ii) to investigate the effect of protection on the diversity of fish species by comparing species richness between the protected and exploited areas at each location of the inshore MPA.

- iii) and finally to further explore the effect of protection on Primary and Vulnerable Fisheries Species groups by comparing MaxN and Total Biomass between the protected and exploited areas at each location of the inshore MPA.

3.2 METHODS

Data collected from the inshore Amathole MPA and adjacent inshore exploited areas were analysed for variation in MaxN, and Total Biomass in response to the explanatory variables management (*protected* and *exploited*), location (*Gxulu*, *Gonubie*, and *Kei*) and substrate (*sand* and *reef*). Response variables and explanatory variables are defined in section 2.2.4 of Chapter 2.

3.2.1 COMMUNITY ANALYSIS

Multivariate analysis of MaxN of all observed species was carried out to test for differences in fish assemblages based on management (*protected* or *exploited*) as detailed in section 2.2.4.3 of the methods chapter. Homogeneity of dispersion was tested using the PERMDISP routine in order to infer about the causes for differences detected in subsequent tests. Sequential PERMANOVA was used to test whether different fish assemblages characterise *protected* and *exploited* areas. The continuous covariates % water column, % obstruction, visibility, temperature, and depth followed by the categorical variables; substrate, location and management were added, in that order, to the analyses. To visualise the groupings according to management and to identify species correlated to the groupings, nMDS analysis was carried out. This was followed by CAP analysis to provide insight into the strength of the grouping variables as predictors. Finally, the contribution of individual species to the observed differences between *protected* and *exploited* areas was determined by the SIMPER routine.

3.2.2 UNIVARIATE ANALYSIS

Univariate GLMs were used to model the influence of management on species richness and on the abundance and biomass of species groups. Data exploration revealed collinearity between depth and visibility, resulting in spurious results in models. As such the term visibility was omitted from the analyses (Zuur et al. 2010). The responses in species richness and MaxN and Total Biomass of Primary and Vulnerable Fisheries Species were modelled using GLMs. The continuous covariates % water column, % obstruction, temperature and depth followed by the categorical variables location, substrate, management and the interaction between location and management were included, in that order, in the saturated model for each analysis.

The resultant saturated model, prior to the elimination of terms took the form:

$$f(\text{response variable}) = \alpha + \beta_1(\% \text{ water column}) + \beta_2(\% \text{ obstruction}) + \beta_3(\text{temperature}) + \beta_4(\text{depth}) + \beta_5(\text{substrate}) + \beta_6(\text{location}) + \beta_7(\text{management}) + \beta_8(\text{location} \times \text{management}) + \varepsilon \quad \text{Eq. 1}$$

Where α is the intercept, β_i refers to the regression coefficients, and ε is the noise (Zuur et al. 2013).

Analysis of deviance was carried out on the optimised models to determine which of the included terms significantly influenced variability in the data. Model summaries were used to examine the direction of influence of each term and to calculate the relative contribution of each one to overall variability. Predicted response values for standard average values of significant variables were then plotted to visualise the response.

3.3 RESULTS

3.3.1 SAMPLING SPREAD AND FOOTAGE SUCCESS

One hundred and forty-nine stereo-BRUVs samples were collected from the three protected areas comprising the inshore Amathole MPA and corresponding inshore exploited areas, from depths between 12 and 65 m. Poor visibility, technical errors, and inappropriate camera angle (where the system landed with the camera aimed either at the substrate or the surface) rendered 33 samples unsuitable for MaxN analysis and 41 samples unsuitable for length analysis. This resulted in an unbalanced distribution of the remaining samples between the levels of the factors substrate, location, and management, with more samples from *reef* substrate than *sand*, more from *protected* management areas than from *exploited* and more from *Gonubie* than *Gxulu* or *Kei* locations (Table 3.1).

Table 3.1: Distribution of baited remote underwater stereo-video samples in the Amathole Marine Protected Area and adjacent exploited areas of comparable depth range suitable for abundance and length analysis according to management (*protected* and *exploited*), location (*Gxulu*, *Gonubie* and *Kei*) and substrate (*sand* and *reef*). The number of successful samples is given in each case.

		<i>Gxulu</i>		<i>Gonubie</i>		<i>Kei</i>	
		Abundance	Length	Abundance	Length	Abundance	Length
<i>Exploited</i>	<i>Sand</i>	3	3	6	6	1	0
	<i>Reef</i>	13	12	17	16	4	3
<i>Protected</i>	<i>Sand</i>	11	11	12	11	9	9
	<i>Reef</i>	5	4	20	18	15	15

3.3.2 GENERAL OVERVIEW

In the 116 inshore samples analysed for MaxN, 74 species were detected. Fifty-three species of bony fish were detected (25 of these from the sparid family) and 21 were cartilaginous species (Table 3.2). There were, on average, nine species detected per sample, with a standard deviation of four species.

Small to medium-sized fish were most abundant in the inshore samples. Fransmadam (*Boopsoidea inornata*), panga (*Pterogymnus laniarius*), blue hottentot (*Pachymetopon aeneum*), sand soldier (*Pagellus bellottii natalensis*), maasbanker (*Trachurus trachurus*), piggy (*Pomadasys olivaceum*), and steentjie (*Spondylisoma emarginatum*) were the most numerous species (Table 3.3). Though large and vulnerable fisheries species tended to be less dominant in the inshore samples, *C. cristiceps* was among

the most abundant species in *protected* areas and *C. laticeps* was among the most abundant in *exploited* areas.

Table 3.2: Summary of results from stereo-BRUVs sampling of the inshore Amathole Marine Protected Area and adjacent inshore exploited areas.

	Total	Protected	Exploited
<i>Suitable Samples</i>	116	72	44
<i>Total Species</i>	74	63	65
<i>Osteichthyes</i>	53	44	46
<i>Sparidae</i>	25	23	21
<i>Chondrichthyes</i>	21	19	19
<i>Unique Species</i>	NA	9	11
<i>Ave Species Richness (± SD)</i>	9 ± 4	10 ± 4	8 ± 4
<i>Max Species Richness</i>	21	21	18

Table 3.3: Summary of the most abundant species in the inshore Amathole Marine Protected Area and adjacent inshore exploited areas. The 10 most abundant species from exploited and protected areas are listed. The average (Ave.) MaxN per sample is given with standard deviation (SD) for each species. Species are listed in descending order of overall abundance.

Species	Ave. MaxN ± SD Exploited	Ave. MaxN ± SD Protected
<i>Boopsoidea inornata</i>	16.1 ± 31.3	5.2 ± 8.7
<i>Pterogymnus lanarius</i>	2.6 ± 0.1	1.8 ± 0.0
<i>Pachymetopon aeneum</i>	5.5 ± 0.0	3.7 ± 0.0
<i>Pagellus bellottii natalensis</i>	2.3 ± 0.1	9.4 ± 0.2
<i>Trachurus trachurus</i>	9.2 ± 0.3	1.6 ± 0.6
<i>Pomadasys olivaceum</i>	6.1 ± 8.9	2.8 ± 4.2
<i>Spondyliosoma emarginatum</i>	5.1 ± 0.2	1.8 ± 0.3
<i>Chrysoblephus laticeps</i>	2.1 ± 0.2	1.4 ± 0.3
<i>Galeichthys feliceps</i>	1.0 ± 0.0	1.6 ± 1.5
<i>Chrysoblephus cristiceps</i>	0.7 ± 0.3	1.4 ± 0.0
<i>Galeichthys ater</i>	1.1 ± 0.1	0.1 ± 0.1

3.3.3 COMMUNITY ANALYSIS - MAXN

PERMDISP results indicated homogeneity of variance for the variables location and management, and heterogeneity of variance for the variable substrate, with higher levels of multivariate dispersion on *reef* substrate than on *sand* (Table A. 1). PERMANOVA analysis indicated that management, location,

substrate, and the interaction between location and management all significantly contributed to variability in MaxN data (Table 3.4). The effect of substrate on the fish assemblage structure was consistent among the levels of location ($p = 0.12$). Pairwise analysis of management within location identified significant differences in the fish assemblage structure between *protected* and *exploited* areas in the *Gonubie* and *Gxulu* locations, but not at *Kei* (Table A. 2). The majority of variability in MaxN data was attributed to substrate (19.33 %) (Table A. 3). Though the contributions of management and location were considerably less than that of substrate, the interaction between them was more influential than either factor alone, contributing 8.69 % to total variability (Table A. 5).

Table 3.4: Results of sequential PERMANOVA analysis to test for effects of substrate, location, and management on fish assemblage structure in the inshore Amathole Marine Protected Area and adjacent inshore exploited areas based on MaxN data. df = degrees of freedom; SS = sum of squares, MS = mean square; Pseudo-F = F-ratios; P (perm) = probability, Unique perms = number of unique permutations.

Source	df	SS	MS	Pseudo-F	P(perm)	Unique perms
% Water column	1	1.266	1.266	2.457	0.002	999
% Obstruction	1	2.322	2.322	4.506	0.001	996
Visibility	1	2.608	2.608	5.061	0.001	999
Temperature	1	2.243	2.243	4.353	0.001	996
Depth	1	3.936	3.936	7.638	0.001	999
Location x Substrate	2	2.142	1.071	1.290	0.117	996
Location x Management	2	2.989	1.495	2.357	0.003	997
Substrate	2	2.136	1.068	2.073	0.002	994
Location	1	9.159	9.159	17.774	0.001	998
Management	1	1.306	1.306	2.535	0.004	996
Pooled	102	52.560	0.515			
Total	115	82.668				

Though nMDS of MaxN data clearly discriminated between substrate groups, no distinction between management groups was apparent (Figure 3.1). The CAP analysis with management and substrate defined as *a priori* groups showed clear separation of fish assemblages according to substrate along CAP axis 1 ($\delta = 0.897$), while the separation according to management groups along CAP axis 2 was more defined on *reef* substrate than on *sand* ($\delta = 0.452$). Species strongly associated with *sand* substrate were the tiger catshark (*Halaelurus natalensis*), hammerhead sharks (*Sphyrna sp.*), evileye pufferfish (*Amblyrhynchotes honckenii*), white sea catfish (*Galeichthys feliceps*), and the lesser guitarfish (*Rhinobatos annulatus*). Of the species associated with *reef* substrate, black sea catfish (*Galeichthys*

ater) and the pyjama shark (*Poroderma africanum*) showed the strongest association to *exploited* areas while *C. cristiceps* was strongly associated with *protected* areas. The association of *C. laticeps* and *P. aeneum* were indistinct. CAP analysis identified 17 axes explaining 80.17 % of the variation in MaxN data, with 71.55 % of samples accurately classified according to substrate (*reef* or *sand*) and management (*protected* or *exploited*; Table 3.5). The higher percentage of accurate classifications on *reef* substrate, regardless of management status, indicated that fish assemblages on *reef* substrate were more homogenous than those on *sand* substrate, consistent with PERMDISP results (Table A. 1).

Table 3.5: Results of cross-validation results of canonical analysis of principal coordinates (CAP) based on modified-Gower Log10 resemblance matrix of MaxN data, indicating degree of accuracy of classification of samples according to substrate and management.

Original Group	Predicted Group				Total	% correct
	Reef Protected	Reef Exploited	Sand Protected	Sand Exploited		
Reef Protected	30	7	2	1	40	75
Reef Exploited	8	24	0	2	34	71
Sand Protected	3	0	22	7	32	69
Sand Exploited	1	0	2	7	10	70

The SIMPER results indicated that on *reef* substrate, fish assemblages in *protected* and *exploited* areas were distinguished primarily by the abundance of smaller sparids in *exploited* areas, such as *B. inornata*, *P. aeneum*, steentjie (*Spondyliosoma emarginatum*), panga (*Pterogymnus laniarius*) and *P. olivaceum* (Table 3.6). *Protected* areas were defined in particular by the abundance of *P. bellottii natalensis* and *C. cristiceps* (Table 3.6). Two Primary Fisheries Species, *P. aeneum* and *C. laticeps*, consistently defined *reef* assemblages, regardless of management status (Table 3.6). A third, *C. cristiceps*, was a defining species for *reef* assemblages in *protected* areas. The absence of fisheries species on *sand* substrate, and their abundance on *reef* substrate, was the defining difference between fish assemblages in the two substrate groups (Table 3.6). In addition, assemblages on *sand* substrates were characterised by the presence of *P. bellottii natalensis*, *G. feliceps*, *R. annulatus* and *H. natalensis*. *Protected sand* communities were distinguished from *exploited* ones in particular by the presence of *R. annulatus* (Table 3.6).

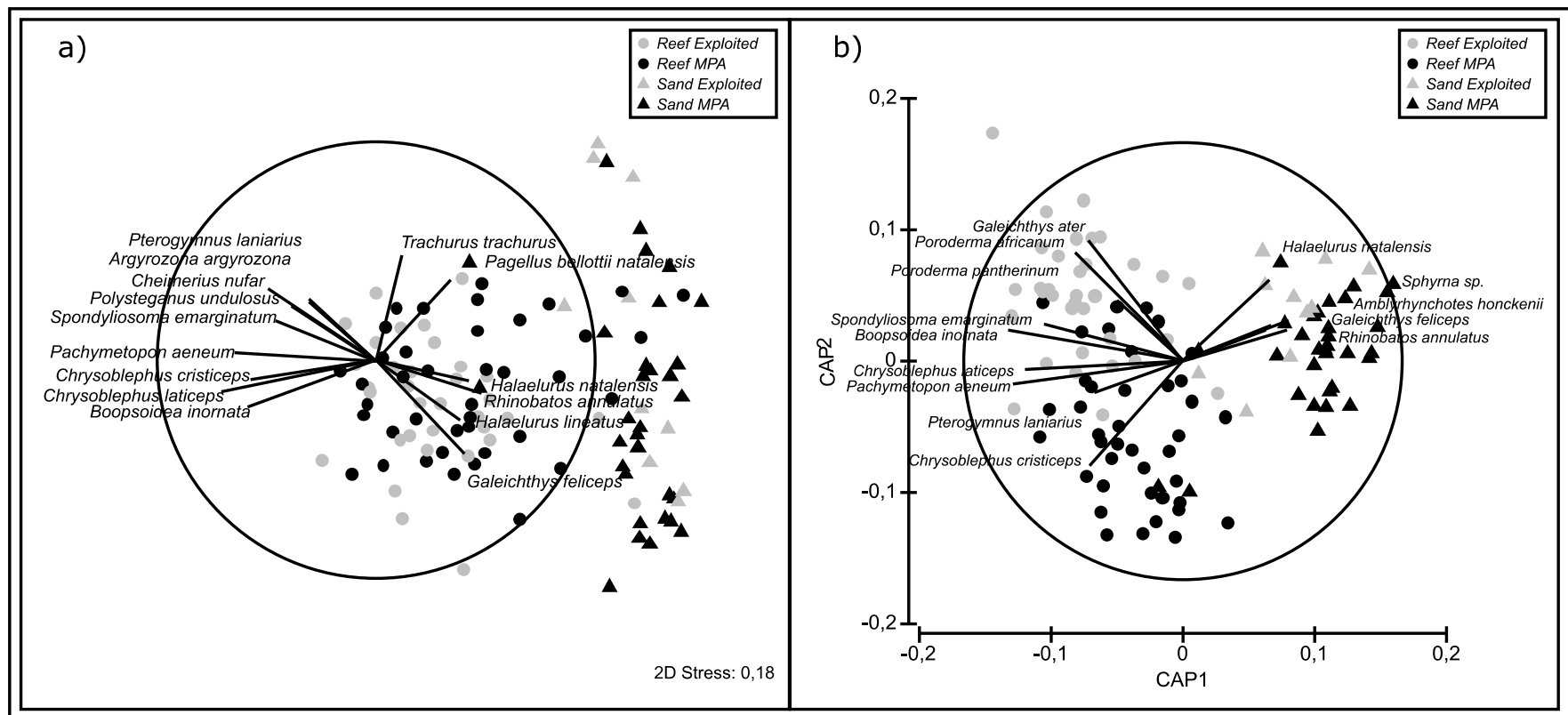


Figure 3.1: Multidimensional ordination plots based on modified-Gower Log10 resemblance matrix of MaxN data of fish assemblages in the Amathole Marine Protected Area and nearby exploited areas, illustrating grouping of samples according to substrate (*reef* or *sand*) and management (*protected* or *exploited*). Species showing a Spearman's correlation of 0.4 or above with ordination axes are represented by vectors overlaid on the plots. a) Non-metric Multidimensional Scaling (nMDS) b) Canonical Analysis of Principal Coordinates (CAP).

Table 3.6: Results of SIMPER analysis of log-transformed MaxN data of fish assemblages in the inshore Amathole Marine Protected Area and adjacent exploited areas, detailing contributions of individual species to within-group similarities (Ave. sim; white cells) and between-group dissimilarities (Ave. dissim; grey cells) for management and substrate groups (exploited/ protected and sand/reef). The contributions (% cont) of those species making up the first 50 % of similarities or dissimilarities are listed in each case. The average abundance (Av.) for each species is given. Species that were more abundant in protected areas are highlighted in grey.

	Sand Protected (SP) Av. sim 24.19				Reef Protected (RP) Av. sim 33.42				Sand Exploited (SE) Av. sim 31.1			Reef Exploited (RE) Av. sim 43.21			
Sand Protected	Species	Av.	% cont		Av. dissim 90.17				Av. dissim 73.79			Av. dissim 90.93			
	<i>G. feliceps</i>	0.86	30.67												
	<i>P. natalensis</i>	1.55	28.42												
Reef Protected	Species	Av. RP	Av. SP	% cont	Species	Av.	% cont		Av. dissim 88.89			Av. dissim 64.05			
	<i>P. natalensis</i>	0.8	1.55	9.4	<i>P. aeneum*</i>	1.53	19.3								
	<i>B. inornata</i>	1.62	0.08	9.04	<i>B. inornata</i>	1.62	19.15								
	<i>P. aeneum*</i>	1.53	0.06	8.14	<i>C. cristiceps**</i>	0.97	11.67								
	<i>G. feliceps</i>	0.29	0.86	5.81	<i>C. laticeps*</i>	0.94	10.32								
	<i>C. cristiceps**</i>	0.97	0.05	5.47	<i>P. natalensis</i>	0.8	7.84								
	<i>C. laticeps*</i>	0.94	0.04	5.01	<i>S. emarginatum</i>	0.84	7.43								
	<i>S. emarginatum</i>	0.84	0.12	4.77											
	<i>P. lanarius*</i>	0.84	0.08	4.72											
Sand Exploited	Species	Av. SE	Av. SP	% cont	Species	Av. SE	Av. RP	% cont	Species	Av.	% cont	Av. dissim 88.59			
	<i>P. natalensis</i>	1.45	1.55	15.42	<i>B. inornata</i>	0	1.62	8.46	<i>P. natalensis</i>	1.45	29.02				
	<i>T. trachurus</i>	1.61	0.44	13.79	<i>T. trachurus</i>	1.61	0	7.82	<i>G. feliceps</i>	0.87	18.26				
	<i>G. feliceps</i>	0.87	0.86	9.82	<i>P. aeneum*</i>	0	1.53	7.74	<i>T. trachurus</i>	1.61	13.03				
	<i>P. olivaceum</i>	1.02	0.32	8.81	<i>P. natalensis</i>	1.45	0.8	7.18	<i>H. natalensis</i>	0.58	11.4				
	<i>H. lineatus</i>	0.59	0.29	6.95	<i>P. olivaceum</i>	1.02	0.5	6.02							
					<i>G. feliceps</i>	0.87	0.29	5.42							
					<i>C. cristiceps**</i>	0	0.97	5.1							
					<i>C. laticeps*</i>	0	0.94	4.72							
					<i>P. lanarius*</i>	0.14	0.84	4.56							
Reef Exploited	Species	Av. RE	Av. SP	% cont	Species	Av. RE	Av. RP	% cont	Species	Av. RE	Av. SE	% cont	Species	Av.	% cont
	<i>B. inornata</i>	2.67	0.08	13.23	<i>B. inornata</i>	2.67	1.62	9.38	<i>B. inornata</i>	2.67	0	12.8	<i>B. inornata</i>	2.67	30.82
	<i>P. aeneum*</i>	1.68	0.06	8.05	<i>P. aeneum*</i>	1.68	1.53	6.65	<i>P. aeneum*</i>	1.68	0	7.82	<i>P. aeneum*</i>	1.68	16.42
	<i>P. natalensis</i>	0.61	1.55	7.48	<i>S. emarginatum</i>	1.42	0.84	6.64	<i>T. trachurus</i>	0.13	1.61	7.18	<i>C. laticeps*</i>	1.15	11.73
	<i>S. emarginatum</i>	1.42	0.12	6.82	<i>P. lanarius*</i>	0.94	0.84	6.16	<i>S. emarginatum</i>	1.42	0.07	6.32			
	<i>C. laticeps*</i>	1.15	0.04	5.66	<i>P. olivaceum</i>	0.8	0.5	5.88	<i>P. olivaceum</i>	0.8	1.02	6.23			
	<i>P. olivaceum</i>	0.8	0.32	4.87	<i>P. natalensis</i>	0.61	0.8	5.34	<i>P. natalensis</i>	0.61	1.45	6			
	<i>G. feliceps</i>	0.26	0.86	4.73	<i>C. cristiceps**</i>	0.42	0.97	4.92	<i>C. laticeps*</i>	1.15	0	5.46			
					<i>C. laticeps*</i>	1.15	0.94	4.75							
					<i>C. nufar*</i>	0.5	0.48	3.61							

* Primary Fisheries Species

** Vulnerable Fisheries Species

3.3.4 SPECIES RICHNESS

The GLM for species richness (defined here as the number of species detected per sample) was fitted with a Poisson distribution. Model selection resulted in the exclusion of the terms % water column, % obstruction and depth (AIC: Full model = 576.7, Best-fit: 574.5 with no difference in deviance explained between models ($p = 0.4$)), resulting in the best-fit model:

$$f(\text{Species Richness}) = \alpha + \beta_1(\text{temperature}) + \beta_2(\text{substrate}) + \beta_3(\text{location}) + \beta_4(\text{management}) + \beta_5(\text{location} \times \text{management}) + \varepsilon \quad \text{Eq. 2}$$

Where α is the intercept, β_i refers to the regression coefficients, and ε is the noise (Zuur et al. 2013).

The best-fit GLM for species richness (Eq. 2) explained 55.73 % of total variability in species richness. Sequential likelihood ratio tests indicated that patterns in species richness were determined by temperature, substrate, and location (Table 3.7). The effect of management and the interaction between location and management were not significant.

Table 3.7: Results of sequential likelihood ratio tests on the best-fit Generalized Linear Model for effects of temperature, substrate, location, management and the interaction between location and management on species richness in the inshore Amathole Marine Protected Area and adjacent inshore exploited areas. df = degrees of freedom; PR(>Chi) = P-value; Relative contribution (%) = contribution of each term to overall variability explained by the model

	df	Residual Deviance	Residual df	Deviance	Pr(>Chi)	Relative contribution (%)
NULL			115	232.02		
Temperature	1	11.168	114	220.85	<0.001	8.64
Substrate	1	98.073	113	122.78	<0.001	75.84
Location	2	18.505	111	104.27	<0.001	14.31
Management	1	0.328	110	103.94	0.567	0.25
Location x Management	2	1.237	108	102.71	0.539	0.96

Gonubie and *Kei* locations were both associated with a lower species richness than *Gxulu* location (mean \pm SD; *Gxulu*: 10 ± 4 ; *Gonubie*: 9 ± 4 ; *Kei*: 7 ± 4 ; Table 3.8). The decrease in species richness relative to *Gxulu* location was significant in the *Kei* location but not in *Gonubie* (Figure 3.2). *Sand* substrate was

associated with a decrease in species richness relative to *reef* (*sand*: 6 ± 6 ; *reef*: 11 ± 4 ; Table 3.8, Figure 3.2).

Table 3.8: Output summary of Generalized Linear Model describing the influence of temperature, substrate, location, management and the interaction between location and management on variability in species richness in the inshore Amathole Marine Protected Area and adjacent inshore exploited areas. Estimate = coefficient estimate; Std. Error = standard error of estimate; $Pr(>|z|)$ = P-value

Coefficients:	Estimate	Std. Error	z value	Pr(> z)
Intercept	1.483	0.268	5.530	<0.001
Temperature	0.073	0.018	4.046	<0.001
<i>Sand</i>	-0.689	0.078	-8.876	<0.001
<i>Gonubie</i>	-0.164	0.102	-1.604	0.109
<i>Kei</i>	-0.442	0.178	-2.489	0.013
<i>Protected</i>	-0.159	0.128	-1.243	0.214
<i>Gonubie Protected</i>	0.175	0.160	1.093	0.274
<i>Kei Protected</i>	0.161	0.225	0.716	0.474

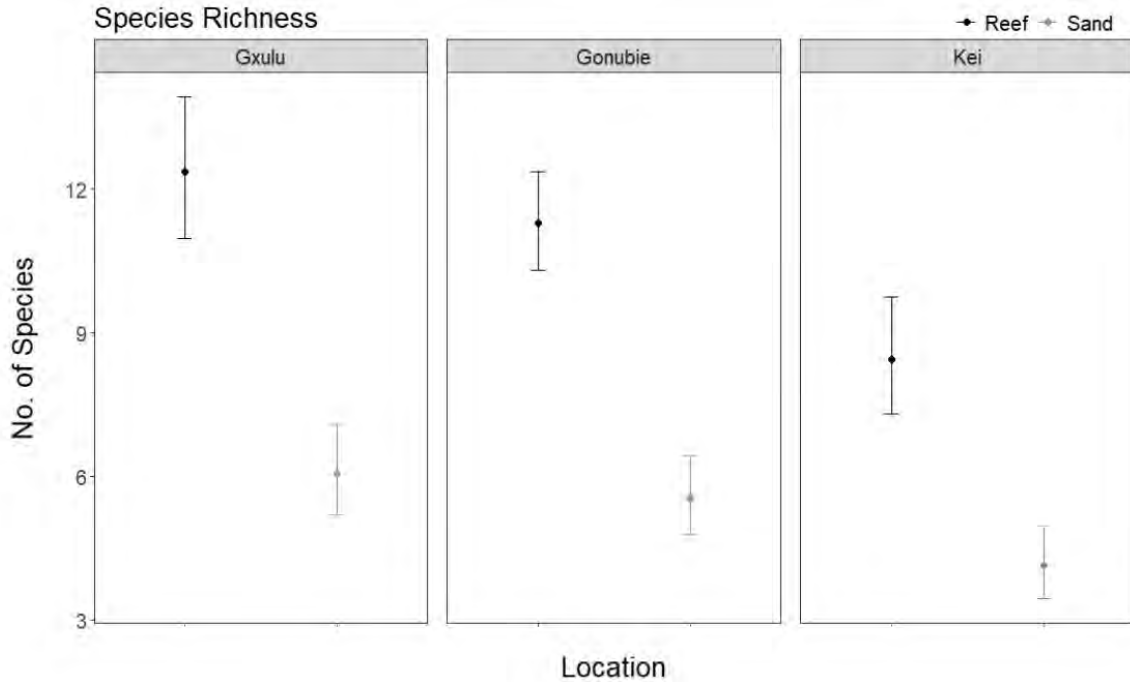


Figure 3.2: Predicted values for species richness (No. of species) on sand and reef substrate for the three locations in the inshore Amathole Marine Protected Area and adjacent inshore exploited areas based on standard average values for temperature, substrate, and location. Error bars represent 95 % confidence intervals. Factors found to be insignificant in analysis of deviance were excluded from the predictive plots.

3.3.5 PRIMARY FISHERIES SPECIES

Although averaged values of MaxN for Primary Fisheries Species did not reveal any obvious distinction between *protected* and *exploited* areas, the average of Total Biomass for several species was notably higher in the *protected* areas (Table 3.9). Biomass of *C. cristiceps*, *C. nasutus*, *E. marginatus*, *P. rupestris* and *P. praeorbitalis* was distinctly higher in the *protected* areas, while that of *M. mustelus* was higher in the *exploited* areas (Table 3.9).

Table 3.9: The average (Av.) MaxN and average (Av.) of the Total Biomass of Primary Fisheries Species where they were detected in the inshore Amathole Marine Protected Area (IP) and adjacent inshore exploited (IE) areas are presented with standard deviation (SD).

Species	MaxN (Av. ± SD)		Total Biomass (kg; Av. ± SD)	
	IE	IP	IE	IP
<i>Argyrozona argyrozona</i>	3 ± 2	5 ± 4	0.8 ± 0.6	1.6 ± 1.8
<i>Cheimerius nufar</i>	2 ± 1	3 ± 3	1.7 ± 1.8	2.6 ± 3.7

<i>Chelidonichthys kumu</i>	1 ± 0	1 ± 1	0 ± 0	0 ± 0
<i>Chrysoblephus cristiceps</i>	2 ± 1	3 ± 3	0.9 ± 0.8	3.7 ± 3.1
<i>Chrysoblephus gibbiceps</i>	2 ± 1	2 ± 1	4.4 ± 5.6	4.1 ± 3.1
<i>Chrysoblephus laticeps</i>	3 ± 1	4 ± 5	1.5 ± 1.1	1.6 ± 1.1
<i>Chrysoblephus puniceus</i>	0 ± 0	0 ± 0	0 ± 0	0 ± 0
<i>Cymatoceps nasutus</i>	4 ± 0	2 ± 2	0.2 ± 0	5.2 ± 3.4
<i>Diplodus capensis</i>	2 ± 2	3 ± 3	0.1 ± 0.1	0.2 ± 0.1
<i>Epinephelus andersoni</i>	0 ± 0	0 ± 0	0 ± 0	0 ± 0
<i>Epinephelus chabaudi</i>	2 ± 0	1 ± 1	2.1 ± 0	1.9 ± 1.2
<i>Epinephelus marginatus</i>	1 ± 0	1 ± 1	0.7 ± 1	2.2 ± 0
<i>Mustelus mustelus</i>	1 ± 0	2 ± 3	6.6 ± 1.5	2.9 ± 1.8
<i>Pachymetopon aeneum</i>	8 ± 8	8 ± 8	0.7 ± 0.6	1 ± 1.3
<i>Petrus rupestris</i>	1 ± 0	1 ± 0	7.7 ± 0	11.5 ± 17.4
<i>Polyprion americanus</i>	0 ± 0	0 ± 0	0 ± 0	0 ± 0
<i>Polysteganus praeorbitalis</i>	0 ± 0	0 ± 0	0 ± 0	3.9 ± 3.3
<i>Polysteganus undulosus</i>	2 ± 1	2 ± 2	0.6 ± 0.7	0.5 ± 0.7
<i>Pterogymnus lanarius</i>	6 ± 4	6 ± 5	0.8 ± 0.8	1 ± 0.8
<i>Rhabdosargus globiceps</i>	0 ± 0	0 ± 0	0.2 ± 0	0 ± 0
<i>Sarpa salpa</i>	2 ± 0	1 ± 1	0.3 ± 0	0 ± 0

3.3.5.1 MAXN

The species comprising the Primary Fisheries Species group are defined in Table 2.1 of the methods chapter. The GLM for MaxN of Primary Fisheries Species (the summed MaxN for all Primary Fisheries Species in each sample, as defined in section 2.2.4.2 of the methods chapter) was fitted with a Negative Binomial distribution after Poisson distribution was found to be over-dispersed (Dispersion statistic 8.86). Model selection resulted in the exclusion of the terms % water column and % obstruction (AIC: Full model = 719.1, Best-fit: 715.9 with no difference in deviance explained between models ($p = 0.7$)), resulting in the best-fit model:

$$f(\text{MaxN Primary Fisheries Species}) = \alpha + \beta_1(\text{temperature}) + \beta_2(\text{depth}) + \beta_3(\text{substrate}) + \beta_4(\text{location}) + \beta_5(\text{management}) + \beta_6(\text{location} \times \text{management}) + \varepsilon \quad \text{Eq. 3}$$

Where α is the intercept, β_i refers to the regression coefficients, and ε is the noise (Zuur et al. 2013).

The best-fit GLM (Eq. 3) explained 51.64 % of total variability in MaxN of Primary Fisheries Species. Sequential likelihood ratio tests indicated that neither location, nor management, nor the interaction between the two had significant influence on MaxN of Primary Fisheries Species (Table 3.10). The effect of substrate on the MaxN of Primary Fisheries Species was significant (Table 3.10), with greater

abundances recorded on *reef* habitats than *sand* (mean \pm SD; *reef*: 18 \pm 14; *sand*: 1 \pm 4; Table 3.11, Figure 3.3).

Table 3.10: Results of sequential likelihood ratio tests on the best fit Generalized Linear Model for effects of temperature, depth, substrate, location, management and the interaction between location and management on the MaxN of Primary Fisheries Species in the inshore Amathole Marine Protected Area and adjacent inshore exploited areas. df = degrees of freedom; PR(>Chi) = P-value; Relative contribution (%) = contribution of each term to overall variability explained by the model

	df	Residual Deviance	Residual df	Deviance	Pr(>Chi)	Relative Contribution (%)
NULL			115	284.21		
Temperature	1	3.079	114	281.13	0.079	2.07
Depth	1	2.205	113	278.92	0.138	1.48
Substrate	1	138.162	112	140.76	<0.001	92.93
Location	2	1.105	110	139.66	0.576	0.74
Management	1	2.205	109	137.45	0.138	1.48
Location x Management	2	1.911	107	135.54	0.385	1.29

Table 3.11: Output summary of Generalized Linear Model describing the influence of temperature, depth, substrate, location, management and the interaction between location and management on variability in MaxN of Primary Fisheries Species in the inshore Amathole Marine Protected area and adjacent inshore exploited areas. Estimate = coefficient estimate; Std. Error = standard error of estimate; PR(>|z|) = P-value

	Estimate	Std. Error	z value	PR(> z)
Intercept	0.222	0.861	0.257	0.797
Temperature	0.128	0.059	2.164	0.030
Depth	0.025	0.008	3.149	0.002
<i>Sand</i>	-2.984	0.247	-12.065	<0.001
<i>Gonubie</i>	-0.430	0.330	-1.302	0.193
<i>Kei</i>	0.141	0.498	0.284	0.776
<i>Protected</i>	0.310	0.408	0.759	0.448
<i>Gonubie Protected</i>	0.212	0.498	0.425	0.671
<i>Kei Protected</i>	-0.559	0.643	-0.869	0.385

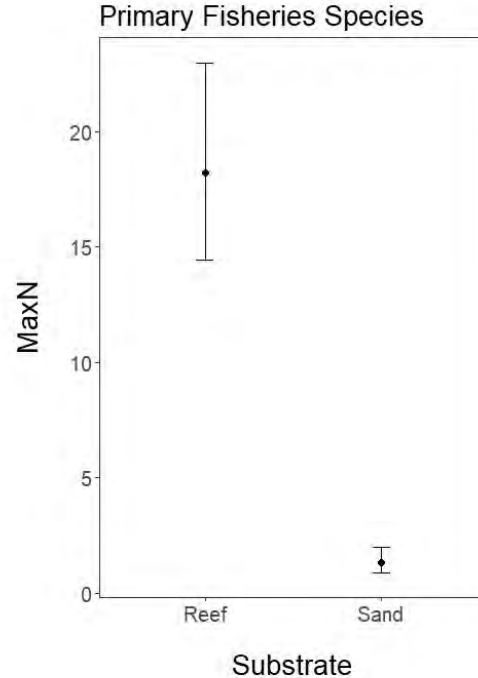


Figure 3.3: Predicted values for MaxN of Primary Fisheries Species on sand and reef substrate in the inshore Amathole Marine Protected Area and adjacent inshore exploited areas based on standard average values substrate. Error bars represent 95 % confidence intervals. Factors found to be insignificant in analysis of deviance were excluded from the predictive plots.

3.3.5.2 TOTAL BIOMASS

The GLM for Total Biomass of Primary Fisheries Species (the summed Total Biomass for all Primary Fisheries Species in each sample, as defined in section 2.2.4.2 of the methods chapter) was fitted with a Tweedie distribution. Model selection resulted in the exclusion of the terms % water column and % obstruction (AIC: Full model = 1 599.4, Best-fit: 1 595.4 with no difference in deviance explained between models ($p = 0.98$) resulting in the best-fit model:

$$f(\text{Total Biomass Primary Fisheries Species}) = \alpha + \beta_1(\text{temperature}) + \beta_2(\text{depth}) + \beta_3(\text{substrate}) + \beta_4(\text{location}) + \beta_5(\text{management}) + \beta_6(\text{location} \times \text{management}) + \varepsilon \quad \text{Eq. 4}$$

Where α is the intercept, β_i refers to the regression coefficients, and ε is the noise (Zuur et al. 2013).

The best-fit GLM (Eq. 4) explained 53.92 % of total variability in Total Biomass of Primary Fisheries Species. Sequential likelihood ratio tests indicated that the observed patterns in Total Biomass were

determined by substrate and management (Table 3.12). Total Biomass was significantly higher on *reef* than on *sand* (mean \pm SD; *reef*: 10.6 \pm 10.7 kg; *sand*: 0.8 \pm 2.7 kg), and inside the *protected* areas compared to adjacent *exploited* areas (mean \pm SD; *protected*: 8.2 \pm 1.2 kg; *exploited*: 4.8 \pm 4.9 kg; Table 3.13, Figure 3.4). Location and the interaction between location and management did not significantly affect Total Biomass of Primary Fisheries Species (Table 3.12).

Table 3.12: Results of sequential likelihood ratio tests on the best fit Generalized Linear Model for effects of temperature, depth, substrate, location, management and interaction between location and management on Total Biomass of Primary Fisheries Species in the inshore Amathole Marine Protected Area and adjacent inshore exploited areas. df = degrees of freedom; PR(>Chi) = P-value; Relative contribution (%) = contribution of each term to overall variability explained by the model

	df	Residual Deviance	Residual df	Deviance	Pr(>Chi)	Relative Contribution (%)
NULL			107	27 950		
Temperature	1	0.2	106	27 950	0.975	0.00
Depth	1	190.2	105	27 759	0.33	1.27
Substrate	1	11 731.5	104	16 028	<0.001	77.84
Location	2	933.1	102	15 095	0.098	6.19
Management	1	1 284.2	101	13 810	0.011	8.53
Location x Management	2	930.1	99	12 880	0.098	6.17

Table 3.13: Output summary of Generalized Linear Model describing the influence of temperature, depth, substrate, location, management and the interaction between location and management on variability in Total Biomass of Primary Fisheries Species in the inshore Amathole Marine Protected Area and adjacent inshore exploited areas. Estimate = coefficient estimate; Std. Error = standard error of estimate; PR(>|z|) = P-value

	Estimate	Std. Error	z value	PR(> z)
Intercept	6.037	1.296	4.658	<0.001
Temperature	0.177	0.089	1.991	0.049
Depth	0.014	0.011	1.325	0.188
<i>Sand</i>	-2.831	0.410	-6.913	<0.001
<i>Gonubie</i>	-0.796	0.496	-1.607	0.111
<i>Kei</i>	-0.888	0.929	-0.956	0.341
<i>Protected</i>	-0.317	0.623	-0.510	0.611
<i>Gonubie Protected</i>	1.455	0.773	1.883	0.063
<i>Kei Protected</i>	1.966	0.107	1.776	0.079

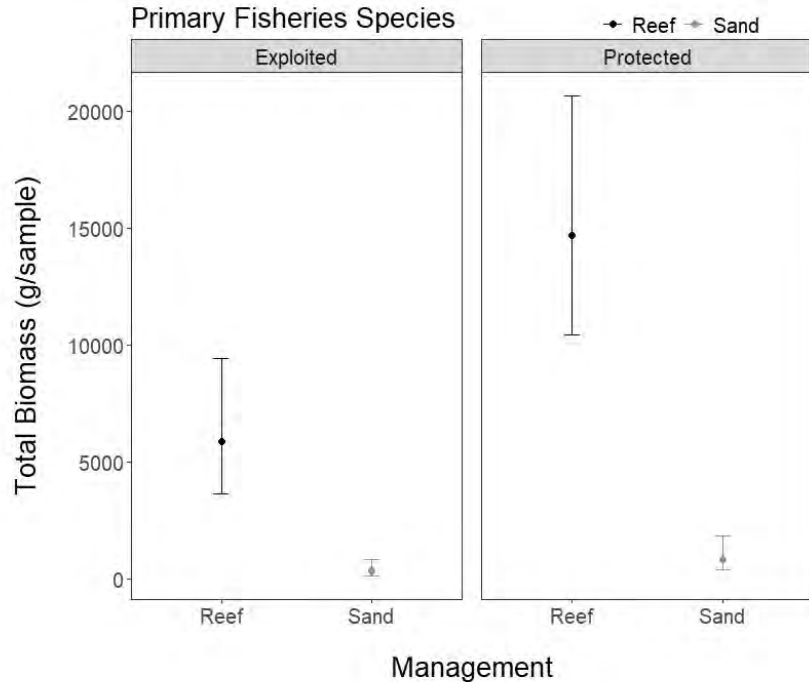


Figure 3.4: Predicted values for Total Biomass of Primary Fisheries Species on sand and reef substrate in the inshore Amathole Marin Protected Area and adjacent inshore exploited areas based on standard average values for substrate and management. Error bars represent 95 % confidence intervals. Factors found to be insignificant in analysis of deviance were excluded from the predictive plots.

3.3.6 VULNERABLE FISHERIES SPECIES

As with Primary Fisheries Species, differences in MaxN based on averaged values were indistinct (Table 3.14). Again, the average of the Total Biomass of *C. cristiceps*, *C. nasutus*, *E. marginatus*, *P. rupestris* and *P. praeorbitalis* was distinctly higher in the *protected* area (Table 3.14).

Table 3.14: The average (Av.) MaxN and average (Av.) Total Biomass of Vulnerable Fisheries Species where they were detected in the inshore Amathole Marine Protected Area (IP) and adjacent inshore exploited (IE) areas are presented. with standard deviation (SD).

Species	MaxN (Av. \pm SD)		Total Biomass (kg; Av. \pm SD)	
	IE	IP	IE	IP
<i>Chrysolephus cristiceps</i>	2 \pm 1	3 \pm 3	0.9 \pm 0.8	3.7 \pm 3.1
<i>Chrysolephus gibbiceps</i>	2 \pm 1	2 \pm 1	4.4 \pm 5.6	4.1 \pm 3.1
<i>Cymatoceps nasutus</i>	4 \pm 0	2 \pm 2	0.2 \pm 0	5.2 \pm 3.4
<i>Diplodus capensis</i>	2 \pm 2	3 \pm 3	0.1 \pm 0.1	0.2 \pm 0.1

<i>Diplodus hottentotus</i>	2 ± 1	2 ± 1	0.4 ± 0.3	0.4 ± 0.7
<i>Epinephelus marginatus</i>	1 ± 0	1 ± 1	0.7 ± 1	2.2 ± 0
<i>Gymnocrotaphus curvidens</i>	1 ± 0	1 ± 1	0 ± 0	0 ± 0
<i>Pachymetopon grande</i>	1 ± 0	1 ± 1	0.1 ± 0	0 ± 0
<i>Petrus rupestris</i>	1 ± 0	1 ± 0	7.7 ± 0	11.5 ± 17.4
<i>Polyprion americanus</i>	0 ± 0	0 ± 0	0 ± 0	0 ± 0
<i>Polysteganus praeorbitalis</i>	0 ± 0	0 ± 0	0 ± 0	3.9 ± 3.3
<i>Polysteganus undulosus</i>	2 ± 1	2 ± 2	0.6 ± 0.7	0.5 ± 0.7
<i>Rhabdosargus globiceps</i>	0 ± 0	0 ± 0	0.2 ± 0	0 ± 0
<i>Rhabdosargus holubi</i>	1 ± 0	2 ± 2	0.2 ± 0.1	0.2 ± 0.2
<i>Rhabdosargus sarba</i>	0 ± 0	0 ± 0	0 ± 0	0 ± 0
<i>Umbrina sp.</i>	1 ± 0	1 ± 0	0 ± 0	0 ± 0

3.3.6.1 MAXN

The species comprising the Vulnerable Fisheries Species group are defined in Table 2.1 of the methods chapter. The GLM for MaxN of Vulnerable Fisheries Species (the summed MaxN for all Vulnerable Fisheries Species in each sample, as defined in section 2.2.4.2 of the methods chapter) was fitted with a Negative Binomial distribution after Poisson distribution was found to be over-dispersed (Dispersion statistic 2.825). Model selection resulted in the exclusion of the terms % water column, % obstruction and depth (AIC: Full model = 430.2, Best-fit: 426.5 with no difference in deviance explained between models ($p = 0.5$)), resulting in the best-fit model:

$$f(\text{MaxN Vulnerable Fisheries Species}) = \alpha + \beta_1(\text{temperature}) + \beta_2(\text{substrate}) + \beta_3(\text{location}) + \beta_4(\text{management}) + \beta_5(\text{location} \times \text{management}) + \varepsilon \quad \text{Eq. 5}$$

Where α is the intercept, β_i refers to the regression coefficients, and ε is the noise (Zuur et al. 2013).

The best-fit GLM (Eq. 5) explained 50.88 % of total variability in MaxN of Vulnerable Fisheries Species. Sequential likelihood ratio tests indicated that the observed patterns in MaxN were determined by temperature, substrate, management, and the interaction between location and management (Table 3.15). Location did not significantly contribute to variability in MaxN of Vulnerable Fisheries Species (Table 3.15).

Table 3.15: Results of sequential likelihood ratio tests on the best fit Generalized Linear Model for effects of temperature, substrate, location, management and interaction between location and management on the MaxN of Vulnerable Fisheries Species in the inshore Amathole Marine Protected Area and adjacent inshore exploited areas. df = degrees of freedom; PR(>Chi) = P-value; Relative contribution (%) = contribution of each term to overall variability explained by the model

	df	Residual Deviance	Residual df	Deviance	Pr(>Chi)	Relative Contribution (%)
NULL			115	245.63		
Temperature	1	10.098	114	235.53	0.001	8.08
Substrate	1	90.810	113	144.72	<0.001	72.66
Location	2	2.086	111	142.63	0.352	1.67
Management	1	11.280	110	131.35	0.001	9.03
Location x Management	2	10.708	108	120.65	0.005	8.57

Increased temperature was associated with an increase in the MaxN of Vulnerable Fisheries Species (Table 3.16). MaxN was significantly higher on *reef* substrate than on *sand* (mean \pm SD; *reef*: 4 ± 4 ; *sand*: 0 ± 0). The influence of management differed according to location (Figure 3.5). On *reef* substrate, predicted MaxN values were significantly higher in *protected* areas than *exploited* areas (mean \pm SD; *protected*: 6 ± 5 ; *exploited*: 3 ± 4) in the *Gonubie* location, and to a lesser extent in the *Kei* location (mean \pm SD; *protected*: 4 ± 4 ; *exploited*: 2 ± 1 ; Figure 3.5). Total MaxN of Vulnerable Fisheries Species was higher in the exploited area relative to the protected area in the *Gxulu* location (mean \pm SD; *protected*: 2 ± 3 ; *exploited*: 3 ± 2 ; Figure 3.5)

Table 3.16: Output summary of Generalized Linear Model describing the influence of temperature, substrate, location, management and the interaction between location and management on variability in MaxN of Vulnerable Fisheries Species in the inshore Amathole Marine Protected Area and adjacent inshore exploited areas. Estimate = coefficient estimate; Std. Error = standard error of estimate; PR(>|z|) = P-value

	Estimate	Std. Error	z value	PR(> z)
Intercept	-3.273	0.980	-3.339	<0.001
Temperature	0.309	0.066	4.688	<0.001
<i>Sand</i>	-2.606	0.321	-8.128	<0.001
<i>Gonubie</i>	-0.736	0.376	-1.958	0.050
<i>Kei</i>	-0.868	0.595	-1.460	0.144
<i>Protected</i>	-0.572	0.478	-1.197	0.231
<i>Gonubie Protected</i>	1.863	0.593	3.143	0.002
<i>Kei Protected</i>	1.850	0.767	2.413	0.016

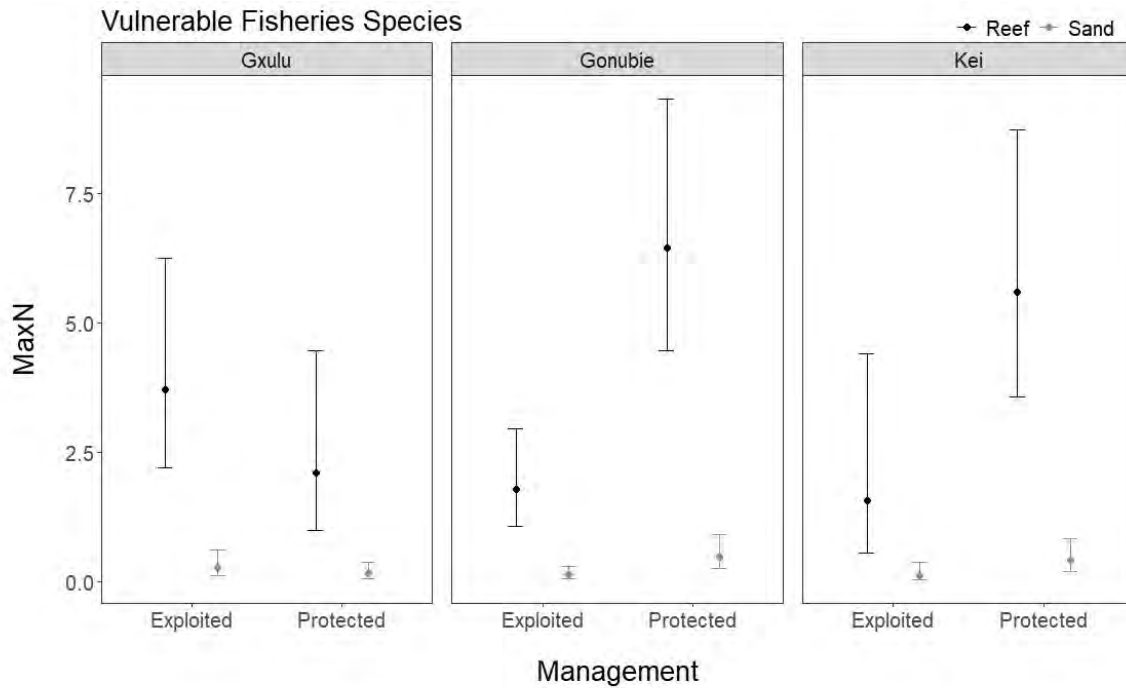


Figure 3.5: Predicted values for MaxN of Vulnerable Fisheries Species on sand and reef substrate for the three locations in the inshore Amathole Marine Protected Area and adjacent inshore exploited areas based on standard average values for temperature, substrate, location, and management. Error bars represent 95 % confidence intervals. Factors found to be insignificant in analysis of deviance were excluded from the predictive plots.

3.3.6.2 TOTAL BIOMASS

The GLM for Total Biomass of Vulnerable Fisheries Species (the summed Total Biomass for all Vulnerable Fisheries Species in each sample, as defined in section 2.2.4.2 of the methods chapter) was fitted with a Tweedie distribution. Model selection resulted in the exclusion of the term depth (AIC: Full model = 5 857.9, Best-fit: 5 856.3 with no difference in deviance explained between models ($p = 0.9$)), resulting in the best-fit model:

$$f(\text{Total Biomass Vulnerable Fisheries Species}) = \alpha + \beta_1(\% \text{ water column}) + \beta_2(\% \text{ obstruction}) + \beta_3(\text{temperature}) + \beta_3(\text{substrate}) + \beta_4(\text{location}) + \beta_5(\text{management}) + \beta_6(\text{location} \times \text{management}) + \varepsilon$$

Eq. 6

Where α is the intercept, β_i refers to the regression coefficients, and ϵ is the noise (Zuur et al. 2013).

The best-fit GLM (Eq. 6) explained 54.5 % of total variability in Total Biomass of Vulnerable Fisheries Species. Sequential likelihood ratio tests indicated that the observed patterns in Total Biomass were determined by substrate, location, management, and the interaction between location and management (Table 3.17).

Table 3.17: Results of sequential likelihood ratio tests on the best fit Generalized Linear Model for effects of % water column, % obstruction, temperature, substrate, location, management and interaction between location and management on Total Biomass of Vulnerable Fisheries Species in the inshore Amathole Marine Protected Area and adjacent inshore exploited areas. df = degrees of freedom; PR(>Chi) = P-value; Relative contribution (%) = contribution of each term to overall variability explained by the model

	df	Residual Deviance	Residual df	Deviance	Pr(>Chi)	Relative Contribution (%)
NULL	1		107	909 170		
% Water Column	1	6 717	106	902 453	0.259	1.36
% Obstruction	1	3 053	105	899 400	0.447	0.62
Temperature	1	24	104	899 376	0.947	0.00
Substrate	1	216 684	103	682 692	<0.001	43.73
Location	2	92 384	101	590 308	<0.001	18.65
Management	1	103 984	100	486 325	<0.001	20.99
Location x Management	2	72633	98	413692	0.001	14.66

Total Biomass of Vulnerable Fisheries Species was significantly lower on *sand* substrate than on *reef* (mean \pm SD; *reef*: 5.3 \pm 8.9 kg; *sand*: 0.4 \pm 1.9 kg Table 3.18). The effect of management was not consistent across locations (Figure 3.6). Total Biomass of Vulnerable Fisheries Species was significantly greater in *protected* areas in *Gonubie* and *Kei* locations (mean \pm SD; *Gonubie protected*: 4.8 \pm 8.6 kg; *Kei protected*: 7.3 \pm 10.1 kg) relative to the corresponding *exploited* areas (mean \pm SD; *Gonubie exploited* 0.7 \pm 1.3 kg; *Kei exploited* 0.9 \pm 1.1 kg; Figure 3.6). Only three samples from *Kei exploited* area were included in the biomass analysis, resulting in a larger confidence interval for that area (Figure 3.6). No significant difference was detected between the *Gxulu protected* and *exploited* areas (mean \pm SD; *Gxulu protected*: 0.8 \pm 1.7 kg; *Gxulu exploited*: 2.1 \pm 4.1 kg; Table 3.17; Figure 3.6). *Gonubie* and *Kei exploited* areas were associated with a slight decrease in Total Biomass relative to the *Gxulu exploited* area (Table 3.18; Figure 3.5). However, biomass increased significantly in both *Gonubie* and *Kei protected* areas compared to *Gxulu protected* area.

Table 3.18: Output summary of Generalized Linear Model describing the influence of % water column, % obstruction, temperature, substrate, location, management and the interaction between location and management on variability in Total Biomass of Vulnerable Fisheries Species in the inshore Amathole Marine Protected Area and adjacent inshore exploited areas. Estimate = coefficient estimate; Std. Error = standard error of estimate; PR(>|z|) = P-value

	Estimate	Std. Error	z value	PR(> z)
Intercept	1.739	2.085	0.834	0.406
% Water Column	0.004	0.006	0.598	0.551
% Obstruction	0.007	0.014	0.512	0.610
Temperature	0.408	0.130	3.145	0.002
<i>Sand</i>	-2.639	0.609	-4.332	<0.001
<i>Gonubie</i>	-1.812	0.807	-2.247	0.027
<i>Kei</i>	-1.411	1.514	-0.932	0.354
<i>Protected</i>	-1.131	0.875	-1.293	0.199
<i>Gonubie Protected</i>	3.786	1.197	3.163	0.002
<i>Kei Protected</i>	4.119	1.729	2.383	0.019

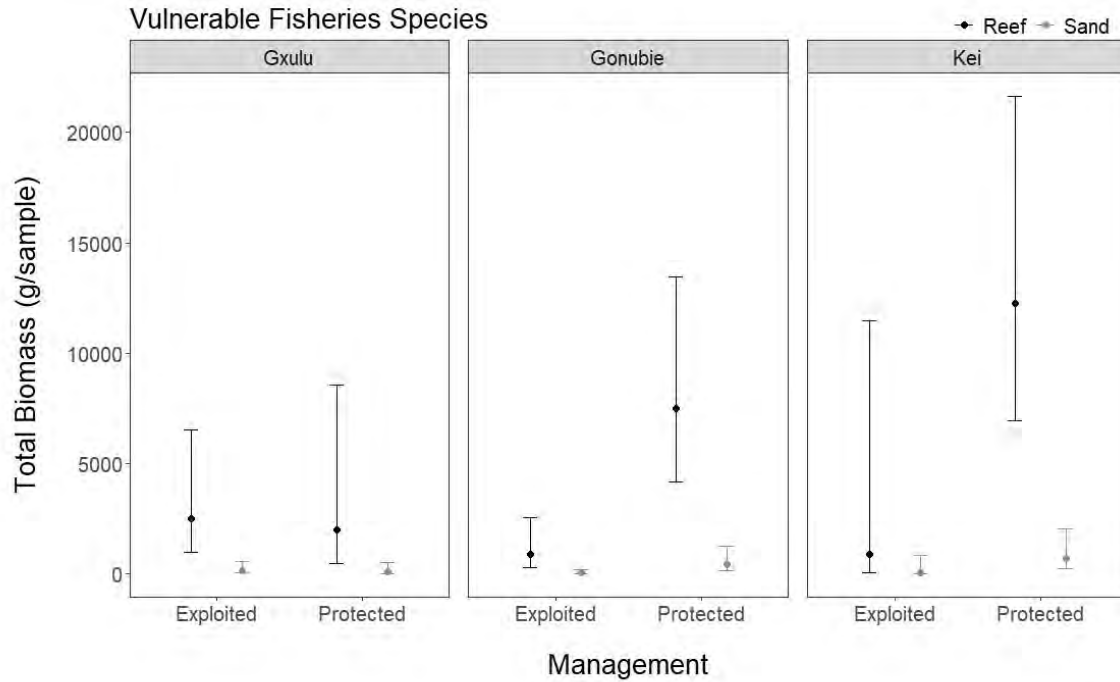


Figure 3.6: Predicted values for Total Biomass of Vulnerable Fisheries Species on sand and reef substrate for the three locations in the inshore Amathole Marine Protected Area and adjacent inshore exploited areas based on standard average values for substrate, location, and management. Error bars represent 95 % confidence intervals. Factors found to be insignificant in analysis of deviance were excluded from the predictive plots.

3.4 DISCUSSION

This chapter investigated whether the inshore Amathole MPA supports the recovery of local populations of reef fish, particularly those species impacted by boat-based exploitation. Significant differences were found between fish assemblage structures in exploited and protected areas at the community level and for species groups (Primary and Vulnerable Fisheries Species). Differences were more pronounced for biomass measures than for abundance (MaxN). Likewise, the response to protection was more apparent for Primary and Vulnerable Fisheries Species than for the full fish assemblage. Substrate was found to exert a particularly strong influence on fish assemblage structure and target species were almost entirely restricted to reef substrate. The amount of reef structure available differed between the three inshore protected areas, with considerably more samples from sand substrate in the Gxulu protected area.

Although species richness was similar between *protected* and *exploited* areas (Figure 3.2) there was significant variability in the structure of the fish assemblages at the community level (Table 3.4) and in populations of target fishery species (Figure 3.4; Figure 3.5; Figure 3.6). At the community level, small-bodied sparid species like *B. inornata*, *P. aeneum*, *S. emarginatum*, and *P. laniarius*, had the strongest influence in variability in the data in multidimensional scaling and SIMPER analyses (Figure 3.1; Table 3.6). The majority of species which exerted a notable influence on variability were more abundant in the exploited areas than in the protected areas (Table 3.6). However, in the analyses restricted to Primary and Vulnerable Target Species (as defined in Table 2.1), total biomass was significantly greater in the protected areas than in the corresponding exploited areas (Table 3.12: Table 3.17), and in the case of Vulnerable Fisheries Species, abundance was also greater in protected areas (Table 3.15). Previous studies have shown that the recovery of fisheries targets, which tend to be larger bodied, higher trophic-level species (Pauly et al. 1998), can drive a decrease in the density of lower trophic-level species in a protected area (Graham et al. 2003, Willis & Anderson 2003, Götz et al. 2009, Kerwath et al. 2013, Heyns-Veale et al. 2019). Although this response to protection has been known to mask reserve effects when carrying out community analysis (Edgar & Stuart-Smith 2009, Lester et al. 2009, Baskett et al. 2011, Heyns-Veale et al. 2019), it is considered an emergent property of a functioning protected area. Indirect effects from predator recovery in a protected area, such as the reduction in abundance of lower trophic level species seen in the community analysis, take longer to manifest than direct increases in abundance and biomass of target species (Heyns-Veale et al. 2019). This suggests that the protection afforded to reef fish by the inshore Amathole MPA, and the historical enforcement of the no-take zones

by local ski-boat fishermen, has resulted in a restructuring of the community, with greater abundance and biomass of larger species (those targeted by fisheries) and lower abundance of small-bodied generalist species in the protected areas.

All analyses conducted in this chapter indicated that the assemblage structure, abundance, and total biomass of fish in the area of the inshore Amathole MPA is determined first by the availability of suitable habitat. For example, in the analysis of the abundance and biomass of Vulnerable Fisheries Species, substrate accounted for 43.7 % and 72.7 %, respectively (Table 3.15; Table 3.17), of the deviance explained by the model. A similar result for substrate was observed for species richness (75.8 %; Table 3.8). Distinct fish communities were associated with sand and reef substrates, with the vast majority of target species being more abundant on reef substrate (Table 3.6). Analysis of dispersion indicated that assemblages on sand were more variable and less diverse than those on reef (Table A. 1). Though this study focused on the benefit of the inshore Amathole MPA to reef-associated fisheries species, it should be noted that sand-associated communities were not merely depleted versions of the reef communities. Though protection of the sand habitat might not provide obvious benefit to reef-associated fisheries species, it supports an invaluable component of the local ecosystem and biodiversity, providing refuge to an array of species not found on reefs, including wide ranging primary fisheries species such as maasbanker (*Trachurus trachurus*) and geelbek (*Atractoscion aequidens*) (Table 3.6).

Overall fish assemblages differed between protected and exploited areas, with greater abundance and total biomass of target species in protected areas. However, it should be noted that fish assemblages from protected areas in the three different locations (Gxulu, Gonubie and Kei) exhibited variable responses to protection. In particular, no significant management effect was detected in the Gxulu location regardless of whether the analysis examined the entire fish assemblage structure (Table A. 2) or focussed on target species (Figure 3.3; Figure 3.4; Figure 3.5; Figure 3.6). This may be due to the lack of suitable inshore reef structure in the protected area at Gxulu. Although every effort was made to sample sites with reef cover, few were detected in the Gxulu protected area (Table 3.1). Since substrate was the most significant influence on fish assemblage structure, it stands to reason that the lack of suitable habitat in the Gxulu protected area limits its conservation value for reef fish species. This could detract from the apparent effectiveness of the inshore Amathole MPA in reaching its current conservation objectives when considered as a whole. However, it is important to remember that the results presented here are focussed on inshore reef fish species and it is likely that the Gxulu protected area does provide benefit other coastal fishes, in particular those associated with sand dominated

habitats. A more comprehensive assessment of the Gxulu protected area to better define its value would be beneficial. Detailed bathymetric mapping of the area and surrounds would assist such an assessment. This highlights the need for clearly defined conservation objectives and proper investigation into the adequacy of an area to meet them when designating a marine protected area.

Though fish assemblage structure in the Kei protected area was not significantly different from that of the corresponding exploited area (Table A. 2), the total biomass of vulnerable species was highest overall in the Kei protected area (Figure 3.6), implying a more mature population structure. This could be due to the difficulty of access, since the Kei protected area is the most remote of the three, or because of the greater size of the Kei protected area compared to Gxulu or Gonubie (Figure 2.2). The particular commitment of members of the Kei Mouth ski-boat club to protect the Kei protected area from poaching (John Rance, BDSAA, pers. comm.) is also likely to have contributed to the success of vulnerable species in this area. The lack of samples from the Kei exploited area may also have detracted from the analysis. Future analysis of this dataset might do better to compare the Kei protected area with samples from the Gonubie exploited area, which falls between Gonubie and Kei protected areas.

It is apparent from the results of this study that the design of the inshore Amathole MPA may be flawed, in particular in terms of the suitability of the Gxulu protected area to support the recovery of reef fish populations. However, given that in its current layout it nonetheless provides demonstrable benefits to threatened species, and that it is well established and largely respected by local fishermen, it would be imprudent to suggest any alteration of its dimensions or position that would encroach on the established inshore fishing grounds alongside without exceptional cause, which has not been identified by this study.

While the majority of target species made relatively minor contributions to variability at community level, two notable exceptions were those of dageraad (*C. cristiceps*) and red roman (*Chrysoblephus laticeps*). These two Primary Fisheries Species occupy remarkably similar ecological niches. Both are distributed along the eastern coast of South Africa, are highly territorial, with juveniles found on reefs up to 30 m deep and adults on reefs up to 100 m deep (Buxton & Allen 1989, Mann 2013). Both feed mainly on reef-dwelling invertebrates (Buxton 1990), are primarily diurnal (Juby 2016) and reproduce between the months of October and January in the Eastern Cape (Buxton 1990, Mann 2013). While *C. laticeps* reach a maximum length of around 50 cm and females reach sexual maturity at around three years, in *C. cristiceps* the maximum length is nearer 70 cm, and females take over seven years to reach maturity (Mann 2013). These differences in size and age at maturity may account for the greater

resilience to fishing pressure demonstrated by *C. laticeps*, which although listed as Near Threatened by the IUCN (Mann et al. 2014b) is considered a potentially sustainable fishery if current management restrictions for this stock are upheld (Mann 2013). *Chrysoblephus cristiceps*, on the other hand, is considered Critically Endangered by the IUCN (Buxton et al. 2014a) and in need of strict protection in order for stocks to recover (Mann 2013, Parker et al. 2016).

While *C. cristiceps* was larger and more abundant inside the protected areas *C. laticeps* was not (Table 3.6, Table 3.9). Though differences in the MaxN and total biomass of *C. laticeps* were less distinct than for *C. cristiceps*, if anything, the tendency was towards greater abundance and biomass of *C. laticeps* in the *exploited* areas (Figure 3.1, Table 3.6, Table 3.9). Since outside of the protected area large individuals of both species are a valued catch, it is intuitive that their numbers would increase in the protected areas. Though this is the case for *C. cristiceps*, the lack of response from *C. laticeps* to protection is noteworthy. Since *C. laticeps* and *C. cristiceps* have highly overlapping niches, it is possible that the recovery of *C. cristiceps* within the protected areas drives the smaller *C. laticeps* to occupy exploited areas where they face less inter-specific competition. Previous studies have also shown density dependent spillover of *C. laticeps* as a result of intra-specific competition, which may also be occurring in the Amathole MPA (Götz et al. 2009, Kerwath et al. 2013). Though further analysis of these species would provide insight into this dynamic, it is clear from these results that the inshore Amathole MPA provides a vital refuge for *C. cristiceps*.

Previous studies have shown that larger carnivorous species, in particular those with limited movement patterns for large portions of their life-histories, show greater responses to protection. (Claudet et al. 2010). However, several of the species from the Amathole region which meet these criteria were notably absent from multidimensional scaling and SIMPER analyses of defining species in the inshore data (Figure 3.1; Table 3.6, Table 3.9). Species such as *P. rupestris*, *P. undulosus*, *C. gibbiceps*, black musselcracker (*Cymatoceps nasutus*) and yellowbelly rockcod (*Epinephelus marginatus*) were not identified as defining species in the inshore data, suggesting that the inshore MPA might not adequately support adult populations of these species.

There are several potential reasons why such species did not appear to benefit from the protection of the inshore MPA. For example, the species listed above are known to take between four and eighteen years for both sexes to reach maturity (Mann 2013), so are likely to take a relatively long time to reflect an increase in abundance due to protection. However, although the inshore Amathole MPA was only officially recognised in 2011, local ski-boat fishermen had voluntarily enforced the no-take zones for

over 20 years prior. It is unlikely, therefore, that the absence of response to protection from these species is entirely a consequence of insufficient duration of protection. The three protected areas comprising the inshore Amathole MPA span less than 20 km of coastline each. If habitual ranging movements of target species exceed the limits of the protected area they will be susceptible to fishing mortality in the adjacent exploited areas. The fact that the species listed above are all endangered raises the possibility that they are not prevalent inshore simply because they are uncommon. Though there are numerous factors which may contribute to the scarcity of large carnivorous reef fish in the inshore MPA, the most conspicuous possibility is that the depth range of the inshore MPA does not cover the preferred habitat of adults of these species. If the preferred habitat of spawner stock of a species falls outside of the depth range of the inshore MPA it is unlikely to derive much benefit from protection therein.

Previous studies along the South African coastline have found that depth plays a critical role in structuring assemblages and populations (Buxton & Smale 1984, Heyns-Veale et al. 2009). However, the results from this research indicated that the depth range sampled did not affect the fish assemblages observed (Table 3.4; Table 3.7; Table 3.10; Table 3.12; Table 3.15; Table 3.17). Considering this result and that this research sampled the full depth range of the inshore MPA, it is possible that the inshore Amathole MPA does not cover a broad enough depth gradient to detect these changes and protect important deeper water habitats.

3.5 CONCLUSIONS

While this study demonstrates that the inshore Amathole MPA has resulted in increased biomass and abundance of numerous vulnerable and threatened reef fish species, large fisheries species were uncommon in the inshore samples. The lack of large fisheries species from the inshore data, including several endangered species whose distributions are centred near the Amathole MPA, suggests that the inshore MPA is restricted in the protection it can provide them. However, the remarkable success of *C. cristiceps* in the inshore Amathole MPA is a perfect example of how a small, fragmented MPA can effectively contribute to the conservation of highly resident species when strategically situated. Considering the critically endangered status of *C. cristiceps*, it is worthwhile investigating the extent of the contribution of the Amathole MPA to the recovery of this species across its distributional range.

The lack of consultation with scientists and MPA planners when the three areas comprising the inshore Amathole MPA were first selected meant that their design was not informed by ecological data. Comprehensive conservation objectives were subsequently developed without further assessment of the adequacy of the MPA to meet them. This puts the Amathole MPA at risk of perceived ineffectiveness and resultant disillusionment of stakeholders. If further analyses confirm the findings of this study, adjustment of the conservation objectives of the inshore Amathole MPA to might help to ensure that the success of the inshore Amathole MPA in protecting inshore reef fish is not obscured by their inability to protect offshore species, or that the value of the Gxulu protected area to sand-associated species does not detract from the apparent benefit of the Gonubie and Kei protected areas to reef-associated species. It is worth investigating the potential benefit and impact on stakeholders of extending the southern limit of the Gxulu protected area to incorporate more reef complexes.

4 COMPARISON OF INSHORE AND OFFSHORE FISH ASSEMBLAGES IN THE AMATHOLE MARINE PROTECTED AREA AND SURROUNDS

4.1 INTRODUCTION AND AIM

The continental shelf in the Amathole region is narrow (< 25 km) in comparison to the majority of the Agulhas Ecoregion, especially the Agulhas Bank to the west that in places stretches 150 km offshore (Dlamini, 2017). The areas comprising the inshore Amathole MPA cover the inner-shelf habitats between the intertidal zone and depths of up to 80 m. The recent offshore extensions to the Amathole MPA cover the outer-shelf and shelf-edge habitats, including terraces and canyons, from 60 to 80 m down to depths in excess of 2000 m (ACEP 2017). The inner shelf descends rapidly from the shoreline to depths of 60 – 80 m within roughly five kilometres from the coast (Dlamini, 2017). The outer shelf then gently descends a further 20 – 30 m over 15 – 25 km, with the shelf break occurring between 100 and 120 m depth (Dlamini, 2017). The greater depth of the outer shelf and shelf break, combined with the change in topography, result in considerably different environmental conditions from the inner shelf and coastal zone (Goschen & Schumann 2011). Currents, temperature, light penetration, fresh water, and sediment inputs change rapidly with an increase in depth modifying the benthic habitat and the communities that inhabit it (ACEP 2017). Given that depth and habitat are known to be two of the most important determinants of fish assemblage structure (Buxton & Smale 1989, Chatfield et al. 2010, Fitzpatrick et al. 2012, Heyns-Veale et al. 2016), the fish assemblages from within the depth range of the inshore MPA are likely to differ significantly from those from the offshore, outer-shelf habitat. While fish species from higher trophic levels are generally more dominant at greater depths and further offshore (Buxton & Smale 1984, Claudet et al. 2010), species richness is higher closer to shore and with greater habitat complexity (Willis & Anderson 2003, Heyns-Veale et al. 2016, Heyns-Veale et al. 2019b). In addition, many fish species show ontogenic shifts in depth preference (Smale 1988, Buxton & Allen 1989, Griffiths & Wilke 2002, Heemstra & Heemstra 2004, Mann 2013). Thus, the offshore extensions of the Amathole MPA stand to provide protection to a distinct, and valuable, array of habitats and communities not represented in the inshore MPA.

Since the South African linefishery has historically focussed its efforts on larger-bodied, higher trophic level species (Pilfold & Pampallis 1993, Hecht & Buxton 1993, Penney et al. 1999, Griffiths 2000, Brouwer & Buxton 2002), many of the species most in need of protection fall within this category. The Amathole region is renowned for its rich linefishery and has an exceptionally high proportion of endemic species, particularly from the sparid family (Buxton & Smale, 1984, Fennessy et al. 2003). Several endangered species are prevalent in the region, including red steenbras (*Petrus rupestris*), seventyfour (*Polysteganus undulosus*), and dageraad (*Chrysoblephus cristiceps*; Brouwer & Buxton 2002, Fennessy et al. 2003).

Petrus rupestris is a South African endemic sparid whose historical range stretched from False Bay in the Western Cape to St. Lucia in northern Kwa-Zulu Natal (Heemstra & Heemstra 2004). Reaching up to two metres and 70 kg (Heemstra & Heemstra 2004), *P. rupestris* takes seven to nine years to reach 50 % maturity and are known to live for as long as 55 years (Andrews et al. 2018). Historical fisheries catch data suggested that by 2012 there had been a 90 % decline in CPUE (catch per unit effort) of *P. rupestris*, with stocks at less than 25 % of recorded levels and less than 5 % of pristine levels (Mann et al. 2014b, Kerwath et al. 2019). This steady decline in *P. rupestris* catches has been consistent across the distributional range of the species, except in the Border and Transkei regions of the Eastern Cape. The historical distribution of adults of this species extended from the Southwestern Cape to Northern Kwazulu-Natal but has now contracted to the stretch between Cape Agulhas and Southern Kwazulu-Natal. Currently, the north-Eastern Cape coast is thought to represent the concentration of the majority of spawner stock (Hecht & Buxton 1993, Kerwath et al. 2019). Sub-adults and adults from areas further south are thought to make a once-off migration to the northern part of the Eastern Cape coast, where they remain for the rest of their reproductive lives (Smale 1988, Hecht & Buxton 1993, Brouwer 2002, Griffiths & Wilke 2002, Mann 2013). While juveniles are common on inshore reefs (less than 50 m deep) throughout the distributional range, adults are usually found on deeper reefs up to 160 m, particularly in the north-Eastern Cape coast, with a smaller population known from the Agulhas Bank (Smale 1988, Griffiths & Wilke 2002). Juvenile *P. rupestris* show high site fidelity and resident adults are thought to be territorial (Brouwer 2002, Heemstra & Heemstra 2004), as well as forming spawning aggregations (Bruce Mann, ORI, pers. obs.) making the species a promising candidate for spatial conservation. This puts the Amathole MPA, which is situated on the north-Eastern Cape coast, in an ideal position to protect reproductive stock of

this heavily depleted species, and previous studies have suggested that an offshore protected area in the region is necessary to adequately protect the remaining spawner stock (Smale 1988, Brouwer 2002).

Polysteganus undulosus is another large endemic sparid listed as Critically Endangered by the IUCN. Overexploitation, in particular of large spawning aggregations in KwaZulu-Natal, led to populations declining to 5 % of pristine levels (Mann et al. 2014). Although a moratorium on catches of *P. undulosus* has been in place since 1998, the species is still subject to illegal fishing, and despite showing some signs of recovery is still considered to be Critically Endangered (Mann et al. 2014). While the distribution of spawner stock of *P. undulosus* is more widespread throughout its range than that of *P. rupestris*, with spawning aggregations taking place in KwaZulu-Natal (Garratt 1988), the Amathole region is nonetheless central in its distribution and is thought to serve as an important nursery area for juveniles (Mann 2013, Mann et al. 2014). Juveniles inhabit inshore reefs while adults form shoals on reefs up to 160 m deep (Mann 2013, Heemstra & Heemstra 2004). As with *P. rupestris*, *P. undulosus* is slow growing, reaching maturity between seven and nine years old and living for over 20 years (Chale-Matsau et al. 2001, Heemstra & Heemstra 2004). Adults, which can reach up to one metre in size and 17 kg in weight are thought to frequent depths of over 70 m, which are poorly represented by the inshore Amathole MPA (Mann 2013, Heemstra & Heemstra 2004). This suggests that the inshore MPA may serve as a nursery area for this species and provide little protection for adults. Since protection of spawner stock has been deemed critical for the recovery of *P. undulosus* (Chale-Matsau et al. 2001), the offshore extension of the Amathole MPA may well provide a decisive boost for the potential recovery of the species.

Dageraad (*Chrysoblephus cristiceps*), is another Critically Endangered South African endemic sparid which is common in the Amathole region (Buxton et al. 2014a, Parker et al. 2016). Adult dageraad occur at depths between 20 and 100 m (Heemstra & Heemstra 2004) and are highly resident (Buxton & Allen 1989). Although not as large as *P. undulosus* or *P. rupestris*, *C. cristiceps* can reach up to 9 kg and 75 cm (Heemstra & Heemstra, 2004). They are slow-growing and long-lived, with females reaching maturity at around 10 years old. In addition, *C. cristiceps* is a protogynous hermaphrodite, changing sex from female to male (Buxton 1990). This has exacerbated the effects of localised overfishing, with female-skewed sex ratios and smaller size at sex-change detected in over-exploited areas (Buxton 1993). In combination with slow-growth

and high residency, this has resulted in the collapse of the population, which has been reflected a massive contraction of its distributional range (Parker et al. 2016). The Amathole region represents one of the last remaining strongholds of this species (Parker et al. 2016) and thus spatial protection in the area is key for its future conservation.

Considering the difference in ecological conditions in the inshore and offshore environments, the habitat preferences of target species, and catch reports from local ski-boat fishermen, it is likely that the offshore environment supports a distinct fish assemblage that is different from the inshore Amathole MPA. In particular, it is likely that adult populations of some target species are found predominantly offshore. By comparing biomass and abundance of species from inshore and offshore zones (Figure 2.3), it is possible to discern differences not only in community structure but in the maturity of populations in each zone, permitting inferences about the reproductive value of each population.

This research chapter aims to investigate whether the fish community in the offshore shelf zone of the Amathole region is significantly different from that of the inshore inner-shelf zone, and whether the offshore extension of the Amathole MPA will provide more meaningful habitat coverage for species of particular conservation interest. In particular, the objectives were:

- i) to determine the effect of depth on the abundance (MaxN) of the entire fish assemblage by comparing the multivariate response of the fish assemblage data between the *inshore* and *offshore* zones.
- ii) to investigate the effect of depth on the diversity of fish species by comparing species richness between the *inshore* and *offshore* zones.
- iii) to explore the effect of depth on Primary and Vulnerable Fisheries Species groups by comparing MaxN and Total Biomass between the *inshore* and *offshore* zones.
- iv) and finally, to investigate the combined effect of depth and protection on *P. rupestris*, *P. undulosus* and *C. cristiceps* by comparing MaxN and Max Biomass across the sampled depth range within *protected* and *exploited* areas.

It must be noted that the sampling for this research was carried out prior to the proclamation of the offshore extension to the Amathole MPA. As a result, it was not possible to compare protected offshore assemblages with assemblages from the inshore MPA. While this is a limitation of the research presented here, the data were collected in the vicinity of the offshore

MPA and it is expected that the observed patterns will be representative of offshore fish assemblages the Amathole region and will provide valuable insight for the management of the offshore MPA.

4.2 METHODS

The data from the inshore Amathole MPA and adjacent inshore exploited areas used in Chapter 3 were compared with additional data collected from offshore exploited areas seaward of the inshore sampling areas. Whereas the inshore analysis (Chapter 3) examined the effect of protection within each of the three locations comprising the inshore Amathole MPA, this offshore analysis considers the effect of depth range (*inshore* or *offshore*), within each management group (*protected* or *exploited*), defined here as the explanatory variable zone (*inshore protected*, *inshore exploited* and *offshore exploited*). Samples from within three nautical miles of the high-tide mark, corresponding with the seaward extent of the inshore MPA, were considered as inshore. The depth of inshore sampling sites ranged from 12 to 65 m. Samples from beyond the three nautical mile inshore zone were considered as offshore, with sampled sites ranging from 76 to 112 m depth. Inshore samples were grouped as either *inshore protected* or *inshore exploited*. Since at the time of sampling the offshore extension of the Amathole MPA had not been designated, all offshore samples were pooled as *offshore exploited*, despite that some of them now coincide with the offshore Amathole Marine Protected Area.

Response variables considered for full assemblages and for species groups were variability in MaxN and Total Biomass. Response variables were analysed according to the explanatory variables zone (*inshore protected*, *inshore exploited* and *offshore exploited*) and substrate (*sand* and *reef*). For individual species, detection probability, MaxN, and Max Biomass were investigated according to management (*protected* or *exploited*) and the continuous covariable depth. Response variables and explanatory variables are defined in section 2.2.4 of Chapter 2.

4.2.1 COMMUNITY ANALYSIS

Multivariate analysis of MaxN of all observed species was carried out to test for differences in fish assemblages based on zone (*inshore exploited*, *inshore protected*, and *offshore exploited*) as detailed in section 2.2.4.3 of the methods chapter. Homogeneity of dispersion was tested using the PERMDISP routine in order to infer about the causes for differences detected in the subsequent tests. Sequential PERMANOVA was used to test whether different fish assemblages characterise the *inshore exploited*, *inshore protected* and *offshore exploited* zones. The continuous covariates % water column, % obstruction, visibility and temperature followed by the categorical variables substrate and zone were added, in that order, to the analyses.

Management and depth were omitted from the analysis as they are both incorporated within the factor zone. To visualise the groupings according to zone and to identify species correlated to the groupings, nMDS analysis was carried out. This was followed by CAP analysis to provide insight into the strength of the grouping variables as predictors. Finally, the contribution of individual species to the observed differences between zones was analysed using the SIMPER routine.

4.2.2 UNIVARIATE ANALYSIS

Univariate GLMs were used to model the influence of zone on species richness and on the MaxN and Total Biomass of species groups (Table 2.1). Data exploration again revealed collinearity between depth and visibility, resulting in spurious results in models. As such the term visibility was omitted from the analyses (Zuur et al. 2010). The continuous covariates % water column, % obstruction and temperature followed by the categorical variables zone and substrate were included, in that order, in the saturated model for each analysis.

The saturated model for species richness and species group responses prior to the elimination of terms took the form:

$$f(\text{response variable}) = \alpha + \beta_1(\% \text{ water column}) + \beta_2(\% \text{ obstruction}) + \beta_3(\text{temperature}) + \beta_4(\text{substrate}) + \beta_5(\text{zone}) + \varepsilon \quad \text{Eq. 7}$$

Where α is the intercept, β_i refers to the regression coefficients, and ε is the noise (Zuur et al. 2013).

The GLMs for individual species responses modelled detection probability, MaxN and Max Biomass according to depth and management, without classification of samples as inshore or offshore. Max Biomass considers the largest individual recorded in each sample at MaxN, providing more information about the size structure of a population than Total Biomass. The analysis of Max Biomass over a continuous depth gradient permits inferences about depth-associated size structure of local populations. The response in MaxN and Max Biomass of *P. rupestris*, *P. undulosus* and *C. cristiceps* to depth (within management) was tested using a Hurdle models (Cragg 1971, Mullahy 1986). This type of model addresses zero-inflation by modelling responses based only on data where the species in question was detected, predicting overall detection probability separately. The hurdle models were run in three parts: first using a

binomial GLM of presence-absence data to investigate patterns in detection probability, second by a Poisson or Negative-Binomial GLM to model abundance (MaxN), and third a Tweedie GLM to model the response of Max Biomass. As *P. rupestris*, *P. undulosus* and *C. cristiceps* were detected no more than twice on sand substrate, the single-species analysis was restricted to reef substrate. Visibility was again discarded from the models due to collinearity with depth.

The resultant saturated model, prior to elimination of terms took the form:

$$f(\text{response variable}) = \alpha + \beta_1(\% \text{ water column}) + \beta_2(\% \text{ obstruction}) + \beta_3(\text{temperature}) + \beta_5(\text{depth} \times \text{management}) + \varepsilon \quad \text{Eq. 8}$$

Where α is the intercept, β_i refers to the regression coefficients, and ε is the noise (Zuur et al. 2013).

Analysis of deviance was carried out on the optimised models to determine which of the included terms significantly influenced variability in the data. Model summaries were used to examine the direction of influence of each term and to calculate the relative contribution of each one to overall variability. Predicted response values for standard average values of significant variables were then plotted to visualise the response.

4.3 RESULTS

4.3.1 SAMPLING SPREAD AND FOOTAGE SUCCESS

In addition to the 149 stereo-BRUVs samples collected from the inshore MPA and adjacent inshore exploited zones (used in Chapter 3), a further 20 samples were collected from exploited sites seaward of the inshore Amathole Marine Protected Area, between depths of 76 and 112 m (Figure 2.2). Of the 20 offshore samples, poor visibility, technical errors, and inappropriate camera angle (where the system landed with the camera aimed either at the substrate or the surface) rendered two samples unsuitable for MaxN analysis and three samples unsuitable for length analysis, as defined in section 2.2.4.2 in methods. Of the 149 inshore samples, 33 had been discarded from MaxN analysis and 41 from length analysis for the same reasons. The remaining samples were distributed unevenly between zones and substrates, with more samples from *inshore* zones than the *offshore exploited* zone, and more samples from *reef* substrate than *sand* (Table 4.1).

Table 4.1: Distribution of baited remote underwater stereo-video systems samples suitable for abundance and length analysis according to substrate (sand and reef) from the inshore Amathole Marine Protected Area, and adjacent inshore and offshore exploited zones. The number of successful samples is given in each case.

Zone	Substrate	Abundance	Length
<i>inshore exploited</i>	<i>sand</i>	10	9
<i>inshore exploited</i>	<i>reef</i>	34	31
<i>inshore protected</i>	<i>sand</i>	32	31
<i>inshore protected</i>	<i>reef</i>	40	37
<i>offshore exploited</i>	<i>sand</i>	4	3
<i>offshore exploited</i>	<i>reef</i>	15	14

4.3.2 GENERAL OVERVIEW

In the 18 offshore samples analysed for MaxN, 28 species were detected, compared to the 74 species found in the inshore samples (Table 4.2). Twenty of the offshore species were bony fish (ten of them sparids) and eight were cartilaginous species. There were, on average, seven species detected per sample (Table 4.2).

Although *P. lanarius* and *P. aeneum* were the most abundant species observed offshore (Table 4.3), and together with *S. emarginatum* and *P. bellottii natalensis* their abundance contributed towards characterising the offshore assemblage, the abundance of several species that were not prevalent in inshore samples defined the offshore environment. These included larger bodied species like *P. undulosus*, *P. rupestris*, and *C. gibbiceps*, and cartilaginous fish like spiny dogfish (*Squalus sp.*), and short tail stingray (*Dasyatis brevicaudata*; Table 4.3).

Table 4.2: Summary of results from stereo-BRUVs sampling of offshore exploited sites in the vicinity of the inshore Amathole Marine Protected Area.

	Offshore	Inshore	Total
<i>Suitable Samples</i>	19	116	135
<i>Total Species</i>	28	74	79
<i>Osteichthyes</i>	20	53	56
<i>Sparidae</i>	10	25	25
<i>Chondrichthyes</i>	8	21	23
<i>Ave Species Richness (± SD)</i>	7 ± 2	9 ± 4	9 ± 4
<i>Max Species Richness</i>	11	21	21

Table 4.3: Summary of the 10 most abundant species from offshore exploited areas adjacent to the inshore Amathole Marine Protected Area. The average (Ave.) MaxN per sample is given with standard deviation (SD) for each species. Species are listed in descending order of overall abundance.

Species	Ave. MaxN ± SD
<i>Pterogymnus lanarius</i>	14.1 ± 11.4
<i>Pachymetopon aeneum</i>	4.9 ± 6.6
<i>Polysteganus undulosus</i>	2.3 ± 4.7
<i>Spondylisoma emarginatum</i>	2 ± 3.6
<i>Argyrozona argyrozona</i>	1.8 ± 3.1
<i>Petrus rupestris</i>	1.3 ± 2.9
<i>Pagellus bellottii natalensis</i>	1.1 ± 3.6
<i>Chrysoblephus gibbiceps</i>	1.0 ± 1.8
<i>Squalus sp.</i>	1.0 ± 1.0
<i>Dasyatis brevicaudata</i>	0.6 ± 0.7

4.3.3 COMMUNITY ANALYSIS – MAXN

PERMDISP results indicated homogeneity of variance for substrate ($p = 0.099$), and heterogeneity of variance for zone, with multivariate dispersion of fish assemblages highest in the *inshore protected* zone and lowest in the *offshore exploited* zone ($p < 0.001$; Table A. 4). PERMANOVA analysis indicated that zone, substrate, and the interaction between the two all contributed to variability in MaxN data (Table 4.4). Pairwise analysis of zones identified significant differences between *inshore protected* and *inshore exploited* zones, *inshore protected* and *offshore exploited* zones, and *inshore* and *offshore exploited* zones (Table A. 5). As with the inshore analysis, substrate was the primary contributor towards overall variability in MaxN data (Table A. 6). However, in this case, the relative contributions of zone and the interaction between substrate and zone were more influential in overall variability.

Table 4.4: Results of sequential PERMANOVA analysis based on modified-Gower log₁₀ resemblance matrix of MaxN of fish assemblages in the inshore Amathole Marine Protected Area and adjacent inshore and offshore exploited zones. df = degrees of freedom; SS = sum of squares, MS = mean square; Pseudo-F = F-ratios; P (perm) = probability, Unique perms = number of unique permutations

Source	df	SS	MS	Pseudo-F	P(perm)	Unique perms
% Water column	1	1.353	1.353	2.426	0.001	997
% Obstruction	1	2.726	2.726	4.889	0.001	998
Visibility	1	4.496	4.496	8.065	0.001	998
Temperature	1	2.240	2.240	4.018	0.001	997
Substrate x Zone	2	6.998	3.499	1.751	0.008	999
Substrate	1	6.606	6.606	11.850	0.001	997
Zone	2	4.626	2.313	4.150	0.001	997
Residual	125	69.682	0.557			
Total	134	98.726				

Separation of the three zones was apparent in both constrained (CAP) and unconstrained (nMDS) multidimensional scaling techniques (Figure 4.1). The CAP plot of MaxN data showed clear separation of fish assemblages in the *offshore exploited* zone from those in the *inshore* zones along CAP axis 1 ($\delta = 0.902$), while the *inshore* zones were separated according to substrate along CAP axis 2 ($\delta = 0.87$; Table 4.5). Slight distinction between *inshore protected* and *inshore exploited* zones was also apparent for *reef* samples along CAP axis 2. Overlaying species

vectors linked to the grouping revealed five species strongly associated with the *offshore* habitat: *P. lanarius*, *C. gibbiceps*, *P. rupestris*, *Squalus sp.* and *D. brevicaudata*. The division of *inshore* species according to *reef* or *sand* habitats and *protected* or *exploited* zones corresponded with what was found in Chapter 3 (Figure 3.1). CAP analysis identified 11 axes explaining 68.46 % of the variation in MaxN data, with 71.11 % of samples accurately classified according to substrate (*reef* or *sand*) and zone (*inshore protected*, *inshore exploited* or *offshore exploited*; Table 4.5). As with the inshore analysis, the higher percentage of accurate classifications on *reef* substrate across all zones indicated that fish assemblages on *reef* substrate were more homogenous than those on *sand* substrate (Table A. 4).

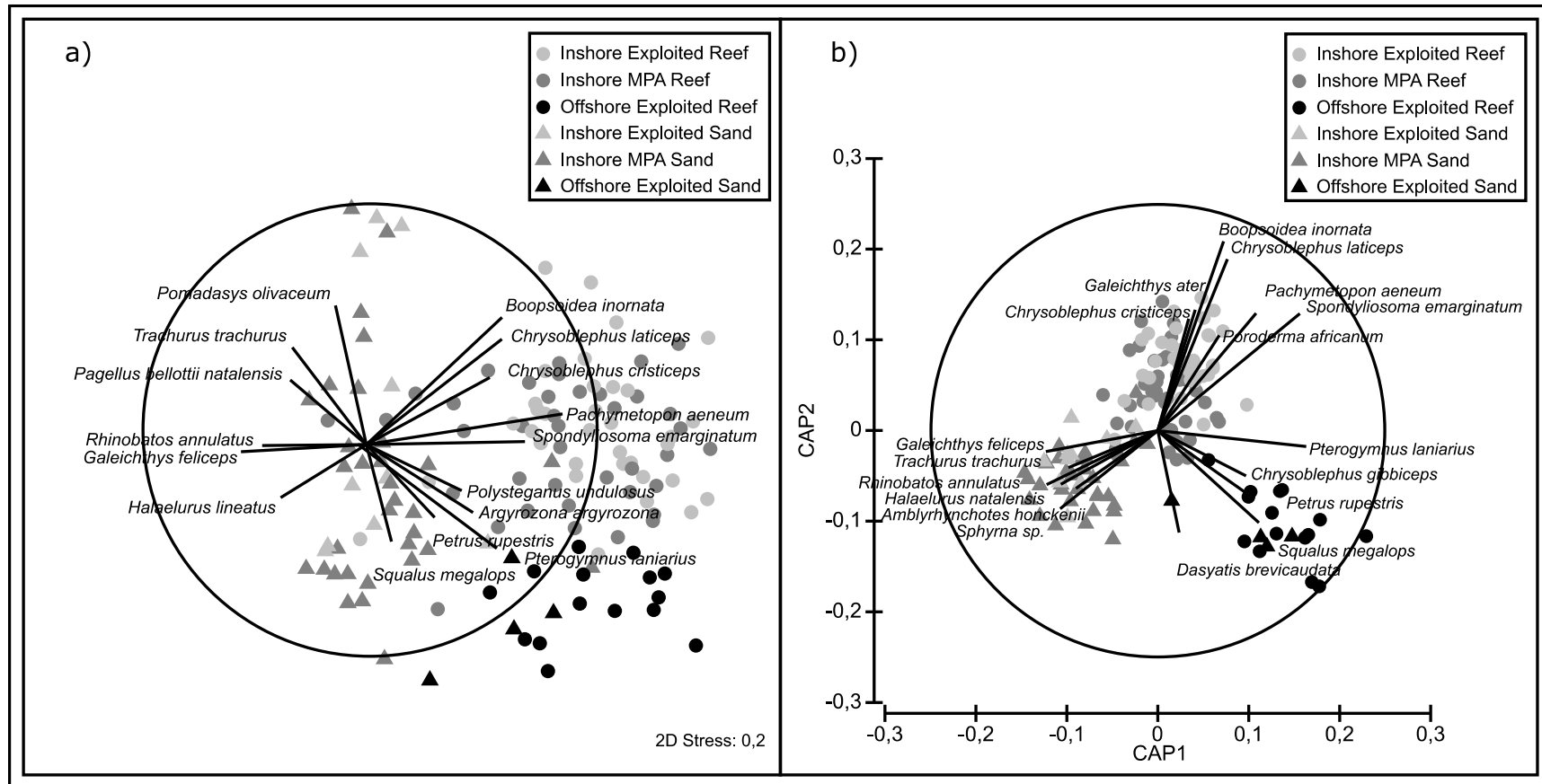


Figure 4.1: Multidimensional ordination plots based on modified-Gower Log10 resemblance matrix of MaxN data of fish assemblages in the inshore Amathole Marine Protected Area, adjacent and offshore exploited zones, illustrating grouping of samples according to substrate (*reef* or *sand*) and zone (*inshore exploited*, *inshore protected* or *offshore exploited*). Species showing a Spearman's correlation of 0.4 or above with ordination axes are represented by vectors overlaid on the plots. a) Non-metric Multidimensional Scaling b) Canonical Analysis of Principal Coordinates (CAP).

Table 4.5: Results of cross-validation results of canonical analysis of principal coordinates (CAP) based on modified-Gower Log10 resemblance matrix of MaxN data, indicating degree of accuracy of classification of samples from the inshore Amathole Marine Protected Area and adjacent inshore and offshore exploited zones according to substrate and zone. Insh. = Inshore, Offsh. = Offshore, Prot. = Protected, Expl. = Exploited.

Original Group	Predicted Group						Total	% correct
	Insh. Prot. Reef	Insh. Prot. Sand	Insh. Expl. Reef	Insh. Expl. Sand	Offsh. Expl. Reef	Offsh. Expl. Sand		
<i>Insh. Prot. Reef</i>	30	3	5	2	0	0	40	75
<i>Insh. Prot. Sand</i>	3	21	0	8	0	0	32	65,63
<i>Insh. Expl. Reef</i>	7	0	25	2	0	0	34	73,53
<i>Insh. Expl. Sand</i>	1	2	0	7	0	0	10	70
<i>Offsh. Expl. Reef</i>	1	0	0	0	11	3	15	73,33
<i>Offsh. Expl. Sand</i>	0	1	0	0	1	2	4	50

The abundance of six species was identified by SIMPER analysis as consistently defining fish assemblages in the *offshore exploited* zone, whether they were compared with assemblages from the *inshore protected* or the *inshore exploited* zones. These were, *A. argyrozona*, *P. undulosus*, *C. gibbiceps*, *P. rupestris*, *Squalus sp.* and *P. lanarius* (Table 4.6). Four species consistently distinguished the *inshore* zones, both *protected* and *exploited*, from the *offshore exploited* zone, namely *B. inornata*, *P. bellottii natalensis*, *G. feliceps* and *C. laticeps*. Several species were detected as defining one of the *inshore* zones when compared to the *offshore exploited* zone but not the other. Those that defined in particular the *inshore protected* zone, *C. cristiceps* and *C. nufar*, are both Primary Fisheries Species, and *C. cristiceps* is Critically Endangered. None of the three species that defined only the *inshore exploited* zone (*T. trachurus*, *P. olivaceum* and *G. ater*) are considered threatened or vulnerable, though the only Primary Fisheries Species of the three, *T. trachurus*, is listed as Vulnerable.

Two more species, *P. aeneum* and *S. emarginatum*, were more abundant in the *offshore exploited* zone when compared to the *inshore protected* zone, but more abundant *inshore* when compared between the *inshore exploited* and *offshore* zone.

Table 4.6: Results of SIMPER analysis of log-transformed MaxN data of fish assemblages in the inshore Amathole Marine Protected Area and adjacent inshore and offshore exploited zones, detailing contributions of individual species to within-group similarities (Av. Sim; white cells) and between-group dissimilarities (Av. Dissim; grey cells) for levels of the variable Zone (*inshore exploited*, *inshore protected* and *offshore exploited*). The contributions (% cont) of species making up the first 70 % of similarities or dissimilarities are listed in each case. The average abundance (Av. ab) for each species is given. Species that were more abundant offshore are highlighted in grey.

	<i>offshore exploited</i> (OE) Av. sim 39.9				<i>inshore exploited</i> (IE) Av. sim 31.20			<i>inshore protected</i> (IP) Av. sim 19.81			
<i>offshore exploited</i>	Species	Av.	% cont		Av. dissim 83.71			Av. dissim 86.38			
	<i>P. lanarius*</i>	2.33	49.83								
	<i>P. aeneum*</i>	1.2	13.3								
	<i>Squalus sp.</i>	0.57	9.22								
<i>inshore exploited</i>	Species	Av. IE	Av. OE	% cont	Species	Av.	% cont		Av. dissim 77.4		
	<i>P. lanarius*</i>	0.76	2.33	10,44	<i>B. inornata</i>	2.07	25.31				
	<i>B. inornata</i>	2.07	0	10,24	<i>P. aeneum*</i>	1.3	13.49				
	<i>P. aeneum*</i>	1.3	1.2	6,57	<i>S. emarginatum</i>	1.11	9.86				
	<i>S. emarginatum</i>	1.11	0.62	5,71	<i>C. laticeps*</i>	0.89	9.63				
	<i>P. natalensis</i>	0.8	0.3	4,84	<i>P. natalensis</i>	0.8	8.33				
	<i>P. olivaceum</i>	0.85	0	4,7	<i>P. olivaceum</i>	0.85	5.38				
	<i>C. laticeps*</i>	0.89	0	4,37							
	<i>P. undulosus**</i>	0.22	0.57	3,42							
	<i>A. argyrozona*</i>	0.22	0.56	3.39							
	<i>Squalus sp.</i>	0	0.57	3.36							
	<i>G. feliceps</i>	0.39	0	2.91							
	<i>G. ater</i>	0.54	0	2.77							
	<i>P. rupestris**</i>	0.02	0.51	2.61							
	<i>T. trachurus</i>	0.47	0	2.6							
	<i>C. gibbiceps**</i>	0.05	0.49	2.52							
<i>inshore protected</i>	Species	Av. IP	Av. OE	% cont	Species	Av. IP	Av. IE	% cont	Species	Av.	% cont
	<i>P. lanarius*</i>	0.5	2.33	13,75	<i>B. inornata</i>	0.94	2.07	9.95	<i>P. natalensis</i>	1.14	21.09
	<i>P. natalensis</i>	1.14	0.3	7,79	<i>P. natalensis</i>	1.14	0.8	7.44	<i>G. feliceps</i>	0.54	11.49
	<i>P. aeneum*</i>	0.87	1.2	7,43	<i>P. aeneum*</i>	0.87	1.3	6.77	<i>P. aeneum*</i>	0.87	10.73
	<i>B. inornata</i>	0.94	0	4,92	<i>S. emarginatum</i>	0.52	1.11	5.87	<i>B. inornata</i>	0.94	10.71
	<i>S. emarginatum</i>	0.52	0.62	4,71	<i>P. olivaceum</i>	0.42	0.85	5.77	<i>C. cristiceps**</i>	0.56	6.52
	<i>G. feliceps</i>	0.54	0	4,29	<i>P. lanarius*</i>	0.5	0.76	4.94	<i>C. laticeps*</i>	0.54	5.77
	<i>Squalus sp.</i>	0	0.57	4,07	<i>C. laticeps*</i>	0.54	0.89	4.68	<i>S. emarginatum</i>	0.52	4.58
	<i>A. argyrozona*</i>	0.26	0.56	4,06	<i>G. feliceps</i>	0.54	0.39	4.64			
	<i>P. undulosus**</i>	0.17	0.57	3.82	<i>T. trachurus</i>	0.2	0.47	3.56			
	<i>C. cristiceps**</i>	0.56	0.09	3.13	<i>C. cristiceps**</i>	0.56	0.32	3.36			
	<i>C. gibbiceps**</i>	0.1	0.49	3.05	<i>G. ater</i>	0.07	0.54	2.95			
	<i>P. rupestris**</i>	0.05	0.51	3.04	<i>C. nufar*</i>	0.32	0.41	2.91			
	<i>C. laticeps*</i>	0.54	0	2.74	<i>H. lineatus</i>	0.14	0.21	2.33			
	<i>D. brevicaudata</i>	0.14	0.41	2.69	<i>H. natalensis</i>	0.21	0.21	2.32			
	<i>C. nufar*</i>	0.32	0.18	2.41	<i>A. argyrozona</i>	0.26	0.22	2.03			

* Primary Fisheries Species

** Vulnerable Fisheries Species

4.3.4 SPECIES RICHNESS

The GLM for species richness (defined here as the number of species detected per sample) was fitted with a Poisson distribution. Model selection resulted in exclusion of the terms % water column and % obstruction (AIC: Full model = 668.5, Best-fit: 666.4 with no difference in deviance explained between models ($p = 0.4$)), resulting in the best-fit model:

$$f(\text{species richness}) = \alpha + \beta_1(\text{temperature}) + \beta_2(\text{substrate}) + \beta_3(\text{zone}) + \varepsilon \quad \text{Eq. 9}$$

Where α is the intercept, β_i refers to the regression coefficients, and ε is the noise (Zuur et al. 2013).

The best-fit GLM (Eq. 9) explained 48.54 % of total variability. Sequential likelihood ratio tests indicated that the temperature, substrate, and zone significantly affected species richness (Table 4.7).

Table 4.7: Results of sequential likelihood ratio tests on the best-fit Generalized Linear Model for effects of temperature, substrate, and zone on species richness in the inshore Amathole Marine Protected Area and adjacent inshore and offshore exploited zones. df = degrees of freedom; PR(>Chi) = P-value; Relative contribution (%) = contribution of each term to overall variability explained by the model

	Df	Residual Deviance	Residual df	Deviance	Pr(>Chi)	Relative contribution (%)
NULL			134	257.15		
Temperature	1	17.090	133	240.06	<0.001	13.69
Substrate	1	96.116	132	143.94	<0.001	77.01
Zone	2	11.601	130	132.34	0.003	9.29

Increased temperature was associated with an increase in species richness (Table 4.8). *Sand* substrate was associated with a decrease in species richness relative to *reef* substrate (mean \pm SD; *sand*: 6 ± 3 ; *reef*: 10 ± 4 ; Table 4.8, Figure 4.2). Both the *inshore protected* zone and the *offshore exploited* zone were associated with lower species richness compared to the *inshore exploited* zone (mean \pm SD; *inshore protected*: 8 ± 4 ; *offshore exploited*: 7 ± 2 ; *inshore exploited* 10 ± 4). However, the decrease was only significant for the *offshore exploited* zone, and only on *reef* substrate (Figure 4.2).

Table 4.8: Output summary of GLM describing the influence of temperature, substrate, and zone on variability in species richness in the inshore Amathole Marine Protected Area and adjacent inshore and offshore exploited zones.

Coefficients:	Estimate	Std. Error	z value	Pr(> z)
Intercept	1.277	0.244	5.234	<0.001
Temperature	0.078	0.016	4.879	<0.001
Substrate <i>sand</i>	-0.656	0.073	-8.981	<0.001
Zone <i>inshore protected</i>	-0.112	0.064	-1.759	0.079
Zone <i>offshore exploited</i>	-0.337	0.103	-3.276	0.001

A significant decrease in species richness was detected on *sand* compared to *reef* substrates (Figure 4.2). Species richness was significantly higher in the *inshore exploited* zone, relative to the *offshore exploited* zone (Figure 4.2). Species richness in the *inshore protected* zone was not measurably different to that observed in *offshore* and *inshore exploited* zones (Figure 4.2).

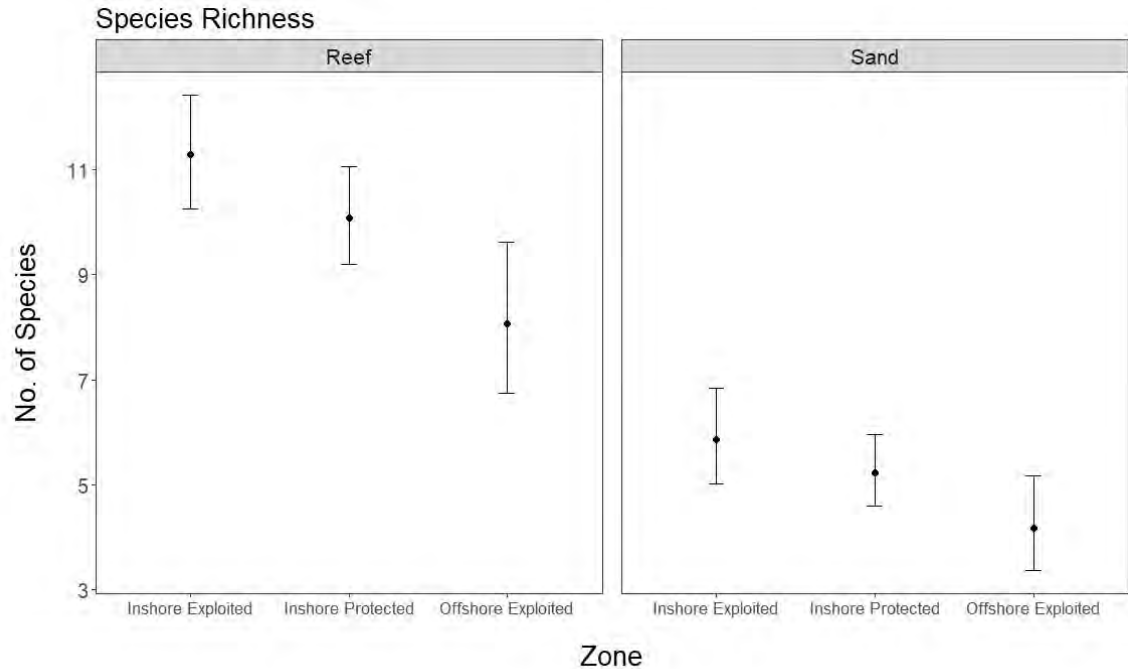


Figure 4.2: Predicted values for species richness (No. of species) on sand and reef substrates in the inshore Amathole Marine Protected Area and adjacent inshore and offshore exploited based on standard average values for all covariates included in Eq. 9. Error bars represent 95 % confidence intervals. Factors found to be insignificant in analysis of deviance were excluded from the predictive plots.

4.3.5 PRIMARY FISHERIES SPECIES

Eight out of 21 Primary Fisheries Species were altogether absent from offshore samples. However, the Total Biomass of several of those that were present was considerably greater offshore than in either of the two *inshore* zones. In particular, *P. rupestris*, *P. undulosus* and *E. marginatus*, and to a lesser degree, *A. argyrozona*, *P. aeneum* and *P. lanarius* (Table 4.9).

Table 4.9: The average (Av.) MaxN and average (Av.) Total Biomass of Primary Fisheries Species where they were detected in the inshore Amathole Marine Protected Area (IP) and adjacent inshore exploited (IE) and offshore exploited (OE) zones are presented with standard deviation (SD).

Species	MaxN (av. \pm SD)			Total Biomass (kg; av. \pm SD)		
	IE	IP	OE	IE	IP	OE
<i>Argyrozona argyrozona</i>	3 \pm 2	5 \pm 4	4 \pm 3	0.8 \pm 0.6	1.6 \pm 1.8	2.3 \pm 1.9
<i>Cheimerius nufar</i>	2 \pm 1	3 \pm 3	2 \pm 1	1.7 \pm 1.8	2.6 \pm 3.7	0.8 \pm 0.8
<i>Chelidonichthys kumu</i>	1 \pm 0	1 \pm 1	1 \pm 0	0 \pm 0	0 \pm 0	0.9 \pm 0
<i>Chrysolephus cristiceps</i>	2 \pm 1	3 \pm 3	2 \pm 1	0.9 \pm 0.8	3.7 \pm 3.1	3.3 \pm 3.4
<i>Chrysolephus gibbiceps</i>	2 \pm 1	2 \pm 1	2 \pm 2	4.4 \pm 5.6	4.1 \pm 3.1	4.7 \pm 7.2
<i>Chrysolephus laticeps</i>	3 \pm 1	4 \pm 5	0 \pm 0	1.5 \pm 1.1	1.6 \pm 1.1	0 \pm 0
<i>Chrysolephus puniceus</i>	0 \pm 0	0 \pm 0	0 \pm 0	0 \pm 0	0 \pm 0	0 \pm 0
<i>Cymatoceps nasutus</i>	4 \pm 0	2 \pm 2	0 \pm 0	0.2 \pm 0	5.2 \pm 3.4	0 \pm 0
<i>Diplodus capensis</i>	2 \pm 2	3 \pm 3	0 \pm 0	0.1 \pm 0.1	0.2 \pm 0.1	0 \pm 0
<i>Epinephelus andersoni</i>	0 \pm 0	0 \pm 0	0 \pm 0	0 \pm 0	0 \pm 0	0 \pm 0
<i>Epinephelus chabaudi</i>	2 \pm 0	1 \pm 1	1 \pm 0	2.1 \pm 0	1.9 \pm 1.2	0 \pm 0
<i>Epinephelus marginatus</i>	1 \pm 0	1 \pm 1	1 \pm 0	0.7 \pm 1	2.2 \pm 0	7.4 \pm 0
<i>Mustelus mustelus</i>	1 \pm 0	2 \pm 3	1 \pm 1	6.6 \pm 1.5	2.9 \pm 1.8	3.9 \pm 2.7
<i>Pachymetopon aeneum</i>	8 \pm 8	8 \pm 8	7 \pm 7	0.7 \pm 0.6	1 \pm 1.3	2.7 \pm 2.5
<i>Petrus rupestris</i>	1 \pm 0	1 \pm 0	2 \pm 4	7.7 \pm 0	11.5 \pm 17.4	24.9 \pm 58.1
<i>Polyprion americanus</i>	0 \pm 0	0 \pm 0	1 \pm 0	0 \pm 0	0 \pm 0	0.2 \pm 0
<i>Polysteganus praeorbitalis</i>	0 \pm 0	0 \pm 0	0 \pm 0	0 \pm 0	3.9 \pm 3.3	0 \pm 0
<i>Polysteganus undulosus</i>	2 \pm 1	2 \pm 2	4 \pm 6	0.6 \pm 0.7	0.5 \pm 0.7	9.1 \pm 10.9
<i>Pterogymnus lanarius</i>	6 \pm 4	6 \pm 5	15 \pm 11	0.8 \pm 0.8	1 \pm 0.8	2 \pm 2.2
<i>Rhabdosargus globiceps</i>	0 \pm 0	0 \pm 0	0 \pm 0	0.2 \pm 0	0 \pm 0	0 \pm 0
<i>Sarpa salpa</i>	2 \pm 0	1 \pm 1	0 \pm 0	0.3 \pm 0	0 \pm 0	0 \pm 0

4.3.5.1 MAXN

The species comprising the Primary Fisheries Species group are defined in Table 2.1 of the methods chapter. The GLM for MaxN of Primary Fisheries Species (the summed MaxN for all Primary Fisheries Species in each sample, as defined in section 2.2.4.2 of the methods chapter) was fitted with a Negative Binomial distribution after Poisson distribution was found to be over-dispersed (Dispersion statistic 7.264). Model selection resulted in exclusion of the terms % water column and % obstruction (AIC: Full model = 863.7, Best-fit: 860.1 with no difference in deviance explained between models ($p = 0.8$), resulting in the best-fit model:

$$f(\text{MaxN Primary Fisheries Species}) = \alpha + \beta_1(\text{temperature}) + \beta_2(\text{substrate}) + \beta_3(\text{zone}) + \varepsilon$$

Eq. 10

Where α is the intercept, β_i refers to the regression coefficients, and ε is the noise (Zuur et al. 2013).

The best-fit GLM (Eq. 10) explained 52.15 % of total variability in MaxN of Primary Fisheries Species. Sequential likelihood ratio tests indicated that the observed patterns in MaxN were determined by substrate and zone (Table 4.10).

Table 4.10: Results of sequential likelihood ratio tests on the best fit Generalized Linear Model for effects of temperature, substrate, and zone on the MaxN of Primary Fisheries Species in the inshore Amathole Marine Protected Area and adjacent inshore and offshore exploited zones. df = degrees of freedom; PR(>Chi) = P-value; Relative contribution (%) = contribution of each term to overall variability explained by the model

	df	Residual Deviance	Residual df	Deviance	Pr(>Chi)	Relative Contribution (%)
NULL			134	338.55		
Temperature	1	0.050	133	338.50	0.824	0.03
Substrate	1	151.253	132	187.25	<0.001	85.66
Zone	2	25.269	130	161.98	<0.001	14.31

Sand substrate was associated with a decrease in MaxN of Primary Fisheries Species compared to *reef* substrate (mean \pm SD; *sand*: 2 ± 3 ; *reef*: 10 ± 13 ; Table 4.11, Figure 4.3). Both the *inshore protected* zone (mean 13, \pm mean \pm SD 13) and the *offshore exploited* zone (mean 25, mean \pm SD 15) were associated with an increase in MaxN compared to the *inshore exploited* zone (mean \pm SD ; *inshore protected*: 13 ± 13 ; *offshore exploited*: 25 ± 15 ; *inshore exploited*: 11 ± 12 ; Table 4.10). However, this was only significant for the *offshore exploited* zone (Figure 4.3). This is consistent with the findings of the inshore analysis in Chapter 3, that MaxN of Primary Fisheries Species was not significantly different between the *inshore protected* and *inshore exploited* zones (Table 3.10).

Table 4.11: Output summary of Generalized Linear Model describing the influence of temperature, substrate, and zone on variability in the MaxN of Primary Fisheries Species in the inshore Amathole Marine Protected Area and adjacent inshore and offshore exploited zones. Estimate = coefficient estimate; Std. Error = standard error of estimate; $Pr(>|z|)$ = P-value

Coefficients:	Estimate	Std. Error	z value	$Pr(> z)$
Intercept	0.452	0.688	0.657	0.511
Temperature	0.153	0.046	3.331	0.001
Substrate <i>sand</i>	-2.600	0.201	-12.941	<0.001
Zone <i>inshore protected</i>	0.144	0.181	0.794	0.427
Zone <i>offshore exploited</i>	1.169	0.247	4.738	<0.001

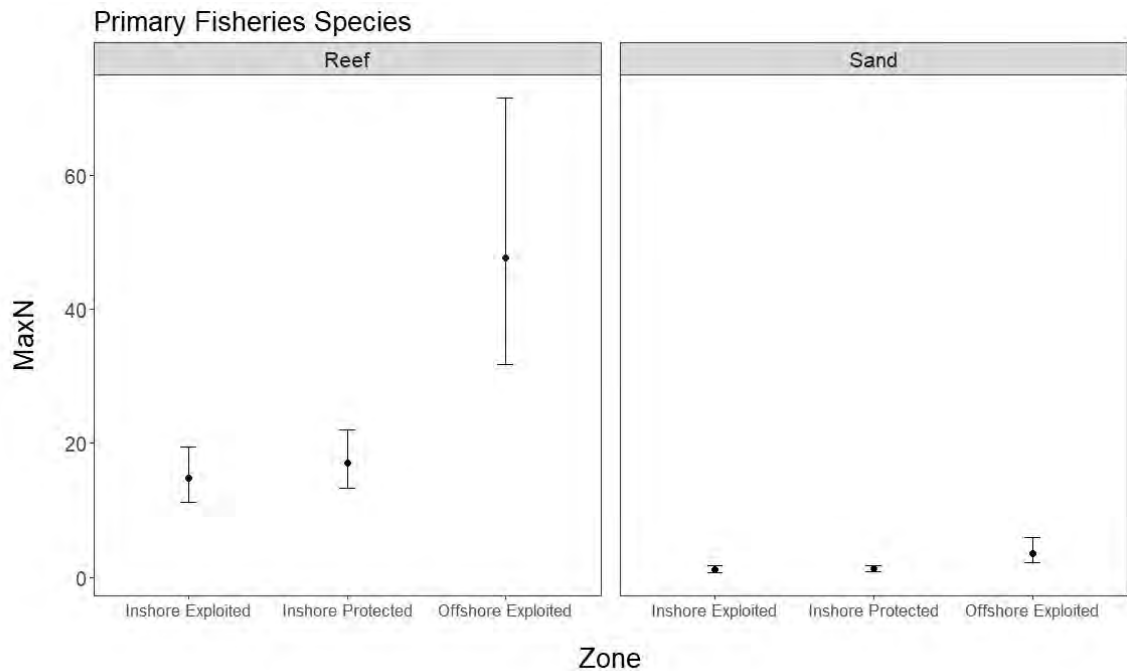


Figure 4.3: Predicted values for MaxN of Primary Fisheries Species on sand and reef substrates in the inshore Amathole Marine Protected Area and adjacent inshore and offshore exploited zones based on standard average values for all covariates included in Eq. 10. Error bars represent 95 % confidence intervals.

4.3.5.2 TOTAL BIOMASS

The GLM for Total Biomass of Primary Fisheries Species (the summed Total Biomass for all Primary Fisheries Species in each sample as defined in section 2.2.4.2 of the methods chapter) was fitted with a Tweedie distribution. Model selection resulted in exclusion of the terms % water column and temperature (AIC: Full model = 2 003.4, Best-fit: 1 806.5 with no difference in deviance explained between models ($p = 0.7$)), resulting in the best-fit model:

$$f(\text{Total Biomass Primary Fisheries Species}) = \beta_2(\% \text{ obstruction}) + \beta_4(\text{substrate}) + \beta_5(\text{zone}) + \epsilon$$

Eq. 11

Where α is the intercept, β_i refers to the regression coefficients, and ϵ is the noise (Zuur et al. 2013).

The best-fit GLM (Eq. 11) explained 58.54 % of total variability in Total Biomass of Primary Fisheries Species. Sequential likelihood ratio tests indicated that the observed patterns in Total Biomass were determined by % obstruction, substrate, and zone (Table 4.12).

Table 4.12: Results of sequential likelihood ratio tests on the best fit Generalized Linear Model for effects of % obstruction, substrate, and zone on the Total Biomass of Primary Fisheries Species in the inshore Amathole Marine Protected Area and adjacent inshore and offshore exploited zones. df = degrees of freedom; PR(>Chi) = P-value; Relative contribution (%) = contribution of each term to overall variability explained by the model

	Df	Residual Deviance	Residual df	Deviance	Pr(>Chi)	Relative Contribution (%)
NULL			124	22 936		
% Obstruction	1	482.7	123	22 453	0.046	4.09
Substrate	1	6 287.1	122	16 166	<0.001	53.27
Zone	2	5 033.1	120	11 133	<0.001	42.64

Sand substrate was associated with a decrease in Total Biomass compared to *reef* substrate (mean \pm SD; *sand*: 20.6 \pm 11.9 kg; *reef*: 30.9 \pm 63.3 kg; Table 4.13, Figure 4.4). Both the *inshore protected* zone and the *offshore exploited* were associated with an increase in Total Biomass compared to the *inshore exploited* zone (mean \pm SD; *inshore protected*: 8.2 \pm 11.7 kg; *offshore exploited*: 35.1 \pm 59.4 kg; *inshore exploited*: 4.8 \pm 4.9 kg; Table 4.13). However, the increase was

only found to be significant for the *offshore exploited* zone, and only on *reef* substrate (Figure 4.4).

Table 4.13: Output summary of Generalized Linear Model describing the influence of % obstruction, substrate, and zone on variability in the Total Biomass of Primary Fisheries Species in the inshore Amathole Marine Protected Area and adjacent inshore and offshore exploited zones. Estimate = coefficient estimate; Std. Error = standard error of estimate; PR(>|z|) = P-value

Coefficients:	Estimate	Std. Error	z value	Pr(> z)
Intercept	8.485	0.276	30.757	<0.001
% Obstruction	0.022	0.013	1.621	0.108
Substrate <i>sand</i>	-2.460	0.362	-6.804	<0.001
Zone <i>inshore protected</i>	1.002	0.314	3.188	0.002
Zone <i>offshore exploited</i>	2.177	0.354	6.156	<0.001

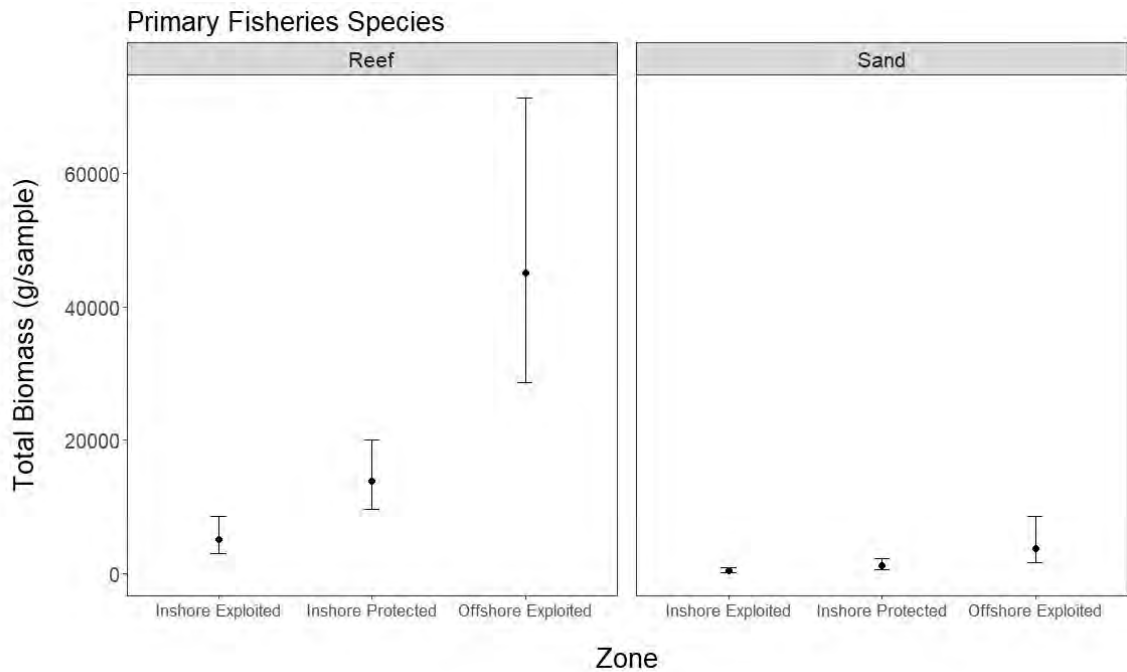


Figure 4.4: Predicted values for Total Biomass of Primary Fisheries Species on sand and reef substrate for the three locations in the Amathole Marine Protected area and adjacent inshore and offshore exploited zones based on standard average values for all covariates included in Eq. 11. Error bars represent 95 % confidence intervals.

4.3.6 VULNERABLE FISHERIES SPECIES

Once again, a large proportion of Vulnerable Fisheries Species were not detected at all in the offshore samples. The biomass of three Vulnerable Fisheries Species, *E. marginatus*, *P. rupestris* and *P. undulosus*, was distinctly greater in the offshore environment, while those of *C. nasutus* and *P. praeorbitalis* were greater inshore (Table 4.14).

Table 4.14: The average (Av.) MaxN and average (Av.) Total Biomass of Vulnerable Fisheries Species where they were detected in the inshore Amathole Marine Protected Area (IP) and adjacent inshore (IE) and offshore (OE) exploited areas are presented with standard deviation (SD).

Species	MaxN (Av. \pm SD)			Total Biomass (kg; Av. \pm SD)		
	IE	IP	OE	IE	IP	OE
<i>Chrysoblephus cristiceps</i>	2 \pm 1	3 \pm 3	2 \pm 1	0.9 \pm 0.8	3.7 \pm 3.1	3.3 \pm 3.4
<i>Chrysoblephus gibbiceps</i>	2 \pm 1	2 \pm 1	2 \pm 2	4.4 \pm 5.6	4.1 \pm 3.1	4.7 \pm 7.2
<i>Cymatoceps nasutus</i>	4 \pm 0	2 \pm 2	0 \pm 0	0.2 \pm 0	5.2 \pm 3.4	0 \pm 0
<i>Diplodus capensis</i>	2 \pm 2	3 \pm 3	0 \pm 0	0.1 \pm 0.1	0.2 \pm 0.1	0 \pm 0
<i>Diplodus hottentotus</i>	2 \pm 1	2 \pm 1	0 \pm 0	0.4 \pm 0.3	0.4 \pm 0.7	0 \pm 0
<i>Epinephelus marginatus</i>	1 \pm 0	1 \pm 1	1 \pm 0	0.7 \pm 1	2.2 \pm 0	7.4 \pm 0
<i>Gymnocrotaphus curvidens</i>	1 \pm 0	1 \pm 1	0 \pm 0	0 \pm 0	0 \pm 0	0 \pm 0
<i>Pachymetopon grande</i>	1 \pm 0	1 \pm 1	0 \pm 0	0.1 \pm 0	0 \pm 0	0 \pm 0
<i>Petrus rupestris</i>	1 \pm 0	1 \pm 0	2 \pm 4	7.7 \pm 0	11.5 \pm 17.4	24.9 \pm 58.1
<i>Polyprion americanus</i>	0 \pm 0	0 \pm 0	1 \pm 0	0 \pm 0	0 \pm 0	0.2 \pm 0
<i>Polysteganus praeorbitalis</i>	0 \pm 0	0 \pm 0	0 \pm 0	0 \pm 0	3.9 \pm 3.3	0 \pm 0
<i>Polysteganus undulosus</i>	2 \pm 1	2 \pm 2	4 \pm 6	0.6 \pm 0.7	0.5 \pm 0.7	9.1 \pm 10.9
<i>Rhabdosargus globiceps</i>	0 \pm 0	0 \pm 0	0 \pm 0	0.2 \pm 0	0 \pm 0	0 \pm 0
<i>Rhabdosargus holubi</i>	1 \pm 0	2 \pm 2	0 \pm 0	0.2 \pm 0.1	0.2 \pm 0.2	0 \pm 0
<i>Rhabdosargus sarba</i>	0 \pm 0	0 \pm 0	0 \pm 0	0 \pm 0	0 \pm 0	0 \pm 0
<i>Umbrina sp.</i>	1 \pm 0	1 \pm 0	0 \pm 0	0 \pm 0	0 \pm 0	0 \pm 0

4.3.6.1 MAXN

The species comprising the Vulnerable Fisheries Species group are defined in Table 2.1 of the methods chapter. The GLM for MaxN of Vulnerable Fisheries Species (the summed MaxN for all Vulnerable Fisheries Species in each sample as defined in section 2.2.4.2 of the methods chapter) was fitted with a Negative Binomial distribution after Poisson distribution was found to be over-dispersed (Dispersion statistic 4.261). Model selection resulted in exclusion of the terms % water column and % obstruction (AIC 527.104 vs AIC of saturated model 529.650, ANOVA comparing models $p = 0.483$), resulting in the best-fit model: A bit clumsy. Rather (AIC: Full

model = 576.7, Best-fit: 574.5 with no difference in deviance explained between models ($p = 0.4$).

$$f(\text{MaxN Vulnerable Fisheries Species}) = \alpha + \beta_1(\text{temperature}) + \beta_2(\text{substrate}) + \beta_3(\text{zone}) + \varepsilon$$

Eq. 12

Where α is the intercept, β_i refers to the regression coefficients, and ε is the noise (Zuur et al. 2013).

The best-fit GLM (Eq. 12) explained 58.63 % of total variability in MaxN of Vulnerable Fisheries Species. Sequential likelihood ratio tests indicated that the observed patterns in MaxN were determined by substrate and zone (Table 4.15).

Table 4.15: Results of sequential likelihood ratio tests on the best fit Generalized Linear Model for effects of temperature, substrate, and zone on the MaxN of Vulnerable Fisheries Species in the inshore Amathole Marine Protected Area and adjacent inshore and offshore exploited zones. df = degrees of freedom; PR(>Chi) = P-value; Relative contribution (%) = contribution of each term to overall variability explained by the model

	df	Residual Deviance	Residual df	Deviance	Pr(>Chi)	Relative Contribution (%)
NULL			134	230.38		
Temperature	1	1.475	133	228.90	0.225	1.55
Substrate	1	79.683	132	149.22	<0.001	83.61
Zone	2	14.141	130	135.08	0.001	14.84

Sand substrate was associated with a decrease in MaxN of Vulnerable Fisheries Species compared to *reef* substrate (mean \pm SD; *sand*: 0 ± 1 ; *reef*: 4 ± 5 ; Table 4.16, Figure 4.5). Both the *inshore protected* zone and the *offshore exploited* zone were associated with a significant increase in MaxN compared to the *inshore exploited* zone on *reef* substrate (mean \pm SD; *inshore protected*: 3 ± 4 ; *offshore exploited*: 5 ± 8 ; *inshore exploited*: 2 ± 3), but not on *sand* (mean \pm SD; *inshore protected*: 0 ± 2 ; *offshore exploited*: 0 ± 0 , *inshore exploited*: 0 ± 0 ; Table 4.16; Figure 4.5).

Table 4.16: Output summary of Generalized Linear Model describing the influence of temperature, substrate, and zone on variability in the MaxN of Vulnerable Fisheries Species in the inshore Amathole Marine Protected Area and adjacent inshore and offshore exploited zones. Estimate = coefficient estimate; Std. Error = standard error of estimate; $PR(>|z|)$ = P-value

Coefficients:	Estimate	Std. Error	z value	Pr(> z)
Intercept	-1.852	0.982	-1.886	0.059
Temperature	0.185	0.065	2.846	0.004
Substrate <i>sand</i>	-2.736	0.328	-8.331	<0.001
Zone <i>inshore protected</i>	0.805	0.257	3.135	<0.001
Zone <i>offshore exploited</i>	1.179	0.343	3.439	<0.001

A significant decrease in MaxN of Vulnerable Fisheries Species was detected on *sand* compared to *reef* substrates (Figure 4.5). While no significant differences in MaxN were observed between zones on *sand* substrate, nor between the *inshore protected* and *offshore exploited* zones on either substrate, MaxN was significantly lower in the *inshore exploited* zone than in the *inshore protected* or *offshore exploited* zones on *reef* substrate.

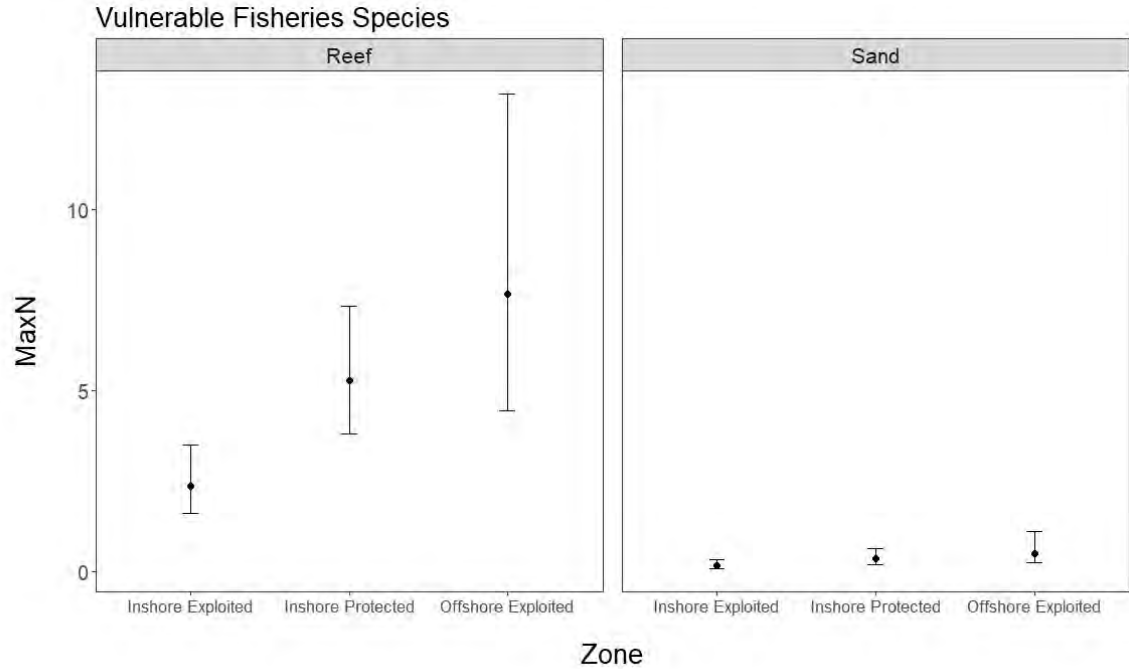


Figure 4.5: Predicted values for MaxN of Vulnerable Fisheries Species on reef and sand substrates in the inshore Amathole Marine Protected Area and adjacent inshore and offshore exploited zones based on standard average values for all covariates included in Eq. 12. Error bars represent 95 % confidence intervals.

4.3.6.2 TOTAL BIOMASS

The GLM for Total Biomass of Vulnerable Fisheries Species (the summed Total Biomass for all Vulnerable Fisheries Species in each sample as defined in section 2.2.4.2 of the methods chapter) was fitted with a Tweedie distribution. Model selection resulted in exclusion of the terms % water column and temperature (AIC: Full model = 1 511.5, Best-fit: 1 507.8 with no difference in deviance explained between models ($p = 0.9$)), resulting in the best-fit model:

$$f(\text{Total Biomass Vulnerable Fisheries Species}) = \alpha + \beta_1 (\% \text{ obstruction}) + \beta_2(\text{substrate}) + \beta_3(\text{zone}) + \epsilon$$

Eq. 13

Where α is the intercept, β_i refers to the regression coefficients, and ϵ is the noise (Zuur et al. 2013).

The best-fit GLM (Eq. 13) explained 53.64 % of total variability in Total Biomass of Vulnerable Fisheries Species. Sequential likelihood ratio tests indicated that the observed patterns in Total Biomass were determined by % obstruction, substrate, and zone (Table 4.17).

Table 4.17: Results of sequential likelihood ratio tests on the best fit Generalized Linear Model for effects of % obstruction, substrate, and zone on the Total Biomass of Vulnerable Fisheries Species in the inshore Amathole Marine Protected Area and adjacent inshore and offshore exploited zones. df = degrees of freedom; PR(>Chi) = P-value; Relative contribution (%) = contribution of each term to overall variability explained by the model

	df	Residual Deviance	Residual df	Deviance	Pr(>Chi)	Relative Contribution (%)
NULL			124	20 533		
% Obstruction	1	515.9	123	20 017	0.043	5.42
Substrate	1	3 459.4	122	16 558	<0.001	36.35
Zone	2	5 542.4	120	11 015	<0.001	58.23

Sand substrate (mean 0.9 kg, SD 3.6) was associated with a decrease in Total Biomass compared to *reef* substrate (mean \pm SD: *sand*: 0.9 \pm 3.6 kg; *reef*: 9.7 \pm 28.2 kg; Table 4.18, Figure 4.6). On reef substrate, the *inshore protected* zone (mean 4.8 kg, SD 2.7) and *offshore exploited* zone (mean 26.6 kg, SD 58) were both associated with an increase in Total Biomass compared to the *inshore exploited* zone (mean \pm SD; *inshore protected*: 4.8 \pm 2.7 kg; *offshore exploited*: 26.6 \pm 58 kg; *inshore exploited* 1.3 \pm 2.7 kg; Table 4.18, Figure 4.6). In addition, Total Biomass in the *offshore exploited* zone was significantly greater than the *inshore protected* zone on reef substrate (mean \pm SD; *inshore protected reef*: 9.5 \pm 12.1; *offshore protected reef*: 31.0 \pm 63.3; Figure 4.6).

Table 4.18: Output summary of Generalized Linear Model describing the influence of % obstruction, substrate, and zone on variability in Total Biomass of Vulnerable Fisheries Species in the inshore Amathole Marine Protected Area and adjacent inshore and offshore exploited zones. Estimate = coefficient estimate; Std. Error = standard error of estimate; PR(>|z|) = P-value

Coefficients:	Estimate	Std. Error	z value	Pr(> z)
Intercept	6.935	0.455	15.242	<0.001
% Obstruction	0.004	0.019	1.938	0.055
Substrate <i>sand</i>	-2.457	0.495	-4.964	<0.001
Zone <i>inshore protected</i>	1.968	0.493	3.990	<0.001
Zone <i>offshore exploited</i>	3.383	0.541	6.249	<0.001

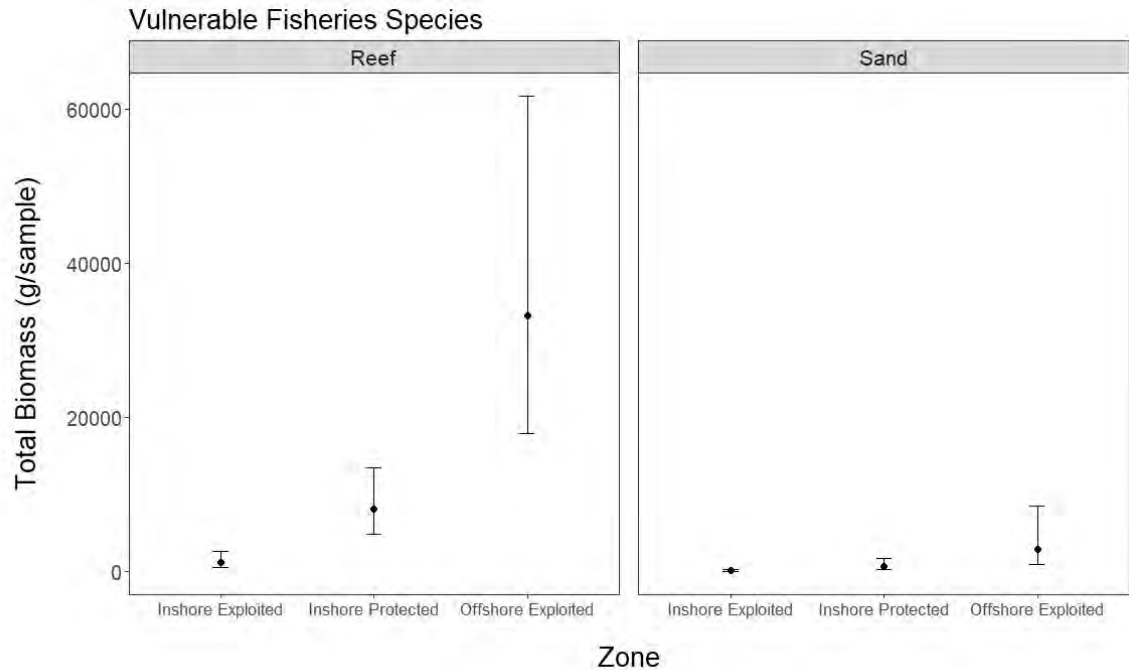


Figure 4.6: Predicted values for Total Biomass of Vulnerable Fisheries Species on reef and sand substrates in the inshore Amathole Marine Protected Area (*inshore protected*) and the adjacent inshore (*inshore exploited*) and offshore (*offshore exploited*) exploited zones based on standard average values for all covariates included in Eq. 13. Error bars represent 95 % confidence intervals.

4.3.7 SINGLE SPECIES ANALYSES

The abundance and biomass of three species of particular conservation interest whose distributions are known to be centred in the Amathole region were analysed according to depth and management. All individuals of *P. rupestris* exceeded the size indicative of 50 % maturity for the species (Table 4.19). *Chrysolephus cristiceps* was largest in the inshore MPA, though even there, the average size was just smaller than the size at change of sex. *Polysteganus undulosus* was largest in the offshore zone, which is the only area where individuals larger than the size at 50 % maturity were recorded. In spite of this, the average size of *P. undulosus* in the *offshore exploited* zone was still below that at 50 % maturity.

Table 4.19: Observed lengths of *Petrus rupestris*, *Polysteganus undulosus* and *Chrysoblephus cristiceps* in the inshore Amathole Marine Protected Area and adjacent inshore and offshore exploited areas. Minimum (Min), maximum (Max) and average (Ave) lengths are reported for each species in mm for the *inshore exploited*, *inshore protected* and *offshore exploited* zones. Average is presented \pm Standard Deviation. The length at 50 % maturity (Length 50 %) and maximum recorded length (Max length) as reported in Mann (2013) is given for each species.

	Length 50 %	Max length	<i>inshore exploited</i>			<i>inshore protected</i>			<i>offshore exploited</i>		
			Min	Max	Ave	Min	Max	Ave	Min	Max	Ave
<i>P. rupestris</i>	575	Historical *1829 Recent *1189	732	732	732 \pm 0	815	1181	960 \pm 195	451	1161	826 \pm 181
<i>P. undulosus</i>	650 – 750	*908	175	355	255 \pm 57	141	360	236 \pm 66	178	657	402 \pm 142
<i>C. cristiceps</i>	Females 275 – 365 Sex change at 435	*615	232	348	293 \pm 30	247	574	414 \pm 87	333	504	440 \pm 93

* Lengths converted from TL to FL (all lengths and conversions from Mann (2013))

Due to the large number of zeros in the datasets for the focus species, a hurdle model approach was followed to investigate patterns in (1) the presence/absence and where present, patterns in (2) the abundance (MaxN) and (3) the maximum recorded individual size (Max Biomass) of *P. rupestris*, *P. undulosus*, and *C. cristiceps*.

4.3.7.1 PETRUS RUPESTRIS

Detection Probability

For the first part of the hurdle model, the analysis focussed on presence-absence values for *P. rupestris* in all of the samples in the dataset. The GLM for detection probability (presence or absence) of *P. rupestris* was fitted with a Binomial distribution. Model selection resulted in the exclusion of the terms % water column and temperature (AIC: Full model = 72.6, Best-fit: 70.8 with no difference in deviance explained between models ($p = 0.3$)), resulting in the best-fit model:

$$f(\text{Detection Probability } P. \text{ rupestris}) = \alpha + \beta_1 (\% \text{ obstruction}) + \beta_4 (\text{depth}) + \beta_5 (\text{management}) + \beta_6 (\text{depth} * \text{management}) + \varepsilon \quad \text{Eq. 14}$$

Where α is the intercept, β_i refers to the regression coefficients, and ε is the noise (Zuur et al. 2013).

The best-fit GLM (Eq. 14) explained 38.11 % of total variability in detection probability of *P. rupestris*. Sequential likelihood ratio tests indicated that the observed pattern in detection probability was primarily determined by depth. (Table 4.20).

Table 4.20: Results of sequential likelihood ratio tests on the best fit Generalized Linear Model for effects of % obstruction, depth, and management on the probability of detecting individuals of *Petrus rupestris* on reef substrate in the inshore Amathole Marine Protected Area and adjacent inshore and offshore exploited areas. df = degrees of freedom; PR(>Chi) = P-value; Relative contribution (%) = contribution of each term to overall variability explained by the model

	df	Residual Deviance	Residual df	Deviance	Pr(>Chi)	Relative Contribution (%)
NULL			134	98.27		
% Obstruction	1	2.050	133	96.220	0.152	5.475
Depth	1	30.880	132	65.340	<0.001	82.465
Management	1	1.365	131	63.975	0.243	3.645
Depth x Management	1	3.151	130	60.824	0.076	8.415

Increased depth was associated with an increased likelihood of detecting individuals of *P. rupestris*, regardless of management status (Table 4.21). The likelihood of detection was considerably greater at depths of over 75 m (Figure 4.7). Since samples from the *inshore* zones did not exceed 65 m, this increased likelihood of detection of *P. rupestris* is only evident for *exploited* samples.

Table 4.21: Output summary of Generalized Linear Model describing the influence of % obstruction, depth, and management on variability in detection probability of *Petrus rupestris* on reef substrate in the inshore Amathole Marine Protected Area and adjacent inshore and offshore exploited areas. Estimate = coefficient estimate; Std. Error = standard error of estimate; $Pr(>|z|)$ = P-value

Coefficients:	Estimate	Std. Error	z value	Pr(> z)
Intercept	-10.959	3.908	-2.804	0.005
% Obstruction	0.093	0.036	2.597	0.009
Depth	0.129	0.047	2.735	0.006
Management <i>protected</i>	6.441	3.803	1.694	0.090
Depth x Management <i>protected</i>	-0.089	0.054	-1.653	0.098

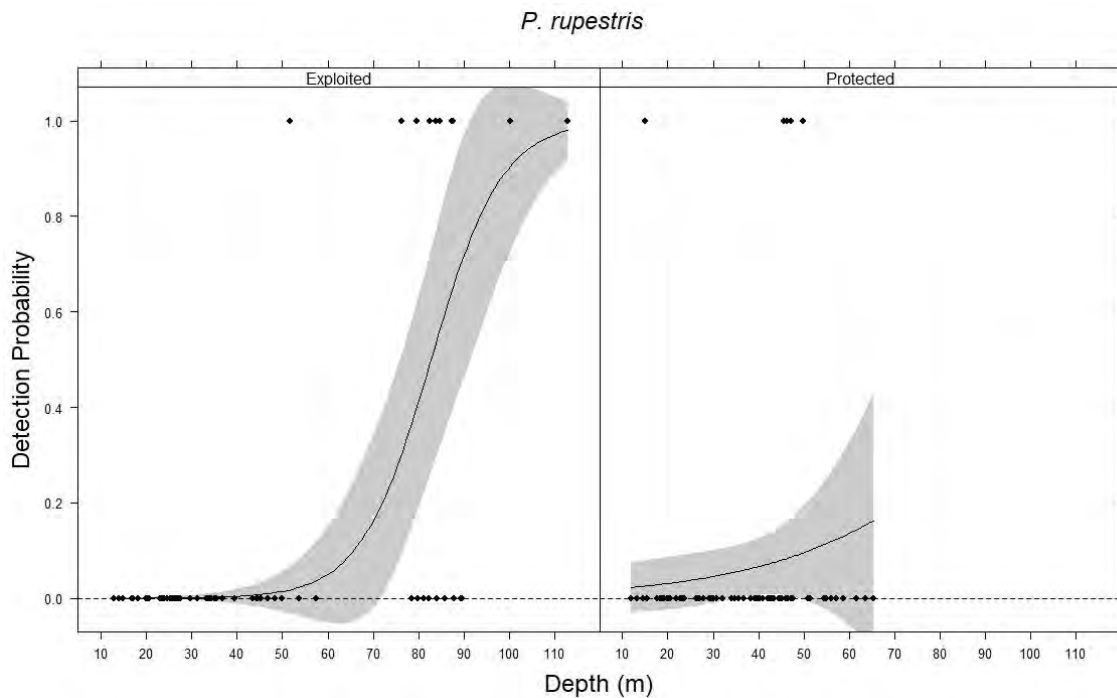


Figure 4.7: Predicted values for detection probability of *Petrus rupestris* on reef substrate according to management group (exploited or protected) and depth in the inshore Amathole Marine Protected Area and adjacent inshore and offshore exploited areas based on standard average values for all covariates included in Eq. 14. Shaded areas represent 95 % confidence intervals.

MaxN

For the second part of the hurdle model, the analysis focussed only on the samples where *P. rupestris* was present. The MaxN of *P. rupestris* was fitted with a Poisson GLM. Model selection resulted in exclusion of the terms % water column and temperature (AIC: Full model = 53.2, Best-fit: 50.8 with no difference in deviance explained between models ($p = 0.4$), resulting in the best-fit model:

$$f(\text{MaxN } P. \text{ rupestris}) = \alpha + \beta_1 (\% \text{ obstruction}) + \beta_2(\text{depth}) + \beta_3(\text{management}) + \varepsilon \quad \text{Eq. 15}$$

Where α is the intercept, β_i refers to the regression coefficients, and ε is the noise (Zuur et al. 2013).

The best-fit GLM (Eq. 15) explained 79.24% % of total variability in MaxN of *P. rupestris*. Sequential likelihood ratio tests indicated that both depth and management significantly contributed to variability in MaxN (Table 4.22). Below 50 m depth, the species was recorded at low abundances, but only within the protected zones (Figure 4.8). At depths greater than 50 m, beyond the depth range of the MPA, MaxN is predicted to increase within increasing depth (Figure 4.8).

Table 4.22: Results of sequential likelihood ratio tests on the best fit Generalized Linear Model for effects of % obstruction, depth, and management on the MaxN of *Petrus rupestris* on reef substrate in the inshore Amathole Marine Protected Area and adjacent inshore and offshore exploited areas. df = degrees of freedom; PR(>Chi) = P-value; Relative contribution (%) = contribution of each term to overall variability explained by the model

	df	Residual Deviance	Residual df	Deviance	Pr(>Chi)	Relative Contribution (%)
NULL			15	34.517		
% Obstruction	1	0,174	14	34,343	0,676	0,636
Depth	1	21,128	13	13,215	<0,001	77,248
Management	1	6,049	12	7,166	0,014	22,116

Table 4.23: Output summary of Generalized Linear Model describing the influence of % obstruction, depth, and management on variability in MaxN of *Petrus rupestris* on reef substrate in the inshore Amathole Marine Protected Area and adjacent inshore and offshore exploited areas. Estimate = coefficient estimate; Std. Error = standard error of estimate; $PR(>|z|)$ = P-value

Coefficients:	Estimate	Std. Error	z value	Pr(> z)
Intercept	-4.95	1.24	-4.005	>0.001
% Obstruction	0.047	0.019	2.452	0.014
Depth	0.061	0.012	5.043	>0.001
Management <i>protected</i>	2.019	0.810	2.491	0.013

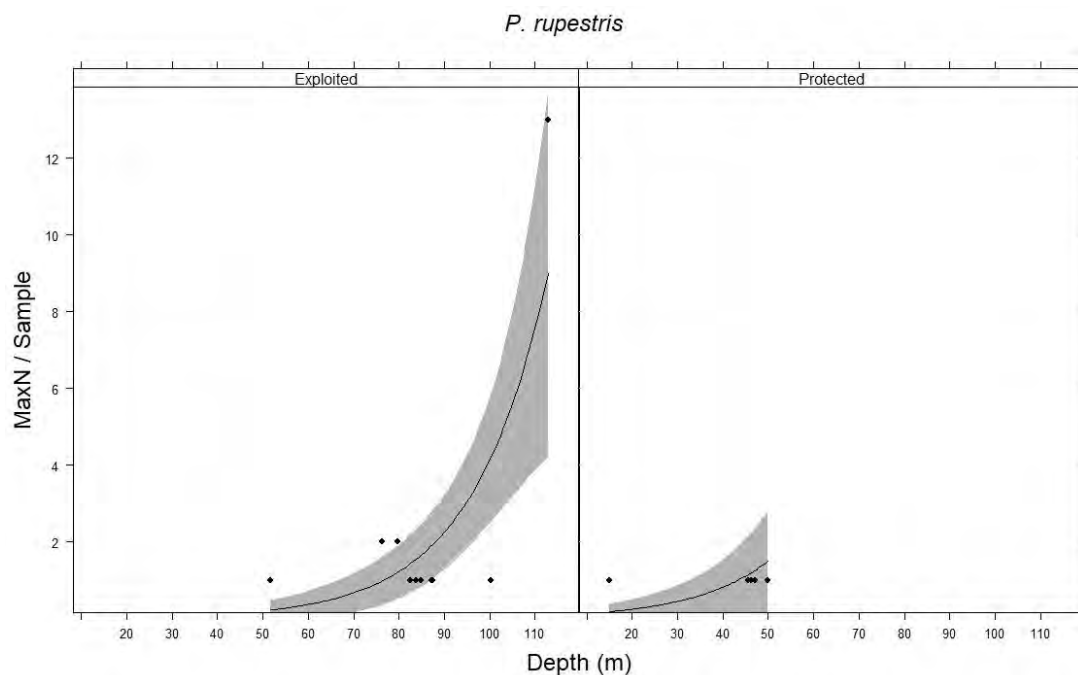


Figure 4.8: Predicted values for MaxN of *Petrus rupestris* on reef substrate according to management group (exploited or protected) and depth in the inshore Amathole Marine Protected Area and adjacent inshore and offshore exploited areas based on standard average values for all covariates included in Eq. 15. Shaded areas represent 95 % confidence intervals.

Max Biomass

For the third part of the hurdle model, the analysis focussed only on the maximum biomass of *P. rupestris* where present. The Max Biomass of *P. rupestris* was fitted with a Tweedie GLM. Model selection resulted in exclusion of the terms % water column and % obstruction and (AIC: Full

model = 294.9, Best-fit: 291.7 with no difference in deviance explained between models ($p = 0.7$), resulting in the best-fit model:

$$f(\text{Max Biomass } P. rupestris) = \alpha + \beta_1(\text{temperature}) + \beta_2(\text{depth}) + \beta_3(\text{management}) + \varepsilon$$

Eq. 16

Where α is the intercept, β_i refers to the regression coefficients, and ε is the noise (Zuur et al. 2013).

The best-fit GLM (Eq. 16) explained 31.39 % of total variability in Max Biomass of *P. rupestris*. Sequential likelihood ratio tests indicated that management had a significant influence on Max Biomass, with greater Max Biomass in *protected* areas than in *exploited* areas (Table 4.24). No significant variation in Max Biomass was found with depth.

Table 4.24: Results of sequential likelihood ratio tests on the best fit Generalized Linear Model for effects of depth and management on the Max Biomass of *Petrus rupestris* on reef substrate in the inshore Amathole Marine Protected Area and adjacent inshore and offshore exploited areas. df = degrees of freedom; PR(>Chi) = P-value; Relative contribution (%) = contribution of each term to overall variability explained by the model

	df	Residual Deviance	Residual df	Deviance	Pr(>Chi)	Relative Contribution (%)
NULL			13	53 388		
Depth	1	307.9	12	56 080	0.752	1.837
Management	1	16451.6	11	36 629	0.021	98.166

Table 4.25: Output summary of Generalized Linear Model describing the influence of depth and management on variability in Max Biomass of *Petrus rupestris* on reef substrate in the inshore Amathole Marine Protected Area and adjacent inshore and offshore exploited areas. Estimate = coefficient estimate; Std. Error = standard error of estimate; PR(>|z|) = P-value

Coefficients:	Estimate	Std. Error	z value	Pr(> z)
Intercept	7.296	1.111	6.567	<0.001
Depth	0.025	0.013	2.016	0.069
Management <i>protected</i>	1.355	0.605	2.239	0.047

The plot of predicted values for Max Biomass of *P. rupestris* is highly restricted by the availability of data from inshore samples, where measurements were only possible for four individuals (three in the *protected* zone and one in the *exploited* zone; Figure 4.9). The available data suggest that, at depths of less than 65 m, *P. rupestris* reaches greater sizes in *protected* areas than in *exploited* areas. Though in the *exploited* samples biomass does appear to increase with depth (Figure 4.9), this effect was found to be insignificant in sequential likelihood ratio tests (Table 4.24). The highest values predicted at 100 m depth in the *exploited* zone are equalled by the highest predicted values in the *protected* zone at 50 m depth (Figure 4.9).

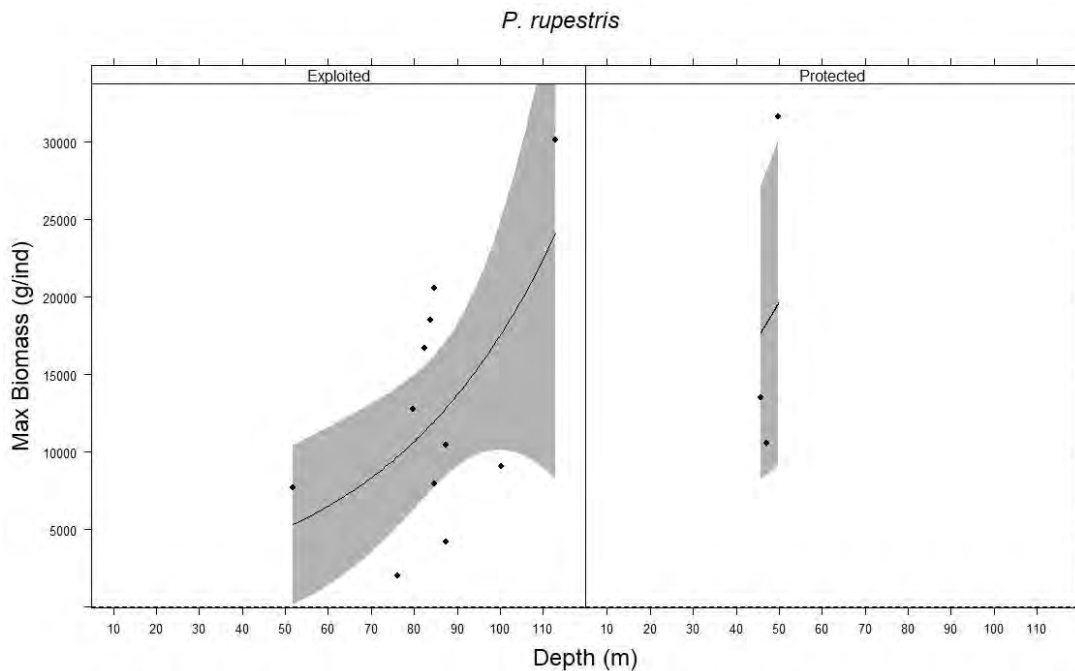


Figure 4.9: Predicted values for Max Biomass of *Petrus rupestris* on reef substrate according to management group (exploited or protected) and depth in the inshore Amathole Marine Protected Area and adjacent inshore and offshore exploited areas based on standard average values for all covariates included in Eq. 16. Shaded areas represent 95 % confidence intervals.

4.3.7.2 *POLYSTEGANUS UNDULOSUS*

Detection Probability

For the first part of the hurdle model, the analysis focussed on presence-absence values for *P. undulosus* in all of the samples in the dataset. The GLM for detection probability of *P. undulosus*

was fitted with a Binomial distribution. Model selection resulted in the exclusion of the term % water column and temperature (AIC: Full model = 138.1, Best-fit: 135.0 with no difference in deviance explained between models ($p = 0.6$)), resulting in the best-fit model:

$$f(\text{Detection Probability } P. \text{ undulosus}) = \alpha + \beta_1(\% \text{ obstruction}) + \beta_2(\text{depth}) + \beta_3(\text{management}) + \beta_4(\text{depth} \times \text{management}) + \varepsilon \quad \text{Eq. 17}$$

Where α is the intercept, β_i refers to the regression coefficients, and ε is the noise (Zuur et al. 2013).

The best-fit GLM (Eq. 17) explained 9.32 % of total variability in detection probability of *P. undulosus*. Sequential likelihood ratio tests indicated that % obstruction and depth both significantly influenced the likelihood of detection (Table 4.26).

Table 4.26: Results of sequential likelihood ratio tests on the best fit Generalized Linear Model for effects of % obstruction, depth, and management on the probability of detecting individuals of *Polysteganus undulosus* on reef substrate in the inshore Amathole Marine Protected Area and adjacent inshore and offshore exploited areas. df = degrees of freedom; PR(>Chi) = P-value; Relative contribution (%) = contribution of each term to overall variability explained by the model

	df	Residual Deviance	Residual df	Deviance	Pr(>Chi)	Relative Contribution (%)
NULL			134	137.84		
% Obstruction	1	4.541	133	133.29	0.033	35.366
Depth	1	7.600	132	125.69	0.006	59.190
Management	1	0.117	131	125.58	0.732	0.911
Depth x Management	1	0.582	130	125.00	0.446	4.533

Increased depth was associated with an increased likelihood of detecting individuals of *P. undulosus*, apparent even within the limited depth range of the inshore MPA (Table 4.27; Figure 4.10). Within this depth range, protection was not associated with an increased likelihood of detecting *P. undulosus* relative to exploited areas (Table 4.27; Figure 4.10)

Table 4.27: Output summary of Generalized Linear Model describing the influence of % obstruction, depth, and management on variability in detection probability of *Polysteganus undulosus* on reef substrate in the inshore Amathole Marine Protected Area and adjacent inshore and offshore exploited areas. Estimate = coefficient estimate; Std. Error = standard error of estimate; $PR(>|z|)$ = P-value

Coefficients:	Estimate	Std. Error	z value	Pr(> z)
Intercept	-2.68198	0.74821	-3.585	<0.001
% Obstruction	0.054	0.023	2.361	0.018
Depth	0.024	0.011	2.098	0.036
Management <i>protected</i>	-0.711	1.272	-0.559	0.576
Depth x Management <i>protected</i>	0.020	0.027	0.753	0.451

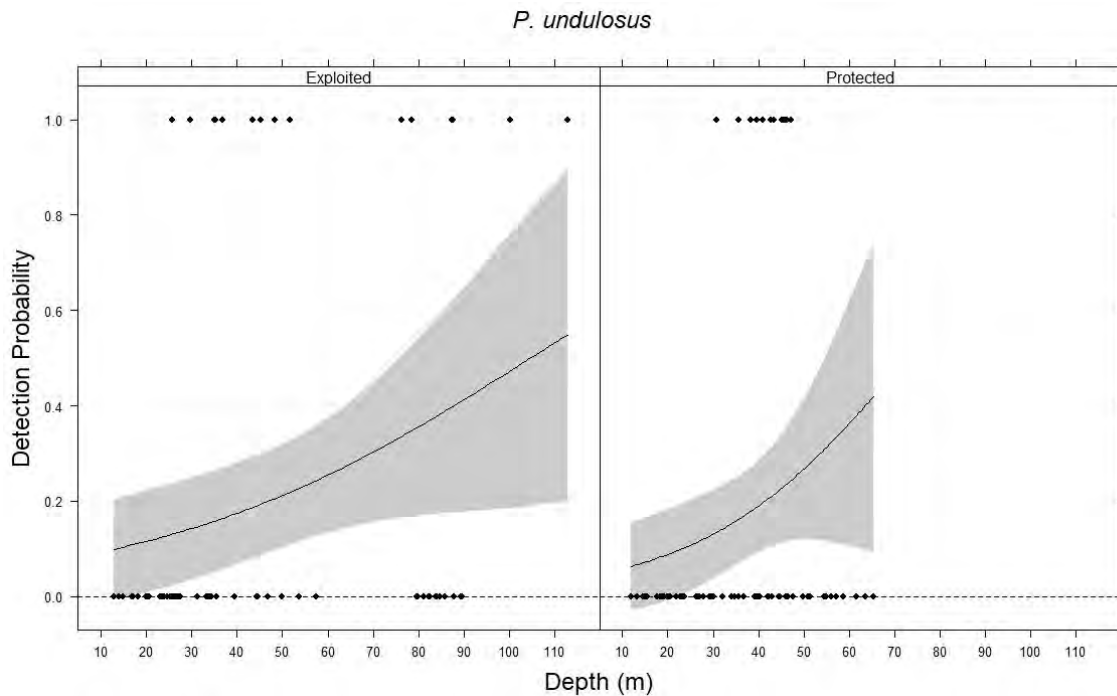


Figure 4.10: Predicted values for detection probability of *Polysteganus undulosus* on reef substrate according to management group (exploited or protected) and depth in the inshore Amathole Marine Protected area and adjacent inshore and offshore exploited areas based on standard average values for all covariates included in Eq. 17. Shaded areas represent 95 % confidence intervals.

MaxN

For the second part of the hurdle model, the analysis focussed only on the samples where *P. undulosus* was present. The MaxN of *P. undulosus* was fitted with a Poisson GLM. Model selection resulted in exclusion of the terms % water column, % obstruction and temperature (AIC: Full model = 127.9, Best-fit: 124.1 with no difference in deviance explained between models ($p = 0.5$)), resulting in the best-fit model:

$$f(\text{MaxN } P. \text{ undulosus}) = \alpha + \beta_1(\text{depth}) + \beta_2(\text{management}) + \varepsilon \quad \text{Eq. 18}$$

The best-fit GLM (Eq. 18) explained 43.13 % of total variability in MaxN of *P. undulosus*. Sequential likelihood ratio tests indicated that the observed patterns in MaxN were determined by depth (Table 4.28), with increased depth associated with an increase in MaxN of *P. undulosus* (

Table 4.29). There was no significant difference between protected and exploited areas within the depth range of the inshore MPA, and the effect of depth was more evident in deeper, offshore areas (Figure 4.11).

Table 4.28: Results of sequential likelihood ratio tests on the best fit Generalized Linear Model for effects of depth and management on the MaxN of *Polysteganus undulosus* on reef substrate in the inshore Amathole Marine Protected Area and adjacent inshore and offshore exploited areas. df = degrees of freedom; PR(>Chi) = P-value; Relative contribution (%) = contribution of each term to overall variability explained by the model

	df	Residual Deviance	Residual df	Deviance	Pr(>Chi)	Relative Contribution (%)
NULL			27	77.115		
Depth	1	31.736	26	45.379	<0.001	94.585
Management	1	1.523	25	43.855	0.217	4.539

Table 4.29: Output summary of Generalized Linear Model describing the influence of depth and management on variability in MaxN of *Polysteganus undulosus* in the inshore Amathole Marine Protected Area and adjacent inshore and offshore exploited areas. Estimate = coefficient estimate; Std. Error = standard error of estimate; $PR(>|z|)$ = P-value

Coefficients:	Estimate	Std. Error	z value	Pr(> z)
Intercept	0.077	0.363	0.213	0.831
Depth	0.020	0.001	4.416	<0.001
Management <i>protected</i>	-0.351	2.152	-1.232	0.218

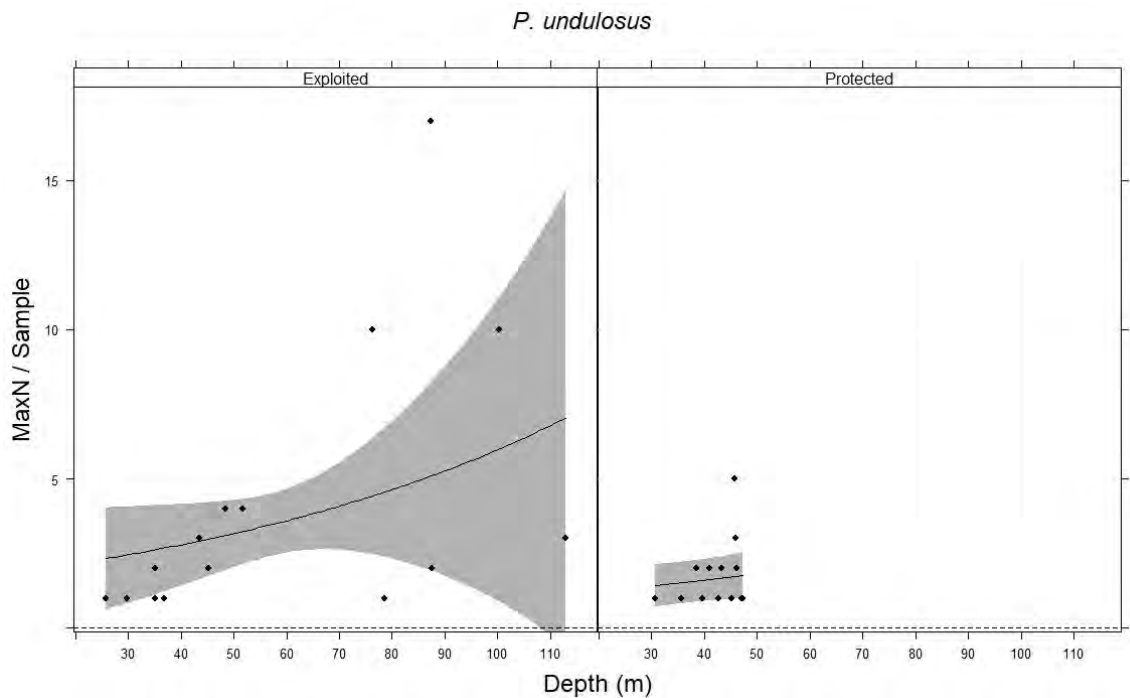


Figure 4.11: Predicted values for MaxN of *Polysteganus undulosus* on reef substrate according to management group (exploited or protected) and depth in the inshore Amathole Marine Protected Area and adjacent inshore and offshore exploited areas based on standard average values for all covariates included in Eq. 18. Shaded areas represent 95 % confidence intervals.

Max Biomass

For the third part of the hurdle model, the analysis focussed only on the maximum biomass of *P. undulosus* where present. The Max Biomass of *P. undulosus* was fitted with a Tweedie GLM. Model selection resulted in exclusion of the terms % water column and % obstruction (AIC: Full

model = 108.2, Best-fit: 102.5 with no difference in deviance explained between models ($p = 0.97$)), resulting in the best-fit model:

$$f(\text{Max Biomass } P. \text{ undulosus}) = \alpha + \beta_1(\text{temperature}) + \beta_2(\text{depth}) + \beta_3(\text{management}) + \varepsilon$$

Eq. 19

The best-fit GLM (Eq. 19) explained 51.65 % of total variability in Max Biomass of *P. undulosus*. Sequential likelihood ratio tests indicated that depth significantly influenced Max Biomass (Table 4.30). Biomass increases with increasing water depth, with the largest individuals recorded in the deepest sample collected for this research (Figure 4.12). As with MaxN (Figure 4.11), Max Biomass did not differ significantly between *protected* and *exploited* areas at shallower depths (Figure 4.12).

Table 4.30: Results of sequential likelihood ratio tests on the best fit Generalized Linear Model for effects of temperature, depth, and management on the Max Biomass of *Polysteganus undulosus* on reef substrate in the inshore Amathole Marine Protected Area and adjacent inshore and offshore exploited areas. df = degrees of freedom; PR(>Chi) = P-value; Relative contribution (%) = contribution of each term to overall variability explained by the model

	Df	Residual Deviance	Residual df	Deviance	Pr(>Chi)	Relative Contribution (%)
NULL			27	22.497		
Depth	1	11.419	26	11.079	<0.001	98.28
Management	1	0.201	25	10.878	0.484	1.72

Table 4.31: Output summary of Generalized Linear Model describing the influence of temperature, depth, and management on variability in Max Biomass of *Polysteganus undulosus* on reef substrate in the inshore Amathole Marine Protected Area and adjacent inshore and offshore exploited areas. Estimate = coefficient estimate; Std. Error = standard error of estimate; PR(>|z|) = P-value

Coefficients:	Estimate	Std. Error	z value	Pr(> z)
Intercept	-0.408	0.393	-1.038	0.309
Depth	0.027	0.006	4.555	<0.001
Management <i>protected</i>	-0.187	1.264	-0.708	0.486

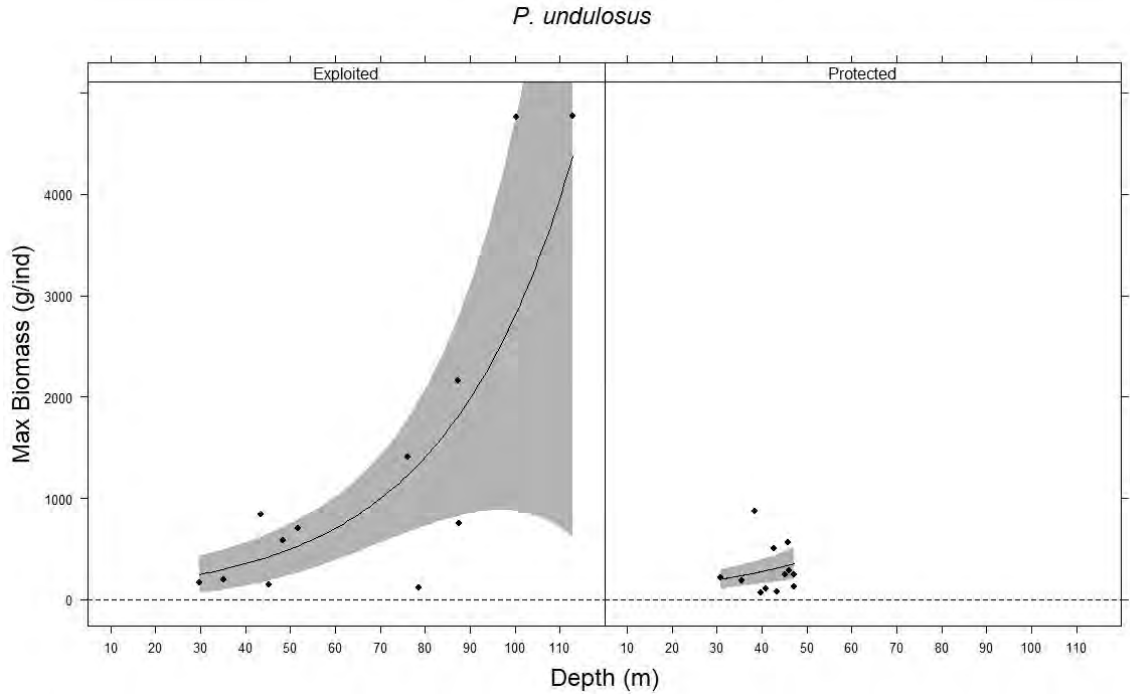


Figure 4.12: Predicted values for Max Biomass of *Polysteganus. undulosus* on reef substrate according to management group (exploited or protected) and depth in the inshore Amathole Marine Protected area and adjacent inshore and offshore exploited areas based on standard average values for all covariates included in Eq. 19. Shaded areas represent 95 % confidence intervals.

4.3.7.3 *CHRYSOBLEPHUS CRISTICEPS*

Detection Probability

For the first part of the hurdle model, the analysis focussed on presence-absence values for *C. cristiceps* in all of the samples in the dataset. The GLM for detection probability of *C. cristiceps* was fitted with a Binomial distribution. Model selection resulted in the exclusion of the term % water column and temperature (AIC: Full model = 168.1, Best-fit: 164.3 with no difference in deviance explained between models ($p = 0.9$)), resulting in the best-fit model:

$$f(\text{Detection Probability}) = \alpha + \beta_1 (\% \text{ obstruction}) + \beta_4 (\text{depth}) + \beta_5 (\text{management}) + \beta_6 (\text{depth} \times \text{management}) + \varepsilon$$

Eq. 20

The best-fit GLM (Eq. 20) explained 9.45 % of total variability in detection probability of *C. cristiceps*. Sequential likelihood ratio tests indicated that the probability of detection was significantly influenced by depth (Table 4.32).

Table 4.32: Results of sequential likelihood ratio tests on the best fit Generalized Linear Model for effects of % obstruction, depth, and management on the probability of detecting individuals of *Chrysoblephus cristiceps* on reef substrate in the inshore Amathole Marine Protected Area and adjacent inshore and offshore exploited areas. df = degrees of freedom; PR(>Chi) = P-value; Relative contribution (%) = contribution of each term to overall variability explained by the model

	Df	Residual Deviance	Residual df	Deviance	Pr(>Chi)	Relative Contribution (%)
NULL			134	170.44		
% Obstruction	1	3.227	133	167.21	0.072	20.043
Depth	1	7.823	132	159.39	0.005	48.590
Management	1	3.208	131	156.18	0.073	19.925
Depth x Management	1	1.843	130	154.34	0.175	11.447

Increased depth was associated with a decrease in the likelihood of detecting individuals of *C. cristiceps* (Table 4.33; Figure 4.13). Although *protected* status was associated with an increase in detection probability at shallower depths (Table 4.33, Figure 4.13), this was determined to be insignificant in the sequential likelihood ratio test (Table 4.32).

Table 4.33: Output summary of Generalized Linear Model describing the influence of % obstruction, depth, and management on variability in detection probability of *Chrysoblephus cristiceps* on reef substrate in the inshore Amathole Marine Protected Area and adjacent inshore and offshore exploited areas. Estimate = coefficient estimate; Std. Error = standard error of estimate; PR(>|z|) = P-value

Coefficients:	Estimate	Std. Error	z value	Pr(> z)
Intercept	-0.663	0.617	-1.076	0.282
% Obstruction	0.037	0.021	1.748	0.081
Depth	-0.015	0.013	-1.214	0.225
Management <i>protected</i>	1.886	0.965	1.954	0.051
Depth x Management <i>protected</i>	-0.032	0.024	-1.349	0.177

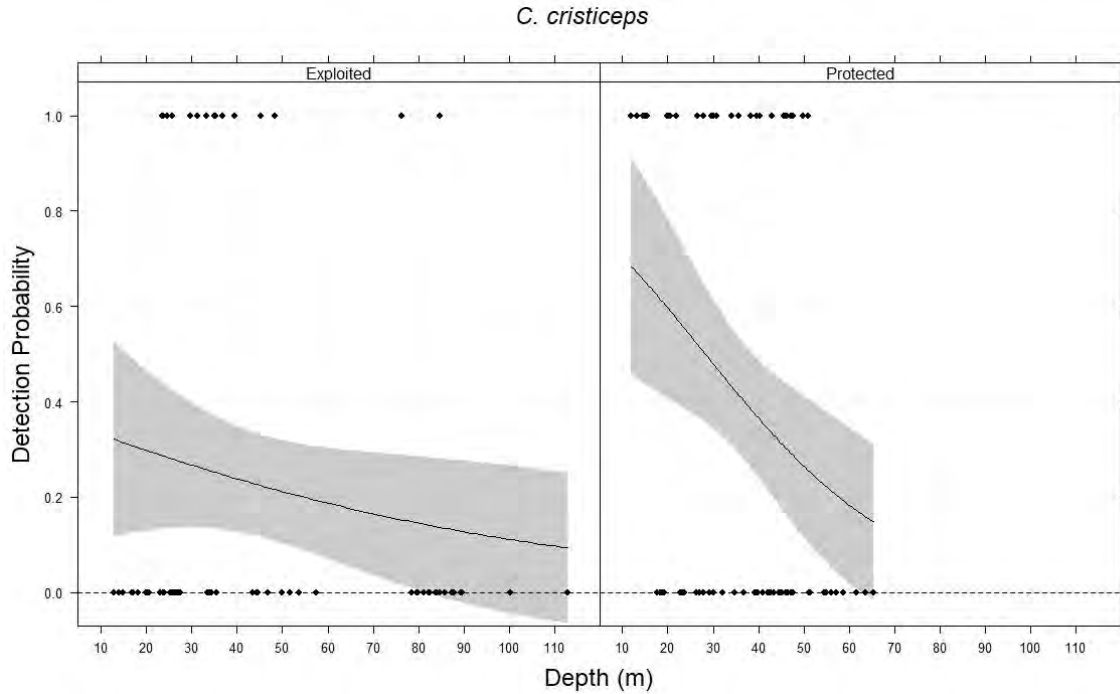


Figure 4.13: Predicted values for detection probability of *Chrysolephus cristiceps* on reef substrate according to management group and depth in the inshore Amathole Marine Protected area and adjacent inshore and offshore exploited areas based on standard average values for all covariates included in Eq. 20. Shaded areas represent 95 % confidence intervals.

MaxN

For the second part of the hurdle model, the analysis focussed only on the samples where *C. cristiceps* was present. The MaxN of *C. cristiceps* was fitted with a Poisson GLM. Model selection resulted in exclusion of the terms % water column, % obstruction and temperature (AIC: Full model = 190.0, Best-fit: 184.5 with no difference in deviance explained between models ($p = 0.9$)), resulting in the best-fit model:

$$f(\text{MaxN } C. \text{ cristiceps}) = \alpha + \beta_1(\text{depth}) + \beta_2(\text{management}) + \beta_3(\text{depth} \times \text{management}) + \varepsilon$$

Eq. 21

The best-fit GLM (Eq. 21) explained 11.65 % of total variability in MaxN of *C. cristiceps*. Sequential likelihood ratio tests indicated that management had a significant effect on MaxN (Table 4.34). *Protected* areas were associated with a significant increase in the MaxN of *C.*

cristiceps compared to *exploited* areas (Table 4.35; Figure 4.14). Depth did not significantly influence MaxN of *C. cristiceps*.

Table 4.34: Results of sequential likelihood ratio tests on the best fit Generalized Linear Model for effects of depth and management on the MaxN of *Chrysoblephus cristiceps* on reef substrate in the inshore Amathole Marine Protected Area and adjacent inshore and offshore exploited areas. df = degrees of freedom; PR(>Chi) = P-value; Relative contribution (%) = contribution of each term to overall variability explained by the model

	df	Residual Deviance	Residual df	Deviance	Pr(>Chi)	Relative Contribution (%)
NULL			43	62.209		
Depth	1	0.791	42	61.418	0.374	6.8
Management	1	6.459	41	54.959	0.011	55.4

Table 4.35: Output summary of Generalized Linear Model describing the influence of depth and management on variability in MaxN of *Chrysoblephus cristiceps* on reef substrate in the inshore Amathole Marine Protected Area and adjacent inshore and offshore exploited areas. Estimate = coefficient estimate; Std. Error = standard error of estimate; PR(>|z|) = P-value

Coefficients:	Estimate	Std. Error	z value	Pr(> z)
Intercept	0.821]	0.304	2.701	0.007
Depth	-0.002	0.006	-0.255	0.799
Management <i>protected</i>	0.507	0.208	2.444	0.015

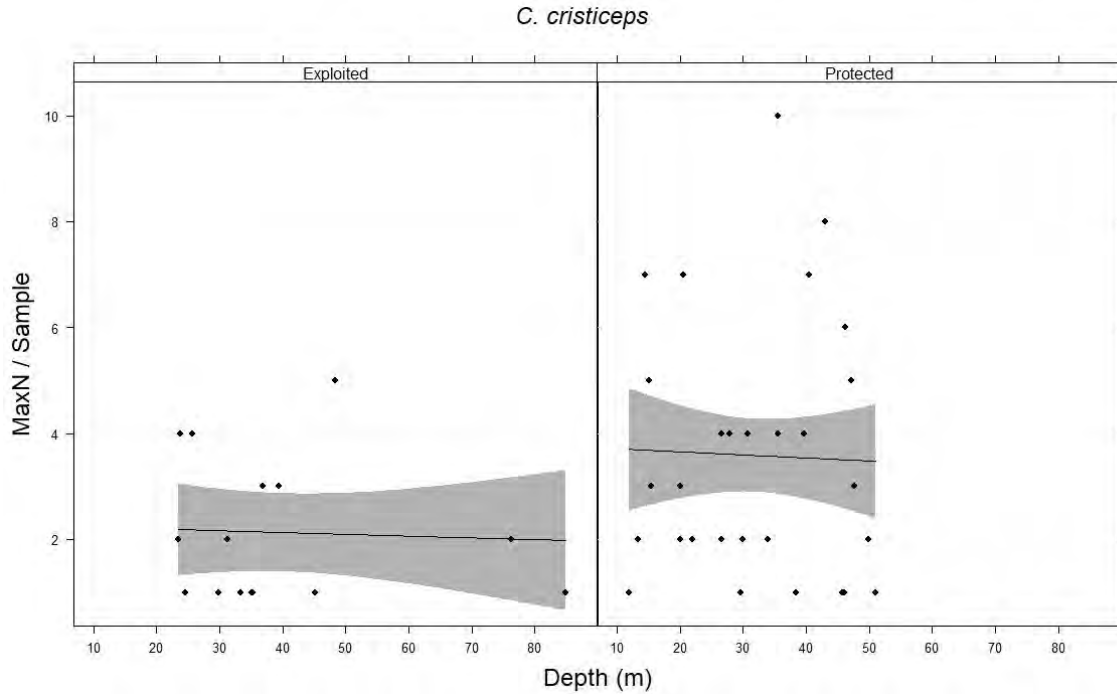


Figure 4.14: Predicted values for MaxN of *Chrysoblephus cristiceps* on reef substrate according to management group (exploited or protected) and depth in the inshore Amathole Marine Protected area and adjacent inshore and offshore exploited areas based on standard average values for all covariates included in Eq. 21. Shaded areas represent 95 % confidence intervals.

Max Biomass

For the third part of the hurdle model, the analysis focussed only on the maximum biomass of *C. cristiceps* where present. The Max Biomass of *C. cristiceps* was fitted with a Tweedie GLM. Model selection resulted in exclusion of the terms % water column, % obstruction and temperature (AIC: Full model = 640.3, Best-fit: 636.3 with no difference in deviance explained between models ($p = 0.5$)), resulting in the best-fit model:

$$f(\text{Max Biomass } C. \text{ cristiceps}) = \alpha + \beta_1(\text{depth}) + \beta_2(\text{management}) + \beta_3(\text{depth} \times \text{management}) + \varepsilon$$

Eq. 22

The GLM run on the best-fit model (Eq. 22) explained 60.59 % of total variability in Max Biomass of *C. cristiceps*. Sequential likelihood ratio tests indicated that management had a significant

influence on Max Biomass (Table 4.36). Though depth alone did not significantly affect Max Biomass, the interaction of depth with management status was significant (Table 4.36).

Table 4.36: Results of sequential likelihood ratio tests on the best fit Generalized Linear Model for effects of depth and management on the Max Biomass of *Chrysolephus cristiceps* on reef substrate in the inshore Amathole Marine Protected Area and adjacent inshore and offshore exploited areas. df = degrees of freedom; PR(>Chi) = P-value; Relative contribution (%) = contribution of each term to overall variability explained by the model

	df	Residual Deviance	Residual df	Deviance	Pr(>Chi)	Relative Contribution (%)
NULL			38	25.223		
Depth	1	0.0579	37	25.165	0.589	0.379
Management	1	13.8808	36	11.285	<0.001	90.826
Depth x Management	1	1.344	35	9.941	0.009	8.794

Protected areas were associated with a significant increase in Max Biomass of *C. cristiceps* compared to *exploited* areas (Table 4.37, Figure 4.15). In *exploited* areas Max Biomass significantly increased with increased depth (Figure 4.15). Despite no significant depth effect in *protected* areas, individuals in the *protected* areas reached larger sizes than those at greater depths in the *exploited* areas (Figure 4.15).

Table 4.37: Output summary of Generalized Linear Model describing the influence of depth and management on variability in Max Biomass of individuals of *Chrysolephus cristiceps* on reef substrate in the inshore Amathole Marine Protected Area and adjacent inshore and offshore exploited areas. Estimate = coefficient estimate; Std. Error = standard error of estimate; PR(>|z|) = P-value.

	Coefficients:	Estimate	Std. Error	z value	Pr(> z)
(Intercept)		5.664	0.276	20.518	<0.001
Depth		0.023	0.006	3.680	0.001
Management <i>protected</i>		2.273	0.370	6.151	0.000
Depth x Management <i>protected</i>		-0.024	0.010	-2.512	0.017

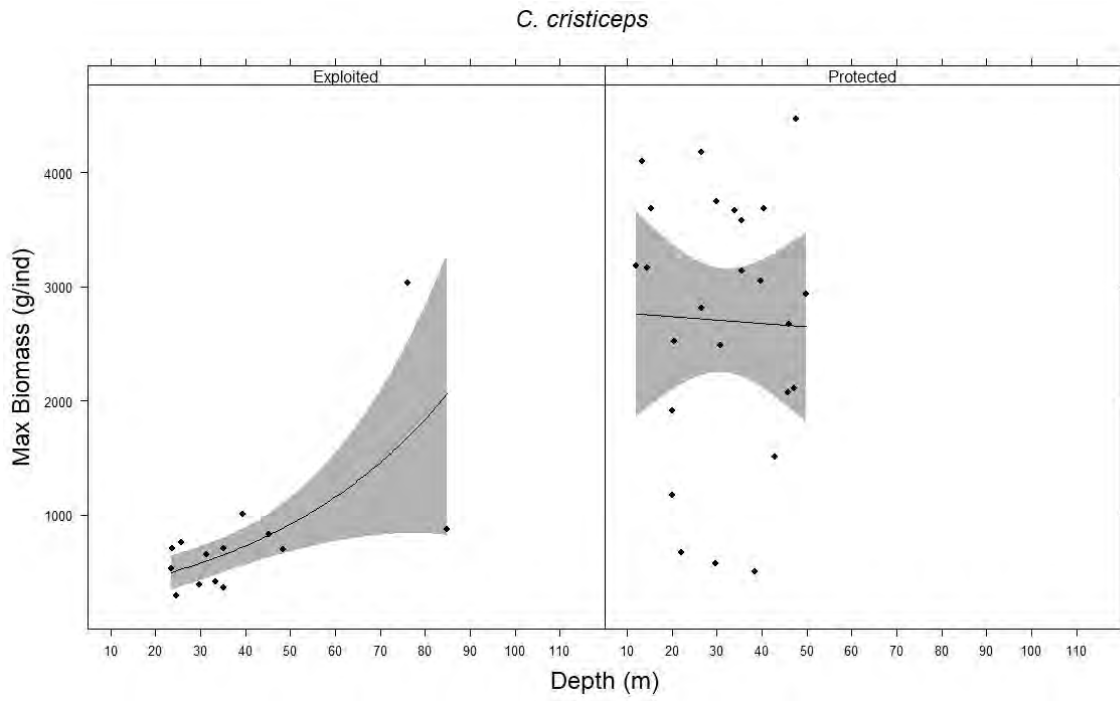


Figure 4.15: Predicted values for Max Biomass of *Chrysolephus cristiceps* on reef substrate according to management group (exploited or protected) and depth in the inshore Amathole Marine Protected area and adjacent inshore and offshore exploited areas based on standard average values for all covariates included in Eq. 22. Shaded areas represent 95 % confidence intervals.

4.4 DISCUSSION

This chapter addressed whether offshore fish assemblages in the vicinity of the Amathole MPA are significantly different from inshore assemblages, and whether the recent offshore extension of the MPA provides more meaningful coverage for species of fisheries and conservation interest, in particular for *P. rupestris*, *P. undulosus* and *C. cristiceps*. Fish assemblages from offshore samples were significantly different from inshore assemblages, regardless of management status. This outcome held at community level, for species groups, for individual species of interest, and for species richness. Fish assemblages in the offshore zone were less diverse than in the inshore zones, with species richness lowest offshore and highest in the inshore exploited zone. The abundance and biomass of Primary and Vulnerable Fisheries Species, however, was highest offshore and lowest in the inshore exploited zone. The three species analysed individually showed variable responses to depth and protection. *Petrus rupestris* and *P. undulosus* were both more abundant with increased depth, and in the case of *P. undulosus*, larger as well. While *P. undulosus* was unaffected by management status, the abundance of *P. rupestris* was found to be higher in *protected* areas than *exploited* areas within the depth range of the inshore protected areas. On the other hand, both the size and abundance of *C. cristiceps* were greatest in the inshore protected areas. Abundance decreased at greater depths, and though size in exploited areas increased with depth, *C. cristiceps* was largest in the inshore MPA.

Differences between zones were more apparent as the analysis was refined to target species, and more apparent for biomass measures than for abundance. Substrate remained an important determinant of assemblage structure offshore (Table 4.4), with greater abundance (Figure 4.3; Figure 4.5) and biomass (Figure 4.4; Figure 4.6) of target species on reef substrate. However, the relative contribution of zone was considerably more influential than that of management alone had been in the inshore analysis, reiterating the importance of the offshore exploited zone in supporting different assemblages and life stages of fish. These findings imply that, when considering greater depth ranges than those encompassed in the inshore MPA, depth, like substrate, strongly determines the structure of fish assemblages in the Amathole region. The inshore MPA alone, as such, cannot be fully representative of local biodiversity, which requires the additional coverage of the recent offshore extension. This finding has important implications for other coastal MPAs in South Africa that were originally established using the three nautical

mile offshore limit. Altering the offshore limits of such areas to ensure that they encompassed deep water shelf habitat, rather than leaving them set at an arbitrary linear distance, could greatly increase the representativeness of biodiversity protected therein.

Offshore fish assemblages were differentiated from those in the inshore zones by the prevalence of larger sparids as well as the presence of several elasmobranchs (Table 4.6). Of the 16 Vulnerable Fisheries Species detected in this study, only six were observed in the offshore zone, and of those, only four appeared to be more abundant there (Table 4.14). However, all four were species of particular conservation interest, namely, *P. undulosus*, *P. rupestris*, *C. gibbiceps* and the Atlantic wreckfish (*Polyprion americanus*) (Note that only one wreckfish was observed, at a depth of 112.8 m).

Previous studies have suggested depth-associated shifts in fish assemblage structure on the South African coast (Buxton & Smale 1989, Heyns-Veale et al. 2016), as well as ontogenic depth preferences for a number of the species in question (Smale 1988, Buxton & Allen 1989, Griffiths & Wilke 2002, Heemstra & Heemstra 2004, Mann 2013). Species richness is known to decrease with depth (Willis & Anderson 2003, Heyns-Veale et al. 2016, Heyns-Veale et al. 2019b) and as large predators become more prevalent (Edgar & Stuart-Smith 2009, Stobart et al. 2009, Maggs 2011). The evidence available from this study suggests that this is indeed the case at Amathole, with dispersion analysis revealing less variability in offshore populations (Table A. 4, which comprise larger individuals of fewer species, several of which are primary fisheries targets and of particular conservation interest (Table 4.3; Figure 4.1; Table 4.6).

Individual analysis of target species confirmed that *P. rupestris* and *P. undulosus* are significantly more abundant at greater depths in the offshore zone (Figure 4.8; Figure 4.11), suggesting that the offshore habitat is of more benefit to them than the inshore habitat. In the case of *P. rupestris* there was no detectable difference in maximum biomass between inshore and offshore zones (Figure 4.9). *Polysteganus undulosus*, however, was found to be larger at greater depths (Figure 4.12), suggesting ontogenic depth distribution of this species, as has been previously described (Heemstra & Heemstra 2004, Mann 2013). Despite this, smaller individuals of *P. undulosus* were not more abundant in the inshore protected areas than in the adjacent inshore exploited areas (Figure 4.11). Further investigation might provide insight into why the inshore MPA does not appear to serve as a juvenile nursery area for *P. undulosus*. It is possible that juveniles of this species roam too extensively to be retained within the limits of the inshore

protected areas. On the other hand, abundance of *P. rupestris* was found to increase in the inshore MPA relative to the inshore exploited areas (Figure 4.8). This suggests that despite the depth limitations of the inshore Amathole MPA, it nonetheless provides some benefit to *P. rupestris*.

These results confirm the premise that species such as *P. rupestris* and *P. undulosus*, which have derived very little benefit from the inshore Amathole MPA, are much more likely to respond to the offshore extension of the protected area. Though the offshore Amathole MPA presents one of the most promising conservation opportunities for these two endangered species in particular, they are representative of a unique offshore assemblage. The conservation of this assemblage and its surrounding ecosystem in the offshore Amathole MPA will undoubtedly have positive impacts on marine life in the Amathole region that would not be possible with the inshore MPA alone.

On the other hand, *C. cristiceps* was shown to be considerably more abundant within the depth range of the inshore MPA, with detection probability declining steadily with depth (Figure 4.13). Although abundance was consistent across the inshore depth range, it was significantly greater in protected samples than in exploited ones (Figure 4.14). The maximum biomass of *C. cristiceps* was also greater overall in the protected samples, where it was unaffected by depth (Figure 4.15). In the exploited samples, although maximum size did increase at greater depths, the largest measured individuals were still smaller than those recorded in the inshore protected samples. In addition, *C. cristiceps* was only detected in two of the offshore samples, with the deepest observation at 85 m. This demonstrates that the inshore Amathole MPA provides sanctuary to adults of *C. cristiceps*, contributing towards spawner biomass of the species with broad-scale benefits for population recovery of the species across its wider distributional range. This result further confirms the findings of the inshore analysis, that despite its small and fragmented design, the inshore Amathole MPA has provided effective protection to a desperately imperilled species. This further strengthens the argument for extending the southern border of the Gxulu MPA to encompass more of the inshore reef habitat that supports the recovery of *C. cristiceps* populations.

4.5 CONCLUSIONS

Depth was confirmed as a key determinant of fish assemblage structure in the area of the Amathole MPA, with the offshore environment supporting an assemblage of species quite distinct from the inshore environment. Though fish assemblages offshore were less diverse than they were inshore, the abundance of several species of particular conservation interest defined the offshore community. The abundance of large individuals of both *P. rupestris* and *P. undulosus* was considerably higher offshore, confirming the suitability of the offshore Amathole MPA to serve as a refuge for the recovery of these species. Further investigation of the offshore community would doubtless reveal its conservation value for many more species of interest. While this study did not take into account the new offshore Amathole MPA and its zonation, the data collected will nevertheless provide a valuable reference point for future studies in the area. Further sampling of the offshore environment will allow a more comprehensive analysis, including comparisons of exploited and protected habitats. The success of *C. cristiceps* within the inshore protected area provides encouragement for the potential of strategically placed MPAs to achieve meaningful results within a limited area and further highlights the importance of protecting the inshore environment.

5 DISCUSSION

The overall aim of this thesis was to determine the effectiveness of the Amathole MPA in protecting representative assemblages of fishes from the Amathole region of South Africa. To achieve this, the study made use of stereo-BRUVs to compare fish communities in the inshore Amathole MPA with those from adjacent exploited sites within a similar depth range and then between the inshore fish assemblages and the fish assemblages found on the outer parts of the continental shelf. The aim of these comparisons were to investigate to what extent the inshore Amathole MPA provides sanctuary to local linefish species, and to describe differences between inshore and offshore fish assemblages and highlight potential conservation gains from the offshore extension of the MPA. The results presented are relevant to the conservation of vulnerable reef fish species and as a reference for assemblage composition in the area of the recently declared offshore Amathole MPA prior to its proclamation.

The overall result indicated that while the inshore Amathole MPA has clearly benefitted several species of particular conservation concern, it falls short of the depth range required to adequately protect larger target species and offshore assemblages. This finding provides valuable evidence to justify the recent extensions seaward of the Kei and Gxulu inshore protected areas.

Availability of reef substrate was the primary influence on target species across the sampled depth range, with species assemblages on sand less diverse and more variable than those on reef substrates. While the inshore analysis revealed no effect of depth on fish assemblages, extension of the depth range considered to include the offshore habitat, revealed that depth does indeed play an important role in structuring fish communities in the vicinity of the MPAs. In keeping with the findings of results of previous studies on the South African coast (Willis & Anderson 2003, Heyns-Veale et al. 2016, Heyns-Veale et al. 2019b), fish assemblages in the offshore zone were less diverse than those inshore, consisting predominantly of larger sparid species and elasmobranchs. However, the abundance and biomass of two species of particular conservation interest, red steenbras (*Petrus Rupestris*) and seventyfour (*Polysteganus undulosus*), were among those that were higher offshore than inshore.

Differences between protected and exploited areas, and between inshore and offshore zones, were more pronounced for biomass than for abundance and as the analyses were refined for target species. Contrarily, community analysis revealed that smaller species from lower trophic levels were more abundant and reached larger sizes in the inshore exploited areas. The apparent response of lower trophic level fishes to the recovery of predatory species is consistent with the findings of previous studies (Edgar & Stuart-Smith 2009, Stobart et al. 2009, Maggs 2011) and a promising indication that historical enforcement of the inshore no-take zones is having the desired effect. In the Amathole MPAs, regulations were historically enforced by local Ski-boat fishermen and coastal stakeholders. This illustrates the benefit of stakeholder investment in the MPA planning process (Hilborn et al. 2004, Rice et al. 2012), not only in securing the approval of such sanctuaries but in their continued advocacy for and defence of the areas against future threats.

When the analysis focussed only on the species targeted by fisheries, the differences between inshore and offshore assemblages was amplified. This implies differential use of the inshore and offshore habitats by these species. The increased difference between zones when considering biomass rather than abundance of target species suggests that there is ontogenic depth distribution for some of these species, with larger individuals found in the deep. This supports the findings of previous studies from South Africa, (Smale 1988, Buxton & Allen 1989, Griffiths & Wilke 2002, Heemstra & Heemstra 2004, Mann 2013) that depth is associated with shifts in fish assemblage structure and ontogenic distribution of species. Such depth associated changes justifies revisiting the representativeness of habitats encompassed by MPAs whose offshore limits were based on linear distance rather than corresponding depth coverage.

The inshore area within the Amathole region appears important for juvenile and immature *P. undulosus*. Management status did not affect the inshore abundance and this could be due to limited residency of juveniles, and/or compliance of local ski-boat fishermen with the moratorium on the capture of this species, which would lead to minimal fishing mortality in the inshore exploited areas. Whether or not this is the case, the culture of compliance fostered by the fishermen's sense of ownership of the protected areas is a proven benefit of this type of stakeholder partnership (Bova et al. 2017).

There was no indication that the inshore area served as a nursery zone for *P. rupestris*, reinforcing the need for an offshore protected area to adequately support spawner stock of this

species in the Amathole region. In addition, this finding highlights the importance of coastal MPAs along South Africa's southern coastline where juvenile *P. rupestris* are known to occur. The inshore MPA did, nonetheless, appear to provide some benefit to adults frequenting the inshore zone, as they were mostly absent from the adjacent exploited areas. Comparison of *P. rupestris* populations from the Amathole MPA with other MPAs within the historical range which also encompass deep water shelf habitat, such as the Agulhas Bank and Protea Bank MPAs, could further substantiate the value of the Amathole area to *P. rupestris*.

The findings of this study differed in several respects from those of the preliminary angling survey carried out by Dr. Malcolm Smale in 2004. The research carried out in 2004 found higher densities of fish in the protected areas but no consistent differences in size for most target species, as well as notable differences in species composition of the assemblage sampled by angling compared to that sampled by stereo-BRUVs here. However, in agreement with Dr. Smale's study, dageraad (*Chrysoblephus cristiceps*) were found to be consistently more abundant and larger in the protected areas than in adjacent exploited areas, with sizes approaching the maximum size on record. This demonstrates that the decades of informal protection of the areas by the ski-boat fishermen have been instrumental in the local protection of *C. cristiceps*, which by all indications are doing well in the inshore MPA. It will be interesting to see if the offshore extension of the MPA results in an expansion of the depth range favoured by *C. cristiceps* in the Amathole area, since in the current study occurrences were restricted mainly to depths of less than 50 m, far below the species limit of 100 m. This encouraging recovery of *C. cristiceps* in the inshore Amathole MPA demonstrates the potential of MPAs to achieve substantial conservation benefits within a limited area and reiterates the benefit of aligning MPA design with objectives.

Of notable difference in the 2004 results was the particularly strong effect of the Gxulu reserve on the size of *C. cristiceps*. The current results indicate, on the contrary, that the absence of suitable reef structure in the Gxulu protected area results in no discernible management effect there. This highlights the need for repeated monitoring of fish communities in the Amathole MPA to account for temporal variability. Further investigation of the 2004 results and comparison with subsequent analyses may provide valuable insight into the evolution of fish assemblage structure in response to spatial protection over time.

Given the apparent benefit of the Kei and Gonubie protected to the recovery of *C. cristiceps* in the area it would also be worth investigating the possibility of extending the boundary of the Gxulu protected area further south to include more reef structure in the protected area. However, careful consideration of current stakeholder usage would be necessary to ensure that support for the MPA is retained. If alteration of the boundaries is not feasible and subsequent monitoring does not reveal seasonal shifts in exposure of reef substrate, it might be desirable to develop the current conservation objectives to define the Gxulu protected area as a sanctuary for sand-associated biodiversity.

While the inshore results have demonstrated the potential of spatial protection for long-lived sparids in the Amathole region, the offshore comparison confirms that protection of larger species like *P. undulosus* and *P. rupestris* requires the depth range provided by the recent extension of the Gxula and Kei MPAs, if MPAs are to have meaningful impact on recovery of these stocks.

5.1 CONCLUSION

Though the inshore Amathole MPA does not entirely meet the conservation objective of protecting vulnerable and threatened reef fish species, since its limited depth extent excludes at least two particularly vulnerable species that are good candidates for spatial protection, it nonetheless provides vital refuge to dageraad and numerous other inshore species, along with the unique ecosystem and biodiversity with which they are associated. While the success of the inshore Amathole MPA exemplifies the utility of spatial protection as a recourse in the absence of detailed ecological information, its shortcomings reinforce the value of clearly defining conservation objectives before the designation an MPA.

This study indicated that the Gxulu protected area provides scant suitable habitat for vulnerable subtidal reef species. However, further research is needed to confirm that this is not simply an artefact of temporal variation in sand deposits. Regardless of the outcome, even in its current state the Gxulu protected area does provide sanctuary local sand communities and those closely associated with the coastline, which, if not of direct importance to fisheries in the area, are at the least a vital component of local biodiversity. Increasing the coastal extent of the Gxulu MPA (if it would achieve better subtidal reef coverage), would be of benefit not only in the additional refuge afforded to *C. cristiceps*, but by improving the overall effectiveness of the inshore

Amathole MPA in meeting its objectives. If stakeholder consultation reveals that such an extension is not feasible, then it might be beneficial to modify instead the conservation objectives of the inshore MPA to include the protection of non-target and sand-associated species.

Further monitoring of all three inshore protected areas will be required to ascertain the level of temporal variation in fish assemblage structure, as well as to extend the area of sampling in the inshore Kei protected area to cover the southern portion, since this study focussed on the northern section.

This study provides the first comprehensive community-level assessment of reef fish in the inshore Amathole marine protected area and surrounds as well as reference measurements from the vicinity of the offshore Amathole MPA prior to its declaration as a protected area. The results support the benefit provided to several endangered species by the inshore no-take zones. The Amathole MPA exemplifies the potential of spatial management within a limited area for highly vulnerable species and establishes a precedent for delimiting the seaward extent of South African MPAs based on depth coverage rather than linear distance from shore. Indeed, the results of this study indicate that failure to do so can deprive some of the most vulnerable species of meaningful spatial protection, missing valuable opportunity to boost recovery of their stocks.

Further research into inter-specific interactions and non-target species, distribution of reef complexes, and temporal variability in fish assemblage would assist future management decisions regarding the Amathole MPAs. Continued observation of the offshore fish assemblages in the MPA will provide insight into the development of community response to offshore protection.

6 REFERENCES

ABESAMIS, R.A., RUSS, G.R. (2005) Density-dependent spillover from a marine reserve: long-term evidence. *Ecological Applications*. 15. DOI:10.1890/05-0174

ACEP (2017) The African Coelacanth Ecosystem Programme Project Overviews 2016/17 – IMIDA: Frontiers Project Overview.

ADENIJI, A., OKOH, O., OKOH, A. (2017) Petroleum Hydrocarbon Fingerprints of Water and Sediment Samples of Buffalo River Estuary in the Eastern Cape Province, South Africa. *Journal of Analytical Methods in Chemistry*. 3. 10.1155/2017/2629365.

AFONSO, P., FONTES, J., SANTOS, R. (2011) Small marine reserves can offer long term protection to an endangered fish. *Biological Conservation*. 144. 2739-2744. 10.1016/j.biocon.2011.07.028.

ADM (AMATHOLE DISTRICT MUNICIPALITY) (2016) Amathole District Municipality Coastal Management Programme.

AGARDY, T., NOTARBARTOLO DI SCIARA, G., CHRISTIE, P. (2011) Mind the gap: Addressing the shortcomings of marine protected areas through large scale marine spatial planning. *Marine Policy*. 35. DOI:10.1016/j.marpol.2010.10.006.

AGARDY, T. (2017) Justified ambivalence about MPA effectiveness, *ICES Journal of Marine Science*. 75(3). <https://doi.org/10.1093/icesjms/fsx083>

AKAIKE, H. (1974) A new look at the statistical model identification. *IEEE Transactions on Automatic Control*. 19(6). DOI:10.1109/TAC.1974.1100705

ANDERSON, M.J. (2001) A new method for non-parametric multivariate analysis of variance. *Austral Ecology*. 26. DOI:10.1111/j.1442-9993.2001.01070.pp.x

- ANDERSON, M.J., WILLIS, T.J. (2003) Canonical Analysis of Principal Coordinates: A Useful Method of Constrained Ordination for Ecology. *Ecology*. 84(2). DOI:10.1890/0012-9658(2003)084[0511:CAOPCA]2.0.CO;2
- ANDERSON, M.J. (2006) Distance-Based Tests for Homogeneity of Multivariate Dispersions. *Biometrics*. 62. DOI:10.1111/j.1541-0420.2005.00440.x
- ANDERSON, M.J., ELLINGSEN, K.E., MCARDLE, B.H. (2006) Multivariate dispersion as a measure of beta diversity. *Ecology Letters*. 9(6). DOI:10.1111/j.1461-0248.2006.00926.x
- ANDERSON, M.J., GORLEY, R.N., CLARKE, K.R. (2008) PERMANOVA+ for PRIMER: Guide to Software and Statistical Methods, PRIMER-E, Plymouth
- ANDERSON, M.J., WALSH, D.C. (2013) PERMANOVA, ANOSIM, and the Mantel test in the face of heterogeneous dispersions: What null hypothesis are you testing? *Ecological Monographs*. 83(4). DOI:10.1890/12-2010.1
- ANDREWS, A., COWLEY, P., SMALE, M. (2018) Fifty-five-year longevity for the largest member of the family Sparidae: the endemic red steenbras *Petrus rupestris* from South Africa. *African Journal of Marine Science*. 40. DOI:10.2989/1814232X.2018.1520148.
- BALLANTINE, B. (2014) Fifty years on: Lessons from marine reserves in New Zealand and principles for a worldwide network. *Biological Conservation*. 176. DOI:DOI:10.1016/j.biocon.2014.01.014
- BASKETT, M., YOKLAVICH, M., LOVE, M. (2011) Predation, competition and the recovery of overexploited fish stocks in marine reserves. *Canadian Journal of Fisheries and Aquatic Sciences*. 68. DOI:10.1139/F06-013.
- BASKETT, M., BARNETT, L. (2015) The Ecological and Evolutionary Consequences of Marine Reserves. *Annual Review of Ecology, Evolution, and Systematics*. 46. DOI:10.1146/annurev-ecolsys-112414-054424.
- BECKLEY, L.E., VAN BALLEGOOYEN, R.C. (1992) Oceanographic conditions during three ichthyoplankton surveys of the Agulhas Current in 1990/91. *South African Journal of Marine Science*. 12(1). DOI:10.2989/02577619209504693

- BERKELEY, S.A., HIXON, M.A., LARSON, R.J., LOVE, M.S. (2004) Fisheries Sustainability via Protection of Age Structure and Spatial Distribution of Fish Populations. *Fisheries*. 29(8). [https://doi.org/10.1577/1548-8446\(2004\)29\[23:FSVPOA\]2.0.CO;2](https://doi.org/10.1577/1548-8446(2004)29[23:FSVPOA]2.0.CO;2)
- BERNARD, A., GÖTZ, A. (2012) Bait increases the precision in count data from remote underwater video for most subtidal reef fish in the warm-temperate Agulhas bioregion. *Marine Ecology Progress Series*. 471. DOI:10.3354/meps10039
- BERNARD, A., GÖTZ, A., PARKER, D., HEYNS, E., HALSE, S., RIDDIN, N., SMITH, M., PATERSON, A., WINKER, H., FULLWOOD, L., LANGLOIS, T., HARVEY, E. (2014) New possibilities for research on reef fish across the continental shelf of South Africa. *South African Journal of Science*. 110. DOI:10.1590/sajs.2014/a0079.
- BIRKELAND, C., DAYTON, P. K. (2005) The importance in fishery management of leaving the big ones. *Trends in Ecology & Evolution*. 20. DOI:10.1016/j.tree.2005.03.015
- BOVA, C.S., HALSE, S.J., ASWANI, S., POTTS, W.M. (2017) Assessing a social norms approach for improving recreational fisheries compliance. *Fisheries Management and Ecology*. 24(2). DOI:10.1111/fme.12218
- BRANCH, G.M., GRIFFITHS, C.L., BRANCH, M.L., BECKLEY, L.E. (1994) Two oceans. A guide to the marine life of southern Africa. David Philip, Cape Town, South Africa. ISBN-13: 978-0864862501
- BROUWER, S.L. (2002) Movement patterns of red steenbras (*Petrus rupestris*) tagged and released in the Tsitsikamma National Park, South Africa. *South African Journal of Marine Science*. 24(1). DOI:10.2989/025776102784528385
- BROUWER, S.L., BUXTON, C.D. (2002) Catch and effort of the shore and ski-boat linefisheries along the South African Eastern Cape Coast. *South African Journal of Marine Science*. 24(1). DOI:10.2989/025776102784528286
- BUXTON, C.D., SMALE, M.J. (1984) A preliminary investigation of the Marine Ichthyofauna in the Tsitsikamma Coastal National Park. *Koedoe - African Protected Area Conservation and Science*. 27. DOI:10.4102/koedoe.v27i1.547.

BUXTON, C.D., SMALE, M.J. (1989) Abundance and Distribution Patterns of Three Temperate Marine Reef Fish (Teleostei: Sparidae) in Exploited and Unexploited Areas Off the Southern Cape Coast. *Journal of Applied Ecology*. 26(2). DOI:10.2307/2404072

BUXTON, C., ALLEN, J. (1989) Mark and recapture studies of two reef sparids in the Tsitsikamma Coastal National Park. *Koedoe - African Protected Area Conservation and Science*. 32. DOI:10.4102/koedoe.v32i1.463.

BUXTON, C. (1990) The reproductive biology of *Chrysoblephus laticeps* and *C. cristiceps* (Teleostei: Sparidae). *Journal of Zoology*. 220. DOI:10.1111/j.1469-7998.1990.tb04321.x.

BUXTON, C. (1993) Life-history changes in exploited reef fishes on the east coast of South Africa. *Environmental Biology of Fishes*. 36. DOI:10.1007/BF00005979.

BUXTON, C.D., HARTMANN, K., KEARNEY, R., GARDNER, C. (2014) When Is Spillover from Marine Reserves Likely to Benefit Fisheries? *PLoS ONE*. 9(9), e107032. <http://doi.org/10.1371/journal.pone.0107032>

BUXTON, C.D., MANN, B.Q., POLLARD, D., CARPENTER, K.E., WINKER, H. (2014) *Chrysoblephus cristiceps*. The IUCN Red List of Threatened Species 2014: e.T170183A1288745. <https://dx.doi.org/10.2305/IUCN.UK.2014-3.RLTS.T170183A1288745.en>.

CAPPO, M., SPEARAE, P., DE'ATH, G. (2004) Comparison of baited remote underwater video stations (BRUVS) and prawn (shrimp) trawls for assessments of fish biodiversity in inter-reefal areas of the Great Barrier Reef Marine Park. *Journal of Experimental Marine Biology and Ecology*. 302. DOI:10.1016/j.jembe.2003.10.006

CAPPO, M., HARVEY, E.S., SHORTIS, M. (2006) Counting and measuring fish with baited video techniques - an overview. In: Lyle, J. M., Furlani, D. M., Buxton, C.D. (eds) *Cutting-edge technologies in fish and fisheries science*. Proceedings of Australian Society for Fish Biology Workshop, pp 101–114

CHALE-MATSAU, J.R., GOVENDER, A., BECKLEY, L.E. (2001) Age, growth and a retrospective stock assessment of an economically extinct sparid fish, *Polysteganus undulosus* from South Africa. *Fisheries Research*. 51(1). DOI:10.1016/S0165-7836(00)00235-6

- CHATFIELD, B.S., VAN NIEL, K.P., KENDRICK, G.A., HARVEY, E.S. (2010) Combining environmental gradients to explain and predict the structure of demersal fish distributions. *Journal of Biogeography*. 37. DOI:10.1111/j.1365-2699.2009.02246.x
- CHRISTENSEN, M.S. (1980) Sea Surface Temperature Charts for Southern Africa, South of 25°S. *South African Journal of Science*. 76. DOI:10.10520/AJA00382353_4461
- CLARKE, A., JOHNSTON, N.M. (1999) Scaling of metabolic rate with body mass and temperature in teleost fish. *Journal of Animal Ecology* 68. DOI:10.1046/j.1365-2656.1999.00337.x
- CLARKE, K.R. (1993) Non-parametric multivariate analyses of changes in community structure. *Austral Ecology*. 18(1). DOI:10.1111/j.1442-9993.1993.tb00438.x
- CLARKE, K.R., WARWICK, R.M. (2001) Change in marine communities: An approach to statistical analysis and interpretation, second ed. PRIMER-E, Plymouth
- CLARKE, K.R., GORLEY, R.N. (2006) PRIMER v6: User Manual/Tutorial. PRIMER-E, Plymouth
- CLAUDET, J., OSENBURG, C.W., BENEDETTI-CECCHI, L., DOMENICI, P., GARCÍA-CHARTON, J., PEREZ-RUZAFÁ, A., BADALAMENTI, F., BAYLE-SEMPERE, J.T., BRITO, A., BULLERI, F., CULIOLI, J., DIMECH, M., FALCÓN, J.M., GUALA, I., MILAZZO, M., SÁNCHEZ-MECA, J., SOMERFIELD, P.J., STOBART, B., VANDEPERRE, F., VALLE, C., & PLANES, S. (2008) Marine reserves: size and age do matter. *Ecology Letters*. 11(5). DOI:10.1111/j.1461-0248.2008.01166.x
- CLAUDET, J., OSENBURG, C.W., DOMENICI, P., BADALAMENTI, F., MILAZZO, M., FALCÓN, J.M., BERTOCCI, I., BENEDETTI-CECCHI, L., GARCÍA-CHARTON, J., GOÑI, R., BORG, J.A., FORCADA, A., DE LUCIA, G.A., PÉREZ-RUZAFÁ, Á., AFONSO, P., BRITO, A., GUALA, I., DIRÉACH, L.L., SANCHEZ-JEREZ, P., SOMERFIELD, P.J., PLANES, S. (2010) Marine reserves: Fish life history and ecological traits matter. *Ecological Applications*. 20. DOI:10.1890/08-2131.1
- CLAUDET, J., GUIDETTI, P. (2010) Fishermen contribute to protection of marine reserves. *Nature*. 464(7829). DOI:10.1038/464673b
- COMEROS-RAYNAL, M.T., POLIDORO, B.A., BROATCH, J., MANN, B.Q., GORMAN, C.E., BUXTON, C.D., GOODPASTER, A.M., IWATSUKI, Y., MACDONALD, T.C., POLLARD, D., RUSSELL, B.,

- CARPENTER, K.E. (2016) Key predictors of extinction risk in sea breams and porgies (Family: Sparidae). *Biological Conservation* 202. DOI:10.1016/j.biocon.2016.08.027
- COMPAGNO, L.J.V., EBERT, D.A., SMALE, M.J. (1989) Guide to the sharks and rays of Southern Africa. Cape Town (South Africa) Struik. ISBN-13 : 978-0869778807
- CONOVER, D.O., MUNCH, B. (2002) Sustaining Fisheries Yields Over Evolutionary Time Scales. *Science*. 297(5578). DOI:10.1126/science.1074085
- COTE, I.M., MOSQUEIRA, I., REYNOLDS, J.D. (2001) Effects of marine reserve characteristics on the protection of fish populations: a meta-analysis. *Journal of Fish Biology*. 59(sA). DOI:10.1111/j.1095-8649.2001.tb01385.x
- COUTANT, C.C. (1987) Thermal preference: when does an asset become a liability? *Environmental Biology of Fishes*. 18(3). DOI:10.1007/BF00000356
- CRAGG, J.G. (1971) Some Statistical Models for Limited Dependent Variables with Application to the Demand for Durable Goods, *Econometrica*, *Econometric Society*, 39(5). DOI:10.2307/1909582
- DAFF (Department of Agriculture, Forestry and Fisheries) (2016), Status of the South African marine fishery resources. Cape Town: DAFF. ISBN:978-0-621-45086-6
- DEDEAT (Department of Economic Development Environmental Affairs and Tourism) (2016) Publishing of public launch sites in the eastern cape in terms of management of public launch sites in the coastal zone regulations in terms of national environmental management: integrated coastal management act, 2008 (Act no. 24 of 2008). *Eastern Cape Provincial Gazette*, No. 3777, Notice 42 of 2016, 19 December 2016.
- DEAT (Department of Environmental Affairs and Tourism) (1997), White paper: a marine fisheries policy for South Africa. Pretoria: Dept. of Environmental Affairs and Tourism. G 68 E.ENVI.97.WHIT
- DEMESTRE, M., SANCHEZ, P., ABELLO, P. (2000) Demersal fish assemblages and habitat characteristics on the continental shelf and upper slope of the north-western Mediterranean. *Journal of the Marine Biological Association of the U.K.* 80. DOI:10.1017/S0025315400003040

DE VOS, L., GÖTZ, A., WINKER, H., ATTWOOD, C.G. (2014) Optimal BRUVs (baited remote underwater video system) survey design for reef fish monitoring in the Stilbaai Marine Protected Area. *African Journal of Marine Science* 36(1). DOI:10.2989/1814232X.2013.873739

DI FRANCO, A., THIRIET, P., DI CARLO, G., DIMITRIADIS, C., FRANCOUR, P., GUTIÉRREZ, N.L., DE GRISAC, A.J., KOUTSOUBAS, D., MILAZZO, M., OTERO, M.D.M., PIANTE, C., PLASS-JOHNSON, J.G., SAINZ-TRAPAGA, S., SANTAROSSA, L., TUDELA, S., GUIDETTI, P. (2016) Five key attributes can increase marine protected areas performance for small-scale fisheries management. *Scientific Reports*. 6(1), 38135. DOI:10.1038/srep38135

DI FRANCO, A., PLASS-JOHNSON, J., DI LORENZO, M., MEOLA, B., CLAUDET, J., GAINES, S., GARCÍA-CHARTON, J., GIAKOUMI, S., GRORUD-COLVERT, K., HACKRADT, C.W., MICHELI, F., GUIDETTI, P. (2018) Linking home ranges to protected area size: The case study of the Mediterranean Sea. *Biological Conservation*. 221. DOI:10.1016/j.biocon.2018.03.012.

DLAMINI, N. (2017) Marine Geology of the East London Continental Shelf. Master's Dissertation, University of Kwa-Zulu Natal, Durban, South Africa. Retrieved from [http://
http://researchspace.ukzn.ac.za/xmlui/handle/10413/15830](http://http://researchspace.ukzn.ac.za/xmlui/handle/10413/15830)

ECSECC (Eastern Cape Socio Economic Consultative Council) (2017), Buffalo City Metro Municipality Socio Economic Review and Outlook, 2017. ECSECC, East London, South Africa. www.ecsecc.org

EDGAR, G.J., STUART-SMITH, R. (2009) Ecological effects of marine protected areas on rocky reef communities – A continental-scale analysis. *Marine Ecology Progress Series*. 388. DOI:10.3354/meps08149.

EDGAR, G.J., STUART-SMITH, R.D., WILLIS, T.J., KININMONTH, S., BAKER, S.C., BANKS, S., BARRETT, N.S., BECERRO, M.A., BERNARD, A.T.F., BERKHOUT, J., BUXTON, C.D., CAMPBELL, S.J., COOPER, A.T., DAVEY, M., EDGAR, S.C., FÖRSTERRA, G., GALVAN, D.E., IRIGOYEN, A.J., KUSHNER, D.J., MOURA, R., PARNELL, P.ED, SHEARS, N.T., SOLER, G.A, STRAIN, E.M.A., THOMSON, R.J. (2014) Global conservation outcomes depend on marine protected areas with five key features. *Nature*. 506(7487). DOI:10.1038/nature13022

FAO (2001) Information on Fisheries Management in the Republic of South Africa. <http://www.fao.org/fi/oldsite/FCP/en/ZAF/body.htm>

FAO (2016) Fisheries and Aquaculture topics. Fish capture technology. Topics Fact Sheets. In: FAO Fisheries and Aquaculture Department [online]. Rome. Accessed 18 July 2018. <http://www.fao.org/fishery/>

FENNESSY, S., MCDONALD, A., MANN, B., EVERETT, B. (2003) An Assessment of the Recreational and Commercial Ski-boat Fishery in the Transkei. *African Journal of Marine Science*. 1. DOI:10.2989/18142320309504001.

FITZPATRICK B.M., HARVEY E.S., HEYWARD A.J., TWIGGS, E.J., COLQUHOUN, J. (2012) Habitat specialization in tropical continental shelf demersal fish assemblages. *PLoS One* 7(6):e39634. DOI:10.1371/journal.pone.0039634

FRIEDLANDER A.M., PARRISH J.D. (1998) Habitat characteristics affecting fish assemblages on a Hawaiian coral reef. *Journal of Experimental Marine Biology and Ecology*. 224. DOI:10.1016/S0022-0981(97)00164-0

FROESE, R., PAULY, D. (Eds) (2018) FishBase. World Wide Web electronic publication. www.fishbase.org

GARCIA, S.M., ZERBI, A., ALIAUME, C., DO CHI, T., LASSERRE, G. (2003) The ecosystem approach to fisheries. Issues, terminology, principles, institutional foundations, implementation and outlook. FAO Fisheries Technical Paper. No. 443. Rome, FAO.

GARRATT, P.A. (1988) Notes on seasonal abundance and spawning of some important offshore linefish in Natal and Transkei waters, Southern Africa. *South African Journal of Marine Science*, 7(1). DOI:10.2989/025776188784379161

GARRATT, P.A. (1996) Threatened fishes of the world: *Polysteganus undulosus* Regan, 1908 (Sparidae). *Environmental Biology of Fishes*. 45. <https://doi.org/10.1007/BF00002528>

GEBCO (2014) The GEBCO_2014 Grid, version 20150318. www.gebco.net

- GELL, F.R., ROBERTS, C.M. (2003) Benefits beyond boundaries: the fishery effects of marine reserves. *Trends in Ecology & Evolution*. 18(9). DOI:10.1016/S0169-5347(03)00189-7
- GIAKOUMI, S., MCGOWAN, J., MILLS, M., BEGER, M., BUSTAMANTE, R., CHARLES, A., CHRISTIE, P., FOX, M., BORBOROGLU, P., GELCICH, S., GUIDETTI, P., MACKELWORTH, P., MAINA, J., MCCOOK, L., MICHELI, F., MORGAN, L., MUMBY, P., REYES, L., WHITE, A., POSSINGHAM, H. (2018) Revisiting “Success” and “Failure” of Marine Protected Areas: A Conservation Scientist Perspective. *Frontiers in Marine Science*. 5. DOI:10.3389/fmars.2018.00223.
- GILL, D.A., MASCIA, M.B., AHMADIA, G.N., GLEW, L., LESTER, S.E., BARNES, M., CRAIGIE, I., DARLING, E.S., FREE, C.M., GELDMANN, J., HOLST, S., JENSEN, O.P., WHITE, A.T., BASURTO, X., COAD, L., GATES, R.D., GUANNEL, G., MUMBY, P.J., THOMAS, H., WHITMEE, S., WOODLEY, S., FOX, H.E. (2017) Capacity shortfalls hinder the performance of marine protected areas globally. *Nature*. 543(7647). <http://dx.doi.org/10.1038/nature21708>
- GOÑI, R., HILBORN, R., DÍAZ, D., MALLOL MARTÍNEZ, S., ADLERSTEIN, S. (2010) Net contribution of spillover from a marine reserve to fishery catches. *Marine Ecology-progress Series*. 400. DOI:10.3354/meps08419.
- GOSCHEN, W.S., SCHUMANN, E.H. (2011) The physical oceanographic processes of Algoa Bay, with emphasis on the western coastal region: A synopsis of the main result of physical oceanographic research in and around Algoa Bay up until 2010. SAEON and IMT. DOI:10.13140/RG.2.1.1823.3767
- GÖTZ, A., KERWATH, S., ATTWOOD, C.G., SAUER, W. (2009) Effects of fishing on a temperate reef community in South Africa 1: Ichthyofauna. *African Journal of Marine Science*. 31(2). DOI:10.2989/AJMS.2009.31.2.12.884.
- GRAHAM, N.A.J., EVANS, R.D., RUSS, G.R. (2003) The effects of marine reserve protection on the trophic relationships of reef fishes on the Great Barrier Reef. *Environmental Conservation*. 30(2). DOI:10.1017/S0376892903000195
- GRIFFITHS, M.H., ATTWOOD, C.G., THOMSON, R. (1999) A new management protocol for the South African line-fishery. In: Mann BQ , *Proceedings of the third southern African marine*

linefish symposium, Arniston, 28 April–1 May 1999. South African Network for Coastal and Oceanic Research. Occasional Report No. 5

GRIFFITHS, M.H. (2000) Long-term trends in Catch and Effort of Commercial Linefish off South Africa's Cape Province: Snapshots of the 20th Century. South African Journal of Marine Science. 22. <https://doi.org/10.2989/025776100784125663>

GRIFFITHS, M., WILKE, C. (2002) Long-term movement patterns of five temperate-reef fishes (Pisces: Sparidae): implications for marine reserves. Marine Freshwater Research. 53. DOI:10.1071/MF01148

GUIDETTI, P., MILAZZO, M., BUSSOTTI, S., MOLINARI, A., MURENU, M., PAIS, A., SPANÒ, N., BALZANO, R., AGARDY, T., BOERO, F., CARRADA, G., CATTANEO-VIETTI, R., CAU, A., CHEMELLO, R., GRECO, S., MANGANARO, A., NOTARBARTOLO DI SCIARA, G., RUSSO, G., TUNESI, L. (2008) Italian marine reserve effectiveness: Does enforcement matter?. Biological Conservation. 141. DOI:10.1016/j.biocon.2007.12.013.

GUTHRIE, D.M. (1986) Role of Vision in Fish Behaviour. In: Pitcher T.J. (eds) The Behaviour of Teleost Fishes. Springer, Boston, MA. ISBN:978-1-4684-8263-8

GWINN, D. C., ALLEN, M. S., JOHNSTON, F. D., BROWN, P., TODD, C. R., ARLINGHAUS, R. (2015) Rethinking length-based fisheries regulations: the value of protecting old and large fish with harvest slots. Fish and Fisheries 16. DOI:10.1111/faf.12053

HALPERN, B.S., WARNER, R.R. (2002) Marine reserves have rapid and lasting effects. Ecology Letters. 5. DOI:10.1046/j.1461-0248.2002.00326.x

HALPERN, B.S. (2003) The impact of marine reserves: Do reserves work and does reserve size matter? Ecological Applications. 13(Suppl). DOI:10.1890/1051-0761(2003)013[0117:TIOMRD]2.0.CO;2

HALPERN, B.S., FRAZIER, M., POTAPENKO, J., CASEY, K.S., KOENIG, K., LONGO, C.S., LOWNDES, J.S., ROCKWOOD, R.C., SELIG, E.R., SELKOE, K.A., & WALBRIDGE, S. (2015) Spatial and temporal changes in cumulative human impacts on the world's ocean. Nature Communications. 6(7615). <https://dx.doi.org/10.1038/ncomms8615>

- HARMAN, N., HARVEY, E.S., KENDRICK, G.A. (2003) Differences in fish assemblages from different reef habitats at Hamelin Bay, south-western Australia. *Marine Freshwater Research*. 54. DOI:10.1071/MF02040
- HARRIS, J., LIVINGSTONE, T., PHADIMA, J., SINK, K., FASHEUN, T., BOYD, A., MFEKA, X. (2014) Phakisa Initiative : fast-tracking establishment of an effective and representative network of Marine Protected Areas for South Africa. From Phakisa: Fast-tracking Ocean Protection in South Africa. Initiative 8: Establishment of an effective and representative MPA network. Technical Report. Conference: Symposium of Contemporary Conservation Practice, At Howick, KwaZulu-Natal, South Africa, Volume: 2014
- HARVEY, E.S., SHORTIS, M. (1995), A system for stereo-video measurement of sub-tidal organisms. *Marine Technology Society Journal*. 29(4).
- HARVEY, E.S., SHORTIS, M.R. (1998), Calibration stability of an underwater stereo-video system: implications for measurement accuracy and precision. *Marine Technology Society Journal*. 32(2).
- HECHT, T., BUXTON, C.D. (1993) Catch trends in the transkei commercial linefishery. *Oceanographic Research Institute, Special Publication 2*: 127-133
- HEDLEY, J. (2003) Vidana 1.0: video analysis for cover estimation. www.marinespatialecologylab.org/recources/vidana/
- HEEMSTRA, P., HEEMSTRA, E. (2004) Coastal Fishes of Southern Africa. National Inquiry Service Centre (NISC) & South African Institute for Aquatic Biodiversity (SAIAB). ISBN:1-9200333-01-7
- HENRIQUES, R., MANN, B.Q., NIELSEN, E.S., HUI, C., VON DER HEYDEN, S. (2020) Extending biodiversity conservation with functional and evolutionary diversity: A case study of South African sparid fishes. *African Journal of Marine Science*. 42(3). DOI: 10.2989/1814232X.2020.1798282
- HEYNS-VEALE, E., BERNARD, A., RICHOUX, N., PARKER, D., LANGLOIS, T., HARVEY, E., GÖTZ, A. (2016) Depth and habitat determine assemblage structure of South Africa's warm-temperate reef fish. *Marine Biology*. 163. DOI:10.1007/s00227-016-2933-8

HEYNS-VEALE, E., BERNARD, A., GÖTZ, A., MANN, B., MAGGS, J., SMITH, M.K.S. (2019) Community-wide effects of protection reveal insights into marine protected area effectiveness for reef fish. *Marine Ecology Progress Series*. 620. DOI:10.3354/meps12970.

HEYNS-VEALE, E., RICHOUX, N.B., BERNARD, A., GÖTZ, A. (2019b) Protected nearshore shallow and deep subtidal rocky reef communities differ in their trophic diversity but not their nutritional condition. *African Journal of Marine Science*. 41. DOI:10.2989/1/814232X.2019.1580614.

HILBORN, R., STOKES, K., MAGUIRE, J., SMITH, T., BOTSFORD, L.W., MANGEL, M., ORENSANZ, J., PARMA, A., RICE, J., BELL, J., COCHRANE, K.L., GARCIA, S., HALL, S.J., KIRKWOOD, G.P., SAINSBURY, K., STEFANSSON, G., WALTERS, C. (2004) When can marine reserves improve fisheries management? *Ocean and Coastal Management*. 47(3/4). DOI:10.1016/j.ocecoaman.2004.04.001

HIXON, M.A., JOHNSON, D.W., SOGARD, S.M. (2014) BOFFFFs: on the importance of conserving old-growth age structure in fishery populations. *ICES Journal of Marine Science*. 71(8). DOI:10.1093/icesjms/fst200

HOEGH-GULDBERG, O., BRUNO, J. F. (2010). The Impact of Climate Change on the World's Marine Ecosystems. *Science*. 328(5985). DOI:10.1126/science.1189930

IUCN (2018) The Red List of Threatened Species. Version 2018-2. Accessed 09/10/2018. <http://www.iucnredlist.org>

JENNINGS, S., KAISER, M.J. (1998) The effects of fishing on marine ecosystems. *Advances in marine biology*. 34. DOI:10.1016/S0065-2881(08)60212-6

JUBY, R. (2017) Diurnal and Nocturnal Activity Patterns and Habitat Use of Algoa Bay's Rocky Reef Fish Community. Master's Thesis. Rhodes University, Makhanda, South Africa. Retrieved from <http://hdl.handle.net/10962/44827>

KELLEHER, G. (1999) Guidelines for Marine Protected Areas. IUCN, Gland, Switzerland and Cambridge, UK. ISBN:978-2-8317-0505-7

- KERWATH S.E., WINKER H., GÖTZ A., ATTWOOD C.G. (2013) Marine protected area improves yield without disadvantaging fishers. *Nature Communications*. 2013(4). DOI:10.1038/ncomms3347
- KERWATH, S., PARKER, D., WINKER, H., POTTS, W., MANN, B., WILKE, C., ATTWOOD, C. (2019) Tracking the decline of the world's largest seabream against policy adjustments. *Marine Ecology Progress Series*. 610. DOI:10.3354/meps12853.
- KRUSKAL, J.B. (1964) Multidimensional scaling by optimizing goodness of fit to a nonmetric hypothesis. *Psychometrika*. 29(1). DOI:10.1007/BF02289565
- LESTER, S.E., HALPERN, B.S. (2008) Biological responses in marine no-take reserves versus partially protected areas. *Marine Ecology Progress Series*. 367. DOI:10.3354/meps07599
- LESTER, S.E., HALPERN, B.S., GRORUD-COLVERT, K., LUBCHENCO, J., RUTTENBERG, B.I., GAINES, S.D., AIRAMÉ, S., WARNER, R.R. (2009) Biological effects within no-take marine reserves : a global synthesis. *Marine Ecology Progress Series*. 384. DOI:10.3354/meps08029
- LUTJEHARMS, J.R.E., COOPER, J., ROBERTS, M. (2000) Upwelling at the inshore edge of the Agulhas Current. *Continental Shelf Research*. 20. DOI:10.1016/S0278-4343(99)00092-8.
- LUTJEHARMS, J. (2006) Three decades of research on the greater Agulhas Current. *Ocean Science Discussions*. 3. DOI:10.5194/os-3-129-2007.
- MAGGS, J. (2011) Fish surveys in exploited and protected areas of the Pondoland Marine Protected Area with consideration of the impact of the MPA on coastal fisheries. DOI:10.13140/RG.2.2.28914.35527.
- MAGGS, J.Q., MANN, B.Q., COWLEY, P.D. (2013) Contribution of a large no-take zone to the management of vulnerable reef fishes in the South-West Indian Ocean. *Fisheries Research*. 144. DOI:10.1016/j.fishres.2012.10.003
- MANN, B.Q. (2013), Southern African marine line fish species profiles. Special publication No. 9. Oceanographic Research Institute: South African Association for Marine Biological Research, Durban. ISBN:978-0-620-58185-1

- MANN, B.Q., BUXTON, C.D., POLLARD, D., CARPENTER, K.E., SADOVY, Y. (2014). *Polysteganus undulosus*. The IUCN Red List of Threatened Species 2014: e.T170206A1293194. Accessed 19/01/2021. <https://dx.doi.org/10.2305/IUCN.UK.2014-3.RLTS.T170206A1293194.en>
- MANN, B.Q., BUXTON, C.D., POLLARD, D., CARPENTER, K.E., WINKER, H. (2014b) *Petrus rupestris*. The IUCN Red List of Threatened Species 2014: e.T170247A1300995. Accessed 19/01/2021. <https://dx.doi.org/10.2305/IUCN.UK.2014-3.RLTS.T170247A1300995.en>.
- MPASA (Marine Protected Areas South Africa). (2020) Accessed 18/07/2020. <https://www.marineprotectedareas.org.za/amathole-offshore-mpa>
- MCARDLE , B. H., ANDERSON, M. J. (2001) Fitting multivariate models to community data: a comment on distance-based redundancy analysis. *Ecology*. 82. DOI:10.1890/0012-9658(2001)082[0290:FMMTCD]2.0.CO;2
- MELLIN, C., MACNEIL, A., CHEAL, A., EMSLIE, M., CALEY, J. (2016) Marine protected areas increase resilience among coral reef communities. *Ecology Letters*. 19. DOI:10.1111/ele.12598.
- MICHELI, F., HALPERN, B.S., BOTSFORD, L.W., WARNER, R.R. (2004) Trajectories and correlates of community change in no-take marine reserves. *Ecological Applications*. 14(6). DOI:10.1890/03-5260
- MICHELI, F., SAENZ-ARROYO A., GREENLEY A., VAZQUEZ L., ESPINOZA MONTES J.A., ROSSETTO, M., DE LEO, G.A. (2012) Evidence That Marine Reserves Enhance Resilience to Climatic Impacts. *PLoS ONE*. 7(7): e40832. doi:10.1371/journal.pone.0040832
- MOMBA, M.N., OSODE, A.N., SIBEWU, M. (2009) The Impact of Inadequate Wastewater Treatment on the Receiving Water Bodies – Case Study: Buffalo City and Nkokonbe Municipalities of the Eastern Cape Province. *Water S.A.* 32. DOI:10.4314/wsa.v32i5.47854.
- MULLAHY, J. (1986) Specification and testing of some modified count data models. *Journal of Econometrics*. 33(3). DOI:10.1016/0304-4076(86)90002-3
- NASH, K., GRAHAM, N. (2016) Ecological indicators for coral reef fisheries management. *Fish and Fisheries*. 17. DOI:10.1111/faf.12157.

- PARKER, D., WINKER, H., ATTWOOD, C.G., KERWATH, S.E. (2016) Dark times for dageraad *Chrysoblephus cristiceps*: evidence for stock collapse. *African Journal of Marine Science*. 38(3). DOI:10.2989/1814232X.2016.1200142
- PAULY, D., CHRISTENSEN, V., DALSGAARD, J., FROESE, R., TORRES, F. (1998) Fishing Down Marine Food Webs. *Science*. 279(5352). DOI:10.1126/science.279.5352.860
- PAULY, D., CHRISTENSEN, V., GUÉNETTE, S., PITCHER, T.J., SUMAILA, U.R., WALTERS, C.J., WATSON, R.A., ZELLER, D. (2002) Towards sustainability in world fisheries. *Nature*. 418(6898). DOI:10.1038/nature01017
- PENNEY, A.J., MANN-LANG, J.B., VAN DER ELST, R.P., WILKE, C.D. (1999) Long-term trends in catch and effort in the KwaZulu-Natal nearshore linefisheries. *South African Journal of Marine Science* 21. DOI:10.2989/025776199784125890
- PILFOLD, S.J., PAMPALLIS, A. (1993) The Natal commercial linefishery. *Oceanographic Research Institute, Special Publication (2)*: 118-121
- R CORE TEAM (2017) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>
- REUSCH, T.B., EHLERS, A., HÄMMERLI, A., WORM, B. (2005) Ecosystem recovery after climatic extremes enhanced by genotypic diversity. *Proceedings of the National Academy of Sciences of the United States of America*. 102(8). DOI:10.1073/pnas.0500008102
- RICE, J., MOKSNESS, E., ATTWOOD, C., BROWN, S.K., DAHLEE, G., GJERDEF, K.M., GREFSRUDE, E.S., KENCHINGTONG, R., KLEIVEN, A.R., MCCONNEY, P., NGOILEI, M.A.K., NÆSJEJ, T.F., OLSENE, E., OLSEN, E.M., SANDERS, J., SHARMA, C., VESTERGAARD, O., WESTLUND, L. (2012) The role of MPAs in reconciling fisheries management with conservation of biological diversity. *Ocean & Coastal Management*. 69. DOI:10.1016/j.ocecoaman.2012.08.001
- ROBERTS, C.M., HAWKINS, J.P., GELL, F.R. (2005) The role of marine reserves in achieving sustainable fisheries. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*. 360(1453). DOI:10.1098/rstb.2004.1578

ROBERTS, M., VAN DER LINGEN, C., WHITTLE, C., BERG, M. (2010) Shelf currents, lee-trapped and transient eddies on the inshore boundary of the Agulhas Current, South Africa: their relevance to the KwaZulu-Natal sardine run. *African Journal of Marine Science*. 32. DOI:10.2989/1814232X.2010.512655.

RSTUDIO TEAM (2016) RStudio: Integrated Development for R. RStudio, Inc., Boston, MA. <http://www.rstudio.com/>

RUSS, G.R., CHEAL, A.J., DOLMAN, A.M., EMSLIE, M.J., EVANS, R.D., MILLER, I., SWEATMAN, H., WILLIAMSON, D.H. (2008) Rapid increase in fish numbers follows creation of world's largest marine reserve network. *Current Biology*. 18(12). DOI:10.1016/j.cub.2008.04.016

S.A. GOVERNMENT (Government of South Africa) (1998) Marine Living Resources Act, 1998 (Act No. 18 OF 1998): Regulations in terms of the Act (Notice R1111). *Government Gazette*, 19205. 02 September 1998.

S.A. GOVERNMENT (Government of South Africa) (2019) National Environmental Management: Protected Areas Act, 2003 (Act no. 57 of 2003): Notice declaring the Amathole Offshore Marine Protected Area in terms of section 22A of the Act. (Notice 763). *Government Gazette*, 42478:26, 23 May 2019.

S.A. GOVERNMENT (Government of South Africa) (2011) Marine Living Resources Act, 1998 (act no. 18 of 1998): Declaration of Amathole Marine Protected Area in the Amathole Region under section 43 of the Act. (Notice R730). *Government Gazette*, 34596:39, 16 September 2011

SCHUMANN, E., BEEKMAN, L. (1984) Ocean temperature structures on the Agulhas Bank. *Transactions of The Royal Society of South Africa*. 45. DOI:10.1080/00359198409519483.

SCHUMANN, E.H. (1987) The coastal ocean off the east coast of South Africa. *Transactions of The Royal Society of South Africa*. 46. DOI:10.1080/00359198709520125

SeaGIS Pty Ltd (2012) EventMeasure [Computer software]. www.seagis.com.au

SINK, K.J., ATTWOOD, C.G., LOMBARD, A.T., GRANTHAM, H., LESLIE, R., SAMAAI, T., KERWATH, S., MAJIEDT, P., FAIRWEATHER, T., HUTCHINGS, L., VAN DER LINGEN, C., ATKINSON, L.J., WILKINSON, S., HOLNESS, S., WOLF, T. (2011) Spatial planning to identify focus areas for offshore

biodiversity protection in South Africa. Final Report for the Offshore Marine Protected Area Project. Cape Town: South African National Biodiversity Institute.

SINK, K. (2016) The Marine Protected Areas debate: Implications for the proposed Phakisa Marine Protected Areas Network. South African Journal of Science. 112. DOI:10.17159/sajs.2016/a0179.

SINK, K.J., VAN DER BANK, M.G., MAJIEDT, P.A., HARRIS, L.R., ATKINSON, L.J., KIRKMAN, S.P., KARENYI, N. (eds). 2019. South African National Biodiversity Assessment 2018 Technical Report Volume 4: Marine Realm. South African National Biodiversity Institute, Pretoria. <http://hdl.handle.net/20.500.12143/6372>.

SMALE, M.J. (1988) Distribution and reproduction of the reef fish *Petrus rupestris* (Pisces: Sparidae) off the coast of South Africa. South African Journal of Zoology. 23(4). DOI:10.1080/02541858.1988.11448113 Operation Phakisa (2018) Accessed 17/03/2018. <https://www.operationphakisa.gov.za>

SMITH, J.L.B (1965) The Sea Fishes of South Africa, Fifth Edition. South Africa, Central News Agency Ltd.

STOBART., B., WARWICK, R., GONZÁLEZ, C., MALLOL, S., DÍAZ, D., REÑONES, O., GOÑI, R. (2009) Long-term and spillover effects of a marine protected area on an exploited fish community. Marine Ecology Progress Series. 384. <https://doi.org/10.3354/meps08007>

THETMEYER, H., KILS, U. (1995) To see and not be seen: the visibility of predator and prey with respect to feeding behaviour. Marine Ecology Progress Series. 126. DOI:10.3354/meps126001

THORSON, J.T., RINDORF, A., JIN GAO, J., DANA H. HANSELMAN, D.H., WINKER, H. (2016) Density-dependent changes in effective area occupied for sea-bottom-associated marine fishes. Proceedings of the Royal Society B: Biological Sciences. 283(1840). DOI:10.1098/rspb.2016.1853

TURPIE, J.K., BECKLEY, L.E., KATUA, S.M. (2000) Biogeography and the selection of priority areas for conservation of South African coastal fishes. Biological Conservation. 92. DOI:10.1016/S0006-3207(99)00063-4

TWEEDIE, M.C.K. (1984) An index which distinguishes between some important exponential families. In: Ghosh, J. K., Roy, J. (Eds), *Statistics: Applications and New Directions*. Proceedings of the Indian Statistical Institute Golden Jubilee International Conference. Indian Statistical Institute, Calcutta, pp. 579–604.

UTNE-PALM, A.C. (2002) Visual feeding of fish in a turbid environment: Physical and behavioural aspects. *Marine Freshwater Behavioural Physiology* 35(1–2). DOI:10.1080/10236240290025644

VAN DER ELST, R. P. (1981) *A Guide to the Common Sea Fishes of Southern Africa*. Struik, Cape Town. ISBN:978-0869771471

WATSON, D., HARVEY, E.S., KENDRICK, G., NARDI, K., ANDERSON, M.J. (2007) Protection from fishing alters the species composition of fish assemblages in a temperate-tropical transition zone. *Marine Biology*. 152. DOI:10.1007/s00227-007-0767-0

WILLIS, T.J., ANDERSON, M.J. (2003) Structure of cryptic reef fish assemblages: relationships with habitat characteristics and predator density. *Marine Ecology Progress Series*. 257. DOI:10.3354/meps257209

WINKER, H., KERWATH, S.E., ATTWOOD, C.G. (2014) Proof of concept for a novel procedure to standardize multispecies catch and effort data. *Fisheries Research*. 155. DOI:10.1016/j.fishres.2014.02.016

WINKER, H., KERWATH, S., ATTWOOD, C., DA SILVA, C., MAGGS, J., PARKER, D. (2017a) Technical Report: The 2017 assessment of carpenter (*Argyrozona argyrozona*) for the South African Linefishery. Cape Town: DAFF. JABBA: Just Another Bayesian Biomass Assessment Project. DAFF/FISHERIES/LSWG/2017/05

WINKER, H., KERWATH, S., ATTWOOD, C., DA SILVA, C., MAGGS, J., PARKER, D. (2017b) Technical Report: The 2017 assessment of hottentot (*Pachymetopon blochii*) for the South African Linefishery. Cape Town: DAFF. JABBA: Just Another Bayesian Biomass Assessment Project. DAFF/FISHERIES/LSWG/2017/07

WINKER, H., KERWATH, S., ATTWOOD, C., DA SILVA, C., MAGGS, J., PARKER, D. (2017c) Technical Report: The 2017 assessment of slinger (*Chrysoblephus puniceus*) for the South African

Linefishery. Cape Town: DAFF. JABBA: Just Another Bayesian Biomass Assessment Project. DAFF/FISHERIES/LSWG/2017/01

WINKER, H., KERWATH, S., ATTWOOD, C., DA SILVA, C., MAGGS, J., PARKER, D. (2017d) Technical Report: The 2017 assessment of silver kob (*Argyrosomus inodorus*) for the South African Linefishery. Cape Town: DAFF. JABBA: Just Another Bayesian Biomass Assessment Project

WOOD, S. N. (2006) Generalized additive models: an introduction with R. Chapman & Hall/CRC Press, Boca Raton. ISBN:9781498728331

WWF-SA (2018) MPA Forum: Amathole. Accessed 04/08/2018. <http://mpaforum.org.za/portfolio/amathole/>

WWF-SASSI (2018) The SASSI list. Accessed 01/08/2018 <http://wwfsassi.co.za/sassi-list/>

ZUUR, A.F., IENO, E.N., ELPHICK, C.S. (2010) A protocol for data exploration to avoid common statistical problems. *Methods in Ecology and Evolution*. 1(1). DOI:10.1111/j.2041-210X.2009.00001.x

ZUUR, A.F., HILBE, J.M., IENO, E.N. (2013) A beginner's guide to GLM and GLMM with R. Highland Statistics Ltd., Newburgh, United Kingdom. ISBN:978-0-9571741-3-9

A APPENDIX

Table A. 1: Results of PERMDISP test for homogeneity of variance for levels of the variables Location, Substrate and Management based on modified-Gower log₁₀ resemblance matrix of MaxN data from fish assemblages in the Amathole Marine Protected Area and adjacent exploited areas. S.E. = standard error, F = Fisher's F-value, Df = degrees of freedom, P(Perm) = P-value

Variable	Levels	Size	Mean	S.E.	F	Df 1	Df 2	P (perm)
Location					0.43	2	113	0.687
	Gxulu	32	0.82	0.022				
	Gonubie	55	0.81	0.020				
	Kei	29	0.84	0.017				
Substrate					5.15	1	114	0.038
	Sand	42	0.80	0.025				
	Reef	74	0.74	0.015				
Management					2.74	1	114	0.105
	Exploited	44	0.79	0.026				
	Protected	72	0.83	0.013				

Table A. 2: Results of pairwise PERMANOVA analysis for levels of the variable management within each location based on modified-Gower log₁₀ resemblance matrix of MaxN data for fish assemblages in the Amathole Marine Protected Area and adjacent exploited areas.

Location	t	P(perm)	Unique perms
Gxulu	1.473	0.017	999
Gonubie	1.739	0.001	998
Kei	0.936	0.575	999

Table A. 3: Estimated component of variation (ECV), square root (Sq. root) of the estimate and percentage contribution (% total) of terms included in PERMANOVA analysis to overall variability in MaxN data of fish assemblages in the Amathole Marine Protected Area and adjacent exploited areas.

Source	ECV	Sq. root	% total
Residual	0.515	0.718	28.91
Substrate	0.231	0.481	19.36
Location x Management	0.047	0.216	8.69
Depth	0.037	0.192	7.72
Management	0.023	0.150	6.04
Location	0.020	0.141	5.69
Visibility	0.019	0.138	5.57
Temperature	0.017	0.130	5.22
% Obstruction	0.016	0.126	5.08
Location x Substrate	0.012	0.111	4.49
% Water Column	0.006	0.080	3.24

Table A. 4: Results of PERMDISP test for homogeneity of variance based on modified-Gower log10 resemblance matrix of MaxN data for levels of the variables substrate and zone in the Amathole Marine Protected Area and nearby exploited areas. S.E. = standard error, F = Fisher's F-value, Df = degrees of freedom, P(Perm) = P-value

Variable	Levels	Size	Mean	S.E.	F	Df 1	Df 2	P (perm)
Substrate					3.000	1	133	0.099
	<i>Sand</i>	46	0.81	0.023				
	<i>Reef</i>	89	0.77	0.014				
Zone					7.765	1	132	0.002
	<i>inshore protected</i>	72	0.83	0.013				
	<i>inshore exploited</i>	44	0.79	0.026				
	<i>offshore exploited</i>	19	0.69	0.033				

Table A. 5: Results of pairwise PERMANOVA analysis of modified-Gower log10 resemblance matrix of MaxN data for levels of the variable zone in the Amathole Marine Protected Area and nearby exploited areas.

Zone	t	P(perm)	Unique perms
<i>inshore protected, inshore exploited</i>	1.544	0.005	998
<i>inshore protected, offshore exploited</i>	2.369	0.001	998
<i>inshore exploited, offshore exploited</i>	2.501	0.001	998

Table A. 6: Estimated component of variation (ECV), square root (Sq. root) of the estimate and percentage contribution (% total) of terms included in PERMANOVA analysis to overall variability in MaxN data of fish assemblages in the Amathole Marine Protected Area and nearby exploited areas.

Source	ECV	Sq. root	% total
Residual	0.557	0.747	34.759
Substrate	0.164	0.405	18.844
Zone	0.065	0.256	11.897
Substrate x Zone	0.059	0.242	11.284
Visibility	0.030	0.173	8.032
% Obstruction	0.016	0.127	5.909
Temperature	0.015	0.122	5.682
% Water Column	0.006	0.077	3.573

Table A. 7: (Part 1) Summary of data for all species detected in the Amathole Marine Protected area and adjacent inshore and offshore exploited areas. The number of detections, average MaxN (Ave. MaxN), and the MaxN for the *inshore exploited* (IE), *inshore protected* (IP) and *offshore exploited* (OE) zones are provided, along with the IUCN conservation status (status), the size and fishery (as per Heyns-Veale et al. 2019), and superclass.

Species	Detections	Ave. MaxN	IE MaxN	IP MaxN	OE MaxN	Status	Size	Fishery	Super-class
<i>Acanthistius sebastoides</i>	9	0	1	3	0	NA	Med	3ary	Ost.
<i>Amblyrhynchotes honckenii</i>	17	0	3	2	0	LC	Med	Non	Ost.
<i>Argyrozona argyrozona</i>	25	1	6	13	10	NT	Large	1ary	Ost.
<i>Atractoscion aequidens</i>	4	0	51	1	0	NT	Large	1ary*	Ost.
<i>Boopsoidea inornata</i>	60	8	106	32	0	LC	Med	2ary	Ost.
<i>Callorhynchus capensis</i>	1	0	1	0	0	LC	Large	2ary	Chond.
<i>Carcharhinus brachyurus</i>	5	0	1	1	0	V	V.large	2ary	Chond.
<i>Carcharhinus obscurus</i>	1	0	0	1	0	E	V.large	2ary	Chond.
<i>Carcharias taurus</i>	13	0	1	1	0	V	V.large	2ary	Chond.
<i>Chaetodon marleyi</i>	2	0	1	1	0	LC	Small	Ornam.	Ost.
<i>Cheilodactylus fasciatus</i>	1	0	1	0	0	LC	Med	3ary	Ost.
<i>Cheilodactylus pixi</i>	18	0	6	3	0	NA	Small	Non	Ost.
<i>Cheimerius nufar</i>	43	1	6	6	3	DD	Large	1ary	Ost.
<i>Chelidonichthys kumu</i>	10	0	1	2	1	LC	Med	1ary	Ost.
<i>Chirodactylus brachydactylus</i>	18	0	2	2	2	NA	Med	2ary	Ost.
<i>Chirodactylus grandis</i>	2	0	1	0	1	NA	Large	2ary	Ost.
<i>Chrysoblephus cristiceps</i>	44	1	5	10	2	CE	Large	1ary	Ost.
<i>Chrysoblephus gibbiceps</i>	20	0	3	3	8	E	Large	1ary	Ost.
<i>Chrysoblephus laticeps</i>	55	1	6	8	0	NT	Med	1ary	Ost.
<i>Chrysoblephus puniceus</i>	1	0	0	1	0	LC	Med	1ary	Ost.
<i>Cymatoceps nasutus</i>	7	0	4	6	0	V	Large	1ary	Ost.
<i>Dasyatidae</i>	1	0	0	1	0	DD	Large	3ary	Chond.
<i>Dasyatis brevicaudata</i> ¹	28	0	1	2	2	LC	V.large	3ary	Chond.
<i>Dasyatis chrysonota</i>	18	0	2	3	1	NT	Large	3ary	Chond.
<i>Dasyatis thetidis</i> ¹	5	0	1	1	0	NA	V.large	3ary	Chond.
<i>Diplodus capensis</i>	14	0	8	5	0	LC	Med	1ary	Ost.
<i>Diplodus hottentotus</i>	8	0	4	2	0	LC	Med	2ary	Ost.
<i>Echeneis naucrates</i>	1	0	0	1	0	DD	Large	Non	Ost.
<i>Epinephelus andersoni</i>	1	0	0	1	0	NT	Large	1ary	Ost.
<i>Epinephelus chabaudi</i>	8	0	2	2	1	LC	Large	1ary	Ost.
<i>Epinephelus marginatus</i>	6	0	1	1	1	V	Large	1ary	Ost.
<i>Galeichthys ater</i>	26	0	4	2	0	NA	Med	3ary	Ost.
<i>Galeichthys feliceps</i>	40	1	7	17	0	NA	Med	3ary	Ost.
<i>Galeocerdo cuvier</i>	1	0	0	0	1	NT	V.large	2ary	Chond.
<i>Gobiidae</i>	1	0	0	1	0	NA	Small	Non	Ost.
<i>Gymnocrotaphus curvidens</i>	4	0	1	1	0	LC	Med	2ary	Ost.
<i>Gymnothorax undulatus</i> ²	1	0	0	0	1	LC	Large	Non	Ost.
<i>Gymnura natalensis</i>	5	0	2	1	2	LC	V.large	2ary	Chond.
<i>Halaelurus lineatus</i>	16	0	4	6	0	LC	Med	Non	Chond.
<i>Halaelurus natalensis</i>	25	0	3	5	0	V	Med	Non	Chond.
<i>Haploblepharus edwardsii</i>	2	0	1	1	0	E	Med	Non	Chond.
<i>Haploblepharus fuscus</i>	3	0	1	1	0	V	Large	Non	Chond.
<i>Lagocephalus sceleratus</i>	1	0	0	1	0	LC	Large	Non	Ost.
<i>Mustelus mustelus</i>	14	0	2	1	2	V	V.large	1ary	Chond.

*Primary fisheries species that were not included in the response group as they are schooling pelagics

¹Genus now changed to *Bathytoshia*

²Species name has been changed to *elaineheemstrae*.

Table A. 9: (Part 2) Summary of data for all species detected in the Amathole Marine Protected area and adjacent inshore and offshore exploited areas. The number of detections, average MaxN (Ave. MaxN), and the MaxN for the *inshore exploited* (IE), *inshore protected* (IP) and *offshore exploited* (OE) zones are provided, along with the IUCN conservation status (status), the size and fishery (as per Heyns-Veale et al. 2019), and superclass.

Species	Detections	Ave. MaxN	IE MaxN	IP MaxN	OE MaxN	Status	Size	Fishery	Super-class
<i>Myliobatis aquila</i>	21	0	2	1	0	DD	Large	3ary	Chond.
<i>Ophisurus serpens</i>	1	0	0	0	4	LC	V.large	Non	Ost.
<i>Oplegnathus conwayi</i>	5	0	2	1	1	NA	Large	2ary	Ost.
<i>Pachymetopon aeneum</i>	79	4	37	26	23	LC	Med	1ary	Ost.
<i>Pachymetopon grande</i>	4	0	2	1	0	NT	Large	2ary	Ost.
<i>Pagellus bellottii natalensis</i>	69	6	23	128	16	LC	Med	3ary	Ost.
<i>Parupeneus rubescens</i>	1	0	1	0	0	LC	Med	Non	Ost.
<i>Petrus rupestris</i>	16	0	1	1	13	E	V.large	1ary	Ost.
<i>Polyamblydon germanum</i>	1	0	2	0	0	LC	Med	2ary	Ost.
<i>Polyprion americanus</i>	1	0	0	0	1	DD	V.large	1ary	Ost.
<i>Polysteganus praeorbitalis</i>	6	0	0	3	0	V	Large	1ary	Ost.
<i>Polysteganus undulosus</i>	28	1	4	5	17	CE	Large	1ary	Ost.
<i>Pomadasys olivaceum</i>	35	3	78	93	0	LC	Med	2ary	Ost.
<i>Pomadasys striatus</i>	5	0	1	1	0	LC	Small	3ary	Ost.
<i>Pomatomus saltatrix</i>	10	0	32	3	0	V	Large	1ary*	Ost.
<i>Porcostoma dentata</i>	15	0	3	2	0	LC	Med	2ary	Ost.
<i>Poroderma africanum</i>	22	0	3	1	2	LC	Large	Non	Chond.
<i>Poroderma pantherinum</i>	8	0	2	1	0	LC	Large	Non	Chond.
<i>Pterogymnus laniarius</i>	56	4	12	16	37	LC	Med	1ary	Ost.
<i>Raja straeleni</i>	8	0	1	1	0	DD	Large	2ary	Chond.
<i>Rhabdosargus globiceps</i>	1	0	0	1	0	V	Med	1ary	Ost.
<i>Rhabdosargus holubi</i>	17	0	2	2	0	LC	Med	2ary	Ost.
<i>Rhabdosargus sarba</i>	1	0	0	1	0	LC	Large	2ary	Ost.
<i>Rhinobatos annulatus</i>	25	0	2	2	0	V	Large	2ary	Chond.
<i>Rostroraja alba</i>	9	0	1	1	1	E	V.large	2ary	Chond.
<i>Sarpa salpa</i>	1	0	2	0	0	LC	Med	1ary	Ost.
<i>Scomber japonicus</i>	2	0	0	12	0	LC	Large	1ary*	Ost.
<i>Serranus knysnaensis</i>	22	0	1	3	2	LC	Med	Non	Ost.
<i>Sphyræna jello</i>	1	0	1	0	0	LC	Large	2ary	Ost.
<i>Sphyrna sp.</i>	12	0	1	1	0	V	V.large	1ary	Chond.
<i>Spondyliosoma emarginatum</i>	62	3	43	23	11	LC	Med	2ary	Ost.
<i>Squalus sp.</i>	11	0	0	0	3	LC	Large	2ary	Chond.
<i>Trachurus trachurus</i>	12	4	157	68	0	V	Large	1ary*	Ost.
<i>Triakis megalopterus</i>	2	0	1	0	0	NA	V.large	2ary	Chond.
<i>Umbrina sp.</i>	3	0	1	1	0	DD	Large	2ary	Ost.

*Primary fisheries species that were not included in the response group as they are schooling pelagics.