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# First survey of fishes in the Betty's Bay Marine Protected Area along South Africa's temperate south-west coast

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This first survey of fish in the Betty's Bay Marine Protected Area (MPA), on the south coast of South Africa, was conducted using baited remote underwater video systems (BRUVs). A total of 58 deployments recorded 42 species in 20 km<sup>2</sup>, including reef, kelp and sand habitats in protected and exploited zones, at between 5 and 40 m depth. Chondrichthyans accounted for 28% of diversity. Teleost diversity was dominated by Sparidae, Cheilodactylidae, Sciaenidae and Ariidae. Diversity (*H'*) was highest in kelp and lowest over sand. Species composition differed among habitat and depths, but protection had no effect. Among four commercial species, only *Pachymetopon blochii* responded positively to protection. The apparent failure of protection may attest to poor compliance, but an investigation into fish size might show an effect. Many species were detected at the western extreme of their range. Diversity in Betty's Bay was predictably lower than in the more eastward Stilbaai MPA, but also lower than in the westward Table Mountain National Park MPA. Fish diversity did not follow a linear increase eastwards from Cape Point. Betty's Bay includes the most easterly protected kelp forests and contains seven species not recorded in the other two areas, and is therefore an important element in the MPA network.

Keywords: BRUVs, fish survey, MPA, species composition, species diversity

# Introduction

### Marine biodiversity protection in South Africa

The southern African coast can be divided into three main biogeographic zones: the cool-temperate West Coast, warm-temperate South Coast and subtropical East Coast (Turpie et al. 2000). These biogeographic zones have been divided into six ecoregions, and further separated into 22 ecozones that incorporate biogeographic and depth patterns (Sink et al. 2012). Each ecozone is considered to have a distinct species assemblage (Sink et al. 2012).

Representation of habitat types in the marine protected area (MPA) network is relatively good, but most fish species are represented in only one MPA or are not represented at all (Solano-Fernández et al. 2012). The West Coast has the lowest number of shelf-inhabiting fish species whereas the East Coast is known for its high species richness, which decreases progressively westward towards Cape Point (Solano-Fernández et al. 2012). The warm-temperate South Coast is home to a number of South African endemic species. Two fish families, namely Sparidae and Clinidae, are particularly well represented among endemics (Turpie et al. 2009). The Sparidae are heavily targeted by fisheries and many of the species are of concern to conservationists (Griffiths 2000).

In all, 21% of the coastline falls within MPAs, and 9% is fully protected from fishing activities (Sink et al. 2012). The distribution of MPAs in South Africa has been examined in relation to diversity patterns, including the distribution of fishes. Survey data of various kinds have revealed that a substantial fraction of fish diversity, some 30% depending on the depth stratum, is not represented in MPAs (Solano-Fernández et al. 2012). The representation is better inshore than offshore. One of the challenges in this type of assessment is the availability of data obtained from broad-spectrum survey techniques that have been applied equally across protected and unprotected areas.

Comprehensive analyses of the fish assemblages across the different ecozones and MPAs are needed to gain better understanding of patterns in biodiversity along the coast and the representation of fish species in the MPA network. Habitat information is an important complement to fish surveys as most fish-habitat linkages and distributional patterns of organisms are poorly understood, especially in temperate areas (Stanley and Wilson 2000; Moore et al. 2011). Numerous studies have described depth-related patterns in habitat and abundance of associated fish, but there can also be important differences in fish assemblages and behaviour between small, often-overlooked, habitat characteristics and patches (Carbines and Cole 2009; Karnauskas and Babcock 2010).

# Lack of consistency of surveys of fish in MPAs and exploited areas

Survey effort has not been consistent across marine protected areas (Attwood and Sink 2008), and fishery-dependent data, by necessity, cannot represent no-take areas. The temperate areas tend to be less-frequently surveyed than the warm, clear East Coast areas, partly because the latter are more conducive to SCUBA survey methods (Solano-Fernández et al. 2012). Capture-based survey techniques, such as angling, have been employed to survey fish assemblages, but they provide little to no information on habitat characteristics, are selective for certain species and size classes, and provide a less comprehensive sample of the fish assemblage than many visual techniques (Willis et al. 2000; Godoy et al. 2006). Furthermore, capture-based survey techniques often conflict with MPA objectives.

The baited remote underwater video system (BRUVs) has been recommended as the most suitable sampling technique for subtidal fish surveys across South Africa's MPAs, because of its ability to sample higher species richness, a wider range of families, and a higher abundance of large-bodied and target species than diver-operated methods (Bernard and Götz 2012; Bernard et al. 2014; De Vos et al. 2014). The relatively low cost and straightforward logistics of deploying and analysing BRUVs also make this technique more suitable than diver-operated surveys as a standardised method across MPAs in South Africa. Implementing a standardised BRUVs procedure for sampling abundance and diversity across different biogeographic zones will allow for comparison among ecozones and more accurate estimations of the representativeness of habitat and fish species in South Africa's MPA network.

In this study we report on the results from the first BRUVs survey, and also the first comprehensive fish survey, of the Betty's Bay MPA and surrounding coastal waters. The primary objectives of this study were: (1) to provide estimates of fish abundance and community composition for protected and exploited areas in Betty's Bay, (2) to describe habitat associations with species composition, and (3) to compare the BRUVs data from Betty's Bay with those from identical surveys in two other MPAs in the Agulhas inshore ecoregion to describe the extent of complementarity and to test for consistency in habitat-associations.

#### Methods

#### Study area

Betty's Bay lies in the Agulhas inshore ecoregion in a transition zone between the West and South-West coasts (Figure 1). This ecoregion is characterised by warm water intrusions from the Agulhas current and notably heterogeneous reef community structures (Sink et al. 2012). Betty's Bay includes reef, kelp, and sand habitats. It is not actually a



Figure 1: Location of the study area at Betty's Bay on the south-west coast of South Africa, as well as other MPAs mentioned in the text

bay, but rather an exposed stretch of coast dominated by an eroding shoreline and a complex sandstone reef structure. It has been identified as a key area to increase reef protection (Sink et al. 2012). A portion of the bay is an MPA that covers 20.1 km<sup>2</sup> and is zoned to allow recreational shore-angling. Although the MPA was designated in 1973, the reef fishes assemblage within it has never been surveyed.

#### Sample sites

Spatially referenced depth measurements from echosounder transects were interpolated in QuantumGIS<sup>™</sup> 2.0.1 (Dufour) using an inverse distance weighted (IDW) algorithm to interpolate a continuous raster surface and create a bathymetric contour map. A study area of 20 km<sup>2</sup> was selected to contain roughly equal parts protected and exploited zones (Figure 2). A list of 58 paired longitude and latitude coordinates were randomly generated within the sampling area using the 'Create Random Points' tool in QGIS. The points were constrained in the interpolated depth layer to fall between 5 and 40 m. BRUVs cannot be safely deployed in the surf zone shallower than about 5 m. The maximum depth for this study was limited to 40 m, which was considered a cautious limit for sufficient light penetration according to a previous BRUVs study along the South-West Coast (De Vos et al. 2014). The selected random points were constrained to be at least 500 m apart in order to avoid overlapping bait plumes and movement of fish between sites, thereby maintaining independent samples (Birt et al. 2012; Santana-Garcon et al. 2014).

#### **BRUVs** description

The rigs were constructed of mild-steel and consisted of a cross-shaped base with two rods extending vertically at either end. A standard definition GoPro Hero2<sup>®</sup> camera in a waterproof housing was mounted facing horizontally on one vertical arm so that the centre of the lens was 24 cm above the seafloor. A perforated PVC bait canister was attached to the other vertical arm 35 cm above the seafloor so that the camera and canister were 1 m apart. A chain



Figure 2: Betty's Bay study area, showing interpolated depth contours (20-m contour in bold) and the sample sites within and adjacent to the MPA. The study area is shallower than 40 m

secured at both vertical arms was attached to a shot line and surface buoy.

# **BRUVs** deployment

Clusters of 8–16 sites were sampled. Clusters were selected randomly for the proximity of the sample-site coordinates. Four BRUVs rigs were deployed simultaneously to increase sampling efficiency. Each deployment used 1 kg of sardine *Sardinops sagax* homogenate as bait, which has been determined to be the best option for attracting a wide range of species (Dorman et al. 2012; Hardinge et al. 2013).

Video recording began at the surface before lowering the rig to the seafloor, where it was left to record for one hour. Studies from South Africa and other temperate environments have shown that a one-hour deployment time is sufficient to record 90–95% of species (Bernard and Götz 2012). Typical deployment time was 3–5 min and the four rigs were deployed within 15 min of each other. All camera stations were completed at least 2 h after sunrise and more than 2 h before sunset to minimise the effect of time of day and to avoid the transition periods between diurnal and nocturnal fish assemblages. Depth measurements and GPS coordinates were taken at each deployment site.

### Video analysis

Video footage was analysed by one of us (LR) using Mac Media Player. Each site was classified as reef, kelp or sand

(Table 1). Samples were discarded if horizontal visibility was <1 m, estimated by means of the visibility of the bait canister, or if >50% of the camera's field of view (FOV) was obstructed.

All species in the video were noted and a MaxN value was recorded for each species at every site, where MaxN is the maximum number of individuals present in any one frame for the duration of the video (Cappo et al. 2003). The MaxN value is a conservative measure of relative abundance that avoids pseudo-replication caused by individuals that swim in and out of the FOV of the camera (Willis et al. 2000). The fish community was grouped into five feeding guilds (Table 2) to test if BRUVs efficiently detect a wide spectrum of fishes.

The relative abundance of each species was calculated as the sum of all MaxN values for that species divided by the total number of sites sampled (n = 58) (Colton and Swearer 2010). The ubiquity of each species (referred to here as the frequency of occurrence) was calculated as the number of samples in which a species was recorded, expressed as a fraction of all samples. The coefficient of variation (CV) of MaxN was calculated to evaluate the level of spatial variation, or dispersion, in abundance. The species accumulation plot was constructed in PRIMER (PRIMER-E 6; Anderson et al. 2008). This procedure randomises the order of samples across 999 permutations and calculates an average curve from these permutations. 
 Table 1: Description of habitat types determined from the field of view (FOV) approximately 4 m ahead of the camera

Habitat type	Description					
Kelp	Any kelp present rising to the surface or full extent of the camera's FOV					
Reef	>50% reef, no kelp present that rises to the full extent of the camera's FOV					
Sand	<50% reef					

 Table 2: Description of feeding guilds used to divide species according to their feeding biology (Heemstra and Heemstra 2004; Branch et al. 2010)

Feeding guild	Feeding preference
Carnivore	Vertebrates and invertebrates
Omnivore	Vertebrates, invertebrates, algae
Herbivore	Algae
Planktonic feeder	Suspended organic particles
Deposit feeder	Organic material in sediment

The plot is used to estimate the rate of recording of new species at various sample sizes.

#### Species diversity and abundance

A Shannon–Wiener diversity index (*H'*) was calculated for each sample, using MaxN as a proxy for abundance. Patterns in *H'* values across the predictor variables Depth, Habitat Type and Protection Status were explored with a generalised additive model (GAM) framework using the 'mgcv' package (Wood 2006) within the statistical platform R (R Core Team 2013). GAMs have proven useful to relate fish abundance or diversity to non-linear spatial predictor variables, such as Depth (Bigelow and Maunder 2007; Bailey et al. 2009; Winker et al. 2013). The GAMs were fitted assuming a Gaussian distribution, which was judged to be appropriate after inspection of residuals. The optimum model for the *H'* index was selected based on analyses of deviance by retaining only those predictor variables that contributed significantly (*p* < 0.05) to the deviance explained.

#### Depth, habitat and area effects on community structure

MaxN values for each species and station were rootroot transformed before computing Bray–Curtis similarities between stations in PRIMER-E (resemblance matrix). A non-metric multidimensional scaling (MDS) ordination was produced from the sample resemblance to represent visually the similarity of species composition between stations according to each factor.

A one-way non-parametric analysis of similarity (ANOSIM) was used to test the null hypothesis that there is no difference in species composition between levels of each of the following categorical factors: Depth (shallow <20 m, deep ≥20 m), Habitat (reef, kelp or sand), Protection Status (protected or exploited), FOV (low, medium or high), and Horizontal Visibility (low, medium or high). Similarity percentages (SIMPER) were calculated to examine the contribution of individual species to the similarity within each level of each significant factor and to identify species

that differentiated levels of such factors. Repeated twoway non-parametric multivariate analyses of variance (PERMANOVA) with the Bray–Curtis similarity coefficient and unrestricted permutations from the raw data tested the effects of, and the interactions between, Depth, Habitat and Protection Status.

## Abundance of four target species

MaxN count observations for four commercially targeted species of seabreams (Sparidae) were related to Habitat Type, Depth and Protection Status using GAMs. The choice of error model was either Poisson, or quasi-Poisson if over-dispersion was evident (cf. De Vos et al. 2014). *Pachymetopon blochii* and *Chrysoblephus laticeps* are highly abundant in linefish catch records; *Pterogymnus laniarius* and *Argyrozona argyrozona* appear in inshore, midwater and deep-sea trawls in addition to linefish records (DAFF 2014). Several rare species of high conservation priority were recorded on the BRUVs survey in Betty's Bay, but their frequency of occurrence was considered too low to obtain reliable abundance trends.

### Comparison with BRUVs data from two MPAs in the Agulhas inshore ecoregion

Community composition data from Betty's Bay were combined with the equivalent data from two previous BRUVs surveys conducted in 2012 in Table Mountain National Park (TMNP) and in 2011 in the Stilbaai MPA (SBMPA). Detailed descriptions of these datasets can be found in Sanguinetti (2013) and De Vos et al. (2014). Samples from TMNP were collected within four spatially separated sites, each with a protected and an exploited component, whereas the samples from SBMPA were restricted to one contiguous, fully protected zone. The study areas also varied in size: Betty's Bay 20 km<sup>2</sup>, TMNP 35 km<sup>2</sup> and SBMPA 11 km<sup>2</sup>. Whereas the Betty's Bay data covered reef, kelp and sand habitats between the 5 and 40 m isobaths, those from TMNP covered only reef and kelp habitats between the 5 and 23 m isobaths, and those from SBMPA covered reef and sand between the 5 and 40 m isobaths. Kelp is absent from SBMPA. Because of these differences, it was not possible to test for patterns in diversity or species composition against each level of each factor.

A one-way analysis of variance (ANOVA) was used to test for differences in H' values between areas (Betty's Bay, TMNP, SBMPA) for reef sites only (94 sample sites). The MaxN values for each species and sample site were rootroot transformed before Bray-Curtis similarities among sample sites were computed in PRIMER-E. Hierarchical clustering (using Bray-Curtis coefficients) and MDS were used to represent graphically the similarity of species composition among study areas. A one-way ANOSIM was used to test the null hypothesis that there is no difference in species composition between study areas for reef sites. A SIMPER calculation was used to examine the contribution of individual species to the similarity within area groups and to identify species that differentiated the area groups. A PERMANOVA of reef sites <26 m depth (69 sample sites) was used to test the effects, and interaction of, area (Betty's Bay, TMNP, SBMPA) and depth categories 'shallow' (0-15 m) and 'deep' (16-25 m). Patterns in the east-west

#### Table 3: Species recorded with BRUVs in Betty's Bay, listed by descending relative abundance

Coiontifio nome		Family	Feeding	Relative		MaxN			
	Common name		guild	abundance	Frequency	Av.	Max.	Min.	CV
Trachurus capensis	Horse mackerel	Carangidae	Planktonic feeder	35.29	34	60.21	400	1	1.62
Pterogymnus Ianiarius	Panga	Sparidae	Carnivore	5.45	43	7.35	28	1	0.85
Pachymetopon blochii	Hottentot	Sparidae	Carnivore	3.97	46	5.00	16	1	0.70
Poroderma africanum	Pyjama catshark	Scyliorhinidae	Carnivore	1.91	46	2.41	6	1	0.63
Argyrozona argyrozona	Carpenter	Sparidae	Carnivore	1.43	21	3.95	30	1	1.72
Haploblepharus edwardsii	Puffadder shyshark	Scyliorhinidae	Carnivore	1.14	42	1.57	3	1	0.49
Chrysoblephus laticeps	Roman	Sparidae	Carnivore	1.12	29	2.24	5	1	0.44
Galeichthys ater	Black seacatfish	Ariidae	Carnivore	1.05	33	1.85	5	1	0.53
Haploblepharus pictus	Dark shyshark	Scyliorhinidae	Carnivore	1.02	35	1.69	3	1	0.45
Pachymetopon aeneum	Blue hottentot	Sparidae	Carnivore	1.02	10	5.90	25	1	1.37
Poroderma pantherinum	Leopard catshark	Scyliorhinidae	Carnivore	0.91	34	1.56	5	1	0.62
Spondyliosoma emarginatum	Steenjie	Sparidae	Carnivore	0.88	18	2.83	11	1	0.98
Notorynchus cepedianus	Sevengill cowshark	Hexanchidae	Carnivore	0.76	33	1.33	2	1	0.36
Eptatretus hexatrema	Sixgill hagfish	Myxinidae	Carnivore	0.45	16	1.63	5	1	0.71
Clinus superciliosus	Super klipfish	Clinidae	Carnivore	0.43	19	1.32	4	1	0.61
Cheilodactylus fasciatus	Redfingers	Cheilodactylidae	Carnivore	0.40	19	1.21	3	1	0.44
Chirodactylus grandis	Bank steenbras	Cheilodactylidae	Carnivore	0.38	10	2.20	7	1	1.15
Boopsoidea inornata	Fransmadam	Sparidae	Carnivore	0.36	6	3.50	8	1	0.74
Chirodactylus brachydactylus	Twotone fingerfin	Cheilodactylidae	Deposit feeder	0.17	7	1.43	2	1	0.37
Chrysoblephus gibbiceps	Red stumpnose	Sparidae	Carnivore	0.14	7	1.14	2	1	0.33
Diplodus hottentotus	Zebra	Sparidae	Carnivore	0.12	5	1.40	2	1	0.39
Atractoscion aequidens	Geelbek	Sciaenidae	Carnivore	0.10	5	1.20	2	1	0.37
Diplodus capensis	Blacktail	Sparidae	Omnivore	0.10	3	2.00	4	1	0.87
Cheilodactylus pixi	Barred fingerfin	Cheilodactylidae	Carnivore	0.09	5	1.00	1	1	0.00
Galeichthys feliceps	White seacatfish	Ariidae	Carnivore	0.09	4	1.25	2	1	0.40
Rhabdosargus globiceps	White stumpnose	Sparidae	Carnivore	0.09	3	1.67	2	1	0.35
Dichistius capensis	Galjoen	Dichistiidae	Omnivore	0.09	3	1.67	3	1	0.69
Dasyatis brevicaudata	Short tailed stingray	Dasyatidae	Carnivore	0.07	4	1.00	1	1	0.00
Halaelurus natalensis	Tiger catshark	Scyliorhinidae	Carnivore	0.07	3	1.33	2	1	0.43
Chelidonichthys capensis	Cape gurnard	Triglidae	Carnivore	0.05	3	1.00	1	1	0.00
Petrus rupestris	Red steenbras	Sparidae	Carnivore	0.05	3	1.00	1	1	0.00
Gymnura natalensis	Diamond butterfly ray	Gymnuridae	Carnivore	0.03	2	1.00	1	1	0.00
Mustelus mustelus	Smoothhound shark	Triakidae	Carnivore	0.03	2	1.00	1	1	0.00
Pachymetopon grande	Bronze bream	Sparidae	Carnivore	0.03	1	2.00	2	2	-
Triakis megalopterus	Spotted gully shark	Triakidae	Carnivore	0.03	2	1.00	1	1	0.00
Argyrosomus inodorus	Silver kob	Sciaenidae	Carnivore	0.02	1	1.00	1	1	-
Caffrogobius nudiceps	Bareheaded goby	Gobiidae	Carnivore	0.02	1	1.00	1	1	-
Congiopodis torvus	Smooth horsefish	Congiopodidae	Carnivore	0.02	1	1.00	1	1	-
Raja clavata	Thornback skate	Rajidae	Carnivore	0.02	1	1.00	1	1	-
Gymnocrotaphus curvidens	Janbruin	Sparidae	Omnivore	0.02	1	1.00	1	1	-
Parascorpis typus	Jutjaw	Parascorpididae	Planktonic feeder	0.02	1	1.00	1	1	-

distribution of species were explored with an MDS ordination of the average MaxN values for each species in each study area.

#### Results

#### Number and distribution of samples in Betty's Bay

In all, 90 BRUVs stations were deployed in Betty's Bay during 12 days at sea. Of these, 58 sites were used in the analysis; the remainder were discarded due to underexposure caused by an algal bloom, interference with the rigs by fishers, inadequate FOV (<50%), inadequate horizontal visibility (<1 m), or if they fell less than 250 m from a previous site (Dorman et al. 2012). Sample-site depth ranged from 5 to 39 m, with an average depth of 21.5 m (SD 8.8). Depth was evenly sampled inside and outside the MPA. The sampling of habitat reflected the distribution in Betty's Bay and was therefore uneven across zones and depth strata. Kelp was more prevalent inside the MPA and sand was more prevalent in the adjacent areas. Kelp does not occur naturally deeper than 20 m in the Agulhas inshore ecoregion.

### Species richness and taxonomic composition

The BRUVs recorded 42 fish species in Betty's Bay (Table 3); 34 species were recorded in the MPA, across 30 samples, and 39 species were recorded on either side of the MPA, across 28 samples.

At class level, Chondrichthyes constituted 28% of the species. At family level, Sparidae (11), Scyliorhinidae (5) and Cheilodactylidae (4) were dominant. Two species were recorded from each of the families Ariidae, Sciaenidae and Triakidae. All other families present were represented by one species only. The majority (85.4%) of the observed species assemblage were carnivores. Omnivores contributed 7.3%, planktonic feeders 4.9% and deposit feeders 2.0%. No obligate herbivores were recorded.

A species accumulation curve based on 999 iterations of randomly reordered samples showed that half of the total species richness was achieved with six stations, and that the rate of new species discovery was 0.13 species (or 0.3% of the total diversity) at the 58th station. The three most-frequently recorded fish species were *P. blochii, Poroderma africanum* and *P. laniarius* (found at 46, 46 and 43 sites, respectively). Overall, *Trachurus capensis*, the pelagic shoaling horse mackerel, was by far the most abundant fish (relative abundance = 35.29). The most abundant benthic species were *P. laniarius* (relative abundance = 5.45) and *P. blochii* (relative abundance = 3.97). Only one individual was observed for each of six of the 42 species records (14%).

### **Diversity patterns**

Despite the lower overall species richness in the MPA, the average Shannon–Wiener index of diversity was greater in the MPA (1.73) than outside (1.47), but the difference was not significant (t = 1.62, p = 0.11). This comparison is partly obscured by the influence of habitat and depth, but even after the GAM accounted for these effects, protection was not a significant source of variation. Sequential *F*-tests showed that the factor Protection Status had no significant contribution to the deviance explained in *H'* values and it was consequently dropped from the model (Table 4). Predicted *H'* values show that species diversity declines in a linear fashion with depth (Figure 3). With respect to habitat, diversity in kelp was greater than on reef and considerably greater than on sand.

#### Species composition

Single-factor ANOSIMs showed that Depth and Habitat were significant factors influencing species composition (Global R = 0.22 and 0.51, respectively, p = 0.01). These results were supported by MDS analyses, which indicated separation of species assemblages between shallow and deep sites and between habitat types reef, kelp and sand (Figure 4). Protection Status, FOV and Horizontal Visibility were insignificant factors. A two-factor PERMANOVA on root-root transformed data confirmed that Habitat and Depth were significant ( $F_{(4,53)} = 4.0956$ , p < 0.001 and  $F_{(4,53)} = 2.4172$ , p < 0.0010.05, respectively), but that the interaction between Depth and Habitat was not significant ( $F_{(4,53)} = 1.0007$ , p = 0.413). Habitat and Depth contributed 23% and 7%, respectively, of the variation explained by the PERMANOVA model. SIMPER analysis indicated that P. africanum was abundant in all three habitats, H. edwardsii, P. laniarius and T. capensis were abundant on reef and sand, and P. blochii was abundant in reef and kelp. The three species contributing most to the similarity among kelp sites were Haploblepharus pictus, C. superciliosus and Notorynchus cepedianus.

Table 4: Summary of the residual deviances of the GAMs fitted to
fish diversity H' in Betty's Bay. The percentage of deviance explained
(% explained) and the significance of each factor are indicated. Total
deviance explained was calculated for the most parsimonious model
including only significant terms indicated by bold $p(\chi)^2$ values

Model	df	Residual deviance	$\stackrel{\Delta}{\text{deviance}}$	% explained	<b>ρ</b> (χ)²
NULL	57	11.50	_	-	_
+Habitat	53	8.78	2.7	23.6	<0.001
+s(Depth)	51	6.97	1.8	15.8	<0.01
+Protection Status	50	6.65	0.31	2.7	0.1232
Total deviance explained				39.4	

To test the effect of Depth and Protection Status on reef, which was equitably distributed across all levels of both factors, sand and kelp sites were removed from the dataset. A two-factor PERMANOVA detected a significant difference in the species assemblage between depth categories shallow and deep ( $F_{(2.35)} = 3.9699$ , p < 0.001), but not between protection levels ( $F_{(2.35)} = 0.8391$ , p = 0.572). The interaction between Depth and Protection was not significant ( $F_{(2.35)} = 0.3720$ , p = 0.914). Depth explained 16% of the variation of fish species composition on barren reefs. SIMPER analysis indicated that shallow sites were dominated by *P. africanum* whereas *T. capensis* was dominant in deep sites. *Pterogymnus Ianiarius* and *P. blochii* were abundant in both depth categories.

#### Abundance and distribution of four target species

Average MaxN values of P. blochii and C. laticeps were greater in protected (5.0 and 1.3, respectively) than exploited zones (2.6 and 0.9, respectively). Conversely, average MaxN values of P. laniarius and A. argyrozona were greater in exploited (6.7 and 1.6, respectively) than protected zones (4.3 and 1.1, respectively). However, sequential F-tests showed that the model most parsimonious to the abundances of C. laticeps, P. laniarius and A. argyrozona included Habitat and Depth, but Protection Status had no significant contribution to the deviance explained once Habitat and Depth were included. The best model for the abundance of P. blochii included Habitat and Depth as highly significant explanatory variables and Protection Status as a significant explanatory variable. Habitat explained the greatest percentage of the residual deviance for P. blochii, C. laticeps and P. laniarius, whereas Depth explained the greatest percentage of the residual deviance for A. argvrozona (Table 5).

Predicted MaxN values show that abundance of *P. blochii*, *C. laticeps* and *A. argyrozona* is greatest in kelp and lowest in sand, whereas abundance of *P. laniarius* is greatest in reef and sand and lowest in kelp (Figure 5). Abundance of *P. laniarius* increases in a quasi-linear fashion with depth. *Pachymetopon blochii* and *C. laticeps* share the same optimal depth range from approximately 12 to 32 m. *Argyrozona argyrozona* exhibits the narrowest optimal depth with a spike around 25 m, although the confidence intervals are large due to its infrequent presence on the BRUVs relative to the other three species (Figure 5).



Figure 3: Predicted values for Shannon–Wiener (*H*') diversity index with 95% confidence intervals, for (a) habitat, standardised to the median observed depth (20 m), and (b) depth (5–39 m), standardised to reef habitat



Figure 4: Multidimensional scaling plots showing the similarity of species composition among sites grouped by (a) depth and (b) habitat categories

**Table 5:** Summary of the residual deviances of GAMs of individual species abundance. Bold  $p(\chi)^2$  values indicate a significant proportion of the residual deviance is explained by the terms in the model. Total deviance explained was calculated for the most parsimonious model

Species	Model structure	df	Residual deviance	$\Delta$ deviance	% explained	$p(\chi)^2$
Pachymetopon blochii	NULL	57	225.5	_	-	_
	+ Habitat	55	172.3	53.2	23.6	<0.001
	+ s(Depth)	51	128.3	44.0	19.5	<0.001
	+ Protection Status	50	115.1	13.2	5.9	<0.05
	Total deviance explained				49.0	
Chrysoblephus laticeps	NULL	57	101.8	_	-	_
	+ Habitat	55	86.7	15.1	14.8	<0.001
	+ s(Depth)	51	73.1	13.6	13.3	<0.01
	+ Protection Status	50	71.3	1.9	1.8	0.175
	Total deviance explained				28.2	
Pterogymnus laniarius	NULL	57	393.8	_	_	_
	+ Habitat	55	255.9	137.9	35.0	<0.001
	+ s(Depth)	53	131.0	124.9	31.7	<0.001
	+ Protection Status	52	128.0	3.0	0.8	0.3
	Total deviance explained				66.7	
Argyrozona argyrozona	NULL	57	286.0	_		_
	+ Habitat	55	253.8	32.2	11.3	<0.05
	+ s(Depth)	52	198.5	55.3	19.3	<0.01
	+ Protection Status	51	195.8	2.7	0.9	0.418
	Total deviance explained				30.5	

# Comparison of BRUVs data from Betty's Bay, TMNP and SBMPA

The combined dataset included 143 one-hour video samples: 58 from Betty's Bay, 56 from TMNP and 29 from SBMPA. Sample depths ranged from 3 to 39 m with an average depth of 17.4 m. Samples in TMNP were limited to <23 m. In all, 95 sites (66%) were classified as reef, 37 (26%) as kelp and 11 (8%) as sand. No sites from TMNP were classified as sand and there is no kelp in the SBMPA. Betty's Bay included samples of all three habitat types.

The BRUVs recorded a total of 60 fish species in the three areas. Forty-two species from 14 families were recorded in Betty's Bay, 36 species from 18 families in TMNP and 38 species from 14 families in SBMPA. Chondrichthyans constituted 30% of the species. Dominant families were Sparidae (20). Scyliorhinidae (5) and Cheilodactylidae (4). The majority (88.3%) of species were carnivores. Omnivores contributed 5.0%, planktonic feeders 3.3% and deposit feeders and herbivores each contributed 1.6% of the observed species assemblage. Only one individual was observed for each of six of the 60 species records (10%). The most frequently encountered species were C. laticeps, P. blochii and P. africanum. These were found at 109, 94 and 94 of the sites, respectively. Excluding the shoaling pelagic species T. capensis, the three most abundant species across all habitat and depth categories in the three areas were P. blochii, Spondyliosoma emarginatum and C. laticeps. The 10 most abundant species were all members of either the Sparidae or Scyliorhinidae (catshark) families.

The species accumulation curves (not shown) showed that half of the total species richness in SBMPA and TMNP was achieved on average with 3 and 4 randomly selected stations, respectively, compared to 6 stations in Betty's Bay. Ten randomly selected stations in Betty's Bay, SBMPA and TMNP recorded 27, 31 and 26 species, respectively.

The average Shannon–Wiener diversity index for reef sites was highest in the SBMPA (H' = 1.94, CV 0.20), followed by TMNP (H' = 1.65, CV 0.30) and then Betty's Bay (H' = 1.56, CV 0.37). Reef sites <26 m followed the same pattern (H' = 1.95, 1.65 and 1.57, CV = 0.20, 0.30 and 0.38 in SBMPA, TMNP and Betty's Bay, respectively). The average H' value for kelp sites was 2.0 in Betty's Bay (CV 0.28) and 1.75 in TMNP (CV 0.26). One-way ANOVAs showed a significant difference in H' values among sites classified as reef ( $F_{(2.92)} = 4.4459$ , p < 0.05) and reef <26 m ( $F_{(2.66)} = 3.1638$ , p < 0.05). Two-tailed *t*-tests showed the differences between H' values for kelp sites in Betty's Bay and TMNP and for reef sites <26 m in Betty's Bay and TMNP were not significant (t = 1.46 and 0.53, p = 0.15 and 0.60, respectively).

An MDS plot of Bray–Curtis coefficients for species in each of the three areas showed groupings of similar species that correspond to the study area (Figure 6). The majority of species unique to one area occurred in the SBMPA (14 species). Seven unique species occurred in Betty's Bay and two species were unique to the TMNP. In all, 19 species were recorded in all three areas and 16 species were recorded in two areas. Species records occurring on sand were excluded because sampling in the TMNP targeted only reef-like habitats.



**Figure 5:** Predicted values for MaxN with 95% confidence intervals, standardised to reef habitat and the median observed depth (20 m) of (a) *Pachymetopon blochii*, (b) *Chrysoblephus laticeps*, (c) *Pterogymnus laniarius* and (d) *Argyrozona argyrozona* 

# Depth, habitat and area trends across the three study areas

The MDS plots of sample sites grouped by study area indicate strong similarities within each area, especially within the SBMPA (Figure 7). Single-factor ANOSIMs showed a significant difference in species composition among reef sites in the three areas (Global R = 0.78, p = 0.01), among reef sites <26 m in the three areas (Global R = 0.78, p = 0.01), among reef sites <26 m in the three areas (Global R = 0.71, p = 0.001), among depth categories for reef sites <26 m (Global R = 0.16, p = 0.01), among kelp sites in Betty's Bay and TMNP (Global R = 0.33, p = 0.03) and among reef sites <26 m in Betty's Bay and TMNP (Global R = 0.33, p = 0.03) and among reef sites <26 m depth confirmed that area and depth categories were significant ( $F_{(4,66)} = 18.667$ , p < 0.001 and  $F_{(4,66)} = 3.119$ , p < 0.05) and the interaction between the two factors was significant ( $F_{(4,66)} = 2.5642$ , p < 0.01).

SIMPER calculations showed that Betty's Bay was more dissimilar to SBMPA than to TMNP (85.4% and 68.0% dissimilarity, respectively). Sites in SBMPA were more



**Figure 6:** MDS plot of similarity among species with respect to abundance on reef (including kelp) in each of the three MPAs under study. The overlaid circles represent the 50% similarity clusters. Clockwise from top the circles indicate species unique to TMNP, species unique to SBMPA, species found in more than one area, and species unique to Betty's Bay. A = *Raja clavata, Congiopodus torvus*; B = *Dasyatis chrysonota, Carcharias taurus*; C = *Epinephelus marginatus, E. andersoni*; D = *Rhabdosargus holubi, Chaetodon marleyi*; E = *Petrus rupestris, Diplodus hottentotus, Galeichthys feliceps.* Full names for species occurring at Betty's Bay are given in Table 3, and those unique to TMNP or SBMPA are as follows: *Pomatomus saltatrix, Argyrosomus inodorus, Pachymetopon grande, Myliobatis aquila, Galeorhinus galeus, Oplegnathus conwayi, Sparodon durbanensis, Cymatoceps nasutus, Squalus acutipinnis, Chrysoblephus cristiceps, Carcharhinus brachyurus, Amblyrhynchotes honckenii, Mustelus mustelus, Cheimerius nufar* 

similar to TMNP than to Betty's Bay even though TMNP lies farther west (75.8% dissimilarity between SBMPA and TMNP). The dissimilarity between Betty's Bay and SBMPA was attributed primarily to the relative abundance of S. emarginatum and C. laticeps in SBMPA, the abundance of Cheimerius nufar in SBMPA and its absence in Betty's Bay, the abundance of P. laniarius, and the abundance of T. capensis and P. blochii in the bay and the absence of these two species in SBMPA. The dissimilarity between Betty's Bay and TMNP was attributed to the relative abundance of T. capensis and P. laniarius in the bay and to the relative abundance of P. blochii, S. emarginatum and C. laticeps in TMNP. Species contributing to the dissimilarities among the three areas for reef sites <26 m were almost identical. The dissimilarity between kelp sites in Betty's Bay and TMNP was attributed primarily to the relative abundance of N. cepedianus, B. inornata and P. africanum in the bay and of P. blochii, H. edwardsii and C. laticeps in TMNP. The dissimilarities between reef sites <26 m in Betty's Bay and TMNP were attributed primarily to the relative abundance of



Figure 7: Multidimensional (MDS) plot of reef (including kelp) sample sites grouped by study area

*T. capensis* and *P. laniarius* in Betty's Bay and of *S. emarginatum, C. laticeps* and *P. blochii* in TMNP.

#### Suitability of BRUVs to monitor reef fish in Betty's Bay

Betty's Bay has been described as harbouring high biodiversity (Tunley 2009) but that assessment was based on very little empirical evidence of fish distribution. Most information on the diversity and abundance of nearshore fish assemblages on the south-west Cape coast comes from catch per unit effort (CPUE) records, derived either from fishery-dependent catches or surveys (Turpie et al. 2009: Solano-Fernández et al. 2012). Betty's Bay does not have a higher diversity of fish catches than areas on either side of it (Solano-Fernández et al. 2012). A total of 33 species were recorded in the National Marine Linefish System (NMLS) database for the period 1985-2011 in the two 5'  $\times$  5' latitude and longitude grid cells encompassing Betty's Bay (Winker et al. 2013). Of these species, 17 were recorded in a survey of shore-angling and spearfishing catches from 1997 to 1999 over a 70-km stretch of coast encompassing Betty's Bay (Attwood and Farguhar 1999).

Of the 42 fish species recorded by BRUVs in Betty's Bay, 24 did not appear in the catch records. Most of these species are from the family Scyliorhinidae or are small reefor kelp-dwelling species not targeted by any fishing sectors, such as Clinus superciliosus and Cheilodactylus fasciatus. Of these, 15 species in the catch records did not appear in the BRUVs survey. Most of the species absent from the BRUVs are migratory pelagic species such as Scomber japonicus, Seriola lalandi and Thyrsites atun, or demersal species such as Merluccius capensis. The BRUVs recorded greater species diversity in a much smaller area over a shorter period of time, indicating that BRUVs data are more appropriate than CPUE-derived data for sampling reef-fish assemblages. Most studies show that BRUVs recorded higher species diversity than CPUE-based techniques such as controlled angling surveys (CAS) or baited traps (Willis et al. 2000; Langlois et al. 2010; Harvey et al. 2012), although Unsworth et al. (2014) found that beach seines recorded more species than BRUVs in a seagrass habitat.

Horizontal visibility ranged from 1 to 7 m and the FOV was often partially obscured by kelp or rocks. However, multivariate analyses of the MaxN values determined that the factors FOV and Horizontal Visibility did not account for variance between sample sites, indicating that the BRUVs data were robust across a range of environmental conditions. Following previous tests we used one hour as the time for deployment, but a recent study by Unsworth et al. (2014) found that two-hour deployments were needed in the poor visibility (<2 m) of north Atlantic kelp beds and seagrass meadows. Additional tests might be needed in South African kelp forests, particularly if the method is to be used on the cold-temperate West Coast.

The application of BRUVs in kelp forests is relatively novel. Surveys of fish in kelp habitats have historically employed underwater visual census (UVC) methods (Ebeling and Bray 1976; Bodkin 1986). A survey of reef and kelp habitats in the TMNP used stationary counts and active searches to observe 28 species during 13 dives over 13 months (Lechanteur and Griffiths 2002). As a boat trip can typically accomplish either two dives or 12 BRUVs deployments in a day, it is clear that BRUVs is the more cost effective of the two methods in kelp forests in terms of boat time.

The single-camera BRUVs rig performed adequately, but required heavier weights to remain upright in dense forests of Ecklonia maxima, the dominant large kelp on the south-west coast of Africa. The BRUVs rigs were not more likely to foul in kelp than on high-profile reef. Harvey et al. (2007) successfully used baited and unbaited cameras in beds of the small kelps Ecklonia radiata, Sargassum spp. and Cystophora spp. Some researchers have experienced difficulties using BRUVs in kelp: Bassett and Montgomery (2011) tethered the system to the vessel to prevent fouling. and Unsworth et al. (2014) recommended changing the design of stereo BRUVs to obtain better length measures in forests of Laminaria spp. The boat we used had difficulty in accessing the middle of dense kelp forests in Betty's Bay. Despite these challenges, however, BRUVs is probably more effective than any other technique in kelp habitats, given the survey biases and high risk of gear entanglement for SCUBA and CAS in kelp forests (Mallet and Pelletier 2014; Unsworth et al. 2014).

#### Habitat representativeness in Betty's Bay

Sink et al. (2012) described 136 habitat types nested in 22 ecozones in South Africa's EEZ. Betty's Bay is located at the western edge of the Agulhas inshore and inner-shelf ecozones in the Agulhas ecoregion. The Betty's Bay MPA is relatively small but encompasses a variety of habitats characteristic of the region, including sand and sediment, low- and high-profile reef, and dense kelp forests. A definitive characteristic of Agulhas inshore reef is its heterogeneity in structure (Sink et al. 2012). The prevalence of dense kelp beds, however, sets Betty's Bay apart from the bulk of the Agulhas ecoregion. The composition of the kelp communities themselves is different to those typical of the cool-temperate West Coast (Field et al. 1980), which suggests that this is a transitional area.

#### Effect of protection status in Betty's Bay

Species richness was greater in the combined exploited areas on either side of the MPA than in the MPA itself, by a slight margin. This result was contrary to the finding of Halpern and Warner (2002), who showed that, in most cases, MPAs were higher in species richness than adjacent zones. Harmelin-Vivien et al. (2008) found that species richness did respond positively to protection, but that overall the gradient was slight (1.1). Claudet et al (2006) found a positive effect of protection on species richness and diversity in the third of three surveys in the Mediterranean, but no effect in the other two. The finding at Betty's Bay may be due in part to the exploited areas being split and therefore covering a more heterogeneous environment than the central MPA. This explanation is supported by the average species diversity per site. Whereas there was no significant difference in H' across the MPA boundary, this measure was higher on average in the MPA than outside it.

Species composition was unaffected by protection in Betty's Bay, even after accounting for habitat effects. This result is at odds with findings on MPA effects in South Africa (Götz et al. 2009) and elsewhere (Micheli et al. 2005; Watson et al. 2005; Barrett et al. 2007). An effect is presumed to be caused by the absence of the reduction of large targeted fishes that is typical of exploited areas (Micheli et al. 2005). Abundance trends were tested for four commercially important species for which sufficient numbers were recorded. *Pachymetopon blochii* showed a significant increase in the MPA relative to outside it, whereas *C. laticeps*, *P. laniarus* and *A. argyrozona* showed no effect. Again, the trend elsewhere is for greater abundance of targeted fishes inside MPAs.

Betty's Bay has been heavily affected by poaching, mostly centred on the lucrative abalone *Haliotis midae* and rock lobster *Jasus Ialandii* resources (Sink et al. 2012), but linefishers have frequently transgressed the regulations as well (Tunley 2009), bringing the efficacy of the area into question. High rates of non-compliance by boat- and shorebased anglers were reported by both the management agency and by local fishers in Betty's Bay (Tunley 2009).

The lack of a protection effect could also reflect an MPA design that is inappropriate for the conservation objectives. One possibility is that the MPA is too small to protect a sufficient area of appropriate habitat for resident reef species, although Halpern and Warner's (2002) meta-analysis showed only a weak effect of MPA size on a number of measures of protection. The shape and size of the MPA, upon proclamation, were not based on assessments of the distribution of key habitats or range sizes of threatened species (Tunley 2009), but the boundaries fortuitously encompass most of the kelp forests found within the survey area and also a substantial amount of reef. The total reef area in the MPA is approximately 12 km<sup>2</sup>, an order of magnitude greater than the home-range sizes of the targeted fish species (Attwood and Bennett 1995; Griffiths and Wilke 2002; Kerwath et al. 2007). It should follow that there would be a significant effect of protection status because the MPA is large enough to encompass the home ranges of these target species. However, an insignificant effect of protection on the abundance of targeted fish species has been found in some MPAs that are zoned for partial protection from fishing (Denny and Babcock 2004; Lester and Halpern 2008). The lack of an effect of protection status is therefore more likely to be a consequence of the legal status offering only partial protection, as shore-angling is permitted inside the MPA boundaries.

The test of protection effects was based on species diversity and abundance. It is conceivable that the inability of the BRUVs to detect differences in fish size masks a benefit provided by the MPA. For example, McLean et al. (2011) found no effect of an MPA in terms of numbers of coral rock trout *Plectropomus leopardus*, but a positive effect in terms of fish length, suggesting that the mean size of fish should be investigated when evaluating protection effects. Fish length data can be obtained from stereo BRUVs, but these instruments are considerably more expensive, require a larger vessel and have a more onerous analysis requirement (Langlois et al. 2010). Single camera BRUVs are feasible as a cost-effective monitoring strategy for South African MPAs. However, the consequence of a lack of size data will need to be considered before this method is advocated as a national standard.

## Characteristics of the observed species assemblage

Fish from a variety of feeding guilds were recorded by the BRUVs in Betty's Bay. There was no clear link between feeding guild and behaviour towards the bait. Individuals of certain carnivorous species, such as *Petrus rupestris*, appeared to disregard the bait entirely. On the other hand, the predominantly herbivorous *P. blochii* approached the bait canister consistently. Although no obligate herbivores were recorded, deposit and planktonic feeders were observed approaching the bait canister. These observations support assertions from prior studies that BRUVs effectively attract a wide range of species, consistently providing high measures of species diversity (Colton and Swearer 2010; Dorman et al. 2012; De Vos et al. 2014).

In general, the array of species recorded by the BRUVs in Betty's Bay was consistent with previous descriptions of this region of the coast (Turpie et al. 2009). Our study was focused on inshore benthic and reef assemblages and, with the exception of the single thresher shark Alopias vulpinus, no large pelagic species were recorded. The only small pelagic species recorded was horse mackerel T. capensis. Pelagic species were recorded in the commercial catch records from the area (Attwood and Farguhar 1999), but these predictably escaped detection by the BRUVs. Some unexpected patterns did emerge in the abundance of the recorded species. The shoaling species A. argyrozona was the fifth-most abundant species. It is typically associated with reef but generally swims high in the water column above rugose reef structures in deep (>40 m) areas (Brouwer and Griffiths 2005). Given these traits and its absence in the BRUVs survey from SBMPA, this species was not expected to be abundant in the Betty's Bay survey. Galeichthys ater was another surprisingly abundant species, appearing at 33 of 58 sites. The congeneric Galeichthys feliceps was recorded in Betty's Bay, TMNP and the SBMPA, but G. ater was observed only in Betty's Bay. The important linefishery target C. laticeps was much less ubiquitous in Betty's Bay than in the SBMPA and TMNP. It was the 11th-most frequently encountered fish in Betty's Bay, the 2nd-most in TMNP and the most frequently encountered species in the SBMPA.

Several important predatory reef fish species reported in historical linefish and shore angling records in Betty's Bay (Attwood and Farquhar 1999) were not observed on the BRUVs. Polysteganus undulosus was landed at Betty's Bay in the past, but the massive decline in this species was associated with a range contraction that left the historical western part of the range unpopulated (Attwood and Farquhar 1999). Despite the implementation of a catch moratorium on the species 20 years ago, which is still in force, there is no sign of a recolonisation of the area. Lithognathus lithognathus, Sparodon durbanensis and Umbrina canariensis are also overexploited species (Buxton and Clarke 1991; Bennett 1993; Hutchings and Griffiths 2010) but are still detected in catch records (Solano-Fernández et al. 2012). The absence of these species from BRUVs data is probably a consequence of the bias against surf-zone species. The BRUVs did record six seabream species that are listed either in one of the 'threatened' categories or as Near Threatened in the IUCN Red List (Mann et al. 2009a, 2009b, 2009c, 2009d, 2009e, 2009f).

Surprisingly, there was no record of the nationally abundant *Sarpa salpa*. This herbivore was one of the three most abundant species recorded in the surveys of TMNP and SBMPA. However, *S. sarpa* is not a target of any fishery sector in the Western Cape and is listed as Least Concern by the IUCN. It is possible that there are inconsistencies in its distribution that have gone unnoticed, and that some habitat requirement is absent from Betty's Bay.

### Longitudinal patterns in species diversity

All three MPAs under discussion are listed in the Agulhas inshore and inner-shelf ecozone within the Agulhas ecoregion, although TMNP is also listed under two ecozones in the Southern Benguela ecoregion: South-Western Cape inshore and inner-shelf and Southern Benguela outershelf (Sink et al. 2012). Patterns in community composition along the South-West Coast are more complex than a simple east-west gradient in species diversity. As expected, the average H' value in Betty's Bay was lower than that in SBMPA, which lies roughly 300 km to the east, despite the survey area being roughly twice as large in Betty's Bay. Surprisingly, the average diversity index for reef-like habitats in Betty's Bay was lower than that in TMNP, which lies roughly 50 km to the west. The coefficient of variation (CV) of the H' values of Betty's Bay was higher for all samples and for only reef habitats, indicating the high spatial variation in species diversity in the survey area.

The lower *H'* values in Betty's Bay than TMNP for reef sites and reef sites <26 m might result from a combination of survey-area size and shape, which are important factors in the recorded species diversity. A larger area is more likely to include a greater variety of habitats and therefore a greater number of species. Although our study in Betty's Bay and that in TMNP had roughly the same number of samples (58 and 56, respectively), the area covered in TMNP was almost twice as large (35 km<sup>2</sup> vs 20 km<sup>2</sup>). Furthermore, the TMNP survey area was long and narrow, stretching along approximately 25 km of coastline and extending from the shore to approximately the 25-m depth contour. Our study included only 11 km of coastline but incorporated depths to 40 m.

Habitat explained a significant portion of the difference in species composition among sites in Betty's Bay, and depth was significant for reef sites. Among the three areas, depth was a significant factor for reef sites <26 m. All of the models showed that area had the strongest effect on species composition among inshore fish assemblages along this stretch of the South-West Coast. The overwhelming effect of area indicates that species assemblages in this region are extremely heterogeneous and do not conform to a simple east–west continuum, either in diversity or composition.

Cluster analysis of reef-like sample sites showed a distinct group of species unique to Betty's Bay and another group unique to SBMPA. The middle group consisted of species common to more than one area. Dissimilarity between Betty's Bay and SBMPA can be attributed to the abundance in Betty's Bay of the typically West Coast species *P. blochii* and two species characteristic of deep, and therefore cooler, waters of the Agulhas Bank, namely *P. laniarius* and *A. argyrozona. Spondyliosoma emarginatum* 

and *C. nufar* were more common in SBMPA. Dissimilarity between Betty's Bay and TMNP can be attributed to the abundance of the shoaling pelagic species *T. capensis* and the cooler water species *P. laniarius* in Betty's Bay and of *S. emarginatum* in TMNP. At higher taxonomic levels, the families Sparidae and Scyliorhinidae dominated the species assemblages in all three areas but the class Chondrichthyes constituted a greater percentage of the species assemblage in SBMPA.

The results of this study show that the transition from the West Coast to the Agulhas inshore ecoregion is not as abrupt as it is often described to be and that False Bay is an anomaly in the longitudinal continuum. The TMNP area is warmer than Betty's Bay, which is an exposed stretch of coast and not a true bay. The colder temperature and upwelling events in Betty's Bay probably explain its more cool-temperate species composition. Four of the six (66%) species records for which only one individual was observed occurred in Betty's Bay, suggesting that this area harbours a relatively large number of species that are either rare or at the edge of their known distributions.

#### Conclusion

The Betty's Bay MPA does not stand out among South African MPAs in terms of its size, but the patterns of species diversity and composition found in the MPA attest to its importance in representing species and habitats at the western extreme of the Agulhas inshore ecoregion. A wide diversity of habitats is represented within the relatively small area of MPA, including a unique assemblage associated with kelp. The species assemblage is a mix of Atlantic and Indian Ocean species, and includes several species at the edge of their known geographical ranges and several species with lower-than-expected abundances for an area in their known distributions. Several species found in Betty's Bay were absent from MPAs on either side. 'Area' was the only significant factor in explaining differences in species diversity and composition across the three study areas, indicating the heterogeneity of the South-West Coast and the strong complementarity of existing reserves in representing reef-fish species. To date, no survey of the De Hoop MPA – situated between Betty's Bay and SBMPA - is available, but its position in the species continuum will render survey data an important addition to the information about the Agulhas ecoregion accumulated so far.

The lack of an identifiable effect of protection status appears to confirm reports that the level of protection of the Betty's Bay MPA is inadequate for the objective of protecting biodiversity and increasing fishery resources. Although not currently available, fish length data from inside and outside the MPA might confirm a possible effect of the current level of protection in the Betty's Bay MPA. However, the habitats and species assemblages encompassed in the MPA are of high conservation value in the context of the regional network of MPAs in South Africa. Five species recorded by the BRUVs are listed in one of the 'threatened' categories and seven are listed as Near Threatened on the IUCN Red List, in addition to two species that have been independently assessed as overexploited (Griffiths 2000). Therefore, the poor performance of the protection status in Betty's Bay does not signify a lack of value of the MPA but rather the potential for improvement if the level of protection is increased.

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