Distribution and community structure of Chaetodontidae (Perciformes) in iSimangaliso Wetland Park with the view to applying the Butterflyfish Indicator Hypothesis in this region of South Africa

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SeaKeys
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Photo: *Chaetodon auriga* (Threadfin) observed in iSimangaliso Wetland Park (Photo credit: Dr. Kerry Sink)

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ABSTRACT

Coral reefs are globally in a vulnerable state, because of both human impacts and environmental alterations. An understanding of coral reef ecosystems and the ability to detect changes in the reef environment early on are necessary to apply effective conservation. The co-evolution of coral and coral feeding fishes means that some species may exhibit interactions useful for indicating reef health, acting as an early warning system. Chaetodontidae (Perciformes) are one such family, containing coral dependent (obligate corallivore) species. This concept is known as the Butterflyfish Indicator Hypothesis (BIH). Through the collection of baseline data for butterflyfish abundance, diversity and species composition, the possible applicability of the BIH was investigated within Marine Protected Areas (MPA's) of iSimangaliso Wetland Park, on the north-eastern coast of South Africa. Other factors possibly impacting butterflyfish distribution were also investigated in this region. These factors were level of MPA protection (sanctuary or partially protected), reef rugosity and site effects. 78 transects across 13 dive sites were swum using Underwater Video Census (UVC) for data capture. Reef rugosity displayed no impact on any of the sampled factors, whilst site and protection level did. Protection was the factor with the greatest influence on butterflyfish species richness (df = 77, t = 2.85, $p < 0.005$), evenness of spread (df = 77, t = 1.79, $p < 0.05$) and total abundance, as revealed by the General Linear Model (GLM) with the lowest Aikake's Information Criterion (AIC) ($y = \beta_o + \beta_1\ (protection)$). None of the factors altered *Chaetodon meyeri* distribution significantly, the only observed obligate corallivore, for which low abundances were observed. Differences in total butterflyfish abundance and species diversity appear to be particularly useful in revealing human impacts on coral health. The lack of *C. meyeri*, likely accounted to low abundances of its preferred coral *Acropora* (Scleractinia: Acroporidae), suggest that the BIH is not useful in this region.

INTRODUCTION

Coral reef ecosystems are in a vulnerable state world-wide. Currently, 30% of the world's reefs are severely damaged and it is predicted that 60% will be lost in the next 15 years (Hughes et al. 2003; 2013). Serious degradation is attributed to coastal development, disease (Harvell et al. 2002) and pollution (Williams et al. 2002; McCulloch et al. 2003). In particular, fishing and diving are two human impacts that have increased in intensity over the last 30 years (Hawkins & Roberts 1993; 2004).

Fishing is the most widespread human impact on the marine environment (Shears & Babcock 2003). Increased fishing pressure can induce trophic cascades through the loss of large predatory fishes (Götz et al. 2009; Currie et al. 2012), while destructive fishing methods can physically damage coral organisms and reef structure (Russ & Alcala 1989; Jackson et al. 2001; Pandolfi et al. 2003).

Scuba diving has grown as a nature based form of tourism, resulting from the rising interest in marine conservation (Harriot et al. 1997; Lucrezi et al. 2013). It is therefore able to contribute to the conservation of reef ecosystems through the involvement of citizen scientists, the growth of local economies and the development of new marine stewards and environmental representatives (Biggs et al. 2012a; 2012b; Teleki 2012). Contrasting these positive developments is the negative environmental impact of increased diving pressure on coral reefs. Divers damage coral and reef structure through kicking, bumping, holding, standing and kneeling, which impacts the reef fish community dependent upon it (Rouphael & Inglis 1997).

Compounding these direct human impacts is the global threat of ocean acidification (Anthony et al. 2011) and steadily increasing ocean temperatures (Hughes et al. 2003; Munday et al. 2012; Green et al. 2014). The ability of coral reefs to absorb these disturbances decreases as the intensity and frequency of such impacts increase (Bellwood et al. 2004). In order to rapidly respond to and effectively manage these human impacts, the coral reef ecosystem dynamics and interactions need to be well understood (Bellwood et al. 2004). The co-evolution of corals and coral-feeding fishes means that these species exhibit interactions that may be useful indicators of reef health (Reese 1977, 1981). A charismatic family of reef fishes that contain coral dependent species is Chaetodontidae (Perciformes), the butterflyfish. As such, they may be suitable in monitoring reef health.

Butterflyfishes (Osteichthyes: Chaetodontidae) are colourful, diurnal, tropical marine fishes that inhabit the shallower waters of coral reefs all around the world (Findley & Findley 2001). The 114 species within the genus *Chaetodon* decrease in species richness from the Indonesia to the Caribbean (Motta 1987; Crosby 1996; Kulbicki et al. 2005; Findley & Findley 2014). Butterflyfishes can range from extremely generalist to highly specialised in their feeding preferences (Crosby 1996). Generalist species are facultative corallivores (partially feeding on coral) and non-coral eating butterflyfish which utilise a large range of resources for food (Crosby 1996; Lawton et al. 2012; Pratchett et al. 2013; Berumen & Pratchett 2007). These include an array of crustaceans, worms, zooplankton, sponges and algae (King 1996), making them less vulnerable to changes in coral cover than the more specialised feeders - the obligate corallivores.

Obligate corallivores are dependent upon the live tissue of coral for food (Crosby and Reese 1996). The intimate relationship between the energetic demands of the fishes and the condition of the coral substrate is thought to make these species good indicators of coral health change on reefs (Crosby 1996) - if the coral is in poor health it will be able to support fewer obligate corallivores. It can thus be inferred that a deterioration in the health of the coral will result in a reallocation of obligate coral feeders to reefs with healthier, more robust corals (Crosby 1996; Ohman et al. 1998). The idea that the relationship between coral feeding butterflyfish and live coral could be used as an early warning system for coral health is a theory established by Hourigan *et al*. (1988). According to Crosby and Reese (1996) this means that "Coral-feeding butterflyfishes respond to declines in coral quality or abundance by behavioural and spatial adjustments that can be easily and rapidly observed." This is known as the Butterflyfish Indicator Hypothesis (BIH).

In order to determine whether the distribution of butterflyfishes is changing, baseline data for the species distribution and community structure is needed. However, the collection of such data requires resources and time that are often not available (Pattengill-Semmens & Semmens 1990). The utilisation of recreational divers to collect and share such data through photography and public online biodiversity databases (for example iSpot (iSpot.org.za)) is known as citizen science. This can be an effective solution to limited funding and manpower (Pattengill-Semmens and Semmes 1990; Goffredo et al. 2010; Teleki 2012), and one of the many reasons why the BIH is appealing - it lends itself easily to the involvement of citizen scientists. Butterflyfish have striking colour patterns and can be easily identified from a distance (Crosby 1996), demanding little skill of the diver. As such, the BIH serves a dual conservation purpose, both by acting as a possible early warning system for coral degradation and by promoting marine ownership and stewardship (Pattengill-Semmens and Semmes 1990; Crosby 1996; Goffredo et al. 2010; Teleki 2012). Butterflyfish are also strongly site attached and long lived (10-12 years) providing the opportunity to observe ecosystem impacts on the same individuals over longer time scales (Crosby & Reese 2005).

The association of butterflyfish to reef habitat has been illustrated globally, in Sri Lanka (Ohman et al. 1998), Hawaii (Cox and Vivien 1994; Crosby and Reese 2005), Japan (Cadoret et al. 1999), the Red Sea (Roberts and Ormond 1987) and the Great Barrier Reef (Fowler 2006). There have however been conflicting reports regarding the correlations found between the corallivore and coral abundances. While there have been strong positive relationships between coral cover and butterflyfish (Bell and Galzin 1984; Bouchon-Navaro et al. 1985; Bouchon-Navaro and Bouchon 1989), relationships have also been found to be weak or absent (Bell et al. 1985; Findley and Findley 1985; Roberts and Ormond 1987; Roberts et al. 1988; Fowler 1990). This has made some experts apprehensive as the global applicability of the BIH (Ohman et al. 1998; Khalaf & Crosby 2005).

Ohman *et al*. (1998) suggested that variability in butterflyfish distribution found amongst studies might stem from variations in the level and type of disturbance that the reef is exposed to. Furthermore, differences in the habitat heterogeneity, complexity and reef rugosities of the study regions may also be responsible for some of the dissimilarities that were found (Bell & Galzin 1984; Findley & Findley 1985; Roberts et al. 1992; Cadoret et al. 1999; Hughes et al. 2003). Lastly, a lack of globally accepted parameters for quantifying behavioural changes, abundances and the extent of habitat degradation is suggested to compound these discrepancies (Ohman et al. 1998). There is, therefore, a need to understand how these variables affect butterflyfish communities within a region before the BIH can be applied.

The iSimangaliso Wetland Park (iSWP) on the north eastern coast of South Africa offers a good study location for testing some of the factors controlling butterflyfish distribution. As one of the world's top dive sites, this region hosts some of the most pristine coral reefs (iSimangaliso Wetland Park 2014), approximately 20 butterflyfish species (King 1996), and around 50 000 dives a year (J Olbourn pers. comm.; Jordan and Samways 2001; Walters and Samways 2001). The iSWP is also home to the largest collection of Marine Protected Areas (MPA's) in the country. These fall within the marine reserves of St. Lucia and Maputaland (Sink et al. 2011), established in 1979 & 1986 respectively (Floros et al. 2013). The reserve stretches along 145 km of coastline and extends 5.6 km seaward (Riegl and Riegl 1996; Schleyer et al. 2008; Currie et al. 2012). Within these reserves, two kinds of MPA's exist; no-take zones (sanctuary sites) and restricted zones (partially protected sites). Sanctuaries prohibit all forms of fishing and diving (with the exception of occasional management) (Lombard et al. 2004; Sink et al. 2011; Floros et al. 2013). Partially protected sites allow varying levels of regulated subsistence and recreational beach angling, boat based game-fishing and spearfishing (Lombard et al. 2004; Sink 2011; Floros et al. 2013). The central, partially protected coastline of iSWP is bordered on the north and the south by sanctuary sites (Figure 1). This clearly defined separation of regions both exposed to and protected from human disturbance allows for the testing of its impact on butterflyfish communities. The latitudinal extent of the reserve also allows for the consideration of what impact geographical site and reef rugosity may be having on their distribution. However, minimal baseline data for butterflyfish abundance and distribution exists in this region of the south-west Indian Ocean (K Sink pers.comm. 2014)

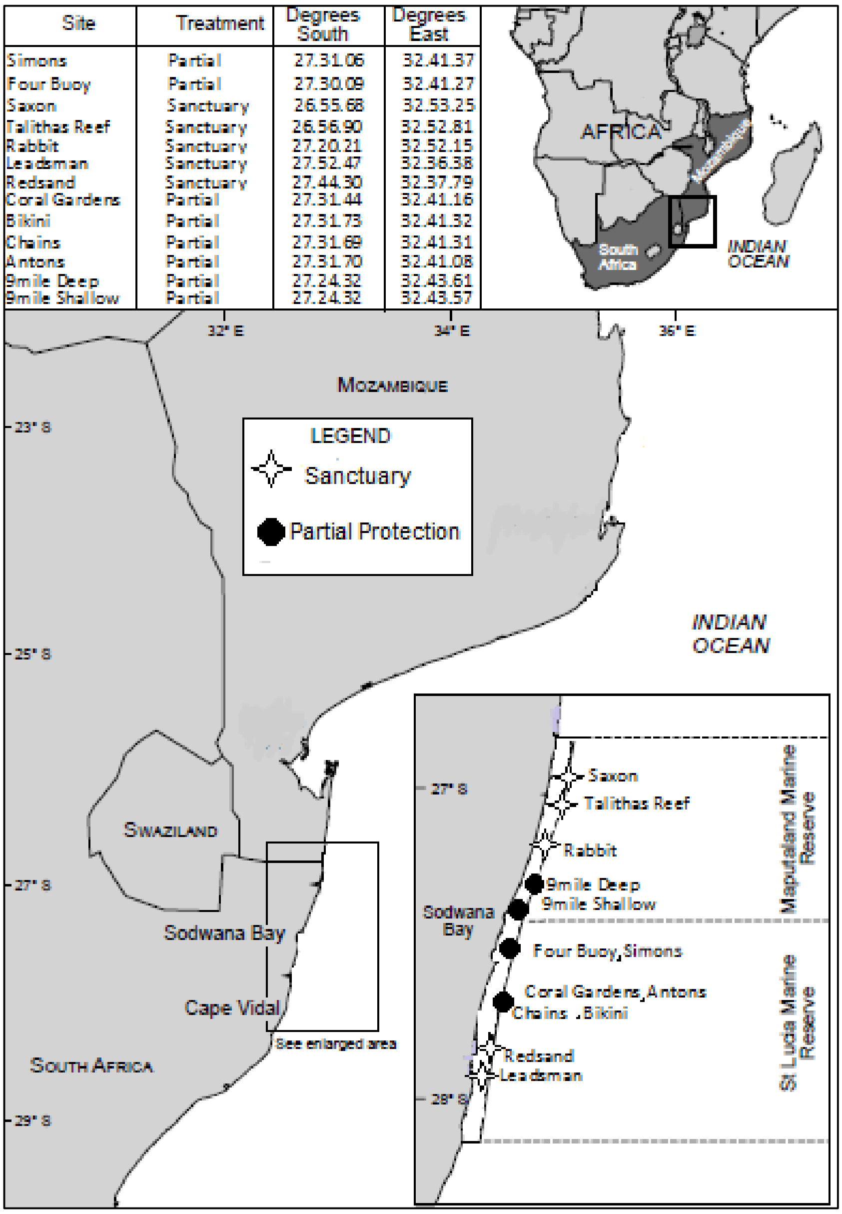
The aim of this study therefore is to (1) collect baseline data for the butterflyfish within iSWP and to (2) test the effects of protection level, reef rugosity and sites on their abundance, species richness and species composition. These first two aims will hopefully allow for investigation into (3) whether the BIH is an appropriate tool for monitoring coral health in this region of the south-west Indian Ocean.

Regarding the effects of factors, protection level and reef rugosity are both hypothesised to alter butterflyfish community structure, diversity and abundance. It is predicted that sanctuary sites will reveal greater diversity and abundance than partially protected sites and that reefs of greater rugosities will also host a greater diversity and abundance of butterflyfish. Site is not predicted to impact diversity, abundance or species composition, due to the short geographic range of the sample region.

MATERIALS AND METHODS

Study Sites

This study was undertaken in May 2014 on reefs along the coastline of the iSimangaliso Wetland Park (iSWP), between 26.5° S and 27.5° S (Fig 1). Sampling bridged five sanctuary sites and eight partially protected sites. All samples fell within the same biogeographic region of the Subtropical East Coast Province and occurred north of the proposed biogeographic break of Cape Vidal (Turpie et al. 2000; Lombard et al. 2004; Sink et al. 2005; Currie et al. 2012). To standardise comparisons, surveys were limited to reefs that were between 8 and 17 m deep, of comparable size (within the order of 100s of metres across), and were at least 200 m from shore (Currie et al. 2012).



Site	Treatment	Degrees South	Degrees East
Simons	Partial	27.31.06	32.41.37
Four Buoy	Partial	27.30.09	32.41.27
Saxon	Sanctuary	26.55.68	32.53.25
Talithas Reef	Sanctuary	26.56.90	32.52.81
Rabbit	Sanctuary	27.20.21	32.52.15
Leadsman	Sanctuary	27.52.47	32.36.38
Redsand	Sanctuary	27.44.30	32.37.79
Coral Gardens	Partial	27.31.44	32.41.16
Bikini	Partial	27.31.73	32.41.32
Chains	Partial	27.31.69	32.41.31
Antons	Partial	27.31.70	32.41.08
9mile Deep	Partial	27.24.32	32.43.61
9mile Shallow	Partial	27.24.32	32.43.57

Figure 1: Map adapted from Currie et al. (2012), illustrating the sites (partially protected and sanctuary) surveyed within the Maputaland Marine Reserve and St. Lucia Marine Reserve of iSimangaliso Wetland Park, South Africa.

Survey method

Underwater Video Census (UVC) (Brock 1954) was used to (1) estimate butterflyfish diversity, abundance and species composition, (2) reveal differences in butterflyfish species richness and diversity between partially protected and sanctuary sites and (3) understand the effects of reef heterogeneity and geographic variability on butterflyfish assemblages.

UVC was the preferred sampling method, due to its superiority over point counts regarding efficiency, variability and bias (Bennett et al. 2009). UVC is non-destructive and able to provide both qualitative and quantitative data on density, population dynamics, community structure and benthic environment of the sampled area (Bennett et al. 2009).

At each site, three sets of two parallel, 50 m strip transects were traversed. This is the most commonly used transect length (Bennett et al. 2009). Diver 1 would descend on SCUBA and lay a weighted 100 m line across an appropriate length of the reef. Divers 2 and 3 would then descend and wait five minutes at a distance of five metres away from the start of the transect line before beginning the video. This time and distance acted as a buffer to minimise the impacts of diver presence on fish behaviour (Bennett et al. 2009). Divers 2 and 3 each held a 60 cm wooden rig with a mounted GoPro Hero 2 in the centre. At the start of each transect the cameras were synchronised and started simultaneously for subsequent ease of analysis. From this point, divers 2 and 3 swam in a straight line, five metres from each side of the transect line and about one metre above the reef. A swimming speed of approximately 10 m per min recorded all fish and benthos 3-5 m on either side of the diver. Three replicates were conducted on each dive to increase the area of reef censused. The second replicate occurred along the latter half of the 100 m line and a third 50 m graduated line was laid for the last replicate. Each transect took approximately five minutes.

In total, 30 transects were conducted in the sanctuary sites and 48 in the partially protected sites. All dives were undertaken by the same divers to avoid between-observer error.

Video Analysis

All videos were analysed using VLC Media Player 2.1.1 and videos were watched at the slowest possible speed with adjusted brightness and contrast to ensure optimal view. All species of butterflyfish in a video were noted and their abundance in each transect recorded. All videos were watched twice to ensure accuracy. Synchronising the starting time for both cameras at the beginning of each transect, through visual finger countdown helped avoid double counting any individuals that might have crossed from one field of view to another during filming. In cases where this occurred, the videos were watched alongside each other and the individual fish followed across both videos. The synchronising of the starting time for both cameras allowed this to occur with ease.

Factor classification

All abundance and species diversity data were compared across the following factors:

-*Protection Level*: As predetermined by experimental design, sampling occurred across two protection levels; sanctuary sites (Saxon, Talithas reef, Rabbit, Leadsman Deep and Redsands) and partially protected sites (Simons, Four Buoy, Coral Gardens, Bikini, Chains, Antons and 9mile Deep).

-*Reef Rugosity*: a ranking system from 1 - 3 was created to infer the habitat heterogeneity of each transect. Ranking 1 represented sites that had a vertical variation of less than 1 m, most of these were fairly flat, homogenous landscapes. Ranking 2 represented transects that had a vertical variation of between 1 - 2 m. Ranking 3 represented transects that had a vertical variation greater than 2 m, these heterogeneous landscapes often included caves and large outcrops.

-*Site*: within the construct of protection, sites were defined according to latitudinal position down the coast. These included the Northern Sanctuary (Saxon, Talithas Reef and Rabbit), 9mile (9mile Deep), 2mile (Simons, Four Buoy, Coral Gardens, Bikini, Chains and Antons) and Southern Sanctuary (Leadsman Deep and Redsands).

Statistical Analysis

Plymouth Routines in Multivariate Ecological Research (PRIMER-E version 6. Clarke and Gorley 2006) was used to calculate abundance and species diversity (species richness and Shannon H' Diversity Index values) for butterflyfish abundance data. The data were square root transformed to down weight abundant species and take into account less common ones. Abundance data for comparisons at the species level, for *Chaetodon meyeri* was subject to Bonferonni's correction so as to counteract the possibility of false significance from multiple comparison tests. The means of these data were compared across the previously defined factors, using the statistical computing environment R (R Development Core Team, 2011).

A one tailed Student t-test was run to compare means of abundance and species diversity across protection level. One-way Analysis of Variance (ANOVA) was run to compare the means of abundance and species diversity data across both reef rugosity and site. Tukey's Honest Significant Difference (HSD) test was applied in combination with the ANOVA's to reveal means that were significantly different from each other.

To determine which factors had the greatest impact on butterflyfish abundance, General Linear Models (GLM) were run. Abundance data were accepted as normal, as was assessed visually and confirmed by a Shapiro-Wilks test. The response variables were therefore assumed to fit a Gaussian distribution. The most suitable model was selected based the minimizations of the model deviance and Aikake's Information Criterion (AIC) using a forward stepwise selection procedure (Appendix 1). Model Validation Plots were used to confirm the normality of the final model. The final model selected is presented:

Final Model: $y = \beta_o + \beta_1 (protection)$

Bray Curtis cluster Analysis and Multidimensional Scaling (MDS) plot was used to compare similarities in species composition amongst protection, reef rugosity and site. Permutational Analysis of Variance (PERMANOVA) was used to test for significant differences in species composition across the categories of protection, reef rugosity and site; as well as the possible effect of diver bias. PERMANOVA models with different combinations and all possible interactions were constructed. These models were evaluated using the pseudo F statistic with 999 permutations of the data using the extension software PERMANOVA + in Primer E version 6 (Clarke & Gorley 2006). The species contributing to the observed patterns in similarity and dissimilarity were revealed using Similarity Percentages (SIMPER).

RESULTS

At the 13 sites that were surveyed, 1067 individual butterflyfish of 16 species were observed across 78 transects. Diver based bias was not significant (df = 1, p > 0.05). The greatest abundance of butterflyfish was found within the Southern Sanctuary with a mean of 18.42 (±3.4) observations per dive. This is in contrast with the Northern Sanctuary, which experienced a mean of only 10.08 (±2.2) individuals per dive (Fig 2). Overall the sanctuary sites displayed both greater species richness and abundances than the two central sites of 9mile and 2mile (Fig 2).

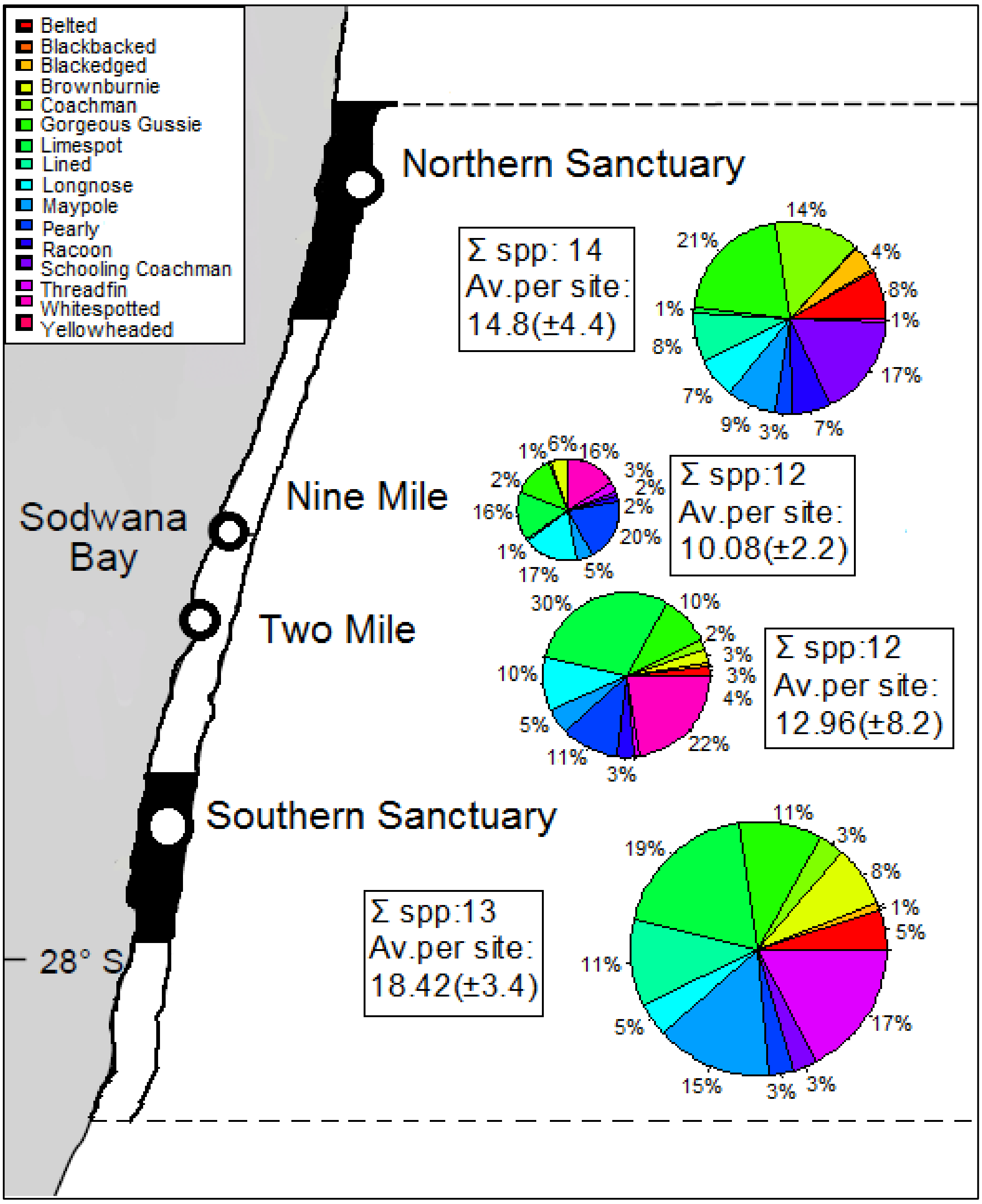


Figure 2: Species richness and mean (± standard error) butterflyfish (Chaetodontidae) count at the community level for all observed butterflyfishes at the four sampled regions (Northern Sanctuary, 9mile, 2mile and Southern Sanctuary) within the iSimangaliso Wetland Park, South Africa. Size of pie approximates total butterflyfish abundance.

Table 1: Dive sites and protection level within sampled reef complexes of the iSimangaliso Wetland Park.

Reef complex	Site	Treatment
2mile	Simons	Partial
2mile	Four Buoy	Partial
Northern	Saxon	Sanctuary
Northern	Talithas Reef	Sanctuary
Northern	Rabbit	Sanctuary
Southern	Leadsman	Sanctuary
Southern	Redsand	Sanctuary
2mile	Coral Garden	Partial
2mile	Bikini	Partial
2mile	Chains	Partial
2mile	Antons	Partial
9mile	9mile Deep	Partial
9mile	9mile Shallow	Partial

Table 2: Butterflyfish (Chaetodontidae) taxa enumerated during transect dives in iSimangaliso Wetland Park, May 2014. Feeding preference indicated as FC (Facultative Corallivore), OC (Obligate Corallivore) and NC (Non Corallivore).

Genus	Species	Common Name	Type of Feeder
Hemitaurichthys	*zoster*	Belted	FC
Chaetodon	*melannotus*	Blackbacked	FC
Chaetodon	*dolosus*	Blackedged	FC
Chaetodon	*blackburnii*	Brownburnie	FC
Heniochus	*accuminatus*	Coachman	FC
Chaetodon	*guttatissumus*	Gorgeous Gussie	FC
Chaetodon	*interruptus*	Limespot	FC
Chaetodon	*lineolatus*	Lined	FC
Forciper	*flavissimus*	Longnose	FC
Chaetodon	***meyeri***	**Maypole**	**OC**
Chaetodon	*madagaskarensis*	Pearly	FC
Chaetodon	*lunula*	Racoon	FC
Heniochus	*diphreutes*	Schooling Coachman	FC
Chaetodon	*auriga*	Threadfin	FC
Chaetodon	*kleinii*	Whitespotted	FC
Chaetodon	*xanthocephallus*	Yellowheaded	NC

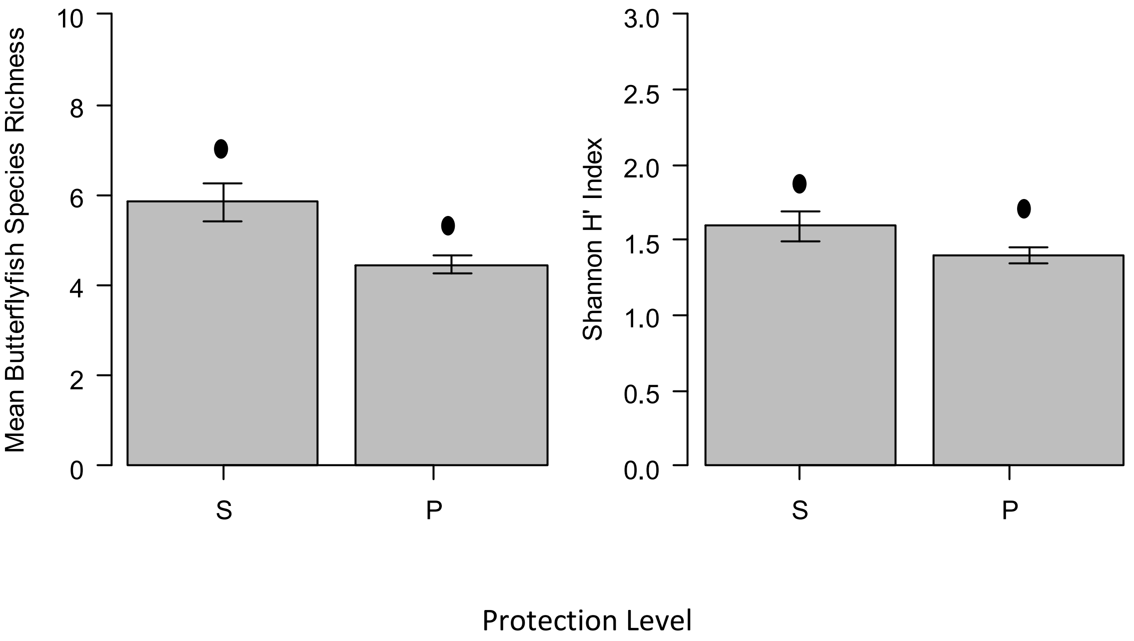


Figure 3: Diversity indices [Shannon H’ Index and mean butterflyfish (Chaetodontidae) species richness] across the two protection treatments [sanctuary (S) and partially protected (P)] within the iSimangaliso Wetland Park. Means that are significantly different are illustrated by the filled circle (●). Error bars denote standard error.

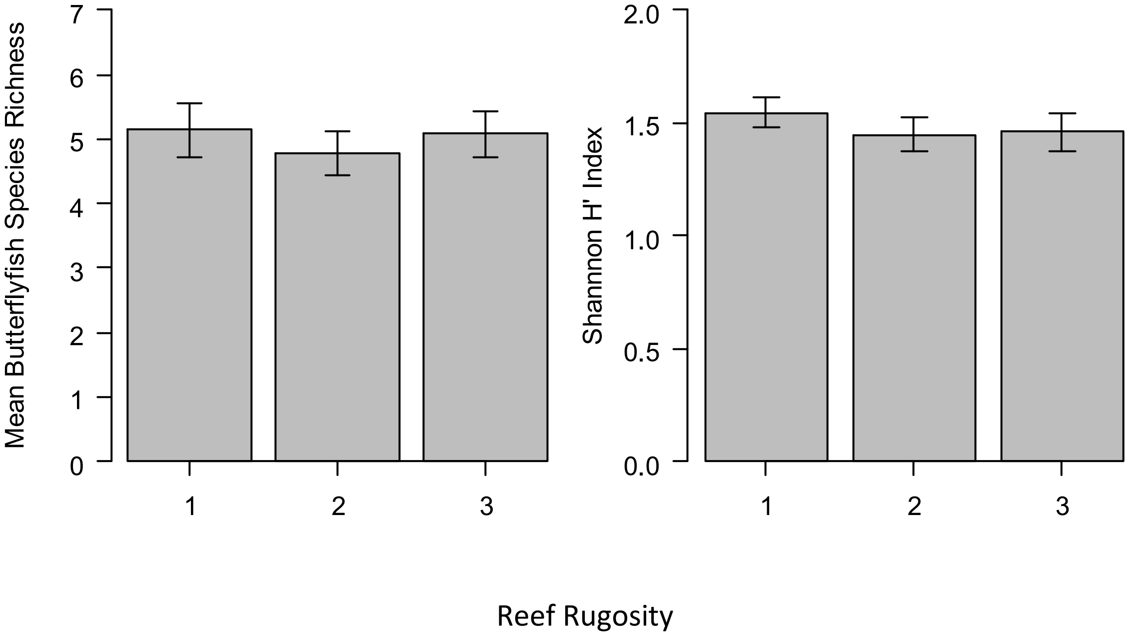


Figure 4: Diversity indices [Shannon H’ Index and mean butterflyfish (Chaetodontidae) species richness] across varying reef rugosities (1, 2 and 3) within the iSimangaliso Wetland Park. Error bars denote standard error.

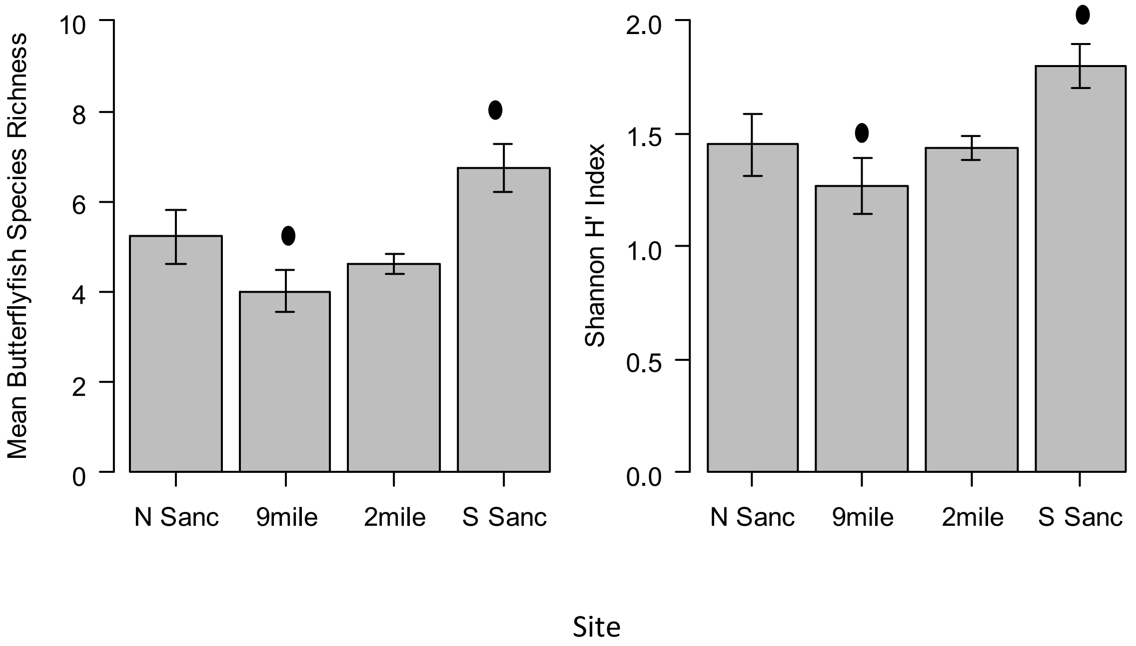


Figure 5: Diversity indices [Shannon H' Index and mean butterflyfish (Chaetodontidae) species richness] across the four sampled regions (Northern Sanctuary, 9mile, 2mile and Southern Sanctuary) of the iSimangaliso Wetland Park. Means that are significantly different from each other are indicated by the filled circle (●). Error bars denote standard error.

Sanctuary sites reveal both a significantly greater species richness and a higher Shannon H' Index than partially protected sites (df = 77, t = 2.85, $p < 0.005$), revealing a more even spread of species (df = 77, t = 1.79, $p < 0.05$) (Fig 3).

Reef Rugosity displayed no noticeable impact on either the butterflyfish species richness or the relative contribution of species within the community (Fig 4). The site of the Southern Sanctuary revealed the greatest species richness and most even spread of species across all sampled sites (Fig 5), this was significant for both diversity indices when compared to 9mile (df = 77, t = 3.94, $p < 0.001$) (df = 77, t = 3.34, $p < 0.001$), though not significant for any other sites (Fig 5).

Total butterflyfish abundance was significantly greater in sanctuary sites than partially protected (Fig 7a). Reef rugosity however did not impact butterflyfish abundance (Fig 7b). Within the sample sites, a significant difference existed between 9mile and 2mile, as well as between 9mile and the Southern Sanctuary (Fig 7c). The GLM with the lowest AIC value includes only protection ($p < 0.05$) (Table 3). When comparing butterflyfish abundances amongst and between protection level, reef rugosity and sites, protection level is therefore the factor that has the greatest impact (Table 3). The validation plots corroborate this model (Fig 6).

Table 3: Results of abundance GLM with Gaussian distribution and identity-link function where df = degrees of freedom, AIC = Akaike's information criterion, *p* = significance level.

Parameter	Residual Df	Df	AIC	Deviance	Δ Deviance	Variation explained	*p*
NULL	77			4307			
+ Protection	76	1	**534.09**	3980.7	326.31	60.457%	**0.0131**
+ Reef Rugosity	75	1	535.86	3969.2	11.52	2.134%	0.6412
+ Sites	74	1	536.97	3924.2	44.95	8.328%	0.3574
+ Protection: Sites	73	1	537.88	3869.5	54.7	10.135%	0.3099
+ Protection: Reef Rugosity	72	1	539.80	3865.8	3.74	0.693%	0.7907
+ Reef Rugosity: Sites	71	1	539.79	3767.3	98.52	18.253%	0.1730
					Total variation explained	12.531%	

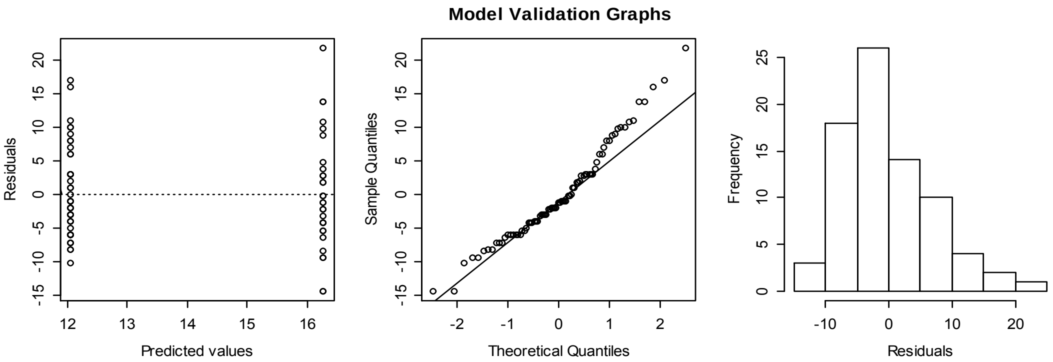


Figure 6: Model Validation Graphs of residuals versus predicted values (left), quantile - quantile plot (middle) and histogram of residuals (right) for mean butterflyfish abundance across Sanctuary and Partially protected sites of the iSimangaliso Wetland Park, South Africa.

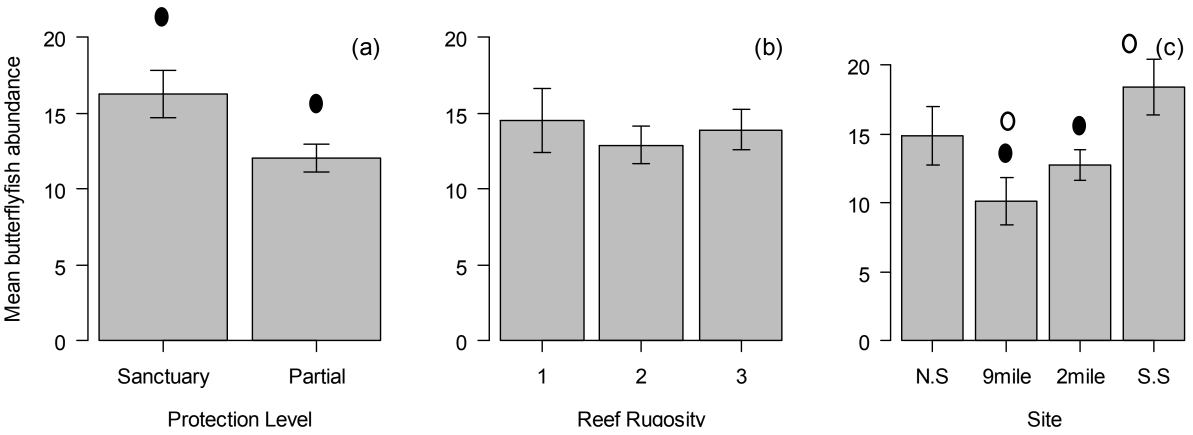


Figure 7: Total mean butterflyfish (Chaetodontidae) abundance across the three sampled factors (a) Protection Level (sanctuary, partial), (b) Reef rugosity (1, 2 and 3) and (c) Site [Northern Sanctuary (N.S), 9mile, 2mile and Southern Sanctuary (S.S)] within the iSimangaliso Wetland Park. Means that are significantly different from each other are indicated by the circles (○, ●). Error bars denote standard error.

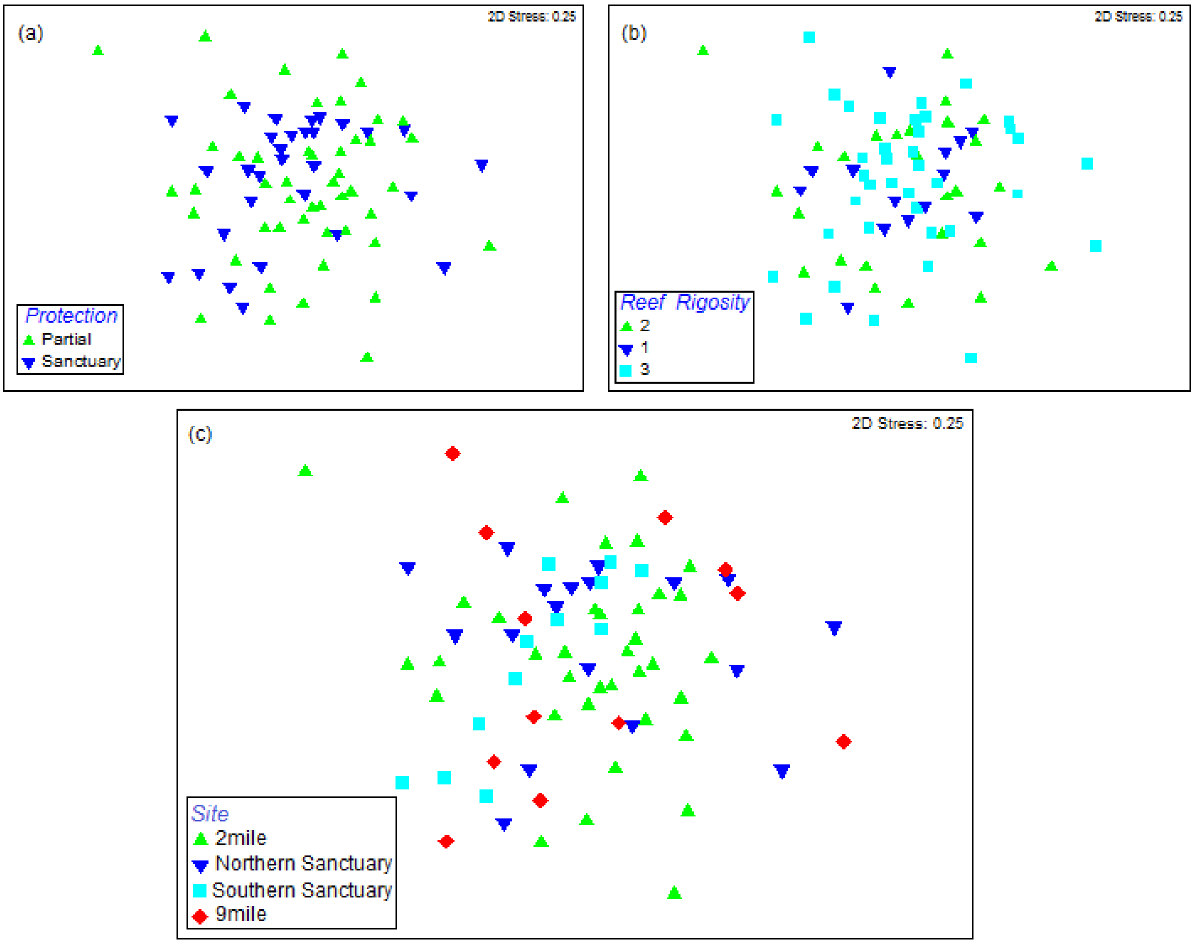


Figure 8: Butterflyfish (Chaetodontidae) species composition and clustering according to (a) Protection level (sanctuary, partial), (b) Reef rugosity (1, 2 or 3) and (c) Site (2mile, Northern Sanctuary, Southern Sanctuary, 9mile) in the iSimangaliso Wetland Park.

A PERMANOVA revealed no significant clustering of species composition (species diversity and relative abundance per transect) between partially protected and sanctuary sites (Fig 8a), though sanctuary sites appeared to share greater intraspecific similarity than within partial sites. Reef rugosity was not responsible for revealing any unique clusters of species composition (Fig 8b). Significant levels of uniqueness were revealed when species composition was clustered according to site ($F = 1.56$, $df = 11$, $p < 0.005$) (Fig 8c). This clustering was not clear, due to high levels of similarity within species composition that still occurred between sites (Fig 8c).

The large overlap in species composition resulted from the five most abundant species which were both the primary contributors to the total similarity within sites and the cause of the dissimilarity among sites, as revealed by SIMPER. The five most abundant species were *Chaetodon interruptus, Chaetodon kleinii, Chaetodon madagskarensis, Chaetodon guttatissumus* and the *Forciper flavissimus*. *C. interruptus* was the most abundant species in the Northern Sanctuary, 2mile and Southern Sanctuary, whilst *C.madagaskarensis* was the most abundant at 9mile (Table 4). Mean *C. meyeri* abundances were low across all factors (Fig 9). This species was most abundant in the Northern Sanctuary, though this was not significantly greater than other sites (Fig 9).

Table 4: The average abundance and contribution to similarity of species composition of five most dominant butterflyfish species (Chaetodontidae) across the four sample sites within iSimangaliso Wetland Park, as revealed by SIMPER in PRIMER.

Site	Species	Average Abundance	Similarity Contribution (%)
Northern Sanctuary	*C. interruptus*	3,11	40,02
	C. kleinii	2,56	24,55
	C. guttatissumus	2,11	10,90
	C. madagaskarensis	1,28	7,45
	C. meyeri	**1,00**	**6,26**
9mile	*C. interruptus*	1,58	28,65
	C. guttatissumus	1,25	20,79
	C. madagaskarensis	**2,00**	17,37
	F. flavissimus	1,75	15,50
	C. kleinii	1,58	8,91
2mile	*C. interruptus*	3,78	34,70
	C. kleinii	2,86	22,68
	C. madagaskarensis	1,44	16,66
	C. guttatissumus	1,22	12,02
	F. flavissimus	1,31	6,57
Southern Sanctuary	*C. interruptus*	3,42	19,67
	C. kleinii	3,17	17,43
	C. madagaskarensis	2,67	17,29
	C. guttatissumus	1,92	13,85
	F. flavissimus	2,00	11,76

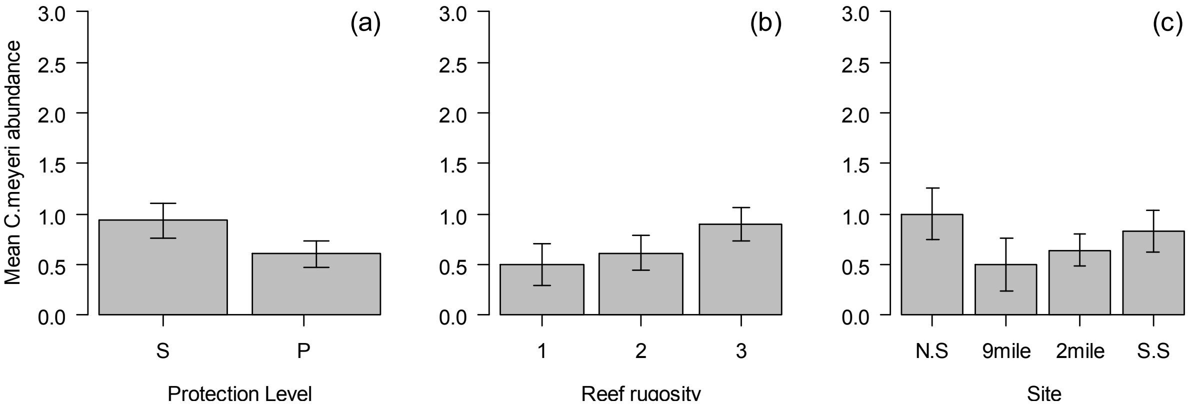


Figure 9: Mean abundance for obligate coral feeder *Chaetodon meyeri,* across the factors of protection level (sanctuary (S) and partial (P)), reef rugosity (1, 2 and 3) and site [Northern Sanctuary (N.S.), 9 mile, 2 mile and Southern Sanctuary (S.S)] within the sampled regions of iSimangaliso Wetland Park. Error bars denote standard error.

DISCUSSION

The aim of this study was to understand the distribution of butterflyfish species along the north-eastern most coast of South Africa and the factors that might be driving these distribution trends. Protection was confirmed to be the factor with the greatest influence on butterflyfish abundance and diversity, whist the hypothesis that reef rugosity was a significant driver of change was rejected for both these variables. The hypothesis that site did not impact diversity, abundance or species composition was also rejected as this factor altered species community and revealed some differences in both abundance and diversity.

Species diversity trends

Species diversity was revealed to be greater within the sanctuary sites than the partially protected ones. Greater diversity is an indication of competition, predation and high energy transfer levels that result from efficient and balanced food webs (Olivier & Poggiale 2013). The absence of fishing in sanctuaries means that trophic cascades, which typically release certain species from predatory control and cause unnatural species dominance in the ecosystem, do not occur (Götz et al. 2009; Olivier & Poggiale 2013). The lack of diving and fishing also means that habitats will be more pristine, as damaging fishing techniques, discarded fishing line and clumsy divers are not compromising the health of the coral reef (Kay and Liddle 1989; Rouphael & Inglis 1997; Schleyer and Tomalin 2000). These results therefore confirm that the health of the coral is one of the factors that impacts species diversity, suggesting that butterflyfishes are useful indicators of reef health.

Whilst coral health is a possible determinant of species diversity, reef rugosity was not found to be a significant driver. This is unexpected, as higher levels of reef rugosity (complexity and habitat heterogeneity) have shown to provide shelter from physical stress (Friedlander and Parrish 1998), increased protection from predators (Hixon 1991; Cadoret et al. 1999) and a greater abundance of feeding sites (Cadoret et al. 1999) . Environmental factors, such as wave exposure and depth, could be influencing observed diversity trends to a greater extent than reef rugosity, or are perhaps masking the impacts. A recent study revealed that wave exposure is an important driver in shaping the foraging behaviour of butterflyfishes (Noble et al. 2014). The greater energetic costs and specific adaptations associated with feeding on reefs exposed to higher wave action leads to lower species diversity in such regions. Depth is a factor that also impacts species diversity and abundance, shallower sites being the preferred habitat for most butterflyfishes (Friedlander & Parrish 1998).

Additionally, it appears that alongside coral health and the possible impacts of environmental factors, the proportion of live coral cover present and the particular species of coral dominant on the reef are important drivers of species diversity. These appear to have a greater impact on species diversity than reef rugosity (Bell & Galzin 1984). Due to the range of feeding preferences and adaptations that butterflyfish display, their distribution appears to be largely determined by preferred food availability (Crosby 1996). The majority of butterflyfish species employ a flexible, generalist feeding approach that allows them to thrive in diverse environments where resource variability is high (Prachett et al. 2013). It is therefore possible that reefs with greater coral diversity also illustrate greater species diversity.

Environmental variations and differences in the composition of the coral species within the sampling region might account for the significant difference in species diversity between the Southern Sanctuary and 9mile. Celliers & Schleyer (2008) revealed that 9mile contains different relative proportions of soft and hard coral than other sites. This may result in the hosting of fewer butterflyfish species. Marine environments are fairly homogenous, experiencing great connectivity through ocean currents and dispersal. Furthermore the distance that the sample sites spanned was short (60km) and all sites fell within the Delgoa Bioregion, north of the Cape Vidal biogeographic break (Turpie et al. 2000; Lombard et al. 2004; Sink et al. 2005; Currie et al. 2012). This further enforces the homogeneity of the habitat and possibly contributes to the similarities in species diversity that were observed across sites. Though the overall effect of site on species diversity was not significant, the two sites with the highest species diversity fell within sanctuary protection. This further supports that sanctuaries host a healthier and more diverse array of corals (Kay & Liddle 1989).

Butterflyfish abundance trends

Although site affected total butterflyfish abundance significantly, the most important factor influencing abundance was protection level. As previously mentioned butterflyfish distribution appears to be primarily affected by food availability (Crosby & Reese 2005; Lawton& Prachett 2012). Sanctuary sites have a greater supply of healthy coral, which can in turn support the feeding of more individual butterflyfishes. As the only human induced differences that exist between protection levels, diving and fishing are the most likely activities resulting in coral reef damage and degradation in this region (Celliers & Schleyer 2008).

Following trends in species diversity, 9mile hosted significantly lower abundances butterflyfish than 2mile, despite 2mile experiencing 97% more diving pressure than 9mile (J Olbourn pers.comm). 9mile is dominated by soft corals within the genera *Lobophytum* (Alcyonacea: Alcyoniidae) and *Sinularia* (Alcyonacea: Alcyoniidae), of which many species are branching (Celliers & Schleyer 2008). In contrast, 2mile has greater abundances of non-branching corals. Whilst these differences in coral cover are likely impacting the species diversity present, they also impact the extent to which the coral is damaged by divers. Delicate branching corals are particularly susceptible to fin damage by divers. This leads to stockier, smaller coral colonies, through the necessary reallocation of energy from growth and reproduction to repair (Hawkins & Roberts 1993). This suggests that the impact of diving is determined less by the quantity of divers than it is by their experience and capability (Kay & Liddle 1989; Rouphael & Inglis 1997). The habitat degradation on reefs with more delicate corals, such as 9mile, is therefore greater. The low abundances of butterflyfish observed at this site suggest that coral health not only impacts species diversity but abundance as well.

Accounting a decline in butterflyfish abundance to targeted reef fishing is likely only possible along the shore regions of 2mile where considerable subsistence and recreational angling takes place. 9mile is a more remote site, which is most frequently accessed by boat. A decline in small benthic reef fish due to targeted shore fishing has been witnessed further north along the Tanzanian coastline (McClanahan et al. 1999). Shore reefs often function as nursery grounds for fish species, the individuals of which move offshore and onto deeper reefs once mature (Currie et al. 2012). The depletion of these nurseries can result in lower levels of recruitment to offshore reefs, decreasing population sizes. Butterflyfish are however, most likely indirectly affected by altered ecosystem interactions through trophic cascades. Top down trophic cascades have the potential to release butterflyfish from piscivorous control if the game fishing has caused butterflyfish predator numbers to significantly decline (Hawkins & Roberts 2004). Fishing might impact butterflyfish through habitat alterations as well. A decline in herbivorous fish decreases grazing pressure and allows algae to overgrow and kill many of the corals (Hawkins & Roberts 2004). Algae also fouls corals when fishing line is discarded and left to tangle around the coral (Schleyer & Tomalin 2000). In these ways, fishing decreases the health of coral structures and reefs.

Species Composition

Five dominant species were present across all sites. These species were *C. interruptus, C. kleinii, C. madagskarensis, C. guttatissumus* and *F. flavissimus.* The significant similarity/clustering within sites and differences revealed amongst sites can be directly attributed to the relative abundances of these five species. The overlap of species composition evident across sites further supports that it is the relative contribution of these species accounting for the similarity and dissimilarity observed.

All of the above mentioned butterflyfish are generalist feeders, largely consuming, though not totally dependent upon, live coral cover for food. They all consume a range of hard and soft corals, present to varying extents across all sites (King 1999; Celliers & Schleyer 2008). The ability of these species to feed flexibly in the presence of great resource variation likely contributes to their widespread presence and abundance (Bell & Galzin 1984). The lack of dominance of other observed facultative butterflyfish on the same reefs suggests that environmental processes might also be influencing species composition across these sites.

C. interruptus, C. kleinii, C. madagskarensis, C. guttatissumus and *F. flavissimus* are morphologically all very different, displaying an array of colorations, sizes, cryptic markings and feeding apparatus adaptations (Motta 1987; McMillan et al. 1999; Kelley et al. 2013). No common phenotypical feature allowing for the outcompeting of other facultative butterflyfish exists among these species and is therefore not a likely cause for their wide range and abundance. The particular species composition observed during this study is possibly a function of fluctuation in larval recruitment and settlement (Findley & Findley 1985). Adult population patterns are a consequence of processes that occur at the settlement stage (Roughgarden et al. 1985). As such they are a subject to variations in ocean currents transporting larvae, differing life history strategies and competition for suitable settlement ground (Findley & Findley 1985; Roughgarden et al. 1985). The major contribution of generalist feeders to the overall species composition is most likely due to their flexible feeding strategy. The dominance of these particular facultative species could however be a more variable trend dependent upon dynamic factors, as mentioned above. A similar study conducted over a longer temporal scale might offer more insight into trends within species composition.

C. meyeri as an indicator species

Of all butterflyfish species documented in this study, *C. meyeri* was the only obligate corallivore. This species was infrequently observed across this region. The lack of significant differences in *C. meyeri* abundance across protection, reef rugosity and site suggests there is a more important factor driving the distribution and abundance of this species. In particular, the low abundances of *C. meyeri* in the Southern Sanctuary, a site with pristine coral reefs, illustrates that one cannot merely use obligate corallivore abundance as a proxy for coral health. As a highly specialised feeder, the *C. meyeri* is dependent on the presence of *Acropora* (Scleractinia: Acroporidae) for food (Lawton et al. 2012; Prachett et al. 2013). The relative absence of *C.meyeri* in all sites except the Northern Sanctuary suggests that *Acropora* is not a widespread or abundant species across the sampled reefs, which is supported in the literature (Celliers & Schleyer 2002; Celliers & Schleyer 2008; Schleyer et al. 2008; Floros et al. 2012).

It has been illustrated in India, French Polynesia, Papua New Guinea, New Caledonia, Japan and the Red Sea that obligate corallivores are the most dominant butterflyfish on coral reefs where their preferred food is abundant (Brock 1979; Cadoret et al. 1999; Prachett et al. 2005; Cole et al. 2010; Lawton et al. 2012; Pratchett et al. 2013). These specialists illustrate priority access to their favoured resource, outcompeting generalists with their superior prey capture and assimilation efficiency (Lawton et al. 2012; Pratchett et al. 2013). The infrequency of *Acropora* across the study sites is however not representative of the entire region. It is in fact a species found in large densities along Four Mile and within some regions of the Northern Sanctuary (Schleyer & Celliers 2005; Celliers & Schleyer 2008). The greater abundance of *C.meyeri* within the Northern Sanctuary than any other site supports the presence of such *Acropora* populations.

Should the Butterflyfish Indicator Hypothesis be applied within iSimangaliso Wetland Park?

In this particular region of the south-west Indian Ocean where various levels of human disturbance exist, differences in total butterflyfish abundance and species diversity appear to be particularly useful in revealing the impacts of diving and fishing on coral health. In fact, the management authorities of the iSWP might consider utilising this indicator family to monitor coral health and adaptively manage human impacts on accessed reefs within these MPA's. Had these clear differences in protection not existed across the sampling region, the use of butterflyfish as indicators of coral health would have been minimal. This is because the BIH is not appropriate at the crude scale of total abundance of multiple species. Rather, it is a more sensitive tool to be applied solely to obligate corallivorous species (Crosby 1996). This study revealed that the abundance of obligate corallivores present is not always an accurate depiction of coral reef health as they were very sparsely observed within the pristine reefs of the Southern Sanctuary. The use of the BIH is therefore constrained to coral reefs upon which obligate corallivores and their preferred coral species occur. As has also been illustrated, it hard to relate changes in a species distribution and abundance to one particular factor when the coral reef environment is so dynamic and alterations could be the result of many environmental and biological influences.

I do not suggest that the BIH is a globally applicable tool, with too many unconsidered variables and detailed prerequisite knowledge of the study site required in order for it to be useful. However, in regions where such knowledge exists, the BIH could be applied alongside other behavioural/coral substrate studies and proven a valuable tool. In order for the BIH to be useful within iSWP, a clearer understanding of the distribution of obligate corallivores within this region is required. Schleyer and Celliers (2005) have discovered large populations of *Acropora* within Four Mile and the northern bounds of iSWP. I suggest that this be the starting point for further studies relating to the BIH in this region. However, for most of the sites that were sampled in this study, where neither *Acropora* nor obligate corallivores were very abundant, the BIH is not able to be applied.

The relevance and possible application of new coral monitoring techniques such as this one are dependent upon the existence of baseline data (Floros et al. 2012). I have demonstrated that the knowledge one gains into ecological processes and species distribution from such acquired data is fundamental when wanting to apply conservation monitoring methods. As such, baseline surveys are the first step toward effective monitoring and conservation (Floros et al. 2012). Through the growing participation of citizen scientists and the utilisation of public online databases such as iSpot, our understanding of butterflyfish distribution, both along this coastline and globally has the potential to expand at much faster rates than could ever be achieved through scientific fieldwork alone. Considering the speed at which global coral decline is occurring, such increased rates of data collection are needed for effective conservation.

With a clear understanding of butterflyfish community and distribution within a region, the usefulness of the BIH can be decided and applied in the appropriate locations. In such cases, coral degradation has the potential to be rapidly recognised and appropriately managed. Early identification and understanding of coral reef threats could greatly improve management efficiency and contribute toward the conservation of these vulnerable coral reef ecosystems.

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APPENDIX

Appendix 1: All possible General Linear Model's (GLMs) with Gaussian distribution and identity-link function that were run for butterflyfish abundance including their Akaike's information criterion (AIC) value.

Model	AIC
$y = \beta_o + \beta_1$ *(protection)*	534.09
$y = \beta_o + \beta_1$ *(protection)* $+ \beta_2$ *(Reef rugosity)*	535.86
$y = \beta_o + \beta_1$ *(protection)* $+ \beta_2$ *(Reef rugosity)* $+ \beta_3$ *(Site)*	536.97
$y = \beta_o + \beta_1$ *(protection)* $+ \beta_2$ *(Reef rugosity)* $+ \beta_3$ *(Site)* $+ \beta_4$ *(Protection*Site)*	537.88
$y = \beta_o + \beta_1$ *(protection)* $+ \beta_2$ *(Reef rugosity)* $+ \beta_3$ *(Site)* $+ \beta_4$ *(Protection*Site)* $+ \beta_5$ *(Protection*Reef rugosity)*	539.8
$y = \beta_o + \beta_1$ *(protection)* $+ \beta_2$ *(Reef rugosity)* $+ \beta_3$ *(Site)* $+ \beta_4$ *(Protection*Site)* $+ \beta_5$ *(Protection*Reef rugosity)* $+ \beta_6$ *(Reef rugosity*Site)*	539.79
Final Model: $y = \beta_o + \beta_1$ *(protection)*	534.09