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Reef fishes of praia do Tofo and praia da Barra, Inhambane, Mozambique

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Abstract

The coral reefs around Praia do Tofo and Praia da Barra, southern Mozambique, are known for their aggregations of marine megafauna, but no studies have yet examined their reef fish biodiversity. This study assesses for the first time the ichthyofaunal diversity of the seas around Praia do Tofo and Praia da Barra. Methods involved underwater observations during recreational dives between February and September 2016, and the use of photographic records from 2015 and 2016. A total of 353 species, representing 79 families, were recorded from 16 patch reefs in the region. The area shows comparable species diversity to protected areas in the southwestern Indian Ocean and has a high proportion of carnivores, together hinting at these reefs being in good condition. However, high primary productivity driven by coastal upwelling may be significantly influencing fish diversity and trophic structure, making these metrics unreliable measures of reef health in this instance. Future studies investigating the sustainability of this ecosystem would benefit from utilising a wide range of reef health measures.

Keywords: Icthyofaunal diversity, Mozambique, checklist, underwater census

Introduction

The ecotourism industry of the Inhambane province in southern Mozambique accounts for approximately 7% of the province's annual income (Mutimucuio & Meyer, 2011). The primary tourism hotspots are the Bazaruto Archipelago National Park (BANP) and the southern area around the Inhambane peninsula. In the latter, the seas around Praia do Tofo and Praia da Barra (hereafter referred to as PTPB) are particularly important due to their resident populations of manta rays and whale sharks (Pierce *et al.*, 2010; Tibirica *et al.*, 2011). Venables *et al.* (2016) estimate that manta ray tourism alone contributes $34 million USD per annum to the province's economy. Scientific research in the PTPB area has thus predominantly focused on these charismatic species (e.g. Rohner *et al.*, 2013; 2014); so far, very little research has been conducted on the biodiversity of resident fish populations. This aspect of the PTPB's marine ecosystem is expected to gain value in the future, as has occurred in the BANP (Schleyer & Celliers, 2005), due to the continued decline of local megafauna populations (Rohner *et al.*, 2013). As of 2014, the United Nations and World Heritage Convention (2014) recommend that the protected area currently represented by the BANP be extended south to include the seas around PTPB. Knowledge of the fish biodiversity of this area will help support this recommendation.

Species richness information is currently missing from the PTPB seas but this data is vital for future ecosystem management. Biodiversity data is necessary to identify key biological components (Pereira, 2000), provide a baseline from which ecosystem stability and function can be assessed (Cleland, 2011), and to predict the effects of biodiversity loss on ecosystem provision (Bellwood & Hughes, 2001; Gillibrand *et al.*, 2007; Maggs *et al.*, 2010). The PTPB area is bordered by the tropical and sub-tropical latitudes of the southwestern Indian Ocean and are home to a number of different reef habitats likely to support diverse reef fish assemblages. The most common habitats are deepwater, offshore patch reefs which are characteristic of southern Mozambique and typically have low levels of coral cover (Pereira, 2000; Motta *et al.*, 2002; Schleyer & Celliers, 2005). Other marine ecosystems in the region include mangrove swamps, estuarine reefs and shallow inshore fringing reefs. This range of reef and coastal environments provides substantial habitat and nursery grounds for fish species in the area. The PTPB area has a relatively large associated human population of over 250,000 people (Instituto Nacional de Estatística, 2007), based primarily in the cities of Maxixe and Inhambane (Fig. 1). However, there is little to no management in place to safeguard the marine ecosystems and the services they provide. This study constitutes a baseline assessment of fish diversity of the reefs surrounding Praia do Tofo and Praia da Barra, and highlights the need for further investigations into the state of these ecosystems.

Materials and Methods

Study Site

Praia do Tofo (23° 51.205' S; 35° 32.882' E) and Praia da Barra (23° 47.541' S; 35° 31.142' E) harbour a number of shallow fringing coral reefs. However, many of the

Figure 1. Map of the study area and its location along the coast of Mozambique (inset). Sampled reefs are indicated by (•); their broad characteristics are described in Table 1.

Table 1. Names and descriptions of sampled reefs, including the underwater survey method used and the amount of time spent surveying each location.

Site Name (Number)	Site Description	Sampling Method	Sampling Time (mins)
Amazon (1)	Offshore, horseshoe reef with an abundance of azooxanthellate soft corals; 23 – 28 metres.	SCUBA	87
Hospital (2)	Offshore, southward sloping reef with occasional short pinnacles; 24 – 26 metres.	SCUBA	80
The Office (3)	Topographically complex offshore reef with an abundance of overhangs and valleys with many encrusting soft corals; 22 – 26 metres.	SCUBA	177
Reggie's (4)	Tall, offshore reef rising between 4 – 8 metres from the seafloor; reef crests are dominated by large colonies of *Tubastrea micranthus*; 22 – 30 metres.	SCUBA	231
Buddies (5)	Shallow, inshore reef subject to persistent swell and fishing pressure; 8 – 10 metres.	SCUBA	97
The Wall (6)	Shallow estuarine reef with daily exposure to strong tidal currents; a combination of seagrass, rocky reef and sand patch microhabitats; 0-4 metres.	Snorkel	70
Mike's Cupboard (7)	Submerged sand dune reef, with many potholes and gullies surrounded by sandy reef flats; 12 – 16 metres.	SCUBA	108
Salon (8)	Shallow inshore reef composed of multiple large pinnacles surrounded by sandy bottom; subject to high turbidity from wave action; 10-14 metres.	SCUBA	175
Sherwood Forest (9)	Offshore reef just outside of Tofo bay, made of one large and one smaller pinnacle both supporting large populations of *Tubastrea micranthus*; 22 – 26 metres	SCUBA	58
Giants Castle (10)	Straight north-south reef with an extensive reef flat and deep reef wall; known within the local dive industry as having the best sighting rate for marine megafauna; 27 – 32 metres.	SCUBA	214
Marble Arch (11)	Inshore reef exposed to minor wave action; large reef flat with a few large potholes and one large rock arch; 14 – 18 metres.	SCUBA	51
Rob's Bottom (12)	Very patchy eastward sloping reef that is often subject to high current with high algal cover; 23 – 27 metres.	SCUBA	158
Manta Reef (13)	A large offshore reef, with a large central reef flat; peripheries are characterised by short, steep reef slopes with a number of tall pinnacles; 18 – 24 metres	SCUBA	365
Outback (14)	Similar reef shape as Giant's Castle, yet with more small inlets that house a number of deep overhangs and archways; 25 – 30 metres.	SCUBA	76
Coconut Bay (15)	Shallow inshore rocky reef with small patches of encrusting soft coral and larger swathes of seagrass; 4 – 8 metres.	Snorkel	53
Paindane Coral Gardens (16)	Small, shallow reef protected from offshore waves by a barrier rock extending from shore; the most abundant coral community in this area, dominated by *Sinularia* spp. soft coral and corymbose acroporids; 1 – 6 metres.	Snorkel	182

sites frequented by the local dive industry are in deeper waters to the north and south. In this study, diversity was recorded on reefs spanning approximately 40 km along the coast of the Inhambane province (Fig. 1). A total of 16 reef sites between 1 and 32 m (Table 1) were surveyed between February and September 2016.

Sampling

The primary method used was underwater observations during a random swim. Species were identified *in situ* if possible and recorded on an underwater PVC slate. If required, a photograph was taken for subsequent species identification. Deep sites (> 8 m) were surveyed using SCUBA, as part of a recreational dive charter operated by Peri-Peri Divers. Shallow sites were assessed by snorkelling. Fifty-four individual surveys, totalling 2218 minutes of observation time were undertaken (total surveying times for each site are shown in Table 1). The species richness recorded from underwater observations was supplemented through the inclusion of species that had been sighted in the year preceding the survey period, and for which there was photographic evidence available from local ecotourism and dive operators (e.g. *Mola mola*). Solicited data from outside the study period was utilised to ensure that rare or seasonally restricted species were recorded. Data collection was approved by the Maritime Administration of the City of Inhambane, and the Ministry of Justice.

Estimated richness and regional comparisons

To determine the number of conspicuous species missed during the visual census, the Coral Fish Diversity Index (CFDI) developed by Allen & Werner (2002) was calculated and compared to the recorded species richness (SR_{obs}). The CFDI examines the diversity of six common and easily observable families as representatives of reef fish species richness. These families are Acanthuridae, Chaetodontidae, Labridae, Pomacanthidae, Pomacentridae and Scaridae. Taxonomic research has suggested that Scaridae be reclassified as a sub-family of Labridae, named Scarinae (Westneat & Alfaro, 2005); however, for the purposes of the present analysis this has no influence on the value of the CFDI. In areas < 2000 km^2, a theoretical species richness (SR_{theor}) is then generated using the equation $SR_{theor} = 3.39(CFDI) - 20.595$ (Allen & Werner, 2002). SR_{theor} was calculated for other reef systems in the southwestern Indian Ocean, using published literature, to draw loose comparisons between the richness of these areas and that observed in the current study (as in Wickel *et al.*, 2014).

Estimating trophic structure

The dietary preference of each species was determined using classifications by Harmelin-Vivien (1979), Hiatt & Strasburg (1960), Hobson (1974), Myers (1999), and FishBase (http://fishbase.org). Where information on a species' feeding habit was not available, feeding habit was assumed from those of congener species and labelled in Table 2 with a '*'. Where congeners were not available the feeding habit was labelled 'unknown' (NA). Eight trophic categories were used, as in Gillibrand *et al.* (2007), Chabanet & Durville (2005), and Durville *et al.* (2003). Trophic categories included herbivore, omnivore, browser of sessile invertebrates, diurnal carnivore, nocturnal carnivore, piscivore, diurnal planktivore, and nocturnal planktivore. The trophic categories, excluding herbivores and omnivores, were then grouped into general carnivores *sensu lato*.

Results

A total of 353 species, representing 79 families, were recorded in the current study from 328 visual observations and 25 past photographic records (Table 2). Of the total number of species recorded, 27 were cartilaginous fish and 326 were bony fish. The CFDI-generated SR_{theor} was 329, lower than the observed species richness (Table 3).

Twelve families represented over half of the total recorded diversity, these included Acanthuridae (17), Balistidae (11), Carangidae (10), Chaetodontidae (18), Holocentridae (10), Labridae (32), Lutjanidae (12), Muraenidae (14), Pomacentridae (21), Scorpaenidae (13), Serranidae (19), and Tetraodontidae (10). Nearly half the recorded families (48%) were represented by one species only. Five of these families are monospecific including, Rachycentridae, Rhincodontidae, Rhinidae, Stegostomatidae, and Zanclidae. The most species-rich genera were *Chaetodon* (12), *Epinephelus* (10) and *Gymnothorax* (10).

General carnivores comprised 78% of the species composition (Fig. 2; Table 4). Seventeen of the species' feeding habits were assumed from those of congener species whilst fifteen were labelled as 'unknown'. The largest single trophic group, the diurnal carnivores, comprised 27% of the species composition (Fig. 2) and included predominantly labrids. The most common nocturnal carnivore families were the lutjanids, the muraenids and the serranids. Chaetodontids made up the majority of the browsers of sessile invertebrates, whilst acanthurids and scarids represented most of the herbivores. There were no other notably common families dominating other trophic groups.

Table 2. Reef fish species checklist from the PTPB area of Mozambique, sighted through surveys (S) and photographic records (P). Where a species' trophic category has been assumed from a congener species, it is labelled with a '*'.

FAMILIES **Species - Authors**	**Sighting Record**	**Trophic Category**
ACANTHURIDAE		
Acanthurus dussumieri Cuvier and Valenciennes, 1835	S	H
Acanthurus leucosternon Bennett, 1833	S	H
Acanthurus lineatus Linnaeus, 1758	S	H
Acanthurus nigrofuscus Forsskål, 1775	S	H
Acanthurus tennentii Günther, 1861	S	H
Acanthurus triostegus Linnaeus, 1758	S	H
Acanthurus xanthopterus Valenciennes, 1835	S	H
Ctenochaetus binotatus Randall, 1955	S	H
Ctenochaetus striatus Quoy and Gaimard, 1825	S	H
Ctenochaetus truncates Randall and Clements, 2001	S	H
Naso brachycentron Valenciennes, 1835	S	H
Naso brevirostris Cuvier, 1829	S	H
Naso elegans Rüppell, 1829	S	H
Paracanthurus hepatus Linné, 1766	S	DPL
Zebrasoma desjardinii Bennett, 1836	S	H
Zebrasoma gemmatum Valenciennes, 1835	S	H
Zebrasoma scopas Cuvier, 1829	S	H
AMBASSIDAE		
Ambassis natalensis Gilchrist and Thompson, 1908	S	DC
ANTENNARIIDAE		
Antennarius coccineus Lesson, 1831	S	Pi
Antennarius commerson Lacepède, 1798	S	Pi
Antennarius nummifer Cuvier, 1817	P	Pi
APOGONIDAE		
Cheilodipterus quinquelineatus Cuvier, 1828	S	NC
Ostorhinchus angustatus Smith and Radcliffe, 1911	S	BSI
Ostorhinchus flagelliferus Smith, 1961	S	BSI
Ostorhinchus fleurieu Lacepède, 1802	S	BSI*
Pristiapogon kallopterus Bleeker, 1856	S	NC
Taeniamia mozambiquensis Smith, 1961	S	NA
ATHERINIDAE		
Atherinomorus lacunosus Forster, 1801	S	NPL

FAMILIES Species - Authors	Sighting Record	Trophic Category
AULOSTOMIDAE		
Aulostomus chinensis Linnaeus, 1766	S	Pi
BALISTIDAE		
Balistapus undulatus Park, 1797	S	DC
Balistoides conspicillum Bloch and Schneider, 1801	S	DC
Balistoides viridescens Bloch and Schneider, 1801	S	DC
Odonus niger Rüppell, 1836	S	DC
Pseudobalistes flavimarginatus Rüppell, 1829	P	DC
Pseudobalistes fuscus Bloch and Schneider, 1801	S	DC
Rhinecanthus aculeatus Linnaeus, 1758	S	DC
Rhinecanthus rectangulus Bloch and Schneider, 1801	S	O
Sufflamen bursa Bloch and Schneider, 1801	S	DC
Sufflamen fraenatum Latreille, 1804	S	DC
Xanthichthys lineopunctatus Hollard, 1854	S	DC*
BLENNIIDAE		
Aspidontus dussumieri Valenciennes, 1836	S	H
Aspidontus taeniatus Quoy and Gaimard, 1834	S	DC
Aspidontus tractus Fowler, 1903	S	DC
Cirripectes stigmaticus Strasburg and Schultz, 1953	S	H
Ecsenius midas Starck, 1969	S	H
Istiblennius edentulous Forster and Schneider, 1801	S	H
Plagiotremus rhinorhynchos Bleeker, 1852	S	NPL
Plagiotremus tapeinosoma Bleeker, 1857	S	O
BOTHIDAE		
Bothus mancus Broussonet, 1782	S	DC
Bothus pantherinus Rüppell, 1830	S	NC
CAESIONIDAE		
Caesio varilineata Carpenter, 1987	S	DPL
Caesio xanthalytos Holleman *et al.* 2013	S	DPL*
Caesio xanthonata Bleeker, 1853	S	DPL
Pterocaesio marri Schultz *et al.*, 1953	S	DPL
Pterocaesio tile Cuvier and Valenciennes, 1830	S	DPL
CALLIONMYIDAE		
Neosynchiropus stellatus Smith, 1963	S	DC

FAMILIES **Species - Authors**	**Sighting Record**	**Trophic Category**
CARANGIDAE		
Alectis ciliaris Bloch, 1787	P	DC
Alectis indica Rüppell, 1830	P	DC
Caranx bucculentus Alleyne and Macleay, 1877	S	DC
Caranx heberi Bennett, 1830	S	DC
Caranx ignobilis Forsskål, 1775	S	DC
Caranx melampygus Cuvier, 1833	S	DC
Caranx sexfasciatus Quoy and Gaimard, 1825	S	Pi
Elagatis bipinnulata Quoy and Gaimard, 1825	S	DC
Gnathanodon speciosus Forsskål, 1775	S	DC
Seriola lalandi Valenciennes, 1833	S	DC
CARCHARHINIDAE		
Carcharhinus amblyrhynchos Bleeker, 1856	S	Pi
Carcharhinus leucas Müller and Henle, 1839	P	DC
Carcharhinus limbatus Müller and Henle, 1839	S	Pi
Carcharhinus melanopterus Quoy and Gaimard, 1824	S	Pi
Carcharhinus obscurus Lesueur, 1818	S	DC
Triaenodon obesus Rüppell, 1837	S	DC
CENTRISCIDAE		
Aeoliscus strigatus Günther, 1861	P	DC
CHAETODONTIDAE		
Chaetodon auriga Forsskål, 1775	S	BSI
Chaetodon blackburnii Desjardins, 1836	S	BSI
Chaetodon dolosus Ahl, 1923	S	BSI
Chaetodon guttatissimus Bennett, 1833	S	BSI
Chaetodon interruptus Ahl, 1923	S	BSI
Chaetodon kleinii Bloch, 1790	S	BSI
Chaetodon lineolatus Cuvier, 1831	S	BSI
Chaetodon lunula Lacepède, 1802	S	BSI
Chaetodon madagaskariensis Ahl, 1923	S	BSI
Chaetodon melannotus Bloch and Schneider, 1801	S	BSI
Chaetodon meyeri Bloch and Schneider, 1801	S	BSI
Chaetodon trifascialis Quoy and Gaimard, 1825	S	BSI
Chaetodon xanthurus Bleeker, 1857	S	BSI

FAMILIES Species - Authors	Sighting Record	Trophic Category
Forcipiger flavissimus Jordan and McGregor, 1898	S	BSI
Hemitaurichthys zoster Bennett, 1831	S	DPL
Heniochus acuminatus Linnaeus, 1758	S	BSI
Heniochus diphreutes Jordan, 1903	S	DPL
Heniochus monoceros Cuvier, 1831	S	BSI
CIRRHITIDAE		
Cirrhitichthys oxycephalus Bleeker, 1855	S	DC
Cyprinocirrhites polyactis Bleeker, 1874	S	DPL
Oxycirrhites typus Bleeker, 1857	P	DPL
Paracirrhites arcatus Cuvier, 1829	S	DC
Paracirrhites forsteri Schneider, 1801	S	DC
CLINIDAE		
Clinus venustris Gilchrist and Thompson, 1908	S	NA
Pavoclinus laurentii Gilchrist and Thompson, 1908	S	NA
CLUPEIDAE		
Gilchristella aestuaria Gilchrist, 1913	S	DPL
CONGRIDAE		
Heteroconger hassi Klausewitz and Eibl-Eibesfeldt, 1959	S	NC
DACTYLOPTERIDAE		
Dactyloptena orientalis Cuvier, 1829	S	NC
DASYATIDAE		
Dasyatis microps Annandale, 1908	S	NC*
Himantura jenkinsii Annandale, 1909	S	NC
Himantura uarnak Gmelin, 1789	S	NC
Neotrygon kuhlii Müller and Henle, 1841	S	NC
Taeniura lymma Forsskål, 1775	P	NC
Taeniura meyeni Müller and Henle, 1841	S	NC
DIODONTIDAE		
Diodon holocanthus Linnaeus, 1758	S	NC
Diodon hystrix Linnaeus, 1758	S	NC
Diodon liturosus Shaw, 1804	S	NC
ECHENEIDAE		
Echeneis naucrates Linnaeus, 1758	S	NC
ENGRAULIDAE		
Thryssa vitrirostris Gilchrist and Thompson, 1908	S	DPL

FAMILIES **Species - Authors**	**Sighting Record**	**Trophic Category**
EPHIPPIDAE		
Platax teira Forsskål, 1775	S	O
FISTULARIIDAE		
Fistularia commersonii Rüppell, 1838	S	Pi
GERREIDAE		
Gerres longirostris Lacepède, 1801	S	DC
GINGLYMOSTOMATIDAE		
Nebrius ferrugineus Lesson, 1831	P	NC
GOBIIDAE		
Amblyeleotris steinitzi Klausewitz, 1974	S	DC
Amblyeleotris wheeleri Polunin and Lubbock, 1977	S	DC*
Caffrogobius saldanha Barnard, 1927	S	NA
Valenciennea strigata Broussonet, 1782	S	DC
HAEMULIDAE		
Diagramma pictum Thunberg, 1792	S	DC
Plectorhinchus flavomaculatus Cuvier, 1830	S	NC
Plectorhinchus gaterinus Forsskål, 1775	S	NC
Plectorhinchus playfairi Pellegrin, 1914	S	DC
Plectorhinchus vittatus Linnaeus, 1758	S	NC
HEMIRAMPHIDAE		
Hyporhamphus affinis Günther, 1866	S	O
HOLOCENTRIDAE		
Myripristis adusta Bleeker, 1853	S	NPL
Myripristis berndti Jordan and Evermann, 1903	S	NC
Myripristis botche Cuvier, 1829	S	NC
Myripristis murdjan Forsskål, 1775	S	NPL
Myripristis vittata Valenciennes, 1831	S	NPL
Neoniphon samara Forsskål, 1775	S	NC
Pagellus natalensis Steindachner, 1903	S	O
Sargocentron caudimaculatum Rüppell, 1838	S	NC
Sargocentron diadema Lacepède, 1802	S	NC
Sargocentron spiniferum Forsskål, 1775	S	NC
ISTIOPHORIDAE		
Istiompax indica Cuvier, 1832	S	Pi
Istiophorus platypterus Shaw, 1792	P	Pi

FAMILIES Species - Authors	Sighting Record	Trophic Category
Makaira nigricans Lacepède, 1802	P	Pi
KYPHOSIDAE		
Kyphosus vaigiensis Quoy and Gaimard, 1825	S	H
LABRIDAE		
Anampses meleagrides Valenciennes, 1840	S	DC
Bodianus anthioides Bennett, 1832	S	DC
Bodianus axillaris Bennett, 1832	S	DC
Bodianus diana Lacepède, 1801	S	DC
Bodianus trilineatus Fowler, 1934	S	DC*
Anampses twistii Bleeker, 1856	S	DC
Cheilinus trilobatus Lacepède, 1801	S	DC
Cheilinus undulates Rüppell, 1835	S	DC
Cheilio inermis Forsskål, 1775	S	DC
Coris aygula Lacepède, 1801	S	DC
Coris caudimacula Quoy and Gaimard, 1834	S	DC
Coris cuvieri Bennett, 1831	S	DC
Coris formosa Bennett, 1830	S	DC
Gomphosus caeruleus Lacepède, 1801	S	DC
Gomphosus varius Lacepède, 1801	S	DC
Halichoeres cosmetus Randall and Smith, 1982	S	DC
Halichoeres hortulanus Lacepède, 1801	S	DC
Halichoeres iridis Randall and Smith, 1982	S	DC
Halichoeres lapillus Smith, 1947	S	DC
Halichoeres nebulosus Valenciennes, 1839	S	DC
Halichoeres scapularis Bennett, 1832	S	DC
Halichoeres zeylonicus Bennett, 1833	S	DC
Halichoeres zulu Randall and King, 2010	S	DC
Labroides bicolor Fowler and Bean, 1928	S	DC
Labroides dimidiatus Valenciennes, 1839	S	DC
Macropharyngodon bipartitus Smith, 1957	S	DC
Macropharyngodon cyanoguttatus Randall, 1978	S	DC*
Novaculichthys taeniourus Lacepède, 1801	S	DC
Pseudocoris heteroptera Bleeker, 1857	S	DC
Thalassoma amblycephalum Bleeker, 1856	S	DC

FAMILIES **Species - Authors**	**Sighting Record**	**Trophic Category**
Thalassoma hebraicum Lacepède, 1801	S	DC
Thalassoma lunare Linnaeus, 1758	S	DC
LUTJANIDAE		
Aprion virescens Valenciennes, 1830	S	Pi
Lutjanus ehrenbergii Peters, 1869	S	NC
Lutjanus fulviflamma Forsskål, 1775	S	NC
Lutjanus gibbus Forsskål, 1775	S	NC
Lutjanus kasmira Forsskål, 1775	S	NC
Lutjanus lutjanus Bloch, 1790	S	NC
Lutjanus monostigma Cuvier, 1828	S	NC
Lutjanus notatus Cuvier, 1828	S	NC
Lutjanus rivulatus Cuvier, 1828	S	NC
Lutjanus sebae Cuvier, 1816	S	NC
Macolor niger Forsskål, 1775	S	NC
Paracaesio sordida Abe and Shinohara, 1962	S	DPL
MALACANTHIDAE		
Malacanthus brevirostris Guichenot, 1848	S	DC
MICRODESMIDAE		
Nemateleotris magnifica Fowler, 1938	S	NPL
Ptereleotris evides Jordan and Hubbs, 1925	S	NPL
Ptereleotris heteroptera Bleeker, 1855	S	DPL
MOLIDAE		
Mola mola Linnaeus, 1758	P	DC
MONACANTHIDAE		
Aluterus scriptus Osbeck, 1765	S	O
Acreichthys tomentosus Linnaeus, 1758	S	DC
Cantherhines fronticinctus Günther, 1867	S	BSI
Cantherhines pardalis Rüppell, 1837	S	BSI
Pervagor janthinosoma Bleeker, 1854	S	NA
Stephanolepis auratus Castelnau, 1861	S	NA
MONOCENTRIDAE		
Cleidopus gloriamaris De Vis, 1882	P	NA
MONODACTYLIDAE		
Monodactylus argenteus Linnaeus, 1758	S	DPL

FAMILIES Species - Authors	Sighting Record	Trophic Category
MULLIDAE		
Mulloidichthys ayliffe Uiblein, 2011	S	NC
Mulloidichthys flavolineatus Lacepède, 1801	S	NC
Mulloidichthys vanicolensis Valenciennes, 1831	S	NC
Parupeneus barberinus Lacepède, 1801	S	DC
Parupeneus indicus Shaw, 1803	S	DC
Parupeneus macronemus Lacepède, 1801	S	DC
Parupeneus trifasciatus Lacepède, 1801	S	DC
MURAENIDAE		
Echidna nebulosa Ahl, 1789	S	NC
Enchelycore pardalis Temminck and Schlegel, 1846	S	Pi
Gymnomuraena zebra Shaw, 1797	S	NC
Gymnothorax breedeni McCosker and Randall, 1977	S	NC
Gymnothorax eurostus Abbott, 1860	S	NC
Gymnothorax favagineus Bloch and Schneider, 1801	S	NC
Gymnothorax flavimarginatus Rüppell, 1830	S	Pi
Gymnothorax griseus Lacepède, 1803	S	NC*
Gymnothorax javanicus Bleeker, 1859	S	NC
Gymnothorax meleagris Shaw, 1795	S	DC
Gymnothorax miliaris Kaup, 1856	S	DC
Gymnothorax nudivomer Günther, 1867	S	NC*
Gymnothorax undulates Lacepède, 1803	S	NC
Rhinomuraena quaesita Garman, 1888	P	Pi
MYLIOBATIDAE		
Aetobatus narinari Euphrasen, 1790	P	DC
Manta alfredi Krefft, 1868	S	DPL
Manta birostris Walbaum, 1792	S	DPL
Mobula japonica Müller and Henle, 1841	S	DPL
ODONTASIPSIDAE		
Carcharias taurus Rafinesque, 1810	S	DC
OPHICHTHIDAE		
Myrichthys colubrinus Boddaert, 1781	S	NC
Myrichthys maculosus Cuvier, 1816	S	NC
Pisodonophis cancrivorus Richardson, 1848	P	NC

FAMILIES **Species - Authors**	**Sighting Record**	**Trophic Category**
OPLEGNATHIDAE		
Oplegnathus robinsoni Regan, 1916	S	O
OSTRACIIDAE		
Lactoria fornasini Bianconi, 1846	S	BSI*
Lactoria cornuta Linnaeus, 1758	S	BSI
Ostracion cubicus Linnaeus, 1758	S	BSI
Ostracion meleagris Shaw, 1796	S	BSI
PEGASIDAE		
Eurypegasus draconis Linnaeus, 1766	S	BSI
PEMPHERIDAE		
Parapriacanthus ransonneti Steindachner, 1870	S	NPL
Pempheris schwenkii Bleeker, 1855	S	NPL
PINGUIPEDIDAE		
Parapercis schauinslandii Steindachner, 1900	S	DC
PLATYCEPHALIDAE		
Papilloculiceps longiceps Cuvier, 1829	S	DC
PLOTOSIDAE		
Plotosus lineatus Thunberg, 1787	S	NC
POMACANTHIDAE		
Apolemichthys trimaculatus Cuvier, 1831	S	O
Centropyge acanthops Norman, 1922	S	O
Centropyge bispinosa Günther, 1860	S	O
Centropyge multispinis Playfair, 1867	S	O
Pomacanthus chrysurus Cuvier, 1831	S	O
Pomacanthus imperator Bloch, 1787	S	O
Pomacanthus rhomboides Gilchrist and Thompson, 1908	S	O*
Pomacanthus semicirculatus Cuvier, 1831	S	BSI
Pygoplites diacanthus Boddaert, 1772	S	BSI
POMACENTRIDAE		
Abudefduf natalensis Hensley and Randall, 1983	S	O
Abudefduf sexfasciatus Lacepède, 1801	S	O
Abudefduf vaigiensis Quoy and Gaimard, 1825	S	O
Amphiprion allardi Klausewitz, 1970	S	O
Amphiprion perideraion Bleeker, 1855	S	O*

FAMILIES **Species - Authors**	**Sighting Record**	**Trophic Category**
Chromis fieldi Randall and DiBattista, 2013	S	DPL
Chromis nigrura Smith, 1960	S	DPL
Chromis opercularis Günther, 1867	S	DPL
Chromis viridis Cuvier, 1830	S	O
Chromis weberi Fowler and Bean, 1928	S	DPL
Chrysiptera brownriggii Bennett, 1828	S	O
Chrysiptera unimaculata Cuvier, 1830	S	O
Dascyllus aruanus Linnaeus, 1758	S	DPL
Dascyllus carneus Fischer, 1885	S	O
Dascyllus trimaculatus Rüppell, 1829	S	DPL
Neopomacentrus cyanomos Bleeker, 1856	S	NA
Plectroglyphidodon dickii Liénard, 1839	S	O
Pomacentrus caeruleus Quoy and Gaimard, 1825	S	O
Pomacentrus pavo Bloch, 1787	S	O
Stegastes fasciolatus Ogilby, 1889	S	H
Stegastes pelicieri Allen and Emery, 1985	S	H
PRIACANTHIDAE		
Priacanthus hamrur Forsskål, 1775	S	NC
PSEUDOCHROMIDAE		
Pseudochromis dutoiti Smith, 1955	S	DC
RACHYCENTRIDAE		
Rachycentron canadum Linnaeus, 1766	S	DC
RHINCODONTIDAE		
Rhincodon typus Smith, 1828	S	DPL
RHINIDAE		
Rhina ancylostoma Bloch and Schneider, 1801	P	NC
RHINOBATIDAE		
Rhinobatus annulatus Müller and Henle, 1841	P	NC
Rhinobatus leucospilus Norman, 1926	S	NC
Rhynchobatus djiddensis Forsskål, 1775	S	NC
SCARIDAE		
Chlorurus cyanescens Valenciennes, 1840	S	H
Chlorurus sordidus Forsskål, 1775	S	H
Scarus ghobban Forsskål, 1775	S	H

FAMILIES **Species - Authors**	**Sighting Record**	**Trophic Category**
Scarus rubroviolaceus Bleeker, 1847	S	H
Scarus scaber Valenciennes, 1840	S	H
Scarus tricolor Bleeker, 1847	S	H
SCOMBRIDAE		
Euthynnus affinis Cantor, 1849	S	DC
Gymnosarda unicolor Rüppell, 1836	S	Pi
Katsuwonus pelamis Linnaeus, 1758	S	DC
Scomberomorus commerson Lacepède, 1801	S	Pi
Scomberomorus plurilineatus Fourmanoir, 1966	P	Pi
Thunnus albacares Bonnaterre, 1788	S	DC
SCORPAENIDAE		
Caracanthus maculatus Gray, 1831	S	NA
Dendrochirus brachypterus Cuvier, 1829	S	NC
Dendrochirus zebra Cuvier, 1829	S	NC
Parascorpaena mossambica Peters, 1855	S	NA
Pterois antennata Bloch, 1787	S	DC
Pterois miles Bennett, 1828	S	Pi
Rhinopias eschmeyeri Condé, 1977	P	Pi*
Rhinopias frondosa Günther, 1892	P	Pi
Scorpaenopsis diabolus Cuvier, 1829	S	Pi
Scorpaenopsis oxycephala Bleeker, 1849	S	Pi
Scorpaenopsis venosa Cuvier, 1829	S	DC
Sebastapistes cyanostigma Bleeker, 1856	S	NA
Taenianotus triacanthus Lacepède, 1802	S	DC
SERRANIDAE		
Cephalopholis argus Schneider, 1801	S	Pi
Cephalopholis miniata Forsskål, 1775	S	NC
Cephalopholis sonnerati Valenciennces, 1828	S	NC
Epinephelus chlorostigma Valenciennes, 1828	S	NC
Epinephelus fasciatus Forsskål, 1775	S	NC
Epinephelus flavocaeruleus Lacepède, 1802	P	Pi
Epinephelus lanceolatus Bloch, 1790	P	NC
Epinephelus macrospilos Bleeker, 1855	S	DC
Epinephelus malabaricus Bloch and Schneider, 1801	S	NC

FAMILIES Species - Authors	Sighting Record	Trophic Category
Epinephelus merra Bloch, 1793	S	Pi
Epinephelus rivulatus Valenciennes, 1830	S	Pi
Epinephelus tauvina Forsskål, 1775	S	Pi
Epinephelus tukula Morgans, 1959	S	NC
Grammistes sexlineatus Thunberg, 1792	S	NC
Nemanthias carberryi Smith, 1954	S	DPL
Plectropomus punctatus Quoy and Gaimard, 1824	S	Pi
Pogonoperca punctata Valenciennes, 1830	S	NC*
Pseudanthias evansi Smith, 1954	S	DPL
Pseudanthias squamipinnus Peters, 1855	S	DPL
SIGANIDAE		
Siganus luridus Rüppell, 1829	S	H
Siganus sutor Valenciennes, 1835	S	H
SOLEIDAE		
Solea turbynei Gilchrist, 1904	S	NA
SPARIDAE		
Chrysoblephus puniceus Gilchrist and Thompson, 1908	S	DC
Diplodus hottentotus Smith, 1844	S	DC
SPHRYNIDAE		
Sphyrna lewini Griffith and Smith, 1834	S	DC
SPHYRAENIDAE		
Sphyraena putnamae Jordan and Seale, 1905	S	NC
STEGOSTOMATIDAE		
Stegostoma fasciatum Hermann, 1783	S	NC
SYNANCEIIDAE		
Synanceia verrucosa Bloch and Schneider, 1801	S	Pi
SYNGNATHIDAE		
Corythoichthys intestinalis Ramsay, 1881	P	DC
Doryrhamphus dactyliophorus Bleeker, 1853	S	DPL
Hippocampus borboniensis Duméril, 1870	S	DPL*
Hippocampus camelopardalis Bianconi, 1854	P	DPL*
Hippocampus histrix Kaup, 1856	S	DPL
Hippocampus kuda Bleeker, 1852	S	DPL
Solenostomus cyanopterus Bleeker, 1854	S	DC

FAMILIES **Species - Authors**	**Sighting Record**	**Trophic Category**
Trachyrhamphus bicoarctatus Bleeker, 1857	S	NA
SYNODONTIDAE		
Synodus dermatogenys Fowler, 1912	S	Pi
Synodus jaculum Russell and Cressey, 1979	S	Pi
TETRAODONTIDAE		
Arothron hispidus Linnaeus, 1758	S	NC
Arothron meleagris Anonymous, 1798	S	NC
Arothron nigropunctatus Bloch and Schneider, 1801	S	NC
Arothron stellatus Anonymous, 1798	S	NC
Canthigaster amboinensis Bleeker, 1864	S	H
Canthigaster bennetti Bleeker, 1854	S	O
Canthigaster janthinoptera Bleeker, 1855	S	O
Canthigaster smithae Allen and Randall, 1977	S	O*
Canthigaster solandri Richardson, 1845	S	O
Canthigaster valentine Bleeker, 1853	S	O
TETRAROGIDAE		
Ablabys binotatus Peters, 1855	S	NA
Ablabys macracanthus Bleeker, 1852	S	NA
TORPEDINIDAE		
Torpedo marmorata Risso, 1810	S	Pi
Torpedo spp.	S	Pi
ZANCLIDAE		
Zanclus cornutus Linnaeus, 1758	S	DC

Trophic Categories: Herbivore (H); Omnivore (O); Browser of Sessile Invertebrates (BSI); Diurnal Carnivore (DC); Nocturnal Carnivore (NC); Piscivore (Pi); Diurnal Planktivore (DPL); Nocturnal Planktivore (NPL); Unknown (NA)

Discussion

This is the first assessment of ichthyofaunal diversity of the seas around Praia do Tofo and Praia da Barra in southern Mozambique. Through the use of underwater observations supplemented by past records, 353 species were recorded from the coral reefs spanning 40 km of the southern coastline of Inhambane province. These results provide a higher estimation of fish species richness than is predicted by the Coral Fish Diversity Index. The diversity of the PTPB area is similar to that recorded in other areas of the southwestern Indian Ocean where visual observations have been the primary data collection method (Table 3) (Maggs *et al.*, 2010; Chabanet & Durville, 2005; Gillibrand *et al.*, 2007; Durville *et al.*, 2003). In particular, SR_{theor} shows high similarity to areas in southern Mozambique and South Africa that are fully or partially protected (e.g. Floros *et al.*, 2012; Maggs *et al.*, 2010; Pereira *et al.*, 2004).

The sub-tropical reefs of the PTPB area have low levels of coral cover (Motta *et al.*, 2002), which may be assumed to result in a low diversity of fish communities (Komyakova *et al.*, 2013). However, the current study found a relatively high fish species richness which is comparable to areas with higher coral cover (e.g. Gillibrand *et al.*, 2007; Table 3). This may be partly explained

Table 3. The diversity of reef fish species and families from other areas in the southwestern Indian Ocean. SRobs = recorded species richness; SRtheor = theoretical species richness predicted by the Coral Fish Diversity Index (Allen & Werner, 2002).

Location	Geographical Coordinates	SR_{obs}	SR_{theor}	No. of families	SR_{obs} to no. of families ratio (2 d. p.)	Source
Praia do Tofo and Praia da Barra	23°51'S, 33°54'E	353	329	79	4.47:1	Present study
Bazaruto Archipelago National Park	21°43'S, 35°27'E	249	359	40	6.23:1	Maggs *et al.* 2010
Maputo Bay	26°S, 32°54'E	327	349	58	5.64:1	Schleyer & Pereira, 2014
Juan de Nova	17°03'S, 42°43'E	299	423	55	5.44:1	Chabanet & Durville, 2005
Andavadoaka	22°05'S, 43°12'E	334	430	58	5.76:1	Gillibrand *et al.* 2007
Glorieuses Islands	11°33'S, 47°20'E	332	451	57	5.82:1	Durville *et al.* 2003
St. Lucia Marine Reserve	27°44'S, 32°40'E	258	349	48	5.38:1	Floros *et al.* 2012
Mafia Island	7°52'S, 39°45'E	394	515	56	7.04:1	Garpe & Ohman, 2003
Europa Island	22°21'S, 40°21'E	389	468	62	6.27:1	Fricke *et al.* 2013
Ponta do Ouro Partial Marine Reserve	26°27'S, 32°56'E	376	318	90	4.18:1	Pereira *et al.* 2004

by the extensive visual sampling design used. The high sampling time employed in this study (over 36 hours of underwater observations) allowed for the observation of some cryptic species that would be missed by shorter visual surveying. For example, four species of gobies and eight species of blennies were recorded on reefs of PTPB (Table 2). Therefore, while visual censuses generally do not accurately capture the diversity of cryptobenthic species (Ackerman & Bellwood, 2000), this limitation can be reduced through extensive sampling. A high number of families were also recorded in comparison to other areas in the region (Table 3), suggesting a high proportion of uncommon species were observed. The impact of greater sampling effort on species records is evident in the results of Gillibrand *et al.* (2007). These authors examined a smaller area than the current study and recorded 334 species by conducting visual observations across a twelve month period. In contrast, Chabanet & Durville (2005) recorded more than 50 fewer species around Juan de Nova Island through 30 hours of visual surveying. This highlights that sampling effort does not solely account for the high fish diversity recorded in the PTPB area.

The present study necessarily examined a large depth range (1-32 m) in order to capture the range of habitats present in the area. As such, a higher number of specialist species are expected to have been identified due to the wider variety of physical habitats and biological conditions (Bridge *et al.*, 2016; Jankowski *et al.*, 2015). Significant changes in fish assemblages with depth have been observed in previous studies (Friedlander & Parrish, 1998) and this is likely to be the same in the current study. This may also explain the high number of families observed (Table 3).

Coastal upwelling in these seas drive high levels of primary productivity and in turn supports abundant populations of large charismatic species (Rohner *et al.*, 2014). It is also likely to influence the reef fish diversity of the area, potentially boosting species richness in two ways. Firstly, cooler waters allow the area to support

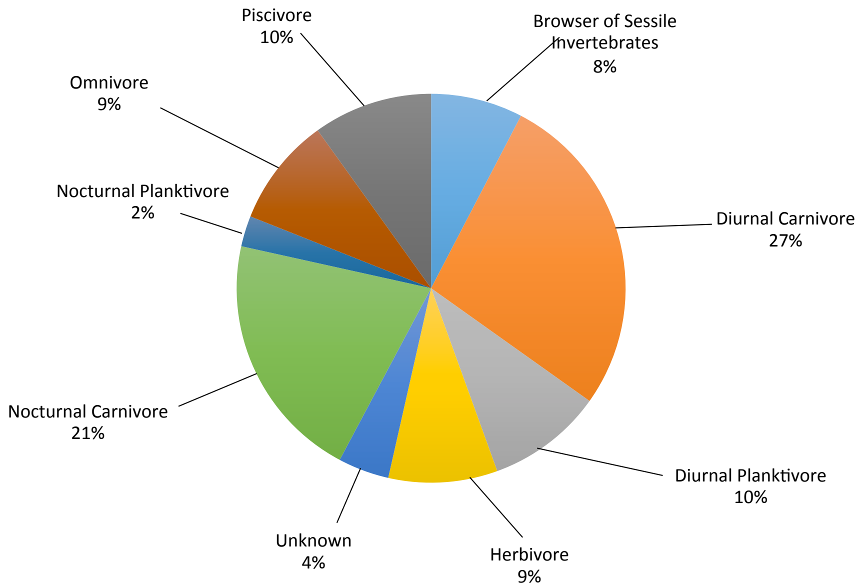

Figure 2. Trophic structure of the PTPB reef fish community estimated from past literature.

species more common in temperate waters (e.g. *Seriola lalandi*, *Oplegnathus robinsoni*). Anderson *et al.* (2015) proposed the appearance of species characteristic of higher latitudes in their sub-tropical study site to regions of cool water upwelling. In the current study water temperatures were recorded between 18-29°C; the influx of cool water may be influencing diversity in the sub-tropical PTPB area. Secondly, upwelling supports high plankton abundance which can reduce competitive exclusion in planktivorous species (Abrams, 1995). This would allow the co-existence of more species on lower trophic levels; an effect which may then propagate up the food chain to produce a higher diversity of secondary and tertiary consumers. The relationship between primary productivity and diversity has been previously acknowledged (Waide *et al.*, 1999). However, the recorded proportion of planktivores in this study is very similar to other areas of the southwestern Indian Ocean (Table 4). Therefore, the effect of high primary productivity in reducing competitive exclusion, if present, appears not to influence this trophic level.

Table 4. Trophic structure recorded from other areas of the southwestern Indian Ocean.

Location	Carnivores (incl. planktivores; % of total)	Planktivores (% of total)	Herbivores (% of total)	Omnivores (% of total)	Source
Bazaruto Archipelago National Park	76	10	12	12	Maggs *et al.*, 2010
Praia do Tofo and Praia da Barra	78	12	9	9	Present study
Juan de Nova	73	13	16	11	Chabanet & Durville, 2005
Andavadoaka	76	11	13	11	Gillibrand *et al.*, 2007
Glorieuses Islands	73	15	15	12	Durville *et al.*, 2003
Geyser and Zelee Banks	72	17	16	12	Chabanet *et al.*, 2002

Carnivores, *sensu lato*, represented the vast majority of the fish diversity in the PTPB area. The relative proportions of carnivores, omnivores and herbivores are similar to other areas in the region (Table 4), supporting the observation of Kulbicki (1988) that the trophic structure of fish communities is consistent across a region. It may suggest that these reefs are in good health (as per Harmelin-Vivien, 1979); however, caution should be exercised when using trophic structure to imply reef health in this instance due to the potentially confounding effect of high primary productivity.

This study demonstrates that the PTPB area is biologically rich beyond its resident megafauna populations, and indicates additional value to the ecotourism industry in the region. Whilst the relatively large sampling extent precludes comprehensive comparisons with other studies in the southwestern Indian Ocean, the results show that the reef ecosystems of PTPB host a fish community comparable to more isolated, or protected areas. This suggests that these reefs are in relatively good condition despite a large associated human population. The high proportion of carnivores recorded here supports this suggestion; however, local upwelling make these metrics questionable measures of reef health. Therefore, targeted research is needed to examine the current health status of these reefs and to provide a stronger baseline for monitoring impacts of future expansion of tourism and fishing activities in the area.

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