

Inventory and Spatial Assemblage Study of Reef Fish in the Area of Andavadoaka, South-West Madagascar (Western Indian Ocean)

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Abstract—This study represents the first qualitative census of the reef fish assemblage of coral reefs in the vicinity of Andavadoaka, south-west Madagascar. Observational data of fish species sightings were collected over the course of a year, while visual census data, with low observer bias, detailing fish assemblage from the four major reef zones of the area were collected in a shorter 5-week period. A total of three hundred and thirty four (334) species from 58 families were recorded throughout the year, while one hundred and eighty seven (187) species were observed during the shorter assemblage study. The trophic habits of the fish population are comparable with other sites in the Western Indian Ocean, and suggest a healthy fish community, despite evidence of broad-scale damage from coral bleaching and associated mortality. The authors suggest that this can be explained by current relatively low levels of anthropogenic impacts from fishing. However, given the extent of regional reef degradation, fish species diversity may now be particularly vulnerable to future anthropogenic or climatic disturbances, such as increased fishing effort or renewed coral bleaching episodes.

INTRODUCTION

Although there have been a number of studies detailing fish populations in Madagascar (Maugé 1967; Harmelin-Vivien 1977; Harmelin-Vivien 1979), few have been undertaken in the last 3 decades, and no such studies have been carried out in the remote northern areas of the large emergent reef system of the South-West of Madagascar. This extensive reef system stretches from Androka in the south to Morombe in the north, a total distance of some 458km (Cooke *et al.* 2000). In the region of Toliara, the reef forms a large barrier (the Grand Récif de Tulear), while further to the north this barrier fragments, comprising a series of patch reefs and fringing reefs, the latter found both adjacent

to the coast and surrounding barrier islands and sand cays.

The region's southern reefs were studied in the 1970s (Clausade *et al.* 1971; Pichon, 1972; Battistini, 1960), although the majority of research focussed on the physical structure and benthic communities of the reefs (Pichon, 1974). Of the few studies of reef fish that have been undertaken in the area, almost all have been restricted to the Grand Récif de Tulear (Maugé, 1967; Harmelin-Vivien, 1977; Harmelin-Vivien, 1979). Coral reefs throughout the region provide a vital resource base for local traditional and artisanal fisheries.

Marine biodiversity is threatened throughout the world's oceans (Bellwood *et al.* 2004; Sala & Nnwlton 2006; Worm *et al.* 2006). From a biogeographical perspective, marine diversity

checklists are critical to identifying geographical variations in species distributions between regions. This knowledge forms a fundamental precursor to understanding processes regulating marine biodiversity, and predicting potential consequences of biodiversity loss to ecosystem function (Bellwood & Hughes 2001). In the Indo-Pacific province such diversity assessments provide a means of understanding longitudinal and latitudinal gradients of species richness away from the Indo-Philippines 'centre' of marine biodiversity (Hughes *et al.* 2002). Coral reef fish species inventories for the western Indian Ocean region are limited in their coverage (Chabanet & Durville 2005) and no data have yet been published detailing reef fish assemblages for the northern areas of the south-west Madagascar reef system. Of particular importance to diversity assessments in the region is a better understanding of faunal differences between the extensive coral reefs of south-west Madagascar and other sites in the south-west Indian Ocean. This study aims to address this gap in published records, presenting research from Andavadoaka to provide

an ichthyological baseline for this poorly known region.

MATERIALS AND METHODS

Description of study site

The small fishing village of Andavadoaka ($22^{\circ}07'S$, $43^{\circ}23'E$, Fig. 1), situated at the extreme northern end of this reef system, some 140 km north of the Grand Récif, lies on the edge of a shallow lagoon, protected from the open Mozambique Channel by extensive coral reefs. In addition to the fringing reefs that characterise much of the coastal marine environment of the south-west, several banks rise up in the shallow waters on the seaward side of these reefs, and a series of 5 offshore islands, numerous uninhabited islets and submerged barrier reefs also support substantial coral growth.

The Andavadoaka reef system comprises 3 major reef types: inshore fringing reefs; seaward fore-reefs and lagoonal patch reefs. Inshore

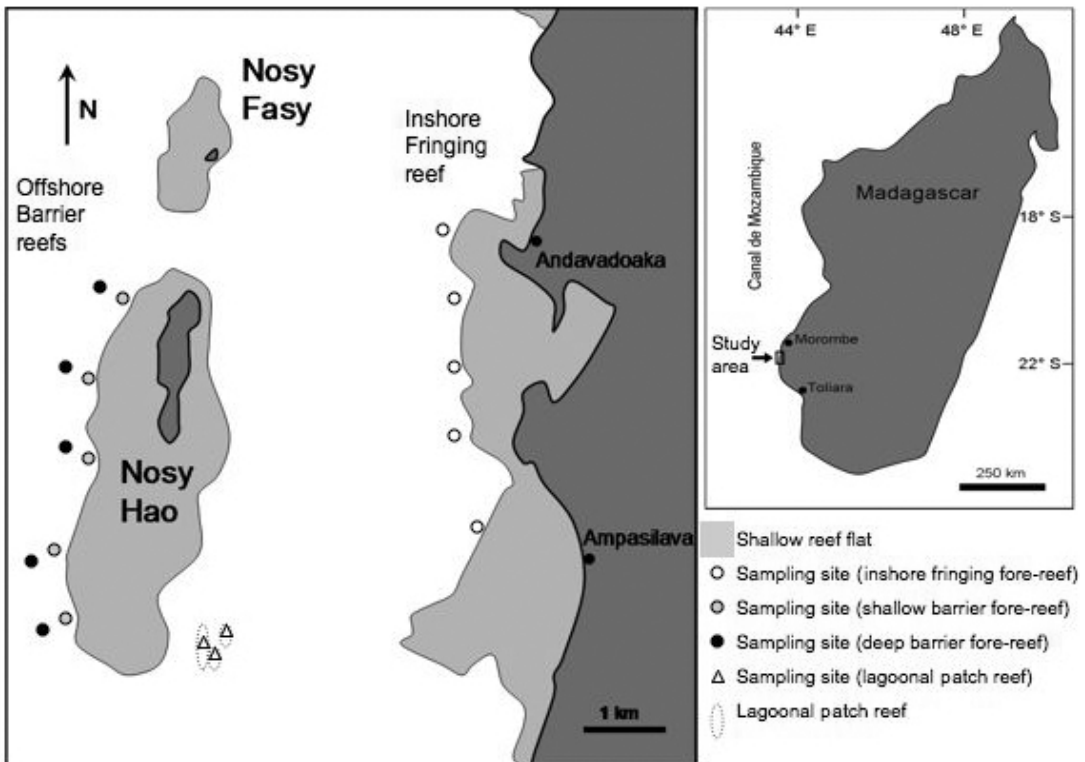


Fig. 1. Location of Andavadoaka and positions of spatial assemblage survey sites

fringing reefs are found adjacent to the coast, following the length of much of the coastline in the region, descending to, and terminating at, the lagoonal floor at approximately 10 m depth. These reefs mark the start of a wide lagoon, between 10 and 30 m in depth, which runs to approximately 8 km offshore before shelving more steeply towards the continental shelf break. Between 6 and 8 km offshore, a broken line of islands and sand cays, each fringed on the seaward side by a barrier fore-reef, protects much of the shallow lagoonal environment from open ocean swells. Within the lagoon itself numerous small patch reefs can be found between 10 and 30 m depth (Figure 1).

Methodology

In order to establish baseline data to compile a regional inventory of fish species present in the region, ongoing sightings of all species were recorded by the authors from all day-time research dives undertaken for a period of one year at reefs throughout the Andavadoaka region, between April 2004 and April 2005.

Alongside this total species census, surveys of spatial assemblages of fish populations were undertaken at a number of selected sites within the region's reef systems, in order to ascertain relative species abundance between different reef types within the region. These studies were carried out through the collection of site-specific fish species assemblage data during daytime dives at the end of the austral summer (February-March 2005) over a 5-week period.

For this site-specific study, inshore fringing fore-reefs were surveyed at a depth of between 5 and 10m. Patch reefs were surveyed at depths between 10 and 18m, and barrier fore-reefs were surveyed in two depth zones; 5-10m and 10-18m. Surveys of all sites were performed by a visual census technique using a single observer to minimise observer bias, according to the visual census methodology of English *et al.* (1997), using 30 minute timed swims, with careful recording of each species observed on an underwater slate. Species unidentifiable *in situ* were recorded with a camera for subsequent expert identification. Estimates of numbers of individuals of each species were made using a semi-quantitative

root 4 scale to facilitate recording of large numbers of fish, as shown in Table 1.

Visual censuses typically underestimate cryptic species (Fowler, 1987). Moreover, it is not possible to standardise the survey effort spent in actively 'hunting' for cryptic species that might be camouflaged on the benthos or concealed in reef crevices. Therefore to minimise observer bias, only non-cryptic species were recorded for the site-specific spatial assemblage study: species that required active searching on the reef were not included. For the purpose of this study, non-cryptic fish species were considered as all fish species not showing cryptic patterning or behaviour, and being large enough to be clearly and immediately visible to surveyors, thus not skewing results of surveys. In excluding cryptic species it was assumed that the proportion of cryptic species at a reef site remains approximately constant between different sites and depths of coral reefs. Based on this assumption, this preclusion would not affect measures of the relative species abundance between sites.

Each selected geomorphological class or reef (inshore fringing fore-reefs; patch reefs; shallow barrier fore-reefs; and deep barrier fore-reefs) was surveyed at five randomly selected survey sites, with the exception of the patch reefs, which were surveyed three times (Figure 1). Efforts were made to ensure that different survey sites within each geomorphological class of reef showed a similar reefscape (Gonzalez-Gandara *et al.* 1999) to the other survey sites carried out within that geomorphological reef class. In addition, the time of surveying was standardised between 0900 and 1400 to avoid the possible effect of temporal variation in assemblages. To minimise the effect of disturbance caused by divers entering the water, prior to each survey divers waited for 5 minutes to allow the fish in the area to return to normal behaviour.

Data Analysis

In addition to basic descriptive analysis of data, multivariate analyses were carried out to test for differences between samples. It was recognised that similarities between samples calculated on original species abundance values were likely to be dominated by a small number of highly abundant species. The root 4 transformation ($\sqrt[4]{y}$),

Table 1: Inventory of the reef fishes of the Andavadoaka region (depths 0-30m). Species in bold observed during spatial assemblage survey

Species	Feeding Habit	Species	Feeding Habit
CARCHARINIDAE		<i>Synanceia verrucosa</i> Bloch & Schneider, 1801	
<i>Carcharhinus falciformis</i> (Müller & Henle, 1839)	6		6
<i>Triaenodon obesus</i> (Rüppell, 1837)	4	SERRANIDAE	
SPHYRNIDAE		<i>Aethaloperca rogae</i> (Forsskål, 1775)	
<i>Sphyrna lewini</i> (Griffith & Smith, 1834)	6	<i>Anyperodon leucogrammicus</i> (Valenciennes, 1828)	6
DASYATIDAE		<i>Cephalopholis argus</i> Bloch & Schneider, 1801	
<i>Taeniura lymma</i> (Forsskål, 1775)	5	<i>Cephalopholis miniata</i> (Forsskål, 1775)	5
MOBULIDAE		<i>Cephalopholis urodeta</i> (Forster, 1801)	
<i>Manta birostris</i> (Walbaum, 1792)	7	<i>Epinephelus caeruleopunctatus</i> (Bloch, 1790)	6
<i>Mobula japonica</i> (Müller & Henle, 1841)	7	<i>Epinephelus fasciatus</i> (Forsskål, 1775)	5
MURAENIDAE		<i>Epinephelus flavocaeruleus</i> (Lacepède, 1801)	
<i>Echidna nebulosa</i> (Ahl, 1789)	5	<i>Epinephelus hexagonatus</i> (Forster in Bloch & Schneider, 1801)	5
<i>Gymnomuraena zebra</i> (Shaw, 1797)	5	<i>Epinephelus lanceolatus</i> (Bloch, 1790)	5
<i>Gymnothorax favagineus</i> Bloch & Schneider, 1801	5	<i>Epinephelus malabaricus</i> (Bloch & Schneider, 1801)	5
<i>Gymnothorax flavimarginatus</i> (Rüppell, 1830)	6	<i>Epinephelus merra</i> Bloch, 1793	6
<i>Gymnothorax javanicus</i> (Bleeker, 1859)	5	<i>Epinephelus ongus</i> Bloch, 1790	5
<i>Gymnothorax meleagris</i> (Shaw, 1795)	4	<i>Epinephelus rivulatus</i> (Valenciennes, 1830)	6
<i>Gymnothorax undulatus</i> (Lacepède, 1803)	5	<i>Epinephelus spilotoceps</i> Schultz, 1953	5
<i>Pseudechidna</i> sp (Bleeker, 1859)	5	<i>Epinephelus tukula</i> Morgans, 1959	5
<i>Rhinomuraena quaesita</i> Garman, 1888	6	<i>Nemanthias carberryi</i> Smith, 1954	7
<i>Siderea picta</i> (Ahl, 1789)	5	<i>Plectropomus laevis</i> (Lacepède, 1801)	5
SYNODONTIDAE		<i>Plectropomus punctatus</i> Quoy & Gaimard, 1824	
<i>Saurida gracilis</i> (Quoy & Gaimard, 1824)	6	<i>Pseudanthias squamipinnis</i> Peters, 1855	7
<i>Synodus dermatogenys</i> Fowler, 1912	6	<i>Variola albimarginata</i> Baissac, 1953	6
HOLOCENTRIDAE		<i>Variola louti</i> (Forsskål, 1775)	
<i>Myripristis adusta</i> Bleeker, 1853	8	APOGONIDAE	
<i>Myripristis berndti</i> Jordan & Evermann, 1903	5	<i>Apogon aureus</i> (Lacepède, 1802)	
<i>Myripristis</i> sp Cuvier, 1829	5	<i>Apogon cookii</i> Macleay, 1881	
<i>Myripristis kuntzei</i> Valenciennes, 1831	8	<i>Apogon cyanosoma</i> Bleeker, 1853	
<i>Myripristis murdjan</i> Forsskål, 1775	8	<i>Apogon fraenatus</i> Valenciennes, 1832	
<i>Neoniphon sammara</i> Forsskål, 1775	5	<i>Archamia fucata</i> (Cantor, 1849)	
<i>Sargocentron caudimaculatum</i> Rüppell, 1838	5	<i>Cheilodipterus macrodon</i> (Lacepède, 1802)	
<i>Sargocentron diadema</i> Lacepède, 1802	5	<i>Cheilodipterus quinquelineatus</i> Cuvier, 1828	
<i>Sargocentron melanospilos</i> Bleeker, 1858	5		
<i>Sargocentron spiniferum</i> Forsskål, 1775	5	PRIACANTHIDAE	
AULOSTOMIDAE		<i>Priacanthus hamrur</i> (Forsskål, 1775)	
<i>Aulostomus chinensis</i> (Linnaeus, 1766)	6	GERREIDAE	
FISTULARIDAE		<i>Gerres oyena</i> (Forsskål, 1775)	
<i>Fistularia commersonii</i> Rüppell, 1838	4	HAEMULIDAE	
SCORPAENIDAE		<i>Diagramma pictum</i> (Thunberg, 1792)	
<i>Pterois antennata</i> (Bloch, 1787)	4	<i>Plectorhinchus chubbi</i> (Regan, 1919)	
<i>Pterois</i> sp Cuvier, 1829	4	<i>Plectorhinchus flavomaculatus</i> (Cuvier, 1830)	
<i>Pterois miles</i> (Bennett 1825)	6		
<i>Scorpaenopsis</i> sp Randall & Eschmeyer, 2001	6		
<i>Scorpaenopsis diabolus</i> (Cuvier, 1829)	6		

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Species	Feeding Habit	Species	Feeding Habit
<i>Plectorhinchus gaterinus</i> (Forsskål, 1775)	5	<i>Parupeneus rubescens</i> (Lacepède, 1801)	4
<i>Plectorhinchus orientalis</i> (Bloch, 1793)	4	KYPHOSIDAE	
<i>Plectorhinchus picus</i> (Cuvier, 1830)	4	<i>Kyphosus cinerascens</i> Forsskål, 1775	1
<i>Plectorhinchus plagiodesmus</i> Fowler, 1935	4	EPHIPPIDAE	
<i>Plectorhinchus playfairi</i> (Pellegrin, 1914)	4	<i>Platax orbicularis</i> (Forsskål, 1775)	2
<i>Plectorhinchus sordidus</i> (Klunzinger, 1870)	5	POMACANTHIDAE	
LUTJANIDAE		<i>Apolemichthys trimaculatus</i> (Lacepède, 1831)	2
<i>Aprion virescens</i> Valenciennes, 1830	6	<i>Centropyge acanthops</i> (Norman, 1922)	2
<i>Lutjanus argentimaculatus</i> (Forsskål, 1775)	5	<i>Centropyge bispinosus</i> (Günther, 1860)	2
<i>Lutjanus bohar</i> (Forsskål, 1775)	5	<i>Centropyge multispinis</i> (Playfair, 1867)	2
<i>Lutjanus fulviflamma</i> (Forsskål, 1775)	5	<i>Pomacanthus chrysurus</i> (Cuvier, 1831)	2
<i>Lutjanus fulvus</i> (Forster in Bloch & Scheider, 1801)	5	<i>Pomacanthus imperator</i> (Bloch, 1787)	3
<i>Lutjanus gibbus</i> (Forsskål, 1775)	5	<i>Pomacanthus semicircularatus</i> (Cuvier, 1831)	3
<i>Lutjanus kasmira</i> (Forsskål, 1775)	5	<i>Pygoplites diacanthus</i> (Boddaert, 1772)	3
<i>Lutjanus lutjanus</i> Bloch, 1790	5	CHAETODONTIDAE	
<i>Lutjanus monostigma</i> (Cuvier, 1828)	5	<i>Chaetodon auriga</i> Forsskål, 1775	3
<i>Lutjanus notatus</i> (Cuvier, 1828)	5	<i>Chaetodon bennetti</i> Cuvier in Cuvier & Valenciennes, 1831	3
<i>Lutjanus sebae</i> (Cuvier, 1816)	5	<i>Chaetodon blackburni</i> Desjardins, 1836	3
<i>Macolor niger</i> (Forsskål, 1775)	5	<i>Chaetodon falcula</i> Bloch, 1793	3
CAESIONIDAE		<i>Chaetodon guttatissimus</i> Bennett, 1832	3
<i>Caesio caerulea</i> Lacepède, 1801	7	<i>Chaetodon unimaculatus interruptus</i> Ahl, 1923	3
<i>Caesio lunaris</i> Cuvier, 1830	7	<i>Chaetodon kleinii</i> Bloch, 1790	3
<i>Caesio striata</i> Rüppell, 1830	7	<i>Chaetodon lineolatus</i> (Quoy & Gaimard, 1831 in Cuvier & Valenciennes)	3
<i>Caesio xanthonota</i> Bleeker, 1853	7	<i>Chaetodon lunula</i> (Lacepède, 1802)	3
<i>Pterocaesio capricornis</i> Smith & Smith, 1963	7	<i>Chaetodon madagaskariensis</i> Ahl, 1923	3
<i>Pterocaesio chrysozona</i> (Cuvier, 1828)	7	<i>Chaetodon melannotus</i> (Bloch & Schneider, 1801)	3
<i>Pterocaesio marri</i> (Schultz, 1953)	7	<i>Chaetodon meyeri</i> Bloch & Schneider, 1801	3
<i>Pterocaesio tile</i> (Cuvier, 1830)	7	<i>Chaetodon trifascialis</i> Quoy & Gaimard, 1825	3
LETHRINIDAE		<i>Chaetodon trifasciatus</i> Mungo Park, 1797	3
<i>Gnathodentex aurolineatus</i> (Lacepède, 1802)	5	<i>Chaetodon vagabundus</i> Linnaeus, 1758	3
<i>Lethrinus borbonicus</i> Valenciennes, 1830	5	<i>Chaetodon xanthocephalus</i> Bennett, 1832	3
<i>Lethrinus conchyliaius</i> (Smith, 1959)	5	<i>Chaetodon zanzibariensis</i> Playfair, in Playfair & Günther, 1867	3
<i>Lethrinus harak</i> (Forsskål, 1775)	5	<i>Forcipiger longirostris</i> (Broussonet, 1782)	2
<i>Lethrinus lentjan</i> (Lacepède, 1802)	5	<i>Hemitaenichthys zoster</i> (Bennett, 1831)	7
<i>Lethrinus microdon</i> Valenciennes, 1830	5	<i>Heniochus acuminatus</i> (Linnaeus, 1758)	3
<i>Lethrinus nebulosus</i> (Forsskål, 1775)	5	<i>Heniochus monoceros</i> (Cuvier, 1831)	3
<i>Lethrinus obsoletus</i> (Forsskål, 1775)	5	ECHENEIDAE	
<i>Lethrinus olivaceus</i> Valenciennes, 1830	5	<i>Echeneis naucrates</i> Linnaeus, 1758	5
<i>Monotaxis grandoculis</i> (Forsskål, 1775)	5	CARANGIDAE	
MULLIDAE		<i>Carangoides ferdau</i> (Forsskål, 1775)	4
<i>Mulloidichthys flavolineatus</i> (Lacepède, 1801)	5	<i>Carangoides fulvoguttatus</i> (Forsskål, 1775)	4
<i>Mulloidichthys vanicolensis</i> (Valenciennes, 1831)	5	<i>Caranx ignobilis</i> (Forsskål, 1775)	4
<i>Parupeneus barberinus</i> (Lacepède, 1801)	4		
<i>Parupeneus trifasciatus</i> (Lacepède, 1801)	4		
<i>Parupeneus cyclostomus</i> (Lacepède, 1801)	4		
<i>Parupeneus indicus</i> (Shaw, 1803)	4		
<i>Parupeneus macronema</i> (Lacepède, 1801)	4		
<i>Parupeneus pleurostigma</i> (Bennett, 1832)	4		

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Species	Feeding Habit	Species	Feeding Habit
<i>Caranx melampygus</i> Cuvier & Valenciennes, 1833	4	<i>Pomacentrus trichrourus</i> Günther, 1877	2
<i>Caranx heberi</i> (Bennet 1830)	4	<i>Pomacentrus trilineatus</i> Cuvier, 1830	2
<i>Elagatis bipinnulata</i> (Quoy & Gaimard, 1825)	4	<i>Stegastes fasciolatus</i> (Ogilby, 1889)	1
<i>Gnathanodon speciosus</i> (Forsskål, 1775)	4		
		LABRIDAE	
CIRRHITIDAE		<i>Anampses caeruleopunctatus</i> Rüppell, 1829	4
<i>Cirrhitiichthys oxycephalus</i> (Bleeker, 1855)	4	<i>Anampses meleagrides</i> Valenciennes, 1840	4
<i>Cirrhitis pinnulatus</i> (Forster, 1801)	4	<i>Anampses twistii</i> Bleeker, 1856	4
<i>Paracirrhites arcatus</i> Cuvier in Cuvier & Valenciennes, 1829	4	<i>Bodianus anthioides</i> Bennett, 1832	4
<i>Paracirrhites forsteri</i> (Bloch & Schneider, 1801)	4	<i>Bodianus axillaris</i> Bennett, 1832	4
		<i>Bodianus bilunulatus bilunulatus</i> (Lacepède), 1801	4
PEMPHERIDAE		<i>Bodianus diana</i> Lacepède, 1801	4
<i>Parapriacanthus ransonneti</i> Steindachner, 1870	8	<i>Cheilinus chlorourus</i> Bloch, 1791	4
<i>Pempheris oualensis</i> Cuvier, 1831	8	<i>Cheilinus fasciatus</i> fasciatus Bloch, 1791	4
<i>Pempheris schwenkii</i> Bleeker, 1855	8	<i>Cheilinus trilobatus</i> Lacépède, 1801	4
<i>Pempheris vanicolensis</i> Cuvier, 1831	8	<i>Cheilinus undulatus</i> Rüppell, 1835	4
		<i>Cheilio inermis</i> Forsskål, 1775	4
POMACENTRIDAE		<i>Coris aygula</i> Lacepède, 1801	4
<i>Abudefduf natalensis</i> Hensley & Randall, 1983	2	<i>Coris caudimacula</i> Quoy & Gaimard, 1834	4
<i>Abudefduf notatus</i> (Day, 1870)	2	<i>Epibulus insidiator</i> Pallas, 1770	4
<i>Abudefduf septemfasciatus</i> (Cuvier, 1830)	2	<i>Gomphosus caeruleus caeruleus</i> Lacepède, 1801	4
<i>Abudefduf sexfasciatus</i> (Lacepède, 1801)	2	<i>Halichoeres hortulanus</i> Lacepède, 1801	4
<i>Abudefduf sordidus</i> (Forsskål, 1775)	2	<i>Halichoeres scapularis</i> Bennett, 1832	4
<i>Abudefduf sparoides</i> (Quoy & Gaimard, 1825)	2	<i>Halichoeres sp.</i>	4
<i>Abudefduf vaigiensis</i> (Quoy & Gaimard, 1825)	2	<i>Hemigymnus fasciatus</i> Bloch, 1792	4
<i>Amblyglyphidodon indicus</i> Allen & Randall, 2002	2	<i>Hemigymnus melapterus</i> Bloch, 1791	4
<i>Amphiprion akallopisos</i> Bleeker, 1853	2	<i>Hologymnosus annulatus</i> Lacepède, 1801	4
<i>Amphiprion latifasciatus</i> Allen, 1972	2	<i>Hologymnosus dolatus</i> Lacepède, 1801	4
<i>Chromis dimidiata</i> (Klunzinger, 1871)	7	<i>Labroides bicolor</i> Fowler & Bean, 1928	4
<i>Chromis lepidolepis</i> Bleeker, 1877	7	<i>Labroides dimidiatus</i> Valenciennes, 1839	4
<i>Chromis leucura</i> Gilbert, 1905	2	<i>Macropharyngodon bipartitus</i> Smith, 1957	4
<i>Chromis nigrura</i> Smith, 1960	7	<i>Novaculichthys macrolepidotus</i> Bloch, 1791	4
<i>Chromis ternatensis</i> (Bleeker, 1856)	7	<i>Oxycheilinus diagrammus</i> Lacepède, 1801	4
<i>Chromis viridis</i> Cuvier, 1830	2	<i>Stethojulis albovittata</i> Bonnaterre, 1788	4
<i>Chromis weberi</i> Fowler & Bean, 1928	7	<i>Thalassoma amblycephalum</i> Bleeker, 1856	4
<i>Chrysiptera annulata</i> (Peters, 1855)	2	<i>Thalassoma hardwicke</i> Bennett, 1830	4
<i>Chrysiptera unimaculata</i> (Cuvier, 1830)	2	<i>Thalassoma hebraicum</i> Lacepède, 1801	4
<i>Dascyllus aruanus</i> (Linnaeus, 1758)	7	<i>Thalassoma lunare</i> Linnaeus, 1758	4
<i>Dascyllus carneus</i> Fischer, 1885	2	<i>Thalassoma trilobatum</i> Lacepède, 1801	4
<i>Dascyllus trimaculatus</i> (Rüppell, 1829)	7	<i>Wetmorella albofasciata</i> Schultz & Marshall, 1954	4
<i>Neoglyphidodon melas</i> (Cuvier, 1830)	4	<i>Xyrichtys pavo</i> Valenciennes, 1840	4
<i>Plectroglyphidodon dickii</i> (Liénard, 1839)	2		
<i>Plectroglyphidodon lacrymatus</i> (Quoy & Gaimard, 1825)	2	SCARIDAE	
<i>Pomacentrus baenschi</i> Allen, 1991	2	<i>Calotomus carolinus</i> (Valenciennes, 1840)	1
<i>Pomacentrus caeruleus</i> Quoy & Gaimard, 1825	2	<i>Cetoscarus bicolor</i> (Rüppell, 1829)	1
<i>Pomacentrus sulfureus</i> Klunzinger, 1871	2	<i>Chlorurus cyaneascens</i> (Valenciennes, 1840)	1
		<i>Chlorurus sordidus</i> (Forsskål, 1775)	1
		<i>Chlorurus strongylocephalus</i> (Bleeker, 1854)	1
		<i>Hipposcarus harid</i> (Forsskål, 1775)	1
		<i>Scarus caudofasciatus</i> (Günther, 1862)	1
		<i>Scarus festivus</i> Valenciennes in Cuvier & Valenciennes, 1840	1
		<i>Scarus frenatus</i> Lacepède, 1802	1

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Species	Feeding Habit	Species	Feeding Habit
<i>Scarus ghobban</i> Forsskål, 1775	1	<i>Naso hexacanthus</i> (Bleeker, 1855)	1
<i>Scarus globiceps</i> Valenciennes, 1840	1	<i>Naso unicornis</i> (Forsskål, 1775)	1
<i>Scarus niger</i> Forsskål, 1775	1	<i>Naso vlamingi</i> (Valenciennes, 1835)	7
<i>Scarus rubroviolaceus</i> Bleeker, 1847	1	<i>Paracanthurus hepatus</i> (Linnaeus, 1766)	7
<i>Scarus russelli</i> Valenciennes, 1840	1	<i>Zebrasoma velifer</i> (Bloch, 1795)	1
<i>Scarus scaber</i> Valenciennes in Cuvier & Valenciennes, 1840	1	<i>Zebrasoma gemmatum</i> (Valenciennes, 1835)	1
<i>Scarus tricolor</i> Bleeker, 1847	1	<i>Zebrasoma scopas</i> (Cuvier, 1829)	1
SPHYRAENIDAE		ZANCLIDAE	
<i>Sphyræna barracuda</i> (Walbaum, 1792)	4	<i>Zanclus canescens</i> (Linnaeus, 1758)	3
<i>Sphyræna flavicauda</i> Rüppell, 1838	4	SIGANIDAE	
<i>Sphyræna sp</i> Cuvier, 1829	6	<i>Siganus argenteus</i> (Quoy & Gaimard, 1825)	1
PINGUIPEDIDAE		<i>Siganus luridus</i> (Rüppell, 1829)	1
<i>Parapercis hexophthalma</i> (Cuvier, 1829)	4	<i>Siganus stellatus</i> (Forsskål, 1775)	1
BLENNIDAE		<i>Siganus sutor</i> (Valenciennes, 1835)	1
<i>Ecsenius nalolo</i> Smith, 1959	1	BOTHIDAE	
<i>Meiacanthus mossambicus</i> Smith, 1959	1	<i>Bothus pantherhinus</i> (Rüppell, 1830)	5
<i>Plagiotremus rhinorhynchus</i> (Bleeker, 1852)	8	SCOMBRIDAE	
<i>Plagiotremus tapeinosoma</i> (Bleeker, 1857)	2	<i>Gymnosarda unicolor</i> (Rüppell, 1836)	6
MICRODESMIDAE		<i>Scomberomorus commerson</i> (Lacepède, 1800)	6
<i>Gunnelichthys sp</i> Dawson, 1968	7	BALISTIDAE	
<i>Nemateleotris magnifica</i> Fowler, 1938	7	<i>Balistapus undulatus</i> (Mungo Park, 1797)	4
<i>Ptereleotris evides</i> (Jordan & Hubbs, 1925)	7	<i>Balistoides conspicillum</i> (Bloch & Schneider, 1801)	4
GOBIIDAE		<i>Balistoides viridescens</i> (Bloch & Schneider, 1801)	4
<i>Amblyeleotris steinitzi</i> (Klausewitz, 1974)	4	<i>Melichthys niger</i> (Bloch, 1786)	2
<i>Amblygobius tekomaji</i> (Whitley, 1940)	4	<i>Odonus niger</i> (Rüppell, 1836)	4
<i>Cryptocentrus strigilliceps</i> (Jordan & Seale, 1906)	4	<i>Rhinecanthus aculeatus</i> (Linnaeus, 1758)	4
<i>Gobiodon citrinus</i> (Rüppell, 1838)	4	<i>Sufflamen bursa</i> (Bloch & Schneider, 1801)	4
<i>Istigobius decoratus</i> (Herre, 1927)	4	<i>Sufflamen chrysopterus</i> (Bloch & Schneider, 1801)	4
<i>Oplopomus oplopomus</i> Valenciennes, 1837	4	MONACANTHIDAE	
<i>Valenciennæna strigata</i> (Broussonet, 1782)	4	<i>Amanses scopas</i> (Cuvier, 1829)	3
ACANTHURIDAE		<i>Cantherhines pardalis</i> (Rüppell, 1837)	3
<i>Acanthurus dussumieri</i> Valenciennes, 1835	1	<i>Oxymonacanthus longirostris</i> (Bloch & Schneider, 1801)	3
<i>Acanthurus leucosternon</i> Bennet, 1833	1	OSTRACIIDAE	
<i>Acanthurus lineatus</i> (Linnaeus, 1758)	1	<i>Ostracion cubicus</i> (Linnaeus, 1758)	3
<i>Acanthurus mata</i> Russell in Cuvier, 1829	7	<i>Ostracion meleagris</i> Shaw, 1796	3
<i>Acanthurus nigricauda</i> Duncker & Mohr, 1929	1	TETRADONTIDAE	
<i>Acanthurus nigrofuscus</i> (Forsskål, 1775)	1	<i>Arothron hispidus</i> (Linnaeus, 1758)	5
<i>Acanthurus tennentii</i> Günther, 1861	1	<i>Arothron immaculatus</i> (Bloch & Schneider, 1801)	5
<i>Acanthurus thompsoni</i> Fowler, 1923	1	<i>Arothron meleagris</i> (Lacepède, 1798)	5
<i>Acanthurus triostegus triostegus</i> (Linnaeus, 1758)	1	<i>Arothron nigropunctatus</i> Bloch &	
<i>Ctenochaetus binotatus</i> Randall, 1955	1		
<i>Ctenochaetus striatus</i> (Quoy & Gaimard, 1825)	1		
<i>Ctenochaetus strigosus</i> (Bennet, 1828)	1		
<i>Naso annulatus</i> (Quoy & Gaimard, 1825)	1		
<i>Naso brevirostris</i> (Cuvier, 1829)	1		
<i>Naso elegans</i> (Rüppell, 1829)	1		

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Species	Feeding Habit
Schneider, 1801	5
<i>Arothron stellatus</i> (Bloch & Schneider, 1801)	5
<i>Canthigaster bennetti</i> (Bleeker, 1854)	2
<i>Canthigaster solandri</i> (Richardson, 1845)	2
<i>Canthigaster valentini</i> (Bleeker, 1853)	2
<i>Torquigener flavimaculosus</i> Hardy & Randall, 1983	2
DIODONTIDAE	
<i>Diodon liturosus</i> Shaw, 1804	5
BELONIDAE	
<i>Strongylura incisa</i> (Valenciennes, 1846)	6
<i>Tylosurus crocodilus</i> (Péron & Lesueur, 1821)	6
CENTRISCIDAE	
<i>Aeoliscus strigatus</i> (Günther, 1860)	4
DACTYLOPTERIDAE	
<i>Dactyloptena orientalis</i> (Cuvier, 1829)	5
GRAMMISTIDAE	
<i>Grammistes sexlineatus</i> Thunberg, 1793	5
HEMIRAMPHIDAE	
<i>Hemiramphus far</i> Forsskål, 1775	2
NEMIPTERIDAE	
<i>Scolopsis bimaculatus</i> Rüppell, 1828	4
<i>Scolopsis ghanam</i> (Forsskål, 1775)	4
<i>Scolopsis vosmer</i> (Bloch, 1792)	4
ORECTOLOBIDAE	
<i>Stegostoma fasciatum</i> (Hermann, 1783)	5
PLATYCEPHALIDAE	
<i>Papillociliceps longiceps</i> (Cuvier, 1829)	4
PLOTOSIDAE	
<i>Plotosus lineatus</i> (Thunberg, 1787)	5
PSEUDOCROMIDAE	
<i>Pseudochromis dutoiti</i> Smith, 1955	4
RHINOBATIDAE	
<i>Rhynchobatus djiddensis</i> (Forsskål, 1775)	5
SPARIDAE	
<i>Acanthopagrus bifasciatus</i> (Forsskål, 1775)	4
SYNGNATHIDAE	
<i>Corythoichthys</i> sp Dawson & Randall, 1975	4
<i>Doryramphus excisus</i> Kaup, 1856	7

Feeding Habits- 1: Herbivore, 2: Omnivore, 3: Browser of Sessile Invertebrates, 4: Diurnal Carnivore, 5: Nocturnal Carnivore, 6: Piscivore, 7: Diurnal Planktivore, 8: Nocturnal Planktivore

applied when recording data in the field, provided a means of down-weighting the importance of highly abundant species so that sample similarities depended not only on their values but also those of less common ('mid-range') species. Hierarchical agglomerative clustering with group-average linking, based on Bray-Curtis sample similarities (appropriate for delineating groups into distinct community structure) was used to find natural groupings of samples using Primer 6 multivariate analysis software. Sites were then discriminated on the basis of their species composition using non-metric multi-dimensional scaling (MDS) and analysis of similarities (ANOSIM) testing, the latter routine being used to identify significant differences between groups of samples defined a priori. By using the non-metric MDS approach, different reef sites (samples) can be considered to have differing fish community compositions when different samples derived from one reef site form a cluster that is distinct from replicates within other sites.

A theoretical value of species richness (SR_{th}) was calculated, based on the regression formula produced by Allen & Werner (2002), to account for the effect of sampling effort in results obtained from the global species census, and to facilitate comparative analysis of species richness data with other reference sites in the Indo-Pacific region. Calculation of SR_{th} is based on an index of fish diversity (coral reef fish diversity index, CFDI). CFDI is equal to the total number of species observed within the acanthuridae, scaridae, labridae, pomacentridae pomacanthidae and chaetodontidae. The theoretical value $SR_{th} = 4.234$ (CFDI) – 114.446.

In order to analyse spatial variation in trophic assemblages of species recorded at study sites during the one-year study, species were categorised to one of 8 trophic levels using data from previous studies described in literature (Hiatt & Strasburg 1960; Hobson 1974; Harmelin-Vivien 1979) and from FishBase (<http://www.fishbase.org>). The 8 categories of feeding habits were: herbivore; omnivore; browser of sessile invertebrates; diurnal carnivore; nocturnal carnivore; piscivore; diurnal planktivore; and nocturnal planktivore. This approach also enabled subsequent trophic assemblage comparisons with other analyses

conducted in the region (Durville *et al.* 2003, Chabanet & Durville 2005). Planktivores feeding on fish nekton were classified as planktivores rather than piscivores in order to be consistent with the studies of Harmelin-Vivien (1979) and Hiatt & Strasburg (1960).

RESULTS

Species Richness

During the year-long study, a total of 334 species was observed, representing 58 families (Table 1). Of these, 7 species were cartilaginous (Class Chondrichthyes), while the remaining 327 species were bony fish (Class Osteichthyes). 48.2% of the species observed belonged to seven major families: labridae (36 species); pomacentridae (31 species); serranidae (23 families); acanthuridae (22 species); chaetodontidae (18 species); scaridae (16 species); and lutjanidae (12 species). Of the remaining 51 families, 23 showed only a single species. During the 5-week period of the spatial assemblage study, 187 species were observed, 56% of the total number of species recorded in the year-long study.

Trophic Structure

76% of total species observed were carnivores, feeding on fish, invertebrates or zooplankton (Fig. 2). Of these, the largest number of species observed (28% of the total) were diurnal carnivores, such as the labridae. The nocturnal carnivores (such as lethrinidae and lutjanidae) were the second most highly represented, showing 21% of the total species observed. Piscivores (serranidae), browsers of sessile invertebrates (chaetodontidae) and diurnal planktivores (caesionidae) are similarly represented, each showing 8% of total species observed. The final group of carnivores, the nocturnal planktivores (such as apogonidae) are represented by 3% of the total species observed. Omnivores (such as pomacentridae) and herbivores (mainly acanthuridae and scaridae) each represented 11% of the total species observed.

Spatial variation in assemblage

Survey stations showed strong similarity in assemblage within reef types, and distinct dissimilarities in assemblage between different reef types (Figures 3 and 4). MDS ordination plots

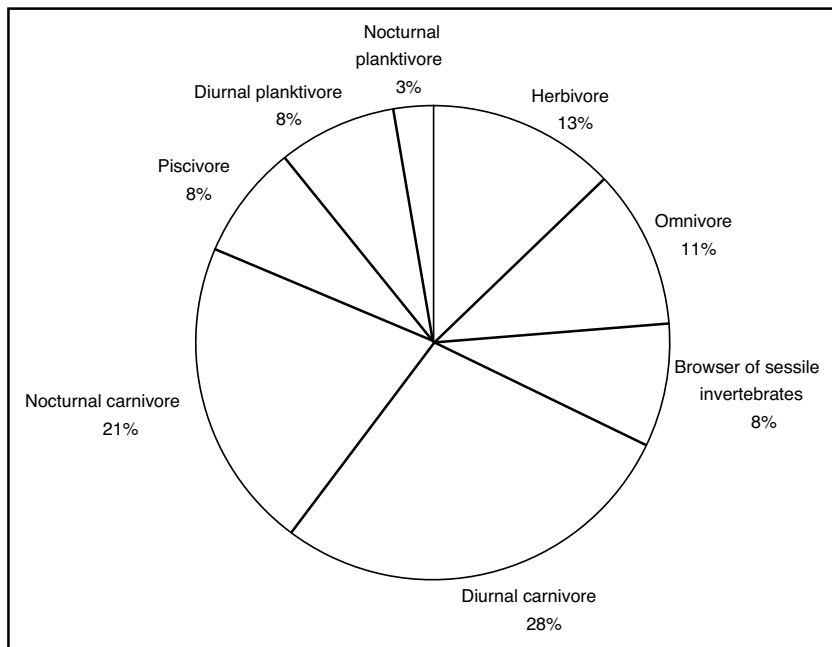


Fig. 2. Trophic guilds of fish species observed in Andavadoaka, expressed as percentage of total species observed during the year-long census study

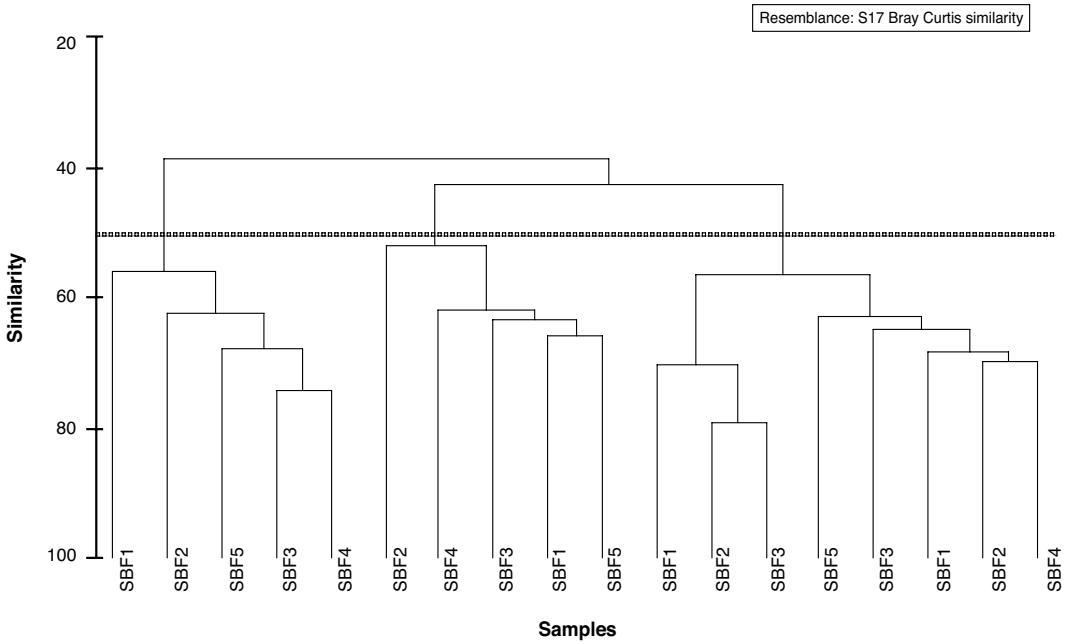


Fig. 3. Hierarchical agglomerative clustering with group-average linking, based on Bray-Curtis sample similarities (appropriate for delineating sample groups by similar community compositions), showing natural groupings of samples from spatial assemblage study (DBF = deep barrier fore-reef; SBF = shallow barrier fore-reef, SFF = shallow fringing fore-reef, DP = deep patch reef)

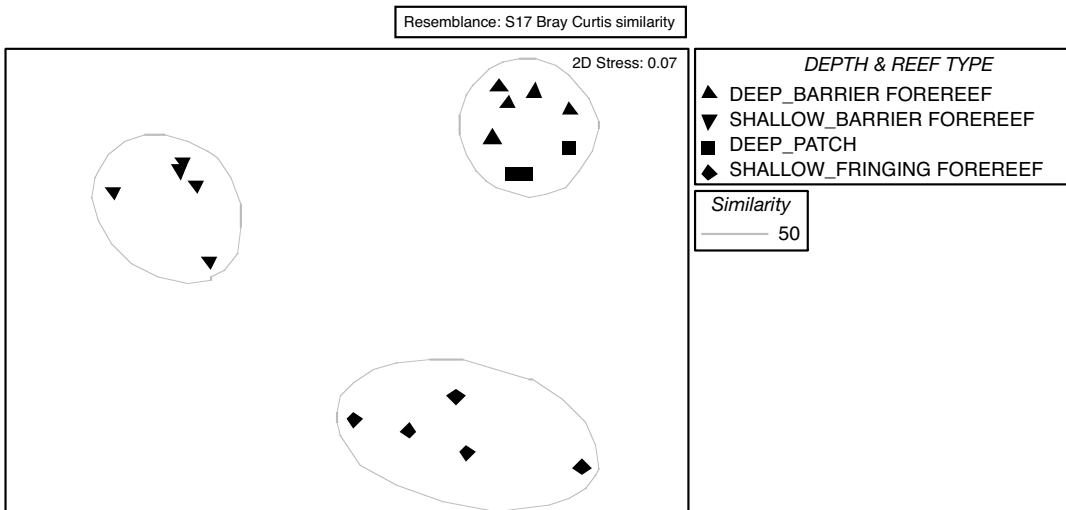


Fig. 4. Non-metric MDS ordination of samples (all depths, all reef types) based on root 4 transformed fish species abundance data showing Bray-Curtis grouping of samples at 50% resemblance

representing samples as points in 2-dimensional space (such that the relative distances between points represent the rank order of Bray-Curtis dissimilarities of samples) provide a useful means of showing similarities in reef composition between sites. Samples split convincingly between depths

and reef types (Figure 4), with the exception of samples from deep barrier forereef and patch reef sites, which group together and independently of other reef types. Superimposition of Bray-Curtis similarity clusters (Figure 3) on this ordination plot emphasises relationships between sample groups.

This observation does not imply that groups have no characteristics in common, but that different characteristic patterns of fish assemblage are found consistently within the different groups. These differences are confirmed by results of a 2-way crossed ANOSIM test for differences between depths and reef zones across all samples. Results show total separation of samples between depths (global $R = 1.0$, $p = 0.8\%$) and very strong separation between reef types (global $R = 0.98$, $p = 0.1\%$). In both cases, the observed sample statistic and significance level rejects the null hypotheses that there is no difference in fish species assemblage between different depths and reef types. Fish species assemblages found at deep barrier fore-reef and lagoonal patch reef sites show the strongest between-group similarities (Figure 4): deep barrier fore-reef areas showed an average of 82 species per survey, very similar to the lagoonal patch reefs (average 88 species per survey). All shallow fore-reef and inshore fringing reef survey sites showed markedly lower numbers of species per survey (59 and 61 respectively).

DISCUSSION

Species Richness

A total of 334 species was observed over the year of sampling. As with all visual censuses, underestimation of cryptic species makes it likely that total species numbers are considerably higher than those found in this study (Fowler, 1987). Seasonal variation was observed in certain species, most noticeably in the seasonal arrival of large shoals of *Sphyraena flavicauda* in the months of February and March. The majority of reef species (for example *Ctenochaetus striatus*) were present in surveys throughout the year. This figure of species richness is comparable to that found during other studies in the Western Indian Ocean (Durville *et al.* 2003; Chabanet 1994; Chabanet 2002; Chabanet & Durville 2005; Harmelin-Vivien 1979), although some of these studies were performed over much shorter time periods (Durville *et al.* 2003; Chabanet 2002) with more intensive sampling than was possible during this study (Durville *et al.* 2003). The 187 species observed in the limited sampled

surveying during 5 weeks of the spatial assemblage study may represent a temporal “snapshot” of species present at the specific reef zones studied. The species richness for Andavadoaka is higher than that found for the Glorieuses Islands (332 species; Durville *et al.* 2003), Juan de Nova (299 species; Chabanet & Durville 2005), Geyser and Zéléé (294 species; Chabanet 1994), Réunion (257 species; Chabanet, 1994) and Mayotte (239 species; Chabanet 2002). These results are also consistent with the usual trend of isolated island-associated reefs to show lower diversity than equivalent areas associated with larger land masses (Randall, 1998). According to the CFDI predictor formula an approximate total of 453 species could be expected, indicating that 73% of the predicted total fish fauna was surveyed. This difference is proportionately similar to published theoretical (SR_{th}) versus observed (SR_{obs}) species richness values for other sites in the region (Chabanet & Durville 2005).

Despite their comparatively higher species richness, Andavadoaka’s reefs are subject to chronic and rapidly growing subsistence and commercial fishing pressures which are not experienced at less exploited reference sites in the Western Indian Ocean (notably Glorieuses Islands, Juan de Nova, and Geyser and Zéléé). Fishing is the primary economic activity for 71% of Andavadoaka’s population of 1200 (Blue Ventures Conservation unpublished data), and communities throughout the region fish for subsistence as well as for income, selling catches to a rapidly growing commercial export market. The population of the Toliara grew by 324% between 1975 and 1993 (Cooke *et al.* 2000) and limited employment opportunities and low agricultural productivity resulted in a five-fold increase in the region’s fishing population in a period of 17 years leading up until the early 1990s (McVean *et al.*, 2005). Andavadoaka has seen a doubling of population input rate (births and immigration arrivals per year) in the 10 years leading up to 2003, with over 50% of the population being 14 or under (Blue Ventures Conservation unpublished data).

Alongside direct fishing pressure, the reefs of south-west Madagascar have experienced widespread degradation as a result of the coral bleaching and mortality events of 1998 and 2001 (Cooke, 2003). Almost all shallow reef areas in

the region are now highly degraded. Low levels of hard coral and high algal dominance in these areas have resulted in a structurally poor environment, particularly in shallow reef environments; a factor which has been shown to lead to lower fish species richness in other areas (Gratwicke & Speight, 2005).

The adverse effects of bleaching-associated coral mortality and fishing on coral reef fish species richness are well documented (McClanahan 1994; Wantiez *et al.* 1997; Jones *et al.* 2004). It is likely that Andavadoaka's fish species richness has been reduced by these impacts. Supporting this assertion, the two areas of shallow reef studied showed lower species numbers than the deeper areas. These shallow sites experience greater fishing pressures than deeper reefs, and are likely to have experienced greater thermal stress than deeper sites during bleaching events.

Andavadoaka's species richness is far higher than that found on the Grand Récif of Toliara in 1979 by Harmelin-Vivien, despite experiencing widespread reef mortality which was not present at the time of the 1979 study. Fishing pressures were also unlikely to have been at existing levels of intensity during the 1979 Toliara study, which is currently the only comparable fish biodiversity assessment for southern Madagascar. The higher species richness recorded in Andavadoaka, despite their current degraded status, suggests that the area is of significant regional importance for fish biodiversity and conservation.

Trophic Structure

Despite the degraded state of Andavadoaka's shallower reefs, which could be expected to impact the number of carnivorous species observed on the reef (Harmelin-Vivien 1992), 74% of species

observed were carnivores. According to Harmelin-Vivien (1979), observed carnivore levels on a healthy reef are usually between 60 and 80%, depending on geographic location. This suggests that the fish communities of Andavadoaka are in good health, despite the high fishing effort and mortality episodes that have occurred over the last decade. This indication is similar to that of Durville *et al.* (2003), who also found very little impact on fish populations following a bleaching event; although in this case the reefs of the Glorieuses islands are dominated by calcareous algae rather than hard corals, and fish populations may have been less susceptible to the effects of reef bleaching than at Andavadoaka reefs.

Notwithstanding these observations of encouraging species richness in Andavadoaka, the longer-term impacts of past mortality events on fish trophic structure and species richness remain to be seen. If Andavadoaka's degraded reefs remain in an algal-dominated state they are likely to suffer further physical deterioration, erosion and decreasing structural complexity, leading to loss of species within key functional groups of reef fish, and substantial reductions of species richness, as has been recorded elsewhere in the south-west Indian Ocean (Graham *et al.* 2006).

Durville *et al.* (2003) have compared the levels of carnivores/omnivores/herbivores across the western Indian Ocean area, to which the findings of the current study have been added (see Table 3). These data support the assertion of Durville *et al.* that the reefs of the Glorieuses islands and also other reefs of the Mozambique Channel (Geysler, Mayotte, Juan de Nova) come closest to the reefs of south-west Madagascar in terms of reef fish trophic structure.

Spatial variation in assemblage

With the exception of the deep barrier fore-reef and patch reef sites, there are distinct differences in assemblage between reef types, with pronounced differences between the two shallow reef types as well as between shallow and deep sites. It is well established that fish assemblages change along a depth gradient (Harmelin-Vivien, 1977; McGehee, 1994; Williams, 1991), however within this study the additional large difference between

Table 2. Log 4 abundance scale

Root 4 value	Abundance
0:	0
1:	1-4
2:	5-16
3:	17-64
4:	65-256
5:	257+

Table 3. Trophic structure of the fish communities, expressed in percentage of total number of species on different Indo-Pacific coral reefs

		Carnivores	Omnivores	Herbivores
Tuléar (Madagascar)	Harmelin-Vivien, 1979	74	13.5	12.5
Réunion	Chabanet, 1994	51	24	25
Mayotte	Chabanet, 2002	69	12.5	18.5
Geyser & Zélée	Chabanet <i>et al.</i> , 2002	69	16	15
Glorieuses	Durville <i>et al.</i> , 2003	73	12	15
Juan de Nova	Chabanet & Durville, 2005	73	16	11
Andavadoaka (Madagascar)	This study	76	11	13

the two shallow study areas (barrier fore-reef and inshore fringing fore-reef) indicates that there are contributing factors other than depth alone. Both sites are considered to have suffered extensive degradation from the bleaching events of 1998 and 2001 (Cooke, 2002), however the proximity of the inshore fringing fore-reef to the coast, and its easy accessibility to fishers, means that fishing pressure is much higher at this shallow near-shore reef system. The deep-water reef-fishing techniques of the indigenous Vezo population (currently limited to line fishing) play a role in limiting over-exploitation of the deeper reefs, and it is possible that populations of reproductive adults at deeper, less exploited, reef sites may support continued recruitment at more degraded sites in the area, thus maintaining species richness of the shallower sites. In addition to experiencing lower biomass removal through fishing, the shallow barrier fore-reef is a much higher-energy system with greater architectural complexity, exhibiting pronounced spur and groove formations. This habitat is constantly exposed to the prevailing sea surge, and as such is unsuitable for the establishment of territorial benthic herbivores such as pomacentridae. Conversely, the inshore fringing reef is a much lower energy environment, sheltered by the barrier islands and wide lagoon, and capable of supporting higher populations of benthic territorial grazers. As evidence for this suggestion, shallow fore-reef areas showed higher numbers of non-territorial herbivorous species, such as acanthuridae and scaridae, and fewer benthic territorial herbivores.

CONCLUSION

This baseline study indicates that, despite broad-scale loss of reef structure due to bleaching-related coral

mortality, reef fish populations in Andavadoaka are similar both in terms of species richness and trophic structure to those of more “pristine” reefs studied elsewhere in the western Indian Ocean, and have not decreased from historical pre-bleaching studies undertaken elsewhere in southern Madagascar. This observation suggests not only that the levels of bleaching and subsequent reef degradation in Andavadoaka have not yet been sufficient alone to produce the catastrophic decreases in fish biodiversity observed elsewhere (Cumming *et al.* 2000; Bruno *et al.* 2001) but also that direct anthropogenic impacts from fishing have not yet caused a reduction of fish species richness in the Andavadoaka region.

At a local level, however, there are distinct differences in species richness between the four reef types studied in Andavadoaka, which may be due, in part, to fishing pressure. Shallow reefs (shallow barrier fore-reef and inshore fringing fore-reefs) have been heavily degraded by bleaching events and show lower numbers of species and lower abundance of species than deeper sites (deep barrier fore-reef and deep patch reef). In the event of intensified anthropogenic or increased natural and climatic stresses on the region’s reefs (for example a change in fishing gear technology, increase in exploitation, direct reef damage by commercial trawlers, or further severe or prolonged bleaching event), the current low coral cover and poor structural complexity of the region’s reefs may make them vulnerable to a collapse in fish populations and ecosystem function. In light of current growth rates of coastal populations, and predictions of continued increases in sea surface temperature as a result of global climate change (West & Salm, 2003), it is likely that stresses on southern Madagascar’s reef environments will increase, making them more

vulnerable to the potentially severe detrimental effects associated with artisanal fisheries (Watson & Ormond, 1994).

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