Journal of the Marine Biological Association of the United Kingdom, 2018, 98(2), 387–400. © Marine Biological Association of the United Kingdom, 2016
doi:10.1017/S0025315416001399

Linkage between fish functional groups and coral reef benthic habitat composition in the Western Indian Ocean

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Benthic habitat composition is a key factor that structures assemblages of coral reef fishes. However, natural and anthropogenic induced disturbances impact this relationship. This study investigates the link between benthic habitat composition and fish functional groups in four countries in the Western Indian Ocean (WIO). Benthic composition of 32 sites was quantified visually from percentage cover of hard and soft corals, rubble, turf, fleshy and crustose coralline algae. At each site, abundance of 12 coral-associated fish functional groups in 50 × 5 m transects was determined. Cluster analysis characterized reefs based on benthic cover and revealed five habitat types (A, B, C, D and E) typified by decreasing cover of hard corals, increasing cover of turf and/or fleshy algae and differences in benthic diversity. Habitat type A was present in all four countries. Other habitats types showed geographic affiliations: notably Comoros sites clustered in either habitats B or E, northern Madagascar had B, C and D type habitats, whereas sites in central Tanzania and northern Mozambique had habitats D and E. Fish functional groups showed significant linkages with some habitat types. The abundances of corallivores, invertivores, detritivores and grazers were higher in habitat B, whereas planktivores and small excavators showed lower abundances in the same habitat. These linkages between benthic habitat types and fish functional groups are important in informing priority reefs that require conservation and management planning.

Keywords: Ecosystem functionality, reef resilience management, SIMPROF, spatial characterization, phase-shifts

Submitted 13 May 2016; accepted 2 September 2016; first published online 10 October 2016

INTRODUCTION

Habitat composition is a significant environmental factor that structures assemblages of reef fishes (Pereira *et al.*, 2014). Studies on coral reef habitats have mainly proposed and focused on quantification of benthic reef variables encompassing corals (hard, soft and dead corals), invertebrates and algae (calcareous, coralline, turf and fleshy algae) (Obura & Grimsditch, 2009; McClanahan *et al.*, 2011). Of particular interest has been the empirical quantification of the relationship between percentage cover of benthic reef variables, reef fish assemblages and the impacts of fishing (Jennings *et al.*, 1995; Bergman *et al.*, 2000). A strong relationship does exist between benthic habitat structure and fish community and most importantly, the benthic structure influences the relative abundance of fish functional groups (Khalaf & Kochzius 2002a; Garpe & Ohman, 2003; Pittman *et al.*, 2007). Moreover, benthic habitat composition and distribution, and its link with fish abundances and biomass are important in understanding the ecological status of marine environments (Jennings *et al.*, 1995).

Few functional-based fish studies have been reported within the WIO region (e.g. Jennings *et al.*, 1995; Khalaf & Kochzius, 2002a; Samoilys & Randriamanantsoa, 2011) in comparison to taxonomy-based fish investigations (e.g. Samoilys, 1988; Khalaf & Kochzius, 2002b; Kochzius, 2007; McClanahan & Humphries, 2012) despite an increased interest in functionality studies over the last decade (Caliman *et al.*, 2010). Ecosystem functionality emphasizes functional groups and multiple processes involved in transfer of energy and matter over time and space (Reiss *et al.*, 2009). In this regard ecosystem functioning entails the composite effects of all processes that sustain an ecosystem. The relevance of focusing on a functionality approach is to enable description of community-level feeding patterns and determine how for instance, the benthic habitat is influenced by fish functional groups and which species or taxa are critical in maintaining an ecosystem (Edwards *et al.*, 2014). More so, functional diversity as opposed to species diversity augments the ecosystem processes. Two concepts support the functionality approach: (1) concept of redundancy – performance of the same ecological role by several species, and (2) concept of functional groups – grouping of species according to their functional roles. More often feeding guilds are assumed to be synonymous to functional groups representing an assemblage of species performing indistinguishable functions, regardless of their taxonomic affinities (Bellwood *et al.*, 2004). Due to limitation of time and resources, selection of species or taxa to be counted is paramount, though the choice should be informed by prior ecological studies (Bellwood & Wainwright, 2002; Samoilys & Randriamanantsoa, 2011).

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This study investigates the link between the composition of benthic habitats and fish functional groups. The study specifically seeks to characterize the difference between benthic habitats based on benthic cover composition, and assess the linkage of fish functional groups' relative abundances, functional diversity and biomass to the benthic habitats. To achieve these objectives benthic and fish data were collected to test the following null hypotheses: (1) all four geographic areas are similar in benthic habitat composition; (2) there is no association of fish functional groups for particular benthic habitats; and (3) there is no difference in biomass of fish functional groups across different benthic habitats.

MATERIALS AND METHODS

Study area

Benthic and fish surveys were done between March 2010 and October 2011 at 32 sites in Tanzania, Mozambique, Comoros and Madagascar (Figure 1, Table 1). Sites were selected haphazardly and ranged from shallow, fringing protected reefs to deep, exposed fore-reef slopes to maximize the range of reef habitats in each country, though constrained by time and resources. Reef type of each site was defined based on the coral reef habitats in the Atlas of Western Indian Ocean Coral Reefs (Andréfouët *et al.*, 2009). The sites were further categorized based on their exposure to oceanic seas and trade winds (Table 1).

Benthic surveys

Benthic composition was assessed to give a broad-scale indication of the structure and condition of the coral reefs considering the equilibrium between corals and algae. It was quantified visually from the benthic variables comprising percentage cover of live hard and soft corals, fleshy, turf and crustose coralline algae (CCA), and rubble. Live hard corals constitute the calcified reef building corals; soft corals are the non-reef building corals lacking a rigid calcium carbonate skeleton; fleshy algae are the non-calcareous brown and green algae with large fronds; turf algae are assemblages of green, red and brown algae that are considered inhibitors of corals. CCA are calcified encrusting algae varying from whitish to dark brown colour and considered important in promoting coral recruitment and binding of reef framework. Rubble is the available loose substratum indicating suitability for coral recruitment and growth (Obura & Grimsditch, 2009). At each site, one or two visual estimates of the benthic variables were undertaken following methods developed by the International Union for Conservation of Nature (IUCN) working group on Climate Change and Coral Reefs (Obura & Grimsditch, 2009). The methods were similar to manta tow techniques (Sweatman *et al.*, 2001) and involved rapid assessment of benthic variables by visually sampling a broad-scale area, usually with no or low replication.

Fish surveys

Fish survey sites corresponded to the same sites as the benthic surveys, and were done to assess the health of coral reefs. A broad range of taxa was selected for the surveys that were then assigned to specific trophic groups relevant in assessing health of the coral reefs, where health refers to the reef's ecological resilience – its ability to resist threats and to recover to a healthy state when an impact does occur (Table 2). Fish densities and size classes of selected taxa were estimated using Underwater Visual Census (UVC) belt transect (English *et al.*, 1994; Samoilys, 1997; Samoilys & Carlos 2000). The selected taxa comprised species representing seven main fish functional groups: piscivores, omnivores, corallivores, invertivores, planktivores, detritivores and herbivores (Table 2). The herbivores further constituted an ecologically diverse group consisting of six functional groups: large excavators, small excavators, scrapers, browsers, grazers and grazers-detritivores (after Green & Bellwood 2009). Fish were counted in 50 × 5 m transects with generally $N = 5$ transects per reef site, collected on two dives (stations), or occasionally only $N = 3$ replicate transects from one station where a second dive was not possible (Table 1). During each dive, the minimum and maximum depths for the station was recorded. In each transect, fish were surveyed to species level so that they could be easily assigned to an appropriate trophic group. However, the Balistidae and Pomacanthidae were aggregated to family level and their behaviour of either benthic or planktonic recorded, to ensure accurate assigning of trophic group during the analysis. The total length (TL) of species was estimated in 5 cm size classes. Species identifications were checked using photographs, taxonomic references and photographic guides (Choat & Randall, 1986; Heemstra & Randall, 1993; Lieske & Myers, 1996; Kuiter, 2002; Kuiter & Debelius, 2006). Verification of species names was done using the online catalogue of fishes (Eschmeyer, 2012).

Data analysis

To identify differences in benthic habitats, all benthic survey data were arcsine square root transformed to bring percentage data close to normal distribution (Friedlander *et al.*, 2014), and analysed with PRIMER 6.0 (Primer-E Ltd, Plymouth, UK), where a Bray–Curtis similarity matrix was calculated from the transformed data. Hierarchical cluster analysis was thereafter performed using a Similarity Profile (SIMPROF) test set at a significance level of $P = 0.05$. The test provides a means of preventing unnecessary further analysis of the benthic sub-cluster (Clarke *et al.*, 2008). Each sub-cluster consisted of several sites, which were significantly different from other sub-clusters. These sub-clusters were defined as benthic habitats. One-way similarity percentage analysis (SIMPER) was utilized to identify a composite of benthic variables contributing most to the similarity within the benthic habitats (Clarke, 1993). To assess habitat diversity, Shannon–Wiener index (H') was calculated based on benthic variables for each site. The H'-values from the different habitats as identified by SIMPROF were compared using a one-way ANOVA and significantly different pairs identified from Tukey HSD test.

The abundance, functional diversity and biomass of fish functional groups were calculated from each site-based transect. Relative abundances were determined from the densities (number of individuals m^{-2}) of fish functional groups. Functional diversity was calculated from density data using two diversity indices: H' and Pielou's evenness index (J'). H' is a diversity index that incorporates both abundance and number of functional groups in its calculation, while J' is a

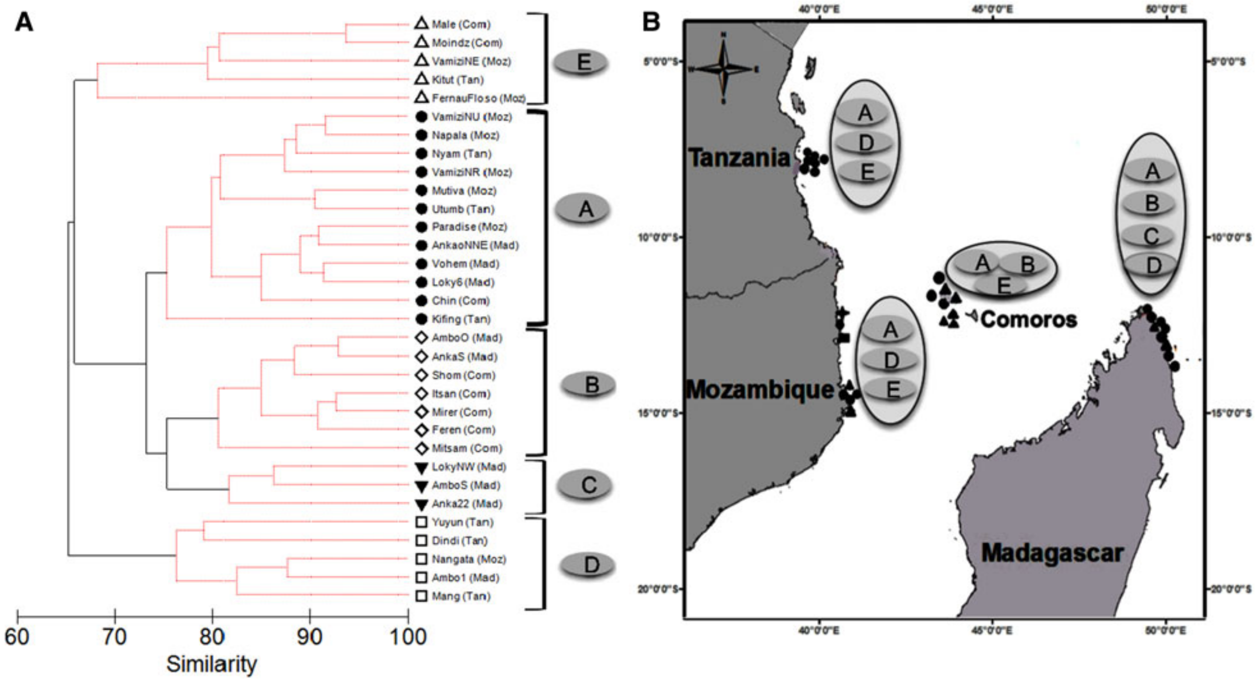

Fig. 1. (A) Cluster analysis of benthic composition – hard corals, soft corals, turf algae, fleshy algae, coralline crustose algae, and rubble from coral reefs in the Western Indian Ocean. Black solid lines join significant clusters groups, identified as habitat type A, B, C, D and E. The suffixes in brackets are the site geographic locations: Com – Comoros, Mad – Madagascar, Moz – Mozambique and Tan – Tanzania. (B) Map of the study sites showing number of fish transects at each site represented by black symbols, and habitat type enclosed by geographic location. Closed triangles = 3, closed square = 4, closed circles = 5, star = 7 fish transects. The habitat types are described in Table 3.

measure of equitability indicating how evenly distributed functional groups are among different benthic habitats (Clarke & Warwick, 2001). Biomass was only estimated for six functional groups: piscivores, omnivores, large excavators, small excavators, scrapers and browsers. Biomass was computed by firstly converting the median of species length size class to weight using the formula $W = aL^b$ with W as weight, L as length, a as constant and b as slope. Length–weight relationship coefficients (a and b) were obtained from published literature (Letourneur *et al.*, 1998; Kulbicki *et al.*, 2005; Green & Bellwood, 2009; Froese & Pauly, 2012). Secondly, the biomasses of species representing each fish functional group within each transect were summed together and converted to kilogram per hectare ($\mathrm{kg\ ha^{-1}}$). Two Bray–Curtis similarity matrices were created from the arcsine transformed relative abundance and log $(x + 1)$ biomass data of fish functional groups. The specific transformations were undertaken to bring data close to normal distribution, and reduce skewness and influence of outliers (Zar, 1999). A permutation-based hypothesis testing analysis of similarities (ANOSIM) was used to compare (1) the relative abundance and (2) biomass, across the clustered benthic habitats. ANOSIM significance test has two important terms: P as the significance level and Global R, which ranges between 0 and 1 indicating the level of similarity between the tested groups (Clarke & Warwick, 2001). One-way SIMPER was applied to identify the fish functional groups contributing most to the observed pattern of similarity within the benthic habitats (Clarke, 1993). These analyses were performed in PRIMER 6.0.

The abundance and biomass of fish functional groups from each habitat were graphed using box and whisker plots. Significance of differences was tested with the non-parametric Kruskal–Wallis test, after failing to conform to the assumptions of parametric statistics (Zar, 1999). Functional diversity indices across the identified habitats were compared using the Kruskal–Wallis test. A post-hoc non-parametric multiple comparison test using 'kruskalmc' from the R-package 'pgirmess' (Giraudoux, 2013) was performed on fish functional groups and functional diversity indices that showed an overall difference across the clustered benthic habitats. These analyses were performed with R v.0.97.551 (R Core Development Team, 2012).

RESULTS

Identification and description of benthic habitats

Hierarchical cluster analysis of the benthic variables using SIMPROF revealed that survey sites clustered into five distinct groups A, B, C, D and E, henceforth identified as habitats (Figure 1A). Particular habitats showed geographic affiliations with habitat A being found in all geographic locations. Comoros sites clustered in either habitats A, B or E, northern Madagascar had A, B, C and D type habitats, whereas central Tanzania and northern Mozambique sites had habitats A, D and E (Figure 1B). Since Habitat C was only found at three sites (all in Madagascar), conclusions on this substrate type are limited. The five habitats were characterized by a composite of different benthic variables that included varying percentage cover of live hard corals, soft corals and turf algae (Table 3). Live hard corals declined in cover from habitat A (59.7%) to E (14.4%), in contrast to turf algae, which generally

Table 1. Summary of site's coordinates, reef types, exposure to oceanic conditions, depth ranges, number of benthic estimates, fish transects of surveyed sites from coastal areas of four countries within the Western Indian Ocean province.

Country	Site	Date of survey	Latitude	Longitude	Reef type	Exposure[a]	Min. depth (m)	Max. depth (m)	No. of benthic estimates	No. of fish transects
Tanzania	Dindini	26/03/2011	−7.9198	39.8262	Forereef	5	4	17	1	5
	Kifinge	22/03/2011	−7.8467	39.8649	Forereef	5	1.6	16.5	1	5
	Kitutia	25/03/2011	−8.1253	39.6480	Shallow terrace	2	2	14	1	5
	Mange	24/03/2011	−8.0678	39.6011	Shallow terrace	2	0.5	10	1	5
	Nyamalile	23/03/2011	−8.0443	39.5197	Shallow terrace	2	3	14	2	5
	Utumbi	27/03/2011	−7.9484	39.7880	Shallow lagoonal terrace	1	5	16	1	5
	Yuyuni	28/03/2011	−7.9831	39.8128	Forereef	5	5	20	1	5
Mozambique	FernauVloso	27/09/2011	−14.4704	40.6808	Diffuse fringing reef	1	2	22	1	5
	Mutiva	28/09/2011	−14.4286	40.7212	Forereef	2	7	21	2	5
	Nangata	30/09/2011	−14.1995	40.7388	Deep terrace	3	8	29	2	5
	Napala	01/10/2011	−14.4584	40.6607	Forereef	2	3	20	1	3
	Paradise	02/10/2011	−14.4495	40.6774	Diffuse fringing reef	2	7	19	2	3
	VamiziNE	11/10/2011	−10.9956	40.7194	Forereef	4	5	22	2	7
	VamiziNR	10/10/2011	−10.9925	40.6858	Deep terrace	3	7	19	2	4
	VamiziNU	10/10/2011	−11.0148	40.6336	Deep terrace	2	5	22	2	5
Comoros	Chindini	15/03/2010	−11.9352	43.4837	Forereef	5	5	20	1	5
	Ferenga	20/03/2010	−12.4034	43.6985	Deep terrace	4	15	19	1	3
	Itsandra	14/03/2010	−11.6676	43.2634	Forereef	3	5	20	1	5
	Male	18/03/2010	−11.8800	43.5134	Forereef	5	10	20	1	3
	Mirereni	21/03/2010	−12.3619	43.6953	Forereef	3	6	20	1	3
	Mitsamiouli	16/03/2010	−11.3762	43.3019	Forereef	3	7	20	1	5
	Moindzaza	17/03/2010	−11.7766	43.2410	Forereef	3	2	17	1	3
	Shomoni	23/03/2010	−11.6271	43.3933	Forereef	5	2	11	1	3
Madagascar	Ambo Inner	28/03/2010	−12.3725	49.4404	Shallow terrace	1	3	11	2	3
	Ambo Outer	30/03/2010	−12.3453	49.4505	Forereef	3	10	19	2	5
	Ambo S	29/03/2010	−12.3655	49.4554	Shallow terrace	2	3	15	1	5
	Ankao NE	12/04/2010	−12.7668	49.8222	Forereef	3	6	11	1	3
	Ankao NNE	11/04/2010	−12.7866	49.8116	Shallow lagoonal terrace	2	2	9	2	5
	Ankao S	11/04/2010	−12.8281	49.8128	Shallow lagoonal terrace	2	1	8	1	5
	Loky S	31/03/2010	−12.7311	49.6955	Forereef	2	6	20	1	5
	Loky NW	01/04/2010	−12.7131	49.6664	Diffuse fringing reef	2	7	19	1	5
	Vohemar N	04/04/2010	−13.3307	50.0142	Forereef	5	9	19	2	5

[a] 1 = bay, 2 = semi-protected inner reef complex or N/NW facing with some protection e.g. from island, land mass, 3 = open sea facing N/NW/W, 4 = open sea facing S/SE/E with some protection from trade winds (e.g. submerged reef or bank or land mass further offshore), 5 = facing S/SE/E with full exposure to trade winds and oceanic conditions.

Table 2. Composition and functional roles of the surveyed fish (after Samoilys & Randriamanantsoa, 2011) from coral reefs in the Western Indian Ocean.

Fish functional group	Functional relevance	Family	Composition (common English name/genera/species)
(1) Piscivores	Exert top-down control on fish of lower trophic level	Serranidae	Groupers
		Lutjanidae	*Aprion viriscens* Valenciennes, 1830
(2) Omnivores	Feed on highly diversified diets including small fish, invertebrates and dead animals	Haemulidae	Sweetlips
		Lethrinidae	Emperors
		Lutjanidae	Snappers, except *Aprion viriscens*
(3) Corallivores	Obligate and facultative corallivores feed on coral polyps	Chaetodontidae	*Chaetodon bennetti* Cuvier, 1831, *C. lineolatus* Cuvier, 1831, *C. melannotus* Bloch and Schneider, 1801, *C. meyeri* Bloch and Schneider, 1801, *C. ornatissimus* Cuvier, 1831, *C. trifascialis* Quoy and Gaimard, 1825, *C. trifasciatus* Park, 1797, *C. zanzibarensis* Playfair, 1867
(4) Invertivores	Feed on coral competitors	Pomacanthidae	Angelfish except *Centropyge* spp.
		Balistidae	Triggerfish (e.g. *Sufflamen* spp.)
		Chaetodontidae	Butterfly fish except the listed corallivore species, *Hemitaurichthys zoster* (Bennett, 1831) and *Heniochus diphreutes* Jordan, 1903
5) Planktivores	Feeds on planktonic food, including zooplankton or phytoplankton.	Balistidae	Triggerfish (e.g. *Melichthys* spp. Swainson, 1839, *Odonus niger* (Rüppell, 1836))
		Chaetodontidae	*Hemitaurichthys zoster* and *Heniochus diphreutes*
		Acanthuridae	*Acanthurus mata* (Cuvier, 1829), *A. nubilus* (Fowler and Bean, 1929), *A. thompsoni* (Fowler, 1923), *Paracanthurus* and *Naso* spp. >20 cm.
		Caesionidae	Fusiliers
(6) Detritivores	Feed on organic matter in sediment and on reef surface	Acanthuridae	*Ctenochaetus* spp.
(7) Herbivores	Feed on benthic primary producers thereby regulating competition between fleshy algae and corals		
Large excavators	Remove considerable substratum and plays a major role in bioerosion	Scaridae	*Bolbometopon muricatum* (Valenciennes, 1840), *Chlorurus* spp. >35 cm, *Cetoscarus bicolor* (Rüppell, 1829)
Small excavators	Remove substrate – plays a slighter role in bioerosion	Scaridae	*Chlorurus* spp. <36 cm
Scrapers	Scraps the substrate removing algae, sediment and other material	Scaridae	*Scarus* spp. and *Hipposcarus spp.*
Browsers	Feed on large macro-algae	Scaridae	*Calotomus* spp. and *Leptoscarus* spp.
		Acanthuridae	*Naso unicornis* (Forsskål, 1775), *Naso tuberosus* Lacepède, 1801 and *Naso* spp. <21 cm
		Ephippidae	Bat fish
		Kyphosidae	Rudder fish
Grazers	Graze on epilithic algal turfs, which can also limit growth of macroalgae	Acanthuridae	*Acanthurus nigrofuscus* (Forsskål, 1775), small *Acanthurus* spp., *Zebrasoma* spp.
		Siganidae	*Siganus* spp. except *S. canaliculatus*
Grazer-detritivores	Feed on algal turf, sediment and some animal material	Acanthuridae	*Acanthurus blochii* Valenciennes, 1835, *A. dussumieri* Valenciennes, 1835, *A. leucocheilus* Herre, 1927, *A. nigricauda* Duncker and Mohr, 1929, *A. xanthopterus* Valenciennes, 1835, *A. tennenti* Günther, 1861.
		Pomacanthidae	*Centropyge* spp.

Table 3. Description of habitats A, B, C, D and E from coral reefs in four countries in the Western Indian Ocean based on SIMPER analysis of cover of benthic variables contributing about 90% of within habitat similarity.

Benthic variable	Av. cover	Av. similarity	% contribution
(a) Habitat A (Average similarity: 83.0%)			
Hard coral	59.72	38.89	46.85
Turf algae	12.22	16.02	19.30
Soft coral	15.93	15.91	19.17
CCA	2.89	6.92	8.34
(b) Habitat B (Average similarity: 85.4%)			
Hard coral	48.30	30.70	35.97
Turf algae	24.74	21.72	25.45
Rubble	10.87	12.00	14.06
CCA	5.76	9.71	11.38
Soft coral	3.61	5.97	7.00
(c) Habitat C (Average similarity: 71.1%)			
Hard coral	39.82	25.80	36.27
Soft coral	30.85	20.55	28.88
Turf algae	18.38	17.91	25.17
(d) Habitat D (Average similarity: 78.9%)			
Fleshy algae	42.20	28.53	36.16
Hard coral	21.91	18.44	23.37
Turf algae	12.22	15.09	19.12
Soft Coral	12.22	12.98	16.46
(e) Habitat E (Average similarity: 76.6%)			
Turf algae	47.06	32.58	42.52
Hard coral	14.39	18.55	24.21
CCA	7.83	10.34	13.49
Soft coral	2.56	7.60	9.91

Number of sites per habitat: A (N = 12), B (N = 7), C (N = 3), D (N = 5) and E (N = 5).

increased in cover from habitat A (12.2%) to E (47.1%). The cover of soft corals was highest in habitat C (30.9%) and lowest in habitat E (2.6%), whereas fleshy algae dominated Habitat D (Table 3).

Shannon–Wiener index of diversity (*H'*) was significantly different across the five benthic habitats (ANOVA, $F = 4.98$, df = 4, $P = 0.004$). Tukey HSD tests showed habitats B and C were more diverse (both $H' = 1.6 \pm 0.1$ SD) than A (1.4 ± 0.2 SD) (Figure 2).

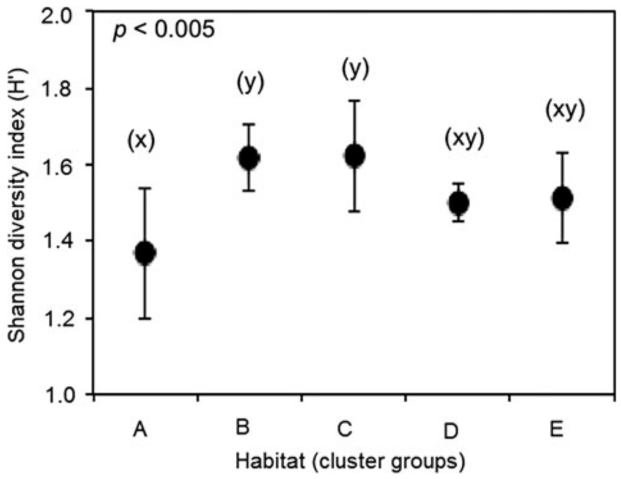

Fig. 2. Shannon–Wiener index of diversity (mean ± SD) of benthic composition grouped by habitat type from coral reefs in the Western Indian Ocean. Habitats with identical lowercase letters are not significantly different based on Tukey HSD test. Description of five habitats is given in Table 3.

Site information

The surveys were conducted at six reef types with 53% of the sites occurring on forereef, 16% on shallow terrace, 13% on deep terrace and 9% each on shallow lagoonal terrace and diffuse fringing reef (Table 1). The sites ranged from shallow to deep, and from semi-protected to exposed forereefs and terraces. Habitat A occurred in all reef types and consisted of sites with mixed exposure to oceanic seas and trade winds but generally in less exposed semi-protected inner reef complexes. Habitat B occurred in forereef, deep terrace and shallow lagoonal terrace reef types that were in the semi-protected inner complex or open sea facing north or north-west. Habitats C and E were found in forereef, diffuse fringing reef and shallow terrace. Sites that clustered in habitat C were less exposed to oceanic conditions occurring in semi-protected inner complex or open sea facing north or north-west. Habitat D occurred in most reef types except diffuse fringing reef and shallow lagoonal terrace. Habitat D and E occurred at sites with all levels of exposure ranging from bay, semi-protected inner complex, open seas and fully exposed to trade winds and oceanic conditions.

Linking fish functional groups to benthic habitats

RELATIVE ABUNDANCE

A total of 145 fish species were counted, excluding Balistidae and Pomacanthidae that were counted at a family level. ANOSIM results of the fish functional groups across the identified benthic habitats showed significant differences

Table 4. SIMPER analysis of relative abundance of fish functional groups from coral reefs in the Western Indian Ocean contributing about 90% similarity within habitats A, B, C, D and E. Description of habitat types is found in Table 2.

Functional groups	Av. abundance	Av. similarity	% contribution
(a) Habitat A (Average similarity: 45.4%)			
Detritivores	13.89	8.61	18.96
Invertivores	10.88	6.46	14.22
Grazers	10.24	6.10	13.42
Planktivores	16.78	5.60	12.32
Scrapers	11.75	5.45	11.99
Omnivores	13.18	3.77	8.31
Small excavators	6.56	3.07	6.76
Corallivores	6.69	2.53	5.56
(b) Habitat B (Average similarity: 53.1%)			
Detritivores	23.65	15.93	29.97
Invertivores	16.96	11.91	22.40
Grazers	17.18	9.67	18.20
Corallivores	6.76	3.86	7.25
Grazer-detritivores	8.56	3.30	6.22
Scrapers	8.27	2.98	5.60
Browsers	4.23	1.96	3.69
(c) Habitat C (Average similarity: 54.6%)			
Invertivores	16.84	13.73	25.10
Detritivores	20.28	12.65	23.14
Scrapers	14.10	7.77	14.21
Grazer-detritivores	9.28	5.17	9.46
Corallivores	6.76	4.19	7.66
Browsers	10.00	3.95	7.22
Small excavators	5.99	2.40	4.38
(d) Habitat D (Average similarity: 43.0%)			
Grazers	13.21	8.33	19.34
Detritivores	13.74	7.27	16.88
Invertivores	12.55	6.08	14.12
Omnivores	13.53	4.87	11.30
Scrapers	8.20	3.37	7.82
Planktivores	13.17	3.36	7.80
Grazer-detritivores	5.38	2.95	6.85
Browsers	7.76	2.46	5.71
Small excavators	4.50	1.67	3.89
(e) Habitat E (Average similarity: 46.9%)			
Planktivores	25.83	13.01	27.71
Grazers	13.62	8.52	18.14
Detritivores	15.26	7.67	16.33
Omnivores	12.48	5.60	11.93
Scrapers	8.10	2.82	6.00
Invertivores	5.59	2.77	5.90
Grazer-detritivores	6.42	2.04	4.35

despite the low Global R ($R = 0.091$, $P = 0.001$). Pair-wise habitat comparisons revealed significant differences in fish functional group composition, though with low R values ($R < 0.32$). Habitat B differed from habitats A, D and E while habitat E differed significantly from habitat C.

SIMPER analysis of fish functional groups based on a cut-off of 90% contribution, showed habitats B and C had a better within-habitat average similarity of fish functional groups compared with the other habitats. Detritivores and invertivores were the typical fish functional groups in habitats A, B and C, both functional groups cumulatively contributing to the within-similarity of 33.2, 52.4 and 48.2% respectively (Table 4). Grazers and detritivores typified habitat D contributing 19.3 and 16.9% correspondingly. Higher abundance of planktivores and grazers characterized habitat E, together contributing 45.9% of the similarity.

Abundances of piscivores, invertivores, corallivores, planktivores, detritivores, small excavators, browsers and grazers showed significant differences across the five habitats ($P < 0.05$, Figure 3). However, pair-wise comparisons of the relative abundance within the habitat types disclosed differences in only six fish functional groups. Detritivores were more abundant in habitat B than in A, while grazers were more abundant in habitats B and E, than in habitat C. Corallivores and invertivores were higher in abundance in habitats B and C, than in E. Invertivores were also lower in abundance in habitat A in comparison to B. Highly diverse benthic habitats (B and C) were generally associated with higher relative abundances of corallivores, invertivores, detritivores and grazers. Conversely, planktivores were lower in abundance in habitat B than in E. Small excavators were also lower in abundance in habitat B than in A and C. The fish functional groups contributing

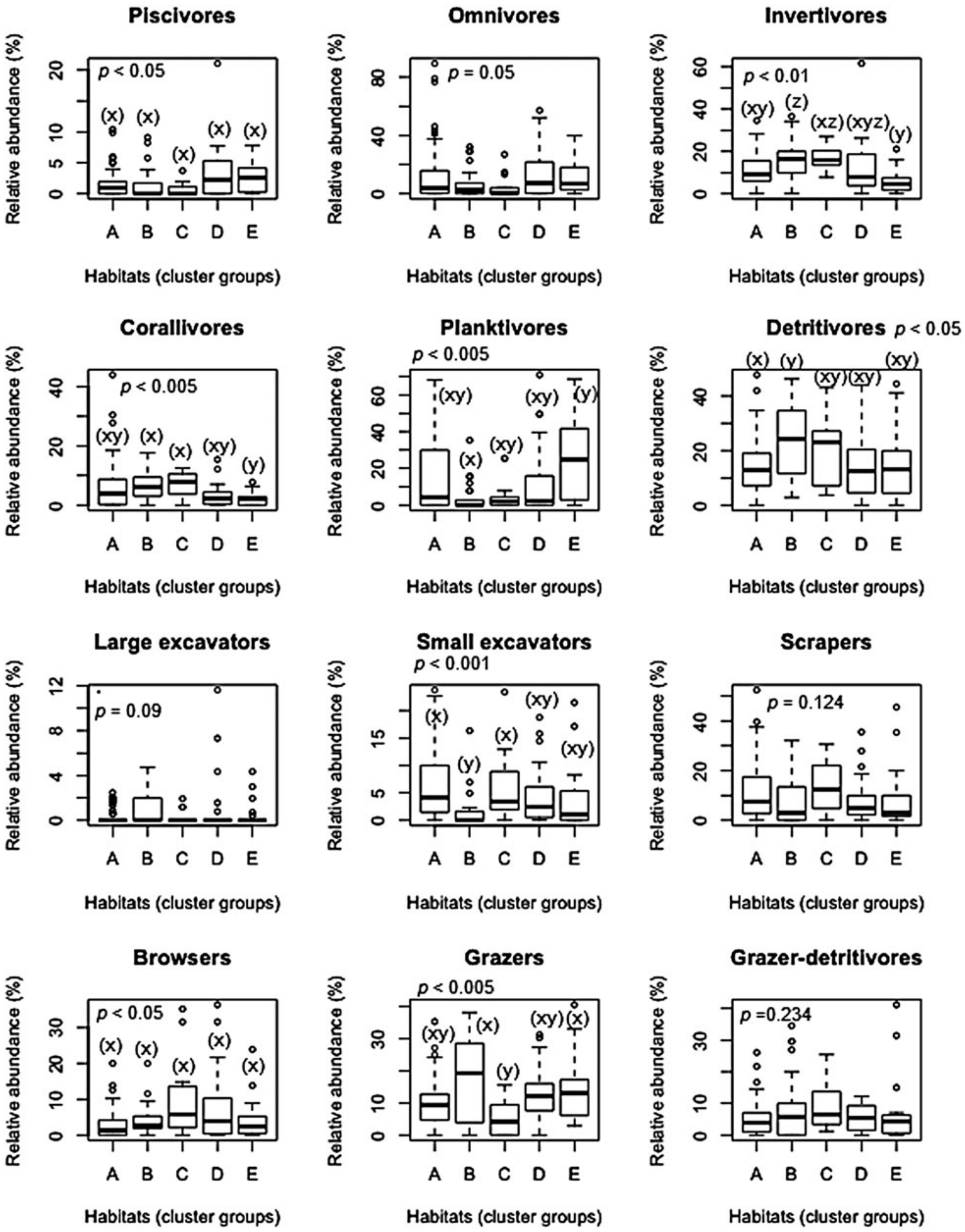

Fig. 3. Boxplots showing median relative abundance of 12 fish functional groups by habitats from coral reefs in the Western Indian Ocean. Number of fish transects per habitat were A (N = 55), B (N = 29), C (N = 13), D (N = 23) and E (N = 23). Habitats with the identical lowercase letters are not significantly different based on Kruskal–Wallis post-hoc test. Open dots indicate outliers. Note different scales along y-axis. Descriptions of the five habitats A to E are given in Table 3.

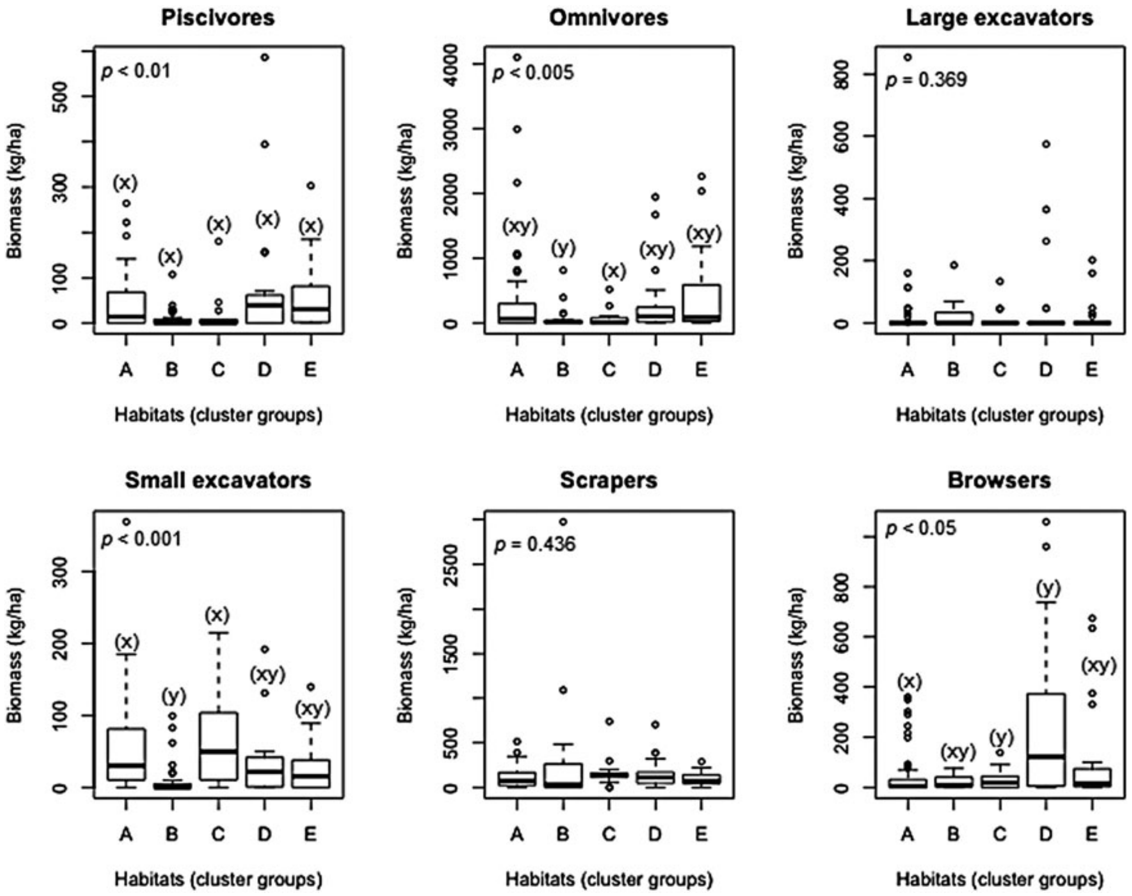

Fig. 4. Boxplots showing median biomass of six fish functional groups by habitats from coral reefs in the Western Indian Ocean. Number of fish transects per habitat were A (N = 55), B (N = 29), C (N = 13), D (N = 23) and E (N = 23). Habitats with identical lowercase letters are not significantly different based on Kruskal–Wallis post-hoc test. Dots indicate outliers. Note different scales along y-axis and description of the five habitats A to E are given in Table 3.

most to the within-habitat similarity as shown in Table 4, corroborated these multiple comparison results.

FUNCTIONAL DIVERSITY

Shannon–Wiener diversity of fish functional groups was similar across habitats ($P > 0.05$). However, the evenness (J') of fish functional groups across habitats differed significantly (Kruskal–Wallis $\chi^2 = 12.48$, $df = 4$, $P = 0.014$). Pair-wise multiple comparisons showed that J' was higher in habitat C compared with habitat E.

BIOMASS

ANOSIM results using clustered habitats as *a priori* factors showed significant differences despite low Global R ($R = 0.102$, $P = 0.004$). ANOSIM pair-wise comparisons among habitats found that the biomass of the six fish functional groups was significantly different ($P < 0.05$), though with low R values ($R < 0.30$). The differences in biomass were between habitats A and B, B and D, and C and E.

Of the six functional groups analysed for differences in biomass across the habitats, only the piscivores, omnivores, browsers and small excavators were found to differ significantly in all habitats ($P < 0.05$). However, pairwise comparison of piscivore biomass across the five habitats did not show any significant difference (Figure 4). Omnivores were higher in biomass in habitat E compared with B. Browsers showed a higher biomass in habitat D compared with A. Small excavators were lower in biomass in habitat B than in habitats A and C.

DISCUSSION

Habitat environmental conditions and distribution

Healthy coral reefs are characterized by a dominance of live hard corals but due to persistent disturbances can often undergo phase-shifts to an alternate degraded state dominated by macroalgae (Bellwood *et al.*, 2004; Hughes *et al.*, 2007). Disturbances caused by overfishing, declining water quality and climate change have exacerbated the vulnerability of coral reefs to phase-shifts worldwide (Hughes, 1994; Chong-seng *et al.*, 2012). Dominance of live hard corals in habitats A, B and C suggests a healthy state of coral reefs in sites in these clusters. In contrast, the dominance of fleshy algae in habitat D may indicate sites where a coral-algal phase shift has occurred through, for example, eutrophication or coral mortality from bleaching (Obura *et al.*, 2011). Coral mortality from bleaching may also explain the dominance of turf algae in habitat E, but with no fleshy algae and the presence of calcareous algae this habitat is not indicative of a

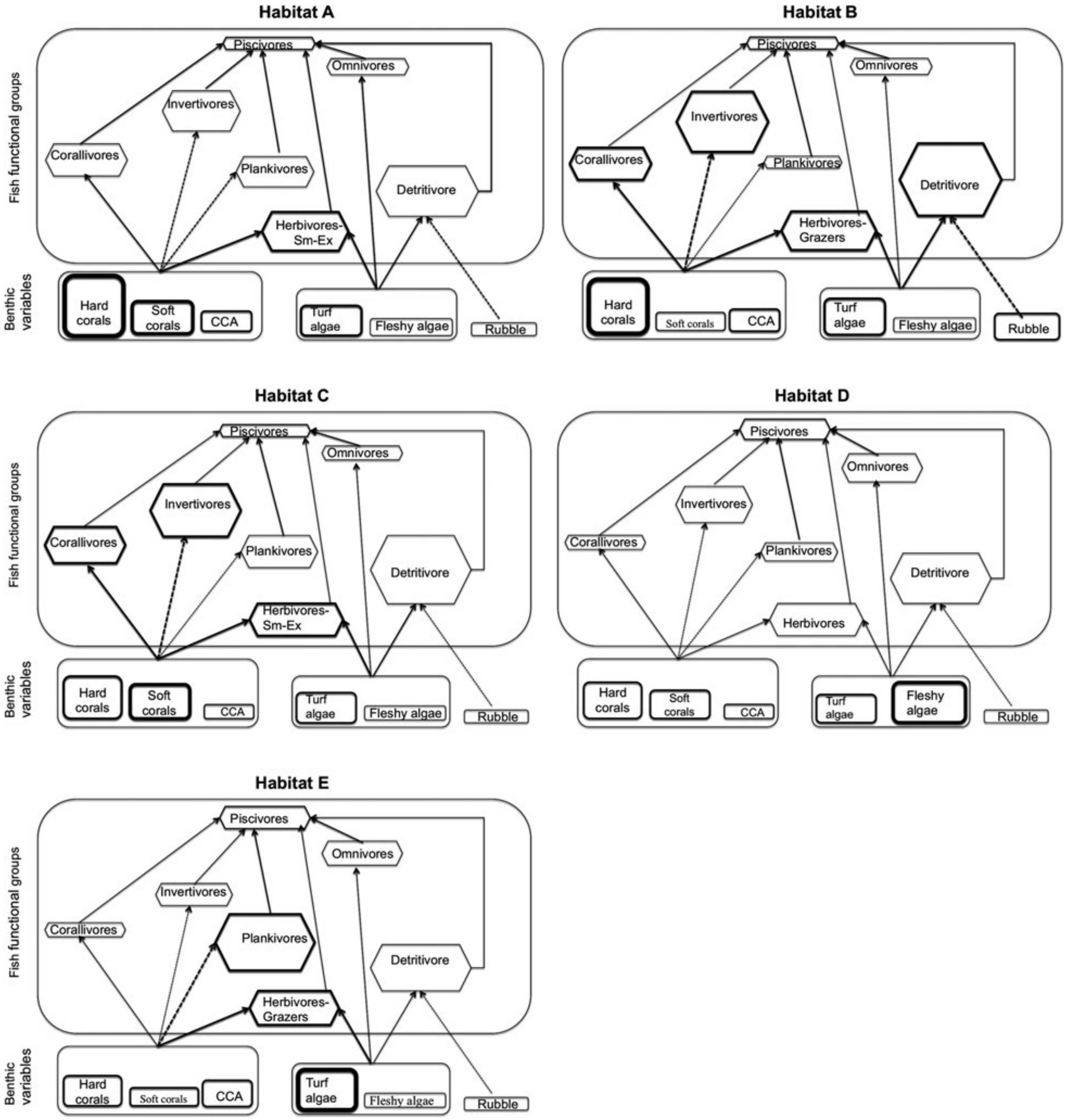

Fig. 5. Diagrammatic representation of the link between the cover of benthic composition of five habitats and relative abundance of fish functional groups from coral reefs in the Western Indian Ocean. The size of the boxes is proportional to the cover and relative abundance of benthic variables and fish functional groups. Bolded boxes represent: benthic variable(s) contributing most to within habitat similarity or a fish functional group found to be higher in the habitat as compared with other habitats. Herbivores constituted six functional groups (see Table 2) and only those significantly higher in abundance are provided. Sm-Ex = small excavators.

phase-shift. If the balance between corals and algae is taken to indicate level of disturbance, reefs in central Tanzania and Mozambique exhibit habitats that are either in a low (habitat A) or high (habitats D and E) state of disturbance. Presence of habitat types B and C may indicate more variable substrate (near mangroves and sand) and oceanic conditions less conducive to hard coral growth and/or an intermediate state of disturbance. The intermediate state of disturbance is supported by the high benthic diversity and relatively high rubble cover, which at a low level is an indicator of previous natural disturbance such as storms, but at a high level can indicate extreme disturbance caused by dynamite fishing or mortality and collapse of corals after bleaching (Obura & Grimsditch, 2009; Wells, 2009). Habitat C, which had more than double the cover of soft coral than any other habitat, was only present in northern Madagascar, possibly caused by nutrient loads from freshwater runoff from land (Obura *et al*., 2011), though the small sample size (N = 3 sites), limits further deductions on this substrate type. Notably, the other four habitat types were well represented across a large number of highly variable sites, which spanned different reef typologies, depths and exposure to oceanic conditions. This provides strong support for the categorizing of these WIO reefs by habitat type.

Fish functional groups and habitats association

A wide variety of biological factors encompassing recruitment, competition, predation, availability of preferred food and shelter affect the abundance and spatial patterns of reef fishes (Choat & Ayling, 1987; Roberts & Ormond, 1987; Doherty and Williams, 1988; Turner & Mittelbach, 1990; Hixon & Jones, 2005; White & Warner, 2007; Chesson & Kuang, 2008). On the other hand, depth and exposure of reefs to currents are among the abiotic factors that may also influence the abundance of reef fishes (Khalaf & Kochzius, 2002a). High variability in estimates of fish abundance from UVC surveys is therefore inevitable (Samoilys & Carlos 2000) and was partially addressed in this study through high replication at the site level and at the reef type level. Despite the high variability in fish abundance our study found that six functional groups differed significantly with benthic composition, which we illustrate diagrammatically (Figure 5). For example, comparing habitats A and B shows higher abundance of herbivorous small excavators associated with higher hard coral in Habitat A and an increased abundance of corallivores, detritivores, invertivores and herbivorous grazers in the higher cover of rubble and lower cover of soft corals in habitat B. The higher cover of soft corals in habitat C is linked to a higher abundance of corallivores, invertivores and herbivorous small excavators. The significantly higher cover of fleshy algae in habitat D is associated with no increase in abundance of any functional group. The highest cover of turf algae and CCA seen in habitat E is associated with an increased abundance of planktivores and herbivorous grazers. From this diagrammatic representation, four hypotheses are generated which require further experimental research to determine the directionality of the relationship: (1) an increase in the cover of rubble coupled with a reduction in soft corals will lead to an increase in abundance of detritivores; (2) moderate cover of hard coral and/or soft corals attracts a higher abundance of corallivores and invertivores; (3) presence of a high cover of turf algae and CCA correlates with high abundance of planktivores; and (4) herbivorous fish functional groups are not correlated with habitats dominated by fleshy algae.

RUBBLE SUBSTRATE AND DETRITIVORES

Substrate type is an important component shaping fish communities with rubble providing an important substrate for the recruitment and successive growth of many sessile invertebrates (Duckworth & Wolff, 2011). Our study showed that detritivores contributed the most to the within-habitat similarity of habitat B, which had the highest cover of rubble. The to and fro movement of water due to wave action can move and overturn rubble creating turbulence that churns out settled detritus, which is an important food source for detritivores and grazer-detritivores.

HARD CORAL SUBSTRATE, CORALLIVORES AND INVERTIVORES

Reef habitat structure provides food resources and shelter through structural complexity (Hixon, 1991). Studies on the link between soft coral and reef fishes are few, though the habitat is not a favourable replacement for hard corals (Syms & Jones, 2001). Site-specific fish, such as butterfly fish, show a more positive correlation with habitat structure than species exhibiting a wide home range (Roberts & Ormond, 1987). The strong positive relationship between habitat types B and C with corallivores such as the butterfly fish, which are either obligate or facultative corallivores (Choat & Ayling, 1987; Pratchett & Berumen, 2008), supports the theory that a high percentage of hard coral is a prerequisite for high abundances of Chaetodontidae (Reese, 1989; Khalaf & Kochzius, 2002b). High abundance of corallivores is indicative of a healthy coral reef (Cole *et al*., 2008; Green & Bellwood, 2009). The high abundance of invertivores which feed on coral competitors may help maintain the high hard coral cover in habitats B and C.

TURF ALGAE AND PLANKTIVORES

Planktivores were negatively associated with high benthic diversity. Planktivores included fishes that feed on demersal zooplankton from coral reefs (e.g. *Acanthurus mata*) and pelagic zooplankton transported oceanically (e.g. *Caesio* spp., *Hemitaurichthys zoster* and *Heniochus diphreutes*) (Froese & Pauly, 2012). Planktivores feeding on pelagic planktonic food would only depend on the reef for provision of shelter, and can still survive on the relatively degraded reefs of habitat E. Through experiments, planktivores have also been shown to avoid predators (mainly piscivores) by exhibiting behavioural activities including shifting habitat use, changing diel activity patterns or reducing movement (Turner & Mittelbach, 1990). This implies that if the structure of degraded coral reef habitats is still intact, planktivores that feed on both pelagic and reef plankton can persist.

ALGAE HABITATS AND HERBIVOROUS FISHES

Herbivorous fishes are predominant consumers of benthic algae and hence substantially affect the abundance and distribution of algae (Hixon, 1997). The highly degraded habitat D reflecting a phase shift from coral to macro-algae, showed no linkage with the abundance of herbivorous fishes; in contrast the semi-degraded habitat E with high turf algae did show a linkage with herbivorous grazers. The strong correlation of grazers to habitat E may be driven by availability of food. Fishing pressure may also have removed the herbivores constricting more linkages with the two algal habitats (Russ, 2003). Indeed experimental research has demonstrated dominance of turf and fleshy algae after exclusion of herbivores (Burkepile & Hay, 2006). Further, algal habitats tend to be ecologically homogeneous and undesirable by other functional groups such as obligate corallivores (Chong-Seng *et al*., 2012) hence reducing competition and allowing grazers to increase. The two algal habitats thus show differential linkages with herbivorous fishes, which suggest these functional groups prefer turf algae habitats to macro-algae.

Benthic habitats and biomass of functional groups

The highest mean biomass of all functional groups combined was associated with specific habitat types: 866 kg ha^{-1} in habitat D and 745 kg ha^{-1} in habitat E. Omnivores feed on highly diverse diets and their biomass can be high in semi-degraded habitats like habitat E. The high biomass of browsers in habitat D likely relates to the importance of fleshy algae for providing shelter for reproduction and resting for adult reef fishes (Vroom *et al*., 2006). Nevertheless, the role browsers play in fleshy-algae dominated habitats is still poorly understood (Chong-Seng *et al.*, 2012).

Fishing and large-bodied functional groups

Marine ecosystems are some of the most heavily exploited and continue to deteriorate due to increasing fishing pressure (Worm *et al.*, 2006). Fisheries target fish at higher trophic levels and after being overfished, shift to those of lower trophic levels (Pauly *et al.*, 1998). In the WIO fishing pressure may be masking habitat associations with piscivores and large excavators. Lack of habitat association was also evident in the Seychelles (Chong-Seng *et al.*, 2012), and may denote high fishing pressure in all identified habitats (Samoilys & Randriamanantsoa, 2011). Removal of fish from the marine environment at rates that cannot be sustained by natural recruitment will significantly alter the habitat-fish association (Coll *et al.*, 2008).

Summary of key findings

We show that reef habitat types relate to broad geographic patterns of reefs in the WIO. Overlaid is evidence of natural disturbance and anthropogenic impacts. In turn these habitat types show relationships with fish functional groups with key groups showing clear associations with particular habitat types. Such information can help focus conservation planning by targeting efforts to priority reefs that support diverse habitat types and diverse fish communities (Roberts *et al.*, 2002; Pittman *et al.*, 2007). Focusing conservation on reefs that support high abundances of herbivores is also important since such reefs are likely to be more resilient in the long term (Bellwood *et al.*, 2004). Management measures geared towards maintenance of a high diversity and biomass of fishery species will also make important contributions towards poverty alleviation and food security in the WIO countries (Allison *et al.*, 2009). Given the importance of the association between habitats and fish functional groups strategic management and protection through area closures continues to be an essential approach for the WIO.

ACKNOWLEDGEMENTS

We thank the institutions and foundations that have made our work possible: Western Indian Ocean Marine Science Association (WIOMSA) for funding fieldwork through the Marine Science for Management (MASMA) programme grant number MASMA/OR/2008/05; Vlaamse Interuniversitaire Raad – Universitaire Ontwikkelingssamenwerking (VLIR-UOS) for a scholarship to K.O. under the framework of the programme 'Master of Marine and Lacustrine Science and Management' at the Universiteit Antwerpen, Vrije Universiteit Brussel and Universiteit Gent (Belgium; www.oceansandlakes.be); the competent authorities for permits; Majambo Jarumani for assisting in creating the map.

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