Marine Pollution Bulletin 148 (2019) 182–193

Contents lists available at ScienceDirect

Marine Pollution Bulletin

journal homepage: www.elsevier.com/locate/marpolbul

Healthy and diverse coral reefs in Djibouti – A resilient reef system or few anthropogenic threats?

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A R T I C L E I N F O

Keywords:
Coral reef
Resilience
Ecosystem health
Fisheries
Red Sea
Coral bleaching

A B S T R A C T

Djiboutian coral reefs are poorly studied, but are of critical importance to tourism and artisanal fishing in this small developing nation. In 2014 and 2016 we carried out the most comprehensive survey of Djiboutian reefs to date, and present data on their ecology, health and estimate their vulnerability to future coral bleaching and anthropogenic impacts. Reef type varied from complex reef formations exposed to wind and waves along the Gulf of Aden, to narrow fringing reefs adjacent to the deep sheltered waters of the Gulf of Tadjoura. Evidence suggests that in the past 35 years the reefs have not previously experienced severe coral bleaching or significant human impacts, with many reefs having healthy and diverse coral and fish populations. Mean coral cover was high (52%) and fish assemblages were dominated by fishery target species and herbivores. However, rising sea surface temperatures (SSTs) and rapid recent coastal development activities in Djibouti are likely future threats to these relatively untouched reefs.

1. Introduction

Coral reefs are crucial ecosystems both in terms of the biodiversity they possess and the ecosystem services they provide (Mace et al., 2012; Costanza et al., 2014). Globally reefs are being degraded by a combination of climate change (Bellwood et al., 2004; Claar et al., 2018; Stuart-Smith et al., 2018), increased sedimentation from coastal development and land-use change (McClanahan and Obura, 1997; Erftemeijer et al., 2012), and ecological changes associated with the over-harvesting of reef resources (Hughes, 1994; Mumby et al., 2006). Based on our current understanding of reef resilience to coral bleaching and other human stressors, key indicators have been proposed to inform resilience-based management (Maynard et al., 2010; McClanahan et al., 2012). However, despite increased efforts in monitoring reefs in recent years (Arif et al., 2014, Hume et al., 2015, Osman et al., 2018, Hadaidi et al., 2018, Paparella et al., 2019), many areas of the Red Sea are lacking key information about the health and resilience of their reefs (PERSGA, 2010; Berumen et al., 2013), and therefore limiting appropriate management strategies.

Reef resilience to disturbance by coral bleaching is a function of factors that: (Muir et al., 2017) reduce a reef's exposure to bleaching by avoiding thermal stress; (2) reduce coral sensitivity to thermal stress; and (3) allow the coral community to recover if mortality occurs (West and Salm, 2003). These three components can be used to understand a reef's vulnerability to future climate pressures (Cinner et al., 2012; Belokurov et al., 2016) and be used to advise resilience based management (McLeod et al., 2019). Bleaching exposure is reduced when the amount of light and temperature during a bleaching event (Coles and Jokiel, 1978). For example, high wave exposure is generally experienced on ocean facing fore-reefs, where wave energy and currents mix cooler deeper waters during stress events, whereas sheltered bays and inland seas suffer from greater surface warming and little mixing of the thermocline (West and Salm, 2003; Obura, 2005). Various mechanisms for coral community adaptation and coral colony acclimation to thermal stress have been proposed, including taxonomic shift to thermally tolerant coral genera (McClanahan et al., 2014), a shift to thermally tolerant zooxanthellae clades (Baker et al., 2004) and increases in photo-protective chemicals in coral tissues (Brown et al., 2002). Hence a reef's bleaching response during thermal stress is a combination of local physical conditions and the nature of the coral community. Recovery from bleaching mortality is dependent on factors that promote coral regrowth, which include coral recruitment, suitable substrate, low pollution and sedimentation, low macroalgae cover and healthy herbivorous fish populations (Fabricius, 2005; Mumby et al., 2006; Obura and Grimsditch, 2009). Management of local human stressors, such as overfishing and pollution, can enhance a reef's ability to recover and

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https://doi.org/10.1016/j.marpolbul.2019.07.040
Received 27 March 2019; Received in revised form 11 July 2019; Accepted 18 July 2019
Available online 17 August 2019

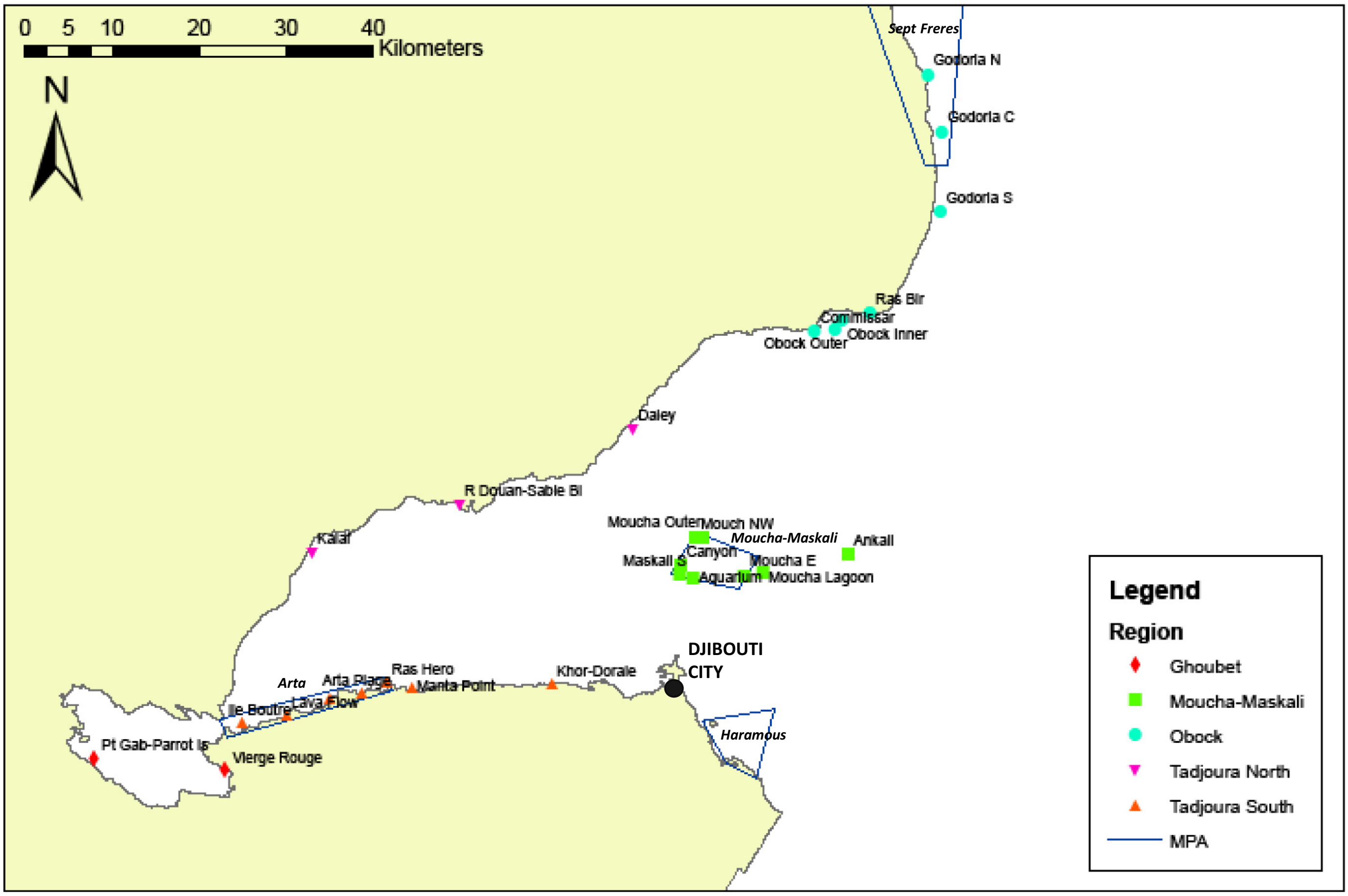

Fig. 1. Map of the Djibouti coastline showing location of dive sites, bathymetry, major urban centres and ports. The sites are divided into five regions indicated by different symbols and sites from 1998 assessments repeated in this study are marked with a white dot. Coast line and shallow reef derived from Landsat 7ETM+ satellite data courtesy of the U.S. Geological Survey. Bathymetric contours derived from Shuttle Radar Topography Mission (SRTM).

hence its overall resilience to coral bleaching (West and Salm, 2003; Bellwood et al., 2004).

In this study, we measured the health of coral reefs and assessed their vulnerability to coral bleaching in the Republic of Djibouti, a small desert nation located in the Horn of Africa at the junction between the Red Sea and the Gulf of Aden (Fig. 1). The population of Djibouti is 850,000, with the greatest densities in the capital, Djibouti City, where a major port and military facilities are found at this geographically strategic location. The 340 km coastline is fringed by approximately 450 km^2 of coral reef (Spalding et al., 2001) and those near Djibouti city, such as around the islands of Moucha and Maskali (Fig. 1), are important for a growing tourist industry. The reef fishery is small, artisanal, and considered under-exploited, employing approximately 2000 fishers who catch grouper (*Epinephelidae*), sweetlips (*Haemulidae*), snapper (*Lutjanidae*), emperors (*Lethrinidae*) and pelagic fishes (Morgan, 2004; Colléter et al., 2015). Much of the coastline outside of Djibouti City is uninhabited desert.

Previous reef surveys were completed in late-1998 by PERSGA (Regional Organisation for the Red Sea and Gulf of Aden) (PERSGA/ALESCO, 2003) and the IUCN (Obura, 1999), and, in 2002 by PERSGA around Sept Frères, in the Bab-el-Mandeb strait, and the adjacent mainland coast (Barker et al., 2002). These surveys contributed to preparing management plans for newly proposed marine protected areas (PERSGA/GEF, 2004). The 1998 survey was after the El-Niño Southern Oscillation (ENSO) and found some coral bleaching related mortality (20–30%), but moderate coral cover (~40%) in many sites (Obura, 1999). Some evidence suggests that the reefs in the Red Sea and the Arabian Gulf may be more resilient to increasing sea temperatures because the corals or their symbionts have adapted to the naturally high and variable temperatures in this region, with summer maximums of 35 °C and an annual range of 10 °C in some locations (Baker et al., 2004; Coles and Riegl, 2013; Howells et al., 2016; Krueger et al., 2017; Smith et al., 2017). However, since 1998 sea temperatures have continued to rise (Raitsos et al., 2011; Heron et al., 2016), with the largest global coral bleaching event ever recorded in 2016 (Furby et al., 2013; Hughes et al., 2017; Monroe et al., 2018; Riegl et al., 2018; Burt et al., 2019). In addition local stressors have increased as Djibouti City and its major international port have developed and its fisheries has grown (Colléter et al., 2015). In this paper, we present the biodiversity and condition of coral and fish communities of Djibouti and provide estimates of their potential vulnerability to coral bleaching and anthropogenic impact, as a basis to inform conservation planning and management efforts.

2. Methods

2.1. Study area

Djibouti's eastern coastline abuts the Gulf of Aden and Bab el-Mandeb at the entrance of the Red Sea (Fig. 1). Much of Djibouti's coastline follows the Gulf of Tadjoura, a submarine canyon running west to east where the Great Rift Valley meets the sea. At the western tip of the Gulf an extremely narrow (< 1 km) channel connects to a basin called the Ghoubet-el-Kharab, the geologically youngest section of Djibouti's coastline. A total of 27 sites were surveyed in September 2014 and February 2016, covering the majority of Djibouti's coastline (Fig. 1, Table S1). Nine of these sites (MM1, MM3, MM4, MM5, MM6,

Table 1
Indicators used to describe the reef's condition, exposure and sensitivity to bleaching and recovery potential from an acute disturbance. Target fish biomass = target species in local fishery. Herb-detritivore = herbivorous and detritivorous (see Green and Bellwood, 2009) fish species combined.

Indicator	Unit	Type
Coral cover	%	Reef condition
Coral genus richness	No. of genera	Reef condition
Target fish biomass	kg per ha	Reef condition
Coral Fish Diversity Index (CFDI)	No. of species	Reef condition
Wave exposure	5-point scale	Bleaching exposure
Shading	5-point scale	Bleaching exposure
Proximity to deep water	5-point scale	Bleaching exposure
Thermally sensitive corals	%	Bleaching sensitivity
Herb-detritivore fish density	Individuals per ha	Recovery potential
Macroalgal cover	%	Recovery potential
Recruit density	Individuals per m^2	Recovery potential
Unconsolidated substrate	%	Recovery potential

MM7, OB6, TN1 & TS2) were previously visited in late 1998, after mass coral bleaching in the Western Indian Ocean had ended (Obura, 1999).

2.2. Site-based field surveys

At each site data were collected on the fish and coral community composition, benthic cover and various physical features of the reef. Physical features of the reef that were recorded included slope, estimated in degrees (°), and rugosity, estimated on a 5-point scale based on the macro-topographical features of the reef (Polunin and Roberts, 1993). Environmental factors were also recorded and included: reef exposure (E) to coral bleaching including, physical shade from sunlight from cliffs or reef slope aspect, high wave exposure and proximity to deep water and upwelling (West and Salm, 2003; Obura, 2005). The bleaching exposure factors were estimated on a 5-point scale, with 1 being the best for the corals (lowest bleaching exposure) and 5 being the worst (Table 1).

Adult corals were recorded in belt transects covering of between 50 and 100 m^2 at each site. Each colony was identified to genus level and assigned to a size class based on the longest axis of the colony (10–20 cm, 20–40, 40–80, 80–160, 160–320, > 320 cm). Coral recruit (< 5 cm) densities were recorded in 1m^2 quadrats placed along belt transects, with between 5 and 15 quadrats surveyed at each site. Additional 1m^2 quadrats were placed near the transect for measuring benthic cover, with 40 quadrats per site in 2014 and 15 quadrats per site in 2016. Nine benthic categories were recorded in these quadrats: hard coral, soft coral, other sessile invertebrate, macroalgae, turf algae, coralline algae, bare substrate, rubble, and sand. The 1998 benthic surveys were conducted using a rapid assessment method, where by the an observer swims around a 100m^2 circle (radius = 5.6 m) and estimates the amount of cover of hard corals, soft corals, sessile invertebrates, fleshy algae, turf algae, coralline algae, hard rock, loose rubble and sand cover (Obura and Mangubhai, 2011). Similar rapid survey methods have been found to be comparable to the photo-quadrat technique used in modern surveys (Wilson et al., 2007).

Fish from 11 families (*Acanthuridae, Balistidae, Caesionidae, Chaetodontidae, Epinephelidae, Haemulidae, Lethrinidae, Lutjanidae, Pomacanthidae, Scarinae (Labridae)* and *Siganidae*) were counted in 50 × 5 m (250 m^2) belt transects, with five transects (total of 1250 m^2) per site (Samoilys and Carlos, 2000). The total length of each fish was estimated to the nearest 5 cm, and the species was noted. The biomass of fish was estimated using length-weight coefficients based on Kulbicki et al. (2005) and updated, where appropriate, from Fishbase (Froese and Pauly, 2019). During the same dive the observer also noted the presence of fish species during a 75 min period, from the 11 families mentioned above and also *Carangidae, Labridae, Monacanthidae, Mullidae, Nemipteridae, Ostraciidae, Pomacentridae* and *Tetraodontidae* (19 families in total) to provide an index of fish diversity (sensu Samoilys and Randriamanantsoa, 2011). No fish surveys were conducted in 1998.

2.3. Data analyses

The fish species' density data (11 families) and coral genus density were compared with the explanatory variables, coral cover, unconsolidated substrate (sand and rubble combined) cover, wave exposure, rugosity and slope, using a Canonical Correspondence Analysis (CCA). These explanatory variables were checked for multi-colinearity using a Variance Inflation Factor analysis and were found not to be colinear (all variables: VIF < 1.6). The significance of explanatory variables in the CCA model was estimated using an ANOVA-like permutation test (Oksanen, 2012). The CCA was performed using the R package 'vegan' (Oksanen et al., 2016).

Fish species were assigned to 11 trophic groups (sensu Green and Bellwood, 2009, Samoilys et al., 2018) and their density and biomass calculated. Lutjanidae, Lethrinidae, Epinephelidae and Haemulidae fish taxa are targeted by artisanal fishing in Djibouti (Morgan, 2004), which correspond to the piscivore and omnivore trophic groups. These groups were combined to define the biomass of fishery target species. Reef condition was defined using the indicators: coral cover, coral genus richness, biomass of fishery target species and the coral fish diversity index (CFDI). CFDI is a commonly used biodiversity index that uses the richness of the six most specious reef fish families, the Chaetodontidae, Pomacanthidae, Pomacentridae, Labridae, Scarinae (Labridae) and Acanthuridae (Allen and Werner, 2002).

Reef resilience to future coral bleaching was described using components of a vulnerability equation (Eq. (1)), namely the system's exposure and sensitivity to the threat and its ability to recover from any damage (Cinner et al., 2012; Belokurov et al., 2016). The sensitivity (S) of the reefs to bleaching was estimated by the percentage of coral cover of genera that are usually most sensitive in the Indo-Pacific (*Acropora, Alveopora, Montipora, Stylophora, Seriatopora, Pocillopora* and branching *Porites*) (Loya et al., 2001; McClanahan and Ateweberhan, 2007; Muir et al., 2017). The recovery (R) potential of reefs was described using the following measures: macroalgal cover, unconsolidated substrate cover, coral recruit density and the density of herbivore and detritivore fishes (Table 1). Herb-detritivore fishes was calculated as the combined abundance of: detritivores, grazer-detritivores, grazers, scrapers, excavators and browsers (Green and Bellwood, 2009).

Sensitivity and recovery indicators were scored on a 5-point scale, whereby the range in values for each indicator was divided into 5 categories with equal breaks (i.e. range/5). Exposure and sensitivity indicators are ordered from good (Muir et al., 2017) to bad (5) for resilience, whereas for recovery indicators the order is reversed. The overall bleaching exposure (E), sensitivity (S) and recovery (R) scores for each site were calculated by taking the mean score of the individual indicators used in that component (Table 2).

Vulnerability equation (sensu Cinner et al., 2012)

$$Vulnerability\ (V) = \frac{[Exposure\ (E) + Sensitivity\ (S)]}{Recovery\ (R)} \tag{1}$$

Past thermal stress affecting reefs in Djibouti was investigated using Sea Surface Temperature (SST) data, which were derived from the Advanced Very High Resolution Radiometer (AVHRR) pixel centred at 11.875°N, 43.125°E from January 1982 to December 2016. The data were accessed from http://las.incois.gov.in/las. The threshold temperature for bleaching, the maximum monthly mean (MMM), was calculated as the mean of the temperatures during the warmest months of the years 1985–1990 and 1993 and the coral bleaching threshold was assumed to be MMM +1 °C (Liu et al., 2003). The severity of thermal stress was measured using 'Degree Heating Weeks' (DHWs), where 1 DHW is a + 1 °C anomaly above MMM lasting for 1 week (Liu et al., 2003).

Table 2
Fish species and sites associated with important environmental differences on Djiboutian reefs, based on the results of the CCA (Fig. 2).

Explanatory variable	Sites	Characteristic species	Ubiquitous species
Wave exposure	Commissar (OB3) and Godoria (OB5–7)	*Acanthurus sohal, Plectorhinchus schotaf, P. gaterinus, Melichthys indicus, Rhinecanthus assasi, Siganus rivulatus*	*Pomacanthus maculosus, Balistoides viridescens, Scarus ferrugineus, Chaetodon fasciatus*
Unconsolidated substrate	Ras Bir (OB4) and Moucha Outer (MM6)	*Siganus luridus, Lutjanus ehrenbergi, Chlororus sordidus*	
Steep reef slopes	Tadjoura South (TS1–6) and the Ghoubet (GB1–2)	*Anyperodon leucogrammicus, Sufflamen spp., Lutjanus kasmira, L. mahsena, Pygoplites diacanthus Pomacanthus asfur*	
High coral cover	Southern Moucha-Maskali (MM8, MM3, MM4), Obock (OB1, OB2), Sable Blanc (TN1) and Ile Boutre (TS7)	*Lutjanus bengalensis, Cetoscarus ocellatus Chaetodon lineolatus C. trifascialis*	

3. Results

3.1. Coral reef variation

A total of 183 fish species from the 19 family sub-set were observed (Table S2), of which 105 were from the six CFDI families. The species reflect typical Red Sea/Gulf of Aden fish communities, with 40 of the species observed being endemic to this region, especially among the Chaetodontidae (butterflyfish) and Scarinae (parrotfish). The structure of the fish assemblages correlated with two CCA components which reflected gradients from reefs with high wave exposure versus steep slopes (CCA1) and reefs with high coral cover versus unconsolidated substrate (CCA2, Fig. 2a). Significant explanatory variables were unconsolidated substrate ($F = 1.89$, $p = 0.030$), wave exposure ($F = 2.00$, $p = 0.023$) and slope ($F = 1.88$, $p = 0.034$). Certain fish species associated with these different explanatory variables while other species were ubiquitous across all sites (Table 2).

A total of 56 coral genera were observed, including species of the Western Indian Ocean endemic genera: *Anomastrea, Horastrea* and *Parasimplastrea* (Table S2). The distribution of coral genera was significantly explained by wave exposure ($F = 4.82$, $p = 0.002$), reef slope ($F = 3.72$, $p = 0.011$) and coral cover ($F = 3.20$, $p = 0.032$) (Fig. 2b).

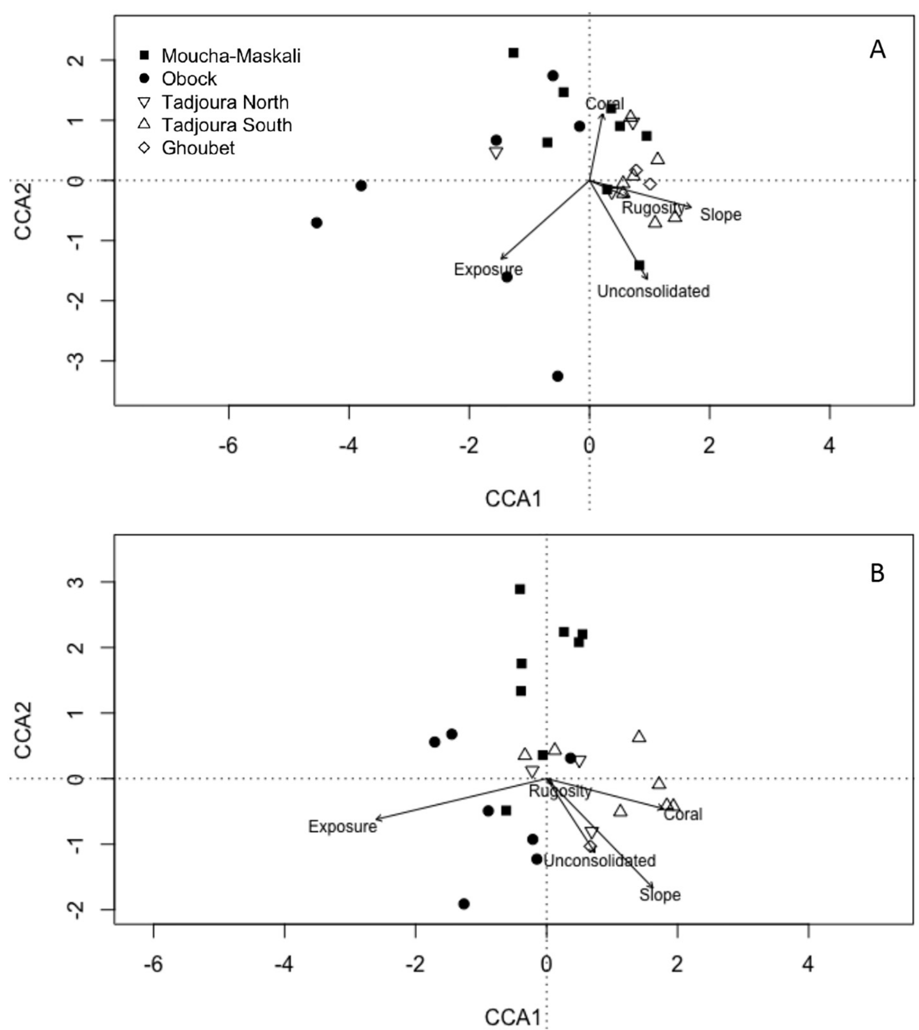

Fig. 2. Canonical correspondence analysis (CCA) plot of A. fish species density from 11 fish families and B. coral genus density. Sites are arranged by symbol for different regions. Note: 'Exposure' refers to wave exposure and 'Unconsolidated' refers to the combined cover of sand and rubble. Species and genus positions are not shown.

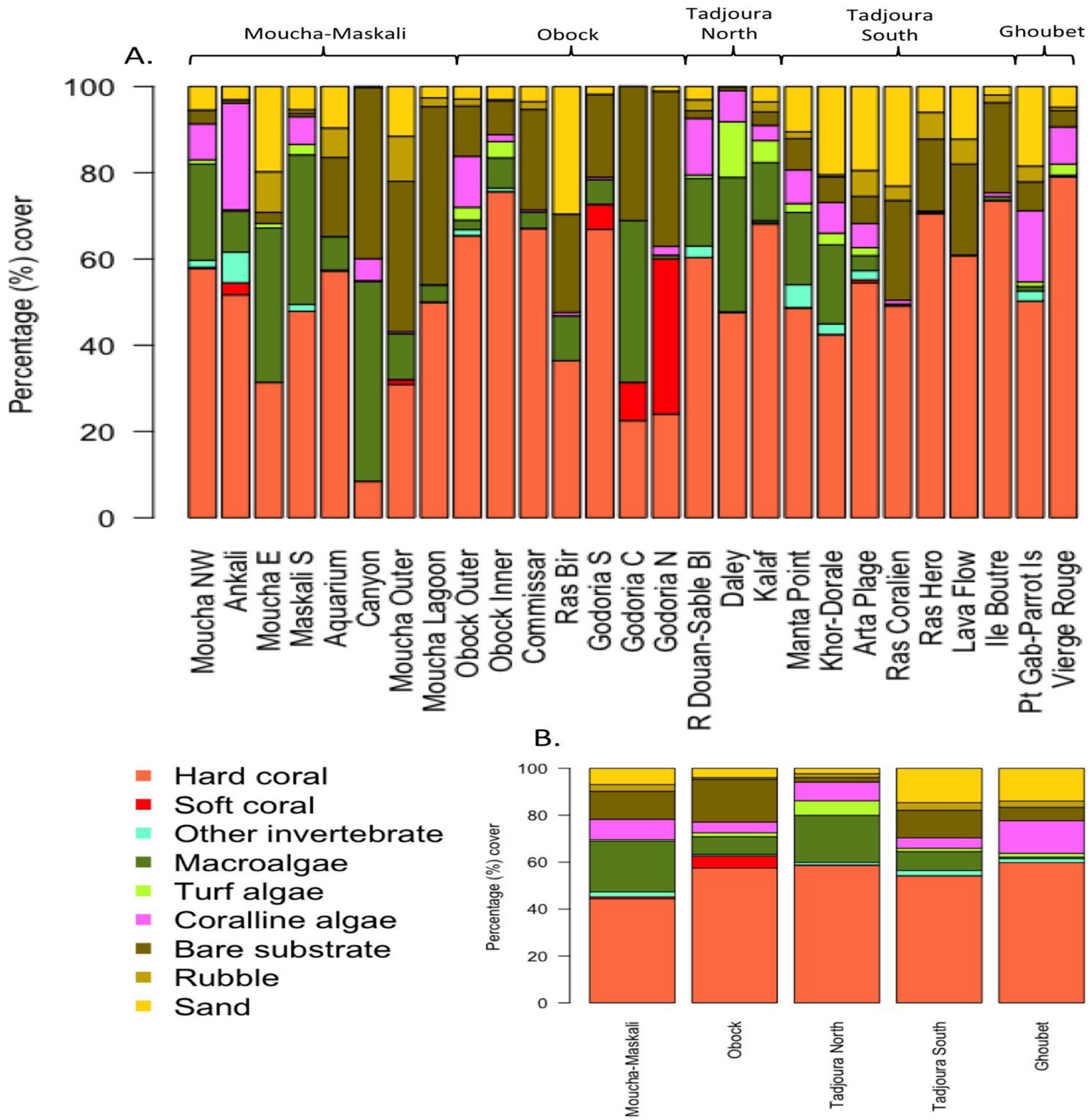

Fig. 3. Cover of major benthic categories by site and region.

Steep slopes and high coral cover reefs in Tadjoura South and the Ghoubet were characterised by encrusting *Montipora, Pavona* and *Echinopora*, whereas wave exposed reefs in Moucha-Maskali and Obock were characterised by massive *Favites, Platygyra* and *Lobophyllia*. The centroids for *Acropora, Pocillopora* and *Porites* were located near the origin of the CCA plot, indicating these genera were found in similar abundances on all reefs.

3.2. Reef condition

The number of coral genera per site ranged from 13 at Moucha Outer (MM6), to 30 at Ras Bir (OB4). The region with the highest coral diversity was Obock with an average of 24.6 (SE ± 1.64) genera per site, whereas Tadjoura North and Ghoubet had the lowest with 16.5 (SE ± 0.87). Coral cover was high at most sites, with an average of 51.8% (SE ± 3.38) and reaching > 70% at sites in Tadjoura South and Ghoubet (Fig. 3, Table 3). Moucha-Maskali had the lowest average coral cover with 41.9% (SE ± 6.03), but was very variable from 8.4% at Canyon (MM7) to > 55% at Moucha North-West (MM1) and Aquarium (MM5). Records from nine sites that were surveyed in 1998 show that there has been no significant change in coral cover between 1998 and 2014–2016 (paired *t*-test: $t = -0.303$, $p = 0.770$) (Fig. 4).

Fish diversity was relatively low at all sites with CFDI values ranging from 28 at Ras Hero (TS5) to 60 at Obock Outer (OB1) (Table 3), with a site average of 44.6 species (SE ± 3.97). There were no obvious regional differences in CFDI, with region averages between 40 and 50. However, total fish density and biomass values (all 11 families combined) were very high in most regions, with mean densities of 8562 (SE ± 1657.8) indiv./ha in Obock, 7270 (SE ± 974.9) in Tadjourah South, 6269 (SE ± 1635.3) in Tadjourah North, 5679 (SE ± 1089.5) in Moucha-Maskali and 5399 (SE ± 1185.3) in Ghoubet. In most sites planktivores were the most abundant fish trophic group, with an overall mean of 2264 (SE ± 330.6) indiv./ha, followed by the omnivores with an overall mean 1741 (SE ± 310.1), except in Moucha-Maskali where scrapers and grazers were more abundant in several sites (Fig. 5a). Total biomass values ranged from 2488 (SE ± 1066.7) kg/ha in Obock, 2327 (SE ± 1206.0) in Ghoubet, 1770 (SE ± 367.0) in Tadjourah South, 1748 (SE ± 300.4) in Tadjourah N and 1379 (SE ± 305.9) in Moucha-Maskali (Fig. 5b). The omnivores had the highest biomass of all trophic groups, followed by the herbivore-detritivores and the planktivores (Fig. 5b). Target fishery species biomass was high in many sites (Fig. 5b), with mean regional values ranging from 718 to

Table 3
Reef condition indicators coral cover, coral genus richness, target fishery species biomass (fish biomass) and Coral Fish Diversity Index (CFDI) of each site and the regional mean and standard errors. *Mean target fish biomass for Obock excludes anomalous value from Ras Bir.

	Coral cover	Coral genera	Target fish biomass	CFDI
Moucha-Maskali	*41.9 (SE ± 6.03)*	*18.6 (SE ± 1.36)*	*376.7 (SE ± 122.17)*	*44.8 (SE ± 2.97)*
Moucha NW	57.8	18	242	41
Ankali	51.7	18	154	55
Moucha E	31.4	16	356	52
Maskali S	47.9	17	285	55
Aquarium	57.2	21	582	38
Moucha Outer	30.9	13	1138	32
Canyon	8.4	26	211	42
Moucha Lagoon	50.0	20	45	43
Obock	*51.1 (SE ± 8.56)*	*24.6 (SE ± 1.64)*	*718.2 (SE ± 150.68)**	*43.0 (SE ± 3.79)*
Obock Outer	65.4	19	1100	60
Obock Inner	75.6	19	1101	54
Commissar	67.1	28	610	35
Ras Bir	36.4	30	6744	39
Godoria S	66.8	27	585	42
Godoria C	22.5	23	123	36
Godoria N	24.0	26	790	35
Tadjoura North	*58.7 (SE ± 6.01)*	*16.5 (N/A)*	*957.5 (SE ± 198.70)*	*49.7 (SE ± 2.03)*
R Douan-Sable Bl	60.4	15	1353	53
Daley	47.5	18	795	46
Kalaf	68.1	N/A	725	50
Tadjoura South	*57.1 (SE ± 4.42)*	*20 (SE ± 0.84)*	*751.2 (SE ± 180.2)*	*41.9 (SE ± 3.95)*
Manta Point	48.6	18	1508	40
Khor-Dorale	42.5	17	794	57
Arta Plage	54.5	18	891	54
Ras Coralien	49.1	22	245	36
Ras Hero	70.4	21	274	28
Lava Flow	60.9	22	396	35
Ile Boutre	73.6	22	1151	43
Ghoubet	*64.6 (N/A)*	*16.5 (N/A)*	*795.3 (N/A)*	*51.0 (N/A)*
Pt Gab-Parrot Is	50.3	18	1228	50
Vierge Rouge	79.0	15	363	52

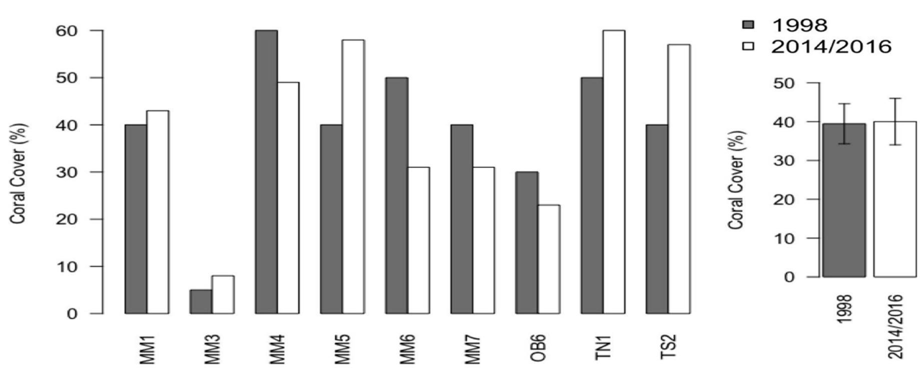

Fig. 4. Coral cover change at sites investigated in late-1998 that were revisted in this study, showing the average and standard error of cover from these sites in the two periods.

958 kg/ha, except in Moucha_Maskali where 377 kg/ha was recorded (Table 2). The target fishery species biomass was significantly lower in the Moucha-Maskali region, compared to other sites ($t = -2.594$, $p = 0.020$). An anomalously high piscivore-omnivore biomass (6744 kg/ha) was recorded in Ras Bir (OB4), due to very large schools of Lutjanidae (snappers) and numerous large (~1 m) *Plectorhinchus albovittatus* (giant sweetlips), therefore this site was excluded in the mean calculation for Obock region (Table 2).

3.3. Past thermal stress and reef resilience to future bleaching

The maximum monthly mean (MMM) was 30.9 °C, thus the bleaching threshold is 31.9 °C (MMM + 1) (Fig. 6). The mean winter temperature for the time series was 25.9 °C (SE ± 0.06), giving an annual range of approximately 5 °C. The historical temperature profile of Djibouti revealed that in the years 1997 and 2002 there were > 4 DHWs, which is considered enough thermal stress to trigger coral bleaching, but only in 1998 did thermal stress exceed 8 DHWs, which is a level of stress where extensive coral bleaching and mortality can occur (Liu et al., 2003). In 2016 there were no anomalously high temperatures or DHWs recorded.

Sheltered lagoonal sites in Moucha-Maskali and Obock (e.g Aquarium (MM5), Maskali South (MM4) and Obock Inner (OB2) were estimated to have the highest exposure to coral bleaching because of the lack of either wave exposure, nearby deep water or physical shading (Table 3, Fig. 7). Other sites in Obock and Moucha-Maskali had low bleaching exposure due to high wave exposure and proximity to deep oceanic waters. Sites in the Ghoubet had low bleaching exposure as a result of physical shading from steep cliffs and steep reef profiles. Bleaching sensitivity of the coral community was high in the southern part of Moucha-Maskali (MM3, MM5 and MM8) and at Ile Boutre (TS7) with > 60% of the coral community composed of *Acroporidae* and

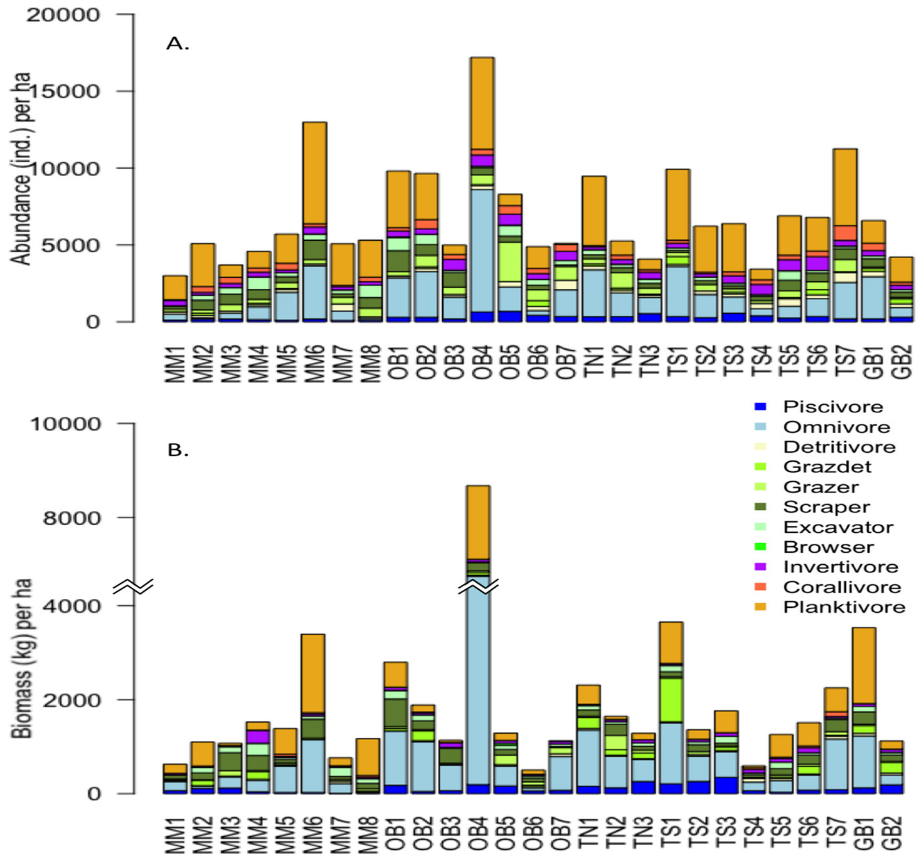

Fig. 5. Fish trophic groups, showing A. the density and B. the biomass per hectare at each site.

Pocilloporidae. Bleaching sensitivity was lowest in Obock, Tadjoura North and the northern part of Moucha-Maskali (MM1, MM2, MM4, MM6 and MM7) with < 25% cover of bleaching sensitive corals. The combination of low bleaching exposure and low bleaching sensitivity at sites such as Moucha Outer (MM6), Ras Bir (OB4), Ras Douan-Sable Blanc (TN1) and Manta Point (TS1), suggests that they will be resistant to future bleaching events (Table 4, Fig. 7).

The potential recovery ability of reefs varied greatly between sites. Macroalgae formed a significant portion of benthic cover (10–20%) at many sites (Table 4, Fig. 3). Exceptions were sites in the Ghoubet and in the western part of Tadjoura South (TS4-TS7), where macroalgal cover was < 1%. The proportion of unconsolidated substrate ranged from 0% in Godoria Central (OB6) to 29.2% in Moucha East (MM3), with higher levels of loose sediment on reefs in Tadjoura South and Ghoubet. The site with the least suitable substrate for coral recruitment and growth (i.e. high macroalgae and loose sediment) was Moucha East (MM3). Herb-detritivore fish density was lowest in Moucha North-West (MM1) with 410 ind. Per ha, and highest at 4000 ind. per ha in Godoria South (OB5) (Table 4). Coral recruit density was < 10 recruits per m^2 in most sites, but in Vierge Rouge (GB2), Parrot Island – Point Gabrielle (GB1) and Manta Point (TS1) recruit density was > 25 per m^2. The sites with the highest overall recovery potential were Obock Inner (OB2) and Obock Outer (OB1), while sites with the lowest recovery potential include Moucha East (MM3), Ras Bir (OB4), Arta Plage (TS3) and Ras

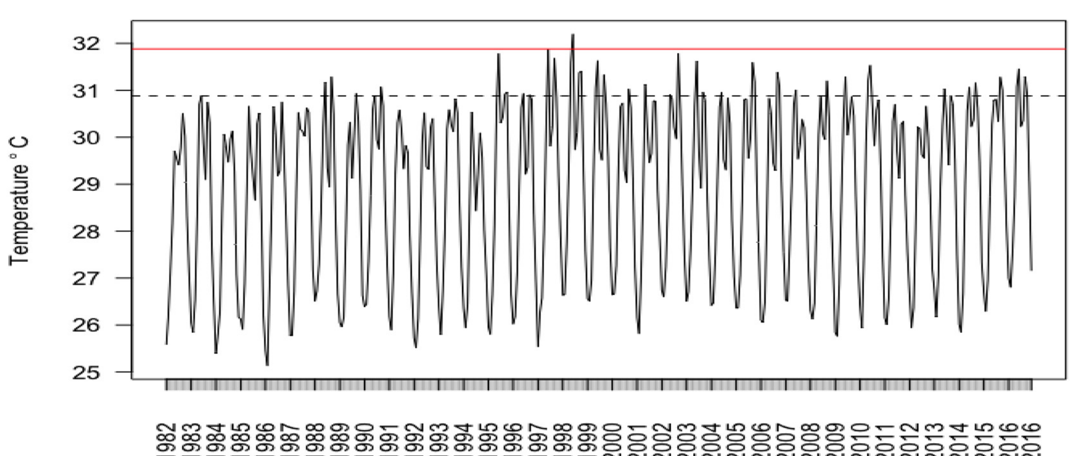

Fig. 6. Sea surface temperatures (SSTs) each month from 1982 to 2016, showing the maximum monthly mean (MMM) indicated with a dashed line and the bleaching threshold (MMM +1 °C) indicated with a solid line.

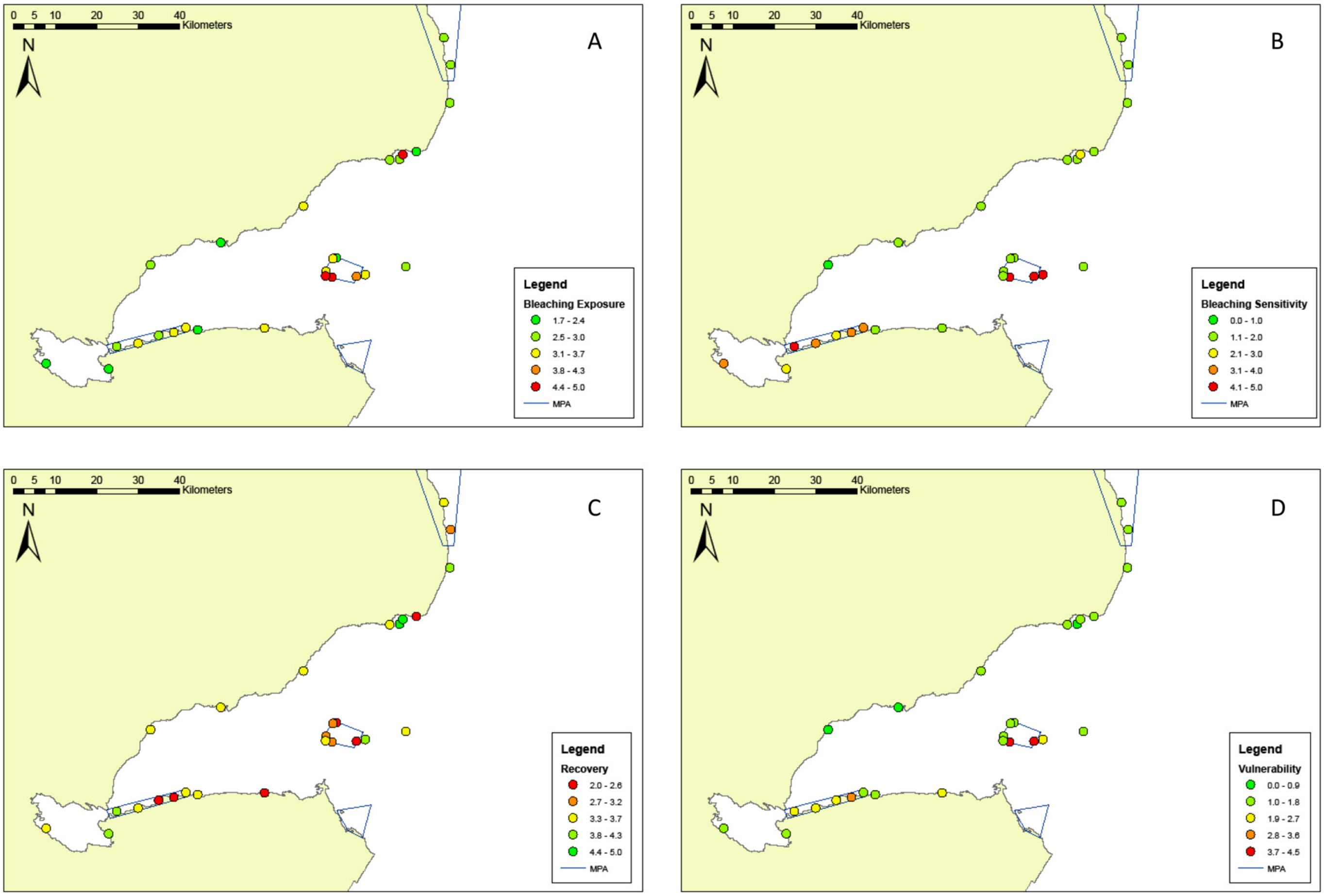

Fig. 7. The vulnerability of reefs to coral bleaching showing a) bleaching exposure, b) bleaching sensitivity, c) recovery potential and d) overall vulnerability. The range in each score for each component was divided into 5 classes of equal width and coloured from good (green) to bad (red). Scores denoting good to bad were reversed for recovery potential as per Eq. (1). Coastline and shallow reef derived from Landsat 7ETM+ satellite data courtesy of the U.S. Geological Survey. Bathymetric contours derived from Shuttle Radar Topography Mission (SRTM). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Corallien (TS4).

The estimated overall vulnerability of most sites was low, either because of low exposure and sensitivity to coral bleaching and/or because of high recovery potential, with the lowest vulnerability to bleaching at Obock Inner (OB2) and Ras Douan-Sable Blanc (TN1). Moucha East (MM3) and Aquarium (MM5) had the highest vulnerability to future bleaching because these shallow lagoon sites were dominated by bleaching sensitive genera and had low recovery potential (Table 4, Fig. 7).

4. Discussion

4.1. Reef types, biodiversity and biogeography

This paper provides the first comprehensive assessment of Djibouti's coral reefs in 18 years and shows a range of reef types within the relatively short coastline of 340 km. Coral reefs were found on all areas of the coastline (Fig. 1), except at river mouths (wadis) where high sedimentation appeared to be preventing coral growth. High turbidity in the coastal waters, probably a result of wind-blown desert sand, was found to limit coral growth in most places to a maximum of 20 m deep (B. Cowburn pers. obs). Variation between reefs appears to be primarily driven by wave exposure, reef slope and unconsolidated substrate of sand and rubble. This may be explained by the geology of the Djibouti coastline: to the east, reefs are found on extensive shallow continental shelves, similar to other reefs in the Southern Red Sea (Spalding et al., 2001; Klaus, 2015) with wide (1-5 km) reef structures, including lagoons, seagrass beds and some small areas of mangroves. The geologically youngest reefs are in the Ghoubet, where the separation of the Somali and African plates is extending the Gulf of Tadjoura westwards (Makris and Ginzburg, 1987). Here, reef structures were small and corals were found growing on the steeply sloping underlying basalt rock in the proximity of deep water in a highly sheltered environment. Reefs in the Gulf of Tadjoura are more developed on a limestone framework, but in many places confined to a narrow band (< 500 m) with a steep slope into deeper water. These patterns in reef type influenced the taxa and abundance of fish and coral, as observed on reefs elsewhere (Friedlander et al., 2003; Pinca et al., 2012). Thus, conservation planning should capture these regional geomorphological and habitat differences.

The biogeographical affinity of these reefs is predominantly Red Sea which is characterised by a high percentage of endemic species of fish (14%) and hermatypic corals (5.5%), where endemism is expressed as the percentage of unique fauna to a region (Randall, 1994; DiBattista et al., 2015). Several species The coral genus diversity was moderate to high with 56 genera, compared to other locations in the WIO with between 40 and 65 genera (Obura, 2012). However, the diversity of reef fish was lower compared to western Indian Ocean (WIO) sites, with a CFDI value of 105 for the whole country, compared to values of 172 in North-East Madagascar (Samoilys and Randriamanantsoa, 2011) and 167 in Cabo Delgado, Mozambique (M. Samoilys 2015, unpubl. data). Certain families are depauperate in the Red Sea/Gulf of Aden compared

Table 4
Reef resilience indicators values per site showing the combined score for bleaching exposure factors, the bleaching sensitivity scores, recovery potential of the site and the final vulnerability score. The range in each score for each component was divided into 5 classes of equal width and coloured from good (green) to bad (red). Scores denoting good to bad were reversed for recovery potential as per Eq. (1).

		Bleaching Exposure				Bleaching Sensitivity		Recovery Potential					Vulner -ability
Region	Site	Wave Exposure	Deep Water	Shading	*Score (E)*	Sensitive Corals	*Score (S)*	Macroalgae	Herbivore Abundance	Loose substrate	Recruit density	*Score (R)*	*Score (V)*
	Moucha NW	4	3	4	3.7	1.7	1.0	22.3	410	5.5	9.7	2.8	1.70
	Ankali	2	1	5	2.7	16.8	1.0	9.5	1216	3.1	N/A	3.7	1.00
	Moucha E	3	4	5	4.0	75.9	5.0	35.8	1480	29.2	N/A	2.0	4.50
Moucha-Maskali	Maskali S	4	5	5	4.7	7.4	1.0	34.7	1856	6.2	N/A	3.3	1.70
	Aquarium	5	5	5	5.0	82.5	5.0	7.8	1240	16.5	0.3	2.8	3.64
	Moucha Outer	2	1	4	2.3	10.4	1.0	46.3	1373	0.2	4.0	2.5	1.33
	Canyon	4	3	4	3.7	7.4	1.0	10.7	2080	22.0	6.6	2.8	1.70
	Moucha Lagoon	3	3	5	3.7	65.7	4.0	4.0	2160	4.7	4.7	4.0	1.92
	Obock Outer	2	2	4	2.7	7.1	1.0	2.2	2576	4.5	19.4	4.5	0.81
	Obock Inner	5	5	5	5.0	22.9	2.0	7.0	2336	3.4	N/A	5	1.40
	Commissar	2	2	4	2.7	9.8	1.0	3.8	1693	5.3	7.7	3.5	1.05
Obock	Ras Bir	2	1	2	1.7	11.6	1.0	10.4	1467	29.6	7.5	2.3	1.19
	Godoria S	1	3	5	3.00	4.1	1.0	5.8	4000	1.8	3.1	4	1.00
	Godoria C	1	3	5	3.00	13.8	1.0	37.5	1893	0.0	5.0	2.8	1.45
	Godoria N	1	3	5	3.00	1.6	1.0	0.9	1813	1.1	6.1	3.8	1.07
	R Douan-Sable Bl	4	1	1	2.0	6.6	1.0	15.7	1088	5.6	18.9	3.5	0.86
Tadjoura N	Daley	2	3	5	3.33	3.8	1.0	31.2	1600	0.1	N/A	3.3	1.30
	Kalaf	3	3	3	3.00	N/A	N/A	13.5	1016	5.9	24.2	3.3	N/A
	Manta Pt	3	1	3	2.3	18.4	1.0	16.8	1072	12.1	31.3	3.3	1.03
	Khor-Dorale	4	3	4	3.67	16.2	1.0	18.3	1144	21.0	12.1	2.5	1.87
	Arta Plage	4	3	3	3.33	37.0	3.0	3.5	696	25.5	N/A	2.3	2.71
Tadjoura S	Ras Coralien	5	3	1	3.00	23.0	2.0	0.4	813	26.4	8.4	2.3	2.22
	Ras Hero	5	3	2	3.33	36.5	3.0	0.4	2253	12.2	8.3	3.8	1.69
	Lava Flow	5	3	2	3.33	42.2	3.0	0.0	1827	18.0	8.1	3.3	1.95
	Ile Boutre	3	3	3	3.00	87.8	5.0	0.9	2227	3.8	7.4	4.0	2.00
Ghoubet	Pt Gab-Parrot Is	3	1	2	2.0	50.2	3.0	1.0	1248	22.1	40.2	3.5	1.43
	Vierge Rouge	5	1	1	2.3	28.6	2.0	0.0	1016	5.6	29.3	4.0	1.08

to other Indian Ocean reef fish assemblages (Randall, 1994), including the Acanthuridae (surgeonfish and unicornfish), Haemulidae (sweetlips), Ostracidae (boxfish) and Monacanthidae (filefish). Lower fish diversity but high endemism are common features of Red Sea reefs as a result of their geographical isolation compared to other Indo-Pacific reefs (Bellwood and Wainwright, 2002; Hughes et al., 2002; Golani and Bogorodsky, 2010; DiBattista et al., 2015; DiBattista et al., 2016).

4.2. Reef condition

High coral cover was observed at most sites, with an average coral cover of 52% and a maximum of 79%. This is at the upper end of the range reported for the Red Sea of 30–50% (PERSGA, 2010) and also higher than many locations in the WIO (Ateweberhan et al., 2011; Obura et al., 2017). The SST profile in Djibouti over the past 30 years suggests there has only been one major bleaching event in 1998, when mass coral bleaching was observed globally (Wilkinson, 2008). Observations of reefs in Djibouti in late 1998 showed that there was little coral mortality at most sites, with a maximum of 20–30% mortality in the Sept Frère islands (Obura, 1999; Barker et al., 2002), with no significant change in coral cover in sites with repeated observations in 2014/2016. Elsewhere in the region, severe coral bleaching and mortality was reported in 1998 from Socotra (DeVantier et al., 2004) and Saudi Arabia (DeVantier et al., 2000; PERSGA, 2010), but region wide levels did not approach the 50–80% mortality observed across countries such as Kenya and the Maldives in 1998 (Ateweberhan et al., 2011). Unfortunately no data were collected post-El Niño 2016 to verify whether the low thermal stress indicated by SST trends resulted in low bleaching, but chance observations of several sites in Moucha-Maskali during January 2017 found healthy coral communities with only partial mortality of *Pocillopora* colonies on shallowest reef (0-3 m) (B. Cowburn – Pers. Obs.) This included Canyon (MM7), which had the lowest coral cover of both 1998 and contemporary sites, again suggesting the 'unhealthy' condition of some reefs may be natural.

Reduction in coral cover in the Red Sea has also been observed near Jeddah in the central Saudi Arabia and near resorts along the Egyptian coast, associated with land reclamation, coastal development and eutrophication from urban areas (Price et al., 2014; Peña-García et al., 2014; Naumann et al., 2015). These impacts may explain the lower coral cover, high unconsolidated substrate and high macroalgae at the three northern sites of the Moucha-Maskali islands near the main shipping route to Djibouti port. However, these conditions were also observed on one of the three remote northern reefs near Godoria, which may be caused by nutrient rich deep-water upwelling and high wave exposure from the Gulf of Aden (Klaus, 2015). Thus, unlike many other reefs globally that have experienced severe bleaching on several occasions (Heron et al., 2016), or local anthropogenic threats (Burke et al., 2011), it appears that the coral communities of Djibouti have experienced relatively low impacts.

The fish assemblages of Djibouti were characterised by very high density and biomass in many sites, with mean total density of 6883 (SE ± 630.0) indiv/ha and a mean total biomass of 1879 (SE ± 309.5) kg/ha. While the use of total fish biomass may be considered a simplistic metric it enables quick comparisons with other reef systems and in particular "reference' unfished systems (Samoilys et al., 2019). The total biomass values recorded in Djibouti are on a par with regions in the western/central Indian Ocean considered to represent reefs that are protected from all human impacts except climate change, such as the Chagos Archipelago (Graham et al., 2013) and the Iles Eparses (Chabanet et al., 2016). In Chagos in 2014, mean total fish biomass values, based on the same families as the current study, ranged from 1700 kg/ha to 3400 kg/ha, while mean total density ranged from 4500 to 7500 individuals/ha (Samoilys et al., 2018). In the Iles Eparses the highest value recorded was 3500 kg/ha (Chabanet et al., 2016). Notably, the biomass estimates in the current study are lower than those reported in Sudan (5001 kg/ha) and Saudi Arabia (4050 kg/ha), which included top predators such as sharks and large (> 1 m) jacks (Carangidae) (Kattan et al., 2017) that were not seen in Djibouti. The fish biomass values suggest higher levels of productivity on Djibouti's reefs compared with the western Indian Ocean. Ocean productivity has been linked to high fish biomass (Williams et al., 2015; Samoilys et al., 2019); possibly high nutrient levels in the Gulf of Aden may also be contributing to the exceptionally high fish biomass found on Djibouti's reefs.

Some fishing impacts within the Djibouti coastline are suggested by results from sites in Moucha-Maskali which had significantly lower fishery target species biomass than other regions; this was also reported in the 1990s (Gladstone et al., 1999). Historically the Somali and Afar peoples of Djibouti were pastoralists and did not fish, but artisanal fishing has grown significantly post-independence (1977) with financial assistance from the new government for the sector (Colléter et al., 2015) and in response to drought related food shortages (Gladstone et al., 1999; Morgan, 2004). However to date the coastal fishery remains small, considered underexploited and predominantly targets pelagic species rather than reef species (Morgan, 2004, Kotb, 2010, World Bank, 2011, K Osuka 2015 pers. obs.).

4.3. Future threats and conservation considerations

Corals in the Red Sea and the Arabian Gulf experience some of the highest summer temperatures globally with a large annual range (Kleypas et al., 1999; Coles and Riegl, 2013). This chronic thermal stress can lead to corals becoming more resistant to acute thermal stress and therefore reducing their vulnerability to bleaching (Fitt et al., 2001; Furby et al., 2013; Ziegler et al., 2017), which has led to suggestions that corals of this region may be best suited to face increasing ocean warming in the future (Coles and Riegl, 2013; Fine et al., 2013). However, the Red Sea has also experienced a rate of SST warming faster than other regions around the world (Raitsos et al., 2011; Heron et al., 2016) and is not immune to coral bleaching events (DeVantier et al., 2000, 2004; Furby et al., 2013). Repeated bleaching has now been recorded on 3 occasions during the past 25 years on the central Saudi Arabian coast (Monroe et al., 2018) and in nearby southern Arabian Gulf *Acropora* corals have been locally extripated (Burt et al., 2019). Our observations indicate reduced exposure to bleaching because of the physical shading from cliffs and steep reef slopes and the proximity to cool deeper waters in many sites along the Gulf of Tadjoura and the Ghoubet. However, these reefs may also be sensitive to bleaching because of the dominance of thermally sensitive *Acroporidae* and *Pocilloporidae* corals. Our vulnerability formula, based on sensitivity, recovery and exposure to bleaching measures, indicates the most vulnerable reefs are in shallow lagoons in Moucha-Maskali and Obock because of low coral recruitment, lack of mixing with deeper waters and the presence of macroalgae. It is unfortunate that these reefs could not be revisited after El-Niño 2016 to test the predictions of the vulnerability model or compare bleaching level in Djibouti to other impacted reefs in the region. However, the low levels of mortality in 1999 data and casual observations in 2017, along with the dominance and large size of thermally sensitive *Acropora* colonies, suggest that this area has experience very little bleaching to date.

Although much of the coastline of Djibouti is uninhabited and undeveloped due to its desert climate, threats to the marine environment from pollution, sedimentation and nutrification near the capital city and main port facility are growing (PERSGA/GEF, 2003; IUCN, 2016). This likely explains the highest vulnerability and lowest resilience measures on reefs in the Moucha-Maskali islands, near Djibouti city. The Government of Djibouti is also increasing the level of economic development around the country focussing on transport, fishing and tourism sectors. Under the 'Vision 2035' programme, several new ports are planned or have begun development including a new port for salt export in the Ghoubet (Fig. 1). This port was not present during the 2014 surveys, but was complete and operational by 2016 (B. Cowburn pers. obs. 2016), demonstrating the rapid rate at which Djibouti is developing. Nevertheless, the Government of Djibouti has recognised its valuable and unique marine environment by establishing four marine parks, located in Arta Plage, Îles Moucha-Maskali, Îles Haramous and Sept Frères (PERSGA/GEF, 2004). A marine spatial planning (MSP) exercise was carried out for the Gulf of Tadjourah with key government bodies and other stakeholders from 2014 to 2016 (IUCN, 2016; Klaus, 2016) and incorporated data collected in the current study. MSP is a holistic and cross-sectoral way to encompass biodiversity conservation, sustainable development and economic growth. The government is also supporting community-based approaches through the introduction of locally managed marine areas which are widely viewed as effective tools for coral reef fisheries management and biodiversity conservation (Rocliffe et al., 2014; Kawaka et al., 2016).

In summary, Djibouti's reefs in 2014 supported healthy coral communities with abundant fish assemblages, likely due to the lack of previous acute thermal stress events, low levels of human impacts and possibly higher ocean productivity. However, future global projections suggest they are likely to be impacted by coral bleaching (van Hooidonk et al., 2016). Further, while the corals on Djibouti's reefs may be well adapted to high temperatures and variable conditions, the high proportion of bleaching sensitive corals, combined with limited historical exposure to bleaching, suggest that corals on these reefs may be vulnerable to future thermal stress. Nevertheless, possibly the biggest current threat to Djibouti's reefs is the rapid development of large coastal infrastructure projects that are being constructed at a rate that is outpacing environmental regulation. It is critical, therefore, that better environmental regulations are put in place, the existing protected areas are effectively managed and the MSP implemented to ensure the rich and valuable biodiversity of Djibouti's coral reefs can continue to provide valuable economic goods and services to the local population.

Acknowledgements

This work was partly funded by the European Union through the IGAD Biodiversity Management Programme in the Horn of Africa through a grant to the IUCN, Coastal Oceans Research and Development - Indian Ocean (CORDIO) and Equipe Cousteau. The contents of this paper are the sole responsibility of the authors (CORDIO, Equipe Cousteau) and can in no way be taken to reflect the views of the European Union. Additional funding was provided by the International Fund for Agricultural Development (IFAD), through PRAREV. We are also grateful to the Ministry of Housing, Urban Affairs & Environment (MHUE) and the following people who all provided invaluable support: Leo Niskanen, Houssein Rayaleh, Tarik Chekchak, Ibrahim Mohamed Abdou, Hassan Mohamed Abass, Ahmed Darar Djibril and Beydane Miyir.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.marpolbul.2019.07.040.

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