



## Through bleaching and tsunami: Coral reef recovery in the Maldives

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### ABSTRACT

Coral reefs are degrading worldwide, but little information exists on their previous conditions for most regions of the world. Since 1989, we have been studying the Maldives, collecting data before, during and after the bleaching and mass mortality event of 1998. As early as 1999, many newly settled colonies were recorded. Recruits shifted from a dominance of massive and encrusting corals in the early stages of recolonisation towards a dominance of *Acropora* and *Pocillopora* by 2009. Coral cover, which dropped to less than 10% after the bleaching, returned to pre-bleaching values of around 50% by 2013. The 2004 tsunami had comparatively little effect. In 2014, the coral community was similar to that existing before the bleaching. According to descriptors and metrics adopted, recovery of Maldivian coral reefs took between 6 and 15 years, or may even be considered unachieved, as there are species that had not come back yet.

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## 1. Introduction

Global climate change, with consequent seawater warming, sea level rise and ocean acidification, is causing coral reef degradation worldwide (Knowlton and Jackson, 2008; Lasagna et al., 2014). Extreme climatic anomalies related to global warming, in particular, have triggered extensive bleaching and mass mortality events across most tropical regions (Baker et al., 2008). In association with local natural (storms, cyclones, tsunamis, crown-of-thorns starfish outbreaks, etc.) and anthropogenic (tourism, fishing, coral mining, anchoring, pollution, etc.) disturbances, climate change is at the origin of the so-called 'coral reef crisis' (Bellwood et al., 2004; Brown et al., 2013; Ban et al., 2014). Under projections of global climate change and local stressors, significant alterations in the ecology, structure and function of coral reefs are expected (Rogers et al., 2015). Recovery of degraded coral reef ecosystems may prove difficult (Graham et al., 2011) and their decline under climate change has been predicted (Descombes et al., 2015).

Recent global analyses indicate that about 75% of world coral reefs are severely threatened by global and local pressures of anthropogenic origin, and, given the present escalation of human

impacts, it is estimated that 90% of them will be at risk by 2050 (Wilkinson, 2008; Burke et al., 2011). Coral reefs survived Quaternary climatic oscillations (Pandolfi and Jackson, 2006), but the recent increase in scale and frequency of disturbances may lead to 'phase shifts', i.e., changes in community structure and composition (Dudgeon et al., 2010; Montefalcone et al., 2011; Mumby et al., 2013).

Estimating magnitude, patterns and trajectories of change is necessary to evaluate the possibility of recovery of coral reefs, but requires information on previous conditions of coral-reef communities (Bruno and Selig, 2007). Unfortunately, this kind of historical data are extremely rare for most regions of the world ocean. Best known examples come from the Wider Caribbean and the Great Barrier Reef, worldwide international initiatives (such as Reef Check) being more recent (Hughes et al., 2010). Little information is available for Indian Ocean coral reefs (Ateweberhan et al., 2011).

The rise in sea-surface temperature linked to the 1997–1998 El Niño event caused massive bleaching and coral mortality throughout the Indian Ocean (Plass-Johnson et al., 2015). The Maldives has been among the most affected countries, with 60–100% coral mortality reported, depending on species and locality (Bianchi et al., 2003). This was not the first bleaching event in the Maldives (Edwards et al., 2001), but has probably been the most severe.

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We have been studying the coral reefs of the Maldives for the last 25 years. Early studies consisted of snapshot assessments in Ari (Morri et al., 1995), Felidhoo (Bianchi et al., 1997) and North Malé Atolls (Morri et al., 2010), but since 1997 we conducted research with yearly scientific cruises (Bianchi et al., 1998, 2009). Thus, we had the opportunity to collect data on the state of coral reefs before, during and after the mass mortality event of May 1998 (Bianchi et al., 2003). The first results of this monitoring activity indicated that recolonisation already started in 1999, with many newly settled colonies recorded (Bianchi et al., 2006). Six years after the 1998 mass mortality, tabular *Acropora* corals were again abundant and large (Lasagna et al., 2010a). This notwithstanding, the recovery of the coral community as a whole appeared slow, suggesting there was an ongoing risk of degradation of these reefs (Lasagna et al., 2008, 2010b). Recovery was still in progress when the Sumatra–Andaman tsunami of December 2004 hit the Maldivian atolls, potentially causing further damage to the reef (Gischler and Kikinger, 2006).

This paper aims at describing the recovery trajectory of Maldivian coral reefs to 2014, taking into consideration multiple descriptors: (1) composition of coral reef communities; (2) coral recruitment; (3) hard coral cover, considering also historical data; (4) reef rugosity, at two different spatial scales; (5) coral ecosystem functioning, in terms of constructional capacity and trophic structure.

## 2. Methods

### 2.1. Study area and field activity planning

The Maldives, comprised of 27 atolls and ca. 1120 islands, form the central part of the Chagos–Maldives–Laccadive ridge in the central Indian Ocean, stretching in a north–south direction from about 7°07' N to 0°40' S in latitude and 72°33' E to 73°45' E in longitude (Risk and Sluka, 2000; Gischler et al., 2014). The climate in the Maldives is monsoon-dominated, with a wet summer monsoon (April to November) due to winds blowing to the northeast and a dry winter monsoon (December to March) with winds blowing westward. Such a wind regime controls the formation of the typical Maldivian reefs called faros (Kench et al., 2006). Although the earliest field investigations on the Maldivian coral reefs date back to the turn of the 20th century (Gardiner, 1901–1905; Agassiz, 1903), thorough studies on coral communities started with the Xarifa expedition in the late 1950s (Wallace and Zahir, 2007 and references therein). Recent reference for the ecology of Maldivian coral reefs is provided by Andréfouët (2012).

Our scientific cruises took place annually (except in 2011) in April, on board of the M/y *Eagle Ray*, *Maavahi*, *Conte Max*, or *Duca di York*. The cruises visited eight atolls: Ari, Felidhoo, Huvadhoo, North Malé, Rasdhoo, South Malé, Thoddoo, Vattaru. Due to weather conditions and logistic constraints or other opportunities, the actual route of the cruises differed from year to year. Every year, 8 sites, chosen randomly, were surveyed along the route of the cruise: 4 ocean reef sites (ocean-facing sides of faros situated on the atoll rim) and 4 lagoon reef sites (lagoon faros or lagoon-facing sides of the atoll rim) (Lasagna et al., 2010b). Sites were located on the British Admiralty Chart No 1013 and their position recorded using a GPS. It happened that some sites were revisited years apart. All data were collected by scuba diving, using different protocols according to the specific survey done.

### 2.2. Data collection and management

#### 2.2.1. Coral reef communities

The composition of reef communities was described using 23 benthic categories (Morri et al., 2010): 20 'lumped' levels of

classification of sessile organisms, combining taxa with growth-forms, and 3 non biotic physiognomic attributes (Table 1). For each of these benthic categories, the percent substratum cover was estimated in three depth zones: outer flat (4–6 m), upper slope (10–12 m), and intermediate slope (16–18 m). Three replicated 20 m long point intercept transects (Bianchi et al., 2004) were laid parallel to the reef edge from an arbitrarily selected starting point in three depth zones and two reef types (ocean and lagoon). In total, 1224 transects (17 years × 2 reef types × 4 sites × 3 depth zones × 3 replicates) were employed.

The matrix containing percent cover data of the 23 benthic categories in the 1224 transects was submitted to Correspondence Analysis (CA), after arcsine  $\sqrt{(x/100)}$  transformation (Legendre and Legendre, 1998). Significance of the axes ( $p < 0.05$ ) was evaluated through Lebart's tables (Lebart, 1975).

#### 2.2.2. Coral recruitment

Commencing 1999, hard coral recruitment was quantified by counting small corals with approximately circular outlines in 12 replicated quadrats of 0.25 m<sup>2</sup>, randomly placed in the same sites and the same depth zones as the community transects described in Section 2.2.1 above. Coral colonies smaller than 5 cm in diameter were called 'recruits', whereas the term 'juveniles' was used for colonies ranging between 5 and 15 cm (Cardini et al., 2012). Both recruits and juveniles were divided into three categories: *Acropora*, *Pocillopora*, others (Bianchi et al., 2003, 2006). The total number of quadrats surveyed was 4320 (15 years × 2 reef types × 4 sites × 3 depth zones × 12 replicates).

Recruit density (number·m<sup>-2</sup>) data were subjected to 4-way analysis of variance (Underwood, 1996), with reef types as fixed factor with 2 levels (ocean and lagoon), years as fixed factor orthogonal to reef types with 15 levels (from 1999 to 2014, except 2011), depth zones as fixed factor orthogonal to years and with 3 levels (4–6 m; 10–12 m; 16–18 m), sites as random factor nested within depth zones and years with 4 levels, and quadrats as replicates ( $n = 4$ ). Temporal autocorrelation was avoided by randomly

**Table 1**

List of benthic categories (together with their codes as used in Fig. 3) chosen to describe reef communities during our yearly cruises in the Maldives.

Benthic categories	Codes
BIOTIC	
<i>Acropora</i> branching	CAB
<i>Acropora</i> digitate	CAD
<i>Acropora</i> tabular	CAT
Coral branching	CB
Coral foliose	CF
Coral massive	CM
Coral encrusting	CE
<i>Tubastrea micranthus</i>	CT
<i>Helioipora coerulea</i>	H
<i>Millepora</i>	M
Corallimorpharians	CMR
<i>Palythoa</i>	P
Soft corals (alcyonarians) zooxanthellate	SZ
Soft corals azooxanthellate	SA
Whip- and wire-corals (to include the gorgonian <i>Junceella</i> and the anthipatarians <i>Cirripathes</i> and <i>Stichopathes</i> )	W
Sea fans (gorgonians and anthipatarians with planar or bushy colonies)	V
Algae (including <i>Tydemania expeditionis</i> and <i>Halimeda</i> )	A
Sponges	SP
Clams ( <i>Tridacna</i> )	TR
Tunicates	TU
NON-BIOTIC	
Dead coral/coral rock	RK
Coral rubble	R
Sand	S

selecting sites each year (Legendre and Legendre, 1998). Homogeneity of variance was tested by Cochran's C-test, while the Student-Newman-Keuls (SNK) test was applied *a posteriori* to detect significant differences between levels.

An indirect estimation of yearly survival of small corals was attempted using the formula: Survival% =  $100 J_{t-1}/R_t$ , where  $R_t$  is the number of recruits in the year considered and  $J_{t-1}$  is the number of juveniles in the previous year. Coral survival data were subjected to 4-way analysis of variance following the same design as for the recruits.

### 2.2.3. Hard coral cover

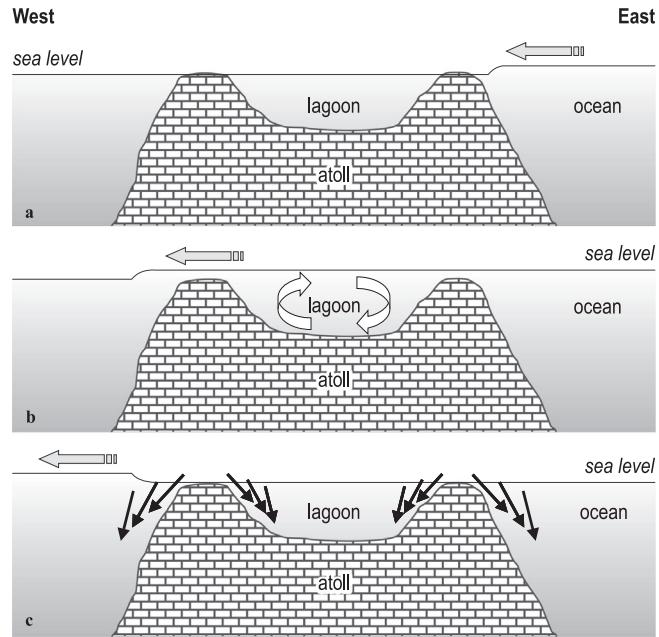
Historical data on hard coral cover obtained from published sources, including grey literature (Stoddart, 1966; Scheer, 1971, 1972, 1974; Spencer Davies et al., 1971; Brown and Dunne, 1988; Risk et al., 1994; Allison, 1995a,b, 1996; Sluka and Reichenbach, 1996; Clark and Edwards, 1999; Rajasuriya et al., 1999, 2002, 2004; McClanahan, 2000; Zahir, 2000, 2002; Edwards et al., 2001; Bianchi et al., 2003, 2006; Zahir et al., 2005, 2011; Graham et al., 2008; Lasagna et al., 2008, 2010b; Muthiga, 2008; Solandt and Wood, 2008; Morri et al., 2010; Solandt and Hammer, 2012; Tkachenko, 2012; Jaleel, 2013; Solandt et al., 2013, 2014; McClanahan and Muthiga, 2014), were merged with our post-1997 data collected as described in Section 2.2.1 above: specifically, for *Acropora* branching, *Acropora digitate*, *Acropora tabular*, coral branching, coral foliose, coral massive, coral encrusting, *Tubastrea micranthus*, *Heliofungia coerula* and *Millepora*.

An overall yearly mean of hard coral cover (historical + ours) was computed irrespective of reef type, site and depth zone (flat and slope, approximately 1–20 m) to describe the general trend of coral cover on Maldivian reefs during the last decades.

### 2.2.4. Reef rugosity

Notwithstanding the severe loss in living coral cover after the mass bleaching of 1998, the three-dimensional structure of the reef was preserved, dead coral colonies still being in place. By 2000, these dead coral colonies started to be destroyed by physical and biological erosion; by 2002, the three-dimensional structure of the reef was largely lost due to the breakage of dead colonies, which were reduced to rubble and sand (Lasagna et al., 2006). A great amount of these loose detrital elements accumulated in place (Lasagna et al., 2010b). When in December 2004 the Sumatra-Andaman tsunami reached Maldivian atolls, it caused submersion of low islands, erosion and displacement of sand cays, and resuspension of sediment (Fig. 1). Waves were not destructive *per se* (Wilkinson et al., 2006), but sand, rubble, detritus and wrecks were driven to shallow bottoms, hit and partially broke the recently grown coral colonies (Lasagna et al., 2014), and eventually deposited on reef slopes (Gischler and Kikinger, 2006), smoothing the substrate and obliterating notches and small terraces.

To document these two effects, we compared both ocean and lagoon reef rugosity before (2004) and after (2005) the tsunami at two spatial scales: (i) small scale (metres), using 90 replicate 2 m long chain transects (Bianchi et al., 2004) laid randomly between 5 and 20 m depth parallel to the reef edge; (ii) large scale (tens of metres), using 12 depth transects (Lasagna et al., 2010b) laid perpendicular to the reef edge, from the reef flat to 20–40 m depth, according to the site. An index of rugosity for the small scale was calculated dividing the length of the chain deployed on the substratum by the length of its horizontal projection. For the large scale, vertical profiles were plotted from depth transect data, and the complexity of each profile was estimated by computing its fractal dimension (Tokeshi and Arakaki, 2012). When available, profiles describing the same site in different years were compared to illustrate any change in topography.



**Fig. 1.** Scheme of the impact of the Sumatra-Andaman tsunami on Maldivian reefs. (a) Incoming wave from the East, causing rise in sea level of ca 1.5–1.8 m. (b) High water passing over reefs and lagoon dislodging sediments and debris. (c) Dumping of sand and rubble on reef slopes after the passage of the wave.

### 2.2.5. Coral ecosystem functioning

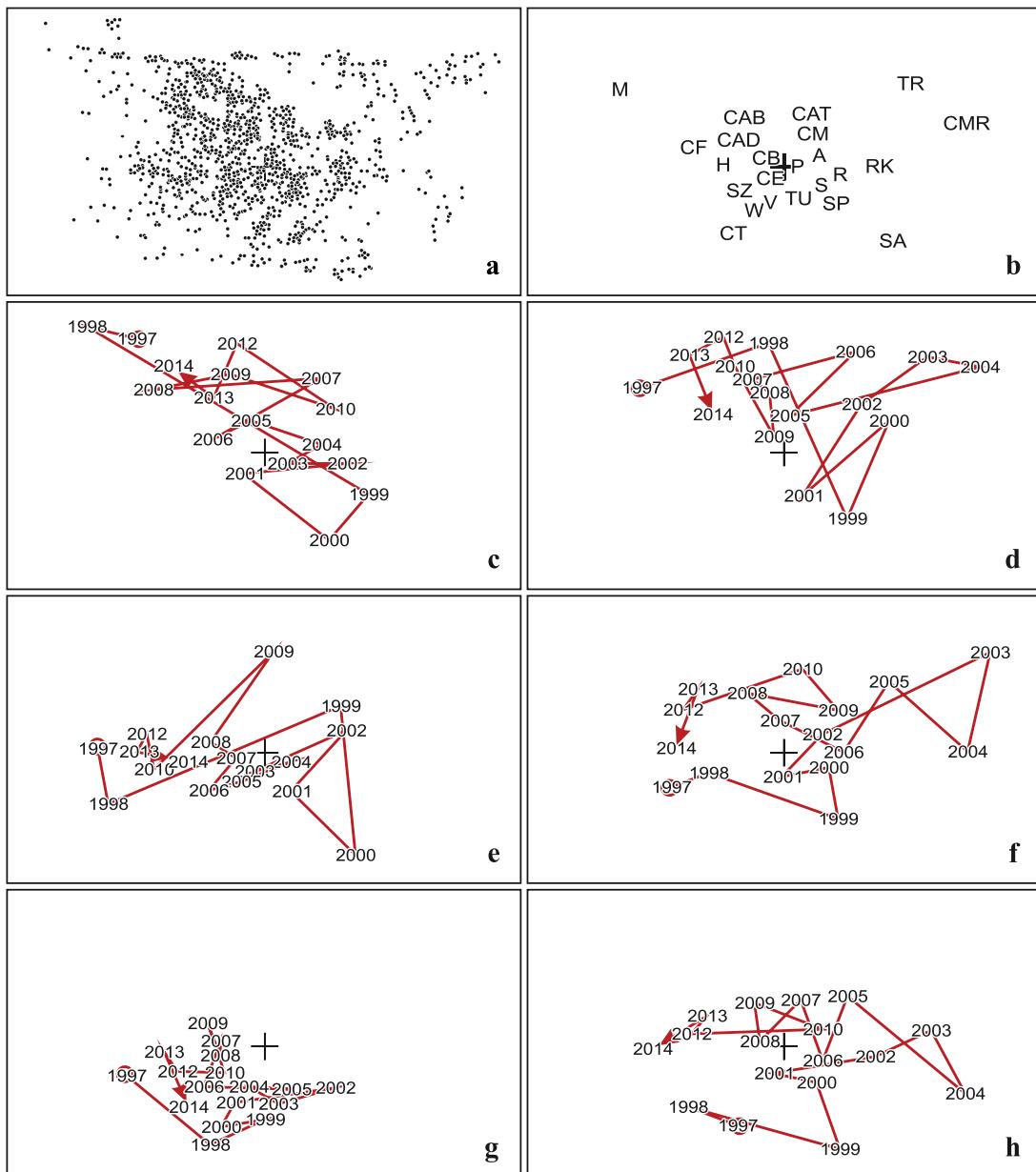
Two major functional aspects were evaluated: constructional capacity and trophic structure. For both aspects, three descriptors were employed. For the constructional capacity, hard-bodied organisms (mostly scleractinian corals, plus occasional large clams), soft-bodied organisms (mostly soft corals, sponges and fleshy macroalgae) and non-biotic substrate (rock, sand, rubble) were considered. Trophic structure was assessed using autotrophs (algae), heterotrophs (planktotrophic invertebrates), and polytrophs (planktotrophic invertebrates with autotrophic endosymbionts, such as zooxanthellate corals and clams, and zoocyanellate sponges and ascidians).

The percent cover of all descriptors was assessed in the field with the plan view technique of Wilson et al. (2007) in 6 replicate spots (each an unmarked area of around 20 m<sup>2</sup>) at 5, 10, 20, 30, 40 and 50 m depth in 3 ocean reefs and at 5, 10, 20 and 30 m depth in 3 lagoon reefs. These surveys were carried out twice before the mass coral bleaching (1997 and 1998) and twice after both bleaching and tsunami (2012 and 2013). In total, 720 surveys (4 years × 3 sites × 6 depth zones in ocean reefs and 4 depth zones in lagoon reefs × 6 replicates) were done. Results were illustrated by triangular (ternary) diagrams (Graham and Midgley, 2000).

## 3. Results and discussion

### 3.1. Coral reef communities

Correspondence analysis gave four significant axes, explaining together 49.4% of the total variance (1st axis = 15.4%; 2nd axis = 14.0%; 3rd axis = 10.8%; 4th axis = 9.2%). For the sake of simplicity, only the first two axes are discussed here (Fig. 2). The general shape of the ordination plot is a main elliptical cloud of points disposed obliquely from the upper left to the lower right corner of the graph. Some points scatter towards the (upper) right: these mostly correspond to the lagoon transects in 2003 and 2004. As for benthic categories, most points are located around the centre of the axes, indicating comparative ubiquity in space and



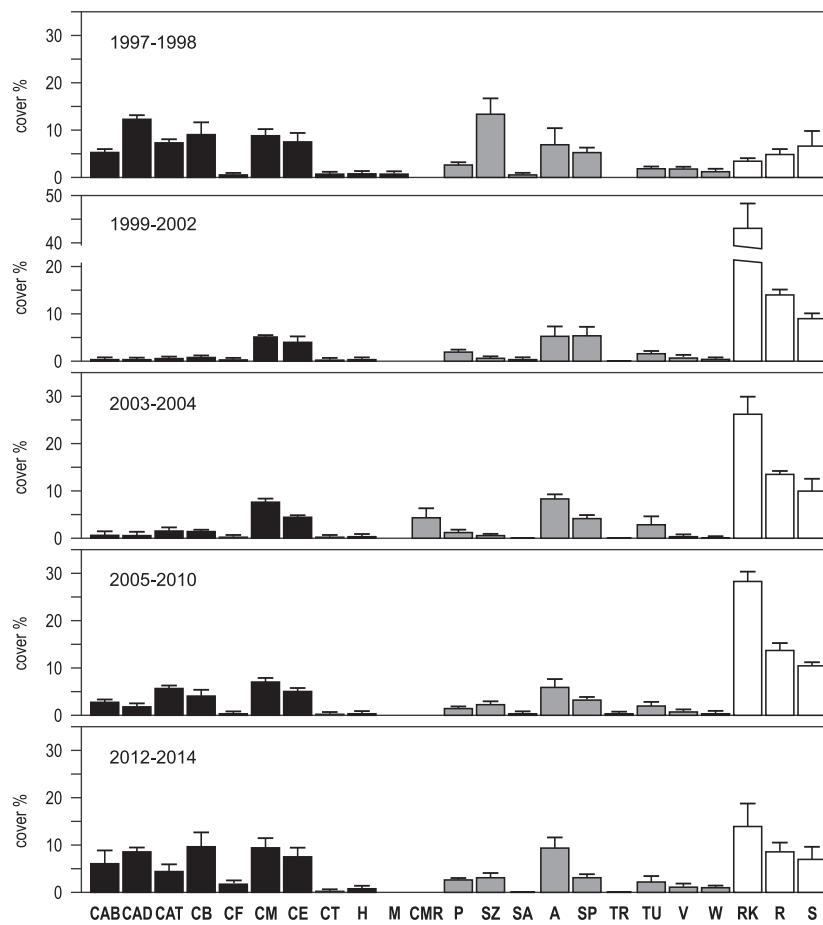
**Fig. 2.** Ordination plot on the first two axes from correspondence analysis: 1st axis is horizontal, 2nd axis is vertical; the cross depicts the centre of the axes. The total plot has been split in six separate graphs to improve readability. (a) All points cloud, each dot representing one transect. (b) Position of the 23 benthic categories, indicated with their codes as in Table 1. (c) Time trajectory of the year centroids for the ocean outer flat. (d) Time trajectory of the year centroids for the lagoon outer flat. (e) Time trajectory of the year centroids for the ocean upper slope. (f) Time trajectory of the year centroids for the lagoon upper slope. (g) Time trajectory of the year centroids for the ocean intermediate slope. (h) Time trajectory of the year centroids for the lagoon intermediate slope.

persistence in time. The point of *Millepora* (M), which was found in both ocean and lagoon outer flats and in ocean upper slope in 1997 and 1998, lies towards the upper left corner of the graph, whereas the point of azooxanthellate soft corals (SA), which were formerly common on ocean slopes, lies at the opposite end of the main ellipse. The points representing clams (TR) and corallimorpharians (CMR) lie in correspondence of the scattered points on the right.

The trajectories connecting year centroids for each reef type and depth zone all describe a conspicuous change between 1997–1998 and 1999–2000, followed by a slow and irregular return to the initial situation of 1997 and 1998. The main difference between lagoon and ocean trajectories is a deviation of lagoon sites trajectories towards the right side of the graph in 2003 and 2004, while the main difference among depth zones is that the trajectories of

shallow sites are longer than that of the deeper sites, especially in ocean reefs. The mass mortality that followed the coral bleaching of May 1998 hit more severely shallow reefs (Bianchi et al., 2003), which explains the relatively minor change at depth.

In all, the time trajectories of reef change, all sites combined, may be divided into five main phases: (i) 1997–1998; (ii) 1999–2002; (iii) 2003–2004; (iv) 2005–2010; (v) 2012–2014 (Fig. 3). In 1997–1998, before the mass bleaching event, Maldivian reefs were dominated by hard and soft corals, followed by algae and sponges; many other organism groups were also present, while non-biotic attributes exhibited comparatively low cover values. In 1999–2002, following the bleaching, hard and soft corals virtually disappeared, with the exception of massive (CM) and encrusting corals (CE), which had been less affected by mass mortality (Bianchi



**Fig. 3.** Mean (+ standard error) percent cover of the benthic categories (coded as in Table 1), on Maldivian reef communities in five time periods, all reef types and depth zones combined. Black bars illustrate hard corals, grey bars other organisms, white bars non-biotic attributes.

et al., 2003). The cover of other organisms did not change significantly, while that of non-biotic attributes, and especially of dead coral/coral rock (RK), increased tremendously. In 2003–2004, the cover of all categories of hard corals started to increase again, that of dead coral/coral rock (RK) to decrease; corallimorpharians (CMR) became abundant in lagoon reefs. In 2005–2010 corals, and especially tabular (CAT) and branching *Acropora* (CAB) and branching corals (CB), continued increasing, corallimorpharians (CMR) disappeared, non-biotic attributes remained similarly abundant as in the previous period. Finally, in 2012–2014, although non-biotic attributes were still comparatively abundant, the cover of hard coral categories returned to the pre-bleaching value. *Millepora* (M), however, was never found again, and zooxanthellate corals (SZ) remained scarcer than before bleaching. All the remaining categories changed little through the whole period of study.

The transient but comparatively high cover of corallimorpharians in 2003–2004 in lagoon reefs might have played an important role in the recovery of the reef community. In these years, coral rubble (mostly 7–15 cm long segments of *Acropora* branches) formed extensive loose accumulations on the slopes of lagoon reefs. Corallimorpharians nearly completely covered this rubble, especially down to 15 m depth (Fig. 4). Algae (including encrusting corallines and *Halimeda*), the bleaching-resistant coral *Goniopora* (McClanahan, 2004; McClanahan et al., 2004) and other organisms (including sponges) were by far less abundant.

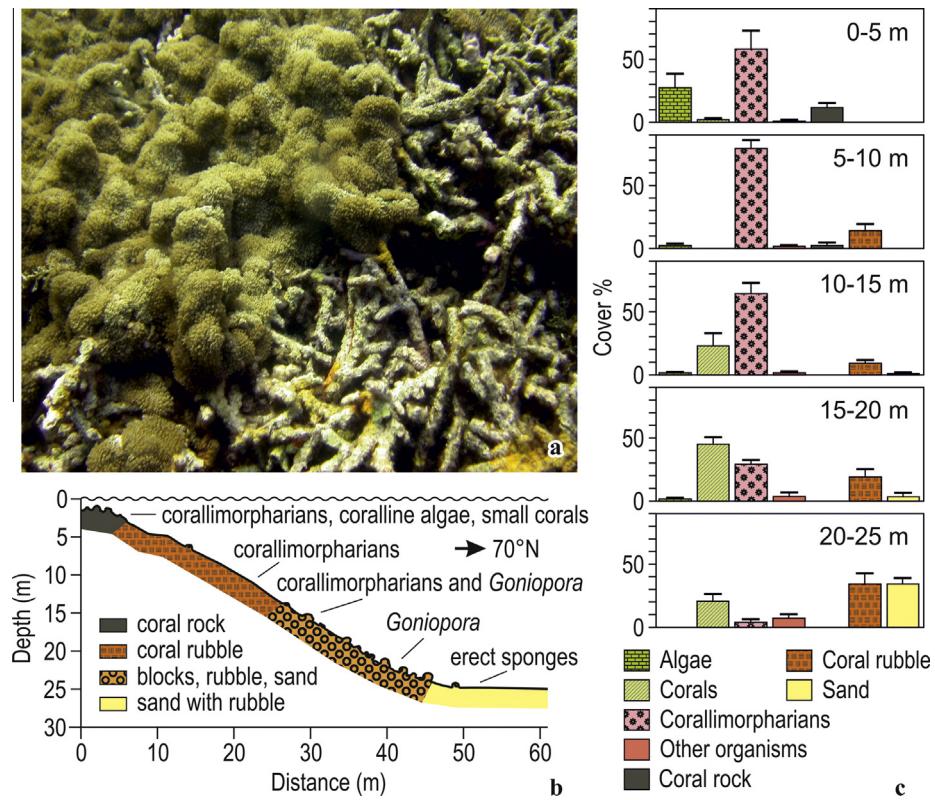
Organisms settling on coral rubble are considered to play a key role for reef regeneration, as they are presumed to act as precursors for rigid binding (Rasser and Riegl, 2002). Corallimorpharians, however, are known to be able to monopolize substratum surface

to the detriment of other potential settlers, including calcified binders and coral recruits (Langmead and Chadwick-Furman, 1999). Thus, despite a potential role for coral framework recovery, “soft binding” by a corallimorpharian might in reality have impeded the settlement of “true binders”, thus preventing, or slowing down, the recovery process. The tsunami of December 2004 dislodged this unconsolidated rubble, and corallimorpharians virtually disappeared from Maldivian reefs.

### 3.2. Coral recruitment

Analysis of variance highlighted great variability in the density of all recruits (*Acropora*, *Pocillopora* and others) both in space and time (Table 2). The interaction implying the factor site was highly significant. SNK test indicated that *Acropora* between 1999 and 2008 and *Pocillopora* between 1999 and 2005 recruited similarly in both ocean and lagoon reefs at all depths. Recruits got more abundant in lagoon outer flats from 2008 onwards for *Acropora*, in ocean outer flats and ocean upper slopes since 2005 for *Pocillopora*. Recruitment of others was higher in 1999 at most sites and depths.

Despite high spatial variability, consistent with the results of similar studies elsewhere (Connell et al., 1997; Hughes et al., 1999; Glassom et al., 2004, 2006), a general temporal trend was recognizable in both lagoon and ocean reefs at all depths (Fig. 5). Four distinct phases can be described. In 1999, recruitment by *Acropora* and *Pocillopora*, which suffered high mortality in 1998 (Bianchi et al., 2003), was low, while that of the others was extremely high: this has been interpreted as the result of the



**Fig. 4.** Incidence of corallimorpharians in lagoon reefs in 2003–2004. (a) Corallimorpharians overgrowing and binding *Acropora* rubble at shallow depth. (b) Benthic communities along a reef profile at Dega Thila, Ari Atoll. (c) Cover data (means + standard errors) of different benthic categories at five depth ranges in the same site.

**Table 2**  
Results of ANOVAs on coral recruitment of *Acropora*, *Pocillopora* and others.

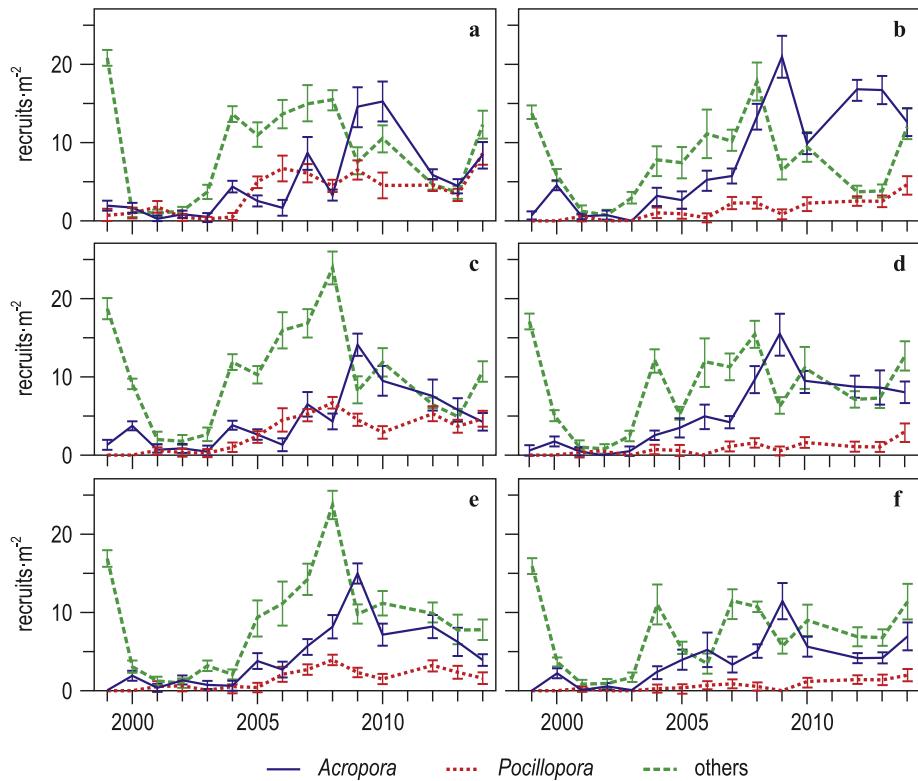
Source	df	<i>Acropora</i>			<i>Pocillopora</i>			Others		
		MS	F	P	MS	F	P	MS	F	P
Reef types (R)	1	201.07	2.25	0.155	52.40	21.26	0.000	622.59	4.59	0.050
Years (Y)	14	1295.62	37.73	0.000	9.68	29.40	0.000	1943.11	38.71	0.000
Depth zones (D)	2	439.47	10.86	0.000	12.66	24.55	0.000	218.61	2.97	0.067
Sites (S) (Y × D)	135	34.33	3.70	0.000	0.33	2.08	0.000	50.19	3.30	0.000
R × Y	14	89.20	3.51	0.000	2.46	6.18	0.000	135.64	3.71	0.000
R × D	2	235.86	3.51	0.044	2.43	5.39	0.010	45.56	0.83	0.447
R × S (Y × D)	135	25.41	2.73	0.000	0.40	2.52	0.000	36.53	2.40	0.000
Y × D	28	40.45	1.18	0.264	0.51	1.57	0.048	73.61	1.47	0.078
R × Y × D	28	67.27	2.65	0.000	0.45	1.13	0.311	54.91	1.50	0.066
Residual	720	9.29			0.16			15.20		
Cochran's C-test		C = 0.059, ns			C = 0.028, ns			C = 0.031, ns		
Transformation		None			Sqrt(x + 1)			None		

'emergency spawning' of massive and encrusting corals following the thermal stress (Loch et al., 2002). Between 2000 and 2003 recruitment of all corals was extremely low, possibly due to the scarcity of living adult colonies. From 2004 to 2008, recruitment rate increased, especially for the others, which showed dominant at all depths in both lagoon and ocean sites. Finally, in the period 2009–2014, recruitment rate by the others slowed down while that of *Acropora* increased: *Acropora* became dominant on outer flats and co-dominated with the others on the slopes; *Pocillopora* recruits, always scarce in the previous phases, became comparatively abundant, especially on shallow ocean reefs.

Results of the analysis of variance on survival data were similar to those on recruit density: the interaction implying sites was always significant and variability was large in both space and time (Table 3). Survival changed significantly with the years, especially on lagoon reefs. SNK highlighted that survival of *Acropora* in lagoon

reefs was lower than in ocean reefs at all depths, but increased since 2009. Survival of *Pocillopora* in lagoon reefs was lower than in ocean reefs, and was higher in outer flats than in slopes. No differences were generally found between ocean and lagoon reefs in the survival of the others to 2004, since when survival was higher in lagoon reefs.

Differential success of the three coral categories in different reef types and depth zones was therefore due to a combination of recruitment and survival (Fig. 6). Neglecting the obvious change with time, *Acropora* exhibited higher recruitment on lagoon outer flats, but higher survival in lagoon slopes; *Pocillopora* had higher recruitment on shallow ocean reefs and higher survival on both lagoon and ocean outer flats; the others did not show any particular spatial pattern. These results suggest that the typical coral zonation is already established in the early phases of coral settlement and colonisation (Miller et al., 2000).



**Fig. 5.** Time trends between 1999 and 2014 of coral recruits (means  $\pm$  standard errors) in two reef types and three depth zones. (a) Ocean outer flat. (b) Lagoon outer flat. (c) Ocean upper slope. (d) Lagoon upper slope. (e) Ocean intermediate slope. (f) Lagoon intermediate slope.

**Table 3**

Results of ANOVAs on coral survival of *Acropora*, *Pocillopora* and others.

Source	df	<i>Acropora</i>			<i>Pocillopora</i>			Others		
		MS	F	P	MS	F	P	MS	F	P
Reef types (R)	1	62377.01	62.73	0.000	79716.93	88.61	0.000	13403.59	12.00	0.000
Years (Y)	12	9663.44	10.06	0.000	6815.09	9.01	0.000	20533.60	14.92	0.000
Depth zones (D)	2	8666.77	9.03	0.000	5372.17	7.10	0.001	1830.78	1.33	0.268
Sites (S) (Y $\times$ D)	117	960.27	1.60	0.000	756.74	1.43	0.004	1376.50	1.80	0.000
R $\times$ Y	12	11803.88	11.87	0.000	5034.29	5.60	0.000	7364.54	6.59	0.000
R $\times$ D	2	5602.02	5.63	0.005	280.08	0.31	0.733	388.72	0.35	0.707
R $\times$ S (Y $\times$ D)	117	994.40	1.65	0.000	899.64	1.70	0.000	1117.09	1.46	0.003
Y $\times$ D	24	1412.59	1.47	0.091	646.88	0.85	0.661	907.56	0.66	0.881
R $\times$ Y $\times$ D	24	1479.87	1.49	0.085	827.32	0.92	0.576	1404.79	1.26	0.210
Residual	624	601.46			528.79			765.50		
Cochran's C-test		C = 0.018, ns			C = 0.020, ns			C = 0.014, ns		
Transformation		None			None			None		

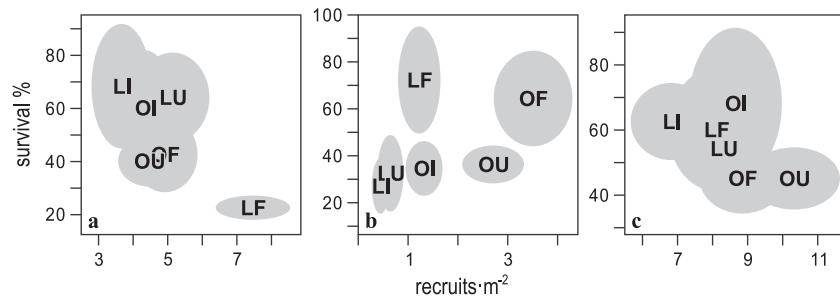
### 3.3. Hard coral cover

The earliest data on coral cover in the Maldives come from the *Xarifa* expedition in the late 1950s (Wallace and Zahir, 2007). Maldivian coral reefs at that time might be considered near pristine conditions, and coral cover averaged 65–75% (Scheer, 1971, 1972, 1974). Early development, from coastal works at the British military base of Addu in the 1960s (Stoddart, 1966) to increased extraction of coral rock as building material (Brown and Dunne, 1988; Brown et al., 1995; Sluka and Miller, 1998) and growing tourism (Allison, 1996) through the 1980s, was accompanied by a fall of coral cover to about 50%. A bleaching event in 1987 caused considerable mortality but no data are available to allow a precise quantification (Edwards et al., 2001): the fall of cover recorded in 1992 (Allison, 1995a,b) may well be the outcome of that event. The disturbance regime changed in the 1990s: Maldivian coral reefs experienced not only increased human pressure, implying sediment loading and eutrophication

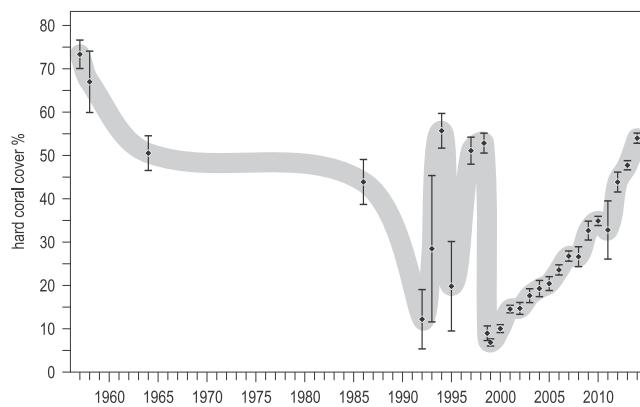
(Allison, 1995a,b), but also local attacks by the crown-of-thorn starfish *Acanthaster planci* (Ciarapica and Passeri, 1993; Morri et al., 2010) and “minor” bleaching events (Ciarapica and Passeri, 1999). Severe reductions of coral cover down to 10–30% were nevertheless followed by rapid recovery to values >50% (Fig. 7). Things showed completely different after the mass bleaching of 1998, which caused living coral cover to fall to 2–8% (Bianchi et al., 2003). Although recovery started soon (McClanahan, 2000; Edwards et al., 2001), coral cover has been increasing at an extremely low pace (Lasagna et al., 2008; McClanahan and Muthiga, 2014), and returned to values >50% only in 2014.

### 3.4. Reef rugosity

The comparison of chain transect data of 2004 and 2005 indicated substrate smoothing at small scale (metres) following the sediment displacement caused by the tsunami of December



**Fig. 6.** Spatial pattern of recruit density and survival, all years combined: OF = ocean outer flat; OU = ocean upper slope; OI = ocean intermediate slope; LF = lagoon outer flat; LU = lagoon upper slope; LI = lagoon intermediate slope. Position of the letters indicates the mean, shadowed areas standard errors. (a) *Acropora*. (b) *Pocillopora*. (c) Others.



**Fig. 7.** Mean ( $\pm$  standard error) hard coral cover in the Maldives, 1956–2014. The shadowed band illustrates the putative time trend.

2004. At large scale (tens of metres), a comparable result holds for lagoon reefs but not for ocean reefs (Fig. 8).

Comparing the vertical profiles of reefs revisited years apart highlighted no change in slope and morphology among years before or after the tsunami, but indicated a reduction of slope steepness of up to  $20^\circ$  between the two periods, especially between 10 m and 30 + m (Fig. 9). Not only were notches and small terraces obliterated, but the deposit of large amount of detrital material caused a reef progradation of several metres. Thus, although reduced reef rugosity may be detrimental for biodiversity (Dunn and Halpin, 2009), reef progradation may offer new scope for reef growth.

### 3.5. Coral ecosystem functioning

As far as constructional capacity is concerned, hard-bodied organism dominance at 5 m and 10 m depth appeared restored

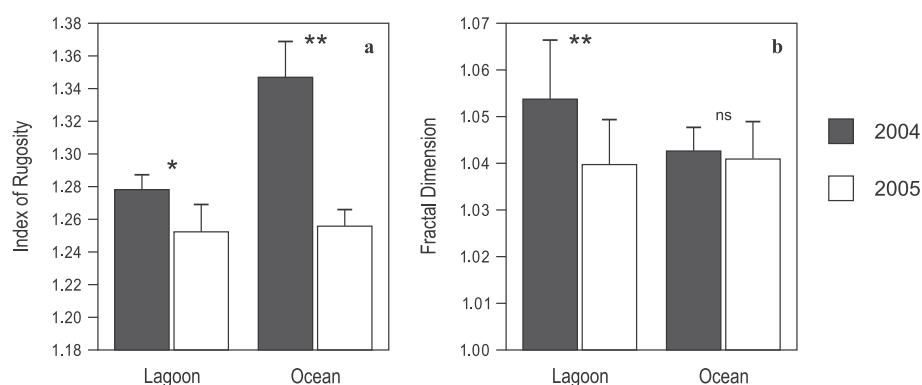
in 2012–2013. However, there were differences between ocean and lagoon reefs (Fig. 10): in the former, the cover of hard-bodied organisms was lower than in 1997–1998, while the reverse is true in the latter. In ocean reefs, hard-bodied organisms, soft-bodied organisms and non-biotic substrate were similarly represented at 20 m and 30 m depth in both periods; on the contrary, at 40 m and 50 m non-biotic substrate was more abundant in 2012–2013 than in 1997–1998, to the detriment of soft-bodied organisms.

Significant constructional capacity resulted therefore limited to the shallowest depths (<20 m), which is consistent with results on Holocene reef growth in the Maldives (Kench et al., 2009). No obvious change was detected with respect to the pre-bleaching situation.

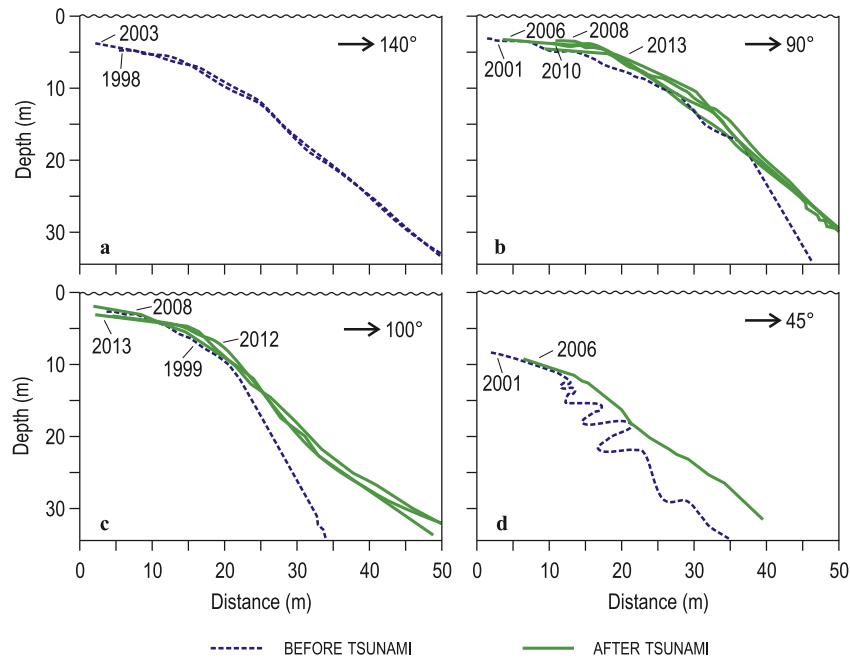
Analysis of trophic structure showed the dominance of polytrophs down to about 20 m depth (Fig. 11). However, in 2012–2013 the cover of polytrophs was reduced in favour of autotrophs at all depths in ocean reefs with respect to 1997–1998. In lagoon reefs, autotrophs increased to the detriment of heterotrophs, while polytrophs showed proportionally more abundant, especially at 20 m and 30 m depth.

### 4. Conclusions

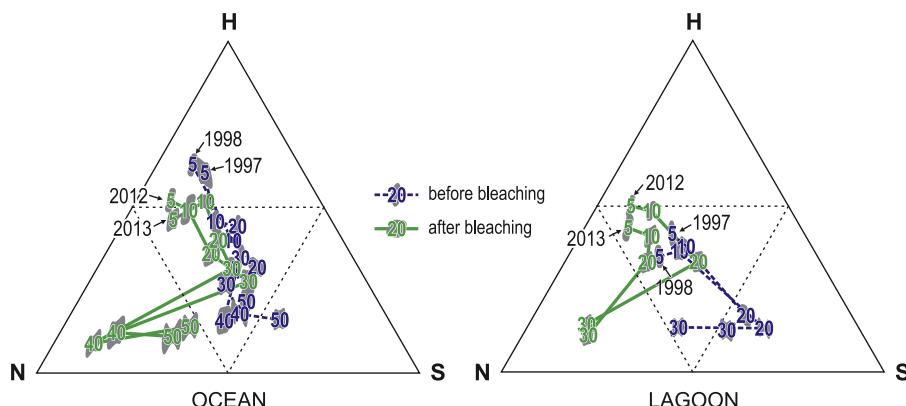
The most common metric of coral reef recovery after major disturbances is the percentage of hard coral cover (Baker et al., 2008; Graham et al., 2011). We combined literature information with our own data to reconstruct the historical trend of hard coral cover in the Maldives. Notwithstanding a long gap between the 1960s and the 1980s and high local variability in the 1990s, Maldivian hard coral cover maintained values around 50% till the massive mortality of 1998, when it dropped to <10% (McClanahan, 2000; Zahir, 2000; Edwards et al., 2001; Bianchi et al., 2003). Recovery to the



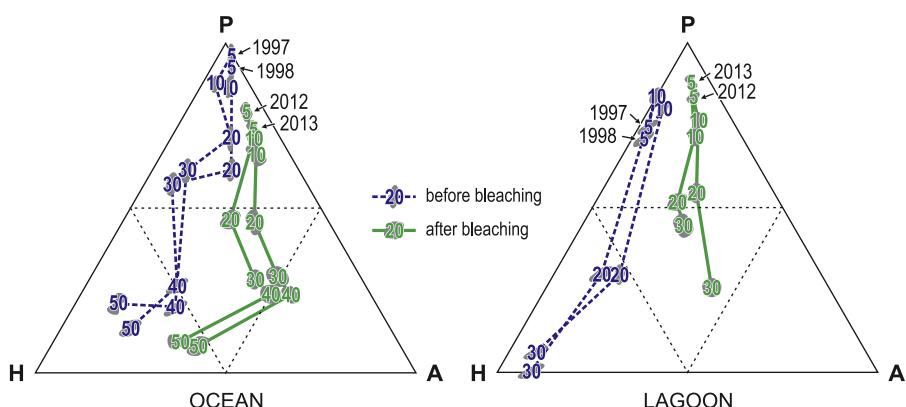
**Fig. 8.** Reef rugosity (mean  $\pm$  standard error) before and after the tsunami of December 2004, at two different spatial scales. (a) Small scale (chain transects). (b) Large scale (depth transects). \* =  $p < 0.05$ , \*\* < 0.01, ns = not significant (Student's t test).



**Fig. 9.** Comparison of reef profile in sites that have been revisited in years before and after the tsunami of December 2004. (a) Makunufushi, South Malé Atoll. (b) Maadhoo, South Malé Atoll. (c) Kandooma, South Malé Atoll. (d) Mushimasgali, Ari Atoll.



**Fig. 10.** Triangular diagrams of reef constructional capacity at different depths in years before (1997 and 1998) and after (2012 and 2013) both bleaching and tsunami, in ocean and lagoon sites: **H** = hard-bodied organisms; **S** = soft-bodied organisms; **N** = non-biotic substrate. Depth values indicate the position of the mean, shadowed areas represent standard errors. Lines trace depth zonation.



**Fig. 11.** Triangular diagrams of reef trophic organisation at different depths in years before (1997 and 1998) and after (2012 and 2013) both bleaching and tsunami, in ocean and lagoon sites: **P** = polytrophs; **A** = autotrophs; **H** = heterotrophs. Depth values indicate the position of the mean, shadowed areas represent standard errors. Lines trace depth zonation.

pre-bleaching values took as many as 15 years. This contrasts with the fast coral recovery observed in the neighbouring Chagos (Sheppard et al., 2008) and in other remote Indian Ocean locations (Gilmour et al., 2013) with similar oceanographic conditions. However, the latter studies concerned nearly uninhabited islands, while the Maldives are experiencing a still moderate but nevertheless growing human pressure because of coastal development and tourism growth (Jaleel, 2013).

Climate change interacting with existing human pressure is expected to result in the loss of coral diversity and critical reef habitat (Darling et al., 2013). Our study addressed these aspects using, in addition to hard coral cover, other descriptors and metrics, ranging from recruitment and community composition to geomorphological and functional aspects.

Earlier studies on coral recruitment in the Maldives (Edwards et al., 2001) found that in 1990–1994 the great majority (94%) of recruits belonged to branching corals (Acroporidae and Pocilloporidae). In March 1999, i.e. 10 months after the mass bleaching event of May 1998, the same authors observed a reduced but still maintained dominance (67–78%) of branching coral recruits. On the contrary, data taken in April 1999 (McClanahan, 2000) showed few recruits of Acroporidae and Pocilloporidae and a large dominance of massive and encrusting corals. This notwithstanding, total recruits density was similar in the two above-mentioned studies:  $28.9 \pm 3.3$  recruits·m<sup>-2</sup> (McClanahan, 2000) vs.  $23.2 \pm 2.4$  recruits·m<sup>-2</sup> (Edwards et al., 2001). Discrepancies in the relative proportions might depend on the different survey methods (and especially on what was intended with 'recruits' by the different authors) or simply reflect the large spatial variability of recruitment, as observed in the present study: McClanahan (2000) surveyed 11 sites in the eastern central atolls, Edwards et al. (2001) one site in North Malé. Edwards et al. (2001) also hypothesised that recruits of branching species had been less affected by bleaching compared to larger colonies, as had been shown by other studies (e.g. Mumby, 1999 in Belize), and persisted cryptically on the reef during bleaching.

From 2000 to 2008, massive and encrusting corals, which suffered comparatively lower mortality rates both in the Maldives (Bianchi et al., 2003) and elsewhere in the Indian Ocean (Tamelander, 2002), dominated the recruits' community. Adult colonies of *Acropora* and *Pocillopora* had been nearly extirpated in 1998 (Bianchi et al., 2003) and their recruitment could increase only after the newly settled colonies matured (Gilmour et al., 2013): *Acropora* species have been shown to reproduce for the first time at ages of 3–4 years (Iwao et al., 2010; Baria et al., 2012). Starting from 2009, *Acropora*, a spawning coral (Hughes et al., 2002) with high competitive ability (Darling et al., 2012), became dominant or co-dominant in the recruit community, while *Pocillopora*, a brooding coral (Hughes et al., 2002) with opportunistic life-trait, increased slowly and always showed less abundant than *Acropora* and the other corals. On the contrary, *Pocillopora* was the dominant recruiting coral in Kenyan reefs recovering from the mass bleaching of 1998 (O'Leary and Potts, 2011), consistently with most pocilloporid species traits (Darling et al., 2012).

Recruit community composition in 2014 roughly mirrored adult community composition: acroporids, massive and encrusting corals (i.e., the others in the recruitment counts), and branching corals (mostly pocilloporids) characterised Maldivian coral reefs as in 1997–1998. Recovery trajectories differed according to reef types and depth zones, which may be partly due to different sites normally being studied in different years (McClanahan and Muthiga, 2014). The causes of temporal irregularities in the trajectories may have been the mild bleaching events that occurred in the Indian Ocean in 2003, 2005, 2007 and 2010 (Tkachenko, 2012; McClanahan, 2014). Similar high spatial (habitat) and temporal

variability in decadal studies of coral recovery have been observed in Australian reefs (Done et al., 2007).

Notwithstanding Maldivian coral communities in 2014 showed roughly similar to the pre-bleaching situation, many subtle differences in composition still remained. *Millepora*, which used to characterise distinctive "zones" at shallow depths (Morri et al., 1995; Bianchi et al., 1997), has not been recorded anymore. Soft corals decreased noticeably, foliose corals increased. Among *Acropora* growth-forms, the original dominance of digitate colonies appeared reduced in favour of branching colonies. Maldivian reefs, therefore, underwent community reassembly as other Indo-West Pacific reefs did (Adjeroud et al., 2009; van Woesik et al., 2011; Johns et al., 2014): obvious at the gross taxonomic level reported here, such a community reassembly is likely to be even greater if viewed at the species level (McClanahan, 2014), and may express adaptation to warmer water temperature (McClanahan and Muthiga, 2014). In 2005, the coral community composition in the Maldives was distinct from those of any other Indian Ocean reefs (McClanahan et al., 2007).

Geomorphological and functional aspects, such as those considered in the present paper, have received little or no attention by other studies of coral reef recovery. Reduction in reef rugosity after the mass mortality of 1998 was noticeable: the large amount of rubble and sand generated by the fragmentation of dead coral colonies covered and levelled down the substrate. In a first phase, coral recruits settled abundantly on rubble, where they suffered high mortality due to substrate instability that easily rolled and turned. Soft-binding of rubble by corallimorpharians in lagoon reefs was a further impediment to recolonisation by corals. The 2004 tsunami displaced the rubble downward, consistently with analyses of past sedimentary records in the lagoon of Rasdhoo Atoll (Klostermann et al., 2014). The loose sediment eventually deposited on reef slopes, thus obliterating many morphologies that were previously visible and reducing slope steepness. The geomorphological consequences of ecological crises such as mass coral mortality may therefore be twofold: on one hand, reef aggradation is halted, leading to the risk of platform drowning (Ciarapica and Passeri, 1993); on the other hand, the huge detrital deposit on slopes allows for reef progradation. Our observations in the Maldives following bleaching and tsunami suggest that overall reef accretion is a discontinuous process occurring in two distinct phases: (1) gradual aggradation, during "normal" periods of coral colony development; (2) abrupt progradation, after major disturbances.

The constructional capacity of Maldivian reefs exhibited little change with respect to what observed before the mass mortality of 1998, at least in shallow water, suggesting full recovery from the regressive stage described in 2008 (Lasagna et al., 2010). At 40–50 m depth, sand and rubble, possibly deposited after the tsunami, were more abundant than in 1997–1998: this deposit had probably been responsible for reduced cover of the soft-bodied epibenthic biota.

As for the trophic structure, polytrophs generally decreased in favour of autotrophs. This notwithstanding, the Maldives did not experience a phase shift to a macroalgae-dominated state (McClanahan and Muthiga, 2014), contrary to what was observed in coral reefs of the Seychelles (Graham et al., 2015).

The adoption of several descriptors and metrics in this study allowed the complexity of coral reef recovery in the Maldives to be illustrated and may serve as an example on how coral reef resilience could be measured. The recovery from disturbances of reefs in French Polynesia was characterised by resilience in terms of coral cover, but plasticity in terms of community composition (Adjeroud et al., 2009), and the same seems true for the Maldives. It may be estimated that Maldivian coral reefs recovery after the mass-mortality of 1998 took between 6 years, when

recruitment rates returned to high levels, and 15 years, when hard coral cover bounced back to pre-bleaching values, or may even be considered unachieved, as there are species that have not come back yet and reef complexity is still reduced. Rather than just looking for recovery, research should address how climate change is reshaping coral reef communities (Darling et al., 2013). The functional consequences of compositional change and reduced structural complexity still needs to be evaluated and, in this regard, long term monitoring remains the only means to track the future evolution of coral reefs.

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