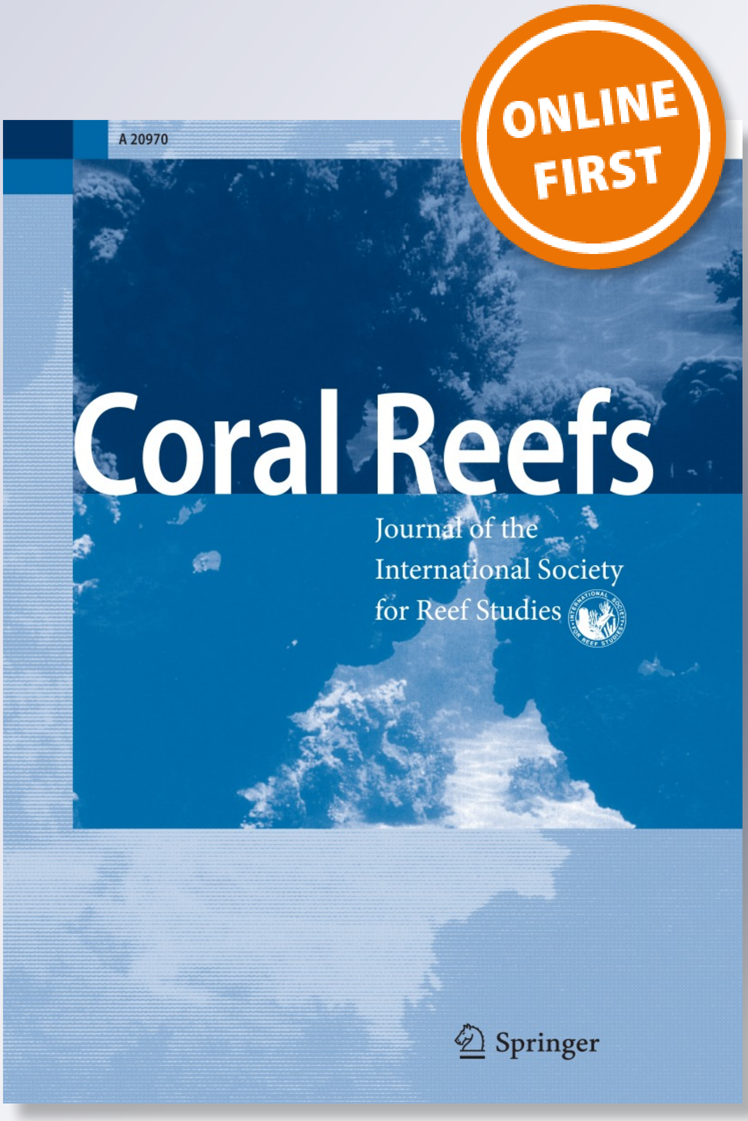
# *Long-lived groupers require structurally stable reefs in the face of repeated climate change disturbances*

**R. Karkarey, N. Kelkar, A. Savio Lobo, T. Alcoverro & R. Arthur**

**Coral Reefs**
Journal of the International Society for Reef Studies

ISSN 0722-4028

Coral Reefs
DOI 10.1007/s00338-013-1117-y



Coral Reefs
DOI 10.1007/s00338-013-1117-y

REPORT

# Long-lived groupers require structurally stable reefs in the face of repeated climate change disturbances

**R. Karkarey · N. Kelkar · A. Savio Lobo ·
T. Alcoverro · R. Arthur**

Received: 22 May 2013 / Accepted: 14 December 2013

**Abstract** Benthic recovery from climate-related disturbances does not always warrant a commensurate functional recovery for reef-associated fish communities. Here, we examine the distribution of benthic groupers (family Serranidae) in coral reef communities from the Lakshadweep archipelago (Arabian Sea) in response to structural complexity and long-term habitat stability. These coral reefs that have been subject to two major El Niño Southern Oscillation-related coral bleaching events in the last decades (1998 and 2010). First, we employ a long-term (12-yr) benthic-monitoring dataset to track habitat structural stability at twelve reef sites in the archipelago. Structural stability of reefs was strongly driven by exposure to monsoon storms and depth, which made deeper and more sheltered reefs on the eastern aspect more stable than the more exposed (western) and shallower reefs. We surveyed groupers (species richness, abundance, biomass) in 60 sites across the entire archipelago, representing both exposures and depths. Sites were selected along a gradient of structural complexity from very low to high. Grouper biomass appeared to vary with habitat stability with significant differences between depth and exposure; sheltered deep reefs had a higher grouper biomass than either sheltered shallow or exposed (deep and shallow) reefs. Species richness and abundance showed similar (though not significant) trends. More interestingly, average grouper biomass increased exponentially with structural complexity, but only at the sheltered deep (high stability) sites, despite the availability of recovered structure at exposed deep and shallow sites (lower-stability sites). This trend was especially pronounced for long-lived groupers (life span >10 yrs). These results suggest that long-lived groupers may prefer temporally stable reefs, independent of the local availability of habitat structure. In reefs subject to repeated disturbances, the presence of structurally stable reefs may be critical as refuges for functionally important, long-lived species like groupers.

**Keywords** Coral reefs · Structural change · Habitat stability · Natural refugia · Groupers

## Introduction

Among the most significant long-term impacts of climate change on tropical reefs is the loss of architectural complexity (Wilson et al. 2006) due to recurrent ocean warming events like the El Niño Southern Oscillation (ENSO), which are now increasingly frequent (Hoegh-Guldberg et al. 2007). While earlier predictions saw reefs destined for collapse under this repeated disturbance (Pandolfi et al. 2003), a more complex picture of mixed decline and recovery is now emerging (Arthur 2000; Arthur et al. 2005; McClanahan et al. 2007; Sheppard et al. 2008;

Communicated by Biology Editor Dr. Stephen Swearer

**Electronic supplementary material** The online version of this article (doi:10.1007/s00338-013-1117-y) contains supplementary material, which is available to authorized users.

R. Karkarey (✉) · N. Kelkar · A. S. Lobo · T. Alcoverro ·
R. Arthur
Nature Conservation Foundation, 3076/5, IV Cross, Gokulam
Park, Mysore 570 002, India
e-mail: rucha@ncf-india.org
URL: www.conservation.in

T. Alcoverro
Department of Marine Ecology, Centre d'Estudis Avançats de
Blanes (CEAB, CSIC), Accés a la Cala S. Francesc 14,
17300 Blanes, Girona, Spain
e-mail: teresa@ceab.csic.es

Graham et al. 2011). The ability for rapid benthic recovery suggests that coral reefs may have a greater ability to cope with climate-related disturbances than previously assumed (Halford et al. 2004). Whether this reflects a commensurate functional recovery for reefs and associated fauna is still not clearly understood (Berumen and Pratchett 2006; Bellwood et al. 2012).

Reef architecture, or the structural complexity of reefs, is linked closely with its ecological functioning as it greatly influences fish population densities (Graham and Nash 2013). Structural complexity is associated with increasing fish diversity through the provision of shelter and diverse physical niches, which mitigate the impacts of predation, competition and physical disturbance (Caley and John 1996; Syms and Jones 2000; Almany 2004a, b; Garpe et al. 2006; Feary et al. 2007). Although the ability to quickly recover coral structure after disturbance events may be vital to the recovery of coral-associated fish assemblages (Sano 2000), even short-lived fish, usually in lower trophic groups, have shown a limited ability to recover (Berumen and Pratchett 2006; Bellwood et al. 2012). Additionally, it is still uncertain if longer-lived (K-selected) species that generally belong to higher trophic groups are resilient to such physical disturbances. Given that the generational recovery time for long-lived species may be much longer than disturbance frequencies (Fulton 2011), the effects of repeated disturbances on long-lived species might be multiplicative (Paine et al. 1998), seriously compromising their ability to recover (Bellwood et al. 2012).

As some of the longest-lived top predators, groupers (Serranidae) are among the most important functional species on coral reefs (Grandcourt 2005). Top predators like groupers often play key roles in regulating communities (Goeden 1989; Hixon and Beets 1993) and their reduction has been clearly linked with declines in ecosystem functioning (Bohnsack 1982; Dulvy et al. 2004a; Heithaus et al. 2008). Groupers are highly dependent on structurally complex reef environments (Sluka and Reichenbach 1996; Lindberg et al. 2006). Reefscape and habitat attributes strongly influence the success of their predatory strategies either directly by changing the effectiveness of ambush strategies (Samoilys 1997; Auster 2005) or indirectly by changing resource densities of smaller fish, crustaceans and other prey species (Almany 2004a). In addition, their slow growth rates, longevity and relatively low fecundity (Grandcourt 2005), make them particularly vulnerable to both natural and anthropogenic exploitation (Russ and Alcala 1998; Sadovy de Mitcheson et al. 2012). Taken together, these characteristics make groupers particularly susceptible to declines in reef habitat as a result of climate change and related disturbances.

Separating the effects of fishing from climate-related structural change on grouper communities is often difficult because of high selective fishing pressures on benthic top predators in most tropical reefs (Myers and Worm 2003; Sadovy de Mitcheson et al. 2012). The Lakshadweep archipelago in India offers a unique opportunity in this context, since the reefs here have had relatively low levels of reef fishing for at least the last four decades (Arthur et al. 2005; Spalding et al. 2001). Further, the Lakshadweep reefs suffered two catastrophic bleaching events in the last decade and a half (1998 and 2010), where a total loss of over 90 % (Arthur et al. 2006) and 70 % (RA, personal observations) live-coral cover has been documented, respectively. Smaller-scale bleaching events (~10–20 % coral bleaching, RA, personal observations), related to increased sea-surface temperature have been observed in 2005 and 2007.

Local hydrodynamics linked to monsoonal exposure and depth were shown to strongly influence benthic resistance and recovery rates within the archipelago, after the 1998 bleaching event (Arthur et al. 2006). Wave exposure and depth have long been identified as major controllers of coral zonation and benthic distribution on reefs (Done 1999; Madin and Connolly 2006; Chollett and Mumby 2012). Exposure and depth work together in mitigating temperature-mediated bleaching responses in corals and in facilitating reef recovery processes (West and Salm 2003). These physical factors, in addition to reef structural complexity and benthic composition, are known to synergistically affect the distribution of reef-associated fish communities (Gust 2002; Sabetian 2003; Floeter et al. 2007). The long-term interaction between habitat characteristics, physical disturbances that disrupt habitats, and species life-history characters, 'filters' unfavourable species from habitats of characteristic disturbance regimes (Southwood 1977). Thus, understanding the long-term influence of exposure and depth-mediated hydrodynamics on benthic structure may be crucial to predicting the effects of increasing multiple disturbances, not only for corals (Madin and Connolly 2006) but for reef-associated fish communities as well.

Our primary objective was to determine the effect of local structural complexity and the long-term habitat structural stability on the distribution of grouper communities across the archipelago. We first employ a 12-yr benthic cover data series from three representative atolls to classify reefs across the archipelago according to long-term structural stability based on exposure (either exposed or sheltered from monsoon storms) and depth (shallow and deep reefs). We then use this habitat stability classification (exposure and depth) to test for differences in grouper communities across a gradient of structural complexity by surveying 60 reef sites across the entire archipelago.

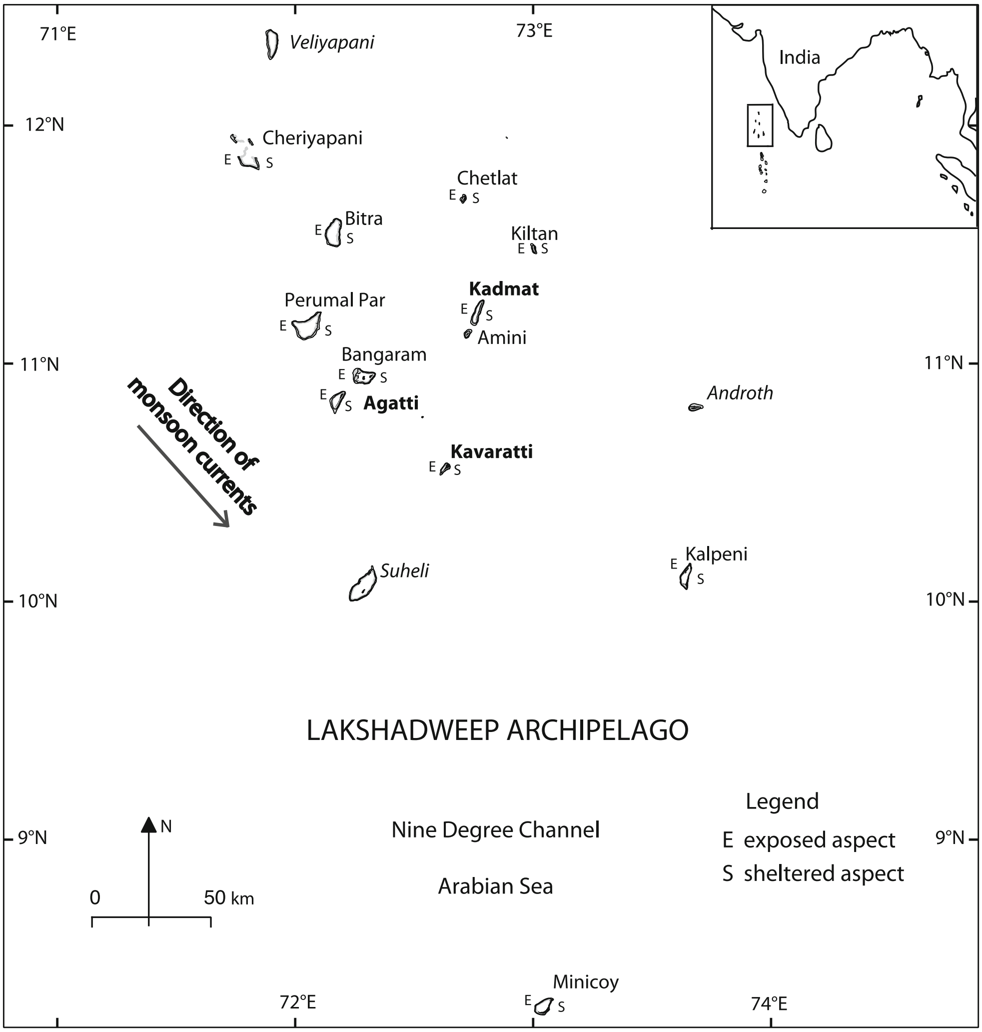


**Fig. 1** Map of Lakshadweep with sampled atolls and banks, direction (southeasterly) of currents during the monsoon season (May–October). The western and eastern aspects of atolls are represented as E (exposed) and S (sheltered), respectively, in relation to their orientation to the monsoon currents. Atolls in *bold* (Agatti, Kadmat and Kavaratti) represent atolls where permanent plots have been established and monitored since 1998; other atolls were sampled during this study in 2011, except those marked in *italics*

## Materials and methods

### Study area

The Lakshadweep archipelago in the northern Indian Ocean comprises 12 coral atolls and submerged banks with 36 small atolls (Fig. 1), occupying a total land area of around 32 km$^2$ between 8°N–12°N, and 71°E–74°E. The Lakshadweep region is heavily influenced by strong wave and current conditions during the southwestern monsoon season between mid-May and mid-October during which the currents in the Arabian Sea are known to flow in the southeasterly direction (Shanker et al. 2001). All atolls are oriented in a nearly north–south direction creating a distinct windward or exposed (west) and leeward or sheltered (east) direction during the monsoon months (Fig. 1). This difference in exposure to monsoon storms was a key factor affecting benthic recovery processes on these reefs after the 1998 mass-bleaching mortality (Arthur et al. 2006).

### *Reef fishing pressure in Lakshadweep*

Pole and line fishing for Skipjack tuna (*Katsuwonus pelamis*) has been practiced by local fishermen since the early 1900s (Hornell 1910). Developments in this fishery were facilitated in 1959 by the Fisheries Department and since then the tuna fishery has become the mainstay of local fishermen in Lakshadweep (Jones and Kumaran 1959; James et al. 1986). The pole and line tuna fishery requires the use of bait fish which includes a number of small-sized species including sprats, fusiliers, damselfish and cardinal fish, captured in the lagoons and adjoining reefs of the

**Table 1** Total fisheries landings (2011): total fisheries landings (metric tons, Mt) in year 2011 from 9 atolls, as documented by the Lakshadweep Fisheries Department

| Fishery type | Total annual catch (Mt) | Percent of total annual catch |
|---|---|---|
| Pelagic | 1,020.984 | 7.7 |
| Reef associated | 411.102 | 3.1 |
| Reef/lagoon | 849.347 | 6.4 |
| Tuna | 10,863.382 | 82.6 |

Fisheries catch recorded as

*Pelagic* sailfish, seer-fish, barracuda, flying-fish

*Reef associated* rainbow runners, reef sharks, carangids, rays

*Reef benthic* perches, coral fishes, lagoon fishes, goatfish, 'others'

*Tuna* Tuna

islands (Pillai et al. 1986). The growth of the tuna fishery requiring a regular supply of bait was closely shadowed by the growth in the reef- and lagoon-based bait fishery in Lakshadweep. This, interestingly, had shifted fishing pressure away from coral reefs in the past four decades (Arthur et al. 2005). Pelagic tuna stocks generate considerable trade revenue (Newton et al. 2007) and have become increasingly important in these regional waters including the neighboring Maldives. In contrast, the near-shore coral reef and lagoon-associated fisheries remain largely artisanal and subsistence in nature in the northern Indian Ocean region (Spalding et al. 2001).

No systematic study on Lakshadweep tuna and other fisheries has been conducted [but see Tamelander and Hoon (2008) for a study of artisanal fishing in Agatti atoll]. The Fisheries Department, however, conducts a voluntary catch-monitoring program of fisheries, but no direct monitoring of landings is undertaken. Total reef fishery yield for 2011 (from 9 atolls) was estimated at 849.3 Mt. These data need to be interpreted with caution, but catch records for 2011 suggest that the pole and line fishery for tuna constitutes 82 % of total landings followed by an 8 % contribution by a pelagic fishery and a 6.4 % contribution by fish associated with reef and lagoon habitats (see Table 1). We additionally conducted a series of key informant fisher interviews ($n = 12$) in two of the surveyed islands, Kadmat and Bitra, to get an understanding of (1) patterns of reef access and (2) local preference for reef fish. Key informants reported that the western reefs were completely inaccessible during the monsoon months (May–October) and fishing is focused inside the lagoon and eastern reefs during this lean period. Fishers also reported a low local preference for groupers (*Serranidae*), while snappers (*Lutjanidae*), jacks and trevallys (*Carrangidae*), needlefish (*Belonidae*), goatfish (*Mullidae*) and napoleon wrasses (*Cheilinus undulatus*) were the most preferred food fish locally, making up a greater proportion of fish catches from the lagoon and reef.

## Field methods

### *Measuring structural complexity (percent standing coral structure)*

Structural complexity was estimated at each site by placing five 1-$m^2$ photo quadrats located at regular intervals on 50 m transect lines (total transects $n = 5$–6 and $n = 30$–35 quadrates per site). Within each quadrat, the percent areal cover of hard coral was estimated with image processing software (ImageJ version 1.44o) by overlaying a 10 × 10 grid on the photo quadrat. Hard coral cover was further classified into coral forms: branching, massive, tabular and encrusting. We calculated a measure of structural complexity, defined as the percent cover of intact hard coral structure, both living and dead, recorded within the quadrat (loose rubble was excluded from this measure). We conducted a standardization to compare our measure of structural complexity with other commonly used techniques: reef rugosity (chain-link method, see Luckhurst and Luckhurst 1978) and vertical coral canopy height (Wilson et al. 2006; Obura and Grimsdith 2009). For the standardization, we measured structural complexity using all three methods at sites that varied considerably in their structural characteristics from nearly bare platforms to very complex reef sites ($n = 9$ samples). As our measure of structural complexity correlated positively and significantly with rugosity (Pearson's product–moment correlation, $r\,(7) = 0.72$, $t = 2.78$, $P = 0.027$) and vertical coral canopy height (Pearson's product–moment correlation, $r\,(7) = 0.79$, $t = 3.5$, $P = 0.009$), it was therefore used as a proxy for structural complexity in this study.

### *Classifying sites based on their structural stability (rate of change in structural complexity)*

To classify reef sites according to their structural stability through time, we used data from 12 long-term monitored reef sites (hereafter called permanent sites) established in 1998 for long-term monitoring of benthic cover. Permanent sites were established at three representative atolls (Agatti, Kadmat and Kavaratti) at two depths (shallow 5–10 m and deep 11–20 m) and two aspects (hereafter known as exposures; eastern aspect, sheltered from monsoon storms and western aspect, exposed to monsoon storms; total sites $n = 12$).

Sites were sampled by transect surveys using SCUBA. At each site, we tracked changes in structural complexity (see above) over a 12-yr period for the sampled years (from 1999 to 2003, 2007 and 2009, $n = 7$ yrs). Mean values of structural complexity for each site were regressed against years during the recovery period between the two coral mass mortality events ($n = 7$ sampled years) and we used the slope of the linear regression (mean slope 2.7 ± 0.62 SE, $R^2 = 0.48$, $F_{(23,46)} = 1.48$, $P < 0.05$) to represent the rate of structural change or turnover in structural complexity (i.e., the loss and recovery of hard coral structure). We use this as an index of structural stability through time for each location.

### *Archipelago-wide survey of groupers and structural complexity*

To determine the relationship between groupers, structural complexity and structural stability we undertook a large-scale survey across the Lakshadweep archipelago between December 2010 to March 2011 at 10 atolls (Agatti, Amini, Bangaram, Bitra, Chetlat, Kiltan, Kadmat, Kavaratti, Kalpeni and Minicoy) and 2 sunken banks (Cheriyapani and Perumal Par, Fig. 1). The sampling was designed to include a gradient of present structural complexity and the two main attributes that determine structural stability, i.e., exposure and depth (see earlier). We sampled 4 sites at each atoll (2 depths and 2 exposures) except for a few large atolls where we sampled multiple sites for better representation. A total of 60 sites were surveyed across the entire archipelago. At each site, we measured present structural complexity in 4–5 random transects located on the reef. Data on structural complexity were collected with the same techniques as the long-term monitoring, using 5–6 photo quadrates per transect (total quadrates per site = 20–25).

At each site, we estimated fish abundance using 5–8 random visual belt transects ($50 \times 10\ \text{m} = 500\ \text{m}^{-2}$ transect area). Along each transect, we recorded species composition and abundance of groupers (family Serranidae). Species were identified following Lieske and Myers (2002). Individual groupers were visually classified into four size classes (<10, 11–30, 31–50, 51 cm and above). Biomass was estimated using published length–weight relationship data for grouper species from www.fishbase.org (Froese and Pauly 2012), with the power function $W = aL^b$, where $W =$ weight of the individual (in gm), $L =$ total length of the individual, and $a$ and $b$ are species-specific constants. We used published life-history information to broadly classify grouper species as relatively short lived (<10 yrs) or long lived (>10 yrs). Groupers of the genus *Aethaloperca*, *Anyperodon*, *Cephalopholis*, *Epinephelus*, *Gracila* and *Plectropomus* were classified as long-lived groupers ($n = 14$ species, Grandcourt 2005; Pears et al. 2006). Smaller coral hinds of the genus *Cephalopholis* were classified as relatively 'short-lived' groupers ($n = 5$ species, Cabanban et al. 2008; Liu and Choat 2008).

## Statistical analysis

### *Patterns in long-term structural stability (structural stability regimes)*

We conducted a two-factorial analysis of variance (two-way ANOVA) at the site level with exposure (two levels: sheltered and exposed aspects) and depth (two levels: shallow and deep reefs) as explanatory variables, and the rate (slope of the regression over a period of 7 yrs, see above) of structural change ($n = 12$ sites), as the dependent variable. The results of the ANOVA and Tukey's post hoc comparisons were used to classify sites across the archipelago based on their structural stability.

### *Archipelago-wide patterns in benthic structural complexity and grouper variables (biomass, abundance and species richness)*

We used generalized linear mixed-effects models (GLMMs) to determine how structural complexity (2011), as well as grouper variables: biomass, abundance and species richness, varied between exposure (sheltered, exposed) and depth (deep, shallow). The GLMM families used were based on visual analysis of frequency distributions of the data. We used Poisson, zero-inflated Poisson and negative binomial GLMMs for these response variables either because they were count data or could be effectively treated as count data (no negative values, discretization naturally possible in the case of continuous variables). Exposure (sheltered, exposed) and depth (deep, shallow) were the fixed effects while atolls ($n = 10$) and sites ($n = 60$, nested within atolls) were random effects. The general GLMM formulation was represented as follows, for example:

$$\begin{aligned}\text{Structural complexity } [ijk] &\sim \text{exposure } [i] + \text{depth } [i] \\ &+ \text{exposure } [i] \times \text{depth } [i] + \text{random}\left(1 \left| \frac{\text{atoll}[j]}{\text{site}[k]} \right.\right)\end{aligned}$$

or

$$\begin{aligned}\text{Grouper variables } [ijk] &\sim \text{exposure}[i] + \text{depth}[i] \\ &+ \text{exposure}[i] \times \text{depth}[i] + \text{random}\left(1 \left| \frac{\text{atoll}[j]}{\text{site}[k]} \right.\right)\end{aligned}$$

where exposure × depth indicates an interaction between exposure and depth category for each site, and the variance term of the random effects (atoll, site) indicate random intercept models, i.e., different intercepts on the response variable for each site, atoll (Zuur et al. 2009). Model selection was undertaken by calculating the Akaike's information criterion (AIC) based on the trade-off between model deviance and parsimony (Crawley 2007). Data were checked for normality by visual inspection of plots of the residuals and fitted values. All data were analyzed with the packages nlme, lme4 and glmmADMB in the statistical software R (R Development Core Team 2011; Pinheiro et al. 2012; Bates et al. 2012; Bolker et al. 2012). Percentage composition of coral forms and grouper size class distributions at the four structural stability regimes (*SD* sheltered deep, *SS* sheltered shallow, *ED* exposed deep, *ES* exposed shallow) are reported using dot charts.

### *Relationship between structural complexity and grouper biomass across structural stability regimes*

Relationships between long-lived and short-lived grouper biomass with structural complexity were explored using generalized linear models (GLMs) at locations of different structural stabilities, as identified from our long-term data. Based on the visual analysis of frequency distributions of the data, we used the negative binomial (NB) family for the discretized response variable of grouper biomass. Zero-inflated negative binomial (ZiNB) models were used to account for zero inflation, when present in the dataset. A logarithmic link function was used to link mean biomass to the predictor function as this ensures positive fitted values (Zuur et al. 2009). For each stability regime, the general model formulation for the GLM was:

$$\text{Grouper biomass}[i] \sim e^{\alpha+\beta\times\text{structural complexity}[i]}$$

where $\alpha$ and $\beta$ are the intercept and slope, respectively. The R packages MASS (Venables and Ripley 2002) and pscl (Zeileis et al. 2008) were used to conduct this GLM analysis.

## Results

### Structural stability regimes

Our long-term benthic data show that the rate of change in benthic structure (structural stability) was strongly influenced by both exposure and depth (Table 2), structural stability was highest at sheltered, deep reefs (mean slope: 0.37 ± 0.15 SE; Fig. 2). Tukey's post hoc tests showed a sixfold difference in structural stability between sheltered, deep sites (which were highly stable through time) and exposed, shallow sites (which were structurally dynamic through time, mean slope: 5.9 ± 0.15; Fig. 2). Even at the same depth, sheltered deep sites (mean slope 0.37 ± 0.15 SE) were thrice as stable as exposed deep sites (mean slope 1.9 ± 0.40). Sheltered deep locations showed the lowest values of structural change through the sampled years, while exposed shallow locations had the highest values. Exposed deep (mean slope: 1.9 ± 0.40) and sheltered shallow locations (mean slope: 2.56 ± 0.44 SE) showed intermediate structural stability values (Table 2; Fig. 2). These comparisons give rise to a gradient of structural stability in the archipelago; high stability (sheltered deep sites), medium stability (exposed deep and sheltered shallow sites) and low stability (exposed shallow sites).

**Table 2** Structural stability regimes: two-factorial analysis of variance (two-factorial ANOVA) for joint effect of exposure and depth on the rate of change of structural complexity (structural stability) over a 7 years (1999–2003, 2007, 2009)

| Source of variation | *df* | Sum of squares | Mean square | *F* |
|---|---|---|---|---|
| Exposure | 1 | 18.377 | 18.376 | 59.73* |
| Depth | 1 | 28.44 | 28.44 | 91.81* |
| Exposure × depth | 1 | 2.332 | 2.33 | 7.58** |
| Model | 3 | 48.95 | 16.31 | 53.05* |
| Error | 8 | 2.461 | 0.307 | |
| Total (corrected) | 11 | 51.41 | | |

$R^2 = 0.65$ (adjusted $R^2 = 0.63$), significant at alpha = 0.05 level

* $P < 0.01$, ** $P < 0.001$

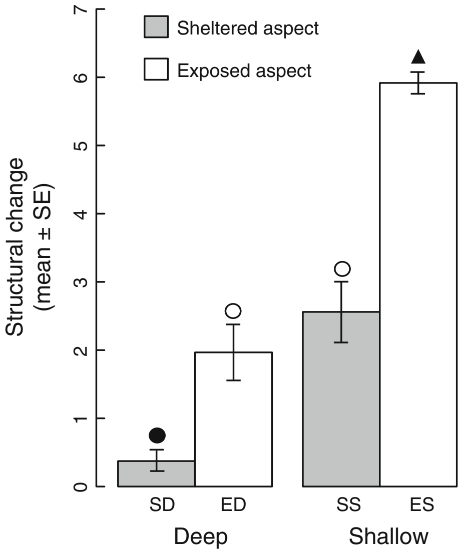


**Fig. 2** Structural stability (mean slope of structural change ± SE) at 12 permanent monitoring locations (Agatti, Kadmat and Kavaratti atolls, established in 1998), tracked during a recovery period between two major mass-bleaching catastrophes (1999 and 2009, $n = 7$ yrs). Sites factored by exposure and depth ($n = 12$). Tukey's HSD indicates three significantly different categories of structural stability at the two depths, represented by high-stability sites *filled circle*, medium-stability sites *open circle*, low-stability sites *filled triangle*. Site code: *SD* sheltered deep, *SS* sheltered shallow, *ED* exposed deep, *ES* exposed shallow

**Table 3** Summary of Poisson generalized linear mixed effect model (Poisson GLMM) showing the effect of exposure and depth on structural complexity (2011)

Selected top model:
structural complexity ~ exposure + depth + random (site)

| Fixed effects mean ± (SE) | | Corresponding $z$ statistic | Random effects variance term ± (SD) | |
|---|---|---|---|---|
| Intercept = exposure (sheltered), depth (deep) | 4.35 (0.05) | 80.54*** | Sites | 0.04 (0.22) |
| Exposure (exposed) | −0.05 (0.08) | −0.7 | | |
| Depth (shallow) | −0.06 (0.02) | −3.25** | | |

The table shows the best-selected model indicating parameter means with standard errors for fixed effects, and variance terms with standard deviation for random effects. Exposure and depth are fixed effects and site represents random effects

** $P < 0.001$ and *** $P < 0.0001$

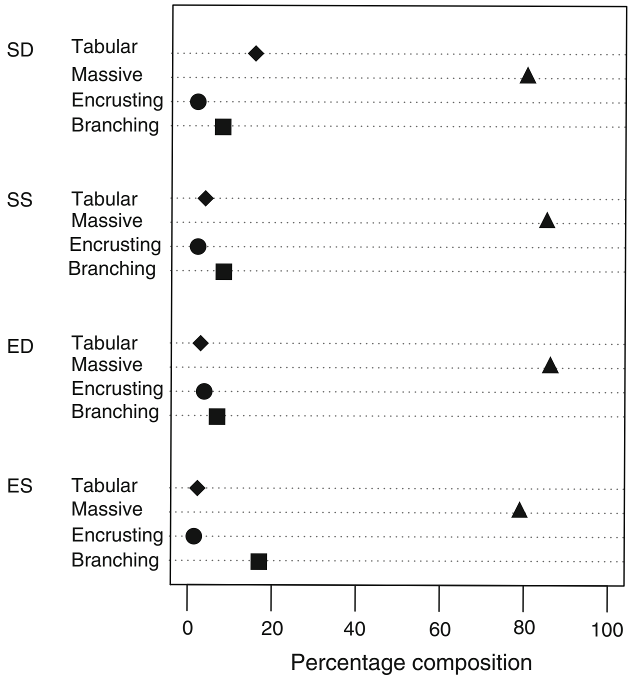


**Fig. 3** Percentage composition of coral forms: branching, encrusting, massive and tabular at four stability categories. Site code: *SD* sheltered deep, *SS* sheltered shallow, *ED* exposed deep, *ES* exposed shallow

## Patterns in structural complexity

Generalized linear mixed-effects models (GLMMs) showed that structural complexity did not significantly change with exposure but showed a weak positive effect of depth (Table 3).

Post-2010 bleaching, the composition of coral forms showed that massive corals dominate the composition of all stability regimes (>70 %, Fig. 3). The percentage contribution of structure-forming tabular and branching corals is low in general throughout the study area, lower than 20 %. Exposed shallow reefs had the highest percentage of branching corals (17.04 %) and the lowest percentage of tabular corals (2.3 %). Sheltered deep reefs had the highest percentage of structure-forming tabular corals (8 %) among all the reefs (Fig. 3).

## Patterns in grouper biomass, diversity and species richness

Mean grouper biomass significantly changed with depth and exposure (Table 4). Within the same depth class, mean grouper biomass was significantly higher at deep sites on the sheltered aspect (Fig. 4a), which had, on average, twice the amount of grouper biomass than deep sites on the exposed aspect. Similarly, comparing between depth classes, sheltered deep sites had six times the biomass of exposed shallow sites (Fig. 4a). Grouper abundance (density) and species richness did not change significantly with exposure or depth (Table 4; Fig. 4b, c). Across the archipelago, 50 % of average grouper biomass was concentrated at merely 10 reef sites (16 % of sites sampled, Fig. 6a), all of which were sites of high structural stability (sheltered deep, Fig. 2), and were also characterized by high structural complexity (more than 80 % structure, Fig. 6a).

The proportion of individuals in large-size classes (31–50 and 51+ cm) was highest in sheltered deep reefs (46.4 and 15 %, respectively; Fig. 5). Sheltered reefs (deep and shallow) were dominated by individuals of length 31–50 cm (~60 %) as compared to exposed reefs (deep and shallow), which were dominated by medium individuals of length 11–30 cm (~50 %). The proportion of very small individuals (≤10 cm) was greater in exposed reefs, both deep and shallow (Fig. 5).

## Relationship between structural complexity and grouper biomass across stability regimes

Biomass of long-lived grouper species increased significantly and exponentially (mean biomass $\sim e^{5.64+0.04*\text{mean structural complexity}}$) with structural complexity but only at the high-stability sites, i.e.,

**Table 4** Generalized linear mixed effect models (GLMMs) showing the effect of exposure, and depth on grouper variables (biomass, abundance and species richness)

| Selected top model | Fixed effects mean ± (SE) | | Corresponding $z$ statistic | Random effects variance term ± (SD) | |
|---|---|---|---|---|---|
| Biomass[a] ~ exposure × depth + random (atoll) | Intercept = exposure (sheltered), depth (deep) | 7.77 (0.20) | 36.98*** | Atoll | 0.03 (0.17) |
| | Exposure (exposed) | −0.76 (0.30) | −2.54* | | |
| | Depth (shallow) | −0.84 (0.31) | −2.67** | | |
| | Exposure (exposed): depth (shallow) | −0.14 (0.46) | −0.3 | | |
| Abundance[b] ~ exposure × depth + random (atoll\|site) | Intercept = exposure (sheltered), depth (deep) | 1.19 (0.16) | 7.18*** | Atoll | 0.08 (0.29) |
| | Exposure (exposed) | −0.22 (0.21) | −1.04 | Atoll: site | 0.14 (0.37) |
| | Depth (shallow) | −0.25 (0.17) | −1.43 | | |
| | Exposure (exposed): depth (shallow) | −0.14 (0.26) | 0.54 | | |
| Species richness[c] ~ exposure + depth + random (atoll) | Intercept = exposure (sheltered), depth (deep) | 1.12 (0.09) | 12.27*** | Atoll | 0.05 (0.23) |
| | Exposure (exposed) | −0.14 (0.08) | −1.69 | | |
| | Depth (shallow) | −0.49 (0.08) | −5.70 | | |

Exposure and depth are fixed effects and site (nested within atoll) and/or sites or atolls alone as random effects. Table provides the best-selected top models indicating parameter means with standard errors for fixed effects, and variance terms with standard deviations for random effects

* $P < 0.01$, ** $P < 0.001$ and *** $P < 0.0001$

GLMM families used: [a] negative binomial (NB = 0.296, SE = 0.024), [b] negative binomial (NB = 1.948, SE = 0.317), [c] Poisson

deep sites on the sheltered aspect (Table 5; Fig. 6a). Further, based on the following estimate:

$$\text{Pseudo}\,R^2 = 1 - \frac{\text{residual deviance}}{\text{null deviance}} \times 100$$

(Zuur etal. 2009),

structural complexity predicted about 79 % variation in long-lived species biomass at these high-stability sites.

In contrast, long-lived grouper biomass did not show even weakly significant relationships with structure for similar levels of structural complexity at all other locations of medium and low stability (Table 5; Fig. 6b–d). Short-lived species biomass was not significantly influenced by structural complexity at any depth or exposure (Table 5).

## Discussion

Although the ability of some reefs to rapidly recover their structure after major mortality events is encouraging, our results indicate that long-term stability of habitats and not merely the availability of structure after rapid coral recovery may be far more important for long-lived species such as groupers. Our 12-yr temporal data shows differential rates of structural change (due to degradation and recovery from multiple bleaching events) across Lakshadweep. The structurally stable, sheltered deep sites across the entire archipelago appear to be highly preferred habitats for long-lived groupers. These 'high-stability' sites support about 50 % of grouper biomass recorded in our study. In comparison, even sites with high structural complexity, which have recovered rapidly from bleaching events (exposed deep sites or both shallow sites), do not support the same biomass of groupers as the high-stability sites. Our results suggest that a quick recovery of benthic structure alone may not influence the distribution of long-lived benthic fish associates, especially on reefs subject to recurrent disturbance events.

In many tropical reefs, groupers are highly targeted species, and this offtake pressure can often play a major role in their distribution (Chiappone et al. 2000). The Lakshadweep reef system is fairly unique in this respect because, despite having a dense human population, reef fishing here is a largely artisanal enterprise and contributes little to overall fishing pressure (Table 1). Grouper biomass in our study was, on average, 88 kg ha$^{-1}$ across the archipelago, comparable with biomass estimates from relatively unfished reefs and well-established marine-protected areas, which can have grouper biomasses of between 20 and 130 kg ha$^{-1}$ dependent on the location (Chiappone et al. 2000; Unsworth et al. 2007; McClanahan 2011). In the absence of robust direct estimates of fishing pressure from the Lakshadweep, these estimates are perhaps the strongest evidence for low grouper fishing from these waters. However, even low levels

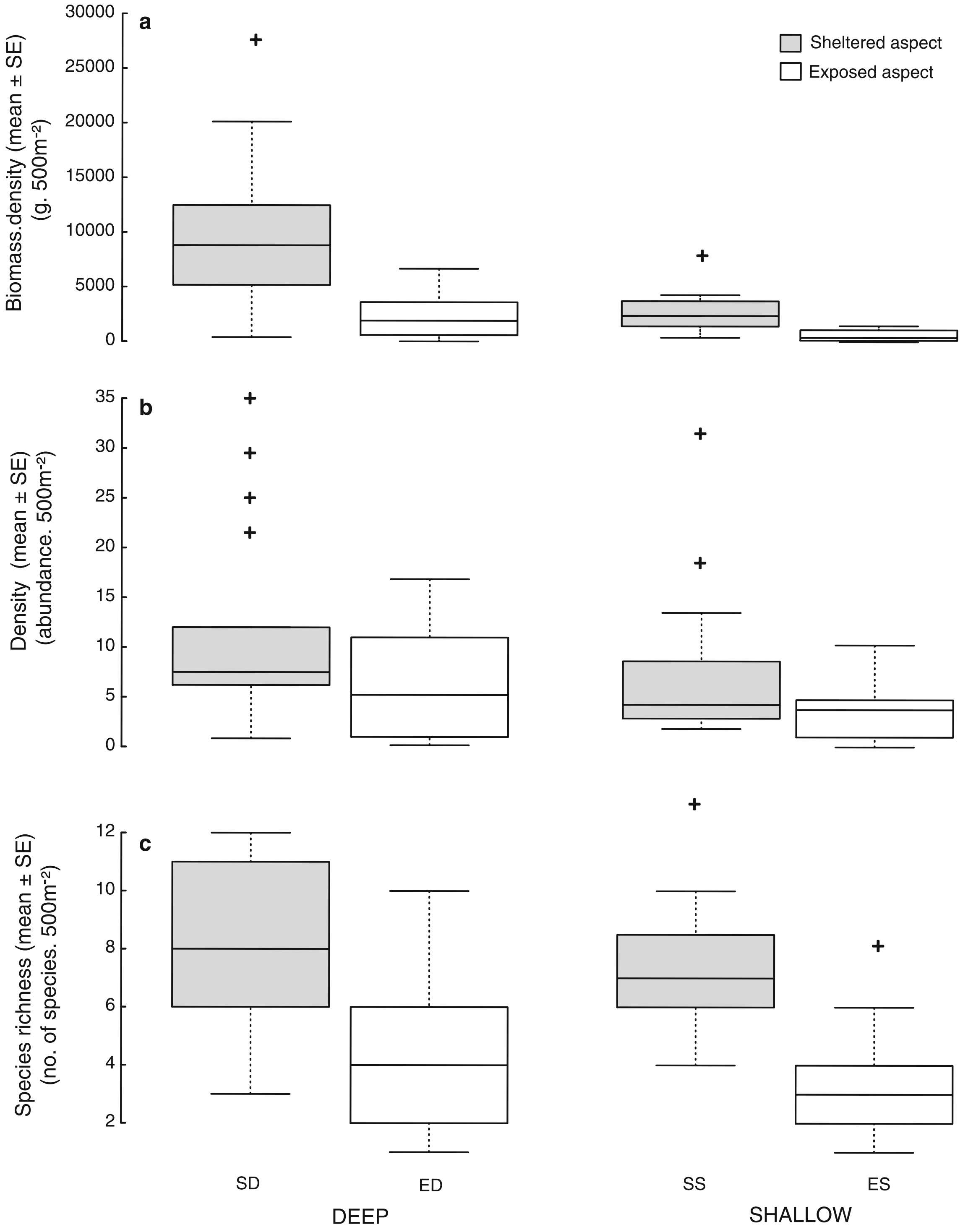


**Fig. 4** **a** Grouper biomass density (mean ± SE), **b** abundance density (mean ± SE) and **c** species richness (mean ± SE) at exposed and sheltered locations and two depths (deep and shallow). Site code: *SD* sheltered deep, *SS* sheltered shallow, *ED* exposed deep, *ES* exposed shallow

of fishing can leave a distinct signature on the distribution and size of reef fish, particularly for long-lived species (Dulvy et al. 2004b). Our results, however, show that eastern reefs, despite being open year-round to light to moderate fishing, consistently show the highest biomass of groupers. The key informant fishers we interviewed also confirmed that groupers were a fairly low-preference food fish locally, and earlier studies indicate that levels of grouper fishing can be low compared with grouper offtake from the nearby Maldives (Tamelander and Hoon 2008; Sattar et al. 2011).

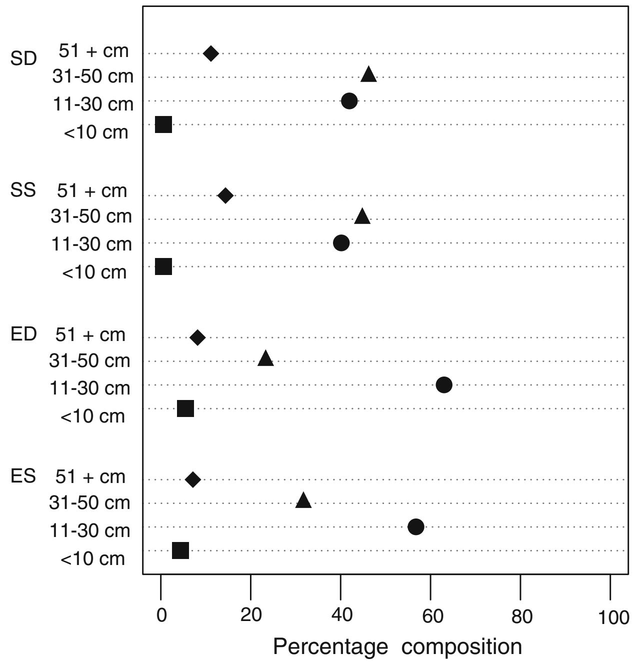


**Fig. 5** Percentage composition of grouper size classes: <10, 11–30, 31–50 and 51+ cm at four stability categories. Site code: *SD* sheltered deep, *SS* sheltered shallow, *ED* exposed deep, *ES* exposed shallow

Taken together, this suggests that reef fishing pressures do not drive the observed patterns and sheltered deep locations may support higher densities (high-stability habitats) over exposed deep and shallow locations (Fig. 4), potentially even offsetting low to moderate reef fishing pressures. More detailed studies on fishing intensity, access and species selectivity need to be undertaken to confirm the impact of fishing on grouper distributions.

Few reefs across the Indo-Pacific (McClanahan et al. 2007; Graham et al. 2011, and our study sites) have shown remarkable ability for benthic recovery after bleaching mass mortality events. Benthic recovery in the Lakshadweep proceeded rapidly after the 1998 El Niño bleaching event (Arthur et al. 2006), influenced strongly by the interaction of depth and protection from monsoonal storms. Exposed shallow sites incurred the highest amount of coral degradation and recovery from the 1998 mass-bleaching event, being dominated by the fast-growing and fragile *Acropora* corals (Arthur et al. 2005). As a result, these sites were structurally unstable, going through cycles of very high and very low structural complexity during the 12-yr period we sampled. Sheltered deep sites, on the other hand, appear to have maintained their structure (in spite of coral mortality) since the 1998 mass-bleaching disturbance. Our data support this observation (Fig. 3), and we find that tabular coral forms, which are most susceptible to wave exposure (Madin and Connolly 2006), were highest in sheltered, deep reefs. Similarly, branching coral forms, which contributed largely to the low stability of exposed shallow reefs, were highest in these reefs, despite the recent bleaching disturbance of 2010.

Most atolls in the archipelago are oriented in a north–south direction with a distinct windward and leeward aspect in relation to the annual southwesterly monsoon. The monsoon system has historically played an important role in shaping the geomorphology of the Laccadives—Chagos archipelago (Siddiquie 1980). Thus, even with a simple binary classification of exposure, our temporal data (12 sites, 3 atolls) is highly representative of archipelago-wide hydrodynamics and we can therefore extrapolate trends in structural stability to the entire archipelago. These results show that structural stability of reefs across the

**Table 5** Generalized linear model (GLM) showing the relationship between grouper biomass (long-lived and short-lived species) and structural complexity at different stability regimes (1) high-stability (SD)-sheltered deep sites, (2) medium-stability (ED)-exposed deep sites (3) medium-stability (SS)-sheltered shallow sites) (4) low-stability (ES)-exposed shallow sites

| Stability regimes | GLM family | Intercept | Structural complexity | $z$ value, $df = 15$ |
|---|---|---|---|---|
| Long-lived species | | | | |
| High (SD) | Negative binomial (NB = 2.5, SE = 1.1) | 5.56 (0.89) | 0.04 (0.01) | 4.03* |
| Medium (ED) | Negative binomial (NB = 1.5, SE = 0.5) | 8.49 (0.97) | − 0.009 (0.01) | −0.73 |
| Medium (SS) | Negative binomial (NB = 0.55, SE = 0.18) | 4.6 (2) | 0.03 (0.02) | 1.43 |
| Low (ES) | Zero-inflated negative binomial (ZINB = 0.98, SE = 0.42) | 2.28 (0.94) | 0.05 (0.01) | 1.89 |
| Short-lived species | | | | |
| High (SD) | Negative binomial (NB = 0.30, SE = 0.11) | 3.3 (2.3) | 0.01 (0.02) | 0.57 |
| Medium (ED) | Negative binomial (NB = 0.42, SE = 0.1) | 5.4 (1.85) | 0.006 (0.02) | 0.26 |
| Medium (SS) | Zero-inflated negative binomial (ZINB = 000.9, SE = 0.47) | 0.55 (3.92) | 0.06 (0.04) | 1.3 |
| Low (ES) | Negative binomial (NB = 0.28, SE = 0.107) | 4.77 (2.42) | 0.009 (0.33) | 0.29 |

Table gives parameter mean ± SE for the explanatory variable (structural complexity), model intercept and corresponding $z$ statistic for $df = 15$

* $P < 0.01$

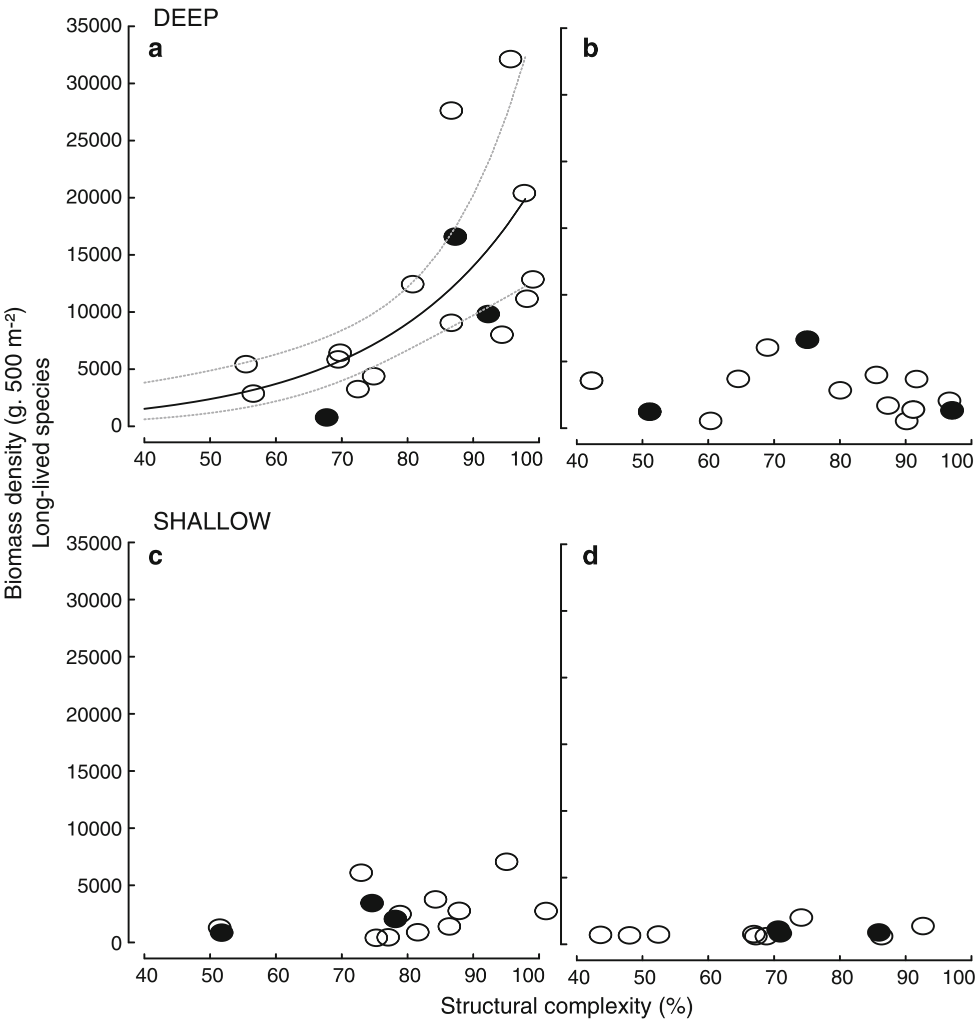


**Fig. 6** Effect of increasing structural complexity on mean biomass density of long-lived grouper species ($n = 14$ species), at exposed and sheltered locations at two depths (deep and shallow) **a** SD, $n = 17$, **b** ED, $n = 14$, **c** SS, $n = 14$, **d** ES, $n = 14$, using GLMs. Relationship between grouper biomass and structural complexity at high-stability locations (a) is fitted by the model: long-lived grouper biomass $\sim e^{5.46*\text{structural complexity}*0.04}$ (*black solid line*), bounded by 95 % confidence intervals (CI, *gray dashed lines*). *Solid circles* indicate permanent monitoring sites at three atolls (Agatti, Kadmat and Kavaratti), *open circles* indicate sites sampled only in 2011. Site code: *SD* sheltered deep, *SS* sheltered shallow, *ED* exposed deep, *ES* exposed shallow

Lakshadweep archipelago increases with depth and degree of protection from the monsoon storms, and sites can be classified, based on their recent history of structural changes as low-stability (exposed shallow), medium-stability (exposed deep, sheltered shallow) or high-stability (sheltered deep) sites.

Independent of structural history, a few years after the last mass-bleaching event, mean structural complexity in Lakshadweep appears to be comparable between sites. Structural complexity is a crucial resource, influencing communities across various ecosystems (MacArthur and MacArthur 1961; Friedlander and Parrish 1998). Yet, in spite of the availability of structure, we see vast differences in grouper biomass between sites of differing structural stabilities, especially between deeper locations. In the absence of any temporal data on fish abundance across the entire archipelago, it is difficult to ascertain whether patterns in biomass represent the response of long-lived fish communities to multiple mass-bleaching disturbances or if they merely reflect a natural distribution with respect to depth and exposure (Sabetian 2003). In our survey, depth does emerge as an important factor by itself, positively affecting grouper biomass and structural complexity. It is however, compelling that even at the same depth (deep), sheltered deep sites with very stable structure support twice the amount of grouper biomass as sites with relatively low stability (exposed deep, Fig. 4a). Further, long-lived groupers show an exponential numerical response to increasing structural complexity only in the high stability, sheltered deep sites in spite of the availability of suitable habitat (80 % structural complexity) at other, less-stable locations (Fig. 6).

Patterns in biomass were driven by a few large-bodied and long-lived species like *Plectropomus laevis*, *Plectropomus areolatus*, *Cephalopholis argus*, *Epinephelus malabaricus*, *Epinephelus caeruleopunctatus* and *Variola louti*, which were common only in sheltered deep sites at all the atolls we surveyed (Electronic Supplemental Material, ESM Appendix 1, Fig. 5). In contrast, short-lived species like the coral hinds (*Cephalopholis leopardus*, *Cephalopholis urodeta*, *Epinephelus fasciatus*) occurred commonly everywhere and did not seem to respond to structural complexity across the stability regimes (ESM Appendix 1, Fig. 5). This suggests that unlike their long-lived counterparts, shorter-lived species, with faster population turnover rates, may not be limited by structural change or may even benefit from the decline of long-lived top predators on unstable reefs. The breakdown of an important resource-abundance relationship in unstable reefs calls into question the ability of functionally important long-lived fish species to survive and recover from repeated environmental disturbances.

Several factors potentially interact to make structurally stable sites in the Lakshadweep critical for long-lived groupers. The observed trends in biomass could largely reflect strong habitat selectivity by grouper species for specific habitat types (Sluka 2000). Coral morphology, the principle structural element on reefs (Kerry and Bellwood 2012), differs in its functional utility to reef fish (Syms 1995; Samoilys 1997; Harmelin and Harmelin-Vivien 1999; Shibuno et al. 2008; Wilson et al. 2008; Kerry and Bellwood 2012). Differences in the composition of structural forms between sites may be an essential factor limiting adult groupers from colonizing low-stability reefs. High-stability, sheltered deep sites, with a mix of coral structures, may provide ideal conditions for small and large groupers (Figs. 3, 5).

The pattern of grouper distribution in Lakshadweep, like other species of reef fish, could also have been largely driven by patterns in prey availability (Shpigel and Fishelson 1989; Beukers-Stewart and Jones 2004), which may fluctuate rapidly in low-stability sites. Species with narrower niche widths in terms of diet, modes of predation and dependence on structure may be unable to survive in low-stability locations where resources are in a state of flux from multiple disturbance events. Similarly, these rapid fluctuations in resources may have created bottlenecks for important population-level processes like reproduction, recruitment, post-recruitment survival, migration, which may only be reflected in the populations after a decadal lag period. The patterns we find suggest the possibility of differential mortality of long-lived species from low-stability sites or adult migrations to high-stability locations. Further studies addressing these various processes are necessary to gain valuable insights into the effects of multiple disturbances on benthic grouper communities.

Independent of the specific mechanisms, these structurally stable reef sites may serve as vital refuge areas for fish populations on coral reefs, especially as climate change increases the frequency and intensity of benthic disturbances (Hoegh-Guldberg et al. 2007). Such stable refugia can have important ramifications for overall reef resilience, serving as important insurance locations for functionally important, keystone predators. Reef benthic predators like groupers are highly vulnerable because, apart from the insidious influences of declining reef architecture on their populations, they are often prized fishery targets feeding a growing live fish trade (Sadovy de Mitcheson et al. 2012). Lakshadweep presents a unique situation where the targeted fishing of groupers and reef fish is generally low in comparison to several regions across the tropics, but it is highly vulnerable today to future external market forces. Our results indicate that even these unexploited populations of benthic predators may be subject to community-wide impacts in the wake of climate change even in relatively unfished reefs like the Lakshadweep. Neither a quick benthic recovery nor the relatively low fishing pressure is sufficient to stem these losses to long-lived groupers, making structurally stable habitats all the more critical to the overall resilience of reef systems. Identifying these historically stable refugia should be an important first step in prioritizing reef management initiatives in the face of rapid climate change and expanding reef fisheries.

**Acknowledgments** We would like to thank the Lakshadweep Administration, Department of Environment and Forests, Department of Fisheries and the Department of Science and Technology for permits and logistic support. In addition, we thank Lacadives, Department of tourism (SPORTS) and supporters in the Lakshadweep: J. Hisham, Idris B., and Ibrahim M.K. For support and critical feedback, we thank Dr. K. Shanker, M.D. Madhusudan and Dr. Howells. We would also like to thank two anonymous reviewers, the editor and T.R. Shankar Raman for their critical inputs to improving the MS. This study was conducted with funding and in-kind support from Rufford Small Grants Foundation, National Geographic and Idea Wild.

## References

Almany GR (2004a) Does increased habitat complexity reduce predation and competition in coral reef fish assemblages? Oikos 106:275–285

Almany GR (2004b) Differential effects of habitat complexity, predators and competitors on abundance of juvenile and adult coral reef fishes. Oecologia 141:105–113

Arthur R (2000) Coral bleaching and mortality in three Indian reef regions during an El Niño southern oscillation event. Curr Sci (Bangalore) 79:1723–1729

Arthur R, Done TJ, Marsh H (2005) Benthic recovery four years after an El-Nino-induced coral mass mortality in the Lakshadweep atolls. Curr Sci (Bangalore) 89:694–699

Arthur R, Done TJ, Marsh H, Harriott V (2006) Local processes strongly influence postbleaching benthic recovery in the Lakshadweep Atolls. Coral Reefs 25:427–440

Auster, PJ (2005) Predatory behavior of piscivorous reef fishes varies with changes in landscape attributes and social context: integrating natural history observations in a conceptual model. In: Diving for Science 2005, Proceedings of the American Academy of Underwater Sciences, Connecticut Sea Grant, Groton, pp 115–127

Bates D, Maechler M, Bolker B (2012) Linear mixed-effects models using S4 classes. R Package version 0.99-0

Bellwood DR, Baird AH, Depczynski M, González-Cabello A, Hoey AS (2012) Coral recovery may not herald the return of fishes on damaged coral reefs. Oecologia 170:567–573

Berumen ML, Pratchett MS (2006) Recovery without resilience: persistent disturbance and long-term shifts in the structure of fish and coral communities at Tiahura reef, Moorea. Coral Reefs 25:647–653

Beukers-Stewart BD, Jones GP (2004) The influence of prey abundance on the feeding ecology of two piscivorous species of coral reef fish. J Exp Mar Biol Ecol 299:155–184

Bohnsack JA (1982) Effects of piscivorous predator removal on coral reef fish community structure. In: Cailliet GM, Simenstad CA (eds) Gutshop '81: Fish food habits studies. Washington Sea Grant Publication, Seattle, Washington, pp 258–267

Bolker B, Skaug H, Magnusson A, Nielsen A (2012) Generalized Linear Mixed Models using AD Model Builder. R package version 0.6.5

Cabanban AS, Myers R, Yeeting B, Pollard D, Kulbicki M, Fennessy S (2008) *Cephalopholis sexmaculata*. In: IUCN 2012. IUCN Red List of Threatened Species. Version 2012.1 www.iucnredlist.org. Downloaded on 18 September 2012

Caley MJ, John JST (1996) Refuge availability structures assemblages of tropical reef fishes. J Anim Ecol 65:414–428

Chiappone M, Sluka R, Sullivan KS (2000) Groupers (Pisces: Serranidae) in fished and protected areas of the Florida Keys, Bahamas and northern Caribbean. Mar Ecol Prog Ser 198:261–272

Chollett I, Mumby PJ (2012) Predicting the distribution of *Montastraea* reefs using wave exposure. Coral Reefs 31:493–503

Crawley MJ (2007) The R book. John Wiley & Sons, Ltd. Chichester: West Sussex PO19 8SQ, England

Done T (1999) Coral community adaptability to environmental change at the scales of regions, reefs and reef zones. Am Zool 39:66–79

Dulvy NK, Freckelton RP, Polunin NVC (2004a) Coral reef cascades and the indirect effects of predator removal by exploitation. Ecol Lett 7:410–416

Dulvy NK, Polunin NVC, Mill AC, Graham NAJ (2004b) Size structural change in lightly exploited coral reef fish communities: evidence for weak indirect effects. Can J Fish Aquat Sci 61:466–475

Feary D, Almany GR, McCormick MI, Jones GP (2007) Habitat choice, recruitment and the response of coral reef fishes to coral degradation. Oecologia 153:727–737

Floeter SR, Krohling W, Gasparini JL, Ferreira CEL, Zalmon IR (2007) Reef fish community structure on coastal islands of the southeastern Brazil: the influence of exposure and benthic cover. Environ Biol Fish 78:147–160

Friedlander AM, Parrish JD (1998) Habitat characteristics affecting fish assemblages on a Hawaiian coral reef. J Exp Mar Biol Ecol 224:1–30

Froese R, Pauly D (eds) (2012) FishBase. World Wide Web electronic publication. www.fishbase.org, version (08/2012)

Fulton EA (2011) Interesting times: winners, losers and system shifts under climate change around Australia. ICES J Mar Sci 68:1329–1342

Garpe KC, Yahya SAS, Lindahl U, Öhman MC (2006) Long-term effects of the 1998 coral bleaching event on reef fish assemblages. Mar Ecol Prog Ser 315:237–247

Goeden GB (1989) Intensive fishing and a "keystone" predator species: Ingredients for community instability. Biol Conserv 22:273–281

Graham NAJ, Nash KL (2013) The importance of structural complexity in coral reef ecosystems. Coral Reefs 32:315–326

Graham NAJ, Nash KL, Kool JT (2011) Coral reef dynamics in a changing world. Coral Reefs 30:283–294

Grandcourt E (2005) Demographic characteristics of selected epinepheline groupers (family: Serranidae; subfamily: Epinephelinae) from Aldabra Atoll, Seychelles. Atoll Res Bull 593:200–216

Gust N (2002) Scarid biomass on the northern Great Barrier Reef: the influence of exposure, depth and substrata. Environ Biol Fish 64:353–366

Halford A, Cheal AJ, Ryan D, Williams DMCB (2004) Resilience to large-scale disturbance in coral and fish assemblages on the Great Barrier Reef. Ecology 85:1892–1905

Harmelin JG, Harmelin-Vivien M (1999) A review on habitat, diet and growth of the dusky grouper *Epinephelus marginatus* (Lowe, 1834). Mar Life 9:11–20

Heithaus MR, Alejandro F, Wirsing AJ, Worm B (2008) Predicting ecological consequences of marine top predator declines. Trends Ecol Evol 23:202–210

Hixon MA, Beets JP (1993) Predation, prey refuges and the structure of coral-reef fish assemblages. Ecol Monogr 63:77–101

Hoegh-Guldberg O, Mumby PJ, Hooten AJ, Steneck RS, Greenfield P, Gomez E, Harvell CD, Sale PF, Edwards AJ, Caldeira K, Knowlton N, Eakin CM, Iglesias-Prieto R, Muthiga N, Bradbury RH, Dubi A, Hatziolos ME (2007) Coral reefs under rapid climate change and ocean acidification. Science 318:1737–1742

Hornell J (1910) Report on the results of a fishery cruise along the Malabar Coast and the Laccadive Islands in 1908. Madras Fisheries Bulletin 4:71–126

James PSBR, Pillai CSG, Pillai PP, Livingston P, Mohan M (1986) Marine fisheries research in Lakshadweep - a historical resume. Mar Fish Inf Serv 68:7–9

Jones S, Kumaran M (1959) The fishing industry of Minicoy Island with special reference to the tuna fishery. Indian J Fish 6:30–57

Kerry JT, Bellwood DR (2012) The effect of coral morphology on shelter selection by coral reef fishes. Coral Reefs 31:415–424

Lieske E, Myers R (2002) Coral reef fishes: Indo-Pacific and Caribbean. Princeton Pocket Guides, Princeton University Press

Lindberg WJ, Frazer TK, Portier KM, Vose F, Loftin J, Murie DJ, Mason DM, Nagy B, Hart MK (2006) Density-dependent habitat selection and performance by a large mobile reef fish. Ecol Appl 16:731–746

Liu M, Choat JH (2008) *Cephalopholis argus*. In: IUCN 2012. IUCN Red List of Threatened Species. Version 2012.1. www.iucnredlist.org. Downloaded on 18 September 2012

Luckhurst BE, Luckhurst K (1978) Analysis of influence of substrate variables on coral-reef fish communities. Mar Biol 49:317–323

MacArthur RH, MacArthur JW (1961) On bird species diversity. Ecology 42:594–598

Madin JS, Connolly SR (2006) Ecological consequences of major hydrodynamic disturbances on coral reefs. Nature 444:477–480

McClanahan TR (2011) Coral reef fish communities in management systems with unregulated fishing and small fisheries closures compared with lightly fished reefs–Maldives vs. Kenya. Aquat Conserv: Mar Freshw Ecosyst 21:186–198

McClanahan TR, Ateweberhan M, Graham NAJ, Wilson SK, Sebastian CR, Guillaume MMM, Bruggemann JH (2007) Western Indian Ocean coral communities: bleaching responses and susceptibility to extinction. Mar Ecol Prog Ser 337:1–13

Myers AR, Worm B (2003) Rapid worldwide depletion of predatory fish communities. Nature 423:280–283

Newton K, Côté IM, Pilling GM, Jennings S, Dulvy NK (2007) Current and future sustainability of island coral reef fisheries. Curr Biol 17:655–658

Obura DO, Grimsdith G (2009) Resilience assessment of coral reefs-Assessment protocol for coral reefs, focusing on coral bleaching and thermal stress. IUCN working group on Climate Change and Coral Reefs. IUCN, Gland, Switzerland

Paine RT, Tegner MJ, Johnson EA (1998) Compounded perturbations yield ecological surprises. Ecosystems 1:535–545

Pandolfi JM, Bradbury RH, Sala E, Hughes TP, Bjorndal KA, Cooke RG, McArdle D, McClenachan L, Newman MJH, Paredes G, Warner RR, Jackson JBC (2003) Global trajectories of the long-term decline of coral reef ecosystems. Science 301:955–959

Pears RJ, Choat HJ, Mapstone BD, Begg GA (2006) Demography of a large grouper, *Epinephelus fuscoguttatus* from Australia's Great Barrier Reef: implications for fishery management. Mar Ecol Prog Ser 307:259–272

Pillai PP, Kumaran M, Pillai CSG, Mohan M, Gopakumar G, Livingston P, Srinath M (1986) Exploited and potential resources of live-bait fishes of Lakshadweep. Mar Fish Inf Serv 68:25–32

Pinheiro J, Bates D, DebRoy S, Sarkar D and the R Development Core Team (2012) nlme: Linear and Nonlinear Mixed Effects Models. R package version 3.1-104

R Development Core Team (2011) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL http://www.R-project.org/

Russ GR, Alcala AC (1998) Natural fishing experiments in marine reserves 1983-1993: roles of life history and fishing intensity in family responses. Coral Reefs 17:399–416

Sabetian A (2003) The association of physical and environmental factors with abundance and distribution patterns of groupers around Kolombangara Island, Solomon Islands. Environ Biol Fish 68:93–99

Sadovy de Mitcheson Y, Craig MT, Bertoncini AA, Carpenter KE, Cheung WWL, Choat JH, Cornish AS, Fennessy ST, Ferreira BP, Heemstra PC, Liu M, Myers RF, Pollard DA, Rhodes KL, Rocha LA, Russell BC, Samoilys MA, Sanciangco J (2012) Fishing groupers towards extinction: a global assessment of threats and extinction risks in a billion dollar fishery. Fish Fish 14:1–18

Samoilys MA (1997) Movement in a large predatory fish: coral trout, *Plectropomus leopardus* (Pisces: Serranidae), on Heron Reef, Australia. Coral Reefs 16:151–158

Sano M (2000) Stability of reef fish assemblages: responses to coral recovery after catastrophic predation by *Acanthaster planci*. Mar Ecol Prog Ser 198:121–130

Sattar SA, Najeeb A, Afzal MS, Islam F, Wood E (2011) Review of the Maldivian grouper fishery and export industry. Darwin Research Project, Marine Research Centre/Marine Conservation Society, UK, p 36

Shanker D, Vinayachandran PN, Unnikrishnan AS, Shetye AR (2001) The monsoon currents in the north Indian Ocean. Prog Oceanogr 52:63–119

Sheppard CRC, Harris A, Sheppard ALS (2008) Archipelago-wide coral recovery patterns since 1998 in the Chagos Archipelago, central Indian Ocean. Mar Ecol Prog Ser 362:109–117

Shibuno T, Nakamura Y, Horinouchi M, Sano M (2008) Habitat use patterns of fishes across the mangrove-seagrass-coral reef seascape at Ishigaki Atoll, southern Japan. Ichthyol Res 55:218–237

Shpigel M, Fishelson L (1989) Food habits and prey selection of three species of groupers from the genus *Cephalopholis* (Serranidae: Teleostei). Environ Biol Fish 24:67–73

Siddiquie HN (1980) The ages of the storm beaches of the Lakshadweep (Laccadives). Mar Geol 38:11–20

Sluka RD (2000) Grouper and napoleon wrasse ecology in Laamu atoll, republic of Maldives: part 1. Habitat, behavior, and movement patterns. Atoll Res Bull 491:1–26

Sluka R, Reichenbach N (1996) The density and diversity of groupers at two sites in the Republic of Maldives. Atoll Res Bull 438:1–16

Southwood TRE (1977) Habitat, the templet for ecological strategies? J Anim Ecol 46:337–365

Spalding MD, Ravilious C, Green EP (2001) World atlas of coral reefs. Univ of California Press, pp 215–217

Syms C (1995) Multi-scale analysis of habitat association in a guild of blennioid fishes. Mar Ecol Prog Ser 125:31–43

Syms C, Jones GP (2000) Disturbance, habitat structure, and the dynamics of a coral-reef fish community. Ecology 81:2714–2729

Tamelander J, Hoon V (2008) The artisanal reef fishery on Agatti Island, Union Territory of Lakshadweep, India. In: Obura D, Tamelander J and Linden O (eds) Ten years after bleaching–facing the consequences of climate change in the Indian Ocean. CORDIO Status Report 2008. CORDIO (Coastal Oceans Research and Development, Indian Ocean)/Sida-SAREC, Mombasa

Unsworth RKF, Powell A, Hukom F, Smith DJ (2007) The ecology of Indo-Pacific grouper (Serranidae) species and the effects of a small scale no take area on grouper assemblage, abundance and size frequency distribution. Mar Biol 152:243–254

Venables WN, Ripley BD (2002) Modern applied statistics with S, 4th edn. Springer, New York

West JM, Salm RV (2003) Resistance and resilience to coral bleaching: Implications for coral reef conservation and management. Conserv Biol 17:956–967

Wilson SK, Graham NAJ, Pratchett MS, Jones GP, Polunin NVC (2006) Multiple disturbances and the global degradation of coral reefs: are reef fishes at risk or resilient? Global Change Biol 12:2220–2234

Wilson SK, Fisher R, Pratchett MS, Graham NAJ, Dulvy NK, Turner RA, Cakacaka A, Polunin NVC, Rushton SP (2008) Exploitation and habitat degradation as agents of change within coral reef fish communities. Global Change Biol 14:2796–2809

Zeileis A, Kleiber C, Jackman S (2008) Regression Models for Count Data in R. Journal of Statistical Software, 27(8). URL http://www.jstatsoft.org/v27/i08/

Zuur AF, Ieno EN, Walker NJ, Saveliev AA, Smith GM (2009) Mixed effects models and extensions in ecology with R. Springer, New York, NY