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Samoilys, Melita; Roche, Ronan; Koldewey, Heather ; Turner, John

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Patterns in reef fish assemblages: insights from the Chagos Archipelago

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Abstract:	Understanding the drivers of variability in the composition of fish assemblages across the Indo-Pacific region is crucial to support coral reef ecosystem resilience. Whilst numerous relationships and feedback mechanisms between the functional roles of coral reef fishes and reef benthic composition have been investigated, certain key groups, such as the herbivores, are widely suggested to maintain reefs in a coral-dominated state. Examining links between fishes and reef benthos is complicated by the interactions between natural processes, disturbance events and anthropogenic impacts, particularly fishing pressure. This study examined fish assemblages and associated benthic variables across five atolls within the Chagos Archipelago, where fishing pressure is largely absent, to better understand these relationships. We found high variability in fish assemblages among atolls and sites across the archipelago, especially for key groups such as a suite of grazer-detritivore surgeonfish, and the parrotfishes which varied in density over 40-fold between sites. Differences in fish assemblages were significantly associated with variable levels of both live and recently dead coral cover and rugosity. We suggest these results reflect differing coral recovery trajectories following coral bleaching events and a strong influence of 'bottom-up' control mechanisms on fish assemblages. Species level analyses revealed that Scarus niger, Acanthurus nigrofuscus and Chlororus strongylocephalos were key species driving differences in fish assemblage structure. Clarifying the trophic roles of herbivorous and detritivorous reef fishes will require species-level studies, which also examine feeding behaviour, to fully understand their contribution in maintaining reef resilience to climate change and fishing impacts.
Order of Authors:	Melita Samoilys
	Ronan Roche
	Heather Koldewey
	John Turner
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CORDIO East Africa

coastal oceans research and development indian ocean

P.O. Box 24562,
Nairobi 00502, Kenya
Mobile : +254 721498713/+447393622355
Email: melita.samoilys@gmail.com
www.cordioea.net

14th November 2017

Dr Heather Patterson
Scientific Editor,
PLOS ONE

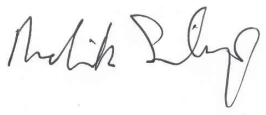
Dear Dr Patterson

Thank you for the second review of our paper: *Patterns in reef fish assemblages: insights from the Chagos Archipelago*.

We have addressed the comments from the two reviewers and your editorial comments in the revised manuscript. In making our revisions we have addressed your concerns that the conclusions of the study are overstated, there is a general lack of clarity in the paper and the points raised can be dealt with in a re-write, particularly in the Discussion. We also provide a response to each comment raised by the reviewers in the two tables appended below.

We trust that the manuscript now meets Plos One's publication criteria.

Yours sincerely



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Patterns in reef fish assemblages: insights from the Chagos Archipelago

Melita Samoilys[1,2] Ronan Roche[3], Heather Koldewey[4,5], John Turner[3]

[1.] CORDIO East Africa, PO Box 24562, Nairobi 00502, Kenya

[2.] Zoology Department, University of Oxford, Oxford OX1 3PS, UK

[3.] School of Ocean Sciences, Bangor University LL59 5AB, UK

[4.] Conservation Programmes, Zoological Society of London, Regents Park, London NW1 4RY, UK

[5.] Centre for Ecology & Conservation, University of Exeter Cornwall Campus, Penryn, Cornwall, TR10 9FE, UK

Abstract

Understanding the drivers of variability in the composition of fish assemblages across the Indo-Pacific region is crucial to support coral reef ecosystem resilience. Whilst numerous relationships and feedback mechanisms between the functional roles of coral reef fishes and reef benthic composition have been investigated, certain key groups, such as the herbivores, are widely suggested to maintain reefs in a coral-dominated state. Examining links between fishes and reef benthos is complicated by the interactions between natural processes, disturbance events and anthropogenic impacts, particularly fishing pressure. This study examined fish assemblages and associated benthic variables across five atolls within the Chagos Archipelago, where fishing pressure is largely absent, to better understand these relationships. We found high variability in fish assemblages among atolls and sites across the archipelago, especially for key groups such as a suite of grazer-

detritivore surgeonfish, and the parrotfishes which varied in density over 40-fold between sites. Differences in fish assemblages were significantly associated with variable levels of both live and recently dead coral cover and rugosity. We suggest these results reflect differing coral recovery trajectories following coral bleaching events and a strong influence of 'bottom-up' control mechanisms on fish assemblages. Species level analyses revealed that *Scarus niger*, *Acanthurus nigrofuscus* and *Chlororus strongylocephalos* were key species driving differences in fish assemblage structure. Clarifying the trophic roles of herbivorous and detritivorous reef fishes will require species-level studies, which also examine feeding behaviour, to fully understand their contribution in maintaining reef resilience to climate change and fishing impacts.

Introduction

Coral reefs are complex and highly biodiverse systems that are subject to a broad range of natural and anthropogenic factors, operating from local to global scales, which drive or impact reef fish population abundance and assemblage structure [1–4]. Reef degradation from fishing pressure and climate-change induced coral bleaching and mortality have been invoked to explain patterns in the structure of coral reef fish assemblages across multiple scales in the Indo-Pacific [5–7]. Other studies point to scale dependence in drivers of fish assemblages with geomorphology and biogeography, for example, playing a significant role at larger regional scales, and fishing and reef benthic structure operating at local scales [8–10]. Understanding the mechanisms by which these drivers interact and their relative contributions to controlling reef fish assemblages is critical in underpinning conservation planning and effective reef fisheries management.

One of the dominant paradigms used to explain impacts from the external stressors of climate change and fishing on coral reefs and their fish assemblages revolves around potential shifts from coral to algal-dominated reef states [11,12]. Herbivorous fishes have been shown to play a leading role in preventing this shift by controlling algal abundance [2,13]. The regulatory pathways involve both resource (bottom-up) and predation (top-down) control of the reef ecosystem. Changes in coral cover represent bottom-up control while top-down control is seen when herbivores are depleted through fishing activities, which can lead to their functional role becoming compromised [4,14]. Coral reef fish assemblages are known to vary in relation to several environmental characteristics such as exposure to oceanic conditions, rugosity, depth, benthic composition and recent coral mortality [8–10,15–18]. Bottom-up control of reef fish populations by reef benthic composition has been well established [10,15,18–20], and long term studies in the Philippines, for example, have shown that this pathway is the primary driver of the herbivorous parrotfishes [21]. Thus, top-down and bottom-up pathways can either dominate or co-occur, depending on the characteristics within the coral reef ecosystem.

From a management perspective, it is important to be able to attribute the relative contribution of casual factors driving the structure of reef fish assemblages. The objective of this study was to determine which of a range of largely biotic factors may be driving the structure of reef fish assemblages in the absence of fishing. Our hypothesis was that without the top-down influence of fishing in the Chagos Archipelago the fish assemblages should reflect the relative contribution of natural drivers, both bottom up (e.g. food availability) and top-down (e.g. predation), of fish populations, and one anthropogenic stressor – coral mortality related to bleaching events. We also sought to describe the characteristic reef fish assemblages of the atolls of the Chagos Archipelago to build on

earlier work that examined fish responses to declines in coral cover caused by the coral bleaching event of 1998 [22] and found little change in reef fish species richness except in corallivores [23]. We also examined the abundance and biomass of reef fishes from the full range of trophic groups to test for relationships between trophic group and reef benthic composition and so examine the functional roles of fish species in reef resilience.

The Chagos Archipelago (British Indian Ocean Territory) is an isolated archipelago of atolls spanning ~60,000 km^2 and 2 degrees of latitude on the north eastern border of the western Indian Ocean Province [24–26], with an area of ~9,400 km^2 of shallow coral reefs (<40m depth) [27]. The islands are uninhabited except for the southern-most atoll, Diego Garcia, which is classified as a Permanent Joint Operating Base of the UK and US governments and hosts a US naval support facility. The archipelago, with the exception of Diego Garcia where a recreational fishery is permitted, was declared a no-take marine protected area (MPA) in 2010 by the UK Government [26]. Indeed, reef fish biomass in the Chagos Archipelago is demonstrably one of the highest of any coral reef ecosystem in the Indo-Pacific [23]. The Chagos Archipelago therefore provides an ideal location for investigating the relationship between fish assemblages and variability in reef benthic habitat and typology, in the absence of impacts from fishing and human populations. Our study assumed that reef fish species distributions did not differ biogeographically across the Chagos Archipelago due to the direction of major current systems in the western Indian Ocean (WIO), and the connectivity of the pelagic larvae of most reef fish [13–16]. We do, however, recognise that self recruitment [32] and local oceanographic dynamics [33] within and among atolls of the archipelago may affect larval recruitment patterns. An earlier study reported that reef fish assemblages were highly homogeneous across the northern atolls [28]. Here we use datasets from a range of atolls in the archipelago, from

the northernmost atolls to Diego Garcia in the south, to examine variation in the abundance and species structure of fish assemblages, and to identify drivers of this variability.

By confining this study to an isolated archipelago of reefs that are relatively unfished and free of pollution and development, this study contributes to a better understanding of intact Indian Ocean reef fish assemblages. As such, it provides a regional context for interpreting coral reef fish assemblages in the wider Indian Ocean where anthropogenic impacts are more prevalent.

Methods

Study sites

We surveyed reef fish assemblages and coral reef benthic assemblages in March 2014 at a total of 13 (fish) and 11 (benthic) sites across 5 atolls in the Chagos Archipelago (decimal minutes: 05.237333 S 71.81498 E to 07.26195 S 72.44333 E, Fig 1, Table S1). Locations included the fully submerged Blenheim Reef atoll, reefs fringing islands on the west side of the Great Chagos Bank (GCB) and the large, well formed Peros Banhos and Salomon atolls. Reef types were defined based on the Andrefoute et al. [34] classification of coral reefs and included forereefs and terraces on the outside of the atolls and pinnacles and inner slopes in the atoll lagoons (Table S1). These were categorised as exposed (outside atolls) or protected (inside lagoons) from oceanic seas. The British Indian Ocean Territory Administration Section of the Foreign and Commonwealth Office, UK Government, granted the research permit to the Darwin Initiative 2014 Expedition to work within

126 the whole Territory. Permission was granted to all authors to visit and dive in the strict
127 nature reserves of the Chagos Archipelago Marine Park.
128
129 **Fig. 1.** Map of the Chagos Archipelago showing atolls surveyed and locations of dive
130 survey sites.
131
132 *Benthic surveys*
133
134 Underwater video transects were recorded using a Sony HDRCX550 camera in a Light
135 and Motion Bluefin housing with Fathom 90 wide angle port and red filter, onto which red
136 lasers with a spacing of 10 cm were mounted to provide scale. Surveys were conducted at
137 each site which ranged in depth from 5–25m. The video aimed for a constant speed (~0.1
138 m s^{-1}), with 10 min within each of four depth zones (25–20 m, 20–15 m, 15–10 m, 10–5
139 m) approximately 1 m above the substrate [32]. Percentage cover of all hard coral and
140 *Acropora* spp. alone, dead coral (defined as recently dead coral skeleton with intact
141 corallite structure), soft coral, crustose coralline algae (CCA), fleshy macroalgae, turf
142 algae, rubble and sand were assessed by randomly selecting 20 video frames from each
143 depth range, and recording what lay beneath 15 randomly selected points per frame, for a
144 total of 300 points per transect, assigned using Coral Point Count software [36]. The
145 rugosity of the reef along each transect was estimated visually using a six point scale
146 following Polunin and Roberts [37], ranging from no vertical structural complexity to
147 highly-developed reefs with large coral colonies, caves and crevasses.
148
149 *Fish surveys*
150

All fish species from 13 pre-selected families that span the full range of trophic groups, from piscivores to detritivores (see Table S2) were counted in 50 x 5 m transects. Two dives were conducted at each site, each approximately 300 m along the reef edge, in which 2–3 transects were run parallel to the reef edge (5–6 replicate transects in total per site). Transects spanned the depth range of the reefs (3m - 26m), with the maximum imposed by dive safety regulations. Fish counts at each site therefore had broad depth ranges, from a minimum of 4m to a maximum of 18m ($\bar{x}$ = 10.2m across 13 sites), depending on the reef profile. This design was used to maximise survey coverage of the fish assemblage on the reef. These corresponded to the dive sites at which the benthic video transects were placed; both methods spanned the same depth range at each site. Siganids (rabbitfishes) were not observed at all and therefore a total of 12 families were counted (Table S2). The density and size classes of species were estimated using standard underwater visual census (UVC) techniques for coral reef fishes [38,39]. The size of all species >5 cm total length (TL) were estimated in 5 cm size classes (e.g. 6–10 cm TL, 11–15 cm TL, 16–20 cm TL etc), to obtain biomass values based on published length–weight relationships [40–42]. Biomass was calculated as a derived variable for the fish assemblage because it is a good indicator of energy flow within the coral reef ecosystem. A fixed size category for the smallest species was used because: simplifying counting procedures across a wide range of species improves accuracy [39,43]; any differences in biomass in these small species between sites will be smaller than the 5 cm size class accuracy used; and to enable these small species to be included in total biomass calculations. Fixed size classes were as follows: i) all Chaetontidae species were assigned a length size class of 6–10 cm, with the exception of *C. xanthocephalos*, *C. lineolatus* and *Heniochus* spp. which were recorded as 11–15 cm; ii) small acanthurids, *Ctenochaetus* spp., *Acanthurus nigrofuscus, A. leucosternon* and *Zebrasoma scopas,* were assigned a length size class of 11–15 cm; iii)

Centropyge spp. (Pomacanthidae) –were assigned a length size class of 6–10 cm. A total of 110 species were identified and assigned to 12 functional trophic groups (piscivores, omnivores, corallivores, invertivores, planktivores, detritivores, grazer-detritivores and 5 herbivore categories, *sensu* Green and Bellwood [44] using a classification system for the WIO [45] (Table S2).

Data Analyses

For analyses, the data were organised into a series of matrices: i) fish species numerical density and biomass (13 sites); ii) fish functional group numerical density and biomass (13 sites); iii) benthic habitat variables (11 sites) that were natural log-transformed and standardised (11 variables).

Fish assemblages

Spatial autocorrelation in fish assemblages across the Chagos Archipelago was tested by implementing a Mantel test using the ade4 package [46] in R [47] on a matrix of geographic distances between sampling sites and a dissimilarity matrix based on fish density computed using the Bray-Curtis index. The Mantel statistic was further calculated within Peros Banhos, GCB and Salomon atolls, to test for a relationship with geographic distance between sites within atolls. Correlations between both numerical density and biomass matrices were tested for significance using 9999 permutations.

In order to visualise variation in the composition of fish assemblages across the archipelago, we used non-metric multidimensional scaling (nMDS) on Bray-Curtis dissimilarity distance measures obtained from fish data matrices of both abundance and

biomass. To determine which of the fish trophic groups were significantly related to the ordination, we carried out random permutation testing using 9999 permutations. To further examine for groupings within the fish assemblage data, a Ward cluster analysis based on Euclidean distances was performed on hellinger-transformed data, using similarity profile analysis (SIMPROF) to test the significance of clustered groups [48].

Relationships between datasets

We tested for autocorrelation within benthic variables and identified variables that were correlated at $r \geq 0.7$. Three variables (calcareous substrate, sand/rubble, and other benthic) were removed from further analysis and no remaining pairwise correlations between variables greater than $r = 0.53$ were found. The remaining 8 variables were further tested by a variance inflation factor (VIF) analysis which found that each of the retained environmental variables resulted in a VIF of <10.

The Adonis function within the Vegan package [49] was used to examine for significant relationships between categorical variables (atoll, reef type and exposure) and the fish assemblages surveyed, also using permutation testing set at 9999 permutations. We used the envfit function within the Vegan package to estimate the direction and strengths of the correlation between the nMDS of fish species and the reef benthic variables surveyed. Finally, we used a variation of the BIO-ENV [50] routine, termed BIO-BIO, to identify the subset of fish species which best correlated to the overall biological pattern of the dissimilarity matrix, using both numerical density and biomass data. They produced similar results, thus density alone was presented.

Results

A total of 110 fish species from the 12 families were recorded across the Chagos Archipelago. The matrices of mean species density and biomass are provided in Tables S3 and S4, respectively. Multivariate ANOVA (Adonis) permutation results found significant differences in the fish species matrices between atolls for both density and biomass datasets ($F_{4,12} = 2.068$, $P = 0.002$; $F_{4,12} = 1.760$, $P = 0.010$) and between three reef types (forereef; terrace & forereef; lagoons (2 types combined), Table S1) for fish biomass ($F_{2,12} = 1.673$, $P = 0.035$). With a limited number of sites, these differences between reef types could not be tested further. There were no significant differences found in species' density or biomass between sites classified as exposed (outer reefs) or protected (lagoon) sites ($P>0.05$).

Mantel tests indicated that dissimilarity in the fish assemblages using species density data was strongly related to geographic distance across the archipelago (Monte Carlo observation = 0.512; $P = 0.002$). However, within Peros Banhos, Salomon and GCB atolls there was no significant relationship between geographic distance between sites and the fish assemblages present (Peros Banhos: Monte Carlo Observation = -0.317, $P = 0.499$; Salomon: Monte Carlo Observation = -0.718, $P = 0.835$; GCB, Monte Carlo Observation = -0.224, $P = 0.497$).

Ordination of species density data across the archipelago revealed three dissimilar groups corresponding to the atolls of Peros Banhos, Salomon and reefs of the GCB (Fig. 2a). Fish assemblages at GCB separated most strongly from other atolls, while Peros Banhos and Salomon were more similar. These differences in fish assemblages were further verified

by the Ward cluster analysis (Fig. 2b), which showed four significant clusters (>60% dissimilarity) though one cluster (cluster 3) comprised of a single site – Diego Garcia Atoll's terrace and forereef, which differed from all other sites (>1.0 dissimilarity). This Euclidian analysis provides a more detailed examination of dissimilarity in the fish assemblages across sites: cluster 1 was most dissimilar from all other sites and consisted of northern sites at Blenheim and Salomon Atoll forereefs; cluster 2 contained all lagoon sites, 3 from Peros Banhos but also 1 site from each of Salomon and Diego Garcia; whilst cluster 4 consisted of two sub-groups, Eagle and Egmont forereefs at GCB and Three Brothers forereef (GCB) and two Peros Banhos sites (a forereef and a lagoon pinnacle). Total fish density and biomass also showed broad-scale differences across the archipelago with the highest densities recorded on reefs at GCB, the highest biomass recorded at Peros Banhos Atoll and the lowest biomass at Diego Garcia Atoll (Fig. 3).

Fig. 2. Spatial variation in reef fish species assemblages across the 13 sites in the Chagos Archipelago: a) non-metric multidimensional scaling plot, coloured ellipses show 95% confidence intervals of site grouping; b) Ward cluster analysis, colours in dendrogram highlight the four significantly different groups found (<0.6 dissimilarity).

Fig. 3. Total fish a) density (number of individuals per hectare) and b) biomass (kg per hectare) by atoll, based on 12 reef-associated families surveyed at 13 sites. Error bars are standard errors.

When fish species were categorised into the 12 trophic groups, permutation tests showed only 3 trophic groups were significant in explaining the pattern in the species assemblages: grazer-detritivores and corallivores for fish density and grazer-detritivores

and planktivores for fish biomass (Table 1, Fig. 4). These three trophic groups all significantly explained fish density differences when the permutation test was stratified by atoll (Table 1). Grazer-detritivores comprise a group of acanthurids and the angelfishes *Centropye* spp. (Table S2). Acanthurid species in this trophic group, such as *Acanthurus tennenti* and *A. xanthopterus*, typically feed on sand and hard surfaces to extract detritus and microbes, as well as epilithic algae. The densities and biomass of these grazer-detritivores were nearly three times greater at GCB and Diego Garcia compared to the other atolls (Fig. 4), representing the largest difference in the fish assemblages across the archipelago. The corallivores consisted of six obligate coral feeding butterflyfishes out of the 18 Chaetodontidae observed in the Chagos Archipelago and were more abundant at Peros Banhos and Salomon atolls, compared to other reefs (Fig. 4). When biomass was considered, the planktivores, comprised of balistid, acanthurid and chaetodontid species, differed significantly between the atolls with biomass at GCB three times higher than any of the other reef sites (Table 1, Fig. 4).

Table 1. Random permutation results of 12 fish trophic groups showing only those significantly related to differences: a) across all sites and; b) stratified by atoll.

Density			**Biomass**		
a) All sites					
Trophic group	r^2	*p*-value	Trophic group	r^2	*p*-value
Grazer-detritivores	0.769	<0.001	Grazer-detritivores	0.792	<0.001
Corallivores	0.598	0.009	Planktivores	0.515	0.026
b) Stratified by atoll					
Grazer-detritivores	0.769	0.006	Grazer-detritivores	0.641	0.016
Planktivores	0.268	0.030	Planktivores	0.515	0.034
Corallivores	0.598	0.048			

Fig. 4. Mean density (number of individuals per hectare) and biomass kg per hectare) by atoll for the three functional trophic groups that were significantly related to fish assemblage differences. Error bars are standard errors. Functional trophic groups are explained in Table S2.

Benthic reef characteristics and fish assemblages

The benthic cover at reef sites was highly variable among the atolls of the archipelago. Total live coral cover ranged from 15.7% (±1.6 SD) to 47.2 % (±24.1 SD), *Acropora* spp. coral cover from 1.1 (±1.4 SD), to 28.1% (±12.4 SD), and dead standing coral from 5.9% (±3.1 SD) to 26.4% (±13.1 SD). Non-metric multi-dimensional scaling of the relative contribution of the eight benthic variables to the differences between fish assemblages across the archipelago showed that reef sites grouped along two main axes (Fig. 5): the Y axis with high macro-algae such as GCB reefs, versus sites with higher soft coral (Diego Garcia); and the X axis with sites with high hard coral, dead coral, live *Acropora*, rugosity and turf algae, at Salomon Atoll and Perhos Banhos, versus reefs at GCB with higher CCA. GCB reefs had the lowest levels of hard coral, ranging from 15.7% (±5.6 SD) to 28.7% (±17.7 SD). However, hard coral and dead coral (i.e. structural components) were the only benthic categories that were significantly related to differences in fish assemblage structure when analysed with fish density data; when tested with fish biomass data, rugosity also became significant (Table 2). When the permutation analysis was stratified by atoll, hard coral and dead coral were no longer significant; instead soft coral showed a significant correlation with fish density and CCA with fish biomass (Table 2). These results corroborate the geographic differences in fish assemblages between different atolls,

driven by hard and dead coral cover, whereas within atolls only CCA and soft coral were significantly correlated with the fish species data matrices.

Fig. 5. nMDS diagram showing the relationship between benthic variables at 11 reef sites overlaid on the fish assemblage ordination (see Fig. 2) across the Chagos Archipelago. The relative contribution of each benthic variable is displayed by the length of the vector.

Table 2. Significant permutation correlations between benthos and the fish species matrix, for density and biomass at a) all sites and b) stratified by atoll.

Density			**Biomass**		
a) All sites					
Benthic Group	r^2	*p*-value	Benthic group	r^2	*p*-value
Hard Coral	0.63	0.021	Hard Coral	0.7	0.001
Dead Coral	0.66	0.013	Dead Coral	0.7	0.001
			Rugosity	0.55	0.034
b) Stratified by atoll					
Soft Coral	0.38	0.004	Crustose Corraline Algae	0.310	0.042

Fish species

A species-level ordination (BIOBIO) of the density of the 110 fish species which determined which species were most correlated with differences in the fish assemblages across all reef sites showed that 13 species best explained (rho=0.832) the fish assemblages across the sites: *Acanthurus lineatus, A. nigrofuscus, Zebrasoma desjardinii* (grazers), *Cetoscarus ocellatus, Chlorurus strongylocephalus B* (large excavators), *Hemitaurichthys zoster, Paracanthurus hepatus* (planktivores), *Lutjanus bohar*

(piscivore), *Lutjanus fulvus*, *Lutjanus gibbus*, *Lutjanus kasmira*, *Lethrinus enigmatus* (omnivores), *Scarus niger* (scraper), *Sufflamen* spp. (invertivore) (Table 3, Table S2, Fig. 6). Note that none of these species were from the significant trophic groups detected in the permutation tests except for *Paracanthurus hepatus*. When the ordination was restricted sequentially, it showed that *Scarus niger* alone was highly correlated (rho=0.569) with species assemblage differences. Further, a combination of only 6 species achieved a very high correlation (rho=0.802) with species assemblage differences. Although the 13 species illustrated in Fig. 6 are the best fit, other species consistently appeared in highly correlated subsets (Table 3), and therefore were likely to drive differences between fish assemblages across the archipelago. These included *Acanthurus thompsoni (*planktivore), *A. tennenti*, *A. xanthopterus* (grazer-detritivores), *Scarus frenatus* (scraper), the invertivores *Chaetodon madagascariensis* and *Sufflamen* spp. and *Lethrinus microdon* (omnivore).

Fig. 6. The relationship between individual species and the fish species density ordination based on the 13 fish survey sites.

Table 3. Species strongly correlated with differences in density of fish species assemblages across the Chagos Archipelago, based on a species level ordination (BIO-BIO) of 110 species.

Number of Species in subset	Fish Species	Spearman's Rank Correlation (rho)
1	*Scarus niger*	0.569
2	*Acanthurus thompsoni, Scarus niger*	0.715
3	*Acanthurus tennenti, Acanthurus thompsoni, Scarus niger*	0.762
4	*Acanthurus thompsoni, Naso hexacanthus S, Scarus niger, S.russelli*	0.767
5	*Acanthurus leucosternon, Cephalopholis sexmaculata, Lethrinus obsoletus, Scarus niger, Scarus psittacus*	0.783
6	*Acanthurus thompsoni, Chaetodon madagascariensis, Lethrinus obsoletus, Scarus niger, Sufflamen spp., Zebrasoma desjardinii*	0.802

7	*Acanthurus thompsoni, Chaetodon madagascariensis, Lethrinus obsoletus, N. hexacanthus S, Scarus niger, Sufflamen spp., Zebrasoma desjardinii*	0.815
8	*Acanthurus tennenti, Acanthurus xanthopterus, Chaetodon madagascariensis, Lutjanus bohar, Scarus frenatus, Scarus niger, Sufflamen spp., Zebrasoma desjardinii*	0.813
9	*Acanthurus tennenti, Acanthurus xanthopterus, Chaetodon madagascariensis, Lutjanus bohar, Lethrinus microdon, Scarus frenatus, Scarus niger, Sufflamen spp., Zebrasoma desjardinii*	0.818
10	*Acanthurus tennenti, Acanthurus xanthopterus, Canthigaster bennetti, Chaetodon madagascariensis, Lutjanus bohar, Lethrinus microdon, Scarus frenatus, Scarus niger, Sufflamen sp., Zebrasoma desjardinii*	0.821
11	*Acanthurus tennenti, Acanthurus xanthopterus, Canthigaster bennetti, Chaetodon madagascariensis, Lutjanus bohar, Lethrinus microdon, Odonus niger, Scarus frenatus, Scarus niger, Sufflamen spp., Zebrasoma desjardinii*	0.823
12	*Acanthurus tennenti, Acanthurus xanthopterus, Canthigaster bennetti, Chaetodon madagascariensis, Lutjanus bohar, Lethrinus microdon, Odonus niger, Paracanthurus hepatus, Scarus frenatus, Scarus niger, Sufflamen spp., Zebrasoma desjardinii*	0.820
13	*Acanthurus lineatus, Acanthurus nigrofuscus, Cetoscarus ocellatus, Chlorurus strongylocephalus B, Hemitaurichthys zoster, Lutjanus bohar, Lutjanus fulvus, Lutjanus gibbus, Lutjanus kasmira, Lethrinus enigmatus, Paracanthurus hepatus, Scarus niger, Zebrasoma desjardinii*	0.831
14	*Acanthurus lineatus, Acanthurus nigrofuscus, Cetoscarus ocellatus, Chlorurus strongylocephalus B, Chaetodon striatus, Hemitaurichthys zoster, Lutjanus bohar, Lutjanus fulvus, Lutjanus gibbus, Lutjanus kasmira, Lethrinus enigmatus, Paracanthurus hepatus, Scarus niger, Zebrasoma desjardinii*	0.824

Three broad types of fish assemblages in the Chagos Archipelago are suggested through a combination of highly significant species within the ordination (Fig. 6), significant benthic associations (Fig. 5) and clustering of fish species (Fig. 2b). These can be defined as those aligned with: 1) higher hard coral cover (27–43%), or recently dead coral; 2) high rugosity and *Acropora* cover; and 3) higher soft coral, CCA, and macro-algal cover but low cover of live hard coral (12–22%; Table 4). The former (groups 1 and 2, Table 4) were found across Salomon and Peros Banhos atolls, whereas the latter (group 3, Table 4) was largely at GCB. It is noteworthy that two of the largest excavating parrotfishes, *Cetoscarus ocellatus* and *Chlorurus strongylocephalos* (B), showed opposing patterns of correlation

(Fig. 6). *Cetoscarus ocellatus* was also closely associated with *Scarus niger* on certain reefs in Salomon and Peros Banhos and both these species characterise group 1 and 2 assemblage types (Table 4). Fish assemblages at Diego Garcia Atoll forereef site were significantly different and may represent a fourth assemblage type, but there were too few survey sites to assess this. Note that 3 species were rare, present only at 1 reef (*A. lineatus*, *Lethrinus enigmatus* and *Lutjanus fulvus*, Table 4, Table S3).

Table 4. Synthesis of results from Figures 2b, 5 and 6 and Tables S3 and S4, to define three broad types of fish assemblages across the Chagos Archipelago, the sites at which they were found and the corresponding reef benthic characteristics. Species and benthos listed are the highest abundance/cover and were significant within analyses. *= rare species seen only at 1 reef. Diego Garcia Atoll forereef was an outlier and is not included.

No.	Fish Species	Reefs	Benthos
1			
	Scarus niger (Scraper)	**Salomon**	Hard coral
	Acanthurus nigrofuscus (Grazer)	- terrace & forereef	*Acropora*
	Hemitaurichthys zoster (Planktivore)	(2 sites)	Soft coral
	Cetoscarus ocellatus (Excavator)	**Blenheim**	Rugosity
2			
	Scarus niger (Scraper)	**Peros Banhos**	Dead coral
	Lutjanus kasmira (Omnivore)	- lagoon (2 sites)	Rugosity
	Cetoscarus ocellatus (Excavator)	**Salomon**	Turf algae
	*A. lineatus** (Grazer)	- lagoon	Hard coral
	L. gibbus (Omnivore)	**Diego Garcia**	*Acropora*
	Z. desjardinii (Grazer)	- lagoon	
3			
	Chlor. strongylocephalos (Excavator)	**GCB**	Soft coral
	Paracanthurus hepatus (Planktivore)	- forereefs	CCA
	*Lethrinus enigmatus** (Omnivore)	**Peros Banhos**	Macro-algae
	Lutjanus bohar (Piscivore)	- forereef	
	*Lutjanus fulvus** (Omnivore)	- lagoon	

Species of conservation and fisheries interest

The widespread Indo-Pacific coral trout grouper *Plectropomus laevis* was abundant and observed at all but 3 sites, with a mean density and biomass of 17.85 ± 1.54 SD individuals/ha and 104.8 ± 170.5 SD kg/ha, including several very large individuals (91–110 cm TL), close to maximum size for this species. *Plectropomus punctatus*, the coral trout grouper endemic to the Indian Ocean was never observed, yet it was recorded from the Chagos Archipelago in the 1990s by Winterbottom and Anderson [51]. No siganids were observed during the current survey, though *Siganus argenteus* and *S. canaliculatus* are known from the archipelago [51]. The abundance of the larger species of grouper such as *Epinephelus fuscoguttatus*, *E. malabaricus*, *E. multinotatus* and *E. tauvina* was extremely low, ranging from a mean of 0.0–0.77 $\pm$1.54 SD fish/ha.

Discussion

Large regional-scale [7,52] or long temporal-scale analyses [2] in the Indian Ocean and across the Indo-Pacific [6] have shown that fishing and climate change are primary drivers of fish assemblage structure. We found significant differences in fish assemblage structure among the atolls of the Chagos Archipelago which we attribute to natural environmental drivers and climate change, as reflected in the significant correlations between fish assemblages and reef benthic composition. However, temporal changes before and after coral bleaching events remain unknown; future work on this would greatly enhance

410 interpretation of the results of the current study. We can, however, assume that fishing
411 effects are minimal due to the lack of resident human populations on any of the atolls
412 since the 1960s (with the exception of Diego Garcia) and because of the establishment of a
413 no-take MPA in 2010. Indeed, the Chagos Archipelago is used as a benchmark for largely
414 unfished reefs in the Indian Ocean [6,23]. Further, our study assumed that reef fish species
415 distributions did not differ biogeographically because of the relatively small geographic
416 range of the Chagos Archipelago fed by the easterly flowing East African Coastal Current
417 and South Equatorial Countercurrent, both emanating from the east African mainland
418 [29], and the connectivity of the pelagic larvae of most reef fishes [30,31]. Of the 110
419 species in the dataset, there was no apparent disjunct in their distribution between the
420 northern atolls (Peros Banhos, Salomon and Blenheim) and the southern atolls (GCB and
421 Diego Garcia) except for *Acanthurus tristis*, *Chaetodon madagascariensis* and *Chlorurus*
422 *capistratoides*, which were only found in the south, and *Chaetodon lunula* which was only
423 found in the north. Of these, only *C. madagascariensis* was a significant species in the
424 ordination analysis.
425
426 *Patterns in fish species and benthic communities*
427
428 Differences in fish assemblages were significantly correlated with geographic distance
429 between sites; the relative density of the 110 fish species across the archipelago differed
430 most significantly between atolls. These atoll-scale differences were also apparent in total
431 density and biomass values (12 families), with the highest fish densities recorded on the
432 reefs of the western edge of the GCB, the highest fish biomass recorded at Peros Banhos
433 Atoll and the lowest fish biomass at Diego Garcia Atoll. Reef benthic composition also
434 varied between atolls, most notably in the relative cover of live hard coral, recently dead

standing coral and rugosity, and permutation testing showed that these differences were significantly related to fish density (hard and dead standing coral) and fish biomass (hard coral, dead standing coral, rugosity). These results are not surprising since strong positive correlations between fish density or biomass and live hard coral and rugosity, benthic variables that co-vary and reflect reef habitat structural complexity, are widely reported [15,16,53–56]. Therefore, patterns in the fish assemblages reported here likely reflect bottom-up control.

A major alteration in the benthic composition of coral reefs across the Indian Ocean occurred following the severe coral bleaching event of 1998 [57]. This thermal anomaly resulted in a reduction of living coral cover in the Chagos Archipelago from 50–75% cover prior to the event to ~10% live coral remaining on all six atolls in 1999 [22]. However, a majority of reef sites across the archipelago recovered rapidly and reached pre-bleaching condition by 2010 [26]. The strong benthic differences between atolls observed in our surveys in 2014 possibly reflect different levels of bleaching and differing recovery patterns following the 1998 event, though with little historic data this remains unknown. However, early reports of highly homogenous fish assemblages across reefs in the northern atolls prior to 1998 [28] suggest that the differences in the structure of the fish assemblages found in 2014 are recent and may therefore, be due to differing recovery patterns.

Fishing effects

This study was not designed to look at fishing effects because it was based on the premise that there is no reef fishing in Chagos Archipelago, however, there was a small Mauritian

460 fishery targeting grouper (Epinephelidae) and snapper (Lutjanidae), which operated from
461 the 1970s until 2010 when the Chagos MPA was designated [23]. Populations of
462 piscivore and omnivore trophic categories were similar between atolls, exemplified by the
463 coral trout grouper *Plectropomus laevis*, which was abundant and observed at all but three
464 sites. However, two snappers *Lutjanus bohar* (piscivore) and *Lutjanus gibbus* (omnivore)
465 were significantly correlated with differences in fish assemblages across atolls. The
466 highest biomass of these two species was found in Peros Banhos lagoon sites (up to 861
467 kg/ha and 530 kg/ha, for *L. bohar* and *L. gibbus*, respectively). Apparently the fishery did
468 not operate in the lagoons (BIOT Fisheries Officer, pers. comm. 2014), but since our study
469 is the first to report on fish biomass in the lagoons there are no previous comparable data.
470 For *L. bohar* moderate biomass levels were found on forereefs at Salomon, Peros Banhos
471 and Blenheim, but were lower at Diego Garcia and GCB, while biomass of *L. gibbus* was
472 highly variable across all forereefs. Our surveys also suggest that three large species of
473 grouper, *Epinephelus fuscoguttatus, E. multinotatus* and *E. tauvina* may have been
474 overfished since their populations were extremely depleted across all sites. While there is
475 also some illegal fishing in BIOT, 80% by weight of illegal catches detected by the BIOT
476 patrol vessel is shark [58], therefore this poaching can be considered minimal in terms of
477 impacts on reef fishes. Our results are inconclusive and suggest that further research is
478 needed to distinguish between possible latent fishing effects or natural biotic/abiotic
479 drivers of some grouper and *Lutjanus bohar*.
480
481 A recreational fishery operates outside the MPA at the naval base in Diego Garcia and is
482 having an impact on fish biomass [23]. Our total biomass estimates with maximum values
483 of ~3,500 kg/ha (12 families) do not include sharks and trevally and therefore cannot be
484 directly compared with the estimates of >9,000 kg/ha reported from 2010–2012. However,

485 comparing relative biomass between atolls from the 2010–2012 survey [23] with our
486 survey in 2014 shows similar differences, with highest values at Peros Banhos, followed
487 by GCB, then Salomon, and the lowest values at Diego Garcia. This supports Graham et
488 al.'s [23] conclusions that the recreational fishery is having an impact. Nevertheless, we
489 measured extremely high biomass values at 10 of the 13 sites (1,501-3,000 kg/ha at six
490 sites, and > 3,000 kg/ha at four sites). These are similar, when the same families are
491 considered, to biomass at other uninhabited and protected reefs of the French territories in
492 the Mozambique Channel [59], providing strong support for using Chagos Archipelago as
493 a reference benchmark for unfished reef fish populations in the western Indian Ocean.
494
495 *Trophic dynamics in the reef fish assemblages*
496
497 Herbivory and detritivory contribute significantly to the trophic dynamics and hence
498 biomass production on coral reefs [60,61]. Indeed, the diversity of herbivores and
499 detritivores seen on modern reefs, illustrated by the parrotfishes (Labridae: Scarinae) and
500 surgeonfishes (Acanthuridae), has been linked to the massive expansion of shallow coral
501 reef habitats over the last 5 million years [62]. In the Chagos Archipelago, the grazer-
502 detritivores was the trophic group that differed most significantly between atolls. This
503 group comprises a suite of acanthurids ("ring-tail" surgeonfishes [44]), such as
504 *Acanthurus tennenti* and *A. xanthopterus,* that harvest mouthfuls of soft sediment on dead
505 coral substrate, as well as on sand, which contain the diatoms and microbes of their diet
506 [63,64]. Their highest densities at GCB and Diego Garcia (>500 and >600 individuals/ha,
507 respectively) corresponded with low hard coral cover. In contrast, low numbers of these
508 surgeonfishes were seen at Peros Banhos, Salomon and Blenheim (<130, <14, <170
509 individuals/ha, respectively), where hard coral cover was high. These results suggest that

these “grazer-detritivore” surgeonfish species may thrive where their benthic food sources have increased due to coral mortality [65] and can therefore serve as important indicators of reef degradation. The prevalence of the detritivory role is also supported by one of the most common reef fishes in the world, the bristletooth surgeonfishes *Ctenochaetus* spp. [66], with the combined density of two species *Ctenochaetus truncatus* and *C. striatus* at ~850 individuals/ha being the second highest (*Caesio* spp. density was the highest: 936 individuals/ha) of all the 110 species surveyed. We propose that the importance of detritivory in recovery of degraded reefs and in cycling carbon within coral reef systems is not well quantified and therefore an important area for future research.

A strong relationship between hard coral cover and corallivores has been widely reported [23,56,67] and was confirmed here with significantly higher densities of obligate coral-feeding butterflyfishes at Peros Banhos and Salomon atolls where there was relatively higher live coral cover. These coral specialists are clearly highly vulnerable to coral mortality and, as such, have long been used as potential indicator species for monitoring coral reef health [68]. The third trophic group that differed significantly between atolls was the planktivores, comprising several acanthurids (three *Naso* spp., *Acanthurus thompsoni* and *Paracanthurus hepatus)*, two chaetodontids, two balistids and *Caesio* spp. The biomass of this group was three times higher at GCB, with a mean biomass of 1,045 kg/ha, compared to 338kg/ha for other atolls, and this was largely due to the caesionids and *Naso hexacanthus* and *N. brevirostris*. Further, three planktivores were strongly correlated with the ordination: *Paracanthurus hepatus, Acanthurus thompsoni* and the chaetodon *Hemitaurichthys zoster*. Drivers of planktivore populations on coral reefs are still poorly understood, but their food items are associated with reef edges and proximity to deep water [69]. These acanthurid species are all zooplanktivores [70], suggesting

waters at GCB may be zooplankton-rich. Thus, higher Acanthuridae densities overall at GCB reefs appear to reflect two different and unrelated trophic pathways: increased access to soft benthic surfaces due to coral mortality for the grazer-detritivores and higher zooplankton densities for planktivores. Finally, it was notable that the density and biomass of the piscivore and omnivore trophic groups, species that represent important target fishery species [23,39], were not significantly correlated with fish assemblage patterns across the archipelago, suggesting that benthic differences did not directly affect these higher trophic level taxa. Thus, when data were aggregated by trophic group, only three groups differed significantly and these appeared to be influenced by reduced coral cover due to climate change [22] and natural variability in zooplankton, both bottom-up control pathways.

It was surprising that none of the five herbivore trophic groups, which include all the parrotfishes, were significant in explaining differences in fish assemblages between sites. We found species-level analyses were more informative than aggregated trophic group analyses and demonstrated species from within seven trophic groups were highly related to differences in the fish assemblages across the reefs of the Chagos Archipelago. *Scarus niger* had the strongest correlation with fish assemblage structure across the archipelago, with highest biomass on the high coral cover northern atolls (182 kg/ha at Peros Banhos), and the lowest at Diego Garcia and the low coral cover reefs of GCB (3 kg/ha and 11–27 kg/ha, respectively). This species is one of the most ubiquitous parrotfishes across the Indo-Pacific [71,72] and feeds on the top 1–2 mm of dead coral substrate [62,73], though it probably removes epilithic algae while feeding. *Scarus niger* was associated with the highly abundant surgeonfish *Acanthurus nigrofuscus*, known to graze similar substrate types but feeding on epilithic algae [63,64]. These two species correlated most closely

560 with the assemblages at Salomon Atoll sites, particularly on the outer forereefs where live
561 hard coral, *Acropora* and rugosity were highest, but also at the Peros Banhos lagoon sites
562 where turf algae and dead coral were relatively high. This result may reflect "feeding
563 complimentarity" by a parrotfish and a surgeonfish, accessing different algal prey within
564 the same benthic substrate [74]. It also illustrates the challenges in using trophic
565 categories as a proxy for ecological function. Herbivorous fishes have been implicated in
566 the top-down control of reef benthos, as their grazing of recently dead coral substrate
567 prevents the rapid colonisation of macroalgae. Further, over-fishing of herbivores has been
568 invoked to explain declines in coral cover and they are consequently considered to play a
569 key functional role in maintaining coral reef resilience [4,11,12,75–77]. Parrotfishes
570 (Labridae; Scarinae) are a significant component of this herbivorous fish community on
571 account of their size, numerical abundance and hence biomass [14]. They are also targeted
572 in many reef fisheries and are frequently used as indicators for the condition or resilience
573 of reefs [14,39,44,61,78]. However, recent work on the intricacies of parrotfish feeding
574 modes and diets [14,62,73] indicates that assigning species with similar feeding modes
575 into broad trophic groups may over-simplify their functional role in reef resilience.
576 Further, we show that parrotfish population densities can vary by up to 43-fold between
577 reef sites in the absence of fishing and so caution against assumptions that declines in
578 parrotfish populations are necessarily due to fishing.
579
580 The largest parrotfishes, *Cetoscarus ocellatus* and *Chlororus strongylocephalos*, showed
581 completely opposing patterns in their distribution with *Cetoscarus ocellatus* closely
582 associated with healthy reefs with high coral cover at the northern atolls (Peros Banhos
583 and Salomon). In contrast, *Chlorurus strongylocephalos* was strongly correlated with reefs
584 at GCB which had the lowest live coral and the highest cover of calcareous algae, soft

585 coral and macroalgae. This opposing pattern in the distribution of these two high-biomass
586 parrotfish, functionally termed “excavators” [14,44,65], can be explained by their feeding
587 behaviour. *Cetoscarus ocellatus* are territorial, non-schooling, harvest small areas of reef
588 and are associated with reefs of high live coral cover (M. Samoilys, pers. obs.). In
589 contrast, *Chlorurus strongylocephalos* prefers disturbed reefs which offer a larger benthic
590 surface area for excavating the dead coral reef matrix [73]. They feed on these substrates,
591 typically in large schools if the disturbed substrate is of sufficient area (H. Choat, James
592 Cook University, pers. comm. 2016). The Indian Ocean endemic, *Chlorurus*
593 *enneacanthus*, was observed to have a similar feeding strategy to *Chlorurus*
594 *strongylocephalos* (M. Samoilys pers. obs.). These *Chlorurus* species conform to reports
595 from the Philippines where some parrotfish species prefer areas of reef that have become
596 damaged, for example from cyclones [21]. The patterns seen here suggest bottom-up
597 control of parrotfish populations by coral cover in positive (e.g. *S. niger*, *C. ocellatus*) or
598 negative (e.g. *C. strongylocephalos*) relationships. These pathways therefore need to be
599 considered when examining the role of parrotfishes in influencing coral recovery
600 trajectories.
601
602 *Conclusions*
603 The isolated Chagos Archipelago provides a valuable ecological benchmark for
604 understanding the structure of reef fish assemblages when fishing impacts are minimal.
605 Differences in fish assemblages across the archipelago were associated with variation in
606 reef benthic condition, which suggested a bottom-up response of fish populations to
607 changes in coral cover. Our results support the concept that herbivory and detrivory are
608 significant functions provided by reef fishes [60–62], but we propose that separating diet
609 from the structural impact of these feeding modes will improve our understanding of their

functional role in reef resilience. The large variation in parrotfish abundance found in the Chagos Archipelago supports studies (e.g. Russ et al. [21]) that caution against assumptions elsewhere that parrotfish population abundances are largely driven by fishing. We found surgeonfish species that graze epilithic algae and parrotfish species that exploit bare substrate to access nutrients within the calcareous matrix [63,64,73] are two key taxa responsible for differences in fish assemblages among the atolls. Both may function to keep macro-algal levels down, but the drivers of their populations are different. Parrotfishes have evolved highly successful traits to exploit food sources on reefs and contribute significant biomass on coral reefs [14, 62], including during declines in coral cover [21,65] and some species are impacted negatively by fishing [65]. Clarifying these trophic dynamics is vital to refine functional trait approaches for understanding the impacts of climate change and fishing on coral reef biodiversity.

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635

636 **Figure Captions**

637 **Fig. 1.** Map of the Chagos Archipelago showing atolls surveyed and locations of dive
638 survey sites.

639 **Fig. 2.** Spatial variation in reef fish species assemblages across the 13 sites in the Chagos
640 Archipelago: a) non-metric multidimensional scaling plot, coloured ellipses show 95%
641 confidence intervals of site grouping; b) Ward cluster analysis, colours in dendrogram
642 highlight the four significantly different groups found (<0.6 dissimilarity).

643 **Fig. 3.** Total fish a) density (number of individuals per hectare) and b) biomass (kg per
644 hectare) by atoll, based on 12 reef-associated families surveyed at 13 sites. Error bars are
645 standard errors.

646 **Fig. 4**. Mean density (number of individuals per hectare) and biomass kg per hectare) by
647 atoll for the three functional trophic groups that were significantly related to fish
648 assemblage differences. Error bars are standard errors. Functional trophic groups are
649 explained in Table S2.

650 **Fig. 5.** nMDS diagram showing the relationship between benthic variables at 11 reef sites
651 overlaid on the fish assemblage ordination (see Fig. 2) across the Chagos Archipelago.
652 The relative contribution of each benthic variable is displayed by the length of the vector.

653 **Fig. 6.** The relationship between individual species and the fish species density ordination
654 based on the 13 fish survey sites.

655

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Fig1

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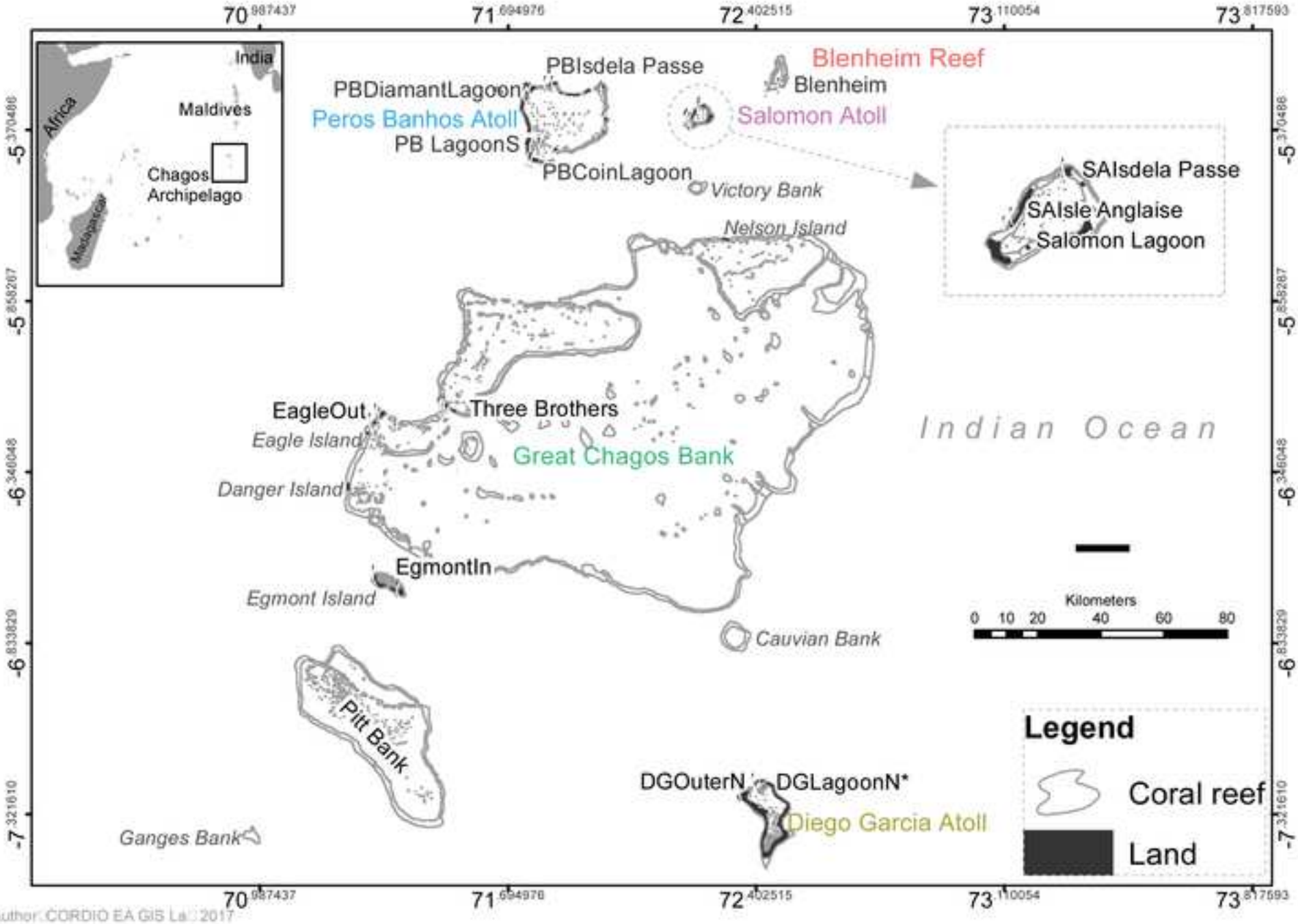

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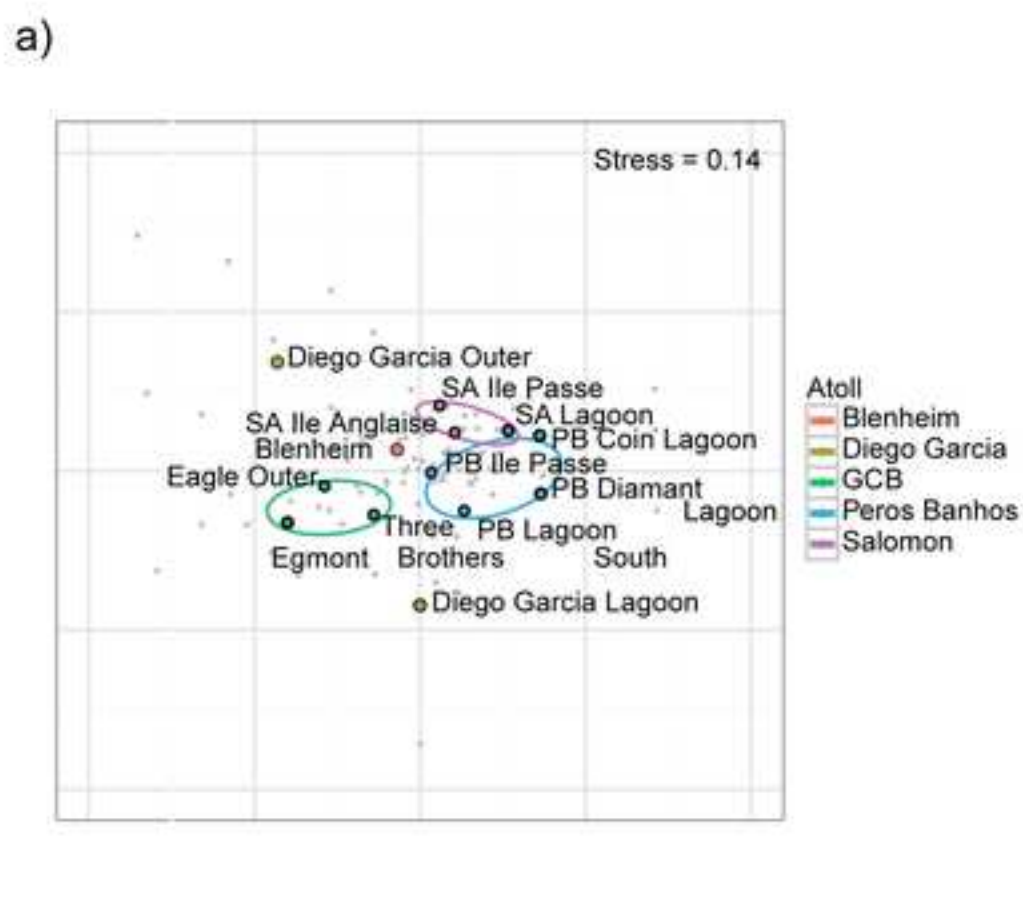

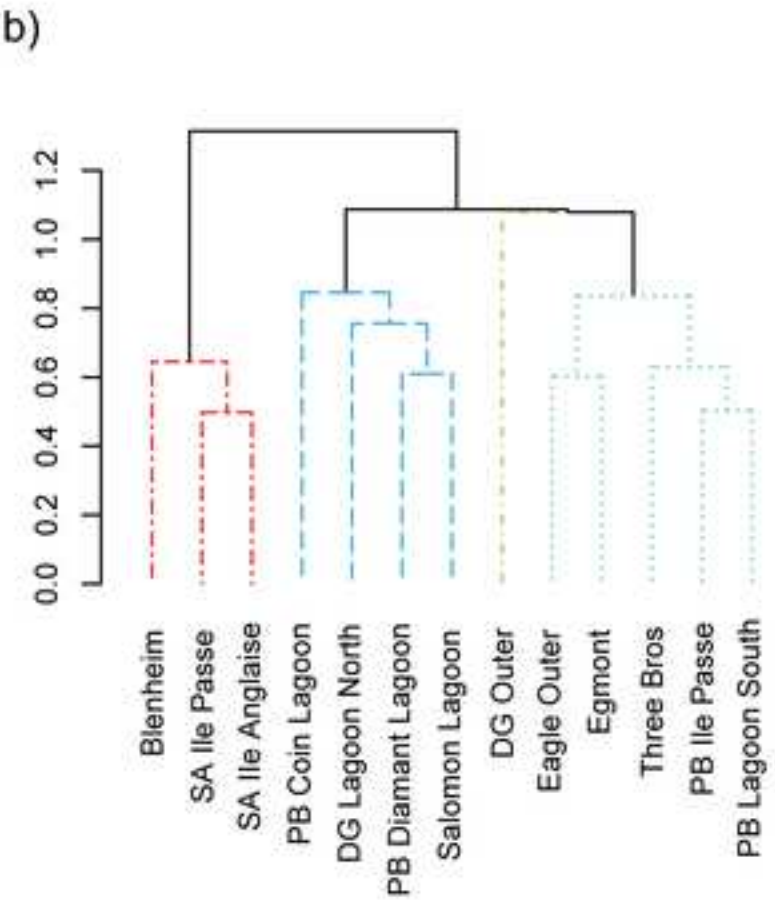

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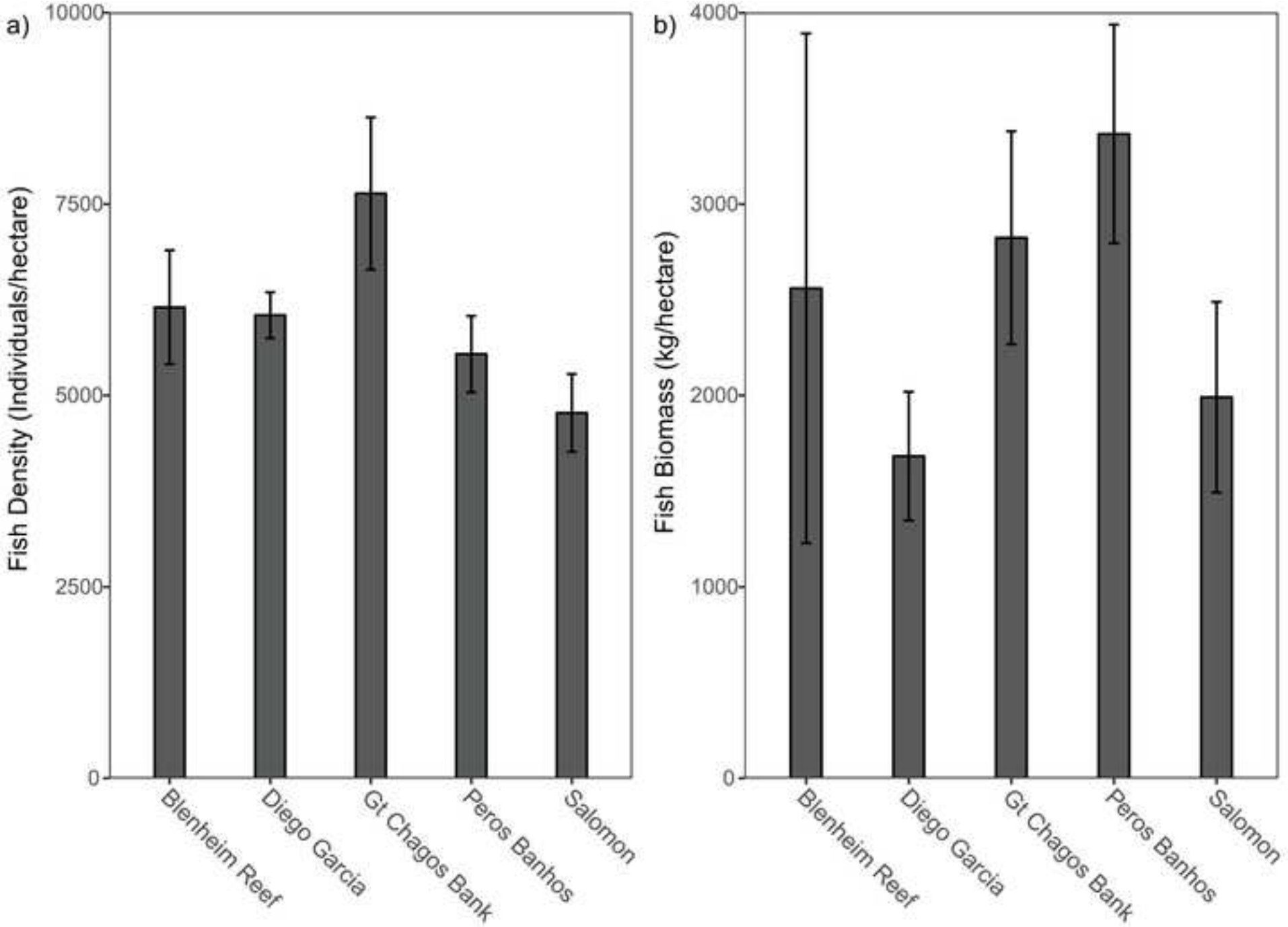

Fig4

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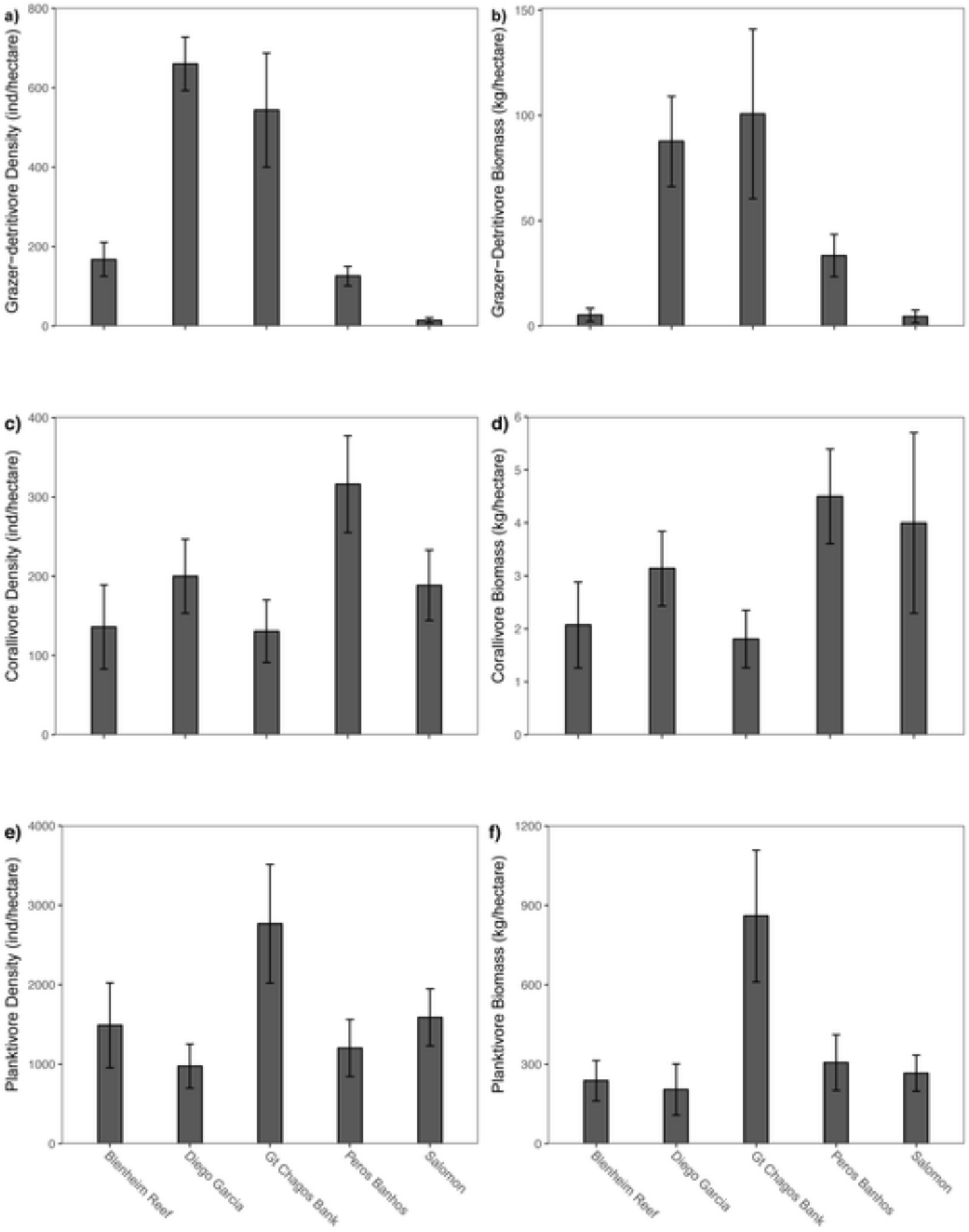

Fig5

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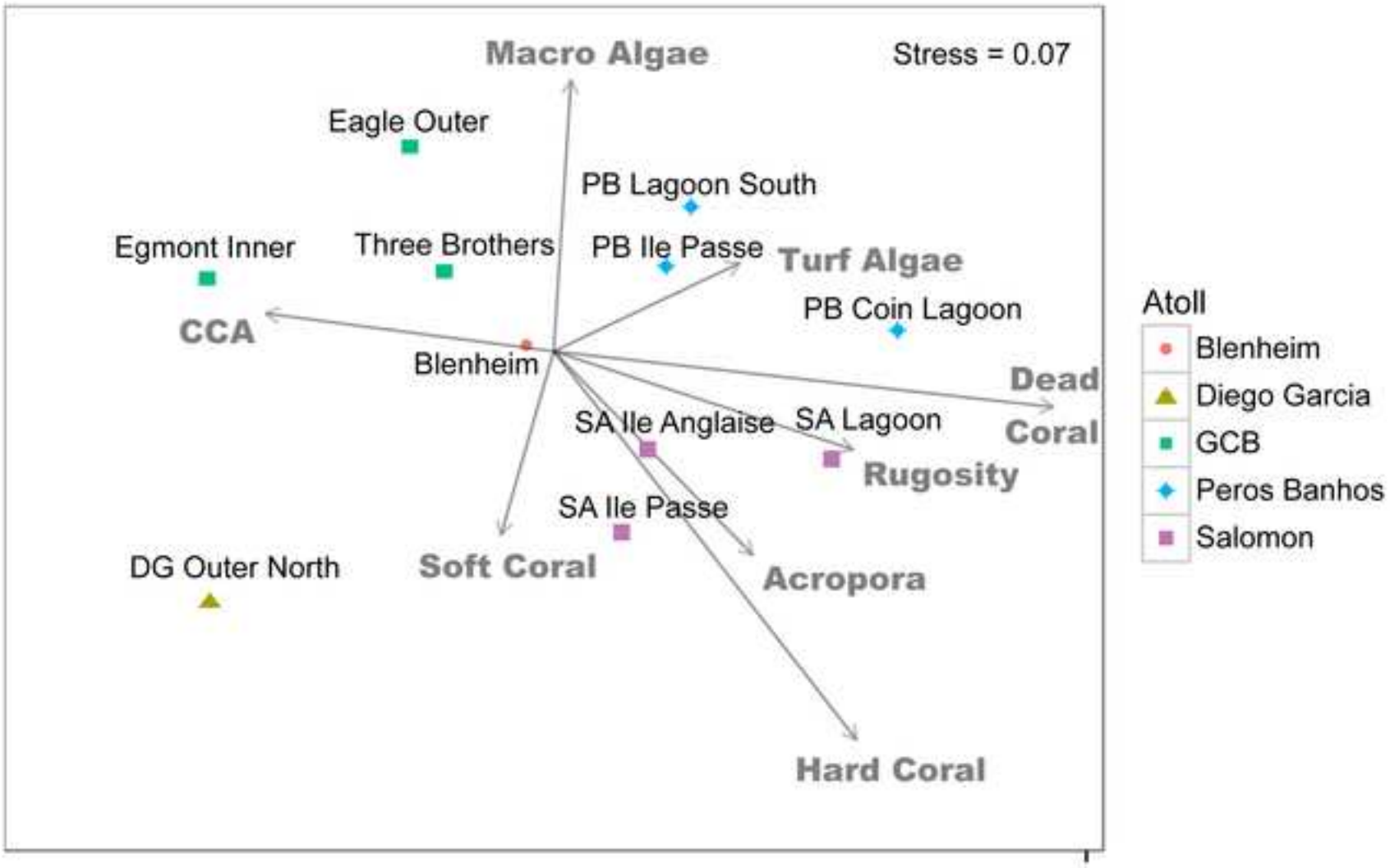

Fig6

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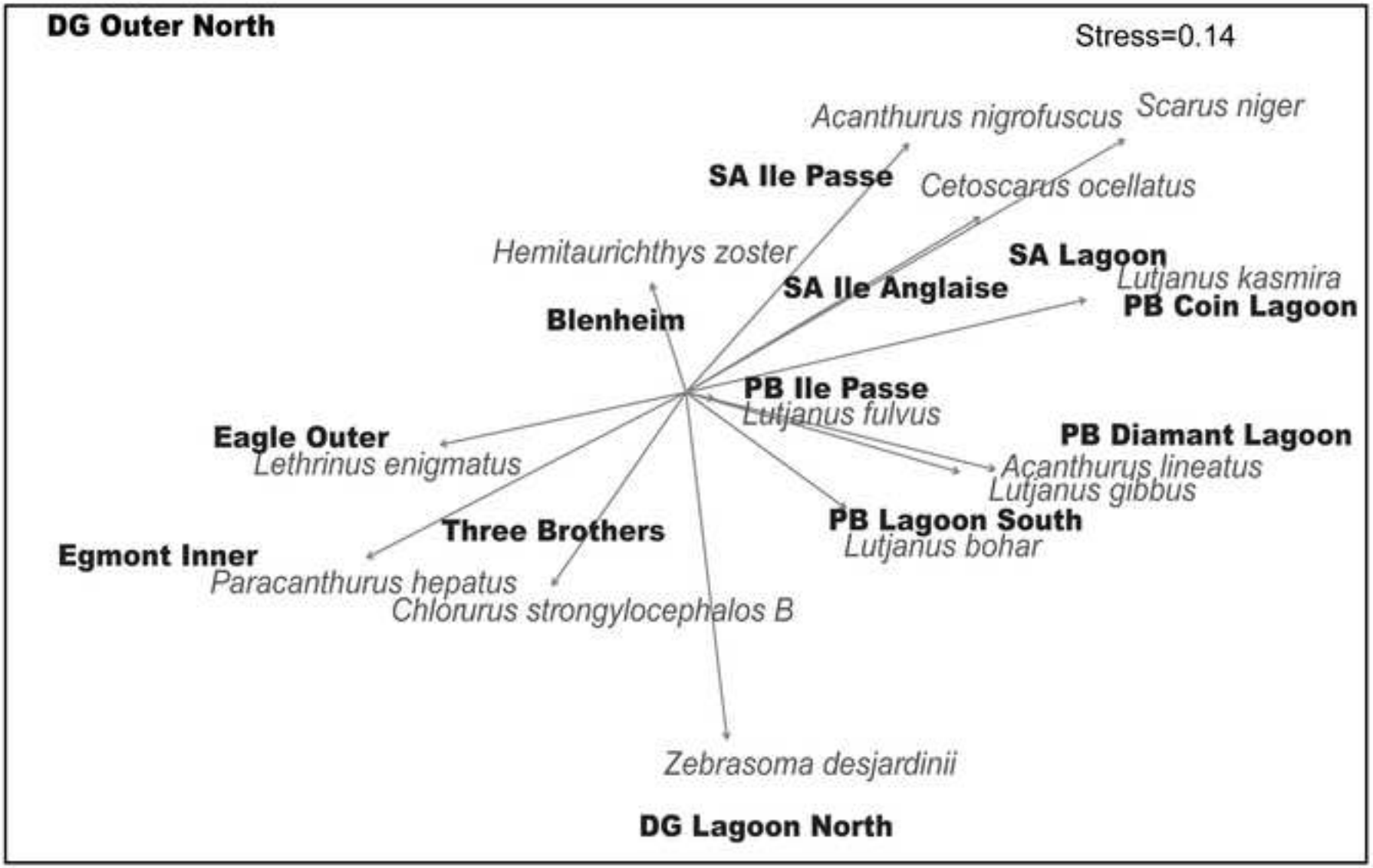

Study sites

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Fish taxa and trophic groups

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Fish species density

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Fish and reef benthos in the Chagos Archipelago

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Patterns in reef fish assemblages: insights from the Chagos Archipelago

Melita Samoilys[1,2] Ronan Roche[3], Heather Koldewey[4,5], John Turner[3]

[1.] CORDIO East Africa, PO Box 24562, Nairobi 00502, Kenya

[2.] Zoology Department, University of Oxford, Oxford OX1 3PS, UK

[3.] School of Ocean Sciences, Bangor University LL59 5AB, UK

[4.] Conservation Programmes, Zoological Society of London, Regents Park, London NW1 4RY, UK

[5.] Centre for Ecology & Conservation, University of Exeter Cornwall Campus, Penryn, Cornwall, TR10 9FE, UK

Abstract

Understanding the drivers of variability in the composition of fish assemblages across the Indo-Pacific region is crucial to support coral reef ecosystem resilience. Whilst numerous relationships and feedback mechanisms between the functional roles of coral reef fishes and reef benthic composition have been investigated, certain key groups, such as the herbivores, are widely suggested to maintain reefs in a coral-dominated state. Examining links between fishes and reef benthos is complicated by the interactions between natural processes, disturbance events and anthropogenic impacts, particularly fishing pressure. This study examined fish assemblages and associated benthic variables across five atolls within the Chagos Archipelago, where fishing pressure is largely absent, to better understand these relationships. We found high variability in fish assemblages ~~between~~ among atolls and sites across the archipelago, especially for key groups such as a suite of

grazer-detritivore surgeonfish and the parrotfishes, which varied in density over 40-fold between sites. Differences in fish assemblages were significantly associated with variable levels of both live and recently dead coral cover and rugosity. We ~~and~~ suggest these results reflect differing coral recovery trajectories following coral bleaching events and~~ed~~ a strong influence of 'bottom-up' control mechanisms on fish assemblages. Species level analyses revealed that *Scarus niger*, *Acanthurus nigrofuscus* and *Chlororus strongylocephalos* were key species driving differences in assemblage structure~~We highlight the importance of examining variability in feeding behaviour within herbivorous and detritivorous fishes to explain their relationship with reef benthic composition~~. Clarifying the trophic roles of herbivorous and detritivorous reef fishes will require species-~~-~~level studies which also examine feeding behaviour to fully understand their contribution in maintaining reef resilience to climate change and fishing impacts.

Introduction

Coral reefs are complex and highly biodiverse systems that are subject to a broad range of natural and anthropogenic factors, operating from local to global scales, which drive or impact reef fish population abundance and assemblage structure [1–4]. Reef degradation from fishing pressure and climate-change induced coral bleaching and mortality have been invoked to explain patterns in the structure of coral reef fish assemblages across multiple scales in the Indo-Pacific [5–7]. Other studies point to scale dependence in drivers of fish assemblages with geomorphology and biogeography, for example, playing a significant role at larger regional scales, and fishing and reef benthic structure operating at local scales [8–10]. Understanding the mechanisms by which these drivers interact and their

relative contributions to controlling reef fish assemblages is critical in underpinning conservation planning and effective reef fisheries management.

One of the dominant paradigms used to explain impacts from the external stressors of climate change and fishing on coral reefs and their fish assemblages revolves around potential shifts from coral to algal-dominated reef states [11,12]. Herbivorous fishes ~~are postulated~~have been shown to play a leading role in preventing this shift by controlling algal abundance [2,13]. The regulatory pathways involve both resource (bottom-up)~~,~~ and predation (top-down) control of the reef ecosystem. Changes in coral cover represent bottom-up control while top-down control is seen when herbivores are depleted through fishing activities, which can lead to their functional role becoming compromised [4,14]. Coral reef fish assemblages are known to vary in relation to several environmental characteristics such as exposure to oceanic conditions, rugosity, depth, benthic composition and recent coral mortality [8–10,15–18]. ~~,~~Bottom-up control of reef fish populations by reef benthic composition has been well established [10,15,18–20], and long term studies in the Philippines, for example, have shown that this pathway is the primary driver of the herbivorous parrotfishes [21]. Thus, top-down and bottom-up pathways can either dominate or co-occur, depending on the characteristics within the coral reef ecosystem.

From a management perspective, it is important to be able to attribute the relative contribution of casual factors driving the structure of reef fish assemblages. The objective of this study was to determine which of a range of largely biotic ~~and abiotic~~ factors may be driving the structure of reef fish assemblages in the absence of fishing. Our hypothesis was that without the top-down influence of fishing in the Chagos Archipelago the fish

assemblages should reflect the relative contribution of ~~largely bottom-up~~ natural drivers, both bottom up (e.g. food availability) and top-down (e.g. predation), of fish populations, and one anthropogenic stressor – coral mortality related to bleaching events. We also sought to describe the characteristic reef fish assemblages of the atolls of the Chagos Archipelago to build on earlier work that examined fish responses to declines in coral cover caused by the coral bleaching event of 1998 [22] and found little change in reef fish species richness except in corallivores [23]. We also examined the abundance and ~~size~~ biomass of reef fishes from the full range of trophic groups to test for relationships between trophic group and reef benthic composition and so examine ~~species'~~ the functional roles of fish species in reef resilience.~~. .~~

The Chagos Archipelago (British Indian Ocean Territory) is an isolated archipelago of atolls spanning ~60,000 km^2 and 2 degrees of latitude on the north eastern border of the western Indian Ocean Province [24–26], with an area of ~9,400 km^2 of shallow coral reefs (<40m depth) [27]. The islands are uninhabited except for the southern-most atoll, Diego Garcia, which is classified as a Permanent Joint Operating Base of the UK and US governments and hosts a US naval support facility. The archipelago, with the exception of Diego Garcia where a recreational fishery is permitted, was declared a no-take marine protected area (MPA) in 2010 by the UK Government [26]. Indeed, reef fish biomass in the Chagos Archipelago is demonstrably one of the highest of any coral reef ecosystem in the Indo-Pacific [23]. The Chagos Archipelago therefore provides an ideal location for investigating the relationship between fish assemblages and variability in reef benthic habitat and typology, in the absence of impacts from fishing and human populations. Our study assumed~~s~~ that reef fish species distributions ~~will~~ did not differ biogeographically across the Chagos Archipelago due to the direction of major current systems in the

100 western Indian Ocean (WIO), and the connectivity of the pelagic larvae of most reef fish
101 [13–16]. We do, however, recognise that self recruitment [32] and local oceanographic
102 dynamics [33] within and among atolls of the archipelago may affect larval recruitment
103 patterns. An earlier study reported that reef fish assemblages were highly homogeneous
104 across the northern atolls [28]. Here we use datasets from a range of atolls in the
105 archipelago, from the northernmost atolls to Diego Garcia in the south, to examine
106 variation in the abundance and species structure of fish assemblages, and to identify
107 drivers of this variability.
108
109 By confining this study to an isolated archipelago of reefs that are relatively unfished and
110 free of pollution and development, this study contributes to a better understanding of
111 intact Indian Ocean reef fish assemblages. As such, it provides a regional context for
112 interpreting coral reef fish assemblages in the wider Indian Ocean where anthropogenic
113 impacts are more prevalent.
114
115 **Methods**
116
117 *Study sites*
118
119 We surveyed reef fish assemblages and coral reef benthic assemblages in March 2014 at a
120 total of 13 (fish) and 11 (benthic) sites across 5 atolls in the Chagos Archipelago (decimal
121 minutes: 05.237333 S 71.81498 E to 07.26195 S 72.44333 E, Fig 1, Table S1). Locations
122 included the fully submerged Blenheim Reef atoll, reefs fringing islands on the west side
123 of the Great Chagos Bank (GCB) and the large, well formed Peros Banhos and Salomon
124 atolls. Reef types were defined based on the Andrefoute et al. [34] classification of coral

reefs and included forereefs and terraces on the outside of the atolls and pinnacles and inner slopes in the atoll lagoons (Table S1). These were categorised as exposed (outside atolls) or protected (inside lagoons) from oceanic seas. The British Indian Ocean Territory Administration Section of the Foreign and Commonwealth Office, UK Government, granted the research permit to the Darwin Initiative 2014 Expedition to work within the whole Territory. Permission was granted to all authors to visit and dive in the strict nature reserves of the Chagos Archipelago Marine Park.

Fig. 1. Map of the Chagos Archipelago showing atolls surveyed and locations of dive survey sites.

Benthic surveys

Underwater video transects were recorded using a Sony HDRCX550 camera in a Light and Motion Bluefin housing with Fathom 90 wide angle port and red filter, onto which red lasers with a spacing of 10 cm were mounted to provide scale. Surveys were conducted at each site which ranged in depth from 5–25m. The video aimed for a constant speed (~0.1 m s^{-1}), with 10 min within each of four depth zones (25–20 m, 20–15 m, 15–10 m, 10–5 m) approximately 1 m above the substrate [32]. Percentage cover of all hard coral and *Acropora* spp. alone, dead coral (defined as recently dead coral skeleton with intact corallite structure), soft coral, crustose coralline algae (CCA), fleshy macroalgae, turf algae, rubble and sand were assessed by randomly selecting 20 video frames from each depth range, and recording what lay beneath 15 randomly selected points per frame, for a total of 300 points per transect, assigned using Coral Point Count software [36]. The rugosity of the reef along each transect was estimated visually using a six point scale

following Polunin and Roberts [37], ranging from no vertical structural complexity to highly-developed reefs with large coral colonies, caves and crevasses.

Fish surveys

All fish species from 13 pre-selected families that span the full range of trophic groups, from piscivores to detritivores (see Table S2) were counted in 50 x 5 m transects ~~run parallel to the reef edge~~. Two dives were conducted at each site, each approximately 300 m along the reef edge, in which 2–3 transects were run parallel to the reef edge (5–6 replicate transects in total per site). Transects spanned the depth range of the reefs (3m - 26m), with the maximum imposed by dive safety regulations. Fish counts at each site therefore had broad depth ranges, from a minimum of 4m to a maximum of 18m ($\bar{x}$ = 10.2m across 13 sites), depending on the reef profile. This design was used to maximise survey coverage of the fish assemblage on the reef. These corresponded to the dive sites at which the benthic video transects were placed; ~~thus~~ both methods spanned the same depth range at each site. Siganids (rabbitfishes) were not observed at all and therefore a total of 12 families were counted (Table S2). The density and size classes of species were estimated using standard underwater visual census (UVC) techniques for coral reef fishes [38,39]. The size of all species >5 cm total length (TL) were estimated in 5 cm size classes (e.g. 6–10 cm TL, 11–15 cm TL, 16–20 cm TL etc), to obtain biomass values based on published length–weight relationships [40–42]. Biomass was calculated as a derived variable for the fish assemblage because it is a good indicator of energy flow within the coral reef ecosystem. A fixed size category for the smallest species was used because: ~~a)~~ simplifying counting procedures across a wide range of species improves accuracy [39,43]; ~~b)~~ any differences in biomass in these small species between sites will be smaller

than the 5 cm size class accuracy used; and ~~c)~~ to enable these small species to be included in total biomass calculations. Fixed size classes were as follows: i) all Chaetontidae species were assigned a length size class of 6–10 cm, with the exception of *C. xanthocephalos*, *C. lineolatus* and *Heniochus* spp. which were recorded as 11–15 cm; ii) small acanthurids, *Ctenochaetus* spp., *Acanthurus nigrofuscus*, *A. leucosternon* and *Zebrasoma scopas*, were assigned a length size class of 11–15 cm; iii) *Centropyge* spp. (Pomacanthidae) –were assigned a length size class of 6–10 cm. A total of 110 species were identified and assigned to 12 functional trophic groups (piscivores, omnivores, corallivores, invertivores, planktivores, detritivores, grazer-detritivores and 5 herbivore categories, *sensu* Green and Bellwood [44] using a classification system for the WIO [45] (Table S2).

Data Analyses

For analyses, the data were organised into a series of matrices: i) fish species numerical density and biomass (13 sites); ii) fish functional group numerical density and biomass (13 sites); iii) benthic habitat variables (11 sites) that were natural log-transformed and standardised (11 variables).

Fish assemblages

Spatial autocorrelation in fish assemblages across the Chagos Archipelago was tested by implementing a Mantel test using the ade4 package [46] in R [47] on a matrix of geographic distances between sampling sites and a dissimilarity matrix based on fish density computed using the Bray-Curtis index. The Mantel statistic was further calculated within Peros Banhos, GCB and Salomon atolls, to test for a relationship with geographic

distance between sites within atolls. Correlations between both numerical density and biomass matrices were tested for significance using 9999 permutations.

In order to visualise variation in the composition of fish assemblages across the archipelago, we used non-metric multidimensional scaling (nMDS) on Bray-Curtis dissimilarity distance measures obtained from fish data matrices of both abundance and biomass. To determine which of the fish trophic groups were significantly related to the ordination, we carried out random permutation testing using 9999 permutations. To further examine for groupings within the fish assemblage data, a Ward cluster analysis based on Euclidean distances was performed on hellinger-transformed data, using similarity profile analysis (SIMPROF) to test the significance of clustered groups [48].

Relationships between datasets

We tested for auto-correlation within benthic variables, and identified variables that were correlated at $r \geq 0.7$. Three variables (calcareous substrate, sand/rubble, and other benthic) were removed from further analysis and no remaining pairwise correlations between variables greater than $r = 0.53$ were found. The remaining 8 variables were further tested by a variance inflation factor (VIF) analysis which found that each of the retained environmental variables resulted in a VIF of <10.

The Adonis function within the Vegan package [49] was used to examine for significant relationships between categorical variables (atoll, reef type and exposure) and the fish assemblages surveyed, also using permutation testing set at 9999 permutations. We used the envfit function within the Vegan package to estimate the direction and strengths of the correlation between the nMDS of fish species and the reef benthic variables surveyed.

Finally, we used a variation of the BIO-ENV [50] routine, termed BIO-BIO, to identify the subset of fish species which best correlated to the overall biological pattern of the dissimilarity matrix, using both numerical density and biomass data. They produced similar results, thus density alone was presented.

Results

A total of 110 fish species from the 12 families were recorded across the Chagos Archipelago. The matrices of mean species density and biomass are provided in ~~Supplementary~~ Tables S3 and S4, respectively. Multivariate ANOVA (Adonis) permutation results found significant differences in the fish species matrices between atolls for both density and biomass datasets ($F_{4,12} = 2.068$, $P = 0.002$; $F_{4,12} = 1.760$, $P = 0.010$)~~;~~ and between three reef types (forereef; terrace & forereef; lagoons (2 types combined), Table S1) for fish biomass ($F_{2,12} = 1.673$, $P = 0.035$). With a limited number of sites, these differences between reef types could not be tested further. There were no significant differences found in species' density or biomass between sites classified as exposed (outer reefs) or protected (lagoon) sites ($P>0.05$).

Mantel tests indicated that dissimilarity in the fish assemblages using species density data was strongly related to geographic distance across the archipelago (Monte Carlo o~~O~~bservation = 0.512; $P = 0.002$). However, within Peros Banhos, Salomon and GCB atolls there was no significant relationship between geographic distance between sites and the fish assemblages present (Peros Banhos: Monte Carlo Observation = -0.317, $P = 0.499$; Salomon: Monte Carlo Observation = -0.718, $P = 0.835$; GCB, Monte Carlo Observation = -0.224, $P = 0.497$).

Ordination of species density data across the archipelago revealed three dissimilar groups corresponding to the atolls of Peros Banhos, Salomon and reefs of the GCB (Fig. 2a). Fish assemblages at GCB separated most strongly from other atolls, while Peros Banhos and Salomon were more similar. These differences in fish assemblages were further verified by the Ward cluster analysis (Fig. 2b), which showed four significant clusters (>60% dissimilarity) though one cluster (cluster 3) comprised of a single site – Diego Garcia Atoll's terrace and~~&~~ forereef, which differed from all other sites (>1.0 dissimilarity). This Euclidian analysis provides a more detailed examination of dissimilarity in the fish assemblages across sites: cluster 1 was most dissimilar from all other sites and consisted of northern sites at Blenheim and Salomon Atoll forereefs; cluster 2 contained all lagoon sites, 3 from Peros Banhos but also 1 site from each of Salomon and Diego Garcia; whilst cluster 4 consisted of two sub-groups, Eagle and Egmont forereefs at GCB~~,~~ and Three Brothers forereef (GCB) and two Peros Banhos sites (a forereef and a lagoon pinnacle). Total fish density and biomass also showed broad~~-~~-scale differences across the archipelago with the highest densities recorded on reefs at GCB, the highest biomass recorded at Peros Banhos Atoll and the lowest biomass at Diego Garcia Atoll (Fig. 3).

Fig. 2. Spatial variation in reef fish species assemblages across the 13 sites in the Chagos Archipelago: a) non-metric multidimensional scaling plot, coloured ellipses show 95% confidence intervals of site grouping; b) Ward cluster analysis, colours in dendrogram highlight the four significantly different groups found (<0.6 dissimilarity).
~~Significant fish species assemblages across 13 sites in the Chagos Archipelago based on a) nMDS analysis of fish species density data and b) Ward cluster analysis showing four significant groups (>0.6 dissimilarity).~~

Fig. 3. Total fish a) density (number of individuals per hectare) and b) biomass (kg per hectare) by atoll, based on 12 reef-associated families surveyed at 13 sites. Error bars are standard errors.

When fish species were categorised into the 12 trophic groups, permutation tests showed only 3 trophic groups were significant in explaining the pattern in the species assemblages: grazer-detritivores and corallivores for fish density and grazer-detritivores and planktivores for fish biomass (Table 1, Fig. 4). These three trophic groups all significantly explained fish density differences when the permutation test was stratified by atoll (Table 1). Grazer-detritivores comprise a group of acanthurids and the angelfishes *Centropye* spp. (Table S2). Acanthurid species in this trophic group, such as *Acanthurus tennenti* and *A. xanthopterus*, typically feed on sand and hard surfaces to extract detritus and microbes, as well as epilithic algae. The densities and biomass of these grazer-detritivores were nearly three times greater at GCB and Diego Garcia compared to the other atolls (Fig. 4), representing the largest difference in the fish assemblages across the archipelago. The corallivores consisted of six obligate coral feeding butterflyfishes out of the 18 Chaetodontidae observed in the Chagos Archipelago and were more abundant at Peros Banhos and Salomon atolls, compared to other reefs (Fig. 4). When biomass was considered, the planktivores, comprised of balistid, acanthurid and chaetodontid species, differed significantly between the atolls with biomass at GCB three times higher than any of the other reef sites (Table 1, Fig. 4).

Table 1. Random permutation results of 12 fish trophic groups showing only those significantly related to differences: a) across all sites and; b) stratified by atoll.

Density			**Biomass**		
a) All sites					
Trophic group	r^2	*p*-value	Trophic group	r^2	*p*-value
Grazer-detritivores	0.769	<0.001	Grazer-detritivores	0.792	<0.001
Corallivores	0.598	0.009	Planktivores	0.515	0.026
b) Stratified by atoll					
Grazer-detritivores	0.769	0.006	Grazer-detritivores	0.641	0.016
Planktivores	0.268	0.030	Planktivores	0.515	0.034
Corallivores	0.598	0.048			

Fig. 4. Mean density (number of individuals per hectare) and biomass kg per hectare) by atoll for the three functional trophic groups that were significantly related to fish assemblage differences. Error bars are standard errors. Functional trophic groups are explained in Table S2.

Benthic reef characteristics and fish assemblages

The benthic cover at reef sites was highly variable among the atolls of the archipelago. Total live coral cover ranged from 15.7% (±1.6 SD) to 47.2 % (±24.1 SD), *Acropora* spp. coral cover from 1.1 (±1.4 SD), to 28.1% (±12.4 SD), and dead standing coral from 5.9% (±3.1 SD) to 26.4% (±13.1 SD). Non-metric multi-dimensional scaling of the relative contribution of the eight benthic variables to the differences between fish assemblages across the archipelago showed that reef sites grouped along two main axes (Fig. 5): the Y axis with high macro-algae such as GCB reefs, versus sites with higher soft coral (Diego Garcia); and the X axis with sites with high hard coral, dead coral, live *Acropora*, rugosity

and turf algae, at Salomon Atoll and Perhos Banhos, versus reefs at GCB with higher CCA. GCB reefs had the lowest levels of hard coral, ranging from 15.7% (±5.6 SD) to 28.7% (±17.7 SD). However, hard coral and dead coral (i.e. structural components) were the only benthic categories that were significantly related to differences in fish assemblage structure when analysed with fish density data; when tested with fish biomass data, rugosity also became significant (Table 2). When the permutation analysis was stratified

Density	Biomass

by atoll, hard coral and dead coral were no longer significant; instead soft coral showed a significant correlation with fish density and CCA with fish biomass (Table 2). These results corroborate the geographic differences in fish assemblages between different atolls, driven by hard and dead coral cover, whereas within atolls only CCA and soft coral were significantly correlated with the fish species data matrices.

Fig. 5. nMDS diagram showing the relationship between benthic variables at 11 reef sites overlaid on the fish assemblage ordination (see Fig. 2) across the Chagos Archipelago. The relative contribution of each benthic variable is displayed by the length of the vector.

Table 2. Significant permutation correlations between benthos and the fish species matrix, for density and biomass at: a) all sites and; b) stratified by atoll.

a) All sites					
Benthic Group	r^2	*p*-value	Benthic group	r^2	*p*-value
Hard Coral	0.63	0.021	Hard Coral	0.7	0.001
Dead Coral	0.66	0.013	Dead Coral	0.7	0.001
			Rugosity	0.55	0.034
b) Stratified by atoll					
Soft Coral	0.38	0.004	Crustose Corraline Algae	0.310	0.042

Fish species

A species-level ordination (BIOBIO) of the density of the 110 fish species which determined which species were most correlated with differences in the fish assemblages across all reef sites showed that 13 species best explained (rho=0.832) the fish assemblages across the sites: *Acanthurus lineatus, A. nigrofuscus, Zebrasoma desjardinii* (grazers), *Cetoscarus ocellatus, Chlorurus strongylocephalus B* (large excavators), *Hemitaurichthys zoster, Paracanthurus hepatus* (planktivores), *Lutjanus bohar* (piscivore), *Lutjanus fulvus, Lutjanus gibbus, Lutjanus kasmira, Lethrinus enigmatus* (omnivores), *Scarus niger* (scraper), *Sufflamen* spp. (invertivore) (Table 3, Table S2, Fig. 6). Note that none of these species were from the significant trophic groups detected in the permutation tests except for *Paracanthurus hepatus*. When the ordination was restricted sequentially, it showed that *Scarus niger* alone was highly correlated (rho=0.569) with species assemblage differences. Further, a combination of only 6 species achieved a very high correlation (rho=0.802) with species assemblage differences. Although the 13 species illustrated in Fig. 6 are the best fit, other species consistently appeared in highly correlated subsets (Table 3), and therefore were likely to drive differences between fish assemblages across the archipelago. These included *Acanthurus thompsoni (*planktivore), *A. tennenti, A. xanthopterus* (grazer-detritivores), *Scarus frenatus* (scraper), the invertivores *Chaetodon madagascariensis* and *Sufflamen* spp. and *Lethrinus microdon* (omnivore).

359

360 **Fig. 6.** The relationship between individual species and the fish species density ordination

361 based on the 13 fish survey sites.

362

363 **Table 3.** Species strongly correlated with differences in density of fish species

364 assemblages across the Chagos Archipelago, based on a species level ordination (BIO-

365 BIO) of 110 species.

Number of Species in subset	Fish Species	Spearman's Rank Correlation (rho)
1	*Scarus niger*	0.569
2	*Acanthurus thompsoni, Scarus niger*	0.715
3	*Acanthurus tennenti, Acanthurus thompsoni, Scarus niger*	0.762
4	*Acanthurus thompsoni, Naso hexacanthus S, Scarus niger, S.russelli*	0.767
5	*Acanthurus leucosternon, Cephalopholis sexmaculata, Lethrinus obsoletus, Scarus niger, Scarus psittacus*	0.783
6	*Acanthurus thompsoni, Chaetodon madagascariensis, Lethrinus obsoletus, Scarus niger, Sufflamen spp., Zebrasoma desjardinii*	0.802
7	*Acanthurus thompsoni, Chaetodon madagascariensis, Lethrinus obsoletus, N. hexacanthus S, Scarus niger, Sufflamen spp., Zebrasoma desjardinii*	0.815
8	*Acanthurus tennenti, Acanthurus xanthopterus, Chaetodon madagascariensis, Lutjanus bohar, Scarus frenatus, Scarus niger, Sufflamen spp., Zebrasoma desjardinii*	0.813
9	*Acanthurus tennenti, Acanthurus xanthopterus, Chaetodon madagascariensis, Lutjanus bohar, Lethrinus microdon, Scarus frenatus, Scarus niger, Sufflamen spp., Zebrasoma desjardinii*	0.818
10	*Acanthurus tennenti, Acanthurus xanthopterus, Canthigaster bennetti, Chaetodon madagascariensis, Lutjanus bohar, Lethrinus microdon, Scarus frenatus, Scarus niger, Sufflamen sp., Zebrasoma desjardinii*	0.821
11	*Acanthurus tennenti, Acanthurus xanthopterus, Canthigaster bennetti, Chaetodon madagascariensis, Lutjanus bohar, Lethrinus microdon, Odonus niger, Scarus frenatus, Scarus niger, Sufflamen spp., Zebrasoma desjardinii*	0.823
12	*Acanthurus tennenti, Acanthurus xanthopterus, Canthigaster bennetti, Chaetodon madagascariensis, Lutjanus bohar, Lethrinus microdon, Odonus niger, Paracanthurus hepatus, Scarus frenatus, Scarus niger, Sufflamen spp., Zebrasoma desjardinii*	0.820
13	*Acanthurus lineatus, Acanthurus nigrofuscus, Cetoscarus ocellatus, Chlorurus strongylocephalus B, Hemitaurichthys zoster, Lutjanus bohar, Lutjanus fulvus, Lutjanus gibbus, Lutjanus kasmira, Lethrinus enigmatus, Paracanthurus hepatus, Scarus niger, Zebrasoma desjardinii*	0.831

14	*Acanthurus lineatus, Acanthurus nigrofuscus, Cetoscarus ocellatus, Chlorurus strongylocephalus B, Chaetodon striatus, Hemitaurichthys zoster, Lutjanus bohar, Lutjanus fulvus, Lutjanus gibbus, Lutjanus kasmira, Lethrinus enigmatus, Paracanthurus hepatus, Scarus niger, Zebrasoma desjardinii*	0.824

Three broad types of fish assemblages in the Chagos Archipelago are suggested through a combination of highly significant species within the ordination (Fig. 6), significant benthic associations (Fig. 5) and clustering of fish species (Fig. 2b). These can be defined as those aligned with: 1) ~~those aligned with~~ higher hard coral cover (27–43%), or recently dead coral; 2) ~~with~~ high rugosity and *Acropora* cover; and 3) ~~those associated with~~ higher soft coral, CCA, and macro-algal cover but low cover of live hard coral (12–22%; Table 4). The former (groups 1 and 2, Table 4) were found across Salomon and Peros Banhos atolls, whereas the latter (group 3, Table 4) was largely at GCB. It is noteworthy that two of the largest excavating parrotfishes, *Cetoscarus ocellatus* and *Chlorurus strongylocephalos* (B), showed opposing patterns of correlation (Fig. 6). *Cetoscarus ocellatus* was also closely associated with *Scarus niger* on certain reefs in Salomon and Peros Banhos and both these species characterise group 1 and 2 assemblage types (Table 4). Fish assemblages at Diego Garcia Atoll forereef site were significantly different and may represent a fourth assemblage type, but there were too few survey sites to assess this. Note that 3 species were rare, present only at 1 reef (~~:~~ *A. lineatus*, *Lethrinus enigmatus* and *Lutjanus fulvus*, ~~(~~Table 4, Table S3).

Table 4. Synthesis of results from Figures 2b, 5 and 6 and ~~Suppl.~~ Tables S3 and S4, to define three broad types of fish assemblages across the Chagos Archipelago, the sites at which they were found and the corresponding reef benthic characteristics. Species and

benthos listed are the highest abundance/cover and were significant within analyses. *= rare species seen only at 1 reef. Diego Garcia Atoll forereef was an outlier and is not included.

No.	Fish Species	Reefs	Benthos
1			
	Scarus niger (Scraper)	**Salomon**	Hard coral
	Acanthurus nigrofuscus (Grazer)	- terrace & forereef	*Acropora*
	Hemitaurichthys zoster (Planktivore)	(2 sites)	Soft coral
	Cetoscarus ocellatus (Excavator)	**Blenheim**	Rugosity
2			
	Scarus niger (Scraper)	**Peros Banhos**	Dead coral
	Lutjanus kasmira (Omnivore)	- lagoon (2 sites)	Rugosity
	Cetoscarus ocellatus (Excavator)	**Salomon**	Turf algae
	A. lineatus (*Grazer)	- lagoon	Hard coral
	L. gibbus (Omnivore)	**Diego Garcia**	*Acropora*
	Z. desjardinii (Grazer)	- lagoon	
3			
	Chlor. strongylocephalos (Excavator)	**GCB**	Soft coral
	Paracanthurus hepatus (Planktivore)	- forereefs	CCA
	*Lethrinus enigmatus** (Omnivore)	**Peros Banhos**	Macro-algae
	Lutjanus bohar (Piscivore)	- forereef	
	*Lutjanus fulvus** (Omnivore)	- lagoon	

Species of conservation and fisheries interest

The widespread Indo-Pacific coral trout grouper *Plectropomus laevis* was abundant and observed at all but 3 sites, with a mean density and biomass of 17.85 ± 1.54 SD individuals-/-ha and 104.8 ± 170.5 SD kg/ha, including several very large individuals (91–110 cm TL), close to maximum size for this species. *Plectropomus punctatus*, the coral trout grouper endemic to the Indian Ocean was never observed, yet it was recorded from

the Chagos Archipelago in the 1990s by Winterbottom and Anderson [5145]. No siganids were observed during the current survey, yet though two species, *Siganus argenteus* and *S. canaliculatus* were reported fromare known from the archipelago in the 1990s [51]. The abundance of the larger species of grouper such as *Epinephelus fuscoguttatus*, *E. malabaricus*, *E. multinotatus* and *E. tauvina* was extremely low, ranging from a mean of 0.0–0.77 ±1.54 SD fish-/-ha.

Discussion

Large regional-scale [7,52] or long temporal-scale analyses [2] in the Indian Ocean and across the Indo-Pacific [6] have shown that fishing and climate change are primary drivers of fish assemblage structure. We found significant differences in fish assemblage structure among the atolls of the Chagos Archipelago which we attribute to natural environmental drivers and climate change, as reflected in the significant correlations between fish assemblages and reef benthic composition. However, temporal changes before and after coral bleaching events remain unknown; thus, future work on this would greatly enhance interpretation of the results of the current study. We found significant differences in fish assemblage structure between the atolls of the Chagos Archipelago which we attribute to natural environmental drivers and climate change.We can, however, We assumed that fishing effects would beare minimal due to the lack of resident human populations on any of the atolls since the 1960s (with the exception of Diego Garcia) and because of the establishment of a no-take MPA in 2010. Indeed, the Chagos Archipelago is used as a benchmark for largely unfished reefs in the Indian Ocean [6,23]. Further, our study assumed that reef fish species distributions did not differ biogeographically because

of the relatively small geographic range of the Chagos Archipelago fed by the easterly flowing East African Coastal Current and South Equatorial Countercurrent, both emanating from the east African mainland [29], and the connectivity of the pelagic larvae of most reef fishes [30,31]. Of the 110 species in the dataset, there was no apparent disjunct in their distribution between the northern atolls (Peros Banhos, Salomon and Blenheim) and the southern atolls (GCB and Diego Garcia) except for *Acanthurus tristis*, *Chaetodon madagascariensis* and *Chlorurus capistratoides*, which were only found in the south, and *Chaetodon lunula* which was only found in the north. Of these, only *C. madagascariensis* was a significant species in the ordination analysis.

Patterns in fish species and benthic communities

Differences in fish assemblages were significantly correlated with geographic distance between sites; the relative density of the 110 fish species ~~fish~~ across the archipelago differed most significantly between atolls. These atoll-scale differences were also apparent in total density and biomass values (12 families), with the highest fish densities recorded on the reefs of the western edge of the GCB, the highest fish biomass recorded at Peros Banhos Atoll and the lowest fish biomass at Diego Garcia Atoll. Reef benthic composition also varied between atolls, most notably in the relative cover of live hard coral, recently dead standing coral and rugosity, and permutation testing showed that these differences were significantly related to fish density (hard and dead standing coral) and fish biomass (hard coral, dead standing coral, rugosity). These results are not surprising since strong positive correlations between fish density or biomass and live hard coral and rugosity, benthic variables that co-vary and reflect reef habitat structural complexity, are widely reported [15,16,53–56]. Therefore, patterns in the fish assemblages reported here likely

reflect bottom-up control.

A major alteration in the benthic composition of coral reefs across the Indian Ocean occurred following the severe coral bleaching event of 1998 [57]. This thermal anomaly resulted in a reduction of living coral cover in the Chagos Archipelago from 50–75% cover prior to the event~~,~~ to ~10% live coral remaining on all six atolls in 1999 [22]. However, a majority of reef sites across the archipelago recovered rapidly and reached pre-bleaching condition by 2010 [26]. The strong benthic differences between atolls observed in our surveys in 2014 possibly reflect different levels of bleaching and differing recovery patterns following the 1998 event, though with little historic data this remains unknown. However, early reports of highly homogenous fish assemblages across reefs in the northern atolls prior to 1998 [28] suggest that the differences in the structure of the fish assemblages found in 2014 are recent and may therefore, be due to differing recovery patterns. ~~We propose this reflects differing trajectories of coral bleaching and recovery between the atolls since the 1998 extreme thermal anomaly.~~

Fishing effects

This study was not designed to look at fishing effects because it was based on the premise that there is no reef fishing in Chagos Archipelago, however, ~~Most reef fishes in the Indian Ocean are targeted, and in many cases are over-exploited, within multi-species fisheries [58,59]. In the Chagos Archipelago,~~ there was a small Mauritian fishery targeting grouper (Epinephelidae) and snapper (Lutjanidae), which operated from the 1970s until 2010 when the Chagos MPA was designated [23]. Populations of piscivore and omnivore trophic categories were similar between atolls, exemplified by the coral trout grouper

Plectropomus laevis, which was abundant and observed at all but three sites. However, two snappers *Lutjanus bohar* (piscivore) and *Lutjanus gibbus* (omnivore)~~,~~ were significantly correlated with differences in fish assemblages across atolls. The highest biomass of these two species was found in Peros Banhos lagoon sites (up to 861 kg~~-~~/ha and 530 kg~~-~~/ha, for *L. bohar* and *L. gibbus*, respectively). Apparently the fishery did not operate in the lagoons (BIOT Fisheries Officer, pers. comm. 2014), but since our study is the first to report on fish biomass in the lagoons there are no previous comparable data. For *L. bohar*~~,~~ moderate biomass levels ~~(175–263 kg/ha)~~ were found on forereefs at Salomon, Peros Banhos and Blenheim, but were lower at Diego Garcia and GCB, while~~(69–108 kg/ha and 16–148 kg/ha, respectively). For *L. gibbus*,~~ biomass of *L. gibbus* was highly variable across all forereefs. Our surveys also suggest that three large species of grouper, *Epinephelus fuscoguttatus*, *E. multinotatus* and *E. tauvina* may have been over~~-~~fished since their populations were extremely depleted across all sites. ~~It is also likely that~~While there is also some illegal fishing ~~is ongoing~~in BIOT, 80% by weight of illegal catches detected by the BIOT patrol vessel is shark [58], therefore this poaching can be considered minimal in terms of impacts on reef fishes.~~:~~ ~~anecdotal reports from India cite grouper landings reputedly captured in the Chagos Archipelago (MS pers. obs).~~ ~~These~~Our results are inconclusive ~~but~~ and suggest that further research is needed to distinguish between possible latent fishing effects or natural biotic/abiotic drivers ~~on~~ of some ~~species~~ grouper and *Lutjanus bohar*~~at certain atolls~~.~~-~~

A recreational fishery operates outside the MPA at the naval base in Diego Garcia and is having an impact on fish biomass [23]. Our total biomass estimates with maximum values of ~3,500 kg/ha (12 families)~~,~~ do not include sharks and trevally and therefore cannot be directly compared with the estimates of ~~-~~>9,000 kg/ha reported from 2010–2012.

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However, comparing relative biomass between atolls ~~during~~ from the 2010–2012 survey [23] with our survey in 2014 shows similar differences, with highest values at Peros Banhos, followed by GCB, then Salomon, and the lowest values at Diego Garcia. This supports Graham et al.'s [23] conclusions that the recreational fishery is having an impact. Nevertheless, we measured extremely high biomass values at 10 of the 13 sites (1,501-3,000 kg/ha at six sites, and > 3,000 kg/ha at four sites). These are similar, when the same families are considered, to biomass at other uninhabited and protected reefs of the French territories in the Mozambique Channel [59], providing strong support for using Chagos Archipelago as a reference benchmark for unfished reef fish populations in the western Indian Ocean.

Trophic dynamics in the reef fish assemblages

Herbivory and detritivory contribute significantly to the trophic dynamics and hence biomass production on coral reefs [60,61]. Indeed, the diversity of herbivores and detritivores seen on modern reefs, illustrated by the parrotfishes (Labridae: Scarinae) and surgeonfishes (Acanthuridae), has been linked to the massive expansion of shallow coral reef habitats over the last 5 million years [62]. In the Chagos Archipelago, the grazer-detritivores was the trophic group that differed most significantly between atolls. This group comprises a suite of acanthurids ("ring-tail" surgeonfishes [44]), such as *Acanthurus tennenti* and *A. xanthopterus*, that harvest mouthfuls of soft sediment on dead coral substrate, as well as on sand, which contain the diatoms and microbes of their diet [63,64]. Their highest densities~~y~~ at GCB and Diego Garcia (>500 and >600 individuals/ha, respectively) corresponded with low hard coral cover. In contrast, low numbers of these surgeonfishes were seen at Peros Banhos, Salomon and Blenheim (<130,

<14, <170 individuals/ha, respectively), where hard coral cover was high. These results suggest that these "grazer-detritivore" surgeonfish species may thrive where their benthic food sources have increased due to coral mortality [65] and ~~may~~ can therefore serve as important indicators of reef degradation. ~~They may also help reduce the growth of macroalgae.~~ The prevalence of the ~~The~~ detritivory role is also supported by one of the most common reef fishes in the world, the bristletooth surgeonfishes *Ctenochaetus* spp. [66], with the combined density of two species ~~ous~~ *Ctenochaetus truncatus* and *C. striatus* at ~850 individuals/ha being the second highest (*Caesio* spp. were the highest: 936 individuals/ha) ~~spp. are one of the most common reef fishes in the world [66] and *C. truncatus* and *C. striatus* were the most abundant~~ of all the 110 species surveyed~~, with densities of up to 1,800 individuals/ha~~. We propose that ~~*These results suggest that this genus* is highly successful and~~ the importance of detritivory in recovery of degraded reefs and in cycling carbon within ~~these~~ coral reef systems ~~systems~~is not well quantified and therefore an important area for future research.

A strong relationship between hard coral cover and corallivores has been widely reported [23,56,67]~~;~~ and was confirmed here with significantly higher densities of obligate coral-feeding butterflyfishes at Peros Banhos and Salomon atolls where there was relatively high~~er~~ live coral cover~~, and the highest densities of corallivores in the lagoons of Peros Banhos where the highest coral cover was recorded~~. These coral specialists are clearly highly vulnerable to coral mortality and, as such, have ~~been~~ long been used as potential indicator species for monitoring coral reef health [68]. The third trophic group that differed significantly between atolls was the planktivores, comprising several acanthurids (three *Naso* spp., *Acanthurus thompsoni* and *Paracanthurus hepatus)*, two chaetodontids, two balistids and *Caesio* spp. The biomass of this group was three times higher at GCB,

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with a mean biomass of ~~860~~ 1,045 kg/ha, compared to ~~277kg~~338kg/ha for other atolls, and this was largely due to the caesionids and *Naso hexacanthus* and *N. brevirostris*. Further, three planktivores were strongly correlated with the ordination: *Paracanthurus hepatus*, *Acanthurus thompsoni* and the chaetodon *Hemitaurichthys zoster*. Drivers of planktivore populations on coral reefs are still poorly understood, but their food items are associated with reef edges and proximity to deep water [69]. These acanthurid species are all zooplanktivores [70], suggesting waters at GCB may be zooplankton-rich. Thus, higher Acanthuridae densities overall at ~~the more degraded~~ GCB reefs appear to reflect two different and unrelated trophic pathways: increased access to soft benthic surfaces due to coral mortality for the grazer-detritivores and higher zooplankton densities for planktivores. Finally, it was notable that the density and biomass of the piscivore and omnivore trophic groups, species that represent important target fishery species [23,39], were not significantly correlated with fish assemblage patterns across the archipelago, suggesting that benthic differences did not directly affect these higher trophic level taxa. Thus, when data were aggregated by trophic group, only three groups differed significantly and these appeared to be influenced by reduced coral cover due to climate change [22] and natural variability in zooplankton, both bottom-up control pathways.

It was surprising that none of the five herbivore trophic groups, which include all the parrotfishes, were significant in ~~the aggregated trophic group analyses~~explaining differences in fish assemblages between sites. We found species–level analyses were more informative than aggregated trophic group analyses and demonstrated species from within seven trophic groups were highly related to differences in the fish assemblages across the reefs of the Chagos Archipelago. *Scarus niger* had the strongest correlation with fish assemblage structure across the archipelago, with highest biomass on the high coral cover

northern atolls (182 kg/ha at Peros Banhos), and the lowest at Diego Garcia and the low coral cover reefs of GCB (3 kg/ha and 11–27 kg/ha, respectively). This species is one of the most ubiquitous parrotfishes across the Indo-Pacific [71,72] and feeds on the top 1–2 mm of dead coral substrate [62,73], though it probably removes epilithic algae while feeding. *Scarus niger* was associated with the highly abundant surgeonfish *Acanthurus nigrofuscus*, known to graze similar substrate types ~~but~~ but feedings~~s~~ on epilithic algae [63,64]. These two species correlated most closely with the assemblages at Salomon Atoll sites, particularly on the outer forereefs where live hard coral, *Acropora* and rugosity were highest, but also at the Peros Banhos lagoon sites where turf algae and dead coral were relatively high. This result may reflect "feeding complimentarity" by a parrotfish and a surgeonfish, accessing different algal prey within the same benthic ~~-~~substrate [74]. It also illustrates the challenges in using trophic categories as a proxy for ecological function. Herbivorous fishes have been implicated in the top-down control of reef benthos, as their grazing of recently dead coral substrate prevents the rapid colonisation of macro~~-~~algae,~~;~~ F~~f~~urther, over-fishing of herbivores has been invoked to explain declines in coral cover and they are consequently considered to play a key functional role in maintaining coral reef resilience [4,11,12,75–77]. Parrotfishes (Labridae; ~~—~~Scarinae) are a significant component of this herbivorous fish community on account of their size, numerical abundance and hence biomass [14]. They are also targeted in many reef fisheries and are frequently used as indicators for the condition or resilience of reefs [14,39,44,61,78]. However, recent work on the intricacies of parrotfish feeding modes and diets [14,62,73] indicates that assigning species with similar feeding modes into broad trophic groups may over-simplify their functional role in reef resilience. Further, we show that parrotfish population densities can vary by up to 43-fold between reef sites in the absence of fishing

and so caution against assumptions that declines in parrotfish populations are necessarily due to fishing.

The largest parrotfishes, ~~the excavators~~ *Cetoscarus ocellatus* and *Chlororus strongylocephalos*, showed completely opposing patterns in their distribution with *Cetoscarus ocellatus* closely associated with healthy reefs with high coral cover at the northern atolls (Peros Banhos and Salomon). In contrast, *Chlorurus strongylocephalos* was strongly correlated with reefs at GCB which had the lowest live coral and the highest cover of calcareous algae, soft coral and macroalgae. This opposing pattern in the distribution of these two high~~-~~biomass parrotfish, functionally termed "excavators" [14,44,65], can be explained by their feeding behaviour. *Cetoscarus ocellatus* are territorial, non-schooling, harvest small areas of reef and are associated with reefs of high live coral cover (M. Samoilys, pers. obs.). In contrast, *Chlorurus strongylocephalos* prefers disturbed reefs which offer a larger benthic surface area for excavating the dead coral reef matrix [73]. They feed on these substrates, typically in large schools if the disturbed substrate is of sufficient area (H. Choat, James Cook University, pers. comm. 2016). The Indian Ocean endemic, *Chlorurus enneacanthus*, was observed to have a similar feeding strategy to *Chlorurus strongylocephalos* (M. Samoilys pers. obs.). These *Chlorurus* species conform to reports from the Philippines where some parrotfish species prefer areas of reef that have become damaged, for example from cyclones [21]. The patterns seen here suggest bottom~~-~~up control of parrotfish populations by coral cover in positive (e.g. *S. niger, C. ocellatus*) or negative (e.g. *C. strongylocephalos*) relationships. These pathways therefore need to be considered when examining the role of parrotfishes in influencing coral recovery trajectories. ~~Our results are consistent with recent findings~~

~~from the Pacific where the responses of herbivorous fishes to biophysical attributes of reefs differed between five trophic groups [65].~~

Conclusions

The isolated Chagos Archipelago provides a valuable ecological benchmark for understanding the structure of reef fish assemblages ~~in the absence of fishing~~when fishing impacts are minimal. Differences in fish assemblages across the archipelago were associated with variation in reef benthic condition, ~~confirming~~ suggesting a bottom-up response of fish populations to changes in coral cover. Our results support the concept that herbivory and detrivory are significant functions provided by reef fishes [60–62], but we propose that separating diet from the structural impact of these feeding modes will improve our understanding of their functional role in reef resilience. The large variation in parrotfish abundance found in the Chagos Archipelago supports studies (e.g. Russ et al. [21]) that caution against ~~the~~ assumptions elsewhere that parrotfish population abundances~~s~~ are largely driven by fishing. We found surgeonfish species that graze epilithic algae and parrotfish species that exploit bare substrate to access nutrients within the calcareous matrix [63,64,73] are ~~-~~two key taxa responsible for differences in fish assemblages between the atolls. Both may function to keep macro-algal levels down, but the~~ir~~ drivers of their populations are different. Parrotfishes have evolved highly successful traits to exploit food sources on reefs and contribute significant biomass on coral reefs [14, 62], including during declines in coral cover [21,65] and some species are impacted negatively by fishing [65]. Clarifying the~~se~~ trophic dynamics is vital to refine functional trait approaches for understanding the impacts of climate change and fishing on coral reef biodiversity.

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Figure Captions

Fig. 1. Map of the Chagos Archipelago showing atolls surveyed and locations of dive survey sites.

Fig. 2. ~~Significant fish species assemblages across 13 sites in the Chagos Archipelago based on a) nMDS analysis of fish species density data and b) Ward cluster analysis showing four significant groups (>0.6 dissimilarity).~~ Spatial variation in reef fish species assemblages across the 13 sites in the Chagos Archipelago: a) non-metric multidimensional scaling plot, coloured ellipses show 95% confidence intervals of site grouping; b) Ward cluster analysis, colours in dendrogram highlight the four significantly different groups found (<0.6 dissimilarity).

Fig. 3. Total fish a) density (number of individuals per hectare) and b) biomass (kg per hectare) by atoll, based on 12 reef-associated families surveyed at 13 sites. Error bars are standard errors.

Fig. 4. Mean density (number of individuals per hectare) and biomass kg per hectare) by atoll for the three functional trophic groups that were significantly related to fish assemblage differences. Error bars are standard errors. Functional trophic groups are explained in Table S2.

Fig. 5. nMDS diagram showing the relationship between benthic variables at 11 reef sites overlaid on the fish assemblage ordination (see Fig. 2) across the Chagos Archipelago. The relative contribution of each benthic variable is displayed by the length of the vector.

Fig. 6. The relationship between individual species and the fish species density ordination based on the 13 fish survey sites.

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P.O. Box 24562,
Nairobi 00502, Kenya
Mobile : +254 721498713/+447393622355
Email: melita.samoilys@gmail.com
www.cordioea.net

14th November 2017

Dr Heather Patterson
Scientific Editor,
PLOS ONE

Dear Dr Patterson

Thank you for the second review of our paper: *Patterns in reef fish assemblages: insights from the Chagos Archipelago*.

We have addressed the comments from the two reviewers and your editorial comments in the revised manuscript. In making our revisions we have addressed your concerns that the conclusions of the study are overstated, there is a general lack of clarity in the paper and the points raised can be dealt with in a re-write, particularly in the Discussion. We also provide a response to each comment raised by the reviewers below.

We trust that the manuscript now meets Plos One's publication criteria.

Yours sincerely

Dr Melita Samoilys
Director

Authors' Response to Editor and Reviewers

Please Note: the Line numbers refer to the marked up revision version of the ms.

Editor's editorial comments

All the editorial corrections have been made on the revised manuscript, or have been addressed during the revisions made as outlined in the tables below, with one exception:

Line 546: Awkward, should be 'but also feeds on…..'
The sentence has been revised differently as the point being made is that *A. nigrofuscus* feeds on epilithic algae while *Scarus niger* does not, though both are feeding on the same sort of substrate. The revised text clarifies this better (Line 677). The point is further explained later under "feeding complimentarity" (Lines 686-687).

Reviewer #3:

Reviewer's comment	*Authors' response*
the hypothesis (Line 68-72) states that since there is no fishing pressure, the fish assemblages should reflect bottom-up drivers. I understand that they see humans as the top-down force here, but in a system where the natural (fish) predator population is intact, it is likely that these organisms would in fact have a stronger top-down influence than in fished systems. Thus, the premise of this hypothesis needs a stronger justification.	Agreed. Text changed in Lines 80-81 to acknowledge the inputs from natural top-down control of fish populations through predation.
The authors state that there may be some poaching in this reserve area, although the presumption is that it is 'minimal' (line 404) due to lack of human residents here. Yet later (line 470), it is stated that it is likely there is some poaching from afar. It would be helpful to know how well patrolled the area is, and if poaching incidents have been observed, if any of the studied reef areas are more vulnerable.	The BIOT MPA is patrolled by the BIOT Patrol Vessel (BPV). Due to the illegal nature of poaching activity within BIOT, and the difficulties in detection and monitoring, it is challenging to make definitive statements regarding its prevalence. The most detailed and up to date data are available in a Clark et al. 2015 MRAG report entitled "Update on the catch and bycatch composition of illegal fishing in the British Indian Ocean Territory (BIOT) and a summary of abandoned and lost fishing gear." Between one and twelve vessels have been detained annually on suspicion of illegal fishing activities between 1996 and 2015. The mean catch per vessel detained from 2006 to 2015 was 2,558 kg or 386 individuals. Sharks were present on 91% of vessels and formed 60% of total catch numbers and 80% of total weight. Thus it can be clearly observed that a range of shark species are the main group targeted by illegal fishing activity. As to whether any of the studied reef areas are more vulnerable, a map of the locations of vessel detentions within the MRAG report suggests that poaching effort is spread evenly across the Archipelago, with the possible exception that vessels do not appear to venture close to Diego Garcia, likely due to US navy presence. The text has been changed to incorporate this briefly (Line 547-550).
It is stated that massive bleaching occurred 15 yrs prior (line 439) & that recovery occurred (line 441) -if site-specific data could be obtained from the Sheppard et al 2012 study, this would allow a much stronger argument for bottom up forcing, as it is stated that fish assemblages were previously homogenous. Varying levels of coral recovery coincided with changes in	This is a valuable point, however there are two main issues which we see with attempting to obtain and analyses data from the Sheppard et al 2012 publication. The data referred to in Sheppard et al 2012 were obtained using eye-estimates of coral cover within quadrats, which is different from the video transect technique used in the present study, so comparability is not clear. There is also an issue in that the specific sites are not the same in the present study and the 2012 study, which would further jeopardize the ability to carry out such an analysis.

management in this area, so there is a chance to look more deeply into these drivers if earlier data could be utilized.	
In the paragraph beginning on line 486 the authors discuss feeding of 2 types of *Acanthurus*. Line 493 needs clarification on whether these species feed in sandy areas, or just on the detritus overlying dead coral substrate. This is important for the comment on line 500 - if they are feeding in sand patches, it is unlikely that these species have any impact on macroalgae growth.	The text has been changed (Line 599-600) to clarify that these species feed on soft sediment on dead coral substrate, as well as sand, and therefore may impact macroalgal growth.
The sentence on Line 503-505 needs to be re-written - detritivory seems tacked on, making a broad statement.	Agreed. The lines 609-615 have been re-written to clarify the statements on detritivory.
Line 526 - it sounds like there is a suggestion that coral mortality leads to increase in zooplankton. Please provide references to substantiate this link.	This was not intended at all, and is not a correct interpretation. The sentence states there are apparently two different pathways (line 654) for the higher acanthurid densities at GCB: higher zooplankton for the planktivorous acanthurids (e.g. *Naso* spp.) and dead coral for the detritivorous acanthurids (ring tail *Acanthurus* spp. and *Ctenochaetus*). We have revised this sentence to spell this out more clearly.
Lines 528-530 state that the bottom-up processes only act on the lowest trophic levels - if this is the case, it undermines the bottom-up conclusion.	The sentence at 528-530 does not specifically state "that the bottom-up processes only act on the lowest trophic levels". It states that "the density and biomass of the piscivore and omnivore trophic groups, species that represent important target fishery species [23,39], were not significantly correlated with fish assemblage patterns across the archipelago, suggesting that benthic differences did not affect these higher trophic level taxa." To improve this text to avoid the reviewer's interpretation we have added the word "directly" (Line 659). We recognize that piscivores and omnivores are affected by bottom up processes through their prey which are in turn affected directly by bottom up benthic condition.
Line 532- provide a reference to support the link between the previous coral mortality and climate change so that this is a stronger statement rather than a presumption.	The following reference has been added (Line 662) and replaces an earlier paper by Sheppard for reference no. 22. Sheppard, C. R. C., A. Harris, and A. L. S. Sheppard. "Archipelago-wide coral recovery patterns since 1998 in the Chagos Archipelago, central Indian Ocean." *Marine Ecology Progress Series* 362 (2008): 109-117.
Line 535: The authors seem to set up a straw man, aggregating fish	The functional groups used are quite finely divided (12 functional groups) rather than broad scale, and are

into broad trophic groups, and then using the failure of those broad groups to show clear trends to say we need to look more fine-scale. There are many excellent studies, some of which are cited, that have clearly shown that within-trophic group differences can be strong and important - this is re-stated line 562, so I wonder why the attempt at over-simplification was even made. The authors again caution against doing what they themselves did in line 600. There are great opportunities with this dataset for a deeper exploration.	based on widely used guidance for using fishes as indicators of coral reef resilience (Green & Bellwood 2009), and refined for the Indian Ocean specific groupings (Samoilys & Randriamanantsoa 2011). Many studies have used far more broadly defined functional groups; for example, Graham, Nicholas AJ, et al. "Lag effects in the impacts of mass coral bleaching on coral reef fish, fisheries, and ecosystems." *Conservation biology* 21.5 (2007): 1291-1300, utilised five groups in their assessment of fish and coral benthos interactions within the Seychelles. So an exploration of the utility of the "best currently available" fish functional groups for the Indian Ocean within this dataset from the Chagos Archipelago, where such an analysis has not previously been carried out, is in the opinion of the authors, a valuable and logical methodology to incorporate into the study. Deeper exploration which extends beyond functional groupings has also been carried out within the study, in the BIO-BIO analysis, which utilised each individual species, and multiple permutations of species-level groupings to come to its findings. Some comparison between the two approaches is therefore valid.
Lines 563-566: it is mentioned that parrotfish populations declined (though not via fishing). Support that what you found was a decline, rather than increases (presumably these data can be compared to the pre-bleaching study?). And once again, the potential for even 1 big poaching event to have a big impact cannot be ignored.	We do not state that parrotfish declined in our study. Our study is one point in time and therefore we can only compare and discuss differences between sites across the archipelago, not differences over time. The point being made here is that the difference in parrotfish population densities between atolls was very large and this cannot be assigned to fishing. Parrotfishes have not been fished in Chagos, except perhaps minimally by the recreational fishery in Diego Garcia. They are not a commercial target and therefore poaching is not an issue. This point is made clear in the section on the effects of fishing where the commercial Mauritian fishery that used to operate targeted just two families of reef fishes – grouper and snapper.
Lines 584-588 state that the parrotfish are bottom-up controlled, but I still am not convinced by the correlative nature of this study that this is the case. Using these same results, one could easily argue that the parrotfish have been influential in determining coral recovery trajectories in this region, so are a top-down force.	We stand by this statement that our results "suggest that parrotfish are bottom-up controlled", because the significance testing in our results was done on the basis of permutation testing not just on the existence of a correlation between datasets. We agree that parrotfish may be/are influential in determining coral recovery trajectories, our statements do not contradict this, but we cannot test this with our data at one point in time. But we have now added some text to include this point (Line 727-729).
Line 600: clarify whether the assumption of fishing as a driver of parrotfish is meant to be just for Chagos or everywhere.	Sentence changed to include "elsewhere" (Line 749).

Reviewer #4:

Reviewer's comment	*Authors' response*
You state that abiotic and biotic factors are assessed, when really the data are just on the benthic habitat and fish associations. Line 67 - what abiotic factors were considered in this study - none is my understanding	Agreed, since the testing of exposure and reef geomorphology type were limited and inconclusive due to limited sample size. Line 77 revised to read "largely biotic factors". Exposure and reef geomorphology type were tested and the results of significant differences in exposure cannot be interpreted further due to limited replication.
You state that one of the main aims was to look at size structure, but this is not assessed at all. Line 76 - where is the size structure component to this study then?	Fish size is incorporated into biomass estimates (the latter derived from fish size using species' length-weight relationships). We have changed "size" to "biomass" eg Line 92.
you say upfront in the discussion that the major differences in the fish assemblage you describe are due to environmental conditions and climate change - there is nothing to support this statement based on the results currently.	We have re-worded and expanded the statement originally at 402 (now Line 457-458) to qualify that environmental drivers and climate change are reflected in the reef's benthic composition.
Line 57 top-down control can also be mediated by predation by larger fishes, not just fishing.	The text has been changed to clarify this point in Line 80-81.
Especially worrisome is the huge noise around the large bodied planktivores, which then becomes one of your main results you discuss. It looks to me like you just happened upon a large school, so making inferences on the GCB being really plankton rich is not very compelling. It is also counter to what I would expect, surely the island with oceanic sides would have greater plankton resources available, with cool deeper water bringing food in? This warrants a bit more discussion, or checking of the raw data, to see if it is just a couple of large school sitings that are causing this result.	The reefs that were surveyed on the western side of Great Chagos Bank are on forereefs and terraces off the islands. Most of GCB is a vast, largely sunken, atoll and it is extensive compared to the other atolls of the archipelago which are more discreet and isolated. We would counter that it is not that surprising that plankton might be richer here. Since there are no published results on plankton in Chagos these discussions are somewhat conjectural and we do not believe merit a major emphasis in the paper. We do not feel it is a "main result". Nevertheless, the planktivores were one of 3 significant trophic groups out of 12 in the analyses and therefore warrant some discussion. The higher planktivorous densities at GCB are not explained by 1-2 very large schools. For example, *Naso brevirostris* and *Melichthys* spp. were highly abundant at Three Brothers reef on GCB, with *Melichthys* spp. also very abundant at the forereef at Diego, whereas *Naso hexacanthus* was highly abundant at Egmont Inner reef on GCB, but also at one site at Peros Banhos atoll. In contrast *Naso vlamingii* was highly abundant at some sites in all three atoll groups, though the highest density was at a GCB site. Importantly, we maintain that while the dataset is

	small and variances are high, typical of UVC surveys of reef fishes, particularly those that school, which include many of the planktivorous species counted here, the statistical tests (random permutation tests having first tested for spatial autocorrelation) were robust. Therefore, the significant differences are likely real and not spurious.
The focus you make of using the Chagos as a benchmark for other Indian Ocean reefs - it would be useful to know how the estimates of biomass compare.	Text added at Lines 587-592 to make this point clearly.
How is terrace and fore reef combined classified? and how does it differ from just from forereef. It would be beneficial to add the exposed or protected classification to Table S1, as well as the number of surveys performed at each site.	Terrace is a substantial shallow sloping area. The forereef is a more steeply sloping area. A characteristic feature of the atolls is a terrace that then gives way to a forereef as opposed to fringing continental reefs which tend to have just forereefs. However, at two islands at GCB there was no terrace. The exposed or protected classification is inherent in whether a site is a lagoon site or not. All non-lagoon sites are exposed, therefore, we feel adding an additional classification is unnecessary. One survey (consisting of multiple transects of both fish and benthos, as outlined in the methods) was performed at each of the sites.
To quickly allow for comparisons across Fig1 and 2, I suggest you use the same color coding on the map as you've used in the dissimilarity plots	Good suggestion, Fig.1 has been changed.
Fig 2 legend - what does significant fish species assemblages mean? The figure legend could be more informative.	The legend for Fig 2 has now been changed to be more informative (lines 298 and 786)
Line 219 - reference for VIF < 10 being acceptably low for colinearity. I thought 3 was a widely accepted threshold.	There are no universally accepted thresholds for an acceptable VIF level. Less than 2.5/3 is one level, less than 10 is another level. Certainly greater than 15 or 20 is unacceptably high. Whilst widely referred to in a variety of publications the original reference for the <10 level is: Chatterjee, S., A. S. Hadi, and B. Price. 2000. Regression analysis by example. John Wiley and Sons, New York, New York, USA.
Line 389 - Siganus argenteus Siganus canaliculatus - is this just due to not surveying the right habitat? Or encountering of their large schools?	The point being made here is that the lack of siganids should not be interpreted to mean that there are no siganids in Chagos. We have re-worded the text to make this clearer (Lines 445-446). Aspects of habitat and school size are valid but exploring these factors is beyond the scope of our dataset.
Line 402 - there is no information presented in this ms on the environmental conditions at Chagos, or across the reefs surveyed, or any	We partly agree with this comment – certainly no temporal data are presented. We have re-worded and expanded the statement (now Line 457-472) to qualify that environmental drivers and climate

temporal component to this work, so it seems a large leap to take this descriptive study that nicely differentiates between reefs in one location at one point in time, to making inferences on the drivers of these differences.	change are reflected in the reef's benthic composition.
Line 404 - the inference that generally fishing effort is low or minimal impact is counter to the statement below on the grouper fishery, as well as illegal fishing, as well at the recreational fishery. It would be a relatively easy thing to separate out targeted and non targeted species to compare biomass/abundance in areas where the recreational fishery is operating, and this could substantiate the focus you have made on fishing effects in the discussion.	The "focus on fishing effects in the discussion" is not a major element of the study because the study was not designed with the intention of examining fishing effects, and therefore the data are inadequate for examining any fishing effects around Diego Garcia. We cover potential fishing effects in the discussion to make as clear as possible what are the deviations from the assumption of minimal fishing impact within the Chagos Archipelago and its MPA. Further, the information on possible illegal fishing from India is purely anecdotal. We mentioned it to illustrate some uncertainty over the unfished status of Chagos. On the basis of this reviewer's comment the text has been revised to remove the anecdotal report from India as it adds confusion, and have made it clear that fishing effects cannot be tested with the current dataset. (Lines 528-529, 554-556).
Line 449 - I tend to disagree with this follow on assumption that if acanthurids are more abundant where their food is, where their food resources are high is because of coral mortality. These species can thrive in areas which are continually disturbed, where coral never becomes dominant, or recruits never get established, such as a crustose coralline algal dominant reef crest which is in the surf impact zone. This limits their utility as an indicator species and also the framing oversimplifies the view of what a coral reef ecosystem is, ignoring their naturally very variable status. I think you could just deal with this with a bit more careful wording in this paragraph.	This interpretation was not intended at all, and is not correct. The sentence states there are apparently two different pathways for the higher acanthurid densities at GCB: higher zooplankton for the planktivorous acanthurids (e.g. some *Naso* spp.) and dead coral for the detritivorous acanthurids (ring tail *Acanthurus* spp. and *Ctenochaetus*). We have edited this sentence to spell this out more clearly (Line 658). We agree entirely with this reviewer that coral reefs are naturally very variable, hence the difficulty in assigning drivers to differences in fish assemblages.
Line 535 - Explain this sentence further. Significant in what? Line 537 - more informative to what?	Text has been revised to explain the two sentences, Line 670-672.
Line 564 - As a general comment, that applies throughout - your reports of biomass per hectare should also include the standard deviations, which	Where biomass is reported in the results text and figures (eg Fig. 3) we provide error terms. We do not feel we need to clutter the Discussion with error terms, particularly when discussing biomass, we

for S.niger are rather enormous. Did you encounter a couple of large schools?I'm concerned you are making inferences from a behavioural event that leads to inflated mean estimates to imply that that number of fish is generalizable per hectare in that location. I agree with the point, parrotfish biomass can vary widely independent of fishing effects, but I think the extreme range more likely reflects a limited sample size, or an encounter with a large school.	tend to refer to a range or a maximum, e.g. > 3,000 kg/ha. The concern that UVC estimates of reef fish populations can be biased by 1-2 large schools is valid. We selected a standard fish UVC method based on 5 replicate 50x5m transects per site after Samoilys and Carlos 2000 which tested a variety of UVC methods weighing up their relative accuracy and precision, and found that scarinae were well estimated by this method. Further, while the dataset is small and variances are high, typical of UVC surveys of reef fishes, random permutation tests having first tested for spatial autocorrelation) were robust, accomodating the variances and still found significant differences. We therefore maintain these are valid. Regarding schooling behavior of parrotfishes and one-off events eg for *Scarus niger*. The mean biomass of this species was consistently high across reefs in Peros Banhos and Salomon atolls, ranging from 102 to 181 kg/ha except for PB Ilse de la Passe where the biomass was slightly lower at 67 kg/ha. In contrast the biomass at the other atolls ranged from 3 to 38 kg/ha with zero at DG lagoon. The PB and Salomon biomass estimates are based on a total of 7 sites with 5 replicate transects per site. The variances are high (see table S4) but the statistical tests detected differences.
Line 584 and Line 594 - It is difficult to infer anything about bottom-up control from this observational data on the habitat characteristics of where these species are most abundant.	We are not clear exactly what the reviewer means by this comment. The habitat characteristics were quantified (benthic surveys, see Methods) and are not therefore "observational". The statement regarding bottom-up control, originally at 584 (now Line 729-731) reflects our interpretation of the significant permutation tests of the benthic data (Table 2, Fig. 5) and the ordination analysis on species' density (Fig.6, Table 3).
Line 586 - Yes, apart from you found no differences between herbivore trophic groups (Line 535) - you've uncovered species specific patterns not evident at the functional group level.	We have removed the reference to the Heenan et al. paper here (Line 733). The Heenan paper (recommended by a previous reviewer) is excellent but requires too much text to explain its significance here, so we edited the citation to it in the conclusions (Line 759-760).
Line 591 - You have stated previously that there has been an grouper fishery at Chagos and and likely there is some illegal take going on, as well as a recreational fishery. It seems more appropriate to say minimal fishing impact, rather than total absence	Text amended, Line 737.
Line 604 - drivers or mechanisms?	Drivers. We mean drivers of the populations of parrotfishes and surgeonfishes. Sentence has been edited (Line 757).