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# Marine reserve recovery rates towards a baseline are slower for reef fish community life histories than biomass

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Ecological baselines are disappearing and it is uncertain how marine reserves, here called fisheries closures, simulate pristine communities. We tested the influence of fisheries closure age, size and compliance on recovery of community biomass and life-history metrics towards a baseline. We used census data from 324 coral reefs, including 41 protected areas ranging between 1 and 45 years of age and 0.28 and 1430 km$^2$, and 36 sites in a remote baseline, the Chagos Archipelago. Fish community-level life histories changed towards larger and later maturing fauna with increasing closure age, size and compliance. In high compliance closures, community biomass levelled at approximately 20 years and 10 km$^2$ but was still only at approximately 30% of the baseline and community growth rates were projected to slowly decline for more than 100 years. In low compliance and young closures, biomass levelled at half the value and time as high compliance closures and life-history metrics were not predicted to reach the baseline. Biomass does not adequately reflect the long-time scales for full recovery of life-history characteristics, with implications for coral reef management.

## 1. Introduction

Heavy fishing pressure, and associated declines in stocks and biomass is widespread throughout the world's fisheries [1,2]. Declining biomass is associated with changes in the taxonomic composition and life-history characteristics of the fish communities—typically towards species with small body sizes, early maturation, lower trophic levels, and those that benefit from prey or competitor release [3–6]. Taxa with fast life histories can maintain populations and production in the face of high fishing mortality but, nevertheless, are expected to undergo phenotypic or genetic change under new conditions and associated selection pressures. This ecological and evolutionary selection has been shown to influence the life histories of species, such as size and age at maturation, sometimes with negative consequences for fisheries production [7–9]. Consequently, holistic management of fisheries needs to understand the complex interactions between fishing and fish community's life history and to develop metrics, models and baselines that consider fishing pressure impacts [10,11].

A number of studies have shown that fishing moratoria or closures (marine reserves) result in recovery of fish numbers and biomass, frequently on the scale of 15–25 years [12–15], but sometimes reported as more rapid [16] or slower [1]. Recovery at the population level is, however, not assured and may depend on the history and intensity of fishing, population characteristics and interactions with the environment [11,17]. For example, closures will differentially influence fish life histories depending on whether or not the taxa are of commercial value, low or high mobility, their body sizes, schooling or territorial behaviour, and their feeding and depth preferences [12,15,18–20]. In some cases, life-history responses can be weakly coupled with biomass and change after biomass has stabilized [21]. Specifically, community biomass asymptotes early, probably owing to limits of production, but density or biomass-dependent processes are hypothesized to cause further shifts in taxonomic composition, size

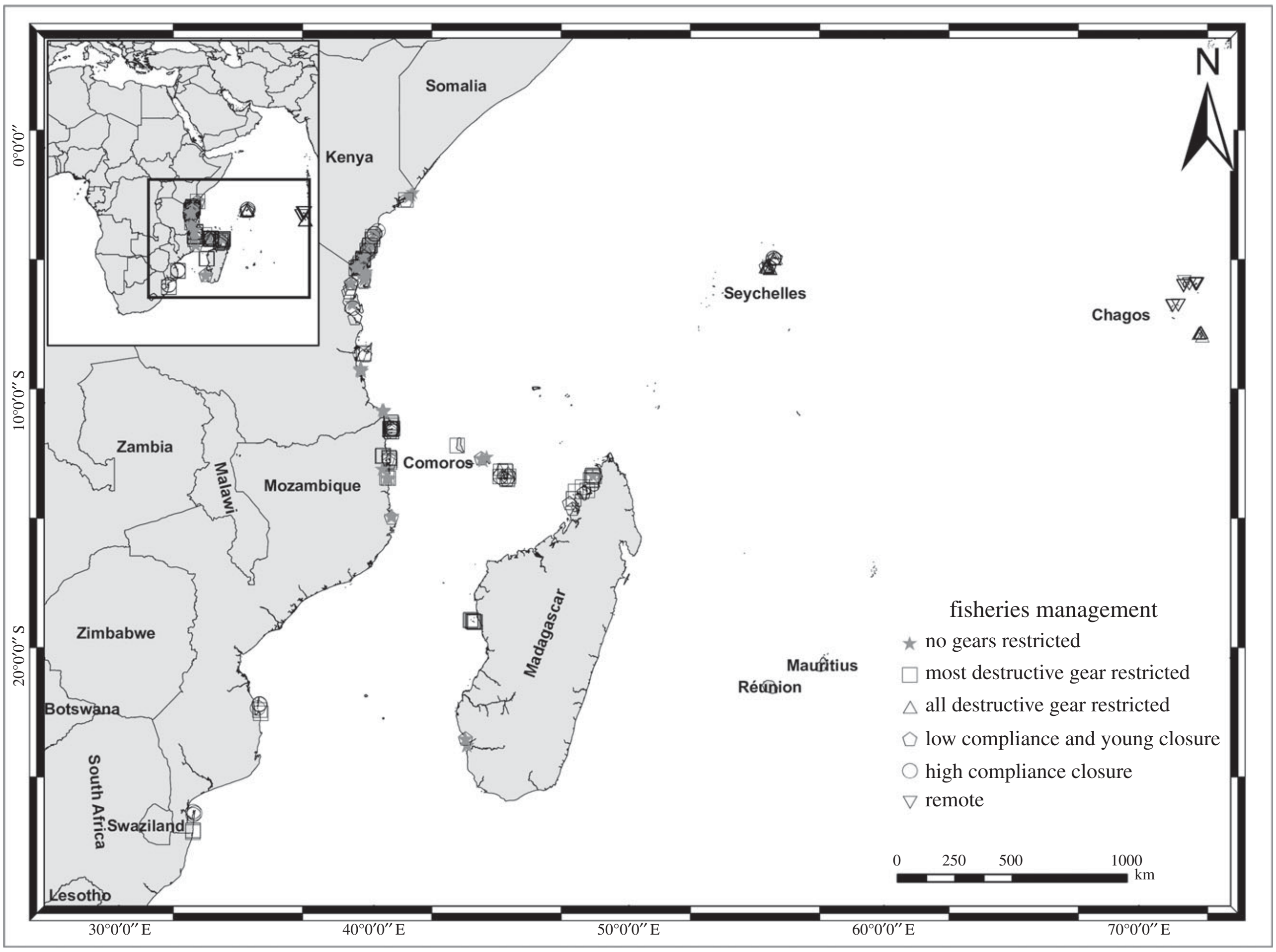

**Figure 1.** Map of the study locations in the western Indian Ocean, including the various categories of fished areas, closures and remote wilderness sites. Details of each location are given in table 1.

composition and life histories. Conditions of limited productivity and increased biotic interactions are expected to promote slower maturation and larger body sizes [21,22]. These findings beg the need to better understand rates of recovery towards baseline conditions and to develop management that recognize not only fisheries production targets, but also life history and ecosystem considerations [23].

In order to better understand the impacts of fishing and recovery, we evaluated changes in key life-history characteristics of coral reef fishes across the Indian Ocean. We evaluated the roles of closure age, size and compliance on the weighted life histories of the fish community in 324 coral reef sites, of which 47 sites were in high compliance and 52 were in low compliance and young closures that ranged in age from 1 to 45 years and size from 0.28 to 1430 km$^2$. These life-history characteristics were compared to a remote baseline system in the region, the Chagos archipelago [24], and also to fisheries using different forms of gear management [20]. These comparisons of gear management, closure compliance, size and age, and remote wilderness were designed to determine life-history responses and more fully understand fisheries and management impacts. Our central hypotheses were: (i) that life histories would change towards larger and later maturing taxonomic composition after community biomass levelled, (ii) that 45 years would not be sufficient time to reach the fish community life-history states of remote wilderness areas, and (iii) the compliance status of the closure would influence state and rate estimates.

## 2. Material and methods

### (a) Site descriptions

Coral reef fish assemblages were surveyed at 324 sites in eight countries of the Indian Ocean, including the Chagos archipelago, the Comoros, Kenya, Madagascar, Mayotte, Mozambique, Seychelles and Tanzania (figure 1). We sampled common coral reef fish in sites that ranged from 1 to 20 m in depth (mean = 4.6 m depth). Sites were located along the back and fore reef of typical carbonate reefs dominated by hard corals and other benthic organisms, including turf and encrusting coralline algae, and lower abundance of soft corals, sponge and erect fleshy algae.

The 324 study sites were classified into six dominant management categories following [20]. The first three were all nominally unfished, protected reefs containing 135 sites: (i) large, uninhabited remote protected area, which includes sites in the 640 000 km$^2$ Chagos Marine Reserve ($n = 36$ sites); (ii) high compliance closures, which include marine parks with active patrols and parts of the Maldives where there is a national policy of highly restricted benthic fishing ($n = 47$ sites); (iii) low compliance and young closures, which include closures without regular or effective patrolling and enforcement ($n = 52$ sites). The other three management categories were 189 reefs open to fishing but the types of fishing gears allowed varied. These included: (iv) all destructive gears restricted, which are sites where only line fishing and traps were permitted ($n = 22$ sites); (v) most destructive gears restricted, which are sites where spearguns and gill nets were also used ($n = 87$ sites); and (vi) no gears restricted, which are sites where drag or small meshed net seines and explosives were also used ($n = 80$ sites). These classifications were based on a mixture of national laws, discussions with fishers and managers, local reports and publications, and our own observations during the sampling periods. In the high compliance and low compliance and young closures, the ages since full closure and sizes were extracted from published information, but sometimes modified based on local knowledge of when management systems actually began, as opposed to legal establishment (electronic supplementary material, table S1). Comparisons of these management systems in space were presented in [20] and here we focus on the changes in fish communities with the age of the closures.

## (b) Field methods

Data were collected from 1988 to 2014, resulting in a database of 527 site–time combinations. Samples in the fishing categories were pooled for all times, whereas the closure categories were only pooled when the sites were sampled in the same year. This resulted in the final 324 reef site replicates used in the analyses. The abundance and size of diurnally active, non-cryptic, reef-associated fishes was quantified at each site using underwater visual census techniques. The studied taxa are mostly site-attached species that occupy reefs, with few being generalist, mobile and large taxa that travel large distances and occupy more habitats and depths. Fish families surveyed included: Acanthuridae, Aulostomidae, Balistidae, Carangidae, Carcharhinidae, Chaetodontidae, Diodontidae, Fistularidae, Ginglymostomatidae, Haemulidae, Holocentridae, Labridae, Lethrinidae, Lutjanidae, Mullidae, Pempheridae, Penguipedidae, Pomacanthidae, Pomacentridae, Scaridae, Scorpaenidae, Serranidae, Siganidae, Sphyraenidae and an ‘Others’ category for the uncommon taxa. In the Comoros, Kenya, Madagascar, Mayotte, Mozambique, the Maldives and Tanzania fishes were counted within one to five 500 $m^2$ belt transects [25]. In Seychelles, fishes were surveyed within eight point counts, each covering a 154 $m^2$ area [26]. In Chagos, fishes were surveyed within four 250 $m^2$ belt transects [24]. In all methods, observers avoided confusion and double counting by surveying larger mobile species first (i.e. Lutjanidae, Scaridae, Serranidae), followed by site-attached species (i.e. Labridae, Pomacentridae). There may be small amounts of variation associated with different survey techniques; however, studies comparing methods have found little difference between belt transects and point counts in estimating fish abundance and community biomass [12,27,28].

## (c) Data analyses

Community-level biomass was estimated from individual fish-length data using length–weight relationships for species or families [29,30]. Of these 25 groups of fish sampled, 16 of the common families were used for community life-history analysis and chosen because they were abundant, had life-history data for a number of the common species, and they were taxa commonly caught in the coral reef fisheries. For example, the Pomacentridae were removed from the analyses, as they are not strongly influenced by fishing and their inclusion added variance most probably due to their responses to benthic habitat or plankton concentrations, which were not effects of fishing being examined here.

The two shark families, Carcharhinidae and Ginglymostomatidae, were almost exclusively found in the remote sites. We were particularly interested in the recovery relative to the remote category baseline but recognized that this could be sensitive to the inclusion or exclusion of sharks in the analyses. It is possible that most fisheries closures in human-dominated shallow reefs will not support large populations of sharks or, at least, that they are difficult to sample in standard daytime visual census transects. Consequently, we evaluated the metrics with and without sharks using one factor ANOVA tests prior to estimating their recovery to a baseline.

Life-history characteristics of the 16 families were compiled using life-history data available in FishBase [30]. The life-history parameters included were: maximum length (cm), growth rate (cm $yr^{-1}$), natural mortality (M), lifespan (yr), generation time (yr), age at first maturity (yr), length at first maturity (cm), length to achieve optimum yield (cm) and trophic level. We extracted the values from the dominant species we counted in transects and used the averages of these in our family-level evaluations as described in [21]. Calculations of community life histories are weighted values such that the mean value for a site was calculated as the biomass of each family group times the mean life-history metric for the specific metric, summed for all families and divided by the total biomass.

A previous study evaluated life-history parameters at the species and family level in three of the countries (Seychelles, Chagos and Maldives) and found little difference in species versus family evaluations [20]. Because the family-level data were more inclusively sampled in terms of spatial replication, the analysis here is based on family-level data where life histories are based on average values of the common taxa in these families in the region. The removal and pooling of some taxa had a small effect on the total community biomass evaluated. For example, 7.3% of the total biomass was not accounted for in the community life-history calculations and 5.6% if sharks were excluded in biomass calculations.

Mean values of the three fisheries management categories (no, some, all destructive gear restricted), and the remote areas were calculated for comparison with the closures. Data at the transect level were pooled into reef sites and times for the analyses, such that variance for closures and ages could be calculated for replicated sites and times. The age, size and compliance of closures were the main categories used for the analyses. The Bazaruto National Park, Mozambique was approximately 40 times larger than the next largest closures, and we therefore removed it from size based analyses. Data collected from a single ecosystem and region constrains variability and we believe the space-for-time substitution proxy method used here should therefore reflect temporal change adequately [12,13,21].

The effects of size, age and their interactions were tested by two-factor ANOVA for the low and high compliance closures separately. Community biomass and life-history metrics against age and size were tested against a number of common models, including linear, logistic, asymptotic and Ricker equations. Akaike information criterion (AIC) and $R^2$-values of the best-fit models were compared to evaluate the most likely relationships for high and low compliance and young closures. We solved the logistic and asymptotic equations to obtain the time to 90 and 95% recovery, to estimate a recovery time that was not sensitive to the long-tail-end dynamics of these equations. All analyses were run in R v. 3.1.3 (R Team 2013) or JMP-Stats v. 11.0 [31].

# 3. Results

## (a) Community biomass responses

Community biomass in the high compliance closures recovered on the scale of 20 years (figure 2). Ricker, logistic and asymptotic equations had similar fits (delta AIC $< 2.5$) and predicted between 36 and 38% of the variance (electronic supplementary material, table S2*a*). Both the logistic and asymptotic equations predicted a biomass levelling at approximately 1150 kg $ha^{-1}$ and reached 95% of this value at approximately 18 and 23 years, respectively. Biomass in the low compliance and young closures recovered on the scale of 10 years but to maximum values of approximately 600 kg $ha^{-1}$. The Ricker equation with its deflection after peak values was the best-fit equation and predicted 29% of the variance. The good fit to the Ricker model indicates a decline in biomass after 10 years

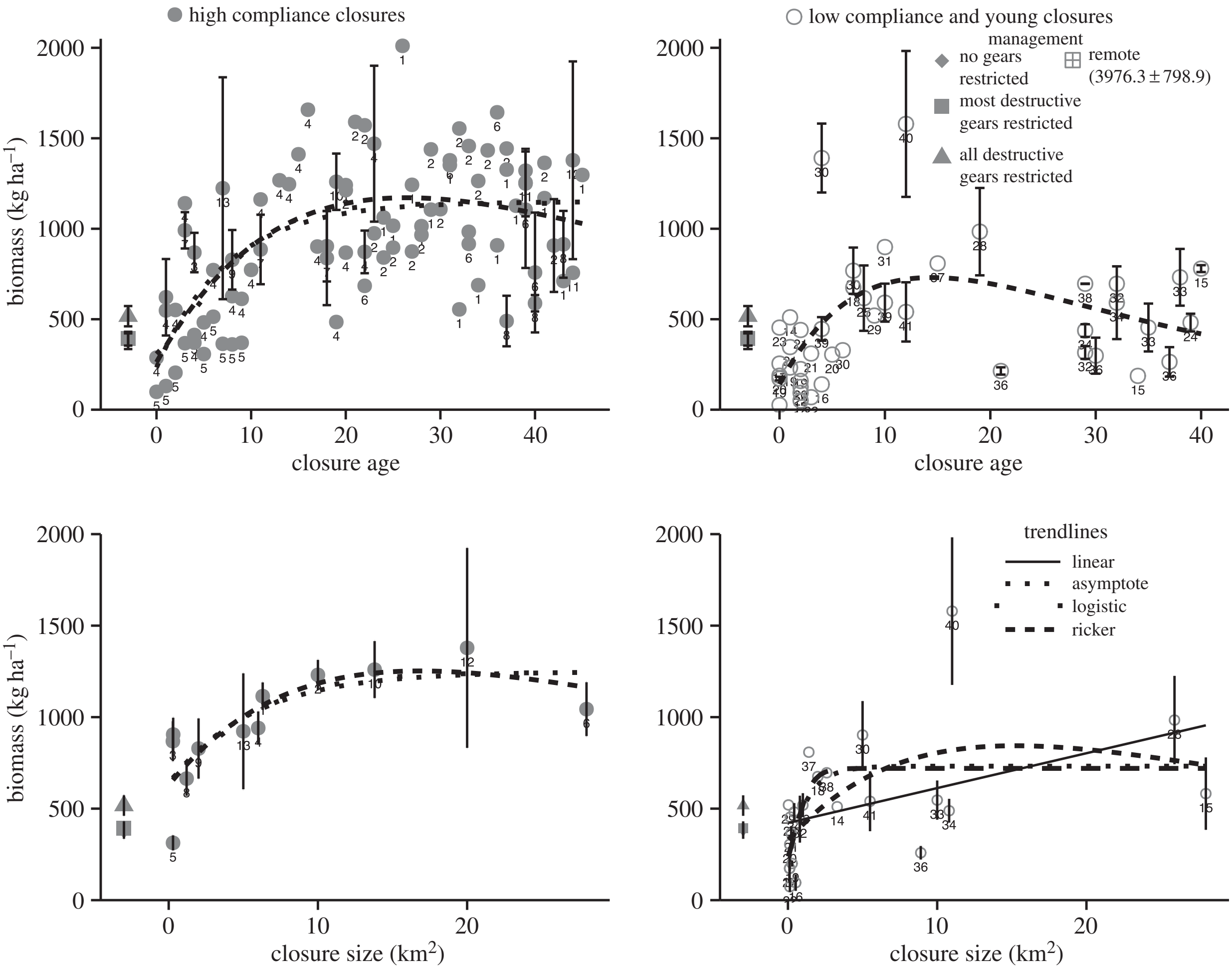

**Figure 2.** Reef fish biomass as a function of age and size of closures for high and low compliance classifications. Numbers indicate the closure used in the analysis and names and other details are given in table 1. Full statistical evaluations are presented in the electronic supplementary material, table S2*a*. Lines of the best-fit model equations indistinguishable based on AIC are shown.

to approximately 400 kg ha$^{-1}$ by approximately 40 years in this closure system. Biomass in remote areas was highly variable and not different for comparisons with and without sharks, with values approximately 3700 kg ha$^{-1}$. Biomass in the high and low compliance and young closures was approximately 29% and approximately 11% of the remote areas, respectively (figure 3). Fished reefs in the three gear restriction categories had biomass levels that aligned well with the early closure values and ranged from approximately 10 to 13% of the remote baseline community biomass.

Community biomass responses with the size of the closure was stronger for high than low compliance and young closures and indicated a biomass maximum of approximately 1150 kg ha$^{-1}$ at approximately 10–15 km$^2$ (electronic supplementary material, table S2*b*). Biomass in low compliance and young closures was quite variable with closure size and levelled at approximately 600 kg ha$^{-1}$ at 2–10 km$^2$. Size and age interactions were statistically significant and negative in both high and low compliance and young closures suggesting that the two factors interact antagonistically and this interaction is stronger in the low than the high compliance closures (low compliance: $t = -4.1$, $p < 0.0001$, high compliance: $t = -2.4$, $p < 0.02$; electronic supplementary material, table S3).

## (b) Life-history responses

When comparing community life histories with and without sharks in the remote sites, only the length measurements were affected by the inclusion of sharks (table 1). For example, maximum lengths in the remote reefs reached approximately 72 and approximately 52 cm with and without sharks included. Community weighted maximum length, length at maturity and optimum yield without sharks were auto-correlated and displayed similar responses and fits to the Ricker, asymptotic and logistic models with the age of closure (figure 3 and electronic supplementary material, table S2*a*). These length metrics increased with the age of the closures and model fits predicted between 32 and 36% and 17 and 25% of the variance for the high and low compliance and young closures, respectively. Body lengths in low compliance and young closures were weakly and linearly associated with the size of closures predicting approximately 20% of the variance (electronic supplementary material, table S2*b*).

In high compliance closures, maximum community body length of 41 cm was predicted to reach 95% of its maximum at approximately 45 years, or the end of the data time series. In low compliance and young closures, the 95% of maximum lengths was approximately 45 cm and was reached at approximately 27 years. Length at maturity of approximately 24 cm reached the 95% of maximum at approximately 31 and 33 years in high and low compliance and young closures, respectively. Length at optimum yield of approximately 27 cm reached 95% of maximum at 31 and 32 years in high and low compliance and young closures, respectively. The remote wilderness values were quite different from the other five management categories with maximum lengths between

**Table 1.** One-way ANOVA comparing the biomass and life-history characteristics of the remote sites of the Chagos evaluated with and without sharks. Per cent difference of the various management categories compared to the Chagos wilderness baseline with sharks. (The values for the high and low compliance and young closures are the equilibrium end-state values. n.s., not significant.)

| life history | biomass | maximum length | length at maturity | length at optimum yield | lifespan | generation time | age at maturity | growth rate | natural mortality | trophic level |
|---|---|---|---|---|---|---|---|---|---|---|
| (*a*) one-way ANOVA | | | | | | | | | | |
| remote with sharks | 3976.3 ± 4793.7 | 71.9 ± 39.4 | 35.4 ± 16.3 | 43.7 ± 25.3 | 11.1 ± 1.6 | 3.4 ± 0.6 | 2.54 ± 0.32 | 0.39 ± 0.05 | 0.78 ± 0.09 | 2.99 ± 0.51 |
| remote without sharks | 3605.5 ± 4358.9 | 51.8 ± 4.9 | 27.2 ± 2.4 | 31.0 ± 3.1 | 10.7 ± 1.5 | 3.2 ± 0.5 | 2.51 ± 0.34 | 0.39 ± 0.05 | 0.79 ± 0.08 | 2.86 ± 0.50 |
| *F* ratio | 0.12 | 9.28 | 8.82 | 9.0 | 1.19 | 2.62 | 0.38 | 0.02 | 1.78 | 2.13 |
| *p*-value | n.s. | 0.0033 | 0.0041 | 0.0037 | n.s. | n.s. | n.s. | n.s. | n.s. | n.s. |
| (*b*) percentage of remote baseline (Chagos) | | | | | | | | | | |
| high compliance closures | 28.8 | 65 | 69.9 | 63.5 | 91.9 | 91.8 | 95.7 | 108 | 111.3 | 93.3 |
| low compliance and young closures | 10.5 | 63.8 | 68.8 | 62.4 | 90.5 | 91.5 | 95.3 | 112.7 | 117.9 | 96.3 |
| all destructive gears restricted | 13 | 70.5 | 72.6 | 66.4 | 89.2 | 88.2 | 92.5 | 112.8 | 114.1 | 89.6 |
| most destructive gears restricted | 9.9 | 57.2 | 62.1 | 55.6 | 88.3 | 91.2 | 93.7 | 115.4 | 123.1 | 99 |
| no destructive gears restricted | 9.5 | 56.3 | 61 | 54.2 | 87.4 | 88.2 | 92.9 | 117.9 | 125.6 | 97.7 |

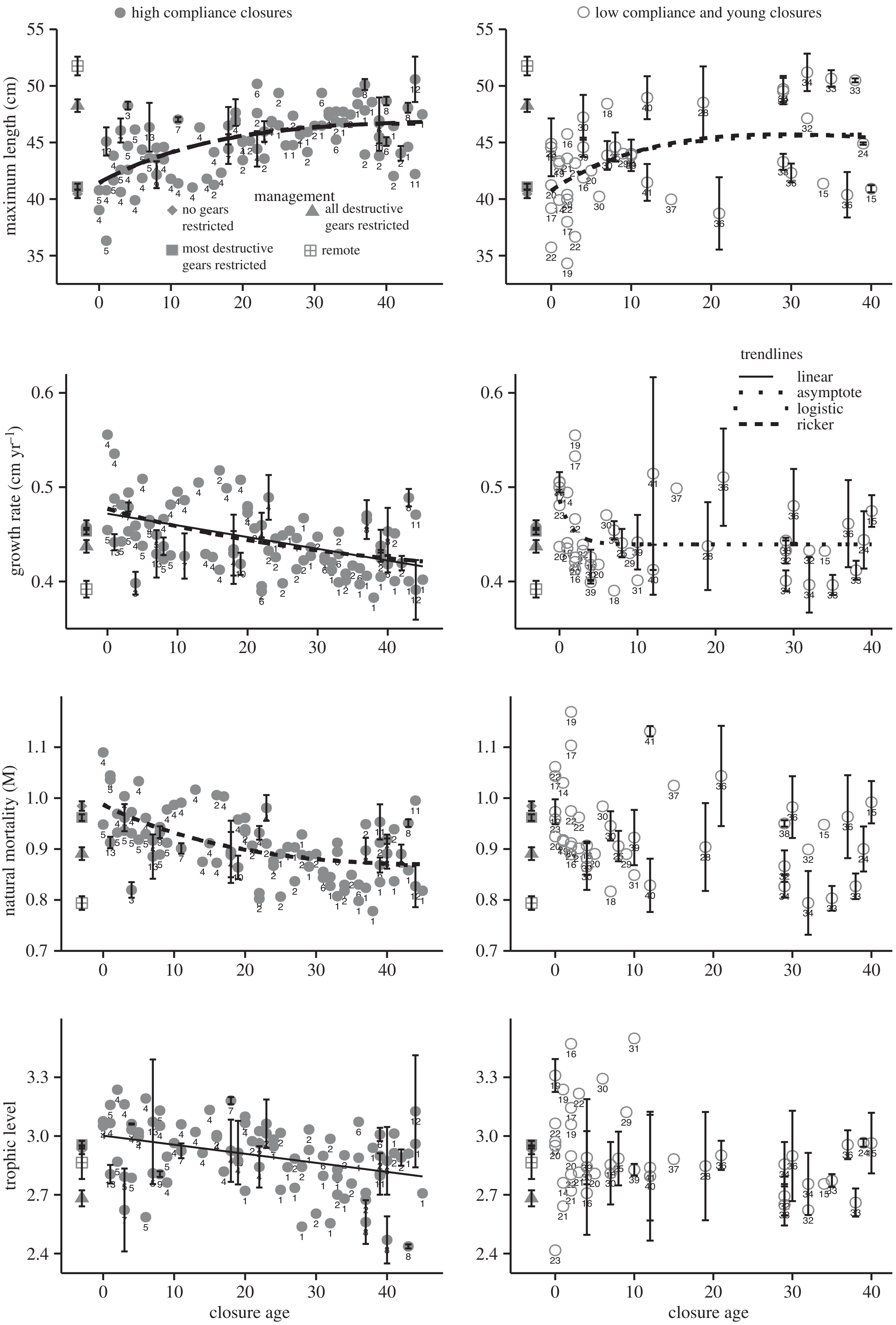

**Figure 3.** Reef fish biomass and length-based life-history values relative to the wilderness baseline of the Chagos. Length-based metrics were different for analysis with and without sharks, whereas other metrics not as shown are presented in the electronic supplementary material, table S3.

56 and 70% of remote values without sharks. Sites where all of the destructive gear were restricted had the longest community body lengths (table 1).

Community lifespan, generation time and age at maturity were not different with or without sharks and all increased significantly with the age of the high compliance closures. Model fits with age and size were weak, however, and best-fit equations in high compliance closures predicting only 5 and 8% of the variance. These three life-history metrics were not statistically significant for age- or size-of-closure evaluations within low compliance and young closures. These metrics also lay between 87 and 95% of the remote management category with slightly higher values in the two closures than the fisheries management categories.

Community growth rates, natural mortality and trophic level all declined with the age of the high compliance closures. Growth rates in high compliance closures declined throughout the time series and all equations predicted approximately 24% of the variance. Best-fit equations suggest that the minimum growth rate is reached beyond the data extent, or 106 and 118 years required before reaching the 95% of minimum value for the asymptotic and logistic equations, respectively. Growth rates in the low compliance and young closures declined marginally ($p < 0.04$), predicting 15% of the variance and minimum values were reached in approximately 4 years by both the logistic and asymptotic equations.

Natural mortality was predicted well in high compliance closures by all equations explaining 29 and 33% of the variance. Ninety-five per cent of minimum values were reached beyond the extent of the empirical data or at 52–56 years for the logistic and asymptotic equations, respectively. Trophic level declined linearly over time in high compliance closures and the best-fit linear model predicted 14% of the variance. Growth rates and natural mortality rates were higher in the two closures and fisheries restrictions management categories compared with remote reefs and rates increased as the number of restrictions declined. Trophic-level values were between 89 and 98% of the remote reefs and the lowest values were found in the high compliance closures and all-gear-restricted categories. The size of a closure was not statistically significant with community life-history variables of growth rate, generation time, age at maturity, natural mortality and trophic level (electronic supplementary material, table S2*b*).

## 4. Discussion

The central hypotheses of this study were supported; that is, community life histories changed towards larger, slower growing and later maturing fauna over closure time, the recovery time of life histories was considerably longer than the recovery of community biomass, and estimates of reef community end states and rates were sensitive to the compliance status of the closures. Categorizing management effectiveness helped to tease apart the various influences and led to a better understanding of how fishing changes the life histories of fish communities by reducing biomass and associated rates of growth, mortality and body size characteristics. These findings would not have been evident unless high compliance closures were present in the region and evaluated separately from low compliance closures. For example, closure compliance levels influenced estimated recovery times and levels of peak biomass and life-history composition, which also interacted with closure size. Reducing closure size slowed recovery rates, particularly in the low compliance and young closures. Community biomass in high compliance closures reached maximum values nearly twice as high as low compliance and young closures and took twice the time to recover. Similarly, important community-level fish life histories metrics like maximum lengths, natural mortality, growth rates and trophic level were predicted to level or reach the remote baselines at closure ages beyond the empirical time series of 45 years in the high but not low compliance and young closures.

Our findings suggest that relying on measurements that arise from the many low compliance and young closures, often included in protected areas evaluations, can underestimate recovery times and asymptote levels, as well as the final compositional state of fish communities [32,33]. Not only do these findings indicate the importance of acknowledging compliance in evaluations of closure management [13] but also the value of high compliance closure and remote wilderness areas in estimating baselines states and recovery rates in marine fisheries [24]. A global meta-analysis of fisheries closures also concluded that young closures were not as effective in promoting fish abundance as reserves older than 15 years [15]. Given recent efforts to create small community closures in this region [34,35], the final biomass levels may be an overestimate and recovery times may be an underestimate for these recently created small closures. Only two small community closures (Vipingo and Kibuyuni sizes were less than 0.3 km$^2$; electronic supplementary material, table S1) were included in the high compliance closure evaluations and were not likely to have had a large influence on the final biomass and recovery rate estimates. This is indicated by the stronger age-size interactive affect in low compliance and young compared with high compliance closures. Nevertheless, the initial biomass levels in the closures and the three fisheries restrictions categories were comparable, suggesting closures started at biomass levels similar to fished reefs in the region. Therefore, the recovery rates in these early stages of closure presented here should apply to currently fished sites, if they are closed to fishing.

Previous predictions for responses of small and large fishes and trophic cascade effects to closure [15] have used categorical and not continuous life-history metrics. Yet, we found continuous and weighted community variables to be important in our regional and single-ecosystem evaluation. A global evaluation of community change across a 40 year time horizon [1] also found continuous community composition and biomass change over the full time series. Consequently, evaluations of fisheries impacts and closures lacking sufficient time, life history and compliance contexts are not likely to detect the full suite of changes. While community biomass is often well correlated with diversity and life-history characteristics [20,36], this study indicates that continuous changes in life histories occur well beyond the time at which biomass reaches its maximum levels.

Our study found that fishing reduces biomass and changes life histories towards faster and more productive communities. While this is an adaptation or community-level compensation to fisheries mortality that promotes taxa better able to tolerate high mortality, it may increase fisheries production through compensatory community change processes promoted by increasing fishing effort [37]. These changes have a number of consequences for the fish community and associated reef ecology. On ecological time scales, there are a number of taxa that will be extirpated or, at minimum, no longer contribute significantly to ecological processes, such as predation and reef erosion [1,24]. Further, the intensity and length of fishing have been shown to influence recovery rates and the ability to rebuild fisheries [11]. Accordingly, intense fishing can promote fast recovery of some stocks but a long history of heavy fishing can reduce the capacity to rebound and increase the uncertainty of rebuilding stocks. Clearly, as reflected in the

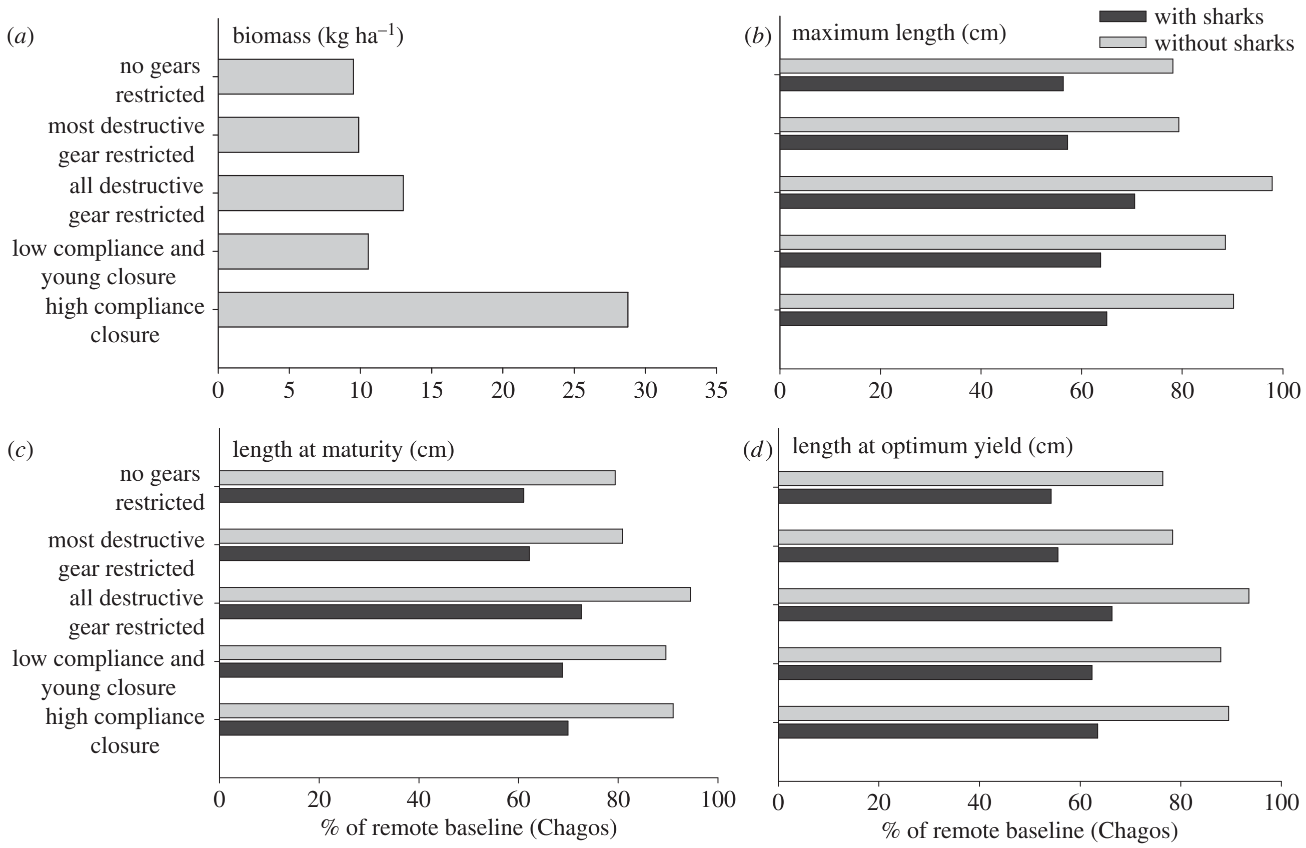

**Figure 4.** Weighted life-history metric changes in the reef fish community as a function of the age of the high compliance and low compliance and young closures. Full statistical evaluations are presented in the electronic supplementary material, table S2*b*.

continuous processes that unfolded in our community-level metrics, life histories and the time since resource extraction is stopped are expected to influence the population rebuilding rates and potential.

On evolutionary time scales, high fishing mortality without refuge is expected to change the biology of species and responses that do not always contribute to fisheries productivity. These changes include slow growth, early maturation at small size, higher reproductive output rather than somatic growth, lower activity and less sex change [38–41]. When heavy fisheries-induced selection pressure reduces genetic variance, it can influence recovery rates to pre-fishing genotypes [10]. This reduced genetic variance should be more common in the absence of fisheries closures or marine wilderness, which can have negative feedbacks on fisheries. For example, Audzijonyte *et al*. [42] modelled small declines in maximum body lengths typical of fisheries and found this could increase natural predation and reduce catches of these shrinking species. These findings indicate the importance of retaining a portfolio of life histories and fisheries management systems, including old closures and wilderness. To date, fisheries-induced evolutionary change studies are limited to temperate species, suggesting a need to evaluate the genetics of impacted coral reef species.

This study has the advantages of investigating change in a single ecosystem and region but has various limits, including the use of space-for-time substitution [12], the use of static and family-level averaged life-history estimates [20], differing habitat features [43], the possible sampling and behavioural effects of fishes in various human impact environments [44], possible changes in fishing pressure and fish communities over recent historical time [34], as well as gradients of compliance that are not easily quantified [32]. Further, community biomass and some life-history variables showed an antagonistic interaction between the age and size of the closure indicating that closure size effects, particularly in the low compliance and young closures, influenced recovery estimates. Given that the best models only predicted approximately 35% of the total variance, it is likely that these limits, interacting factors, historical contingency and data-need trade-offs are among other unstudied factors that contributed to this unexplained variance. Nevertheless, the patterns of recovery in high compliance closures generally confirm the patterns observed in the various management categories. Thus, fish communities in the oldest and best-protected closures had not converged towards remote communities even after 45 years.

Sharks are found and frequently counted in remote coral reefs, but they are scarce and seldom counted in reefs with greater human occupation or impact [24,45–47]. The magnitude of these differences may, in part, be owing to behavioural responses of the sharks to divers [48], but the lack of sharks in human-populated areas is almost certainly owing to their vulnerability to fishing [49]. Indeed, only very large closures are likely to capture the home range of sharks and protect them from fishing impacts [24]. When sharks are included in our analyses, they have an influence on body length community life-history estimates but not the other weighted rate and trophic-level traits. When included, they did not significantly increase the biomass estimates of the remote reefs. This is partly owing to the high spatial variation but also there are reports of episodic shark fishing in the Chagos [50]. This may explain the weak effect and, therefore, our findings and conclusions must consider this possible influence on our baseline. The lack of wholly intact baselines makes it difficult to fully understand and contribute to understanding the role of sharks on reef ecology [51,52].

Research findings on the effects of closure size on fish community metrics have been variable and may depend on a number of sampling and environmental factors [15,18,19,53]. Here we found a 10 km$^2$ peak for biomass, while a study using a more limited set of closures found a weaker effect with a peak response at approximately 5 km$^2$ [13]. The weak effect has a number of potential sources that include mobility of the reef fish species and fishing intensity or buffer zones on the borders. However, it appears from these studies that closures should be at least 5–10 km$^2$ to reach their potential within fished seascapes and avoid the slower recovery predicted by limited size. Size of closures will need to be larger still when promoting the abundance of larger taxa, such as sharks and jacks, is a management objective [24,47].

This study has highlighted the importance of evaluating multiple ecological proxies when evaluating management success and developing guidelines for implementation. Recommendations based solely on reef fish abundance or biomass would suggest relatively small and short times for closures. These metrics would, however, neglect the ongoing changes in the life-history characteristics, which can take much longer to stabilize and have consequences for both ecological and evolutionary processes. We suspect from our comparisons and predictions that the full recovery process will take over 100 years given enough space. Rates will be sensitive to the closure areas and full recovery to a baseline will not be possible in small closure areas less than 10 km$^2$. The full implications of human impacts and management decisions are being lost as ecological baselines in the Indian Ocean and other regions become degraded (figure 4).

Data accessibility. Meta- and summary data from these surveys will be deposited in the Wildlife Conservation Society research data repository, http://programs.wcs.org/databases/.

Authors' contributions. Both authors collected and compiled the data, conceptualized the study, and wrote the manuscript.

Competing interests. We have no competing interests.

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