

RESEARCH ARTICLE

# Simplification of Caribbean Reef-Fish Assemblages over Decades of Coral Reef Degradation

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## Abstract

Caribbean coral reefs are becoming structurally simpler, largely due to human impacts. The consequences of this trend for reef-associated communities are currently unclear, but expected to be profound. Here, we assess whether changes in fish assemblages have been non-random over several decades of declining reef structure. More specifically, we predicted that species that depend exclusively on coral reef habitat (i.e., habitat specialists) should be at a disadvantage compared to those that use a broader array of habitats (i.e., habitat generalists). Analysing 3727 abundance trends of 161 Caribbean reef-fishes, surveyed between 1980 and 2006, we found that the trends of habitat-generalists and habitat-specialists differed markedly. The abundance of specialists started to decline in the mid-1980s, reaching a low of ~60% of the 1980 baseline by the mid-1990s. Both the average and the variation in abundance of specialists have increased since the early 2000s, although the average is still well below the baseline level of 1980. This modest recovery occurred despite no clear evidence of a regional recovery in coral reef habitat quality in the Caribbean during the 2000s. In contrast, the abundance of generalist fishes remained relatively stable over the same three decades. Few specialist species are fished, thus their population declines are most likely linked to habitat degradation. These results mirror the observed trends of replacement of specialists by generalists, observed in terrestrial taxa across the globe. A significant challenge that arises from our findings is now to investigate if, and how, such community-level changes in fish populations affect ecosystem function.

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## Introduction

Habitat degradation modifies the structure of ecological assemblages by altering biotic interactions and ecosystem dynamics. The extent of a species' reliance on specific habitat features is one of the characteristics that should determine how well it will fare under most scenarios of habitat change [1,2]. While habitat specialists should be relatively sensitive to the degradation of their preferred habitat, generalists may be less affected, or could even benefit from new habitat arrangements or from the reduction in abundance or disappearance of other species (i.e., predators and competitors) via ecological compensation [3,4]. Across various taxa and geographical regions, specialist species appear to be declining and experiencing higher extinction risk in response to habitat change compared to generalist species, leading to homogenization and simplification of communities over time [5]. Measuring how species or groups of functionally similar species within communities differ in their responses to habitat change is therefore crucial to understand and predict the consequences of habitat loss and environmental degradation for species assemblages and ecosystem functioning. In fact, trends in the abundance of specialist species are now used as national and international indicators of development sustainability (e.g., [6]).

Coral reefs are changing rapidly, worldwide. This is particularly evident in the Caribbean where the structural complexity of many reefs has greatly declined, due to loss of coral cover and changes in the composition of coral assemblages [7–9]. The ecological repercussions of long-term decline in architectural complexity are likely to be substantial. For many reef fishes and invertebrates, the risk of predation is influenced by access to refuges; thus, the richness, abundance and biomass of these species are influenced by habitat complexity [10,11]. The consequences for coral reef fishes are of particular concern because this group plays key roles in ecosystem functioning (e.g., [12,13]) and reef fisheries are important for the livelihood of many human coastal communities [14]. In a large-scale meta-analysis, Paddock et al. [15] found that since the late 1990s the overall density of Caribbean reef fishes has declined consistently across the region. This reduction was attributed in part to declines in coral cover and reef complexity, which began as early as the 1970s [7,16].

Species seldom all respond similarly to changes in habitat. In the Indo-Pacific region, for example, a variety of species in a range of taxa depend nearly exclusively on live coral for food or shelter and, predictably, these specialists have often declined more precipitously in response to coral loss than less dependent species [10,17–19]. In the Caribbean, very few reef fishes are as heavily reliant on live corals as their Indo-Pacific counterparts [20]. However, this does not mean that all Caribbean reef fishes are generalists. Ecological specialization is not a dichotomous state but instead ranges along a continuum [21]. Caribbean reef fishes vary in terms of the extent to which they use non-reef as well as reef habitats, and the extent to which they clearly associate with specific features of reef structure or microhabitats (e.g., [22–24]). The recent changes in Caribbean reef fish density could therefore have been accompanied by shifts in relative abundance of slightly more and slightly less specialised species that are more subtle than those observed in the Indo-Pacific region.

The rate of change in population size is one of the most sensitive metrics for assessment of long-term biodiversity change [25–28]. Changes in abundance provide information about both variability and quantity of biodiversity (25,27), and can be used to detect shifts in community composition (26) and to infer changes in habitats and/or intensity of threats, such as exploitation (25). Here, we test the hypothesis that fishes that are more specialised in terms of coral reef habitat use have declined more in abundance than have habitat-generalists at the same locations across reef distributed throughout much of the Caribbean. We apply a novel method designed to measure the state of biodiversity based on species population trends [29] to a large,

regional-level database of temporal variation in the abundances of Caribbean reef fishes to examine large-scale trends of change in habitat-specialists and habitat-generalists. Furthermore, by examining the trends for fished and unfished species in those two groups, we test whether any differences in trajectories are attributable to fishing rather than causes such as changes in habitat structure.

## Methods

### Database and species grouping

We used a subset of the database that was compiled by Paddack et al. [15] of temporally replicated, quantitative data on Caribbean reef fish density (individuals  $m^{-2}$ ) from *in situ* surveys conducted by trained scientific observers (see details in Paddack et al. [15]). To be included, each study needed to have (i) reported a density estimate of at least one reef fish species from a reef site within the Caribbean region, (ii) surveyed the same species at the same site over more than one year, and (iii) replicated measurements during each survey. In the current analysis we used only common species, which we defined as those observed in at least 50% of the surveys in a time series. With this restriction, we aimed to control for the potentially influential effect of zero-density values in short (2–5 years) time series.

Specialization can be quantified by measuring the narrowness of use of a particular gradient of resource or habitat [25]. Because no Caribbean fish species relies exclusively on live corals and very few are closely associated with live coral [30,31], we based our specialization categories on the strength of association with coral reef habitat in general. Thus we classed as ‘specialists’ those species that are only found on coral reefs, and as ‘generalists’, those species that are associated with a broader range of habitat types, including less complex habitats such as sea-grass beds, gorgonian fields, sponge beds and macroalgal stands. For our analyses we used the specialist/generalist assignment of species made by Luiz et al. [32] who categorized fish species using data on habitat-use and latitudinal-range obtained from bibliographic sources and online databases, supplemented with field records (see Luiz et al. [32] for details). Species were classified as specialists or generalists prior to analyses and before exploring the general trends from each group in the database. In total we categorized 81 species from 27 families as habitat-specialists and 80 species from 26 families as habitat-generalists (S1 Table). Fish species in each of the two habitat-use groups were also separated into two sub-groups based on their level of exploitation. We obtained the fishing status categorization from Paddack et al. [15] and FishBase [33]. Unfished species included those that are not marketed, have unknown fishing status, or are targeted only lightly by the aquarium trade. Fished species included those that are marketed as food-fish or are heavily targeted by the aquarium trade.

The majority of the data came from studies that methodically collected abundance estimates for many species in each reef fish assemblage (see [15]). As such, our study is unlikely to over-represent species of special interest (e.g., threatened species), which is a common caveat in studies of this kind (e.g., [29, 34]).

### Trend analysis

To generate overall density trends for habitat-specialist and habitat-generalist species we used an aggregated index of change in abundance. This index of abundance was developed to provide scientists, policy-makers, and the general public with information on trends in the abundance of vertebrate populations across the globe [35]. This index represents an effective heuristic instrument for indicating trends in global biodiversity [29], and has been adopted as a key indicator of the state of global biological diversity at the international level [28,36]. In

addition, it can be used to evaluate broad scale trends for biogeographic realms, biomes, habitats, and particular taxonomic groups (e.g., [29, 34]).

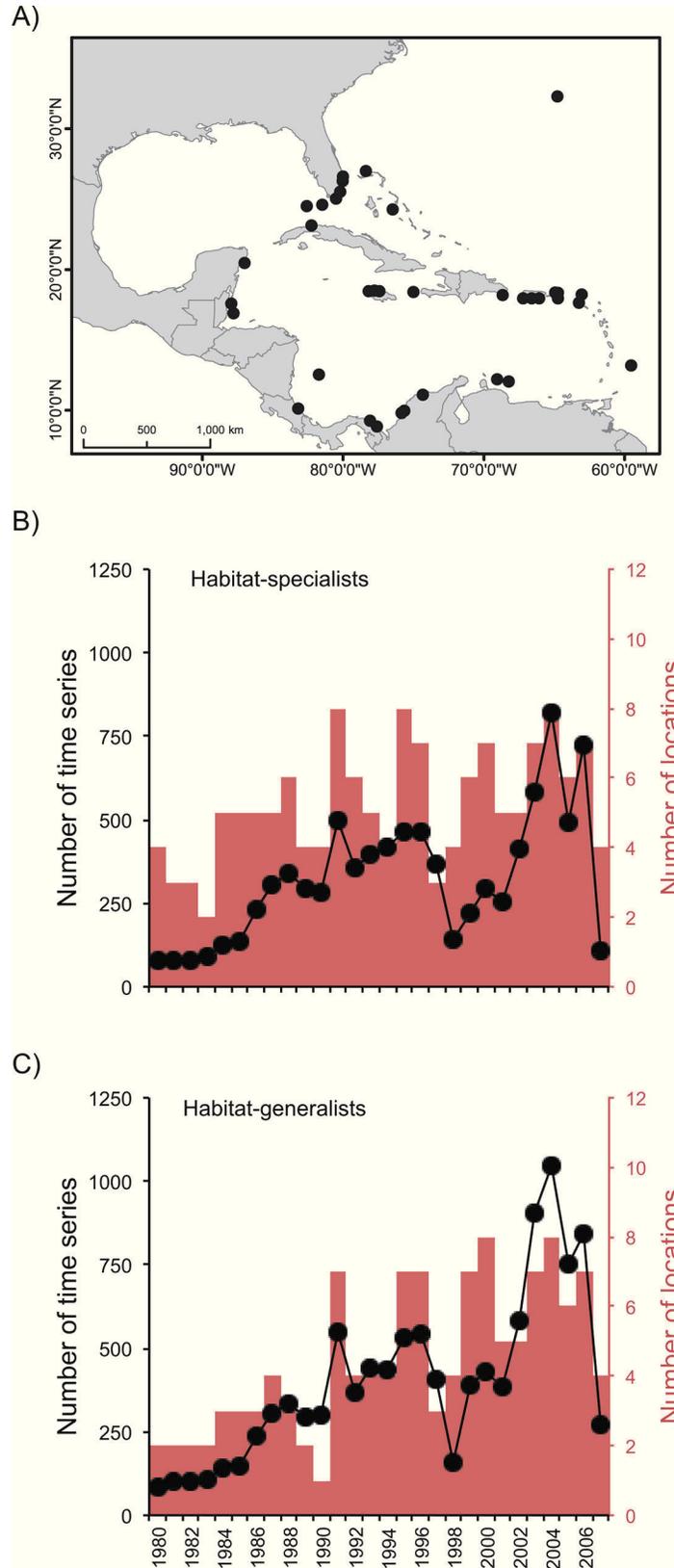
We outline the main steps for abundance-index computation here, although a more thorough description of the method and equations is provided in [S1 Appendix](#). For each time series, the change in density from each year to the next was calculated. In the case of incomplete time series, zero values were replaced by one percent of the mean population value for the whole time series, and missing values for yearly censuses were derived from interpolation of the preceding and the subsequent years with measured values (see [29]). Missing value interpolations were applied to most of the time series, given the gaps in data collection in the majority of monitoring schemes ([S1 Fig](#)). Two different methods were then used to generate estimates of change for each time series: log-linear models (the chain method in Loh et al. [35]) were used to compute values for short time series ( $n < 6$  time intervals; 70% of the total), and generalized additive models were used to compute values for all other time series. The use of this smoothing approach accounts better for non-linear variation [29,37].

Trends of all populations of the same species were averaged to produce species-specific trends. The average rate of change in each year across all species was then calculated. Finally, the average annual species change in each year was chained to the previous year to generate a continuous index, starting with an initial value of 1 in the first year of the database, which was 1980 in this study. All populations within species were given equal weight in the calculation of species-specific trends because we had no information on the relative importance of different populations to region-wide species abundance. Similarly, each species contributed equally to the calculation of the index. An advantage of giving equal weighting to all species is that common species or highly abundant populations do not have a disproportionate influence on the index trajectory. Separate indices were computed for habitat-specialist and habitat-generalist species and then, for fished and unfished species within each of those two habitat-use groups.

The uncertainty of the index estimates was assessed with bootstrapped 95% confidence intervals (CI). For each year, 1000 index values were calculated from randomly sampled species-specific population changes [35]. We considered a divergence of the overall trend as significant when the CI did not encompass the overall population baseline (i.e., Index of Abundance = 1).

## Results and Discussion

Our analysis included 3727 population trends for 161 common reef fishes from sites distributed throughout the wider Caribbean region ([Fig 1A](#)). As is common in this type of study, the number of sites and times series represented in the analyses tended to increase over time ([Fig 1B and 1C](#)); however, the geographical representativeness of the data has been regionally comprehensive since the 1990s ([S1 Fig](#)). We found that abundance trends differed markedly between habitat-generalists and habitat-specialists. The abundance of specialists began declining in the mid-1980s, reaching a low of ~60% of the 1980 baseline abundance by the late-1990s ([Fig 2A](#)). Average abundance and variation have increased somewhat since the early 2000s, although the average is still well below the baseline level of 1980. In contrast, the abundance of generalist species has remained relatively stable since 1980, with a marked but non-significant upswing since 2000 ([Fig 2B](#)). The trends of change of specialists and generalists were significantly different from each other between late-1980s and late-1990s, but the differences became less apparent during the 2000s due to the high variability associated with both trends (see CIs in [Fig 2A and 2B](#); and [S2 Fig](#)). The patterns uncovered here are not due to the presence of different time series in different parts of the study period. Monitoring at many sites used in the analyses ceased or began in the late-1990s ([S1 Fig](#)); however, when only time series that span



**Fig 1. Spatial and temporal distribution of time-series of abundance of Caribbean reef fishes.** (A) Location of the study sites is shown as black dots (note that one dot usually represents multiple reefs). Numbers of time series (black dots) and sites (red bars) included in the Index of Abundance for (B) habitat-specialists, and (C) habitat-generalists.

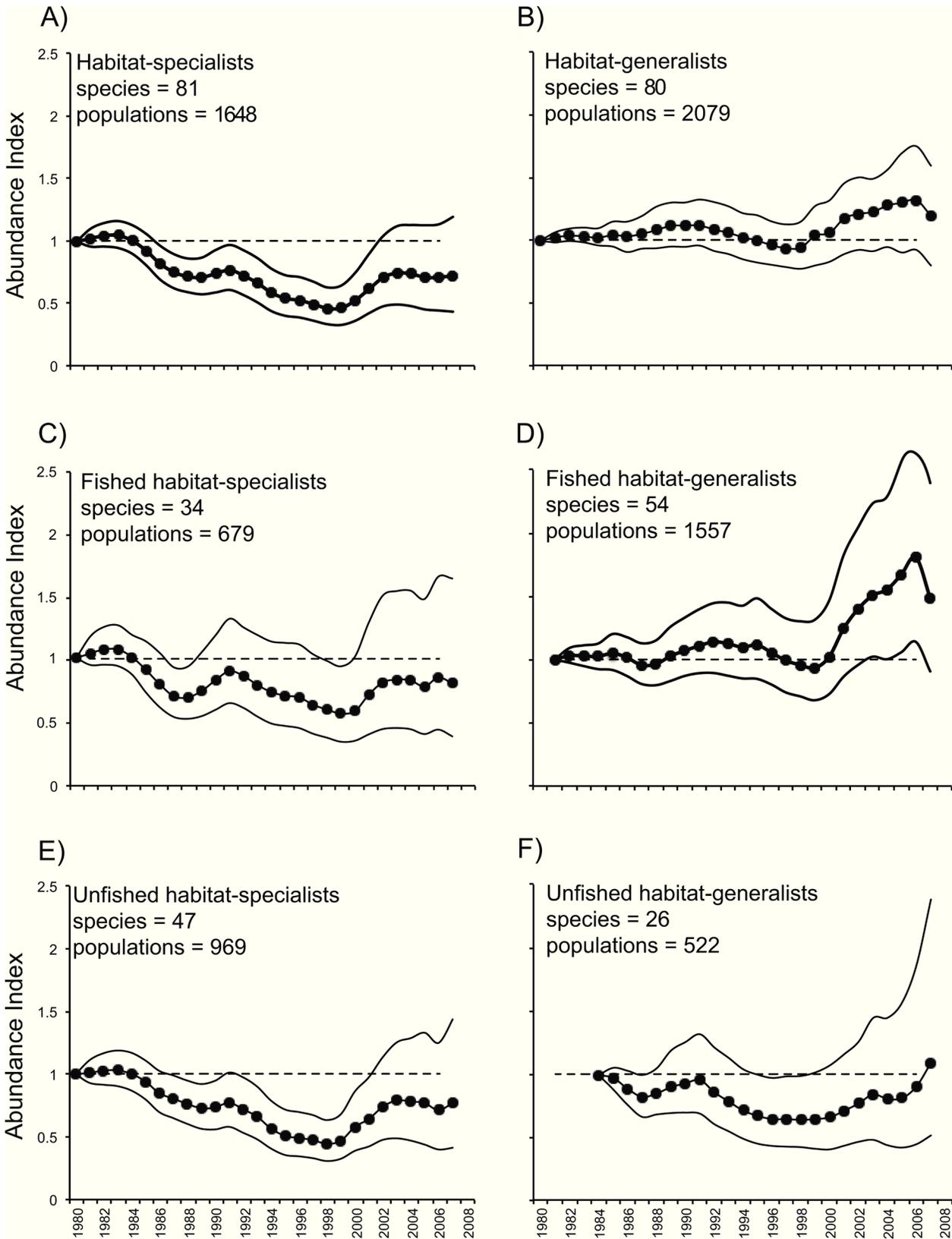
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most of the study duration are used, the average trends are similar, albeit with larger confidence intervals owing to the smaller sample sizes (S3 Fig).

The decline of habitat-specialist fishes we find here began soon after periods of rapid declines in coral cover and reef complexity during the early 1980s [7,16,38] (S4 Fig). The widespread mortality of morphologically complex, branching *Acropora* corals in the Caribbean, owing to white-band disease starting in the mid-1970s [39], likely accounts for some of these early changes to reef habitats. Caribbean *Acropora* reefs tend to support higher fish abundance and species richness than areas with lower structural complexity [40]. Thus, it is likely that the near-disappearance of these corals from many areas reduced drastically the amount of a major structural habitat feature throughout the 1980s [39], and affected populations of a number of reef fishes. While it is not possible to determine whether the decline of specialist species began before 1980, the ~4–5 years of relative stability at the start of the temporal trend suggest that populations of those species were not already undergoing a steep decline at that time (Fig 2A). Thus, specialist species may have experienced a lagged response to the loss of reef complexity, which started a few years earlier ([7,16]; Fig 2A). Several factors may have contributed to this delayed effect: (i) a lag in the degradation of microhabitat structure sufficient to have a measurable effect on specialist populations; (ii) reduced recruitment by fishes that need fine-scale structure as settlement microhabitat; and (iii) reductions in survivorship and/or reproductive output of specialists, owing to loss of shelter or food resources [10,17,41].

The decline in abundance of habitat-specialists continued steadily through the 1990s, with some evidence of modest recovery since 2000 (Fig 1A). This pattern of increase is unlikely to be the result of any improvement in habitat quality on Caribbean reefs, as it occurred in a decade when, at the regional scale, coral cover remained relatively low and reef architectural complexity declined steeply [7,16,38] (S4 Fig). The overall increase in the index values of specialist species in the 2000s is accompanied by an increasing variance (Fig 2A): while some populations were recovering, many more were continuing to decline (Figs 3 and 4). Biological traits and geographic distribution are usually poor predictors of population change on a broad scale (e.g., [42,43]); hence we did not attempt to investigate the identity or location of the species driving changes in the abundance of either specialists or generalists. However, we found no evidence that the increasing trend during the 2000s is related to positive changes in the abundance of a discrete subset of specialist species: most species show a mixture of declining and increasing populations during the 2000s (Fig 3). There were some geographic differences in recovery, with the Greater Antilles posting relatively more recovering than declining populations of habitat-specialists during the 2000s (Fig 4). This pattern contributed to the large confidence intervals that characterize all of the overall trends (Fig 2) in the last decade of the study period. Understanding the reasons for this geographic pattern will require further investigation.

In contrast to specialist fishes, the abundance of generalists on Caribbean reefs has remained relatively constant throughout the three decades spanned by this study (Fig 2B). This pattern suggests that fishes in this group were not negatively affected by changes occurring on coral reefs, and some may even have benefited from the reduced abundance of some other species (e.g., of food competitors) and/or from the loss of reef architectural complexity [3, 5, 44]. Generalist reef fishes may have relatively plastic preferences for settlement microhabitats, allowing them to recruit more successfully onto degraded reefs and alternative habitats than habitat specialists. For example, parrotfishes that sometimes exhibit strong recruitment associations with



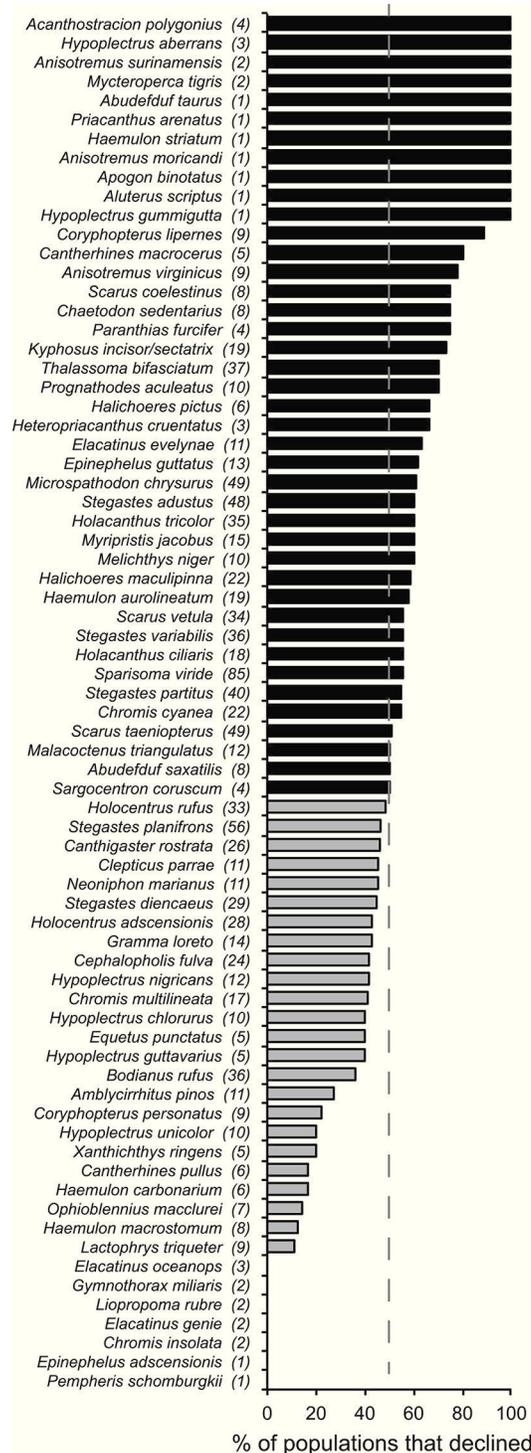
**Fig 2. Temporal trends in overall Caribbean reef fish abundance, relative to 1980 as depicted by the Index of Abundance.** Plots show average change ( $\pm$  95% CI, see [Methods](#)), with dashed line at  $y = 1$  indicating the 1980 value. The numbers of species and populations used to generate each panel are indicated. (A) all habitat-specialists; (B) all habitat-generalists; (C) habitat-specialists targeted by fisheries; (D) habitat-generalists targeted by fisheries; (E) unfished habitat-specialists; and (F) unfished habitat-generalists.

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specific coral microhabitats (e.g., [24]) also recruit onto macroalgae on reefs with low coral cover [45]. It has been suggested that fishes at higher trophic levels (which are mostly generalists; [S1 Table](#)) might experience lagged reductions due to declines in habitat-dependent prey fishes [10]. However, we did not find any evidence in support of this in our regional analysis. The abundance of generalist species remained relatively constant independently of the declines in the abundance of specialist species.

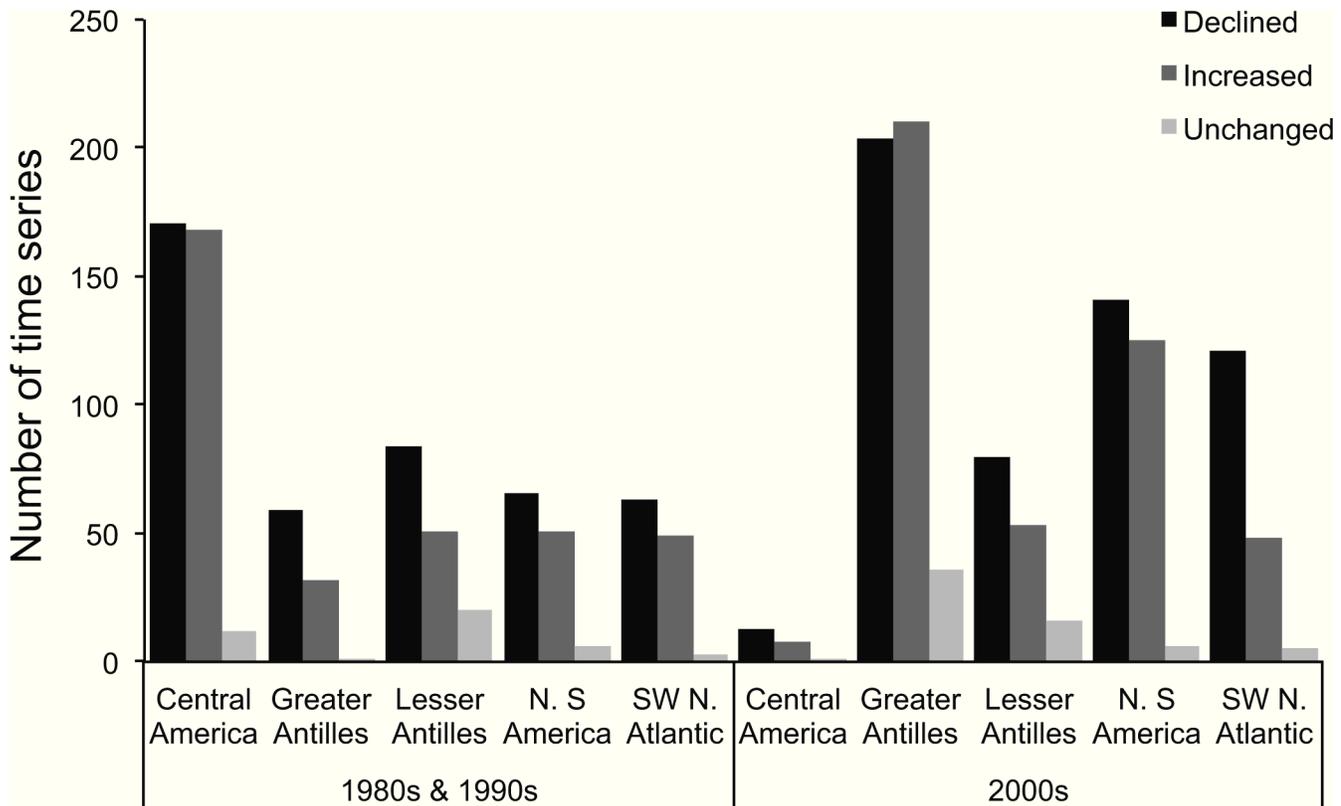
Fishing could be inferred to drive overall changes in Caribbean reef fish assemblages if fished species declined while unfished species did not. We found no evidence for such a fishing effect. Fished and unfished specialists show much the same abundance dynamics ([Fig 2C vs. 2E](#)). Note, however, that the uncertainty is high for exploited specialist fishes, probably due to the relatively low sample size. This observation supports our view that declines in the abundance of specialist species through the 1980s and 1990s were likely a consequence of reef degradation. The trends of fished and unfished generalists are not significantly different from each other (CIs overlap in [Fig 2D vs. 2F](#)). Although the uncertainty in the trends of both fishes and unfished habitat-generalists is large, particularly over the last five years of the series ([Fig 1F](#)), fished generalists increased distinctly more than unfished generalists during the last third of the study period ([Fig 2D](#)). In a previous study, Paddock et al. [15] also found similar rates of change of fished and unfished species in general, supporting the notion that fishing has not been a main driver of the recent changes in the abundance of reef fishes. It remains possible that fishing pressure and indiscriminate fishing methods may have affected unfished species indirectly through bycatch or by altering food-web dynamics (e.g., predation release; [46]). However, such effects would be difficult to assess with our data.

The slight increase in abundance of many fished generalist species in the last decade of the study is surprising because it is produced largely by significant increases in species of commercial importance such as groupers and snappers ([S5 Fig](#)). Changes in fisheries management are unlikely to be responsible for this pattern. The number and extent of species, gear and other effort restrictions vary widely across Caribbean nations [47]. For this reason, and because of poor compliance and enforcement remain problems in the region [48], it seems unlikely that a regional-scale increase in abundance of exploited generalist species is the result of multiple independent changes in national catch and effort regulations. Similarly, it is unlikely that the increasing use of marine protected areas (MPAs) as fishery management tools (cf., [49]) explains the increase in abundance of fished generalists. Only 8% of our time series stemmed from monitoring sites in marine protected areas, and the number of populations from such sites actually decreased over time ([S6 Fig](#)). The relative increase in abundance of fished species in the last third of our study period may be a reflection of the time horizon of our study. Many of the populations of exploited generalist species likely were already heavily depleted well before the start of our study [50,51]. Hence, the increase we recorded since the turn of the millennium is likely to be relatively small in comparison to original population sizes. That is, a 'shifting baseline' effect, due to a heavily depressed level at the start of the study (1980), may have amplified the *apparent* size of any subsequent increase. Although it remains difficult to understand why this mechanism would affect fished generalists more than their unfished counterparts, it is important to remember that the apparent increase in abundance of fished generalists does not necessarily indicate healthy populations of commercially important species, or that the negative effects of fishing have ceased in the Caribbean. Fishing often truncates the age and size



**Fig 3. Percentage of time-series (= populations) of each habitat-specialist species that declined between the first and the last year of their monitoring period between 2000 and 2007.** This time period spans the apparent partial recovery of specialist species in the early 2000s (see Fig 2A). The total number of time-series by habitat-specialist species is indicated in parentheses. The 72 species are ranked from the highest to the lowest percentage of declining time-series. Habitat-specialist species with 50% or more of declining time-series (black bars), and less than 50% (grey bars) are identified. In total, 557 populations declined, 446 increased and 64 were stable (no change). Note that this figure does not show the magnitude of the changes.

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**Fig 4. Number of time series (= populations) of habitat-specialist species that show a decline, a recovery or remained stable between the first and last year of their monitoring period.** The data are presented by geographical region (as in S1 Fig) and for two time periods (1980s-1990s, and 2000s). These two time periods were selected based on the overall trend of Fig 2A, which shows partial recovery of specialist species in the early 2000s. In the 1980s-1990s, a total of 443 populations declined, 351 increased and 42 were stable (no change). In the 2000s, a total of 562 species declined, 441 increased, and 64 remained stable. Note that this figure does not show the magnitude of the changes.

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structure of populations [52]. Thus, the trend of commercially important generalists might be driven by increases in the abundance of small-sized individuals (e.g., juveniles) rather than increases in individual size and biomass that are needed to effect population recovery. Shifts in species composition from large-bodied to smaller-bodied species via a compensatory response are also possible.

Our results indicate that Caribbean reef-fish assemblages have been experiencing profound changes in community composition since 1980, probably largely due to habitat degradation. We found evidence of an apparent replacement of habitat-specialists by generalist species over a 30-year period. Such a shift is symptomatic of disturbed ecosystems around the world [4,6] and, in some cases, results in large-scale spatial homogenisation of previously diverse species assemblages [5, 53]. The ecological replacement of specialized species by generalists could have consequences for ecosystem integrity and function. For example, the loss of specialist species is likely to reduce the variability in community responses to disturbances and environmental change, and modify species interaction networks, which could result in the loss of key ecosystem functions [1,5,21,54]. Further research assessing the links between habitat specialisation and ecosystem functioning, in terms of species replacement triggering trophic cascades, altering energy flux, and changing functional redundancy, is crucial to fully understand the consequences of habitat degradation for coral reef diversity and for the resources they provide to humanity.

## Supporting Information

### S1 Appendix. Calculation of the Abundance Index.

(PDF)

**S1 Fig. Time series of data available from different census sites that, together, provided the 3727 populations included in this study.** Each line showed the time span of a time series. Time series are colour-coded by sub-region of the Caribbean to show the geographic spread of the data.

(PDF)

**S2 Fig. Significance ( $p$  values) of the annual difference between the trends of habitat-generalists and habitat-specialists shown in Fig 2A and 2B.**  $p$  values were derived from T tests comparing the final index values and 95% CIs of the specialist and generalist trends. The dashed line shows the critical value below which differences are statistically significant.

(PDF)

**S3 Fig. Temporal trends in the Abundance Index (+/- 95% CI, see Methods for calculations) of habitat-specialist (left column) and habitat-generalist (right column) Caribbean reef-fish species in long time-series that either stop in 1998 (top row) or span 1998 (middle row).** The baseline year is indicated by a dashed line. Panels (A) and (B) from Fig 2 are shown to facilitate the visual interpretation.

(PDF)

**S4 Fig. Long-term trajectories of change in coral cover, reef rugosity and habitat-specialist fishes on Caribbean reefs.** A) Region-wide changes in mean coral cover and reef rugosity based on a meta-analysis of ecological studies across the Caribbean from 1977 to 2008 (Redrawn from Alvarez-Filip et al. 2011; *Global Change Biol.* 17:2470–2477). B) Temporal trends in the overall abundance of habitat-specialist fishes, relative to 1980 as depicted by the Abundance Index (Redrawn from Fig 2A). The grey dotted line indicates the year 2000, when at the regional scale, the abundance of habitat-specialist fishes started to recover but coral cover and reef rugosity continued to decline. The two panels derive from different data sources due to the lack of site overlap between the habitat (coral cover and reef rugosity) and fish datasets.

(PDF)

**S5 Fig. Temporal trends in aggregate abundance (Abundance Index, with 95% CI) of two major taxa of commercially important Caribbean reef fishes: Serranidae (groupers) and Lutjanidae (snappers).** Baseline year is 1986 (dashed line at  $y = 1$ ).

(PDF)

**S6 Fig. Number of populations (i.e., time series) collected from inside (red bars) and outside (blue bars) Marine Protected Areas in the Caribbean in each year of the study.** Between 1980 and 1988 all times series for inside MPAs are from only one study in Florida, USA. From 1991 to 2007, the number of studies contributing information for sites inside MPAs ranged between one and two, and represented only three other countries/territories (Saba, Costa Rica and Curaçao). Due to the scatter spatial and temporal distribution of the data, it was not possible to further explore the trends of change inside MPAs with the Abundance Index.

(PDF)

**S1 Table. Species included in this study, their habitat categorisation according to the use of reef habitats.** Specialists use only coral reef habitats, and generalists use coral reefs as well as one or more other coastal habitats (classification from Luiz et al. 2012). Fishing status is from Paddock et al. (2009). See Methods for description.

(PDF)

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## Author Contributions

Conceived and designed the experiments: LAF IMC. Analyzed the data: LAF BC. Contributed reagents/materials/analysis tools: LAF MJP DRR BC IMC. Wrote the paper: LAF MJP DRR BC IMC.

## References

1. Olden JD, Poff NL. Ecological processes driving biotic homogenization: Testing a mechanistic model using fish faunas. *Ecology*. 2004; 85: 1867–1875.
2. Devictor V, Julliard R, Couvet D, Lee A, Jiguet F. Functional homogenization effect of urbanization on bird communities. *Conserv Biol*. 2007; 21: 741–51. PMID: [17531052](#)
3. Colles A, Liow LH, Prinzing A. Are specialists at risk under environmental change? Neoecological, paleoecological and phylogenetic approaches. *Ecol Lett*. 2009; 12: 849–63. doi: [10.1111/j.1461-0248.2009.01336.x](#) PMID: [19580588](#)
4. Purvis A, Gittleman JL, Cowlishaw G, Mace GM. Predicting extinction risk in declining species. *Proc R Soc Biol Sci*. 2000; 267: 1947–1952. PMID: [11075706](#)
5. Clavel J, Julliard R, Devictor V. Worldwide decline of specialist species: toward a global functional homogenization? *Front Ecol Environ*. 2011; 9: 222–228.
6. Gregory RD, van Strien A, Vorisek P, Gmelig AW, Noble DG, Foppen RPB, et al. Developing indicators for European birds. *Proc R Soc Biol Sci*. 2005; 360: 269–88.
7. Alvarez-Filip L, Côté IM, Gill JA, Watkinson AR, Dulvy NK. Region-wide temporal and spatial variation in Caribbean reef architecture: is coral cover the whole story? *Global Change Biol*. 2011a; 17:2470–2477.
8. Alvarez-Filip L, Dulvy NK, Côté IM, Watkinson AR. Coral identity underpins reef complexity on Caribbean reefs. *Ecol Appl*. 2011b; 21: 2223–2231 PMID: [21939056](#)
9. Alvarez-Filip L, Carricart-Ganivet J, Horta-Puga G, Iglesias-Prieto R. Shifts in coral-assembly composition do not ensure persistence of reef functionality. *Scientific reports*. 2013; 3: 3486. doi: [10.1038/srep03486](#) PMID: [24336631](#)
10. Pratchett MS, Munday PL, Wilson SK, Graham NAJ, Cinner JE, Bellwood DR, et al. Effects of climate-induced coral bleaching on coral-reef-fishes ecological and economic consequences. *Oceanogr Mar Biol Annu Rev*. 2008; 46: 251–296.
11. Graham NJ, Nash KL. The importance of structural complexity in coral reef ecosystems. *Coral Reefs*. 2012; 32: 315–326
12. Holmlund CM, Hammer M. Ecosystem services generated by fish populations. *Ecol Econom*. 1999; 29: 253–268.
13. Kennedy EV, Perry CT, Halloran PR, Iglesias-Prieto R, Schönberg CHL, Wisshak M, et al. Avoiding coral reef functional collapse requires local and global action. *Curr Biol*. 2013; 23: 912–8. doi: [10.1016/j.cub.2013.04.020](#) PMID: [23664976](#)
14. Allison EH, Perry AL, Badjeck MC, Adger WN, Brown K, Conway D, et al. Vulnerability of national economies to the impacts of climate change on fisheries. *Fish Fish*. 2009; 10, 173–196. doi: [10.1007/s10162-009-0161-3](#) PMID: [19247714](#)
15. Paddack MJ, Reynolds JD, Aguilar C, Appeldoorn RS, Beets J, Burkett EW, et al. Recent region-wide declines in Caribbean reef fish abundance. *Curr Biol*. 2009; 19: 590–595. doi: [10.1016/j.cub.2009.02.041](#) PMID: [19303296](#)
16. Alvarez-Filip L, Dulvy NK, Gill JA, Côté IM, Watkinson AR. Flattening of Caribbean coral reefs: region-wide declines in architectural complexity. *Proc R Soc Biol Sci*. 2009; 276: 3019–3025 doi: [10.1098/rspb.2009.0339](#) PMID: [19515663](#)

17. Jones GP, McCormick MI, Srinivasan M, Eagle JV. Coral decline threatens fish biodiversity in marine reserves. *Proc Natl Acad Sci*. 2004; 101: 8251–8253. PMID: [15150414](#)
18. Munday PL. Habitat loss, resource specialization, and extinction on coral reefs. *Global Change Biol*. 2004; 10: 1642–1647.
19. Wilson SK, Burgess SC, Cheal AJ, Emslie M, Fisher R, Millet I, et al. Habitat utilization by coral reef fish: implications for specialists vs. generalists in a changing environment. *J Anim Ecol*. 2008; 77: 220–228. PMID: [18081778](#)
20. Bellwood DR, Hughes TP, Folke C, Nyström M. Confronting the coral reef crisis. *Nature*. 2004; 429: 827–833. PMID: [15215854](#)
21. Devictor V, Clavel J, Julliard R, Lavergne S, Mouillot D, Thuiller W, et al. Defining and measuring ecological specialization. *J Appl Ecol*. 2010; 47: 15–25.
22. Robertson DR. Cohabitation of competing territorial damselfishes on a Caribbean coral reefs. *Ecology*. 1984; 65: 1121–1135.
23. Tolimieri N. Contrasting effects of microhabitat use on large-scale adult abundance in two families of Caribbean reef fishes. *Mar Ecol Prog Ser*. 1998a; 167: 227–239.
24. Tolimieri N. The relationship among microhabitat characteristics, recruitment and adult abundance in the stoplight parrotfish, *Sparisoma viride*, at three spatial scales. *Bull Mar Sci*. 1998b; 62: 253–268.
25. Balmford A, Green RE, Jenkins M. Measuring the changing state of nature. *Trends Ecol Evol*. 2003; 18: 326–330
26. Buckland ST, Magurran AE, Green RE, Fewster RM. Monitoring change in biodiversity through composite indices. *Philos Trans R Soc Lond B Biol Sci*. 2005; 360: 243–254. PMID: [15814343](#)
27. Pereira HM, Cooper DH. Towards the global monitoring of biodiversity change. *Trends Ecol Evol*. 2006; 21: 123–129. PMID: [16701487](#)
28. Collen B, Nicholson E. Taking the measure of change. *Science*. 2014; 346: 166–167 doi: [10.1126/science.1255772](#) PMID: [25278506](#)
29. Collen B, Loh J, Whitmee S, McRae L, Amin R, Baillie JEM. Monitoring change in vertebrate abundance: the Living Planet Index. *Conserv Biol*. 2009; 23: 317–27. doi: [10.1111/j.1523-1739.2008.01117.x](#) PMID: [19040654](#)
30. Coker DJ, Wilson SK, Pratchett MS. Importance of live coral habitat for reef fishes. *Rev Fish Biol Fish*. 2013; 24: 89–126.
31. Cole AJ, Pratchett MS, Jones GP. Diversity and functional importance of coral-feeding fishes on tropical coral reefs. *Fish Fish*. 2008; 9: 286–307.
32. Luiz OJ, Madin JS, Robertson DR, Rocha LA, Wirtz P, Floeter SR. Ecological traits influencing range expansion across large oceanic dispersal barriers: insights from tropical Atlantic reef fishes. *Proc R Soc Biol Sci*. 2012; 279: 1033–1040. doi: [10.1098/rspb.2011.1525](#) PMID: [21920979](#)
33. Froese R, Pauly D. FishBase. Available: [www.fishbase.org](http://www.fishbase.org). Version 07/2010
34. Galewski T, Collen B, McRae L, Loh J, Grillas P, Gauthier-Clerc M, et al. Long-term trends in the abundance of Mediterranean wetland vertebrates: From global recovery to localized declines. *Biol Conserv*. 2011 144: 1392–1399.
35. Loh J, Green RE, Ricketts T, Lamoreux J, Jenkins, Kapos V, et al. The Living Planet Index: Using species population time series to track trends in biodiversity. *Philos Trans R Soc Lond B Biol Sci*. 2005; 360: 289–295. PMID: [15814346](#)
36. Butchart SHM, Walpole M, Collen B, van Strien A, Scharlemann JPW, Almond REA, et al. Global biodiversity: indicators of recent declines. *Science*. 2010; 328: 1164–1168. doi: [10.1126/science.1187512](#) PMID: [20430971](#)
37. Fewster RM, Buckland ST, Siriwardena GM, Baillie SR, Wilson JD. Analysis of population trends for farmland birds using generalized additive models. *Ecology*. 2000; 81: 1970–1984.
38. Schutte V, Selig E, Bruno J. Regional spatio-temporal trends in Caribbean coral reef benthic communities. *Mar Ecol Prog Ser*. 2010; 402: 115–122.
39. Bruckner AW. Proceedings of the Caribbean *Acropora* Workshop, Potential Application of the US Endangered Species Act as a Conservation Strategy. US Dept. of Commerce, National Oceanic and Atmospheric Administration, National Marine Fisheries Service; 2003
40. Lirman D. Reef fish communities associated with *Acropora palmata*: Relationships to benthic attributes. *Bull Mar Sci*. 1999; 65: 235–252.
41. Wilson SK, Graham NAJ, Pratchett MS, Jones GP, Polunin NVC. Multiple disturbances and the global degradation of coral reefs: Are reef fishes at risk or resilient? *Global Change Biol*. 2006; 12: 2220–2234.

42. Mace GM, Collen B, Fuller RA, Boakes EH. Population and geographic range dynamics: implications for conservation planning. *Philos Trans R Soc Lond B Biol Sci.* 2010; 365: 3743–3751. doi: [10.1098/rstb.2010.0264](https://doi.org/10.1098/rstb.2010.0264) PMID: [20980321](https://pubmed.ncbi.nlm.nih.gov/20980321/)
43. Collen B, McRae L, Deinet S, De Palma A, Carranza, Cooper N, et al. Predicting how populations decline to extinction. *Philos Trans R Soc Lond B Biol Sci.* 2011; 366: 2577–2586 doi: [10.1098/rstb.2011.0015](https://doi.org/10.1098/rstb.2011.0015) PMID: [21807738](https://pubmed.ncbi.nlm.nih.gov/21807738/)
44. Pratchett MS, Coker DJ, Jones GP, Munday PL. Specialization in habitat use by coral reef damselfishes and their susceptibility to habitat loss. *Ecol Evol.* 2012; 2: 2168–80. doi: [10.1002/ece3.321](https://doi.org/10.1002/ece3.321) PMID: [23139876](https://pubmed.ncbi.nlm.nih.gov/23139876/)
45. Paddack MJ, Sponaugle S. Recruitment and habitat selection of newly settled *Sparisoma viride* to reefs with low coral cover. *Mar Ecol Prog Ser.* 2008; 369: 205–212.
46. Heithaus MR, Frid A, Wirsing AJ, Worm B. Predicting ecological consequences of marine top predator declines. *Trends Ecol Evol.* 2008; 23: 202–10. doi: [10.1016/j.tree.2008.01.003](https://doi.org/10.1016/j.tree.2008.01.003) PMID: [18308421](https://pubmed.ncbi.nlm.nih.gov/18308421/)
47. McManus E, Lacambra C. Fisheries regulations in the wider Caribbean region. Project summary. United Nations Environment Program, World Conservation Monitoring Centre, Cambridge, UK. 2005.
48. Haughton EO. Compliance and enforcement of fisheries regulations in the Caribbean. *Annu Proc Gulf Caribb Fish Inst.* 2004; 54: 188–201.
49. Polunin N, Roberts CM. Greater biomass and value of target coral-reef fishes in two small Caribbean marine reserves. *Mar Ecol Prog Ser.* 1993; 100: 167–176.
50. Jackson JBC. What was natural in the coastal oceans? *Proc Natl Acad Sci.* 2001; 98: 5411–5418. PMID: [11344287](https://pubmed.ncbi.nlm.nih.gov/11344287/)
51. McClenachan L. Historical declines of goliath grouper populations in South Florida, USA. *Endanger Species Res.* 2009; 7: 175–181.
52. Berkeley S, Hixon M, Larson R, Love M. Fisheries sustainability via protection of age structure and spatial distribution of fish populations. *Fisheries.* 2004; 29: 23–32.
53. Le Viol I, Jiguet F, Brotons L, Herrando S, Lindström, Pearce-Higgins JW, et al. More and more generalists: two decades of changes in the European avifauna. *Biology Letters.* 2012; doi: [10.1098/rsbl.2012.0496](https://doi.org/10.1098/rsbl.2012.0496)
54. Lurgi M, López BC, Montoya JM. Novel communities from climate change. *Philos Trans R Soc Lond B Biol Sci.* 2012; 367: 2913–22 PMID: [23007079](https://pubmed.ncbi.nlm.nih.gov/23007079/)

## Online supplementary material

### Calculation of the Abundance Index

We used 2 different methods to generate index values: a chain method (Loh et al. 2005) and a generalized additive modeling technique (Fewster et al. 2000; Buckland et al. 2005). We followed Loh et al. (2005) to implement the chain method; however, as per Collen et al (2009) we calculated the logarithm of the ratio of population abundance for successive years ( $d$ ), rather than for 5 yearly intervals:

$$d_t = \log_{10}(N_t/N_{t-1}), \quad (1)$$

where  $N$  is the population measure and  $t$  is the year. One percent of the mean population abundance value for the whole time series was added to all years when  $N =$  zero. Missing values were imputed with log-linear interpolation (no values were extrapolated):

$$N_i = N_p \left( N_s / N_p \right)^{(i-p)/(s-p)}, \quad (2)$$

where  $i$  is the year for which the value is interpolated,  $p$  is the preceding year with a measured value, and  $s$  is the subsequent year with a measured value. For species with more than one time series, the mean value of  $d_t$  was calculated across all time series for that species. Species-specific values for  $d_t$  were combined:

$$\bar{d}_t = \frac{1}{n_t} \sum_{i=1}^{n_t} d_{it}. \quad (3)$$

The index value ( $I$ ) was then calculated in year  $t$  as

$$I_t = I_{t-1} 10^{\bar{d}_t} \quad (4)$$

with the index value set to 1 in 1980, the first year of the time series. Insufficient data were available to run the index prior to 1980 or continue it beyond 2007 (because of a lag in publication of data).

Time series with  $n < 6$  were analyzed with the chain method. Following Collen et al. (2009) for all other time series, we implemented a generalized additive model (GAM), specified with the mgcv package framework in R (Wood 2006). For each time series we:

1. fitted a GAM on observed values with  $\log_{10}(N_t)$  as the dependent variable and year ( $t$ ) as the independent,

2. set the smoothing parameter to the length of the population time series divided by 2 (Wood 2006),
3. selected the smoothing-parameter value by comparing the estimated degrees of freedom when the smoothing parameter was successively incremented by 1,
4. used fitted GAM values to calculate predicted values for all years (including those with no real count data), and
5. averaged and aggregated  $d$  values from the imputed counts as described above.

A GAM framework might be advantageous in long-term trend analysis because it allows change in mean abundance to follow any smooth curve, not just a linear form (Fewster et al. 2000). The GAM method has greater flexibility for drawing out the long-term nonlinear trends that are generally not elicited in the discrete annual estimates of the chain method. We weighted the analysis, as described above, with species with more than one time series averaged across all the time series for that species. We combined specific values with geometric means at each time point and calculated the index.

### Calculation of confidence limits

We used a bootstrap resampling technique to generate confidence limits around index values. To calculate a bootstrap replicate, for each interval,  $t-1$  to  $t$ , a sample of  $n_t$  species-specific values of  $d_t$  was selected at random with replacement from the  $n_t$  observed values. We implemented the bootstrap procedure 10,000 times and used the bounds of the central 9,500  $I$  values for each year to represent the 95% confidence interval for the index in that year (Loh et al. 2005). Setting the base year (1980) to unity did not mean there was no uncertainty associated with it, rather that the uncertainty was inherited by the rest of the values in the series.

### Literature Cited

- Buckland, S. T., A. E. Magurran, R. E. Green, and R. M. Fewster. 2005. Monitoring change in biodiversity through composite indices. *Philosophical Transactions of the Royal Society of London B* **360**:243-254.
- Crawley, M. J. 2002. *Statistical computing: an introduction to data analysis using S-Plus*. Wiley, Chichester, United Kingdom.
- Collen B, Loh J, Whitmee S, McRae L, Amin R, Baillie JEM (2009). Monitoring change in vertebrate abundance: the Living Planet Index. *Conserv Biol* 23: 317-27.
- Fewster, R. M., S. T. Buckland, G. M. Siriwardena, S. R. Baillie, and J. D. Wilson. 2000. Analysis of population trends for farmland birds using generalized additive models. *Ecology* **81**:1970-1984.
- Loh, J., R. E. Green, T. Ricketts, J. F. Lamoreux, M. Jenkins, V. Kapos, and J. Randers. 2005. The living planet index: using species population time series to track trends in biodiversity. *Philosophical Transactions of the Royal Society of London B* **360**:289-295.
- R Development Core Team. 2006. *R: language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna.
- Wood, S. N. 2006. *Generalized additive models: an introduction with R*. Chapman & Hall/CRC, Boca Raton, Florida.

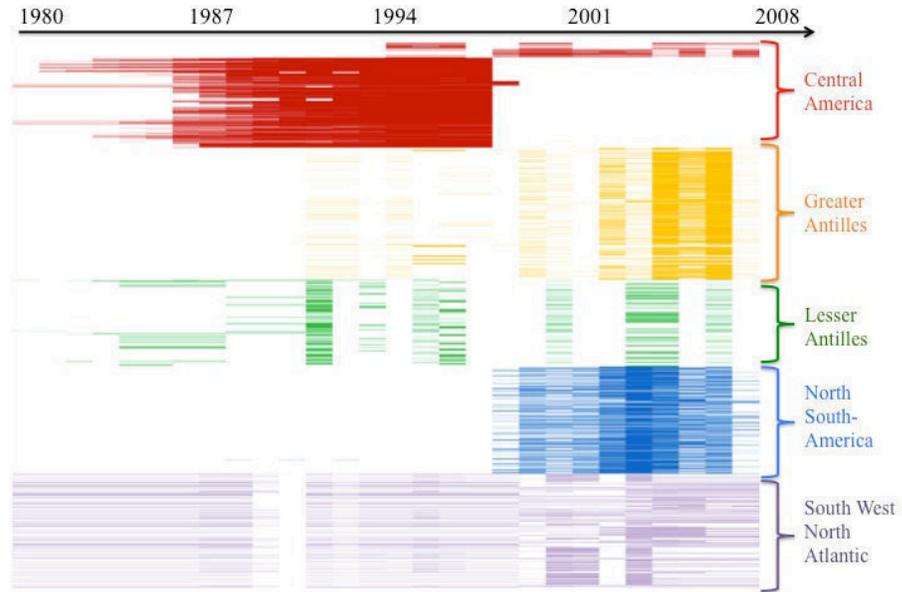


Figure S1. Time series of data available from different census sites that, together, provided the 3727 populations included in this study. Each line showed the time span of a time series. Time series are colour-coded by sub-region of the Caribbean to show the geographic spread of the data.

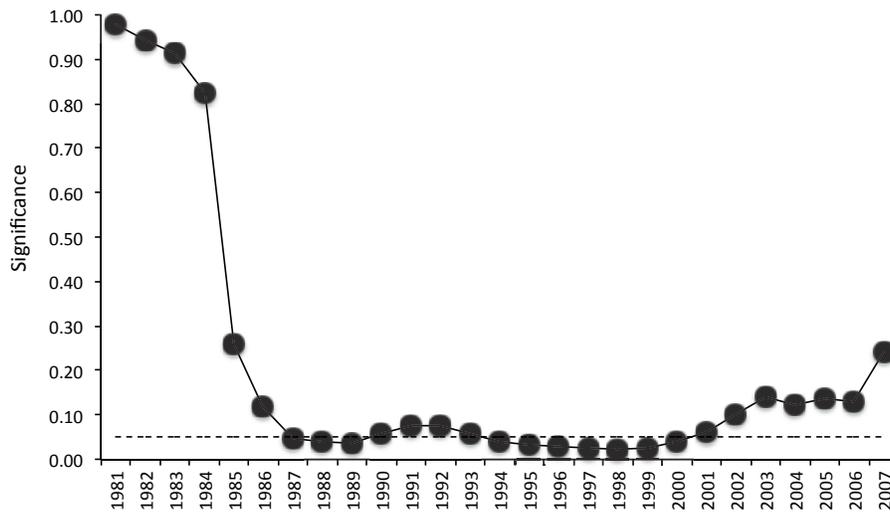


Figure S2. Significance ( $p$  values) of the annual difference between the trends of habitat-generalists and habitat-specialists shown in Fig 2A and B.  $p$  values were derived from T tests comparing the final index values and 95% CIs of the specialist and generalist trends. The dashed line shows the critical value below which differences are statistically significant.

As can be seen in Figure S1, monitoring at many sites either ceased or began around 1998. We explored the effect of this change-over of sites by analysing only the time series that span this time period. The patterns are shown in Figure S3 and are consistent with the trend shown by time series ending in 1998 and by the complete data set (Figs 2A & B in main paper, reproduced below), indicating that the turnover of monitoring sites did not drive the main findings of our analyses.

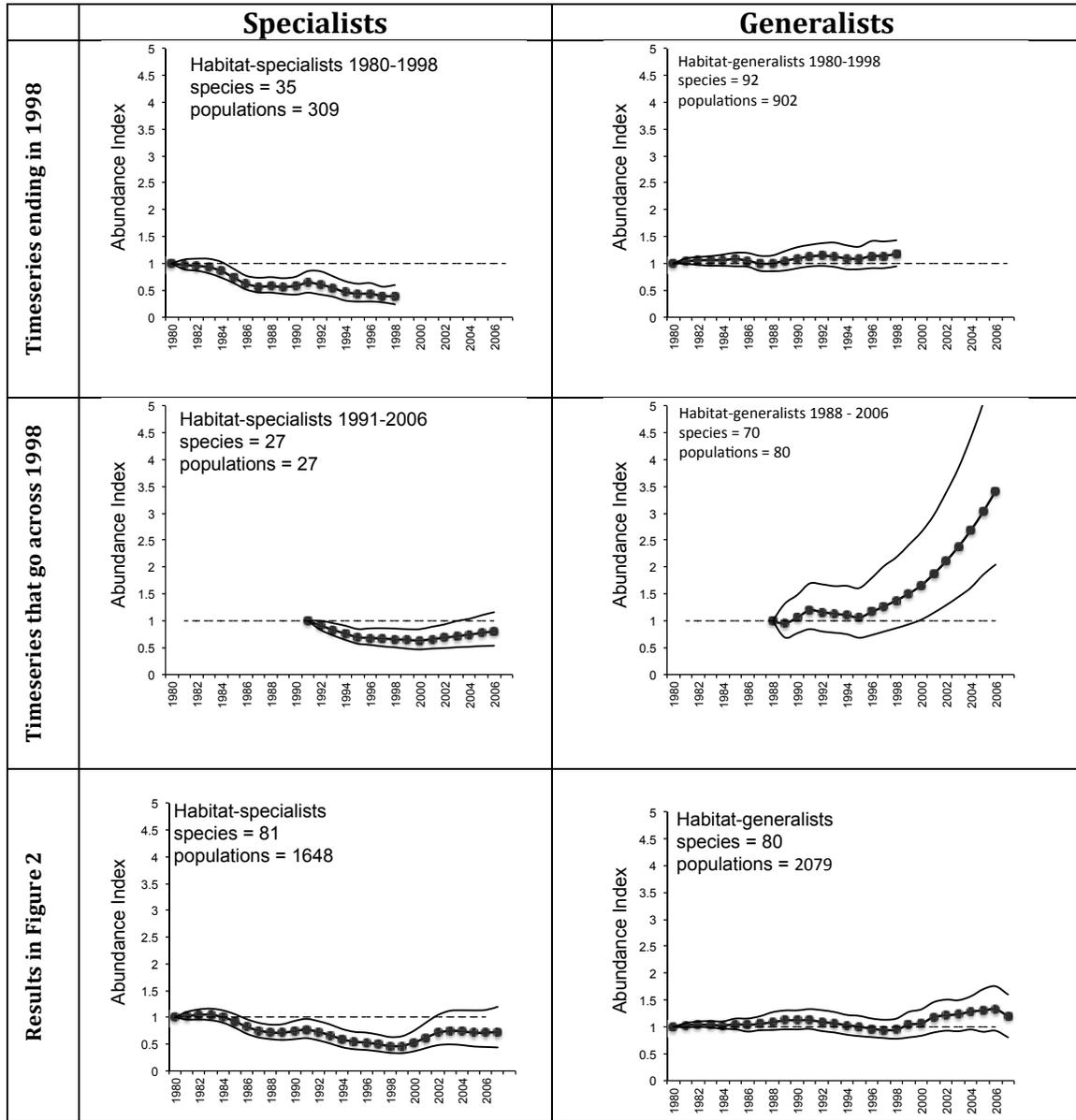


Figure S3. Temporal trends in the Abundance Index ( $\pm$  95% CI, see Methods for calculations) of habitat-specialist (left column) and habitat-generalist (right column) Caribbean reef-fish species in long time-series that either stop in 1998 (top row) or span 1998 (middle row). The baseline year is indicated by a dashed line. Panels (A) and (B) from Figure 2 are shown to facilitate the visual interpretation.

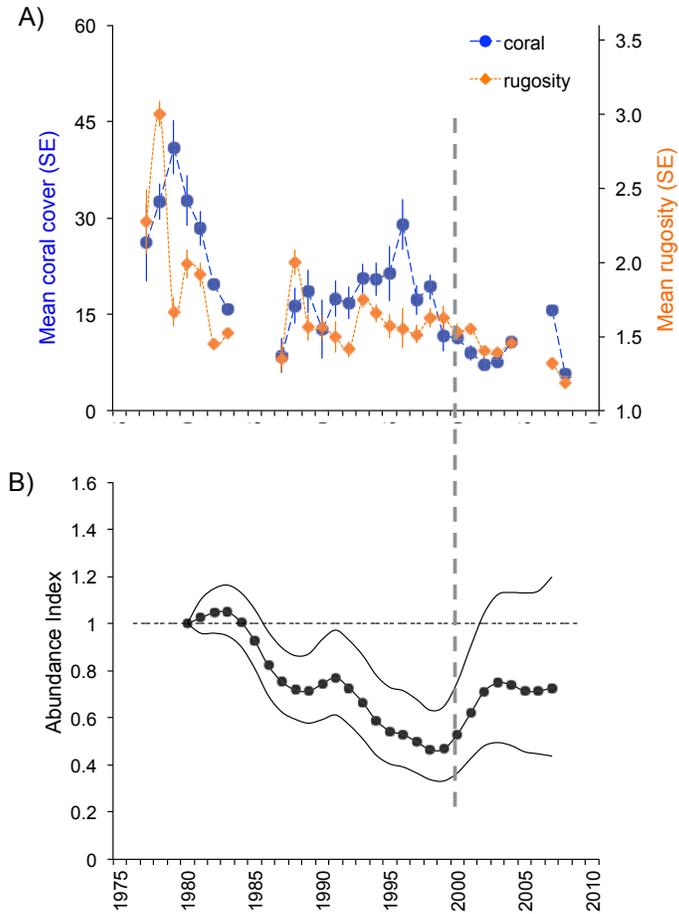


Figure S4. Long-term trajectories of change in coral cover, reef rugosity and habitat-specialist fishes on Caribbean reefs. A) Region-wide changes in mean coral cover and reef rugosity based on a meta-analysis of ecological studies across the Caribbean from 1977 to 2008 (Redrawn from Alvarez-Filip et al. 2011; *Global Change Biol.* 17:2470-2477). B) Temporal trends in the overall abundance of habitat-specialist fishes, relative to 1980 as depicted by the Abundance Index (Redrawn from Figure 2A). The grey dotted line indicates the year 2000, when at the regional scale, the abundance of habitat-specialist fishes started to recover but coral cover and reef rugosity continued to decline. The two panels derive from different data sources due to the lack of site overlap between the habitat (coral cover and reef rugosity) and fish datasets.

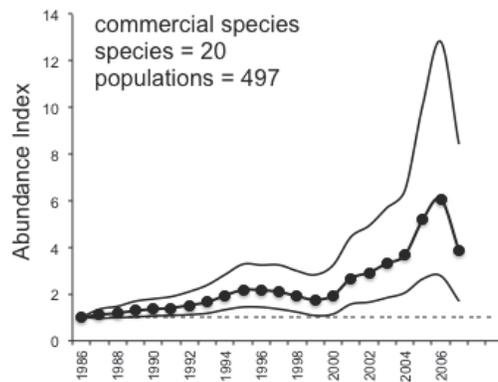


Figure S7. Temporal trends in aggregate abundance (Abundance Index, with 95% CI) of two major taxa of commercially important Caribbean reef fishes: Serranidae (groupers) and Lutjanidae (snappers). Baseline year is 1986 (dashed line at  $y = 1$ ).

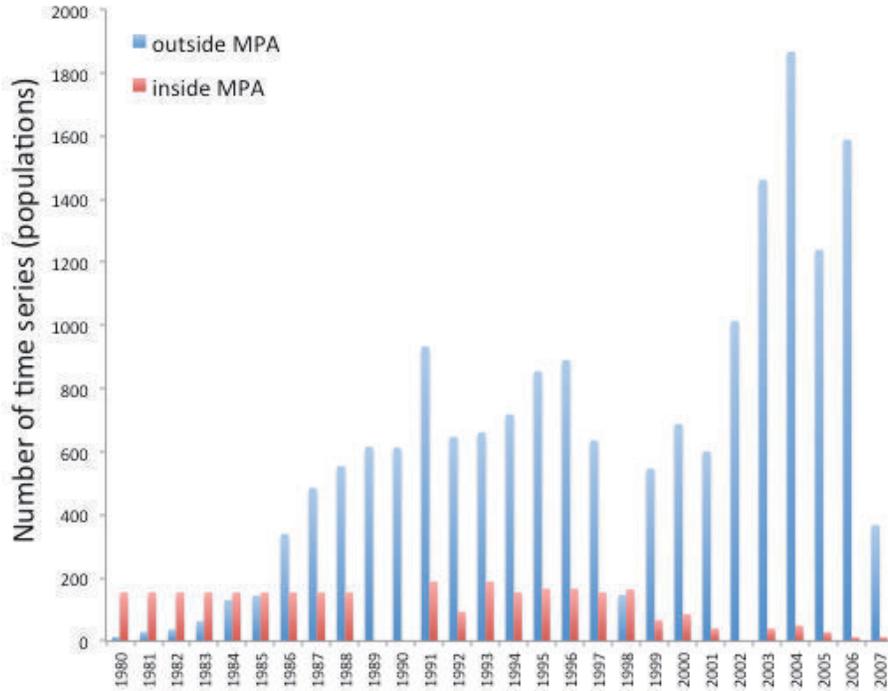


Figure S8. Number of populations (i.e., time series) collected from inside (red bars) and outside (blue bars) Marine Protected Areas in the Caribbean in each year of the study. Between 1980 and 1988 all times series for inside MPAs are from only one study in Florida, USA. From 1991 to 2007, the number of studies contributing information for sites inside MPAs ranged between one and two, and represented only three other countries/territories (Saba, Costa Rica and Curaçao). Due to the scatter spatial and temporal distribution of the data, it was not possible to further explore the trends of change inside MPAs with the Abundance Index.