Report

Recent Region-wide Declines in Caribbean Reef Fish Abundance

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Summary

Profound ecological changes are occurring on coral reefs throughout the tropics [1–3], with marked coral cover losses and concomitant algal increases, particularly in the Caribbean region [4]. Historical declines in the abundance of large Caribbean reef fishes likely reflect centuries of overexploitation [5–7]. However, effects of drastic recent degradation of reef habitats on reef fish assemblages have yet to be established. By using meta-analysis, we analyzed time series of reef fish density obtained from 48 studies that include 318 reefs across the Caribbean and span the time period 1955–2007. Our analyses show that overall reef fish density has been declining significantly for more than a decade, at rates that are consistent across all subregions of the Caribbean basin (2.7% to 6.0% loss per year) and in three of six trophic groups. Changes in fish density over the past half-century are modest relative to concurrent changes in benthic cover on Caribbean reefs. However, the recent significant decline in overall fish abundance and its consistency across several trophic groups and among both fished and nonfished species indicate that Caribbean fishes have begun to respond negatively to habitat degradation.

Results and Discussion

A thorough search for fishery-independent, quantitative time-series data on Caribbean reef fish density yielded 23 peer-reviewed papers, 4 reports, and 21 unpublished data sets, which together spanned 53 years, 273 reef fish species, and 20 countries and dependent territories. A rate of change in fish density was calculated for each of the 12,897 species × reef-specific time-series obtained from these 48 studies. A meta-analysis of these data revealed that annual rates of change in reef fish density in the Caribbean shifted from being positive or indistinguishable from zero to negative over the period from 1955 to 2007 (Figure 1). Averaged over the entire time period, the annual rate of change in fish density was statistically indistinguishable from zero (A_r, of 0.53%; bias-corrected 95% confidence interval, CI = −0.39% to 1.48%, which is not significant because it overlaps zero), but this averaging of rates from different time periods masks significant differences among them (Q_M = 25.89, p = 0.004). Between 1955 and 1995, rates of change in fish density were indistinguishable from zero or significantly positive (1981–1985). For both of the final two time periods (1996–2000 and 2001–2007), rates of change in fish density were significantly negative (Figure 1). The only time period showing positive change (1981–1985) coincides with an important ecological event in the Caribbean, the mass mortality of a once ubiquitous reef herbivore, the sea urchin *Diadema antillarum* [8]. A positive response in fish populations to this event [9, 10] may have delayed the onset of the downward trend.

There was also significant variation in annual rates of change in fish density among subregions (Q_M = 52.00, p = 0.001). Three of the five major subregions of the Caribbean (Figure S1 available online)—the SW N Atlantic, the Lesser Antilles, and Central America—show significant negative rates of change in fish density between 1996 and 2007 (Figure 2). The causes of variation among subregions are unclear, but two potential sources can be ruled out. Marine protected areas (MPAs) usually have higher fish densities [11, 12], and unequal contributions of MPAs across subregions could, therefore, generate variation in trends in fish density. However, only 5% of density estimates were derived from MPAs, and removing these data did not alter the overall rate of change ($A_{r \text{ without MPAs}}$ = 0.48%, CI = −0.41% to 1.46%) nor did it remove the heterogeneity among subregions (Q_M = 48.34, p = 0.001). Geographic variation in rates of change of fish density also cannot be explained by geographic differences in rates of loss of coral cover, because no evidence of such regional variation was found in a meta-analysis of more than 250 Caribbean reefs [4]. Moreover, geographic variation in rates of change of fish density were not attributable to absolute loss of coral cover over the past 30 years, which has varied among subregions [4], as indicated by the fact that areas with the greatest absolute declines in coral cover (e.g., parts of the Greater Antilles [4]) had nonsignificant rates of change in fish density. Nonetheless, our results suggest that declines in reef fish densities have occurred recently and across most reefs of the region.

We found little evidence for a role of fishing in driving the recent declines in Caribbean reef fishes. Rates of change in density of fished and nonfished species were similar (Q_M = 0.47, p = 0.59), with both groups posting significantly negative annual rates of change in the most recent time period (2001–2007, fished species: A_r = −2.90%, CI = −4.26% to −1.49%; nonfished species: A_r = −3.55%, CI = −5.44% to −1.58%). Moreover, large-bodied species and those at higher trophic levels which are usually most strongly impacted by fishing pressure [13–15] showed no greater declines than other groups as indicated by a lack of a relationship between rate of change in density and maximum attainable total length of each species (slope < 0.0001, p = 0.34). Furthermore, piscivorous fishes, which are heavily fished in the region [16, 17], showed no evidence of decline (Figure 3). Previous studies indicate that the long history of intensive fishing in the Caribbean depleted populations of top-level predators long before the first scientific surveys in this area [5]. As a result, populations of such species may now be persisting at low densities owing to strong density dependence. The declines across a wide range of species, including lower trophic levels and smaller-bodied species not targeted by fisheries, suggest that they are not due to fishing pressure alone.

Counterintuitively, the decline in fish density that we document could be caused by recovery of large predators. These species live at low densities but can consume large numbers of smaller reef fishes, reducing overall fish density [18, 19]. Such an effect has been observed in comparisons of relatively pristine and heavily exploited Pacific reefs and appears attributable to the abundance of large sharks on unfished reefs [20–22]. There is no evidence, however, that populations of sharks or piscivorous fishes have been increasing in the Caribbean region [23, 24]. Thus, we find no evidence that declines in density of Caribbean reef fishes have been driven by recovery of large predators in the region.

During the period of decline (1996–2007), three trophic groups—the herbivores, invertivores, and generalist carnivores—had significantly negative annual rates of change (i.e., CIs did not overlap zero), whereas the three other groups had rates of change that were indistinguishable from zero (Figure 3). Nevertheless, because of largely overlapping confidence intervals, trophic groups did not differ significantly from each other in mean rate of change (Q_M = 10.23, p = 0.26). The decline in herbivorous fishes is of particular concern, given the role of this group in maintaining low algal biomass, thus facilitating coral recruitment and survival [25, 26].

Corals have declined drastically across the Caribbean region in the past few decades, with an 80% reduction in cover
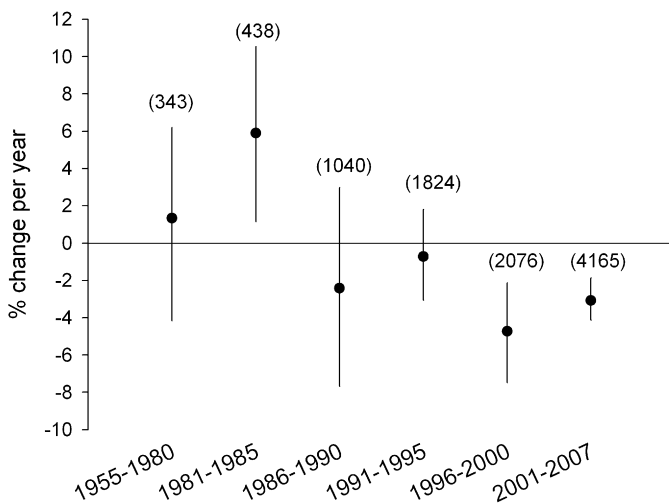
Figure 1. Annual Percent Change in Fish Density m^{-2} per 5-Year Period

Bars are 95% confidence intervals. Two time periods (pre-1980 and post-2000) included more than 5 years to avoid low sample sizes. Sample sizes are given in parentheses and represent the number of individual fish density estimates included in the analysis for each group.

Caribbean reef fish may not depend on corals to the same extent as do their Indo-Pacific counterparts. Noncoral habitats appear to have been important for speciation and persistence of Caribbean fish taxa, particularly during periods of high coral extinction rates [32–36]. Today, a few small-bodied species in the Caribbean associate closely with coral substrata [37, 38], but in contrast to Indo-Pacific species, no Caribbean fish feeds exclusively on corals [39]. Nonetheless, structural complexity is important for Caribbean fishes [40, 41] and it is likely that the three-dimensional relief of Caribbean reefs has been gradually deteriorating, particularly in recent years as corals—the building blocks of reef platforms—have been reduced to very low abundance.

Our study reveals recent region-wide declines in Caribbean coral reef fish density that are largely consistent across subregions and in three of six trophic groups. Although Caribbean reef fishes seem to have been slower in responding to degradation of coral reef habitats than Indo-Pacific reef fishes, declines have recently become evident. The consistency of these declines across a range of species with varying ecologies and an array of reefs throughout the Caribbean suggests a degradation debt, with fishes in this region now declining in response to habitat-related changes.

Experimental Procedures

Systematic Data Search

Temporally replicated, quantitative data of Caribbean reef fish density (no. of individuals m^{-2}) from in situ surveys conducted only by highly trained scientists were identified via (1) electronic and manual searches of published literature, (2) manual searches of unpublished reports and theses, and (3) contributions of raw data by researchers. Electronic literature searches were conducted with ISI Web of Science (1900–2008), Aquatic Sciences and Fisheries Abstracts (ASFA; 1971–2008), and ProQuest Digital Dissertations (1861–2008). References cited in these publications were also checked. Manual searches of unpublished reports and theses were carried out at Caribbean research institutions with significant library holdings

since the mid-1970s [4]. The overall lack of congruence between the trajectory of fish density and that of coral cover within this time period is surprising, considering that declines in density of many coral reef fish species have been linked to loss of coral in other regions [27–31]. Responses of fish populations to loss of coral in the Indo-Pacific have been shown to lag by 5–10 years [29]. In contrast, in the Caribbean, where coral has been lost gradually since at least the mid-1970s [4], our analyses indicate that overall reef fish density began to decline significantly only in the last decade (Figure 1). The lag in response to coral loss by Caribbean reef fish may therefore be longer than for Indo-Pacific fishes.

The regional difference in lag times may simply reflect differences in the temporal scale of coral loss, because this study examines changes in reef fish density throughout a multidecadal period of continual coral loss, whereas the Indo-Pacific studies followed discrete catastrophic coral mortality events. However, differences between Caribbean and Indo-West Pacific fishes in response to declines in coral cover may be real and reflect differing historical and ecological causes.
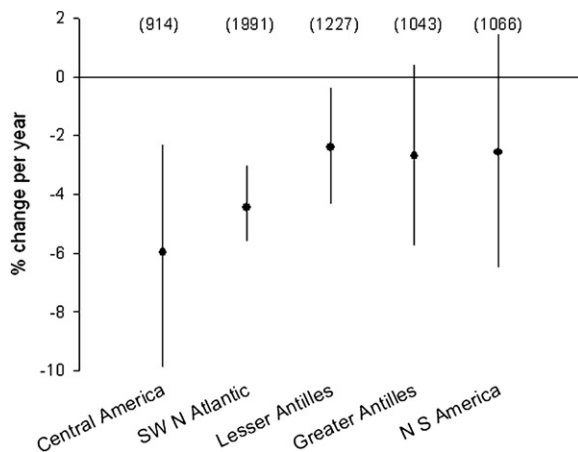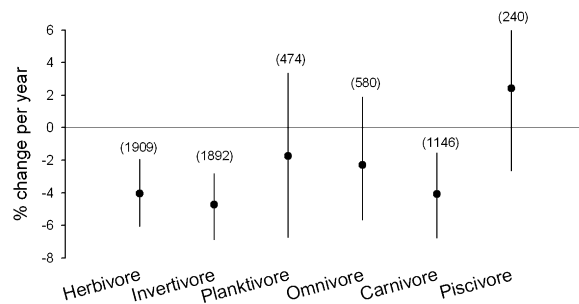

Figure 2. Annual Percent Change in Fish Density m^{-2} across Five Subregions of the Caribbean Basin 1996–2007

Bars are 95% confidence intervals. Sample sizes are given in parentheses and represent the number of individual fish density estimates included in the analysis for each group.

Figure 3. Annual Percent Change in Fish Density m^{-2} by Major Trophic Group during the Time Period 1996–2007

Bars are 95% confidence intervals. Sample sizes are given in parentheses and represent the number of individual fish density estimates included in the analysis for each group.

and/or research programs. These included the Smithsonian Tropical Research Institute in Panama, Bellairs Research Institute, Barbados Fisheries Institute and the University of the West Indies in Barbados, Caribbean Marine Biology Institute in Curaçao, Discovery Bay Marine Laboratory, Montego Bay Marine Park, the University of the West Indies in Jamaica, the University of Puerto Rico, the University of the Virgin Islands and the National Park Service in the Virgin Islands, Rosenstiel School for Marine and Atmospheric Science and NOAA Southeast Fisheries Science Center in Miami, the Centro de Investigación en Ciencias del Mar y Limnología (CIMAR) from the Universidad de Costa Rica, in San José, Costa Rica, and Universidad Autónoma de Yucatán and CINVESTAV in Mexico. Finally, an advertisement of the project with request for data was posted to an international list-serve of coral reef researchers ("coral-list") managed by the National Oceanic and Atmospheric Administration.

To be included, each study needed to have (1) reported a density estimate of at least one reef fish species from a reef site within the Caribbean region, (2) surveyed the same species at the same reef site over more than one year, and (3) replicated measurements within each survey.

Data were compiled from 48 multiyear quantitative surveys of reef fish density, which included 12,897 reef- and species-specific time series. When data from published sources were presented in aggregated form, disaggregated data were sought directly from the authors. When species-specific data were not available, the lowest taxonomic or trophic group possible was used (e.g., some studies only reported to family, or by trophic group, such as "herbivores"). The data spanned the years 1955–2007, came from both published (56%) and unpublished sources, and encompassed 273 species (Table S2) from 318 reefs in 20 countries and dependent territories (Table S1, Figure S1).

Meta-analysis is a method specifically designed to synthesize quantitatively the results of separate studies. It entails the calculation of an "effect size" for each study, i.e., a common currency by which to measure the magnitude of the response of interest *within* each study, which are then combined into an overall effect size across studies in order to detect whether trends are consistent across studies. Meta-analytic methods can overcome the limited spatial and temporal extent of many coral reef monitoring programs and are used increasingly in ecological and conservation studies [4, 27, 42–44].

The effect size used here was the annual rate of change in density, A_R, measured as:

$$A_R = [\log A_e - \log A_i]/d$$

where A_e and A_i are numerical densities of a given reef fish species at the end and start, respectively, of the time series at a given reef, and d is the length of the time series in years. Individual effect sizes were weighted by the spatial area covered in each fish survey (e.g., area of transect multiplied by number of replicate transects per survey), because this has been found to be a robust and relevant weighting factor for meta-analyses involving subtidal data [45]. Mean effect sizes (overall or within-group) were therefore calculated as:

$$\overline{A}_r = \frac{\sum_{x=1}^{n}(W_x * A_{r\,x})}{\sum_{x=1}^{n}W_x}$$

where w is the reef area surveyed. Confidence intervals (CI) were calculated as:

$$CI = A_r \pm t_{a/2[n-1]} * \sqrt{1/\sum_{x=1}^{n}}$$

A significant effect is one for which the CI does not encompass 0.

Heterogeneity in the overall mean effect size was evaluated with the test statistic Q_T [46], which measures the extent to which individual effect sizes coincide in direction and magnitude. To investigate the causes of any significant heterogeneity, data were subdivided into biologically meaningful groups to partition the variation, and differences among groups were evaluated via the test statistic Q_M [43]. This test determines whether there are significant differences in magnitude and direction of response among categorical groups. Note that it is possible to have a similar magnitude and direction of response among groups (i.e., a nonsignificant Q_M) while some or all individual groups show a significant effect size (i.e., individual CIs do not overlap zero). We examined four categorical groupings: subregion, time period, trophic group, and fishing status. Five broad subregions within the Caribbean were considered: the southwestern North Atlantic, the Greater

Antilles, the Lesser Antilles, northern South America, and Central America. Time periods were evaluated in 5-year intervals, with two exceptions: years prior to 1981 (31 years) and after 2000 (7 years) were combined because of low sample sizes included in these intervals. The earliest time interval (<1981) includes data from the 1970s and the only older study available (1955), so extrapolation of the results to pre-1970s should be considered cautiously; however, results are unchanged by the removal of the 1955 study (pre-1981 rate of change in fish density, with 1955 study: A_r = 1.34%, CI = −3.86% to 5.97%; without 1955 study: 2.54%, CI = −2.43% to 7.55%). Note that the total sample size for the temporal analysis (9886 time series) was lower than that of the overall analyses because some time series did not have replicate surveys within a given 5-year interval, so could not be included. We repeated the temporal analysis with longer time intervals (12 years), and patterns were consistent (i.e., significant decline in the most recent time interval: 1996–2007: A_r = −2.97%, CI = −4.52% to −1.42%). Fish species were categorized into one of six major trophic groups (Table S2), similar to those designated by previous authors [47, 48] and representing potentially important differences in ecological roles and behavior and thus in susceptibility to impacts such as fishing pressure or habitat change. The trophic groups were (1) herbivores (consume detritus, turf algae, and/or macroalgae, <10% of diet is animal matter); (2) invertivores (consume benthic-associated invertebrates, <10% of diet by volume contains algae/plants/detritus); (3) piscivores (prey on living fishes, <10% invertebrates or plant/algae/detritus); (4) carnivores (eat both invertebrates and fishes, and if plants/algae/detritus, <10% by volume); (5) omnivore (diet contains both animal and plant matter, >10% of both); and (6) planktivores (consume macro and micro zooplankton, including larval fishes). Finally, fish species were also separated into two categories of fishing status: fished or unfished. Fished species were identified by conducting searches in FishBase (http://www.fishbase.org) and primary literature. Nonfished species include those that are not marketed, have unknown fishing status, or are included only in the aquarium trade. Designations are listed in Table S2.

The effect of one continuous variable, maximum attainable total length of species, on annual rates of change in density was also examined. Maximum total length data were obtained from FishBase (http://www.fishbase.org) (Table S2). The significance of this meta-regression is reported as the probability of the slope being different than zero [46].

We tested for nonindependence, publication, and methodological biases in several ways. The calculation of overall effect size was repeated multiple times, excluding sequentially individual studies with >50 species or >5 reefs. The results remained consistent, indicating that no single, large study had an undue influence on the overall result. Publication bias could occur if studies are published only when they show a strong effect. We compared the overall effect sizes obtained with only peer-reviewed and only non-peer-reviewed data sources and found no significant difference (Q_M = 1.24, p = 0.36). A lack of publication bias was also evident in the clear funnel shape exhibited by the relationship between individual effect sizes and sample sizes [46]. There was no relationship between annual rate of change in fish density and study duration (slope = 0.0003, p = 0.33), and the effect sizes generated by studies of short duration (i.e., two years) were as variable as those from studies of longer duration (short studies: Q_T = 1202.22, p < 0.001; longer studies: Q_T = 20465.14, p < 0.001). Finally, to examine potential biases introduced by combining studies with different surveying methods, we compared the rates of change in overall fish density obtained with transects, cine-transects, point counts, quadrats, and whole-reef counts—the five methods used in the studies included—for the decade in which we had the most data (1996–2007). This revealed no significant differences among methods (Q_M = 11.39, p = 0.08).

All A_R and CI are presented as back-transformed data so that they can be easily interpreted as percent change in fish density per year. Insufficient data were available to permit analyses of changes in fish length, biomass, or species composition (because not all studies examined the entire species assemblage).

Supplemental Data

Supplemental Data include one figure and two tables and can be found with this article online at http://www.current-biology.com/supplemental/S0960-9822(09)00751-9.

Acknowledgments

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