Exploitation, secondary extinction and the altered trophic structure of Jamaican coral reefs.

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Coral reef communities of the Greater Antilles in the Caribbean have a long history of anthropogenic disturbance, driven by the exploitation for food of both vertebrate and invertebrate species [1,2]. Exploitation, coupled with region-wide declines of coral environments [3–6] has resulted in local and regional vertebrate extinctions. The impact of those extinctions on reef communities, however, remains largely unexplored. Here we show, using a highly resolved model coral reef-seagrass food web, that at least 40 of 188 expected vertebrate species are absent from Jamaican coral reefs. Twenty one of the absent species are of high trophic level and are exploited by humans. The remainder of the absent species are unexploited, and comprises a significantly high proportion of specialized reef foragers. Many of those species are also more trophically specialized than their closest trophic competitors. We conclude that the absence of unexploited species from Jamaica is caused by the overexploitation of high trophic level species, and consequent trophic cascades and secondary extinction among their prey in an increasingly degraded reef environment. The result is a reef community depauperate of both exploited high trophic level predators, and unexploited, specialized lower

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trophic level reef foragers.

Many exploited vertebrate species have been extirpated from various islands in the Caribbean, or persist at dramatically reduced population sizes. Numerous studies have addressed the effects of the loss of herbivorous species [7–10] or higher trophic level consumers [4,6,11] on coral communities. Here, based on a highly resolved food web network model of coral communities in the Greater Antilles, we report on the alteration of trophic structure caused by the absence of both exploited and unexploited species over a broad range of trophic levels.

Our construction of the food web network relied upon records of community composition and ecology from across the Greater Antilles, but we focused on Jamaica because of its documentation of pre-historic and post-Columbian fishing [2,12–14]. The final network comprises 750 primary producer, invertebrate and vertebrate species, and 34,545 intra- and interspecific predatory interactions (SI Table 1). There is a total of 188 vertebrate species, and these were organized into foraging groups as species that forage primarily on coral reefs (reef foragers), in seagrass beds (seagrass foragers), or frequently in both habitats (reef-seagrass foragers) [15]. This model is henceforth referred to as the expected network of a Greater Antillean reef. The network was used in conjunction with the REEF Volunteer Survey Program database [16] to search for vertebrate species that are expected to occur on Jamaican coral reefs, yet do not. We recorded all species that are both present in the network, and have been observed at least once in Jamaica in the past 10 years. This number varies between 58 and 123 in the six designated REEF zones. Our estimate of species absent from Jamaica is conservative, however, since we considered the presence of a species at a single locality

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to count for the entire island. This allows for the possibilities that the survey overlooked species, and that individuals at one locality could relocate to or reproductively seed another locality. Furthermore, we ignored demographic data such as estimated population densities, and recorded a species as present if only a single individual was observed. Nevertheless, the final estimate yielded 40 vertebrate species which have not been observed by the REEF survey in Jamaica for at least the past 10 years, yet are expected to be present based on the network model. We examined the changes that the removal of these 40 species would precipitate in the expected network, and how their absence has caused the observed Jamaican food web to deviate from the expected.

The number of prey per consumer (in-links) for the entire network has a right-skewed, long-tailed distributon (mode=30) (Fig. 1). A distinct mode within the range of the distribution distinguishes this food web from other published food webs, most of which have decay (e.g. exponential) distributions [17–19]. The distribution for vertebrates only is similar to the overall distribution. The long tails of the overall and vertebrate-only distributions indicate the presence of generalized feeders, and suggest that this food web possesses the tolerance to node removal typical of other real-world networks [20]. Food webs with long-tailed link distributions are resistant to secondary extinction and collapse when nodes are removed randomly [21,22]. Resistance, or structural robustness [23] is generated by the presence of highly-linked species, in this case trophic generalists. Removing the 40 missing species from the Greater Antillean network predicted a single secondary extinction, the striated frogfish (*Antennarius striatus*), which is indeed one of the species absent from Jamaica. The removals also represent the loss of 2,401 links (Fig. 2), altering the network's distribution significantly, and increasing connectance [24] from 0.061 to 0.064. An increase can result

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only from a biased removal of link-poor trophic specialists. This is supported by the significantly lower in-link distribution of species absent from Jamaica when compared to species which are present (Fig. 1). The difference, however, stems from the reef foraging group only, and not the seagrass or reef-seagrass foraging groups. Jamaican reef communities therefore have fewer reef foraging vertebrate species than would be expected for a Greater Antillean reef.

The trophic levels of absent species is another food web feature biased according to foraging group. Trophic level was measured as fractional trophic level (ftl) [25,26], with secondary and higher consumers of the expected network having a mean ftl of 3.38 (Fig. 3). Changing the ftl of a single species in a food web changes the trophic levels of higher trophic level species linked to it by predatory chains. The removal of the 40 missing species (ftl reduced to zero) consequently resulted in the alteration of ftl for 39 other vetebrate species that are direct or indirect consumers of one or more of the absent species, but the ftl distribution is not altered significantly. Furthermore, whether ftl alteration (Δftl) is an increase or decrease is unrelated to original ftl, being determined instead by the trophic levels of absent prey species. The majority of changes in ftl are minor (Δftl < 0.1). Absent species, however, are of significantly higher ftl than would be expected if they were selected randomly. This bias is generated by a difference between absent and present species within the reef-seagrass foraging group only. Examples of these species include the mutton hamlet (*Alphestes afer*, ftl=4.44) and the oceanic whitetip shark (*Carcharhinus longimanus*, ftl=4.48). There are no biases, however, within the reef or seagrass foraging groups. Species absent from the reef-seagrass foraging group in Jamaica are therefore of unexpectedly high trophic levels.

Twenty-one of the 40 absent species are exploited by humans [12,15,27,28] (SI Table 2). They are also of significantly higher ftl compared to other vertebrates in the expected network (mean ftl = 3.64, Kolmogorov-Smirnov, n=187, p = 0.011), and to other vertebrates currently exploited in Jamaica (Kolmogorov-Smirnov, n=127, p = 0.001). The impact of fishing, combined with traits generally correlated with high trophic level, such as smaller population sizes, is therefore the likeliest explanation for their absences. It is not necessarily the only factor, however, and does not explain the absence of unexploited species, at least not directly. Additional explanations include being overlooked by surveys, undocumented fishing, and the degradation of Jamaican reefs. Being overlooked by REEF surveys is not a likely explanation because the surveys account for numerous similar species. For example, the unexploited and absent downy blenny (*Labrisomus kalisherae*) is no more difficult to observe than the seaweed blenny (*Parablennius marmoreus*), which is recorded in the Jamaica survey. Undocumented fishing is also an unlikely explanation given the available records of recent Jamaican fisheries [12,15,28]. The decreased quality of Jamaican coral reefs, including the reduction of spatial heterogeneity of the reef [3,5] is a more supportable hypothesis. Additionally, we hypothesize that the exploitation of predatory species and consequential trophic cascades is a factor in the absence of unexploited species.

Secondary extinctions caused by top-down effects, such as trophic cascades, cannot be demonstrated with demographically unparameterized networks [22,23]. There is, however, circumstantial evidence. We reasoned that if unexploited species are absent because of trophic cascades, then those unexploited species could be competitively inferior to other prey of the same predators. We tested this hypothesis by first observing the network structure of the absent species only.

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Thirty-nine of the 40 absent species are linked in a single component or sub-network (Fig. 4). Randomly selected sub-networks with comparably large single components occur only when generalist predators are included, namely carcharhinid sharks. The in-link structure of the observed sub-network of absent species is indeed dominated by generalist predators, with 93 of the 97 in-links belonging to only 11 exploited, predatory species.

Next we compared two properties relevant to interspecific interactions. First, body length is representative of important predatory, anti-predatory and competitive traits. Second, the number of in-links measures the degree of trophic specialization. We then identified the closest potential competitors of all the absent species, defining competitors as species within the same foraging group, with which an absent species shares at least 50% of its prey species, and which are prey to the same predators among the absent species. For example, the absent molly miller (*Scartella cristata*) and the present redlip blenny (*Ophioblennius atlanticus*) share 100% of their in-links. Thirty-eight competitors were consequently identified for 17 of the 40 absent species (SI Table 3). There is no significant difference in body length between the absent species and potential competitors (Wilcoxon signed rank test, n=60, p = 0.352), but absent species do have significantly fewer in-links (Wilcoxon signed rank test, n=60, p = 0.0039). Specifically, absent, exploited species have no fewer in-links than their competitors (Wilcoxon signed rank test, n=31, p = 0.289), but unexploited species do (Wilcoxon signed rank test, n=29, p = 0.0018). Although number of species compared is low (8 exploited and 9 unexploited species), the indication is that unexploited species absent from Jamaican reefs are more trophically specialized than their present competitors. The result is a reduction of trophic specialization in the vertebrate component of the reef community.

The structure of Jamaican coral reefs therefore differs significantly from what is expected of a Greater Antillean reef. The historic targeting of high trophic level species would have generated trophic cascades [1,2] and altered the competitive environments of lower trophic level prey. Unexploited, absent species are apparently at a disadvantage relative to trophic competitors during cascades. Those species may also be more sensitive to changes of reef quality [29]. It remains to be seen if other regional coral reefs in the Greater Antilles have exhibited similar responses to exploitation, and whether protective measures have preserved or restored trophic structure [30].

Methods Summary

The composition of coral reef and associated seagrass communities in the Greater Antilles was assessed by reviewing the available literature extensively. Taxa present elsewhere in the Caribbean Sea or Gulf of Mexico, but not recorded explicitly from one of the Greater Antillean islands or the United States Virgin Islands, were omitted from the dataset. Only species for which reasonable detail of prey and predators, as well as foraging area could be obtained, were included. Most primary producer and invertebrate species were organized into functional trophic guilds [22] unless consumer diets are highly specialized and known with specificity. Cartilaginous and bony fish diets were obtained from Opitz's report [15]. We searched the REEF Volunteer Survey database [16] for records of every vertebrate species in our dataset. Those species in the dataset that are not part of the survey, but are present in our dataset were automatically considered to be present. All REEF zones in Jamaica were queried individually, but the results were combined to construct the Jamaican species list.

Fractional trophic level of a species was calculated as one plus the average trophic level of all its prey. Primary producers therefore have ftl=1, while primary consumers have ftl=2. Beyond that, species' ftl values may be real numbers, reflecting dietary diversity and the extent to which a species feeds at multiple trophic levels. The nearest trophic competitors of an absent species were determined by comparison to all members of its foraging group, and measurement of in-link overlap. Body lengths were obtained from Fishbase [27]. The extent of trophic competitive overlap was measured as the number of prey possessed in common by the species.

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Supplementary Information is linked to the online version of the paper at www.nature.com/nature. A figure summarizing the main result of this paper is available in Supplementary Information.

Author Contributions P.D.R. designed the study and assembled the Greater Antillean and Jamaican food webs. R.H. searched the REEF databases and determined exploited/unexploited statuses of species. P.D.R. performed statistical analyses. Both authors wrote the text and assembled data tables for Supplementary Information.

Author Information The authors declare that they have no competing financial interests. Reprints and permissions information is available at npg.nature.com/reprintsandpermissions. Correspondence and requests for materials should be addressed to P.D.R. (email: proopnarine@calacademy.org).

Figure 1   Trophic in-link (number of prey) distributions. a, Trophic in-link distribution for expected Greater Antillean network. b, The distribution for vertebrate species absent from Jamaica (black line) is significantly lower than that of the vertebrate-only component of the expected network (green histogram) (Kolmogorov-Smirnov, n=187, p=0.003). c, Stacked area graph of distributions for the reef (solid black), seagrass (stippled) and reef-seagrass (gray) foraging groups. The reef group differs significantly from that of species present in Jamaica (Kolmogorov-Smirnov, n=94, p=0.001), but the seagrass and reef-seagrass groups do not (Kolmogorov-Smirnov; n=29, p=0.793; n=64, p=0.202 respectively).

Figure 2   Vertebrate component of the coral reef food web. Upper - expected Greater Antillean network, lower - observed Jamaican network. The Jamaican network lacks 40 species present in the expected network. Species with idential prey and predators have been collapsed into single nodes in order to increase the clarity of these figures (see Methods Summary). Nodes are arranged on the periphery of the networks, and the lines or edges represent predator-prey links. The in-link distributions of the networks differ significantly (Wilcoxon signed rank test, p<0.0001).

Figure 3   Fractional trophic level (ftl) distribtions. a, Distributions of species present in Jamaica (histogram) and those absent (black line) differ significantly, with mean secondary consumer ftl being greater for absent species (t-test, n=177, p=0.0067). Primary consumers (yellow bar) are omitted from the comparison. b, The difference between distributions in (a) is generated primarily by the absence of higher ftl species in the

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reef-seagrass foraging group (histogram) compared to species still present (t-test, n=64, p=0.0024). The reef (maroon line) and seagrass (blue line) groups do not differ from expected ftl values (t-test; n=89, p=0.383 and n=25, p=0.417 respectively).

Figure 4   Sub-network (upper) of species absent from Jamaica. Lower network, randomly selected sub-network of the samke size. A single component in the random network is expected, since sub-networks comprising any 40 verterbate species yield component sizes of 39-40 9% of the time (out of 100 randomly selected sub-networks). Generalist predators: A - blacknose shark (*Carcharhinus acronotus*), B - lemon shark (*Negaprion brevirostris*), C - tiger shark (*Galeocerdo cuvier*), D - bonnethead shark (*Sphyrna tiburo*).

Methods

The compositions of coral reef and associated seagrass communities were assessed by reviewing the available literature [31–137]. We included only species for which reasonable detail of prey and predators, as well as foraging habitat could be obtained. Primary producer and invertebrate species were organized into trophic guilds [22] unless consumer diets are highly specialized and known with specificity (SI Table 1). Fish diets were obtained primarily from Randall [137] and Opitz [15]. Many fish dietary items, however, are present in very small amounts, and may represent only occassional feeding rather than major dietary components, or are probably ingested incidentally. We therefore included only those prey items which comprised 1% or more of a species' diet.

The REEF Volunteer Survey database [16] was searched for records of every vertebrate species in our dataset (SI Table 2; 53x column headings refer to REEF geographic zones in Jamaica. The first column of numbers for each zone refers to percent sighting frequency, and the second column are estimates of population density). Species in the dataset that are not part of the REEF survey were automatically considered to be present. Our queries covered the period 1999-2009. Also, though species were assigned to one of three reef or seagrass foraging groups, our documentation does not preclude their presence in other coastal areas. Trophic in-link distributions of the complete network and the Jamaican network were compared with the non-parametric Wilcoxon signed rank test because of the distinct non-normality of the distributions. Transformations of the data did not resolve their deviation from normality.

Similarly, the Kolmogorov-Smirnov test was used for comparisons of subsets of those distri-

butions, and the small subsets of the fractional trophic level distributions. Fractional trophic level of a species was calculated as one plus the average trophic level of all its prey. Primary producers therefore have ftl=1, while primary consumers have ftl=2. Beyond that, species' ftl values may be real numbers, reflecting dietary diversity and the extent to which a species feeds at multiple trophic levels. The ftl distributions of the complete and Jamaican networks were suitable for comparison with t-tests because of larger sample size and symmetric, peaked (though platykurtic) shapes.

Vertebrate sub-networks were constructed from the complete network randomly by selecting 40 species randomly out of the 187 vertebrate species. The size of the largest component of the resulting sub-network was recorded as the number of species linked into the single largest component.

Whether a species is or was exploited was assessed from several sources [12,27,28]. The nearest trophic competitors of an absent species were determined by comparison to all members of its foraging group, and measurement of in-link overlap. Body lengths were obtained from Fishbase [27]. The extent of trophic competitive overlap was measured as the number of prey possessed in common by the species.

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│ species             │
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