Functionally diverse reef-fish communities ameliorate coral disease

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Edited by David M. Karl, University of Hawaii, Honolulu, HI, and approved August 18, 2009 (received for review January 13, 2009)

Coral reefs, the most diverse of marine ecosystems, currently experience unprecedented levels of degradation. Diseases are now recognized as a major cause of mortality in reef-forming corals and are complicit in phase shifts of reef ecosystems to algal-dominated states worldwide. Even so, factors contributing to disease occurrence, spread, and impact remain poorly understood. Ecosystem resilience has been linked to the conservation of functional diversity, whereas overfishing reduces functional diversity through cascading, top-down effects. Hence, we tested the hypothesis that reefs with trophically diverse reef fish communities have less coral disease than overfished reefs. We surveyed reefs across the central Philippines, including well-managed marine protected areas (MPAs), and found that disease prevalence was significantly negatively correlated with fish taxonomic diversity. Further, MPAs had significantly higher fish diversity and less disease than unprotected areas. We subsequently investigated potential links between coral disease and the trophic components of fish diversity, finding that only the density of coral-feeding chaetodontid butterflyfishes, seldom targeted by fishers, was positively associated with disease prevalence. These previously uncharacterized results are supported by a second large-scale dataset from the Great Barrier Reef. We hypothesize that members of the charismatic reef-fish family Chaetodontidae are major vectors of coral disease by virtue of their trophic specialization on hard corals and their ecological release in overfished areas, particularly outside MPAs.

biodiversity | ecosystem function | marine protected area | coral reef

Coral reefs remain under increasing threat from poor water quality, habitat degradation, and destructive fishing practices (1–3). These disturbances have abetted drastic shifts in reef community structure (4), reduced productivity (5), and lowered resilience (6–8). More recently, outbreaks of infectious diseases have become a significant cause of coral mortality and habitat loss (9). In the Caribbean basin, for example, diseases of coral reef organisms have become the most important factor in the decline of coral reefs throughout that region (10). However, despite a concerted global effort to characterize coral diseases since the early 1990s, the ecological drivers of these phenomena—and the ultimate consequences for coral reef communities—remain poorly understood (11, 12).

Fish are a dominant structuring force on coral reefs, controlling the distribution and abundance of many reef taxa (13–16). However, if subject to sustained heavy fishing, entire functional groups can be lost (17, 18), resulting in a cascade of effects. These can include population increases of species released from predation and competition (19), reduced diversity, and simplified community structure. This, in turn, disrupts numerous weaker, higher-order interactions thought to be directly linked to ecosystem stability (20–22) and which otherwise buffer the effects of agents of mortality, such as pathogens, their vectors, or predators with “boom and bust” population cycles (17, 23, 24). Ultimately, the resilience of coral reefs is compromised (6, 17). In light of evidence that the diversity and abundance of host, vector, or reservoir species can affect the epizootiology of a disease (25–27), we speculate that diverse, less-impacted reef-fish communities can promote coral health.

Hence, to examine whether functionally diverse fish communities play a role in ameliorating coral disease, we surveyed 14 sites [seven marine protected areas (MPAs) and seven adjacent fished sites] across the central Philippines and examined 1,260 m² of reef for the disease status of 21,646 coral colonies. We tested the hypothesis that reefs with more intact fish communities had significantly lower levels of coral disease. We used well-managed MPAs to ensure intact fish communities, along with companion sites open to fishing but with otherwise comparable benthic communities, to investigate the potential role of reef fish in coral disease dynamics.

Results and Discussion

Factors varying at spatial scales less than that of the study region (circa 12,000 km²) appeared responsible for disease prevalence across sites (“site” refers to a portion of a reef that was surveyed; two sites per reef: one MPA and one fished area). Mean prevalence of all six coral diseases recorded (white syndrome, ulcerative white spots, growth anomalies, black band, skeletal eroding band, and brown band) differed widely among sites, from a low of 0.25% to a high of 7.9% (Fig. 1), although the number of diseases per site did not (Wilcoxon $H = -0.808$, $P = 0.4191$). There was a strong spatial component to disease at the regional scale. Sites differed significantly in the prevalence of diseases (two-way ANOVA $F = 13.68$; $P < 0.0001$), with sites closer together more likely to have similar disease prevalence than those farther away ($r = 0.367$, $P = 0.0009$; simple Mantel test). Thus, despite the potentially high connectivity between the sites in this archipelagic marine system, variation in disease prevalence depended more on aspects of transmission operating at the scale of average intersite distances, 10 km–50 km.

Overall, MPAs had a powerful effect on reducing coral disease, with significantly lower disease prevalence than that of unprotected sites ($\bar{x} \pm 1$ SE: 2.8 ± 0.9 vs. 4.5 ± 1.2 ; two-way ANOVA $F = 5.17$; $P = 0.02$). At all reefs, disease prevalence was lower in MPAs than in fished sites (Fig. 1). These results were not due to differences in percent total coral cover between MPAs and fished sites (57.0 ± 4.5 vs. 57.3 ± 3.4), percent cover of *Porites*, the dominant hard-coral genus and disease host (40.0 ± 3.4 vs. 40.2 ± 4.0), mean total number of coral colonies per transect (342.2 ± 29.1 vs. 356.8 ± 31.4), or physical damage to colonies (0.14 ± 0.02 vs. 0.10 ± 0.02). Moreover, community-level comparisons, as measured by Bray–Curtis similarities in benthic attributes between sites, revealed no differences (global $R = -0.029$, $P = 0.58$) (27). The prevalence of coral disease was instead most strongly reduced on reefs completely protected from fishing; i.e., in MPAs.

Author contributions: L.J.R. and A.P.M. designed research; L.J.R. and A.P.M. performed research; L.J.R., A.R.H., and A.M.K. analyzed data; and L.J.R., A.R.H., and A.M.K. wrote the paper.

The authors declare no conflict of interest.

This article is a PNAS Direct Submission.

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This article contains supporting information online at www.pnas.org/cgi/content/full/0900365106/DCSupplemental.

Fig. 1. Mean total disease prevalence for six disease states in 14 sites surveyed in the Central Visayas. Mean $\pm$ SE presented; $n = 3$ –6 transects per site.

Because of its manifold potential effects on fish diversity, fishing could be acting in several ways to exacerbate coral disease, and these ways are not necessarily mutually exclusive. Hence, to clarify the relationship between disease and fish diversity per se, we regressed disease prevalence against the average taxonomic distinctness of the fish assemblages at each site. The latter variable summarizes fish diversity as a function of taxonomic relatedness and is allied with trophic and functional diversity (28–30). For example, low distinctness indicates limited taxonomic representation and has been used to indicate reef degradation (31). Disease prevalence was significantly negatively correlated with fish taxonomic distinctness, regardless of a site's protection status, when controlling for spatial effects and coral cover with a partial Mantel test (all sites: $r = -0.753$, $P < 0.001$; Fig. 2A). Moreover, six of seven MPAs showed higher taxonomic distinctness than their paired fished sites (paired t test: $t = 2.49$;

$P = 0.053$). This relationship suggests an important role, as seen in other systems (24, 32), for high diversity in limiting disease through ecological control of vector species.

To examine this idea, we tested which taxonomic components of fish diversity were linked to variation in coral diseases by separately regressing disease prevalence against densities of the 27 most abundant functional groups/taxa (Table 1). We found no significant associations between coral disease and any functional group/taxon (all sites: $r \leq 0.371$; $P \geq 0.110$). However, when we examined only sites with coral cover $\geq 50\%$, a single significant and positive relationship was revealed between disease prevalence and the butterflyfish family Chaetodontidae ($r = 0.680$, $P = 0.028$; Fig. 2B and Table 1). This is consistent with a threshold effect of host-coral density in diseases spread through secondary infection (33). Further, within the family, corallivorous species were associated with disease ($r = 0.750$, $P = 0.022$), noncorallivorous species only marginally so ($r = 0.503$, $P = 0.067$), and obligate corallivores explained more variation in disease than did facultative species ($r = 0.686$, $P = 0.039$ vs. $r = 0.587$, $P = 0.049$). Chaetodontids were more abundant at sites with taxonomically depauperate fish assemblages ($r = -0.692$, $P = 0.022$; Fig. 2C), most likely because they are not targeted by fishers (34) or are released by other indirect, top-down interactions. These results support the hypothesis that corallivorous butterflyfishes can act as vectors of coral diseases.

To test the generality of these findings in other Indo-Pacific reefs, we examined a second large-scale public-domain dataset (35) from the Great Barrier Reef (GBR), Australia, which permitted comparisons of the abundance of taxonomic components of fish assemblages to counts of diseased coral colonies. Chaetodontids again emerged as the single fish family significantly and positively associated with disease prevalence ($r = 0.513$, $P = 0.0081$; Fig. 2D and Table 2) at sites with moderate to high coral cover ($\geq 40\%$) while controlling for spatial autocorrelation effects and holding coral cover constant.

Although the etiologies of the disease states we documented remain under study and likely involve multiple mechanisms of

Fig. 2. Simple linear regressions on relationships between coral disease and fish diversity per reef site. Dashed lines represent 95% confidence intervals; closed circles, MPAs; open circles, fished sites. (A–C) Philippines. (D) GBR. (A) Average taxonomic distinctness of fish assemblages vs. mean coral disease prevalence, all sites. (B) Average taxonomic distinctness vs. chaetodontid abundance, sites with $\geq 50\%$ live coral cover. (C) Chaetodontid abundance vs. mean coral disease prevalence, sites with $\geq 50\%$ live coral cover. (D) Chaetodontid abundance vs. coral disease counts, sites with $\geq 40\%$ live coral cover.

This measure is independent of sample size, which circumvents a problem confounding many of the other more commonly used measures of diversity. It is more sensitive to disturbance effects than traditional indices, such as Shannon diversity (51). The master list of coral reef fishes of the Philippines was compiled from a query to FishBase (www.fishbase.org/search.php).

To assess the generality of the results from the Philippines, we also performed partial Mantel regressions on a comparable dataset from the GBR, which provides publicly available information on population trends of corals and reef fishes for 93 reefs spanning 2,000 km of the GBR (34). We could not, however, compare fish taxonomic distinctness or trophic status within taxa between regions because the GBR data are grouped to the family level. Further, recent rezoning of no-take areas within the GBR precluded our

making comparisons between different management regimes (52). We used the most current dataset for each reef (2006 or 2007), which included mean site abundance for 10 fish families and diseased coral colony counts.

ACKNOWLEDGMENTS. We acknowledge field assistance from K. Rosell, P. Cadiz, and P. Rojas. Discussions with C. D. Harvell, B. Willis, R. Rowan, J. McIlwain, P. Mumby, and the Raymundo lab group significantly improved this manuscript, as did comments from two anonymous reviewers. We acknowledge the logistical support of the Coastal Conservation and Education Foundation Inc., Cebu City, Philippines. Funding for this work was provided by the Global Environment Facility/World Bank Coral Reef Targeted Research Program. This is contribution number 624 of the Marine Laboratory, University of Guam.

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