EcoHealth 5, 338–345, 2008
DOI: 10.1007/s10393-008-0196-7

ECOHEALTH

Original Contribution

Reef Fishes Have Higher Parasite Richness at Unfished Palmyra Atoll Compared to Fished Kiritimati Island

Kevin D. Lafferty,[1] Jenny C. Shaw,[2] and Armand M. Kuris[2]

[1]*Western Ecological Research Center, U.S. Geological Survey, Marine Science Institute, University of California, Santa Barbara, CA 93106*
e-mail: lafferty@lifesci.ucsb.edu
[2]*Department of Ecology, Evolution and Marine Biology and Marine Science Institute, University of California, Santa Barbara, CA 93106*

Abstract: We compared parasite communities at two coral atolls in the Line Islands chain of the central Pacific (Kiritimati Island and Palmyra Atoll). Palmyra Atoll is relatively pristine while Kiritimati Island is heavily fished. At each island, we sampled five fish species for helminth and arthropod endoparasites: *Chromis margaritifer*, *Plectroglyphidodon dickii, Paracirrhites arcatus*, *Acanthurus nigricans*, and *Lutjanus bohar*. The surveys found monogeneans, digeneans, cestodes, nematodes, acanthocephalans, and copepods. Parasite richness was higher at Palmyra compared to Kiritimati for all five fish species. Fishes from Palmyra also tended to have more parasites species per host, higher parasite prevalence, and higher parasite abundance than did fishes from Kiritimati. The lower parasitism at Kiritimati may result from a simplified food web due to over fishing. Low biodiversity could impair parasite transmission by reducing the availability of hosts required by parasites with complex life cycles. Most notably, the lower abundances of larval shark tapeworms at Kiritimati presumably reflect the fact that fishing has greatly depleted sharks there in comparison to Palmyra.

Key words: parasites, fishing, Line Islands, biodiversity, richness, abundance

INTRODUCTION

''Shark-infested'' conjures up a dangerous—but accurate—image of a pristine coral reef. But most Pacific atolls are no longer pristine. Fishing has greatly reduced standing-stock biomass of fishes, particularly top predators such as sharks (Friedlander and DeMartini, 2002). Here, we argue that coral reefs may be losing their parasites along with their sharks.

Some studies link fishing to a reduction in parasitism (Amundsen and Kristoffersen, 1990; Kuris and Lafferty, 1992; Ward and Lafferty, 2004). There are at least three potential reasons fishing might directly reduce parasitism. Firstly, parasites of fished species may experience reduced transmission efficiency if host abundance declines (Dobson and May, 1987). Secondly, because a decrease in the diversity of hosts can reduce the diversity of parasites with complex life cycles (Hechinger and Lafferty, 2005), fishing one host from a complex life cycle could result in a decline in the parasites of non-fished species as well. Parasites with complex life cycles include larval trypanorynch and tetraphyllidean tapeworms (whose predator hosts are elasmobranches), and larval nematodes, larval digeneans, and larval acanthocephalans (whose predator hosts are usually teleosts). Thirdly, fishing mortality shifts size-frequency distributions towards younger, smaller individuals (Sala and Knowlton, 2006), who tend to have fewer parasites (Combes, 2001).

Published online: October 10, 2008

Correspondence to: Kevin D. Lafferty, e-mail: lafferty@lifesci.ucsb.edu

Fishing can also indirectly increase parasitism. Predator removal could release prey species from top-down control. Such prey species may increase in abundance and mean body size and, therefore, accumulate more parasites, particularly directly transmitted parasites (Packer et al., 2003; Lafferty, 2004).

To compare parasitism under fished and non-fished conditions, we would ideally have sampled from a large number of sites and then looked for associations between fishing pressure and parasitism. However, logistical constraints led us to examine two coral atolls in the Line Islands chain that represent endpoints in their degree of human impact. Palmyra Atoll (N 5.881, W -162.076) has no permanent human population, while Kiritimati (Christmas) Island (N 1.885, W -157.411) supports a recently enlarged human settlement (~8000 persons per 642 km^2) and local fisheries (Stevenson et al., 2007). Palmyra is presently a marine protected area and its lack of regular human settlement since World War II represents a relatively long history with little to no exploitation. In contrast, the human population on Kiritimati relies on fish as a primary source of protein. Furthermore, commercial fisheries export fish, shark fins, and aquarium specimens from Kiritimati.

At Palmyra, the biomass of fishes is more than four times higher than at Kiritimati, mostly due to a dramatically higher abundance of top predators, which at Palmyra consist of reef sharks (82%), snappers (15%), and jacks (3%) (Stevenson et al., 2007). These large fishes account for 56% of the fish biomass at Palmyra and 3% of the fish biomass at Kiritimati (Stevenson et al., 2007). The biomass of herbivorous fishes is also higher at Palmyra than at Kiritimati, but there is no difference in the biomass of lower-level carnivorous fishes (Stevenson et al., 2007).

Other differences exist between the two atolls. The preponderence of small fishes (primarily planktivores) at Kiritimati is associated with a threefold higher count density of fishes at Kiritimati compared with Palmyra (Sandin et al., 2008). Furthermore, coral disease is higher and coral recruitment is lower at Kiritimati than at Palmyra (Sandin et al., 2008). In addition, the algal community at Palmyra is mostly crustose coraline algae, while turf algae dominates at Kiritimati (Sandin et al., 2008). The differences between Kiritimati and Palmyra are consistent with a broader pattern of the effects of fishing at many different coral reefs (Friedlander and DeMartini, 2002; Stevenson et al., 2007; Sandin et al., 2008).

We hypothesized that the reduction in fish biomass and simplification of the food web at Kiritimati would lead to a net reduction in the diversity and abundance of fish parasites at Kiritimati compared with Palmyra. In particular, we expected a decrease in parasites that used top predators in their life cycles.

Methods

Five fish species common to Palmyra and Kiritimati were selected to represent an array of Indo-Pacific coral reef fish taxonomic and ecological diversity. These were, from smallest to largest in size, the zooplankton predator *Chromis margaritifer* (bicolor chromis) (N = 25 at Palmyra, 25 at Kiritimati), the territorial algal gardener/grazer, *Plectroglyphidodon dickii* (Dick's damsel) (N = 25 at Palmyra, 25 at Kiritimati), the microcarnivore, *Paracirrhites arcatus* (arc-eyed hawkfish) (N = 24 at Palmyra, 25 at Kiritimati), the herbivore, *Acanthurus nigricans* (whitecheek surgeonfish) (N = 25 at Palmyra, 26 at Kiritimati), and the piscivore, *Lutjanus bohar* (two-spot red snapper) (N = 11 at Palmyra, 27 at Kiritimati).

Fish were captured by spear, trap, hook and line, and, at Kiritimati, application of clove oil. Fish were sampled from multiple sites (nine at Kiritimati and seven at Palmyra, chosen for ease of boat access) to increase the chance that samples were representative of the entire island, not just a specific collection site. Kiritimati sites usually occurred near populated areas; Palmyra sites were distributed to avoid other research projects. Collections were standardized to the fore reef at 10 m depth. Fish were kept fresh on ice until dissection.

We systematically evaluated each fish for parasites. Although we inspected the exterior of the fish, we did not use data on parasites from the skin of fishes in analyses because they were rare or absent (perhaps lost at capture or difficult to observe). The body cavity was eviscerated. The heart, stomach, left fillet, intestine, mesenteries, spine, and left eye were squashed between slides and visually inspected for parasites with the aid of a dissecting microscope. Gall bladders were squashed for myxozoans in the Palmyra fishes, but we dropped this step at Kiritimati due to the rarity of fishes infected with Myxozoans at Palmyra. (We found one *Thalassoma amblycephalum* infected with a balloon-shaped myxozoan with two nuclei, single filament sometimes exiting at the point of balloon; however, we had

insufficient microscopy power to further identify it and, furthermore, *T. amblycephalum* was dropped as a host species from our Kiritimati Island samples.) The gill arches were removed from the left side of the fish, placed in a vial of fresh water, and shaken to dislodge parasites. We removed gills and visually inspected them and the heavier particles from the wash. Intestinal contents were placed into jars of seawater, shaken, and the supernatant decanted. We viewed settled items under the dissecting scope and screened them for parasites. We doubled parasite counts for those bilateral body parts for which we only sampled the left side.

The parasite species were likely undescribed, so field identification was possible only to broad taxonomic levels. We photographed representative individuals of each parasite species (photo documentation available on request). When enough parasite material was available, we either fixed vouchers in Berland's fluid (nematodes), AFA, or 4% formalin, or we preserved them in 95% EtOH for future inspection by taxonomic experts. However, for the analyses in this article, we grouped parasites into operational taxonomic units. This grouping, though coarse, allowed the calculation of several indices of parasite species diversity and abundance that did not rely on species-level identifications.

We compared parasite communities between Palmyra and Kiritimati as a proxy for effects of human disturbance (primarily fishing). Because differences in sampling effort can confound the comparison of species lists, we controlled for variation in the number of host individuals dissected (Table 1) by using richness estimates. We calculated jackknife estimators to project the total parasite species richness of a fish species at each island (Zelmer and Esch, 1999). We also used bootstrapping (resampling with replacement) to estimate the total number of parasite species in a common sample size (10 fish). To compare parasite richness between islands, we ran paired *t*-tests, using fish species as replicates, and calculated 95% confidence limits for each estimate. Differences in fish body size between our samples could lead to a difference in parasite richness because parasitism tends to increase with fish size. For this reason, we also constructed a general linear model with the number of parasite species per fish individual (square-root transformed to meet assumptions of normality) as the dependent variable, fish weight as a covariate, and island and fish species as factors.

Although comparing parasite species richness was the main goal of our investigation, we also explored differences in parasite burdens between the islands (with fish weight as a covariate, and fish species and island as factors). We first assessed the prevalence of infection (% of fish parasitized) with a logistic regression. We then used a generalized linear model (with an assumed Poisson distribution and a log-link function for over dispersion) to examine factors associated with parasite abundance (number of parasite individuals per host, by parasite group).

Results

At each location, the parasites found were not clearly consistent with parasites previously described for the host species investigated. For this reason, our analysis is limited to broad patterns of richness and abundance of morphospecies conservatively grouped into broad taxonomic categories. Further analysis of this parasite community will require species identifications and knowledge of life cycles.

The parasite community was richer at Palmyra than at Kiritimati for all fish species. On average, jackknife estimates of parasite species richness for a particular fish species were 70% higher at Palmyra than at Kiritimati (Fig. 1, fish species as replicates, two-tailed paired *t*-test, df = 19, $P = 0.022$). Rarefied estimates of parasite species richness were, on average, 123% higher at Palmyra than at Kiritimati (borderline significant, fish species as replicates, two-tailed, paired *t*-test, df = 19, $P = 0.060$). However, in samples from Kiritimati, *Acanthurus nigricans* and *Paracirrhites arcatus* were larger, whereas in samples from Palmyra, *Lutjanus bohar* and *Chromis margaritifer* were larger, contributing to our concerns that differences in fish weight among our samples might drive some of the differences in parasite richness among sites.

Individual fish had more parasite species at Palmyra than at Kiritimati after accounting for fish weight and fish species. In the general linear model, all main effects (weight, island, fish species) were significant, explaining 37% of the variation in parasite species richness per fish individual. Independent of fish species and fish weight, individual fish from Palmyra had nearly twice the richness of parasites (least squared means [±SE] = 1.08 [0.076] vs. 0.56 [0.07]) than did individuals from Kiritimati (square-root transformed richness, $F_{1,230} = 18.29$, $P < 0.0001$). Parasite richness differed significantly among fish species (square-root transformed richness, $F_{4,230} = 21.93$, $P < 0.0001$), with *A. nigricans* having the most parasite species per fish individual, followed by *C. margaritifer, L. bohar, P. arcatus,*

Table 1. Summary of Parasite Data for Palmyra and Kiritimati[a]

Fish sp.	Parasite sp.	Prevalence (%)	Mean Intensity
Palmyra			
Acanthurus nigricans $N = 25$	TREM.AD.01	68	20
	NEMA.AD.02	56	3
	NEMA.LA.01	16	1
	TREM.AD.02	8	3
	ACAN.AD.01	4	1
	CEST.LA.01	4	2500
Chromis margaritifer $N = 25$	COPE.LA.01	28	3
	CEST.LA.05	8	14
	CEST.LA.09	8	1
	COPE.LA.02	4	2
	NEMA.LA.05	4	4
	TREM.ME.01	4	1
Lutjanus bohar $N = 11$	TREM.AD.05	36	9
	TREM.AD.03	27	6
	CEST.LA.05	27	1
	TREM.AD.04	27	5
	TREM.AD.06	27	15
	COPE.04	18	5
	MONO.01	18	10
	TREM.AD.07	18	4
	COPE.03	9	1
	MONO.06	9	2
	NEMA.AD.03	9	1
	NEMA.AD.04	9	1
	TREM.AD.08	9	2
	CEST.LA.04	9	1000
Paracirrhites arcatus $N = 24$	CEST.LA.06	63	3
	TREM.AD.12	29	2
	NEMA.LA.05	21	8
	NEMA.AD.06	4	1
	TREM.AD.11	4	1
Plectroglyphidodon dickii $N = 25$	NEMA.LA.08	20	2
	COPE.05	4	1
	MONO.03	4	10
	NEMA.AD.07	4	1
	TREM.ME.01	4	1
Kiritimati			
Acanthurus nigricans $N = 26$	TREM.AD.01	81	97
	NEMA.LA.01	12	8
	TREM.AD.02	12	120
	CEST.LA.02	4	2
Chromis margaritifer $N = 25$	CEST.LA.03	4	1
	COPE.LA.01	4	2
	TREM.ME.02	4	2

Table 1. continued

Fish sp.	Parasite sp.	Prevalence (%)	Mean Intensity
Lutjanus bohar	NEMA.AD.04	26	1
$N = 27$	TREM.AD.04	15	3
	TREM.AD.09	11	2
	COPE.LA.03	7	2
	TREM.AD.01	7	2
	TREM.AD.10	7	1
	MONO.02	4	2
	TREM.AD.02	4	1
	TREM.AD.03	4	1
Paracirrhites arcatus	NEMA.LA.05	52	20
$N = 25$	TREM.AD.11	12	2
	CEST.LA.07	8	16
Plectroglyphidodon dickii	CEST.LA.08	4	1
$N = 25$	NEMA.LA.09	4	1

[a]Parasite species codes reflect broad taxonomic groups, life stages, and species identification number (ID). For example, ACAN.AD.01 refers to Phylum Acanthocephala, adult, species 01. ID numbers were assigned to specimens that appeared as morphologically distinct species. Codes are as follows: ACAN, Ph. Acanthocephala; CEST, Class (C.) Cestoda; COPE, Class Copepoda; MONO, Cl. Monogenean; NEMA, Ph. Nematoda; TREM, Subclass Digenea; AD, adult; LA, larva; ME, metacercaria. Life stage was omitted for monogeneans (all adults) and specimens where stage could not be identified. Prevalence represents the percentage of hosts infected with a particular parasite species, whereas mean intensity is the average parasite load, of that parasites species, per infected host (Bush et al., 1997).

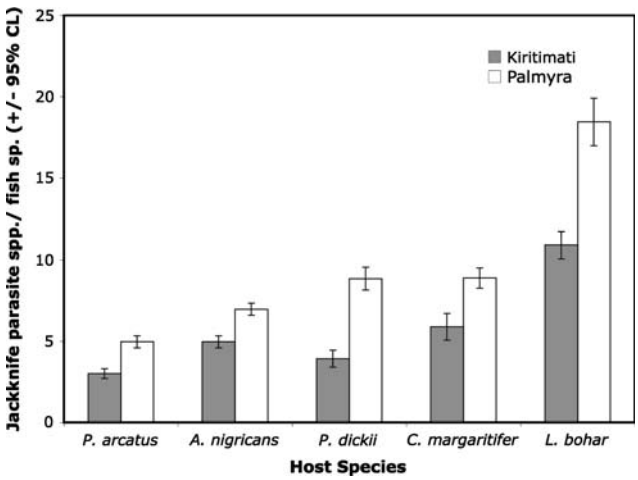

Figure 1. Jackknife species richness estimates for the parasite assemblage of five coral reef fish species at Palmyra Atoll (unfished) and Kiritimati Island (fished). Error bars are 95% confidence intervals. Paired *t*-test with fish species as replicates indicates a significant difference between the islands as $P = 0.022$.

and Plectroglyphidodon dickii. After controlling for fish species and island, the number of parasite species in a fish increased with the weight of the fish (slope [SE] of untransformed relationship between weight and richness = 0.0006 [0.0001] parasite species per g fish) (square-root transformed richness, $F_{1,230} = 5.18$, $P = 0.0237$).

For each broad group of parasites, species richness was higher at Palmyra than at Kiritimati, with the exception of monogeneans, where we found three species at each island (Table 1). When prevalence of a parasite group varied between islands, there was a trend towards higher prevalence at Palmyra. Here, we present the logistic regression statistics for significant and nominally significant effects of island, but note that fish species was also a significant effect (weight was not significant), and that each specific test was subject to weaknesses of multiple comparisons. When we found a significant island by species interaction, fish species were analyzed separately. Monogeneans were more prevalent at Palmyra than at Kiritimati (Chi-square = 5.34, $P = 0.021$, particularly for *Lutjanus bohar* and *Plectroglyphidodon dickii*). Cestode prevalence was much higher at Palmyra than at Kiritimati (Fig. 2, Chi-square = 17.5, $P < 0.0001$, particularly for *L. bohar* and *Paracirrhites arcatus*). The prevalence of copepods was significantly higher at Palmyra than at Kiritimati (Chi-square = 10.63, $P = 0.0011$, particularly for *Chromis margaritifer*). Nematodes were significantly more prevalent at Palmyra than Kiritimati for *Acanthurus nigricans* (Chi-square = 16.08,

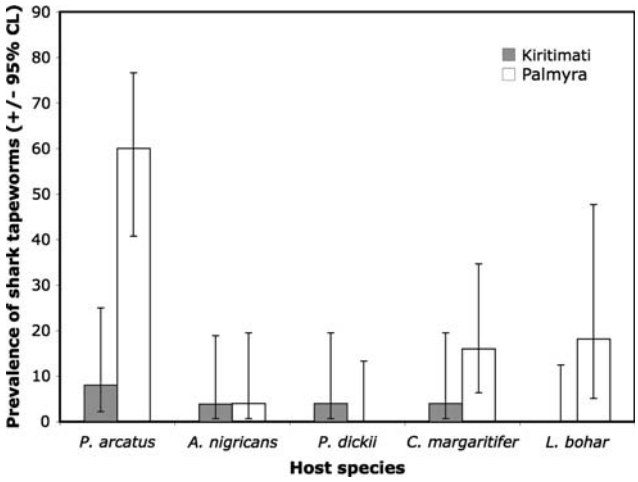

Figure 2. Prevalence of larval shark tapeworms (cestodes) in five coral reef fishes at Palmyra Atoll (unfished) and Kiritimati Island (fished). Logistic regression (controlling for fish weight and using fish individuals as replicates) indicated an overall higher prevalence of cestodes at Palmyra, an effect significant at the species level for *P. arcatus* and *L. bohar,* and marginally significant for *C. margaritifer.*

$P < 0.001$) (and nominally for *P. dickii,* Chi-square = 3.27, $P = 0.07$), but nominally higher at Kiritimati than Palmyra for *P. arcatus* (Chi-square = 3.83, $P = 0.05$). Trematode prevalence did not differ significantly between islands for any of the fishes (trematode prevalence was nominally higher at Palmyra than Kiritimati for *P. arcatus*, Chi-square = 3.82, $P = 0.05$).

Parasites were usually more abundant at Palmyra than at Kiritimati. Fish weight was not a significant factor in any generalized linear model of parasite abundance. A significant fish species by island interaction required us to run separate analyses for each fish–parasite combination (see Table 2). Two combinations (trematodes in *Acanthurus nigricans* and nematodes in *Paracirrhites arcatus*) were significantly more abundant at Kiritimati than at Palmyra. Seven combinations (nematodes in *Plectroglyphidodon dickii*, copepods in *C. margaritifer*, and trematodes, cestodes, copepods, and monogeneans in *Lutjanus bohar*) were significantly more abundant at Palmyra than at Kiritimati. The 16 remaining comparisons were not significant. Acanthocephalans were found only at Palmyra and were too rare for meaningful comparisons between islands.

Pathology was grossly evident for only one parasite species, a juvenile nematode in the coelom of the hawkfish, *Paracirrhites arcatus*. Aggregations of these worms often occurred in the posterior coelom, where they elicited a strong host response and were enveloped in melanized tissue. Hawkfish from Kiritimati had a higher mean abundance of this nematode species than did fish from Palmyra (Chi-square = 7.67, $P = 0.0056$).

Discussion

The data suggested that parasite richness, prevalence, and abundance were generally higher at unfished Palmyra than at fished Kiritimati. The consistent differences between parasite richness across five fish species lend additional support to the interpretation that the two islands differ in their parasite communities. Island differences in parasite richness (per fish), prevalence, and abundance occurred independent of differences in the individual weight of fishes. In addition, the significant increase in parasite spe-

Table 2. Comparison of Mean (95% CI) Parasite Abundances for Both Sampling Sites[a]

Host species	Parasite	Kiritimati	Palmyra	Chi-sq	*P*
A. nigricans	Trematode	96.5 (68.7–135.5)	13.7 (5.4–34.3)	23.6	<0.0001
P. arcatus	Nematode	10.6 (5.5–20.4)	1.75 (0.3–9.1)	5.76	0.016
P. dickii	Nematode	0.04 (0.004–0.410)	0.36 (0.16–0.78)	5.2	0.022
C. margaritifer	Copepod	0.16 (0.02–1.43)	2.16 (1.1–3.9)	10.25	0.0014
L. bohar	Trematode	0.85 (0.3–2.7)	11.5 (7.0–18.8)	24.9	<0.0001
L. bohar	Cestode	0	91 (32.4–255.4)	8.95	0.0028
L. bohar	Copepod	0.22 (0.04–1.32)	2 (0.79–5.09)	5.91	0.015
L. bohar	Monogenean	0.15 (0.006–3.47)	3.81 (1.44–10.1)	7.69	0.0056
P. arcatus	Trematode	0.12 (0.03–0.539)	0.542 (0.26–1.11)	4.1	0.044

[a]Sixteen NS comparisons not shown. Statistics computed with a generalized linear model. Df = 1 for all Chi-square tests. The resulting *P*-values derive from 25 independent tests, suggesting that a Bonferroni-adjusted critical *P*-value of 0.002 be used to evaluate significance, though this correction remains controversial among ecologists.

cies per fish with fish weight adds another important result to our study; reductions in fish size distributions due to fishing, as is seen in snapper at Kiritimati (Sandin et al., 2008), should also reduce the amount of parasites in the ecosystem.

High host density should increase the transmission efficiency of directly transmitted infectious diseases. While three of our five fish species are more abundant at Palmyra, the two damselfish (*Plectroglyphidodon dickii, Chromis margaritifer*) are more abundant at Kiritimati (Stevenson et al., 2007; Sandin et al., 2008). Thus, we might have expected damselfish to support more directly transmitted parasites at Kiritimati; yet, damselfish parasites (directly and indirectly transmitted) were consistently less abundant and rich at Kiritimati.

A higher degree of food-web complexity is one possible explanation for the higher richness of parasites at Palmyra than at Kiritimati, because complex food webs should create more opportunities for the completion of parasite life cycles (Lafferty et al., 2006). For instance, spottail shiners from the St. Lawrence River have less parasite diversity in areas with simplified food webs (Marcogliese et al., 2006). The larval cestodes we observed all use elasmobranchs as final hosts. Therefore, the greater abundance of metacestode larvae at Palmyra than at Kiritimati likely reflects the high abundance of sharks at Palmyra. While coral reefs without sharks and parasites may sound like a tropical paradise, such simplified systems reflect degraded and simplified food webs.

Sharks are important reef predators that have been broadly subjected to over fishing. However, their low density, wide ranges, and ability to elude detection make them difficult to quantify (Wirsing et al., 2007). We propose that sampling larval cestodes in small teleost hosts, like the sedentary arc-eyed hawkfish, is a convenient method for assessing spatial variation in shark distribution. Parasites make cost-effective indicators for estuarine habitats (Huspeni and Lafferty, 2004) and may hold promise for coral reefs.

Palmyra and Kiritimati were chosen because they were both small, isolated islands known to vary primarily in their extent of fishing (Stevenson et al., 2007; Sandin et al. 2008). However, other environmental differences between the islands could affect parasite communities. Palmyra (12 km^2) is much smaller than Kiritimati (642 km^2) and further north of the equator. All things being equal, a larger island like Kiritimati should have a higher richness of parasites. Kiritimati also receives substantially less rainfall than does Palmyra, but since our studies were conducted on the fore reef (as opposed to the lagoon), we do not expect a substantial effect of rainfall on these data. It is not clear how the greater degree of coral disease or the higher cover of turf algae would directly reduce parasites at Kiritimati. It remains possible that other unknown island differences drove the observed differences in parasitism.

Heavy fishing at Kiritimati remains a logical explanation for the reduction in parasite diversity and abundance seen there in comparison to unfished Palmyra. However, with a lack of replication, we cannot statistically determine if the two islands differ in parasitism solely because they vary in fishing pressure. Comparing a large number of physically similar islands that vary in fishing pressure is a possible avenue for future work. In addition, one could consider parasite communities of fishes along a gradient of human impact at a single island. For example, at Kiritimati, there are reef areas far from human settlements, potentially allowing for replicated samples along a finer-scale gradient of fishing.

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