Fishing drives declines in fish parasite diversity and has variable effects on parasite abundance

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Abstract. Despite the ubiquity and ecological importance of parasites, relatively few studies have assessed their response to anthropogenic environmental change. Heuristic models have predicted both increases and decreases in parasite abundance in response to human disturbance, with empirical support for both. However, most studies focus on one or a few selected parasite species. Here, we assess the abundance of parasites of seven species of coral reef fishes collected from three fished and three unfished islands of the Line Islands archipelago in the central equatorial Pacific. Because we chose fish hosts that spanned different trophic levels, taxonomic groups, and body sizes, we were able to compare parasite responses across a broad cross section of the total parasite community in the presence and absence of fishing, a major human impact on marine ecosystems. We found that overall parasite species richness was substantially depressed on fished islands, but that the response of parasite abundance varied among parasite taxa: directly transmitted parasites were significantly more abundant on fished than on unfished islands, while the reverse was true for trophically transmitted parasites. This probably arises because trophically transmitted parasites require multiple host species, some of which are the top predators most sensitive to fishing impacts. The increase in directly transmitted parasites appeared to be due to fishing-driven compensatory increases in the abundance of their hosts. Together, these results provide support for the predictions of both heuristic models, and indicate that the direction of fishing’s impact on parasite abundance is mediated by parasite traits, notably parasite transmission strategies.

Key words: anthropogenic environmental change; biodiversity; disease; disturbance; fishing; parasites.

INTRODUCTION

For the past several decades, ecologists have worked to document impacts of anthropogenic environmental change on the distributions of free-living species. But despite the ubiquity of parasites, which constitute at least 40% of animal species on the planet (Dobson et al. 2008) and make up the majority of species in 27 of its 42 recognized animal phyla (Poulin and Morand 2000, deMeeus and Renaud 2002), we still have only a rudimentary understanding of how human impacts affect parasite abundance and diversity. Understanding how parasite biodiversity will change in a changing environment is important for a number of reasons. First, a growing body of evidence suggests that parasites are ecologically influential in some ecosystems (Gomez et al. 2012). They can regulate host populations (e.g., Hudson et al. 1998), mediate the species composition of free-living communities (e.g., Mouritsen and Poulin 2005, Wood et al. 2007), comprise a substantial proportion of the total biomass of an ecosystem (e.g., Kuris et al. 2008, Preston et al. 2013), and redirect energy flow within and among food webs by behaviorally manipulating (e.g., Lafferty and Morris 1996, Sato et al. 2011) or killing (Suttle 2005) their hosts. Given their influence, change in parasite abundance is likely to have reverberating impacts on ecosystem function (Gomez et al. 2012). Second, understanding the impacts of anthropogenic environmental change on the abundance and diversity of parasites gives us insight into current and future disease risk for hosts of special concern, like humans (Keesing et al. 2010), commercially valuable domestic (Cleaveland et al. 2001), and wild (McCallum et al. 2005, Shields 2012) animals, and endangered species (Daszak 2000). For a full accounting of the impacts of human activities on ecosystems and for projecting future disease risk, it is therefore critical that ecologists answer the question: How does anthropogenic environmental change impact parasite abundance and diversity?

Only a few empirical studies have assessed the effects of human disturbance across a broad range of parasite species, and these tend to find mixed responses to disturbance. In the Atlantic lowlands of Costa Rica, McKenzie (2007) found that, among three species of amphibian hosts collected from clear-cut cattle pasture and forest habitats, six metazoan parasite species were more abundant in pasture than forest, two species were more abundant in forest than pasture, and 13 species did...
not differ significantly between the two habitats. Aeb y et al. (2011) found that, while prevalence of growth anomalies (a tumor-like disease of unknown etiology) of Porites spp. corals increased with increasing density of nearby human populations across the Hawaiian Islands, the prevalence of trematodiasis (infection by trematode metacercariae) decreased across this impact gradient. A number of studies have compared parasite prevalence and diversity between marine reserves, where human environmental impacts are legally excluded, and open-access areas where such impacts continue. Some have found higher parasite abundance and diversity in reserves than in open-access areas (Sonnenholzner et al. 2011), or have failed to find significant differences in abundance and diversity between reserve and open-access areas (Ternengo et al. 2009). In a meta-analysis, Lafferty (1997) showed that the overall response of aquatic parasites to pollution impacts is weak, primarily because parasite groups diverge in their responses to pollution, and different types of pollution impacts (e.g., eutrophication vs. heavy metal contamination) can generate divergent responses of abundance within parasite groups. Together, these results suggest that the response of parasites to environmental change is variable and context specific. But several key questions remain. First, when we look across a wide diversity of parasite taxa, will most populations increase, decrease, or remain unchanged in response to anthropogenic impacts? Second, what taxonomic groups of parasites tend to exhibit sensitivity to anthropogenic impacts, what groups tend to increase in abundance as impacts accumulate, and what characteristics might drive these divergent responses?

To address these questions, we focused on a marine model system affected by fishing (Sandin et al. 2008), one of the most intense and longest-standing impacts on the world’s oceans (Jackson et al. 2001, Halpern et al. 2008). We aimed to test how fishing-driven alterations in the fish community affect the abundance, species composition, and diversity of marine fish parasites by comparing, between three fished and three unfished coral islands, the parasite assemblages of seven host fish species spanning a variety of trophic levels, taxonomic groups, and body sizes. We attempted to select a representative cross-section of the fish community, composed of the most abundant fish species from a variety of fish trophic groups, to maximize the taxonomic and life history diversity of parasites detected. For each parasite, we calculated a “response to fishing” to indicate the magnitude and direction of the difference in abundance between fished and unfished islands, a difference which may arise from either direct or indirect effects of fishing. Direct effects of fishing include, for example, fishing of a host, which might reduce the density and size structure of that host population, reducing transmission of its directly transmitted parasite and resulting in lower parasite abundance on fished than on unfished islands. Indirect effects of fishing include fishing the predator or competitor of a host, which can cause compensatory increases in host density (e.g., Demartini et al. 2008), increasing transmission of a directly transmitted parasite, and resulting in higher abundance on fished than on unfished islands. We use the word “fishing” to refer to the ecosystem-level effects of fishing, not just its host-population-level effects, and the term therefore encompasses both the direct and indirect effects of fishing on hosts and non-hosts.

A previous study conducted in the Line Islands system examined the parasite communities of five reef fishes from one fished (Kiritimati) and one unfished (Palmyra) island, finding higher parasite richness in all host species at the unfished island (Lafferty et al. 2008). Lafferty et al. (2008) also found higher abundance on the fished than the unfished island for two parasite taxa, higher abundance on the unfished than the fished island for seven other taxa, and no significant differences for the 16 remaining taxa detected. While these effects could be driven by fishing, they could also be due to other differences between the islands, including oceanography or biogeography. We thus designed a natural experiment by replicating within each level of the fishing “treatment,” that is, by expanding the experimental design from one fished and one unfished island to three fished and three unfished islands, with the goal to decouple fishing effects from the physical and oceanographic differences among the sampled islands. This allowed us to attribute observed differences between levels of the fishing “treatment” to the effect of fishing and to rule out other sources of inter-island variability. For each of our research questions, we formulated several a priori hypotheses originating from previous findings (Lafferty et al. 2008), as well as from theoretical (Keesing et al. 2006, Dunn et al. 2009, Colwell et al. 2012, Lafferty 2012) and synthetic (Wood et al. 2010) work.

**Question 1: How does richness of parasite taxa differ between fished and unfished islands?**

**Hypothesis 1 (H1). Negative effect of fishing on parasite diversity.**—In our study system, fishing has the effect of reducing the abundance of a number of fish taxa, including many of the large-bodied, high-trophic-level predators likely to serve as definitive hosts of trophically transmitted parasites, as well as other species likely to serve as intermediate hosts of trophically transmitted parasites or sole hosts of directly transmitted parasites (Sandin et al. 2008). Because fish hosts constitute habitats and resources for parasites, we expected that fishing impacts would result in depressed species richness of parasite taxa on fished islands (Lafferty 2012), as has been observed for disturbances such as coastal development (Huspeni and Lafferty...

Question 2: For each species of parasite, are parasites more abundant, less abundant, or equally abundant on fished relative to unfished islands?

The impacts of fishing on parasite abundance might be positive, negative, or neutral. A key question is, what proportion of parasites should be expected to exhibit each response? We made three predictions for the response of parasite abundance to fishing. As a null hypothesis, we may expect parasites to be equally abundant across environmental contexts (Bush and Kennedy 1994); instead, parasites might be (Hypothesis 2) more abundant (Keesing et al. 2006) or (Hypothesis 3) less abundant (Wood et al. 2010), on fished relative to unfished islands. These predictions are not mutually exclusive, as different parasite taxa might exhibit different responses.

Hypothesis 2 (H2). Positive effect of fishing on parasite abundance.—If fishing facilitates compensatory increases in the density of low-trophic-level hosts through removal of their predators (susceptible host release) or stresses hosts to the extent that immunological defenses against parasites are compromised (immunity reduction [Bly et al. 1997, Hoole 1997]), fishing should drive increases in parasite abundance (i.e., higher abundance on fished than unfished islands [Keesing et al. 2006]).

Hypothesis 3 (H3). Negative effect of fishing on parasite abundance.—If fishing reduces the density of hosts (reduced direct transmission), mean host size (reduced habitat availability), or the complexity of the food web (reduced trophic transmission [Wood et al. 2010]), fishing should drive declines in parasite abundance (i.e., higher abundance on unfished than fished islands).

Question 3: What host and parasite attributes predict whether a parasite species is more abundant, less abundant, or equally abundant between fished and unfished islands?

Hypothesis 4 (H4). Transmission strategy.—Trophi-
cally transmitted parasites (i.e., those parasites with complex life cycles, which pass through multiple parasitic life stages that each require different host species and which are transmitted through predator–prey interactions among those species, like trematodes, cestodes, nematodes, and acanthocephalans) should be more likely to decline in abundance on fished islands than are directly transmitted parasites (i.e., those parasites that can be transmitted among conspecific hosts, like copepods and monogeneans). This is expected to arise because trophically transmitted parasites must use multiple host species to complete their life cycle, and as the number of obligately required hosts increases, so should the likelihood that one of those hosts will be negatively impacted by fishing (Lafferty and Kuris 2009, Rohr et al. 2011, Colwell et al. 2012, Lafferty 2012).

Hypothesis 5 (H5). Host specificity.—Generalist parasites (i.e., those parasites with broad host ranges per parasite life stage) should be more likely to increase in abundance on fished islands than are specialist parasites, since a generalist parasite will be more likely to benefit from increases in one of the many host species within its host range (i.e., susceptible host release), and will be better able to compensate for the loss of one or a few host species to fishing (Colwell et al. 2012, Lafferty 2012).

Hypothesis 6 (H6). Host response.—Fish species have divergent responses to fishing, with some decreasing in abundance due to direct fishing pressure (e.g., top predators [Sandin et al. 2008]), and others experiencing compensatory increases in abundance due to release from predation or competition by fished species (e.g., planktivores, mesopredators [DeMartini et al. 2008, Sandin et al. 2008]). If transmission efficiency of parasites is strongly dependent on host density, then parasite abundance should track host abundance (McCallum et al. 2005). Therefore, we predicted an overall positive relationship between host response to fishing (the difference between host density on fished vs. unfished islands; hereafter, “host response”) and parasite response to fishing, and we expected this relationship to be strongest for directly transmitted parasites, since the transmission efficiency of these parasites can depend exclusively on the density of their hosts. In contrast, the efficiency of trophic transmission is determined by the density of multiple host species (Lafferty 2012).

We tested these hypotheses by comparing parasite abundance and diversity between three fished and three unfished coral islands within the same archipelago, in a natural experiment. Our results demonstrate that fishing depresses parasite diversity and has variable effects on parasite abundance, with directly transmitted parasites increasing in response to fishing pressure and trophically transmitted parasites showing the opposite pattern.

Methods

Study sites

We quantified parasite abundance and diversity in fish collected from three fished and three unfished coral islands of the Line Islands, in the central equatorial Pacific (Fig. 1). The unfished islands Jarvis, Kingman, and Palmyra are U.S. possessions incorporated into the U.S. Pacific Remote Islands Marine National Monument in 2009 (Bush 2009), and prior to that, protected as U.S. National Wildlife Refuges (beginning in 1974 for Jarvis and in 2001 for Kingman and Palmyra [Maragos et al. 2008a]). Both designations include a strict ban on fishing, but all of these islands were probably only sporadically and lightly fished prior to formal protection, due to their extreme inaccessibility (Maragos et al. 2008b). In contrast, Teraina, Tabuaeran, and Kiritimati
are islands of the Republic of Kiribati, and are each inhabited by between several hundred and several thousand people who engage in subsistence fishing as a primary economic activity (see Sandin et al. 2008: Supplemental Data S1). Fishing is primarily by hook-and-line, supplemented with a limited amount of spearfishing on Teraina, and tends to target predatory species of fish (S. A. Sandin, personal observation). Previous studies have shown strong divergence in the fish communities between these three fished and three unfished islands, with higher fish biomass and abundance of top predators on unfished islands, and higher abundance of low-trophic-level fishes like planktivores on fished islands, possibly due to release from predation pressure (DeMartini et al. 2008, Sandin et al. 2008). Island size, latitude, average sea surface temperature, and productivity are not confounded with fishing pressure among the six islands, and pooling data within the three fished and three unfished islands allowed us to homogenize the influence of oceanographic factors across the archipelago (Sandin et al. 2008; C. L. Wood, J. Baum, S. Walsh, R. Trebilco, S. A. Sandin, B. Zgliczynski, A. Briggs, and F. Micheli, unpublished manuscript; Fig. 1). This system is therefore a suitable natural experiment for testing the impacts of fishing-driven environmental change on a variety of ecosystem parameters, including parasite abundance and biodiversity.

Host sampling

Sampling was conducted at six islands of the Line Islands archipelago (from north to south: Kingman Reef, Palmyra Atoll, Teraina/Washington Island, Tabuaeran/Fanning Island, Kiritimati/Christmas Island, and Jarvis Island; Fig. 1) from a research vessel between October and November 2010. At each of these six islands, we sampled seven species of reef fishes (Table 1). We selected species (1) that were among the most abundant species for their respective trophic group across the six islands, and (2) that spanned a range of body sizes, trophic levels, and taxonomic groups. Fish were collected by scuba divers using three-pronged spears (for fish >10 cm) and hand nets (for fish <10 cm). We sampled at least 25 individuals of each species from each island, and exceeded 25 individuals for most species–island combinations (Appendices A and B). In a handful of cases, particular species–island combinations had been collected in previous expeditions, and to minimize sampling impacts on those populations, were not targeted again in the 2010 sampling effort. Where we lacked data on parasite abundance for a species–island combination, we supplemented from three data sources: (1) parasite sampling conducted by C. L. Wood with specimens from Palmyra Atoll collected by our team in a separate expedition in 2009 (Appendix C), (2) parasite sampling conducted by C. L. Wood with specimens from
Table 1. A list of species sampled from fished and unfished atolls in the Northern Line Islands archipelago.

<table>
<thead>
<tr>
<th>Scientific name</th>
<th>Common name</th>
<th>Family</th>
<th>Diet</th>
<th>Relative body size</th>
<th>Largest total length attained (cm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cephalopholis arodata</td>
<td>darkfin hind</td>
<td>Serranidae</td>
<td>small fishes (68% of diet), crabs, shrimps, mantis shrimps</td>
<td>medium</td>
<td>26.5</td>
</tr>
<tr>
<td>Ctenochaetus striatus</td>
<td>bluespotted bristletooth</td>
<td>Acanthuridae</td>
<td>detritus and algae</td>
<td>medium</td>
<td>29</td>
</tr>
<tr>
<td>Acanthurus nigricans</td>
<td>whitecheek surgeonfish</td>
<td>Acanthuridae</td>
<td>filamentous algae</td>
<td>medium</td>
<td>21.3</td>
</tr>
<tr>
<td>Paracirrhites acratus</td>
<td>arc-eye hawkfish</td>
<td>Cirrhitidae</td>
<td>shrimps, small fishes, crustaceans, fish eggs</td>
<td>medium</td>
<td>14</td>
</tr>
<tr>
<td>Stegastes aureus</td>
<td>golden gregory</td>
<td>Pomacentridae</td>
<td>algal turf</td>
<td>small</td>
<td>9.9</td>
</tr>
<tr>
<td>Chromis margaritifer</td>
<td>bicolor chromis</td>
<td>Pomacentridae</td>
<td>zooplankton</td>
<td>small</td>
<td>9</td>
</tr>
<tr>
<td>Pseudanthias bartlettorum</td>
<td>Bartlett’s anhias</td>
<td>Serranidae</td>
<td>zooplankton</td>
<td>small</td>
<td>6.2</td>
</tr>
</tbody>
</table>

Note: Diet and body size information adapted from Randall (2005).

Kiritimati Island collected in 2010 and 2011 (C. L. Wood, J. Baum, S. Walsh, R. Trebilco, S. Sandin, B. Zgliczynski, A. Briggs, and F. Micheli, unpublished manuscript), and (3) parasite sampling conducted by C. L. Wood with specimens from Kiritimati Island collected in 2009 (Appendix C). These three additional data sources used methods identical to those described here, and all collections were conducted between May and August of 2009, 2010, or 2011 (Appendix C). This supplementation resulted in excellent representation across the islands, except for Palmyra Atoll (Appendices A and B), where we lack individuals from three of the seven host species: Paracirrhites acratus, Acanthurus nigricans, and Chromis margaritifer. The use of fish collected in different years and seasons introduces the potential for temporal variability in parasite abundance or species composition to confound our inter-island comparisons. However, given the relative longevity of these parasites in their hosts (Lafferty and Kuris 2002), and the fact that the vast majority of our fish samples (90.2%) came from the expedition conducted in October and November of 2010 (Appendices A, B, and C), the effect of this variability in timing of fish collection is likely to be minimal.

Because habitat type and wave exposure of collection sites might influence estimates of parasite abundance, we attempted to hold these variables constant by conducting most sampling on the leeward fore reef of each island. In several instances, sea conditions required us to collect in backreef or patch reef habitats (Appendices C and D). All sampling was completed at depths between 5 and 25 m, with the vast majority of samples taken between 11 and 18 m (Appendix C). To account for possible depth-dependent variation in parasite abundance, we included the depth at which the host was collected in all statistical analyses. Fishes were collected from between 2 and 10 sites at each island (Appendices C and D).

Fishes were immediately frozen after collection, and we recorded several items of meta-data for each fish before and after freezing. Total length, standard length, fork length, and mass were measured. In all analyses, total length was used as a proxy for fish body size. Fish were kept frozen until being thawed for dissection.

Fish counts were conducted by a team of divers at each island to characterize the fish assemblage and estimate the density, biomass, and size-structure of all coral reef fish species >3 cm TL (total length). Fish were identified to species and counted in belt transects constrained to depths between 7 and 15 m in fore-reef habitat. Three belt transects were completed at each station. In each transect, divers tallied all fishes ≥20 cm TL along a 25 m long × 4 m wide swath on the first pass, and tallied all fishes <20 cm TL along a 25 m long × 2 m wide swath on the return pass. Surveys were conducted in 2005 on Kingman, Palmyra, Tabuaeran, and Teraina (Sandin et al. 2008), in 2005 and 2010 on Teraina, and biennially between 2002 and 2010 on Jarvis (Williams et al. 2011). The total number of transects was 25 on Kingman, Tabuaeran, and Kiritimati, 26 on Palmyra, 9 on Teraina, and 29 on Jarvis. Details of the survey protocols are described in Friedlander et al. (2010).

Parasite sampling

We performed a comprehensive examination of each fish, designed to detect most metazoan parasites. We did not count mobile skin parasites or micropredators, as these are easily lost when the host is captured, and we did not search for myxozoan gall bladder parasites, but all other metazoans should have been easily detected with our protocol. We adapted the dissection protocol to the morphology of each species, and departures from the generalized dissection protocol described next are detailed in Appendix E. Within species, the dissection protocol was consistent. Although several technicians prepared fish for examination (e.g., removing viscera and gills), only one observer (C. L. Wood) counted parasites for all 945 fish dissected (with the exception of some intestinal parasites, where C. L. Wood trained technicians to perform counts). For most host species, the right pectoral, right pelvic, anal, dorsal, and caudal fins were removed and examined with strong transmitted light under a dissecting microscope, to detect trematode metacercariae and encysted sarcocaitic copepods. The gills, right eye, and viscera were removed and the buccal
and body cavities carefully examined. If the right-side bilateral organs were damaged (e.g., by a spear wound), the left-side organs were taken instead. The visceral organs and eye were separated, squashed between glass plates, and examined with strong transmitted light under a dissecting microscope. The gill arches were cut apart from one another, shaken in a jar of seawater to remove mucus, and the entire gill arch, along with the wash, was examined under magnification for crustacean and monogenean gill parasites. The right fillet was removed, squashed between glass plates, and examined with strong transmitted light under magnification for encysted nematodes, cestodes, and trematode metacercariae. The inner surface of the skin removed from that fillet was examined for trematode metacercariae. Stomachs were used for gut content analysis and were not analyzed for parasites, but intestines were subject to a thorough parasitological examination. For large herbivorous and detritivorous fishes (Acanthurus nigricans and Ctenochaetus marginatus, which have long intestines containing large masses of material), intestines were cut into sections, slit open, and the contents and lining washed through a 150-μm sieve. The material retained in the sieve was then examined under a dissecting microscope. This analysis was performed by technicians trained by C. L. Wood, and with these extra personnel, we were able to examine more intestines than whole fishes (Appendix B), increasing replication for intestinal parasites in these herbivorous and detritivorous host species. For the remaining fish species, the intestine was slit open and squashed between glass plates. For all bilateral organs where we examined only one side, parasite counts were doubled. When an organ was missing or damaged (e.g., part of fin was missing), we recorded “n/a,” not 0, for any parasite species typically found in that organ (e.g., fin metacercariae). Photographs of each parasite species (along with detailed images of diagnostic morphological features) and voucher specimens were archived and are available for examination by request to the corresponding author. We identified parasite species to the lowest possible taxonomic level (Appendix F). As general guides for identifications we used Kabata (2003) and Yamaguti (1963) for copepods, Schultz (1969) for isopods, Gibson et al. (2002), Bray et al. (2005), and Bray et al. (2008) for trematodes, Skrabin (1991) for nematodes, and Khalil et al. (1994) for cestodes. We supplemented with taxonomic literature from the Indo-Pacific region, where available, to achieve more taxonomically resolved identifications.

Information on the life cycle and natural history of each parasite was surveyed from this literature and collated (Appendix F). Each parasite was classified according to its broad taxonomic group (Subphylum Crustacea, Class Monogenea, Class Trematoda, Phylum Nematoda, Class Cestoda), transmission strategy (direct vs. trophic transmission, where directly transmitted parasites are transmitted among conspecific hosts, and trophically transmitted parasites are parasitic in multiple life stages among hosts of different species), and host specificity (ranked 1–6 based on Brusca [1981], Sasal et al. [1998], and Jones et al. [2007], with 1 indicating high specificity). We defined “specialists” as those parasites known to use a narrow range of host species for the stage in the life cycle most likely to parasitize a fished species (e.g., the adult stage of trophically transmitted parasites). Because the natural histories of the parasites we detected are poorly known, we surmised life history traits for each parasite based on its membership in higher-order taxonomic groups (i.e., phylum, subphylum, or class level), based on previous assessments (Brusca 1981, Sasal et al. 1998, Jones et al. 2007). While this is a coarse approach, host specificity is known to be phylogenetically conserved within these higher-order taxonomic groups (Sasal et al. 1998, Mouillot et al. 2006), and until life cycles and species identities are worked out for the parasite fauna of the Line Islands, this approach is a strong approximation for understanding how parasite traits might mediate the direction of parasites’ response to anthropogenic environmental change.

**Statistical analysis**

**Parasite diversity.**—We tested for differences in parasite taxonomic diversity between fished and unfished islands (Hypothesis 1). Because differences in sampling effort can confound the comparison of diversity among communities, we accounted for differences in number of hosts sampled and number of parasites detected by calculating richness estimates. We included in our analysis all parasite taxa detected. We used the non-parametric jackknife estimator to project parasite taxon richness at the saturation of the species accumulation curve for each host–island combination (Zelmer and Esch 1999), calculated using the SPECIES package in R (R 2.11.1 GUI 1.34; R Development Core Team 2010). To compare richness between fished and unfished islands, we ran a mixed-effects general linear model with fishing status (fished vs. unfished) as a fixed effect and island and host species as random effects, where replicates were jackknife-estimated parasite taxon diversity for each host–island combination. We included the covariates latitude (average latitude within island), depth (average depth at which hosts of a given species were collected within islands), and host body size (average host TL within host species within islands) to ensure that these factors were not driving patterns in parasite diversity. Covariates were removed from the model through backwards elimination if they were not significant at α = 0.10. This level of α was chosen so as to include even marginally influential covariates in the overall model, but α = 0.05 was used as the standard for assessing statistical significance in hypothesis testing. This analysis was conducted using the lmer function (package lme4) in R, and P values were extracted with pvals.fnc (package languageR). To test whether the
response of parasite diversity to fishing was related to the response of host species abundance to fishing, we ran a simple linear regression between the response of parasite taxon diversity to fishing (standardized coefficient for the effect of fishing on jackknife parasite taxon diversity from ANOVA models performed within host species) and the response of host abundance to fishing (standardized coefficient for the effect of fishing on host density from ANOVA models performed within host species), with the covariates mean host body size (measured as total length), mean collection latitude, and mean collection depth, where replicates were islands within hosts.

Parasite abundance.—We began our analysis of parasite abundance by assessing the response to fishing of each parasite taxon individually. We analyzed the abundance of every host–parasite combination that was observed in at least one host individual on at least $n = 3$ islands, where $n$ was the total number of islands where that host species was collected, for a total of 44 host–parasite combinations (out of 77 total combinations detected; Appendix F). For each host–parasite combination, we used a mixed-effects generalized linear model (GLMM) with negative binomial error and correction for zero-inflation to assess the response of parasite abundance to fishing pressure, with fishing status (fished vs. unfished) as a fixed factor and island (Jarvis, Kingman, Palmyra, Teraina, Tabuaeran, Kiritimati) as a random factor. Three covariates with the potential to influence parasite abundance were also included: body size of the host (measured as total length [TL]), and latitude and depth of collection of the host. Latitude was included to account for the potential influence of the latitudinal gradient of productivity in influencing parasite abundance (C. L. Wood, J. Baum, S. Walsh, R. Trebilco, S. Sandin, B. Zgliczynski, A. Briggs, and F. Micheli, unpublished manuscript). We used backwards elimination to remove covariates (TL, latitude, depth) until we arrived at models in which either (1) all parameters were significant at $\alpha = 0.10$, or (2) only fishing status and the random effect of island remained as predictors. These analyses were performed with the glmmadmb function (package glmmADMB) in R. Since many statistical tests were performed, we applied a correction for multiple comparisons (false discovery rate, or FDR correction) to all $P$ values (Benjamini and Hochberg 1995).

We used a meta-analytic approach to assess the responses of parasites to fishing across parasite taxa. For effect size estimates, we used regression coefficients for the effect of fishing status on abundance of each parasite in each host, extracted from the GLMMs described previously. All analyses were performed with the metafor package in R. We first calculated a cumulative effect size across all 44 host–parasite combinations, using a fixed-effects model weighted by the inverse of the variance for each effect size. We tested for heterogeneity within these effect sizes with the test statistic $Q_T$. Where heterogeneity was detected, we hypothesized that it was due to underlying ecological differences among host–parasite combinations. We tested our hypotheses with several meta-analytic fixed-effects general linear models. One model tested our a priori hypothesis that parasite higher-order taxonomic grouping would influence the mean response of parasites to fishing pressure; another tested a priori hypotheses about the interaction between parasite and host traits; and the last was used to conduct a post hoc exploration of the influence of highly divergent parasite responses. The first model included the moderator higher order taxonomic grouping of the parasite (Crustacea, Monogenea, Trematoda, Cestoda, Nematoda), and was designed to test Hypothesis 4. Because it explicitly tested for heterogeneity within and between taxonomic groupings, the single acanthocephalan taxon we detected was excluded from this analysis. The second model included parasite transmission strategy (direct vs. trophic; H4), host specificity (1–6, as described previously, with 1 indicating high host specificity; 5), host response to fishing (calculated as the standardized regression coefficient for the effect of fishing status on the density of hosts, with negative values indicating that host density is lower on fished than on unfished islands; standardized regression coefficients were used to reduce the influence of highly variable values of host response; Hypothesis 6), and the interaction between parasite transmission strategy and host response to fishing (H6). The third model contrasted the response of trematodes to the remainder of the trophically transmitted parasites, in order to parse their influence on overall estimates of mean effect size for the trophically transmitted parasites.

To confirm the findings of the diversity and abundance analyses described previously, we also analyzed the data with a multivariate approach, using non-parametric statistics based on the Bray–Curtis dissimilarity index. Methods, results, and interpretation of this analysis are presented in Appendix G.

RESULTS

Question 1: How does richness of parasite taxa differ between fished and unfished islands?

Our diversity analysis revealed that parasite diversity was lower on fished relative to unfished islands, with >50% more parasite taxa on unfished compared to fished islands (Fig. 2; Appendix H; $7.37 \pm 1.46$ parasite taxa [intercept $\pm SE$], effect of fishing status [unfished] = $3.99 \pm 1.80$ parasite taxa, $f_{33} = 2.23$, $P = 0.033$). This pattern was consistent with Hypothesis 1, and was driven by two factors: (1) the modestly higher raw taxon richness detected on unfished relative to fished islands (Appendix I), and (2) the influence of rare parasite species on jackknife estimates of taxon richness. Rare parasite species, that is, species observed in only one or two host individuals, were more common on unfished islands (Appendix J). These rare parasites increased the jackknife estimate of parasite taxon richness at satura-
tion because their presence suggests that additional sampling will yield more rare parasite taxa. Taxonomic richness was not significantly related to latitude ($t_{30} = 0.758, P = 0.455$), depth of collection of hosts ($t_{31} = 0.990, P = 0.330$), or body size of hosts ($t_{32} = 1.68, P = 0.104$), and these covariates were therefore omitted from the model. The response of parasite richness to fishing was unrelated to the response of host density to fishing; that is, whether parasite diversity increased or decreased in response to fishing pressure was unrelated to whether host density increased or decreased in response to fishing pressure (Fig. 2b; linear regression, effect of change in host density $= 0.586 \pm 1.800$, $F_{1,5} = 0.106, P = 0.758$).

**Question 2:** Are parasites more abundant, less abundant, or equally abundant on fished relative to unfished islands?

Across the 44 host–parasite combinations that were abundant enough to be compared between fished and unfished islands, 13.6% of combinations (6 of 44) showed significantly higher parasite abundance on unfished than fished islands, 22.7% (10 of 44) showed higher abundance on fished than unfished islands, and 63.6% (28 of 44) showed no significant response to fishing (Fig. 3; summary of results in Appendix K, full results in Appendix L). Two host–parasite combinations with opposite responses to fishing, live and dead larval nematodes in *Cephalopholis urodeta*, were considered to be members of the same taxonomic group, and though they are displayed separately in Fig. 3, were combined for the purposes of analysis (Appendix M).

**Question 3:** What host and parasite attributes predict whether a parasite is more abundant, less abundant, or equally abundant between fished and unfished islands?

Meta-analysis demonstrated substantial heterogeneity in response to fishing among host–parasite combinations. The cumulative effect size across all 44 host–parasite combinations was significantly greater than zero ($0.163 \pm 0.076$ [mean $\pm$ SE], $z = 2.16, df = 43, P = 0.031$), suggesting that the overall effect was toward higher parasite abundance on fished than unfished islands. However, significant heterogeneity in the cumulative effect size ($Q_T = 251, df = 43, P < 0.0001$) indicated substantial differences in response among parasites. In the first meta-analysis model, focused exclusively on parasite traits, parasite higher order taxonomic grouping was a significant moderator, indicating that parasite groups varied in their overall response to fishing (Fig. 4; $R^2 = 0.364, Q_M = 90.5, df = 4, P < 0.0001$; Appendix N). In the second meta-analysis model, focused on the interaction between parasite and host traits, transmission strategy (H4) and the interaction between transmission strategy and host response (H6) were significant predictors of parasite response to fishing.
fishing, but host specificity (H5) was not \( R^2 = 0.285, \quad Q_M = 71.7, \quad df = 4, \quad P < 0.0001; \) Appendix N).

**Hypothesis 4: Transmission strategy.**—Directly transmitted parasites were significantly more abundant on fished than on unfished islands (estimate = 1.06 ± 0.246, \( z = 4.30, \quad df = 39, \quad P < 0.0001 \)), and exhibited a significantly more positive response to fishing pressure than did trophically transmitted parasites (Fig. 4; Appendix N; estimate = \(-1.24 ± 0.329, \quad z = -3.77, \quad df = 39, \quad P = 0.0002 \)). Within the trophically transmitted parasites, *Stephanostomum* sp. metacercariae and some other trematodes showed strong positive responses to fishing (Fig. 3a). The third meta-analysis model \( R^2 = 0.345, \quad Q_M = 86.6, \quad df = 2, \quad P < 0.0001; \) Appendix N) partitioned the influence of *Stephanostomum* sp. and other trematodes, and after excluding the trematodes, the remainder of the trophically transmitted parasites were significantly more abundant on unfished than on fished islands (Fig. 4; estimate ± SE = \(-2.15 ± 0.232, \quad z = -0.27, \quad df = 41, \quad P < 0.0001 \)). The directly transmitted crustaceans and monogeneans had significant positive responses to fishing, the trophically transmitted cestodes

![Fig. 3. Standardized partial regression coefficient (z score) for the effect of fishing status on parasite abundance for each parasite taxon within host species. Values more than 2 indicate host–parasite combinations for which significantly more parasites were found on fished islands than on unfished islands (brown bands) and values less than –2 indicate host–parasite combinations for which significantly more parasites were found on unfished islands relative to fished islands (blue bands). P values are false discovery rate (FDR) corrected for multiple comparisons.](image-url)
and nematodes had significant negative responses to fishing, and the trophically transmitted trematodes did not have a significant response to fishing (Fig. 4; Appendix N).

**Hypothesis 5: Host specificity.**—Host specificity was not a significant moderator in the overall model (Appendices N and O), indicating that there was no relationship between specificity for the definitive host (i.e., the host most likely to be affected by fishing) and a parasite’s response to fishing. Accordingly, no additional analyses were performed.

**Hypothesis 6: Host response to fishing.**—Some hosts were more abundant on fished islands, while others were more abundant on unfished islands (Figs. 2b and 4b). The correlation between the response of hosts to fishing and the response of parasites to fishing differed between directly and trophically transmitted parasites, with directly transmitted parasites exhibiting more pronounced increases in abundance with fishing-driven increases in host abundance (Fig. 4b; Appendix N; host response × transmission strategy interaction, estimate = −1.10 ± 0.373, z = −2.96, df = 39, P = 0.003).

Multivariate analysis confirmed findings of the meta-analytic approach (Appendix G).

**DISCUSSION**

We found that parasite taxonomic diversity was substantially reduced on fished relative to unfished islands, but patterns for parasite abundance were more variable. While the abundance of directly transmitted parasites responded positively to fishing, trophically transmitted parasites tended to respond negatively. Parasite abundance was positively related to host abundance for directly transmitted parasites, indicating that heightened abundance of directly transmitted parasites on fished islands might be due to compensatory increases in host density. Overall, neither positive nor negative responses to fishing dominated; instead, parasite responses were mediated by parasite traits and the host’s response to fishing.

**Question 1: How does richness of parasite taxa differ between fished and unfished islands?**

Parasite taxon richness across all host–parasite combinations detected was significantly reduced on fished relative to unfished islands: jackknife taxon richness was, on average, >50% higher on unfished islands than on fished islands. This was due in part to modestly higher raw taxon richness detected on unfished relative to fished islands for some host species (Appendix I), and in part to the fact that several rare parasite species were observed on unfished islands that were not observed on fished islands (Appendix J). Rare species may be vulnerable to stochastic loss in fished ecosystems, due to fishing-driven reductions in host abundance (Stephens and Sutherland 1999, Torchin et al. 2003). The effect of fishing on parasite taxon richness was unrelated to the effect of fishing on host density (Fig. 2b), and is therefore probably related to the effects of fishing on other hosts whose density was not measured here. This suggests that overall food web simplification, not merely the exploitation of one or a few hosts, drives declines of parasite diversity. It is also possible that parasite diversity in the fish species we screened is linked with abiotic factors correlated with fishing (e.g., fishing reduces habitat complexity, which reduces the abundance of invertebrate intermediate hosts and the diversity of parasites that these hosts transmit to fish hosts). This result is consistent with prior studies of the effects of fishing (Sasal et al. 1996, Bartoli et al. 2005, Lafferty et al. 2008, Marzoug et al. 2012) and marine invasions (Bartoli and Boudouresque 1997) on fish parasites, and of salt marsh habitat destruction (Huspeni and Lafferty 2004, Hechinger and Lafferty 2005) and hurricanes (Aguirre-Macedo et al. 2011) on estuarine snail parasites, all of which find negative impacts of disturbance on parasite diversity. These data should therefore reinforce ecologists’ concern that anthropogenic disturbance might be causing widespread, cryptic declines in parasite biodiversity (Dunn et al. 2009, Wood et al. 2010, Colwell et al. 2012).

**Question 2: Are parasites more abundant, less abundant, or equally abundant on fished relative to unfished islands?**

The response of parasite abundance to fishing was variable among parasite taxa. For the 44 host–parasite combinations that were sufficiently abundant to analyze, about 13.6% of taxa decreased in abundance in response to fishing pressure, 22.7% increased, and 63.6% showed no significant response to fishing. This result clearly indicates that neither the positive (H2) nor negative (H3) relationships dominate the response of parasite abundance to disturbance. Instead, as has often been documented among free-living species (e.g., McKinney and Lockwood 1999), there appear to be “winners and losers” among parasites in a changing environment. The “winners” in this ecosystem are primarily copepod gall parasites and *Stephanostomum* sp. metacercariae, which were consistently (i.e., across different host species) more abundant on fished than on unfished islands. While the potential for such increases in disease prevalence should continue to concern ecologists (Keesing et al. 2010), these “winners” did not constitute the majority of parasites in the community we studied, comprising only 10 of 44 host–parasite combinations, or eight unique parasite taxa (since three of the significant host–parasite combinations were *Stephanostomum* sp.). Furthermore, few metazoan fish parasites are known to exert strong pathological effects on their hosts, except for the purpose of facilitating trophic transmission or in rare examples of high-intensity infection (Sindermann 1987), suggesting that increases in parasite abundance might not lead to increases in rates of fish disease. In addition to the slight but real possibility of rising disease burdens, our data suggest that another, more probable outcome of
fishing-driven environmental change is parasite species decline (discussed in the following passages). A large number of the parasite taxa we detected did not vary in abundance between fished and unfished islands, consistent with Hypothesis 3. This might be the case among (1) parasite taxa for which fishing did not have disruptive effects on hosts, or (2) parasite taxa with substantial resilience to host loss. Though there are marked differences in the fish community between our fished and unfished islands, fishing pressure on Teraina, Tabuaeran, and Kiritimati is probably relatively light when compared to intensely fished or overfished coral reef ecosystems globally (Sandin et al. 2008). Alternately, parasites might be exceptionally resilient to loss of hosts due to their ability to expand their host range, high evolutionary rates, and high reproductive potential (Bush and Kennedy 1994). Surely transient, natural reductions in host abundance are events that have occurred through evolutionary time, creating selective pressure on parasites for plasticity and genetic diversity sufficient for adaptability in the face of change. But despite the large number of individual host–parasite combinations that did not show significant differences between fished and unfished islands, when we synthesized across combinations, certain parasite taxonomic and ecological groupings were particularly vulnerable, and others particularly resilient, to fishing.

Question 3: What host and parasite attributes predict whether a parasite is more abundant, less abundant, or equally abundant between fished and unfished islands?

Transmission strategy was a strong predictor of parasite response to fishing. Directly transmitted parasites tended to increase in response to fishing, while trophically transmitted parasites tended to decrease.

Hypothesis 4. Transmission strategy.—Meta-analysis revealed that trophically transmitted parasites (excluding the trematodes) were significantly more abundant on unfished than on fished islands, consistent with Hypothesis 4. When trophically transmitted parasites were broken down into taxonomic groupings, both cestodes and nematodes were significantly more abundant on unfished than on fished islands. This pattern probably arises because trophically transmitted parasites must use multiple host species to complete their life cycles, and as the number of hosts increases, so should the likelihood that one of these obligately required hosts will be negatively impacted by fishing (sensu Rohr et al. 2011, Colwell et al. 2012). Additionally, many of the trophically transmitted parasites, especially the cestodes, nematodes, and acanthocephalans, use large apex predators as their final hosts (Appendix F), and these species are particularly susceptible to human impacts (Purvis et al. 2000a, b, Cardillo 2003, DeMartini et al. 2008, Sandin et al. 2008). A complex life cycle could conceivably confer resilience to short-term fluctuations.
in the abundance of one host. Because many parasitic infections are long lived (e.g., trematodes in long-lived snail first intermediate hosts), a complex life cycle could provide opportunities for parasites to “bide their time” in one host, buffering against fluctuations in the abundance of the hosts of other life stages. However, our data indicate that, for cestodes and nematodes in particular, possessing a complex life cycle puts a parasite at greater risk for fishing-driven decline.

Other studies have highlighted the potential sensitivity to fishing pressure of larval cestodes that use elasmobranchs as final hosts (Lafferty et al. 2008). Because the tetraphyllidean and trypanorhynch tapeworms we detected are obligate parasites in elasmobranch intestines in their adult life stages (Khalil et al. 1994), and because elasmobranchs are exceptionally sensitive to fishing pressure due to life history traits (e.g., slow growth, late sexual maturity, low fecundity) and strong fishing pressure on their populations (Stevens et al. 2000, Fowler et al. 2005, Bender et al. 2013), this example demonstrates that complex life cycle parasites with fishery-targeted hosts are likely to be sensitive to fishing impacts (see Plate 1). In fact, non-elasmobranch hosts used in the course of the cestode life cycle probably benefit from fishing. Since tapeworm larvae are trophically transmitted from second intermediate teleost hosts to elasmobranchs, those teleost hosts might experience compensatory increases in abundance where elasmobranch predation pressure is reduced by fishing. Despite this, cestodes displayed reduced abundance on fished relative to unfished islands, probably because fishing of shark hosts creates a “life cycle bottleneck”. Such bottlenecks have been observed in mathematical models of the impact of biodiversity loss on parasites (Lafferty 2012). We surmise that a similar mechanism generates the observed pattern of reduced abundance of nematodes on unfished relative to fished islands. Like cestodes, nematodes have a complex life cycle and obligately require multiple hosts (Skryabin 1991). In adult stages, these nematodes use predatory teleosts, elasmobranchs, marine mammals, and birds, all taxa that have probably experienced disturbance-related reductions on fished islands (Sherley 2001, Sandin et al. 2008).

In contrast with the findings for the other trophically transmitted parasites, meta-analysis revealed that trematodes exhibited widely divergent responses to fishing: we found that three trematode taxa were significantly more abundant on unfished than on fished islands, while two were more abundant on fished than unfished islands (Fig. 3a). This result is consistent with Lafferty et al. (2008), who found that two trematode taxa were more abundant on unfished Palmyra than on fished Kiritimati, and one taxon was more abundant on Kiritimati than Palmyra. We speculate that the divergent responses of trematode taxa to fishing are due to complex indirect effects of fishing on trematode hosts (see Idiosyncratic responses).

Hypothesis 5. Host specificity.—We anticipated that generalist parasites would be more abundant on fished than on unfished islands, since a generalist parasite should be more likely to benefit from increases in one of the many host species within its host range (i.e., susceptible host release), and better able to compensate for the fishing-driven decline of one or a few host species (sensu Colwell et al. 2012). However, we found no relationship between degree of parasite specialization and the effect of fishing on parasite abundance, and Hypothesis 5 was therefore not supported. One constraint that compromised our ability to detect the hypothesized effect was the absence of taxonomically resolved natural history information for the parasites detected in this study. Because we lacked species-level information on these parasites, we inferred their degree of specialization from information on higher-order taxonomic levels (Brusca 1981, Sasal et al. 1998, Jones et al. 2007). Specialization is strongly conserved within our taxonomic groupings (Sasal et al. 1998, Mouillot et al. 2006), but we have nonetheless probably summarized over a substantial amount of variation. This constraint reduces our confidence in the conclusion that there is no relationship between host specificity and parasite response to fishing, although we did not find any evidence for such a link in this data set.

Hypothesis 6. Host response to fishing.—We found that directly transmitted parasites were significantly more abundant on fished than on unfished islands, consistent with Hypothesis 3 (Fig. 4a). This pattern appears to be driven in part by directly transmitted parasites’ positive response to host density, consistent with Hypothesis 6 (Fig. 4b). That is, directly transmitted parasites were more abundant on fished islands in part because their focal hosts were more abundant there (Fig. 4b). This finding suggests that fishing-driven compensatory increases in host abundance may drive increases in the abundance of directly transmitted parasites in fished environments. This effect influences the abundance of directly transmitted parasites but not trophically transmitted parasites, probably because while directly transmitted parasites are positioned to capitalize on an increase in host abundance, trophically transmitted parasites might be “rate-limited” by the least abundant host in the life cycle. Bottlenecks in the complex life cycle, particularly at the adult stage (e.g., the shark host of cestode adults), might reduce the ability of trophically transmitted parasites to capitalize on increases in abundance of hosts at other life cycle stages. However, it should be noted that a substantial proportion of variability among parasite responses was unexplained by host response and the other included predictors (as indicated by $Q_2$ statistics). This unexplained variability may be attributable to additional factors that vary between fished and unfished islands or to the interaction of those factors with parasite traits.

Another important caveat for this analysis relates to the relatively low trophic level of our focal hosts.
Though the seven host species that we chose for this assessment span a variety of trophic levels, the highest-trophic-level species (*Cephalopholis urodeta*) is not a top predator. As a result of the relatively low trophic level of the fish species sampled, few of these species declined in density with fishing, and many instead increased, presumably due to release from predation pressure on fished relative to unfished islands (Figs. 2b and 4b). Our findings might have differed had we focused instead on higher-trophic-level hosts. Specifically, we predict that parasites would be more likely to decline with fishing in higher-trophic-level hosts, since these hosts are more likely to experience strong reductions in density due to the direct effects of fishing. We would expect this to hold true even for the fishing-resilient directly transmitted parasites, given their strong dependence on host density (Fig. 4b). In choosing focal host species, we were limited by the logistical constraints of collecting very high-trophic-level species like predatory snappers and sharks, including their pelagic nature, ability to evade capture, the danger they pose to collectors, their rarity at fished sites, and our concern for further depleting populations of these highly valued and highly threatened species. If these constraints can be addressed, it would be informative to sample parasites in high-trophic-level hosts in future studies. Given the lack of replication at the level of host traits (i.e., we chose only one representative from each of several major functional groupings of coral reef fishes), it would also be informative to add additional host species that replicate the functional groups and trophic levels of hosts represented in this study. This would provide more scope for drawing conclusions about how host trophic level, response to fishing, body size, and other factors influence the response of parasites to fishing.

Finally, it is worth considering whether the use of fish collected in different years and seasons allowed for our inter-island comparisons to be confounded with temporal fluctuations in parasite abundance. Given the relative longevity of the metazoan parasites we detected (Lafferty and Kuris 2002), and the fact that the vast majority of our fish samples (90.2%) came from the expedition conducted in October and November of 2010 (Appendices A, B, and C), we anticipated that the effect
of this variability in timing of fish collection would be minimal. Indeed, because host individuals from outside the primary sampling period of October and November 2010 were only ever used for one of the six islands within each host species (Appendices A and B), and because statistical tests accounted for the variability within and between fished and unfished islands, it is unlikely that timing of sampling contributes to patterns reported here.

Idiosyncratic responses

The trematodes showed high variability in their response to fishing pressure, and one metacercaria, *Stephanostomum* sp., had a strong positive response to fishing. Because increases in the abundance of snail first intermediate hosts can drive dramatic increases in the prevalence of trematodes in downstream hosts (e.g., Picquet et al. 1996, Johnson et al. 2007), we speculate that fishing-related changes in these first intermediate hosts might be the driver of increased *Stephanostomum* sp. abundance and variable abundance of the remaining trematodes on fished islands.

While the first intermediate hosts of cestodes and nematodes are planktonic crustaceans like copepods, trematode first intermediate hosts are usually gastropods. Given the oceanic nature of islands, the abundance of planktonic crustaceans at our sampling sites is probably determined to a large extent by oceanic productivity, and to a lesser extent by local biotic interactions (Leichter et al. 1998, Hamner et al. 2007). Therefore, fishing might affect cestode and nematode life cycles primarily by acting on hosts of other life stages, for example, by directly reducing the abundance of a definitive host. In contrast, coral reef gastropod abundance can be strongly affected by fishing-driven change in the local food web (McClanahan 1989). If fishing reduces the abundance of the predator of a gastropod, it could cause a compensatory increase in gastropod abundance and a concomitant increase in trematode abundance. For example, fishing has been shown to release a variety of gastropods from predation pressure on Kenyan coral reefs, resulting in concomitant increases in their density (McClanahan 1989). Therefore, the effect of fishing on trematode abundance could depend on the interaction between the direct and indirect effects of fishing on the definitive host and indirect effects of fishing on the first intermediate host, making the direction of a trematode’s response to fishing difficult to predict.

The complexity of fishing’s effects on the multiple obligate hosts of trematodes might further explain the highly divergent responses of *Stephanostomum* sp. metacercariae. The identities of the first intermediate and definitive hosts of the *Stephanostomum* sp. metacercariae identified in this study are unknown, but the life cycles of several marine congeners have been demonstrated. *Stephanostomum baccatum* has been reported in *Buccinum undatum* and *Neptunea decemcosmatum* (Wolfgang 1954), as well as *Neptunia antiqua* (MacKenzie and Liversidge 1975), and *Stephanostomum caducum* has been documented to infect *Natica alderi* (Koie 1978). Of these four known gastropod hosts, three are whelks in the superfamily Buccinoidea, and one is a moon snail in the superfamily Naticoidea; all utilize mud or sand flat habitat. Based on this host specificity, we conjecture that the first intermediate host of the *Stephanostomum* sp. metacercaria we observed might also be a buccinoid whelk or naticoid moon snail from mud- or sand-bottom habitat, potentially from the sandy habitat that surrounds the reefs where these fish were collected. Since all of these potential snail hosts are predators, we suspect that they are not strongly responsive to the increased nutrient inputs of fished and inhabited relative to unfished and uninhabited islands (Sandin et al. 2008). Therefore, it seems improbable that increased *Stephanostomum* sp. abundance would be driven by nutrient enrichment on inhabited islands. However, these large mollusks are probably prey for a number of fish targeted by fishing. If the first intermediate hosts of *Stephanostomum* sp. are released from predation pressure on unfished islands, then their increase in abundance could facilitate an increase in transmission of cercariae to our focal hosts, and could therefore account for the increased abundance of metacercariae we observed on fished relative to unfished islands. *Stephanostomum* sp.’s unique suite of first intermediate hosts might therefore explain the strong divergence in response to fishing between it and the remainder of the trophically transmitted parasite taxa.

Another interesting contrast is that between live and dead/melanized larval nematode parasites in *Cephalopholis urodeta*. Combining the abundance of live and dead larvae shows that there are more nematode larvae overall and that a greater proportion of these nematodes are inactivated by the host immune response on unfished than on fished islands, possibly because fish on these islands have higher immune function or a different age structure. This contrast is explored in depth in Appendix M.

Comparison with other studies

The results from this study are in strong agreement with those of Lafferty et al. (2008), who contrasted the parasite assemblages of a similar suite of fish hosts (*Paracirrhites arcatus*, *Acanthurus nigricans*, and *Chromis margarifer*, as well as *Plectroglyphidodon dickii* and *Lutjanus bohar*) between Kiritimati Island and Palmyra Atoll. As in our study, Lafferty et al. found lower parasite taxon richness in the presence of fishing than in its absence. Where Lafferty et al. found that jackknife estimates of parasite richness were on average 70% higher at Palmyra than at Kiritimati, we found that jackknife estimates were on average 54% higher on three unfished islands than on three fished islands (Lafferty et al. 2008). Although Lafferty et al. did not identify parasites but instead grouped like parasites into
morphospecies, photographs of representative specimens allow tentative comparison of the abundance of individual parasite taxa between the two studies. As in our study, Lafferty et al. found that the response of parasite abundance to fishing varied among parasite taxa. Notably, Lafferty et al. demonstrate much higher prevalence of cestode parasites on Palmyra relative to Kiritimati, in agreement with our findings that cestode responses to fishing tend to be negative. Of the 25 host–parasite combinations evaluated by Lafferty et al., two were more abundant within hosts on Kiritimati than Palmyra, seven were more abundant on Palmyra than Kiritimati, and 16 were not significantly different between the two islands. Among the nine significant combinations, three were shared in common between the two studies. Of these, the two studies agreed on the direction of the relationship for one parasite taxon (microscaphid sp. in A. nigricans) and disagreed for two taxa (grandiunguid sp. in C. margaritifer, and larval nematodes in P. arcatus). We attribute these differences to the influence of individual island-to-island variability in the Lafferty et al. study. Because our experimental design includes replication within fishing status (i.e., three islands within each fishing status category, rather than one), our study extends the findings of Lafferty et al. by demonstrating differences that are attributable to the impact of fishing and not merely to island-to-island variability. In general, both of these studies conclude that fishing depresses parasite diversity and can have variable effects on parasite abundance, and both studies identify negative responses to fishing among trophically transmitted parasites.

Conclusions and implications for other disease systems

With data on 77 host–parasite combinations from 945 individuals of seven fish species collected from three fished and three unfished islands, we demonstrate that fishing has negative effects on parasite diversity and variable effects on parasite abundance, which appear to be mediated by parasite traits. Overall, neither positive nor negative relationships dominate the response of parasites to fishing. Instead, as for free-living species, there are likely to be winners and losers among parasites in a changing environment, with losers including trophically transmitted parasites and winners including directly transmitted parasites whose hosts benefit from fishing.

What lessons can we draw from these data to predict fishing-driven change in marine ecosystems? Relative to many marine habitats, especially those subject to commercial fisheries, the fished islands of the Line Islands are lightly fished (Halpern et al. 2008), and are therefore an imperfect, probably conservative, representation of the differences between fished and unfished ecosystems. Furthermore, while results from this study are relevant for similar coral reef habitats, it is unclear how these patterns might differ in other marine ecosystems. Given these caveats, our data suggest that directly transmitted parasites could pose a growing disease risk in fished marine ecosystems. Equally important, trophically transmitted parasites appear to be sensitive to fishing impacts, and might be at risk of local extirpation in fished environments. Within trophically transmitted parasites, taxa that use apex predators as final hosts appear to be especially vulnerable, while parasites with hosts that benefit from fishing (e.g., trematodes with snail intermediate hosts) appear to be buffered against fishing impacts. The positive correlation between host density and directly transmitted parasite abundance suggests that directly transmitted parasites with fishing-sensitive hosts might also be at risk. Since parasite taxon richness was negatively related to fishing in our data set, this study also highlights the potential for fishing to drive steep yet cryptic declines in parasite biodiversity (Wood et al. 2010). Such a loss is of special concern given the important ecological role that parasites are known to play in ecosystems (Gomez et al. 2012).

It appears that both increasing disease risk (Keesing et al. 2010) and loss of parasite biodiversity (Colwell et al. 2012, Gomez et al. 2012) are likely outcomes in a changing environment. The direction of response of parasites to environmental change appears to be driven in part by parasite traits. An improved understanding of how parasite traits and other factors influence the likelihood of parasite increase or decrease across impacted ecosystems will better equip ecologists to predict how disease will change in a changing world.

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SUPPLEMENTAL MATERIAL

Appendix A
Number of individual hosts dissected from each unfished and fished island, for each of the seven fish species sampled (*Ecological Archives* E095-170-A1).

Appendix B
Number of individual intestines dissected from each unfished and fished island, for each of two herbivorous fish species sampled (*Ecological Archives* E095-170-A2).

Appendix C
Metadata on sampling sites within islands (*Ecological Archives* E095-170-A3).

Appendix D
Map of sampling sites within islands (*Ecological Archives* E095-170-A4).

Appendix E
Detailed dissection protocols for each host species (*Ecological Archives* E095-170-A5).

Appendix F
Parasite taxa detected in each host species, with natural history information (*Ecological Archives* E095-170-A6).

Appendix G
Multivariate analysis (*Ecological Archives* E095-170-A7).

Appendix H
Species accumulation curves for each of the seven host species (*Ecological Archives* E095-170-A8).

Appendix I
Raw parasite taxon richness on each island (*Ecological Archives* E095-170-A9).

Appendix J
Some examples of parasite species that were influential in jackknife estimates of diversity (*Ecological Archives* E095-170-A10).

Appendix K
Summary of results of GLMMs for each host–parasite combination (*Ecological Archives* E095-170-A11).

Appendix L
Results of full and reduced GLMMs for each host–parasite combination (*Ecological Archives* E095-170-A12).

Appendix M
Contrast between live and dead larval nematode parasites in *Cephalopholis urodeta* (*Ecological Archives* E095-170-A13).

Appendix N
Results of general linear models for meta-analysis (*Ecological Archives* E095-170-A14).

Appendix O
Plot of effect size for each parasite taxon as a function of host specificity score (*Ecological Archives* E095-170-A15).