How have fisheries affected parasite communities?

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SUMMARY

To understand how fisheries affect parasites, we conducted a meta-analysis of studies that contrasted parasite assemblages in fished and unfished areas. Parasite diversity was lower in hosts from fished areas. Larger hosts had a greater abundance of parasites, suggesting that fishing might reduce the abundance of parasites by selectively removing the largest, most heavily parasitized individuals. After controlling for size, the effect of fishing on parasite abundance varied according to whether the host was fished and the parasite's life cycle. Parasites of unfished hosts were more likely to increase in abundance in response to fishing than were parasites of fished hosts, possibly due to compensatory increases in the abundance of unfished hosts. While complex life cycle parasites tended to decline in abundance in response to fishing, directly transmitted parasites tended to increase. Among complex life cycle parasites, those with fished hosts tended to decline in abundance in response to fishing, while those with unfished hosts tended to increase. However, among directly transmitted parasites, responses did not differ between parasites with and without fished hosts. This work suggests that parasite assemblages are likely to change substantially in composition in increasingly fished ecosystems, and that parasite life history and fishing status of the host are important in predicting the response of individual parasite species or groups to fishing.

Key words: biodiversity, disease, fishing, freshwater, marine, meta-analysis.

INTRODUCTION

How parasites affect fisheries is of immediate and significant economic and social relevance. The converse, how fisheries affect parasites, receives less attention. Here, we present the results of a meta-analysis that suggests fishing can alter aquatic parasite assemblages, and we argue that these changes can indirectly alter ecosystem function and its associated services.

Why should we care whether fishing alters parasite communities? In certain circumstances, parasites can regulate host populations (e.g. Hudson *et al*. 1998) and mediate the species composition of free-living communities (e.g. Mouritsen and Poulin, 2005; Wood *et al*. 2007). There is also an increasing awareness that parasites can shape entire aquatic food webs (e.g. Lafferty *et al*. 2008*a*). Parasites are extremely diverse: at least 40% of animal species are parasitic (Dobson *et al*. 2008), as are the majority of species in 27 of the 42 recognized animal phyla (Poulin and Morand, 2000; deMeeus and Renaud, 2002). In some aquatic ecosystems, parasites can comprise a large proportion of total biomass, surpassing the biomass even of top predators in estuarine salt marshes (Kuris *et al*. 2008) and insects in freshwater ponds (Preston *et al*. 2013). In addition to representing a large proportion of food web nodes and of the biomass within those nodes, parasites can also account for a large proportion of the linkages between nodes: in an analysis of four food webs, parasite–host links outnumbered predator–prey links (Lafferty *et al*. 2006), and parasites increased food web connectance (Lafferty *et al*. 2006), with implications for overall food web stability (Dunne *et al*. 2002). Parasites might also influence the strength of linkages between their hosts and other species by affecting host growth, survival, behaviour, reproductive investment and competitive ability (Lafferty, 2008). A common adaptation of many parasites is to manipulate host behaviour to facilitate transmission, particularly by inducing behaviours in an intermediate host that make it susceptible to predation by a definitive host (Moore, 2002). Because such trophically transmitted parasites are common in aquatic ecosystems (Marcogliese, 2002*b*), it is possible that this manipulation is widespread; if so, parasites might broadly increase the interaction strength of predator–prey relationships that would otherwise be weak, with implications for the abundance, biomass and population dynamics of both predators and prey (Lafferty, 2008). These examples illustrate that parasites are ecologically influential. Here, we ask how fishing

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affects parasites and what this means for the influence they exert on aquatic ecosystems.

Historical data on aquatic parasite assemblages are too scarce to indicate what parasite communities were like prior to intensive fishing. Instead, researchers have made contemporary comparisons of fished *vs* unfished areas, documenting effects of fishing or protection against fishing on aquatic parasite assemblages at geographically diverse sites from the Mediterranean to the tropical equatorial Pacific. However, most of these studies are unreplicated contrasts between a single unfished or lightly fished area (e.g. marine reserve) *vs* a single fished area (e.g. a nearby open-access area). The findings of these studies are diverse: many report reductions in parasite species diversity in response to fishing pressure (e.g. Sasal *et al*. 1996; Lafferty *et al*. 2008*b*; Marzoug *et al*. 2012), but how parasite abundance responds to fishing pressure varies among parasite species and among studies. We combined data across parasite life history strategies, host types, and other factors to better understand how broad groups of parasites might respond to fishing.

Our goal is to examine how fisheries affect parasite assemblages and to assess the potential ecological importance of these changing parasite assemblages. We begin by outlining some hypotheses for how fishing might affect parasites, focusing on specific predictions that take into account the ecological diversity among aquatic parasites. We test these hypotheses with a meta-analysis, using a comprehensive dataset assembled from a thorough search for studies contrasting parasite assemblages in heavily fished and lightly fished or unfished areas. This dataset is included as Supplementary Material (Appendix 1) so that others can investigate the influence of factors we do not consider here, or update our analysis when additional studies become available.

HYPOTHESES

Aquatic parasites are taxonomically and ecologically diverse (Poulin, 1998; Poulin and Morand, 2000; Marcogliese, 2002*a*), and this diversity makes it difficult to envision a consistent response to fishing across all – or even most – aquatic parasites. Instead, we expect that parasites will exhibit a diversity of responses to fishing pressure, including positive, negative and neutral changes. However, the diversity of responses does not mean that we cannot make predictions. The direction of a parasites' response to fishing pressure might be predictable based on parasite traits, host traits and environmental context. Here, we present several, non-mutually exclusive hypotheses for the context-dependency of parasite responses to fishing pressure, which we test with meta-analysis below.

Hypothesis 1: Fishing reduces the diversity of parasites in an ecosystem because it simplifies host communities and this disrupts parasite transmission.

Prediction 1: Overall parasite species diversity should be higher in unfished than in fished areas. (Parasite species diversity in unfished areas > parasite species diversity in fished areas.)

This is expected under the assumption that fishing simplifies marine communities by reducing free-living biodiversity. Parasite diversity is tied to host diversity and hosts do not need to be lost completely from the system for parasites to suffer. Evidence for the local extirpation of parasites below a threshold in host density is strong (e.g. Arneberg *et al*. 1998; McCallum *et al*. 2005) and low host density has also been linked to low parasite diversity (e.g. Morand and Poulin, 1998; Arneberg, 2002; Hechinger and Lafferty, 2005).

Hypothesis 2: Fishing reduces the abundance of parasites (i.e. number of parasites per host) of fished hosts because lower host density reduces parasite transmission.

Prediction 2: Parasites that use a fished host in their life cycle will be less abundant in fished areas than in unfished areas, even when measured in another host in the life cycle. (Mean response to fishing among parasites with a fished focal host or some fished host in the life cycle <0.)

As previously noted, parasite transmission can be strongly tied to host density (e.g. Arneberg *et al*. 1998; McCallum *et al*. 2005) and, since fishing acts to directly reduce fish density, we expect fishing to drive declines in the abundance of parasites of fished hosts (Dobson and May, 1987). This is a simple and direct hypothesis about the effects of fishing, because it focuses on single host species, not the entire ecosystem. Here, we specify that the effect of fishing on a parasite species of a fished host can be measured by the abundance of parasites in that host or in other hosts in the life cycle. The abundance of parasites within the environment (i.e. number of parasites per unit area) is a function of both the number of parasites per host and host density. From this perspective, parasites will often have smaller populations where fishing reduces the density of their hosts (e.g. Wood *et al*. 2013) – a prediction that we do not test specifically due to lack of consistent data on host density.

Hypothesis 3: Fishing can indirectly increase the abundance of parasites of unfished hosts if those hosts benefit from the fishing of their competitors or predators.

Prediction 3: Parasites that use only unfished hosts in their life cycle should be more abundant in fished areas than in unfished areas. (Mean response to fishing among parasites with an unfished focal host and no other fished host in the life cycle >0.)

Although fishing often has the effect of reducing the density of fished populations, its effects at

a community level are more complex: because fishing pressure often focuses on high trophic-level, large-bodied species (Pauly and Watson, 2005; Pauly *et al*. 2005), it can generate trophic cascades that release lower trophic-level species from regulation, resulting in fishing-driven reductions in the density of some host species and compensatory increases in the density of others (e.g. Myers *et al*. 2007; Baum and Worm, 2009; Casini *et al*. 2009).

Hypothesis 4: Life-cycle complexity can alter the outcome of the above hypotheses.

Prediction 4.1: Parasites with complex life cycles are more likely to decline in response to ecosystem simplification associated with fishing than are directly transmitted parasites. (Mean response to fishing among complex life cycle parasites < mean response to fishing among directly transmitted parasites.)

Complex life cycle parasites (trematodes, nematodes, cestodes, acanthocephalans) should be more likely to decline in the presence of fishing than are directly transmitted parasites (crustaceans, monogeneans, eulimid gastropods, bacteria). First, definitive host species of complex life cycle parasites tend to be large bodied and high trophic level: exactly the fish species that are most sought-after by fishermen (Pauly and Watson, 2005; Pauly *et al*. 2005). For example, cestodes tend to use elasmobranchs as their definitive hosts, and sharks are among the marine species most negatively affected by fishing (Stevens *et al*. 2000; Fowler *et al*. 2005; Bender *et al*. 2013). The impact of the loss of sharks might be observed in the down-stream life stages of the parasite (for instance, at the larval stage in fish hosts; Lafferty *et al*. 2008*b*). Second, for complex life cycle parasites, each stage needs to have at least one host species present. If any life stage loses its host, the parasite cannot complete its life cycle, creating a 'life cycle bottleneck' that prevents transmission, even if hosts for other stages in the life cycle are unaffected (Wood *et al*. 2010; Rudolf and Lafferty, 2011; Lafferty, 2012). Such a sequential dependence on multiple host species – in and of itself – should increase the likelihood that a parasite will require a host that is negatively affected by fishing.

Prediction 4.2: Among complex life cycle parasites, those using at least one host that is fished (or responds negatively to fishing) should be more likely to decline than those that use no fished hosts (or whose hosts respond positively to fishing). (Among complex life cycle parasites, mean response to fishing for those parasites with at least one fished host in the life cycle < mean response to fishing for those parasites with no fished host in the life cycle.)

The abundance of parasites with complex life cycles depends on the success of all the hosts in the life cycle. While fishing might depress the abundance of some host groups, it could increase the abundance of other host groups (e.g. Myers *et al*. 2007; Baum and Worm, 2009; Casini *et al*. 2009), which might

lead to increased transmission of a parasite. For instance, trematodes typically have non-fished molluscs as first intermediate hosts and these might have indirect positive responses to fishing if they are released from predation in fished environments. For a given parasite whose hosts diverge in their response to fishing pressure, the outcome for parasite abundance will be difficult to predict, although due to life cycle bottlenecks, we predict that the parasite's response will tend to be negative. With no fished hosts in the life cycle, there is potential for a parasite to increase in abundance if its hosts experience compensatory increases in response to fishing.

Prediction 4.3: Among directly transmitted parasites, parasites of unfished hosts should increase in response to fishing, while parasites of fished hosts should decline. (Mean response to fishing for parasites with an unfished host >0, mean response to fishing for parasites with a fished host <0.)

In contrast with complex life cycle parasites, the abundance of directly transmitted parasites can be dependent on the density of a single host species (e.g. Arneberg *et al*. 1998; McCallum *et al*. 2005). We therefore predict that directly transmitted parasite abundance will track their hosts' response to fishing: increasing where hosts experience compensatory increases in abundance, and decreasing where hosts are fished.

We tested these predictions by analysing the results of studies that compared the parasite assemblages of fished and unfished areas. We found support for *Predictions 1* (fishing reduces parasite diversity), *3* (fishing increases abundance of parasites with unfished hosts), *4.1* (complex life cycle parasites respond more negatively to fishing than do directly transmitted parasites), and *4.2* (complex life cycle parasites with fished hosts respond more negatively to fishing than do complex life cycle parasites with unfished hosts), and equivocal support for *Predictions 2* (fishing reduces abundance of parasites with fished hosts) and *4.3* (directly transmitted parasites with fished hosts respond more negatively to fishing than do directly transmitted parasites with unfished hosts). Study-to-study variability and ecological factors not considered among our predictions may also be important in determining parasite responses to fishing pressure.

MATERIALS AND METHODS

Data selection

We established several a priori criteria for inclusion of studies in our meta-analysis. Included studies were required to contrast the abundance of at least one parasite species in the same host species between heavily fished and lightly fished or unfished areas. We accepted the fishing intensity rating of the original

authors and included studies conducted in marine and freshwater ecosystems on both fish and invertebrate hosts. All studies gave a quantitative estimate of the abundance of parasites within each host sampled (e.g. average number of parasites per host, qualitative but consistently applied infection intensity score).

We searched for appropriate studies with Web of Science (Thomson Reuters), using the following search string:

(fishing or exploit* or (protected area*) or reserve) AND

(parasit* or disease* or pathogen* or infect* or prevalence or nematod* or cestod* or trematod* or acanthoceph* or virus* or bacteri* or ectoparasit* or endoparasit* or worm* or protozoa* or protist* or (mass and mortalit*))

This search returned 8088 studies. Each study's title was screened by CLW and, if relevant, further evaluated for adherence to the criteria outlined above. Of the 8088 studies returned, 12 were deemed appropriate for inclusion (Amundsen and Kristoffersen, 1990; Sasal *et al*. 1996, 2004; Loot *et al*. 2005; Lafferty *et al*. 2008*b*; Freeman and MacDiarmid, 2009; Ternengo *et al*. 2009; Marzoug *et al*. 2012; Sonnenholzner *et al*. 2011; Sala-Bozano *et al*. 2012; Wootton *et al*. 2012; Wood *et al*. 2013). Each unique host–parasite combination was treated as an independent datum, resulting in multiple data points arising from each study: from the 12 suitable studies found during our literature search, we obtained 149 host–parasite combinations. For each datum, we recorded parasite identity, host identity, whether the host in which the parasite was detected or another host in the life cycle was subject to fishing pressure in fished areas (see next paragraph for full explanation of this distinction), the higher-order taxonomic grouping of the parasite (Crustacea, Monogenea, Trematoda, Cestoda, Nematoda, Acanthocephala, Gastropoda, Bacteria), and the response of the parasite to fishing (positive, negative or neutral, based on the authors' interpretation).

We categorized whether a host was fished (for the purposes of testing *Predictions 2, 3* and *4*) in two ways. First, we determined whether the focal host (i.e. the host in which the parasite was measured) was fished using the assessments of the original authors. We called this predictor 'fishing status of the focal host'. However, complex life cycle parasites detected as larvae in an unfished focal host might have other hosts (particularly definitive hosts) that are fished. To capture this effect of fishing, we used the following criteria to define the 'fishing status of all hosts':

1. Any parasite with a fished focal host was classified as 'fished'.

2. Any directly transmitted parasite with an unfished focal host was classified as 'unfished'.

3. Any complex life cycle parasite known or suspected to use a fished host at some point in the life cycle was classified as fished. For example, since most cestodes use top predators as definitive hosts, and top predators are subject to strong fishing pressure, we classified cestode larvae as 'fished'. For non-cestode larval parasites, we classified a species as 'fished' if its focal host was large, which suggests that its predator would be of sufficient body size to be subject to fishing pressure. For non-cestode larval parasites of small focal hosts, we used criteria 4 and 5, below.

4. Any complex life cycle parasite suspected of using exclusively unfished hosts was classified as unfished. For example, a trophically transmitted parasite using a small, unfished host as its definitive host is unlikely to cycle through larger, fished hosts at other points in its life cycle.

5. Any complex life cycle parasite where insufficient information existed to make a determination about the likely fishing status of all hosts in the life cycle was classified as 'uncertain'.

These classifications resulted in two ways of characterizing the likely fishing pressure experienced by a parasite: fishing pressure experienced by the focal host and fishing pressure experienced by all hosts in the life cycle.

To explore how parasite life cycle complexity interacts with effects fishing on hosts (i.e. to test *Predictions 4.1, 4.2, 4.3* and *4.4*), we further broke down these categories by differences in life-cycle complexity across parasites. We created six non-exclusive groups based on the host fishing status categorizations above:

1. Directly transmitted parasites with fished focal hosts.

2. Directly transmitted parasites with unfished focal hosts.

3. Complex life cycle parasites with unfished focal hosts and no other fished hosts in the life cycle.

4. Complex life cycle parasites with a fished focal host or at least one fished host elsewhere in the life cycle.

5. Complex life cycle parasites with unfished focal hosts, regardless of the fishing status of other hosts in the life cycle.

6. Complex life cycle parasites with fished focal hosts, regardless of the fishing status of other hosts in the life cycle.

Throughout the remainder of the paper, we refer to these groups as 'life-cycle complexity–fishing status groupings'.

One key impediment to meta-analysis of these findings was the potential correlation of host body size with both per-host parasite abundance and fishing status of the sampling area. That is, large hosts tend to carry more parasites, and areas protected from fishing tend to contain larger hosts. All the studies we found controlled for this potential effect of host body size, but they did not provide consistent measurements of the relative effect of fishing independent of host body size. For example, some authors performed statistical tests that controlled for host body size (e.g. by including body size as a covariate), but reported mean parasite abundance values in heavily fished and lightly/unfished areas. Other authors reported regression coefficients for the effect of fishing – a value that reflects the contribution of fishing independent of the contribution of body size, if body size is also included in the statistical model. These variations prevented us from calculating a consistent effect size from published information on each host–parasite combination. To circumvent these constraints, we sought the raw datasets for all studies, obtained data for a large subset of these studies, and extracted regression coefficients for the effects of both fishing and body size for each host–parasite combination. We then used these consistent metrics to perform a quantitative meta-analysis across the studies for which we were able to obtain raw data. We include our meta-analytic dataset in Appendix 1. We also summarize results for the effect of body size on parasite abundance, independent of the effect of fishing, using the meta-analytic approach described below.

Parasite diversity (Prediction 1)

To test *Prediction 1*, we assessed the response to fishing of parasite diversity across five studies that quantified this effect. Diversity metrics varied across papers; we used the metric that was reported by the authors and calculated a standardized effect size by subtracting the overall diversity of unfished areas (i.e. across multiple host species, for papers that reported results from multiple host species) from the diversity of fished areas and then dividing by the diversity of unfished areas (see Appendix 1). We then performed a one-sample *t*-test to assess whether this value differed significantly from zero. We also repeated this analysis using host species as the unit of replication: that is, some studies investigating the effect of fishing on parasite diversity report results from multiple host species, so we derived an effect size as above for each host species, and subjected this value to a one-sample *t*-test.

Parasite abundance (Predictions 2–4)

We performed a quantitative meta-analysis with the subset of studies for which we could obtain raw data by contacting authors and requesting data at the individual host level (i.e. for each host: parasite abundance, body size and collection site). This quantitative meta-analysis was not possible to conduct for diversity, because raw data were not available from a large proportion of the studies testing for a diversity effect. However, of the 149 host–parasite combinations originally identified, we were able to obtain raw data on abundance for 74 (see Appendix 1). We excluded one study where data were not available at the individual host level (i.e. prevalence was reported across many hosts; this study reported a positive relationship between fishing the predator of a host and parasitism of that host; Lafferty, 2004). For each study where we were able to obtain suitable raw data, we tested for the effect of fishing (heavily fished *vs* lightly fished/unfished area) on parasite abundance while controlling for host size, using a generalized linear model with Poisson error structure (glm in R version 3.0.2 base package; R Foundation for Statistical Computing). If there was more than one site within each fishing status group, site was included as a random effect (glmer in package lme4). If the heavily fished *vs* lightly/unfished contrast was temporal rather than spatial, we split the time period into 'before' and 'after' fishing (Amundsen and Kristoffersen, 1990). We report the effects of fishing and host body size as regression coefficients with associated s.e. (see Appendix 1).

We used a quantitative meta-analytic approach to assess the responses of parasites to fishing across host–parasite combinations. For effect size estimates, we used regression coefficients for the effect of fishing status on abundance of each host–parasite combination, extracted from the Poisson regressions described above. We first calculated a cumulative effect size across all 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. The four models tested our a priori hypotheses regarding the influence of various factors on the response of parasite abundance to fishing pressure: whether the focal host (i.e. the host in which the parasite was observed) is fished (*Predictions 2* and *3*, Model A), whether any host in the life cycle is fished (*Predictions 2* and *3*, Model B; see above for criteria used to assess whether any host in the life cycle is fished), whether the parasite has a complex or direct life cycle (*Prediction 4.1*, Model C), and life cycle–host fishing status grouping (*Predictions 4.2, 4.3* and *4.4*, Models D and E). All analyses were performed with the *metafor* package in *R*.

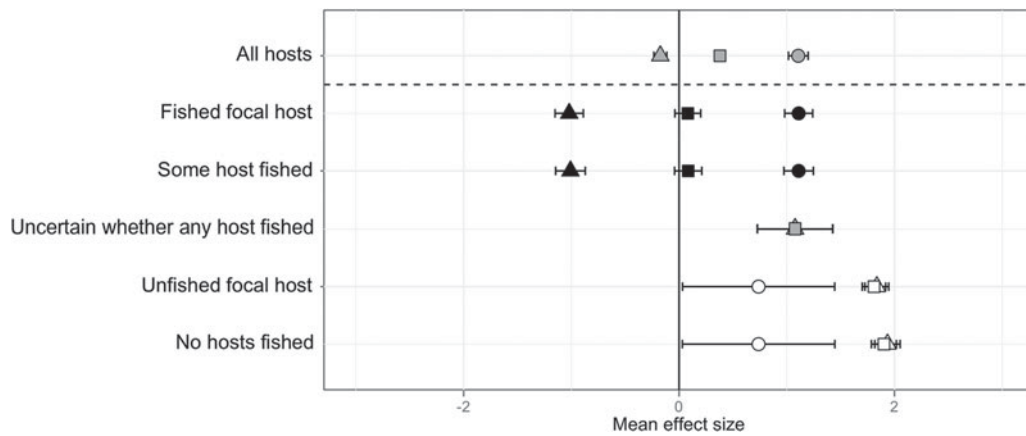We used a similar meta-analytic approach to summarize the effect of host body size on parasite

Fig. 1. Mean effect size and 95% confidence interval for the response of parasite abundance to fishing within groups: parasites across all hosts, parasites with fished focal hosts, parasites with some host in the life cycle fished, parasites for which it is uncertain whether any host is fished, parasites with unfished focal hosts, and parasites with no fished hosts in the life cycle. Triangles indicate complex life cycle parasites, circles indicate directly transmitted parasites, and squares indicate all parasites for a given group. Positive values indicate groups of host–parasite combinations for which more parasites were found in heavily fished areas than in lightly fished or unfished areas and negative values indicate groups of host–parasite combinations for which more parasites were found in lightly fished or unfished areas relative to heavily fished areas. Colour reinforces values on the y-axis: black represents fished hosts, white represents unfished hosts, and grey represents all hosts or hosts for which fishing status is uncertain.

abundance across host–parasite combinations. For effect size estimates, we used regression coefficients for the effect of host body size on abundance of each host–parasite combination, extracted from the Poisson regressions described above. We calculated a cumulative effect size across all host–parasite combinations, using a fixed-effects model weighted by the inverse of the variance for each effect size. We also tallied the number of host–parasite combinations with significant negative, significant positive and no relationship between host body size and parasite abundance.

RESULTS

Parasite diversity (Prediction 1)

Results for parasite diversity were consistent with *Prediction 1*. There was a marginally significant negative effect of fishing on overall parasite diversity when results were analysed by study (mean effect $\pm$ s.e. $= -0 \cdot 29 \pm 0 \cdot 10$, $t = -2 \cdot 91$, df $= 4$, $P = 0 \cdot 0436$). There was a similar, but strongly significant negative effect of fishing on overall parasite diversity when results were analysed by host species (mean effect $\pm$ s.e. $= -0 \cdot 32 \pm 0 \cdot 06$, $t = -5 \cdot 64$, df $= 9$, $P = 0 \cdot 0003$; see Appendix 1 for details).

Parasite abundance (Predictions 2–4)

Quantitative meta-analysis demonstrated substantial heterogeneity in the response of abundance to fishing among host–parasite combinations. The cumulative effect size across all 74 host–parasite combinations was significantly greater than zero

(mean $\pm$ s.e. $= 0 \cdot 379 \pm 0 \cdot 023$, $z = 16 \cdot 4$, df $= 73$, $P < 0 \cdot 0001$), suggesting that the overall effect was toward higher parasite abundance in heavily fished relative to lightly fished/unfished areas. However, significant heterogeneity in the cumulative effect size ($Q_T = 3790$, df $= 73$, $P < 0 \cdot 0001$) indicated substantial differences in response among host–parasite combinations.

In the first meta-analysis model (Model A), which tested the effect of whether the focal host itself is the target of fishing pressure, host fishing status was a significant moderator, indicating that parasites with unfished focal hosts are more likely to respond to fishing with increases in abundance than are parasites of fished focal hosts (Fig. 1; Appendix 2; $Q_M = 801$, df $= 1$, $P < 0 \cdot 0001$). Parasites with unfished focal hosts had a significant positive response to fishing (mean effect size $= +1 \cdot 81$, s.e. $= 0 \cdot 06$, $n = 30$, $P < 0 \cdot 0001$), consistent with *Prediction 3*. Contrary to *Prediction 2*, parasites with fished focal hosts did not have a significant response to fishing (mean effect size $= +0 \cdot 08$, s.e. $= 0 \cdot 06$, $n = 44$, $P = 0 \cdot 18$).

Results from the second meta-analysis model (Model B) indicated that parasites with no fished hosts in the life cycle were more likely to respond positively to fishing with increases in abundance than were parasites with at least one fished host in the life cycle, while parasites with an unknown number of fished hosts had an intermediate response (Fig. 1; Appendix 2; $Q_M = 814$, df $= 2$, $P < 0 \cdot 0001$). Parasites with no fished hosts in the life cycle had a significant positive response to fishing (mean effect size $= +1 \cdot 90$, s.e. $= 0 \cdot 06$, $n = 11$, $P < 0 \cdot 0001$), consistent with *Prediction 3*. Parasites for which we could not determine whether there were fished hosts in the

life cycle also had a significant positive response to fishing (mean effect size = +1·08, s.e. = 0·18, $n = 9$, $P < 0.0001$). Contrary to *Prediction 2*, parasites with at least one fished host in the life cycle did not have a significant response to fishing (mean effect size = +0·08, s.e. = 0·06, $n = 54$, $P = 0.19$).

The third meta-analysis model (Model C) demonstrated that complex life cycle parasites were more likely to decline in response to fishing pressure than were directly transmitted parasites, consistent with *Prediction 4.1* (Fig. 1; Appendix 2; $Q_M = 756$, df = 1, $P < 0.0001$). Complex life cycle parasites had a significant negative response to fishing (mean effect size = −0·174, s.e. = 0·031, $n = 67$, $P < 0.0001$), while directly transmitted parasites had a significant positive response to fishing (mean effect size = +1·11, s.e. = 0·05, $n = 42$, $P < 0.0001$).

The fourth meta-analysis model (Model D) tested the effect of parasite life stage–host fishing status group, and found significant heterogeneity among groups (Fig. 1; Appendix 2; $Q_M = 2570$, df = 4, $P < 0.0001$). Consistent with *Prediction 4.2*, complex life cycle parasites with at least one fished host responded negatively to fishing (mean effect size = −1·01, s.e. = 0·07, $n = 48$, $P < 0.0001$), while complex life cycle parasites with no fished hosts responded positively (mean effect size = +1·94, s.e. = 0·06, $n = 12$, $P < 0.0001$). These responses were significantly different from one another (mean effect size = −2·94, $P < 0.0001$). Contrary to *Prediction 4.3*, both directly transmitted parasites with fished (mean effect size = +1·11, s.e. = 0·07, $n = 35$, $P < 0.0001$) and unfished (mean effect size = +0·738, s.e. = 0·361, $n = 7$, $P = 0.0410$) hosts tended to increase in abundance in response to fishing and there was no significant difference between their responses (mean effect size = −0·372, $P = 0.30$).

Host body size

Across all 74 host–parasite combinations, 17 had a significant positive relationship between host body size and parasite abundance, 8 had a significant negative relationship, and 49 had no significant relationship. According to quantitative meta-analysis, the cumulative effect size across all 74 host–parasite combinations was significantly greater than zero (mean ± s.e. = +0·002 ± 0·0001, $z = 17·81$, df = 73, $P < 0.0001$), suggesting that the overall effect was toward higher parasite abundance in large fish relative to small fish.

DISCUSSION

Overall, parasites were more abundant in large than in small host individuals, consistent with previous work on host body size (Pacala and Dobson, 1988; Lo *et al*. 1998; Poulin, 2000). Because fishing tends

to reduce mean host body size (e.g. Bianchi, 2000; Jennings and Blanchard, 2004), areas protected from fishing often contain larger individuals than do those that are heavily fished (Lester *et al.* 2009). Our other analyses controlled for effects of host body size, and therefore, the effects we report below are additive to the effects of fishing on host size. Although responses of parasite abundance to fishing pressure varied dramatically, we were able to explain some of this variation in ways more or less consistent with most of our predictions.

Hypothesis 1: *Fishing reduces the diversity of parasites in an ecosystem because it simplifies host communities and this disrupts parasite transmission*

Our meta-analysis demonstrated a negative effect of fishing on parasite species diversity, consistent with *Hypothesis 1*. We would expect this effect if fishing had a strongly negative effect on the abundance of some subset of parasite species, to the extent that these parasites are driven to a level of rarity where they are not sampled by observers. What are the consequences of this effect? The contribution of parasite diversity to aquatic ecosystem function remains relatively unexplored but, given the potentially general effect of fishing on parasite diversity, deserves further scientific attention.

Hypothesis 2: *Fishing reduces the abundance of parasites of fished hosts because lower host density reduces parasite transmission*

The quantitative meta-analysis revealed that fishing status of the host was influential in determining the response of parasites to fishing pressure: parasites of unfished hosts tended to have more positive responses to fishing pressure than did those of fished hosts. However, the response of parasites of fished hosts was equivocal with respect to *Prediction 2*: across all the host–parasite combinations compiled, there was no significant response of parasites whose focal hosts were fished, or parasites with at least one fished host in the life cycle.

A large proportion of the host–parasite combinations we compiled (66 of 74, or 89%) showed no significant response to fishing pressure, according to the authors' original analyses (see Appendix 1). Quantitative meta-analysis allowed us to leverage both significant and non-significant host–parasite combinations and pool them across studies to gain statistical power to detect an effect, but the lack of a response to fishing among parasites of fished hosts remained. There are potential explanations for this pattern. It is possible that most studies lack the power to detect differences between heavily fished and lightly fished/unfished areas. We find this explanation probable, but we do not believe that it

alone can explain the large number of parasites that have no significant response to fishing pressure, because across the studies we included in our meta-analysis, minimum sample sizes were relatively large, always exceeding 25 individuals per heavily fished or lightly fished/unfished area. This level of replication should provide adequate statistical power to detect large differences in parasite abundance between areas. This suggests that parasites are somehow resilient to fishing impacts. One possible source of resilience lies with the social behaviour of hosts. Parasite transmission is based on local host density, and schooling and other aggregating behaviours can maintain contact rates between infectious and susceptible hosts even as host abundance declines. There are few examples of this, but replicated laboratory experiments with guppies show that social behaviour, not host density, drives transmission of monogenean parasites (Johnson *et al*. 2011). There may be other reasons that parasites persist at low host density. Perhaps most parasite species have experienced reductions in host density through evolutionary time, and possess adaptations and plasticity to compensate for these reductions. In addition to parasite resilience, it might be the case that the community-level effects of fishing can counterbalance one another: for example, fishing might reduce the density of a primary host, but if that host's competitor is an alternative host for a given parasite, release of the competitor might compensate for loss of the primary host. However, when we disaggregated parasite species into life history groups, we observed that this resilience to fishing holds only for directly transmitted parasites: complex life cycle parasites tended to decline in presence of fishing (see *Hypothesis 4*, below).

Hypothesis 3: *Fishing can increase the abundance of parasites of unfished hosts if those hosts indirectly benefit from the fishing of their competitors or predators*

There was a strong and consistent increase in the abundance of parasites of unfished hosts in response to fishing, consistent with *Prediction 3*. This was expected because parasite transmission is linked to host density (e.g. Arneberg *et al*. 1998; McCallum *et al*. 2005), and because fishing should tend to increase the density of unfished hosts, which stand to benefit from compensatory increases arising from the loss of their fished competitors and predators (e.g. Myers *et al*. 2007; Baum and Worm, 2009; Casini *et al*. 2009). This finding has important implications for how parasite assemblages are expected to differ between fished and unfished environments. These data suggest that a fished environment should contain more parasites of the low trophic-level, unfished hosts experiencing compensatory increases in abundance. What these compositional changes will mean

at a community or ecosystem level will likely depend upon the identities and traits of the parasites involved.

We note that it is exceptionally difficult to predict indirect effects in complex ecosystems. A good example is the contrast between the results of Lafferty (2004) and Sonnenholzner *et al*. (2011). Both studies address how parasites of unfished sea urchins respond to the fishing of sea urchin predators. In both cases, sea urchin abundance increased in response to the release from predation pressure produced by fishing. As expected, bacterial epidemics among sea urchins increased in response to this host release (Lafferty, 2004). But eulimid gastropod parasites of urchins decreased in abundance, because these were preyed on by small crabs that benefited indirectly from fishing (Sonnenholzner *et al*. 2011).

Hypothesis 4: *Life-cycle complexity can alter the outcome of the above hypotheses*

We hypothesized that complex life cycle parasites would be more likely to decline in the presence of fishing than would directly transmitted parasites (*Prediction 4.1*), and the data strongly supported this expectation. Complex life cycle parasites had a significant negative response to fishing, while directly transmitted parasites had a significant positive response. We expected this pattern because complex life cycle parasites tend to use the large, high trophic-level hosts most vulnerable to fishing pressure, and because they require multiple hosts in the life cycle, increasing the probability that some hosts will be fished. These data therefore suggest that, in addition to containing more parasites of the low trophic-level, unfished hosts experiencing compensatory increases in abundance, fished environments are also likely to contain fewer complex life cycle parasites.

The data were also consistent with our prediction that, among complex life cycle parasites, those with at least one fished host should decline in abundance, while those with no fished hosts should increase (*Prediction 4.2*). In addition to their high trophic-level definitive hosts, complex life cycle parasites also pass through low trophic-level intermediate hosts. These hosts can range from planktonic crustaceans (first intermediate hosts for cestodes, nematodes and acanthocephalans) to benthic gastropods (first intermediate hosts for trematodes) to fish or benthic macro-invertebrates (second intermediate or paratenic hosts for trematodes, cestodes, nematodes and acanthocephalans). Some of these hosts, especially the planktonic crustaceans, should be relatively insensitive to fishing impacts; although the abundance of zooplankton can be affected by trophic cascades in cases of extreme overfishing (e.g.

Frank *et al*. 2005), bottom-up effects like oceanic productivity are usually more influential in determining the abundance of these species (Leichter *et al*. 1998; Hamner *et al*. 2007). In contrast, other intermediate hosts, particularly benthic snails, can be prey of fished species and therefore stand to benefit from fishing impacts. For example, on Kenyan coral reefs, fishing causes compensatory increases in the abundance of benthic snails (McClanahan, 1989). This might benefit the parasites that use these snails as intermediate hosts (mostly trematodes), particularly if their definitive hosts are not fished (Wood *et al*. in press). These data therefore suggest that, among complex life cycle parasites, those with fished hosts are likely to be less common in fished environments, while those with unfished hosts might exhibit increases in response to fishing.

Contrary to our expectations, directly transmitted parasites of fished and unfished hosts did not differ in their response to fishing pressure (*Prediction 4.3*). The overall response of directly transmitted parasites to fishing was significantly positive for both groups. Why might directly transmitted parasites increase in abundance in response to fishing pressure, regardless of the fishing status of their host? It is possible that most directly transmitted parasites have a sufficiently broad host range that they are able to capitalize on fishing-driven increases in some host other than the focal host, even when the focal host is fished. Or, as above, directly transmitted parasites might be at least insensitive to decreases in host density due to social behaviours of their hosts. These results make clear that an increase in the abundance of directly transmitted parasites is a possible outcome of increasing fishing pressure.

Together, these results are consistent with a forthcoming, comprehensive study of the differences in parasite assemblages between fished and unfished coral islands of the central equatorial Pacific (Wood *et al*. in press). In agreement with the completely independent results presented here, Wood *et al*. documented lower parasite diversity, lower abundance of complex life cycle parasites, and higher abundance of directly transmitted parasites on fished relative to unfished atolls. However, their work also found that directly transmitted parasites were likely to follow the trajectory of their hosts, including exhibiting declines when hosts decline in response to fishing. The broad agreement of these results suggests that some generality is beginning to emerge in our understanding of how fishing can affect aquatic parasites.

In interpreting these results, it is important to bear in mind the potential for non-independence among data points taken from the same study or arising from phylogenetic relationships among hosts. Under typical circumstances, we would have controlled for this potential non-independence by including random effects of study identity and host phylogeny in meta-analytic models. However, most of the studies included in our analysis report results for only one host species, with the result that very few of these studies contain the full range of potential causal variables (e.g. host fishing status). The inclusion of study or host taxa as random effects would obscure most of the variation we would like to account for, because that variation exists more among studies than it does within studies. To be able to test our hypotheses, we therefore had to make the simplifying assumption of independence among data points taken from the same study and phylogenetically similar hosts. We recognize that there probably exists heterogeneity among included studies due to intrinsic differences in the way that the studies were carried out, and that some proportion of variation is attributable to phylogenetic relatedness of hosts. This is an alternative hypothesis that may explain the patterns we report here. We encourage future researchers considering an update to our analysis to include random effects to control for study identity and host phylogeny when data are sufficiently abundant to allow this. We also encourage more studies that explicitly contrast the response of parasites with fished and unfished hosts, to further disentangle the effects of fishing on parasite assemblages.

WHY DOES FISHING-DRIVEN CHANGE IN PARASITE ASSEMBLAGES MATTER?

Our meta-analysis suggests that parasite assemblages will experience several predictable compositional changes as fishing proceeds, including declines in parasite diversity, increases in the abundance of parasites of low trophic-level, unfished hosts, decreases in the abundance of complex life cycle parasites (such as cestodes), and increases in the abundance of directly transmitted parasites. What do these changes mean for aquatic ecosystem function?

Parasites that increase in fished areas might fill the void left behind when fisheries reduce the abundance of top predators. For instance, one study found that bacterial epidemics in sea urchins were higher in fished areas and that this partly compensated for the missing regulatory effect of fished spiny lobsters on sea urchin populations (Behrens and Lafferty, 2004; Lafferty, 2004). Redundancies such as this are important for buffering how ecosystems respond to change. In other words, the presence of parasites can help increase the robustness of the ecosystem to fishing by regulating non-fished species that might otherwise increase strongly in abundance. On the other hand, fishing-driven increases in directly transmitted parasites could result in greater disease burdens in an increasingly fished ocean (e.g. Harvell *et al*. 2004).

For the complex life cycle parasites that decline with fishing, there are potential effects on non-fished

hosts as well as entire communities. For instance, fishing of sharks could lead to the reduction of larval cestodes in prey species, providing to those prey species a release from both predation and parasitism. As another example of the potential ecological implications of loss of complex life cycle parasites, consider the fact that many of these parasites behaviourally manipulate their hosts to facilitate transmission to the next host in the life cycle, usually by predation on the intermediate host (Moore, 2002). Because complex life cycle parasites increase the susceptibility of many prey individuals to predation, the loss of complex life cycle parasites could conceivably result in an overall weakening of predator–prey interactions.

These are but a few examples of the potential knock-on effects of fishing-driven change in parasite assemblages. Our understanding of parasites' ecological influence is in its infancy, but mounting evidence suggests that parasites are important players in some ecosystems (Gomez *et al*. 2012). In certain circumstances, parasites 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 behaviourally manipulating (e.g. Lafferty and Morris, 1996; Sato *et al*. 2011) or killing (Suttle, 2005) their hosts. If parasites are influential in a particular ecosystem, then we should expect changes in their diversity, abundance and species composition to have reverberating effects in that ecosystem. The nature and generalizability of these effects remain to be quantified, and these interesting questions should be the focus of further research in ecological parasitology.

CONCLUSIONS

Our meta-analysis is the most comprehensive study to date of the effect of fishing on aquatic parasite assemblages. The results indicate that fishing has negative effects on parasite diversity and the abundance of complex life cycle parasites, and positive effects on the abundance of parasites with unfished hosts and of directly transmitted parasites. Overall, our results show that change in parasite assemblages in response to mounting fishing pressure will be complex, with some parasite groups increasing and others decreasing. Given what we know of parasites' ecological role, these compositional changes are likely to affect marine ecosystem function and services, but further research is needed to identify these effects.

SUPPLEMENTARY MATERIAL

To view supplementary material for this article, please visit http://dx.doi.org/S003118201400002X.

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