

Productivity and fishing pressure drive variability in fish parasite assemblages of the Line Islands, equatorial Pacific

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Abstract. Variability in primary productivity and fishing pressure can shape the abundance, species composition, and diversity of marine life. Though parasites comprise nearly half of marine species, their responses to these important forces remain little explored. We quantified parasite assemblages at two spatial scales, across a gradient in productivity and fishing pressure that spans six coral islands of the Line Islands archipelago and within the largest Line Island, Kiritimati, which experiences a west-to-east gradient in fishing pressure and upwelling-driven productivity. In the across-islands data set, we found that increasing productivity was correlated with increased parasite abundance overall, but that the effects of productivity differed among parasite groups. Trophically transmitted parasites increased in abundance with increasing productivity, but directly transmitted parasites did not exhibit significant changes. This probably arises because productivity has stronger effects on the abundance of the planktonic crustaceans and herbivorous snails that serve as the intermediate hosts of trophically transmitted parasites than on the higher-trophic level fishes that are the sole hosts of directly transmitted parasites. We also found that specialist parasites increased in response to increasing productivity, while generalists did not, possibly because specialist parasites tend to be more strongly limited by host availability than are generalist parasites. After the effect of productivity was controlled for, fishing was correlated with decreases in the abundance of trophically transmitted parasites, while directly transmitted parasites appeared to track host density; we observed increases in the abundance of parasites using hosts that experienced fishing-driven compensatory increases in abundance. The within-island data set confirmed these patterns for the combined effects of productivity and fishing on parasite abundance, suggesting that our conclusions are robust across a span of spatial scales. Overall, these results indicate that there are strong and variable effects of anthropogenic and natural drivers on parasite abundance and taxonomic richness. These effects are likely to be mediated by parasite traits, particularly by parasite transmission strategies.

Key words: chlorophyll a concentration; directly transmitted parasites; fishing pressure; host specificity; human disturbance; Line Islands archipelago; marine parasites; primary productivity; trophically transmitted parasites; upwelling.

INTRODUCTION

In ocean ecosystems, spatial and temporal variability in primary productivity is a dominant structuring force (Frank et al. 2007). Increasing nutrient concentrations increase the abundance of phytoplankton and echo to higher trophic levels, affecting zooplankton (e.g., Verheyen 2000), planktivorous fishes (e.g., Chavez et al.

2003), and predators, including seabirds (e.g., Ballance et al. 1997), turtles (e.g., Saba et al. 2008), and pelagic teleosts and sharks (e.g., Block et al. 2011). Natural and anthropogenic top-down processes, including predation and fishing, can combine and interact with bottom-up control to shape populations and communities (e.g., Hunt and McKinnell 2006, Baum and Worm 2009). Despite our advanced understanding of the influence of bottom-up and top-down forces on free-living marine species, their influence on marine parasites remains poorly understood (Marcogliese 2001).

This gap in our understanding elicits an important question; does the response to productivity of marine parasites match the response of free-living marine

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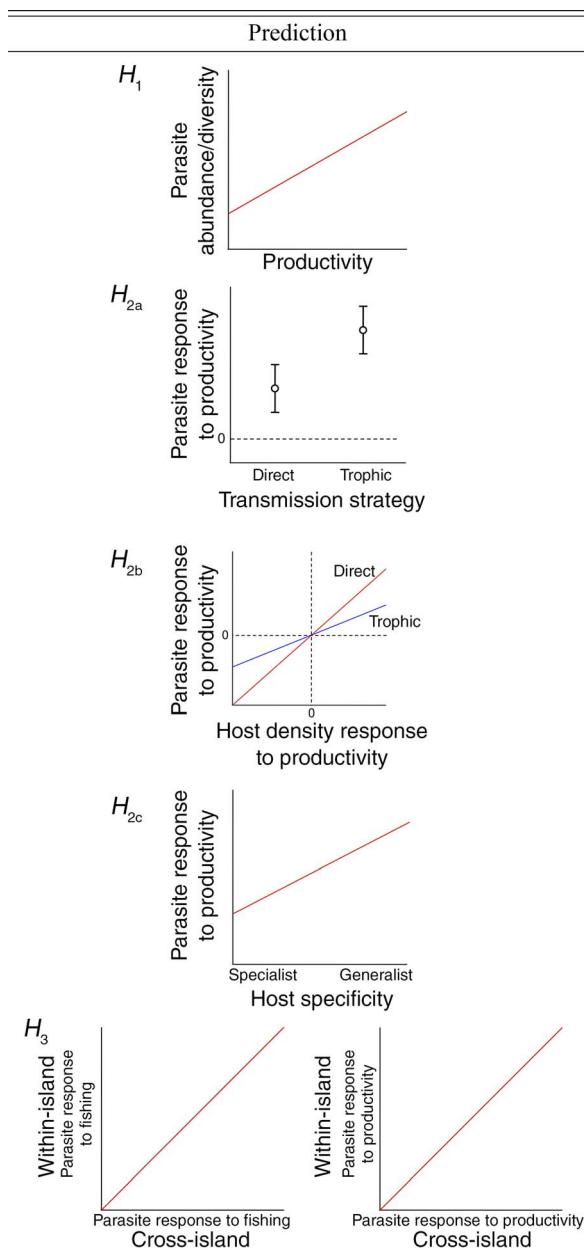
TABLE 1. Research questions (*Q*) and hypotheses (*H*) for the across-islands and within-island data sets, and a brief summary of the outcome for each hypothesis.

Data set and question	Hypothesis	Outcome
Across islands		
<i>Q</i> ₁ : What is the net effect of variability in primary productivity on parasite abundance and diversity?	<i>H</i> ₁ : Positive parasite–productivity relationship, wherein, if marine parasites follow patterns established for aquatic parasites across anthropogenic eutrophication gradients (e.g., Lafferty 1997) and, for freshwater parasites across natural productivity gradients (e.g., Baldwin 2000, Goater et al. 2005), then parasite abundance and diversity should increase with increasing productivity.	Supported for abundance but not diversity
<i>Q</i> ₂ : What host and parasite attributes predict the magnitude and direction of the response of parasite abundance to productivity?	<i>H</i> _{2a} : Transmission strategy, wherein the positive parasite–productivity relationship should be stronger for trophically transmitted parasites than for directly transmitted parasites, because increasing productivity should increase the availability of intermediate hosts for trophically transmitted parasites (e.g., planktonic crustaceans, and herbivorous snails).	Supported
	<i>H</i> _{2b} : Host density response, wherein, although the effects of bottom-up forces such as productivity enrichment tend to attenuate with increasing trophic level (Gruner 2004), fishes can increase in density in response to increasing productivity (Chavez et al. 2003). If a host responds to an increase in productivity with an increase in density, transmission efficiency and, therefore, abundance of its parasites should increase (McCallum et al. 2005). This relationship should be strongest for directly transmitted parasites, because their abundance can be dependent upon the density of a single host species, and therefore may be highly sensitive to changes in the density of that host. In contrast, the abundance of trophically transmitted parasites is necessarily dependent upon the density of multiple host species, which may make them less dependent on the density of any one host species. Therefore, we anticipate that there should exist an overall positive relationship between host density response to productivity (the direction and magnitude of the relationship between host density and productivity; hereafter, “host density response”) and parasite response to productivity, and that this relationship should be strongest for directly transmitted parasites.	Not supported; predicted direction
	<i>H</i> _{2c} : Host specificity, wherein host generalists should be more responsive to increases in productivity than are host specialists, because generalist parasites can take advantage of productivity-driven increases in any host, whereas specialist parasites might increase or decrease in abundance, depending on the effects of productivity on the abundance of one or a few hosts (Zander and Reimer 2002, Johnson and Carpenter 2008, Johnson et al. 2010).	Not supported; response of specialists > response of generalists
Within and across islands		
<i>Q</i> ₃ : Are across-island patterns in the relationship of parasite abundance to productivity and fishing pressure reflected in the within-island data set?	<i>H</i> ₃ : Concordance between data sets, wherein across six Line Islands, fishing pressure affects the abundance and diversity of parasites. Directly transmitted parasites are significantly more abundant on fished than on unfished islands due to positive effects of fishing on the density of low-trophic level hosts, while the reverse is true for trophically transmitted parasites (Wood et al. 2014). We hypothesized that patterns of parasite abundance and diversity detected in the within-island analysis would be consistent with patterns of the across-islands analysis, both for the effect of fishing (Wood et al. 2014) and for the effect of productivity (<i>H</i> ₁).	Supported

species? Studies conducted across gradients of anthropogenic nutrient pollution suggest that this is the case. Several meta-analyses across marine, freshwater, and terrestrial parasites suggest a strong positive relationship between nutrient enrichment and parasite abundance (Lafferty 1997, McKenzie and Townsend 2007, Vidal-Martinez et al. 2009), although one meta-analysis fails to find this pattern (Blanar et al. 2009). Further, both parasite abundance and taxonomic richness are expected to decline at very high levels of eutrophication, when host density is reduced and physical conditions (e.g., hypoxia) make the eutrophied habitat inhospitable for

parasite transmissive stages (Galli et al. 1998, Zander and Reimer 2002; reviewed in Johnson and Carpenter 2008). While the natural range of variability in productivity is narrower than the range generated by anthropogenic nutrient enrichment (e.g., Brush 2001, Osterman et al. 2005), evidence from freshwater ecosystems indicates that the trend for parasite abundance to increase with increasing productivity holds within natural ranges of variability in productivity (Baldwin 2000, Goater et al. 2005). Though little direct evidence exists concerning the relationship between natural variability in primary productivity and marine

TABLE 1. Continued.



parasite abundance and taxonomic diversity, we expect that these relationships are also likely to be positive.

There are several hypothesized mechanisms for a positive relationship between primary productivity and parasite abundance. First, increasing productivity might increase the abundance of intermediate hosts: planktonic and benthic crustaceans for cestodes, nematodes, and acanthocephalans, and herbivorous snails for trematodes (e.g., Hanzelova 1992, Galli et al. 1998, Johnson et al. 2007). Primary productivity can also have positive effects on focal host density, and increases in host density might facilitate transmission by increasing

contact rates between susceptible and infected individuals or between susceptible individuals and parasite transmissive stages (hereafter, the response of focal host density to primary productivity is termed “host density response”; Lafferty and Holt 2003, McCallum et al. 2005). Finally, increasing productivity can increase subsidies to pathogens (e.g., as when pathogens take up additional nutrients directly; Bruno et al. 2003) or increase the amount of host resources available for sequestration by pathogens (e.g., Hall et al. 2009).

Productivity is not the only factor likely to influence parasite abundance in marine ecosystems; fishing may also be influential (Marcogliese 2002, Wood et al. 2010). Fishing pressure can drive declines in parasite taxonomic diversity and either increases or decreases in parasite abundance, depending on parasite traits (Wood and Lafferty 2014, Wood et al. 2014). Specifically, the abundance of trophically transmitted parasites (i.e., those parasites that are transmitted via predator-prey interactions at any point in their life cycle) tends to decline with increasing fishing pressure, because trophically transmitted parasites require multiple host species to complete their life cycles, and many of these are the top predators most sensitive to fishing impacts. In contrast, directly transmitted parasites tend to track their hosts, increasing in abundance if hosts experience compensatory increases in response to fishing, and decreasing if their hosts decline with fishing (Wood et al. in 2014). Fishing pressure is a spatially extensive impact on ocean ecosystems at the global scale (Halpern et al. 2008). Because fishing and productivity are likely both to affect parasite assemblages and to coincide spatially, we were interested in quantifying their joint effects.

We assessed the role of productivity and fishing pressure in shaping parasite abundance and taxonomic diversity by comparing parasite assemblages from two data sets of fish parasites collected from the Line Islands archipelago: across-islands, a data set of parasites from seven fish host species collected at three fished and three unfished coral islands situated within a natural, upwelling-driven primary productivity gradient; and within-island, a data set of parasites from five fish host species collected across gradients of fishing pressure and natural, upwelling-driven primary productivity at Kiritimati, one of the fished islands from the across-islands data set (Appendix A). Our goals were to account for the joint effects of fishing and of productivity in both data sets, to explore the strength of the productivity effects in both data sets, and to compare results for fishing in the across-islands data set (reported in Wood et al. 2014) with results for fishing in the within-island data set (reported in this paper). Using both data sets allowed us to assess the effects of productivity and fishing at different spatial scales, provided a comprehensive test of our hypotheses, and offered the opportunity to validate patterns uncovered in the across-islands data set using a fully independent data set. We posed research questions and tested several hypotheses for both the across-islands and

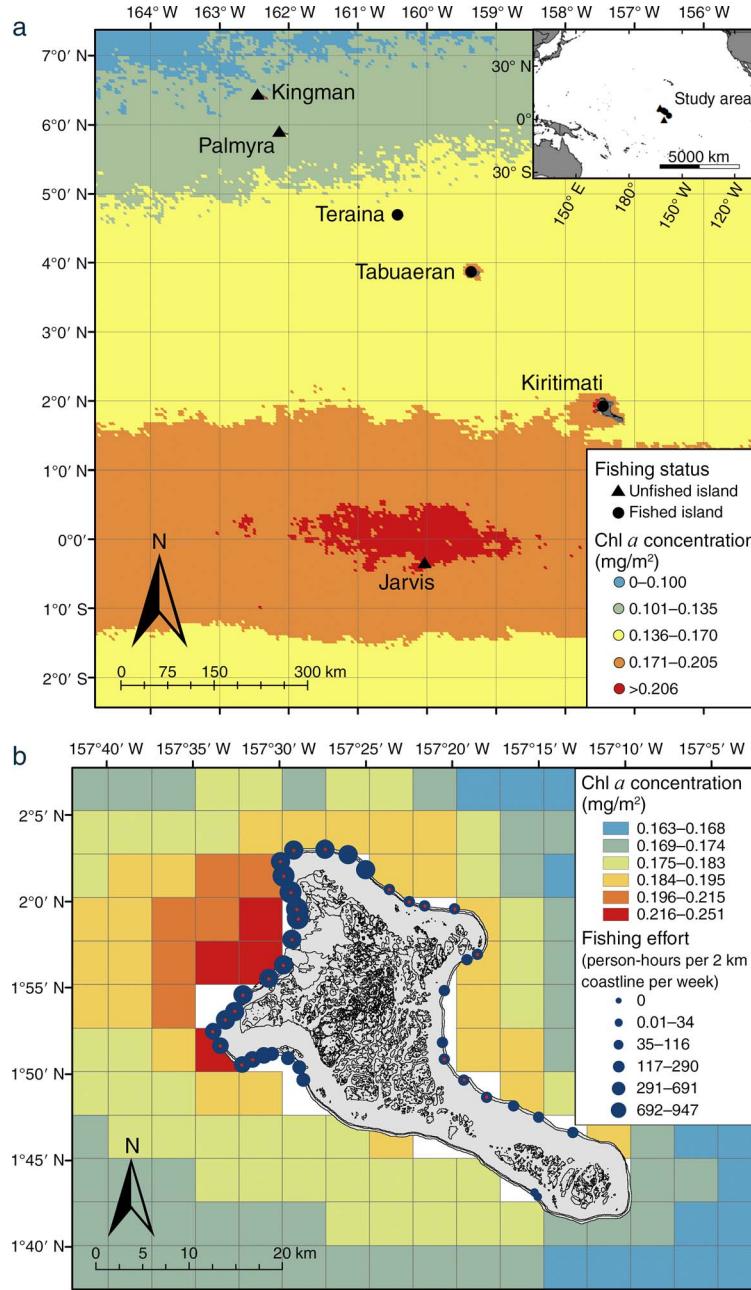
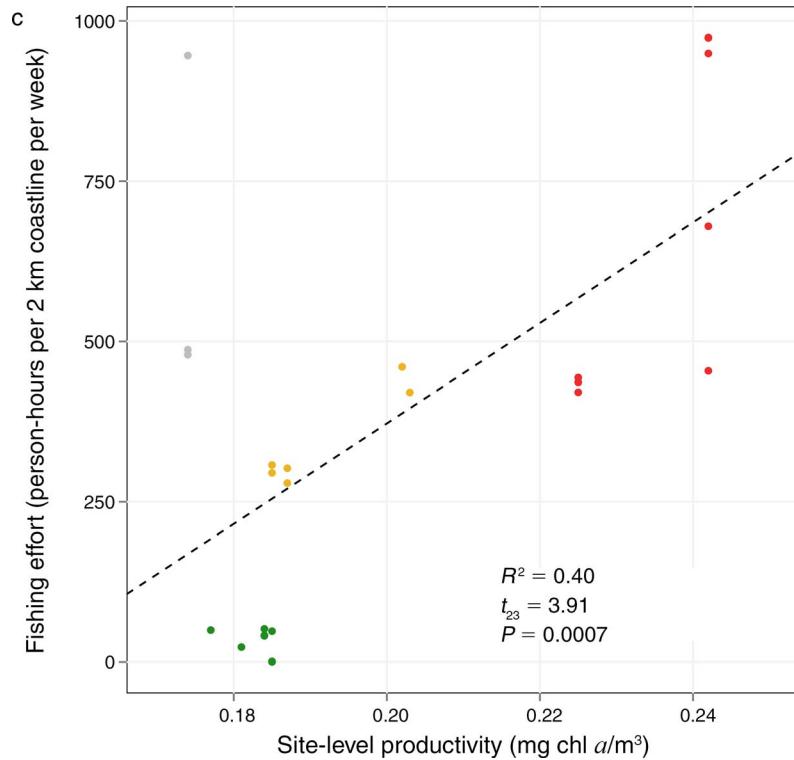


FIG. 1. (a) Study sites of the across-islands data set: three unfished islands (Kingman, Palmyra, and Jarvis) and three fished islands (Teraina, Tabuaeran, and Kiritimati) in the Line Islands archipelago. (b) Study sites of the within-island data set (Kiritimati Island), indicated with red dots. (c) Within-island study sites are categorized into three productivity–fishing effort site-groupings. Group 1 (green) is low fishing effort and productivity; group 2 (yellow) is intermediate fishing effort and productivity; and group 3 (red) is high fishing effort and productivity. Sites not included in the analysis are indicated in gray (see methodological details in Appendix C). Data points are jittered along the y -axis to allow visualization of overlapping points. The dashed line shows the regression of site-level productivity on effort hours.

within-island data sets. Questions, hypotheses, and outcomes are all shown in Table 1. We were specifically interested in potential differences between responses of trophically transmitted parasites (i.e., parasites with complex life cycles that pass through multiple life stages

and are transmitted through predator–prey interactions, such as trematodes, cestodes, nematodes, and acanthocephalans) vs. directly transmitted parasites (i.e., parasites that can be transmitted among conspecific hosts, such as crustaceans and monogeneans), and between



is exposed to both heavy fishing pressure and high levels of productivity (Walsh 2011). Due to the island's large size (388 km² in land area, ~150 km in perimeter), most fishing occurs in the vicinity of population centers on the western side of the atoll (Fig. 1b; DeMartini et al. 2008, Walsh 2011). This side of the atoll also experiences high-nutrient, low-temperature conditions, possibly due to prevailing east-to-west currents that drive island wake upwelling (Fig. 1b and c; Walsh 2011). To investigate the combined influence of fishing and productivity on parasite abundance and taxonomic diversity on Kiritimati, we included fishing and productivity as a single predictor in statistical models (see details in *Statistical analysis: parasite abundance*), and used inferences from the across-islands analysis to interpret patterns detected on Kiritimati. This conservative approach allowed us to avoid spurious conclusions about the relative influence of productivity and fishing that can arise from interpreting unstable parameter values generated by collinear statistical analyses, while still gaining insight into how these two factors shape parasite assemblages. Using both the across-islands and within-island data sets also allowed us to assess the effects of productivity and fishing at different spatial scales, providing a comprehensive test of our hypotheses.

Host sampling

For the across-islands analysis, sampling was conducted at the six islands (Fig. 1a; Appendices C and D) by scuba divers deployed from a research vessel between October and November 2010. We sampled 945 individual fish across seven species of reef fishes, aiming for 25 fish of each species from each of the six islands (Appendix E; Wood et al. 2014). Fish counts were also conducted at each island to characterize the fish assemblage and estimate the abundance, biomass, and size-structure of all coral reef fish species >3 cm total length. For the within-island analysis, sampling was conducted at 25 sites around Kiritimati Island (Fig. 1b) in May and June 2010 by scuba divers deployed from small boats or from shore. We sampled 894 individuals across five species of reef fishes, aiming for >150 fish of each species, distributed across the west-to-east productivity–fishing gradient (Appendix F).

Parasite sampling

For each fish collected, we performed a comprehensive examination designed to detect most metazoan parasites. We adapted the dissection protocol to the morphology of each host species (see Wood et al. 2014). Although several technicians prepared fish for examination (e.g., removing viscera and gills), only one observer (C. L. Wood) counted parasites for all 1839 fish dissected (with the exception of some intestinal parasites, where Wood trained technicians to perform counts). For each fish, we quantified abundance (number of individual parasites, including zeroes; Bush et al. 1997) for every parasite species.

Information on the life cycle and natural history of each parasite was surveyed from the literature and collated (Appendix G). Each parasite was classified according to its broad taxonomic group (subphylum Crustacea, class Monogenea, class Trematoda, phylum Nematoda, and class Cestoda), transmission strategy (direct vs. trophic transmission), 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 Northern Line Islands, this approach is a strong approximation for understanding how parasite traits might mediate the direction of parasites' response to anthropogenic environmental change.

Oceanography

We used chlorophyll *a* (chl *a*) concentration as a proxy for primary productivity and mapped remotely sensed chl *a* data to characterize variability in productivity among islands for the across-islands analysis (Appendix C and H) and among sites (Fig. 1b; Appendix I) for the within-island analysis. Values were extracted from the Ocean Color Radiometry Online Visualization and Analysis Monthly Data tool in NASA Giovanni's Ocean Portal.¹⁰

Statistical analysis: parasite abundance

For each host–parasite combination in the across-islands data set, we used a generalized linear mixed effects model (GLMM) with negative binomial error structure and correction for zero-inflation to assess the response of parasite abundance to productivity and fishing pressure, with productivity (measured as mean chl *a* for each island) and fishing status (fished vs. unfished) as fixed factors and island (Jarvis, Kingman, Palmyra, Teraina, Tabuaeran, or Kiritimati) as a random factor to account for the nested observations of parasite abundance for the numerous individual fish from each island. (It should be noted that the random factor of island has the same levels as the fixed factor of

¹⁰ <http://disc.sci.gsfc.nasa.gov/giovanni>

productivity. Using both of these terms would be unacceptable due to collinearity, were island included as a fixed factor, but is not an issue when island is included as a random factor [Henderson 1982]). Two additional covariates with the potential to influence parasite abundance were also included: body size of the host (measured as total length) and depth of collection of the host. Although results for dead nematodes are presented in plots and in Appendix M of Wood et al. (2014), dead nematodes were not included in any subsequent analyses. We present results for an alternate formulation of the statistical analysis (one in which host density is included as a fixed factor in GLMMs) in Appendix N.

Across the 25 collection sites in the within-island data set, fishing pressure and productivity were correlated and, therefore, represented collinear predictors of parasite abundance ($R^2 = 0.400$, $t_{23} = 3.91$, $P = 0.0007$; Fig. 1c; fishing effort [person-hours] derived from household survey data by Walsh [2011]). To circumvent this constraint, we collapsed the collinear predictors into a single predictor in all statistical models. Specifically, we retained the productivity variable, renamed it productivity–fishing gradient value, and interpreted the response of parasite abundance to this predictor as a joint function of productivity and fishing pressure (as recommended by Dormann et al. 2013). We then analyzed abundance for each host–parasite combination with a generalized linear model (GLM) with negative binomial error, zero-inflation, and including productivity–fishing gradient value as a predictor and host body size as a covariate. All of the aforementioned analyses were performed with the glmmadmb function in R (R 2.11.1 GUI 1.34; Fournier et al. 2012, R Core Team 2013, Skaug et al. 2013) and we applied the FDR (false discovery rate) correction for multiple comparisons to all P values within each suite of statistical tests (Benjamini and Hochberg 1995).

To investigate differences in the response to productivity among groups of parasite taxa detected in the across-islands data set, we performed meta-analyses. For effect size estimates, we used regression coefficients for the effect of productivity on abundance of each parasite, extracted from our modeling. We began by calculating a cumulative effect size of productivity across all host–parasite combinations, using a fixed-effects model weighted by the inverse of the variance for each effect size, to test hypothesis H_1 (Table 1). We tested our remaining hypotheses with several meta-analytic fixed-effects general linear models. Model 1 included the moderator higher order taxonomic grouping of the parasite, and was designed to test H_{2a} (Table 1). Model 2 included parasite transmission strategy (H_{2a} and H_{2b}), host specificity (H_{2c}), response of host density to productivity (standardized coefficient for the effect of productivity on host density from ANOVA models performed within host species; H_{2b}), and the

interaction between host density response and parasite transmission strategy (H_{2b}) as well as the interaction between host density response and host specificity (H_{2c} ; Table 1). All analyses were performed with the metafor package in R (Viechtbauer 2010, R Core Team 2013). This meta-analytic approach allowed us to gain power by pooling replication across parasite taxa within parasite groups, essentially, averaging across the idiosyncratic responses of individual taxa to get at the general relationship that characterizes larger groups of taxa sharing certain traits.

To investigate the degree to which results from the within-island analysis were consistent with results from the across-islands analysis (H_3), we compared effect sizes for each of the parasite higher-order taxonomic groupings between the two data sets (Table 1). We began by calculating mean effect sizes for the within-island data set using the same meta-analytic approach described in this section (models 3 and 4). To test for correspondence between the across-islands and within-island data sets, we ran a linear model predicting the z score for the effect of the Kiritimati productivity–fishing gradient on abundance of Crustacea, Monogenea, Trematoda, Cestoda, and Nematoda (from model 3) with two factors, z score for the effect of productivity on abundance of these parasite taxa from the across-islands analysis (from model 1) and z score for the effect of fishing on abundance of these parasite taxa from the across-islands analysis (from Wood et al. 2014). This analysis allowed us to circumvent the problem of collinearity of fishing and productivity in the within-island data set. Instead of attempting to disentangle the influence of fishing vs. productivity as predictors of parasite abundance, we quantified their joint effect on parasite abundance and then asked whether the response of parasites to the within-island productivity–fishing gradient was consistent with the patterns uncovered in the across-islands analysis.

Statistical analysis: parasite taxonomic diversity

We also tested for differences in parasite taxonomic diversity as a function of productivity. We used the non-parametric jackknife estimator to project parasite taxon richness at the saturation of the species accumulation curve (Zelmer and Esch 1999), calculated using the SPECIES package in R (Wang 2011, R Core Team 2013). This analysis was conducted for each host–island combination in the across-islands analysis, and for each host–site-grouping combination (Fig. 1c) in the within-island analysis.

For the across-islands analysis, we ran a mixed-effects general linear model with island-level productivity (chl a), fishing status (fished vs. unfished), and their interaction as fixed effects and island and host species as random effects, where replicates were jackknife-estimated parasite taxon richness for each host species (H_1 ; Table 1). We included the covariates collection

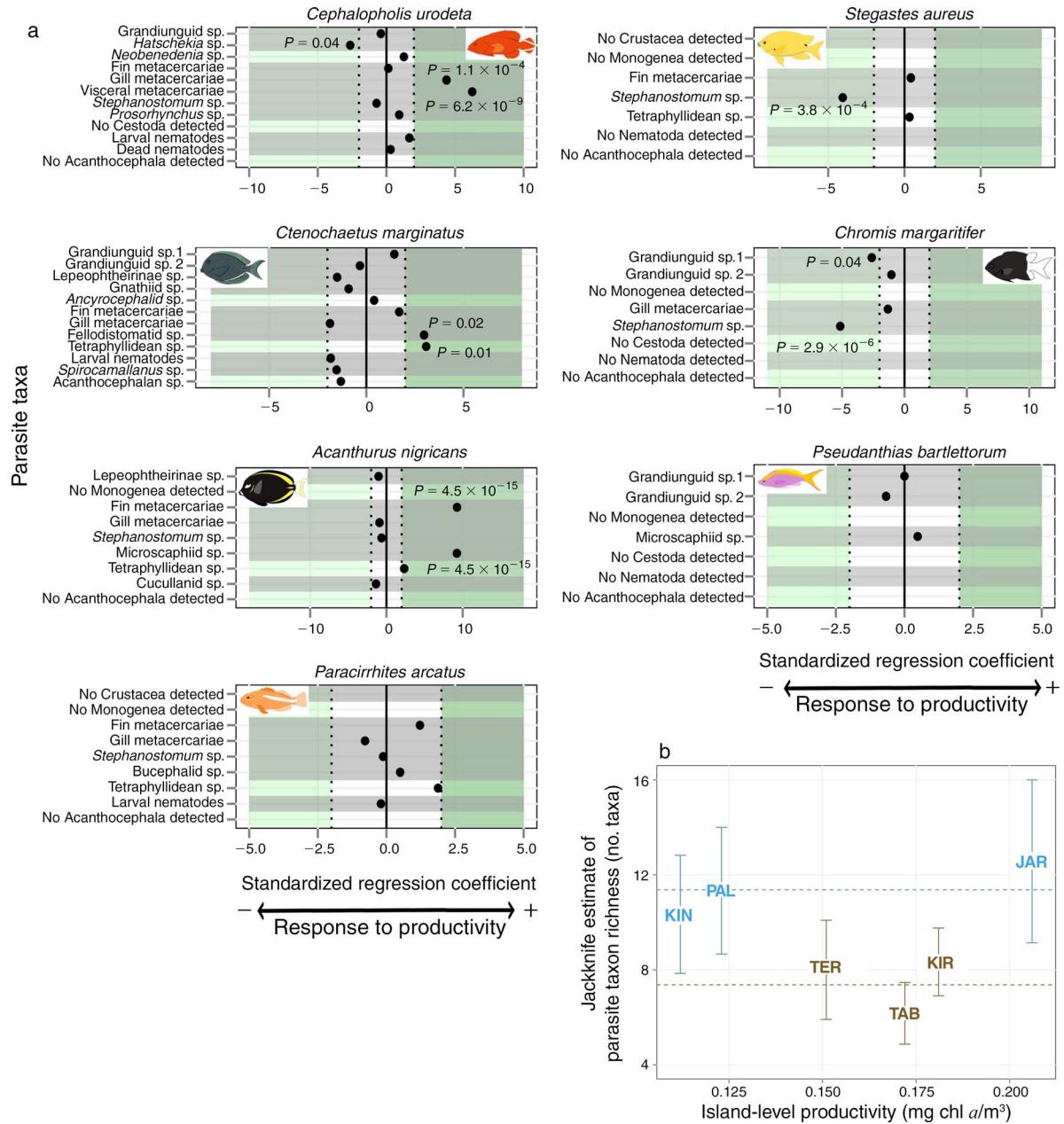


FIG. 2. (a) Standardized partial regression coefficients for the effect of productivity on parasite abundance for each parasite taxon from the across-islands analysis. Values > 2 indicate host-parasite combinations for which parasite abundance had a significant positive association with productivity (dark bands), and values < -2 indicate a significant negative association with productivity (light bands). P values are FDR (false discovery rate)-corrected for multiple comparisons. See Appendix H for details of statistical models. (b) Mean jackknife estimates of parasite taxon richness and 95% confidence interval as a function of island-level chl a , from the across-islands analysis. Overall means for fished and unfished islands are presented as brown and blue dashed lines, respectively. Islands represented are Kingman (KIN), Palmyra (PAL), Teraina (TER), Tabuaeran (TAB), Kiritimati (KIR), and Jarvis (JAR). See Wood et al. (2014) for additional details of the fishing status-parasite taxon diversity relationship. (c) Standardized partial regression coefficients for the effect of the within-island productivity and fishing gradients on parasite abundance for each parasite taxon. See Appendix I for details of statistical models. (d) Jackknife estimates of parasite taxon diversity for each host in each productivity-fishing effort site-grouping for the within-island analysis. *Cephalopholis argus* (CEPARG), *Acanthurus nigricans* (ACANIG), *Paracirrhites arcatus* (PARARC), *Plectroglyphidodon dickii* (PLEDIC), and *Chromis margaritifer* (CHRMAR) are shown. Across the within-island data set, fishing pressure and productivity were correlated and represented collinear predictors of parasite abundance. For more information on the productivity and fishing scale, see Methods: Statistical analysis, parasite abundance. Sea life drawings are courtesy of Cynthia Clark.

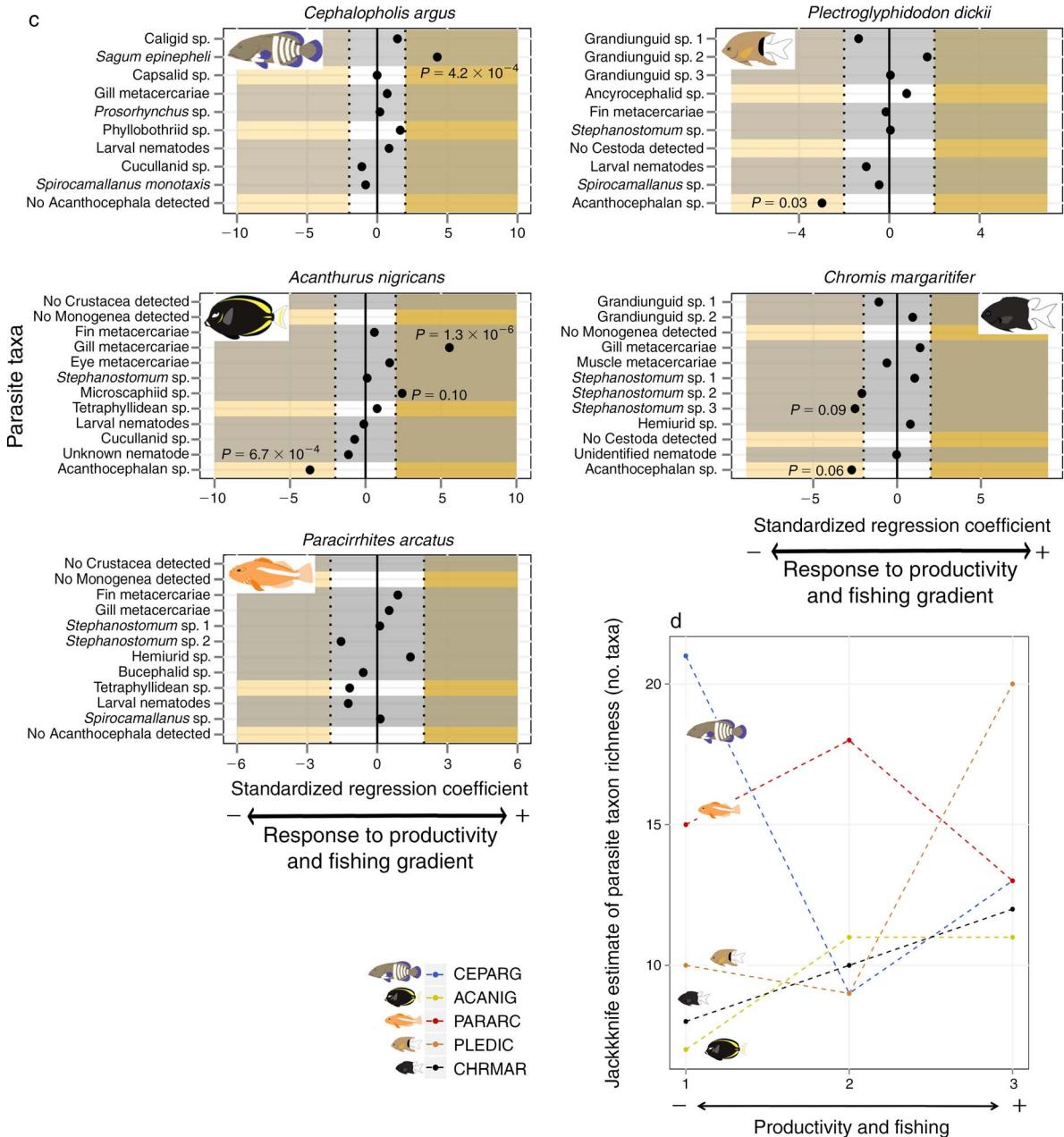


FIG. 2. Continued.

depth and host body size. To evaluate how parasite taxon richness varied among sites within Kiritimati Island, we split sites into three natural groupings in [chl *a*]–fishing pressure space (Fig. 1c). We assigned sites to groups of low, intermediate, and high productivity–fishing effort by considering their position along the regression line in Fig. 1c. We then ran mixed-effects general linear models with productivity–fishing effort site-grouping (Fig. 1c) as a fixed effect, host species as a random effect, and host body size as a covariate, where replicates were jackknife-estimated parasite taxon richness for each host–site-grouping combination (H_3 ; Table 1). Both of these analyses were conducted using the lmer function in R (Bates et al. 2013, R Core Team 2013), and P values were extracted with pvals.fnc (Baayen 2011).

RESULTS

In the across-islands data set, we found that increasing productivity was correlated with increased parasite abundance overall, but that the effects of productivity differed among parasite groups. Trophical-

ly transmitted parasites increased in abundance with increasing productivity, but directly transmitted parasites did not exhibit significant changes. We also found that specialist parasites increased in response to increasing productivity, while generalists did not. After the effect of productivity was controlled for, fishing was correlated with decreases in the abundance of trophically transmitted parasites, while directly transmitted parasites appeared to track host density. We observed increases in the abundance of parasites using hosts that experienced fishing-driven compensatory increases in abundance. The within-island data set confirmed these patterns for the combined effects of productivity and fishing on parasite abundance, suggesting that our conclusions are robust across a span of spatial resolutions.

Question 1: What is the net effect of variability in primary productivity on parasite abundance and taxonomic diversity?

Of the 45 abundant host-parasite combinations detected in the across-islands data set, six increased with increasing productivity, two decreased with increasing productivity, and 37 had no significant response to productivity (Fig. 2a; Appendix J). These results controlled for the influence of fishing, because they are based on regression coefficients from models containing terms for both productivity and fishing (results for fishing are detailed in Wood et al. 2014 and summarized under Question 3). The cumulative effect size across all combinations was significantly greater than zero (Fig. 3a; mean \pm SE = 9.59 ± 1.22 , df = 44, $P < 0.0001$), indicating that the overall effect was that parasite abundance increased with increasing productivity, consistent with H₁. However, heterogeneity in the total cumulative effect size ($Q_T = 287$, df = 44, $P < 0.0001$) indicated that host-parasite combinations differed significantly in their responses to productivity, and this was investigated through additional meta-analyses (see Question 2).

Jackknife richness was not related to the interaction between fishing status and productivity (Fig. 2b; $t_{29} = -0.189$, $P = 0.85$) or to the main effect of productivity ($t_{30} = 0.708$, $P = 0.48$), contrary to H₁, but richness was significantly higher on unfished than on fished islands (Fig. 2b; $t_{33} = 2.23$, $P = 0.0331$; reported in Wood et al. 2014). The covariates depth ($t_{31} = -0.990$, $P = 0.33$) and mean host body size ($t_{32} = 1.68$, $P = 0.1035$) were not significant predictors of jackknife richness and were therefore excluded from the final model.

Question 2: What host and parasite attributes predict the magnitude and direction of the response of parasite abundance to productivity?

We tested several hypotheses to examine the positive relationship between productivity and parasite abundance. Both meta-analytic model 1 (parasite taxonomic

grouping) and model 2 (parasite traits) contained significant moderators (Appendix K). In model 1, both trematodes and cestodes exhibited a significant positive response to productivity, while the response of the remainder of the parasites did not differ significantly from zero (Fig. 3b). In model 2, trophically transmitted parasites had a significantly more positive response to productivity than did directly transmitted parasites, consistent with H_{2a} (Fig. 3a; effect of transmission strategy[trophic]: estimate \pm SE = 59.2 ± 12.2 , $z = 4.86$, df = 39, $P < 0.0001$). The response of directly transmitted parasites to productivity did not differ significantly from zero, falsifying H_{2b} (Fig. 3a; estimate \pm SE = 6.24 ± 15.5 , $z = -0.401$, df = 39, $P = 0.68$). However, as predicted in H_{2b}, the response of parasite abundance to productivity was positively related to the response of their hosts to productivity for directly transmitted parasites and unrelated for trophically transmitted parasites (Fig. 3c; effect of [transmission strategy(trophic)]/[host density response interaction] is estimate \pm SE = -16.0 ± 5.05 , $z = -3.17$, df = 39, $P = 0.0015$). Specialist parasites exhibited a more positive response to increasing productivity than did generalist parasites (Fig. 3d; estimate \pm SE = -12.2 ± 3.65 , $z = -3.33$, df = 39, $P = 0.0009$), contradicting H_{2c}. This relationship held even after two outliers with effect sizes >200 were removed from the data set (Fig. 3d). Specialist parasites were less responsive to increases in the abundance of their focal hosts than were generalist parasites (estimate \pm SE = 2.97 ± 1.41 , $z = 2.12$, df = 39, $P = 0.0343$), also contradicting H_{2c}.

Question 3: Are across-island patterns in the relationship of parasite abundance to productivity and fishing pressure reflected in the within-island data set?

Of the 47 abundant host-parasite combinations detected in the within-island data set, two increased with increasing productivity–fishing gradient value, two decreased with increasing gradient value, and 43 had no significant response to gradient value; of the 43 without a significant response, two had marginally significant (corrected $P \leq 0.10$) negative responses and one had a marginally significant positive response (Fig. 2c; Appendix L). Jackknife parasite taxonomic richness was unrelated to the productivity–fishing effort site-grouping (Fig. 2d; $t_{12} = 0.715$, $P = 0.49$) or mean host body size ($t_{12} = 1.73$, $P = 0.11$). Meta-analysis revealed pattern in the response to productivity–fishing gradient value across host-parasite combinations (Appendix K). The cumulative effect size across all combinations was significantly greater than zero (Fig. 4a; mean \pm SE = 4.00 ± 1.50 , df = 46, $P < 0.0001$), indicating that the overall effect was for increasing parasite abundance with increasing gradient value. However, heterogeneity in the cumulative effect size ($Q_T = 123$, df = 46, $P < 0.0001$) indicated that host-parasite combinations differed significantly in their responses. Both meta-analytic

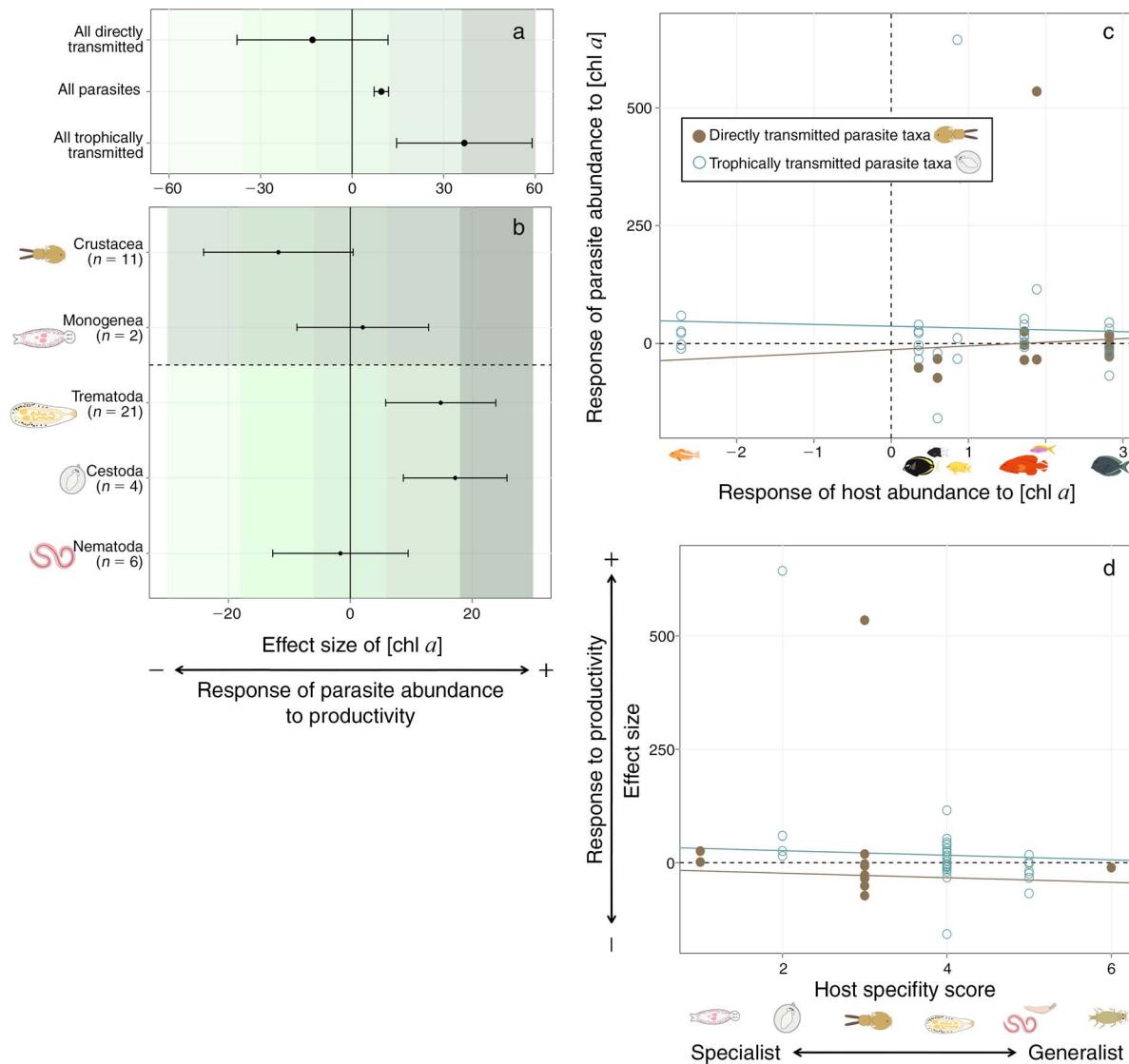


FIG. 3. Mean effect size and 95% confidence interval for the effect of productivity on across-island parasite abundances for (a) all parasites combined, all trophically transmitted parasites, and all directly transmitted parasites and (b) parasite higher-order taxonomic groupings. (c) Effect size for each parasite taxon (i.e., partial regression coefficient for the response to productivity, [chl a]) as a function of the host's response to fishing (standardized regression coefficient for the response of the host to productivity, [chl a]) from across-islands analysis. Fish images indicate the host's response to fishing for each fish species. Across the within-island data set, fishing pressure and productivity were correlated and represented collinear predictors of parasite abundance. (d) Effect size for each parasite taxon (i.e., partial regression coefficient for the response to productivity) as a function of the host specificity score (ranked 1–6 based on Brusca [1981], Sasal et al. [1998], and Jones et al. [2007], with 1 indicating high specificity) from across-islands analysis. Parasite images indicate the host specificity of each parasite taxon. See key in Fig. 3c. Sea life drawings are courtesy of Cynthia Clark.

model 3 (parasite taxonomic grouping) and model 4 (parasite traits) contained significant moderators (Appendix K). In model 3, crustaceans exhibited a significant positive response to productivity–fishing gradient value, acanthocephalans exhibited a negative response, and the response of the other parasites did not differ significantly from zero (Fig. 4b). In model 4, the response of trophically transmitted parasites to the productivity–fishing gradient value was significantly

more negative than that of directly transmitted parasites ($Q_M = 4.11$, $df = 1$, $P = 0.0426$). The response of directly transmitted parasites was significantly greater than zero and the response of trophically transmitted parasites was not significantly different from zero (Fig. 4a).

Responses in the within-island analysis (Fig. 4a and 4b) appeared to be consistent with the combined effects of fishing (Fig. 4c and 4d, from Wood et al. 2014) and productivity (Fig. 3a and 3b) inferred in the across-

islands analysis. In the across-islands data set, we found that directly transmitted parasites, including crustaceans and monogeneans, responded positively to fishing (Fig. 4c and 4d). We also found that trophically transmitted parasites, including nematodes, cestodes, and acanthocephalans, tended to respond negatively (Fig. 4c and 4d). Full details of the effect of fishing on parasite abundance and taxonomic richness are presented in Wood et al. (2014).

The regression comparing responses of parasites from the within-island data set to those from the across-islands data set revealed that both across-islands fishing (Fig. 5a; $t_2 = 6.40$, $P = 0.0236$) and across-islands productivity (Fig. 5b; $t_2 = 5.81$, $P = 0.0284$) were significant predictors of the within-island response to the productivity–fishing gradient. This indicates that results from the within-island analysis were consistent with those from the across-islands analysis, and the data therefore supported H_3 .

DISCUSSION

Question 1: What is the net effect of variability in primary productivity on parasite abundance and taxonomic diversity?

Our finding of a positive relationship between productivity and parasite abundance is consistent with H_1 and an extensive literature on anthropogenic eutrophication (Lafferty 1997, McKenzie and Townsend 2007, Johnson et al. 2010). This conclusion generates readily testable hypotheses regarding global marine parasite biogeography. For example, parasite abundance might be greater along the high-productivity eastern margins of the Pacific and Atlantic Oceans than along their low-productivity western margins. Parasite abundance should also be greater in high-productivity temperate waters than in the low-productivity tropics, all else equal. Interestingly, we did not find a relationship between parasite taxon richness and productivity (Fig. 2b), perhaps because the examined productivity gradient did not span a large range of values (0.112–0.206 mg/m³; Appendix C). Alternately, oceanic productivity might not have strong effects on parasite taxonomic diversity; this interpretation is consistent with studies of parasite biogeography, which document increasing parasite taxon richness with declining latitude (Rohde 2002), despite the fact that oceanic productivity declines with declining latitude. Overall, our data suggest a positive relationship between productivity and parasite abundance but no relationship between productivity and parasite taxon richness. (See Appendix M for discussion of possible correlates of productivity.)

Question 2: What host and parasite attributes predict the magnitude and direction of the response of parasite abundance to productivity?

The positive effect of productivity on parasite abundance revealed in our data appears to be due to

productivity-driven increases in trophically transmitted parasites (supporting H_{2a}) and parasites with a high degree of host specificity (refuting H_{2c}). Directly transmitted and generalist parasites did not have strong responses to productivity, though there is evidence from the across-islands data set that directly transmitted parasites exhibited more positive responses to productivity where their hosts experienced productivity-driven increases in density (Fig. 3c). These patterns are inconsistent with predictions (Johnson and Carpenter 2008, Johnson et al. 2010) and data (Zander and Reimer 2002) from the literature on anthropogenic eutrophication, where ecologists have generally anticipated increases in directly transmitted and generalist parasites with increasing productivity. The patterns in our data are probably driven by several mechanisms.

One potential mechanism is the influence of intermediate hosts in facilitating productivity-mediated change in parasite abundance. This is suggested by the fact that, in our data set, trophically transmitted parasites increased in abundance with increasing productivity, while directly transmitted parasites did not. Oceanic primary productivity is robustly linked to the abundance of planktonic crustaceans such as copepods (e.g., Verheyen 2000), and these crustaceans serve as obligate intermediate hosts for many trophically transmitted parasites, notably cestodes and nematodes. Links between the availability of intermediate host zooplankters and the prevalence of trophically transmitted fish parasites have been established in some freshwater ecosystems (Hanzelova 1992, Galli et al. 1998). Productivity is also linked to the abundance of herbivorous snails (e.g., Johnson et al. 2007), the first intermediate hosts of many trematode parasites. We suggest that productivity effects on intermediate hosts are the primary reason that the abundance of trophically transmitted parasites responds to increased productivity in our data set.

Why host specialist parasites, but not generalist parasites, increased in abundance at enriched productivity sites (Fig. 3d) is uncertain. Based on the literature on anthropogenic eutrophication (Zander and Reimer 2002, Johnson and Carpenter 2008, Johnson et al. 2010), we expected that the response to productivity of generalist parasites would be more positive than would be the response of specialist parasites (H_{2c}), but our data suggest the opposite pattern. This might be because specialist parasites tend to be more strongly limited by definitive host availability than are generalist parasites, and increasing productivity could alleviate this definitive host limitation by increasing host density. The significant interaction between parasites' specificity for their definitive host and host density response suggests that, the less specific a parasite is for its definitive host, the more responsive it is to productivity-driven increases in its focal host's density, probably because generalist parasites are less limited by the availability of definitive hosts than specialist parasites (i.e., the definitive host

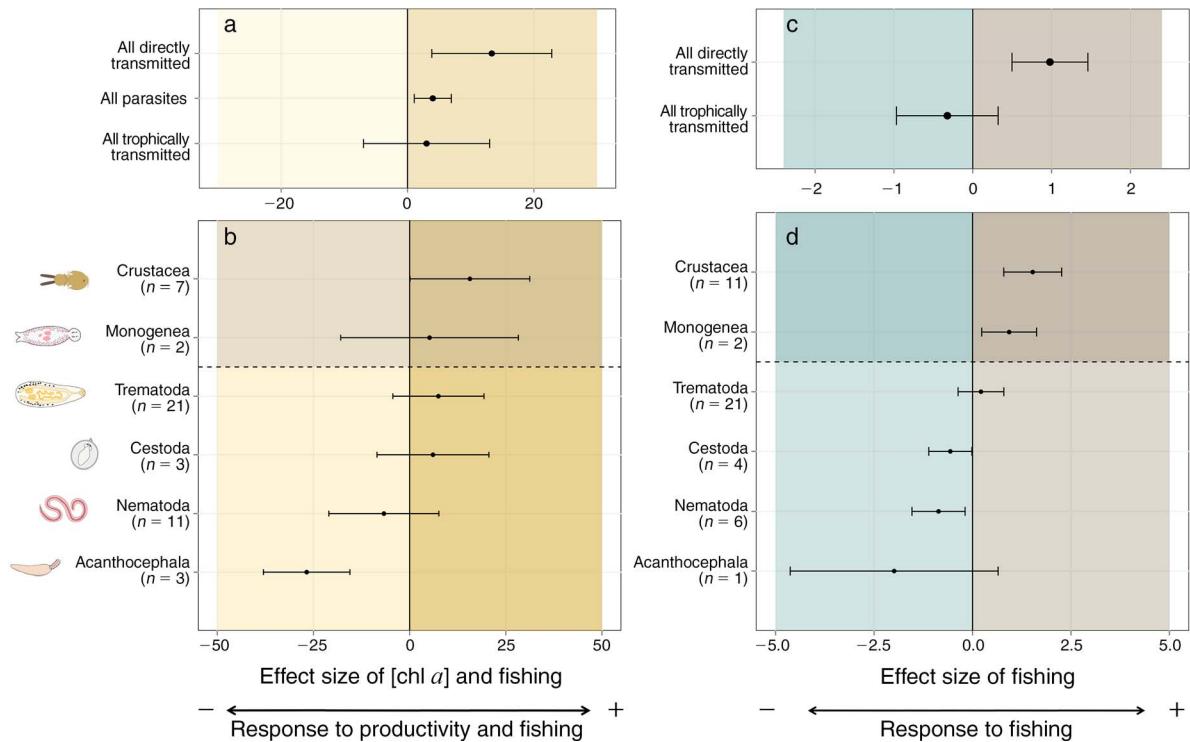


FIG. 4. (a and b) Mean effect size and 95% confidence interval for the effect of productivity and fishing gradients on within-island parasite abundance for (a) all parasites combined, all trophically transmitted parasites, and all directly transmitted parasites and (b) parasite higher-order taxonomic groupings. (c and d) Mean effect size and 95% confidence interval for the effect of fishing status on across-island parasite abundance for (c) all parasites combined, all trophically transmitted parasites, and all directly transmitted parasites and (d) parasite higher-order taxonomic groupings. Sea life drawings are courtesy of Cynthia Clark.

does not create a life-cycle bottleneck as the number of parasite propagules produced by the focal host increases). To our knowledge, only one study has demonstrated greater responsiveness to eutrophication among generalist relative to specialist parasites (Zander and Reimer 2002). Natural variability occupies a truncated range of the productivity values generated by anthropogenic nutrient enrichment (e.g., Brush 2001, Osterman et al. 2005), so it is possible that the response of parasite abundance to anthropogenic eutrophication (previous work) will differ from the response to natural variability in productivity (our work). However, this possibility remains to be explicitly tested.

We predicted an overall positive relationship between host density response to fishing and parasite response to fishing, and we expected this relationship to be strongest for directly transmitted parasites (Table 1). The data matched this expectation, providing support for H_{2b} . However, despite the positive response of directly transmitted parasites to productivity-driven increases in the density of their hosts, directly transmitted parasites were not significantly more abundant per host on islands with enriched productivity. This might be because, although parasites with hosts that increased in response to productivity were more abundant on more

productive atolls, not all hosts were strongly responsive to productivity.

Our finding that trophically transmitted parasites increased with increasing productivity, but that directly transmitted parasites did not, contrasts with the prediction that directly transmitted parasites should be more responsive to anthropogenic eutrophication than are trophically transmitted parasites (Johnson and Carpenter 2008, Johnson et al. 2010). However, the effects of bottom-up forces such as productivity enrichment tend to attenuate with increasing trophic level (Gruner 2004). Hence, productivity should have a stronger effect on the abundance of zooplankters and herbivorous snails that serve as intermediate hosts for trophically transmitted parasites than it would have on higher trophic-level fishes that are the sole hosts of directly transmitted parasites. However, increasing abundance of the hosts of directly transmitted parasites is still a possible outcome of increasing productivity, consistent with the positive relationship that we found between the response of hosts to productivity and the response of their parasites. Perhaps effects of enrichment on directly transmitted parasites become noticeable only when enrichment is substantial enough to generate large increases in fish host densities.

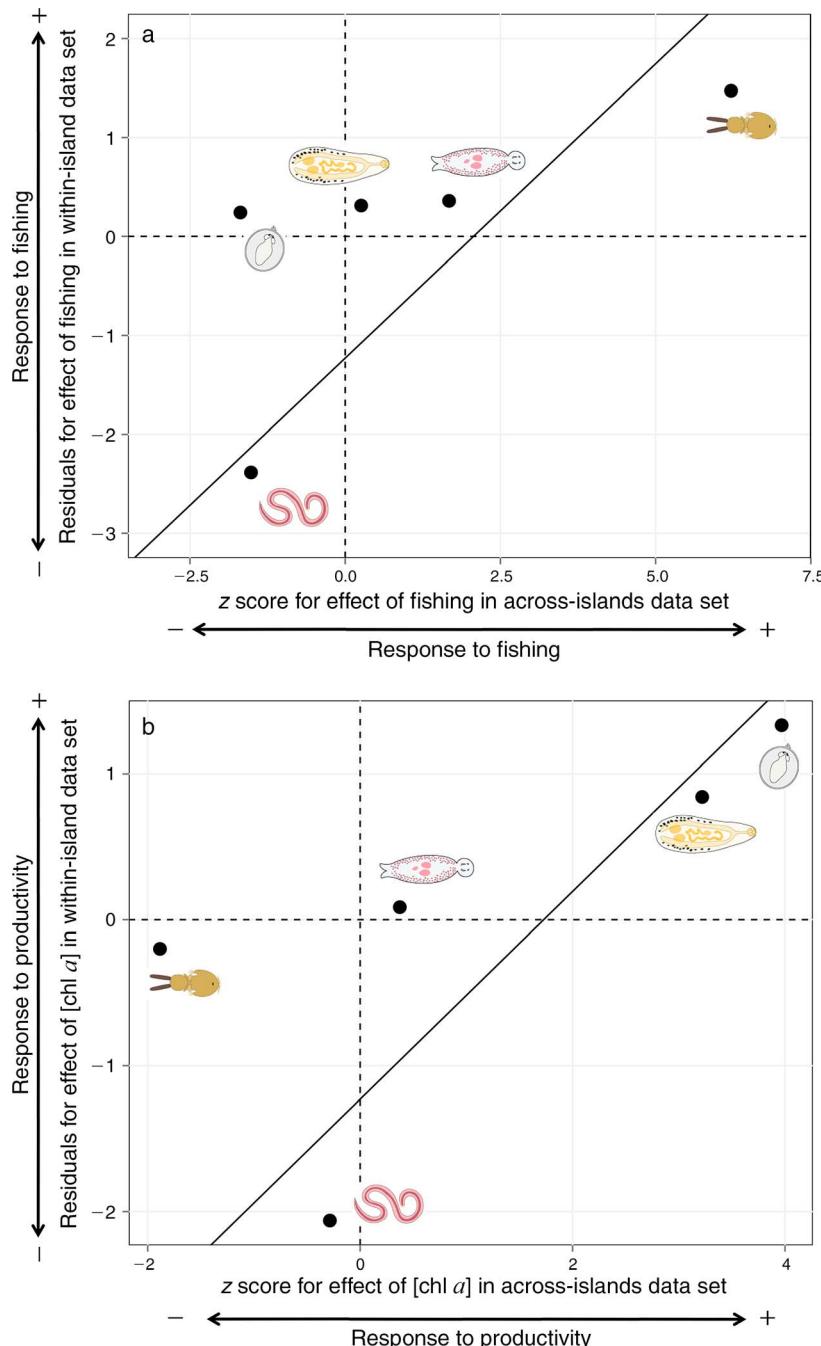


FIG. 5. Relationship between results from across-islands and within-island analysis. Plotted are responses for each of the parasite higher-order taxonomic groupings for across-islands (x-axis) and within-island (y-axis) data sets. (a) Residuals for the effect of fishing on the within-island analysis, as a function of the effect of fishing in the across-islands analysis and (b) residuals for the effect of productivity on the within-island analysis, as a function of the effect of productivity in the across-islands analysis. Images are courtesy of Cynthia Clark.

Question 3: Are across-island patterns in the relationship of parasite abundance to productivity and fishing pressure reflected in the within-island data set?

Comparison with the independent, within-island data set allowed us to assess the robustness of the conclusions

from the across-islands analysis. It also allowed us to disentangle the response of parasite abundance to productivity and to fishing pressure across the confounded within-island productivity–fishing gradient. Coarse comparison of the meta-analytic results from the two data sets (Fig. 4a and b vs. Fig. 4c and d)

suggested strong correspondence, which was confirmed by a statistical model (Fig. 5a and 5b). This regression showed that patterns of parasite abundance detected in the across-islands analysis were consistent with patterns of the within-island analysis. Specifically, results from the within-island analysis support the conclusion that fishing can increase the abundance of directly transmitted parasites and decrease the abundance of trophically transmitted parasites (Wood et al. 2014). These fishing-related changes in parasite abundance modulate the positive response of parasites to productivity.

Conclusions

Our study tests the influence on parasite abundance and taxonomic diversity of natural variability in primary productivity, a factor that is recognized as important in determining the abundance and distribution of a variety of free-living marine species (Frank et al. 2007). We found that parasite abundance tended to increase with increasing productivity. However, our results diverged surprisingly from previous studies by demonstrating that trophically transmitted parasites and parasites with high host specificity are more responsive to increases in productivity than are directly transmitted or generalist parasites. By comparing results from the across-Line Islands analysis with those from the within-Kiritimati Island analysis, we were able to confirm our general conclusions about productivity as well as conclusions about fishing pressure (Wood et al. 2014), namely, that fishing depresses the abundance of trophically transmitted parasites and can increase the abundance of directly transmitted parasites. Overall, our results suggest that the effects of anthropogenic and natural drivers on parasite abundance and taxonomic diversity will be mediated by parasite traits, particularly parasite transmission strategy.

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SUPPLEMENTAL MATERIAL

Ecological Archives

Appendices A–N are available online: <http://dx.doi.org/10.1890/13-2154.1.sm>