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Spatial covariation in nutrient enrichment and fishing of herbivores in an oceanic coral reef ecosystem

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Abstract

Both natural and anthropogenic stressors are increasing on coral reefs, resulting in large-scale loss of coral and potential shifts from coral- to macroalgae-dominated community states. Two factors implicated in shifts to macroalgae are nutrient enrichment and fishing of reef herbivores. Although either of these factors alone could facilitate establishment of macroalgae, reefs may be particularly vulnerable to coral-to-algae phase shifts in which strong bottom-up forcing from nutrient enrichment is accompanied by a weakening of herbivore control of macroalgae via intense fishing. We explored spatial heterogeneity and covariance in these drivers on reefs in the lagoons of Moorea, French Polynesia, where the local fishery heavily targets herbivorous fishes and there are spatially variable inputs of nutrients from agricultural fertilizers and wastewater systems. Spatial patterns of fishing and nutrient enrichment were not correlated at the two landscape scales we examined: among the 11 interconnected lagoons around the island or among major habitats (fringing reef, mid-lagoon, back reef) within a lagoon. This decoupling at the landscape scale resulted from patterns of covariation between enrichment and fishing that differed qualitatively between cross-shore and long-shore directions. At the cross-shore scale, nutrient enrichment declined but fishing increased from shore to the crest of the barrier reef. By contrast, nutrient enrichment and fishing were positively correlated in the long-shore direction, with both increasing with proximity to a pass in the barrier reef. Contrary to widespread assumptions in the scientific literature that human coastal population density correlates with impact on marine ecosystems and that fishing effort declines linearly with distance from the shore, these local stressors produced a complex spatial mosaic of reef vulnerabilities. Our findings support spatially explicit management involving the control of anthropogenic nutrients and strategic reductions in fishing pressure on herbivores by highlighting specific areas to target for management actions.

KEYWORDS
bottom-up forcing, coral reefs, coral–macroalgae phase shifts, local-scale fisheries, nutrient enrichment, reef resilience, top-down forcing

INTRODUCTION

Both natural and anthropogenic stressors are increasing on coral reefs, resulting in large-scale loss of coral and potential shifts from coral-dominated to macroalgae-dominated community states. Nutrient enrichment of nearshore waters and overfishing of herbivorous fishes both have been identified as key local drivers that can influence the proliferation of macroalgae (Gilby et al., 2015; Graham et al., 2013; McCook, 1999; Rasher et al., 2012). Chronic anthropogenic nutrient loading of nitrogen from sewage or agricultural runoff can accelerate the growth of benthic algae, leading to persistent blooms (Adam et al., 2021; Lapointe et al., 2005; Naim, 1993; Smith et al., 2010). Reductions in the abundance or biomass of herbivorous fishes can decrease herbivory and reduce top-down control of algae (Adam et al., 2011; Holbrook et al., 2016, 2018; Schmitt et al., 2019). Although either of these factors alone could facilitate macroalgae cover, reefs where both operate together could be particularly vulnerable to shifts to macroalgal dominance, especially following loss of coral cover from other disturbances (e.g., bleaching, cyclones). Knowledge of the patterns of spatial covariation in levels of nutrient enrichment and intensity of fishing for herbivores could contribute to local management strategies for coral reefs by identifying the reef areas to target for tailored management actions.

Nutrient inputs and fishing pressure can vary greatly in space in both tropical and temperate coastal zones (Walsh, 2011). Nutrient enrichment has been especially well studied in this regard at both regional and local spatial scales. At regional scales of tens to hundreds of square kilometers, declining nutrient enrichment has been documented with increasing distance from population centers (Duran et al., 2018; Lapointe et al., 2010; Reopanichkul et al., 2010) and from inshore to offshore as terrestrial inputs disperse and are diluted (Cooper et al., 2007; Fabricius et al., 2005; Jupiter et al., 2008; Lirman & Fong, 2007). For example, water quality varied across the Great Barrier Reef, with particulate nutrients declining from nearshore reefs in the coastal zone to offshore islands (Cooper et al., 2007). Similar cross-shelf gradients in nutrient enrichment have been observed in the Florida Reef Tract (Lirman & Fong, 2007). Nutrient enrichment gradients have also been identified at smaller spatial scales of a few kilometers or less (Adam et al., 2021; Knee et al., 2016; Lapointe et al., 2004; Lin & Fong, 2008). These gradients can arise from a variety of activities such as mariculture farms (Garren et al., 2008; Lin & Fong, 2008), waste disposal and wastewater outflows (Costa et al., 2008; Costa 2007; Reopanichkul et al., 2010) or terrestrial agriculture (Costa 2007, Costa et al. 2008). Spatial patterns can be shaped by processes such as submarine groundwater discharge (Knee et al., 2016; Street et al., 2008) and river inputs to bays that carry agricultural runoff or sewage (Fabricius et al., 2005).

Spatial patterns of fishing can be complex and affected by many social, economic, and ecological factors. The spatial behavior of fishers has generally received the most research attention in temperate commercial fisheries (Branch et al., 2006; Daw et al., 2011), for which the richest data are often available. Some studies have revealed that fishing effort measured at spatial scales of many square kilometers in nearshore systems declines with increasing distance from port or shore (Boenish & Chen, 2018; Cinner et al., 2018; Harborne et al., 2018; Saul & Die, 2016; Zellmer et al., 2018). For example, Stewart-Smith et al. (2008) tested the perception that commercial and recreational fishing on temperate reefs generates spatial impacts that diminish with distance from fisher access points and found greater fishing impacts at more accessible sites along the Tasmanian coastline. Small-scale tropical fisheries have received far less attention in this regard (Aswani, 1998; Daw et al., 2011; Teh et al., 2012; Walsh, 2011). In the small-scale fishery of Sabah, Malaysia, fishers in most villages had preferences for fishing grounds closest to the location of their village, although other factors such as safety and ocean conditions also influenced their choices (Teh et al., 2012). By contrast, in the western Solomon Islands fishers focused more on habitat type than travel distance and their preferences shifted seasonally from inner lagoon habitats to fore reef sites (Aswani, 1998). Despite the variety of factors that shape spatial patterns of fishing, bio-economic models used to explore alternative options for nearshore management often assume that effort and impact of fishing are correlated with coastal human population density and decline at locations that are farther from port or shore (e.g., Rassweiler et al., 2012; Sampson, 2018), as do spatial analyses predicting fishing-associated impacts and vulnerability (Thiault et al., 2017).

The fact that both nutrient enrichment and fishing intensity vary spatially suggests that certain reef areas could potentially experience chronic high levels of both stressors, and, for coral reefs, heightened risk of proliferation of

macroalgae. Conversely, some reefs could persistently experience low levels of both stressors, providing more resilience of the coral state or acting as refuges in the face of larger scale impacts. However, the degree to which nutrient enrichment and fishing intensity covary across space, and at what spatial scales, has not been well studied, particularly in a coral reef context. We examined spatial covariation of the two stressors for an oceanic island—Moorea, French Polynesia—that has a thriving small-scale lagoon fishery that heavily targets herbivorous fishes (Leenhardt et al., 2016; Rassweiler et al., 2020; Thiault et al., 2017) and whose lagoon patch reefs are vulnerable to coral to macroalgae phase shifts (Schmitt et al., 2019).

Moorea is a high volcanic island surrounded by a barrier reef that encloses 11 lagoons. Because its inhabitants are not evenly distributed around the island, levels of nutrient enrichment and fishing pressure on herbivores could vary around the island as a function of the size of local communities adjacent to each lagoon. This motivated us to first assess whether the two stressors were positively correlated at the relatively coarse, island-wide spatial scale of Moorea's 11 interconnected lagoons. We then explored covariation in the stressors at a finer spatial scale, that is, among the major lagoon habitats ranging from the fringing reefs adjacent to the shore to the back reefs located just inshore of the reef crest. In Moorea, lagoons are ~1 km wide from shore to reef crest, and fringing reefs might be expected to be more heavily impacted by anthropogenic stressors than reefs further from shore. Moorea's inhabitants live on a narrow coastal strip and, as both nutrients and fishers enter the lagoons along the coast, their impacts have been assumed to be concentrated on these more accessible fringing reefs and decline further out into the lagoon. Our analyses enabled us to explore which reef areas were likely to be most and least vulnerable at the two landscape scales (among lagoons, and across habitats/zones within lagoons). Our study tested widespread assumptions that anthropogenic stressors to nearshore marine ecosystems covaried and were positively correlated with coastal human population density, and that fishing intensity declined linearly with distance from shore. Furthermore, our findings have substantial implications for the development of spatially explicit management actions, particularly in coral reef settings.

METHODS

Ecological and social context

Moorea, French Polynesia (17°30′S, 149°50′W) is a small (~135 km^2) volcanic island located near the island of Tahiti in the central South Pacific. The island is surrounded by a barrier reef located ~1 km offshore that is interrupted by 11 major reef passes that connect the 11 shallow (generally <3 m depth) protected lagoons inside the barrier reef with the open ocean (Appendix S1: Figure S1). Shoreward of the reef crest is a distinct back reef habitat that is dominated by patch reefs separated by sand, coral rubble, and reef pavement. Moving toward the shore, back reef habitats are gradually replaced by a more open, mid-lagoon zone, characterized by sandy areas containing numerous patch reefs. Directly adjacent to land are shallow fringing reefs, in some cases separated from the mid-lagoon zone by a deeper channel. Water flow within the lagoons is wave driven with waves forcing water over the crest, through the lagoons and out the deep passes (Leichter et al., 2013).

Moorea has over 17,000 inhabitants (ISPF, French Polynesian Population Census 2017) residing in five *communes associées* or districts: Afareaitu, Haapiti, Paopao, Papetoai, and Teavaro (Appendix S1: Figure S1) subdivided into 20 villages. As a result of the steep topography, residents tend to live along the island's 60 km-long perimeter road, with additional population centers located in several large valleys. Moorea has undergone substantial economic development in recent decades, including intensification of commercial agriculture (e.g., pineapple plantations) and the development of tourist facilities (including hotels) that have contributed to anthropogenic nutrient enrichment in the lagoon (Loiseau et al., 2021). However, fishing remains a widespread activity (Leenhardt et al., 2016; Rassweiler et al., 2020; Thiault et al., 2017, 2019). Nearly two-thirds of households reported fishing activity using hook and line, spearguns, or nets (Leenhardt et al., 2016; Rassweiler et al., 2020), and ~20% of the adult population practice fishing as a cash-earning occupation (whether primary or secondary) (Appendix S1: Table S1). Fish are caught for household consumption, sharing in the community, and for sales at small stands along the perimeter road (Leenhardt et al., 2016, Rassweiler et al., 2020). Our previous analyses of fish sold at the roadside stands revealed that at least 60 genera of fishes are represented in the catch, the bulk of which is caught by free-diving spearfishers. However, six genera of herbivorous fishes (*Naso*, *Scarus*, *Siganus*, *Chlorurus*, *Acanthurus*, *Calotomus*) together comprise almost 60% of the abundance and biomass of the catch (Rassweiler et al., 2020). These herbivorous fishes are critical to the resilience of the reefs because of their potential to prevent proliferation of macroalgae (Han et al., 2016).

Spatial scales of study

We explored the relationships between nutrient enrichment in the lagoons and the intensity of fishing for

herbivorous fish at two spatial scales. The first involved comparisons among the 11 lagoons around the island (Appendix S1: Figure S1). The goal of investigating this landscape scale was to delineate island-wide patterns in the two drivers and identify potentially vulnerable areas around the island where the stressors were both elevated. The second spatial scale that we investigated involved comparisons of fishing intensity and nutrient enrichment at smaller reef habitat scales, both across the major lagoon habitats at different distances from shore—fringing reef, mid-lagoon, and back reef—and alongshore, comparing habitats at different distances from the reef passes. To address these within-lagoon spatial scales, we selected study areas in three districts (Haapiti, Afareaitu, Papetoai; Appendix S1: Figure S1), one on each side of the island, where we obtained detailed data about fishing practices and locations through household surveys, informal interviews, and participant observation.

Bathymetry, habitat classification, and lagoon geometry

We mapped the inner edge of the reef crest, the shore line and openings to each of the 11 passes on Moorea based on LiDAR-based digital elevation maps produced from an airborne LiDAR campaign conducted in 2015 (Collin et al., 2018). Furthermore, we created a spatial habitat layer that classified areas of the lagoon 3 m or shallower into three habitats: fringing reef, mid-lagoon, and back reef. Areas closest to shore were classified as fringing reef, with the edge typically delineated by a deeper channel. In lagoons lacking a channel, the boundary between fringing reef and mid-lagoon was chosen based on the depth profile (e.g., set at the deepest point) and coral cover (e.g., drawing the boundary through areas with little reef). Back reef habitats were defined as areas within 200 m of the reef crest on the shoreward side. Shallow areas (0–3 m) located between the fringing reefs and back reefs were classified as mid-lagoon. In addition to these habitat classifications, any location in the lagoon was described by its distance to the nearest pass and its relative distance to shore. The relative distance to shore was calculated as the distance to the nearest point on the shore as a fraction of the total distance from the shore to the reef crest passing through that point, such that locations on the shore have a value of 0 and locations at the reef crest have a value of 1. Finally, depth for any location within lagoons was assigned based on LiDAR data (Collin et al., 2018), averaged within each 25 × 25 m grid cell.

Spatial patterns of fishing

Several types of information, including census data, household surveys, fish-seller surveys, and ethnographic participant observation, allowed us to gain an understanding of fishing practices and spatial variation in fishing at both spatial scales. At the among-lagoon scale, we used data from the 2017 French Polynesian Population Census (ISPF 2017) to calculate an estimate of overall fisher density for each lagoon based on population size and number of adults (here considered as over 15 years of age) engaged in fishing (Appendix S1: Table S1). Along with demographic data, French Polynesian census data cover employment and occupation information, including engagement in the fishery as a primary or secondary cash-earning occupation.

Information about spatial variation in fishing across the different reef habitats (within-lagoon scale) was derived from data gathered in 2014–2015 through an extensive household survey of 351 households (Rassweiler et al., 2020). This survey utilized convenience and reputational sampling methods and aimed to achieve an even distribution across each district's designated survey area. During these interviews we gathered detailed information about fishing practices from households with at least one active fisher ($N = 222$). Interviewed fishers enumerated the gears they used and, for each gear, the three main taxa they targeted. Most interviewed fishers also agreed to participate in a mapping exercise in which they drew their fishing grounds for each mentioned gear on a laminated satellite image of Moorea's lagoons ($N = 173$; Afareaitu $N = 65$, Haapiti $N = 55$, Papetoai $N = 53$). From these maps, in total, 330 spatial polygons were digitized, which together with the specific locations of each household, enabled us to estimate the average distance fishers traveled from their home to their fishing grounds. Fish-seller surveys conducted at roadside stands provided additional insight into the location of the catch relative to the fisher's residence (Rassweiler et al., 2020).

Patterns of N enrichment in the lagoons

We used data from a previous study (Adam et al., 2021) to delineate spatial patterns of nutrient enrichment in the lagoons. To obtain estimates of nutrient enrichment, tissue samples of the brown alga *Turbinaria ornata* were analyzed for nitrogen (N) content. *Turbinaria* responds to N pulses by storing surplus N (Schaffelke, 1999) and therefore N tissue content can provide a time-integrated measure of N availability (Atkinson & Smith, 1983; Fong et al., 1994; Shantz et al., 2015). On Moorea, spatial variation in *Turbinaria* N content is explained by the proximity from known anthropogenic nutrient sources (primarily sewage) (Adam et al., 2021). Samples of *Turbinaria* were

collected at 0.5–2 m depth at 171 sites around the island, at least 0.5 km apart and situated to cover major reef habitats, including fringing reefs, mid-lagoon, back reef, reef passes, and bays. At each site we collected thalli from 10 different random individuals of *Turbinaria* within an area of ~500 m^2 and averaged the N values from the 10 individuals. Here we considered only samples collected in May 2016, at the end of the rainy season. This time point followed several months when nutrient delivery to the lagoons from anthropogenic sources was likely to be the highest due to runoff from agricultural areas and inputs of groundwater. Total N content was determined via elemental analysis using a CHN Carlo-Erba elemental analyzer (NA1500) at the University of Georgia, Center for Applied Isotope Studies.

Island-scale (among-lagoon) patterns of fishing intensity and nutrient enrichment

A lagoon-scale metric of fisher density was calculated using census data (ISPF, French Polynesian Population Census 2017). The number of adults (>15 years) engaging in the fishery as a cash-earning occupation was retrieved from the census data for each land unit adjacent to Moorea's 11 lagoons. To standardize fisher density across lagoons and land units of varying sizes, we calculated densities by normalizing the number of fishers by the extent of the adjacent shallow lagoon area (≤3 m), a depth range that provides a good proxy for the extent of the most desirable fishing grounds.

To calculate variation among lagoons in nutrient enrichment, we estimated the mean percentage N in *Turbinaria* tissue for each lagoon. N enrichment varies among reef habitats (i.e., from shore to the reef crest), and these habitats are unequally represented among the different lagoons. Therefore, we obtained estimates of enrichment for each lagoon from a mixed effects model with habitat type modeled as a random effect using the R packages "nlme" (Pinheiro et al., 2020) and "emmeans" (Lenth, 2020). For this analysis, we only used data from back reef, mid-lagoon, and fringing reef sites, as these habitats were sampled in every lagoon. Sample sizes are listed in Appendix S1: Table S1. Further details regarding spatial patterns of nutrient enrichment are found in Adam et al. (2021).

Reef habitat scale (within-lagoon) patterns of fishing intensity and nutrient enrichment

Using the spatial data from the household survey mapping exercise we were able to quantify spatial patterns of fishing intensity and explore its variation across habitats within the study areas. As we were interested in analyzing how fishing might reduce top-down control of algae, we excluded from our household survey dataset line and net fishers who did not report any herbivorous species (i.e., Acanthuridae, Kyphosidae, Siganidae, and Scaridae) as one of their top-three targeted species. However, we retained all fishing grounds reported by spearfishers—regardless of the target species they mentioned—as we have learned through participant observation and analysis of catch data that spearfishers who seek out carnivorous species also opportunistically shoot herbivores. The filtering process reduced the number of fishing ground maps in our sample from 173 to 136.

To depict spatial patterns of fishing and nutrient enrichment, we created heat maps for each of our three study areas (Haapiti, Afareaitu, Papetoai; Appendix S1: Figure S1). We divided the adjacent lagoon into a 25 × 25 m grid, extending from shore to the reef crest and cropped at the boundaries of the study areas (shore, barrier reef crest). For each grid cell we estimated fishing intensity by counting the number of fishers who included or intersected the given grid cell when mapping their fishing grounds. To standardize these fishing intensity values for comparison across study areas, we calculated a ratio by dividing each grid cell's value (i.e., absolute number of fishers identifying it as an area they target) by the total number of fishers who participated in the mapping exercise in that study area. To visualize fine-scale spatial heterogeneity in nutrient enrichment within the lagoons, we interpolated patterns of N enrichment from our lagoon-wide sampling of *Turbinaria* for each of the three study areas. Interpolations were generated via ordinary kriging with a spherical variogram model as implemented in the R package "kriging" (Olmedo, 2014).

For statistical analysis of the relationships between fishing intensity and nutrient enrichment, we overlaid the nutrient data (sampling locations) on the fishing intensity heat maps. Using *ArcGIS*, we extracted the pixel value of fishing intensity for each point where nutrients had been sampled. This resulted in 64 total points (Afareaitu: 19; Haapiti: 20; Papetoai: 25) with both nutrient and fishing intensity values. These points were assigned habitats (fringing reef: 29; mid-lagoon: 17; back reef: 18), depth, and distance to the nearest pass and relative distance from shore as described above. Points were then plotted as scatterplots, and Pearson's R correlations calculated.

To explore the distribution of fishing intensity within each habitat type, a random distribution of 10,000 points spaced at least 10 m apart was overlaid onto the lagoon habitat spatial layer. To remain consistent with the nutrient data depth range, we removed points that were not

between 0–3 m depth. Finally, only the random points overlapping with the fishing intensity heat maps of our three study areas were retained in the analysis. This resulted in 516 points in Afareaitu (fringing reef: 31; mid-lagoon: 199; back reef: 286), 1019 points in Haapiti (fringing reef: 236; mid-lagoon: 351; back reef: 432), and 632 points in Papetoai (fringing reef: 227; mid-lagoon: 175; back reef: 230).

For both the nutrient data and fishing intensity data, we explored associations with variables characterizing their position within the lagoon (relative distance from shore and distance from pass) using linear mixed effects models (LMERs) with the R package "lme4" (Bates et al., 2015). We assumed a Gaussian family normal distribution for both response variables. Diagnostics were run on model outputs to confirm model assumptions were met. For the model using fishing intensity as the response variable, we used all 2167 random fisher intensity points described above. We treated distance to reef pass and relative distance to shore as continuous fixed effects and location (study area) as a categorical random effect. For the linear model with nutrient values as the response variable, we used all 171 nutrient data points sampled in May 2016, using points from all around the island (not just within the three study areas). We treated distance to reef pass and relative distance to shore as continuous fixed effects. Using the R package "sjPlot" (Lüdecke, 2020), we plotted the relationships estimated by these regression models.

RESULTS

Island-scale (among-lagoon) patterns of fishing and nutrient enrichment

Both fisher density and nutrient enrichment varied among the 11 lagoons (Figure 1). Not surprisingly, two of the three lagoons with the highest values for nutrient enrichment (N2 and N3) were situated on either side of Paopao's bay adjacent to the island's main population centers and to a major watershed where pineapple farming occurs. However, other lagoons with high nutrient enrichment values (e.g., W1 and W2) were located in sparsely populated areas, and there was no significant correlation between nutrient enrichment and population size at the island scale (Pearson's $r = 0.25$, $p = 0.46$). Lagoons with high fisher density were located on both

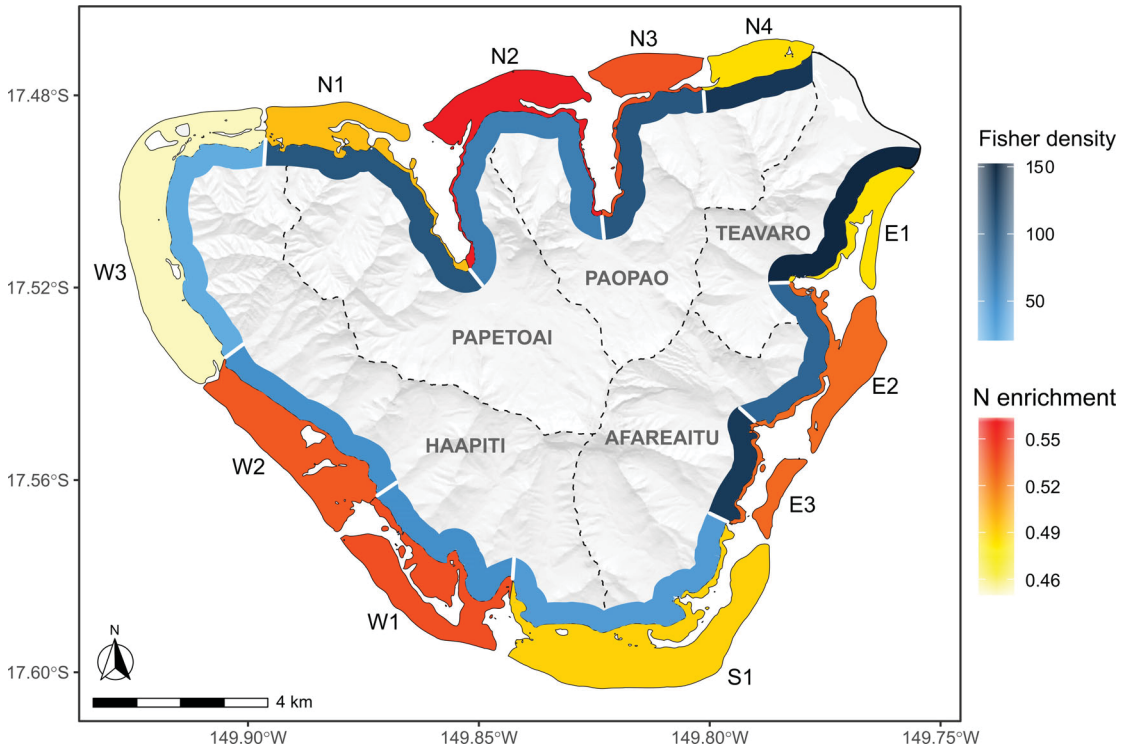

FIGURE 1 Spatial patterns of nutrient enrichment (percentage N) and fisher density (fishers per km^2) in the 11 lagoons around Moorea. Lagoons are delineated as areas located between two passes and have been coded according to their location running clockwise around the island. Fisher density is expressed as number of fishers per km^2 of estimated fishable lagoon habitat (depth <3 m) and is represented by the line along the coast. Levels of nutrient enrichment (percentage of nitrogen found in *Turbinaria ornata*) are indicated by the color coding of the lagoons

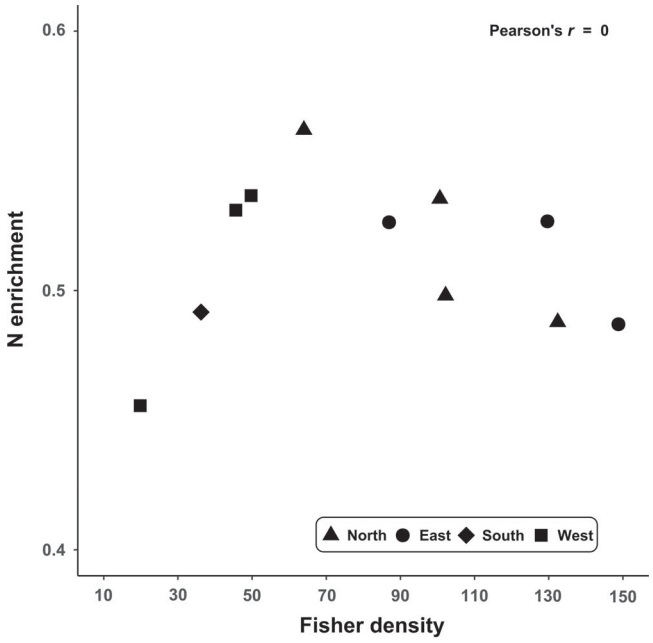

FIGURE 2 The relationship between the values of nutrient enrichment and fisher density depicted in Figure 1. Nutrient enrichment represents the percentage of nitrogen found in *Turbinaria ornata* samples, while fisher density represents the number of fishers per km^2 of estimated fishable lagoon habitat. The 11 lagoons are indicated by their geographic position on the island (triangles, North shore; circles, East; diamond, South; squares, West)

the north and east sides. While the absolute number of fishers living adjacent to each lagoon did covary positively with population size (Pearson's $r = 0.64$, $p = 0.03$), there was no relationship between population size and our metric of fisher density (Pearson's $r = 0.1$, $p = 0.77$). This is because the extent of desirable fishing grounds (i.e., shallow lagoon area) was independent of the population size adjacent to each lagoon (Pearson's $r = -0.05$, $p = 0.88$). For example, the extent of shallow lagoon available across the island's major population center on the north shore (N3) was relatively small; conversely, the second largest lagoon was located across one of the least populated sectors of the island (W3).

When considering the relationship between fisher density and nutrient enrichment, there was no correlation at the among-lagoon scale (Pearson's $r = 0$, $p = 0.99$; Figure 2), and there were no marked geographic patterns or gradients of covariation.

Our measure of spatial variation in fisher density among the 11 lagoons used census data that quantified population sizes and fishing activity, relative to the amount of fishable area in each lagoon. This approach assumed that fishing mainly occurred close to where the fisher lives, that is, in the lagoon adjacent to their residence. Data from both our roadside market surveys and our household surveys supported this assumption. Interviews with sellers during the roadside surveys indicated that more than 75% of fishing occurred near the fishers' villages of residence or in fishing areas offshore of their neighboring villages (Figure 3). During household surveys, fishers delineated their fishing grounds on maps; and, on average, fishing grounds were less than 2 km from fishers' households ($N = 173$, mean = 1.8 km, SD = 1.3 km) (Table 1).

Reef habitat scale (within-lagoon) patterns of fishing intensity and nutrient enrichment

Based on household survey data from three study areas (Afareaitu, Haapiti, Papetoai), one on each side of the island (Appendix S1: Figure S1), fishing intensity for herbivores varied among different habitats and zones, and the patterns were largely similar in all three study areas (Figure 4). Fringing reefs had generally low levels of fishing, while the back reef, mid-lagoon, and the edges of passes had variable—but often high—fishing intensity (Figure 4). The heat maps of nutrient enrichment revealed patterns of spatial variation characterized by the highest levels on nearshore fringing reefs and adjacent to reef passes (Figure 4).

Similar to our findings for the among-lagoon spatial scale (Figure 2), when examined at the finer spatial scale, levels of fishing intensity and nutrient enrichment were not significantly correlated (Pearson's $r = -0.11$, $p = 0.38$; Figure 5). The heterogeneity in the data motivated further exploration of spatial patterns of fishing intensity and nutrient enrichment among habitat types and with distance from shore (cross-shore direction) and from reef passes (long-shore direction).

The spatial pattern of fishing intensity varied among the major lagoon habitats but shared consistent features across the three focal study areas (Figure 6). The fringing reef was less heavily fished than the mid-lagoon or back reef habitats, which were characterized by a much wider range of fishing intensity, including the highest levels of fishing intensity (Figure 6). As a result of this consistency across the study areas, we pooled the data from all three in a linear mixed effects regression (LMER) model, which revealed that fishing intensity was higher in areas close to reef passes ($p = 0.006$) and in areas of lagoons relatively farther from the shore (i.e., closer to the barrier reef crest, $p < 0.001$; Figure 7). Results of the analysis for nutrient enrichment revealed similar alongshore patterns, with nutrient enrichment greater near reef passes ($p < 0.001$; Figure 7). However, in contrast with the pattern for fishing, nutrient enrichment declined with

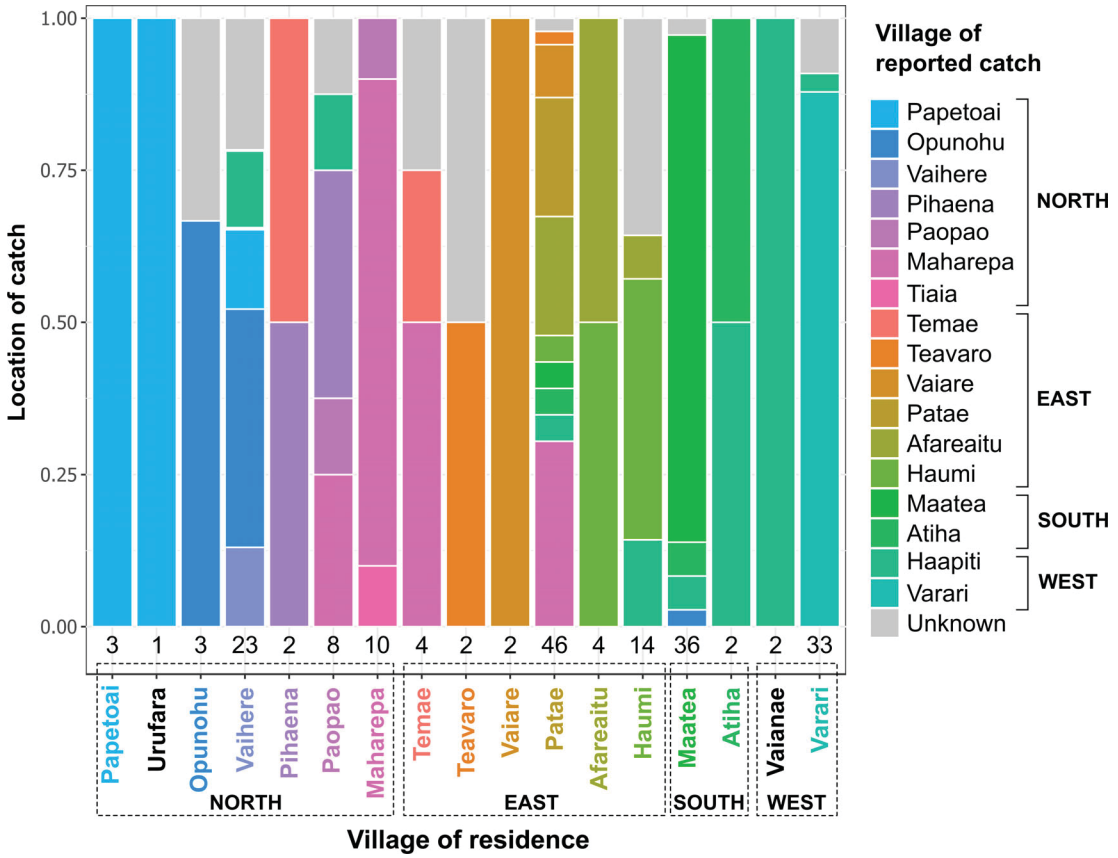

FIGURE 3 Catch location of fish sold by the roadside by fishers living in 17 villages in Moorea. $N = 195$ events (an event is a fisher selling catch by the roadside, indicated in black numbers along the *x*-axis). Villages are coded by color and ordered corresponding to their location running clockwise around the island starting from the island's northwest corner. Colors of labels on the *x*-axis match those in the legend (labels in black are villages of residence that were not reported as catch locations)

TABLE 1 Average distances (km) traveled to fishing grounds estimated from fishing maps drawn by 173 fishers

District	N	Mean (SD)
Afareaitu	65	1.93 (1.43)
Haapiti	55	1.62 (1.28)
Papetoai	53	1.85 (1.24)
All Districts	**173**	**1.83 (1.32)**

Note: Data (mean [SD]) are given for study areas in three districts, one on each side of the island.

increasing distance from shore ($p < 0.001$). While both models were highly significant, they explained only 23% of the spatial variation in fishing, and 22% of the variation in nutrient enrichment (Appendix S1: Table S2).

Collectively, these qualitatively different cross-shore and long-shore relationships resulted in weak and variable correlations between fishing intensity and nutrient enrichment within each of the three main lagoon habitats (Figure 8). Fringing reefs experienced generally low fishing intensity but highly variable nutrient enrichment, with some nearshore reefs having the highest levels of nutrients that we measured in this study (Figure 8). There was also a trend for a negative relationship between fishing intensity and nutrient input on fringing reefs (Pearson's $r = -0.33$, $p = 0.08$). These results refuted our expectation that the fringing reef would have many locations experiencing both intense fishing and high nutrient enrichment. Compared with the fringing reef, the mid-lagoon and back reef habitats were somewhat less variable in the degree of nutrient enrichment, but experienced a wide range of fishing intensity. In the mid-lagoon, fishing intensity and nutrient enrichment were weakly positively correlated (Pearson's $r = 0.48$, $p = 0.05$), while there was no significant relationship between the two variables on the back reef (Pearson's $r = 0.03$, $p = 0.91$).

We also explored the relationships between intensity of fishing and nutrient enrichment among the three study areas (Appendix S1: Figure S2). The three areas showed generally similar patterns in the range of nutrient

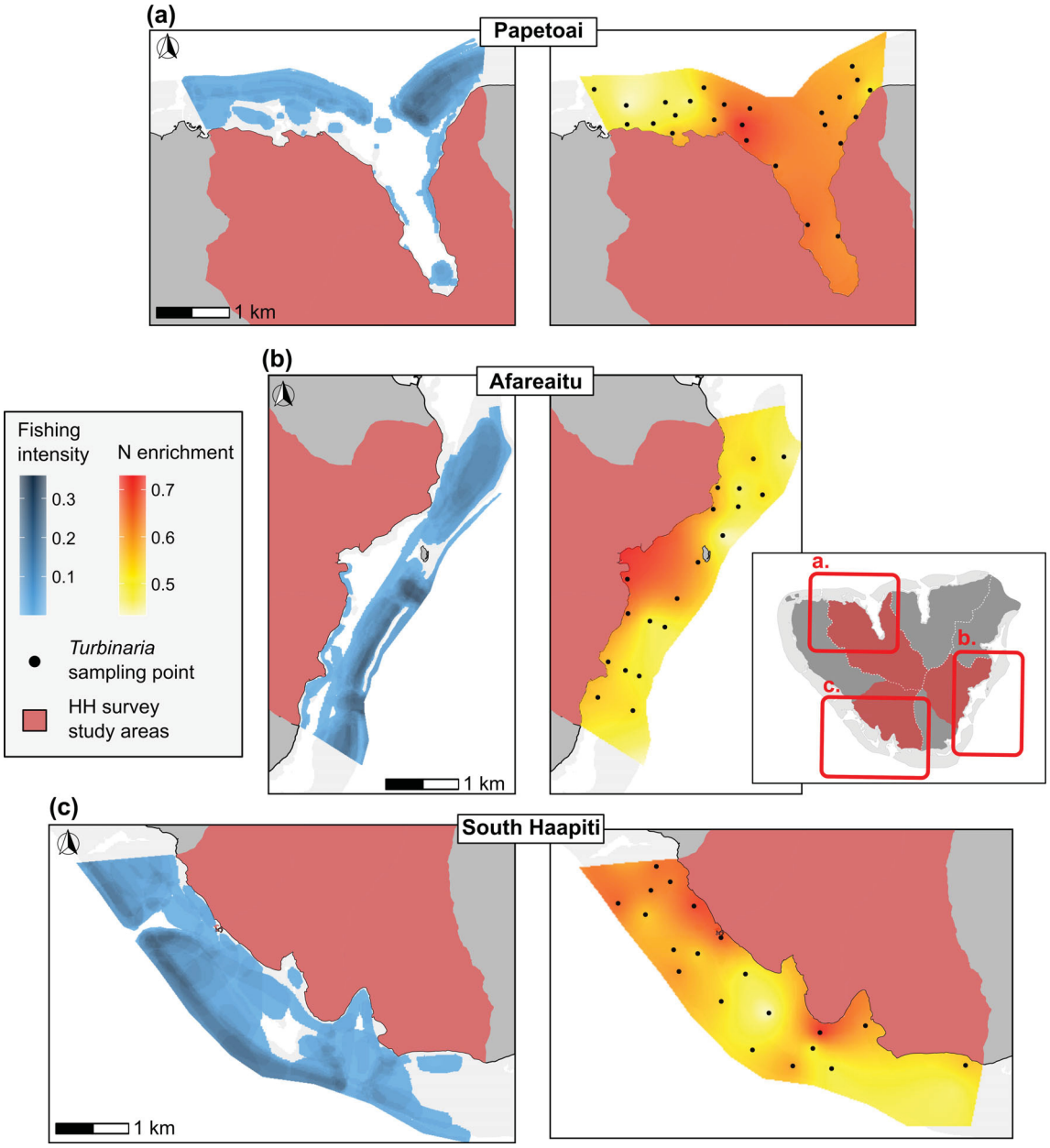

FIGURE 4 (a–c) Heat maps of fishing intensity for herbivores (left) and nutrient enrichment (right) at the three study areas in the Papetoai, Afareaitu, and South Haapiti districts of Moorea. The areas where household (HH) surveys were conducted to estimate fishing intensity are indicated by the colored area in each map inset. Dots on the nutrient heat maps indicate locations ($N = 64$) where the alga *Turbinaria ornata* was sampled for estimation of nutrient enrichment

enrichment and intensity of fishing, and none of the relationships between the two variables was statistically significant.

DISCUSSION

Many coral reef systems worldwide are experiencing population growth, coastal development, and agricultural intensification that increase nutrient inputs to reefs, with simultaneously increasing fishing pressure on herbivorous fish populations. These chronic, local drivers can affect the proliferation of macroalgae and promote shifts from a coral-dominated to an algae-dominated state. This is particularly the case following disturbances that result in landscape-scale loss of coral cover, which is increasing due to climate change. Spatial patterns of variation in nutrient enrichment or in fishing have been quantified in some nearshore systems. However, knowledge of how and at what spatial scales these two factors covary on coral reefs is much more limited, and spatial data on fishing intensity are

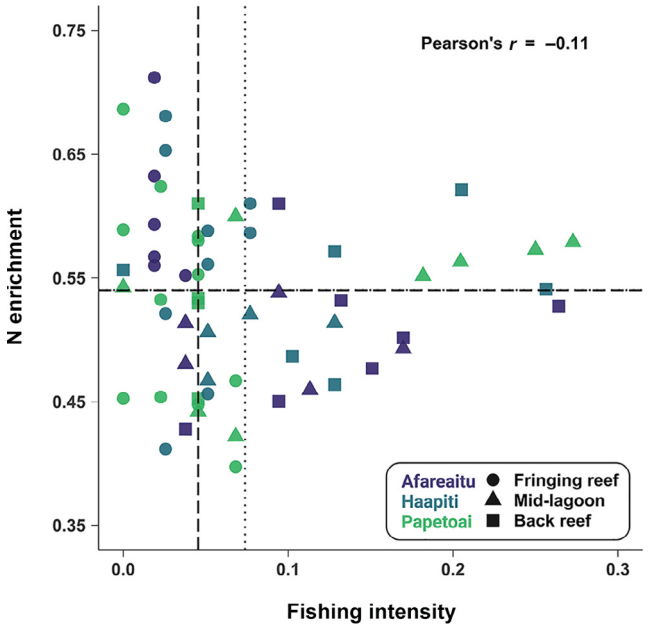

FIGURE 5 Relationship between nutrient enrichment and fishing intensity for three study areas (in Afareaitu, Haapiti, and Papetoai districts) and in the three major lagoon habitats (fringing reef, mid-lagoon, back reef). Nutrient enrichment represents the percentage of nitrogen found in *Turbinaria ornata* samples, while fishing intensity is the proportion of fishers in that study area that included that location within one of their reported fishing areas. Each symbol represents fishing intensity at a location in the lagoon (as depicted on the maps in Figure 4) where samples of the alga *T. ornata* were taken to estimate nutrient enrichment ($N = 64$). Means (N enrichment, 0.54; fishing intensity, 0.07) and medians (N enrichment, 0.54; fishing intensity, 0.05) are indicated by the dotted and dashed lines, respectively

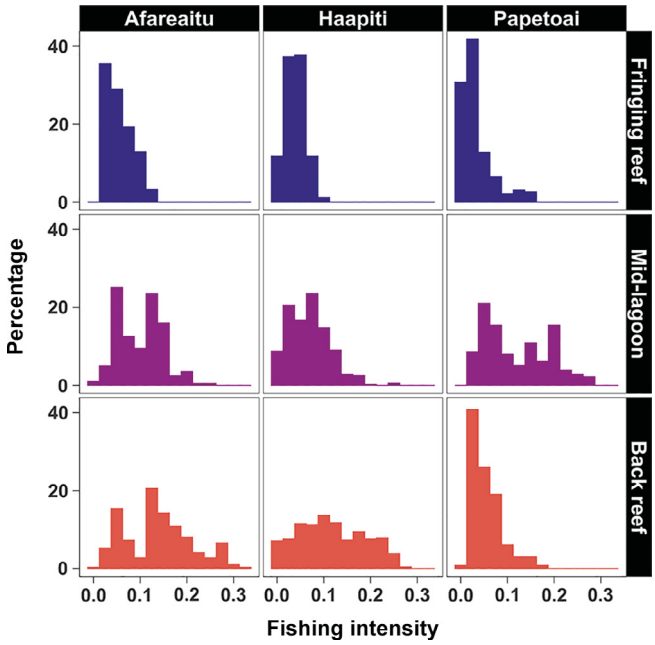

FIGURE 6 Distribution of fishing intensity among the three main lagoon habitats (fringing reef, mid-lagoon, back reef) for three study areas (in Afareaitu, Haapiti, and Papetoai districts). Fishing intensity is the proportion of fishers in that study area that included that location within one of their reported fishing areas. Histograms are based on fishing intensity at a set of randomly selected points in the study area (Afareaitu $N = 799$; Haapiti $N = 1476$; Papetoai $N = 1191$). Each plot represents the percentage of the set of randomly selected points that fell into the corresponding binned values of fishing intensity

particularly limited for small-scale reef fisheries. Moorea is an ideal setting for studying the spatial patterns and covariance of nutrients and fishing, because increasing population growth and changes in land use have fostered nutrient enrichment in some areas of the lagoon (Adam et al., 2021), and because herbivorous species are selectively targeted by the local fishery (Rassweiler et al., 2020). Understanding whether the intensities of these stressors are spatially correlated, and at what scales, could enable more effective management strategies targeted at areas of highest or least concern.

The degree to which locations with intense fishing and high nutrient inputs are particularly vulnerable to overgrowth by macroalgae is not well understood. It has long been argued that responses of coral reefs to disturbance can only be understood by considering multiple stressors (Hughes & Connell, 1999). While experiments have demonstrated that changing nutrients and fishing simultaneously could have greater effects than altering either alone (e.g., Gil et al., 2016; Zaneveld et al., 2016), the degree to which the combined effects might be synergistic, as opposed to simply additive, is exceptionally difficult to predict (Ban et al., 2014). Nevertheless, even additive (noninteracting) effects can have dire consequences if they increase the probability of a phase shift into persistent macroalgal dominance (Hughes et al., 2017).

Our study revealed spatial variation in anthropogenic stressors on Moorea. Among the 11 lagoons, combinations of high and low values for nutrient enrichment and fisher density were observed, with no marked geographic gradients. It is not surprising that the lagoons varied in nutrient enrichment, given the patchiness of human settlement and the variation in land use and size of the watersheds around the island, factors that have been shown to drive nutrification in nearshore waters in other systems. Adam et al. (2021) documented the highest levels of nutrient enrichment near Moorea's large watersheds on the north and west sides of the island where inputs of nitrogen (N) from sewage and agriculture are high. This pattern was seasonally persistent despite variation in rainfall and wave strength (which drives lagoon circulation and delivery of nutrients), and isotopic

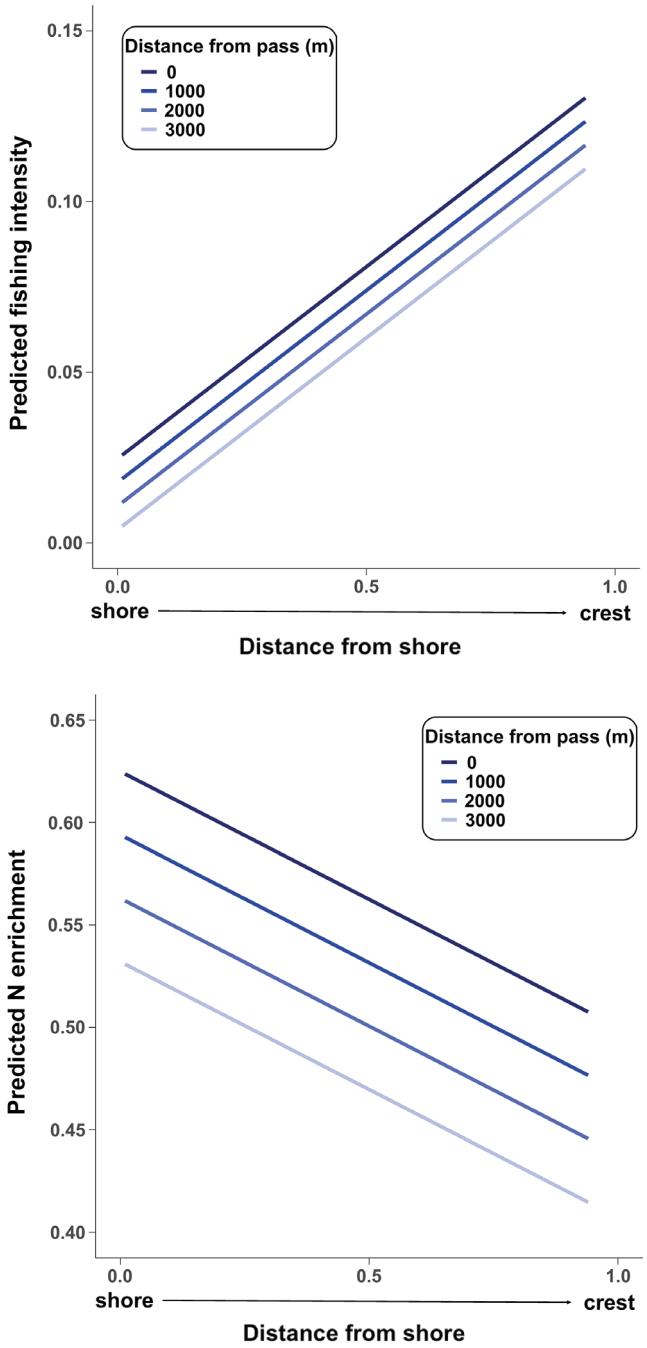

FIGURE 7 (Upper) Results of a linear mixed effects model examining fishing intensity in the three main habitat zones of the lagoon (fringing reef, mid-lagoon, and back reef) with respect to the proximity to the nearest reef pass (m) and distance from shore. Fishing intensity is the proportion of fishers in that study area that included that location within one of their reported fishing areas. Distance from shore is expressed as a ratio of the distance from shore divided by the total distance from shore to reef crest. (Lower) Results of a linear mixed effects model examining the amount of nutrient enrichment in the three main habitat zones of the lagoon with respect to proximity to the nearest reef pass (m) and the distance from shore. Nutrient enrichment represents the percentage of nitrogen present in *Turbinaria ornata* samples

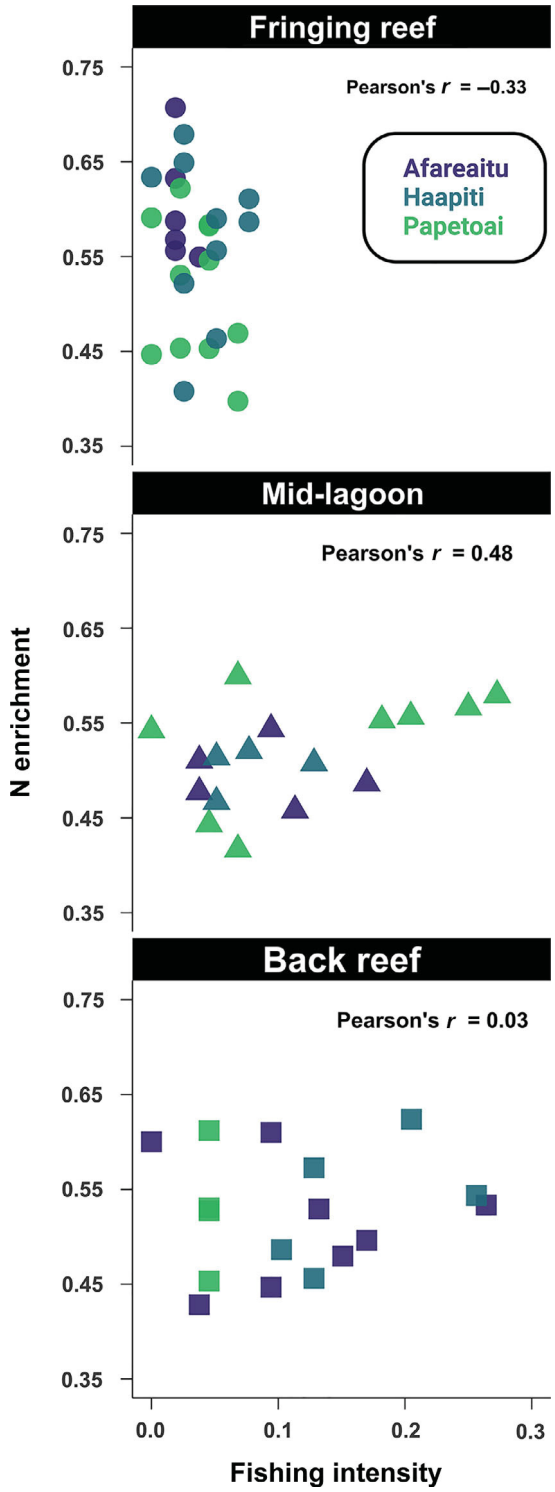

FIGURE 8 Relationships between nutrient enrichment and fishing intensity. Nutrient enrichment represents the percentage of nitrogen found in *Turbinaria ornata* samples, while fishing intensity is the proportion of fishers in that study area that included that location within one of their reported fishing areas. Panels show data from the three main habitat zones of the lagoon (fringing reef, mid-lagoon, back reef) while symbol colors indicate study areas

signatures of N in high-enrichment areas were consistent with terrigenous rather than oceanic sources of N (Dailer et al., 2010; Lin & Fong, 2008; Page et al., 2013). Such sources include fertilizers, waste from livestock and aquaculture, and sewage (Adam et al., 2021). Additionally, time-series data indicated that lagoon areas close to major watersheds on Moorea are likely to have experienced nutrient enrichment for at least the past decade (Adam et al., 2021). These lagoons contrast with areas with sparser populations and less intense land-use activities on the northwest and southern tips of the island that experience lower levels of nutrient enrichment (Figures 1 and 2).

Our island-scale metric for fisher density used the number of adults who engaged in fishing as a cash-earning occupation within the land adjacent to the lagoon, adjusted for the area of shallow lagoon suitable for fishing. Great variation in both lagoon size and the spatial distribution of the population around Moorea resulted in substantial variation in fisher density (Figure 2). It was lowest on the south and west portions of the island where lagoons are large and populations sparse, compared with the more densely populated north shore with its smaller lagoons. Importantly, at the among-lagoon scale, the intensity of fishing and levels of nutrient enrichment were not correlated, suggesting that the predictive power of broad measures of human impact such as population density or human gravity (e.g., Cinner et al., 2018) that aggregate different kinds of human-induced stressors should be approached with caution. In particular, while human coastal population density may seem like a convenient proxy for different types of human impacts to marine ecosystems, and is commonly used as such in the scientific literature including as an indicator of fishing pressure (Stallings, 2009; Thiault et al., 2017; Ward-Paige et al., 2010), nutrient inputs (Smith et al., 2003), or generic anthropogenic pressure (Feist & Levin, 2016; Welle et al., 2017), our results suggested that these stressors may often show more complex relationships with population density.

The initial approach we used to quantify fishing effort used census data, which revealed that on average, ~20% of the adult population engaged in fishing as an occupation (Appendix S1: Table S1). However, data from our household surveys in the three study areas revealed that approximately two-thirds of households had at least one person who engaged in fishing, and 93% of informants had fished at some point in their lives. Similar to practices elsewhere in the Pacific (Cinner, 2014; Daks et al., 2018), there is a wide continuum of engagement in the reef fishery ranging from food security and income generation to cultural practices. Results from our household survey added value to information from the census data, as they enabled us to capture spatial patterns of fishing for specific fish taxa and provided a more complete assessment of fishing activity.

Fishing in the three study areas showed similar patterns in the frequency of use of the major lagoon habitats, with the fringing reef used less often for fishing for herbivores than areas further offshore (the mid-lagoon and back reef; Figure 6). The pattern also held when we considered total fishing effort (for herbivorous and non-herbivorous fish taxa). This finding refuted the expectation that the fringing reef would be most heavily fished, because it is the most accessible and suggested that the use of linear diffusion models that are often used for nearshore marine ecosystems to approximate fishing effort as a function of distance from shore could be problematic in the context of small-scale fisheries. Our market surveys revealed that most of the catch originated from areas close to fishers' residences (Figure 3), and in household surveys fishers indicated that the distance from home to their fishing spots was relatively small (averaging ~1.8 km; Table 1; see also Thiault et al., 2017) compared with the distance traveled in temperate commercial fisheries. Nonetheless, these shorter travel distances still allowed most fishers to potentially access all three habitats within the relatively narrow lagoons. If diffusion models were to be used to estimate fishing effort in this context, it might be more appropriate for them to be directional (describing probability of travel along the coastline but not across the lagoon to the reef crest).

The inverse relationship between distance from shore and fishing intensity may seem to conflict with previous work suggesting that fishers prefer to target more accessible locations closer to their homes. However, much of the existing work on distance effects has involved comparing patterns of fishing effort over tens to hundreds of km (Cinner et al., 2018; Zellmer et al., 2018), in which the costs involved in travel decisions are likely to be much more significant than in coral reef fisheries, in contexts such as Moorea's lagoons where the reef crest is <2 km offshore. Even in systems that exhibit strong declines in fishing effort with distance from port, this is only one of many interacting socioeconomic and cultural factors that influence fishing effort such as social status, variation in skill, territoriality, knowledge transmission, spatial management regulations, or marine tenure (e.g., Boenish & Chen, 2018; Lauer & Aswani, 2009). It is likely that fishers travel across smaller spatial scales in many coral reef fisheries. In these cases, other environmental factors such as habitat suitability, depth and fish distributions, or cultural factors such as fish species preferences attenuate distance effects and can result (as in our case) in an inverse relationship between fishing and distance from shore (García-Quijano, 2009). More

broadly, our findings suggested that generalizations inferred from large-scale commercial fisheries such as the relationship between distance to shore and fishing intensity may not be applicable to small-scale coral reef fisheries.

Fringing reefs experienced generally lower fishing pressure than other lagoon habitats, but they often had high levels of nutrient enrichment (Figure 8, Adam et al., 2021). Indeed, fishing intensity and nutrient enrichment showed opposite cross-shore trends (Figure 7). The observation of reduced fishing intensity on the fringing reef could indicate that this zone is less vulnerable because it does not have high levels of both stressors. However, this pattern might be the result of the combined long-term exposure of fringing reefs to ever-increasing nutrient inputs, modification of the habitat for coastal development (Madi Moussa et al., 2019), and historically high intensity fishing, making these habitats, in the present day, less suitable for fishes and therefore poor attractors for fishers. This is consistent with observations made by older interviewed fishers who noted the decreasing abundance of desirable fish near the shore and the near disappearance of on-foot harpooning as a fishing technique (Conte, 1999), driving a trend of fishing further from home and in deeper areas.

In summary, we found that fishing pressure and nutrient enrichment were spatially variable and not strongly correlated with one another at the island (among-lagoon) and among-habitat (within-lagoon) scales around the island of Moorea. The low spatial covariance at these two landscape scales arose from opposing nutrient–fishing relationships between cross-shore (inversely correlated) and long-shore (positively correlated) directions, which resulted in a mosaic of vulnerabilities to coral–macroalgae phase shifts among lagoon reefs. These results suggested that these two local stressors that are known to facilitate shifts from coral to macroalgal dominance are not simply a function of human population density around the island. Furthermore, the lack of a spatial coherence has important management implications for this and potentially other coral reef systems. Areas with high levels of both stressors at either scale are likely to be more vulnerable to other disturbances that may facilitate a transition to macroalgal dominance (e.g., coral bleaching, storm or anchor damage, crown-of-thorns sea star outbreak). By contrast, areas with low levels of both stressors may be more resilient to other disturbances and could serve as important coral refuges. Importantly, different management levers are required to reduce fishing on herbivores (e.g., implementing potentially temporary or seasonal protected areas; encouraging fishing of non-herbivorous species through species regulations or gear restrictions) and to reduce nutrient inputs (e.g., restricting certain land-use activities; regulating coastal development and sewage treatment). Understanding the spatial patterns of these stressors can enable more efficient allocation of management effort at scales that more appropriately match site-specific social and ecological processes (Hunter et al., 2018).

Translating our findings into specific management actions depends in part on whether stakeholders prioritize management to reduce stressors in high impact areas, or to protect the most resilient or low impact areas. For example, the two lagoons on the north shore that had high levels of both stressors could be considered for efforts to reduce fishing on herbivores and/or control nutrient inputs. The lagoon on the west shore with low fishing and low nutrients could be a high priority for protection via conservation measures to maintain this low impact status into the future. At the habitat scale, mid-lagoon and back reef habitats had higher fishing but lower nutrient inputs. If stakeholders wanted to reinforce this trend and prevent increasing fishing pressure on fringing reefs in the future that experience the highest nutrient loadings, they could combine habitat-specific protected areas, targeting the fringing reefs with increased subsidies and helping fishers to acquire larger boats and motors. This would enable them to reach the least vulnerable habitats to nutrient inputs, even in inclement weather. Regardless, based on our results and those previously reported (Adam et al., 2021), there is a clear need to prioritize the reduction of inputs of anthropogenically derived nutrients into the lagoons of Moorea. In addition to management actions, our results could inform where reef managers, scientists, or community-based organizations should focus monitoring effort to assess and better understand temporal trajectories of fishing pressure, nutrient enrichment, and the implications of these two factors for coral-to-algae phase shifts, and a template for how to couple natural and social science data to achieve such aims.

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research was approved by the San Diego State University's Institutional Review Board (HS-2017-0179).

CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHOR CONTRIBUTIONS

Sally J. Holbrook, Matthew Lauer, Andrew Rassweiler, Sarah E. Lester, and Russell J. Schmitt conceptualized the study and secured funding; Thomas C. Adam, Dana C. Cook, Sally J. Holbrook, Scott D. Miller, Russell J. Schmitt, Matthew Lauer, and Jean Wencélius designed and performed the ecological field work; Chelsea E. Hunter, Matthew Lauer, and Jean Wencélius designed and performed the social science field work; Jean Wencélius, Thomas C. Adam, Andrew Rassweiler, and Alexandra K. Dubel analyzed and visualized data; Thomas C. Adam oversaw collection and processing of nutrient data; Sally J. Holbrook wrote the initial manuscript draft; all authors contributed to data interpretation and manuscript revisions.

DATA AVAILABILITY STATEMENT

Nutrient data are available at EDI Data Portal (Moorea Coral Reef et al., 2020): https://doi.org/10.6073/pasta/1197c058ca1672c6f21bdd25d536e25a. Human subjects data are sensitive and not publicly available; these data can be obtained by researchers with appropriate credentials from Matthew Lauer, Dept. of Anthropology, San Diego State University.

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REFERENCES

Adam, T.C., D.E. Burkepile, S.J. Holbrook, R.C. Carpenter, J. Claudet, C. Loiseau, L. Thiault, A.J. Brooks, L. Washburn, and R.J. Schmitt. 2021. "Landscape-Scale Patterns of Nutrient Enrichment in a Coral Reef Ecosystem: Implications for Coral to Algae Phase Shifts." *Ecological Applications* 31(1): e02227. https://doi.org/10.1002/eap.2227

Adam, T.C., R.J. Schmitt, S.J. Holbrook, A.J. Brooks, P.J. Edmunds, R.C. Carpenter, and G. Bernardi. 2011. "Herbivory, Connectivity and Ecosystem Resilience: Response of a Coral Reef to a Large-Scale Perturbation." *PLoS One* 6(8): e23717.

Aswani, S. 1998. "Patterns of Marine Harvest Effort in Southwestern New Georgia, Solomon Islands: Resource Management or Optimal Foraging?" *Ocean and Coastal Management* 40: 207–35.

Atkinson, M., and S. Smith. 1983. "C: N: P Ratios of Benthic Marine Plants." *Limnology and Oceanography* 28: 568–74.

Ban, S.S., N.A.J. Graham, and S.R. Connolly. 2014. "Evidence for Multiple Stressor Interactions and Effects on Coral Reefs." *Global Change Biology* 20: 681–97.

Bates, D., M. Maechler, B. Bolker, and S. Walker. 2015. "Fitting Linear Mixed-Effects Models Using lme4." *Journal of Statistical Software* 67: 1–48.

Boenish, R., and Y. Chen. 2018. "Spatiotemporal Dynamics of Effective Fishing Effort in the American Lobster (*Homarus americanus*) Fishery along the Coast of Maine, USA." *Fisheries Research* 199: 231–41.

Branch, T.A., R. Hilborn, A.C. Haynie, G. Fay, L. Flynn, J. Griffiths, K.N. Marshall, et al. 2006. "Fleet Dynamics and Fishermen Behavior: Lessons for Fisheries Managers." *Canadian Journal of Fisheries and Aquatic Sciences* 63: 1647–68.

Cinner, J. 2014. "Coral Reef Livelihoods." *Current Opinion in Environmental Sustainability* 7: 65–71.

Cinner, J.E., E. Maire, C. Huchery, M.A. MacNeil, N.A.J. Graham, C. Mora, T.R. McClanahan, et al. 2018. "Gravity of Human Impacts Mediates Coral Reef Conservation Gains." *Proceedings of the National Academy of Sciences of the United States of America* 115: E6116–25.

Collin, A., C. Ramambason, Y. Pastol, E. Casella, A. Rovere, L. Thiault, B. Espiau, et al. 2018. "Very High Resolution Mapping of Coral Reef State Using Airborne Bathymetric LiDAR Surface-Intensity and Drone Imagery." *International Journal of Remote Sensing* 39: 5676–88.

Conte, E. 1999. "Pêches pré-européennes et survivances en Polynésie Française." In *Les petites activités de pêche dans le Pacifique Sud*, edited by G. Blanchet, 27–40. Paris: IRD.

Cooper, T.F., S. Uthicke, C. Humphrey, and K.E. Fabricius. 2007. "Gradients in Water Column Nutrients, Sediment Parameters, Irradiance and Coral Reef Development in the Whitsunday Region, Central Great Barrier Reef." *Estuarine, Coastal and Shelf Science* 74: 458–70.

Costa, O.S., Jr. 2007. "Anthropogenic Nutrient Pollution of Coral Reefs in Southern Bahia, Brazil." *Brazilian Journal of Oceanography* 55: 265–79.

Costa, O.S., Jr., M. Nimmo, and M.J. Attrill. 2008. "Coastal Nitrification in Brazil: A Review of the Role of Nutrient Excess on Coral Reef Demise." *Journal of South American Earth Sciences* 25: 257–70.

Dailer, M.L., R.S. Knox, J.E. Smith, M. Napier, and C.M. Smith. 2010. "Using δ15N Values in Algal Tissue to Map Locations and Potential Sources of Anthropogenic Nutrient Inputs on the Island of Maui, Hawai'i, USA." *Marine Pollution Bulletin* 60: 655–71.

Daks, R., T. Ticktin, S.D. Jupiter, and A. Friedlander. 2018. "Drivers of Fishing at the Household Scale in Fiji." *Ecology and Society* 23(1): 37.

Daw, T., J. Maina, J. Cinner, J. Robinson, and A. Wamukota. 2011. The Spatial Behaviour of Artisanal Fishers: Implications for Fisheries Management and Development (Fishers in Space). Fishers in Space Final Report. December 2011. 79 p

Duran, A., A.A. Shantz, D.E. Burkepile, L. Collado-Vides, V.M. Ferrer, L. Palma, A. Ramos, and P. González-Díaz. 2018. "Fishing, Pollution, Climate Change, and the Long-Term Decline of Coral Reefs off Havana, Cuba." *Bulletin of Marine Science* 94: 213–28.

Fabricius, K., G. De'ath, L. McCook, E. Turak, and D.M.C.B. Williams. 2005. "Changes in Algal, Coral and Fish Assemblages along Water Quality Gradients on the Inshore Great Barrier Reef." *Marine Pollution Bulletin* 51: 384–98.

Feist, B.E., and P.S. Levin. 2016. "Novel Indicators of Anthropogenic Influence on Marine and Coastal Ecosystems." *Frontiers in Marine Science* 3: 113.

Fong, P., R.M. Donohoe, and J.B. Zedler. 1994. "Nutrient Concentration in Tissue of the Macroalga *Enteromorpha* as a Function of Nutrient History - an Experimental Evaluation Using Field Microcosms." *Marine Ecology Progress Series* 106: 273–82.

García-Quijano, C.G. 2009. "Managing Complexity: Ecological Knowledge and Success in Puerto Rican Small-Scale Fisheries." *Human Organization* 68: 1–17.

Garren, M., S. Smriga, and F. Azam. 2008. "Gradients of Coastal Fish Farm Effluents and their Effect on Coral Reef Microbes." *Environmental Microbiology* 10: 2299–312.

Gil, M.A., S.U. Goldenberg, A. Ly Thai Bach, S.C. Mills, and J. Claudet. 2016. "Interactive Effects of Three Pervasive Marine Stressors in a Post-Disturbance Coral Reef." *Coral Reefs* 35: 1281–93.

Gilby, B.L., P.S. Maxwell, I.R. Tibbets, and T. Stevens. 2015. "Bottom-up Factors for Algal Productivity Outweigh no-Fishing Marine Protected Area Effects in a Marginal Coral Reef System." *Ecosystems* 18: 1056–69.

Graham, N.A.J., D.R. Bellwood, J.E. Cinner, T.P. Hughes, A.V. Norström, and M. Nyström. 2013. "Managing Resilience to Reverse Phase Shifts in Coral Reefs." *Frontiers in Ecology and the Environment* 11: 541–8.

Han, X., T.C. Adam, R.J. Schmitt, A.J. Brooks, and S.J. Holbrook. 2016. "Response of Herbivore Functional Groups to Sequential Perturbations in Moorea, French Polynesia." *Coral Reefs* 35: 999–1009.

Harborne, A.R., A.L. Green, N.A. Peterson, M. Beger, Y. Golbuu, P. Houk, M.D. Spalding, et al. 2018. "Modelling and Mapping Regional-Scale Patterns of Fishing Impact and Fish Stocks to Support Coral-Reef Management in Micronesia." *Diversity and Distributions* 24: 1729–43.

Holbrook, S.J., T.C. Adam, P.J. Edmunds, R.J. Schmitt, R.C. Carpenter, A.J. Brooks, H.S. Lenihan, and C.J. Briggs. 2018. "Recruitment Drives Spatial Variation in Recovery Rates of Resilient Coral Reefs." *Scientific Reports* 8: 7338.

Holbrook, S.J., R.J. Schmitt, T.C. Adam, and A.J. Brooks. 2016. "Coral Reef Resilience, Tipping Points and the Strength of Herbivory." *Scientific Reports* 6: 35817.

Hughes, T.P., M.L. Barnes, D.R. Bellwood, J.E. Cinner, G.S. Cumming, J.B.C. Jackson, J. Kleypas, et al. 2017. "Coral Reefs in the Anthropocene." *Nature* 546: 82–90.

Hughes, T.P., and J.H. Connell. 1999. "Multiple Stressors on Coral Reefs: A Long-Term Perspective." *Limnology and Oceanography* 44: 932–40.

Hunter, C.E., M. Lauer, A. Levine, S. Holbrook, and A. Rassweiler. 2018. "Maneuvering towards Adaptive Co-Management in a Coral Reef Fishery." *Marine Policy* 98: 77–84.

Jupiter, S., G. Roff, G. Marion, M. Henderson, V. Schrameyer, M. McCulloch, and O. Hoegh-Guldberg. 2008. "Linkages between Coral Assemblages and Coral Proxies of Terrestrial Exposure along a Cross-Shelf Gradient on the Southern Great Barrier Reef." *Coral Reefs* 27: 887–903.

Knee, K.L., E.D. Crook, J.L. Hench, J.J. Leichter, and A. Payton. 2016. "Assessment of Submarine Groundwater Discharge (SGD) as a Source of Dissolved Radium and Nutrients to Moorea (French Polynesia) Coastal Waters." *Estuaries and Coasts* 39: 1651–68.

Lapointe, B.E., P.J. Barile, M.M. Littler, and D.S. Littler. 2005. "Macroalgal Blooms on Southeast Florida Coral Reefs II. Cross-Shelf Discrimination of Nitrogen Sources Indicates Widespread Assimilation of Sewage Nitrogen." *Harmful Algae* 4: 1106–22.

Lapointe, B.E., P.J. Barile, C.S. Yentsch, M.M. Littler, D.S. Littler, and B. Kakuk. 2004. "The Relative Importance of Nutrient Enrichment and Herbivory on Macroalgal Communities near Norman's Pond Cay, Exumas Cays, Bahamas: A "Natural" Enrichment Experiment." *Journal of Experimental Marine Biology and Ecology* 298: 275–301.

Lapointe, B.E., R. Langton, B.J. Bedford, A.C. Potts, O. Day, and C. Hu. 2010. "Land-Based Nutrient Enrichment of the Buccoo Reef Complex and Fringing Coral Reefs of Tobago, West Indies." *Marine Pollution Bulletin* 60: 334–43.

Lauer, M., and S. Aswani. 2009. "Indigenous Ecological Knowledge as Situated Practices: Understanding Fishers' Knowledge in the Western Solomon Islands." *American Anthropologist* 111: 317–29.

Leenhardt, P., M. Lauer, R. Madi Moussa, S.J. Holbrook, A. Rassweiler, R.J. Schmitt, and J. Claudet. 2016. "Complexities and Uncertainties in Transitioning Small-Scale Coral Reef Fisheries." *Frontiers in Marine Science* 3: 70.

Leichter, J.L., A.L. Alldredge, G. Bernardi, C.A. Carlson, R.C. Carpenter, P.J. Edmunds, M.R. Fewings, et al. 2013. "Biological and Physical Interactions on a Tropical Island Coral Reef: Transport and Retention Processes on Moorea, French Polynesia." *Oceanography* 26: 52–63.

Lenth, R. 2020. emmeans: Estimated Marginal Means, Aka Least-Squares Means. R Package Version 1.5.1. https://CRAN.R-project.org/package=emmeans

Lin, D.T., and P. Fong. 2008. "Macroalgal Bioindicators (Growth, Tissue N, δ15N) Detect Nutrient Enrichment from Shrimp Farm Effluent Entering Opunohu Bay, Moorea, French Polynesia." *Marine Pollution Bulletin* 56: 245–9.

Lirman, D., and P. Fong. 2007. "Is Proximity to Land-Based Sources of Coral Stressors an Appropriate Measure of Risk to Coral Reefs? An Example from the Florida Reef Tract." *Marine Pollution Bulletin* 54: 779–91.

Loiseau, C., L. Thiault, R. Devillers, and J. Claudet. 2021. "Cumulative Impact Assessments Highlight the Benefits of Integrating Land-Based Management with Marine Spatial Planning." *Science of the Total Environment* 787: 147339.

Lüdecke, D. 2020. sjPlot: Data Visualization for Statistics in Social Science. R Package Version 2.8.6. https://CRAN.R-project.org/package=sjPlot.

Madi Moussa, R., L. Fogg, F. Bertucci, M. Calandra, A. Collin, A. Aubanel, S. Polti, et al. 2019. "Long-Term Coastline Monitoring on a Coral Reef Island (Moorea, French Polynesia)." *Ocean and Coastal Management* 180(1): 104928.

McCook, L. 1999. "Macroalgae, Nutrients and Phase Shifts on Coral Reefs: Scientific Issues and Management Consequences for the Great Barrier Reef." *Coral Reefs* 18: 357–67.

Moorea Coral Reef LTER, D. Burkepile, and T. Adam. 2020. MCR LTER: Coral Reef: Landscape-Scale Patterns of Nutrient Enrichment in a Coral Reef Ecosystem: Implications for Coral to Algae Phase Shifts, Adam et al., Ecol. Appl. ver 10.

Environmental Data Initiative. https://doi.org/10.6073/pasta/1197c058ca1672c6f21bdd25d536e25a

Naim, O. 1993. "Seasonal Responses of a Fringing Reef Community to Eutrophication (Reunion Island, Western Indian Ocean)." *Marine Ecology Progress Series* 99: 137–51.

Olmedo, O. E. 2014. Kriging: Ordinary Kriging. R Package Version 1.1. https://CRAN.R-project.org/package=kriging.

Page, H.M., A.J. Brooks, M. Kulbicki, R. Galzin, R.J. Miller, D.C. Reed, R.J. Schmitt, S.J. Holbrook, and C. Koenigs. 2013. "Stable Isotopes Reveal Trophic Relationships and Diet of Consumers in Temperate Kelp Forest and Coral Reef Ecosystems." *Oceanography* 26: 180–9.

Pinheiro, J., D. Bates, S. DebRoy, D. Sarkar, R Core Team. 2020. nlme: Linear and Nonlinear Mixed Effects Models. R Package Version 3.1-148. https://CRAN.R-project.org/package=nlme.

Rasher, D.B., S. Engel, V. Bonito, G.J. Fraser, J.P. Montoya, and M. E. Hay. 2012. "Effects of Herbivory, Nutrients, and Reef Protection on Algal Proliferation and Coral Growth on a Tropical Reef." *Oecologia* 169: 187–98.

Rassweiler, A., C. Costello, and D.A. Siegel. 2012. "Marine Protected Areas and the Value of Spatially Optimized Fishery Management." *Proceedings of the National Academy of Sciences of the United States of America* 109: 11884–9.

Rassweiler, A., M. Lauer, S.E. Lester, S.J. Holbrook, R.J. Schmitt, R. Madi Moussa, K. Munsterman, et al. 2020. "Perceptions and Responses of Pacific Island Fishers to Changing Coral Reefs." *Ambio* 49: 130–43.

Reopanichkul, P., R.W. Carter, S. Worachananant, and C.J. Crossland. 2010. "Wastewater Discharge Degrades Coastal Waters and Reef Communities in Southern Thailand." *Marine Environmental Research* 69: 287–96.

Sampson, G.S. 2018. "Economic Spillovers in Spatial Harvest Behavior." *Ecological Economics* 145: 57–74.

Saul, S., and D. Die. 2016. "Modeling the Decision-Making Behavior of Fishers in the Reef Fish Fishery on the West Coast of Florida." *Human Dimensions of Wildlife* 21: 567–86.

Schaffelke, B. 1999. "Short-Term Nutrient Pulses as Tools to Assess Responses of Coral Reef Macroalgae to Enhanced Nutrient Availability." *Marine Ecology Progress Series* 182: 305–10.

Schmitt, R.J., S.J. Holbrook, S.L. Davis, A.J. Brooks, and T.C. Adam. 2019. "Experimental Support for Alternate Attractors on Coral Reefs." *Proceedings of the National Academy of Sciences of the United States of America* 116(10): 4372–81.

Shantz, A.A., M.C. Ladd, E. Schrack, and D.E. Burkepile. 2015. "Fish-Derived Nutrient Hotspots Shape Coral Reef Benthic Communities." *Ecological Applications* 25: 2142–52.

Smith, J.E., C.L. Hunter, and C.M. Smith. 2010. "The Effects of Top-Down Versus Bottom-Up Control on Benthic Coral Reef Community Structure." *Oecologia* 163: 497–507.

Smith, S.V., D.P. Swaney, L. Talaue-Mcmanus, J.D. Bartley, P.T. Sandhei, C.J. McLaughlin, V.C. Dupra, et al. 2003. "Humans, Hydrology, and the Distribution of Inorganic Nutrient Loading to the Ocean." *Bioscience* 53: 235–45.

Stallings, C.D. 2009. "Fishery-Independent Data Reveal Negative Effect of Human Population Density on Caribbean Predatory Fish Communities." *PLoS One* 4(5): e5333.

Stewart-Smith, R.D., N.S. Barrett, C.M. Crawford, S.D. Frusher, D. G. Stevenson, and G.J. Edgar. 2008. "Spatial Patterns in Impacts of Fishing on Temperate Rocky Reefs: Are Fish Abundance and Mean Size Related to Proximity to Fisher Access Points?" *Journal of Experimental Marine Biology and Ecology* 365: 16–5.

Street, J.H., K.L. Knee, E.E. Grossman, and A. Paytan. 2008. "Submarine Groundwater Discharge and Nutrient Addition to the Coastal Zone and Coral Reefs of Leeward Hawai'i." *Marine Chemistry* 109: 355–76.

Teh, L.C.L., L.S.L. Teh, and M.J. Meitner. 2012. "Preferred Resource Spaces and Fisher Flexibility: Implications for Spatial Management of Small-Scale Fisheries." *Human Ecology* 40: 213–26.

Thiault, L., A. Collin, F. Chlous, S. Gelcich, and J. Claudet. 2017. "Combining Participatory and Socioeconomic Approaches to Map Fishing Effort in Small-Scale Fisheries." *PLoS One* 12(5): e0176862.

Thiault, L., L. Kernaléguen, C.W. Osenberg, T. Lison de Loma, Y. Chancerelle, G. Siu, and J. Claudet. 2019. "Ecological Evaluation of a Marine Protected Area Network: A Progressive-Change BACIPS Approach." *Ecosphere* 10(2): e02576.

Walsh, S.M. 2011. "Ecosystem-Scale Effects of Nutrients and Fishing on Coral Reefs." *Journal of Marine Biology* 2011: 187248.

Ward-Paige, C.A., C. Mora, H.K. Lotze, C. Pattengill-Semmens, L. McClenachan, E. Arias-Castro, and R.A. Myers. 2010. "Large-Scale Absence of Sharks on Reefs in the Greater-Caribbean: A Footprint of Human Pressures." *PLoS One* 5(8): e11968.

Welle, P.D., M.J. Small, S.C. Doney, and I.L. Azevedo. 2017. "Estimating the Effect of Multiple Environmental Stressors on Coral Bleaching and Mortality." *PLoS One* 12(5): e0175018.

Zaneveld, J.R., D.E. Burkepile, A.A. Shantz, C.E. Pritchard, R. McMinds, J.P. Payet, R. Welsh, et al. 2016. "Overfishing and Nutrient Pollution Interact with Temperature to Disrupt Coral Reefs Down to Microbial Scales." *Nature Communications* 7: 11833.

Zellmer, A.J., J.T. Claisse, C.M. Williams, and D.J. Pondella. 2018. "Long-Term, Spatial Marine Harvest Intensity as an Indicator of Human Impact on Shallow Rocky Reef Ecosystems." *Marine Ecology* 39: e12463.

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Additional supporting information may be found in the online version of the article at the publisher's website.

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