Running Head: nutrient enrichment on a coral reef Landscape-scale patterns of nutrient enrichment in a coral reef ecosystem: implications for coral to algae phase shifts

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Landscape-scale patterns of nutrient enrichment in a coral reef ecosystem: implications for coral to algae phase shifts

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Abstract

Nutrient pollution is altering coastal ecosystems worldwide. On coral reefs, excess nutrients can favor the production of algae at the expense of reef-building corals, yet the role of nutrients in driving community changes such as shifts from coral to macroalgae is not well understood. Here we investigate the potential role of anthropogenic nutrient loading in driving recent coral-to-macroalgae phase shifts on reefs in the lagoons surrounding the Pacific island of Moorea, French Polynesia. We use nitrogen (N) tissue content and stable isotopes ($\delta^{15}N$) in an abundant macroalga (*Turbinaria ornata*) together with empirical models of nutrient discharge to describe spatial and temporal patterns of nutrient enrichment in the lagoons. We then employ time series data to test whether recent increases in macroalgae are associated with nutrients. Our results revealed that patterns of N enrichment were linked to several factors, including rainfall, wave-driven circulation, and distance from anthropogenic nutrient sources, especially human sewage. Reefs near large watersheds, where inputs of N from sewage and agriculture are high, have been consistently enriched in N for at least the last decade. In many of these areas, corals have decreased and macroalgae have increased, while reefs with lower levels of N input have maintained high cover of coral and low cover of macroalgae. Importantly, these patchy phase shifts to macroalgae have occurred despite substantial island-wide increases in the density and biomass of herbivorous fishes over the time period. Together, these results indicate that nutrient loading may be an important driver of coral-to-macroalgae phase shifts in the lagoons of Moorea even though the reefs harbor an abundant and diverse herbivore assemblage. These results emphasize the important role that bottom-up factors can play in driving coral-to-macroalgae phase shifts and underscore the critical importance of watershed management for reducing inputs of nutrients and other land-based pollutants to coral reef ecosystems.

Key words: *coral reef; phase shift; macroalgae; nutrient pollution; nitrogen; sewage; top-down; bottom-up;* Turbinaria ornata*; stable isotopes; $\delta^{15}N$; herbivory*

Introduction

Nutrient pollution is a major anthropogenic force altering coastal ecosystems worldwide (Carpenter et al. 1998, Howarth 2008). Anthropogenic inputs of nitrogen and phosphorous can facilitate blooms of harmful algae, reduce water clarity, alter food webs, and deplete oxygen leading to dead zones (Boesch 2002), ultimately disrupting fisheries and harming human health (Anderson et al. 2012). These adverse effects of excess nutrients on coastal ecosystems are likely to be exacerbated in coming decades by continued changes in land-use as well as altered precipitation regimes and ocean warming due to climate change (Altieri and Gedan 2015, Gobler et al. 2017, Sinha et al. 2017).

Excess nutrients can be especially harmful to oligotrophic systems such as coral reefs. High levels of nutrient loading can lead to persistent blooms of algae that can dramatically alter the structure and function of reef ecosystems (Naim 1993, Loya 2004, Lapointe et al. 2005). Even moderate nutrient loading can favor algae and heterotrophic filter feeders that compete with corals and other reef building taxa (Fabricius 2005, Rice et al. 2020), thereby impeding coral recovery following a disturbance (Graham et al. 2015, MacNeil et al. 2019). Nitrogen (N) loading can be particularly harmful to coral reefs, as excess N can negatively impact coral growth and survival in addition to fueling algal growth (D'Angelo and Wiedenmann 2014, Shantz and Burkepile 2014, Morris et al. 2019). Thus, understanding the sources and impacts of anthropogenic N is critical for conservation and management of coral reef ecosystems.

In some cases, N pollution can be traced to a specific point source (e.g., sewage outfall) (Smith et al. 1981, Dailer et al. 2010). However, most N input to coastal ecosystems is derived from diffuse nonpoint sources (Carpenter et al. 1998). On coral reefs, N from nonpoint sources tends to be delivered in surface water runoff during episodic rainfall events and via discharge of submarine groundwater. After reaching the ocean, N-rich water is then transported and mixed via local hydrodynamic features. Small-scale hydrodynamics also influence rates of nutrient uptake by modifying boundary-layer conditions of benthic organisms (Carpenter et al. 1991). Thus, the movement and ultimate fate of anthropogenically-derived N in nearshore ecosystems are complex and will depend on many interacting factors, including the location of N sources, the timing of rainfall, and the hydrodynamic environment (Brocke et al. 2015).

A more complete understanding of the impacts of N pollution on nearshore ecosystems requires knowledge of the spatial and temporal patterns of enrichment and how the physical environment modulates these patterns. In many locations, water column nutrients are measured periodically in mandated water quality monitoring programs. These programs can provide valuable information on decadal-scale trends and large-scale spatial patterns of nutrient availability (De'Ath and Fabricius 2010, Duprey et al. 2016, Lapointe et al. 2019). However, the coarse temporal and spatial resolution of most water column monitoring programs precludes building a mechanistic understanding of the causes and consequences of nutrient enrichment in many coastal systems. This is particularly true on coral reefs, where researchers have used N content and isotopic signatures in benthic algae to resolve patterns of N enrichment at relatively small spatial scales (Umezawa et al. 2002, Lin and Fong 2008, Dailer et al. 2010). However, these studies generally have not linked enrichment patterns to benthic community dynamics or ecosystem processes (but see Lapointe 1997). As a result, there is widespread disagreement

regarding the levels of nutrient enrichment that are harmful to coral reefs and how important nutrients are for impacting coral reef community dynamics (Lapointe 1999, Szmant 2002, D'Angelo and Wiedenmann 2014, Arias-González et al. 2017, Bruno et al. 2019).

Here we quantify the spatial and temporal patterns of N availability on coral reefs around the South Pacific island of Moorea, French Polynesia. The coral reefs around Moorea have undergone multiple cycles of disturbance and recovery over the past four decades. While the oligotrophic fore reef has shown remarkable resilience to disturbances (Adjeroud et al. 2009, 2018, Holbrook et al. 2018, Kayal et al. 2018), the reefs within the lagoons have exhibited contrasting dynamics, with some reefs shifting from coral- to macroalgae-dominated communities (Schmitt et al. 2019). Nutrient input could be a major driver of algal proliferation within the lagoons, but to date, no studies have evaluated the spatial or temporal patterns of enrichment or how those patterns relate to benthic community dynamics. Here, we combine N content and stable isotopes ($\delta^{15}N$) in the tissue of the macroalga *Turbinaria ornata*, together with empirical models of nutrient discharge and time series data on the dynamics of benthic algae and coral to address the following questions: 1) What are the spatial patterns of N enrichment and how do these patterns vary across seasons with different levels of rainfall and wave forcing? 2) To what extent are spatial patterns of N enrichment related to anthropogenic inputs? and 3) Are recent increases in macroalgae related to N enrichment?

Methods

Site Description

Moorea, French Polynesia (17 º 30′S, 149 º 50′W) is a small (~ 135 km^2) volcanic island located near the larger island of Tahiti in the central South Pacific. The ocean surrounding

Moorea is oligotrophic, with levels of dissolved inorganic nitrogen (DIN) often at or below detection limits (nitrate plus nitrite in the top 25 m of the water column: 0.38 +/- 0.84 uM; mean +/- SD) (Alldredge and Carlson 2019). The island is surrounded by a well-developed barrier reef located ~ 1 km offshore that is intersected by 12 reef passes that connect the shallow protected lagoons inside the barrier reef to the open ocean (Fig. 1a). Shoreward of the reef crest is a distinct back reef habitat that is less than 3 m deep and is dominated by patch reefs separated by sand, coral rubble, and reef pavement. Directly adjacent to land are shallow fringing reefs that in some locations are separated from shallow back reef habitats by a channel (> 10 m deep) that connects to a reef pass.

Tidal amplitudes are small (< 30 cm), and circulation within the lagoon is primarily driven by wave forcing across the reef crest, which creates flow into the lagoon and out of the reef passes (Hench et al. 2008, Leichter et al. 2013). Wave forcing is largely driven by long period swells originating from storms thousands of kilometers away. As a result, wave exposure (and thus circulation patterns) varies seasonally and among sides of the island concurrent with seasonal differences in storm activity in the northern and southern hemispheres. The west and east shores receive the most wave energy, with peak wave energy occurring during winter in the southern hemisphere (hereafter 'austral winter') from May to October. In contrast, peak wave energy on the north shore occurs from November to April during winter in the northern hemisphere ('austral summer') (Edmunds et al. 2010). Moorea's climate is characterized by a warm, wet season from November to April and a cooler and drier season from May to October.

Due to the steep topography, the island's ~ 17,000 residents are concentrated along its 60 km coastline, with population centers located in several large valleys. Rapid population increases in recent decades have coincided with substantial land clearing for agriculture and urbanization

(Walker et al. 2014). In contrast to ocean waters, DIN concentrations can be very high (> 100 uM) in groundwater and streams (Knee et al. 2016, Haßler et al. 2019). Major sources of N to the lagoons include treated and untreated human sewage, animal waste from livestock, and fertilizer from agriculture and landscaping (Haßler et al. 2019).

What are the spatial patterns of N enrichment and how do these patterns vary across seasons with different levels of rainfall and wave forcing?

To quantify seasonal variation in nutrient delivery mechanisms, we obtained daily rainfall and wave data. Rainfall data were from a meteorological station in Faaa, Tahiti (Global Historical Climatology Network ID:FP000091938), ~ 15 km east of Moorea. We calculated a 30-day moving sum for October 2015 through August 2016, which corresponded with our high resolution N sampling, and plotted the LOESS smoothed values together with the monthly means during the different sampling intervals using the R package ggplot2 (Wickham 2016).

Wave data have been collected continuously at three sites on the exposed fore reef of Moorea (one site on each of the island's three sides) since 2005 as part of the MCR LTER project (http://mcrlter.msi.ucsb.edu/cgi-bin/showDataset.cgi?docid=knb-lter-mcr.30; Washburn 2018). At each site, data from bottom-mounted Wave & Tide recorders (SBE 26plus; Sea-Bird Electronics, Inc., Bellevue, WA, USA) and bottom-mounted Acoustic Doppler Current Profilers (Sentinel ADCPs: Teledyne RD Instruments, Poway, CA, USA) were used to estimate significant wave height (H_s) and dominant wave period (T_p) at 2 h sampling intervals. Daily averages of H_s and T_p were then calculated and total wave power (P) per linear meter of reef was estimated using deep-water approximations as $P = \rho g^2 H_s^2 T_p / 32 \pi$ where ρ is seawater density (1025 kg m^{-3}) and g is the acceleration of gravity (9.81 ms^{-2}).

We used ADCPs as the primary instrument to quantify patterns of wave forcing on the three shores of the island because ADCPs had fewer missing values compared to the SBE 26s during our study; to obtain a complete record we used data from the SBE 26s when ADCP data were missing. To ensure that data from the two instruments were comparable, we used the full time series of wave data in least squares linear regressions to estimate the site-specific log-log relationships between P as measured by the SBE 26s and ADCPs. The relationships were strong (r^2 ranging from 0.86 to 0.90), and missing ADCP data were gap filled with the predicted values based on these site-specific relationships. We then calculated daily mean wave power for each shore of the island during each 90-day period preceding our sampling efforts. We focused on a 90-day period assuming that N tissue content in the thalli of *Turbinaria ornata* (hereafter, '*Turbinaria*'), the species of macroalgae we used to map N availability, reflects the nutrient environment during a period of up to three months prior to its collection. This estimate is based on the growth rates and longevity of *Turbinaria* thalli (Davis 2018, Schmitt et al. 2019). However, because little is known about N storage and turnover in *Turbinaria* we also describe rainfall and wave conditions during the 45-day period prior to *Turbinaria* collection (Appendix S1: Figs. S1 and S2) since these two time scales (45 and 90 days) are likely to bracket the period of influence.

To map N availability in the lagoons of Moorea, we collected samples of *Turbinaria* at ~ 180 sites around the island during three different sampling periods, corresponding with different rainfall and wave regimes (January 2016, May 2016, and August 2016) (Adam and Burkepile 2020). Sites were at least 0.5 km apart and were spaced to maximize coverage of the different reef habitats within the lagoons, including the fringing reefs, mid-lagoon/back reef, reef crest, reef passes, and bays (Fig. 1a). Like other macroalgae, *Turbinaria* responds to N pulses by

storing surplus N (Schaffelke 1999) and consequently N tissue content is believed to be an excellent time-integrated indicator of N availability (Atkinson and Smith 1983, Fong et al. 1994, Shantz et al. 2015). Sampling was conducted over ~ 3 weeks during each of the three sampling periods; due to logistic constraints, some sites were not sampled in all three sampling periods (January n = 184, May n = 171, August n = 173). At each of the sites, we collected thalli from 10 different patches of *Turbinaria* across an area of ~ 500 m^2. Samples were immediately placed on ice and transported to the laboratory. One blade from each of 10 thalli was sampled at 5 cm below the apical tip. Blades were scrubbed of epiphytes and rinsed with fresh water before being dried at 60° C to a constant weight and ground to a fine powder. 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.

In addition to analyzing N content of algal tissue, we also conducted stable isotope analyses to help determine the sources of N. The use of naturally occurring stable isotopes of N (^{15}N: ^{14}N, expressed as $\delta^{15}N$) is particularly useful for distinguishing between natural and sewage-derived N because natural sources generally have low signatures while sewage-derived N is high in ^{15}N (with $\delta^{15}N$ values ranging from ~ 5% to 20%) (Risk et al. 2009, Kendall et al. 2012). In the lagoons of Moorea, N likely comes from a mix of oceanic and terrestrial sources, the latter including synthetic and organic fertilizers, livestock, and human sewage. Because synthetic fertilizers tend to have $\delta^{15}N$ signatures that are similar to or lower than natural sources (generally ranging from -4 to 4%) (Dailer et al. 2010), elevated $\delta^{15}N$ values would indicate that human sewage or animal waste are important sources of N but would not rule out the importance of fertilizers or other sources. Isotopic analysis on dried and ground algal tissue was conducted using a Thermo Finnigan Delta-Plus Advantage isotope mass spectrometer with a Costech EAS

198 elemental analyzer at the University of California, Santa Barbara, Marine Science Institute
199 Analytical Laboratory.

200 Spatial patterns of N enrichment (total N expressed as % of dry weight) were visualized
201 using ordinary kriging with a spherical variogram model as implemented in the R package
202 'kriging' (Olmedo 2014). To test whether enrichment patterns were consistent across sample
203 periods at the scale of individual sites we used linear correlation, with separate correlations
204 conducted for each side of the island. Finally, we used ANOVA to test whether N levels varied
205 among our three sample periods. Because of significant spatial autocorrelation among sites, we
206 analyzed the mean % N on each of the island's three shores as a conservative test, using data
207 only from the set of 155 sites that were surveyed in all three sample periods.

208 Visual inspection of N interpolations suggested that spatial patterns of enrichment were
209 related to wave power (see Results). Therefore, we used the results of the correlation analysis
210 described in the previous paragraph to test whether temporal consistency depended on variation
211 in wave forcing. Specifically, we used Pearson's correlation to test whether the correlation
212 coefficient describing the temporal correlation in N enrichment (% N) was related to differences
213 in mean wave power (specific to each shore) across the different sample periods.

214 **To what extent are spatial patterns of nitrogen enrichment related to anthropogenic**
215 **inputs?**

216 To test whether spatial patterns of N enrichment were associated with anthropogenic N
217 inputs into the lagoons, we modeled the distribution of N from sewage and agriculture based on
218 spatially explicit data from the urban planning office of French Polynesia and the Institut de la
219 Statistique de la Polynésie Française (ISPF). We mapped the relative input of nutrients from

agriculture in the lagoon using a three-step procedure. First, for each catchment area (n = 119), we calculated the total farmed area based on data available from the urban planning office of French Polynesia, and used it as an estimate of "agriculture intensity". Second, we estimated the maximum diffusion potential of each catchment (MDP_w) using the following formula:

$MDP_w = a * A_w + b$ where A_w is the size of the catchment *w* in square km and a and b are the slope (a= 0.0022) and intercept (b= 15.82) of the linear relationship, obtained from Adjeroud & Salvat (1996). This approach is consistent with global (Burgers et al. 2014) and local (Brown et al. 2017) studies highlighting the positive correlation between A_w and nutrient discharge to the marine environment, and has been widely used in cumulative impact assessments (Halpern et al. 2008, Ban et al. 2010, Micheli et al. 2013). Third, we applied a kernel density function at each river mouth that linearly decays "agriculture intensity" of the associated watershed basin from the river mouth (maximum value) to the MDP_w (null value) to disperse these watershed-scale values onto Moorea's reefs. Then, values were re-scaled from 0 to 1 in order to represent the relative level of nutrient input from agriculture with the final layer having 5 m resolution. Kernel estimation was completed using the Heatmap plugin in QGIS v2.18.14 (QGIS Development Team 2016).

We mapped the relative sewage discharge by combining household density along the coast and the water treatment system used in each individual household (n = 8,614). Each treatment system was assigned a value based on its overall environmental impact (no treatment = 2; treatment with a sump = 1; and treatment with a plant = 0; data from ISPF) which was subsequently used as a weighting component of household density. We then extrapolated onto the reef using linear decay, assuming that pollution from sewage discharge spread linearly into

242 the lagoon from the source. Kernel estimation was completed using the Heatmap plugin in QGIS
243 v2.18.14 (QGIS Development Team 2016).

244 To test whether spatial patterns of N enrichment were related to anthropogenic inputs we
245 used a two-step approach. First, we tested whether the isotopic signature ($\delta^{15}N$) of *Turbinaria*
246 was related to the modeled distributions of N from agriculture and sewage. We found that $\delta^{15}N$
247 signatures were well predicted by modeled sewage input, particularly during the rainy season,
248 suggesting that $\delta^{15}N$ is a good proxy for anthropogenic nutrients (see Results). Thus, to test
249 whether the overall N enrichment patterns were driven by anthropogenic N input we tested for a
250 relationship between $\delta^{15}N$ and total N. Because we had no a priori expectation of the functional
251 forms of the relationships between anthropogenic nutrient input, isotopic signature ($\delta^{15}N$), and
252 total N, we used boosted regression tree (BRT) analyses; BRTs are a powerful machine learning
253 approach to model fitting that use the data to characterize the relationships between variables
254 (Elith et al. 2008, De'Ath and Fabricius 2010). BRT models were conducted using the 'dismo'
255 package in R (Hijmans et al. 2017) and parameterized according to Elith et al. (2008). Island
256 shore was included in all models. In addition, to explore whether models had greater prediction
257 power for some shores compared to others we also created separate models for each island shore.
258 To aid in data interpretation we show both the fitted relationships from the BRT analyses as well
259 as correlation plots of the raw data.

260 **Are recent increases in macroalgae related to nitrogen enrichment?**

261 To track long-term variation in N availability to benthic organisms, we collected data on
262 N content of *Turbinaria* tissue annually between 2007 and 2013 as part of the Moorea Coral
263 Reef Long-Term Ecological Research (MCR LTER) program (http://mcrlter.msi.ucsb.edu/cgi-
264 bin/showDataset.cgi?docid=knb-lter-mcr.20; Carpenter 2018). This time frame captures the

period when macroalgae increased markedly at some locations in the lagoons. We sampled 10 *Turbinaria* from 18 locations on six cross-shore transects (corresponding to the six core MCR LTER sites), with samples taken on the fringing reef, back reef, and reef crest during the last week of May or first week of June. Total N content was determined via CHN analysis on a model CEC 440HA organic elemental analyzer at the University of California, Santa Barbara, Marine Science Institute Analytical Laboratory. To determine whether N enrichment varied consistently among sites, habitats, and years we used ANOVA and AICc to select among models with and without interaction coefficients (Burnham and Anderson 2002). For this and other linear models, we inspected model residuals to ensure the assumptions of the tests were met.

To characterize the dynamics of macroalgae and coral, we collected data annually in three habitat types (fringing reef, back reef, and fore reef) at six sites (two on each of the three sides of the island) from 2006 to 2018 as part of the Moorea Coral Reef Long-Term Ecological Research (MCR LTER) program (http://mcrlter.msi.ucsb.edu/cgi-bin/showDataset.cgi?docid=knb-lter-mcr.8; Carpenter 2019). Here we focus on the back reef habitat, where macroalgae increased in abundance in some locations (Schmitt et al. 2019). At each site, the dominant space holders are characterized using point contacts at 50 fixed locations on five permanent 10 m long transects (n = 10, 0.25 m^2 quadrats per transect). Macroalgae are identified to species in situ with other benthic space holders categorized to functional group (e.g., turf algae, scleractinian coral, etc.). In addition to benthic space holders, annual data on the abundance and biomass of fishes are collected at the same sites via visual surveys on four 50 m long by 5 m wide fixed transects (http://mcrlter.msi.ucsb.edu/cgi-bin/showDataset.cgi?docid=knb-lter-mcr.6; Brooks 2018).

To determine whether the persistent increases in macroalgae that occurred on the back reef were related to spatial patterns of N enrichment and/or herbivore biomass we tested for an association between the change in the mean percent cover of macroalgae at each of our six long-term sites and 1) mean N enrichment, and 2) mean biomass of herbivorous fishes during the time when the coral-to-macroalgae phase shifts occurred (between 2007 and 2013). Ideally, we would use a model selection framework to disentangle the multiple factors that may be driving increases in macroalgae. Yet, with only six sites this was not possible. Instead we used two separate Spearman's rank correlations to independently test for an association between N and macroalgae and herbivore biomass and macroalgae. A positive correlation between N and macroalgae would indicate that reefs that have been consistently enriched in N were more likely to experience increases in macroalgae than less enriched reefs but would not rule out the importance of other factors. Similarly, a negative correlation between herbivore biomass and macroalgae would indicate that reefs with the highest biomass of herbivores were least likely to experience increases in macroalgae.

Results

What are the spatial patterns of N enrichment and how do these patterns vary across seasons with different levels of rainfall and wave forcing?

Rainfall varied among the three sample periods, reflecting typical seasonal patterns in Moorea. During 2016, mean monthly rainfall was more than 3-fold greater prior to the May sampling, compared to the January and August sampling (January = 121 mm, May = 372 mm, August = 110 mm) due to abundant rainfall during February, March, and April (Fig. 1b).

Wave power varied greatly among the three sides of the island and exhibited different seasonal patterns reflecting differences in exposure to waves generated from storms in the southern and northern hemispheres (Fig. 1c-e). Wave power was most variable on the north shore (among period CV = 70%), intermediate on the west shore (among period CV = 40%), and least variable on the east shore (among period CV = 28%). Mean daily wave power was consistently high on the north shore prior to the January and May sampling periods but dropped precipitously in May and remained low throughout the austral winter (Fig. 1c). The result was a seven-fold decline in wave power on the north shore in the three months leading up to the August sampling relative to the previous three months. Wave power was consistently high on the west shore, with wave power exceeding the north shore during all sampling periods (Fig. 1e). Wave power was especially high on the west shore during the austral winter, with wave power ~ 2-fold greater in the three months leading up to the August sampling compared to the three-month period preceding the January sampling (Fig. 1e). Mean wave power on the east shore was intermediate between the north and west shores. Similar to the west shore, wave power was greatest on the east shore during the austral winter and least during the austral summer (Fig. 1d).

Nitrogen content of *Turbinaria* tissue revealed evidence for enrichment hotspots on all three sides of the island (Fig. 2). Algae were enriched in N near bays and large watersheds and were also frequently enriched near reef passes. In contrast, algae tended to be lower in N near the reef crest and in the mid-lagoon (Fig. 2). Enrichment patterns varied through time and were related to seasonal changes in wave power and rainfall. Algae were more enriched in N in May following the rainy season compared to January and August, which followed drier periods (ANOVA, $F_{2,6} = 18.4$, $P = 0.003$; Post hoc Tukey tests comparing % N in May to January and August, $P < 0.01$ for both). The spatial extent of enrichment appeared to be related to the wave

regime. During periods of low wave forcing (e.g., the north shore during August), enrichment signals were constrained to nearshore fringing reefs and reef passes compared to periods of high wave forcing (e.g., the west shore during August) when enrichment signals extended farther into the lagoons (Fig. 2).

Enrichment patterns were more consistent throughout the year on some sides of the island compared to others. Spatial patterns of enrichment were highly consistent on the east shore, where wave forcing was least variable among seasons (Appendix S1: Fig. S3). In contrast, enrichment patterns were much more variable on the north shore where wave forcing was highly variable (Appendix S1: Fig. S4). Spatial patterns of enrichment on the west shore were intermediate in consistency compared to the other two shores (Appendix S1: Fig. S5). Pairwise correlation of algal N content among sites during different seasons was strongest when wave power was similar, as indicated by a negative association between the among-period correlation coefficient and the difference in mean wave power during the 90-day period immediately preceding sampling (Pearson's correlation, $r = -0.59$, $P = 0.09$; Appendix S1: Fig. S6).

To what extent are spatial patterns of nitrogen enrichment related to anthropogenic inputs?

Isotopic signature ($\delta^{15}N$) of *Turbinaria* exhibited strong spatial patterns that varied considerably among sample periods (Fig. 3b, Appendix S1: Fig. S7). During the rainy season, when anthropogenic inputs of N are likely to be highest, kernel density estimates of human sewage derived from data on household sanitation predicted well $\delta^{15}N$ values in *Turbinaria* (Fig. 3a-e) (BRT full model cross validation correlation = 0.51; relative importance of modeled sewage = 75%). The fitted relationship between modeled sewage and $\delta^{15}N$ was positive and roughly linear across most of the range of the data (Appendix S1: Fig. S8). $\delta^{15}N$ was also

positively related to modeled nutrients from agriculture (Appendix S1: Fig. S8), though agriculture had little predictive power compared to sewage (BRT relative importance = 7%). Kernel density estimates of human sewage were also correlated with $\delta^{15}N$ during the January and August sampling (Appendix S1: Figs. S8, S9), though the correlations were less strong (January: full model cross validation correlation = 0.48; relative importance of modeled sewage = 59%; August: full model cross validation correlation = 0.38; relative importance of modeled sewage = 30%) and the fitted relationships were highly non-linear with $\delta^{15}N$ initially decreasing with predicted sewage before increasing at higher levels (Appendix S1: Fig. S8).

Model performance also varied for different sides of the island. For example, during the rainy season, modeled sewage predicted as much as 73% of the variation in $\delta^{15}N$ on the east shore of the island (BRT cross validation correlation = 0.73; relative importance of modeled sewage = 100%). In contrast, modeled sewage during the rainy season only predicted 24% of the variation in $\delta^{15}N$ on the west shore (BRT cross validation correlation = 0.32; relative importance of modeled sewage = 100%) and 53% of the variation in $\delta^{15}N$ on the north shore (BRT cross validation correlation = 0.55; relative importance of modeled sewage = 97%). Modeled nutrients from agriculture consistently had little predictive power (BRT relative importance < 10%).

Nitrogen tissue content was positively associated with $\delta^{15}N$ during all sample periods, but the relationship was particularly strong (and roughly linear across most of the range of data) during the rainy season (Fig. 3f-h; Appendix S1: Figs. S10 and S11) (BRT full model cross validation correlation = 0.61; relative importance of $\delta^{15}N$ = 89%). The association between $\delta^{15}N$ and total N was strongest for the north and east shores of the island. For example, during the rainy season, $\delta^{15}N$ predicted 75% and 81% of the variation in total N on these shores, respectively (BRT cross validation correlation north shore = 0.75, east shore = 0.81) while

predicting a more modest 35% of the variation in total N on the west shore (BRT cross validation correlation = 0.35).

Are recent increases in macroalgae related to nitrogen enrichment?

Annual sampling of *Turbinaria* from three habitats at our six long-term sites revealed strong spatial patterns that were consistent through time (model without interactions outperformed all other models with a delta AICc $\geq$ 13). Algal N content varied strongly among habitats (ANOVA, Habitat: $F_{2,108} = 23.3$, $P < 0.001$) and sites (ANOVA, Site: $F_{5,108} = 3.2$, $P = 0.009$ (Fig. 4). Algae were enriched in N on nearshore fringing reefs, and to a lesser extent the back reef, relative to the reef crest (Fig. 4a). These differences mirror long-term differences in water column DIN over the same time period (Appendix S1: Fig. S12). In addition to these differences among reef habitats, algae also tended to be more enriched in N at the north shore sites compared to sites on the east and west shores (Fig. 4b).

Beginning at or shortly after the onset of our benthic time series in 2007, corals began to decline and macroalgae began to increase on the back reef at permanent study sites LTER 1, LTER 2, and LTER 3 (Fig. 5). By 2013 at LTER 1 and LTER 2, and 2014 at LTER 3, the cover of macroalgae exceeded coral cover (Fig. 5). Since 2014, coral cover at these sites has continued to decline or stabilize at low (< 5%) levels while the cover of macroalgae has remained high. Species composition of algal assemblages varies somewhat among sites; dominant taxa include the brown algae *Turbinaria ornata*, *Sargassum pacificum*, and *Dictyota bartayresiana* as well as the red alga *Amansia rhodantha* (Fig. 5). Over the same time period, coral cover has remained high, and macroalgae cover low at permanent study sites LTER 4, LTER 5, and LTER 6, which experience lower nutrient conditions compared to LTER 1, LTER 2, and LTER 3 (Fig. 5). Increases in macroalgae were strongly correlated with the long-term nutrient environment, with

higher N associated with greater increases in macroalgae (Spearman correlation, $r_s = 0.94$, P = 0.02; Fig. 6a). In contrast, there was no significant association between increases in macroalgae and the mean biomass of herbivorous fishes (Spearman correlation, $r_s = 0.20$, P = 0.71; Fig. 6b). Higher N was also associated with coral decline, although the correlation was only marginally significant (Spearman correlation, $r_s = -0.77$, P = 0.10; Appendix S1: Fig. S13).

Discussion

Patterns of N enrichment in the lagoons of Moorea were related to several factors, including rainfall, wave power, and distance from anthropogenic nutrient sources, particularly sewage. High resolution maps of N enrichment revealed several patterns that were consistent among the three sample periods. During all sampling periods, algae had higher N on nearshore fringing reefs compared to the mid-lagoon and reef crest. In addition, algae were consistently enriched in N near large watersheds, where inputs of N from sewage and agriculture are high. Our long-term data indicate that areas of the lagoon that are near shore and close to major watersheds have been consistently enriched in N for at least a decade. During this time, corals have decreased and macroalgae have increased at back reef locations with high N, while reefs with lower levels of N have maintained high cover of coral and low cover of macroalgae. Importantly, these patchy phase shifts to macroalgae have occurred despite island-wide increases in the biomass of herbivorous fishes. Similar coral-to-macroalgae phase shifts have been observed on many reefs globally (e.g., Hughes 1994, Graham et al. 2015, Bozec et al. 2019), and are often associated with reductions in the biomass of herbivorous fishes due to overfishing. Our observation that nutrient loading, and not herbivory, is strongly associated with phase shifts in the lagoons of Moorea emphasizes that bottom-up factors, such as nutrient pollution from

sewage and agriculture, can also be important drivers of coral-to-macroalgae phase shifts on tropical reefs.

Influences of rainfall and wave-driven flow on seasonal patterns of nitrogen enrichment

Many of the enrichment patterns we observed in our high-resolution sampling were consistent among seasons, yet there were also differences that were related to seasonal differences in wave forcing and rainfall. For example, overall levels of N in *Turbinaria* tissue were higher in May following the wet summer period compared to January and August which followed periods with less rainfall. In addition, spatial patterns of enrichment were related to wave forcing, which varied asynchronously around the island due to seasonal differences in wave exposure. During periods of low wave energy, enrichment signals were constrained to nearshore fringing reefs and embayments, while during periods of higher wave energy enrichment signals extended farther into the lagoons. The precise mechanisms driving these spatial patterns are unknown but are likely to be related to circulation since waves are the primary driver of circulation in the lagoons (Hench et al. 2008, Leichter et al. 2013).

Irrespective of the precise mechanism, our finding that rainfall and waves can interact to determine spatial patterns of nutrient enrichment in a lagoonal coral reef system has important implications. For example, on the north shore of Moorea where the wave climate is highly seasonal, the rainy season corresponds with a period of high wave energy. Because increased rainfall results in N enriched conditions in the lagoons and waves appear to be important for delivering N to the reef crest, the coincidence of the rainy season with a period of large waves could result in nutrient pulses to wide reaches of the lagoon that otherwise might be restricted to the fringing reefs when waves are smaller. Given that waves drive circulation patterns on many

444 tropical oceanic islands (Hench et al. 2008), seasonality in wave-driven circulation could be an
445 important mechanism driving patterns of nutrient enrichment on many coral reefs.

446 *Anthropogenic nitrogen sources*

447 We observed the highest levels of N enrichment near areas with dense human populations
448 and known nutrient sources, particularly sewage. In addition, isotopic signatures of N in areas of
449 high enrichment were consistent with terrigenous rather than oceanic sources of N (Lin and Fong
450 2008, Dailer et al. 2010, Page et al. 2013). While it was not possible for us to quantify the
451 relative contributions of all the possible N sources to the lagoons, the strong association between
452 the predicted spatial distribution of human sewage and the $\delta^{15}N$ signature in *Turbinaria* tissue
453 strongly suggests that algae are incorporating sewage-derived N. In addition, the fact that the
454 $\delta^{15}N$ signature predicted well total N tissue content suggests that anthropogenic sources of N
455 (including sewage) are driving spatial patterns of N availability across the lagoons.

456 In contrast to sewage, our model of N enrichment from agricultural fertilizer was not a
457 good predictor of the isotopic signature or total N content in *Turbinaria* tissue. The lack of an
458 isotopic signature is unsurprising, given that $\delta^{15}N$ values of fertilizers are often similar to natural
459 sources (Kendall et al. 2012). Our ability to detect an effect of fertilizer on N tissue content also
460 may have been limited by the assumptions we made when modeling fertilizer input to the
461 lagoons. A key assumption of our predictive model was that N from fertilizer was delivered to
462 the lagoons in surface water runoff via one of several dozen streams around the island. In
463 contrast, we modeled sewage assuming diffusion from the source based on the assumption that
464 sewage contamination would primarily reach the lagoons via groundwater. While little is known
465 about the extent of submarine groundwater discharge in Moorea or the relative importance of
466 groundwater versus surface water runoff for delivering different types of nutrients, recent studies

in Moorea suggest that septic waste and animal manure in groundwater are likely an important source of N to the lagoons (Knee et al. 2016, Haßler et al. 2019). Given the potential importance of anthropogenic N input for shaping the structure and function of coral reef ecosystems, future work is needed to better characterize the sources and delivery pathways of anthropogenic N to the lagoons.

The role of nitrogen enrichment in driving coral-to-algae phase shifts

Patterns of N enrichment have important implications for understanding the dynamics of benthic algae, which can strongly influence overall ecosystem health. Nutrient enrichment can allow for the proliferation of algae that are physiologically unable to grow under nutrient poor conditions. In addition, excess nutrients can also facilitate algae indirectly through the loss of top-down control if adding nutrients causes algal production to outpace herbivory (Scheffer et al. 2008, Arias-González et al. 2017, Briggs et al. 2018). In this study, we found that several species of macroalgae have recently increased in abundance on back reef habitats of Moorea, but only where levels of N are relatively high. Benthic algal blooms have been noted on some nearshore fringing reefs in Moorea in the past (Payri 1987, Adjeroud and Salvat 1996, Gattuso et al. 1997), and it had been hypothesized that those blooms could be related to waste water discharge (Wolanski et al. 1993, Gattuso et al. 1997). Our results support this hypothesis and also suggest that the impacts of nutrients may extend beyond nearshore fringing reefs to back reef habitats farther from shore.

Several factors in addition to nutrient enrichment could be contributing to the increases in macroalgae in the lagoons of Moorea. Phase shifts to macroalgae frequently occur following large coral-killing disturbances that liberate space for the growth of benthic algae, particularly in systems with low levels of herbivory due to overfishing (Done et al. 1991, Hughes 1994, Graham

et al. 2015). The reefs in Moorea experienced two large coral-killing disturbances in the late 2000's, including an outbreak of corallivorous crown-of-thorns seastars (*Acanthaster planci*; COTS) and a large cyclone that together reduced the cover of living coral to near zero on the fore reef (Adam et al. 2011, 2014, Kayal et al. 2012). While reefs in the lagoons were much less impacted by these disturbances, some reefs have experienced a period of protracted coral decline that appears unrelated to these recent disturbances (Han et al. 2016, Schmitt et al. 2019, this study). Coral decline on both the fore reef and within the lagoons coincided with an increase in the biomass of herbivorous fishes (Adam et al. 2011, 2014, Lamy et al. 2015, Han et al. 2016, Dubois et al. 2019). Yet, unlike the fore reef, where herbivores controlled the proliferation of algae and corals have rapidly recovered (Holbrook et al. 2016, 2018), many reefs within the lagoons have become dominated by persistent algal assemblages, despite the presence of a diverse and abundant herbivore assemblage (Han et al. 2016, Edmunds et al. 2019). Higher nutrient loading in the lagoons is one possible explanation for why many reefs within the lagoons have become dominated by macroalgae while macroalgae have remained uncommon on the fore reef despite increases in herbivore biomass in both habitats. Likewise, differences in nutrient enrichment among lagoons may help explain why reefs in some lagoons have undergone persistent phase shifts to macroalgae, while others remain coral dominated despite similar increases in the biomass of herbivorous fishes.

Patterns of N loading may have also influenced the heterogeneous decline in corals across the lagoons. In addition to the positive correlation between long-term N enrichment and increase in macroalgae, N enrichment was also related to the loss of coral cover. Part of the impact of N on corals could be mediated by the rise in macroalgae, as algae can outcompete juvenile and adult corals (Bulleri et al. 2013, Brown and Carpenter 2014) and inhibit coral

recruitment (Kuffner et al. 2006, Mumby et al. 2016, Bulleri et al. 2018). But, excess nutrients also can directly negatively impact corals by increasing the prevalence and severity of coral disease (Bruno et al. 2003, Vega Thurber et al. 2014) and by exacerbating coral bleaching and mortality during thermal stress events (Wiedenmann et al. 2013, Zaneveld et al. 2016, Burkepile et al. 2019, Donovan et al. 2020). Human sewage may be particularly harmful to corals as it both delivers excess nutrients as well as pathogenic microbes that cause coral disease and mortality (Patterson et al. 2002, Sutherland et al. 2010). Nutrients from sewage and other land based sources of pollution are also commonly associated with toxins, organic carbon, and sediments, all of which have direct detrimental effects on corals (Fabricius 2005, Wear and Thurber 2015).

Conclusion

Spatial patterns of N availability in the lagoons of Moorea, a small oceanic island in the South Pacific, are shaped by terrigenous inputs even though lagoons are continuously flushed with oligotrophic ocean water. Long-term data indicate that reefs experiencing the highest levels of N enrichment have undergone persistent phase shifts to a macroalgae-dominated state despite the presence of a diverse and abundant herbivore assemblage. These results indicate that anthropogenic nutrient pollution is likely an important driver of reef degradation in Moorea. Persistent phase shifts from coral to macroalgae are a problem on many reefs worldwide and are often associated with declines in the abundance of herbivorous fishes. Our results emphasize that bottom-up factors can also play an important role in driving these algal phase shifts. Future work is necessary to better characterize the sources and impacts of anthropogenic nutrients on Moorea, but sewage from septic systems appears to be an important contributor. Impacts of nonpoint sources of N are difficult to isolate yet are likely widespread in tropical countries with coral

reefs, underscoring the critical importance of managing watersheds to reduce inputs of nutrients and other land-based pollutants to coral reef ecosystems.

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Authorship Statement

TCA, DEB, SJH, RJS and RCC designed the study and secured funding; TCA, DEB, AJB, and RCC performed field work; JC, CL, and LT created empirical models of nutrient discharge; LW oversaw collection and processing of wave data; TCA conducted analyses and wrote the initial manuscript draft. All authors contributed to manuscript revisions.

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Figure Legends

Figure 1. (a) Map of Moorea showing the locations of the six MCR LTER sites and the sampling grid for the high resolution nutrient maps with sample locations colored according to habitat type. Shallow lagoon habitat is shown in gray. White space within the lagoons represents non-reef area (e.g., deep water sandy areas). Land is displayed as a digital elevation model with a hillshade to show ridgelines and valleys. (b) Rainfall from October 2015 until September 2016 in Faaa, Tahiti ~ 15 km east of Moorea. Blue curve is the LOESS smoothed 30-day sum. Black lines are monthly means for each of the three 90-day periods preceding the January, May, and August sampling. Note that we expect the nutrient content of macroalgal tissue (*Turbinaria ornata*) to reflect the nutrient environment during the ~ 3-month period prior to its collection. Patterns of wave forcing from October 2015 until September 2016 on the (c) north, (d) east, and (e) west shores of Moorea. Blue lines are daily wave power calculated from ADCPs. Black lines are daily means for each of the three 90-day periods preceding the January, May, and August sampling. Note the highly seasonal pattern of wave forcing on the north shore, with minimal wave forcing during the austral winter (June to September). Also note the different scales on the y axes.

Figure 2. Spatial patterns of nitrogen enrichment (% N) in tissue from the macroalga *Turbinaria ornata* for the (a) January, (b) May, and (c) August sampling. Arrows are proportional to the mean wave power on each of the three sides of the island during the 90 days preceding each of the three sampling efforts. Note that the color scale for %N differs among sample periods. Algae were consistently enriched in N at fringing reef sites and near reef passes compared to sites near the reef crest. Enrichment is especially strong near large watersheds, most notably the areas

around the two large bays on the north shore of the island as well as the smaller bays on the east and west shores.

Figure 3. (a) Modeled N enrichment based on locations of septic systems and sources of untreated sewage. (b) Empirical patterns of $\delta^{15}N$ in *Turbinaria ornata* tissue during the rainy season. Association between modeled N from sewage and $\delta^{15}N$ for the (c) north, (d) east, and (e) west shores of Moorea during the rainy season. Association between $\delta^{15}N$ and nitrogen content (% N) of *Turbinaria ornata* tissue during the rainy season on the (f) north, (g) east, and (h) west shores of Moorea.

Figure 4. Mean (+/- SE) N content of *Turbinaria ornata* tissue in (a) three habitats (fringing reef, back reef, and reef crest) and (b) at six long-term MCR LTER sites (two sites on each of the three sides of the island) between 2007 and 2013. Note that N is consistently enriched at the fringing reef sites relative to the back reef and reef crest. Also note that LTER sites 1, 2, and 3 tend to be enriched relative to sites 4, 5, and 6.

Figure 5. Area plot showing the percent cover of coral and algae at the six MCR LTER back reef sites (three sites with relatively high nitrogen: LTER 1, LTER 2, and LTER 3 and three sites with relatively low nitrogen: LTER 4, LTER 5, and LTER 6) from 2007 through 2018. Also shown is the mean biomass of herbivorous fishes for the same time period. All values are from annual sampling.

Figure 6. Correlation between the change in the percent cover of macroalgae between 2007 and 2013 at each of the six MCR LTER back reef sites and the mean (a) nitrogen content of *Turbinaria ornata* tissue and (b) biomass of herbivorous fishes during the same time period.

Figure 1

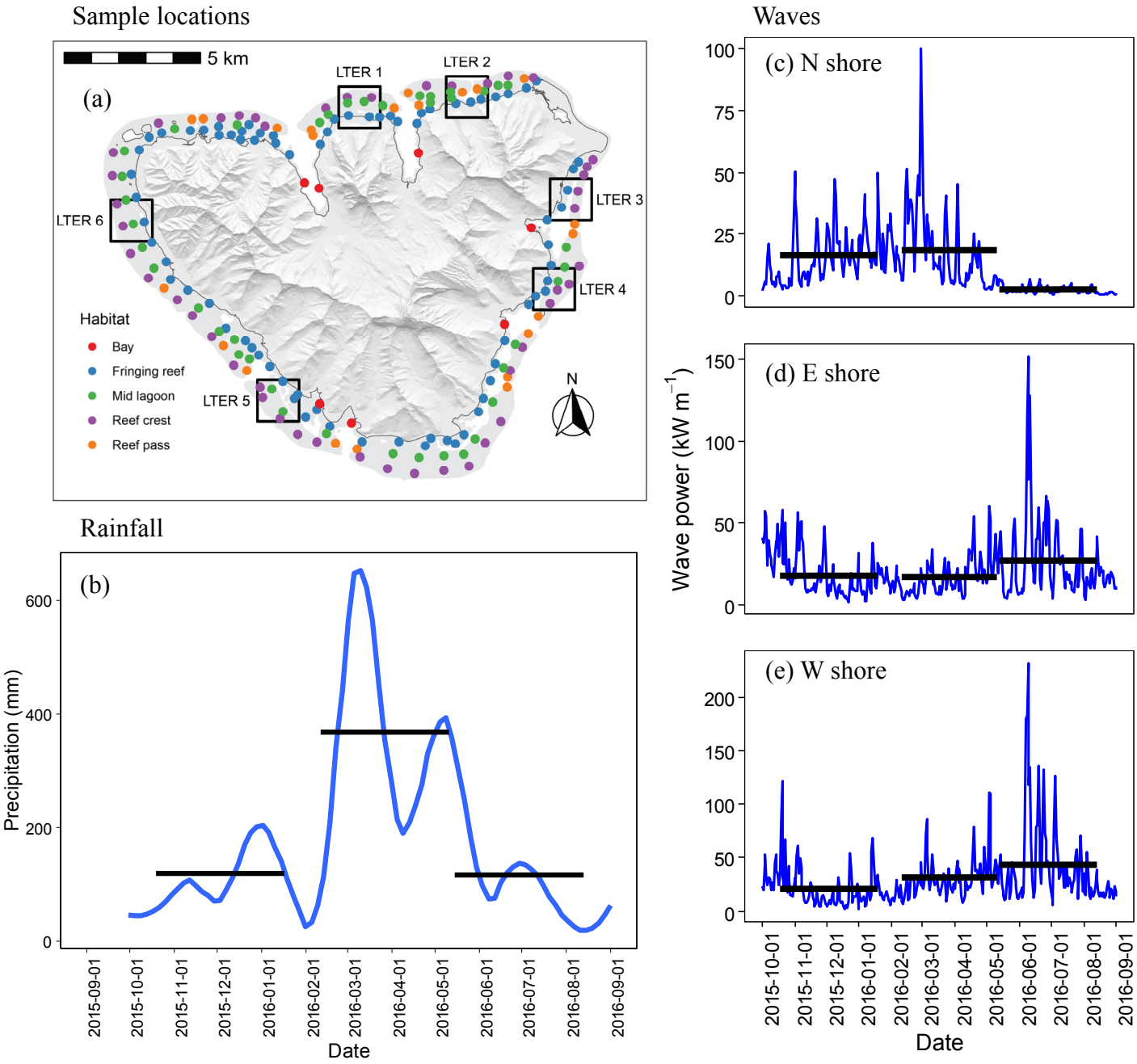
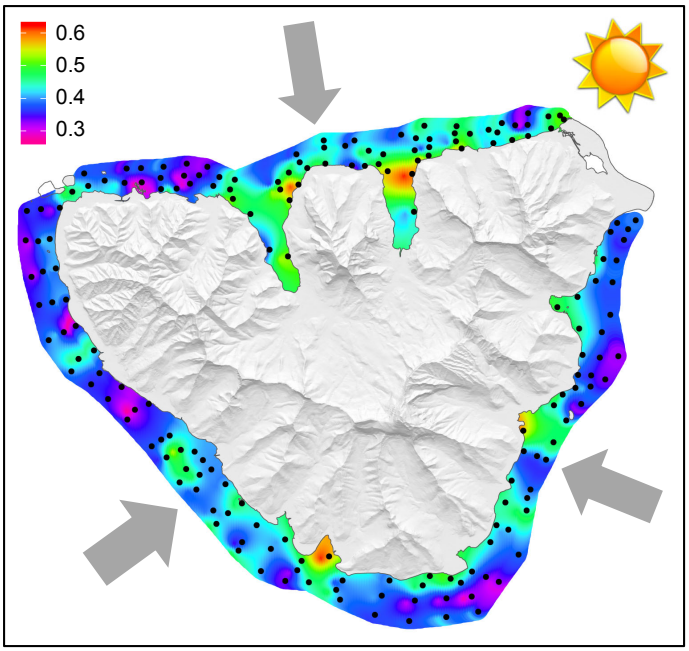
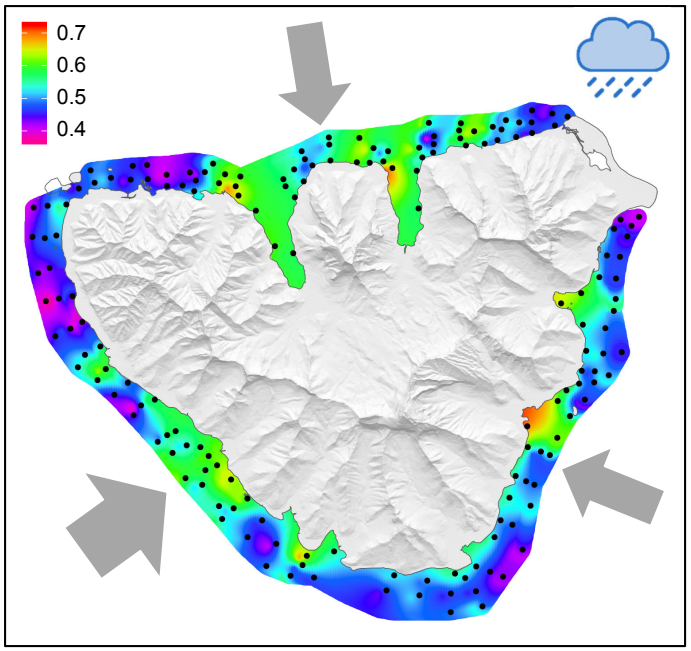

Sample locations
5 km
(a)
LTER 1
LTER 2
LTER 3
LTER 4
LTER 5
LTER 6
Habitat
Bay
Fringing reef
Mid lagoon
Reef crest
Reef pass
N
Rainfall
(b)
Precipitation (mm)
0
200
400
600
2015-09-01
2015-10-01
2015-11-01
2015-12-01
2016-01-01
2016-02-01
2016-03-01
2016-04-01
2016-05-01
2016-06-01
2016-07-01
2016-08-01
2016-09-01
Date
Waves
(c) N shore
(d) E shore
(e) W shore
Wave power (kW m^{-1})
0
25
50
75
100
150
200
2015-10-01
2015-11-01
2015-12-01
2016-01-01
2016-02-01
2016-03-01
2016-04-01
2016-05-01
2016-06-01
2016-07-01
2016-08-01
2016-09-01
Date

Figure 2

(a) January sampling (dry season)



(b) May sampling (rainy season)



(c) August sampling (dry season)

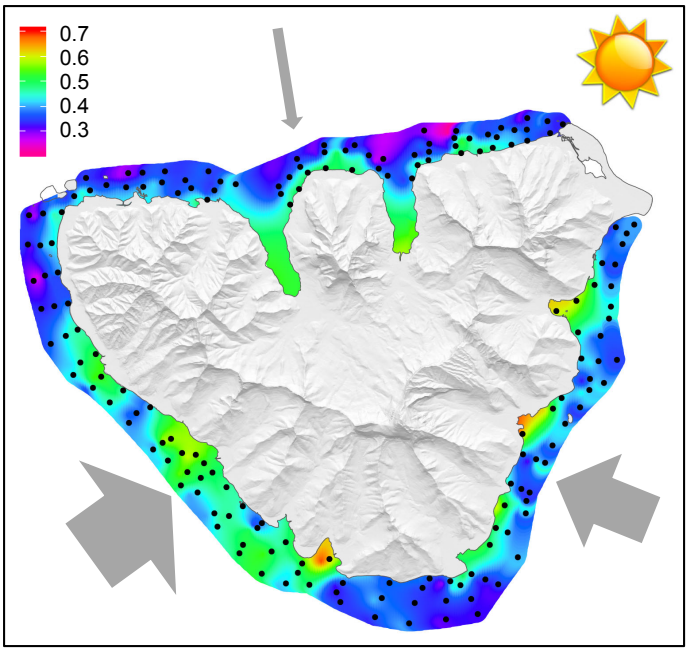


Figure 3

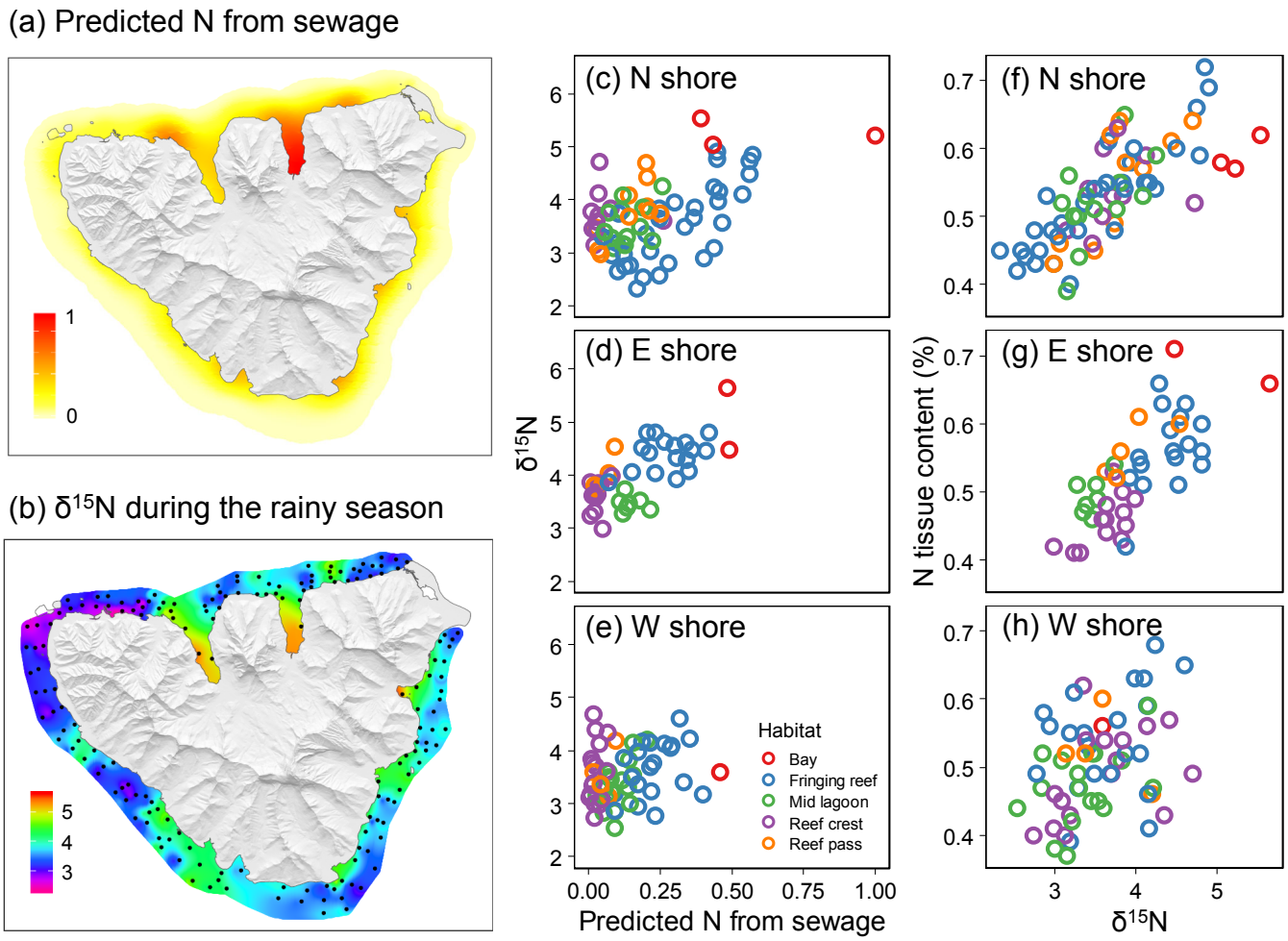

(a) Predicted N from sewage
1
0
(b) δ15N during the rainy season
5
4
3
(c) N shore
(d) E shore
(e) W shore
(f) N shore
(g) E shore
(h) W shore
δ15N
N tissue content (%)
Predicted N from sewage
δ15N
Habitat
Bay
Fringing reef
Mid lagoon
Reef crest
Reef pass

Figure 4

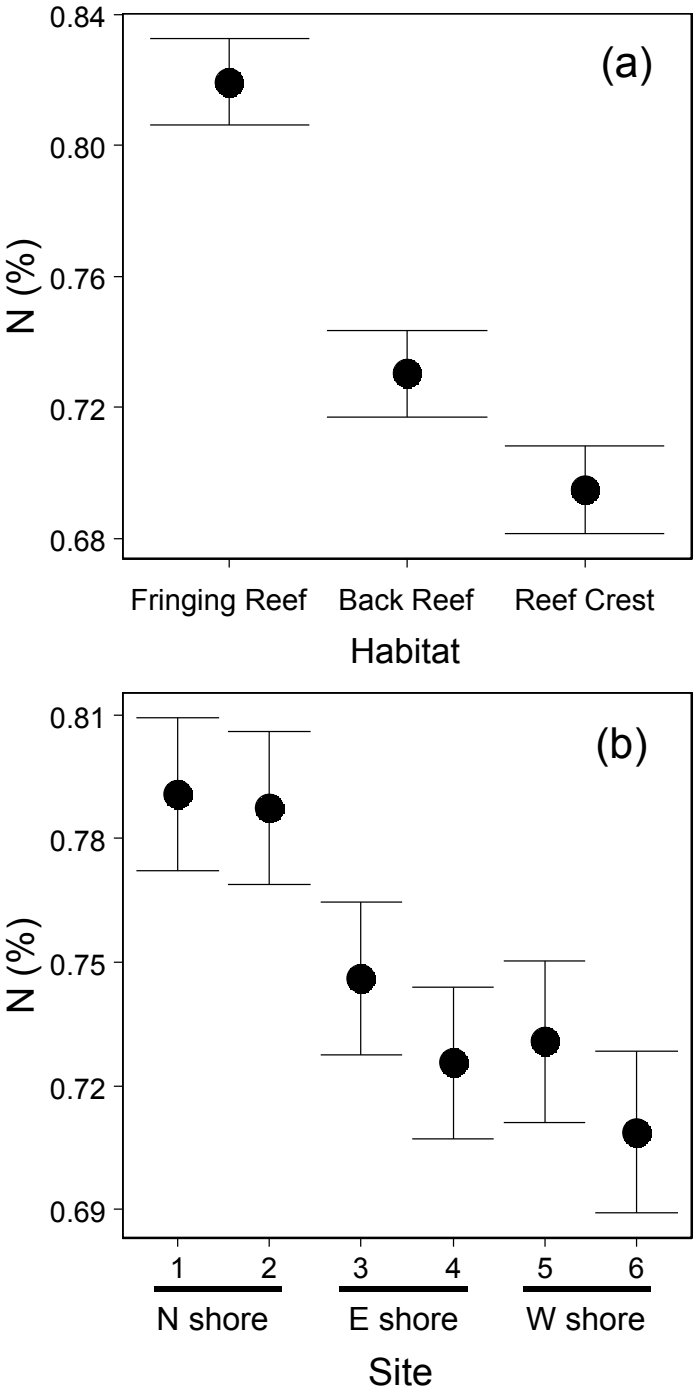

(a)
0.84
0.80
0.76
0.72
0.68
N (%)
Fringing Reef
Back Reef
Reef Crest
Habitat
(b)
0.81
0.78
0.75
0.72
0.69
N (%)
1
2
3
4
5
6
N shore
E shore
W shore
Site

Figure 5

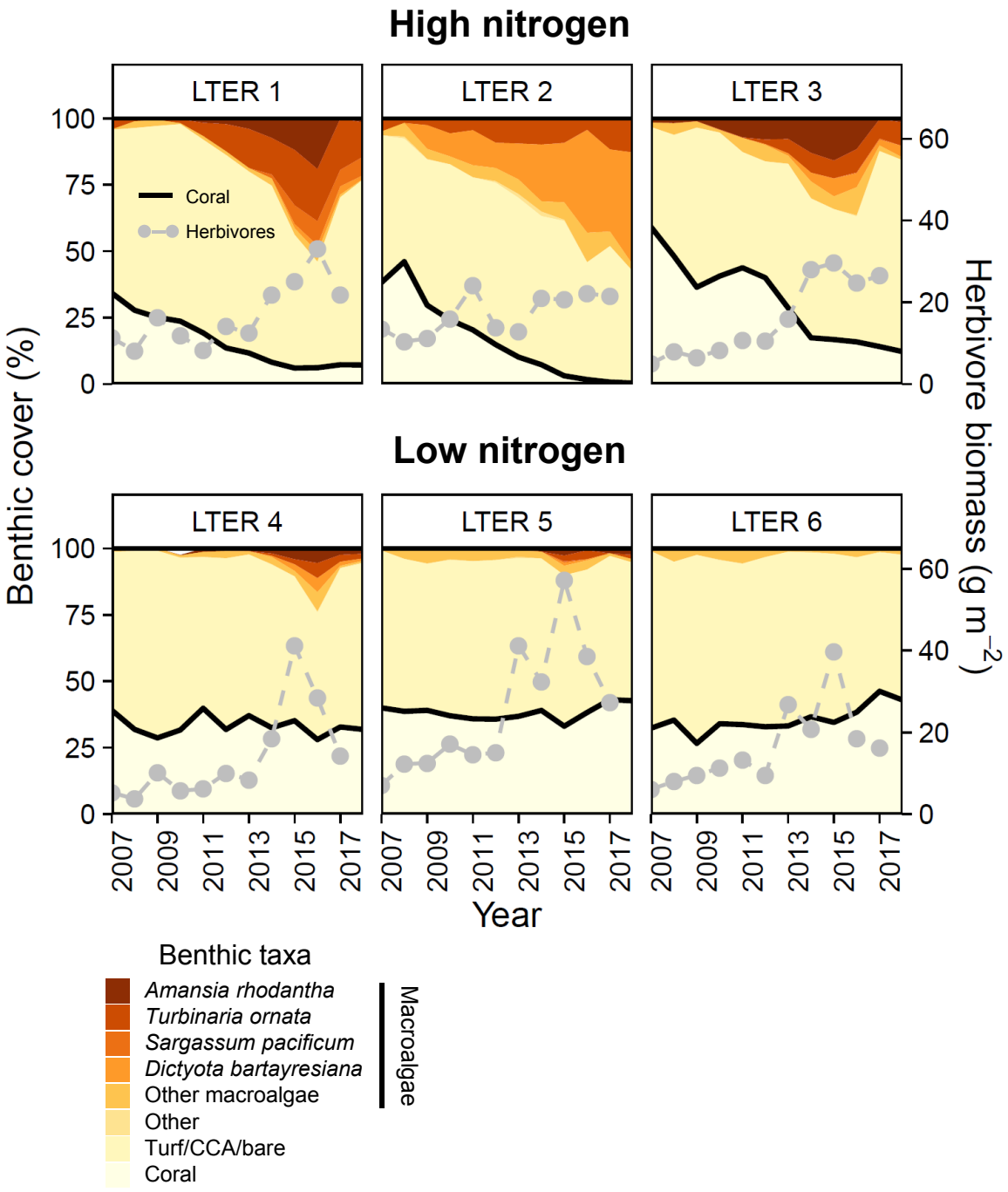
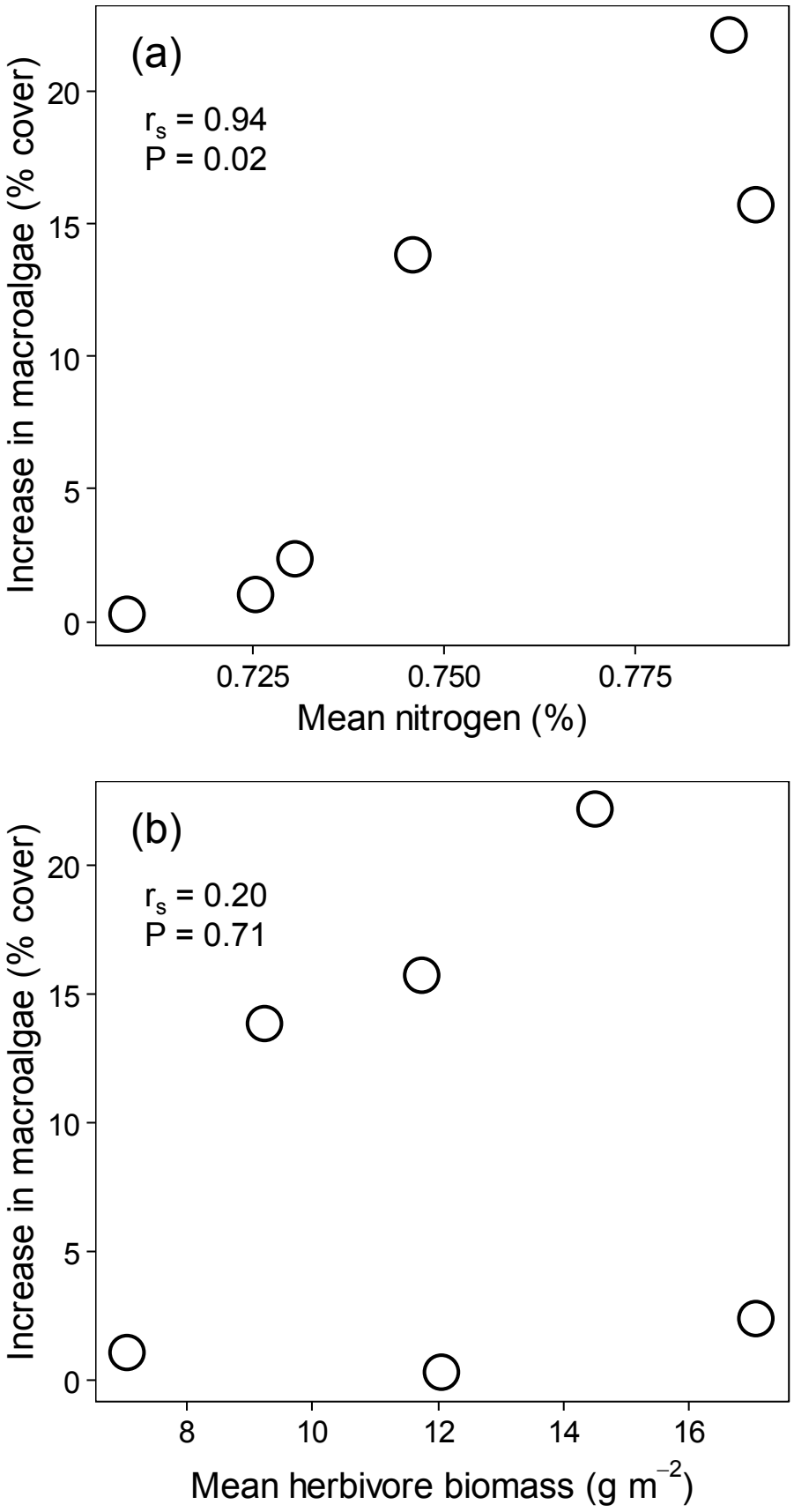

High nitrogen
LTER 1
LTER 2
LTER 3
Low nitrogen
LTER 4
LTER 5
LTER 6
Coral
Herbivores
Benthic cover (%)
Herbivore biomass (g m^{-2})
Year
Benthic taxa
Amansia rhodantha
Turbinaria ornata
Sargassum pacificum
Dictyota bartayresiana
Other macroalgae
Other
Turf/CCA/bare
Coral
Macroalgae

Figure 6


(a)
r_s = 0.94
P = 0.02
Increase in macroalgae (% cover)
0
5
10
15
20
0.725
0.750
0.775
Mean nitrogen (%)
(b)
r_s = 0.20
P = 0.71
Increase in macroalgae (% cover)
0
5
10
15
20
8
10
12
14
16
Mean herbivore biomass (g m^{-2})