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Nutrient thresholds to protect water quality, coral reefs, and nearshore fisheries

Peter Houk [a,*], Fran Castro [b], Andrew McInnis [a], Michael Rucinski [b], Christy Starsinic [a], Teddy Concepcion [b], Storm Manglona [a], Edwin Salas [c]

[a] University of Guam Marine Laboratory, UOG Station, Mangilao 96923, Guam
[b] University of Guam Sea Grant, UOG Station, Mangilao 96923, Guam
[c] Guam Environmental Protection Agency, Barrigada 96913, Guam

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ABSTRACT

A ridge-to-reef framework was developed for 26 watersheds around Guam. Dissolved inorganic nitrogen (DIN) data were collected for one year at the base of streams while coral and fish surveys were conducted on adjacent reefs. Two independent analyses revealed a similar 0.10 mg/l DIN threshold beyond which negative impacts to water quality and coral reefs existed. The influence of DIN was next partitioned with respect to a second primary stressor, fishing pressure. While coral diversity was negatively influenced by DIN, the cover of some stress-tolerant corals increased, such as *Porites rus*, making coral cover alone a poor indicator of watershed pollution. Less intuitive, DIN predicted increased food-fish biomass that was accounted for by generalist herbivores/detritivores, representing homogenized assemblages, while fishing pressure reduced biomass. Our DIN thresholds resonated with a similar study in American Samoa suggesting broader guidance for water quality legislation may be emerging.

1. Introduction

Two significant and ubiquitous forms of watershed pollution on coral reefs are sediments and nutrients (Lapointe et al., 2019; Tuttle et al., 2020; Zhao et al., 2021). Sediments transported by rainfall events reduce sunlight, bury reef organisms, and deplete oxygen for corals and other substrates. Corals buried by only 2 to 3 mm of organic sediment for 3 days showed significant mortality through several pathways related to respiration (Weber et al., 2012), and many attributes of sedimentation have been related to reductions in coral cover and diversity (Comeros-Raynal et al., 2021; Fabricius et al., 2012). Similarly, fishes exposed to high turbidity and sediments may have altered ecology (i.e., feeding and behavior) and physiology (i.e., gill structure and even larval development), reducing and displacing their populations (Wenger et al., 2015). Clearly reefs adjacent to watershed discharge are exposed to direct sediment impacts and burial, yet the spatial and temporal impacts beyond the core discharge zone are variable and influenced by sediment characteristics and flocculation, oceanographic currents, winds, waves, and tides (Bainbridge et al., 2018; Bartley et al., 2014; Delandmeter et al., 2015).

Dissolved nutrients are a second major form of watershed pollution that may or may not be associated with sediments. Dissolved nutrients such as nitrogen-nitrate quickly perpetuate through marine food webs given their rapid uptake by sessile organisms and phytoplankton that are exposed to freshwater-discharge plumes with varying amounts of sediment (Burkepile et al., 2020; Lapointe et al., 2019; Zhao et al., 2021). Thus, many studies have revealed predictable relationships between nutrient discharge concentrations and reef assemblages. For instance, dissolved inorganic nitrogen (DIN) concentrations were examined across one year at the base of 34 watershed around Tutuila, American Samoa, to examine potential impacts on adjacent coral reefs (Houk et al., 2020). Watersheds where DIN concentrations exceeded 0.1 $mg{\cdot}l^{-1}$, 20 % of the time or more within a year, were associated with diminished diversity and size structure of coral assemblages. The 20 % exceedance criteria resonated with both undesirable biological changes on the reefs and United States Environmental Protection Agency (USEPA) recommendations for developing water quality standards (EPA, 2001). A similar study from the Great Barrier Reef linked measurements of marine water quality data with several attributes of reef assemblages but found weaker relationships with DIN that were

* Corresponding author.
E-mail address: houkp@triton.uog.edu (P. Houk).

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suggested to be an artifact of the rapid transformation and uptake DIN in marine environments where sampling occurred (Fabricius et al., 2012). Meanwhile, a long-term study in the Florida Keys revealed links between increasing groundwater DIN concentrations and the gradual loss of coral cover through many mechanisms over four decades (Lapointe et al., 2019).

Previous research between DIN, watershed pollution, and coral reefs makes DIN one good candidate for use within regulatory standards, management policies, and for further research (Houk et al., 2020; Lapointe et al., 2019; McCloskey et al., 2021). One pressing question is whether the relationships and thresholds revealed for any island or location are specific to localized geology, oceanography, and/or ecology? Alternatively, are relationships similar across (some) tropical environments and could they offer generalized guidance for proactive management (Cooper et al., 2009; Fabricius et al., 2012; Houk et al., 2020; Jameson et al., 2004)? A second pressing question is how to

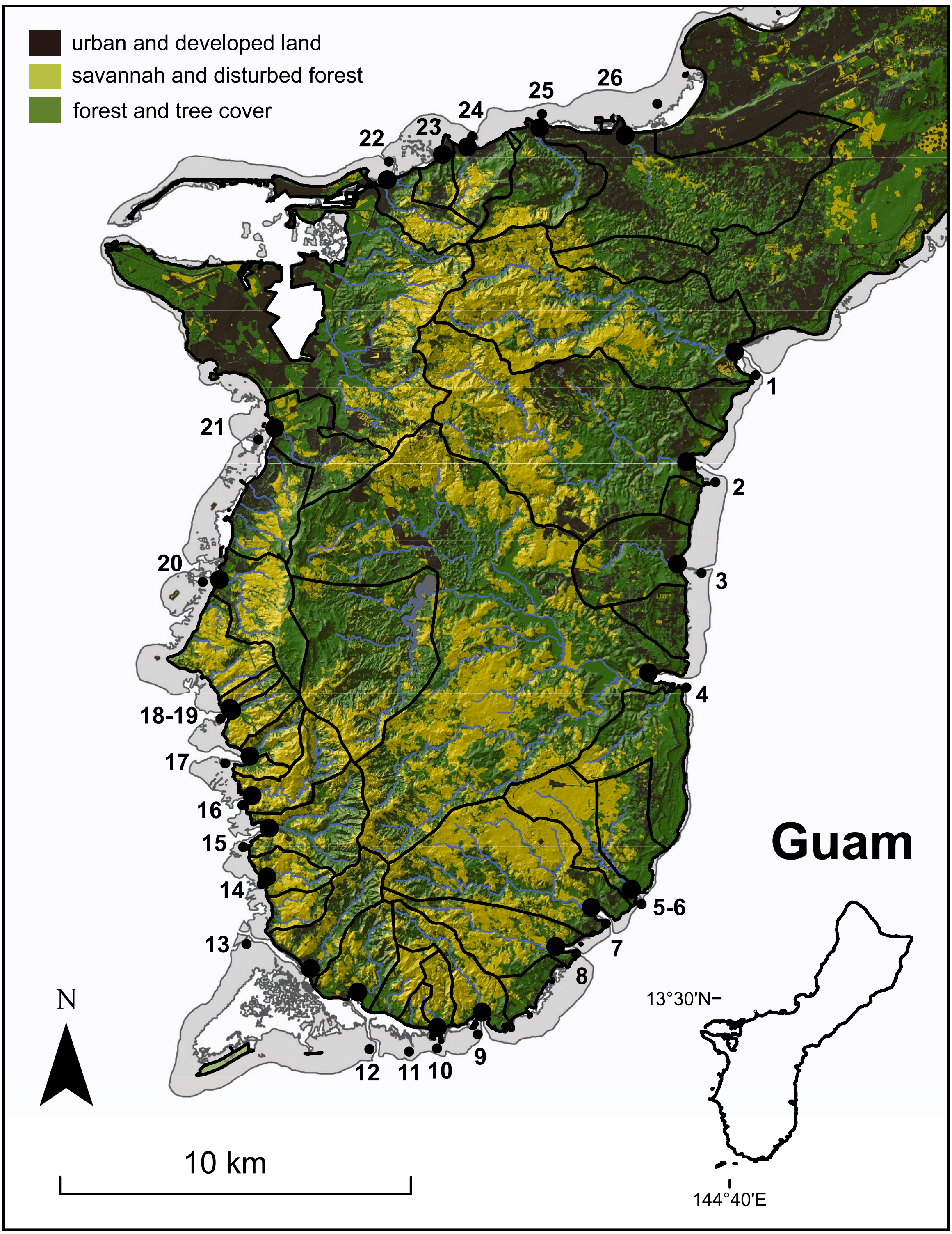

Fig. 1. Map of Guam, Micronesia, highlighting the volcanic southern watersheds (numbers) where water quality (large black circles) and coral reef (small black circles) data were collected. Two watersheds had two perennial streams within each that were sampled (5–6 and 18–19) (*Material and methods*).

partition the influences of DIN versus other local stressors when examining biological assemblages?

This study established a ridge-to-reef framework around Guam, Micronesia, to evaluate DIN concentrations within watersheds and evaluate impacts to coral, benthic, and fish assemblages. DIN was examined at the base of 26 freshwater streams to capture seasonality and evaluate thresholds using two independent approaches. Thresholds were first estimated based upon water quality exceedance criteria (i.e., the % of time that DIN exceeded a threshold concentration). Thresholds were also examined by partitioning the influences of DIN and fishing pressure, representing two priority stressors, on coral, benthic, and fish assemblages. The results posited broader guidance for managing water quality and DIN across the tropical Pacific and revealed specific ecological outcomes for each priority stressors at the site-and-island scale.

2. Materials and methods

Guam is a high island and urban center of Micronesia, in the tropical northwest Pacific Ocean (Fig. 1). The island is split geologically with raised limestone aquifers in the north and volcanic watersheds in the south. The most recent population estimate in 2020 was 168,783 people spread across 549 km^2 of land. The Guam Environmental Protection Agency is responsible for protecting stream and coastal water quality and regularly revisits their permitting and discharge regulations to adapt and improve their regulatory oversight. We examined 26 streams that represented a gradient of low-to-high human influence around the volcanic watersheds of southern Guam. Our goals were to: 1) identify whether point versus non-point sources of pollution were major contributors to DIN concentrations in each watershed, 2) decouple natural and human drivers of DIN to model annual DIN discharge and develop exceedance criteria, 3) partition the influence of DIN and fishing pressure to understand their contributions to reef assemblages, and 4) compare DIN thresholds developed using USEPA exceedance criteria guidance versus DIN thresholds that caused negative impacts to reef assemblages.

2.1. Water-quality data

Water-quality data were collected monthly at the base of our 26 study watershed streams between April 2020 to May 2021. Sampling was conducted during low tides associated with new and full moons to minimize salinity intrusion from adjacent ocean waters and focus our data collection on freshwater discharge. During each sampling event, all streams were sampled within the same 3-hour period by several teams of standardized observers using calibrated instruments. This sampling design aimed to control for extrinsic environmental variation across the watersheds, and best allow for comparisons, including our mixed-modeling statistical approach outlined below. Samples were collected by filtering 500 ml of water through 0.45 μm Cole-Palmer filters into polyethylene bottles. Samples were placed on ice and either processed immediately or frozen until analysis. Frozen samples were analyzed within 1-week of collection. DIN concentrations were analyzed using the QuikChem 8500 Flow Injection Analyzer developed by Lachat Instruments. Dissolved inorganic nitrogen (DIN) was defined by the sum of nitrate, nitrite, and ammonium, however nitrite was negligible. In addition to DIN sampling, YSI Professional Plus hand-held instruments were used to collect temperature, conductivity, and dissolved oxygen. Salinity was calculated using temperature and conductivity data. Water quality data were provided in the Supplemental information (Table S1).

2.2. Ecological data

Coral, benthic, and fish assemblage data were collected on reefs adjacent to each watershed. Survey locations were similarly located at the southern edge of each channel associated with watershed discharge (Fig. 1). Five, 50 m transects were laid along the 8–10 m reef slope contour and field protocols followed previous studies designed to address statistical power needs for site-level resolution (Houk et al., 2015; Houk and Van Woesik, 2013). Benthic substrates were evaluated using fifty photos taken at 1 m intervals along each transect line. The benthic substrates under five randomly allocated dots were evaluated within each photo (n = 250 data points per transect, and 1250 points per site). Corals, macroalgae, other common invertebrates, were identified to the genus-growthform level (i.e., *Porites* massive), while other substrates were grouped into functional categories (crustose coralline algae, poorly-calcifying encrusting red and brown algae known to overgrow corals, turf, and sand) (Ballantine and Ruiz, 2011; Edmunds et al., 2019). Coral-assemblage data were collected from sixteen, 0.25 m^2 quadrats placed along the transect lines at 15 m intervals. Coral colonies with centerpoints inside of the quadrat boundary were identified and measured for the maximum diameter (x), and for the diameter perpendicular to the maximum (y). Surface area was calculated assuming colonies were elliptical. Food-fish assemblages were estimated from 12 stationary-point counts (SPC) conducted at ~20 m intervals along the transect lines. During each SPC, the trained observer recorded the species name and the size of all food-fish within a 5–6 m radius for a period of 3 min. Food-fish were defined as acanthurids, scarids, serranids, carangids, labrids, lethrinids, lutjanids, balistids, kyphosids, mullids, holocentrids, and sharks. Fish sizes were converted to biomass using coefficients from regional fishery-dependent data when available, or from FishBase (www.fishbase.org). Ecological data were deposited into the Micronesia Reef Monitoring online database that hosts data, provides data access, and offers collaborations with interested individuals and organizations (https://micronesiareefmonitoring.com/).

2.3. Condition scores

Latent variables associated with coral, benthic, and fish assemblages were derived from field surveys to generate condition scores that could be evaluated against DIN and other environmental and human factors that are described below. The condition scores were previously defined by a team of researchers for a regional conservation movement to represent desirable attributes related to reef processes, which combine to perform essential ecosystem functions (Houk et al., 2015). For example, the metric of fish size structure was related to grazing potential, which in turn facilitates recruitment and growth of corals. The combined metrics were considered condition scores. Coral condition metrics included: (i) Shannon-Weaver evenness, (ii) skewness, (iii) species richness, and (iv) assemblage heterogeneity defined by the multivariate dispersion associated with replicate quadrats. Heterogeneity was measured by multivariate Bray-Curtis dissimilarities, which were highest when species composition changed the most among replicate coral quadrats (Beals, 1984). Skewness provided information on the size structure of coral assemblages and was also a good indicator of coverage. Benthic condition metrics were derived from photo-quadrat surveys and included: (v) coral cover, (vi) macroalgal cover, (vii) coral evenness, and (viii) benthic-substrate ratio derived from the cover of crustose coralline algae divided by poorly-calcifying encrusting algae, turf algae, and macroalgae. Fish condition metrics included: (ix) assemblage heterogeneity, (x) mean size, (xi) overall biomass, and (xii) piscivore biomass. Individual metrics were all scaled in a low-to-high intuitive manner and then standardized. The mean was taken to represent a latent variable describing the coral, benthic, or fish assemblage. Analyses were first performed on the condition scores, but subsequently performed with individual metrics that were most influential.

2.4. Environmental data to predict DIN

Previous studies suggested rainfall, windspeed, and sea-surface temperatures (SST) were drivers of stream DIN variability in a Pacific island setting (Houk et al., 2020). Rainfall transports watershed pollution to the base of the study streams and was hypothesized to be the primary predictor of stream DIN. Wind-driven waves have the potential to restrict flow out of river basins, or alternatively, improve flushing. Seasonal fluctuations in air temperature can change nitrogen mineralization in watersheds thereby influencing streams, and seasonal fluctuations in SST can change the background levels of DIN in marine waters (Eldredge, 1983; Jack Brookshire et al., 2011). SST served as a proxy for both. Rain and wind data were gathered from the airport weather station in Guam (NOAA climate data center, https://www.ncdc.noaa.gov/cdo-web/) while SST data were gathered from the oceanographic monitoring buoy off the east coast of Guam (National Data Buoy Center Buoy 52200, https://www.ndbc.noaa.gov/).

In contrast to these environmental factors that determine day-to-day variability in DIN concentrations, human factors were expected to influence mean annual DIN across the study watersheds. Numerous studies have revealed that watershed development and human population were strong predictors of time-integrated DIN due to general non-point pollution sources such as septic systems, urban runoff, and agriculture. Meanwhile, watershed size and slope may represent influential covariates that influence the nature and rate of transport. Watershed metrics were calculated from geographic information system base layers served online through the University of Guam Water and Environmental Research Institute (http://south.hydroguam.net/gis_download.php). These layers provided i) estimates of human development defined by agriculture, barren, and urban areas, ii) estimates of human populations ultimately derived from census data, iii) watershed sizes, and iv) watershed slopes.

2.5. Data analyses

Three watersheds on the southeast had consistently high salinities due to topography and ocean influx and thus were removed from DIN analyses (sites 8 to 10). For all remaining watersheds, only 10 % of samples had high salinities due to ocean influxes, leaving 90 % of the data for analyses. Relationships between cumulative rainfall 2-days prior to sampling and DIN concentrations were first examined to characterize the nature of watershed pollution. Watersheds with significant, least-squares regressions between DIN and rainfall had low DIN concentrations (below 0.10 mg/l) in the dry season but DIN increased, often tripling during the peak of the wet season ($P < 0.05$ and normal residuals, Fig. S1). We hypothesized indiscriminate non-point sources of pollution from human presence within these watersheds that was transported by rainfall events (i.e., septic systems, agriculture, or confined animals). In contrast, watersheds with non-significant rainfall relationships had consistently high DIN across the year above 0.20 mg/l. Given that only one permitted point-source discharge existed within our study streams (site 14, artificial wetlands to treat sewage from ~4000 people, DIN consistently below 0.20 mg/l suggesting compliance), we used these results to hypothesize the presence of unclassified point-sources of pollution. Our hypothesized classifications of point-versus-non-point pollution were further investigated in the second set of models that examined mean annual DIN concentrations with respect to human and watershed characteristics described above. Watershed size, slope, human population density, and development were examined for their individual, additive, and interactive ability to predict mean annual DIN. The best-fit model was considered based upon fit (R^2), confidence (*P*-value), stability (Akaike Information Criterion, AIC scores), and residual normality. We expected that watersheds with point sources of pollution would have weak-or-no relationships with indiscriminate human presence, while non-point pollution would be associated with human presence variables noted above.

Next, we used generalized linear mixed-effects modeling to predict daily DIN concentrations for each watershed. Rainfall, SST, and wind data represented fixed effects that were hypothesized to impact daily DIN similarly across all watersheds. These environmental data were examined for several time periods prior to sampling to search for best-fit models (1-day, 2-days, and 1-week). In contrast, watershed identities were represented by random effects (i.e., differing y-intercepts), which were hypothesized to be an artifact of differing human factors described above. Mixed modeling was performed using package *lme4* in the R software platform using the maximum likelihood approach (Bates et al., 2015). We first built a null model, and then compared subsequent models using analyses of variance (ANOVA) to test between the residual deviance estimates. The best-fit model was selected based upon a step-wise comparison of both residual deviance and AIC scores.

The mixed-modeling results provided predictions of daily DIN concentrations across 2021 that represented continuous hindcasts. Daily hindcasts were visualized against monthly sampling events and then used to establish DIN thresholds that were exceeded 10 %, 20 %, and 30 % of the time. These exceedance criteria were based upon guidance provided by the United States Environmental Protection Agency (USEPA) (EPA, 2001).

2.6. DIN, fishing pressure, and reef assemblages

The conditions of coral, benthic, and fish assemblages were last examined with respect to several environmental variables, proxies to fishing pressure, and DIN. Predictor terms included wave energy, distance to nearest land-based fishing access, distance to nearest boat-based fishing access, distance to watershed discharge point, and DIN. Long-term wave energy data around Guam was previously developed based upon 10-year windspeed and wind direction data that were used to calculate energy incident upon each study reef (http://south.hydroguam.net/map-coast-wave-exposure.php). Least-squares regression modeling followed the same process described above.

3. Results

3.1. Watershed classifications

Non-point source pollution was the hypothesized, primary contributor of DIN in 17 of the 23 watersheds where positive relationships existed with rainfall and sampling consistently occurred in low-salinity watershed discharge (Figs. 2, S1). DIN across these 17 watersheds ranged between 0.02 and 0.20 mg/l and human population density and disturbed land were predictors of mean annual DIN ($R^2 = 0.37$, 0.36, and 0.41 with *P*-values<0.01 for regressions between mean annual DIN at each site and log human population, disturbed land, and log population × disturbed land, Fig. 2b). In contrast, unclassified point-source pollution was the hypothesized, primary contributor of DIN in the remaining 6 watersheds where rainfall had non-significant relationships with DIN and concentrations were consistently ≥0.20 mg/l (Fig. 2). For these watersheds, mean annual DIN was not predicted by watershed characteristics or human factors (Fig. 2).

3.2. Daily DIN modeling

Mixed-effects regression modeling revealed that cumulative rainfall 2-days prior to sampling was the strongest predictor of daily DIN values for all watersheds with hypothesized non-point source pollution ($\chi^2 = 129.8$, $P < 0.001$, $\Delta AIC = 127.8$, ANOVA comparison against null model, $n = 224$ samples within 18 non-point watersheds). However, significant random effects existed whereby each watershed had a differing y-intercept that represented differing baseline DIN concentrations. In support, the random y-intercept terms of the model were highly correlated with mean annual DIN ($r = 0.94$, Pearson's correlation), which as noted above, was well predicted by human population and watershed development. Therefore, the modeling process partitioned natural factors (i.e., rainfall) as fixed effects that explained daily DIN variation, and human factors as random effects that led to differing y-intercepts, or differing baselines.

Predictions from mixed-effects models were used to hindcast daily DIN for each non-point source watershed between 2020 and 2021

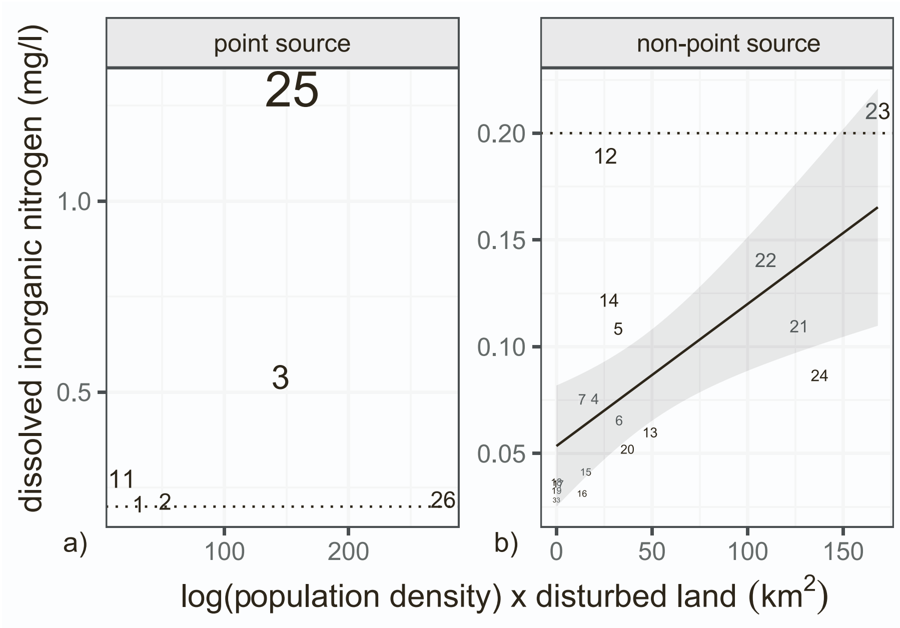

Fig. 2. a–b. Relationships between human populations, disturbed land, and the mean dissolved inorganic nitrogen (DIN) concentrations from samples collected across the study year. Numbers on the plot were scaled by DIN and identify individual watersheds in Fig. 1. Watersheds were classified as having point source DIN contributions if no relationship with rainfall existed and DIN was consistently above 0.20 mg/l (a, dotted line), or were classified as having non-point source contributions if significant relationships with rainfall existed and DIN was variable with season (b). Note, axis scales differ.

(Fig. 3). From these hindcasts, DIN concentrations associated with 10 %, 20 %, and 30 % exceedances were derived for each site (Fig. 3b). Unpopulated watersheds with little barren and developed land had DIN concentrations between 0.05 and 0.08 mg/l within this range of exceedance criteria, while watersheds with moderate human population and developed land had concentrations between 0.08 and 0.18 mg/l. Therefore, conservative recommendations of DIN thresholds for water quality regulations were suggested by the transition between unpopulated and moderately populated watersheds using the 20 % exceedance criteria, or at approximately 0.10 mg/l.

3.3. DIN, fishing pressure, and reef assemblages

Condition scores for both benthic substrates and coral assemblages were predicted by a similar suite of environmental variables, DIN, and fishing pressure proxies. When examining all reeftypes together, wave energy was the only significant, but weak, predictor of benthic and coral condition (Table 1, Appendix Figs. S2–S3). High wave energy was associated with higher condition, and there was a strong break between the eastern exposed reefs and the western leeward reefs that weakened residual normality. Predictions were much stronger when stratifying within eastern and western reefs. Coral condition was diminished by DIN and proximity to boat access (i.e., fishing pressure), and increased with distance from watershed discharge (i.e., dilution) ($R^2 = 0.84$ and 0.95, respectively for coral assemblages on the west and east, Table 1). Partial regression plots that isolated upon each predictor term while controlling for others revealed that negative impacts to the coral assemblages began when DIN exceeded 0.10 mg/l, providing a second independent estimate of a DIN threshold that resonated with the USEPA water quality exceedance criteria (Fig. 4). Benthic condition on the eastern reefs had the exact same predictors as coral condition, however, on the west coast, benthic condition was similarly low across all sites except for the marine protected areas (MPA), matching the trends with fish conditions.

Fish condition scores across all reeftypes decreased with proximity to boat access, increased in marine protected areas (MPA), and increased with DIN and wave energy (Fig. 5, Table 1, Appendix Fig. S4). The less-intuitive increases with DIN and wave energy were driven by increased biomass of small-bodied herbivores and detritivores, and greater presence of a few large generalist herbivores that increased size structures (i.e., *Kyphosus* spp.) (Appendix Figs. S5–S6). Further stratification revealed that fish condition scores on the west were influenced by MPA, whereby the only MPA had significantly higher condition than other reefs. Fish condition on the east was predicted by proximity to boat/land access and the smaller gradient in wave energy among eastern reefs, but not significantly influenced by MPA status (Table 1).

We last provided a summary of the correlation structure between individual condition metrics for fish, coral, and benthic assemblages to better understand contextual relationships between DIN, fishing pressure, and individual reef attributes (Appendix Figs. S5–S6). Fish condition scores were driven most by biomass and size (r ~ 0.9, Pearson's moment correlation between metric and overall score for both east and west reefs), moderately by heterogeneity and predator biomass for west reefs where rare but influential encounters with larger fish occurred (r ~ 0.37), and uninformed by evenness (r ~ 0). Coral condition scores were driven most by evenness (r ~ 0.95) and skewness (r ~ 0.80 to 0.90, east and west reefs), heterogeneity on west reefs where rare but influential encounters with larger coral colonies existed (r ~ 0.85), and moderately by species richness on east reefs (r ~ 0.55). Benthic condition scores on the west were driven most by evenness and the benthic substrate ratio (r ~ 0.82 for both), with little influence from coral cover due to positive relationships between tolerant corals such as *Porites rus* and DIN, but negative relationships with other corals. However, benthic scores on the wave-exposed east were driven by evenness and coral cover that was comprised mainly of Merulinidae and Acroporidae corals (r ~ 0.42 and 0.79, respectively). Last, the overall condition scores for corals, fish, and benthic assemblages were positively correlated, especially benthic and fish scores, suggesting feedback loops existed between the assemblages which was furthered in the discussion (r ~ 0.35 to 0.50, Appendix Fig. S7).

4. Discussion

We developed a 'ridge-to-reef' framework to link sources of watershed pollution with stream DIN concentrations and specific attributes of coral-reef assemblages. Tangible outcomes included (i) identifying unclassified point-sources of pollution in 6 watersheds that were not associated with any permitted point-source discharges, and (ii) recommending a ~0.1 mg/l DIN threshold beyond which exceedances of DIN were limited to 20–30 % of the time and no negative impact to adjacent

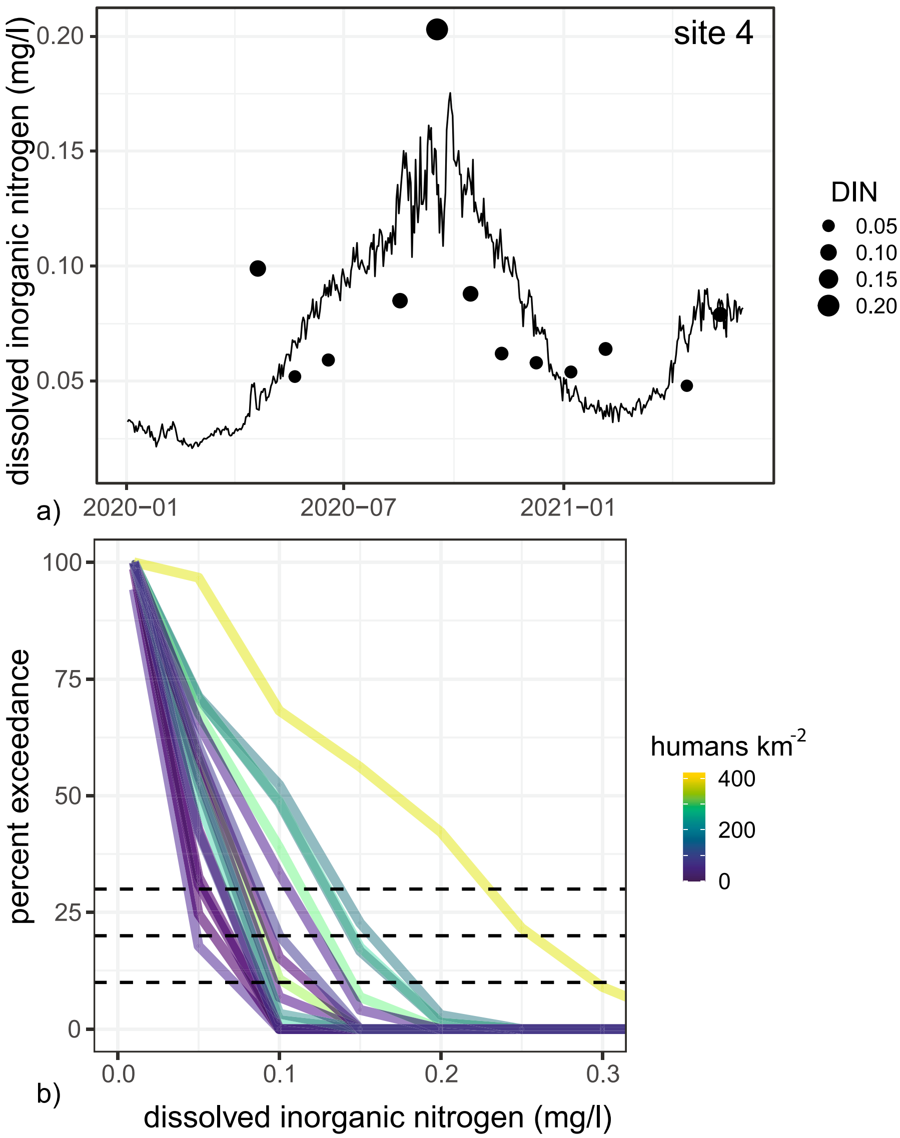

Fig. 3. a–b. Predicted daily DIN concentrations for one representative watershed across the study year when stream sampling occurred (a) (site 4, black line, Fig. 1). Black dots indicate monthly sampled DIN concentrations used to build hindcast models. Similar hindcasts were created for each watershed and clipped to cover a 1-year period. The percent of time each watershed exceeded specific DIN concentrations was then plotted (b, dashed horizontal lines show 10, 20, and 30 % exceedance times). Color gradient lines represents each watershed with colors scaled to human population.

coral and benthic assemblages were detected. Interestingly, studies from American Samoa reported a similar 0.1 to 0.15 mg/l stream DIN threshold was also associated with the 20 % DIN exceedance criteria and negative changes to the coral and benthic assemblages (Comeros-Raynal et al., 2021; Houk et al., 2020). Given consistencies between these two tropical islands that differed in watershed sizes, soils, geology, and slope, generalized guidance to benefit Pacific islands may be emerging. However, generalized guidance hinges upon key questions such as: 1) Do uninhabited watersheds from differing high islands process available DIN to similar extents and yield similar baseline stream discharge concentrations? 2) Are relationships and thresholds between human populations, developed land, and DIN similar across islands? Currently, many Pacific islands lack infrastructure and resources to determine locally-relevant water quality standards and rely upon guidance from developed, often continental nations that may not be relevant as development permits continue to be issued. In these cases, our DIN thresholds could be implemented proactively until resources exist to conduct independent sampling.

Beyond water quality legislation, our results provided further clarity into two primary local stressors and their impacts to coral-reef assemblages (Foo et al., 2021). We summarize that high DIN exposure: i) reduced evenness, richness, and heterogeneity of coral assemblages (Fabricius et al., 2012), however, ii) increased the biomass and size structure of generalist fish assemblages, and contextually, iii) increased the cover of the stress-tolerant corals such as *Porites rus* on several leeward reefs but reduced coral cover elsewhere (Darling et al., 2013), while lastly, iv) reduced the coverage of non-coral calcifying substrates on western reefs only where low wave energy and limited flushing existed (Lapointe et al., 2019) (Fig. 6). Broadly, this translated to a homogenization of many Guam reefs where lower diversity and less rugose reef assemblages benefit generalist herbivores and detritivores (Emslie and Pratchett, 2018; Taylor et al., 2015), with total food fish biomass dependent on wave energy and fishing access. This type of ecological homogenization has been seen in many other systems exposed to diverse stressors, with notable tradeoffs between increasing or maintaining production and yield despite diminishing ecosystem resilience and biodiversity (McKinney, 2006; Mori et al., 2015; Richardson et al., 2018; Riegl et al., 2012).

At the individual reef scale, we highlighted significant interplay between wave energy, fishing pressure, and DIN concentrations. It was desirable to embrace the interplay between these factors and reef attributes to provided higher-resolution management guidance pertaining to DIN and fishing pressure (Bradley et al., 2009; Comeros-Raynal et al., 2021; Mumby et al., 2007; Van de Leemput et al., 2016). For instance, successful fisheries management policies are expected to have stronger benefits to coral, fish, and benthic assemblages given the ubiquitous,

Table 1
Summary statistics of regression models between reef condition scores, dissolved inorganic nitrogen (DIN), fishing pressure proxies, and other environmental factors. Significant model terms included *DIN*, *disch.dist* representing distance from watershed discharge point, *land* or *boat.access* representing distances fishers must travel, *MPA* representing marine protected areas, *wave* representing wave energy (methods). The best-fit models presented here were based upon residual normality and Akaike Information Criterion scores, while controlling for any outliers that were >2 standard deviations above the mean. Numbers in parentheses of outlier sites refer to Fig. 1.

Dependent variable	Geography	Model estimates	R^2	P-value	Site omission
Coral condition	All (n = 20)	0.41 ± 0.07 *wave*	0.61	<0.001	–
	West (n = 10)	−0.64 ± 0.15 *DIN* 0.05 ± 0.01 *land* × *boat. access*	0.84	<0.001	*DIN* > 2SD (25) *c_score* < 2SD (21)
	East (n = 7)	−0.36 ± 0.08 *DIN* 0.19 ± 0.04 *boat.access* 0.44 ± 0.05 *DIN* × *disch.dist*	0.95	0.007	*disch.dist* > 2SD (12)
Benthic condition	All (n = 20)	0.20 ± 0.10 *wave*	0.14	0.06	–
	West	–	–	–	–
	East (n = 7)	−0.20 ± 0.08 *DIN* 0.14 ± 0.04 *boat.access* 0.27 ± 0.05 *DIN* × *disch.dist*	0.86	0.03	*disch.dist* > 2SD (12)
Fish condition	All (n = 23)	0.21 ± 0.10 *boat.access*, 0.65 ± 0.25 *MPA*, 0.07 ± 0.03 *DIN* × *wave*	0.44	0.002	–
	West (n = 12)	1.60 ± 0.41 *MPA*	0.56	0.003	–
	East (n = 8)	−0.25 ± 0.09 *wave*, 0.12 ± 0.05 *land* × *boat. access*	0.72	0.02	–

negative relationships with boat/land access (i.e., fishing pressure proxies) compared to contextual relationships with DIN. However, fisheries policies alone would be most relevant where fisher preferences are driven by biomass and size, and not species selectivity which would require additional DIN pollution management. In contrast, watershed policies are expected to best protect coral and habitat diversity that are known to improve reef rugosity, accretion, and benefit recreational uses and tourism. While we appreciate that each watershed/reef system investigated has differing fishing pressure and DIN contributions, our results quantified their individual influences in each watershed to help prioritize management intervention.

4.1. *DIN concentration versus discharge volume*

It is important to consider the present study evaluated DIN concentrations but not discharge volumes. Our hypothesis was that watershed size or slope might be significant covariates in reef assemblage models because they help to scale DIN concentrations to discharge volumes (e.g., watershed size is a proxy of discharge volume). Yet, two factors may explain why watershed size and slope did not improve our predictions of reef condition. First, watershed sizes on the western, leeward side of the island were mainly similar and thus DIN concentrations would be the primary source of variability that determines discharge volumes (mean watershed size = 4.1 km^2 ± 1.5 SD). Second, while watershed sizes differed substantially on eastern reefs (mean = 15.9 km^2 ± 19.1 SD), there was a strong correlation between distance from watershed discharge and size (r = 0.77), and distance modulated the negative impacts to benthic and coral assemblages within best-fit regression models.

5. Conclusions

The present study used calibrated survey teams to simultaneously collect water quality data at the base of 26 Guam watersheds at monthly intervals for a full year to capture seasonal cycles. This design controlled for inherent variation that is known to influence water quality and facilitated the development of discharge models to predicted DIN. Both water-quality exceedance criteria and the responses of biological assemblages both concluded that 0.10 mg/l DIN represented a useful threshold to protect stream water quality and adjacent reef assemblages.

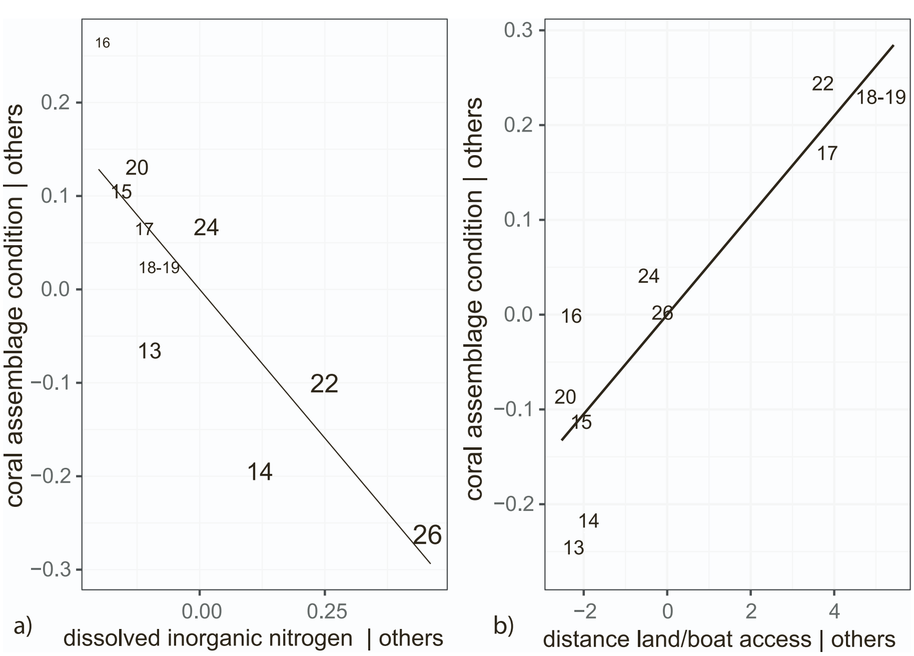

Fig. 4. Added variable regression plots showing the individual influences of DIN concentrations (a) and fishing pressure proxies (b) on coral condition scores for western Guam watersheds (see Table 1 for full model details). The axes of added variable plots represent standardized values for each predictor after accounting for all others. Numbers correspond to Fig. 1 and numbers in (a) were scaled by mean annual DIN concentration (low-small and high-large, with a range of 0.035 to 0.22 mg/l). Notably, the 0.10 mg/l DIN threshold was crossed when moving between sites 13 and 24, where a negative effect on coral condition scores began to emerge. Similar findings existed for eastern Guam watersheds (Table 1, also see Appendix Fig. S2).

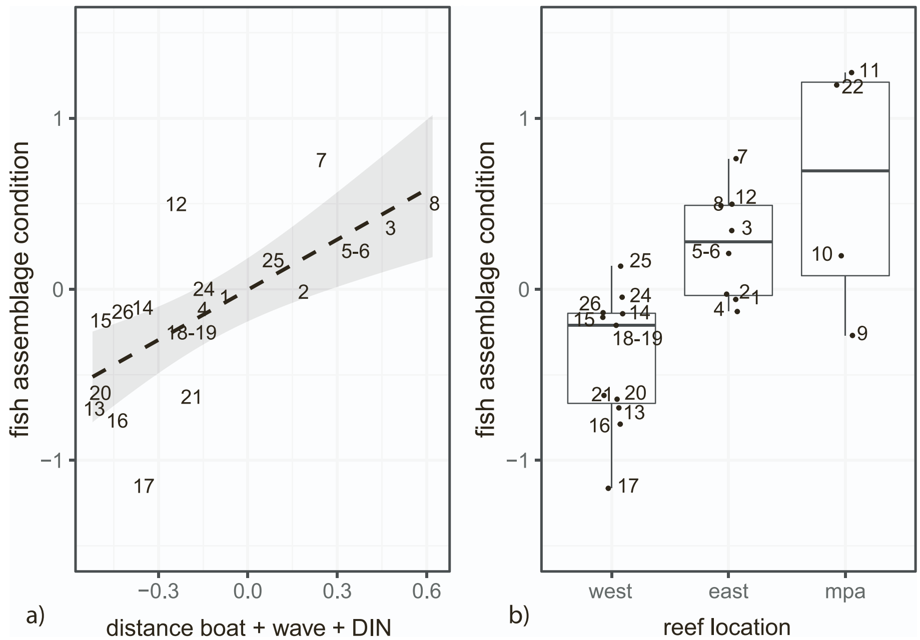

Fig. 5. a–b. Regression plot (a) showing the positive, additive influences of distance from boat access, wave energy and DIN on fish condition scores for non-MPA reefs (see Table 1 for model details). This best-fit regression model was associated with a clear break in fish condition scores between the west (low) and east (high), and a less-pronounced, positive but contextual influence of marine protected area status (b). Numbers on the plot refer to sites in Fig. 1.

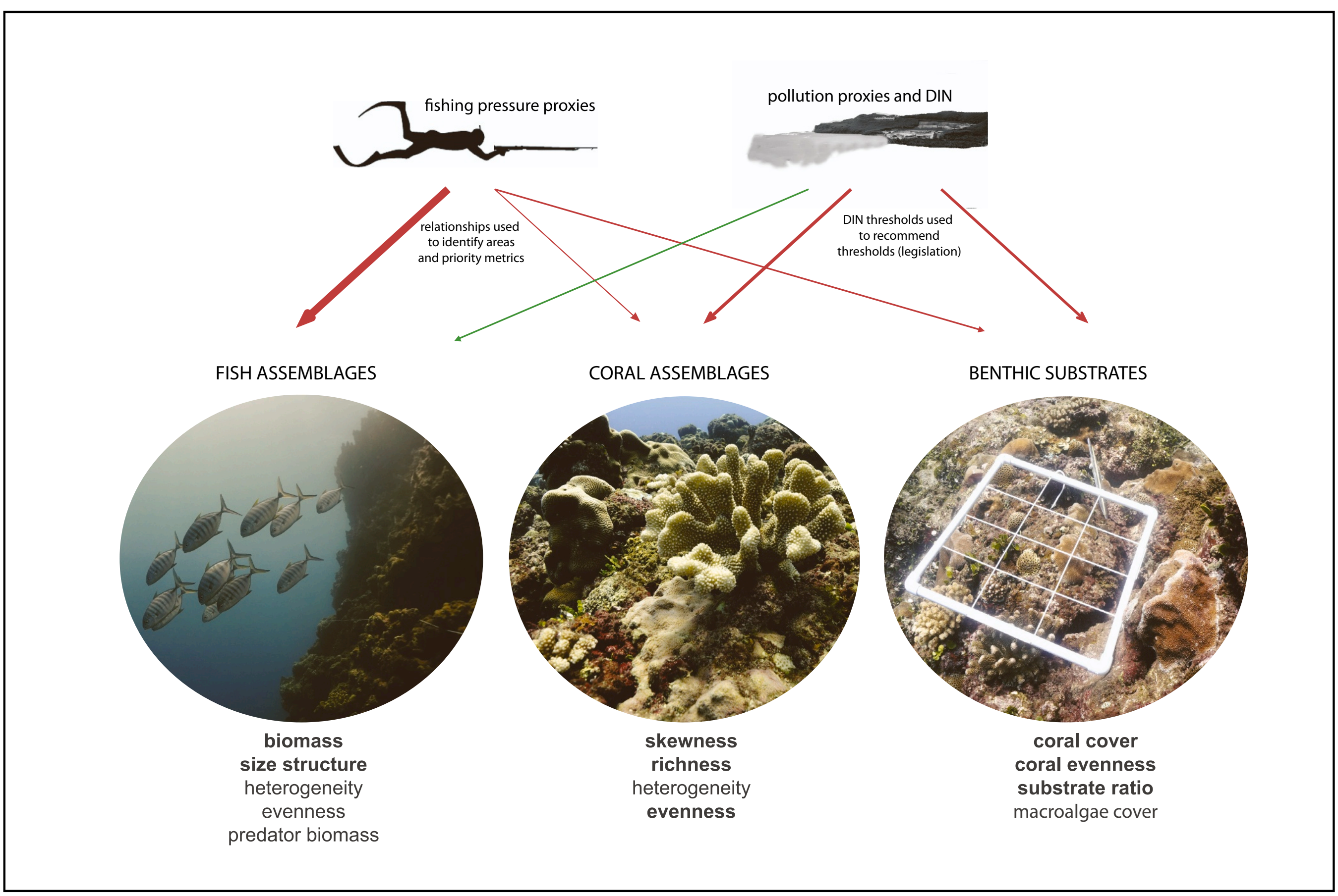

Fig. 6. Visualization of modelled relationships between dissolved inorganic nitrogen (DIN), fishing pressure, and coral-reef assemblages. Arrow thickness was scaled to the predictive power of each term while accounting for all others (see Table 1 for model details), while colors indicate negative (red) or positive (green) effects. The individual metrics that comprised each reef assemblage scores are noted below the pictures and metrics in **bold** had the greatest correlation, or influence, with the overall reef assemblage scores (Appendix Fig. S6). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

While DIN was represented by nitrate and ammonia, nitrate was dominant in our freshwater discharge samples (>85 % of DIN) and has the most significant consequences for coral-reef assemblages that regularly recycle ammonia, but are sensitive to nitrate addition (Burkepile et al., 2020; Zhao et al., 2021). We last revealed contextual consequences of DIN discharge and fishing pressure to the nearshore reef assemblages that helped to link conservation and management objectives with expected, measurable outcomes. As studies continue to examine the suite of watershed pollution indictors such as nutrients, sedimentation, turbidity, and chlorophyll, our results suggested that thresholds for DIN concentrations may be similar across Pacific Islands warranting further investigation.

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CRediT authorship contribution statement

Peter Houk: Conceptualization, Methodology, Visualization, Funding acquisition, Writing – original draft, Data curation. **Fran Castro:** Conceptualization, Methodology, Visualization, Funding acquisition, Writing – original draft, Data curation. **Andrew McInnis:** Data curation. **Michael Rucinski:** Data curation. **Christy Starsinic:** Data curation. **Teddy Concepcion:** Data curation. **Storm Manglona:** Data curation. **Edwin Salas:** Data curation.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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