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SANTA CRUZ

**THE INFLUENCE OF SEABIRD GUANO ON PACIFIC CORAL REEF
ECOSYSTEMS**

A dissertation submitted in partial satisfaction
of the requirements for the degree of

DOCTOR OF PHILOSOPHY
in
ECOLOGY & EVOLUTIONARY BIOLOGY
by

Susanna Erin Honig

September 2015

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Abstract

The Influence of Seabird Guano on Pacific Coral Reef Ecosystems

By

Susanna E. Honig

The biosphere is composed of a mosaic of ecosystems that are connected to one another through biological and physical processes. Animals that migrate over large spatial scales can play a significant role in vectoring nutrients and energy from one ecosystem to another. For example, seabirds forage in pelagic ecosystems on fish, krill, and squid and then migrate thousands of kilometers to breeding islands where they deposit large concentrations of nutrient-rich feces, or guano. Over sixty years ago, G.E. Hutchinson hypothesized that nutrients from seabird guano could increase primary productivity in recipient marine ecosystems. The nutrients in seabird guano have been widely documented to dramatically alter recipient terrestrial and freshwater ecosystems, but the influence of guano on nearshore marine ecosystems remains elusive. In the following dissertation, I assess the impact of seabird guano on one of the most biodiverse marine ecosystems on earth; coral reefs. First, I examine the influence of seabird guano subsidies on coral reef benthic community composition and fish biomass across one of the largest marine protected areas on earth, the Pacific Remote Islands Marine National Monument. I demonstrate that coral reefs next to

islands with high densities of seabird guano have more herbivorous fishes and significantly different benthic communities. Next, I use stable isotope analysis and benthic percent cover data to evaluate the nitrogen-footprint from seabirds on coral reef macroalgae adjacent to Rose Atoll, American Samoa. I demonstrate that algae adjacent to Rose Island, which is home to a large seabird colony, is enriched in $\delta^{15}\text{N}$. However, algal ecological responses to seabirds are taxon-specific: fleshy algal cover increases with increasing proximity to Rose Island, whereas calcareous algal cover decreases with increasing proximity to Rose Island. Finally, I assess relative differences in seawater nutrients and algal nitrogen isotope values in the complex, anthropogenically-modified coral reefs of Oahu, Hawaii to see how seabird community subsidies may alter coral reefs in pristine vs. impacted Pacific islands. Even in the midst of anthropogenic fishing and nutrient enrichment, I demonstrate that islets with large seabird colonies have greater dissolved phosphate values and higher algal $\delta^{15}\text{N}$ compared to islets with small seabird colonies. Together, these three data chapters are the first test of Hutchinson's local enrichment hypothesis in coral reef ecosystems, and they provide strong evidence that seabirds significantly influence coral reef ecology and biogeochemistry via cross-ecosystem nutrient subsidies. Coral reefs and seabirds are two of the most threatened marine communities on the planet, but they are currently managed in isolation. The results of this research indicate that seabirds should no longer be ignored as a significant source of nutrients on coral reefs. Instead, seabird and coral reef conservation should be

integrated in order to maximize efficient and potentially synergistic management of these two globally-imperiled marine communities.

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Chapter 1

Introduction

Ecosystems are characterized as discrete units made up of interacting species and their physical environment, but boundaries that separate adjacent ecosystems are not impermeable. Instead, the flux of organic and inorganic material across ecosystem borders can occur via direct transport of organisms, detritus, or nutrients across space (Polis et al. 1997, 2004). Unidirectional flow of donor-controlled resources from one ecosystem into another are considered spatial subsidies if they increase productivity in recipient ecosystems (Polis et al. 1997). Cross-ecosystem subsidies can therefore be important drivers of bottom-up food web regulation, particularly when resources from nutrient-replete systems are vectored into nutrient-deplete or oligotrophic habitats with consequences for higher trophic levels. Spatial subsidies are vectored across a myriad of ecosystems that span terrestrial and aquatic environments through abiotic (e.g. wind, currents) or biotic (e.g. direct organismal transport) processes. Organisms that transport nutrients from one ecosystem to another may play a large role in the functioning of adjacent ecosystems. Seabirds, which feed exclusively from the ocean, are well-documented vectors of spatial subsidies.

Seabirds transport nutrients across space through the deposition of feces, or guano. These top predators feed in pelagic ecosystems on fish, krill, and squid, and migrate thousands of kilometers to islands where they breed and concentrate guano

that is rich in nitrogen and phosphorus (Smith and Johnson 1995). Over sixty years ago, G.E. Hutchinson hypothesized that seabirds could increase marine primary productivity in nearshore ecosystems (Hutchinson 1950). Since then, guano-derived subsidies have been documented to dramatically alter ecosystem productivity in terrestrial (Anderson and Polis 1999, Croll et al. 2005, Young et al. 2010) and freshwater ecosystems (Payne and Moore 2006), but the impact of seabird guano in marine ecosystems remains debated. Studies that have addressed the impact of seabird guano in marine ecosystems have mostly been in temperate upwelling zones (e.g. Wootton 1991), where offshore pulses of cold, nutrient-rich water may overwhelm local seabird guano inputs. However, recent work in an oligotrophic lagoon highlights the potential for seabird guano to influence nutrient-deplete marine ecosystems (McCauley et al. 2012), increasing the abundance of zooplankton and planktivorous consumers like manta rays.

Coral reef ecosystems offer an ideal location in which to address Hutchinson's marine enrichment hypothesis because they are characteristically low in nutrients (Szmant-Froelich 1983) and coupled with seabird colonies via tropical islands or atolls. Seabirds have been breeding on islands adjacent to coral reefs for millions of years, and tropical seabird populations were likely much larger and biodiverse in the past prior to human-driven extinctions, particularly in the Pacific Islands (Steadman 1995). This historic association between birds and adjacent reefs highlights the potential importance of seabird guano as a source of localized nutrients for remote coral ecosystems.

The possible implications of seabird community subsidies on coral reef ecosystems are not trivial; seabirds and coral reefs are two of the most threatened marine communities on earth. Nearly a third of all seabird species are at risk of extinction (Spatz et al. 2014), and around sixty percent of coral reefs worldwide are threatened by anthropogenic stressors (Burke et al. 2011). However, these two at-risk marine communities are currently managed separately by conservation practitioners. Anthropogenic nutrient enrichment from sewage effluent, agricultural fertilizer, and urban runoff can threaten coral reef health by favoring the proliferation of weedy algal species over corals (Smith et al. 2010), increasing coral disease (Bruno et al. 2003), and even promoting species invasions (Brodie et al. 2005). In systems where nutrient enrichment is coupled with overfishing, coral-dominated ecosystems may undergo phase shifts into algal-dominated barrens (Hughes 1994). Given the consequences of human-derived nutrients on coral reef ecology and health, it is essential to understand the potential influence guano may be having on coral reefs that are coupled with seabird islands. Identifying any existing links between these two imperiled communities can facilitate integrated management and aid in the development of accurate predictions for reef resilience and recovery with and without seabird colony restoration. This knowledge is vital for the simultaneous preservation of seabird and coral reef communities worldwide.

In the following doctoral dissertation, I evaluate the influence of seabird community subsidies on adjacent coral reef ecosystems with three data chapters:

In **Chapter 2**, I perform a comparative analysis across 7 islands with varying seabird abundance in the Pacific Remote Islands Marine National Monument to assess the relative influence of guano production on coral reef benthic community composition and fish biomass. I use regression techniques to understand how guano production influences the percent cover of benthic functional groups and the biomass of herbivorous fishes. I then use multivariate ordination to reduce benthic community composition into three dimensions and employ alternative regression models to address the relative influence of guano production on these dimensions of community composition in addition to other oceanographic and biological covariates. Finally, I examine individual benthic taxa that are important drivers of community composition to understand how specific taxonomic groups that make up the benthic community may respond to seabird guano enrichment.

In **Chapter 3**, I address the influence of seabird guano on macroalgal biogeochemistry and ecology at Rose atoll in American Samoa. Rose atoll is a small, uninhabited Marine National Monument composed of two coral cays that are home to 140,000 breeding seabirds. I begin by assessing the mean $\delta^{15}\text{N}$ (a proxy for seabird-derived nitrogen) in a calcareous macroalga, *Halimeda* sp., at Rose atoll, and I compare these values to those observed at Tutuila and Ofu & Olosega (other islands in the archipelago). I then examine the algal $\delta^{15}\text{N}$ content within Rose atoll at coral reef sites that are varying distances from shore. Finally, I analyze the relationship between distance from shore and percent cover of four common chlorophytes, *Halimeda* sp., *Caulerpa* sp., *Dictyosphaeria* sp., and *Microdictyon* sp., with the

hypothesis that chlorophytes responding to guano-derived nutrients will be higher in abundance closer to shore.

In **Chapter 4**, I use seawater nutrient sampling and stable isotope analysis on macroalgae to evaluate the chemical signal of seabird guano in coral reefs adjacent to four islets offshore of southeast Oahu, Hawaii. This chapter combines techniques used in previous chapters but applies them to a complex, human-dominated system that is inundated with other sources of nitrogen and phosphorus from sewage effluent, agricultural fertilizer, urban runoff, and freshwater streams to see if guano-derived nutrients are important in the midst of anthropogenic enrichment.

Together, these three chapters are the first test of Hutchinson's seabird enrichment hypothesis in coral reef ecosystems, and they address his hypothesis at the landscape level, across 14 islands in the remote tropical and subtropical Pacific. This landscape level approach exposes patterns occurring along gradients of human impact, equatorial upwelling, sea surface temperature, and biogeography. These patterns provide a framework from which mechanistic processes should be further explored and evaluated (synthesized in **Chapter 5**), with important consequences for seabird and coral reef ecology and conservation.

Chapter 2

The influence of seabird guano on coral reef communities at the landscape level

Abstract

Nutrient-replete seabird breeding islands and nutrient-deplete marine ecosystems co-occur throughout the world. Sixty-five years ago Hutchinson hypothesized that runoff of feces or guano from these islands could locally enrich surrounding waters. Although seabird subsidies of nutrients to recipient terrestrial and freshwater ecosystems have been well documented, support for Hutchinson's local enrichment hypothesis in marine ecosystems has been little studied. We assessed the relationship between guano inputs and coral reef community composition at seven islands in one of the world's largest marine protected areas, the Pacific Remote Islands Marine National Monument, by linking seabird guano production to benthic cover and fish biomass data. Chi square results revealed that high-guano sites had a greater biomass of browsing herbivorous fishes but no difference in macroalgal cover, suggesting that enrichment was manifest in production not standing stock of macroalgae. In addition, generalized additive models revealed that sites next to islands with increased guano enrichment and high herbivory were fundamentally different in benthic community composition relative to low-guano islands. Taken together, our results suggest that seabird guano provides a bottom-up nutrient resource that fuels production at higher trophic levels with consequences that

reverberate back to the benthic community through top-down effects, supporting both Oksanen and Fretwell's exploitation ecosystems hypothesis and Hutchinson's local enrichment hypothesis. These findings further suggest opportunities for linked management of tropical seabirds and coral reefs, two of the most threatened marine groups.

Introduction

Seabirds forage offshore, but roost and breed on islands where they deposit nutrient-rich feces (guano). Over six decades ago, Hutchinson (Hutchinson 1950) proposed that guano runoff could increase marine productivity in nearshore habitats surrounding breeding islands. Subsequent studies in terrestrial and freshwater habitats have demonstrated the importance of seabird-derived nutrient subsidies (Lindeboom 1984, Polis and Hurd 1996, Anderson and Polis 1999, Schmidt et al. 2004, Payne and Moore 2006, Young et al. 2010) and highlighted the negative impacts to biological communities in those habitats when seabirds are lost (Croll et al. 2005, Maron et al. 2006). However, evidence of Hutchinson's original hypothesis about the role of seabird communities as a nutrient subsidy to marine ecosystems has remained elusive (Wootton 1991).

Our limited understanding of the contribution of seabird guano to marine communities stems primarily from studies conducted in temperate ecosystems embedded in nutrient-rich upwelling zones (Zelickman and Golovkin 1972, Bosman and Hockey 1986, Wootton 1991), where the contribution of seabird guano can be

overwhelmed by oceanographically-derived inputs of nitrogen and phosphorus (but see McCauley et al. 2012 for an example in an oligotrophic lagoon). By contrast, many coral reef ecosystems are limited in oceanographically-supplied nutrient input. Hence, island/reef ecosystems present an ideal system to examine the influence of seabird-derived nutrients because 1) high concentrations of guano from island-breeding tropical seabirds are adjacent to nutrient-deplete coral reef communities, many of which are remote from human influences, and 2) seabird abundance varies greatly among otherwise similar islands.

Nutrient over-enrichment on coral reefs from anthropogenic sources (e.g. sewage, agricultural fertilizer) negatively alters coral reef health by inhibiting coral settlement, calcification, and growth (Koop et al. 2001, Fabricius 2005) favoring the proliferation of fleshy macroalgae over scleractinian corals (Smith et al. 2010), and increasing the incidence of disease (Bruno et al. 2003). These impacts can be even more dramatic when coupled with depletion of herbivorous fishes from overfishing (Friedlander and DeMartini 2002, Williams et al. 2011, Weijerman et al. 2013), in extreme cases causing phase shifts from coral to algal domination (Hughes 1994). However, recent work in protected areas in the Pacific has revealed a significant number of reefs without any detectable anthropogenic sources of nutrients with relatively high algal biomass (Sandin et al. 2008, Vroom and Braun 2010, Vroom et al. 2010). These observations call into question the widespread idea that pristine coral reefs are characterized by high coral and low algal cover but also provide the impetus

for the investigation of the potential for the role of nutrient inputs from guano runoff in structuring near-pristine coral reef habitats.

Seabirds and coral reefs are two of the world's most threatened marine communities, and like many communities are currently managed in isolation despite their frequent spatial and temporal co-occurrence. In this paper we evaluate support for Hutchinson's local enrichment hypothesis to assess the role that seabird-mediated nutrient subsidies play in structuring nearshore coral reef communities. Using a landscape-level approach across islands in the Pacific Islands Remote Marine National Monument (Fig. 2.1) with different prevailing oceanographic conditions, we test whether seabird-derived nutrient inputs next to protected coral reefs (no permanent human populations, no legal fishing; (NOAA 2015)) are associated with community-level patterns consistent with bottom-up influence on benthic and fish taxa. We hypothesize that increased guano will favor the proliferation of macroalgae and herbivores that selectively feed on macroalgae (browsers), resulting in significantly altered community structure at sites adjacent to seabird islands.

Methods

Study site

The Pacific Remote Islands Marine National Monument encompasses 7 uninhabited islands or atolls spanning nearly twenty degrees in latitude (Fig. 2.1), and it is one of the largest marine protected areas in the world, including 1,269,075 square kilometers of land and sea (NOAA 2015). The area includes a diverse assemblage of

seabirds, turtles, marine mammals, fish, and invertebrates (Obama 2014), including threatened species, and has been the subject of regular monitoring programs since 2000 (Vroom and Braun 2010). Because the islands comprising the Pacific Remote Islands Marine National Monument are uninhabited and fishing in adjacent waters is prohibited (Obama 2014), these coral reefs represent some of the most pristine in the world, providing an exceptional opportunity to test the natural effect of seabird nutrient subsidies.

Benthic percent cover

The NOAA Pacific Islands Fisheries Science Center's (PIFSC) Coral Reef Ecosystem Division (CRED) conducted research expeditions in the Pacific Remote Islands Marine National Monument during 2009-2011 to characterize baseline coral reef ecology, including species-level benthic cover. Divers measured benthic percent cover using the Line Point Intercept method (e.g. Vroom and Braun 2010) along two consecutive 25-meter transects separated by 5 meters at permanent sites. At 20-centimeter intervals, divers identified benthic composition to the lowest possible taxonomic unit. We pooled data from both transects and summed the number of points identified for each taxon divided by the total number of points (250), multiplied by 100 to obtain percent cover.

Fish biomass

To measure the biomass of fishes from 2000-2009, research biologists followed standard CRED Rapid Ecological Assessment methods using belt transects

(e.g. Williams et al. 2011). Divers swam parallel to three 25-meter transects at each site, and they recorded the size class and count of all fishes observed within visually estimated belt widths. Fishes with total lengths greater than 20 centimeters were identified in belt widths of 4 meters (100 m² area) on the swim out. Fishes with total lengths smaller than 20 centimeters were identified in belt widths of 2 meters (50m² area) on the swim back to the initial starting point. Divers identified fish to the smallest taxonomic unit possible (usually species). We summarized mean fish biomass across all years for functional groups including herbivores that selectively feed on macroalgae (referred to hereafter as browsing fish), herbivores that feed on turf algae (a mixture of grazers, scrapers, and excavators), secondary consumers, planktivores, and piscivores. We assigned fish taxa into functional groups according to expert opinion, CRED consumer guild categories, and published literature (Green and Bellwood 2009, Williams et al. 2011, Weijerman et al. 2013).

Guano production density

For each island with associated coral reef data we used estimates of breeding seabird abundance (Depkin 2002, MCBI 2007, Flint 2015), mass-specific energetic requirements (Birt-Friesen et al. 1989), of all occurring seabird species, and information on species-specific breeding duration, including fledging and incubation (Schreiber and Burger 2002) to calculate guano production (in metric tons yr⁻¹) following Croll et al. (Croll et al. 2005). We incorporated land area (Gove et al. 2013) to characterize guano production density (in MT*km⁻² yr⁻¹).

Data analysis

We calculated the mean benthic proportion cover by site for unambiguous taxonomic units (referred to hereafter as operational taxonomic units (OTUs)) across all available years in forereef habitats occurring in mid-depth zones (6-18 m). An OTU was the resolved systematic grouping that could be identified in field sampling and included species, genera, and in rare cases higher functional categories. We identified functional groups for all OTUs, including turf algae, macroalgae, crustose coralline algae, cyanophytes, scleractinian corals, corallimorphs, octocorals, and zoanthids. Mean fish biomass was determined at each of these sites by functional group. We arcsin-squareroot transformed benthic proportion cover, $\log(x+1)$ transformed guano production density, and $\log(x+1)$ transformed fish biomass data to conform with statistical assumptions (Zar 1999). For each coral reef site, we quantified the linear distance to the nearest island (m) in Google Earth (Google Inc. 2015). No sites were close to more than one island. To remove the possibility that the inherently unbalanced sampling design could bias results, we standardized the number of sites per island to the lowest number at any island. Where the number of sites exceeded this number we dropped those most distant from the island. This yielded 3 sites at each of 7 islands (Fig. 2.1).

Community analyses

We used a stepped approach, described below, to assess potential bottom-up and top-down processes affecting the benthic communities. This approach had three

broad steps. First, we use ordination to characterize the benthic community in a reduced set of dimensions (\ll than the full set of taxonomic groups). Second, we used a model selection approach assessing the strength of association between a set of predictor variables and the benthic community. Third, we decomposed the benthic ordination to assess the importance of the particular taxonomic groups to the models developed in step 2.

To describe benthic community structure, we used nonmetric multidimensional scaling (NMS; Kruskal 1964, Mather 1976). We removed rare taxa (taxa occurring at only one or two sites) prior to the NMS, yielding 21 final taxa. We calculated dissimilarity matrices using Bray-Curtis distance (Bray and Curtis 1957).and used coral reef sites as sample units. We determined the final number of dimensions (axes) for the most appropriate ordination solution by comparing the stress with the number of dimensions. This is a process that uses a measure of lack of fit of an n-dimensional ordination to the similarity matrix as a guide to determining the appropriate number of dimensions in the ordination.

To quantify the impact of guano production density on benthic community structure in addition to bottom-up environmental and top-down biological covariates, we used model selection (generalized additive models (GAMs)) with NMS axis scores (each representing 1 dimension in the ordination described above) as a response. These represent components of community composition. We chose to use a GAM approach rather than a generalized linear modeling (GLM) approach because of

the constraint imposed by parametric fit in GLM's relative to GAM's, where fit is through non-parametric smoothing. One possible issue with GAM's is that that best fit between predictor and response variables can be unpredictably non monotonic if the model is over-fit, precluding easy interpretation of results. We guarded against this by minimizing the number of fitted parameters. We included sea surface temperature, chlorophyll [a], wave energy, and irradiance, averaged at the island level (Gove et al. 2013) as bottom-up oceanographic covariates and fish biomass, averaged by site at the functional-group level, as top-down biological covariates. We iteratively dropped covariates that were not significant ($p>0.05$) until all remaining covariates in the model were significant (Zuur et al. 2009) To assess the direction of the linear relationship among covariates and NMS axes, we calculated Pearson-Kendall correlations. We assessed co-linearity among covariates and eliminated redundant covariates prior to running GAMs.

We verified the importance of covariate values by examining the jackknifed improvement in deviance explained for each generalized additive model. We systematically removed each covariate and then created a model with the remaining covariates, in addition to a model with each covariate in isolation. Deviance explained was re-computed during each iteration and compared to the model with all covariates included. If a covariate was substantially correlated with other covariates, or was independent of other covariates but added little model fit, withholding it will have little impact on model performance. Therefore, an important and non-redundant

covariate will have high explanatory power by itself and its omission from the model will result in a significant reduction in deviance explained.

After identifying key axes of benthic community structure and the environmental and biological factors associated with them, we measured the contribution of particular taxa to these gradients to identify influential groups. This was done by examining the strength of the relationship between community axis scores and each taxonomic group. We calculated the correlation coefficient (r) for each taxon against axis scores, and we regarded taxa as having an interpretable relationship with axis score if more than 10% ($r^2 > 0.1$) of the variance in that variable could be explained by the variance in axis score (Pan et al. 1996, Huff et al. 2005).

Test of models of enrichment

We tested two simple hypotheses to investigate the relationship between guano production density and enrichment at higher trophic levels. For both hypotheses we included distance between sample site and island as a predictor variable to account for dilution of nutrients away from the guano sources.

(1) There would be a positive relationship between guano production (predictor variable) and macroalgae and turf (response variable). This is a straight forward and seemingly intuitive prediction but key to understanding this hypothesis is that our estimate of macroalgae and turf is static; that is, it represents standing stock of primary producers most likely to respond to nutrient enrichment.

(2a) There would be a no relationship between guano production (predictor variable), and macroalgae and turf (response variable), and

(2b) There would be a positive response between guano production (predictor variable) and biomass of fish herbivores (of macroalgae and turf).

Taken together (2a and 2b), the hypothesis is based on the idea that nutrient enrichment is likely to lead to greater production of macroalgae and turf, which will lead to greater numbers of consumers without change in standing stock (at least with respect to cover). Clearly this hypothesis also assumes no anthropogenic impacts that could interfere with the trophic relationship between algal production and consumption by herbivorous fish.

We used a generalized linear modeling approach (normal distribution, identity link) to test these two hypotheses.

Results

Test of models of enrichment

Guano production density varied among islands, with the greatest enrichment at Baker Island and the least at Kingman Reef, a submerged atoll (Fig. 2.2). We found no relationship (Chi sq. = 0.0094, df = 2, p = .9953) between standing stock of macroalgae and turf and enrichment (modeled by guano production density and distance between sample site and island). By contrast, we found a positive relationship (Chi sq. = 9.61, df = 2, p = 0.0082) between browsing herbivorous fish

biomass and enrichment (Fig. 2.3) These results support the idea that in this system nutrient enrichment via guano increases macroalgal and turf production, but not standing stock, and thereby increases standing stock of herbivorous fish.

Community analyses

Non-metric multidimensional scaling ordination (NMS) on benthic taxa revealed that the benthic community composition varied across sites, and that variation, using a Monte Carlo approach, was best explained on three dimensions (Axes). The final ordination was reached after 71 iterations and the final stress value was 0.104, a value considered to indicate a good fit between the ordination and the original similarity matrix. NMS Axes were highly orthogonal (independent); orthogonality was greater than 98% for all three pairwise comparisons of axes. Visual inspection of the NMS revealed that some sites from common islands had similar benthic community composition along Axis 1 and 2 (e.g. Wake Atoll, Palmyra Atoll, Fig. 2.4), but in general sites were spread along a gradient of community composition rather than being clustered by island. All three sites from Baker Island occurred at the high end of the Axis 1 gradient, which was also associated with the high end of the guano production density and browsing fish biomass gradients (Fig. 2.4).

Linear correlations among covariates and axis scores (Table 2.1) revealed that guano production density and browsing fish biomass were both positively and strongly related to Axis 1 scores (Fig. 2.4). Given the univariate association between guano production density and browsing herbivore biomass, we simultaneously

smoothed these variables as a tensor product (the interaction between the two variables) for a Generalized Additive Model (GAM) with Axis 1 as a response, but not for Axis 2 or 3. This allowed assessment of this interaction within the GAM modeling framework but only as they were associated with the benthic community described on Axis 1. For all other covariates, inclusion in GAM was dictated by the model selection approach as described in the methods section. The full set of GAM results (Fig. 2.5) revealed that benthic composition was best explained by a combination of environmental (chlorophyll a and sea surface temperature) and biological covariates (fish biomass). The relative contribution of each of these covariates to axis scores was variable, with guano production density* browsing fish biomass explaining the most deviance individually along Axis 1 (Fig. 2.5).

Benthic community variation modeled along Axis 1 was driven primarily by a subset of benthic taxa belonging to scleractinian coral, macroalgae, turf algae, and crustose coralline algae functional groups (Table 2.1). The direction of each taxon's relationship with Axis 1 scores was variable; in general, scleractinian corals were negatively associated with the community composition gradient, and most algal groups were positively associated with the gradient. Exceptions to this pattern included the scleractinian genus *Acropora*, which was positively associated with the gradient, and the calcareous macroalga *Peyssonnelia*, which was negatively associated with the gradient (Table 2.1).

Browsing fish biomass was positively associated with NMS Axis 1 scores at high guano production density ranges when other significant covariates were accounted for (fixed at their median values), but this relationship was not apparent at low guano production density ranges (Fig. 2.6).

Discussion

It is extraordinarily difficult to document the effects of physical and ecological processes across spatially large communities and biogeography, and it is primarily done using comparative and not experimental approaches. However, when done well, these comparative studies have profoundly influenced our understanding of mechanisms promoting community organization, dynamics, composition, and vulnerability (e.g. Williams et al. 2011, 2015, Connolly et al. 2014). In this study we evaluated a hypothesis derived from Hutchinson (Hutchinson 1950) that effects of subsidies of nutrients from seabird colonies would at least in part influence the structure of coral reef communities. We, like the studies noted above, used a comparative approach based on combining datasets from a variety of sources. We note this because aggregation of disparate datasets is increasingly possible and holds incredible promise as a tool for examination of questions that are geographic or global in scale. However, aggregation comes with a set of problems that can obscure hypothesized patterns and mechanisms. These mainly stem from the reality that the different datasets were likely collected for different reasons, and taxonomic resolution and temporal and spatial scales and replication are typically not coherent in design. Hence, thoughtful development of assembly rules for data aggregation is essential.

Through careful assembly of datasets for benthic cover, fish composition and biomass, guano production, and oceanographic conditions, we were able to demonstrate land to sea flux of seabird guano, which has a significant bottom-up influence on coral reef community structure across the Pacific Remote Islands Marine National Monument.

At the functional group level, chi square results revealed that sites adjacent to islands with higher guano production density had greater biomass of browsing herbivorous fishes despite no effect on algal standing stock, supporting the hypothesis that nutrients from seabird guano favor the production of macroalgae, fueling herbivory by browsing fishes. We tested this hypothesis while including oceanographic and ecological alternatives by characterizing the composition of the benthic community and using it as a response variable. The results from our GAMs showed a strong interaction between guano enrichment and browsing fish biomass on the benthic community, supporting our hypothesis that browsing herbivores are feeding on algal production enriched by seabirds. Together these results support Oksanen and Fretwell's exploitation ecosystems model (Oksanen et al. 1981), where increased nutrient inputs enhance herbivore populations that, in turn, maintain the standing stock of primary producers at a constant level

Indirect impacts of nutrient inputs on herbivore abundance have been quantified in several meta-analyses in marine ecosystems (Worm et al. 2002, Burkepile and Hay 2006) and demonstrated experimentally (Boyer et al. 2004,

Furman and Heck 2008, Burkepile and Hay 2009) and comparatively (Williams et al. 2015) on coral reefs. Collectively, these studies have shown that combined bottom-up effects of nutrient input and top-down effects of herbivory result in complex consequences for associated benthic communities. In this study, variation in community composition scores along Axis 1 was strongly associated with increasing browser biomass when guano production density was high, but not when guano production density was low (Fig. 2.5), signifying interplay between bottom-up and top-down forces. We hypothesize that differences in benthic community composition at guano-enriched sites result from increased overall selectivity by browsing herbivorous fish, favoring the proliferation of benthic taxa that are less preferred or are resistant to herbivory via adaptive chemical defenses (Hay et al. 1994, Bolser and Hay 1996, Rasher et al. 2013). In contrast, variation along Axes 2 and 3 were mostly explained by oceanographic forcing (sea surface temperature and chlorophyll a), which is not surprising given that Jarvis, Howland, and Baker Islands are all heavily influenced by equatorial and topographic upwelling (Brainard et al. 2005, 2014, Gove et al. 2006, Miller et al. 2008, Williams et al. 2015). Hypotheses addressing the influence of oceanographically-driven bottom-up and/or top-down control on benthic community structure are not mutually exclusive from a guano enrichment hypothesis, and they may interact with guano enrichment in unanticipated ways.

Along Axis 1, taxon-specific regressions on ordination-derived composition scores revealed that specific taxa drive the observed gradient in community structure (Table 2.1), highlighting their potential as indicators of guano-enriched herbivory. In

general, we found that increased cover of turf algae, crustose coralline algae, and a highly defended maroalga (*Lobophora*), were associated with positive composition scores along Axis 1, corresponding to high guano production density and high herbivory (Fig. 2.6). In contrast, reduced cover of scleractinian corals was associated with positive composition scores along Axis 1. Decades of research has established a negative, competitive relationship between corals and upright algae and filamentous turfs (reviewed in McCook et al. 2001, Fabricius 2005), which may explain why corals and turf algae are inversely related to community composition. However, this was not consistent among all scleractinian taxa: Montiporids, Pocilloporids, Poritids, and Fungiids were all negatively associated with the community composition gradient, while Acroporids had positive associations. Coral responses to nutrient enrichment can be variable (Szmant 2002, Fabricius 2005), taxon-specific (e.g. Fong and Fong 2014), and source-dependent (Bongiorni et al. 2003). Seabird guano is rich in phosphorus (e.g. Liu et al. 2006) and ammonia (e.g. Schmidt et al. 2004, Riddick et al. 2014) which may impose differential responses on coral taxa. For example, Dunn et al. (Dunn et al. 2012) showed that *Acropora* grew quickly in response to experimental phosphate additions, and others have observed similar effects from fish-derived excreta (e.g. Meyer and Schultz 1985, Bongiorni et al. 2003). Acroporids are important components of coral reefs worldwide because these fast-growing corals are characteristically a chief producer of the calcium carbonate reef framework (Browne 2012), and their positive, significant association with composition scores indicates

that they may be tolerant or potentially enhanced by guano production density and high herbivory.

While benthic communities in our study showed complex, taxon-specific responses to seabird nutrients, it is significant that we did not observe general functional-group level transformations from coral to algal-domination at high-guano study sites. This signifies that seabirds, which have naturally occurred in tropical ecosystems for millions of years, may *not* alter coral reefs in the same manner that anthropogenic nutrients have been shown to globally. This is surprising given the magnitude of guano that is produced on Pacific Islands, which equals or in many cases exceeds nutrient input from intensive agriculture (Smith and Johnson 1995, Young et al. 2010). Herbivorous fish communities, which are protected from fishing in the regions examined in this study, function as key trophic links between primary production and higher trophic levels (Sandin et al. 2008, Williams et al. 2011, Heenan and Williams 2013), and they are likely responsible for transferring subsidized primary production up the food web. The ability of herbivorous fishes to mediate nutrient-flux on coral reefs by increasing grazing rates (Boyer et al. 2004, Burkepile and Hay 2006, 2009) makes them a vitally important functional group for reef health (Green and Bellwood 2009).

These findings provide new insight regarding the role of seabirds in nutrient-cycling on coral reefs, a factor that has traditionally been ignored or assumed to be negligible. Seabirds occupy thousands of islands globally, and coral reefs co-occur on

many tropical seabird-breeding islands, which means that the effects we observed in this study are likely occurring worldwide. However, marine and terrestrial protections on most island/reef ecosystems are limited compared to those on our study systems (Bellwood et al. 2004, Hughes et al. 2010). In most areas of the world coral reefs are locally inundated by anthropogenic pollution and overfishing, in addition to the longer-term risks of global climate change (Friedlander and DeMartini 2002, Fabricius 2005, Hoegh-Guldberg et al. 2007) The relationship we found between seabird guano enrichment and the biomass of browsing herbivorous fishes may break down in areas with added nutrients and fishing pressure.

Nearly 30 percent of all seabird species are currently at risk of extinction (Spatz et al. 2014) and over 60 percent of coral reefs worldwide are threatened (Burke et al. 2011). These co-occurring communities are generally managed in isolation. Our work shows guano nutrient subsidies may complicate management of these ecosystems. Failure to recognize this relationship can lead to incorrect predictions of reef recovery in areas of high guano production, particularly in areas with varying amounts of fishing harvest. Indeed, many coral reef systems that evolved adjacent to dense seabird colonies which once provided important terrestrial to marine nutrient fluxes have experienced significant reductions in these fluxes due to seabird declines. Prior to anthropogenic disturbances, pristine systems may actually have existed across a range of nutrient availability, depending upon proximity to seabird breeding islands and the density of nesting seabirds. Recent fishing-mediated declines in reef-associated herbivorous fish may alter coral reef community structure, with differing

effects depending upon the amount of seabird nutrient flux. Coral reef managers assessing reef health may have more realistic expectations for current and future conditions on island-associated reefs by incorporating seabird-derived nutrients as a factor. The simultaneous preservation of seabird islands and adjacent coral reefs may allow for conservation synergies that promote and maintain the health of both communities at once, protecting these unique habitats.

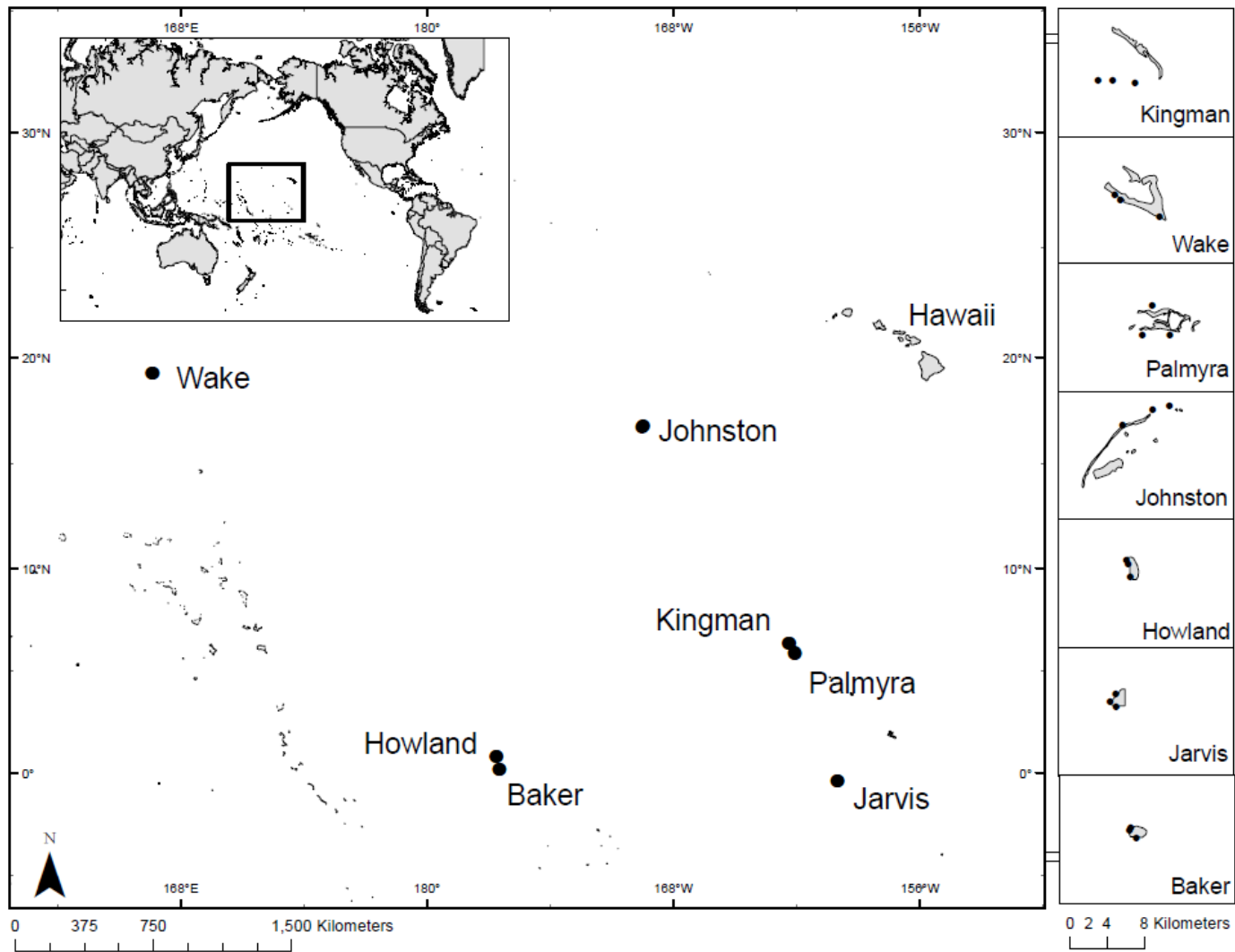


Figure 2.1 Locations of study islands (large black circles) across the Pacific Remote Islands Marine National Monument and coral reef sites (small black circles on inset maps on the right) used as samples within each island in the study. Basemap Source: Esri World Countries.

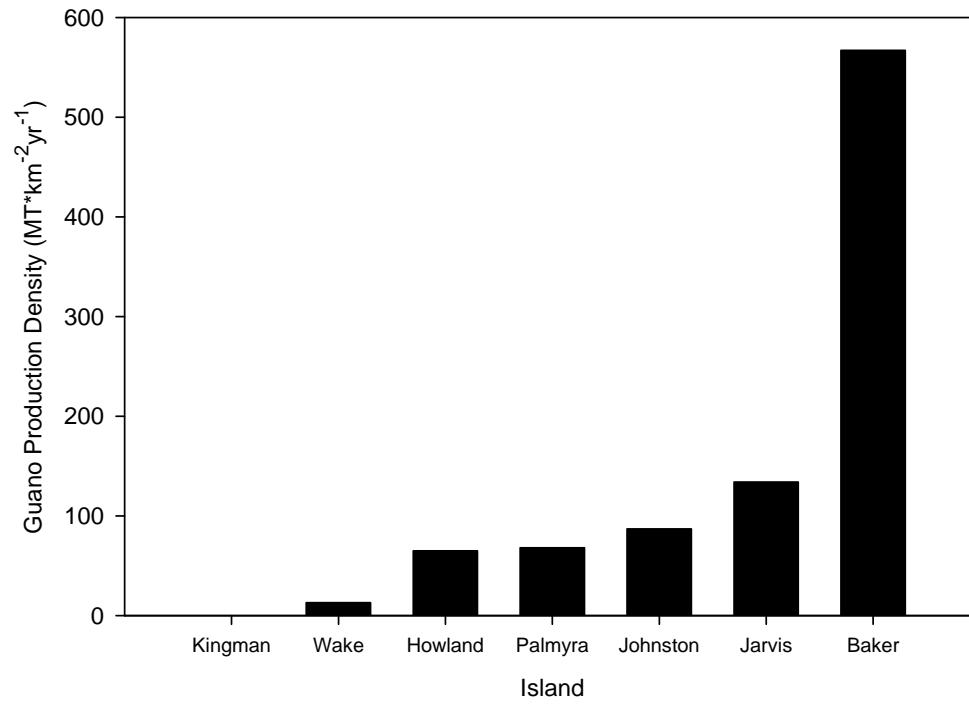


Figure 2.2 Guano production density across seven study islands in the Pacific Remote Islands Marine National Monument.

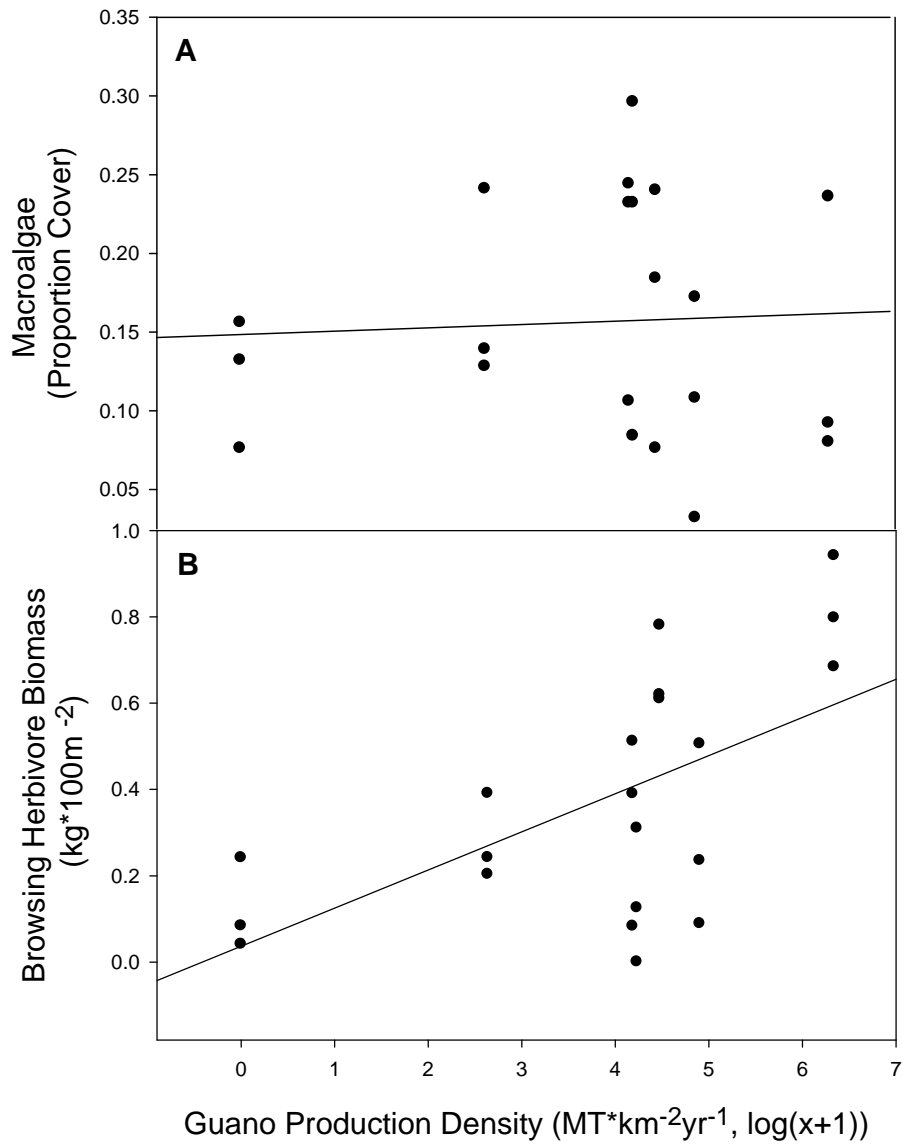


Figure 2.3 The linear relationship between two coral reef functional groups and guano enrichment. (A) shows the relationship between macroalgae and guano enrichment ($R^2 = -0.05$, $F_{1,19} = 0.06$, $p = 0.8170$) and (B) shows the relationship between browsing herbivorous fish and guano enrichment ($R^2 = 0.33$, $F_{1,19} = 10.85$, $p = 0.0038$). Points for both (A) and (B) represent sites ($n = 3$) at each island.

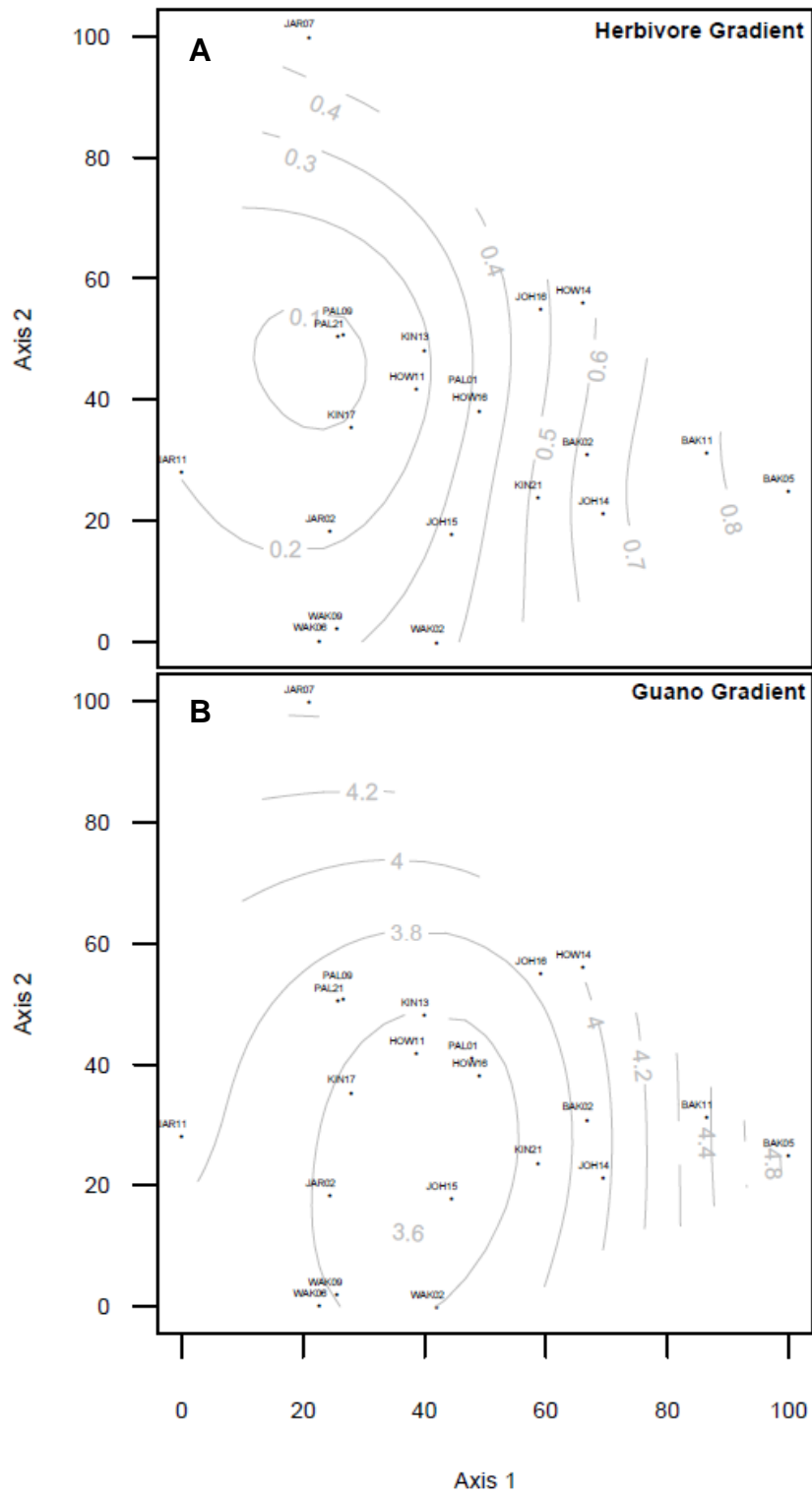


Figure 2.4 Indirect gradient analysis showing NMS Axis 1 vs. Axis 2 scores among 21 sites (7 islands with 3 sites each) overlaid with (A) $\log(\text{browsing herbivorous fish biomass (kg} \cdot 100\text{m}^{-2}) + 1)$ contours and (B) $\log(\text{guano production density (MT} \cdot \text{km}^{-2} \text{yr}^{-1}) + 1)$ contours.

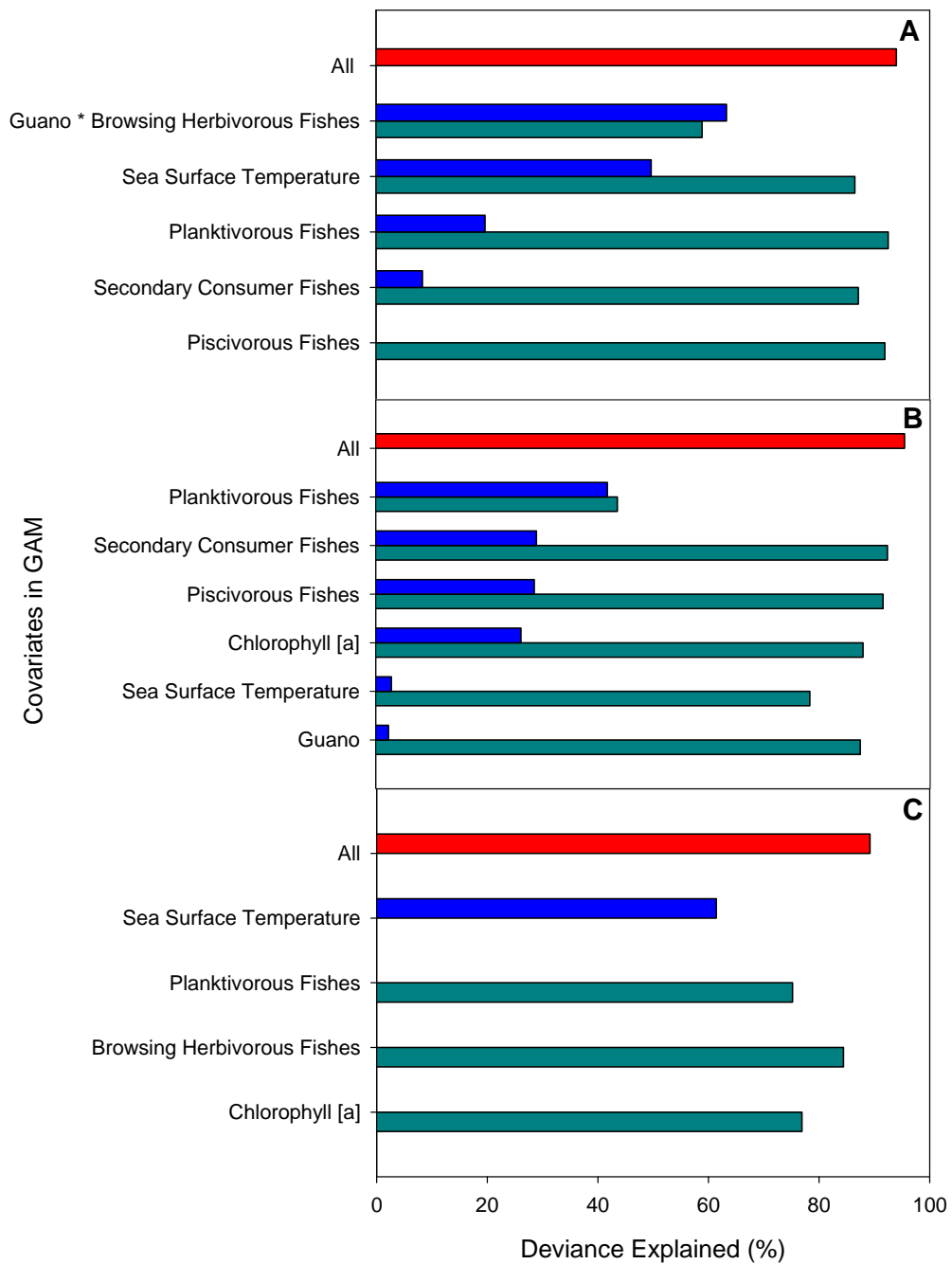


Figure 2.5 Deviance explained individually by each covariate alone (blue bars) vs. without that covariate (cyan bars) compared to total deviance explained by all covariates together (red bars) for (A) Axis 1, (B) Axis 2, and (C) Axis 3 scores following Generalized Additive Models (GAMs).

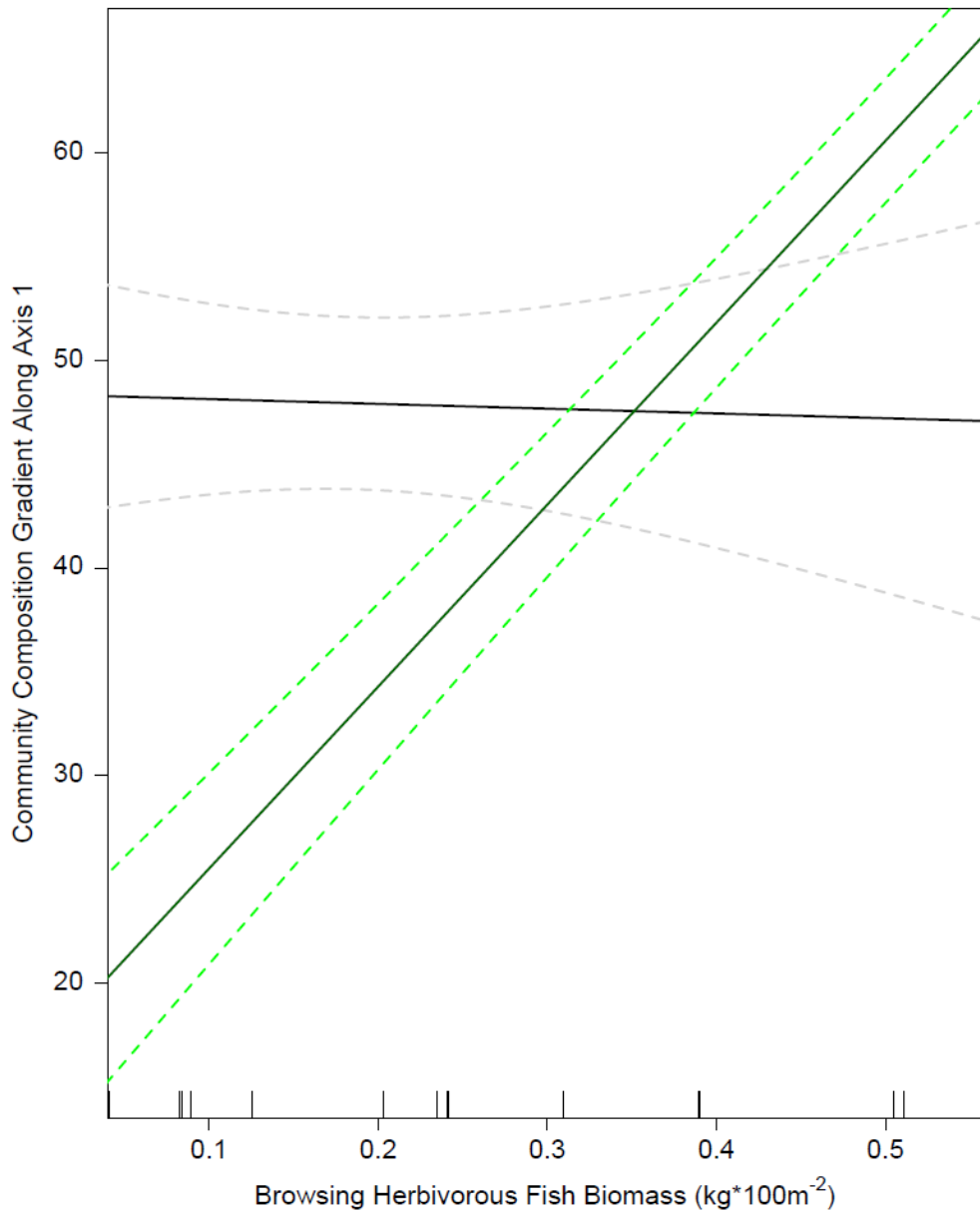


Figure 2.6 Model output of Axis 1 scores calibrated by browsing herbivorous fish biomass (kg*100m⁻²) at low (10%, black) and high (90%, green) guano production density quantiles. All other significant GAM covariates were held at median values. Error bars represent ± 95% Confidence Intervals.

Table 2.1 Summary of Pearson and Kendall correlations with ordination axes for a subset of influential taxa and covariates used in Generalized Additive Models. Taxa shown have $R^2 > 0.1$ versus NMS Axis 1.

Linear Relationships with NMS Axes		Axis 1 <i>R</i>	Axis 2 <i>R</i>	Axis 3 <i>R</i>
Functional Group	Benthic Taxon			
Scleractinian	<i>Montipora</i>	-0.685	-0.349	0.135
Macroalgae	<i>Peyssonnelia</i>	-0.641	-0.117	0.135
Scleractinian	<i>Acropora</i>	0.629	0.164	0.020
Turf Algae	Turf Algae	0.608	-0.53	-0.344
Scleractinian	<i>Pocillopora</i>	-0.524	-0.224	-0.409
Corallimorph	Corallimorph	0.482	0.117	-0.097
Macroalgae	<i>Lobophora</i>	0.426	0.143	0.459
Scleractinian	<i>Porites</i>	-0.399	0.097	-0.306
Crustose coralline algae	Crustose coralline algae	0.383	0.194	0.865
Octocoral	<i>Sinularia</i>	-0.337	0.754	-0.366
Scleractinian	<i>Fungia</i>	-0.337	0.19	-0.031
Covariate				
Browsing Herbivore Biomass (kg 100m ⁻²)		0.772	-0.012	0.182
Log (Guano Production Density+1) (MT*km ⁻² yr ⁻¹)		0.633	0.001	0.008
Planktivore Biomass (kg 100m ⁻²)		-0.346	0.682	-0.326
Turf-feeding Herbivore Biomass (kg 100m ⁻²)		0.318	-0.088	0.021
Sea Surface Temperature (°C)		0.27	0.159	-0.425
Wave Energy (kW m ⁻¹)		-0.25	-0.09	0.261
Piscivore Biomass (kg 100m ⁻²)		-0.232	0.312	-0.207
Secondary Consumer Biomass (kg 100m ⁻²)		-0.228	-0.335	-0.408
Log (Distance) (m)		0.156	0.029	0.675
Irradiance (Einsteins m ⁻² d ⁻¹)		0.136	0.012	0.197
Chlorophyll [a] (mg m ⁻³)		0.067	0.473	-0.036

Chapter 3

Nutrient enrichment by seabirds on coral reef macroalgae at Rose Atoll, American Samoa

Abstract

Seabirds breed on islands that are physically connected to nearshore coral reef ecosystems, but the impact of seabird guano on adjacent algal biogeochemistry and ecology has been little studied. We used nitrogen stable isotope analysis at three islands in American Samoa and benthic percent cover data of chlorophytes adjacent to Rose Atoll, the island with the greatest seabird density, to assess the relationship among seabird populations, algal $\delta^{15}\text{N}$, and relative percent cover of algae. Seabird-derived algal nitrogen, proxied by $\delta^{15}\text{N}$, was greatest at Rose Atoll compared to Tutuila and Ofu & Olosega Islands, and within the reef ecosystems of Rose Atoll $\delta^{15}\text{N}$ declined with distance from Rose Island. Three genera of chlorophytes (*Dictyosphaeria*, *Caulerpa*, and *Microdictyon*) also declined in abundance with increasing distance from Rose Island. However, *Halimeda*, a calcareous chlorophyte, increased significantly with increasing distance from Rose Island. Our results demonstrate that guano from seabirds plays an important a role in nutrient cycling and availability, with impacts to reef algal communities varying across taxa. Seabirds, which have traditionally been ignored as a source of nutrients on coral reefs, should be considered in coral reef management plans.

Introduction

Coral reefs are among the most productive and biodiverse ecosystems on the planet, yet typically occur in clear, nutrient-poor water (Szmant-Froelich 1983). This paradox is explained in part by the mutualism between hermatypic corals and photosynthetic endosymbionts, which together are the structural, nutrient, and energetic underpinning of these ecosystems (Szmant-Froelich 1983, Weis and Allemand 2009). A diversity of studies have shown that nutrients are made available naturally in oligotrophic coral reef systems via nutrient fixing by microbes (e.g. Cardini et al. 2014) atmospheric deposition (e.g. Barile and Lapointe 2005), oceanographic upwelling (e.g. Eidens et al. 2014), geologic weathering (e.g. Perry et al. 2012), excretion from animals living within or adjacent to reef boundaries (e.g. Meyer and Schultz 1985, Holbrook et al. 2008, Layman et al. 2013) and recycling by zooxanthellae. In addition, anthropogenically-derived nutrients can enter oligotrophic reefs via sewage runoff and agricultural fertilizer (reviewed by Fabricius 2005). However, little attention has been given to natural cross-ecosystem nutrient subsidies, particularly the role of seabirds, which are recognized globally for their ability to concentrate marine-derived nutrients on islands and are often found breeding in large numbers on adjacent coral reef islands.

Seabirds are top predators in pelagic ecosystems, migrating thousands of kilometers to breed on oceanic islands where they have been shown to subsidize terrestrial communities through the deposition of feces, or guano (e.g. Lindeboom

1984, Polis and Hurd 1996, Schmidt et al. 2004, Croll et al. 2005, Young et al. 2010). G.E. Hutchinson hypothesized that seabird guano could increase primary production in marine ecosystems adjacent to breeding colonies (1950), and while this question has been examined in temperate, nutrient-replete upwelling systems (e.g. Bosman and Hockey 1986, Wootton 1991), until recently it has only been hypothesized in nutrient-deplete systems (Littler et al. 1991, Smith and Johnson 1995, Schmidt et al. 2004). New insight from the equatorial Pacific indicates that seabird guano may provide significant bottom-up nutrients that reverberate up the food chain to consumers like Manta rays (McCauley et al. 2012). However, Hutchinson's original hypothesis about the direct effect of seabird guano on the biogeochemistry of primary producers remains unaddressed.

Here we investigate the role of seabird enrichment on algal abundance and biogeochemistry adjacent to Rose Atoll, which is home to nearly 140 thousand breeding seabirds (Table 3.1; Wegmann and Holzwarth 2006). Specifically, we examine how macroalgal $\delta^{15}\text{N}$ enrichment (as an indicator of seabird-derived enrichment) varies at Rose Atoll compared to other islands in American Samoa and also how $\delta^{15}\text{N}$ varies within the atoll along a gradient of distance from Rose Island (the dominant seabird breeding colony). Additionally, we examine the relationship between proximity to Rose Island and macroalgal percent cover of four genera of chlorophytes (*Caulerpa*, *Microdictyon*, *Dictyosphaeria*, and *Halimeda*).

Methods

Study site

This study took place in American Samoa, a US territory in the central tropical south Pacific Ocean made up of two coral atolls and five volcanic islands (Brainard et al. 2008, Fenner et al. 2008). The islands in this study (Fig. 3.1) vary in human population, reef area, land area, and seabird breeding abundance (Table 3.1). Rose Atoll, the southernmost atoll in the archipelago, is an uninhabited Marine National Monument and, as one of the smallest atolls in the world, it has disproportionately higher breeding seabird density than other islands in the archipelago (Wegmann and Holzwarth 2006, United States Fish and Wildlife Service 2014). Nearly 140 thousand seabirds breed on Rose Island, which is one of two small sand cays in the atoll. The other sand cay, Sand Island, shifts in shape and size from year to year, is intermittently vegetated, and has only a small number of birds breeding on it at any one time (Wegmann and Holzwarth 2006). Benthic data were collected in 2010 and algal samples were collected in 2012 during coral reef monitoring cruises to American Samoa by the Coral Reef Ecosystem Division of the National Oceanic and Atmospheric Administration (NOAA), Pacific Islands Fisheries Science Center.

Benthic percent cover

We surveyed the percent cover of benthic taxa along the forereef habitat at Rose Atoll using the line point intercept (LPI) method in 2010. At permanent sites in the mid-depth (6-18m) zone, ($n = 10$, Fig 1.), divers swam along two consecutive 25-

m transects separated by a 5-m interval and identified organisms at regular points (every 20 cm) to the highest taxonomic resolution possible (Vroom and Braun 2010). We calculated the mean percent cover for four chlorophyte genera, *Microdictyon*, *Dictyosphaeria*, *Caulerpa*, and *Halimeda* at all sites. We chose to examine chlorophytes because they have been shown to be reliable indicators of nutrient availability in many systems (Smith et al. 1981, Raffaelli et al. 1998). We chose these four particular chlorophyte genera because of their relatively high prevalence at our study islands. We excluded *Valonia* and *Bryopsis* because they each occurred at only 1 and 3 sites respectively and occupied less than 1% of the benthic cover when present. We measured the linear distance (m) from each sampling site to the closest portion of Rose Island using GPS-measured coordinates and Google Earth (Google Inc. 2015).

Algal collection and stable isotope analysis

In 2012, we opportunistically collected six replicate thalli samples of *Halimeda* ($n=54$ thalli) at four permanent forereef sites located around Rose Atoll, two sites located around Tutuila Island, and three sites around Ofu & Olosega Islands (Fig. 1). Samples were frozen immediately following collection and shipped to the University of California, Santa Cruz for processing.

We thawed frozen algae, rinsed it with deionized water to eliminate salt, and manually removed all epiphytes or epifauna with forceps. Cleaned samples were oven-dried at 60 °C for 24-48 hr (e.g. Lapointe et al. 2011) and homogenized using a

porcelain mortar and pestle. Samples were then weighed (mean \pm standard deviation = $12020 \pm 11 \mu\text{g}$) into 5 mm x 9 mm tin capsules (Costech Analytical Technologies). We measured algal $\delta^{15}\text{N}$ using a Carlo Erba 1108 elemental analyzer coupled to an isotope ratio mass spectrometer (ThermoFinnigan Delta Plus XP) at the University of California, Santa Cruz Stable Isotope Laboratory.

Statistical analyses

To examine differences in algal $\delta^{15}\text{N}$ among islands ($n = 3$) in American Samoa, we used one-way analysis of variance (ANOVA). To investigate the relationship among log (distance) to Rose Island and algal $\delta^{15}\text{N}$ and taxa-specific percent cover within Rose Atoll, we used linear regression ($n = 4$ isotope sites, $n = 10$ benthic cover sites). We conducted all statistical analyses in Jmp Pro 11.0.0 and prepared figures using SigmaPlot 10.0. Unless otherwise noted, means \pm standard errors are reported.

Results

Algal $\delta^{15}\text{N}$

Algal $\delta^{15}\text{N}$ values, with enriched values indicative of seabird-derived nitrogen, varied significantly among islands. Rose Atoll had significantly greater ($F_{2,6} = 17.7142$, $p = 0.0030$) $\delta^{15}\text{N}$ values ($6.51 \text{‰} \pm 0.47$), compared to Ofu & Olosega and Tutuila Islands ($5.06 \text{‰} \pm 0.14$ and $5.24\text{‰} \pm 0.18$ respectively), which were not

statistically distinguishable from each other (Tukeys HSD post-hoc analysis, Fig. 3.2).

Within Rose Atoll, variability in algal $\delta^{15}\text{N}$ was significantly explained by distance from the island, with sites farther from Rose Island having lower algal $\delta^{15}\text{N}$ values (Table 3.2, Fig. 3.3A).

Algal percent cover

Dictyosphaeria, *Microdictyon*, and *Caulerpa* percent cover significantly decreased with increasing distance from Rose Island (Table 3.2, Fig. 3.3B-D).

Halimeda showed the opposite pattern, increasing in abundance with greater distance from Rose Island (Table 3.2, Fig. 3.3E).

Discussion

The negative role that anthropogenically-derived nutrient fluxes from land-to-sea play in coral reef ecosystem functioning has been well established (reviewed in Szmant 2002, Fabricius 2005). However, the influence of naturally-derived land-to-sea nutrient fluxes has received significantly less attention, and the consequences of seabird guano on coral reef ecology is virtually unexplored. This gap in knowledge is not trivial; seabird populations are estimated to produce nutrient-rich guano at rates comparable to (if not exceeding) large human populations (Smith and Johnson 1995, Young et al. 2010), and they are well-established vectors of marine-derived nitrogen in terrestrial and freshwater communities (e.g. Lindeboom 1984, Anderson and Polis

1999, Croll et al. 2005, Payne and Moore 2006, Kolb et al. 2010). Moreover, the distribution and abundance of seabirds on tropical and temperate islands are almost certainly less today than they were in the past (Steadman 1995). Globally, dense colonies of breeding seabirds occur adjacent to many coral reefs, and these ecosystems have a long co-evolutionary history. Given the high prey consumption rates and long breeding season of seabirds (Birt-Friesen et al. 1989, Schreiber and Burger 2002), we estimate that Rose Atoll's annual breeding seabird population produces nearly 858 metric tons of guano $\text{km}^{-2} \text{yr}^{-1}$, resulting in the annual delivery of approximately 62 metric tons $\text{km}^{-2} \text{yr}^{-1}$ of N and 12.87 metric tons $\text{km}^{-2} \text{yr}^{-1}$ of P (assuming a similar elemental stoichiometry of guano to that on the Great Barrier Reef (Smith and Johnson 1995)). This deposition rate is greater than that estimated to occur in intensive agriculture (Pearson and Stewart 1993, Young et al. 2010).

Indeed, our stable isotope results indicate that Rose Atoll's seabird population is a significant source of nitrogen in adjacent algae. Nitrogen stable isotopes have been used extensively to estimate the contribution of terrestrial sources of nitrogen to aquatic primary producers (e.g. McClelland et al. 1997, Costanzo et al. 2005) but overlap in source isotope ratios can make it challenging to separate the influence of anthropogenic vs. seabird-derived nitrogen because both occupy high trophic levels and have been found in the range of 12-16 ‰ (e.g. Cabana and Rasmussen 1996, Young et al. 2010). However, our results reveal that algae growing adjacent to Rose Atoll, which is uninhabited by humans and has no agriculture, is significantly enriched in $\delta^{15}\text{N}$ compared to Tutuila Island, which has nearly 400 people/ km^2 and

Ofu & Olosega Islands, which have approximately 30 people/km² (Table 3.1, Pacific Islands Fisheries Science Center 2011). Furthermore, within Rose Atoll, $\delta^{15}\text{N}$ values are significantly greater close to Rose Island, where most of the archipelago's seabirds breed, and $\delta^{15}\text{N}$ values decrease with increasing distance from Rose Island. These results provide evidence suggesting that seabird-derived nutrients are being retained within nearshore algae, a result that has been hypothesized (e.g. Schmidt et al. 2004) but not previously demonstrated at this scale.

Within Rose Atoll, the relationship between proximity to seabird colonies and algal percent cover varied among chlorophytes (Fig. 3.3B-E). Three of the four algal genera decreased significantly in benthic percent cover with increasing distance from Rose Island, a pattern which supports Hutchinson's hypothesis that guano-derived nutrients increase primary production near breeding islands (Hutchinson 1950). However, the fourth genus, *Halimeda*, showed the opposite pattern, with the benthic cover nearing 30 percent at sites over two kilometers distant from Rose Island (Fig. 3.3E). Other studies of algal cover at Rose Atoll have reported similar patterns to those we describe here (*Microdictyon* and *Halimeda*, Aeby et al. 2006, Wegmann and Holzwarth 2006, Brainard et al. 2008); however, this is the first time they have been assessed as a function of proximity to seabirds. *Halimeda* is calcareous while the three genera that increased with proximity to the seabird colony were fleshy. Studies in the Florida Keys demonstrated that nutrient-replete conditions promote the productivity of fleshy algae, while nutrient-deplete conditions are associated with the success of more calcareous forms like *Halimeda* (Delgado and Lapointe 1994). In

particular, P-limitation is more likely for fleshy algae compared to calcareous forms which fix phosphate during the calcification process (Delgado and Lapointe 1994), and seabird guano, which is rich in both elements, has been observed to terrestrially influence soil phosphorus concentrations even without demonstrable differences in nitrogen concentrations between seabird rich and seabird poor islands (Croll et al. 2005). Nutrient limitation was not explicitly tested in this study; however, differential patterns observed among chlorophytes reveal the potential for similar groups of organisms to respond in unique ways to environmental gradients, confirming the value of taxon-specific rather than functional-group level analyses (Fong and Fong 2014). Overall, our results are consistent with Hutchinson's hypothesis, suggesting that seabird guano is used as a source of nutrients by adjacent coral reef producers, with effects possibly reverberating up the food chain to consumers, potentially altering nearshore coral reef ecosystems in unexpected ways.

This study demonstrates that seabirds should not be ignored as a source of nutrients for coral reef macroalgae in coral reef ecosystems. Seabirds and coral reefs are both threatened communities, but they have a history of intimate association that spans millions of years. We have demonstrated that seabird guano significantly alters coral reef macroalgal ecology and biogeochemistry. Consequently, it is likely that activities leading to tropical seabird declines (e.g fisheries bycatch, development, invasive species) and recovery (bycatch reduction, invasive species removal) will also reverberate to changes in adjacent coral reef communities. These ecological processes

in turn will bear on the management and conservation of coral reefs and their adjoining landmass in numerous and sundry ways.

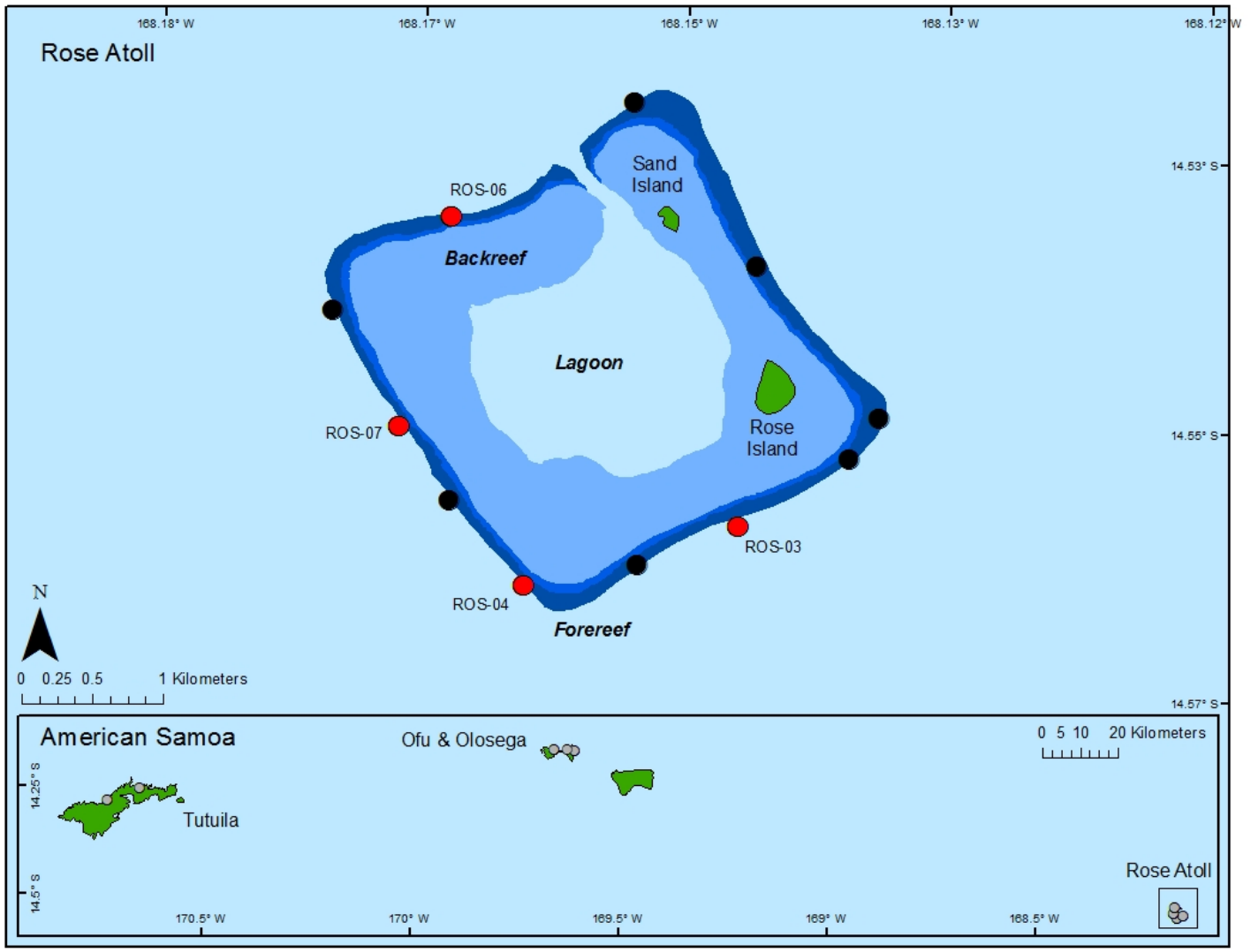


Figure 3.1 Locations of algal collection sites at Rose Atoll (red circles in top panel and grey circles in bottom panel), benthic cover measurements at Rose Atoll (red and black circles in top panel) and algal collection sites at Tuituila and Ofu & Olosega Islands (grey circles in bottom panel). Basemap sources: Benthic habitats of American Samoa prepared by visual interpretation from remote sensing imagery version 1.1, NOAA's Ocean Service, National Centers for Coastal Ocean Science (NCCOS) and Esri World Countries basemap.

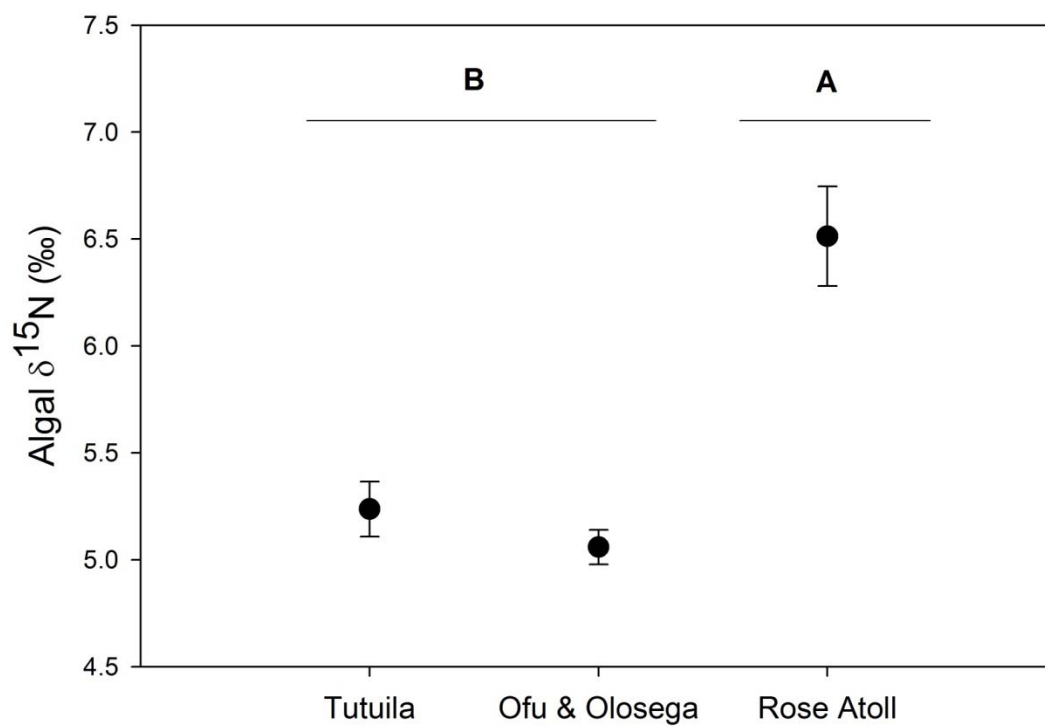


Figure 3.2 Mean $\delta^{15}\text{N} \pm 1\text{SE}$ ‰ ($n = 9$ sites) in *Halimeda* among three islands in American Samoa. Different letters imply significant differences (ANOVA).

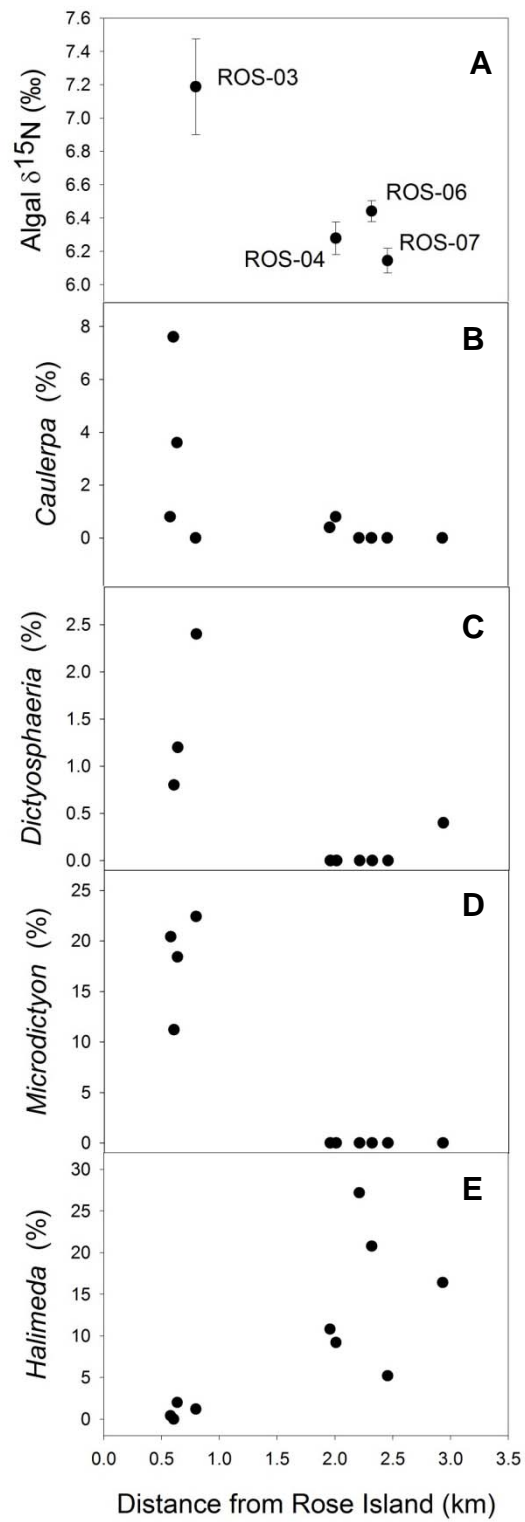


Figure 3.3 The relationship between (A) mean algal $\delta^{15}\text{N} \pm 1\text{SE}$, and benthic percent cover of (B) *Caulerpa*, (C) *Dictyosphaeria*, (D) *Microdictyon*, (E) *Halimeda* and linear distance from Rose Island (km).

Table 3.1 Summary of attributes for three study islands in American Samoa.

Island	Island type ^a	Land area (km ²) ^a	Reef area (km ²) ^a	Human population density (persons/km ²) ^b	Breeding seabirds ^c
Ofu & Olosega	Basalt island	12.61	12.03	27	Data deficient
Rose atoll	Closed atoll	0.09	7.8	0	139,396
Tutuila	Basalt island	137.45	50.89	397	2031

Data come from ^aGove et al. 2013, ^bPacific Islands Fisheries Science Center 2011

^cWegmann and Holzwarth 2006, ^dO'Connor and Rauzon 2004

Table 3.2 Results from linear regression analysis on algal $\delta^{15}\text{N}$ ($n = 4$) and percent cover ($n = 10$) for four algal genera (*Caulerpa*, *Dictyosphaeria*., *Halimeda*, and *Microdictyon*.) vs. log(distance). *($p < 0.05$), ***($p < 0.001$)

Predictor Variable	Response Variable	Slope	y-intercept	F	P	R ²
log (distance)	algal $\delta^{15}\text{N}$	-0.85	12.87	24.9917	0.0378*	0.89
	<i>Caulerpa</i> % cover	-2.34	18.24	5.3314	0.0498*	0.32
	<i>Dictyosphaeria</i> % cover	-2.32	17.99	5.9321	0.0408*	0.35
	<i>Halimeda</i> % cover	10.86	-69.20	11.2526	0.0100*	0.40
	<i>Microdictyon</i> % cover	-13.45	104.48	42.8109	0.0002***	0.82

Chapter 4

Evidence of seabird guano enrichment on coral reefs in Oahu, Hawaii

Abstract

Seabirds and coral reefs are two of the most threatened marine communities on earth, and they co-occur on many tropical islands and subtropical islands and atolls. Seabirds concentrate marine-derived nutrients on breeding islands in the form of feces (guano), and these nutrients dramatically alter terrestrial ecosystem ecology. Recent work in the remote Pacific indicates seabird-derived nutrients may also subsidize nearshore coral reefs, but the consequences of guano on complex, anthropogenically-modified coral reefs are unknown. The impact of seabird guano on nearshore coral reefs around Oahu, Hawaii was investigated using offshore islets as samples. Reefs in close proximity to large seabird breeding colonies (primarily consisting of wedge-tailed shearwaters, *Puffinus pacificus*) had greater concentrations of dissolved phosphate in seawater and greater $\delta^{15}\text{N}$ in adjacent subtidal macroalgae relative to reefs next to small breeding colonies. However, dissolved nitrate was not different among islets, potentially due to enrichment from human sewage, particularly at the islet with lowest seabird abundance. These results indicate that seabirds may be a source of nutrients for coral reef ecosystems that are already inundated with local and global stressors.

Introduction

Seabirds typically forage at sea but breed and roost, sometimes in large numbers, on islands where they deposit guano, rich in nitrogen and phosphorus. Guano is documented to provide a significant nutrient input in terrestrial (e.g. Lindeboom 1984; Polis and Hurd 1996; Anderson and Polis 1999; Schmidt et al. 2004; Croll et al. 2005; Maron et al. 2006; Young et al. 2010) and marine (Bosman and Hockey 1986, Bosman et al. 1986, Wootton 1991) ecosystems, increasing primary production with the potential to fuel production at higher trophic levels (McCauley et al. 2012). Coral reefs are often found adjacent to islands with large populations of breeding or roosting seabirds, providing the opportunity for nutrients derived from seabird guano deposited on the islands to be transported to the adjacent coral reef ecosystems. Many coral reefs are also far from pristine, and are instead subject to local stressors such as overfishing (Pandolfi et al. 2003), nutrient pollution (Fabricius 2005), and habitat transformation (Nystrom et al. 2000) as well as global stressors including ocean acidification, sea level rise, and increasing water temperature (Hoegh-Guldberg et al. 2007). Nutrient pollution from anthropogenic sewage (e.g. Lapointe and Clarke 1992) or agricultural fertilizer (e.g. Fabricius and De'Ath 2004) can harm recipient scleractinian corals directly via reduced growth rates stemming from competition with endosymbionts and indirectly via increased sedimentation, reduced light, and competition with weedy algal species that flourish in the presence of excess nutrients (reviewed in Fabricius 2005). Furthermore, on reefs that are heavily fished, excess nutrients can contribute to phase shifts that transform high biodiversity, coral-dominated reefs into lower diversity algal-

dominated habitats (e.g. Hughes 1994). It is therefore unclear how naturally-derived nutrients from seabird colonies will affect coral reefs experiencing multiple stressors.

Coral reefs in the Main Hawaiian Islands have been exposed to numerous anthropogenic stressors for centuries, the most extreme of which occur on Oahu, the most populated island with almost 1 million inhabitants (Bailey-Brock et al. 2007). Oahu's coral reefs have undergone significant modification stemming from agricultural development, land use change, effluent from human sewage, invasive species, and intensive fishing (Hunter and Evans 1995). Many of these threats are concentrated on reefs adjacent to Honolulu, the island's urban center, but reefs around the entire island are also subject to various levels of anthropogenic stressors.

Many of Oahu's coral reefs are adjacent to small offshore islets where seabirds breed. Oahu's 10 offshore islets are partially isolated from many of the anthropogenic disturbance in comparison to the main island of Oahu, and are thus the breeding site for approximately 98% of the 145,000 seabirds breeding in the Oahu region (Pyle and Pyle 2009). These islets are uninhabited, with varying accessibility to humans. They represent an intermediate level of disturbance when compared with the highly disturbed Main Hawaiian Islands and protected Northwestern Hawaiian Islands (Coles and Swenson 2010). Differences in proximity, protection status, invasive species, and size have resulted in a large gradient in seabird abundance among islets, providing a unique opportunity to use islands as replicates of seabird abundance. Moreover, their proximity to a suite of anthropogenic stressors,

particularly sewage and runoff-derived nutrients, provides the opportunity to examine adjacent reef ecosystem responses to varying combinations of seabird vs. human-derived nutrients.

In this study, we use four island/reef pairs, all exposed to some background level of human-derived nutrients but with varying seabird abundance, to assess whether seabirds are associated with differences in dissolved nutrients (phosphate and nitrate) and macroalgal $\delta^{15}\text{N}$. We hypothesize that coral reef waters next to more abundant seabird colonies will have more dissolved nutrients and that sampled macroalgae will have higher $\delta^{15}\text{N}$ values, a proxy for seabird-derived nitrogen, compared to islets with fewer seabirds.

Methods

Study site

We carried out our study on four small islets offshore of windward Oahu during February through March 2012 (Fig. 1). These islets vary over 100-fold in abundance of breeding seabirds (Pyle and Pyle 2009, Table 4.1) and are all uninhabited seabird sanctuaries managed by the Hawaii Department of Land and Natural Resources Division of Forestry and Wildlife (DLNR DOFAW). The dominant species breeding across these islets are wedge-tailed shearwaters (*Puffinus pacificus*), but other species found breeding on one or all of these islets include Bulwer's petrels (*Bulweria bulwerii*), Christmas shearwaters (*Puffinus nativitatis*) and white-tailed tropicbirds (*Phaethon lepturus*) (Pyle and Pyle 2009). We visited these

sites in the middle of the rainy season, which is November through April, (Timm et al. 2015), with the assumption that nutrients concentrated on islands in the past breeding season (June-August, Pyle and Pyle 2009) may be mobilized during the wet season (e.g. Smith and Johnson 1995).

Seawater nutrients

On the leeward side of each islet, we collected three mid water-column seawater samples at 6 sites adjacent to the islet ($n = 72$ total samples, 18 per islet) in 500 mL acid-washed HDPE bottles. Samples were collected within a range of 45-90 m from the shoreline of each islet. We stored bottles on ice and filtered each sample through Whatman GF/F 25 mm filters using hand-pump vacuum filtration systems upon our return to the Hawaii Institute of Marine Biology. We froze filtrate in 20 mL scintillation vials and shipped them on dry ice to the Marine Analytical Lab at the University of California Santa Cruz. We then analyzed thawed seawater with a Lachat QuikChem 8000 Flow Injection Analyzer to measure dissolved NO_x (nitrate+nitrite) and PO_4^{3-} (phosphate) levels (μM). Manufacturer method detection limits (MDL) were set at $0.02 \mu\text{M}$ for PO_4^{3-} and $0.01 \mu\text{M}$ for NO_x .

Stable isotope analysis

To assess whether seabird-derived nitrogen could be traced in adjacent macroalgae, we used nitrogen stable isotope analysis, which has been widely used to map the signal of seabird guano in primary producers in terrestrial ecosystems (Anderson and Polis 1999, Schmidt et al. 2004, Croll et al. 2005, Young et al. 2010,

Szpak et al. 2012). We collected macroalgal samples ($n = 58$) from the genus *Halimeda* adjacent to each islet near water sample collection sites. We rinsed all thalli with deionized water to eliminate salt and removed epiphytes and epifauna with forceps. We oven-dried algae at 60 °C for 24-48 h. We ground algae into fine, homogenous powder via mortar and pestel, and analyzed algal $\delta^{15}\text{N}$ using a Carlo-Erba 1108 elemental analyzer coupled to an isotope ratio mass spectrometer (ThermoFinnigan Delta Plus XP IRMS) at the University of California Santa Cruz Stable Isotope Laboratory.

Data analysis

To assess significant differences ($\alpha=0.05$) in seawater nutrients among islets, we performed linear Mixed Models with site as a random effect nested within islet. We performed one-way Analysis of Variance (ANOVA) to assess significant differences in algal $\delta^{15}\text{N}$ among islets. We used Tukey HSD post-hoc analysis to compare differences among means when significant differences were observed for seawater nutrients and algal $\delta^{15}\text{N}$. All statistical analyses were performed in Jmp Pro 12.

Results

Seawater nutrients

Mixed Model results revealed that there were significant differences in dissolved phosphate among islets ($F_{3,21} = 6.1664$, $p = 0.0035$), with only 12.9% of

total variance explained by the random effect of site. Tukey HSD post-hoc analyses showed that phosphate levels were significantly higher at Moku Nui, the highest seabird islet, than they were at Popoi'a, Kapapa, or Mokoli'i, and these latter three islets were not statistically distinguishable from one another (Fig. 4.2). In contrast, NO_x was not significantly different among islets ($F_{3,20} = 1.1717$, $p = 0.3454$), with 14.5% of total variance explained by the random effect of site. Mean NO_x values varied among islets, with $X \pm SE = 0.32 \pm 0.14 \mu\text{M}$ at Moku Nui, $X \pm SE = 0.24 \pm 0.12 \mu\text{M}$ at Popoi'a, $X \pm SE = 0.07 \pm 0.03 \mu\text{M}$ at Kapapa, and $X \pm SE = 0.38 \pm 0.12 \mu\text{M}$ at Mokoli'i.

Stable isotope analysis

ANOVA revealed significant isotopic differences among islets (ANOVA, $F_{3,54} = 12.3983$, $p < 0.001$). Tukey HSD post-hoc analyses revealed that macroalgae adjacent to Moku Nui were enriched in $\delta^{15}\text{N}$ compared to all other islets, which were not significantly different from one another (Fig. 4.3).

Discussion

Coral reefs adjacent to islets with large seabird colonies had high values of dissolved phosphate and macroalgal $\delta^{15}\text{N}$ compared to reefs next to smaller seabird colonies. This suggests that seabird guano is delivered in usable forms to nearshore waters and taken up by primary producers. These coral reef results complement previous work on terrestrial islands (Lindeboom 1984, Polis and Hurd 1996, Schmidt

et al. 2004, Croll et al. 2005, Young et al. 2010), temperate marine systems (Bosman and Hockey 1986; Wootton 1991) and oligotrophic lagoons (McCauley et al. 2012), indicating that seabirds provide bottom-up nutrient pulses to a variety of recipient ecosystems.

Dissolved phosphate was enriched at Moku Nui, which has over 5000 nesting wedge-tailed shearwaters (Marie pers comm), more than three times the abundance found at the next largest seabird colony in the study at Popoi'a. Together, Moku Nui and its southern neighbor Moku Iki form the Mokuluas which host more than 10,000 breeding seabirds per year (Table 4.1, Pyle and Pyle 2009), but dissolved nitrate and nitrite values were not different among islets. Seabird guano is rich in both nitrogen and phosphorus, with composition estimates equaling 7.3% nitrogen and 1.5% phosphorus (Smith and Johnson 1995), and we would therefore predict that seabird-enrichment would be reflected by both elements. In the Aleutian Islands, seabird guano was similarly associated with island-level increases in total soil phosphorus but not soil nitrogen (Croll et al. 2005). Phosphorus can be the limiting nutrient in many carbonate reef environments (Smith 1984, Lapointe and Clarke 1992). Nutrient-limitation on coral reefs is predicted to vary depending on geomorphology of adjacent islands (Littler et al. 1991) and anthropogenic sources (Cardini et al. 2014), and it may be that the coral reefs offshore of windward Oahu are limited locally by phosphorus but not nitrogen. Northeast trade winds and high mixing during the sampling season further complicate the ability to track differences in seawater nutrients among islets. Regardless, we still found a strong signal for phosphorus,

indicating that seabird-derived phosphorus may be retained even during mixing periods. Nonetheless, the nutrient sampling in this study provides only a snapshot of reef nutrients across space, which may be much different over a longer time scale and during different seasons and environmental conditions.

In contrast to the short-term snapshot provided by seawater nutrient sampling, stable isotope analysis provides a longer-term record of nutrient enrichment in marine producers (e.g. Costanzo et al. 2005; Mcclelland et al. 2014). Our results indicate that *Halimeda* $\delta^{15}\text{N}$, like phosphate, is highest at Moku Nui, which hosts the largest seabird colony in our study compared to all other islets (Fig.4. 2). Algal samples were collected nearly 100 m from islet shorelines, so the magnitude of enrichment may be even more noticeable closer to shore. In fact, samples collected opportunistically directly adjacent to Popoi'a, Kapapa, and Mokoli'i islets showed higher $\delta^{15}\text{N}$ values compared to more distant algal collections. Unfortunately, we were unable to collect algae in close proximity to shore on Moku Nui so we could not analyze this relationship among all islets (Honig unpubl data). Regardless, our isotopic results support the hypothesis that seabird guano provides nitrogen that is taken up by reef primary producers. It is possible that these nutrients are then transferred up the food chain when macroalgae is consumed by herbivorous fishes and invertebrates, a result that has been seen on terrestrial islands (e.g. Polis and Hurd 1995).

The majority of anthropogenic nutrient sources potentially confounding our results originate in or near Kaneohe Bay, relatively far from Kailua and Lanikai and

the islets with high seabird abundances (Popoi'a and Moku Nui). For example, Mokoli'i, which has the smallest seabird abundance in our study, is also within 600 m of a public restroom at Kualoa Park and 1.2 km from Moli'i fish pond (Google Earth 2015). Kaneohe Bay also has a long history of anthropogenic nutrient enrichment from sewage effluent (Smith et al. 1981, Hunter and Evans 1995). Between 1940-1970, sewage from three separate treatment plants was discharged into the bay, fueling the proliferation of the chlorophyte *Dictyosphaeria cavernosa*, and reducing scleractinian coral cover at patch reefs and fringing reefs prior to sewage diversion in 1980 (Smith et al. 1981, Hunter and Evans 1995, Stimson et al. 2001). Furthermore, Kaneohe Bay is subject to significant intrusion of freshwater runoff from nearby streams, which has resulted in reef kills during extreme storms (e.g. Jokiel et al. 1993). It is unlikely that the isotopic enrichment at Moku Nui represents anthropogenic sewage given that macroalgal $\delta^{15}\text{N}$ surveys on Oahu-based sewage inputs from onsite sewage disposal systems (OSDS) and wastewater injection wells typically reach $\delta^{15}\text{N}$ values >9 ‰ (Amato 2015). Given the variety of anthropogenic pollution sources into Kaneohe Bay, the phosphate and macroalgal $\delta^{15}\text{N}$ enrichment observed offshore of Moku Nui indicates that local nutrient input by seabirds on the four islets in our study is visible in primary producers even in the presence of a myriad of anthropogenic stressors.

It remains unclear how natural nutrient subsidies from seabirds interact with co-existing anthropogenic stressors that are known to increase nutrient delivery, decrease the number of herbivorous fishes, and reduce the overall resilience of coral

reefs (e.g. Hughes et al. 2003). On Jamaican reefs, nutrient enrichment, disease, and overfishing transformed healthy coral reefs from coral-dominated to algal-dominated ecosystems (Hughes 1994), and many of the reefs in the Main Hawaiian Islands are suffering from similar threats (Friedlander and DeMartini 2002, Aeby et al. 2011). Most Oahu reefs have been and are actively fished (Stimson et al. 2001, Williams et al. 2006, 2011), and natural nutrient subsidies by seabirds may pose an additional risk to reefs if primary producers aren't sufficiently regulated by herbivore populations.

Nearly a third of all seabird species are at risk of extinction globally (Spatz et al. 2014), and breeding seabirds in Oahu are in peril of extirpation. The small islets in our study are some of the only isolated habitats available for burrow-nesting birds like wedge-tailed shearwaters, which are extremely vulnerable to human trampling and invasive species (e.g. Young et al. 2013). Seabird conservation efforts in Hawaii have included removing invasive mammals and ants from these islands, and many of these actions have been successful (Smith et al. 2006). However, seabirds are perpetually threatened by species invasions and disturbance. It is unclear how future seabird restoration will affect the already heavily impacted reefs in Kaneohe Bay, but our results suggest that it may increase the delivery of phosphate and isotopically heavy nitrogen to the surrounding marine environment. It is prudent for coral reef managers to consider the potential impacts of increasing or decreasing seabird populations on the islands adjacent to coral reefs. Seabirds naturally occur next to hundreds of coral islands and atolls throughout the globe, but anthropogenic influence may complicate the impact of seabird/reef nutrient fluxes on coral reefs that are

already overfished and polluted. Further empirical evaluation of the ecological influence seabirds have on degraded reefs is necessary to maximize conservation efficacy and minimize the potential unintended consequences of independent marine and terrestrial management.

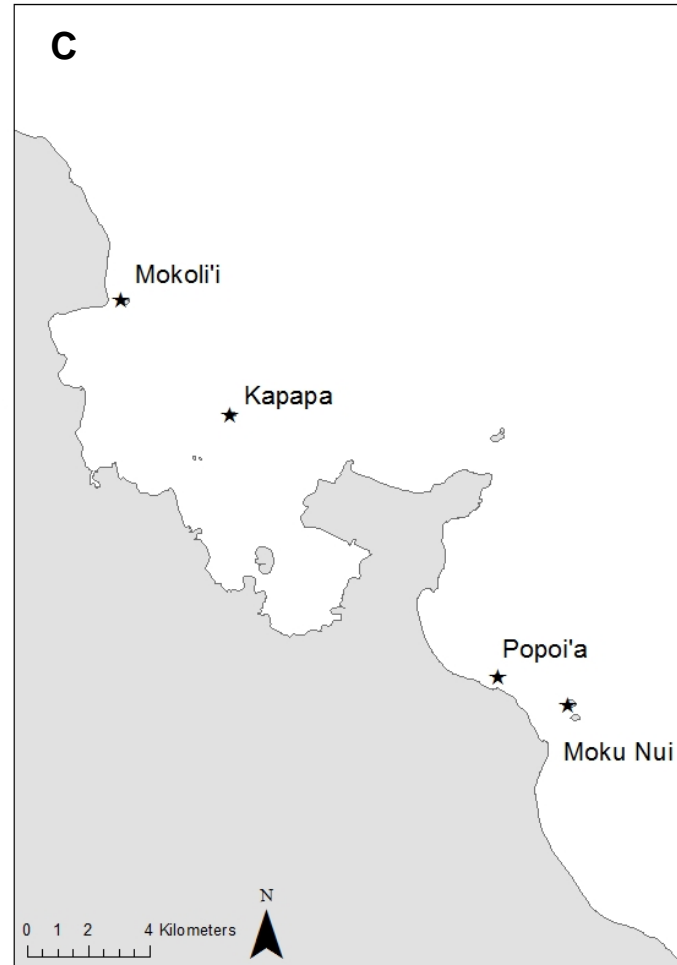
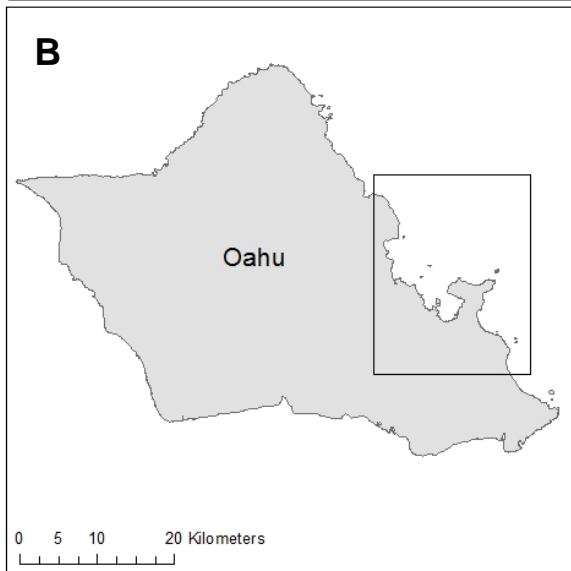
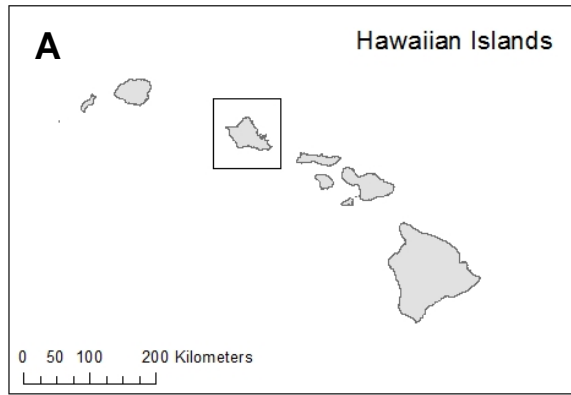


Figure 4.1 Locations of (A) the main Hawaiian Island chain, (B) the island of Oahu, and (C) four study islets (stars) offshore of windward Oahu with varying seabird abundance. Basemap Source: Global Island Database 2015.

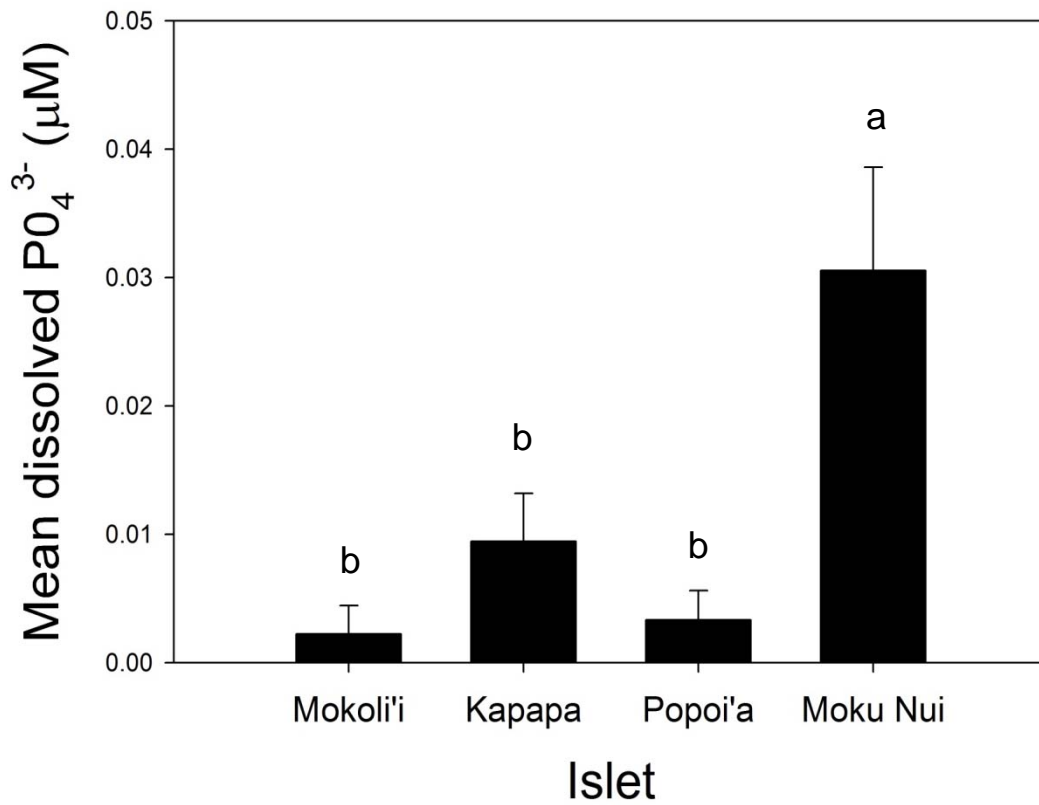


Figure 4.2 Mean dissolved phosphate ± 1 SE μM , $n = 72$ in seawater across Mokoli'i, Kapapa, Popoi'a, and Moku Nui. Different letters imply significant differences.

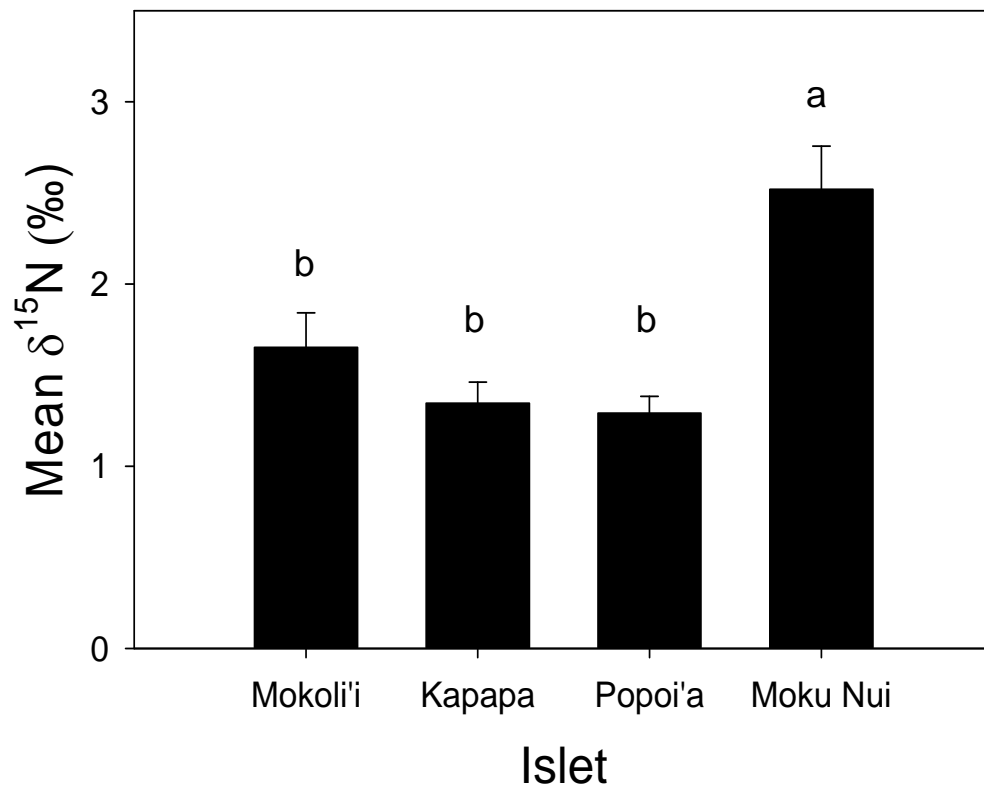


Figure 4.3 Mean $\delta^{15}\text{N} \pm \text{SE} \text{‰}$, $n = 58$ of macroalgae from the genus *Halimeda* across Mokoli'i, Kapapa, Popoi'a, and Moku Nui. Different letters imply significant differences.

Table 4.1 Islet characteristics of Mokoli'i, Kapapa, Popoi'a, and the Mokuluas.

Islet	Latitude	Longitude	Number of breeding seabirds ^a	Number of breeding seabirds along linear coastline (# m ⁻¹) ^b
Mokoli'i	21.51	-157.83	202	0.27
Kapapa	21.48	-157.80	310	0.30
Popoi'a	21.40	-157.72	1,625	2.39
Mokuluas	21.39	-157.69	10,155	6.80

^aEstimate from Pyle and Pyle 2009 and ^bLinear coastline measured with path tool in Google Earth (Google Inc. 2015)

Chapter 5

Synthesis

Do seabird communities subsidize nearshore coral reefs?

Seabird-vectored nutrients are a ubiquitous spatial subsidy in many ecosystems, but their influence in coral reef ecosystems has not been addressed, until now. My dissertation provides biogeochemical and ecological evidence from the remote tropical and subtropical Pacific ocean indicating that nutrients from seabird guano make their way into nearshore coral reef ecosystems and alter benthic community composition and herbivorous fish biomass, providing a bottom-up spatial subsidy for coral reefs. Results from the Pacific Remote Islands Marine National Monument are consistent with the hypothesis that seabird guano increases production, but not standing stock of macroalgal and turf functional groups, and this production is quickly consumed by the browsing herbivorous fish that selectively feed on macroalgae, increasing browser biomass. Combined with results from American Samoa, it seems likely that the impact of seabird guano on algal and coral communities is taxon-specific, which may explain the lack of an effect on benthic functional groups, at least in terms of standing stock.

While these complex, taxon-specific responses by the benthic community to seabird nutrients are important, equally and potentially more important is the absence of a seabird-induced phase shift in coral reef ecosystems from coral-dominated to algal-dominated habitats. This signifies that seabirds, which have naturally occurred

in tropical ecosystems for millions of years, do *not* alter coral reefs in the same manner that anthropogenic nutrients have been shown to globally (e.g. Szmant 2002, Smith et al. 2010), at least in ecosystems protected from fishing. This is surprising given the magnitude of guano that is produced on Pacific Islands, which is comparable in many cases to nutrient loading by intensive agriculture (Smith and Johnson 1995, Young et al. 2010). Herbivorous fish communities, which are protected from fishing in the regions examined in Chapters 1 and 2, function as key trophic links between primary production and higher trophic levels (Sandin et al. 2008, Williams et al. 2011, Heenan and Williams 2013), and they are likely responsible for transferring subsidized primary production up the food web. The ability of herbivorous fishes to mediate nutrient-flux on coral reefs by increasing grazing rates (Boyer et al. 2004, Burkepile and Hay 2006, 2009) makes them a vitally important functional group for reef health (Green and Bellwood 2009). This relationship may break down in areas that are not protected from fishing, where excess algal production is not controlled by grazing. Indeed, results from Chapter 3 indicate that seabird-derived nutrients can be tracked in disturbed coral environments, even when excess sources of anthropogenic runoff are available. The interaction between human-derived nutrients, seabird-derived nutrients, overfishing and their combined influence on coral reef ecology remains to be addressed, but is widely relevant for reef conservation.

What does this mean for the conservation of coral reefs and seabirds?

Seabird colonies are globally at risk of extinction from invasive species, pollution, fisheries bycatch, and climate change (Spatz et al. 2014), and because conservation dollars are limited, seabird restoration efforts are often decided using science-driven prioritization models (e.g. McCreless et al. 2013). Our results indicate that proximity to coral reefs should be used as a factor when prioritizing islands for conservation through tools like invasive species eradication, but the implications of including this information is context-dependent. For example, on uninhabited islands surrounded by marine protected areas, restoring seabird colonies may indirectly benefit recipient coral reef communities by fueling the production of herbivorous fishes. However, on islands with anthropogenic sources of nutrient runoff and heavily fished adjacent reefs, seabird colony restoration may pose consequences for reef resilience, and mitigation of these potential consequences should be considered. Therefore, understanding the unique portfolio of threats and the level of protection existing across the global mosaic of island/reef associations is required to begin predicting the utility of seabird colony restoration as either a tool or a threat for coral reef ecosystem health. In either case, incorporating information linking seabirds and coral reef communities will advance the ability of managers to preserve both communities more effectively with the potential for conservation synergies.

Patterns vs. Processes

The research outlined in this dissertation provides information about coral reef patterns that are exhibited among islands with varying seabird population abundance.

This type of comparative approach is powerful because it takes advantage of naturally occurring gradients in the environment at a broad scale, but there are limitations to the interpretations that can be made from this work. For example, I am only able to speculate about mechanistic processes guiding the patterns I observed in the previous three chapters, and there are additional processes (e.g. topographic upwelling) that require further investigation to disentangle their effects from seabird enrichment. It is imperative that future studies involve manipulative experiments to disentangle the mechanisms driving seabird community subsidies on coral reef ecology. These include but are not limited to: caging experiments that measure algal production and standing stock responses close to and far from shore at islands with and without seabirds, *in situ* palatability and selectivity assays by herbivores on enriched and unenriched algae, and direct tests varying the stoichiometric composition and magnitude of nutrients to reflect guano vs. human sewage and agricultural fertilizer on coral growth rates and disease. These types of studies will greatly enhance our understanding of the interacting processes that drive local, regional, and global patterns in coral reefs as a function of seabird community abundance.

Concluding Remarks

Taken together, the research outlined in this dissertation provides the first evidence linking seabird community subsidies with coral reef ecology, supporting Hutchinson's 65 year old seabird enrichment hypothesis (Hutchinson 1950). The innumerable questions that are prompted by this evidence should be

addressed using experimental approaches with careful attention paid to specific management plans and conservation needs for both imperiled communities. Working toward the integration of marine and terrestrial management for coral reefs and seabirds will improve ecological understanding of both systems and help protect them in the face of global change.

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