Nearshore ecosystems on seabird islands are potentially influenced by invasive predator eradications and environmental conditions: a case study at the Mercury Islands, New Zealand

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ABSTRACT: Seabirds maintain island ecosystem function by providing rich marine-derived nutrients to the islands where they nest. These nutrients are returned to the sea through runoff, fertilizing the nearshore environment. Invasive predators disrupt this bottom-up control by decimating seabird populations. While invasive predator eradications lead to terrestrial recovery on seabird islands, there is little information on the nearshore impact. We determined how nearshore macroalgae communities and seabird-derived nitrogen concentrations are influenced by predator eradications and environmental parameters (sampling depth, season, wave exposure, and runoff). This case study examined 4 islands in the Mercury Islands archipelago, representing 3 eradication histories: never invaded by mammalian predators, eradicated over 30 yr ago, and eradicated 2 yr ago. Macroalgal diversity was highest at never-invaded islands, followed by islands in order of eradication year (eradicated 30 and 2 yr ago). The amount of seabird-derived nitrogen (δ^{15}N) in algae was higher during the rainy season and decreased with sampling depth and wave exposure. Sampling near high runoff points resulted in increased δ^{15}N in red algae alone. Never-invaded islands had the highest δ^{15}N in most species. With species found at both eradicated islands, the recently eradicated island had unexpectedly higher δ^{15}N than the island eradicated over 30 yr ago. This discrepancy may be a result of the recently eradicated island's large size and presence of streams, estuaries, and sheltered bays. Studying nearshore habitats is crucial in understanding the extent to which seabirds act as a conduit of the land–sea interface and the marine impacts of island management.

KEY WORDS: Seabirds · Eradication · Invasive species · Nearshore environment · Macroalgae · Stable isotope analysis · Biodiversity

1. INTRODUCTION

As keystone species and mediators of important subsidies, seabirds are integral to maintaining island ecosystem function. They provide a vital link between marine and terrestrial systems by depositing large amounts of nutrient-rich guano onto the islands on which they breed (Anderson & Polis 1999, Sanchez-Pinero & Polis 2000, Fukami et al. 2006). These nutrients are then returned to the sea through runoff, fertilizing the nearshore environment. This flow of nutrients drives the bottom-up control of many island food webs, promoting productivity, species abundance, and diversity (Polis et al. 1997, Fukami et al. 2006, Post et al. 2008), and leading such islands to be termed 'seabird islands' (Mulder et al. 2011). Seabird

islands are distinctly different from other islands due to the high quantities of marine nutrients (in the form of guano and carcasses) deposited and the physical alteration through burrowing that drives island ecosystem functioning (Mulder et al. 2011). These islands have evolved intricate food webs and relationships that rely on seabird presence.

The vital ecosystem functions governed by seabirds are threatened by invasive mammalian predators (Atkinson 1985, Croll et al. 2005, Towns et al. 2006, Aguirre-Muñoz et al. 2008, Jones et al. 2008). Since most island breeding seabirds evolved without terrestrial predators, they are particularly vulnerable to mammal invasions. Through predation, competition, and habitat damage, invasive mammals can decimate seabird populations, disrupting the bottom-up control of seabird islands (Fukami et al. 2006, Towns et al. 2009). Invaded islands with fewer seabirds have lower concentrations of carbon, nitrogen, and phosphorus in soils (Fukami et al. 2006), lower nitrogen concentrations of leaf-litter and foliage (Wardle et al. 2009), and decreased populations of plants, invertebrates, and reptiles through predation and/or disruption of community relationships (Towns 2009). The impact from drastic seabird population declines and extirpations by invasive predators is markedly severe on these ecologically unique seabird islands.

The destructive effects of introduced mammals have led to widespread attempts at eradicating them from islands (Howald et al. 2007, Aguirre-Muñoz et al. 2008). There have been over 850 successful invasive mammal eradications on islands since 1950 (DIISE 2015) with an increased eradication rate beginning in 1980 (Keitt et al. 2011), largely due to the development of toxicant aerial broadcast in combination with bait stations and other control techniques (Towns & Broome 2003). Successful invasive mammal eradications have led to seabird and ecosystem recoveries across many island systems (Towns 2009, Lavers et al. 2010, Jones et al. 2016).

While the knowledge of terrestrial ecosystem recovery continues to grow, there is little information on how nearshore environments respond to invasive mammal eradications. Nearshore habitats are important to humans and wildlife, providing food and economic stability as well as ecological services (Beck et al. 2003). Coastal fisheries can account for 50–90% of the dietary animal protein in coastal communities (Bell et al. 2009) and provide employment to more local people than offshore fisheries (Gillett 2009). These ecologically and economically important habitats are impacted by marine activities such as overfishing (Pauly et al. 1998, Jackson et al. 2001, Scheffer et al. 2005, Vasas et al. 2007) and terrestrial activities such as wastewater runoff causing eutrophication.

Increases in nutrient loading are associated with changes in nearshore community composition, biodiversity, species distribution, biomass, and nutrient limitations (Cloern 2001, Ringuet & Mackenzie 2005, Schein et al. 2012), favoring undesirable species (Vasas et al. 2007). For example, massive storm events lead to nutrient loading and result in brief increases in phytoplankton biomass, causing primary productivity in the nearshore system to switch from nitrogen- to phosphate-limited (Ringuet & Mackenzie 2005). An increase in fertilizer runoff can result in the replacement of native vegetation with algae that thrives in eutrophic environments, decreasing fish biodiversity (Schein et al. 2012). Protecting coastal environments is an important component of island management, yet monitoring nearshore response to management activities, such as invasive mammal eradications, is uncommon.

Research documenting nearshore differences between seabird islands varying in invasion histories and nest densities can be used to infer nearshore responses to mammal eradication. On the Aleutian Islands, rat invasions created a trophic cascade in the intertidal zone as reduced seabird densities resulted in increased invertebrate abundance and decreased algal cover (Kurle et al. 2008). In the Baltic Sea, islands with high seabird nest densities had a measured increase in marine primary productivity and nitrogen stable isotope ratios, expressed as $\delta^{15}N$ ($\delta^{15}N = [^{15}N/^{14}N_{sample} \, / \, ^{15}N/^{14}N_{standard} - 1] \times 1000$ [‰]), an indication of seabird-derived nitrogen in algae and invertebrates (Kolb et al. 2010, Gagnon et al. 2013). Similarly, high $\delta^{15}N$ was observed in macroalgae near islets with greater seabird densities in Oahu, Hawaii (Honig & Mahoney 2016), and in macroalgae, sponges, and fish on coral reefs near islands without introduced rats in the Chagos Archipelago (Graham et al. 2018).

What remains unclear is how nearshore algal communities, seabird-derived nutrient ratios in macroalgae, and nitrogen concentrations in the water column change following mammal eradications. Seabird guano is rich in nitrogen, most of which is in the organic form as uric acid (~70–80%) and inorganic forms as ammonia and nitrate (~10–17%) (Lindeboom 1984, Staunton Smith & Johnson 1995). Macroalgae are often nitrogen limited. Ammonium and nitrate are more readily absorbed, with the preferred form for uptake being ammonium (DeBoer 1981). Quantifying nitrogen concentrations in the water surrounding seabird colonies as well as nitrogen iso-

tope ratios (δ^{15}N) in macroalgae can be a good predictor of guano-based nitrogen availability for macroalgae. In this case study, we (1) investigated how macroalgae communities vary by island invasion and eradication history through species richness/diversity measurements and community structure descriptions and (2) determined how environmental parameters in addition to invasion/eradication history influence seabird-derived nitrogen in nearshore macroalgae using stable isotope analysis. We expected never-invaded islands and those cleared of invasive mammals earlier to have higher species richness/diversity, leading to unique macroalgae communities based on invasion history. We also expected variables such as wave action, runoff, sampling season, and depth to influence nutrients from guano in macroalgae, affecting seabird-derived δ^{15}N. This study will better define the application of stable isotope analysis in the nearshore environment by measuring influential marine parameters. Documenting differences in nearshore communities at seabird islands varying in invasion histories is crucial in understanding the extent to which seabirds act as a conduit of the land–sea interface and for elucidating their influence on the nearshore marine environments where they nest.

2. MATERIALS AND METHODS

2.1. Study site

New Zealand is a global leader in island invasive management, successfully eradicating mammal pests from over 100 offshore islands in 50 yr (Towns et al. 2013). With the highest seabird diversity in the world, New Zealand's recovering seabird islands are important to global seabird conservation. The passive recovery of these eradicated seabird islands can be slow, as seabirds exhibit strong philopatry, Allee effects, and low reproduction rates (Jones 2010a,b). In the Hauraki Gulf of northern New Zealand, seabird burrow densities are considerably higher on uninvaded islands than on eradicated and invaded islands (Mulder et al. 2009). High density thresholds of nesting seabirds may be required before large-scale recovery is detected in terrestrial systems

(Jones 2010b), taking a minimum of 15 yr on some islands (Jones 2010a). A similar time frame is expected before ecosystem-level changes in community structure and nutrient levels are documented in nearshore communities at recovering islands.

This case study was conducted on 4 islands in the Mercury Island archipelago: Ahuahu/Great Mercury, Korapuki, Atiu/Middle, and Green Islands (Fig. 1). The Mercury Islands are located 8 km off the coast of the Coromandel Peninsula on New Zealand's North Island (36.6445° S, 175.8451° E). Like most of New Zealand's offshore islands, the Mercury Islands have been directly impacted by human settlement and introduced mammals (Bellingham et al. 2010). Fishing regulations at the Mercury Islands are comparable to other islands in the region, with daily catch limits and bans on set netting. Each study island varies in invasion and eradication history, from those that have never been invaded (Atiu/Middle and Green Islands) to those eradicated of mammalian predators (rats and cats) in 1986 (Korapuki Island) (McFadden & Towns 1991) and 2014 (Ahuahu/Great Mercury Island). There are no remaining islands in the Mercury Island chain that still have rats and cats present. We describe differences between the islands based on these invasion histories, which are directly related to
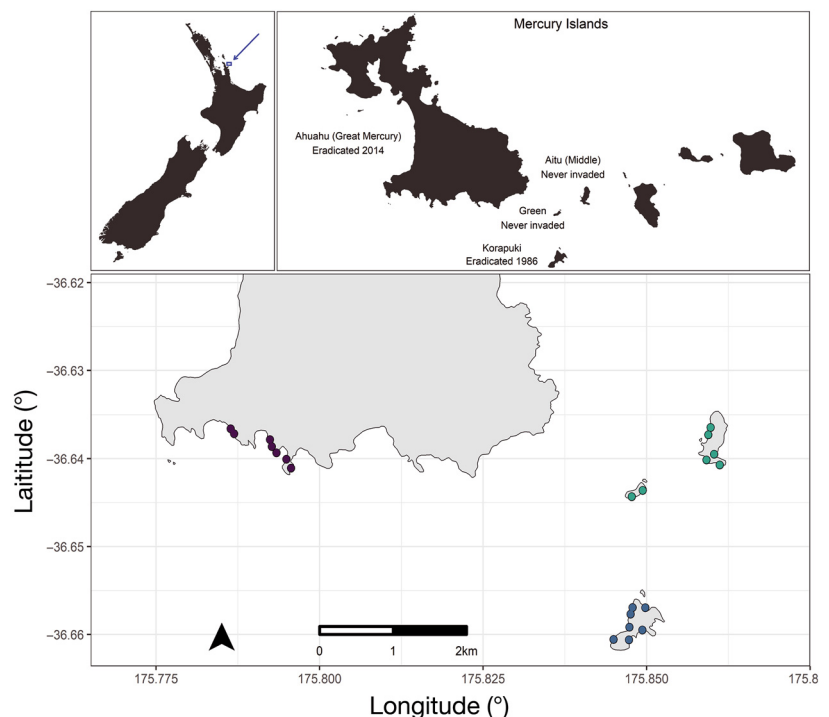

Fig. 1. Sampling sites with reference to location in the Mercury Islands archipelago and New Zealand

mean seabird burrow density, with the never-invaded islands having the highest density followed by the islands eradicated over 30 yr ago and 2 yr ago (Table 1). Korapuki, Atiu/Middle, and Green Islands are uninhabited while Ahuahu/Great Mercury is inhabited by one family with livestock. Given that most human and livestock activity occurs on the northern half of the island, sampling was restricted to the southern coast of Ahuahu/Great Mercury. There are 8 ground-nesting seabird species on the Mercury Islands (Skegg 1963, Atkinson 1964, Southey 1985, Towns & Atkinson 2004) with varying breeding periods, resulting in steady guano deposition onto the islands throughout the year (Table S1 in the Supplement at www.int-res.com/articles/suppl/m661p083_supp.pdf). Heavy rains from June through September provide the main transport of nutrients from the terrestrial to the nearshore environment.

2.2. Macroalgae community sampling

Seven sampling areas were established around each study island, grouped by invasion history: Atiu/Middle and Green (hereafter, never-invaded), Korapuki (hereafter, eradicated over 30 yr ago), and Ahuahu/Great Mercury (hereafter, recently eradicated) (Fig. 1). Atiu/Middle and Green Islands were combined for all analyses and summary descriptions given their similar small size (13 and 2 ha), close proximity (785 m), perimeter/area ratio (0.017 and 0.038), and identical invasion history. Each sampling area consisted of a pair of SCUBA transects ~30 m apart, resulting in 14 transects per study island/invasion history group. Transects began at the shoreline and ran through the intertidal zone, ending in the subtidal zone at a depth of 5 m. Macroalgae species and their percent cover were documented within a 1 × 1 m quadrat placed every meter in depth along the transects. Sampling occurred at the end of the dry season (February and March 2016) and rainy season (September and October 2016) to account for temporal variability in nutrient subsidies. Due to ocean conditions, it was not possible to sample every depth and transect in both seasons. The total number of quadrats ranged from 42–70 per island/group each season.

2.3. Stable isotope sampling

Given that seabirds feed at a high trophic level, primarily on marine prey, their guano is enriched in the heavier ^{15}N isotope (Mathisen et al. 1988, Kline et al. 1990), allowing researchers to track seabird influence through trophic systems (Mizutani & Wada 1988, Wainright et al. 1998, Post 2002, Croll et al. 2005, Jones 2010a). Algal ^{15}N enrichment has been observed at seabird islands with high nest density (Kolb et al. 2010, Gagnon et al. 2013), and researchers have used algal δ^{15}N signatures to trace nitrogen-enriched sewage in mixed coastal waters (Gartner et al. 2002). Never-invaded islands and those cleared of invasive mammals earlier are expected to have higher seabird densities and higher nutrient loads into the nearshore environment, resulting in ^{15}N enrichment.

Samples from the 6 most common macroalgae species found at the study islands were collected from quadrats for stable isotope analysis (see Section 3.2). Each macroalgae sample was cleaned of epiphytic algae, rinsed with deionized water, and dried at 55°C for 48–72 h. The most recent growth from the tip of each sample was removed, ground into a fine powder, weighed (4–7 mg, precision 0.01 mg), packed into tin capsules, and analyzed for δ^{15}N using an elemental analyzer (Costech ECS 4010) coupled with a mass spectrometer (Thermo-Finnigan DELTAplus Advantage), with atmospheric N_2 as the nitrogen standard.

Table 1. Summary of study island characteristics

Study island	Area (ha)	Invasion/eradication history	Current human habitation	Livestock present	Mean seabird burrow density (burrows m^{-2})	Wave exposure (±SE)	Runoff (±SE)
Atiu (Middle)	13	Never invaded	No	No	1.27	80.46 ± 13.31	7.71 ± 2.31
Green	2				Borrelle (2018)		
Korapuki	18	Eradicated 1986	No	No	0.18–0.25 Freschet et al. (2013), Borrelle (2018)	70.40 ± 8.79	13.13 ± 4.54
Ahuahu (Great Mercury)	1860	Eradicated 2014	Yes (1 family)	Yes	0 Borrelle (2018)	67.36 ± 6.26	15.91 ± 6.69

2.4. Water sampling

Given the high nitrogen content of seabird guano, quantifying ammonium and nitrate concentrations in the water surrounding seabird colonies can be a good predictor of guano-based nitrogen availability for macroalgae. High nitrogen concentrations are often found in waters near seabird breeding areas (Bosman & Hockey 1986, McCauley et al. 2012). During SCUBA surveys, 300 ml of seawater were collected in sample jars from each transect roughly 0.5 m above the sediment at a depth of 3 m. Samples were filtered to remove large particles (>0.5 mm), kept in the dark, refrigerated (<8°C), and processed within 48 h. Sample sizes ranged from 24−28 per island invasion history. Water samples were analyzed for ammonia and nitrate concentrations (range 0−1 mg l^{-1}, accuracy ±0.01 mg l^{-1}) using a YSI 9500 field photometer (YSI) during both the rainy and dry sampling seasons.

2.5. Statistical analysis

All statistical analyses were performed in R version 3.4.1 (R Core Team 2017). Macroalgae species richness and diversity, defined as the Shannon index (*H*) (Shannon 1948), were compared between invasion histories. Results are presented as means with 95% CIs. The importance of environmental variables and island invasion history on macroalgae communities was identified using generalized linear models (GLMs) with the 'manyglm' function from the 'mvabund' package (Wang et al. 2020). The influence of these variables was quantified and visualized using a generalized linear latent variable model from the 'gllvm' package (Niku et al. 2020). GLMs are preferred over traditional distance-based analyses because distance-based analyses are potentially susceptible to confounding ef-

fects from the mean−variance relationship; as mean abundance increases so does variance (Warton et al. 2012). Model-based analyses and ordinations are useful for identifying correlation patterns between taxa, measuring environmental influence, and making statistical inferences (Hui et al. 2015, Warton et al. 2015). For all community analyses, there was no significant difference between seasons.

We identified 5 factors (predictor variables) that could potentially influence algal $\delta^{15}N$ values, including invasion history (never-invaded, eradicated 30 yr ago, and recently eradicated), season (rainy and dry), depth (1−5 m), runoff, and wave exposure (Table 2). Runoff is a unitless measure of flow accumulation calculated as a raster of the total number of cells that drain into each individual cell. It is based on flow direction from a digital elevation model (DEM) (Jenson & Domingue 1988) using the flow accumulation algorithm (Hydrology toolset, Spatial Analyst toolbox, ArcGIS). Wave exposure is mean weighted fetch calculated using the 'fetchR' package (Seers 2017). Fetch-based indices are reliable in quantifying wave exposure across large areas in shallow systems (Hill et al. 2010).

The relative importance of each variable in predicting $\delta^{15}N$ was calculated from model averaging of selected linear mixed-effects models (LMMs) for each macroalgae species separately. All models were ranked using second-order Akaike's information criterion (AIC_c) corrected for small sample size (Hurvich & Tsai 1989) using the 'MuMin' R package (Barton 2017). Those with AIC_c weights (w_i) (Johnson & Omland 2004) greater than 0.01 were included in candidate model sets. AIC_c weights represent the relative likelihood of a model to explain the variable relationship. All LMMs in the candidate model set, those with a likelihood greater than 1%, were averaged using the 'AICcmodavg' R package (Mazerolle 2017) to provide individual parameter estimates and rela-

Table 2. Predictor variables examined in linear mixed models to describe algal $\delta^{15}N$ response

Variable	Type	Levels	Description
Invasion history	Categorical	Never invaded	Atiu/Middle and Green Islands
		Previously eradicated (30+ yr ago)	Korapuki Island
		Recently eradicated (2 yr ago)	Ahuahu/Great Mercury Island
Season	Categorical	Rainy	End of winter (September−October)
		Dry	End of summer (February−March)
Depth	Continuous		Sampling depth: 1−5 m
Runoff	Continuous		Flow accumulation at shore
Wave exposure	Continuous		Mean weighted fetch

tive importance. Individual parameters with relative importance greater than 0.9 were considered strongly significant and values between 0.6 and 0.9 were moderately significant. Only parameters that met these values were included in the description of differences between island invasion histories.

Fixed effects included all predictor variables (normally distributed) and 2-way interactions between season and invasion history, season and runoff, and invasion history and depth. The increased nutrient loading in the rainy season could influence how invasion history and runoff amount impact stable isotope values. The effect of sampling depth on isotope values could be impacted by invasion history, as islands with varying guano deposition could also vary in how deep the guano influence is detected. If heterogeneity was detected within the model variances, we adjusted variance weights for season and/or islands depending on the species data set. To account for sample variation across sites and time, random effects were modeled for repeat transects or quadrats. The full models used to define candidate models, including all fixed effects, weights, random effects, and sample size are listed in Table S2. Models were fitted based on a maximum likelihood method and analyses performed using the 'nlme' R package (Pinheiro et al. 2017). We used these analyses to describe differences between islands in this specific archipelago as a case study, recognizing that our inferences cannot be generalized to other island systems. Nitrate and ammonia concentrations were compared between season and island invasion history. Assumptions of ANOVA were evaluated by Q-Q plots for normalcy and Levene's test for homogeneity of variance. Water samples from all islands and seasons were normally distributed while uneven variance was detected in nitrate concentrations during the dry season. Therefore, we used Welch's ANOVA in all water sample analyses.

3. RESULTS

3.1. Macroalgae community

In total, 29 macroalgae species were identified from the SCUBA surveys (Table S3). Species richness and H were lowest at the recently eradicated island, followed by the islands eradicated over 30 yr ago, and were highest at the never-invaded islands (Fig. 2, Table S4). There were different algal communities at varying depths (likelihood ratio test [LRT] = 178, p < 0.001), wave exposures (LRT = 61, p = 0.011), runoff points (LRT = 78, p < 0.001), and islands (LRT = 409, p < 0.001). However, most of the species lacked strong associations with the environmental variables (Fig. S1). Environmental variables (depth, wave exposure, and runoff) explained approximately 14% of the covariation in algae cover (Fig. 3). The addition of island invasion history increased the proportion of variance explained to 25% (Fig. 3).

Red algae species were found most often on the never-invaded islands (68% of the quadrats), followed by the island eradicated 30 yr ago (40%), and least often at the recently eradicated island (12%). Only one species of green algae, *Ulva per-*
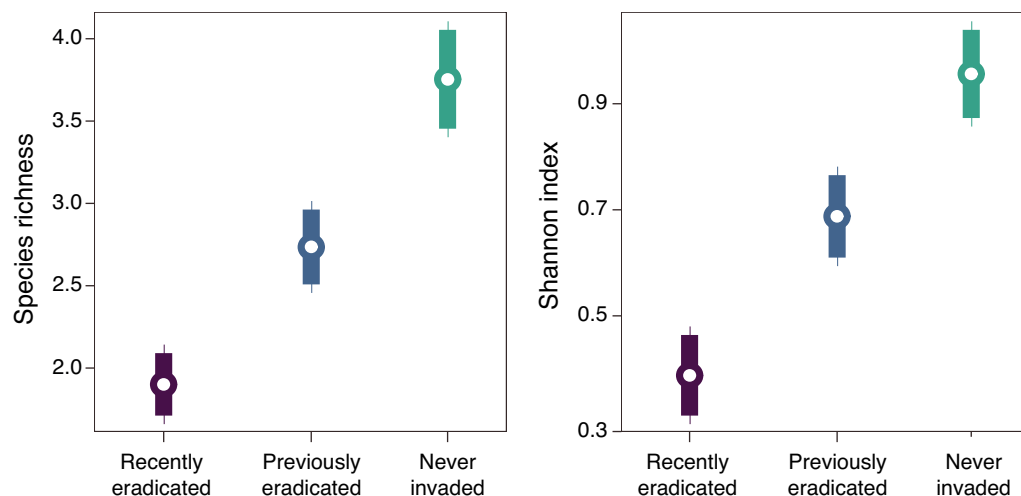

Fig. 2. Species richness and diversity (Shannon index) by invasion history displayed as mean and 95% CIs. 'Previously eradicated': predators were eradicated from the island over 30 yr ago; 'recently eradicated': predators eradicated 2 yr ago
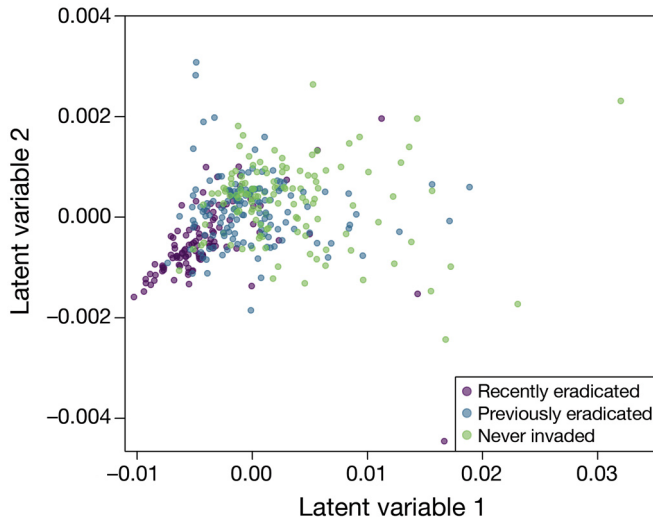
Fig. 3. Ordination of macroalgae communities based on a generalized linear latent variable model with environmental covariates (sampling depth, wave exposure, and runoff). Sites are colored by island invasion history to portray differences in community structure between islands

tusa, was documented during SCUBA sampling, and its presence was limited to the never-invaded islands (26% of the quadrats). The recently eradicated island was dominated by the brown kelp *Ecklonia radiata*, found at 85% of the quadrats with a mean cover of 67%.

3.2. Stable isotope analysis

The algal species selected for stable isotope analysis (including total sample size) were *Carpophyllum flexuosum* (n = 66), *C. maschalocarpum* (n = 56), *C. plumosum* (n = 68), *Ecklonia radiata* (n = 79), *Vidalia colensoi* (n = 35), and *Xiphophora chondrophylla* (n = 93). *V. colensoi* was the only red alga (Rhodophyta) found at most transects while the remaining 5 species belong to the brown algae group (Phaeophyceae). Between 8 and 21 candidate models were identified for each species and included in model averaging to estimate variable importance (Table S5).

Season was a strong predictor in ^{15}N enrichment across all species (relative importance = 1.00) (Table S6). Algae samples collected in the rainy season had higher δ^{15}N values (Table S6, Fig. 4), unsurprisingly given that rain is the main transport vector of guano from the terrestrial to marine system at the study islands. Depth was a strong predictor in ^{15}N enrichment across all species (relative importance >

0.89) except *E. radiata* and *V. colensoi* (Table S6). As depth increased, δ^{15}N decreased across all species except *C. flexuosum* and *X. chondrophylla* (Table S6, Fig. 4). These 2 species exhibited island-specific depth relationships (Table S6, Figs. 4 & S2). As wave exposure increased, δ^{15}N decreased in all species except *E. radiata* (Table S6, Fig. 4) due to greater mixing in the water column. Frequent and strong waves can reduce nutrient residence time in the nearshore water column, quickly transporting nutrients away from land. Increased runoff resulted in increased δ^{15}N only in the red alga *V. colensoi* (parameter importance = 0.75) (Table S6, Fig. 4).

Invasion history was an important predictor in ^{15}N enrichment across all species (relative importance > 0.75), except *E. radiata* (relative importance = 0.08) (Table S6). Never-invaded islands had higher δ^{15}N than the eradicated islands in all species found there, as depicted by parameter estimates and CIs (Table S6, Fig. 5). However, the expected trend of decreasing δ^{15}N by years since eradication did not hold true. With species found at both eradicated islands (*C. flexuosum*, *C. maschalocarpum*, and *X. chondrophylla*), the recently eradicated island had δ^{15}N values roughly equal to or higher than the island eradicated over 30 yr ago (Table S6, Fig. 5). However, the zero overlapping CIs in many of these invasion histories indicate some uncertainty in these relationships (Table S6).

3.3. Water sampling

Ammonia concentrations in the water column did not vary by season (Welch's ANOVA, $F_{1,47} = 0.28$, p = 0.60), while nitrate values were higher during the rainy season for all island invasion histories ($F_{1,68}$ = 115.15, p < 0.001) (Fig. 6, Table S7). In the dry season, ammonia values were highest at the island eradicated over 30 yr ago, followed by the recently eradicated island, and never-invaded islands, although these differences were insignificant (p = 0.16) (Fig. 6, Table S7). This order was reversed in the rainy season (p = 0.13) (Fig. 6, Table S7). All ammonia measurements were low (<0.2 mg l^{-1}), regardless of season. Such values are low on the detection scale of the instrument (0–1 mg l^{-1}), possibly misrepresenting the importance of the results. In the dry season, nitrate values were significantly different between all islands (p < 0.05 for all pairwise comparisons) with the highest concentration observed at the island eradicated over 30 yr ago (Fig. 6, Table S7). However, in the rainy season, nitrate concentrations were highest
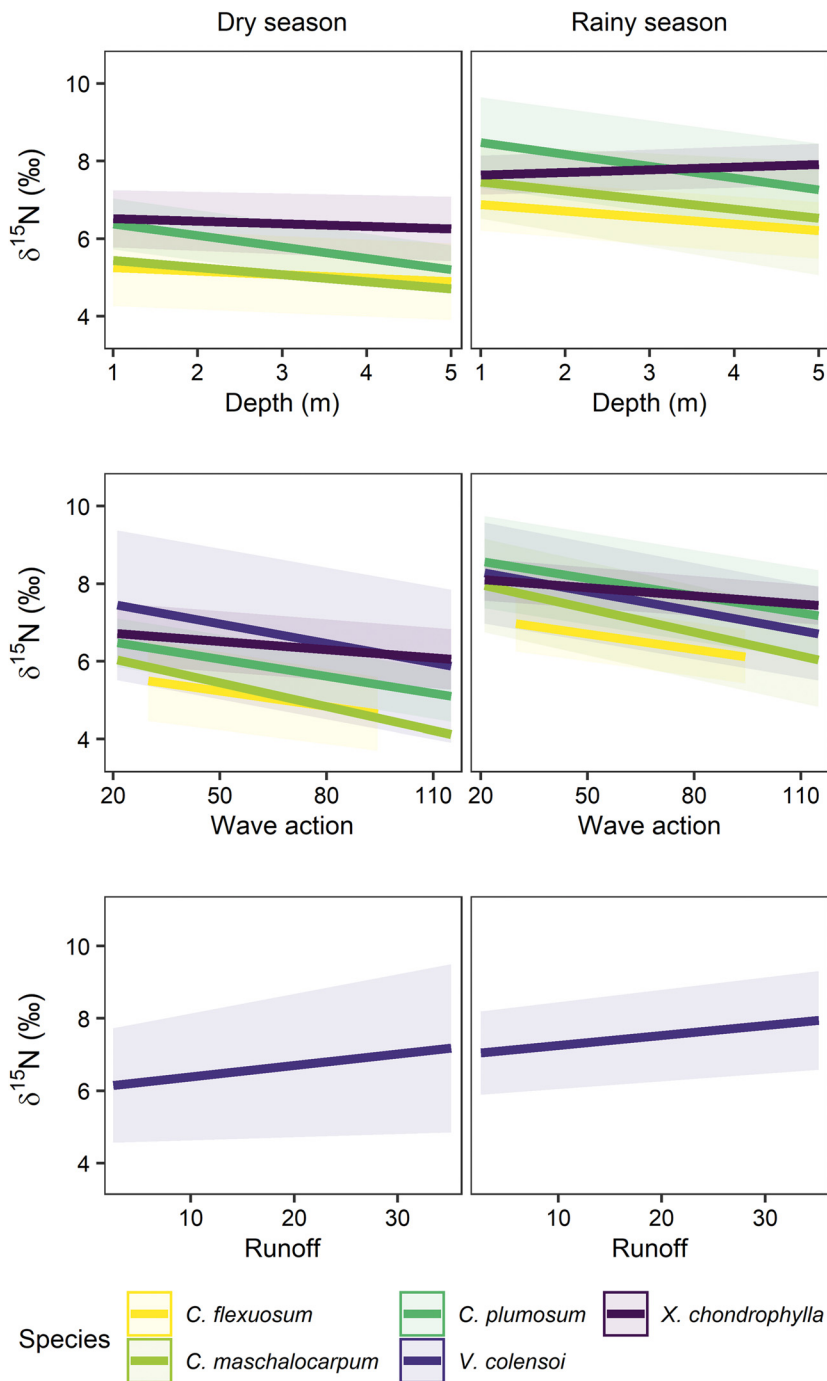
Fig. 4. Linear mixed model averaged predictions of δ15N by season, depth, wave exposure, and runoff. Only species with significant parameter influence on δ15N are presented in each variable plot. Columns: sampling season; colors: species; shaded areas: 95% CIs

Species
- C. flexuosum
- C. maschalocarpum
- C. plumosum
- V. colensoi
- X. chondrophylla

4. DISCUSSION

4.1. Macroalgae community

This study is the first to describe nearshore recovery across invasion histories while measuring additional environmental parameters. Algae communities exhibited differences based on sampling depth, wave exposure, runoff, and island invasion history, indicating that seabird nutrient runoff has the potential to shape nearshore marine communities. Nitrogen stable isotope values also differed among invasion histories, but were heavily influenced by environmental factors including season, sampling depth, and wave action. Not all species responded similarly to environmental factors and invasion histories, demonstrating algal species-specific responses to seabird-derived nutrient uptake.

Given that high seabird density corresponds to high algal species richness and diversity as well as the significant influence of runoff on community structure, it is likely that guano deposition is influencing macroalgae community composition. Similar relationships linking nutrient input to increased aquatic diversity have been described in other studies (Nielsen 2003, Bracken & Nielsen 2004) up until a context-dependent threshold of nutrient enrichment, after which diversity declines (Mittelbach et al. 2001). Guano runoff is shown to increase algal production and provide habitat for marine invertebrates which in turn feed shorebirds and other higher trophic level organisms (Bosman & Hockey 1986), suggesting that mammal eradication could positively impact entire food webs as seabird populations rebound. One study found rat-free islands with high seabird densities had higher δ15N in algae as well as faster growing fish communities with higher biomass (Graham et al. 2018).

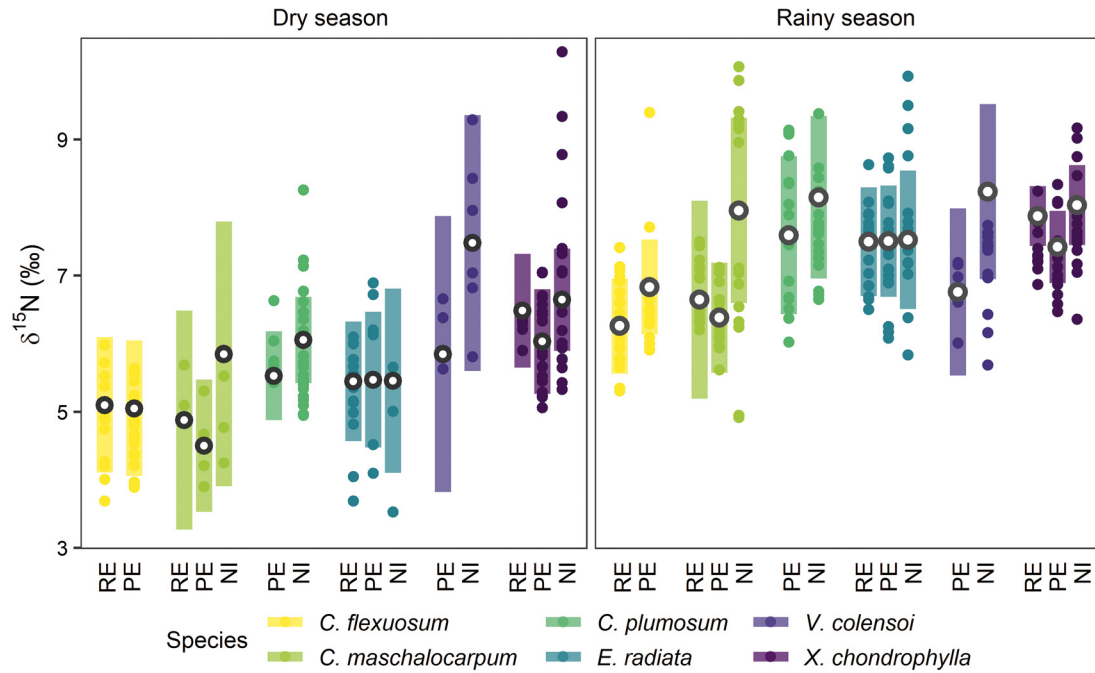The macroalgal communities measured at the never-invaded and older eradicated islands often con-

at the recently eradicated island, followed closely by the never-invaded islands and island eradicated over 30 yr ago, although these relationships were insignificant (p = 0.21) (Fig. 6, Table S7).

Fig. 5. Linear mixed model averaged predictions of δ^{15}N by invasion history (RE: recently eradicated [2 yr ago]; PE: previously eradicated [over 30 yr ago]; NI: never invaded). Colors: species; colored points: δ^{15}N values; outlined white points: model predicted medians; shaded bars: model predicted 95% CIs. Invasion history was an important predictor in ^{15}N enrichment across all species, except *Ecklonia radiata.* The importance of island invasion history was strongest in *Carpophyllum plumosum*, *Vidalia colensoi*, and *Xiphophora chondrophylla* (non-zero overlapping CIs)
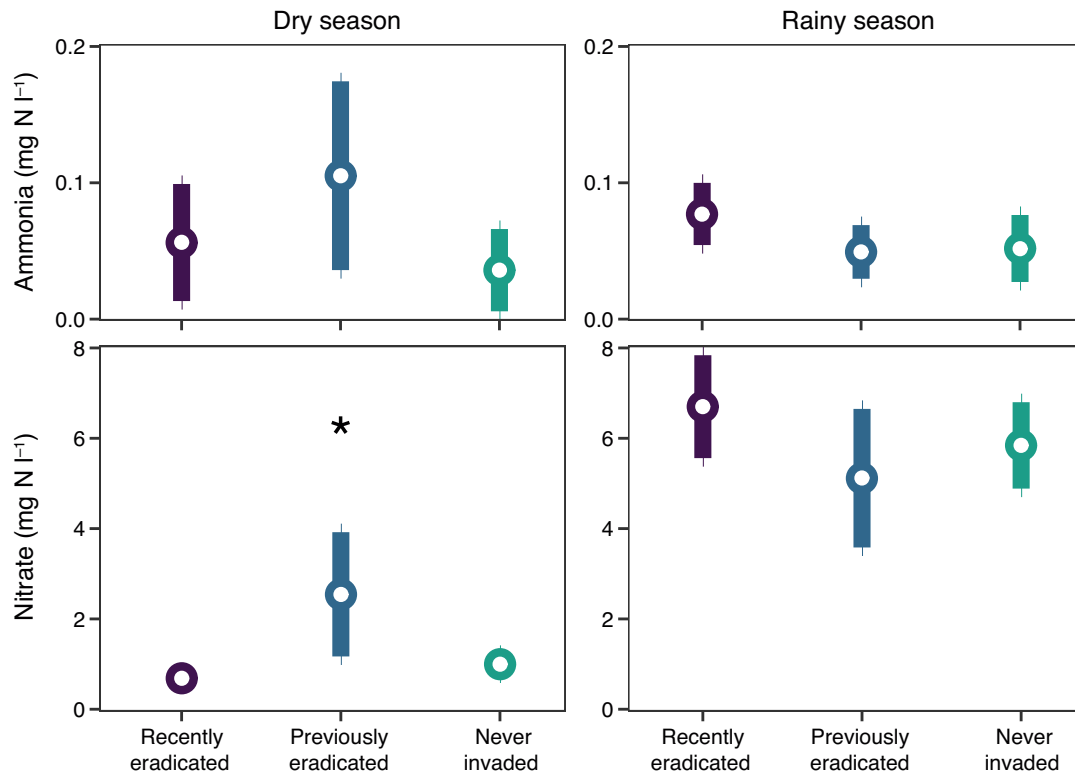

Fig. 6. (a) Ammonia and (b) nitrate concentrations by invasion history and season displayed as mean and 95% CIs. 'Previously eradicated': predators eradicated from the island over 30 yr ago; 'Recently eradicated': predators eradicated 2 yr ago. Asterisk indicates significantly higher nitrate concentration at the previously eradicated island in the dry season

tain red and green algae, which thrive in nutrient-rich environments. Previous research has used algal structure and function to identify functional groups that respond differently to nutrient availability in regards to succession, productivity, and persistence (Littler & Littler 1980). Many species with high nutrient requirements and growth rates in nitrogen-rich environments have thinner tissues, high surface area to volume (SA:V) ratios, and low nutrient storage capabilities (Rosenberg & Ramus 1984, Wallentinus 1984, Nielsen & Sand-Jensen 1990, Hein et al. 1995), allowing them to dominate in eutrophic environments (Littler & Littler 1980). Most green and red algae possess these characteristics, and their presence at the never-invaded and older eradicated islands could indicate a habitat with higher nutrients and their competitive dominance over slower growing species (Valiela et al. 1992, Harlin 1995, Kinney & Roman 1998, Campbell 2001). The higher occurrence of red algae species on the never-invaded and older eradicated islands could be driving the increased diversity and variable community composition documented at these islands.

Conversely, the recently eradicated island had fairly consistent communities comprised primarily of brown algae, a group typified by thick tissues, slow growth, and a low SA:V ratio — characteristics unsuitable for responding to the brief nutrient pulses present in runoff events but beneficial in persisting through periods of nutrient shortage (Carpenter 1990). These communities were dominated by *Ecklonia radiata*, a slow-growing kelp species with low nitrogen requirements (Kirkman 1989, Campbell 2001). Slow-growing macroalgae thrive in nutrient-limited habitats (Duarte 1995), and *E. radiata* can create dense canopies, increasing shading and affecting species abundance as well as species assemblages (Toohey & Kendrick 2008, Wernberg & Goldberg 2008). The kelp dominating the recently eradicated island could have played a role in its relatively lower species diversity than the macroalgal communities surrounding the other islands.

In addition to nutrient subsidies, wave action also influenced macroalgae communities. More diverse communities are sometimes found in areas of intermediate to high wave exposure (Kautsky & Kautsky 1989, Burrows 2012). However, some studies have documented a variable seasonal response or no change in macroalgae assemblage by wave exposure (Kraufvelin 2007, Kraufvelin et al. 2010, Smale et al. 2011, Spatharis et al. 2011). In this study, wave exposure was highest at the never-invaded islands followed by the island eradicated over 30 yr ago and the recently eradicated island (Table 1), correlating with

the island order from higher to lower diversity. Few species exhibited a strong association with wave exposure (Fig. S1), so community differences were not driven by individual species. We found that seabird-derived nutrient deposition and environmental variables such as wave exposure can explain the differences in algal communities.

4.2. Stable isotope analysis

Stable isotope analysis is an effective technique for monitoring terrestrial recovery on seabird islands (Jones 2010a) and measuring seabird influences in the nearshore environment (Kolb et al. 2010, Gagnon et al. 2013). Our analysis demonstrated that guano uptake in macroalgae is species-specific and influenced by multiple environmental factors. Given that the red alga *Vidalia colensoi* was the only study species influenced by runoff amount further indicates that different algal functional forms take up nutrients at different rates and capacities. Previous research found green and red algae enriched in ^{15}N following nutrient exposure, while the brown kelp *E. radiata* had no difference in δ^{15}N values (Gartner et al. 2002). *E. radiata* was the only study species with relatively equal δ^{15}N values across islands regardless of seabird burrow density and guano input. The low nitrogen uptake rate and large structural biomass (low SA:V ratio) of *E. radiata* results in a competitive disadvantage (Wallentinus 1984), requiring long nitrogen exposure time for ^{15}N enrichment. A similar indifference to seabird impact was found in the kelp *Saccharina latissimi*, where δ^{15}N did not vary between islands with and without seabirds in the Arctic (Zmudczyńska-Skarbek et al. 2015, Zmudczyńska-Skarbek & Balazy 2017).

The consistently high δ^{15}N values at the never-invaded islands are most likely a result of the islands' high seabird burrow density compared to the islands eradicated 30 yr ago and 2 yr ago. These never-invaded islands would have greater guano deposition and nutrient runoff, resulting in coastal nitrogen enrichment values similar to seabird islands with high nest densities regardless of eradication history (Kolb et al. 2010, Gagnon et al. 2013, Honig & Mahoney 2016). Comparing δ^{15}N values between the eradicated islands was not as intuitive given that the recently eradicated island had higher nitrogen enrichment than the island eradicated over 30 yr ago. One reason for this discrepancy could be the slightly lower wave exposure at sampling areas around the recently eradicated island, encouraging higher δ^{15}N

values from less mixing. Additionally, samples of *Carpophyllum maschalocarpum* and *Xiphophora chondrophylla* were found at shallower depths at the recently eradicated island compared to the older eradicated island (Table S8). Shallower sampling sites are inherently enriched in ^{15}N due to their proximity to runoff sources on land, therefore the higher δ^{15}N measured at the recently eradicated island could be inflated from their shallow collection depths and potentially not a result of the island's invasion history.

Another potential explanation for enriched isotope values at the recently eradicated island could be the presence of pied shags *Phalacrocorax varius* nesting on tree branches over sampling areas. They forage in water less than 10 m deep and breed year-round, resulting in small yet constant nearshore nutrient deposits compared to large colonies of ground-nesting seabirds common on the other islands. The nitrogen in guano is composed primarily of uric acid with small amounts of ammonium and nitrate (Lindeboom 1984, Staunton Smith & Johnson 1995). When shags deposit guano directly into the nearshore, the small amount of inorganic nitrogen immediately available for algae uptake (ammonium and nitrate) is enriched in ^{15}N (Wainright et al. 1998, Zhu et al. 2009), resulting in higher δ^{15}N values from the algae samples.

4.3. Water sampling

The presumed lack of usable, inorganic nitrogen at the recently eradicated island is supported by the low concentrations of nitrate and ammonium in water samples during the dry season. The unexpectedly high inorganic nitrogen concentrations at the recently eradicated island during the rainy season could be distorted by increased nitrogen runoff from livestock feces, sediment, or forest litter (McColl et al. 1977) since this sizeable island has large stream catchments, which the other islands lack. The best way to understand the complexities in nitrogen cycling from land to sea and the potential differences in algal communities at this island would be future studies comparing the newly established and expanding petrel colonies on the island's headlands with other areas lacking seabirds.

5. CONCLUSIONS

This case study provides some of the first descriptions of how macroalgae communities are more di-

verse at never-invaded and older eradicated islands as well as how sampling depth, season, wave action, and runoff influence stable isotope values in algal species. This study demonstrates the importance of including environmental parameters in nearshore community and stable isotope research. However, it is difficult to draw broader conclusions linking island eradication history and nearshore algal response due to the limited number of islands in this case study. A larger sample size of islands with varied eradication/restoration histories would help us understand if the patterns we observed here can be generalized across similar islands with related invasion histories. Quantifying nearshore recovery is crucial in measuring whole system impacts of island management, maintaining coastal ecological and economic services, and further describing the importance of seabirds in driving the nutrient connection between land and sea.

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