Ecological Applications, 20(5), 2010, pp. 1204–1216

Prognosis for ecosystem recovery following rodent eradication and seabird restoration in an island archipelago

Holly P. Jones[1]

Yale University, 370 Prospect St., New Haven, Connecticut 06511 USA

Abstract. Invasive species are widespread and can have devastating effects on biota, especially insular biota. Invasive species eradications are increasingly employed to promote island recovery to preinvasion states. However, it remains unclear if additional restoration actions may be required on islands that were once heavily reliant on seabird guano for ecosystem functions. Active seabird augmentation has been suggested as necessary to exact ecosystem recovery on contemporary timescales in some cases. I use two experiments on offshore islands in Cook Strait, New Zealand, to test the hypothesis that seabird restoration will restore island ecosystem functioning following invasive rodent removal. The first is a small-scale single-island fertilization experiment that simulates seabird recovery. This experiment tested the recovery potential of offshore islands and was used to infer the density of seabirds needed to elicit ecosystem recovery. The second is a large-scale natural experiment that takes advantage of eight islands with differing rodent eradication and seabird restoration histories. I compared ecosystem functioning variables (δ^{15}N, C:N ratios in soil, plants, and spiders, as well as arthropod abundance and diversity) on two islands that had rodents eradicated and two islands undergoing seabird augmentation with two control islands (never invaded by rodents) and two positive control islands (currently invaded by rodents). The results suggest that islands do have the potential for recovery given nutrient amendments, but that islands with rodents eradicated and islands undergoing seabird augmentation have not recovered most of their ecosystem function. Finer, intra-island analysis showed that seabird restoration projects have the potential to speed the recovery process, but that the projects on the studied seabird restoration islands were not advanced enough to produce island-wide recovery. The results suggest that high seabird densities (5–10 burrows/m^2) are needed to promote recovery to never-invaded control levels. Seabird augmentation, through chick translocation and/or social facilitation with decoys, vocalization playbacks, and/or mirrors can supplement passive seabird recovery on islands where seabirds have been extirpated or extremely reduced by invasive predators. Such restoration efforts may be necessary to promote ecosystem recovery on contemporary timescales.

Key words: Cook Strait, New Zealand; ecosystem recovery; eradication; invasive rodent species; island restoration; seabird restoration; social facilitation; spatial subsidies; stable isotope analysis.

Introduction

Islands have high levels of endemism and are critical areas for biodiversity conservation (Kier et al. 2009). The majority of animal extinctions have occurred on islands, and most, including more than half of all seabird extinctions, were attributed to invasive species (Atkinson 1989, Simberloff 1995, IUCN 2009). This vulnerability of island species has prompted concerted efforts to eradicate invasive species from nonnative ecosystems. One goal of these eradications is to promote ecosystem recovery to preinvasion states (Atkinson 1988). Yet, it is unclear if ecosystems can recover their natural function once invasive species are removed (Beisner et al. 2003). This study tests measures of ecosystem recovery on islands where invasive species have been removed for island restoration.

Ecologists have long recognized that ecosystems can be linked if highly mobile vertebrates such as birds transport nutrients across landscapes (Hutchinson 1950). These linkages are often critical to productivity, nutrient flow, and the abundance and diversity of recipient food webs (Polis et al. 1997, Post et al. 1998, Fukami et al. 2006). Colonial seabirds are often major nutrient vectors on islands free from invasive predators, especially since seabird colonies can comprise millions of individuals. These colonies can have important bottom-up effects on island plant production and trophic structure by infusing massive amounts of guano fertilizer into terrestrial zones (Anderson and Polis 1999, Sanchez-Pinero and Polis 2000, Croll et al. 2005, Fukami et al. 2006).

However, approximately one-third of all seabird species are threatened with extinction (IUCN 2009).

Manuscript received 30 June 2009; revised 23 September 2009; accepted 5 October 2009. Corresponding Editor: M. J. Vander Zanden.

[1] E-mail: holly.jones@yale.edu

Invasive rodents that are commensal with humans (*Rattus exulans*, *R. rattus*, *R. norvegicus*, and *Mus musculus*) are a primary cause of the extirpation or severe reduction of many insular breeding seabird populations (Atkinson 1985, Jones et al. 2008). Rodents impact seabird populations directly via predation (Wanless et al. 2007, Jones et al. 2008) and indirectly via disturbance, which further causes nest abandonment, higher divorce rates, and burrow switching (Jouventin et al. 2003). The loss of seabirds, in turn, has lead to alteration of important ecosystem processes normally supported by guano.

The ecosystem-wide effects of invasive rodents have prompted a global effort to eradicate them from islands (Howald et al. 2007). In island eradication projects, it is important to distinguish between recovery and ecological restoration. If there is no active management other than removal of a disturbance effect such as introduced species, the goal is for passive recovery. Thus, the definition of recovery is a change by natural processes over time without active intervention, whereas the definition of restoration is active intervention to achieve a specific goal (Atkinson 1988). Simberloff (1990) defined successful ecological restoration of an island as a system that does not deviate significantly from an undisturbed reference site, a definition that will be used for the remainder of this manuscript. Whether ecosystems are repaired by passive recovery or by active restoration, measurements of change are necessary to determine to what extent a recovering ecosystem differs from nearby unmodified sites (Atkinson 1988).

Rodent eradication programs have benefited many species of conservation concern, and have been touted as not just benefiting single species, but enabling entire ecosystem recovery. Yet disturbed ecosystems may not recover to their predisturbed states once the source of disturbance is removed, because they have become locked in an alternate stable state (Jones and Schmitz 2009). For many species of seabirds impacted by rodents, most notably hole-nesting procellarids, return to islands within several years of rodent removal is rare because of high natal philopatry (Gaze 2000) and perhaps continued perception of predation risk. Thus, although invasive rodents and other predators may cause ecosystem shifts due to extirpation of seabirds on an island, eradication of these predators may be insufficient to restore allochthonous nutrients due to reluctance of seabirds to recolonize islands (Croll et al. 2005, Mulder et al. 2009, Towns et al. 2009). Barriers to natural recolonization may be overcome by active seabird restoration (Kress 1998) including chick translocation, acoustic vocalization playbacks, and decoys that attract breeding seabirds back to historical breeding islands. The proposition that such recolonization should restore island ecosystem function (e.g., Miskelly et al. 2009) has not been formally tested.

I tested the hypothesis that restoration of seabird populations will restore preinvasion island ecosystem function through two experiments undertaken on offshore islands of New Zealand. The first was a fertilization experiment on a rodent-free but also seabird-free island. This experiment simulated varying seabird colony densities to gauge the recovery potential of offshore islands. The second was a natural experiment that capitalized on existing rodent eradications and seabird restoration projects on islands in New Zealand. I then use these results to offer some prognoses for recovery of ecosystem properties and functions ($\delta^{15}N$, C:N ratios in soil, plants, and spiders, arthropod abundance and diversity) through rodent eradication and seabird restoration.

Study System and Methods

Experimental setup and natural history

Of 30 islands in Cook Strait, New Zealand, eight were suitable for detailed study of the relative impacts of invasive species removal and seabird restoration on ecosystem recovery (Stephens, Middle Trio, Wakaterepapanui, Nukuwaiata, Maud, Mana, Tawhitinui, and Victory; see Fig. 1, Table 1, and Appendix A). Stephens (Takapourewa) and Middle Trio islands have never been invaded by rodents (controls) and have dense populations of colonial seabirds such as Fairy Prions (*Pachyptila turtur*; see Plate 1), Sooty Shearwaters (*Puffinus griseus*), Northern Diving Petrels (*Pelecanoides urinatrix urinatrix*), and Fluttering Shearwaters (*Puffinus gavia*). Rats were eradicated from Wakaterepapaunui (*Rattus exulans* and *R. norvegicus*) in 1999 and Nukuwaiata (*R. exulans*) in 1994 (Howald et al. 2007). Nukuwaiata has remnant natural colonies of Sooty and Fluttering Shearwaters, but Wakaterewepapanui had no colonial seabirds present at the time of study (H. Jones, *personal observation*). Victory (Motuiti) and Tawhitinui currently have rats (positive controls), and Mana and Maud (Te Hoiere) islands are currently undergoing seabird restoration. On Mana seabirds are being restored following the cessation of farming activities and house mouse eradication in 1990. Rodents have never invaded Maud, and the reason for the lack of seabirds is unclear, although its past human use is a likely contributor (Appendix A). Regardless of its invasion history, Maud is the only island that is undergoing seabird restoration with a recent history of seabird absence that is in the geologically and geographically confined study area. Detailed information on the seabird restoration actions on Maud and Mana is provided elsewhere (Appendix A).

I measured recovery response using fast and slow response variables. Annual plant productivity and arthropod abundance are expected to respond quickly to restoration efforts, whereas other variables such as nutrient sources are expected to respond more slowly because of their differing turnover times in ecosystems (Carpenter and Turner 2000). By choosing comparatively fast and slow variables, I aimed to understand how different ecosystem components recovered, if they

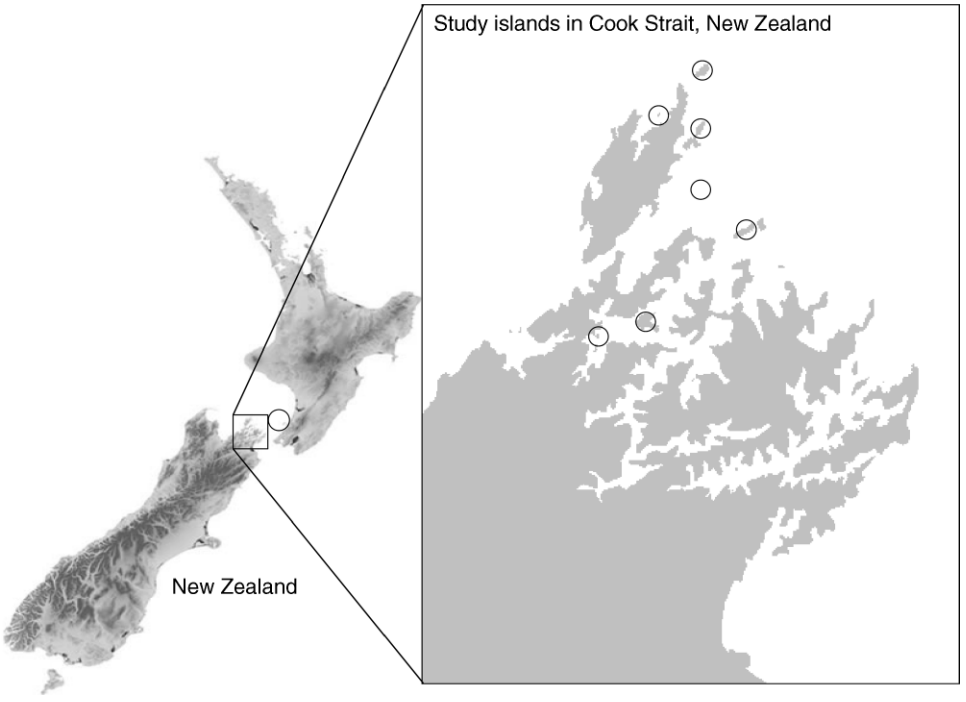

FIG. 1. Locations of islands used for the natural experiment in Cook Strait, New Zealand. The map to the left is of New Zealand, and the map on the right is a close-up of the Marlborough Sounds, where seven of the study islands are located. The seven study islands are indicated by circles.

recover at all. The fertilization experiment was done on a small scale over a short time frame, and thus required fast response variables to gauge the recovery potential of island systems in the face of the potential nutrient pulses that seabirds could provide. The fertilization experiment was also used to estimate the approximate amount of marine-derived nutrients needed to induce ecosystem recovery on islands. The natural experiment was used to gauge recovery on a large scale (whole-island scale) over a relatively long time frame (8–16 years), and thus required a combination of both fast and slow response variables. The natural experiment did not rely on artificial nutrient amendments, which made it possible to trace the fate of seabird-derived nitrogen through island food webs (soil, plants, spiders) and to calculate the amount of seabird-derived nitrogen used by island consumers (spiders). Collectively, both experiments offer insight into nutrient concentrations needed for recovery and whether or not there was measurable recovery of ecosystems on eradicated and seabird restoration islands.

Fertilization experiment sampling scheme and response variables

The fertilization experiment was undertaken on rodent- and seabird-free Maud Island grassland, and assessed the potential of seabird recovery to restore ecosystems. I simulated seabird presence in two ways. I added nutrients using a fertilizer application that mimicked seabird guano. I simulated seabird bioperturbation by digging 20 cm deep holes that emulate nesting burrows.

I used a randomized block study design with five treatments and 10 replicates of 2-m^2 plots. Replicates

TABLE 1. Sizes and treatments of study islands in Cook Strait, New Zealand.

Island	Size (ha)	Restoration treatment	Seabird density†
Stephens	150	never invaded	high
Middle Trio	13	never invaded	high
Victory	16	has rodents	undetectable
Tawhitinui	22	has rodents	undetectable
Wakaterepapanui	74	eradicated (1999)	undetectable
Nukuwaiata	249	eradicated (1994)	low
Maud	309	seabird restoration (since 1991)	undetectable outside of restoration colony
Mana	217	seabird restoration (since 1993)	low

† Author's *personal observation*.

were spaced at least 50 m apart from one another to ensure independence. In each replicate, the five treatments were randomly assigned: (1) control (no fertilizer), (2) low seabird density (1 burrow/m^2), (3) medium seabird density (3 burrows/m^2), (4) medium-high seabird density (5 burrows/m^2), and (5) high seabird density (10 burrows/m^2). I estimated the amount of phosphorus and nitrogen likely to be contributed by seabirds in differing densities should they be present (Appendix B), based on calculations for Fairy Prion nutrient input on Stephens Island (Mulder and Keall 2001) and for other burrow-nesting seabirds (Furness 1991). Seabird guano was unavailable in New Zealand and not legally permissible to import. Therefore, I simulated the organic and marine-derived nature of seabird guano using liquid fish-based fertilizer Verteflow 8.3.6 (Fertilizer New Zealand, Nelson, New Zealand) which contains marine-derived nitrogen and phosphorus. Seabird guano is also high in uric acid, ammonium, and phosphorus. I therefore supplemented Verteflow with urea, ammonium nitrate, and time-release fertilizer (Appendix B). I applied the fertilizer mix twice over a two-month period (once on 7 October and once on 1 November 2007). The reapplication mimicked seabird presence over three months (a typical breeding season).

Four months after the fertilizer application, I evaluated ecosystem response to fertilization by measuring plant litter decomposition rates, aboveground net primary productivity (ANPP), and arthropod consumer abundance during 11–13 March 2008. These variables are integral to ecosystem functioning on islands, are thought to be diminished when seabird populations decline following rodent introduction, and are expected to respond positively to seabird recovery (Croll et al. 2005, Fukami et al. 2006, Towns et al. 2009). In marked plots before fertilization I clipped all vegetation from 10 cm above the ground. I placed preweighed litterbags in each plot to measure decomposition rates. The 5×5 cm litterbags were made with fiberglass window screening and filled with grass clippings from Maud Island. I measured ANPP in three replicates within cages made of chicken wire 28 cm in diameter and 1 m high, with a shade cloth covering to exclude herbivores. In each of the exclosure cages I estimated ANPP by clipping grass to 10 cm and drying and weighing samples. I also clipped grass to 10 cm from the center 0.25 m^2 of each plot and dried and weighed the samples. I estimated the fraction of ANPP moving up the grazing chain (GANPP) as the difference between herbivore exclosures and open plots divided by ANPP measures from the exclosures.

I sampled arthropods by placing 75 mm diameter plastic cups into the ground with the opening flush to the ground surface (Markwell and Daugherty 2002). The cups were filled one-third full with 20% ethanol. I covered all traps with 10×10 mm mesh netting secured with a rubber band to exclude reptiles and any large and perhaps rare or endangered endemic arthropods. I placed square aluminum covers over each pitfall to exclude rain or debris. Arthropod abundance was calculated as the number of individuals caught per trap night.

Natural experiment sampling scheme and response variables

For the natural experiment, I selected a subset of eight islands in Cook Strait that have a wide range of rodent invasion histories and restoration efforts to measure recovery following different eradication and restoration efforts (Fig. 1, Table 1; Appendix A). Study islands were chosen for their balance of island size among treatment groups (Table 1), enabling the creation of an observational experimental study in which two islands are replicates of each of four histories: (1) rodents never invaded; (2) rodents invaded but not eradicated; (3) rodents eradicated; and (4) rodents absent with seabird restoration. Both invaded and never-invaded islands serve as references to gauge the degree to which rodent removal will lead to recovery or if islands remain in a disturbed state. I define recovery as the return of response variables to levels statistically indistinguishable from those observed on reference islands that were never invaded.

I used a nested block study design in which island identity was the nested factor and island treatment (never invaded, invaded, eradicated, seabird restoration) was the nesting factor. Potentially confounding factors such as history, past human use, island perimeter-to-area ratio, and island size vary among islands (Table 1; Appendix A). Out of necessity, because this was a natural experiment, I considered these factors ex-design and corrected for these through group assignment. Effects of island size and perimeter-to-area ratios were addressed through allocation of different island sizes among treatments. Human use factors were addressed by sampling in primary (undisturbed by humans) forest and in vegetation habitats in various successional stages toward reforestation (grassland and mixed regeneration).

On each island, I established three transects from coast to maximum elevation and sampled plots along multiplicative distances from the coast (i.e., 0 m, 10 m, 20 m, 40 m, 80 m) until entering a new habitat type (grassland, mixed regeneration, or forest) or a new seabird treatment (in or out of colony), in which case the multiplicative sampling started over until another habitat or treatment was reached, or until I reached the maximum elevation. The transects were located to transcend seabird colonies on islands with seabirds and to transcend all habitat types available on each island. Because of the high conservation value of the islands, transects were limited to areas determined by the New Zealand Department of Conservation. In particular, no transects were allowed in critical habitat for endemic frogs (*Leiopelma* spp.), in tuatara (*Sphenodon*

punctatus) nesting rookeries, or in sacred Māori cultural sites.

I randomly chose plot locations within each transect, and within each I measured soil pH, temperature, and moisture, plot aspect and slope, percent canopy cover, and the number of active seabird burrows (as indicated by presence of droppings outside burrows or seabirds in burrows) in a 3-m^2 plot.

Delta ^{15}N values provide an index of enrichment of the heavier isotope of nitrogen relative to a standard (air), and are standard measurements used to trace the amount of nitrogen flowing through ecosystems (Post 2002, Croll et al. 2005). I took advantage of the fact that marine nitrogen is enriched in ^{15}N compared to terrestrial nitrogen (Mathisen et al. 1988, Kline et al. 1990) to measure the source and fate of marine-derived nitrogen in trophic levels (soil, plants, arthropods) on study islands. On offshore islands in New Zealand, terrestrial soil samples on seabird-inhabited islands have $\delta^{15}N$ signatures around 17‰, while island soils unaffected by seabirds typically have $\delta^{15}N$ signatures around 10‰ (Markwell and Daugherty 2003). I used a single isotope ($\delta^{15}N$) two-end-member mixing model (Phillips 2001) to estimate the proportion of marine-derived nitrogen used by terrestrial arthropod predators (spiders) in their diet. I assumed 3.4% trophic fractionation (Post 2002). I used terrestrial soil gathered on invaded islands that had no seabirds present (Tawhitinui and Victory) as the terrestrial end member, and seabird-influenced soil gathered on islands with high seabird densities (Stephens and Middle Trio) as the marine end member. Both $\delta^{15}N$ values for terrestrial and marine end members (5.58‰ ± 0.3‰ and 17.26‰ ± 0.4‰, respectively) are in the standard range for soils in New Zealand with and without seabird influence (Markwell and Daugherty 2003).

I measured C:N ratios in soil, plants, and spiders as indicators of ecosystem function on the chosen study islands. I measured nitrate and ammonium concentrations to elucidate the extent of seabird legacies in soil and the ecosystem-level effects of invasive rodents on nutrient cycling. On islands, seabird guano is deposited in soils, and that uric acid is soon hydrolyzed to ammonium and gaseous ammonia. Following nitrification, the main soluble nitrogen forms available for plant consumption are nitrate and ammonium (Schmidt et al. 2004).

I collected one soil and one plant sample (from all plant species available) in each sampling plot. I chose understory shrubs (*Coprosma repens*, *Macropiper excelsum*, and *Myrsine australis*), and grass (*Holcus lanatus*) for stable isotope analysis because they were relatively common among all study islands. I picked the newest growth leaves available from three individuals per sample. I collected soil samples by removing all debris above the soil layer and collecting into a plastic bag 100 g of soil from 0 to 10 cm below the O horizon. I sieved soil samples to 2-mm particle size in the field and later to 0.5 mm in the laboratory.

I collected spider samples in each vegetation type on each transect. Thus, spiders from various sampling points along a transect but from the same habitat type were pooled. For stable isotope analysis, I collected spider samples passively in 2006 using pitfall traps (as in the fertilization experiment). It was more efficient to actively collect spiders, so in 2007 I collected spiders by gathering them at the base of their tunnels or by laying out a light-colored cloth and sorting through ground litter. All spiders were preserved in 70% ethanol until they were brought to the laboratory. All spiders were sorted to species (genus if the species had not yet been described) and identified to feeding locale (above- or belowground) with the aid of expert colleagues at Te Papa Museum in New Zealand. I used only belowground species for isotope analysis because they were found in the most abundant feeding locale (Appendix C).

All isotope samples were washed with distilled water, dried for 48 hours in a 60°C drying oven, ground to a fine powder, and weighed. Spider samples consisted of leg material supplemented with head capsules. I selectively used leg and head capsules to ensure maximum protein content and to reduce the amount of muscle or cuticle in samples. Stable isotope analyses were performed using a stable isotope mass spectrometer at the Yale Earth System Center for Stable Isotopic Studies (ESCSIS). I evaluated soil samples for ammonium and nitrate concentrations by using standard extraction in 2 mol/L KCl. After extraction, I analyzed samples with an automated flow analyzer.

I measured arthropod order richness and abundance as indicators of how nutrient subsidies or lack thereof are realized throughout island food webs. The dominant arthropods in ecosystems are indicators of whether or not materials or nutrients pass up trophic levels. Food web theory suggests that higher primary production should support higher densities of herbivores and high-trophic-level consumers (Polis et al. 1997). I tested this assertion by deploying up to six pitfall traps per transect to capture ground-dwelling arthropods. The number of sampling points per transect was dictated by island shape and size, so pitfall traps ranged from 7 to 18 traps per island. Traps were evenly spaced between habitat and seabird treatments. I sorted arthropod samples to the level of orders. Arthropod richness was calculated as the number of orders per pitfall trap, and abundance was calculated as the number of individuals caught per trap night.

I used ANOVA with post hoc Tukey tests to account for differences in arthropod abundance, productivity consumed by herbivores, and decomposition rates between fertilizer experiment treatments.

Finding no significant differences in variables between years or habitat types for inter-island comparisons, I

pooled years and habitats and used nested ANOVA with post hoc Tukey tests to account for differences between treatments in island-wide mean soil and spider $\delta^{15}N$ and C:N, $\delta^{15}N$ and C:N values for *C. repens*, *M. excelsum*, *M. australis*, and *H. lanatus*, soil nitrate and ammonium concentration, arthropod richness, and arthropod abundance. I used ANOVA with post hoc Tukey tests to account for intra-island differences in soil $\delta^{15}N$, C:N, and ammonium and nitrate concentrations between samples taken in and out of seabird colonies. Sample sizes were too small to compare arthropod and plant measurements inside and outside of seabird colonies. Comparisons inside and outside seabird colonies could only be done for the never-invaded treatment on Stephens Island, as there were no sampling points on Middle Trio that were devoid of seabird burrows. Data were log-transformed as necessary to meet normality assumptions of statistical tests.

Research has shown that nutrient subsidies derived from wind-driven allochthonous resources and carrion/beach-wrack may influence the response variables chosen for this study independently of guano inputs. These subsidies tend to have disproportionately higher influence on island perimeters than on island interiors, and marine-derived subsidies decrease with island size and perimeter-to area-ratio (Polis and Hurd 1996). In addition, topography such as steep cliffs may keep non-seabird nutrient vectors near the edges of islands (Paetzold et al. 2008). Accordingly, there may be a gradient effect from shore to interior that varies with island size and topography. To test the possibility that differing island size (Table 1) introduced gradient rather than rodent effects, I regressed arthropod abundance, soil ammonium and nitrate concentrations, and $\delta^{15}N$ in soils and plants against the distance from the shore for each treatment. I also used ANCOVA with perimeter-to-area ratio as a covariate for $\delta^{15}N$ in soils and plants, arthropod abundance and richness, and soil ammonium and nitrate concentrations for each island. Lastly, I used a dual isotope ($\delta^{15}N$ and $\delta^{13}C$) three-end-member mixing model to estimate the proportion of guano-, marine algae-, and terrestrial-based nitrogen in predatory spider diets on all island treatments. I assumed 3.4‰ trophic fractionation for nitrogen and 0.4‰ trophic fractionation for carbon (Post 2002). I used seabird guano collected from never-invaded islands, the most commonly found species of marine algae (*Carpophyllum* spp.) surrounding study islands, and terrestrial C_3 plant leaves from mainland forests without any marine-derived nitrogen or carbon sources, each as the three end-members in the model. Values of $\delta^{15}N$ and $\delta^{13}C$ for end members (13.86‰ and −20.74‰, 9.67‰ and −12.55‰, and 5.36‰ and −28.42‰ for guano, algae, and C_3 plants, respectively) were consistent with those reported in the literature (Mizutani and Wada 1988, Amundson et al. 2003, Markwell and Daugherty 2003).

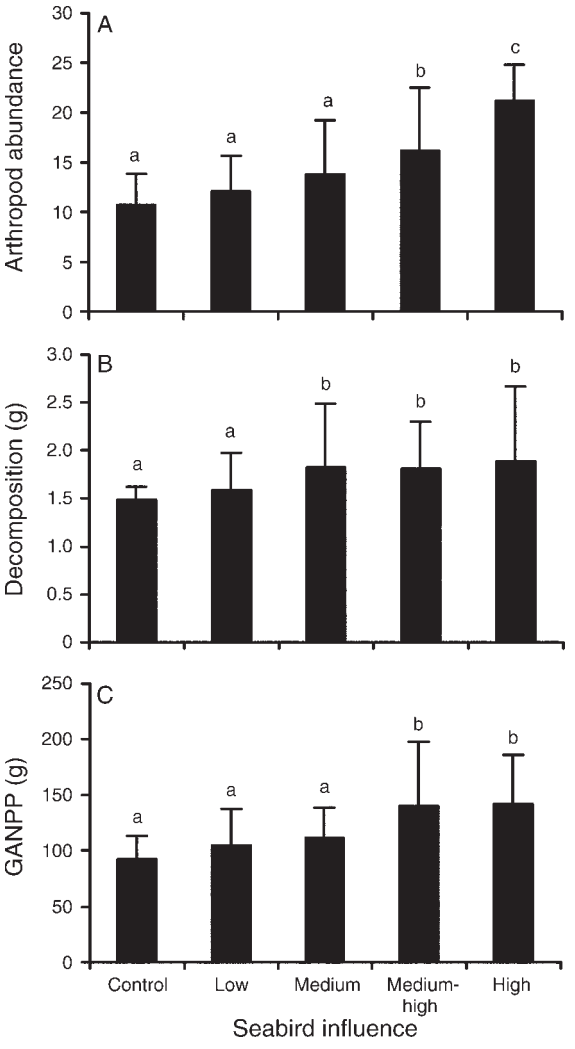

FIG. 2. Responses of (A) arthropods, (B) decomposition rates, and (C) productivity consumed by herbivores to experimental seabird recovery on Maud Island. Control treatments had no nutrient additions, while low, medium, medium-high, and high treatments simulated seabird densities with the addition of nutrients at the level of 1, 3, 5, and 10 seabird burrows/m^2, respectively (see Appendix B for amounts). Seabird influence increases from left to right. Values are means + SE. Arthropod abundance was measured as average arthropod abundance per trap night. Different lowercase letters above the error bars indicate significant differences at the $\alpha = 0.05$ level.

RESULTS

Fertilization plots

After four months, treatments that simulated medium to high seabird density had significantly higher arthropod abundance, decomposition rates, and GANPP than low-density treatments ($P < 0.05$; Fig. 2). Relatively high nutrient additions were necessary to elicit a significant response; a Tukey test revealed that arthropod abundance and GANPP were both significantly

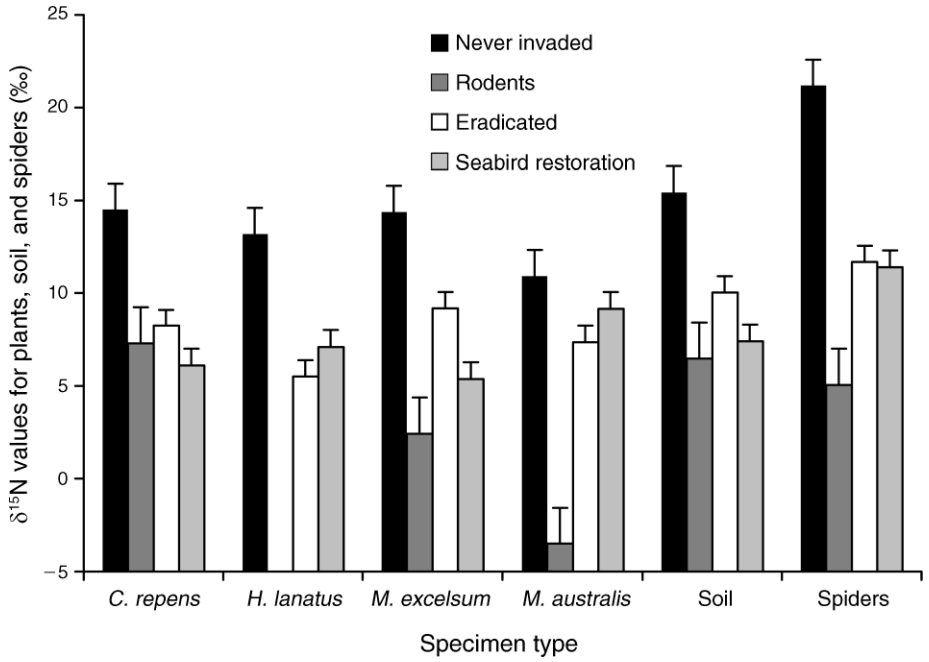

FIG. 3. The figure shows $\delta^{15}N$ values for plants, soil, and spiders across island treatments. Never-invaded treatments have never been invaded by rodents, eradicated treatments have had rodents eradicated, seabird restoration treatments are undergoing seabird restoration, and rodent treatments are currently invaded by rodents. Plants are *Coprosma repens*, *Macropiper excelsum*, *Myrsine australis*, and the grass *Holcus lanatus*. Values are means + SE.

higher than controls only for the two highest seabird density treatments (Fig. 2).

Natural experiment

Interisland comparisons.—The $\delta^{15}N$ levels in soil, spiders, and plants (*C. repens*, *M. excelsum*, *M. australis*, *H. lanatus*) were consistently highest in the never-invaded treatments ($P < 0.01$, 0.001, 0.03, 0.01, 0.03, 0.03, respectively). Recovery of variables to never-invaded control levels was detected only for *M. excelsum* on eradicated islands and *M. australis* on both eradicated and seabird restoration islands ($P > 0.05$ for post hoc tests; Fig. 3). The proportion of marine-derived nitrogen in spider diets was 104% ± 4% for never-invaded islands, indicating that terrestrial-derived nitrogen did not contribute to spider diets. In contrast, the proportion of marine-derived nitrogen was negative for rodent-invaded islands, suggesting marine-derived nitrogen does not play a significant role in spider diets on these islands. The proportion of marine-derived nitrogen in spider diets on both eradicated and seabird restoration islands was similar; 52% and 50% of N in the diet was marine-based on eradicated and seabird restoration islands, respectively.

Plant and spider C:N ratios did not significantly differ among treatments ($P > 0.05$; Fig. 4). Soil C:N was highest (low quality) for invaded islands ($P < 0.001$). Soil C:N values on eradicated and seabird restoration islands were statistically similar to never-invaded islands, indicating full recovery ($P > 0.05$ for post hoc tests; Fig. 4). Soil nitrate and ammonium concentrations were consistently higher in never-invaded treatments ($P < 0.03$, 0.01, respectively), with no recovery detected for eradicated and seabird restoration islands ($P > 0.05$ post hoc tests; Fig. 5). Arthropod richness was higher on never-invaded and seabird restoration islands than on invaded and eradicated islands ($P < 0.03$; Fig. 6). Arthropod abundance was highest on never-invaded islands, and was correspondingly lower on invaded, eradicated, and seabird restoration islands ($P < 0.05$; Fig. 6).

Intra-island comparisons for seabird restoration islands.—Soil $\delta^{15}N$, ammonium, and nitrate concentrations were significantly higher and soil C:N was consistently lower in the natural Sooty Shearwater colony than outside the colony, and in the restoration colony on Mana Island (Table 2). The restoration colony on Mana had higher soil ammonium concentration than outside the colony, but the other three variables were not significantly different (Table 2). Soil $\delta^{15}N$ levels were significantly higher and soil C:N was consistently lower in the Maud Island restoration colony than outside the colony (Table 2). The nutrient subsidy of both the natural and restoration colonies does not appear to extend beyond 50 m from the colony (Fig. 7). In contrast, subsidies on Stephens Island remained statistically similar (except for soil nitrate) at all distances from the colony (Fig. 7, Table 2).

Spatial effects.—Wind-driven spatial subsidies do not seem to play a major role on the study islands, as

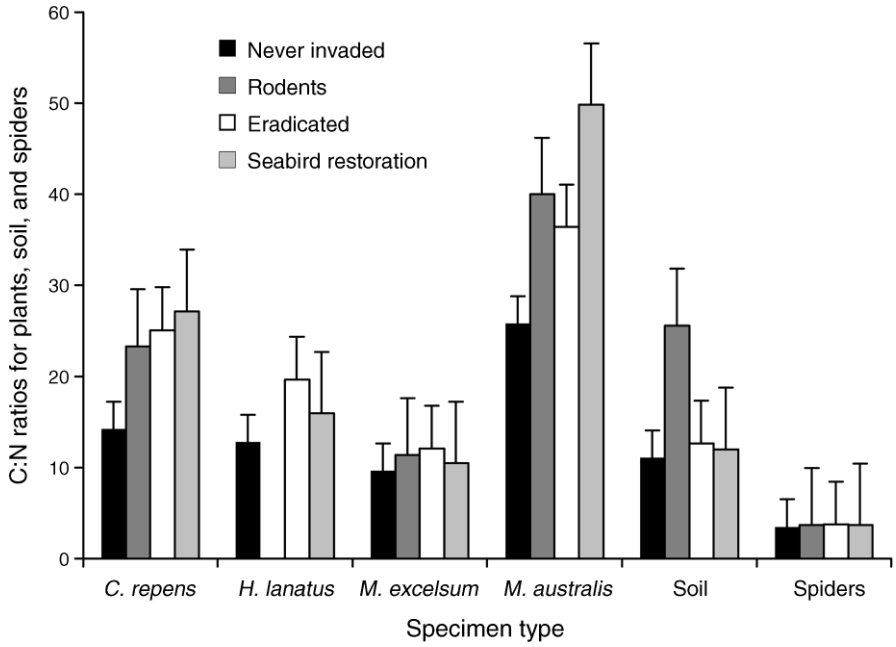

FIG. 4. C:N ratios for plants, soil, and spiders across island treatments. Plants are as in Fig. 3. Values are means + SE.

distance from shore was only significantly related to $\delta^{15}N$ in *C. repens* on seabird restoration islands, and $\delta^{15}N$ in *M. australis* on never-invaded islands ($P < 0.05$). Perimeter-to-area ratio ANCOVAS were significant for 4 out of 18 possible variables; $\delta^{15}N$ in *M. excelsum* and *M. australis*, soil nitrate, and arthropod abundance all had significant interactions with perimeter-to-area ratio ($P < 0.001$, 0.03, 0.01, and 0.03 in these four variables, respectively). The isotope mixing model showed that algae-derived prey do not contribute to spider diet on never-invaded islands 0% ± 1%. Algae-derived prey contribute 11% ± 4%, 14% ± 5%, and 13% ± 4% of spider diets on invaded, eradicated, and seabird restoration islands, respectively. These analyses suggest that beach wrack plays a small role in these food webs, because the steep cliffs present on most study islands (Appendix A) provide a semi-impermeable layer for vector-driven nutrient subsidies other than those delivered by seabirds.

DISCUSSION

Ecological theory offers two views on the prognosis of ecosystem recovery following removal of major disturbance agents. One view holds that ecosystems will recover gradually from disturbances at a rate proportional to the degree to which the disturbance is eradicated (Beisner et al. 2003, McLauchlan et al. 2007), a conventional view in restoration ecology (van

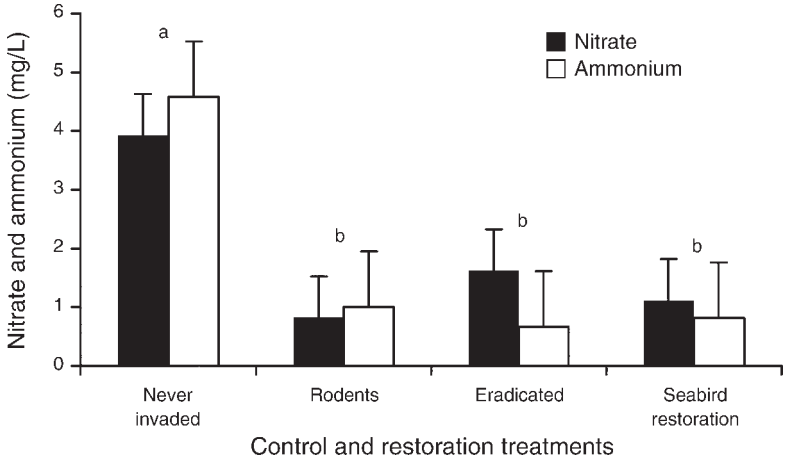

FIG. 5. Soil nitrate and ammonium concentrations across island treatments. Different lowercase letters above each pair of bars indicate significant differences at the $\alpha = 0.05$ level. Values are means + SE.

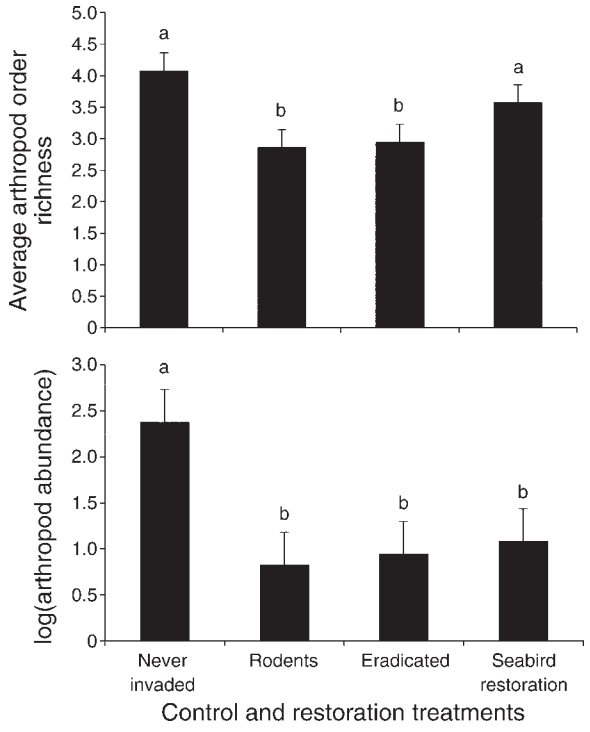

FIG. 6. Average arthropod order richness (number of orders of arthropods) and log abundance (log number of arthropods caught per trap night) across island treatments. For each graph, different lowercase letters above each bar indicate significant differences at the $\alpha = 0.05$ level. Values are means + SE.

Andel and Aronson 2006). The other view holds that ecosystems could get locked into alternative states, thereby precluding recovery following eradication of the disturbance agent without additional restoration efforts (Scheffer et al. 2001, Beisner et al. 2003). The aim of this study was to determine which view was appropriate for island recovery following invasive rodent eradication and thereby give a prognosis for the likelihood of recovery.

The fertilization experiment supports suggestions (Croll et al. 2005, Mulder et al. 2009, Towns et al. 2009) that seabird-driven ecosystems can fail to recover in a contemporary timescale following removal of invasive predators without managed seabird recolonization. At experimental sites, subsidies approaching levels that matched medium to high seabird density were needed to initiate a recovery response in productivity, arthropod abundance, and decomposition rates (Fig. 2). But once the ecosystem variables responded, recovery to levels matching uninvaded islands could be rapid.

The fertilizer experiment also helped to explain why arthropod abundance varied among different restoration treatments on islands. For example, never-invaded control islands (equivalent to medium-high to high fertilizer input) had the highest arthropod abundance (Fig. 6). All other islands had similarly low arthropod abundance, consistent with the low to medium treatment of the fertilizer experiment (Figs. 2 and 6). Together, the fertilization and natural experiment affirm that high seabird densities are required for recovery to preinvasion conditions (Figs. 2 and 6).

The natural experiment indicated that islands free of rodents for 8–13 years have yet to begin recovering their levels of ecosystem function in most variables (Figs. 3–6), even though this time frame is sufficient to observe ecosystem recovery (Jones and Schmitz 2009). Thus, rodent eradication alone is likely insufficient to restore seabird densities and ecosystem function. This corroborates the suggestion that these systems are locked into an alternative state from a lack of seabird recolonization of those islands.

Yet when seabird restoration is implemented, ecosystems recover slowly if at all (Figs. 3–7). This slow recovery can be a consequence of soil structure, and seabird life history and demography. Seabirds have difficulty digging burrows in soils compacted by farming and/or ungulates, thereby preventing burrowing seabirds from breeding in restoration sites (Harris 1974, Stokes and Boersma 1991). However, certain seabird species can overcome soil compaction and dig their own

TABLE 2. Post hoc Tukey test *P* values for ANOVAs between response variables inside and outside colonies and between restoration seabird colonies and natural seabird colonies.

Island	Response variable	Natural colony vs. restoration colony	Natural colony vs. outside colony	Restoration colony vs. outside colony
Mana	soil $\delta^{15}N$	0.006	<0.0001	0.058 (NS)
	soil ammonium	0.032	<0.0001	0.024
	soil nitrate	0.009	<0.0001	0.220 (NS)
	soil C:N ratio	0.042	<0.01	0.102 (NS)
Maud	soil $\delta^{15}N$	NA	NA	0.003
	soil ammonium	NA	NA	0.139 (NS)
	soil nitrate	NA	NA	0.236 (NS)
	soil C:N ratio	NA	NA	0.005
Stephens	soil $\delta^{15}N$	NA	0.190 (NS)	NA
	soil ammonium	NA	0.469 (NS)	NA
	soil nitrate	NA	0.048	NA
	soil C:N ratio	NA	0.051 (NS)	NA

Notes: NS means nonsignificant; NA means not applicable.

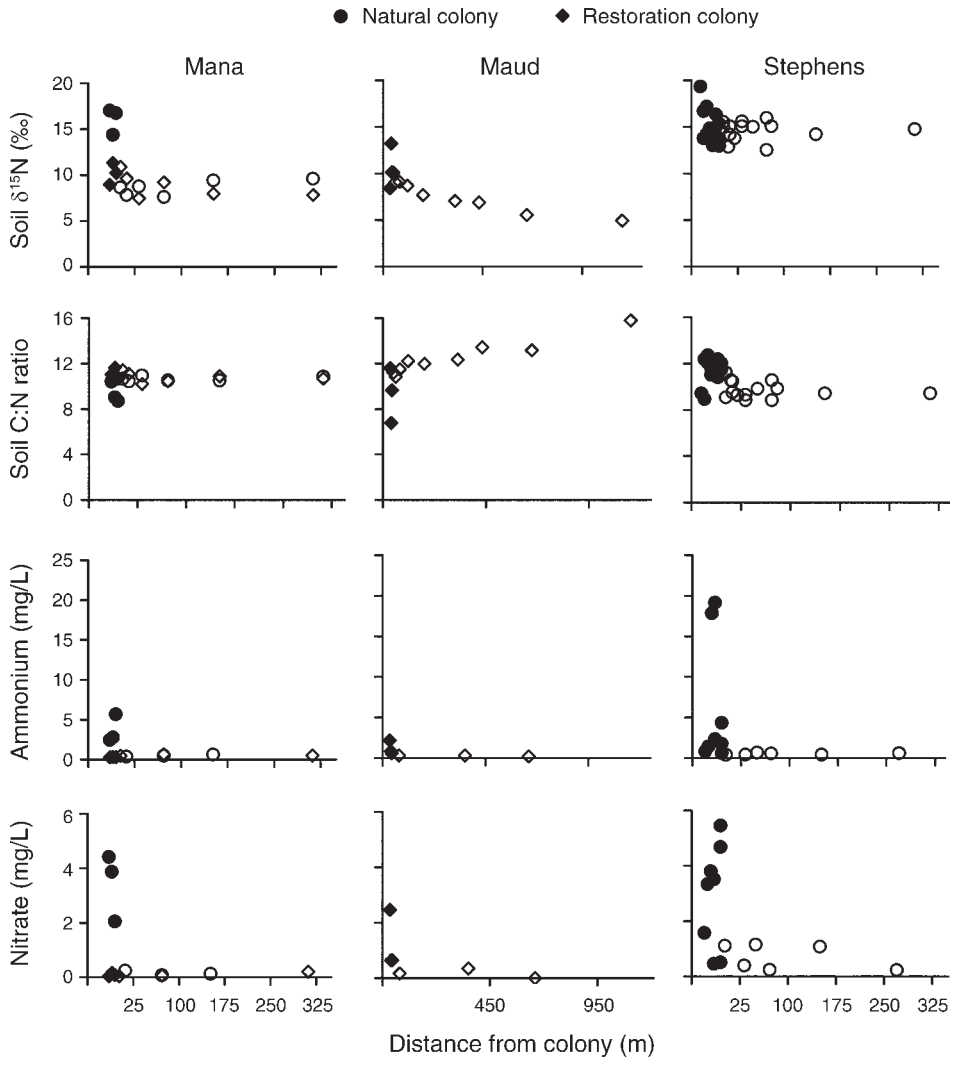

FIG. 7. Soil parameter levels observed on seabird restoration islands (Mana and Maud) and on never-invaded Stephens Island. Open symbols are values measured outside seabird colonies; solid symbols are values inside the colonies.

burrows. On Mana, diving petrels returned to dig their own burrows rather than use the artificial nest boxes to which they were transferred initially as chicks (Miskelly et al. 2009).

Even so, chick translocations only began in 1991 on Maud and in 1997 on Mana. The intervening 10–16 years is relatively short for colony reestablishment relative to seabird life history timescales. Fluttering Shearwaters (translocated to Maud from 1991–1996) take on average seven years to become reproductively mature, and diving petrels (translocated to Mana starting from 1997–1999) take 2–3 years to become reproductively mature (Brooke 2004, Bell et al. 2005). Both species' low reproductive rates (one egg laid per pair [Brooke 2004, Bell 2005]), and the low reproductive rates and relatively strong Allee effects of many seabirds in general (Jouventin et al. 2003), suggest that seabird restoration programs may take decades to produce high enough seabird densities to provide levels of guano input needed for full recovery of ecosystem function. Indeed, the average seabird density in the Stephens Island plots (6.33 burrows/m^2) far exceeded both seabird densities in restored colonies (0.67 and 2.33 burrows/m^2 for Mana and Maud, respectively) and the natural colony density on Mana (3 burrows/m^2). The mechanism for uniform levels of seabird influence on Stephens thus appears to be its relatively high density of seabirds; there may be a seabird density threshold beyond which local seabird colony dynamics play out at the whole-island scale, suggesting again that recovery requires restoration of high seabird densities.

Unassisted seabird recovery or the absence thereof appears dependent on a variety of factors including proximity to a source population and seabird life history characteristics (Jones et al., *in press*). There are a variety of examples of natural seabird recolonization following

PLATE 1. Fairy Prions (*Pachyptila turtur*) landing near their burrows on Stephens Island, New Zealand. Photo credit: H. P. Jones.

predator eradication for seabirds without natal philopatry, with relatively high reproductive rates, and with short prebreeding periods. For example, the eradication of cats (*Felis catus*) from Ascension Island, completed in 2004, resulted in the breeding Sooty Tern (*Onychoprion fuscatus*) population increasing by over 50 000, with adult mortality from predation dropping to virtually zero (Hughes et al. 2008). However, natural recovery is much less often documented for hole-nesting procellariid species, which are some of the most common seabird species in New Zealand and the most common breeders on the study islands. Whether or not the eradicated study islands will exceed the seabird density threshold and fully recover their function naturally over time remains unclear. One way to assess whether recovery will occur naturally is to examine a chronosequence of islands that have undergone eradication while controlling for external factors.

Applied implications

Seabird recolonization following rodent eradication happens naturally in a few cases (e.g., terns on Ascension Island), and is often dependent on the proximity of source populations and the biology of the particular seabird species in question. Hole-nesting procellarid seabirds are probably the least likely to recolonize naturally because of their strong philopatry, Allee effects, and low reproductive rates. Given their strong representation across all seabird species and especially across species threatened with extinction, their lack of ability to naturally recover following predator eradication is concerning. Even if there is natural recolonization, it may not be at a sufficient density to provide timely restoration of the ecosystem, as is the case for Nukuwaiata and Mana Islands. Indeed, my data indicate that seabirds need to reach densities of 5–10 burrows/m^2 to restore nutrient dynamics to a preinvasion state (Figs. 2–6), although such densities can suppress some invertebrate and plant species (e.g., Mulder and Keall 2001, Towns et al. 2009). Thus, simple removal of invasive predators will not be enough to meet the mandate of ecosystem restoration on islands that depend on philopatric, slow-breeding seabirds for ecosystem function (Mulder et al. 2009, Towns et al. 2009).

Where seabird colonies are extirpated or extremely reduced, natural recolonization may require centuries, a time frame that is at least an order of magnitude higher than timelines usually specified in restoration plans. Thus, eradication strategies may need to be supplemented with high-density seabird restoration projects in cases where seabird recovery is protracted or nonexistent. Such projects can involve translocating high numbers of chicks or attracting high numbers of breeding adults to create dense seabird colonies. Artificially increasing colony size and breeding outputs of a seabird colony can help overcome seabird Allee effects and low reproductive rates (e.g., Miskelly et al. 2009). Demographic analyses are also required to identify quantitatively the densities and time frames needed to

reestablish viable colonies and nutrient inputs sufficient to restore ecosystem functions.

Acknowledgments

Os Schmitz, Pete Raymond, David Post, David Towns, Bernie Tershy, and an anonymous reviewer provided helpful comments on the manuscript. For access to study islands, I thank Ngāti Koata, Ngāti Kuia, and Ngāti Toa. Transportation and logistical thanks go to Clare Allen, Mike Aviss, Greg Bettjeman, Maurice Brown, Jon DeVries, Pete Gaze, Colin Miskelly, Nicky Nelson, Grant Timlin, Richard Walle, and Steve Ward. Thanks to Bruce Benseman, Ilse Boerman, Ilse Corkery, Amelia Geary, Monica Gruber, Fiona McDonald, Alice McNatty, and Lennart Suselbeek for help with fieldwork. Mike Fitzgerald identified the spiders. Lucy Hurrey identified the algae. Dan Keltner and Victoria University Wellington's herpetology group provided moral and logistical support. This study was supported by the National Geographic Society's Committee for Research Exploration, the Yale Institute of Biospheric Studies, Yale School of Forestry and Environmental Studies, Yale Earth Systems Center for Stable Isotopic Studies, the American Philosophical Society's Lewis and Clark Exploration Fund, the Sophie Danforth Conservation Biology Fund, and the Leopold Schepp Foundation. Gerry Olack and Jonas Karosas provided laboratory expertise, and Berkley Adrio, Dan Keltner, and Coulter and Zach Schmitz helped with lab work. Data are original and may be used elsewhere in the future.

Literature Cited

Amundson, R., A. T. Austin, E. A. G. Schuur, K. Yoo, V. Matzek, C. Kendall, A. Uebersax, D. Brenner, and W. T. Baisden. 2003. Global patterns of isotopic composition of soil and plant nitrogen. Global Biogeochemical Cycles 17: 1031.

Anderson, W. B., and G. A. Polis. 1999. Nutrient fluxes from water to land: Seabirds affect plant nutrient status on Gulf of California islands. Oecologia (Berlin) 118:324–332.

Atkinson, I. A. E. 1985. The spread of commensal species of Rattus to oceanic islands and their effect on island avifaunas. Pages 35–81 *in* P. J. Moors, editor. Conservation of island birds. International Council for Bird Preservation, Cambridge, UK.

Atkinson, I. A. E. 1988. Presidential address: opportunities for ecological restoration. New Zealand Journal of Ecology 11: 1–12.

Atkinson, I. 1989. Introduced animals and extinctions. Pages 54–75 *in* D. Western and M. C. Pearl, editors. Conservation for the twenty-first century. Oxford University Press, New York, New York, USA.

Beisner, B. E., D. T. Haydon, and K. Cuddington. 2003. Alternative stable states in ecology. Frontiers in Ecology and the Environment 1:376–382.

Bell, M., B. D. Bell, and E. A. Bell. 2005. Translocation of fluttering shearwater (*Puffinus gavia*) chicks to create a new colony. Notornis 52:11–15.

Brooke, M. 2004. Albatrosses and petrels across the world. Oxford University Press, New York, New York, USA.

Carpenter, S. R., and M. G. Turner. 2000. Hares and tortoises: interactions of fast and slow variables in ecosystems. Ecosystems 3:495–497.

Croll, D. A., J. L. Maron, J. A. Estes, E. M. Danner, and G. V. Byrd. 2005. Introduced predators transform subarctic islands from grassland to tundra. Science 307:1959–1961.

Fukami, T., D. A. Wardle, P. J. Bellingham, C. P. H. Mulder, D. Towns, G. W. Yeates, K. I. Bonner, M. S. Durrett, M. N. Grant-Hoffman, and W. M. Williamson. 2006. Above- and below-ground impacts of introduced predators in seabird-dominated island ecosystems. Ecology Letters 9:1299–1307.

Furness, R. 1991. The occurrence of burrow-nesting among birds and its influence on soil fertility and stability. Pages 53–65 *in* P. Meadows and A. Meadows, editors. The environmental impact of burrowing animals and animal burrows. Oxford University Press, Oxford, UK.

Gaze, P. 2000. The response of a colony of sooty shearwater (*Puffinus griseus*) and flesh-footed shearwater (*P. carneipus*) to the cessation of harvesting and the eradication of Norway rats (*Rattus norvegicus*). New Zealand Journal of Ecology 27: 375–379.

Harris, S. W. 1974. Status, chronology, and ecology of nesting storm petrels in northwestern California. Condor 76:249–261.

Howald, G., C. J. Donlan, B. R. Tershy, D. A. Croll, J. Russell, A. Saunders, and M. Clout. 2007. Invasive rodent eradications on islands. Conservation Biology 21:1258–1268.

Hughes, B. J., G. R. Martin, and S. J. Reynolds. 2008. Cats and seabirds: effects of feral domestic cat *Felis silvestris catus* eradication on the population of sooty terns *Onychoprion fuscata* on Ascension Island, South Atlantic. Ibis 150:122–131.

Hutchinson, G. 1950. The biogeochemistry of vetebrate excretion. American Museum of Natual History, New York, New York, USA.

IUCN (International Union for the Conservation of Nature). 2009. 2009 IUCN red list of threatened species. ⟨www.iucnredlist.org⟩

Jones, H. P., and O. J. Schmitz. 2009. Rapid recovery of damaged ecosystems. PLoS ONE 4:e5653.

Jones, H. P., B. R. Tershy, E. S. Zavaleta, D. A. Croll, B. S. Keitt, M. E. Finkelstein, and G. R. Howald. 2008. Severity of the effects of invasive rats on seabirds: a global review. Conservation Biology 22:16–26.

Jones, H. P., D. R. Towns, T. Bodey, C. M. Miskelly, J. Ellis, M. J. Rauzon, S. W. Kress, and M. McKown. *In press*. Chapter 11: Recovery and restoration on seabird islands. *In* C. P. H. Mulder, D. R. Towns, and W. B. Anderson, editors. Seabird islands: ecology, invasion, and restoration. Oxford University Press, Oxford, UK.

Jouventin, P., J. Bried, and T. Micol. 2003. Insular bird populations can be saved from rats: a long-term experimental study of white-chinned petrels *Procellaria aequinoctialis* on Ile de la Possession (Crozet archipelago). Polar Biology 26: 371–378.

Kier, G., H. Kreft, T. M. Lee, W. Jetz, P. L. Ibisch, C. Nowicki, J. Mutke, and W. Barthlott. 2009. A global assessment of endemism and species richness across island and mainland regions. Proceedings of the National Academy of Sciences USA 106:9322–9327.

Kline, T. C., Jr., J. J. Goering, O. A. Mathisen, P. H. Poe, and P. L. Parker. 1990. Recycling of elements transported upstream by runs of Pacific salmon. I: Delta 15N and delta 13C evidence in Sashin Creek, southeastern Alaska. Canadian Journal of Fisheries and Aquatic Sciences 47:136–144.

Kress, S. W. 1998. Applying research for effective management: case studies in seabird restoration. Pages 141–154 *in* J. M. Marzluff and R. Sallabanks, editors. Avian conservation: research and management. Island Press, Washington, D.C., USA.

Markwell, T. J., and C. H. Daugherty. 2002. Invertebrate and lizard abundance is greater on seabird-inhabited islands than on seabird-free islands in the Marlborough Sounds, New Zealand. Ecoscience 9:293–299.

Markwell, T. J., and C. H. Daugherty. 2003. Variability in delta 15N, delta 13C and Kjeldahl nitrogen of soils from islands with and without seabirds in the Marlborough Sounds, New Zealand. New Zealand Journal of Ecology 27:25–30.

Mathisen, O. A., P. L. Parker, J. J. Goering, T. C. Kline, P. H. Poe, and R. S. Scalan. 1988. Recycling of marine elements transported into freshwater systems by anadromous salmon.

Vereinigung für Theoretische und Angewandte Limnologie, Verhandlungen 23:2249–2258.
McLauchlan, K. K., J. M. Craine, W. W. Oswald, P. R. Leavitt, and G. E. Likens. 2007. Changes in nitrogen cycling during the past century in a northern hardwood forest. Proceedings of the National Academy of Sciences USA 104: 7466–7470.
Miskelly, C. M., G. A. Taylor, H. Gummer, and R. Williams. 2009. Translocations of eight species of burrow-nesting seabirds (genera *Pterodroma*, *Pelecanoides*, *Pachyptila* and *Puffinus*): Family Procellariidae. Biological Conservation 142:1965–1980.
Mizutani, H., and E. Wada. 1988. Nitrogen and carbon isotope ratios in seabird rookeries and their ecological implications. Ecology 69:340–349.
Mulder, C. P. H., M. N. Grant-Hoffman, D. R. Towns, P. J. Bellingham, D. A. Wardle, M. S. Durrett, T. Fukami, and K. I. Bonner. 2009. Direct and indirect effects of rats: Does rat eradication restore ecosystem functioning of New Zealand seabird islands? Biological Invasions 11:1671–1688.
Mulder, C., and S. Keall. 2001. Burrowing seabirds and reptiles: impacts on seeds, seedlings and soils in an island forest in New Zealand. Oecologia 127:350–360.
Paetzold, A., M. Lee, and D. Post. 2008. Marine resource flows to terrestrial arthropod predators on a temperate island: the role of subsidies between systems of similar productivity. Oecologia 157:653–659.
Phillips, D. L. 2001. Mixing models in analyses of diet using multiple stable isotopes: a critique. Oecologia (Berlin) 127: 166–170.
Polis, G. A., W. B. Anderson, and R. D. Holt. 1997. Toward an integration of landscape and food web ecology: the dynamics of spatially subsidized food webs. Annual Review of Ecology and Systematics 28:289–316.
Polis, G. A., and S. D. Hurd. 1996. Allochthonous input across habitats, subsidized consumers, and apparent trophic cascades: Examples from the ocean–land interface. Pages 275–285 *in* G. A. Polis and K. O. Winemiller, editors. Food webs: integration of patterns and dynamics. Chapman and Hall, New York, New York, USA.
Post, D. M. 2002. Using stable isotopes to estimate trophic position: models, methods, and assumptions. Ecology 83: 703–718.
Post, D. M., J. P. Taylor, J. F. Kitchell, M. H. Olson, D. E. Schindler, and B. R. Herwig. 1998. The role of migratory waterfowl as nutrient vectors in a managed wetland. Conservation Biology 12:910–920.
Sanchez-Pinero, F., and G. A. Polis. 2000. Bottom-up dynamics of allochthonous input: direct and indirect effects of seabirds on islands. Ecology 81:3117–3132.
Scheffer, M., S. Carpenter, J. A. Foley, C. Folke, and B. Walker. 2001. Catastrophic shifts in ecosystems. Nature (London) 413:591–596.
Schmidt, S., W. C. Dennison, G. J. Moss, and G. R. Stewart. 2004. Nitrogen ecophysiology of Heron Island, a subtropical coral cay of the Great Barrier Reef, Australia. Functional Plant Biology 31:517–528.
Simberloff, D. 1990. Reconstructing the ambigous: Can island ecosystems be restored? Pages 37–51 *in* D. R. Towns, C. H. Daugherty, and I. A. E. Atkinson, editors. Ecological restoration of New Zealand islands. Department of Conservation, Wellington, New Zealand.
Simberloff, D. 1995. Why do introduced species appear to devastate islands more than mainland areas? Pacific Science 49:87–97.
Stokes, D. L., and P. D. Boersma. 1991. Effects of substrate on the distribution of Magellanic Penguin (*Spheniscus magellanicus*) burrows. Auk 108:923–933.
Towns, D. R., D. A. Wardle, C. P. H. Mulder, G. W. Yeates, B. M. Fitzgerald, R. P. Parrish, P. J. Bellingham, and K. I. Bonner. 2009. Predation of seabirds by invasive rats: multiple indirect consequences for invertebrate communities. Oikos 118:420–430.
van Andel, J., and J. Aronson. 2006. Restoration ecology. Blackwell, Oxford, UK.
Wanless, R. M., A. Angel, R. J. Cuthbert, G. M. Hilton, and P. G. Ryan. 2007. Can predation by invasive mice drive seabird extinctions? Biology Letters 3:241.

APPENDIX A

Natural history details of study islands (*Ecological Archives* A020-041-A1).

APPENDIX B

Amounts of nitrogen and phosphorus applied to each seabird density treatment by each fertilizer component (*Ecological Archives* A020-041-A2).

APPENDIX C

Spider species used for stable isotope analysis (*Ecological Archives* A020-041-A3).