Seabird Sentinels: The Barometer for Island Conservation in a Changing World

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Tītī whakatai aro rua
E hoki ra koe
Ki O-te-Patatu.
Ki te pa whakatangi
Ki te koauau,
Ki tauwene ai
E raro i au-e!

Ko Ranginui kei runga
Ko Papatūānuku kei raro
Ka tangi te tītī
Ka tangi hoki ahau
Tihei Mauri Ora!

Ko te Tai-o-Rehuā te moana
Ko Te Waipounamu te waka
Ko Aoraki te māunga
Ko te Kawatiri te awa
Ko Steph Borrelle tōku ingoa

Tēnā koutou, Tēnā koutou, Tēnā koutou katoa.

O titi, bird of the sea,
Bird of the hilltop cave,
Come back to O-te-Patatu,
To the lofty dwelling
Where the sweet sounds are heard,
The sound of the faery flute,
The music of the mountains
That thrilled me through and through!

Ranginui (sky father) above
Papatūānuku (earth mother) below
The sooty shearwater sings
So too do I
Behold there is life!

My ocean is the Tasman Sea
My canoe is the South Island
My mountain is Aoraki
My river is the Buller river
My name is Steph Borrelle

Abstract

Seabirds are the most threatened group of marine animals, 53% of Procellariiformes (albatrosses, petrels, storm petrels, shearwaters, fulmars, and prions) are experiencing population declines; thus, their protection is a global conservation priority. On land, seabirds are vulnerable to invasive mammalian predators, due to physiological, behavioural and demographic traits, such as extended immaturity, low reproductive output and colonial nesting habits. At-sea, seabirds are impacted by human activities; suffering increasing levels of mortality from fisheries bycatch, pollution, and climate change. Land-based conservation actions, such as predator eradication have been the focus of conservation efforts. Currently, gaps remain in our understanding about the recovery of seabirds on islands following predator eradication. Moreover, little is known about the population level impacts of extrinsic stressors. In this thesis, I am to contribute to understanding if invasive predator control will deliver enduring benefits for seabirds and their island ecosystems. To do this, I investigate the factors that influence seabirds returning to islands after predator eradication, how island ecosystems are recovering, new ways of measuring the abundance and recovery of seabirds to islands, and how seabird recovery is affected by intensifying marine threats.

In **chapter 2**, I evaluate the recovery of seabird colonies (n=97) in the Hauraki Gulf, New Zealand; a seabird diversity hotspot (27 species) which has a long history of predator eradications. I conduct a comparative analysis of seabird assemblages on islands with three predator histories: never invaded, eradicated of predators, and with invasive mammalian predators present. I found islands cleared of predators show recovery of seabirds over time and had more unique seabird taxa than islands that never had predators. However, recovery appears to be influenced by a suite of site- and species-specific factors. While time following the eradication is an important factor, space, demographic traits and population dynamics may have a stronger influence on the passive recovery and recolonisation of seabirds to islands. As such, consideration of additional conservation management actions may be necessary to facilitate seabird island recovery.

Seabirds influence island flora and fauna communities through soil disturbance from burrowing, and from subsidies of marine derived nutrients via guano, failed eggs, prey remains, and corpse deposition to their terrestrial breeding grounds. In **chapter 3**, I quantify seabird nutrient distribution on islands where seabirds are recovering. I investigate the ecological factors that may influence the accumulation and distribution of seabird nutrient enrichment to plants using a cross island comparison, on islands with three predator histories: never invaded by non-native predators, cleared of predators (approximately 30 years ago), and newly eradicated (<2 years). I found that there is a strong relationship of soil and leaf variables

with seabird burrow density, but there is variability in the ecological influences on seabird nutrient distribution and accumulation in vegetation. While seabird nutrient influences can be detected rapidly in some foodweb components of island ecosystems, the overall enrichment of the ecosystem, which is a key driver of ecosystem function and composition, may take longer to recover.

While seabirds are a global conservation priority, only a fraction of seabird species or their island habitats are consistently monitored, and in many instances, the monitoring is spasmodic, or insufficient to detect informative changes to populations that are useful for adaptive management strategies. In **chapter 4**, I capitalise on the established relationship between soil-foliar nutrients and spectral reflectance to investigate if seabird nutrient enrichment can be detected in the spectral reflectance of island plant species with a controlled experiment and field testing. I found that nutrient enrichment from seabirds can be detected in the spectral reflectance of pōhutukawa, a common island canopy species, in experimental conditions; however, in field testing the relationship is less apparent. While more work is needed to refine methods, our results suggest that there is potential to use spectral reflectance as a proxy measure for seabird abundance.

The large spatial distribution of seabirds at-sea means they can be exposed to multiple anthropogenic stressors, such as fisheries bycatch, pollution, and climate change, which can be cumulative or interactive in nature. Quantifying the impacts of individual or interactive marine stressors on a seabird species is challenging because of the ambiguity of detecting at-sea mortality, and is confounded by demographic factors (*e.g.,* reproductive factors; age, success, frequency), ecological noise, and how sub-lethal threats potentially manifest at the population level. In **chapter 5** of this Thesis, I explore how these threats may affect the population recovery of seabirds after predator eradication using a theoretical modelling approach. Using a model specifically developed for data-limited species, I calculated the intrinsic population growth rate, and the limit of annual mortality for each population for 81 Procellariiformes. I found the mortality limits were commensurate with IUCN Red List categories, and that body size and spatial distribution are good predictors of the risk of population collapse from marine threats. Furthermore, I found a high phylogenetic signal of the sensitivity of species analysed to demographic impacts by at-sea threats, implying that the model may also help inform other closely related species that have not yet been evaluated.

“I have learned that I still
have a lot to learn”

– Maya Angelou

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Attestation of authorship

“I hereby declare that this submission is my own work and that, to the best of my knowledge and belief, it contains no material previously published or written by another person (except where explicitly defined in the acknowledgements), nor material which to a substantial extent has been submitted for the award of any other degree or diploma of a university or other institution of higher learning.”

Signed:

Date: 14th December 2017

Co-author contributions

The co-authored literature reviews in this thesis have been broken down into five task components, each of which have been given a weighting (% time) to produce the completed output:

Concept & structure = 5%
Article retrieval = 10%
Article assessments = 20%
Writing = 60%
Reviewing & editing = 5%

Chapter 2: *Influences on the recovery of seabirds to islands following predator eradication, with a focus on Procellariiformes* (Borrelle *et al.* 2016)

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	Reviewing & Editing	1%		
C. Gaskin	Reviewing & editing	1%	1%	
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Chapter 3: *Seabird Island Nitroscapes (Borrelle et al. in preparation for the New Zealand Journal of Ecology)*

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	Article assessment	8%		
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Research outputs

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Provencher J.F., **Borrelle S.B.,** Sherley R.B., Avery-Gomm S., Hodum P., Bond A., Major H.L., McCoy K.D., Crawford R., Merkel F., Votier S., Reynolds M., Hatfield J., Spatz D., Mallory M.L. 2018. Seabirds. In *World Seas, Volume III: Ecological Issues and Environmental Impacts*. CRC Sheppard (ed.). Elsevier, Inc.; Cambridge, MA, USA; pp – in press.

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Conference presentations

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Chapter 1| Scope

General introduction and Thesis framework

1.1 Seabirds

A ‘seabird’ is defined as a bird that spends most of its life at sea or makes a living from the ocean (Schreiber & Burger 2002). Species are from the orders Spenisciformes (penguins), Pelecanifromes (pelicans, boobies, cormorants, frigate birds, tropic birds, anhingas), a few in the order Charadriiformes (gulls, skuas, skimmers, terns, auks, and shorebirds), and the truly pelagic species are those in the order Procellariiformes; the albatrosses, petrels, shearwaters, fulmars, and prions. In this thesis, I focus on species in the order Procellariiformes for three main reasons; 1) they are among the most highly threatened group of marine animals (IUCN 2017), thus are a global conservation priority; 2) they are the predominant colonial nesting species on the islands in New Zealand – a seabird diversity hotspot, where my study sites are located for chapters 2, 3 and 4; and 3) are the most severely affected by the marine threats beyond exclusive economic zones (EEZ), including fisheries bycatch, plastic pollution, and climate change, which I address in chapter 5 of this thesis.

Figure 1.1 The New Zealand storm petrel *Fregetta maoriana* in the Hauraki Gulf, Aotearoa, 2017. Photo © S. Borrelle.

Procellariiformes or tube-nosed seabirds, hereafter referred to as 'seabirds', are represented by 139 species, and include the albatrosses (Diomedeidae), petrels, shearwaters, fulmars and prions (Procellariidae), and storm petrels (Hydrobatidae; Oceanitidae; *e.g.,* the New Zealand Storm-petrel *Fregetta maoriana* (Schreiber & Burger 2002; Figure 1.1). Seabirds are *K*-selected species by virtue of their typically long life spans (20-60 years) relative to size, deferred maturity (average of 5 years), low fecundity, high adult survival rates, extended periods of parental care before fledging (40-280 days), and intermittent breeding habits (Schreiber & Burger 2002). Seabirds are present in all of the oceans and seas of the world (Schreiber & Burger 2002; Figure 1.2).

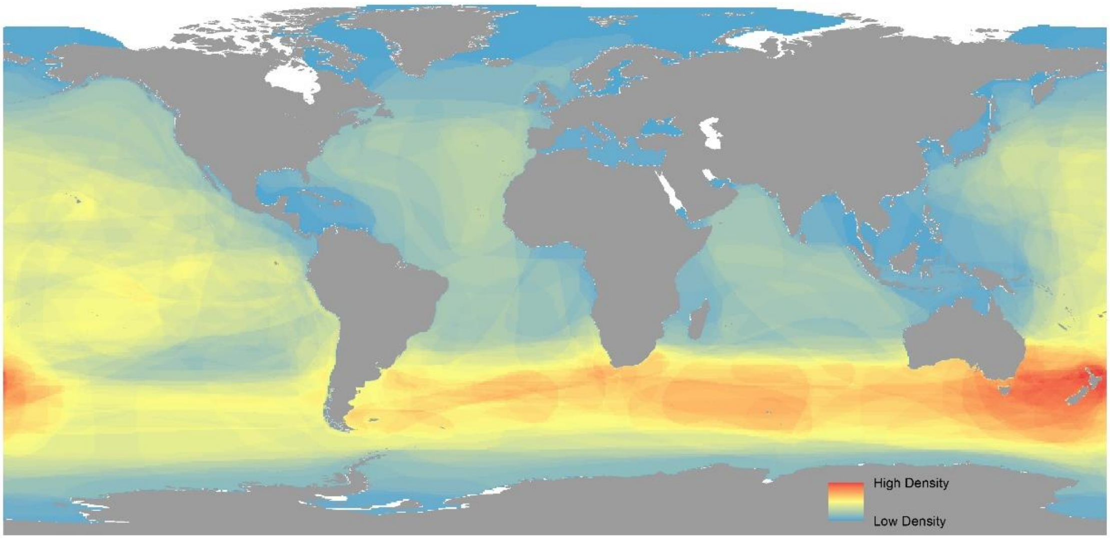

Figure 1.2 Global at-sea distributions of 139 Procellariiforme seabirds. The highest density is in Aotearoa New Zealand with 53 species breeding in the region.

A suite of complex and dynamic biophysical processes influence distribution of seabirds. These are governed by a network of interacting processes operating at mega-macro scales: 1,000s of kilometres (km); *e.g*., upwelling events influencing prey availability, to meso-fine scales: 10s to 100s of km, *e.g.,* diurnal vertical prey movements (Hunt Jr & Schneider 1987). The distance of foraging trips and migration routes between breeding sites varies among species, driven primarily by resource abundance and seasonal climatic fluctuations (Hunt Jr & Schneider 1987; Schreiber & Burger 2002). The distance individual seabirds travel can be astounding. For example, in a sabbatical year, wandering albatrosses *Diomedea exulans* can cover 120,000 km, equivalent to circumnavigating Antarctica two to three times (Weimerskirch et al. 2015). However, during the breeding season seabirds take multi-directional or shorter dispersal routes, such as tākoketai *Procellaria parkinsonii*, which averages 100 -1,200 km per day on foraging trips to the shelf break off northern New Zealand (Freeman et al. 2010). Seabirds are truly marine species, spending most of their lives at-sea, only returning to land to breed and provision chicks (Schreiber & Burger 2002).

Colonial breeding habits are observed in 98% of seabird species, where colony morphology ranges from loose aggregations to dense boisterous colonies (Smith, Mulder, & Ellis 2011). Colony density varies greatly depending on species, and stochastic exogenous forces, such as areas of marine productivity (Furness & Birkhead 1984), fishery pressures, or the presence of invasive predators (Smith et al. 2011). Despite bio-geophysical heterogeneity of islands systems, there is a clear distinction between islands inhabited by seabirds and those without them, in terms of flora and fauna species assemblages, as well as productivity (Smith et al. 2011). So much so, that the term 'seabird island' is often used to describe island ecosystems which are influenced by the marine derived nutrient enrichment from nesting seabirds (Mulder et al. 2011; Smith et al. 2011).

The exchange of resources from a more productive ecosystem to a less productive one is a widespread ecological phenomenon (Ellis 2005). The organisms involved in these exchanges are called allogenic ecosystem engineers, and act as vectors for the movement of nutrients and biomass and modulate resource availability to biotic and abiotic components of the ecosystem at the terminal end (C.P. Jones, Lawton & Shachak 1994; Ellis, Fariña & Witman 2006). Seabirds are allogenic ecosystem engineers of subsidies of marine derived nutrients like guano, failed eggs, prey remains, and corpse deposition to their terrestrial breeding grounds (Mulder et al., 2011; Smith et al., 2011). Seabird guano can enrich soil nitrogen by up to 100 times and phosphorus up to 400 times, compared to island soils without seabirds (Smith et al., 2011). This enrichment can exert strong influences on local foodwebs, contributing to abundance and diversity of island biota (Ellis et al. 2011; Kolb, Young & Anderson 2011).

In seabird driven systems, top level consumers (*e.g.*, spiders, lizards) feed on lower level foodweb members (*e.g.,* flies, aphids), which browse on plants and organic matter enriched by seabird guano (Jones 2010; Kolb, Young & Anderson 2011). Dense seabird colonies influence the composition and abundance of invertebrate communities (Sanchez-Pinero & Polis 2000; Thoresen et al. 2017), and microbial soil communities, most of which are more diverse and abundant than on islands without seabirds (Wright et al. 2010; Thoresen et al. 2017).

The physical impact of seabirds can be predicted by the type of nesting and density of individuals (Smith et al. 2011). There are four main nesting types; cavity, crevice, surface, and burrowing. Cavity and crevice nesting have the least impact on the chemical and physical characteristics of islands, although trampling and litter collection can influence the vegetation structure (Smith et al. 2011). Depending on colony density, surface nesters can exert moderate to high physical and chemical impact through trampling vegetation, litter collection and guano deposition (Smith et al. 2011). New Zealand's seabird avifauna is dominated by colonial burrow-nesting seabirds, such as *Pterodroma* spp. (Taylor 2000), which exert the strongest influence on island ecosystems through nutrient deposition and physical modification from burrowing activity (Smith et al. 2011). In addition, the physical disturbance caused by birds moving through vegetation can increase litter fall and decomposition rates, further influencing soil chemistry and nutrient cycling (Mulder et al. 2011; Smith et al. 2011). The combination of nutrient inputs and physical disturbance affects plant growth rates, either by enhancing or inhibiting biomass production, and influencing vegetation community composition and structure (Bancroft, Garkaklis & Roberts 2005; Ellis 2005; Mulder et al. 2011).

Seasonal breeding habits of many species, particularly temperate and sub-polar ranging species, means island nutrient inputs and physical disturbance regimes can be unevenly distributed over time (Smith et al. 2011). High concentrations of nutrients are imported during breeding periods and the length of time nutrient deposition and disturbances occur is dependent on the species present; ranging from a few weeks to as long as ten months (Schreiber & Burger 2002; Smith et al. 2011). Further, climatic cycles, notably rainfall events, appear to have the strongest influence on the temporal variation in mineralized soil nitrogen (Bancroft, Garkaklis & Roberts 2005). These intense episodic nutrient inputs and accompanying physical damage mean that ornithocoprophilous plant species that have adapted mechanisms to survive extreme nutrients, disturbances, or those opportunistic enough to regenerate are present (Ellis et al. 2011; Figure 1.3).

Figure 1.3 Understory of a 'seabird island', characterised by very little litter and few seedlings present, with trees having been toppled and generally dominated by species with vegetative growth strategies. Photo © S. Borrelle.

The ecosystem engineering effects of colonial nesting seabirds render seabird islands unique repositories of flora and fauna. Thus, seabird islands are of significant conservation value. In fact, while islands account for only 5% of the earth's total land surface, they encompass 20% of global biodiversity and a higher number of endemic species than any other ecosystem (Whittaker & Fernández-Palacios 2007; Kier et al. 2009). However, insular environments are particularly vulnerable to the effects of habitat modification and introduced mammalian predator species (Drake et al. 2002; Towns 2002), which can disrupt a variety of ecosystem processes both directly and indirectly (Fukami et al. 2006; Towns et al. 2009). For island biota, the rules of existence are altered through direct predation, resource competition, changes to primary productivity, nutrient cycling, decomposition rates, and disturbance regimes induced by introduced species (Fukami et al. 2006; Vitousek et al. 1997). Veritably, the impacts of introduced predators are illustrated in the list of recent biological extinctions; 70% of mammals; 90% of reptiles; and 95% of bird species have been island endemics (Doherty et al. 2016; Keitt et al. 2011).

1.2 Seabird conservation

Introduced predators remain one of the major threats to the world's seabird populations, which are experiencing disproportionate population declines compared to their terrestrial cousins (Lascelles et al. 2014; Paleczny et al. 2015). Seabirds account for one quarter of marine extinctions and are the most highly threatened group of marine animals; 29% of seabirds (101 species) are listed by the International Union for Conservation of Nature (IUCN) as being at some risk of extinction (Spatz et al. 2014; IUCN 2017). Of the world's monitored seabird populations, nearly 70% exhibit declining population trends (Paleczny et al. 2015). Procellariiformes are disproportionality represented, with 79.6% of species experiencing rapid declines due to reduced fledgling survival rates, and increased adult mortality (Paleczny et al. 2015). Seabirds are slow-breeding, long-lived species and even a slight declining trend can have alarming consequences, particularly for those species with small populations (Birdlife International 2008). For example, long-term studies from South Georgia Island, in the Southern Ocean revealed the Wandering Albatross *Diomedea exulans* has experienced a 30% population decline over the last four decades (Poncet et al. 2006). Similarly, modelled over 70 years (*ca.* three generations), the Tristan Albatross *Diomedea dabbenena* has projected future population declines of over 80%, primarily due to incidental mortality in commercial long line fishing operations, further compounded by lowered fledgling success because of predation by cats and mice (Polidoro et al. 2009).

Seabird conservation efforts on islands have focussed on the removal of predator species with the aim of minimising further damage and allowing for a degree of recovery (Towns & Broome 2003; Towns et al. 2009; Towns, West & Broome 2013; Jones et al. 2011, 2016), but islands also provide refugia for species that have been affected by habitat loss on mainland sites (Diamond 1990; Bellingham et al. 2010). The rapid increase in successful pest eradications around the world over the last three decades has culminated in >1,182 eradication projects, which have successfully cleared 25 invasive vertebrate species from >1000 islands (Lavers, Wilcox & Donlan 2010; Island Conservation 2017). These impressive conservation efforts have resulted in significant gains for seabirds and island biota globally (Jones et al. 2016).

Of New Zealand's 468 islands that were invaded by invasive mammalian predators (> 1 ha), 31% (143) have had mammals eradicated successfully (invasive mammals died out naturally on an additional six islands), equating to 61,080 ha (Parkes, Byrom & Edge 2017). While the objectives for predator removals often tacitly assume that simply removing the unwanted agent of change will allow for seabird and ecosystem recovery, this is rarely the outcome (Jones et al. 2011).

Introduced predators can affect the community structure of vegetation on seabird islands, altering composition via seed predation, reducing seed dispersers and influencing seedling recruitment (Mulder et al. 2009). When predators are removed, seedling recruitment can be dominated by invasive ruderal species, or those less susceptible to seed predation, thereby potentially altering the successional trajectory of a cleared island (Mulder et al. 2009; Ellis et al. 2011). If seabirds do not return then large inputs of marine derived nutrients no longer enter the system, further altering island biogeochemical processes and biological community assemblages (Jones et al. 2008; Towns et al. 2009; Thoresen et al. 2017). Therefore, the re-instatement of ecosystem function following the removal of introduced mammals requires the return of extirpated seabird species or population growth of remnant seabird populations (Croll et al. 2005).

Most species of seabirds are assumed to be strongly philopatric, returning to their natal site to breed (Schreiber & Burger 2002). This characteristic can influence the establishment of new breeding colonies; however, colonies are not completely closed and dispersal does occur among metapopulations (Brooke et al. 2017; Igual et al. 2007). The passive recovery of seabird populations has been observed on islands around the world (Buxton et al. 2014). Seabird recovery after predator eradication is not straightforward. Recovery of remnant colonies and the recolonization of extirpated species is complicated by species specific life-history traits, population dynamics, intrinsic site specific growth of individual metapopulations, and numerous extrinsic temporal and spatial influences (Buckelew et al. 2011; Rauzon et al. 2011).

In the second chapter of this thesis, I examine the influences on recovery and recolonization of seabirds to islands in the Hauraki Gulf, Aotearoa New Zealand following invasive predator eradication[1]. Capitalizing on the long history of predator eradications in the region, I explore the ecological and demographic factors

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[1] This chapter is published as: Borrelle, S.B., Boersch-Supan, P.H., Gaskin, C.P. & Towns, D.R. (2016) Influences on recovery of seabirds on islands where invasive predators have been eradicated, with a focus on Procellariiformes. *Oryx*, 1–13.

influencing the return of extirpated seabirds and recovery of remnant colonies using a cross-island comparative analysis, based in island biogeography theory. The equilibrium theory of island biogeography was developed on the premise that species richness maintains a dynamic equilibrium over time, strongly controlled by area (MacArthur & Wilson 1967; Simberloff 1974). I compare the seabird species richness of islands that have never been invaded by invasive predators (n=30) to islands that have been cleared of invasive predators (n=31), and on islands that still have predators present (n=37; Figure 1.4). The aim of this chapter is to help understand the complex drivers of seabird recovery to islands following predator eradication.

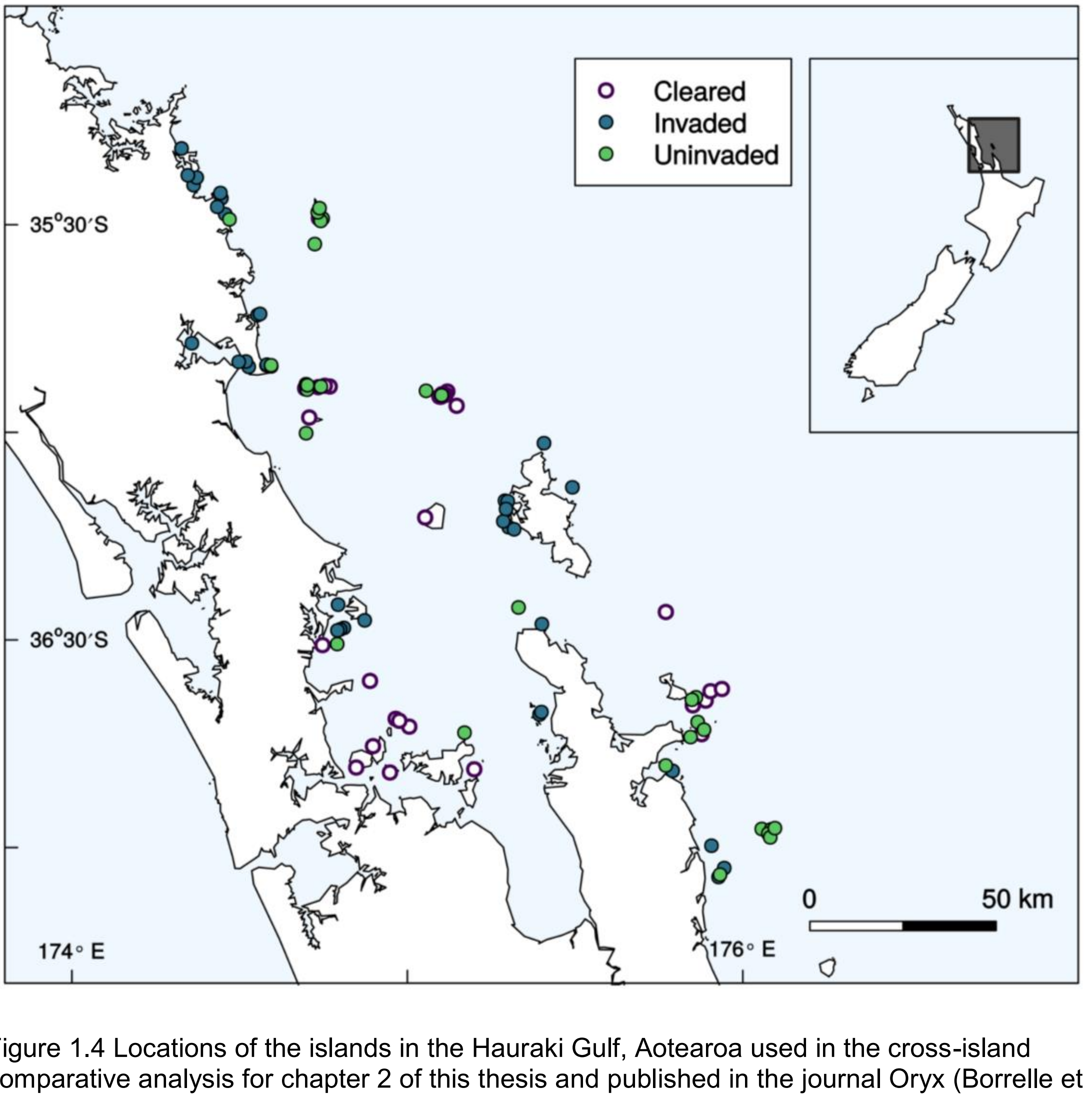


Figure 1.4 Locations of the islands in the Hauraki Gulf, Aotearoa used in the cross-island comparative analysis for chapter 2 of this thesis and published in the journal Oryx (Borrelle et al. 2016).

1.3 Seabird island ecosystem recovery

Resource distribution within a system is a key determinant of the composition, abundance, and distribution of biotic communities (Fukami et al. 2006; Kolb, Young & Anderson 2011). Therefore, the reinstatement of ecosystem processes is an important component of ecological restoration. At the ecosystem level, we can measure the reinstatement of seabird ecosystem engineering effects as seabird populations recover following predator eradication with a variety of approaches (*e.g.,* Jones 2010; Jones & Schmitz 2009; Thoresen et al. 2017; Towns et al. 2016). For example, the recovery of seabird nutrient influences can be traced through ecosystems by measuring stable isotopes of δ^{15}N and δ^{13}C and C/N, which are a means of determining the relative contribution of marine derived sources of nitrogen from seabirds. Post-eradication, seabird nutrient enrichment can be detected relatively quickly once birds return (Jones 2010).

Seabird recovery to islands following predator eradication is often patchy, which means that nutrient resources can be unevenly distributed. Moreover, the underlying regolith will influence the background nutrient levels and rates of recovery (Ollier & Pain 1996). Such factors will limit the ability of some species of plants to survive, from either limitation of key nutrients, such as nitrogen and phosphorus, to creating a toxic environment, thereby influencing the trajectory of ecosystem recovery processes, potentially causing arrested succession (Mulder et al. 2009). While much is known about seabird nutrient influences on some ecosystem components (Jones 2010; Jones et al. 2011; Kolb, Young & Anderson 2011; Thoresen et al. 2017), gaps remain in our understanding about the within-island scale spatial distribution and accumulation of seabird nutrient enrichment to ecosystem components post-eradication, which have been relatively poorly studied (Kolb, Young & Anderson 2011). In the third chapter of this thesis, I aim to contribute to improving our understanding about the distribution and accumulation of seabird nutrient enrichment, and what ecological factors influence the recovery of the ecosystem engineering properties of seabirds.

I sampled from four islands in the Mercury Island group, off the east coast of the Coromandel (Figure 1.5). Atiu island (13.5 ha; -36.63 S, 175.86 E) and Green island (2.5 ha; -36.64 S, 175.84 E: Figure 1.5) have never had invasive mammalian predators and therefore provide ideal ‘pristine’ comparisons of what functioning seabird island ecosystems would look like. Because of the small size of the islands, and the similarities between seabird assemblages and burrow density, and environmental variables, I pooled samples from Atiu and Green for all of the analyses in chapter 3. Ahuahu (1867 ha; -36.64 S, 175.81 E) was invaded by kiore *Rattus exulans* and ship rats *R rattus* and cats *Felis catus*, until 2016 when it was confirmed that the eradication program in 2014 was successful. There are less than 2 pairs of oi *Pterodroma gouldi* within my sampling area on Ahuahu island. I used this island as a 'control' site. Korapuki island (18 ha; -36.65 S, 175.85 E;) was cleared of kiore, and rabbits *Oryctolagus cuniculus* in 1986 and 1987 respectively (Towns & Atkinson 2004).

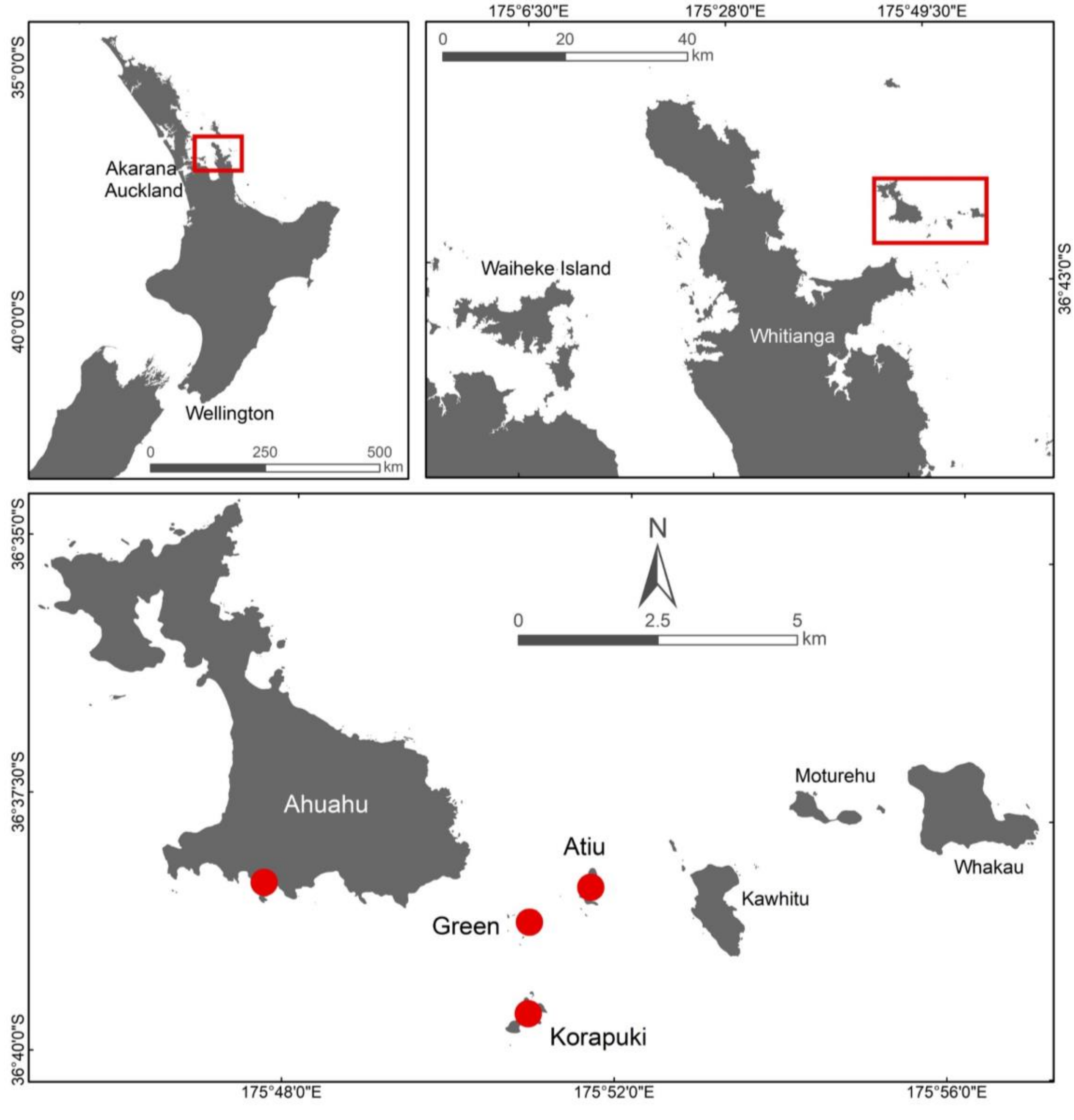


Figure 1.5 Study locations on Ahuahu, Korapuki, Atiu and Green Islands in the Mercury Island group where samples were taken for chapters 3 and 4 of this Thesis.

Because seabirds are still recovering on Korapuki Island, there are areas of dense seabird burrows and areas with few or no burrows. This spatial heterogeneity provided the ideal study system to measure the recovery of seabird nutrient influences at a within island scale for chapter 3 of this thesis. On my study islands, there are six species of burrow nesting seabirds (Table 1.1).

Table 1.1 Burrow-nesting seabird species known to be breeding on the study islands I sampled from for chapters 3 and 4 of this Thesis. The species include: oi/grey-faced petrels *Pterodroma gouldi* (GFPE); Pycroft's petrels *P. pycrofti* (PYPE); toanui /flesh-footed shearwater *Puffinus carneipes* (FFSH); tītī/sooty shearwaters *Puffinus griseus* (SOSH); little shearwaters *P. assimillis* (LISH); kuaka /common diving petrel *Pelecanoides urinatrix* (CDPE). There are also karoro/black-backed gulls *Larus dominicanus* and kororā/little penguins *Eudyptula minor* breeding on the islands.

Island	GFPE	PYPE	FFSH	SOSH	LISH	CDPE
Korapuki	✔	✔	✔	✔	✔	✔
Green	✔		✔		✔	✔
Atiu (Middle)	✔	✔	✔		✔	✔
Ahuahu (Great Mercury)	✔ *	(✔)				(✔)

** There are only 1 or 2 pairs breeding within my sample locations on Ahuahu. PYPE and CDPE are thought to be breeding at some locations post-eradication (J. Russell personal communication.*

Understanding how seabird island systems respond to past conservation interventions can help guide management strategies in the future. Unfortunately, resource limitations and logistical challenges mean that monitoring individual colonies or ecosystem components on numerous remote seabird islands following predator eradications is often impractical, and so seabirds and their island habitats are, at best, spasmodically monitored (Richard & Abraham 2013a; Buxton et al. 2014). In New Zealand, long-term monitoring data exist for only 34% of seabird species breeding on offshore islands (Buxton et al. 2014). Of those species monitored, only 3.6% had both pre- and post-eradication count data to compare population changes following predator management (Buxton et al. 2014).

To evaluate the outcomes of conservation actions of predator eradication on seabird-driven ecosystem recovery, additional tools are needed to measure seabird abundance and ecosystem recovery on islands after predator eradication (Croxall et al. 2012; Buxton et al. 2014). Since every island and species would be logistically and financially impossible to monitor, we need to identify proxies and techniques from which we can glean information about ecosystem status. Essentially, we have to maximize conservation outcomes by deciding which components of systems will provide the most useful information to inform conservation management (Possingham, Fuller & Joseph 2012).

Because seabirds alter island ecosystems through chemical and physical disturbance via the deposition of marine derived nutrients and burrowing activity, concentrations of nitrogen in soils can be positively correlated to seabird burrow density (Ellis, Fariña & Witman 2006; Jones et al. 2011). Photosynthetic rates are directly related to the concentration of nitrogen in plant foliage, which represents a simple, but biologically meaningful link between terrestrial nitrogen (N) stores, plants and N cycling (M. L. Smith et al. 2003). Nitrogen is a key element in chlorophyll, and enzymes needed for the process of photosynthesis, consequently a shortage or excess of N in plants influences leaf biochemistry (Clevers & Gitelson 2013). A strong correlation between chlorophyll and foliar N has been found in numerous plant species (Yoder & Pettigrew-Crosby 1995; Oppelt 2002; Mutanga & Skidmore 2007; Mizusaki, Umeki & Honjo 2013).

The structural and chemical constituents of plant tissues dictate how much light is absorbed and at what wavelength of the electromagnetic spectrum (EMS; Sanchez-Pinero & Polis, 2000). Regions of the EMS have been associated with leaf and canopy level biophysical and chemical characteristics, including water content, nutrients and biomass (Li & Alchanatis 2014; Townsend et al. 2007; Tremblay, Wang, & Cerovic 2012). For example, chlorophyll is the main foliar constituent in determining spectral reflectance in the 450-1500nm range of the electromagnetic spectrum (EMS). Therefore, estimating leaf biochemical properties, such as nutrient status, is possible by looking at these regions of the EMS using spectroscopy techniques (Sanchez-Pinero & Polis 2000). Indeed, remote sensing of forest canopies is emerging as a powerful tool in ecology and conservation for monitoring and research purposes (Gitelson et al. 2003; Rose et al. 2015).

In the fourth chapter of this thesis, I investigate whether the nutrient enrichment from nesting seabirds is able to be detected in the spectral reflectance of island plant species. Because of the strong correlation of chlorophyll and foliar N content, I hypothesised that the nutrient inputs from seabird colonies will be distinguishable in the spectral signatures of the pōhutukawa forest canopy in relation to burrow density. I investigated this hypothesis with a controlled experiment and field tested the approach on seabird islands in the Mercury Islands group (Figure 1.5), off the east coast of the North Island with variable seabird nesting density. This work aims to contribute to developing effective monitoring tools using technology such as satellite remote sensing for monitoring of burrow nesting seabirds using the spectral reflectance of the forest canopy as a proxy for nesting density. Remote sensing potentially offers managers a valuable tool to measure ecosystem recovery, and seabird abundance in a way that is less labour intensive, and possible over much larger spatial scales than traditional monitoring methods (Figure 1.6).

Figure 1.6 Atiu island, the Mercury Island Group, from above. In chapter 4, my research explores the potential to use the nutrient enrichment of seabirds on island plants as a proxy for monitoring seabird nesting density using remote sensing technology. Photo © S. Borrelle.

1.4 Extrinsic influences on recovery

The removal of invasive predators from seabird islands is a necessary strategy for protecting the world's threatened seabird taxa (Jones et al. 2016). Nevertheless, seabirds are impacted by intensifying anthropogenic activities at sea; such as oil pollution, plastic pollution ingestion, fisheries interactions, prey distribution and environmental shifts due to climate change (Croxall et al. 2012; Birdlife International 2013). Therefore, as we shift into an era of post-predator seabird conservation, we must consider the potential impacts from marine threats on seabird recovery and population persistence, particularly as these marine pressures are predicted to increase (*e.g.,* Wilcox, Van Sebille & Hardesty 2015).

Threats from human activities in the marine environment that affect seabirds include: plastic pollution, oils spills, heavy metal contamination (and other industrial pollutants, such as pesticides and radioactive material *e.g.,* Fukushima), climate change, and from interactions with commercial fisheries operations (Croxall et al. 2012; Spatz et al. 2014; Provencher et al. 2018). These threats operate at a range of spatial and temporal scales and affect seabird populations both directly and indirectly. Quantifying the exact effect of a unique stressor is difficult, and in most cases multiple stressors will be acting in unison (Giudici et al. 2010). In my thesis, I discuss the threats to seabirds of plastic pollution, climate change and fisheries bycatch, acknowledging there are a suite of threats that may impact seabird populations (for further discussion on the full suite of marine threats to seabirds see Appendix 3; Provencher et al. 2018). In chapter 5, I explore the population impacts of the three main threats of plastic pollution, commercial fisheries, and climate change, described below, which are those threats where sufficient data were available to conduct an analysis on population level impacts.

***Plastic pollution*:** More than 5.52 trillion pieces of plastic are estimated to exist in the world's oceans (Eriksen et al. 2014). Plastic ingestion by seabirds has been documented from the poles (Provencher et al. 2010; Robards, Piatt & Wohl 1995; van Franeker & Bell 1988), to the tropics (Auman et al. 1997), and oceans in-between (Azzarello & Van Vleet 1987; Laist 2016; Ryan 2008). In New Zealand, the ingestion of plastics was observed as early as 1958 in beach cast prions *Pachyptila* spp. (Gregory 1977, 1978). In the 1970's when systematic surveys were carried out, surveyors noted 'an abundance of plastic pellets and other marine debris' on the beaches in Northern regions, and the number of birds found with plastic increased from ~5% to ~25% over a twenty year period (Gregory 1977, 2009).

Procellariiformes are particularly susceptible to plastic ingestion because of their gut morphology (muscular gizzards), feeding behaviour (surface feeders, omnivorous, and often scavengers), and with the exception of albatrosses, have an inability to eject indigestible matter (Schreiber & Burger 2002). In a 14-year survey, Moser & Lee (1992) evaluated the gut contents of 1033 seabirds and found that Procellariiformes contained the highest loads of plastic, and the frequency of ingestion incidence increased over the study period. Shearwaters have been found to be particularly vulnerable to plastic pollution, causing a reduction in reproductive fitness, chemical residue contamination, and both adult and chick mortality (Cousin et al. 2015; Yamashita et al. 2011).

Figure 1.7 Plastic collected from a beach in Queensland, Australia, 2016. Photo © S. Borrelle.

Reports on the physiological effects of plastic debris ingestion on seabirds include: internal and external wounds, skin lesions and ulcerating sores, ingestion causing general debilitation, inhibiting feeding capacity, eventually leading to starvation, reductions in reproductive capacity, drowning, and impairment of predator avoidance (Azzarello & Van Vleet 1987; Laist 1997; Cousin et al. 2015). Chicks and fledglings can fall victim to loads of plastic debris regurgitated by their parents, suffering dehydration and starvation (Sievert & Sileo 1993). Spear et al. (1995) and Lavers, Bond and Hutton (2014) reported a significant negative relationship between chick body weight and number of ingested plastic particles.

There is growing evidence of acute and chronic poisoning from absorption of toxic compounds associated with marine plastic pollution (Hardesty et al. 2015; Tanaka et al. 2013, 2015). Lavers et al. (2014) suggested that seabird populations on Lord Howe Island, Australia are bioaccumulating organic contaminants, such as heavy metals and poly-chlorinated biphenyls (PCB's), resulting from plastic ingestion. In addition, there is potential for contaminants to be transferred to island soil communities and vegetation and affect whole ecosystem function, although, this has yet to be investigated (Lavers, Bond & Hutton 2014). However, although seabirds have acted as biomarkers for marine pollutants for several decades (Ryan 1987a), and adult mortality can be forensically attributed to pollutants (Furness & Camphuysen 1997; Ryan 2008), the population-level impacts for most marine species affected remain inconclusive (Rochman et al. 2016).

Climate change: Changes to marine primary producers and marine processes induced by climate change can have direct and indirect effects on seabird populations, primarily through changes to prey distributions (Oro 2014). Research into the response of seabirds to changes in climate has been prominent in ornithological studies for more than five decades (Behrenfeld et al. 2006; Schine, van Dijken & Arrigo 2016). There are consistent relationships between rates of primary productivity and Sea Surface Temperature (SST). Shifts in SST affect primary producers, which induces boom and bust population cycles in apex predators, such as seabirds (Crick 2004). El Niño/La Niña driven SST oscillations occur naturally on a 3 - 4 year cycle alternating between the oceans, *i.e.,* when there is a warmer episode in the Pacific, there is a cold episode in the Southern Atlantic. During El Niño years, primary productivity is reduced because oceanic upwelling is inhibited by the warm waters along the west coast of South America (Schreiber & Schreiber 1984).

The reduction in primary productivity can cause fish abundance to crash leading to breeding failures in seabirds that forage off the South American coast (Crick 2004). Another example is the Kerguelen Islands, where warmer winter SST affected zooplankton blooms and consequently the body condition of Blue petrels *Halobaena caerulea*, which forage in the region (Guinet et al., 1998). Barbraud & Weimerskirch (2003) analysed long-term climate and seabird mortality data and found that climate variability exerts a strong influence over seabird survivorship and thus population dynamics and viability. They suggested that colonies can be resilient to anomalous short-term climatic variability, such as El Niño/La Niña, but long-lasting, directional warming anomalies have a negative effect on populations (Barbraud & Weimerskirch 2003; Crick 2004).

Challenges lie in predicting future predator-prey resource distributions or effects on populations because, so far, changes to species distributions attributed to climate change have been challenging to verify (Oro 2014). Homeotherms (*i.e.,* mammals and birds) are unlikely to experience direct physiological impacts from temperature fluctuations and climate change. However, evidence is mounting on the indirect effects of climate on behavioural traits, adult survivability and reproductive fitness in seabirds (Barbraud et al. 2012; Lewison et al. 2012). Furthermore, changes in climate are manifesting as shifts in breeding and migration timings, reproductive performance, and population distribution changes (Crick 2004; Oro 2014).

Commercial fisheries: It is no coincidence that seabird foraging areas and fishery areas overlap. Areas of upwelling of deep nutrient rich ocean waters stimulate enormous algae blooms, providing a rich food source for krill, cephalopods, attracting meso- and apex-predators, such as sharks and seabirds. Karpouzi et al. (2007) investigated the annual consumption by seabirds on a global scale. They calculated the estimated annual food consumption to be 96.4 million mT (95%CI, 78.0 - 114.7 million mT); this quantity is comparable to commercial fisheries operations. While, this does not necessarily mean that there is direct competition between commercial fisheries and seabirds, such may be the case if both are active in the same area at the same time (Furness & Tasker 2000).

Some seabird species face increasing resource competition of fisheries that are targeted by commercial fishing operations, which would otherwise be available as prey (Crick 2004; Oro 2014). Using stable isotope analysis of subfossils, Wiley et al. (2013) found that Hawaiian petrel *Pterodroma sandwichensis* shifted to a lower trophic level prey coinciding with rapid technological advances in commercial fisheries 100 years ago. A reduction of biomass at the surface means seabirds are poorly fed (Cury et al. 2011); the feedback loop from food availability alters the breeding behaviour of seabirds, which are less likely to return to the colony and engage in breeding activities (Montevecchi 2002; Wanless et al. 2005). Conversely, the increase in human exploitation of global fisheries has provided an additional opportunity for some opportunistic seabird taxa to forage discarded by-catch and offal, which is thrown overboard and would otherwise be unavailable (Furness & Tasker 2000; Karpouzi, Watson & Pauly 2007).

In addition to the impact on marine resources below the surface of the ocean, seabirds become the victims of fishing activities and equipment, inadvertently caught on long lines, nets, and trawls (Abraham & Thompson 2011; Žydelis, Small & French 2013). Seabird mortality from long-line commercial fishing activities is estimated to be more than 320,000 birds every year (Anderson et al. 2011), one third of which are

Albatrosses (family Diomedeidae; Birdlife International 2013). However, some work suggests that 320,000 is a gross underestimate, and is less than half of actual mortality, thereby putting numbers closer to three quarters of a million or more seabirds every year (Brothers et al. 2010).

The pressure exerted on seabirds from multiple threats manifests in a variety of population, physiological and behavioural changes (*e.g.,* Barbraud et al. 2012; Chambers et al. 2011; Cousin et al. 2015; Giudici et al. 2010). For example, prolonged or extreme weather events can affect resource availability and cause 'wrecks' (seabirds get caught in storms or are unable to find food and wash up on beaches; Crick 2004; Giudici et al. 2010; Figure 1.8). This can be catastrophic for seabird populations when there are wide-scale adult mortality events which, in turn lower annual reproductive output and chick survival rates (Barbraud & Weimerskirch 2003; Figure 1.9).

Figure 1.8 Beach wrecked prions after a Tasman Sea weather anomaly in 2017. Photo © S. Borrelle.

A reduction in physical condition in breeding birds, from one or more of the aforementioned marine threats, can have a negative effect on reproductive success. Negative effects on reproductive success can be bought on by a reduction in overall physical condition, where individuals may skip breeding to avoid the additional physiological stress of producing an egg, or provisioning a chick(s), although the influences that lead birds to make their reproductive decisions remain poorly understood (Montevecchi 2002; Giudici et al. 2010). An increase in corticosteroids can lead to adverse immunological responses, which can be transferred to the immunological condition of offspring (Auman et al. 1997; Thompson & Hamer 2000). Ultimately, stress related changes to physiological condition can lead to higher mortality of adults and chicks and ultimately declining populations (Giudici et al. 2010).

Environmental conditions, and interactions with these and other anthropogenic threats can act antagonistically on a seabird population, affecting adult survival rates, reproductive capacity, and egg, chick and fledgling survival (Figure 1.9). Changes to vital rates affect population growth rates, often leading to long-term population declines (Croxall et al. 2012; Foden et al. 2013; Rolland et al. 2009). For some species affected by multiple marine threats, even in the absence of predation pressure at their breeding sites, population declines may result in a trajectory towards extinction.

The ideal management strategy for any threatened species is to identify the cause and associated rates of decline in a population using high-resolution data (Wade 1998; Dillingham et al. 2016). Because of the inherent complexity, few studies have investigated the potential impact of multiple anthropogenic threats acting in unison on seabirds (Barbraud et al. 2012; Burthe et al. 2014; Rolland, Barbraud & Weimerskirch 2009), fewer still from a comparative perspective (Rolland, Weimerskirch & Barbraud 2010). Moreover, the effects of marine threats on adult survival are often ambiguous; populations may become extinct before an effect on a key demographic process can be detected (Wade 1998). In the absence of detailed data, models represent a useful tool to explore how populations may respond to threats (Lebreton & Clobert 1991).

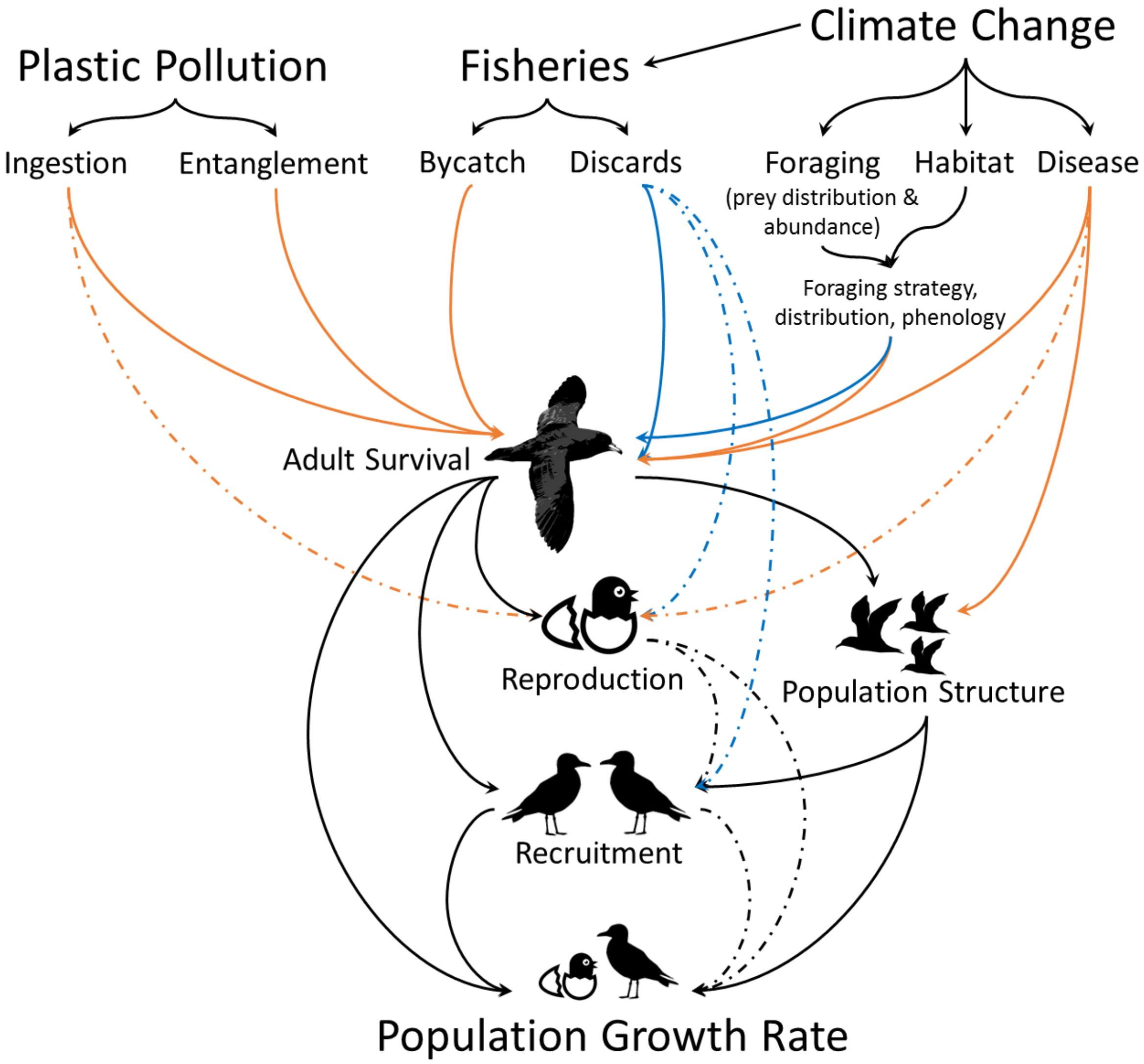


Figure 1.9 Pathways of direct/indirect effects by fisheries, climate change (adapted from Barbraud *et al*., 2012), and plastic pollution on population growth of seabirds. Population growth of these long-lived species is typically mediated by adult survival, the reproductive output of the percentage of breeding individuals in the population, and recruitment rates. Entanglement and ingestion of plastic pollution can cause negative effects (orange lines) on chick and adult survival (Lavers, Bond & Hutton 2014), leading to reduced recruitment rates. Furthermore, plastic ingestion may have negative biophysical effects on reproductive outputs (Burger & Gochfeld 2002). Fisheries may exert negative effects on population growth via mortality of breeding adults; if fishery by-catch of adults occurs during chick provisioning, the remaining parent is unlikely to successfully support a chick to fledging (Montevecchi 2002). Alternatively, fisheries discards may positively benefit (blue lines) a species by positively affecting adult survival, chick survival, and recruitment rates (Montevecchi 2002). Climate change exerts impacts on populations that are more complicated to decipher; these may be negative or positive, and are both spatially and taxonomically specific (Jenouvrier, Barbraud & Weimerskirch 2005; Jenouvrier 2013). Changes to prey abundance and distribution may benefit or impede some populations, similarly, increased temperatures may alter breeding cycles for some species (Schreiber 2002). Heterogeneity in life-history traits (*e.g.,* sex, age) is not included here, but may play important roles in shaping responses of populations to multiple marine threats. The solid lines represent impacts on adult survival (as I deal with this explicitly in chapter 5) and the dashed lines represent how threats might affect populations through changes to egg, chick, and juvenile survival.

In the fifth chapter of this thesis I explore how the aforementioned threats of plastic pollution, fisheries, and climate change may affect seabird population recovery following predator eradication using a theoretical modelling approach. Unravelling the impacts of multiple marine threats on seabird populations and the recovery trajectory of colonies post-predator eradication is somewhat hindered by the paucity of detailed at-sea mortality data and limited demographic data for many species. To overcome this limitation, I use a demographic modelling approach, designed specifically for data-limited species (Niel & Lebreton 2005; Dillingham et al. 2016), expanded to 81 species to cover a macro-ecological perspective.

The Demographic Invariant Method (DIM; Niel & Lebreton 2005) calculates the intrinsic population growth (*r*), the maximum potential growth rate of a population under optimal conditions (Dillingham et al. 2016), for 81 procellariiform species (Table 5.1). Second, with these estimates, I calculated the mortality limit, that is, the maximum number of individuals that can be killed before a decline occurs (M_{limit}; Figure 1.10.B). I validated the utility of this approach, which is based on knowledge of minimal demographic data (*i.e.,* only age of first reproduction and adult survival), by comparing the mortality limits of each species against their IUCN Red List categories, which are designed to capture the extinction potential of a species globally (Croxall et al. 2012). Then, I used phylogenetic methods to identify the leading ecological (foraging strategy, prey preference, at-sea distribution) and demographic and morphological metrics (*e.g.,* body mass) that best predict the risk of a species to marine threats across the 81 species of seabirds. Finally, for a subset of species (n=14) for which I obtained more detailed data on mortality from fisheries, plastic pollution, and climate change, I used perturbation analyses to simulate the population impacts by these threats (Caswell 2008; Figure 1.10.C). The last step allows the evaluation of the role of individual and multiple, interacting marine threats in population recovery after predator eradication.

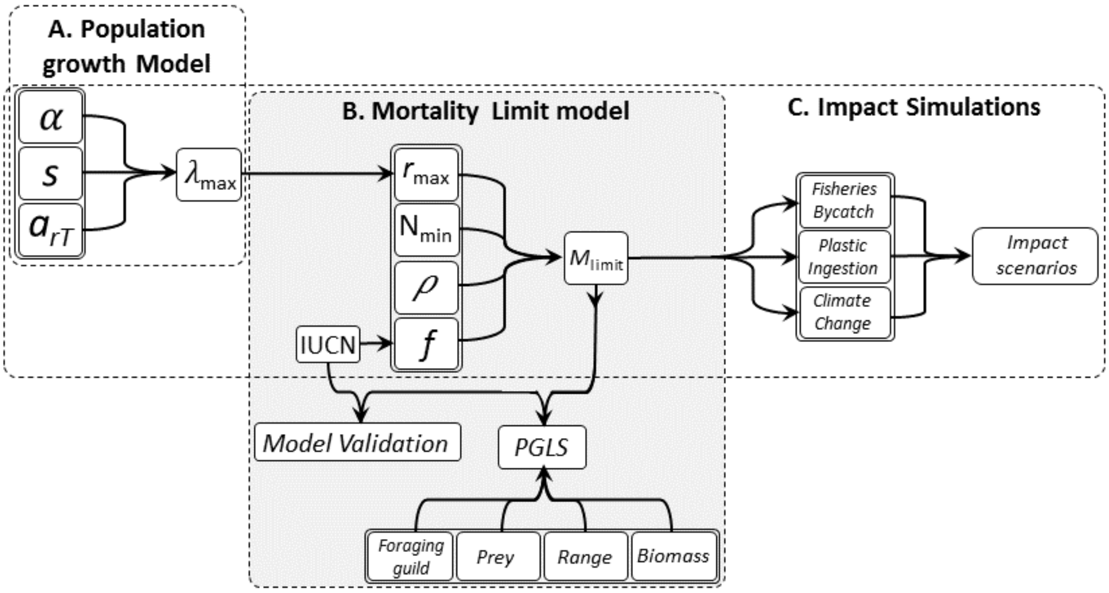
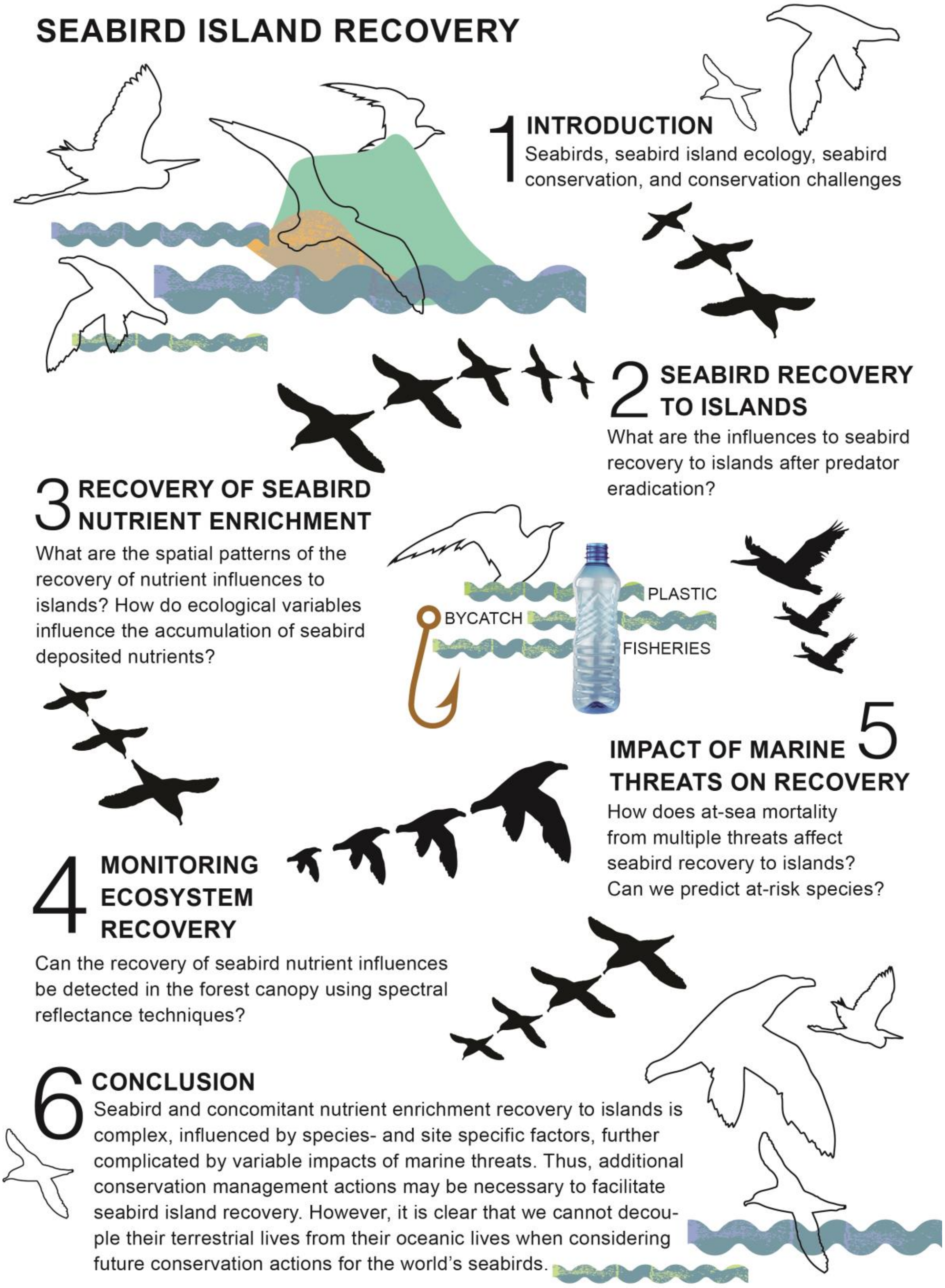


Figure 1.10 Modelling approach to estimate the impact of marine threats on population trends of seabirds. The demographic invariant method (DIM) used here allows us to calculate the asymptotic population growth rate λ_{max}, under optimal conditions (A). Where, *a* is the age of first reproduction, *s* is adult survival, and a_{rT} is the allometric constant (~1; Niel & Lebreton 2005; Dillingham & Fletcher 2011). The allometric constant is based on the relationship between adult body mass to maximum annual growth rate λ_{max} and generation time *T* by a single allometric exponent ~1/4 (Niel & Lebreton 2005). The second step of our approach B) is to calculate the mortality limit, M_{limit}, the maximum number of breeding individuals that could be removed from the population without causing a decline in the population. 3). M_{limit} is a function of (i) r_{max}, the annual maximum population growth above replacement ($r_{max} = \lambda_{max} - 1$), (ii) N_{min}, the minimum breeding population that is compatible with r_{max} (eq. 2), (iii) a calibration factor, *p*, which accounts for overestimation of M_{limit} (Richard & Abraham 2013b), and (iv) a recovery factor *f*, informed by the *IUCN* Red List listing depending on the threat status. The recovery factor (*f*) accounts for the effect of density dependence on demographic performance (e.g., negative density-dependence effects from environmental stochasticity on breeding phenology, whereby mating efficiency is reduced; Votier *et al.* 2009), undetected mortality (e.g., unidentified oil spills; Votier *et al.* 2005), which may create an imbalance in certain age classes such as the most reproductive adults (Lebreton & Clobert 1991), potential errors in population estimates, or unknown biases (Dillingham & Fletcher 2011; Richard & Abraham 2013a).To validated the model M_{limit} outputs to the IUCN Red List threat categories (Figure 5.2). Next, I used phylogenetic generalised least squares (PGLS) to examine predictors of risk with the ecological variables of foraging strategy, primary prey type, at-sea range, and biomass. In the third step C), using prospective perturbation analyses I simulated impacts on adult mortality from fisheries, plastic pollution, and climate change for a subset of 14 seabird species for which I obtained high-quality threat data. The perturbation analysis adjusts the adult survival rate in response to at-sea mortality, thus $\lambda_{max.}$ and mortality limits.

Together, the chapters of this thesis aim to present a more comprehensive understanding of how seabirds and their breeding islands respond to predator eradication. To do this, I use a variety of tool and techniques that integrate the fields of conservation biology, demography and ecology (Figure 1.11). These include: empirical field research techniques, theoretical modelling approaches, and the novel application of spectroscopy methods, which have been used extensively in agricultural applications, but only recently are being applied to ecological research.



SEABIRD ISLAND RECOVERY

1 INTRODUCTION
Seabirds, seabird island ecology, seabird conservation, and conservation challenges

2 SEABIRD RECOVERY TO ISLANDS
What are the influences to seabird recovery to islands after predator eradication?

3 RECOVERY OF SEABIRD NUTRIENT ENRICHMENT
What are the spatial patterns of the recovery of nutrient influences to islands? How do ecological variables influence the accumulation of seabird deposited nutrients?

IMPACT OF MARINE THREATS ON RECOVERY 5
How does at-sea mortality from multiple threats affect seabird recovery to islands? Can we predict at-risk species?

4 MONITORING ECOSYSTEM RECOVERY
Can the recovery of seabird nutrient influences be detected in the forest canopy using spectral reflectance techniques?

6 CONCLUSION
Seabird and concomitant nutrient enrichment recovery to islands is complex, influenced by species- and site specific factors, further complicated by variable impacts of marine threats. Thus, additional conservation management actions may be necessary to facilitate seabird island recovery. However, it is clear that we cannot decouple their terrestrial lives from their oceanic lives when considering future conservation actions for the world's seabirds.

Figure 1.11 Thesis structure and chapter questions that contribute to answering the question: "will predator control deliver enduring benefits to seabird island ecosystems?"

1.5 Thesis motivation

When I was a child, I wanted to fly (like a bird). Sadly, the laws of physics prevent me from ever being able to achieve that goal. Around the same time, I also wanted to save the whales, not any one particular species, just all of the whales.

Decades later, thanks to opportunities presented to me from working under the guidance of David Towns after my Bachelor of Science Degree, I found myself on the Mokohinau islands in the Hauraki Gulf, standing on a cliff in the dark, my headlamp piercing into the blackness.

Then they arrived.

Hundreds of white-faced storm petrels returning to their burrows, flying into the light like moths. I was in awe of these tiny birds (~45 g) living in the unforgiving oceans, faced with numerous marine threats only to return to land to face a suite of terrestrial stressors. They exert strong influences over their island habitats but spend most of their solitary lives at sea. Forget the whales, seabirds are way cooler. Seabirds are impacted by our presence on land; habitat destruction and invasive predators, and our presence at-sea; fisheries, climate change, plastic, pollution. We cannot separate their ocean lives from their terrestrial lives – how are we to manage the conservation of these enigmatic creatures to ensure they persist in the future, and continue to contribute to the islands ecosystems they inhabit and alter?

Natural systems are made up of many and varying components. Separating each component out can tell us much about how an ecosystem operates. But they do not operate in isolation, the biota interacts with each other and the abiotic components across spatial and temporal scales. As tempting as it is to simplify and isolate components, to focus on one or two small pieces of the puzzle, reality frequently and often rudely reminds us that the sum of parts rarely can be disentangled, there are always caveats. My PhD has been a scientific and personal exploration into the caveats of the natural word and my place in it, an opportunity to revisit my childhood dreams of saving ~~the whales~~ seabirds, it has been an opportunity to do something I have wanted to since childhood, be a positive contributor in protecting the world's natural environment, and for all of its challenges, I am forever grateful for the experience.

1.6 Thesis objectives

The main research question of this Thesis is '**Will invasive predator control deliver enduring benefits for seabird island ecosystems?**' Answers to this question will require an understanding of: **1)** the factors that influence seabirds returning to islands cleared of invasive predators, **2)** the patterns of recovery of seabird nutrient influences on island ecosystems **3)** the ways to measure the abundance and recovery of seabirds to islands, and **4)** how marine threats influence the recovery of seabirds following invasive predator eradication (Figure 1.11).

1.7 Thesis structure

My thesis covers three key fields of research that contribute to our understanding of seabird island ecosystems and seabird recovery following predator eradication: ecosystem recovery patterns, investigating new methods of measuring the abundance of seabirds and their ecosystem engineering effects, and the intrinsic and extrinsic influences on seabird recovery (Figure 1.11). It is written in a 'papers pathway' style. That is, each data chapter is a unique question related to the thesis objective written in the style of a journal manuscript, with Supporting information included at the end of each chapter. My PhD Thesis is composed of five manuscripts: chapters 2 and 6 are published in the journals *Oryx* and *Proceedings of the National Academy of Science*, respectively. Chapters 3, 4, and 5 are under final preparation for submission to *The International Journal of Remote Sensing*, The *New Zealand Journal of Ecology*, and *Proceeding of the National Academy of Sciences*, respectively. When I write 'I', I mean 'we' because this work was not possible without the guidance, knowledge, and skills of my advisors and co-authors.

Chapter 2 | Data

Influences on recovery of seabirds on islands where invasive predators have been eradicated, with a focus on Procellariiformes[2]

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[2] This Chapter has been published as: Borrelle, S.B., Boersch-Supan, P.H., Gaskin, C.P. and Towns, D.R., 2016. Influences on recovery of seabirds on islands where invasive predators have been eradicated, with a focus on Procellariiformes. *Oryx*, 52(2) pp.346-358.

2.1 Abstract

Protecting the world’s seabirds is a global conservation priority given that 29% of seabird species are threatened with extinction. One of the most acute threats to seabirds (notably Procellariidae) is introduced predators, which depredate seabirds at all life stages from eggs to adults. Consequently, invasive predator eradication has been identified as an effective and commonly used seabird conservation method. Seabird recovery post-eradication is influenced by complex and interacting environmental and demographic factors, though gaps remain in our understanding of species-specific responses. Here, we reflect on the recovery of seabirds to islands cleared of predators by drawing on the equilibrium theory of island biogeography and synthesise key influences on recovery reported in the literature. To illustrate this synthesis, we present a regionally specific case study on the recovery of seabird colonies (n=98) in the Hauraki Gulf, New Zealand; a seabird diversity hotspot (27 species), which has a long history of invasive predator eradications. We found that islands cleared of predators show recovery of seabirds over time, and surprisingly had more diverse seabird assemblages than islands that never had predators. This recovery appears to be influenced by a suite of site- and species-specific factors. Managers may assume that given enough time following an eradication, seabirds will recolonise. While time is a factor, island spatial distribution has a significant effect on the recolonisation of seabirds, in addition to demographic traits, colonizing ability and habitat suitability. Therefore, integrating expected site and species-specific recovery responses into planning seabird island eradications could help guide post-eradication management actions.

Key words: Biogeography, Restoration, Conservation, Threatened species, Animal Behaviour.

2.2 Introduction

Seabirds are often abundant on islands (Mulder *et al.* 2009). However, colonial nesting habits, low reproductive output and extended periods of parental care at breeding grounds make seabirds vulnerable to predators (Furness & Camphuysen 1997; Baillie, Hilton-Taylor & Stuart 2004; Wolf *et al.* 2006; Croxall *et al.* 2012) Introduced predators are the most acute and wide scale threat to seabirds, for example rats (Kiore *Rattus exulans;* Norway rats *R. norvegicus* and ship rats *R. rattus*), which depredate seabirds at every life-stage have invaded at least 80% of the world's island groups (Towns, Atkinson & Daugherty 2006; Jones *et al.* 2008; Croxall *et al.* 2012; Spatz *et al.* 2014) Consequently, seabirds are now among the most globally threatened group of animals. Of approximately 365 species worldwide, 29% have been listed as globally threatened, another 10% as near threatened and 5% are listed as critically endangered (Birdlife International 2015; IUCN 2017). Accordingly, predator removal is considered to be one of the most effective seabird conservation strategies (Jones 2010; Towns, West & Broome 2013; Jones *et al.* 2016). In fact, the removal of predators can have positive feedbacks for many biota and ecosystem processes affected by predator presence (Towns, Atkinson & Daugherty 2006; Towns *et al.* 2009; Lavers, Wilcox & Donlan 2010; Jones & Kress 2012; Le Corre *et al.* 2015; Jones *et al.* 2016).

Despite considerable investment into the removal of introduced predators from islands, the way seabirds respond subsequently remains poorly understood (Lavers, Wilcox & Donlan 2010; Buxton *et al.* 2014, 2016). Available research has described variable responses among species and islands (Gaze 2000; Lavers, Wilcox & Donlan 2010; Ismar *et al.* 2014). The same traits that make seabirds vulnerable to predation, can also inhibit their natural recovery following predator removal (Jones *et al.* 2011; Buxton *et al.* 2014). Species-specific differences in reproductive output, philopatry and behavioural characteristics influence the response of seabirds to recovery and recolonisation of newly available habitat (Danchin, Boulinier & Massot 1998; Jones *et al.* 2011; Buxton *et al.* 2014). For example, there was no observed increase of flesh-footed shearwater (*Ardenna carneipes*) or sooty shearwater (*Puffinus griseus*) populations following the removal of Norway rats from Titi Island, Marlborough Sounds (-40.95 S, 174.13 E) in the 1970s (Gaze 2000). Similarly, on Raoul, Kermadec Islands (29.26 S, 177.92 W), there was no observed response of white-naped (white-necked) petrels (*Pterodroma cervicalis*) following the removal of Norway rats*,* kiore, and cats (*Felis catus*) between 2002 and 2004 (Veitch *et al.* 2011). Conversely, on the same island there was a notable increase in nesting by black-winged petrels (*Pterodroma nigripennis*), wedge-tailed shearwaters (*Ardenna pacifica*), and recolonisation by Kermadec petrels (*P. neglecta*), Kermadec little shearwaters (*Puffinus assimilis kermadecensis*), and Kermadec storm petrels (Gaskin *et al.* 2011).

Twenty-five species of invasive predators of seabirds have been successfully eradicated from 1016 islands around the world (Jones *et al.* 2016; Island Conservation, 2017). Responses of seabirds and island ecosystems to these eradications are now being evaluated. The putative objective is to identify how seabird colonies recover following predator removals, and if they can recover to a 'restored state' at all (Jones 2010). Understanding the recovery of seabirds through space and time following predator eradication is crucial for informing continued conservation management of seabirds, particularly for species experiencing population declines exacerbated by marine threats (Rolland *et al.* 2009; Croxall *et al.* 2012), such as fisheries by-catch, plastic pollution, and climate change.

The equilibrium theory of island biogeography states that species richness maintains a dynamic equilibrium over time, influenced by area and ecological diversity (Preston 1962; MacArthur & Wilson 1967; Simberloff 1974). Therefore, we would expect that seabird richness on islands to also follow this pattern. By comparing islands cleared of introduced predators to islands that have not been affected by the presence of predators or habitat modification, we may be able to discern the state of recovery post- predator eradication. Here, with a basis of island biogeography theory, we synthesize key influences on seabird recolonisation and recovery reported in the literature. We present a case study to test biogeographical influences by examining whether there has been measurable change to seabird assemblages on a large sample of islands cleared of invasive predators in New Zealand. We discuss how these biogeographical influences and additional factors of behaviour, demography, and within island habitat availability, may be driving seabird recovery. Ideally, pre-eradication population census data should be used for comparative evaluations of species responses to the removal of threats, but in practice such data are rarely available (Duffy 1994). Therefore, we evaluate changes in seabird richness on islands that have been cleared of invasive predators, and compare them to a subset of islands, of comparable area, that remained free of predators and where historical seabird species composition data were available. We focus on the Hauraki Gulf, northern New Zealand, which has 27 species of breeding seabirds (Gaskin & Rayner 2013). We used survey data of seabird richness on islands, where species were confirmed to be breeding as of the Austral winter of 2015.

2.3 Study area

The islands of the Hauraki Gulf are bounded in the north by the Poor Knights (-35.46 S, 174.73 E), the Great Barrier Island group to the east (-36.17 S, 175.52 E), and the Aldermen (Ruamaahua) Islands (-36.96 S, 176.08 E) to the south (Figure 2.1). The islands included in our study represent a range of ecological states from extensively modified either through previous or current influences from invasive mammals (e.g. Rakitu Island; -36.12 S, 175.49 E), to near pristine (e.g. most islands in the Poor Knights group; Table 2.6). We excluded islands <1 ha because of the small island effect (Burns, Paul McHardy & Pledger 2009), and because of the reliability of the survey data, where predator presence, and seabird population data may be unreliable due to survey constraints (Supporting Information). We also excluded islands that have a permanent residential population because of the potential effects of human activities on the establishment of seabird colonies (Le Corre *et al.* 2002). We grouped islands (n=98) into three categories based on predator status. *Uninvaded* islands (*n*=30), *invaded* islands (*n*=37) and *cleared* islands (*n*=31) (Figure 2.1). The climate of the Hauraki Gulf is temperate-humid with a mean annual temperature of 16°C, relative humidity of 87% and mean average rainfall 1202 mm (CliFlo 2017).

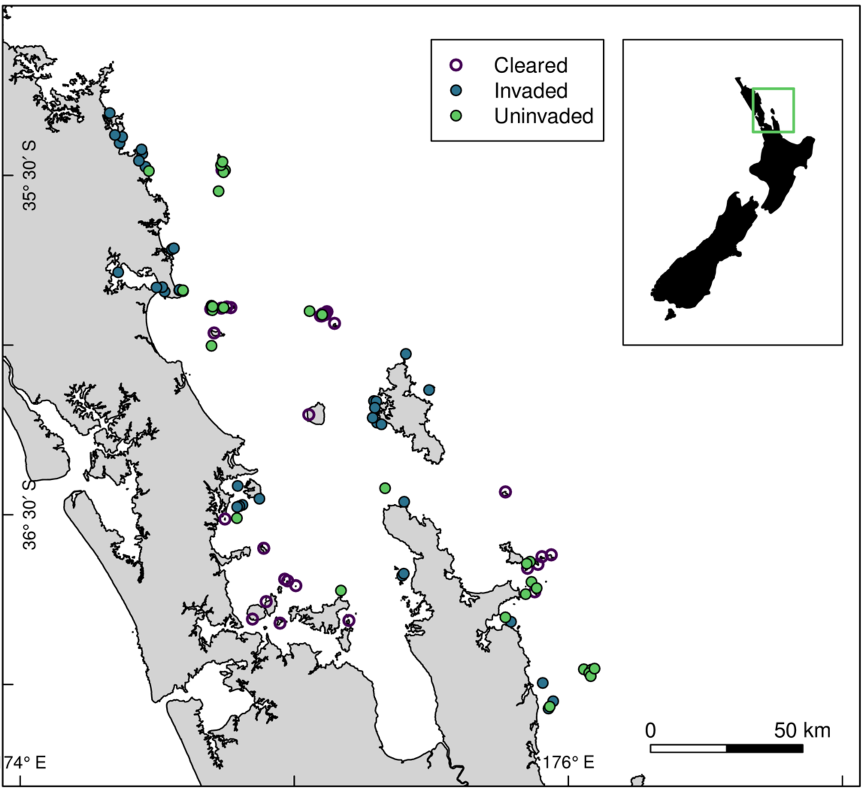

Figure 2.1 The Hauraki Gulf, New Zealand study area and seabird presence data locations (n=98).

2.4 Methods

2.4.1 Data

Long-term survey data of species confirmed to be breeding on the islands as of the Austral winter of 2015 were from C. Gaskin (unpublished data), D.R. Towns (unpublished data) and supplemented by peer reviewed literature (Figure 2.1; Supporting information). The data are presence only. Absence data are rarely available due to more labour-intensive sampling methods and greater economic costs associated with identifying the absence of a species or community (Phillips, Anderson & Schapire 2006). In most cases the data are based on observations on islands that were made up to 30 years ago, with recent presence (*i.e.,* 2004 to present) confirmed through acoustic surveys, occasional island visits and, in some cases, targeted species surveys (*e.g.,* flesh-footed shearwater, Buller's shearwater (*Ardenna bulleri*), grey-faced petrel (*Pterodroma gouldi*), black petrel (*Procellaria parkinsoni*), Cook's petrel (*Pterodroma cookii*), New Zealand storm petrel (*Fregetta maoriana*); C. Gaskin, unpublished data) where additional data on other species have been collected. These reports are based on observations; impressions can vary in quality depending on the methodology, taxon and skill of the observer (see Supporting Information for further discussion). These sampling effort biases may influence our results. However, the majority of data were collected by the same group of researchers, and any potential biases are likely consistent across our study area.

We followed Birdlife International for taxonomy and nomenclature (Birdlife International 2014). We included 16 seabird species in the study: Procellariiformes (n=14), Sphenisciformes (n=1), and Pelecaniiformes (n=1) (Table 2.5). All of these species exhibit natal site philopatry and they have a range of population level responses to introduced predators. Terns (family: Sternidae), gulls (family: Laridae) and shags/cormorants (family: Phalacrocoracidae) were discarded from the analysis because they exhibit ephemeral breeding site selection behaviour (Monaghan 1996; New Zealand Birds Online 2015). We have generalised assumptions about the behavioural traits, such as sex biases and habitat selection preferences.

We included rats (*Rattus rattus, R. novegicus, R. exulans*), mice (*Mus musculus*), cats (*Felis catus*), and pigs (Harris 1970; Medway 2001) as known predators of seabirds. Predator eradication data were obtained from the Department of Conservation, D.R. Towns (unpublished data), Gaskin *et al.* (2011) and the Database of Island Invasive Species Eradications (Island Conservation 2015). Eradications were carried out over 77 years, from 1936 (pigs from Aorangi; -35.48 S, 174.74 E) to 2011 (*R. exulans* from Taranga; -35.96 S, 174.71 E). We used the date of the last successful eradication, where predators had not been identified in biosecurity follow-ups.

Given the paucity of pre-eradication seabird species composition data for *cleared* islands, temporal analysis of seabird recovery is challenging. Therefore, we used the available data for *uninvaded* island census data as a basis for comparisons with seabird species richness of *cleared* islands, i.e. this is essentially a natural experiment (Oksanen 2001). While, this approach simplifies potential ecological complications, we assumed that species richness for a given island area would be comparable given the similar geology, metapopulation proximity and habitat of the islands in the region. In order to assess the stability of these assemblages, we used historical seabird survey data for six *uninvaded* “reference” islands in our study (Table 2.1) with the earliest data collected in 1928. While census surveys on our reference islands were not systematic, these data provide information on the observed stability of seabird species composition over the survey period. Species were only included on the list if they were recorded as breeding at that location. Disturbance history on these islands varied from historical land clearance by burning and agricultural use by Māori to minimal evidence of use (Table 2.1). These sites represent class I and II (Taylor 1989) because of which, we assumed that there was no limitation of available breeding habitat for seabirds.

Table 2.1: Species composition recorded over time on reference islands in the Hauraki Gulf, New Zealand that have never had mammalian predators.

Island	Disturbance History	Seabird assemblages	Dates observed (breeding)
Tawhiti Rahi (-35.45 S, 174.73 E) Poor Knights Islands 155.9 ha	Crop cultivation and seabird harvest (pre-European), burning of the flat areas of the island [9].	Grey-faced petrel	1973 [15], 1981[9]*, 2013 [17]
		Pycroft's petrel	1973 [15], 1981[9]*, 2013 [17]
		Fairy prion	1946 [6], 1973 [15], 1976 [8], 1981[9]*, 2013 [17]
		Buller's shearwater	1946 [5], 1973 [15], 1981[9]*, 2013 [17]
		Fluttering shearwater	1973 [15], 1981[9]*, 2013 [17]
		Little shearwater	1973 [15], 1981[9]*, 2013 [17]
		Common diving petrel	1973 [15], 1981[9]*, 2013[17]
		White-faced storm petrel	1973 [15], 1981 [9]*, 2013[17]
Hongiora (-36.95 S, 176.05 E) Aldermen Islands 15.55 ha	Extensive burning of vegetation prior to 1935. Muttonbird harvest by local Maori [7, 11].	Grey-faced petrel	1973[7], 2013 [17]
		Flesh-footed shearwater	1928 [12], 2013 [17]
		Sooty shearwater	1967 [1] , 2013 [17]
		White-faced storm petrel	1928 [12], 1973[7], 1986[10], 2013 [17]
		Common diving petrel	1958[4], 1963[1], 1973[7], 2013 [17]
		Fluttering Shearwater	2013 [17]
		Little shearwater	2013 [17]
		Little penguin	2013 [17]
		Fairy prion	2013 [17]
Ruamahuaiti (-36.97 S, 176.08 E) Aldermen Islands 23.79 ha	Pigs were briefly on the islands in 1842, but no records of how or when they were removed. The impact on seabirds was likely to be minimal according to observations from McFadden (1986) [10].	Grey-faced petrel	1973 [7], 2013 [17]
		Fluttering shearwater	1928 [12], 1973 [7], 2013[17]
		Little shearwater	1967 [1], 2013 [17]
		Common diving petrel	1973 [7], 2013 [17]
Ruamahuanui (-36.95 S, 176.09 E) Aldermen Islands 32.4 ha	Burned in the late 1800's [11].	Grey-faced petrel	1972 [11], 1973 [7], 2013 [17]
		Fluttering shearwater	1972 [11], 2013 [17]
		Little shearwater	1972 [11], 2013 [17]
		Sooty shearwater	1928 [12], 1972 [11], 2013 [17]
		Little penguin	2013 [17]
		Common diving petrel	2013 [17]

Middle (-36.63 S, 175.86 E) Mercury Islands 11 ha	Few signs of burning, undisturbed condition [2].	Grey-faced petrel:	1962 [3, 16], 1985 [13], 2013 [17]
		Pycroft's petrel	1985 [13] (may not be breeding), 2013 [17]
		Flesh-footed shearwater	1962 [3, 16], 1985 [13], 2013 [17]
		Fluttering shearwater	1962 [3], 1985 [13], 2013 [17]
		Little shearwater	1962 [3], 1985 [13], 2013 [17]
		White-faced storm petrel	1985 [13], 2013 [17]
		Common diving petrel	1962[2, 16], 1985 [13], 2013 [17]
		Little penguin	1962 [3, 16], 1985 [1], 2013[3]
Green (-36.64 S, 175.84 E) Mercury Islands 2.5 ha	Few signs of burning, undisturbed condition [2].	Grey-faced petrel	1962 [3, 16], 1967 [14], 2013 [17]
		Common diving petrel	1962 [2, 16], 1967 [14], 2013 [17]
		Flesh-footed shearwater	1962 [3], 1967 [14], 2013 [17]
		Fluttering shearwater	1962 [16], 1967 [14], 2013 [17]
		Little shearwater	1962 [3, 16], 1967 [14], 2013 [17]
		White-faced storm petrel	1967 [14], 2013 [17]
		Little penguin	1962 [3], 1967 [14], 2013 [17]

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[1] Adams, G.P. 1967. Island survey form (unpublished; Wildlife Branch files). In: Fogarty & Douglas 1973. [2] Atkinson, I.A.E. 1962. Report on the vegetation of the smaller Mercury Islands an Ohena Island. Unpublished Report. [3] Atkinson, I.A.E. 1964. The flora, vegetation, and soils of Middle and Green Islands, Mercury Islands group. *New Zealand Journal of Botany*, 2, 385-402. [4] Blackburn, A. 1958. Island survey form (unpublished; Wildlife Branch files). In: Fogarty & Douglas 1973. [5] Blackburn, A. 1958. Island survey form (unpublished; Wildlife Branch files). In: Fogarty & Douglas 1973. [6] Buddle, G.A. 1946. A second visit to the Poor Knights. *Emu,* 45, 315-318. [7] Fogarty, S.M. and Douglas, M.E. 1973. The birds of the Aldermen Islands. *Tane*, 19, 31-39. [8] Harper, P.C. 1976. Breeding biology of the fairy prion (*Pachyptila turtur*) at the Poor Knights Islands, New Zealand. *New Zealand Journal of Zoology,* 3, 351-371. [9] McCallum, J. 1981. Birds of Tawhiti Rahi Island, Poor Knights Group, Northland, New Zealand. *McCallum (1981) [9] notes that seabirds that have been previously recorded on the island were not present on his visit in 1981, because it did not coincide with the breeding times of these birds. (1981 not confirmed breeding) *Tane,* 27, 59-66. [10] McFadden, I. 1986. Aldermen Islands, unpublished report. [11] Merton, D., Crook, I., Whitaker, A. and Ramsay, G. 1972. Island Survey form (Unpublished surveys). [12] Sladden, B., Falla, R.A. 1958. Island survey form (unpublished; Wildlife Branch files). In: Fogarty & Douglas 1973. [13] Southey, I. 1985. Birds of Middle Island, observations. Unpublished survey. [14] Thoresen, A.C. 1967. Ecological observations on Stanley and Green Islands, Mercury group. *Notornis,* 14, 182-199. [15] Veitch, C.R., Smuts-Kennedy, J.C., Moran, L.R., and Batchelor, C. 1973. Island survey form (unpublished; Wildlife Branch files). [16] Skegg, P.D.G. 1963. Birds of the Mercury Islands group. *Notornis*, 10, 153-168. [17] This study, and P. Lyver, September 2015, personal communication.

2.4.2 Quantitative analysis

All statistical analyses were done in R statistical software v. 3.1 (R Core Team 2013). We used generalized linear models (GLMs) with Poisson-distributed errors to estimate the species-area relationship by predator status for all islands (Supporting Information). While the models of species richness and island area assume there is a linear increase in species as island area increases, in reality this is limited by the number of seabird species in the region. Here, we assume that maximum species richness is constrained by the number of species included in the analysis (n=16). GLM assumptions of a linear-mean variance relationship, and of spatially uncorrelated errors were checked using the dispersion test from the AER package (Kleiber & Zeileis 2008) and spatial correlation tests from the sp, ape and gstat packages (Supporting information; Paradis *et al.,* 2004; Pebesma 2004; Bivand & Rundel 2016).

2.4.3 Species-Area GLM model fitting and selection

We considered three models for the species-area relationship by predator status, all being Poisson regressions of a semilog model (*i.e.,* species count S as response, $\log_{10}(A)$ as predictor). The three models are all Poisson GLMs: $S \sim \text{Poisson}(\mu)$ with log link such that $\log \mu(S) = \boldsymbol{\beta X} i$ where $\boldsymbol{X}$ and $\boldsymbol{\beta}$ are the design matrix and the parameter vector, respectively, and i is the number of variables.

1) **effect of log(area) only:**

$$\log \mu(S) = \beta_0 + \beta_1 \log_{10} A$$

2) **additive effects of log(area) and predator status, i.e. separate intercept per predator status but same slope:**

$$\log \mu(S) = \beta_0 + \beta_1 \log_{10} A + \beta_2 \, Predator$$

3) **interaction of log(area) and predator status, i.e. separate slope and intercept per predator status:**

$$\log \mu(S) = \beta_1 Predator + \beta_2 \log_{10} A \times Predator$$

Multi-model inference based on Poisson GLMs was used to explore possible predictors of species richness for the *cleared* islands (Burnham & Anderson 2003). The predictors explored were size, time since eradication, distance to the mainland, i.e.

the nearest point on the coastline of the North Island, and distance to Auckland city centre (36.85 S, 174.76 E) – the latter two being potential proxies for human disturbance and/or distance to offshore feeding grounds. Distances were calculated using the rgeos package (Bivand & Rundel 2016). We used the MuMIn package (Barton 2015) to generate a complete set of candidate models based on the above predictors and ranked the resulting model fits by AICc.

We used Chi-squared tests (*alpha level* = 0.05) of frequency of occurrence to evaluate the differences among species present on *cleared, uninvaded* and *invaded* islands respectively (R Core Team 2013). Because of poor representation or absence of some species within island categories, analyses used a subset of six widely distributed species (Figure 2.3).

2.4.4 Exploratory AFR analysis

We used a Kruskal-Wallis rank sum test to test for differences in the mean age at first reproduction (AFR), a possible proxy for colonisation ability, for each island assemblage. Species-specific AFR values (Table 2.5) were averaged over all breeding species on a given island.

2.5 Results

The mean area of *uninvaded* islands was 13.88 ha (SD = 31.43), ranging from 1.04 to 155.92 ha and were biased towards <10 ha (n=23 of 30). *Invaded* islands mean area was 24.79 ha (SD = 62.34) and ranged from 1.14 ha to 312.33 ha. The mean area of *cleared* islands was 286.15 ha (SD = 675.7) and represented the most evenly spread area range of all three categories ranging from 1 ha to 2817 ha.

The final model for the species-area relationship included separate slopes and intercepts by predator status. No significant overdispersion was detected (Overdispersion test: dispersion parameter = 0.99; p = 0.53). Weak, but statistically significant spatial autocorrelation in the residuals was indicated by Moran's I (I = 0.1, p = 0.011), and visual inspection of spatial residuals indicated that this was due to the model overpredicting species richness for the islands of the inner Hauraki Gulf (Supporting Information; Figure 2.5). GLM parameter estimates are presented in Table 2.2, and model predictions are illustrated in Figure 2.2.

Table 2.2 GLM parameter estimates for the species-area relationship by predator status. Parameter values are given on the link scale.

Parameter	**Parameter estimate**	**Std. error**	***p***
Predator_statusCleared	1.462	0.160	< 0.001
Predator_statusInvaded	-0.480	0.285	0.092
Predator_statusUninvaded	0.890	0.156	< 0.001
Log10(ha):Predator_statusCleared	0.038	0.036	0.295
Log10(ha):Predator_statusInvaded	0.249	0.096	0.009
Log10(ha):Predator_statusUninvaded	0.259	0.062	< 0.001

For *uninvaded* islands the intercept (i.e. expected species count on a 1 ha island) is 2.43 (95% CI: [1.77, 3.28]; $\hat{\beta} = 0.89$, $p < 0.001$), and for a 10-fold increase in area the species count is expected to increase 1.81-fold (95% CI: [1.36, 2.39]; $\hat{\beta} = 0.26$, $p < 0.001$). For *cleared* islands the intercept is 4.31 (95% CI: [3.12, 5.84]; $\hat{\beta} = 1.46$, $p < 0.001$), and no significant relationship was found between species richness and area ($\hat{\beta} = 0.04$, $p = 0.295$). For *invaded* islands the intercept is 0.62 (95% CI: [0.34, 1.05]; $\hat{\beta} = -0.48$, $p = 0.092$), and for a 10-fold increase in area the species count is expected to increase 1.77-fold (95% CI: [1.14, 2.71]; $\hat{\beta} = 0.25$, $p = 0.009$). Further, regardless of size, invaded islands did not have more than four species (Figure 2.2).

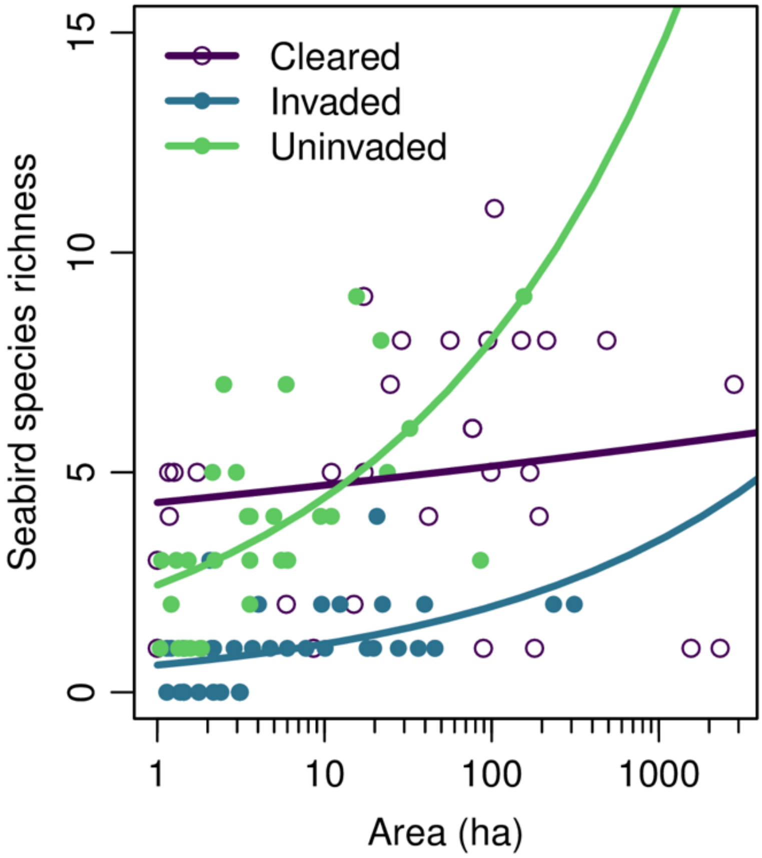
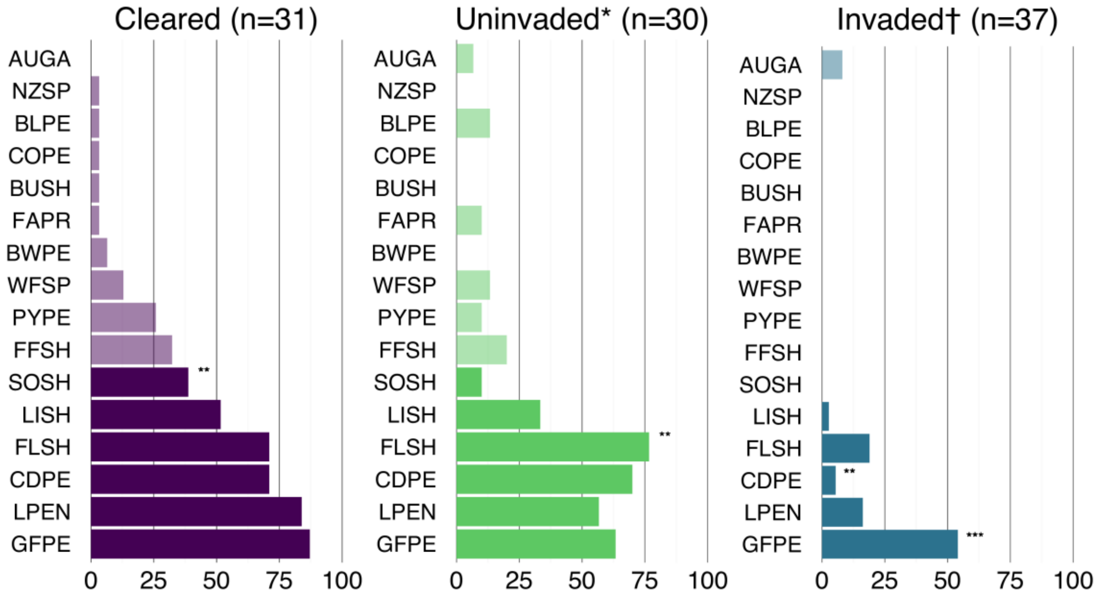


Figure 2.2 Observed species richness and GLM predictions as a function of island area comparing uninvaded islands (intercept = 2.43, slope = 0.26), cleared islands (intercept = 4.31, slope = n.s.), and invaded islands (intercept = 0.62, slope = 0.25). Model parameter estimates are detailed in Table 2.2.

The largest suite of species included in the analysis was on *cleared* islands, with the smallest on *invaded* islands (Figure 2.3). Standard residuals from the Chi-squared test showed a higher proportion of *invaded* islands with grey-faced petrels than expected (p = 0.001, df = 12, standard residual = 4.66). A higher proportion than expected of *cleared* islands had sooty shearwaters (p = 0.023, standard residual = 2.39) and a higher proportion than expected of *uninvaded* islands had fluttering shearwaters (p = 0.033, standard residual = 1.52). On *invaded* islands there were fewer than expected populations of common diving petrels (*Pelecanoides urinatrix*; p = 0.027, standard residual = -1.92). Seven species of seabirds present on *cleared* and/or *uninvaded* islands were absent from *invaded* islands (Figure 2.3).



Note: *$p<0.1$; **$p<0.05$; ***$p<0.01$

Figure 2.3 Proportion of islands with seabird species that are confirmed breeding on cleared, uninvaded and invaded islands in the wider Hauraki Gulf region, New Zealand. The dark bars are those where data met the assumptions of the Chi-squared test. AUGA: Australasian gannet, NZSP: New Zealand storm petrel, BLPE: black petrel, COPE: Cook's petrel, BUSH: Buller's shearwater, FAPR: fairy prion, BWPE: black-winged petrel, WFSP: white-faced storm petrel, PYPE: Pycroft's petrel, FFSH: flesh-footed shearwater, SOSH: sooty shearwater, LISH: little shearwater, FLSH: fluttering shearwater, CDPE: common diving petrel, LPEN: little penguin, GFPE: grey-faced petrel. * Bias of uninvaded islands was towards areas < 10 ha, and † bias of invaded islands was towards areas > 155 ha.

Multi-model inference did not provide strong evidence for a link between the time since eradication and species richness. Distance to Auckland was retained as predictor in all six models that were within 3 AICc units of the optimal model, with higher species richness on islands further from the city. Distance to mainland and island size were each retained in three of the top six models, but effect sizes were close to zero when both predictors were retained in the same model. Island size had a positive effect on species richness, whereas distance to mainland had a negative effect. (Table 2.3; Supporting Information; Figure 2.8).

On the reference islands, species composition was stable for up to 85 years (Table 2.1). No species identified in early reports disappeared from any island, but in one group (Ruamaahua) up to four species not recorded previously were present in 2013 (Table 2.1).

Table 2.3: Parameter estimates and associated standard errors for the top ranked models for species richness on cleared islands. Models were ranked by AICc. Distance to Auckland was retained as a predictor in all six models, which were within 3 AICc units of the optimal model.

	Dependent variable: Species richness							
	(Model 1)	(Model 2)	(Model 3)	(Model 4)	(Model 5)	(Model 6)	(Model 7)	(Model 8)
Intercept	0.527	0.035	0.234	0.025	0.455	0.526	0.218	0.448
	(0.268)	(0.334)	(0.366)	(0.326)	(0.271)	(0.267)	(0.365)	(0.269)
Distance to Auckland (km)	0.015	0.014	0.015	0.013	0.013	0.015	0.014	0.012
	(0.003)	(0.003)	(0.003)	(0.003)	(0.003)	(0.003)	(0.003)	(0.003)
Distance to mainland (km)	-0.012		-0.008			-0.012	-0.007	
	(0.005)		(0.006)			(0.005)	(0.006)	
Island size (log(ha))		0.089	0.059	0.091			0.062	
		(0.040)	(0.048)	(0.040)			(0.049)	
Time since eradication (years)				0.003		0.0005	0.002	0.001
				(0.005)		(0.005)	(0.005)	(0.005)
AICc	129.57	129.59	130.74	131.95	132.17	132.21	133.50	134.55
ΔAICc	0.00	0.02	1.17	2.38	2.60	2.64	3.92	4.98
Model weight	0.28	0.27	0.15	0.08	0.08	0.07	0.04	0.02

Mean assemblage AFR was lowest on invaded islands and highest on uninvaded islands, but these differences were not statistically significant (Kruskal-Wallis rank sum test, chi-squared = 5.72, df = 2, p = 0.057; Figure 2.7.A). Furthermore, across cleared islands mean assemblage AFR increased with time since eradication, although again this result was not statistically significant (OLS regression, $\hat{\beta}$ = 0.013, p = 0.20; Figure 2.7.B).

2.6 Discussion

One of the benefits of invasive predator eradications is to allow affected resident seabird populations to recover and to enable recolonisation by species that have been extirpated (Kappes & Jones 2014). The equilibrium theory of island biogeography states that area should be the best predictor of species richness on islands (Preston 1962; MacArthur & Wilson 1967). In our analysis, we assumed that species richness of seabirds on *cleared* islands should resemble or begin to resemble *uninvaded* islands of a comparable area within a similar biogeographic region. While our data are undoubtedly influenced by variable survey effort, plus temporal and spatial biases such as island size and a lack of pre-invasion census data, we can show that seabirds are recolonizing *cleared* islands in the Hauraki Gulf (Figure 2.2). This recolonisation result is promising, especially since all of the species absent from invaded islands are now breeding on *cleared* islands (Figure 2.3). Furthermore, *uninvaded* islands, Hongiora (-36.95 S, 176.05 E) and Ruamahuanui (-36.95 S, 176.09 E), appear to have recruited species that had not been observed previously (Table 2.1), perhaps as spillover from populations increasing elsewhere as a part of natural assemblage equilibrium processes (Simberloff 1974; Buxton *et al.* 2014).

While differing rates of re-colonisation and local extinction may result in a species richness rebound effect following the removal of predators (Cirtwill & Stouffer 2016), ecological diversity is likely to exert a strong influence on the return of seabird assemblages to equilibrium on *cleared* islands (Preston 1962; MacArthur & Wilson 1967; Simberloff 1974). We posit that, within our case study system, the seabird assemblage structure on cleared islands will likely reflect the effects of five components; 1) spatial distribution of islands influencing proximity to source populations, foraging areas and/or human activities; 2) time since eradication; 3) behavioural influences including interspecific interactions; 4) the availability of suitable habitats; and, 5) the colonising ability of individual species (Figure 2.4). We were able to statistically support the influence of space (1) and to a lesser extent, time (2). However, our model was not able to explain all of the variance. The literature provides some guidance for the behavioural (3), within habitat (4), and demographic (5) influences on seabird recolonisation to islands cleared of invasive predators in the Hauraki Gulf.

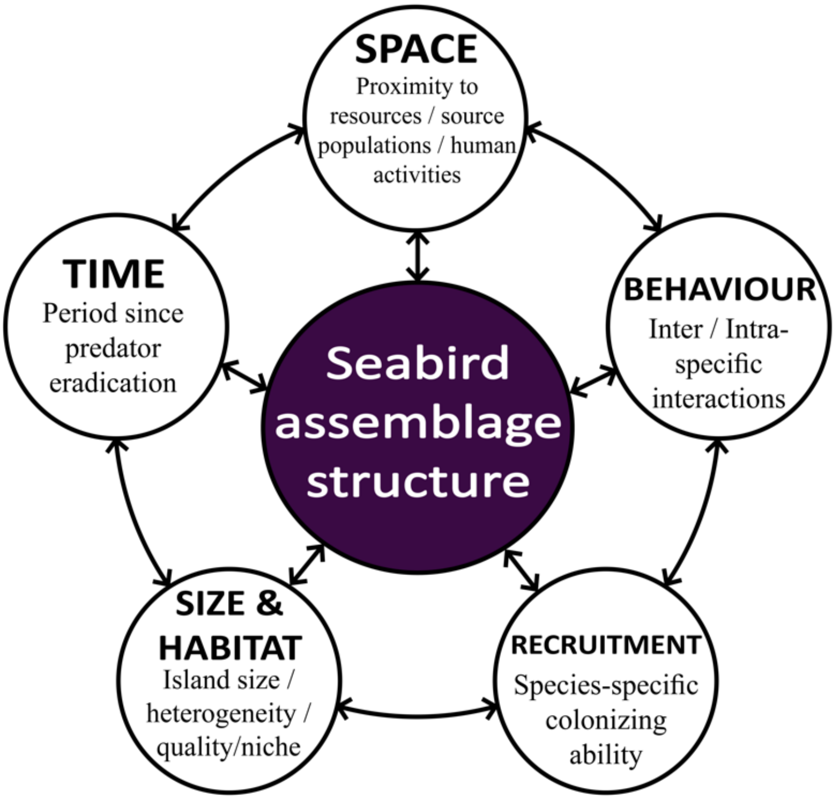


Figure 2.4 Schematic representation of the key influences on seabird recolonisation to islands cleared of predators.

Space: The rate and pattern of seabird recovery appears to be most affected by the proximity of *cleared* islands to source populations, foraging areas and/or human activities. Distance to local populations was the strongest influence on seabird recruitment in Buxton *et al*.'s (2014) study, where the proportion of natural seabird recolonisation response fell below 50% when the source population was equal to or more than 25 km from the recruitment site. Borrelle et al. (2015) found lower than expected species richness on Hauraki Gulf islands beyond the 25 km radius, thus supporting distance to source populations as a key driver of passive seabird recolonization (Buxton *et al.* 2014). Further, the recruitment of some species to cleared islands may be influenced by the proximity to foraging grounds. The ideal situation for species is the juxtaposition of resources that reduces costs to the individual (Estades 2001). Seabirds represent the extreme end of these habitat resource spatial patterns, reflected by foraging grounds often considerable distances from breeding sites and that are discontinuously distributed across space and time (Estades 2001). The disparity between breeding sites and dynamic nature of foraging areas means that these relationships are not well understood (Fernández-Chacón *et al.* 2013). While we found no compelling evidence of spatial correlation, we note that islands located in the Inner Gulf all have negative residuals (Supporting information; Figure 2.5). This may be explained by the results from multi-model inference, which suggested that proximity to Auckland negatively influenced the spatial distribution of seabird recovery (Table 2.3; Supporting Information; Figure 2.8). This could be attributed to a combination of proximity to source populations, optimal foraging theory and greater habitat modification and marine activities in these areas (Borrelle 2013; Gaskin & Rayner 2013). More detailed evaluation of effect modifiers in relation to proximity to human activities and foraging patterns (*e.g.,* using detailed telemetry data) may improve the predictability of the model.

Time: A positive, but statistically not significant increase in species richness was observed with time since eradication. This result may be affected by a strong temporal artefact because our analysis of seabird recovery on some islands reflects predator eradication effort concentrated approximately 20 years ago (Supporting Information; Figure 2.6). Our comparisons of species richness with island area strongly suggest that not all *cleared* islands resemble the seabird richness of *uninvaded* islands of comparable size. This result may indicate that there has been insufficient time for the recolonisation of seabirds to those islands, particularly on larger islands that were cleared more recently following the resolution of logistical and operational challenges (Towns & Broome 2003). Further, variations in the speed and/or capacity of individual seabird species to recolonise may also be a contributing factor. However, given the GLM predictions of species richness of *cleared* islands compared to *invaded* islands, it appears that on many *cleared* islands species richness has increased following predator eradications (Figure 2.2). On some islands, these responses have been rapid and unpredicted. For example, Burgess Island (-35.90 S, 175.11 E) has had remarkable recovery of seven species of procellariiforms (Table 2.4; Ismar et al., 2014). Further, since the eradications of cats (1970s) and kiore (2004) on Te-Hauturu-o-Toi (Little Barrier Island; -36.20 S, 175.08 E), the New Zealand storm petrel has reached sufficient numbers for identification of a breeding population of this hitherto presumed extinct species (Rayner *et al.* 2015). Cirtwill & Stouffer (2016) found that following defaunation on disturbed mangrove islands, species richness increased temporarily once the disturbance (predation) was removed. Species assemblages then stabilised with equilibrium between immigration and extirpation (Cirtwill & Stouffer 2016). A similar process may be operating on some of our study islands following predator eradication. However, little is known about the temporal dynamics of seabird communities during recolonisation of islands. In the case of the volcanic island of Surtsey (Iceland, 63.30 N, 20.60 W), nine seabird species successively established breeding sites over the course of 55 years. Only one of these, the Arctic tern (*Sterna paradisaea*), failed to establish a permanent presence and went locally extinct after three breeding attempts across four years (Petersen 2009).

Table 2.4 Seabird species assemblage on Burgess Island prior to rat eradication in 1990 (McCallum 1980), and post-eradication, from Ismar *et al.* (2014).

Species	**McCallum** (1980)	**2010** October	**2011** September	**2013** February
Australasian gannet		●	●	
Grey-faced petrel	●	●	●	●
Common diving petrel		●	●	●
Little shearwater		●	●	●
Fluttering shearwater		●	●	●
Sooty shearwater		●		●
White-faced storm petrel		●		●
Black-winged petrel				●

Behaviour: Examples of intrinsic effects on seabird recovery can include situations where intra- and inter-specific interactions exert strong influences on recovery rate and recruitment (Danchin, Boulinier & Massot 1998; Parejo, Danchin & Avilés 2004; Buxton *et al.* 2014). Seabird recruitment to new breeding sites may be limited by the number of immature individuals in local metapopulations; because of the life history traits of seabirds, colony growth can be slow (Parejo, Danchin & Avilés 2004). Further, the recruitment of immature individuals is influenced by the availability of suitable habitat and social cues (Danchin, Boulinier & Massot 1998; Parejo, Danchin & Avilés 2004). These interactions can influence breeding success or immigration rates as a result of limited access to nest sites. Passive recolonisation of seabirds on 92 offshore islands in New Zealand following the removal of introduced predators was greater where more than two seabird species were present (Buxton *et al.* 2014); suggesting that this was likely due to conspecific attraction to preferential habitat (Danchin, Boulinier & Massot 1998; Parejo, Danchin & Avilés 2004; Buxton *et al.* 2014). In contrast, numbers of grey-faced petrels appeared to decline on the Poor Knights Islands as Buller's shearwaters increased in abundance, even though grey-faced petrels are abundant on Taranga/Hen Island in the neighbouring Hen and Chickens group (Harper 1983). Inter-specific competition may play a greater role than predator presence in the distribution of grey-faced petrels on the Poor Knight's group given the higher than expected proportion of *invaded* islands with this species (Figure 2.3).

Size & Habitat: We found that four of the 16 seabird species included in our analyses are absent from *uninvaded* islands (Figure 2.3). Instead, we found the full suite of seabird species across *cleared* islands, which indicates rapid recolonisation by seabirds following a release from predation pressure (Cirtwill & Stouffer 2016), and/or area-related limitations on ecological diversity influencing the availability of suitable habitat (Simberloff 1974). Larger *invaded* islands may also be serving as refugia for some species, despite predator presence, because of availability of preferred habitat. For example, Cook's petrels and black petrels are not represented on *uninvaded* islands; however, both species are present on *invaded* islands and *cleared* islands. Cook's petrel was widely distributed on the mainland of New Zealand before the introduction of mammals (Imber, West & Cooper 2003), but is now restricted to only three breeding sites: Codfish Island (-46.77 S, 167.63 E), Aotea (Great Barrier; -36.20 S, 175.40 E) and Te-Hauturu-o-Toi (Towns, 2009). Nest burrows are found in tall forests, generally above 250 m elevation on both islands with the largest population being on Te-Hauturu-o-Toi (Rayner *et al.* 2007). Similarly, tākoketai (black petrels) were once more widely distributed, breeding at five or more sites on the North Island before 1900 (Imber *et al.* 2003). Tākoketai are now restricted to Te-Hauturu-o-Toi and Aotea (estimated at 2,000 breeding pairs; E. Bell, Wildlife Management International Ltd, personal communication 2015), also in colonies largely restricted to high altitude (> 400 m) tall forest (Francis & Bell 2010; Bell *et al.* 2011). For species such as Cook's and tākoketai, habitat suitability and a lack of islands of sufficient size or elevation may be a limiting factor in recruitment to newly predator free sites. Conversely, more ‘generalist’ species, such as grey-faced petrels, common diving petrels and fluttering shearwaters may be less constrained by habitat suitability (Buxton *et al.* 2016).

Recruitment: We found that the proportion of islands with fluttering shearwaters was greatest on *uninvaded* islands (Figure 2.3). Given that fluttering shearwaters are abundant in the region (estimated population of 20,000 pairs; C. Gaskin, unpublished data), we might expect this species to be more widely distributed on *cleared* islands, as was found for sooty shearwaters which have an estimated population of less than 800 pairs (Figure 2.3; C. Gaskin, unpublished data). Their contrary distribution suggests that fluttering shearwaters may have a more limited capacity for recruitment to new breeding sites than species such as sooty shearwaters. Behavioural or sex differences between species may also influence recruitment rates (Dittmann, Ezard & Becker 2007) but there is limited understanding about how these influences might affect recruitment. Additional demographic traits, such as age at first breeding, may influence the species-specific rate of recovery of the islands (Nur & Sydeman 1999), where species that have shorter pre-breeding states may recolonise more quickly. For example, on the Mokohinau Islands, common diving petrel and white-faced storm petrel (*Pelagodroma maoriana*) populations increased dramatically in the two decades following the removal of *R. exulans* (Ismar *et al.* 2014). For white-faced storm petrels and common diving petrels age at first reproduction (AFR) is 2 or 3 years, compared to tākoketai and Pycroft’s petrels with AFR of 5-10 years (New Zealand Birds Online 2015). While we found no statistical evidence of AFR influencing recolonisation potential in our study, the effect of AFR could be masked by the small sample size, the relative recency of most eradications, and/or the lack of time-series observations of the recovery process on individual islands. Further research may provide insight into AFR and recovery rate relationships.

Predator eradication is an effective conservation tool for protecting and enhancing the world’s seabird colonies (Jones 2010; Towns, West & Broome 2013; Jones *et al.* 2016). Such actions can result in fundamental changes to the structure and species richness of island seabird faunas. However, we also found that once these assemblages form, they undergo little change over many decades despite pervasive extrinsic influences such as fisheries bycatch and marine pollution. Constraints on natural recolonisation are nonetheless numerous. For example, despite their mobility over water, seabirds rarely establish new breeding sites due to K-selected traits

(Hamer, Schreiber & Burger 2002; Schreiber & Burger 2002), although some seabird colonies do show emigration and immigration so are not closed (Igual *et al.* 2007; Lawrence, Lyver & Gleeson 2014). Demographic, intrinsic, extrinsic, habitat and spatial factors also complicate seabird recovery following predator eradications, with additional variation caused by strong species, and site-specific effects (Buxton *et al.* 2014). Given the complex influences on recolonisation, seabird conservation that involves invasive species eradications should aim to improve understanding of the species-specific and external effects on demographic traits and population dynamics, since these may elicit responses peculiar to regional faunas. To achieve this, effective and consistent seabird monitoring plans should be an integral component of any seabird island restoration project.

2.7 Supporting information

2.7.1 Taxonomic considerations:

We grouped the subspecies; New Zealand white-faced storm petrel (*Pelagodroma marina maoriana*) and the white-faced storm petrel (*Pelagodroma marina*) together and also the North Island little shearwater (*Puffinus assimilis haurakiensis*) and little shearwaters (*Puffinus assimilis*). Terns (family: Sternidae) and gulls (family: Laridae) were discarded from the analysis because they are confined to coastal areas, exhibit strong intraspecific aggression and individual nest sites are often up to 1 km apart. Shags/cormorants (family: Phalacrocoracidae) were also discarded because they exhibit ephemeral breeding site selection behaviour (New Zealand Birds Online 2015).

Table 2.5 Seabird species, IUCN trend status and age at first reproduction (AFR; mean) included in our review of seabird recovery on islands in the Hauraki Gulf, New Zealand following predator eradication.

Order	Scientific name	Common name	Description	AFR
Pelecaniformes	*Morus serrator*	Australasian gannet	Native IUCN: Least concern Population trend: Increasing	5.5
Procellariiformes	*Procellaria parkinsoni*	Black (Parkinson's) Petrel	Endemic IUCN: Vulnerable Population trend: Stable	6
Procellariiformes	*Pterodroma nigripennis*	Black-winged petrel	Native IUCN: Least concern Population trend: Declining	3
Procellariiformes	*Ardenna bulleri*	Buller's shearwater	Endemic IUCN: Vulnerable Population trend: Stable	~5
Procellariiformes	*Pelecanoides urinatrix*	Common diving petrel	Native IUCN: Least concern Population trend: Declining	2
Procellariiformes	*Pterodroma cookii*	Cook's petrel	Endemic IUCN: Vulnerable Population trend: Increasing	~3
Procellariiformes	*Pachyptila turtur*	Fairy prion	Native IUCN: Least concern Population trend: Stable	3
Procellariiformes	*Ardenna carneipes*	Flesh-footed shearwater	Native IUCN: Least concern Population trend: Declining	5

Procellariiformes	*Puffinus gavia*	Fluttering shearwater	Endemic IUCN: Least concern Population trend: Relict	~5
Procellariiformes	*Pterodroma gouldi*	Grey-faced petrel	Endemic IUCN: Least concern Population trend: Declining	5.5
Sphenisciformes	*Eudyptula minor*	Little penguin	Native IUCN: Least concern Population trend: Declining	2.5
Procellariiformes	*Puffinus assimilis*	Little shearwater	Native IUCN: Least concern Population trend: Declining	~4
Procellariiformes	*Fregetta maoriana*	New Zealand storm petrel	Endemic IUCN: Critically endangered Population trend: unknown	~2.5
Procellariiformes	*Pterodroma pycrofti*	Pycroft's petrel	Endemic IUCN: Vulnerable Population trend: Increasing	3
Procellariiformes	*Ardenna griseus*	Sooty shearwater	Native IUCN: Near threatened Population trend: Declining	6
Procellariiformes	*Pelagodroma marina*	White-faced storm-petrel	Native IUCN: Least concern Population trend: Declining	2.5

2.7.2 Data limitations:

Some of the seabird data are from observations that are out of date, are biased towards heavily studied sites, or that may not be representative of colony densities at un-sampled locations (Rayner *et al.* 2007). Furthermore, the number of records varied substantially in the dataset, with some species represented by a single data point. We did not account for occupancy during the breeding period; instead we assumed that all of the presence records were of breeding colonies (or individuals). Sampling effort bias was not accounted for. Population census data were excluded from the statistical analysis. Estimating population size can be technically and practically challenging because many Procellariiformes nest in rugged inaccessible locations and are nocturnal, and are therefore difficult to count directly (Rayner *et al.* 2007). While these biases mean that making clear inferences from the data are challenging, the dataset represents a relatively comprehensive picture of seabird presence and changes over time in response to predators and predator removals. Further, as the data were collected by a small group of individuals over the time period of the dataset, we believe the biases are likely to be consistent across the study area.

Island status: Island ecological status descriptions are adapted from Taylor (1989; Table 2.6) the islands in the study ranged from class I to class VII. While the categories are broad, and lack specific criteria for a comprehensive description of the ecological status, they provide an overall guideline. We acknowledge that every island is influenced by a variety of biogeochemical and stochastic influences that affect the biological communities, and so classifying the islands into such broad categories may misrepresent the true ecological status of the island.

Table 2.6 Class descriptions of the status of islands included in our study including introduced mammal and habitat modification status (adapted from: Taylor 1989).

Class Code	Class	Description
I	**Near pristine** natural environment	These islands have not had, or known to have had introduced mammals present. The vegetation may have been modified by historical human activity, but has recovered to or near pre-modified condition. The flora and fauna communities are likely to be representative of pristine island systems. Relict populations of rodent or mammal sensitive species are often present.
II	**Outstanding quality** natural environment	Introduced mammals are absent or have been removed. The vegetation has been modified through either land clearance (e.g. fires) or from the effects of introduced mammals. The islands flora and fauna are in mid-late stage recovery; forests are still in successional stages. Fauna are diverse, and include rodent sensitive species.
III	**High Quality** natural environment	Introduced mammals are present, or have recently been removed but are low impact species. These islands have been highly modified from cultural harvesting /land-use, intact forest remnants remain. The flora and fauna communities are recovering, although may be affected by the spread of invasive weeds and the continued disruption to seed dispersal, or seedling recruitment if mammals are still present.
IV	**Moderate quality** natural environment	Introduced mammals are present, and the islands have been extensively modified in the past. No intact forest remnants are present; however, the regeneration of successional stage forest is occurring (High potential for restoration)
V	**Modified**	Introduced mammals are either present or absent. The islands have been significantly modified by cultural or farming activities. The original vegetation is likely to have been completely cleared, and the islands used as farmland. The current vegetation is grassland, patches of shrubland and/or tree ferns (high potential for restoration).

VI	**Recreational**	Introduced mammals are present, and the island is at a high risk of continued reinvasion due to constant public use or is permanently inhabited. The islands are and continue to be extensively modified.
VII	**Inshore**	Introduced mammals are either present or not, but are within the swimming range of commensal rats, deer and stoats, and are at high risk for invasions. Rodent sensitive species may be present.

2.7.3 Additional Poisson GLM results:

Results from the model selection show that model 3 with separate intercepts and slopes by predator status has the lowest AICc (R Core Team 2013; Table 2.7).

Table 2.7 Model selection results for the Poisson GLM of the species-area relationship by predator status.

Predictors	df	AICc
log(area)	2	452.8
log(area) + Predator status	4	377.7
Predator status + log10(area):Predator status	**6**	370.8

The Poisson GLM assumes a linear mean-variance relationship (dispersion parameter =1). We checked this assumption using a dispersion test (Kleiber & Zeileis 2008; R Core Team 2013). The dispersion parameter is estimated to be 0.99 and not significantly different from 1 ($z = -0.09$, $p = 0.53$). Hence, the assumption of a Poisson mean-variance relationship is met. Weak, but statistically significant spatial autocorrelation in the residuals was indicated by Moran's I ($I = 0.1$, $p = 0.01$), and visual inspection of spatial residuals indicated that this was due to the model over-predicting species richness for the islands of the inner Hauraki Gulf (Figure 2.5).

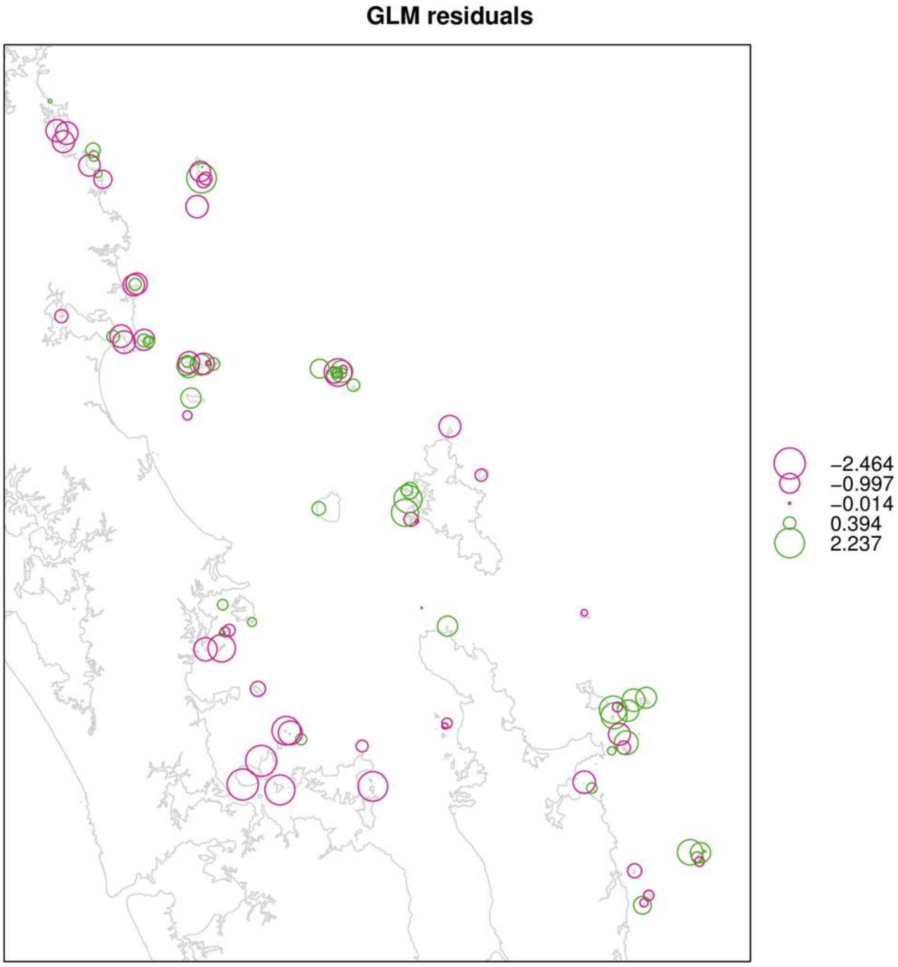


Figure 2.5 Map of GLM residuals for the species-area relationship by predator status.

Cleared Islands GLMs: Multi-model inference based on Poisson GLMs was used to explore possible predictors of species richness for the cleared islands (Burnham & Anderson 2003). The predictors explored were size, time since eradication, distance to the mainland and distance to Auckland – the latter two being potential proxies for human disturbance and/or distance to offshore feeding grounds. Distances were calculated using the rgeos package (Bivand & Rundel 2016). We used the MuMIn package (Barton 2015) to generate a complete set of candidate models based on the above predictors and ranked the resulting model fits by AICc. Multi-model inference did not provide strong evidence for a link between the time since eradication and species richness. Distance to Auckland emerged as a significant predictor in all six models that were within 3 AICc units of the optimal model, with higher species richness on islands further from the city. Distance to mainland and island size were each retained in three of the top six models and had a significant effect size only when they were not retained in the same model. Size had a positive effect on species richness, whereas distance to mainland had a negative effect (Table 2.3; Figure 2.8).

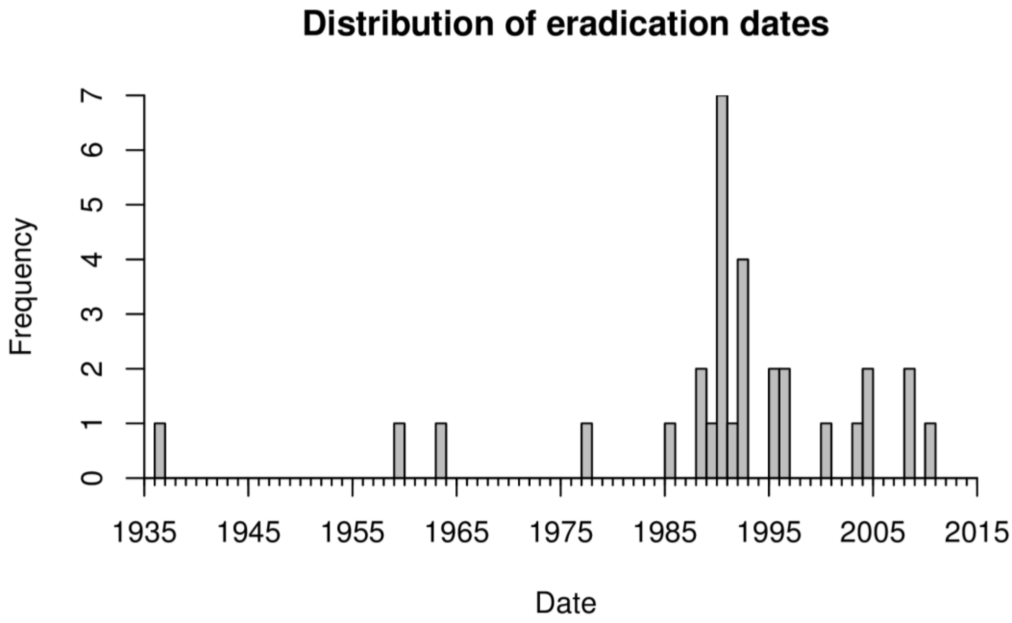


Figure 2.6 Frequency distribution of eradications (n = 31) on islands in the Hauraki Gulf, New Zealand included in our study.

Exploratory AFR analysis: There was no effect of mean age at first reproduction (averaged over all breeding species on a given island) by predator status (Kruskal-Wallis rank sum test, chi-squared = 5.72, df = 2, p-value = 0.057).

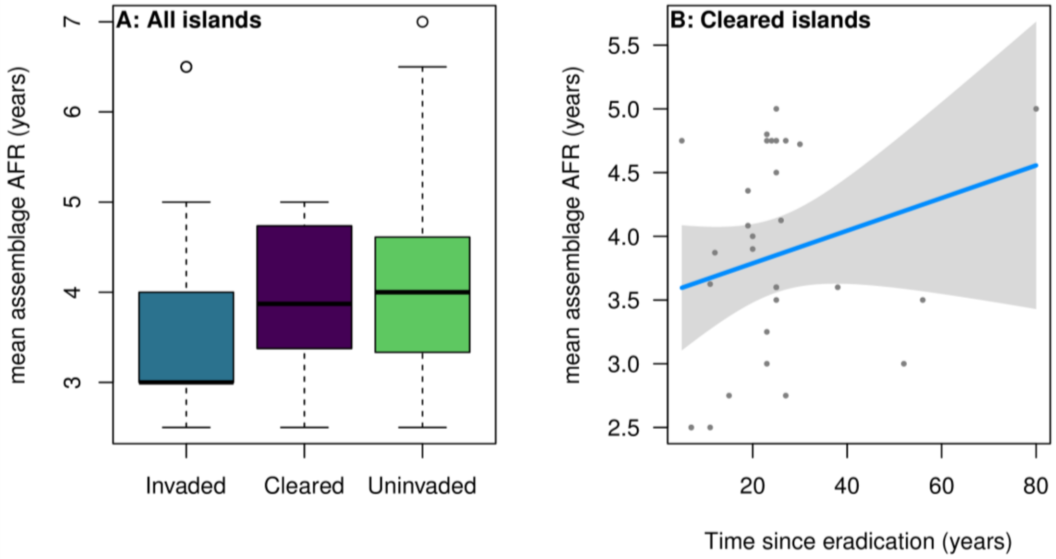


Figure 2.7 There was no effect of mean age at first reproduction (averaged over all breeding species on a given island) by predator status (Kruskal-Wallis rank sum test, chi-squared = 5.72, df = 2, p-value = 0.057). B: Ordinary least squares regression of mean assemblage AFR against time since eradication for the cleared islands. The positive trend is not statistically significant ($\hat{\beta}$ = 0.013, p = 0.20).

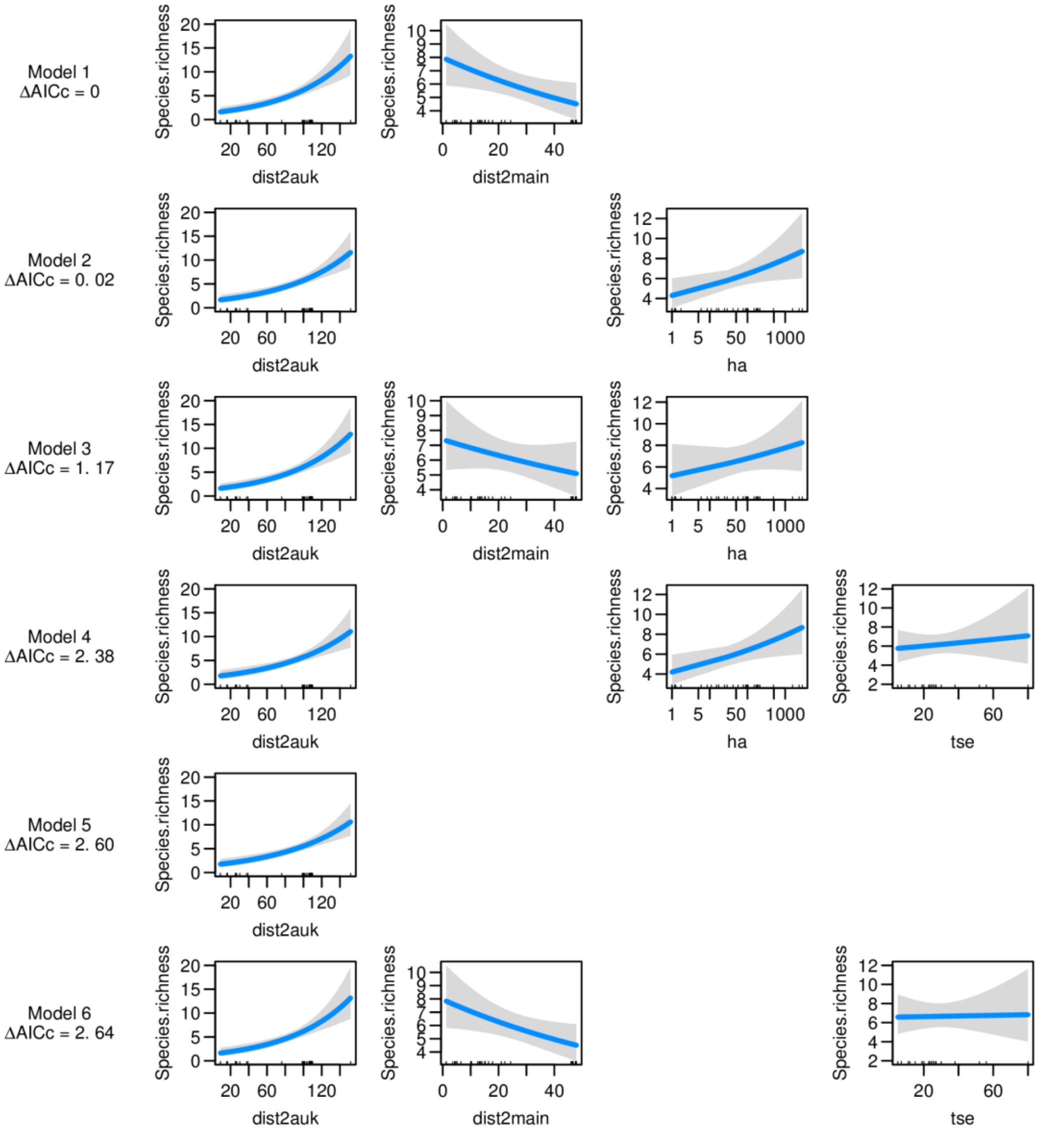


Figure 2.8 Partial effect plots of the top six models of species richness on cleared islands from the multi-model selection procedure. Model parameter estimates and associated standard errors are given in the main manuscript in Table 2.3.

Chapter 3 | Data

Seabird island nitroscapes: predictors of the distribution of seabird nutrient enrichment in soils and leaves

3.1 Abstract

Seabirds are ecosystem engineers by providing nutrient enrichment from guano deposition and disturbance from burrowing activity, and in turn influencing soil properties and flora composition on their island breeding sites. Therefore, the loss of nutrient subsidies when seabird populations decline or are extirpated from islands where invasive mammalian predators are present can result in major alterations to island floral and faunal communities. Few studies have quantified the spatial heterogeneity of seabird nutrient recovery following predator eradication at the within island scale. In this study, we conduct a cross-island comparative analysis quantifying soil and foliar nutrients among islands never invaded by invasive predators – Atiu and Green, an island cleared of predators where seabirds are recovering – Korapuki, and one without seabirds – Ahuahu, in the Mercury Islands group. We explore the potential drivers of spatial variation in nutrient recovery and use high resolution sampling in space to map how seabird density is distributed in soils and plants after predator eradication. We found that there is a strong relationship of soil and leaf nutrient content with seabird burrow density, but there is variability in the ecological influences on seabird nutrient distribution and accumulation in vegetation in response to nutrient enrichment. Understanding the patterns of nutrient enrichment recovery on islands inhabited by burrow-nesting seabirds can help inform management action to achieve long-term island restoration goals.

Key words: ecosystem engineering, predator eradication, restoration,

3.2 Introduction

Biotic communities and ecosystem processes are strongly influenced by the flow of nutrients within systems and across system boundaries, such as the terrestrial-marine interface (*i.e.,* allocthonous subsidies; Polis & Hurd 1996; Wright *et al.* 2010). On offshore islands, colonial nesting seabirds often act as vectors for marine derived nutrients through the deposition of guano, prey remains, failed eggs, and corpses (Mulder *et al.* 2011; Smith, Mulder & Ellis 2011). The annual rate of nutrient enrichment from seabirds is controlled by colony density and nesting type. For example, in a wedge-tailed shearwater (*Puffinus pacificus*) colony at low density (0.15 burrows$\cdot$m^2), the deposition rate of nitrogen (N) is ~51 kg$\cdot$ha^{-1} yr^{-1} (Bancroft, Garkaklis & Roberts 2005). In high density seabird colonies (>1 nest·m^2) enrichment of N can reach 1000 kg·ha^{-1} yr^{-1} for surface nesting birds (Schmidt *et al.* 2004). This extreme fertilization, coupled with the physical disturbance of burrowing activity and birds crashing through the canopy affects soil chemistry, salinity, pH, homogenization, and decomposition rates, which affects plant communities, growth rates, leaf chemistry, and soil microbial and invertebrate communities (Mulder *et al.* 2011; Orwin *et al.* 2016; Thoresen *et al.* 2017).

The loss of allochthonous subsidies if seabird populations decline or are extirpated as a result of invasive mammalian predators can therefore result in major alterations to island floral and faunal communities (Jones *et al.* 2008; Towns *et al.* 2009, 2011). Introduced predators remain one of the major threats to the worlds seabird populations (Paleczny *et al.* 2015). However, the removal of introduced predators from islands can allow for the recolonization and recovery of seabirds (Buxton *et al.* 2014; Borrelle *et al.* 2016; Brooke *et al.* 2017), potentially reinstating nutrient subsidies (Jones 2010), and concomitant ecosystem engineering effects.

Jones (2010) demonstrated that seabird deposited nutrients can be detected in ecosystem components of plants and invertebrates within a relatively short timescale using measures of C/N ratios and stable isotopes. Indeed, soil and leaf chemistry, soil pH, and plant community structure can be explained by seabird burrow density (Fukami *et al.* 2006; Mulder *et al.* 2009, 2011). These studies contribute to our broad understanding of the recovery of seabird ecosystem engineering properties following predator eradication. However, conservation managers are likely to assume that because predator effects are island-wide, seabird nutrient influences on ecosystem components will apply evenly, *i.e.,* provide whole island responses (*e.g.*, Mulder *et al.* 2009). In fact, there are few mechanistic investigations into how abiotic factors influence the within island spatial variation of seabird nesting density to ecosystem components (but see; Wait, Aubrey & Anderson 2005; Durrett *et al.* 2014).

The recovery of seabirds and reinstatement of seabird nutrient influences on ecosystem structure and function following predator removal is not straightforward (Towns 2002; Jones *et al.* 2011; Borrelle *et al.* 2016). The rate and trajectory of recovery of seabird island ecosystems will be influenced site-specific factors, such as the underlying regolith of the island, which determines background nutrient levels in the soils (Ollier & Pain 1996). Furthermore, burrow-nesting seabirds (Procellariidae) have species-specific nesting site preferences, variables such as elevation, slope, aspect, soil type, and forest types (Schramm 1986; Rayner *et al.* 2007; Whitehead *et al.* 2014). Thus, seabird nutrient deposition into a system, and background nutrient levels are not uniformly distributed (Durrett *et al.* 2014). Biological and ecological factors, such as plant and microbial communities, soil quality, topography, vegetation composition, and climatic conditions control the accumulation and movement of nutrients in a system (Irick *et al.* 2015). This spatial variation in deposition and accumulation of seabird nutrients following predator eradication influences successional processes of vegetation recovery and seabird driven ecosystem processes following invasive predator removal. If the seabird engineering effects do not fully recover, island ecosystems may enter a state of arrested succession, ultimately failing to meet restoration goals (Mulder *et al.* 2009).

In this study, we investigate the variation of seabird nutrient enrichment in seabird island forest canopies using comparative analysis of islands with three different predator histories. We also investigate the ecological drivers of nutrient distribution in soil and plants using a high-resolution sampling regime to map soil and foliar nutrient patterns on Korapuki Island, where seabird recovery is patchily distributed following predator eradication ~30 years ago. The purpose of our study is twofold; 1) quantify the levels of soil and foliar nutrients on islands with different predator status in relation to seabird nesting density; and 2) quantify the abiotic factors, including: elevation, slope, aspect, soil compaction, and water availability that drive the spatial variation in soil and foliar nutrient measures. We expect that the effects of seabird nutrient enrichment distribution will be regulated in three ways; 1) nutrient concentration decreases as distance to burrows increases; 2) nutrients run-off during rainfall events and accumulate in valleys, basins and near the shoreline; or 3) a combination of both, dependent on scale-dependant ecological factors.

3.3 Methods

To explore the spatial variation of seabird deposited nutrients following predator eradication and the ecological drivers of nutrient distribution, we measured soil nitrate (NO_3^-) and Carbon C/N of the soils, and foliar N and C/N of the dominant canopy species: pōhutukawa (*Metrosideros excelsa*). Following the rapid hydroxylation of uric acid in guano and nitrification processes, ammonium and NO_3^-, are the most bioavailable forms of N for plants (Jones 2010). Given the high correlation between ammonium and NO_3^- in seabird dominated systems (Jones 2010), and an intense sampling regime (n_{total}=376), we measured only NO_3^- to elucidate seabird nutrient enrichment in island soils.

We conducted a cross-island analysis using four islands to examine the difference between total N, C/N, and NO_3^- on islands where invasive mammalian predators have never invaded ([two] Uninvaded), have been eradicated ~30 years ago (Old Erad), and recently eradicated with few/no nesting seabirds (~3 years ago; New Erad). We explored spatially the relative influence of the ecological variables of; slope, aspect, elevation, rainfall, and soil compaction on nutrient accumulation and distribution in island soils and pōhutukawa leaves. We chose to sample pōhutukawa trees because of the wide distribution of this species on New Zealand's offshore islands. Pōhutukawa are an ecologically opportunistic species, tolerant to the effects of wind driven salt, bare soils, rocky cliffs, and water limitation (Bylsma, Clarkson & Efford 2014), characteristic of seabird islands.

3.3.1 Study sites

The Mercury Islands are located off the east coast of the Coromandel. The island group has been described in detail elsewhere (Towns *et al.* 2016). Briefly, the islands share similar biogeographic features and climate conditions, the soils are homogeneously volcanic and friable but soils on Ahuahu are compacted from stock farming. On all islands, slopes are moderately steep (21–25°) to steep (26–35°) and soil erosion form and degree are slight (1-10%; Landcare Research New Zealand 2017). The climate is humid-temperate, with average annual rainfall of 1832.4 mm, most falling in the Austral winter (238 mm/month) and 83-91% relative humidity. Mean annual temperature is 15˚C (CliFlo 2017).

We sampled four of the seven islands in the group: 1) Korapuki (18 ha; -36.65 S, 175.85 E), which was cleared of kiore (*Rattus exulans*) and rabbits (*Oryctolagus cuniculus*) in 1986-1987 respectively (Old Erad), 2) Atiu (13.5 ha; -36.63 S, 175.86 E) and 3) Green (2.5 ha; -36.64 S, 175.84 E), which have never been invaded by predators (Uninvaded); and 4) Ahuahu (1867 ha; -36.64 S, 175.81 E), which was eradicated of kiore, ship rats (*R. rattus*), and cats (*Felis catus*) in 2014 (Towns *et al.* 2016). For the purposes of our analysis, we pooled data from Atiu and Green islands for two reasons: 1) because of the small sample size for each island and; 2) they have similar seabird assemblages and nesting density, and geophysical characteristics (*i.e.*, steep cliffs, soil type).

The seabird assemblages on Atiu/Green, and Korapuki are such that there is seabird activity year-round, with a short relatively seabird free period in April (Supporting information; Table 3.3). Seabird species breeding on these islands include; oi (*Pterodroma gouldi*), pakahā (*Puffinus gavia*), toanui (*Puffinus carneipes*), little shearwater (*Puffinus assimilis*), takahikare (*Pelagodroma marina*), kuaka (*Pelecanoides urinatrix*), and korora (*Eudyptula minor*). There are only oi breeding on Ahuahu in very low numbers (~1 pair within our sample sites).

On Atiu and Green, the vegetation is a mixed canopy of pōhutukawa, māhoe (*Melicytus ramiflorus*), kanono (*Coprosma macrocarpa*), and ewekuri (*Strebulis banksii*). The canopy species assemblage on Korapuki and Ahuahu is indicative of succession following modification, which is primarily composed of pōhutukawa canopy, and secondary regenerating forest of broadleaf species and coastal shrubs, including māhoe, kanono, kawakawa (*Piper excelsum* subsp. *peltatum*), ewekuri, and māpou (*Myrsine australis*) (Atkinson 2004; Bergin & Hosking 2006). The presence of rats, and grazing sheep and cattle on Ahuahu, and rabbits on Korapuki, led to the dominance of pōhutukawa, and weedy species in forest remnants, because more palatable plant species, such as māhoe, kanono, and kawakawa became heavily browsed (Atkinson 2004).

3.3.2 Sampling design

We selected sites dominated by pōhutukawa trees, and sampled trees approximately 25-40 m apart, but excluded cliffs, unsafe slopes, and unvegetated beaches. Samples sizes were n=132 on Korapuki, n=34 on Ahuahu, and n=13 on Atiu/Green. On Korapuki, we used a strongly dispersed sampling design, where samples were taken approximately 25 m apart, to ensure spatial autocorrelation for interpolation of the variables between samples points (De Gruijter *et al.* 2006). We sampled on two occasions over 10 days, during the Austral summer (February-March 2017; dry; n=179) and winter (August 2016; wet; n=179). We recorded slope, aspect, and elevation at each site using a calibrated Garmin GPSMAP 64s (Garmin Ltd, Lenexa, KS, USA). Burrow density was calculated as burrows per m^2, as a proxy for seabird activity (Fukami *et al.* 2006), within a 5 m radius (78.54 m^2) around each sampled pōhutukawa tree.

We measured soil compaction (top 10 cm; Dickey-John soil compaction tester; Auburn, IL, USA), and soil moisture (Decagon ProCheck and EC-10 soil moisture sensor; Decagon, Pullman, WA, USA). In addition, we used rainfall data from the NIWA Taihoro Nukarangi's National Climate data (CliFlo 2017) for one month, two weeks and one week prior to our sampling dates to test the relative influence of water availability on nutrient distribution and accumulation. The biopedturbation of the soil by seabird burrowing activity has not been found to influence the vertical stratification of soil nutrients in soil depths up to 50 cm (Fukami *et al.* 2006). Using a trowel, we took approximately 100 g of soil to 10 cm depth from three locations around the tree. Each sample was homogenized in the field. In heavily burrowed areas, we took soil samples at the surface to avoid damaging burrows or disturbing birds. Soil pH of a slurry of soil (10 g) with deionized water (50 ml) was measured in the field using an Eketcity handheld pH meter (Anaheim, CA, USA).

Factors other than soil nutrient values can cause variation in foliar nutrients (Vitousek 2004). However, Vitousek (2004) found that foliar nutrients in tropical *Metrosideros* spp. can reflect soil nutrient status when leaves of similar age and position on the canopy are sampled across a range of substrates and topographies. Further, leaf age can affect the concentration of nutrients, where mobile nutrients, such as N decline with age (Snowdon, Ryan & Raison 2005). Therefore, we collected three to five new growth leaves from pōhutukawa trees. We aimed to get leaves of the same age and canopy position. When sampling was unsafe (*i.e.,* tall trees and/or cliffs) we collected the youngest leaves that were accessible.

Soil samples (sieved [1 mm] to remove large debris) and leaves were rinsed in deionized water and oven dried (55°C, ~48 h) and ball milled (400 rpms for 3 and 8 minutes respectively; Retsch PM 100 Ball Mill, Germany). Soil NO_3^- was extracted using a Nitrate (NO_3^-) test kit (API, Chalfont, PA, USA) to solution and a spectrophotometric determination conducted using a UV/Vis absorbance analyser (FLUOstar Omega, BMG Labtech, Ortenberg, Germany), which we reported as NO_3 $g{\cdot}m^2$. The soil and the leaves were analysed for total N, and carbon (C) with a multipoint normalization using acetanilide with an elemental analyser (ECS 4010, Costech Analytical, Valencia, CA) at the Stable Isotope lab at Washington State University, USA, and C/N calculated. Carbon (C) and nitrogen (N) are closely linked with biological processes (Coruzzi & Zhou 2001). The ratio of these products can provide insight into nutrient stocks and cycling processes, turnover, and indicators of ecosystem process recovery after perturbation (Coruzzi & Zhou 2001).

3.3.3 Quantitative analysis

To investigate if there was a difference between island predator histories using generalized linear mixed effects models (GLMMs) with normal errors and identity link function. We used the response variables of; soil NO_3^-, C/N, and foliar leaf total N, C/N as fixed effects, and island history and season as random effects and ranked the resulting model fits by AICc. Model parameters were estimated using the *nlme* package (Pinheiro et al. 2017) in *R* (R Core Team 2013). We performed an analysis of variance ANOVA with post hoc Tukey's tests to test if there is a seasonal (summer and winter) difference for each of the response variables (R Core Team 2013).

In order to explore the ecological influences on the distribution of soil and leaf nutrient properties in relation to burrow density, we used GLMMs, with island predator history and season as fixed effects. We performed step-wise regression using the candidate predictor variables of burrow density, slope, aspect, elevation, rainfall (one month, two weeks and one week prior to sampling) and soil moisture at the time of sampling, and soil compaction on the distribution of soil NO_3^-, C/N and leaf N, C/N. Models were selected using *backward* stepwise regression. The stepwise regressions were carried out with the function *lme* of the *nlme R* package (Pinheiro *et al.* 2009). All models were fitted using spherical spatial correlation structures to account for non-independence of data points arising from the high-density sampling design. All statistical analyses were done in R statistical software v. 3.1 (R Core Team 2013).

For the high-resolution spatial maps of Korapuki Island (Old Erad; Figure 3.1) we used the interpolation technique *Splines with Barriers* in ArcGIS (ESRI 2011). Interpolation techniques (or kriging) rely on spatial autocorrelation to predict values, such as soil nutrients, between each sample point, where the fewest number of samples are needed to create an accurate profile (De Gruijter *et al.* 2006). The interpolations are a prediction of values of the variable of interest between sampling points based on such variables as topography, slope, soil depth and characteristics (De Gruijter *et al.* 2006). We interpolated burrow density (burrows·m^2), and our response variables of soil NO_3^-, soil C/N, Leaf N, and leaf C/N (Figure 3.1). Because we found no difference between seasons for the measured variables on Korapuki, we used the mean value to generate the interpolation maps of each of the measured variables (Figure 3.1). All maps are using the geographic datum NZGD2000 and the New Zealand Transverse Mercator projection.

3.4 Results

3.4.1 Cross-island comparison

On Ahuahu (New Erad), seabird burrow density was nil at all sites except at one sampling location, where there was an unoccupied burrow. On Korapuki (Old Erad) mean burrow density was 0.18 burrows·m^{-2}, with maximum density of 0.73 burrows·m^{-2}, which were found predominantly on elevations > 25 m and within ~100 m of the shoreline (Figure 3.1). On Atiu/Green (Uninvaded) mean seabird burrow density was 1.27 burrow·m^{-2} (min=0.8, max=1.66 burrows·m^{-2}). Ahuahu had a mean soil pH of 5.97, ranging from 4.23 – 7.57, and Korapuki 6.53, ranging from 3.58 – 7.48, and Atiu/Green had mean soil pH of 3.86, with a range of 3.10 – 4.57, significantly lower than Korapuki and Ahuahu islands ($p<0.0001$; Supporting Information; Figure 3.4.A). Korapuki and Atiu/Green had comparable (low) mean soil compaction, different to Ahuahu with high soil compaction ($p<0.0001$); Supporting Information; Figure 3.4.B).

On Atiu/Green, soil NO_3^- was 32.1 % greater in the winter than in the summer ($p=0.003$), but there was no effect of seasonality on Korapuki and Ahuahu in soil NO_3^- (Supporting information; Figure 3.5). Mean soil NO_3^- aggregated for both seasons increased in response to increased burrow density across the island histories. Mean soil NO_3^- on Korapuki was 28 % greater than Ahuahu ($p=0.056$), and Atiu and Green mean soil NO_3^- was 109.2 % and 127.5 % greater than Korapuki and Ahuahu respectively ($p=0.0002$; $p<0$; Table 3.1; Figure 3.2.A).

Table 3.1 Mean and standard errors for the response variables NO_3, soil N, C/N, and pōhutukawa leaf % N, and C/N on the island treatments of newly eradicated, old eradicated and uninvaded by introduced mammalian predators.

Island	Area (ha)	NO_3 g m^{-1}	Soil C/N	Pōhutukawa leaf % N	Pōhutukawa leaf C/N
New Eradicated (Ahuahu)	1867	2.341 (0.355)	18.9:1 (0.36)	0.66 (0.023)	68.53:1 (5.76)
Old Eradicated (Korapuki)	18	3.103 (0.172)	13.76:1 (0.21)	0.49 (0.015)	94.16:1 (4.66)
Uninvaded (Atiu and Green)	13.5 & 2.5	10.569 (0.461)	10.6:1 (0.49)	0.88 (0.029)	49.99: (6.79)

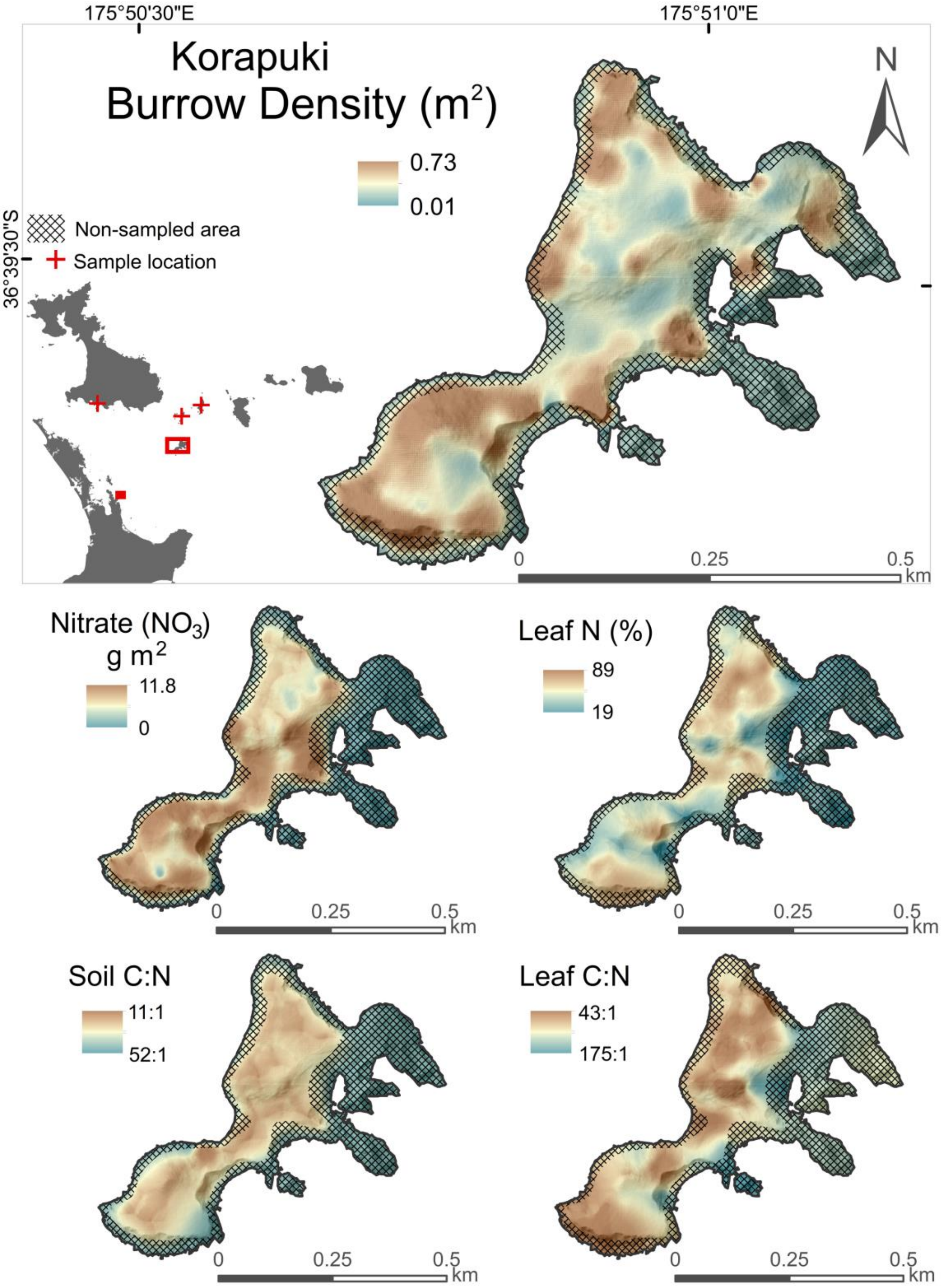


Figure 3.1 The spatial distribution of burrow density (burrows·m^2), soil nitrate (NO_3^-) and soil C/N, and pōhutukawa leaf variables of total leaf N, and leaf C/N on Korapuki Island, values are mean across both seasons and interpolated between sample points (approximately 25m apart). The hatched area represents areas of the island that were not sampled. Sample locations on Atiu/Green and Ahuahu are indicated by red crosses.

In the opposite trend to soil NO_3^- on Atiu/Green, leaf % N decreased 15.4 % between summer and winter (p=0.003), there were no seasonal difference in leaf % N for Korapuki or Ahuahu (Supporting Information; Figure 3.2.B). Leaf % N was different between all island histories but did not follow the same linear increase with burrow density as soil NO_3^-. Korapuki leaf % N was 29.1 % and 56.7 % lower than Ahuahu and Atiu/Green respectively ($p<0.001$; Figure 3.2.B). Leaf % N on Ahuahu was 28.8 % less than Atiu/Green ($p<0.001$; Table 3.1; Figure 3.2.A).

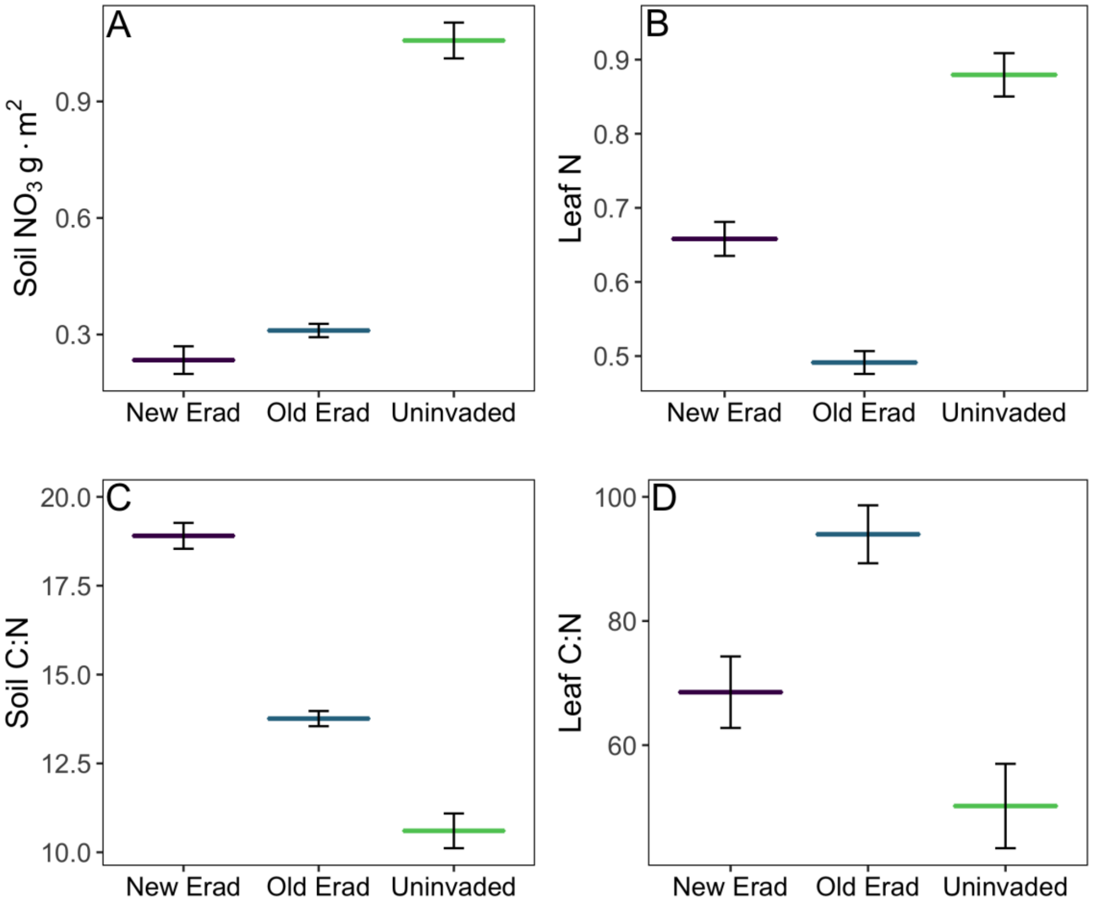


Figure 3.2 Generalized linear mixed effects model (GLMM) predictions (means ± standard errors) of each of the response variables on islands with different predator histories: New Erad - Ahuahu, eradicated of kiore, ship rats and cats in 2014; Old Erad – Korapuki, cleared of kiore and rabbits in 1986-87 respectively, and; Uninvaded – Atiu/Green, never invaded by invasive predators. The response variables are: A) Soil NO_3^-; B) Leaf % N; C) Soil C/N and; D) Leaf C/N.

There were differences among all island histories for soil C/N (Figure 3.2.C; $p<0.0001$ in all cases). Mean soil C/N on Ahuahu was 31.5 % and 56.3 % higher than

Korapuki and Atiu/Green respectively ($p<0.0001$; Figure 3.2.C). Mean soil C/N on Korapuki was 25.9 % higher than Atiu/Green ($p=0.002$; Figure 3.2.C). Mean leaf C/N on Ahuahu was 31.5% lower compared to Korapuki ($p=0.05$; Figure 3.2.D). Atiu/Green mean leaf C/N was 61.3 % and 31.3 % lower than Korapuki and Ahuahu respectively ($p<0.0001$; Table 1; Figure 3.2.D). For all island predator histories, a post hoc Tukey's test showed no seasonal differences for the response variables of soil C/N and leaf C/N (Supporting Information; Figure 3.5.C & D).

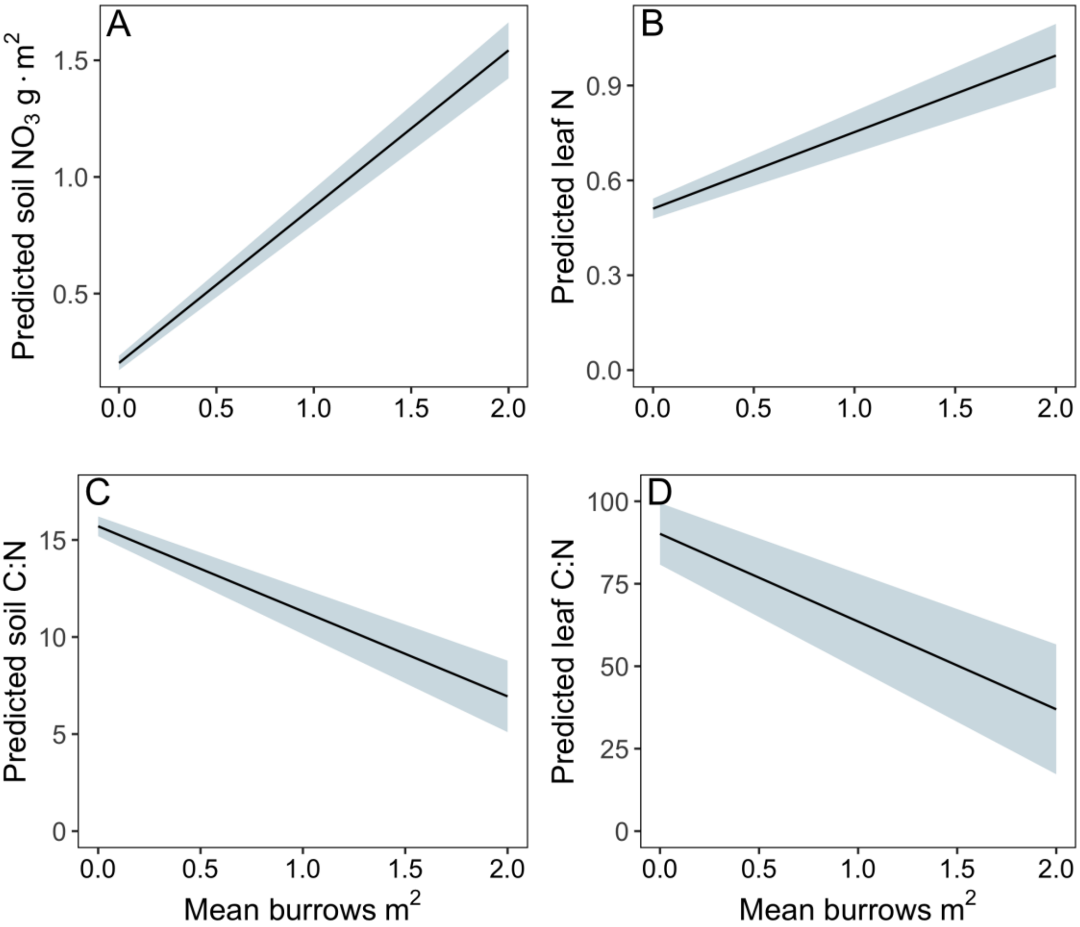


Figure 3.3 Predicted NO_3, soil C/N, and leaf N, and leaf C/N in response to increasing seabird burrow density (burrows·m^2). Shaded polygons denote the regression standard error.

Predicted values for the response variables exhibited expected trends, with soil NO_3^- increasing in response to greater numbers of seabird burrows (Figure 3.3.A), leaf % N followed the soil NO_3^- trend, increasing in response to increasing burrow density (Figure 3.3.B). Both soil and leaf C/N are predicted to decrease, indicating nutrient limitation is decreased in response to increasing seabird nesting density (Figure 3.3.C & D).

3.4.2 Ecological drivers of nutrient distribution

We used stepwise regression analyses to test if burrow density, slope, elevation, soil moisture, soil compaction and aspect predicted the response variables of soil NO_3^-, soil C/N, leaf % N, and leaf C/N. For soil NO_3^-, a significant positive response was found for burrow density (64.52 ± 5.4 SE, df = 173), and significant negative response for elevation (-0.27 ± 0.09 SE, df = 173, AIC= -27.21; Table 3.2), no other predicters were retained in the stepwise regression model. Slope (-0.06 ± 0.01 SE, df = 166), elevation (0.03 ± 0.01 SE, df = 166), and aspect (0.03 ± 0.01 SE, df = 166) were the strongest predictors of soil C/N (Table 3.2). Burrow density and soil compaction were retained in the stepwise regression model predicting leaf % N (0.13 ± 0.06 SE), and burrow density, elevation, soil compaction, and aspect were the strongest predictors of leaf C/N (-29.1 ± 7.88 SE, 0.26 ± 7.88 SE, -0.51 ± 0.1 SE, 0.05 ± 0.02 SE respectively, df = 162; Table 3.2).

Table 3.2 Model coefficient estimates and standard errors (in parentheses) for response variables to ecological predictors from the stepwise regression analysis. All island histories and seasonality treatments were pooled for these analyses (n=376). Rainfall for one week, two weeks, and one month prior to sampling are excluded from the table because there was no predictive power, as with soil moisture (%).

	Response variables			
	Soil NO_3^-	**Soil C/N**	**Leaf %N**	**Leaf C/N**
Intercept	32.79	14.46	0.63	62.71
	(7.54)	(1.99)	(0.082)	(19.79)
Burrow density (m^2)	64.52***		0.13**	-29.07***
	(4.52)		(0.058)	(7.89)
Slope		-0.06***		
		(0.01)		
Elevation (m)	-0.27**	0.03***		0.26*
	(0.09)	(0.011)		(0.14)
Soil moisture (%)				
Soil compaction				-0.51***
				(0.103)
Aspect		0.003*		0.046**
		(0.001)		(0.022)

Note: *p<0.1; **p<0.05; ***p<0.01

3.5 Discussion

Despite the controls seabirds have over ecosystem community composition and functioning on their island breeding sites, few studies have quantified the spatial heterogeneity of seabird nutrient influences and seabird density (Durrett *et al.* 2014). We investigated the spatial pattern of nutrient enrichment recovery using a cross island comparison and high-resolution mapping of an island where seabirds are recovering following predator eradication approximately 30 years ago with varying seabird nesting density. We found that burrow density is a good predictor of soil nitrate (NO_3^-), leaf % N and leaf C/N, but not soil C/N. As predicted, soil NO_3^- accumulates in valleys and basins (Figure 3.1). However, the relationship between seabird nesting density and foliar nutrients is less clear and likely to be more strongly influenced by species-specific physiology and by variable ecological and climatic factors (Snowdon, Ryan & Raison 2005; Niu *et al.* 2016). We discuss the drivers of this variability as explained by our results and draw from the literature to help explicate the complexity of factors controlling seabird nutrient enrichment distribution on islands.

In most terrestrial ecosystems, N is a limiting nutrient for plants, thus the enrichment from seabird activity has a strong influence on the plant communities of seabird islands (Mulder *et al.* 2011). We can assume that on Atiu/Green (Uninvaded) islands, which have remained free of invasive predators, nutrient distribution in soils and vegetation uptake is in a state of stochastic equilibrium (Gundersen *et al.* 1998; Niu *et al.* 2016). Global patterns show N uptake in plants generally increases with fertilization initially and levels off when the plant is N saturated (Niu *et al.* 2016). Lovett & Goodale (2011) detected a 20 % increase in foliar N in oak forest experimentally fertilized with N, which over the long-term remained stable. This pattern is reflected in our results for Atiu/Green in the high soil NO_3^- and leaf % N values, and low leaf C/N indicating that pōhutukawa on Uninvaded islands do not appear to competitively disadvantaged by lower nutrient availability (Figure 3.2.B & D). Conversely, leaf N and C/N results on Korapuki (Old Erad) and Ahuahu (New Erad) suggest that pōhutukawa may have smaller reserves of N due to lower soil nutrient levels (Figure 3.2.B & D). This difference between islands is to be expected given their lower burrow density, and sporadic, patchy distribution of seabird activity (Figure 3.3.A & Figure 3.1). Ahuahu showed higher leaf % N than expected despite having no seabirds present (Figure 3.2.B). On Ahuahu, it is likely that pōhutukawa is capitalizing on nutrient enrichment from livestock that are grazed on the island, as there was evidence of grazing in the forested areas where the samples were taken (SBB's personal observation), which was largely unavoidable given the small patch size of the regenerating native forest.

While our stepwise regression analyses did not select soil moisture, or rainfall levels prior to sampling, as a predictor of soil NO_3^-, nitrate is extremely soluble in water, thus more mobilized nitrogen should reflect strongly in NO_3^- levels (Haynes & Goh 1978). It would be expected that there may be high run-off of soil NO_3^- during the wet season (Haynes & Goh 1978). Gunderson et al. (1998) found that N leaching was greater at enriched sites because N availability may exceed the demand of microbes and plants. However, we observed an increase in soil NO_3^- from summer (dry) to the winter (wet) sampling periods on Atiu/Green (Supporting Information; Figure 3.4.A & B). This likely illustrates the mobilization of NO_3^- and additional guano deposition during the initial stage of the breeding season when birds are returning to the islands (Gaskin & Rayner 2013). Although not significant, we observed a slight decrease in mean soil NO_3^- between seasons on Korapuki and Ahuahu (Supporting Information; Figure 3.5.A), suggesting that some NO_3^- deposited by seabirds during the winter may be running-off or immediately taken up by plants, although further investigation is needed.

On Atiu/Green, there was an increase in leaf % N for pōhutukawa from summer to winter, suggesting that pōhutukawa on unmodified islands may be more adapted to exploit higher concentrations of N. In contrast, although not significant, there was a decrease in leaf % N on Korapuki and Ahuahu (Supporting Information; Figure 3.5.B). The physiological response of pōhutukawa on islands with few seabirds may be to regulate nutrient uptake for times when it is needed for growth to avoid ion imbalances or nutrient toxicity (Niu *et al.* 2016). All vascular plants have evolved regulatory mechanisms to maintain xylem and physiological processes when water is limited. Short term mechanisms to minimize water loss is achieved primarily through stomatal closure to reduce transpiration rates; this also causes decreases in CO_2 diffusion rates affecting carboxylation reactions in photosynthesis (Farquhar & Sharkey 1982). Pōhutukawa are extremely tolerant of drought conditions, and may in fact be limited by waterlogging, given they are not found on wet sites (Bergin & Hosking 2006). Trees sampled on Atiu/Green were predominantly on exposed steep slopes, reducing water retention compared to sites on Korapuki and Ahuahu, which were less steep. Thus, on Korapuki and Ahuahu, an excess of soil moisture in the winter (wet) season may slow photosynthetic rates. Furthermore, light levels may affect photosynthetic capacity among the islands sampled. Indeed, the natural establishment of pōhutukawa is usually restricted to sites with full sunlight (Bergin & Hosking 2006), suggesting light limitation, which would reduce photosynthetic rates and lead to a reduction in chlorophyll and associated leaf % N concentrations, which we observed on Korapuki and Ahuahu (Blackmer & Schepers 1995).

In addition to seabird burrow density (and associated nutrient enrichment), the range in leaf C/N for Korapuki may be attributed to leaf physiology and natural variability. For example, in the physiologically similar genus *Eucalyptus* (also Myrtaceae), the C/N of green leaves can range from 28-65 (Snowdon, Ryan & Raison 2005). This high C/N is because, while C in leaves remains relatively stable, N concentrations can range two orders of magnitude depending on soil C and N concentrations and distribution, growing conditions, and climate (Snowdon, Ryan & Raison 2005). Unravelling the influences on leaf C/N is further complicated by the variability of soil C and N, which can change dramatically over short timescales given environmental conditions, such as organic matter accumulations, water availability, temperature, and microbial activity (Snowdon, Ryan & Raison 2005).

Our data for soil C/N reflected NO_3^- concentrations and ecological drivers of C/N previously described in the literature (Figure 3.2.A & C). Higher C/N values are expected where rates of decomposition are slower and NO_3^- is limited or leaching is high (Lovett, Weathers & Arthur 2002). Furthermore, in areas of high seabird activity, understory vegetation and leaf litter is minimal, influencing decomposition rates, and thus carbon stores (Mulder *et al.* 2011). Leaf litter decomposition rates are likely to be strongly influenced by the leaves of pōhutukawa, which are high in lignin with a waxy cuticle - a physiological mechanism for maintaining water (Bergin & Hosking 2006). Thus, leaf decomposition rates are slower compared to broadleaf species, which are more widely distributed on uninvaded islands (Cameron 1990; Atkinson 2004).

Snowdon et al. (2005) found that a strong predictor of soil C/N was the terrain attribute of slope, where soils on upper slopes had lower C/N than soils on lower slopes and depressions where leaf litter accumulation. Our results support this with a negative relationship for soil C/N and slope (Table 3.2). Finally, species composition can affect soil C/N; Finzi et al. (1998) found soil C/N ranged ± 4.7 among six species of tree in an old growth North American deciduous forest, which they attributed to differences in litter production and decomposition rates of individual species foliage. As the dominant canopy species on Korapuki, the variable decomposition rates of pōhutukawa may exert strong controls over N and C cycling, which may also be controlled by species specific root distribution and microbial biomass and activity in the soils (Vesterdal *et al.* 2008), or by root damage cause by seabird burrowing activity (Mulder *et al.* 2011).

Coupled with topographical and environmental drivers of soil nutrient distribution, the biopedturbation from expanding seabird burrowing activity on Korapuki is likely to exert strong controls on nutrient movement. Indeed, seabird driven soil processes can have a strong influence on nutrient distribution for several reasons: soil aggregation is poor, water infiltration is high; thus nutrient leaching can be high, and environmental conditions can result in high salinity and aridity due to high winds (Bancroft, Garkaklis & Roberts 2005). The level of soil displacement from burrowing activity, and the incorporation or exclusion of leaf litter in the soils will depend on seabird species' physiology and nesting preferences. For example, burrows were most dense on higher elevations, close to the island edge with a north-westerly aspect (Figure 3.1). This infers colony expansion is thus far limited to the most preferential habitat and will likely expand into less ideal habitat over time (Buxton *et al.* 2016), perhaps resulting in a more uniform nutrient profile as on Atiu/Green islands.

The spatial decoupling of burrow density to nutrient distribution is also likely to be influenced by species-specific behavioural and physiological attributes (Wait, Aubrey & Anderson 2005; Durrett *et al.* 2014). For example, larger birds may distribute themselves or behave differently than smaller species of seabirds. One species, oi (550 g), is widely distributed on the islands in the Hauraki Gulf because they are more tolerant to predator invasions, and of the species on Korapuki are recovering most rapidly. However, because of their size, burrow density is generally ~0.26 burrows·m^2, lower than smaller species, such as tītī wainui (120 g *Pachyptila turtur*), which can form upwards of 3 burrows·m^{-2} (Mulder & Keall 2001). Body size is a good indicator of the quantity of guano produced per bird. Additionally, different species also feed at different trophic levels, thereby relative quantities of nitrogen deposited within a system will vary depending on the seabird assemblages and nesting density (Durrett *et al.* 2014).

Behavioural differences among species may also play a role in the unpredictable patterns of nutrient distribution, unrelated to burrow density and distribution on islands during the recovery phase. For example, some larges species of shearwaters use a 'takeoff' tree or promontory, where birds void guano before flight, thus depositing potentially large quantities of guano in an area decoupled from burrow density (Durrett *et al.* 2014). Likewise, there may be sites within the forest where landing site may be preferred due to the density of the forest canopy, creating a 'hotspot' of guano deposition. Additionally, environmental covariates, such as soil type and depth, ground cover and vegetation community influence the distribution of seabird burrows on islands (Buxton *et al.* 2016).

Seabird colony recovery after predator eradication is influenced by variable ecological factors but also species-specific demographic and physiological traits (Buxton *et al.* 2014; Borrelle *et al.* 2016). Thus, the reinstatement of seabird nutrient enrichment on islands cleared of invasive predators is unevenly distributed (Durrett *et al.* 2014). As predicted, we found that burrow density is a good predictor of soil N distribution but not for leaf N distribution. Elevation was the only ecological variable found to influence soil N distribution; however, there are multiple confounding factors driving seabird deposited nutrient distribution. Further influencing the distribution of nutrients is the underlying regolith of the islands and severity of historical habitat modification on soil properties and vegetation communities (Atkinson 2004), and thus the recovery of biotic components affected by the invasion of predators and subsequent removal.

While seabird nutrient influences can be detected in foodweb components of island ecosystems upon their re-establishment and colony expansion (Jones 2010), the overall nutrient enrichment, which is an important driver of species composition and ecosystem function (Jones *et al.* 2011), may take longer to recover. Eventually, we might expect to see the equilibrium of nutrient distribution in soils and foliage on recovering islands as the pōhutukawa canopy diminishes and the plant community structure reflects a more seabird dominated one. While pōhutukawa may be benefitting from the nutrient enrichment of seabirds, they may also slow vegetation recovery to a composition comparable to uninvaded islands. Given that pōhutukawa can live upwards of 300 years (Atkinson 2004), much longer studies will be required where vegetation cover could potentially thwart ecological restoration goals.

3.6 Supporting information

On Korapuki (Old Erad), there are higher densities of oi (grey-faced petrels *Pterodroma gouldi*), which likely contributing more nutrients than other species, particularly during their incubation and provisioning period (June-Jan; Table 3.3). On Ahuahu (New Erad), oi numbers are fewer than 2 pairs at sampling sites (S. Borrelle, D. Towns, pers observations). On Atiu/Green (Uninvaded), flesh-footed and little shearwaters dominate.

In general, soil pH is likely to play a role in the uptake of nutrients by pōhutukawa. A soil pH of ~4.0 has been shown to maximize the absorption of nitrates. Conversely, plants will absorb the maximum amount of ammonium at a soil pH of ~8.0 (Haynes & Goh 1978). Soil pH was most variable on Korapuki, strongly associated with burrow density. Soil pH on Atiu and Green were significantly lower than Korapuki and Ahuahu ($p<0$), which likely influences leaf %N (Figure S1.A). However, because we did not look at multiple forms of nitrogen in the soils, the role of different species of N, soil pH and redox potential in seabird enriched soils warrants further investigation.

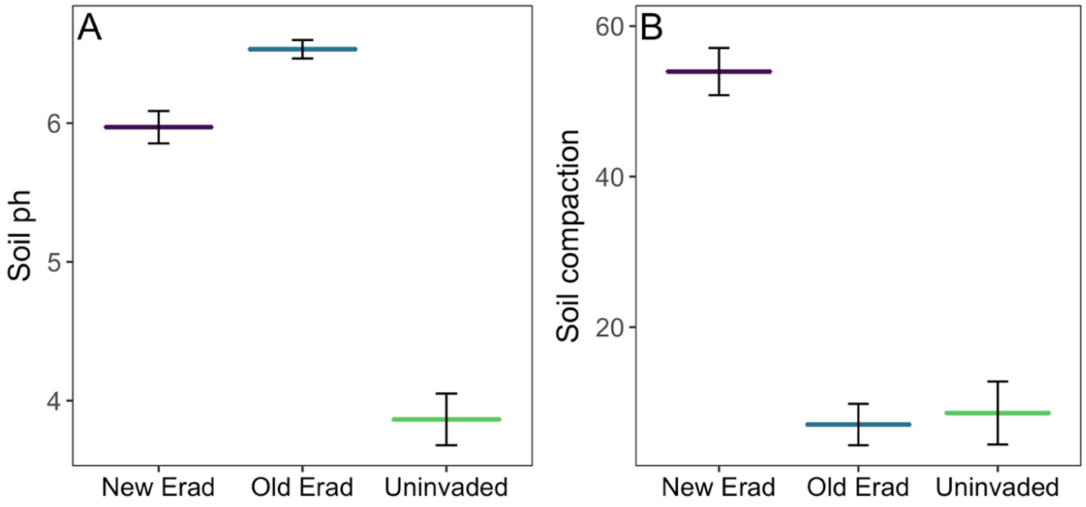


Figure 3.4 Model predicted soil pH (A) and soil compaction (B) for island treatment with season as a random variable.

Table 3.3 Breeding timetable of species on the Mercury Islands study sites.

Species	**Jan**	**Feb**	**March**	**April**	**May**	**June**	**July**	**Aug**	**Sept**	**Oct**	**Nov**	**Dec**
Oi / grey-faced petrel (*Pterodroma gouldi)*	Fledge		Prospecting			Laying		55 days incubation		Provisioning		Fledge
Toanui / flesh-footed shearwater (*Puffinus carneipes)*	~50 days incubation		Provisioning		Fledge				Prospecting			Laying
Pakahā / fluttering shearwater (*Puffinus gavia*)	Fledge						Prospecting		Laying		Provisioning	
Little shearwater (*Puffinus assimilis*)					Prospecting		Laying		Provisioning		Fledge	
Takahikare / white-faced storm petrel (*Pelagodroma marina)*	57 day incubation		Fledge					Prospecting		Laying		
Kuaka / common diving petrel (*Pelacanoides urinatrix)*	Provisioning		Fledge			Prospecting		Laying			53 day incubation	
Kororā / little penguin (*Eydyptula minor)*	36 day incubation		Provisioning		Fledge		Laying (2nd clutch & sometimes rare 3rd clutch)					
Tītī wainui / fairy prion (*Pachyptila turtur)*	44-55 day incubation	Provisioning		Fledge						Laying		44-55 day incubation

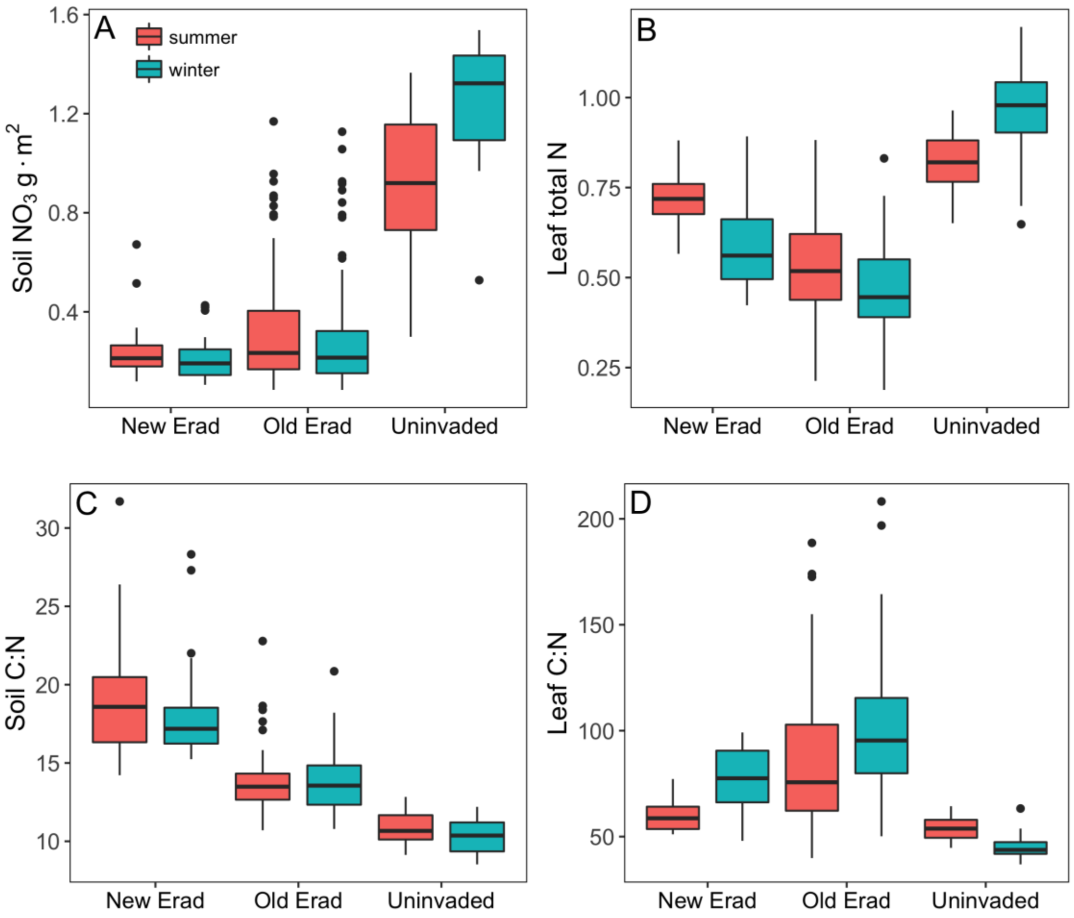


Figure 3.5 Seasonal variation between summer (red) and winter (blue) for each of the response variables of A) soil NO_3^-, B) pōhutukawa leaf total nitrogen, C) soil C/N, and D) pōhutukawa leaf C/N among the treatment islands; New Erad is Ahuahu; Old Erad is Korapuki, and Uninvaded is pooled for Atiu and Green islands.

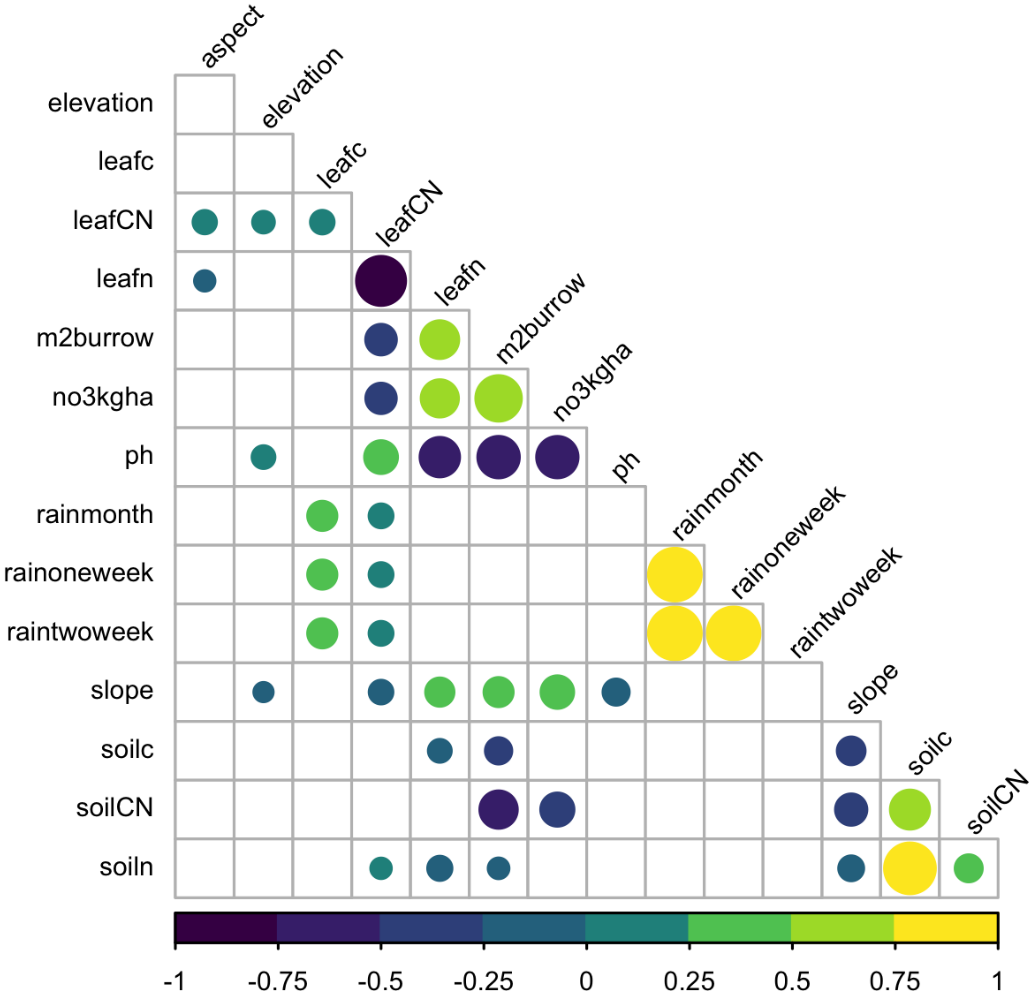


Figure 3.6 Correlation matrix of the environmental variables, blank squares represent non-significant correlations. The size of the circle represents the scale of significance.

Chapter 4 | Data

Foliar spectral reflectance response of three island plant species to seabird nutrient enrichment

4.1 Abstract

Studies have identified correlations between nutrient status and the spectral reflectance of foliage from agricultural fields to diverse forests, an approach that capitalizes on the relationship between soil and foliar nutrients. Seabirds are often the vectors of large quantities of marine derived nutrients to their terrestrial breeding sites. Based on established biochemical relationships between soil-leaf-spectral reflectance, we hypothesize that nutrient enrichment from seabirds can be detected in the forest canopy using spectroscopy techniques. To test this hypothesis, we evaluated the effect of seabird nutrient enrichment on the spectral response of a common island canopy species on Aotearoa's seabird islands – pōhutukawa, in a controlled experiment. We simulated realistic and extremely high levels of seabird nutrient input to detect if there is a threshold of nutrient input necessary to detect spectral responses. We field tested this hypothesis on an island with variable seabird nesting density, and with two additional canopy plant species; māhoe and kanono. We found a strong relationship between soil nutrient status and spectral reflectance with high to extremely high simulated nutrient enrichment for pōhutukawa. However, in field testing, despite underlying soil characteristics reflecting differences in seabird density, we did not find a consistent relationship between seabird density and spectral reflectance, attributed to variable ecological factors. Our results indicate there is promise for using foliar spectral reflectance to measure nutrient influences of burrow-nesting seabirds, but more work is necessary to understand at which seabird densities leaf spectral reflectance responses can be detected.

Synthesis and applications: Seabirds are vulnerable to invasive mammalian predators, which can suppress or eliminate their nutrient subsidies. Thus, predator eradication from seabird islands is a key conservation tool. While further investigation is needed, our results suggest remote sensing has the potential for measuring the recovery nutrient input from burrow-nesting seabirds, capitalizing on the relationship between soil and foliar nutrients. Such an approach would provide managers a valuable tool to monitor the recovery of seabirds to islands eradicated of invasive predators in a less labour-intensive way, and at greater spatial scales than traditional monitoring methods.

Key words: conservation, ecosystem engineering, monitoring, remote sensing, restoration

4.2 Introduction

Nitrogen is a key element in plant growth and photosynthesis; it is abundant in amino acids, proteins, nucleic acids, ATP, and RuBisCo (ribulose-bisphosphate carboxylase-oxygenase), the principle carboxylation enzyme for photosynthesis found predominantly in chlorophyll (Smith, Hollinger & Ollinger 2008; Mizusaki, Umeki & Honjo 2013). A strong correlation between chlorophyll and foliar N has been found in a number of plant species (Blackmer & Schepers 1995; Zhang, Chen & Thomas 2007; Mizusaki, Umeki & Honjo 2013). Nutrient availability strongly influences the structural and biochemical traits of leaves, chlorophyll, and carotenoid pigments (Gitelson *et al.* 2003; Baltzer & Thomas 2005; Asner & Martin 2008). These structural and chemical constituents of plant tissues dictate how much light is absorbed and at what wavelength of the electromagnetic spectrum (EMS) (Zhang, Chen & Thomas 2007; Sanches *et al.* 2013; Li & Alchanatis 2014).

Light radiation is absorbed by chlorophyll in plants for use in photosynthesis, but there is an excess of light that is dissipated, known as spectral reflectance (Tremblay et al., 2012). The spectral reflectance properties of the EMS in the range 400-700 nm have been shown to reliably reflect concentrations of chlorophyll, specifically at the green peak (550 nm; Yoder & Pettigrew-Crosby 1995; Stone, Chisholm & Coops 2001; Mizusaki, Umeki & Honjo 2013). Consequently, the relationships between the absorption of electromagnetic radiation and foliar characteristics enables the estimation of plant biochemical properties using commonly available spectroscopy techniques (Sanches *et al.* 2013). Indeed, measuring foliar reflectance using high resolution spectral sensors has been used to estimate total N content of canopy leaves of temperate, tropical forests and pastoral landscapes from local to regional scales (Yoder & Pettigrew-Crosby 1995; Smith, Hollinger & Ollinger 2008; Tremblay, Wang & Cerovic 2012; Asner *et al.* 2017).

Burrow-nesting seabirds (Family: Procellariidae) are allogenic ecosystem engineers via marine derived nutrient subsidies and physical disturbance from burrowing activity (Smith, Mulder & Ellis 2011). They enrich their terrestrial breeding grounds with often large amounts of nutrients via guano, failed eggs, prey remains, and corpse deposition. The guano deposited by seabirds is rich in nitrogen

(N), typically excretions are between 14.9-28.6% total N content (Bird *et al.* 2008). Uric acid, a major component of seabird guano is rapidly hydrolysed to gaseous ammonia and ammonium, and the nitrification process yields nitrate NO_3^-, which is biologically available for plant use (Bird *et al.* 2008). Deposition rates of seabird guano in low density colonies (0.15 burrows m^2) can be as much as 51 N $kg \cdot ha^{-1}$ yr^{-1} (Bancroft, Garkaklis & Roberts 2005) and upwards of 1000 N $kg \cdot ha^{-1}$ yr^{-1} (Schmidt *et al.* 2004), equivalent to agricultural fertiliser treatments. The intense enrichment by seabirds affects ecosystem composition, vegetation leaf chemistry, plant growth rates, and invertebrate communities (Fukami *et al.* 2006; Smith, Mulder & Ellis 2011; Thoresen *et al.* 2017).

Insular environments, such as the islands on which seabirds breed, are vulnerable to invasive predators (Drake *et al.* 2002). Invasive mammalian predators can suppress or eliminate seabird colonies entirely from invaded islands (Towns *et al.* 2011). The loss of allochthonous nutrient inputs, when seabirds are extirpated or suppressed, can have detrimental impacts to island ecosystem composition and function (Fukami *et al.* 2006; Jones *et al.* 2008; Thoresen *et al.* 2017). Accordingly, invasive predator eradication is a key conservation tool to protect seabirds and reinstate their ecosystem engineering properties to their island habitats (Jones 2010; Jones *et al.* 2011, 2016). Traditional methods of measuring recovery following predator eradication, such as measuring stable isotopes in food web components (Jones 2010), can be labour intensive and expensive. Thus, monitoring ecosystem recovery post-eradication is often limited. Remote sensing is emerging as a powerful tool for ecological applications, notably using vegetation indices as proxy measures for burrow nesting species (Wilschut *et al.* 2018). Here, we explore the potential for using spectral reflectance of the forest canopy to detect seabird nutrient enrichment, which could be used as a proxy for measuring seabird ecosystem recovery.

The aim of our study is twofold; 1) to investigate experimentally the potential for using spectral reflectance to measure the ecosystem engineering properties of seabirds, *i.e.,* nutrient enrichment, in a common seabird island plant species, and; 2) explore if the relationship between soil and foliar nutrients remains detectable under field conditions. Because foliar nutrient concentrations are predicted to increase with the addition of N, and to reflect soil N concentrations (Townsend *et al.* 2003; Vitousek 2004), we hypothesized that the nutrient enrichment from seabird activity will be distinguishable in the spectral signatures of the forest canopy of seabird islands. In a controlled experiment, we examined the in-situ spectral reflectance response of pōhutukawa (*Metrosideros exclesa*), a common canopy species on seabird islands in New Zealand, to variable levels of simulated seabird nutrient enrichment. We then field tested the spectral response of pōhutukawa, and two other common canopy species; māhoe (*Melicytus ramiflorus*) and kanono (*Coprosma macrocarpa*), using leaves and soil variables from an island with variable seabird nesting density. If the relationship between soil and foliar nutrients holds in heterogeneous seabird modified ecosystems, and is detectable using spectroscopy techniques, there is potential to capitalise on this relationship for measuring the recovery of seabird nutrient influences and seabird abundance on islands eradicated of invasive mammalian predators using remote sensing technology.

4.3 Methods

To test the spectral response of pōhutukawa to seabird nutrient enrichment, we conducted a controlled experiment applying simulated seabird guano in four treatment levels to pōhutukawa and measured the spectral reflectance over 47 weeks. We validated our controlled experiment using field collected data, including leaf spectral reflectance, soil nitrate (NO_3^-), and leaf total nitrogen (N) on Korapuki Island, where there is variable seabird nesting density (Figure 4.1). We sampled on two occasions, following a *dry* period, and following a *wet* period to investigate the influence of water availability on foliar spectral responses. In addition to pōhutukawa, we measured the spectral reflectance of two other plant species; māhoe, and kanono, which are common on seabird islands. At both the experimental site and the field collection sites, the climate is humid-temperate, with average annual rainfall of 1832.4 mm, most falling in the Austral winter (238 mm/month) and 83-91% relative humidity. Mean annual temperature is 15˚C (CliFlo 2017).

4.3.1 Experiment

We used juvenile pōhutukawa plants (n=40), approximately 4 m tall, with diameter at breast height ~4 cm. The trees were kept outside at Oratia Natives Nursery in West Auckland (-36.92 S, 174.61 E). All plants received the same amount of rainfall and light as each other over the length of the experiment. We applied simulated seabird guano for three seabird burrow densities: Medium (1 burrow·m^2; n=10), High (5 burrows·m^2; n=10), Extremely High (10 burrows·m^2; n=10), and no treatment (controls; n=10). Nutrient treatment recipes were calculated from Jones (2012; Supporting information; Table 4.2). These nutrient densities are greater than burrow density found at our field sites; however, we used these greater treatment concentrations to evaluate the level of nutrient enrichment needed to detect a spectral response in our study species. We applied the first treatment in March 2015 and repeated treatments every four to six weeks for 47 weeks. We sampled five times during the treatment period, each time we measured soil moisture (Decagon ProCheck and EC-10 soil moisture sensor; Decagon, Pullman, WA), soil temperature, and collected approximately 100g of soil using a trowel from each plant to measure NO_3^-. At the beginning (baseline) and end of the experiment we collected 3-5 new growth leaves from the most sunlight exposed part of the canopy to measure leaf % nitrogen (N) and C/N.

4.3.2 Field collected data

We sampled soils and leaves from Korapuki (18 ha; -36.65 S, 175.85 E) in the Mercury Island Group, off the east coast of the Coromandel, New Zealand (Figure 4.1). Korapuki was historically invaded by kiore (Pacific rats; *Rattus exulans*), and rabbits (*Oryctolagus cuniculus*), which were eradicated in 1986 and 1987 respectively (Towns & Atkinson 2004). Seabird recovery on Korapuki is patchy, thus providing the ability to measure areas with and without seabird activity (Figure 4.1). Slopes on the island are moderately steep (21–25°) to steep (26–35°), and soils are homogeneously volcanic and friable. Soil erosion form and degree for our study islands are slight (Landcare Research New Zealand 2017). Vegetation on the islands is dominated by old growth pōhutukawa and coastal evergreen trees and shrubs including māhoe, kanono, kawakawa (*Piper excelsum* subsp. *peltatum*), ewekuri (*Strebulis banksii*), and māpou (*Myrsine australis*; Atkinson 2004).

At each sampling site (Figure 4.1), we collected eight to ten new growth leaves from pōhutukawa, māhoe, and kanono from the most sunlit part of the canopy where possible considering the topographic and logistical constraints (*i.e.,* cliffs, unsafe slopes, unvegetated beaches were not sampled). Burrow density was calculated as burrows$\cdot$m^2, as a proxy for seabird activity (Fukami *et al.* 2006), within a 5 m radius (78.54 m^2) around each sampled pōhutukawa tree. We measured soil moisture, soil temperature, and collected approximately 100 g of soil using a trowel from three locations around each sample site, as per the experiment. The soil samples from each site were aggregated and sieved in the field. We sampled on two occasions in the Austral summer and autumn of 2017, after a one month period of dry weather (February), then one month following multiple rainfall events (April) to test if water availability influenced the spectral reflectance of the plants (CliFlo 2017).

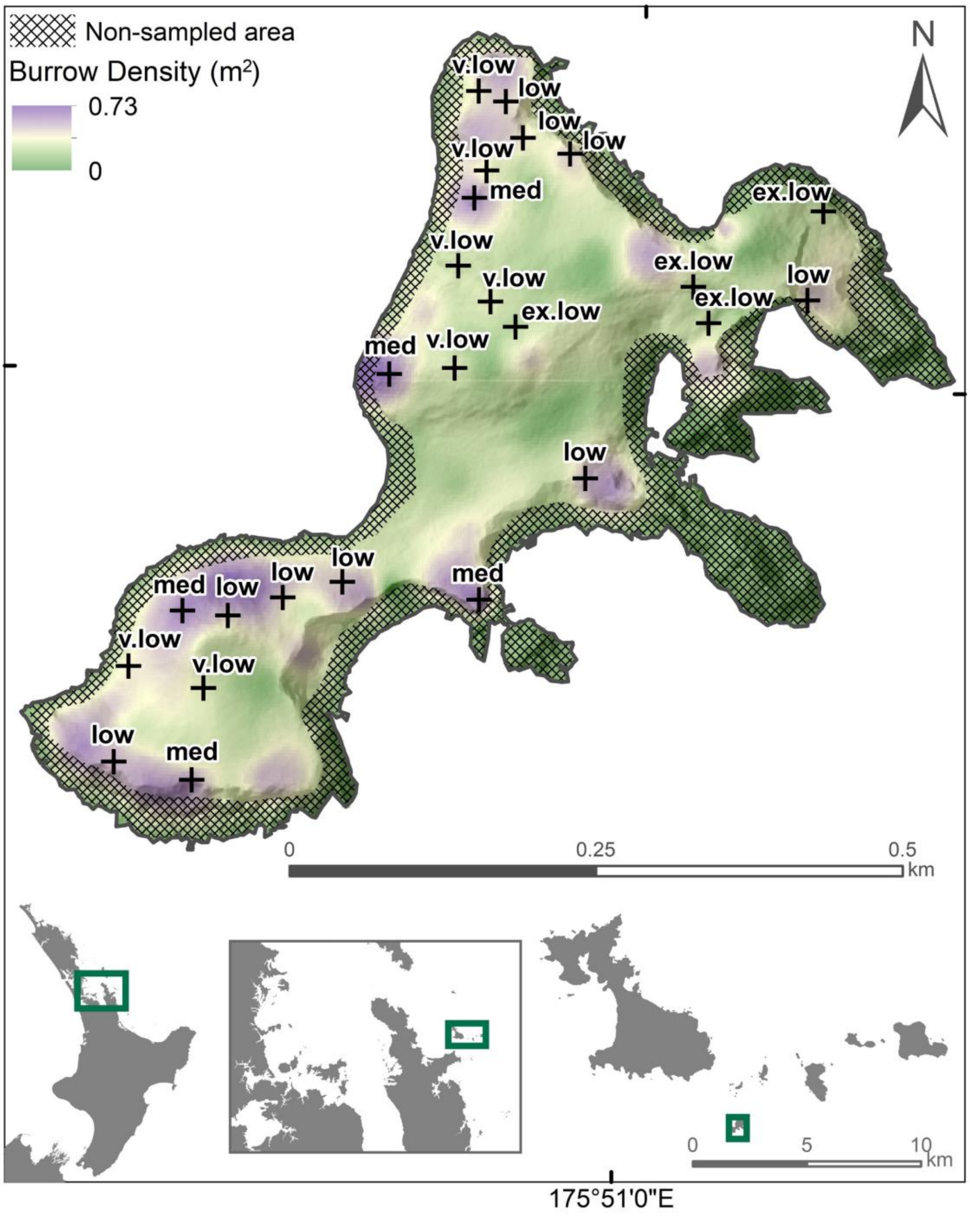


Figure 4.1 Burrow density (Burrows·m²) and sample locations of sites where pōhutukawa, māhoe, and kanono were collected for spectral reflectance and soil and leaf variables, with corresponding burrow density categories of; Extremely Low (ex.low; <0.05 burrows·m², total *n*=12; 4 of each species), Very Low (v.low; 0.05-0.2 burrows·m², total *n*=21; 7 of each species), Low (low; 0.2-0.5 burrows·m², total *n*=27; 9 of each species), and Medium (med; >0.5 burrows·m², total *n*=15; 5 of each species) on Korapuki Island, Aotearoa.

For the experiment and field collected data, three leaves from each plant (rinsed with deionized water) and soil samples (sieved [1mm] to remove large debris) were oven dried (55°C, ~48 h) and ball milled (400 rpms for 10 and 3 minutes, for leaves and soil respectively; Retsch PM 100 Ball Mill, Germany). Soil NO_3^- was extracted to a solution using a Nitrate (NO_3^-) test kit (API, Chalfont, PA, USA) for spectrophotometric determination using a UV/Vis absorbance analyser (FLUOstar Omega, BMG Labtech, Ortenberg, Germany), and calculated to NO_3 $g \cdot m^2$. The leaves from the field, and the first and final sampling session of the experiment were analysed for total N, C with a multipoint normalization using acetanilide with an elemental analyser (ECS 4010, Costech Analytical, Valencia, CA) at the Stable Isotope lab at Washington State University, USA, and C/N calculated. Carbon (C) and nitrogen (N) are closely linked with biological processes and can provide insight into nutrient status of leaves (Coruzzi & Zhou 2001).

4.3.3 Spectral reflectance data

We used a HandHeld 2 Portable Spectroradiometer (Analytical Spectral Devices, Inc, Boulder, CO), which covers wavelengths in the visible light and near infrared (NIR) from 325-1075 nm, at a bandwidth of 1 nm. Spectral readings were taken ~10cm above the leaves, and we took 50-75 spectral readings, which were averaged to obtain a mean reflectance spectrum for each sampled tree (Stone, Chisholm & Coops 2001; Wang *et al.* 2018). For the experimental study, we took spectral signatures of new growth leaves attached to the pōhutukawa trees at the beginning of the experiment, and approximately every two-three months given weather constraints. For the field collected leaves from pōhutukawa, māhoe, and kanono we removed the samples from the tree and measured the spectral reflectance in the open. All spectral measurements were taken on sunny days (<10% cloud cover) as close to solar noon as possible (12 pm in summer, and 11am in winter to account for day-light savings) to reduce inaccuracies in spectral reflectance measurements (Dalponte, Bruzzone & Gianelle 2012).

4.3.4 Quantitative analysis

For the experiment, we calculated the mean and standard deviation for each experimental treatment for NO_3^- and SLA over the treatment period. We performed generalised linear mixed effects models (GLMMs) to test for differences in NO_3^- for each treatment over the length of the experiment at each sampling point (n=5), with soil moisture (dry or wet for the field samples) as a random variable, using the *lme* function of the *nlme* package (Pinheiro *et al.* 2009). For the field-collected spectral reflectance of pōhutukawa, māhoe, and kanono, and biochemical data we grouped the samples into burrow density categories of Medium (>0.5 burrows·m^2, *n*=15), Low (0.2-0.5 burrows·m^2, *n*=27), Very low (0.05-0.2 burrows·m^2, *n*=21), and Extremely Low (<0.05 burrows·m^2, *n*=12; Table 4.1).

Spectral reflectance data were processed and exported as *reflectance* using the *ASCII Export* function in ViewSpec Pro (Analytical Spectral Devices, Inc, Boulder, CO, USA). The data were visually inspected to remove noisy individual spectra, and bands between 400-900 nm were selected (Baltzer & Thomas 2005; Martin *et al.* 2008), corresponding to the region of the EMS associated with N, and within the range of our spectroradiometer. We normalised the spectra, that is the minimum and maximum is contrained between 0-1 using the *procspec* function in the *pavo* package (Maia, Bitton & Eliason 2014). We used the *prospectr* package for spectral analysis of the green peak and to generate figures (Stevens & Ramirez–Lopez 2014). Because of the strong correlation between foliar N and chlorophyll, and because chlorophyll is the main foliar constituent in determining spectral reflectance at the green peak, near 550 nm, we examined in detail if there were differences between treatments in this part of the EMS (Yoder & Pettigrew-Crosby 1995; Stone, Chisholm & Coops 2001). To test for differences in leaf spectral reflectance at the green peak in relation to individual measured ecological variables (simulated seabird guano/burrow density, soil NO_3^-, soil C/N, leaf % N, and leaf C/N), we performed one-way analysis of variance ANOVA with a post-hoc Tukey test of multiple comparison of means (R Core Team 2013). The treatment-level results are presented with standard error of the mean to illustrate the variability within samples (Figure 4.3 & Figure 4.5).

4.4 Results

4.4.1 Simulated seabird guano experiment

Soil nitrate (NO_3^-) concentrations at the start of the experiment were on average 91.8% higher than our Extremely Low field control sites (0.22 ± 0.16 g m^2; Figure 4.4) at the baseline sample mean of 0.6 ± 0.19 g m^2 due to enriched potting mix used at the nursery where the plants were located (Figure 4.2.A). Over the course of the experiment, the nitrate leached from the experimental control plants and by the end of the experiment soil NO_3^- was 0.6% higher than the Extremely Low field control sites.

There was no difference in baseline NO_3^- concentrations among all experimental treatments (p=0.72; Figure 4.2.A). Soil NO_3^- increased for the High and Extremely High treatment over the first 8 weeks; only the Extremely High treatment was different to the control (p=0.008). After 18 weeks of treatment, soil NO_3^- decreased for all treatments, coinciding with the main growth cycle of pōhutukawa in late spring (Bergin & Hosking 2006), and likely due to initial nutrient leaching and plant uptake. Soil NO_3^- for the Extremely High and High treatments were 66% and 51% greater than the Control (p=0.002 and p=0.02 respectively), but there was no difference between the Control and the Medium treatment (p=0.79; Figure 4.2.A). After 33 weeks of treatment, the Extremely High and High treatments had 150% and 126% higher concentrations of soil NO_3^- compared to the Control (p=0.008/p=0.02 respectively), and no difference between the Medium treatment and Control (p=0.26; Figure 4.2.A). At the end of the treatment period, soil NO_3^- for the Extremely High treatment was 127% greater than the control, and 104% for the High treatment (p=0.0001 and 0.001 respectively; Figure 4.2.A). The Medium treatment was not different to the Control (p=0.14).

There was no difference in total leaf % N at the beginning of the experiment (Figure 4.2.B). At the end of the experiment, mean total leaf % N increased 59.2% for the Extremely High and 38.5% for the High treatment (p=0.0002 and p=0.004 respectively). There was no difference in leaf % N between Medium and Control treatments (p=0.52; Figure 4.2.B). Leaf C/N decreased from the beginning of the experiment to the end by 57.4% for the Extremely High treatment and 39.5% for the High treatment (p=0.0002 and p=0.004 respectively; Figure 4.2.C). There was no difference in leaf C/N from the beginning to the end of the experiment for the Control and Medium treatment (p=0.47), although there was an observed decrease in leaf C/N for the Medium treatment (Figure 4.2.C).

The spectral response of pōhutukawa at the green peak (550 nm) was not different among treatments at the beginning of the experiment (p=0.35; Figure 4.3.A) or after 8 weeks (two fertilizer applications; p=0.32; Figure 4.3.B). After 18 weeks, (four fertilizer applications) the spectral reflectance at the green peak of the Extremely High treatment was 3.2% lower than the Control plants spectral reflectance (p=0.02; Figure 4.3.C). Among the Medium and High treatments, there were no differences from the Control in the green peak. The spectral reflectance at the green peak at 33 weeks of simulated seabird guano treatment was 63.2%, 40.7%, and 45.6% lower than the Control for Extremely High, High, and Medium respectively (Extremely High: p=0.025; High: p=0.037; Medium: p=0.05; Figure 4.3.D). The spectral reflectance at the green peak at the end of the experiment was 77.4%, 74.5%, and 53.2% lower than the Control for Extremely High, High, and Medium respectively (Extremely High: p=0.004; High: p=0.004; Medium: p=0.01; Figure 4.3.E).

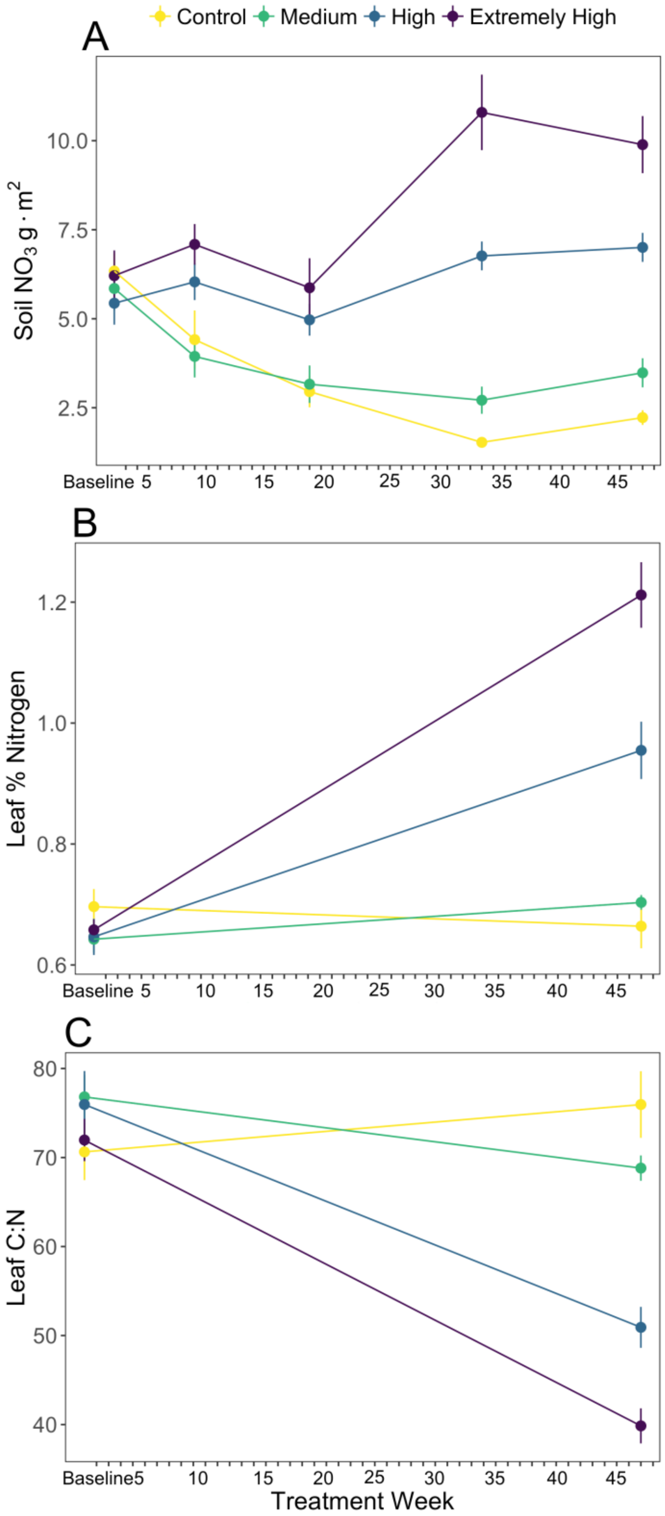


Figure 4.2 Soil NO_3^- concentrations across the five sampling sessions during the treatment period (47 weeks) for pōhutukawa. **B)** Mean distribution and standard deviation of Leaf % N for each simulated seabird burrow density treatment; Control, Medium, High, and Extremely High for the first and last treatments. **C)** Leaf C/N at the beginning of the experiment and at the end.

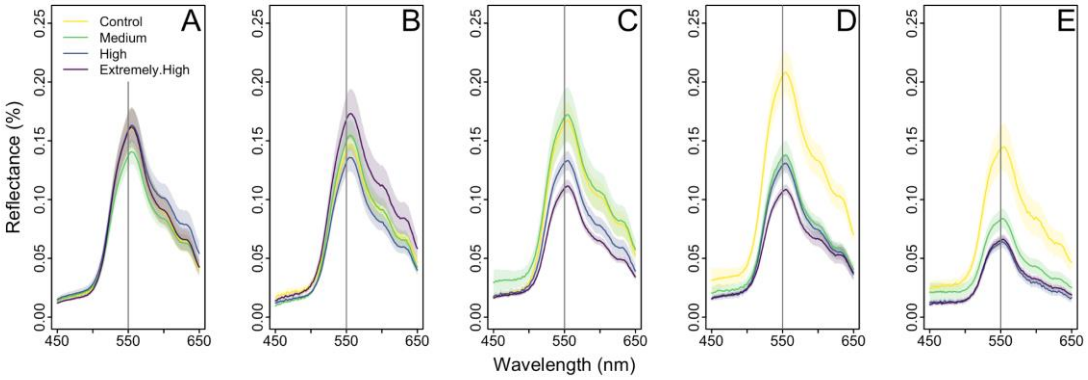


Figure 4.3 The spectral response of pōhutukawa shown as the standard error of the mean for each simulated seabird guano treatment; Control, Medium, High, and Extremely High for the wavelength features between 450-650 nm of the electromagnetic spectrum (EMS), where reflectance is the most sensitive to changes in nitrogen status (Baltzer & Thomas 2005). The vertical lines represent the green peak (550nm), which we used in the statistical analysis to test for differences in the treatments. A) baseline spectral reflectance (July); B) 8 weeks of treatment (September); C) 18 weeks of treatment (November; peak growing season); D) 33 weeks of treatment (February), and; E) 47 weeks of treatments (May).

4.4.2 Field testing of the spectral response to seabird burrow density

At the sampling locations on Korapuki Island, burrow density ranged from 0.03 – 0.66 burrows·m^2 (Figure 4.1; Table 4.1). Rainfall in the month prior to the *dry* sampling session was 95 mm, and the *wet* sampling session followed a period of intense rainfall, where 246.2 mm fell in the month preceding sampling (CliFlo 2017). There was a 28.7% decrease in soil NO_3^- for the Extremely Low burrow density between the dry and wet sampling periods (p=0.02; Figure 4.4). Between the dry and wet sampling periods the Very Low treatment, soil NO_3^- decreased 22% (p=0.07; Supporting information; Figure 4.8). While there was an observable decrease in soil C/N at the High burrow density site, there were no statistical differences for all variables measured among the burrow density treatments and between the dry and wet sampling treatments (Table 4.1; Supporting information; Figure 4.8). A comparison of the variables soil NO_3^-, leaf % N, and leaf C/N among the experimental treatments and the field samples for the dry and wet sampling periods is illustrated in Figure 4.4.

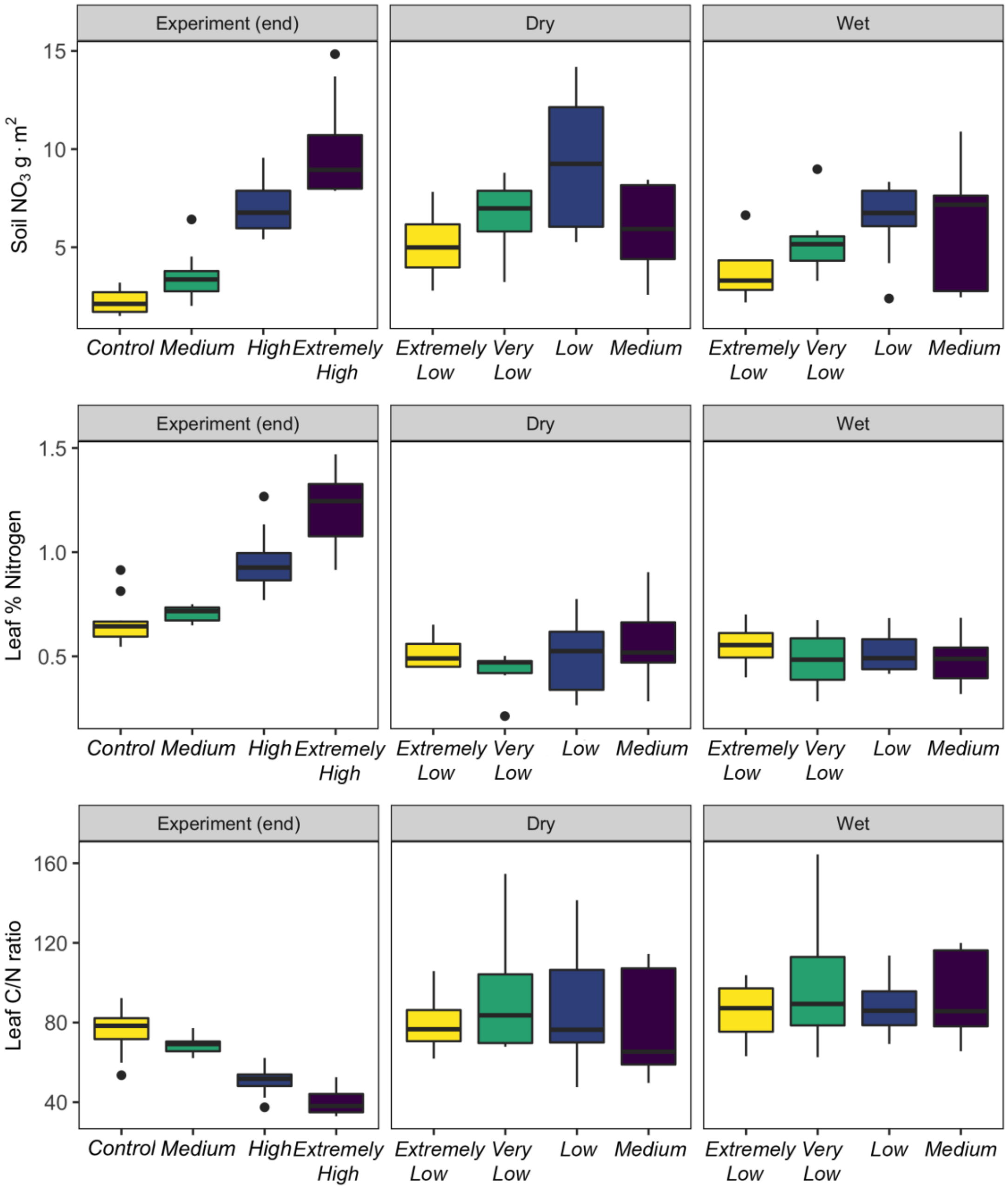


Figure 4.4 A comparison of measured variables of soil NO_3^-, and pōhutukawa leaf % N, and leaf C/N among the four experimental treatments of Control, Medium, High, and Extremely High at the end of the experiment (n=40) and the same for the field seabird densities of Extremely Low, Very Low, Low, and Medium among the dry (n=25) and wet (n=25) sampling sessions for Soil NO_3^-, pōhutukawa leaf % Nitrogen and leaf C/N.

Table 4.1 Soil and leaf variables for the dry and wet sampling from Korapuki Island, Aotearoa.

	Treatment	Burrows (m^2)	Soil NO_3 (g m$^{2)}$	Soil C/N	Leaf %N	Leaf C/N
Dry	Extremely Low (n=4)	0.06 ±0.02	0.52 ± 0.22	13.83 ±1.73	51.95 ±0.10	80.25 ±18.59
	Very Low (n=7)	0.14 ± 0.3	0.66 ± 0.19	13.47 ±2.61	42.5 ±0.10	93.42 ±33.12
	Low (n=9)	0.29 ± 0.5	0.93 ± 0.34	13.86 ±1.67	48.4 ±0.18	87.87 ±32.53
	Medium (n=5)	0.60 ± 0.8	0.59 ± 0.25	13.44 ±0.42	56.78 ±0.23	79.12 ±29.58
Wet	Extremely Low (n=4)	0.06 ±0.02	0.39 ± 0.19	15 ±9.93	55.2 ±0.13	82.13 ±20.47
	Very Low (n=7)	0.14 ± 0.3	0.53 ± 0.19	18.01 ±13.29	48.4 3±0.14	99.91 ±35.36
	Low (n=9)	0.29 ± 0.5	0.65 ± 0.2	15.11 ±5.73	52.91 ±0.10	88.25 ±14.24
	Medium (n=5)	0.60 ± 0.8	0.62 ± 0.36	10 ±1.49	48.58 ±0.14	93.12 ±23.95

We found no difference between the green peak (550 nm) spectral reflectance (%) for either the burrow density treatment, nor the dry and wet treatments among the three study species (Figure 4.5; see Supporting Information; Figure 4.9 & Figure 4.10 for individual species green peak spectral responses, and Figure 4.7 for the full spectrum). There was no relationship between the green peak and any of the measured variables of soil NO_3^-, soil C/N, leaf % N, and leaf C/N for any of our study species (Table 4.1).

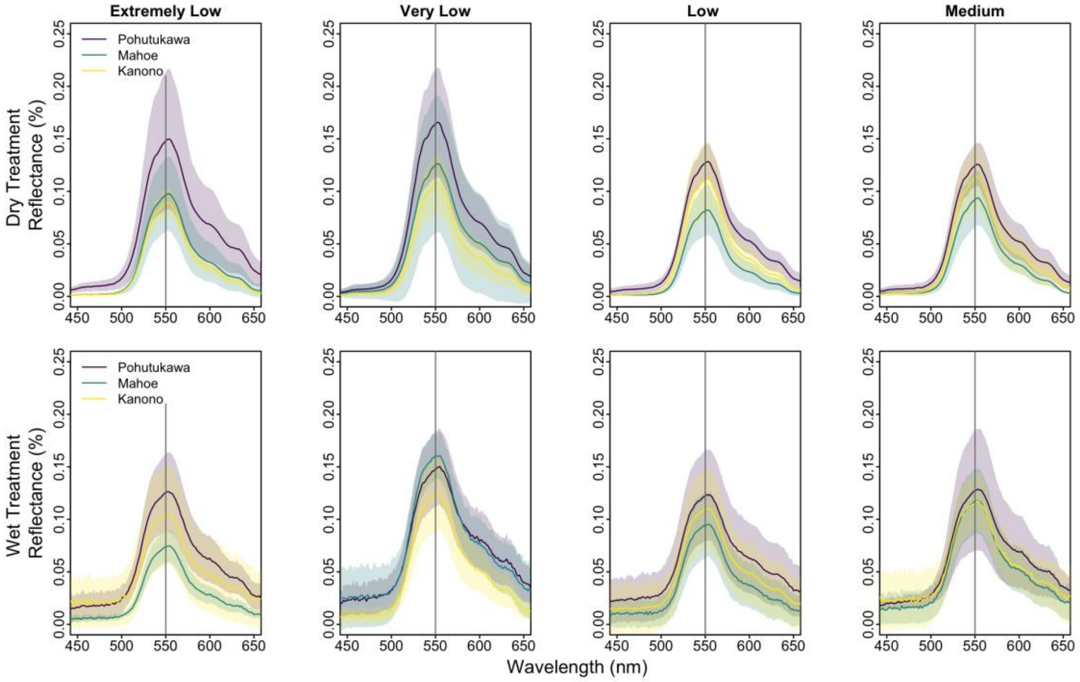


Figure 4.5 The standard error of the mean of spectral reflectance for pōhutukawa (n=25), māhoe (n=25), and kanono (n=25) collected in the field. The top panel is the spectral reflectance measured during a dry period (February), and the bottom panel is measured after a wet period (April). The left to right panels reflect spectral response of the three species at burrow density categories of Extremely Low (<0.049 burrows·m^2, total *n*=12; 4 of each species), Very Low (0.05-0.19 burrows·m^2, total *n*=21; 7 of each species), Low (0.2-0.49 burrows·m^2, total *n*=27; 9 of each species), and Medium (>0.5 burrows·m^2, total *n*=15; 5 of each species) at the sites where the samples were collected.

4.5 Discussion

Our experiment investigating the spectral response of pōhutukawa, a common canopy species on islands with seabirds, indicated a decrease in % spectral reflectance at the green peak (550 nm) under Extremely High and High levels of simulated seabird nutrient enrichment (Figure 4.3). This result was similar to nutrient enrichment experiments of temperate deciduous tree species (Baltzer & Thomas 2005). However, under natural field conditions, the relationship between burrow density, soil nutrients (as a proxy for seabird activity) and spectral reflectance was not detectable in any of our study plant species in either dry or wet conditions. Nevertheless, with further investigation, our experimental results suggest that leaf level spectral reflectance measurements have the potential to be indices for measuring the nutrient enrichment from burrow nesting seabirds.

The Extremely High and High nutrient enrichment experimental conditions do not reflect realistic seabird nesting densities for the species found on our study island. However, the Low and Medium experimental nutrient enrichment treatments reflected soil nitrate levels similar to the field sites of Low and Medium burrow density (Figure 4.4). Therefore, despite soil variables reflecting seabird nesting density, our results suggest that the threshold of seabird nutrient enrichment in field conditions may not be high enough to be detectable in foliar response variables of leaf % N and C/N, or the spectral reflectance of island canopy species. It is likely that the nutrient enrichment from recovering seabird activity is being attenuated through run-off before the trees are able to capitalise on it, due to ecological conditions, such as soil type, slope, soil moisture content, and climatic conditions (Zhang, Chen & Thomas 2007; Van Deventer *et al.* 2015), to an extent that is not detectable within the range of our spectroradiometer.

Climatic cycles, most notably rainfall events, appear to have the strongest influence on the temporal variation in mineralized N, and thus the nutrient status of the foliage (Bancroft, Garkaklis & Roberts 2005). For example, while the chlorophyll red-edge position has been used as a reliable co-variant for mapping N content of leaves (Ramoelo *et al.* 2012); however, the seasonal variation of leaf chlorophyll and nutrient content is poorly understood, and could potentially produce erroneous results in nutrient mapping and monitoring at the canopy scale (Van Deventer *et al.* 2015). While not statistically significant, we measured a decrease in spectral reflectance of pōhutukawa leaves across all of the burrow densities in the dry sampling period (Figure 4.5; Supporting Information; Figure 4.9), suggesting that water availability may be influencing the uptake of soil N, although further research is required to verify this.

Stochastic abiotic and biotic factors can cause variability in soil and leaf nutrient content or plant stress, which can cause damage to the chlorophyll pigments in leaves, altering the spectral reflectance (Zhang, Chen & Thomas 2007; de Jong *et al.* 2012). Moreover, the structural features of leaves, such as the waxy cuticle, non-uniform arrangement of cells and organelles, as well as water content can scatter light unpredictably, which may obscure subtle reflectance and absorption features (Yoder & Pettigrew-Crosby 1995). Our test species, pōhutukawa has a thick waxy cuticle, characteristic of coastal species, and those tolerant to arid conditions (James & Bell 1995). Further confounding the field measurements of foliar spectral reflectance in response to seabird nutrient enrichment further is the light availability for individual trees. Several studies have found that light conditions may play a greater role than nutrients in leaf reflectance via mechanisms such as allocation shifts, photobleaching, photoprotection and leaf surface characteristics (Baltzer & Thomas 2005; Dechant *et al.* 2017). While we did not account for light availability for each sampled tree in the field, further investigation may reveal that light availability for each individual tree may strongly influence the foliar reflectance features compared to our experimental results.

In addition to ecological factors, we posit that seabird burrow density may not be a good indicator of seabird nutrient enrichment in island plant species, due to species-specific seabird physiology and behaviour. For example, smaller species, such as kuaka (common diving petrel *Pelecanoides urinatrix* ~130 g) have higher density of burrows·m^2 than larger species, such as oi (grey-faced petrel *Pterodroma gouldi* ~550 g). Body size determines quantities of guano produced per bird and there are species-specific nesting site preferences, such as slope, elevation, and forest types (Whitehead *et al.* 2014), that influence rates of guano deposition (Durrett *et al.* 2014). Different species also feed at different trophic levels, thereby relative quantities of nitrogen deposited within a system will vary depending on the seabird assemblages and density (Durrett *et al.* 2014). Furthermore, the seasonal breeding habits of many species, particularly temperate and sub-polar ranging species, means island nutrient inputs and physical disturbance regimes may be unevenly distributed over time (Smith, Mulder & Ellis 2011).

The variability in foliar reflectance compared to leaf level characteristics, such as nutrient status, has yielded mixed results in scaling from experimental observations to real world applications (Yoder & Pettigrew-Crosby 1995; Smith, Hollinger & Ollinger 2008; Ollinger 2011). This variation has been attributed to leaf level characteristics (Yoder & Pettigrew-Crosby 1995), canopy structure (Asner & Martin 2008), measurement geometry and background reflectance (Stone, Chisholm & Coops 2001), and geospatial and ecological variables (Asner *et al.* 2017). Finally, given our study focused on a small region of the EMS in the visible light range, hyperspectral regions of the EMS, *i.e.,* those regions beyond the visible light spectrum such as the near infrared (NIR; 700-2500 nm), may provide additional informative measures of the relationship between seabird nutrient enrichment and spectral reflectance. For example, Martin et al. (2008) found a strong correlation between nitrogen concentration and the reflectance in the near infrared region of the EMS at 800-1200 nm. Therefore, further study is needed to explore the ecological factors influencing spectral reflectance, and investigation of other regions of the EMS to accurately evaluate seabird nutrient influences on island forest canopies.

4.6 Conclusion

Seabirds are vulnerable to invasive mammalian predators, which can suppress their ecosystem engineering effects, thereby altering islands ecosystems (Jones *et al.* 2008; Smith, Mulder & Ellis 2011; Towns *et al.* 2011). Thus, predator eradication is a key conservation tool to restore seabird colonies (Towns 2009; Jones *et al.* 2011). However, a major obstacle in evaluating the recovery of often remote seabird islands is a lack of monitoring capacity (Suding 2011). We investigated the potential for using foliar spectral reflectance to measure the nutrient enrichment from burrow-nesting seabirds. We found that in controlled conditions there is a strong spectral response to simulated seabird nutrient enrichment; however, the range of ecological factors influencing field-based foliar spectral reflectance of seabird island canopy species means that further investigation is needed. Our understanding of factors that drive nutrient flow and accumulation in seabird island systems is limited (Chapter 3), veritably influenced by site-specific ecological and climatic features, in addition to species-specific nesting and physiological factors. However, our work is an encouraging step towards the application of remote sensing technologies for monitoring for burrow-nesting seabirds on remote islands.

4.7 Supporting information

4.7.1 Experimental methods

Because importing genuine seabird guano into New Zealand is illegal, we used simulated seabird guano (Jones 2010). The simulated guano was composed of 32.3 g of urea, 23.3 g of ammonium nitrate and 89 g of Vertefert (fish based fertiliser; FertNZ, New Zealand) as described in Jones (2010). Treatment amounts were calculated for Extremely High, High, and Medium nesting seabird density by volume of the planter (Table S1). We used the average sampling depth of seabird nutrient studies (between 10 and 50 cm depth) to calculate treatments by soil volume (Table 4.2; Markwell and Daugherty 2003, Wait et al. 2005, Ellis et al. 2006, Fukami et al. 2006, Jones 2010, Durrett et al. 2014). The treatments were diluted 1:10 with deionised water and applied every 4-6 weeks beginning in July 2015 to May 2016. Water was not controlled for, the plants were housed outside, receiving the same amount of rainfall and sunlight.

Table 4.2: volume of simulated seabird guano applied to experimental pōhutukawa trees. There were two different pot sizes, which were treated by volume.

Planter sizes (Litres)	Extremely High (g)	High (g)	Medium (g)
45	36.00	18.00	3.15
100	80.00	40.00	7.00

4.7.2 Field testing methods

To calculate the green peak (550 nm) we averaged the wavelengths between 545 – 555 nm and performed generalised linear mixed effects models (GLMMs), as per the methods section. We visually examined the full spectrum (390-950 nm) for the experiment (Figure 4.6), and the field collected spectra (Figure 4.7), to see if there were differences between treatments at any other regions than the green peak (550 nm), we could detect no other regions of interest.

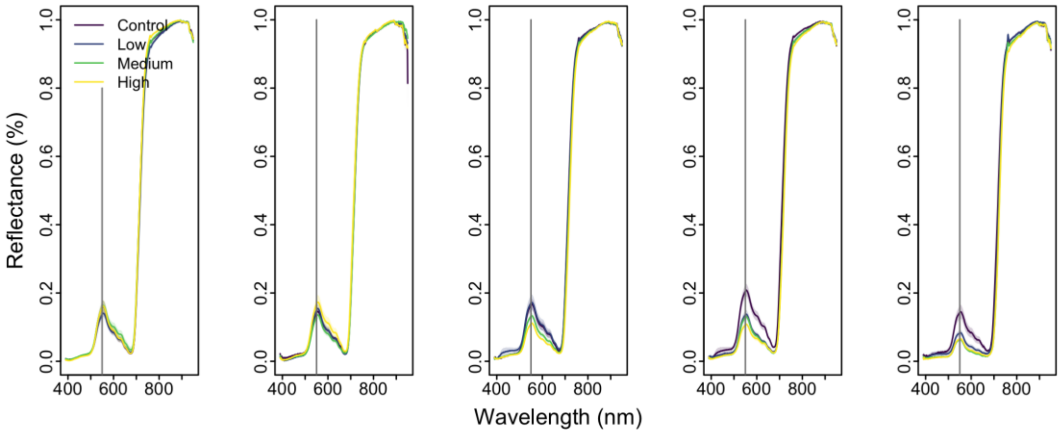


Figure 4.6 Spectral reflectance curve for the experimental nutrient enrichment of pōhutukawa. The spectra is the full measured spectrum (390-950 nm; not including regions cleaned in data wrangling). The grey vertical lines represent the green peak at 550 nm that was used in the statistical analysis.

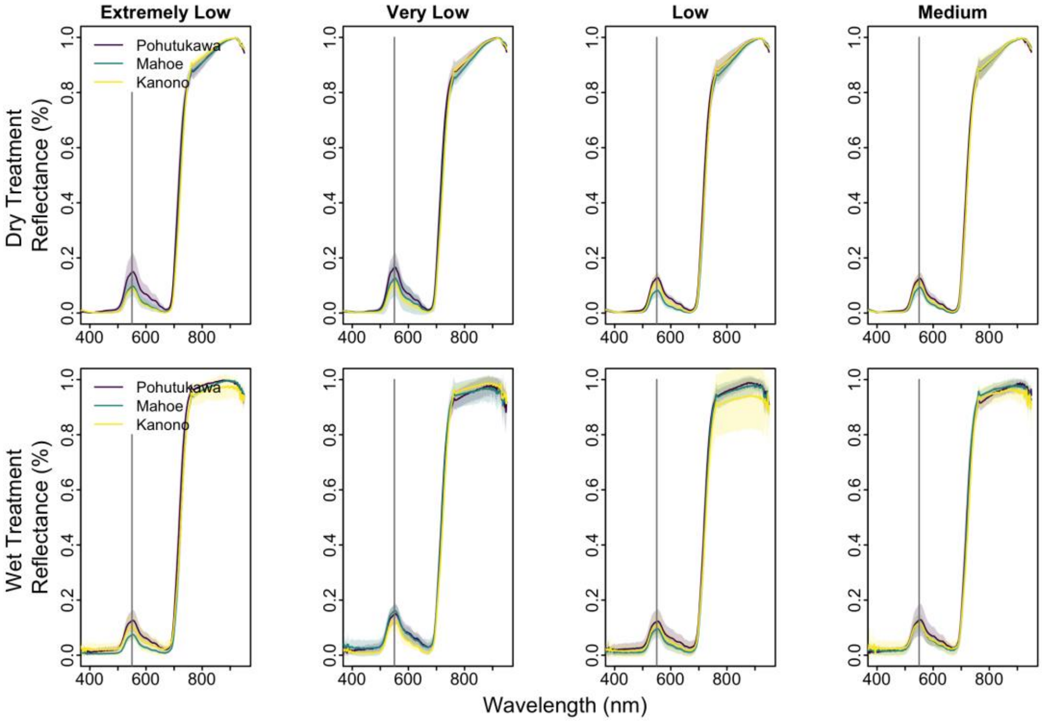


Figure 4.7 Spectral reflectance curve for the field collected spectra of pōhutukawa, māhoe, and kanono. The spectra is the full measured spectrum (390-950 nm; not including regions cleaned in data wrangling). The grey vertical lines represent the green peak at 550 nm that was used in the statistical analysis.

4.7.3 Additional field results

We found a 28.7% decrease in soil NO_3^- for the Extremely Low and 22 % for the Very Low sites between the dry and wet sampling periods from the post hoc Tukey’s test (p=0.017). There were no differences between the dry and wet sampling periods for the Low and Medium treatments in soil NO_3^- (Figure 4.8.A). There were no significant differences for any of the variables among sites or the wet and dry sampling periods (Figure 4.8). The range of soil C/N was much greater during the wet sampling period (Figure 4.8.C), although there were no statistical differences.

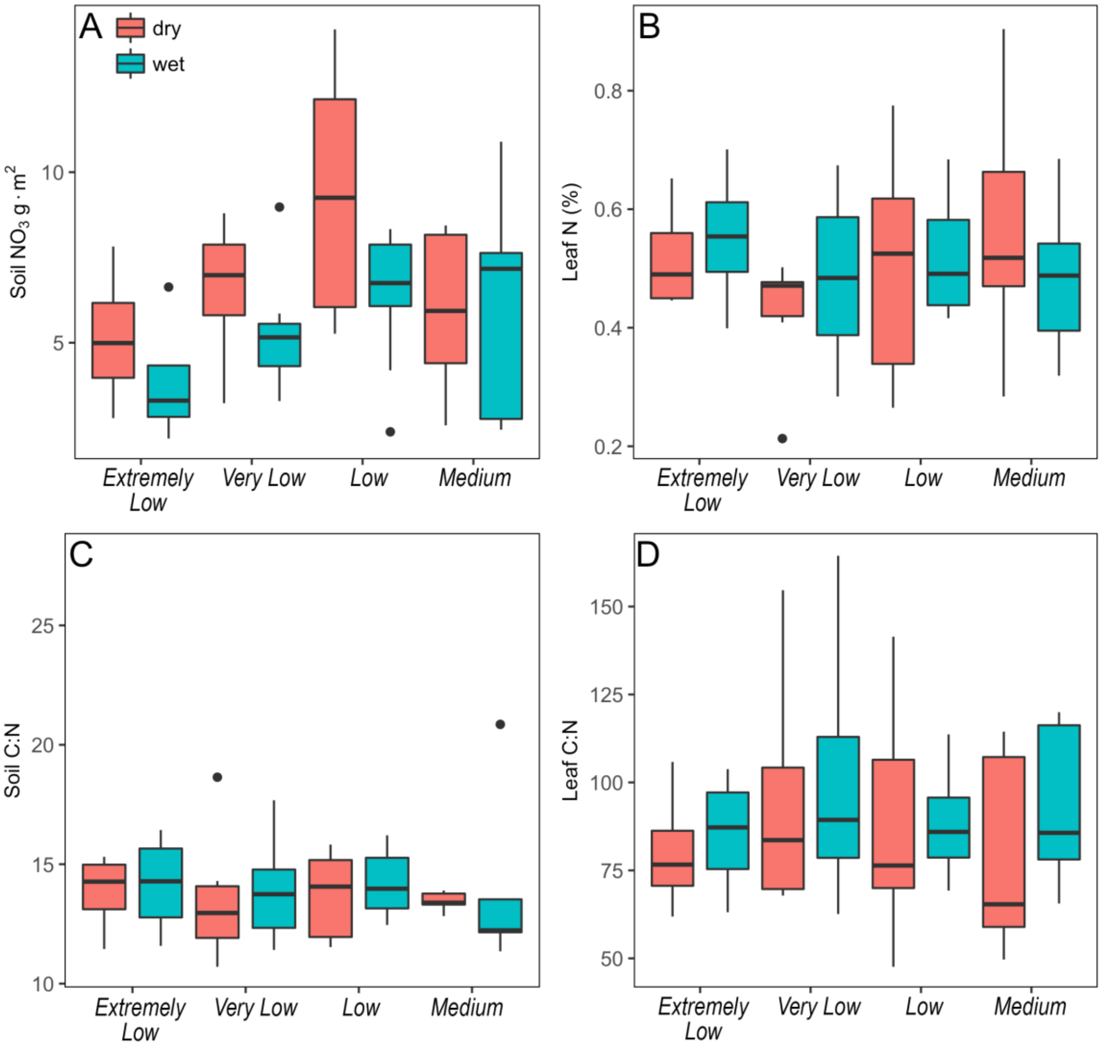


Figure 4.8 Soil NO_3^- for the burrow density treatments and between the dry and wet sampling periods. There was no difference between the Control and the Low and High sites, but a significant difference between the control and Medium burrow density site (p=0.003).

While there were no statistical differences among the burrow density treatments and spectral reflectance for pōhutukawa, on visual inspection, there is a lower mean % reflectance for the Low and Medium treatments (Figure 4.9; top panel). However, this pattern is not reflected in the wet sampling period (Figure 4.10;

top panel). There is no observable difference in spectral reflectance among treatments for māhoe or kanono in either the dry or wet sampling periods (Figure 4.7).

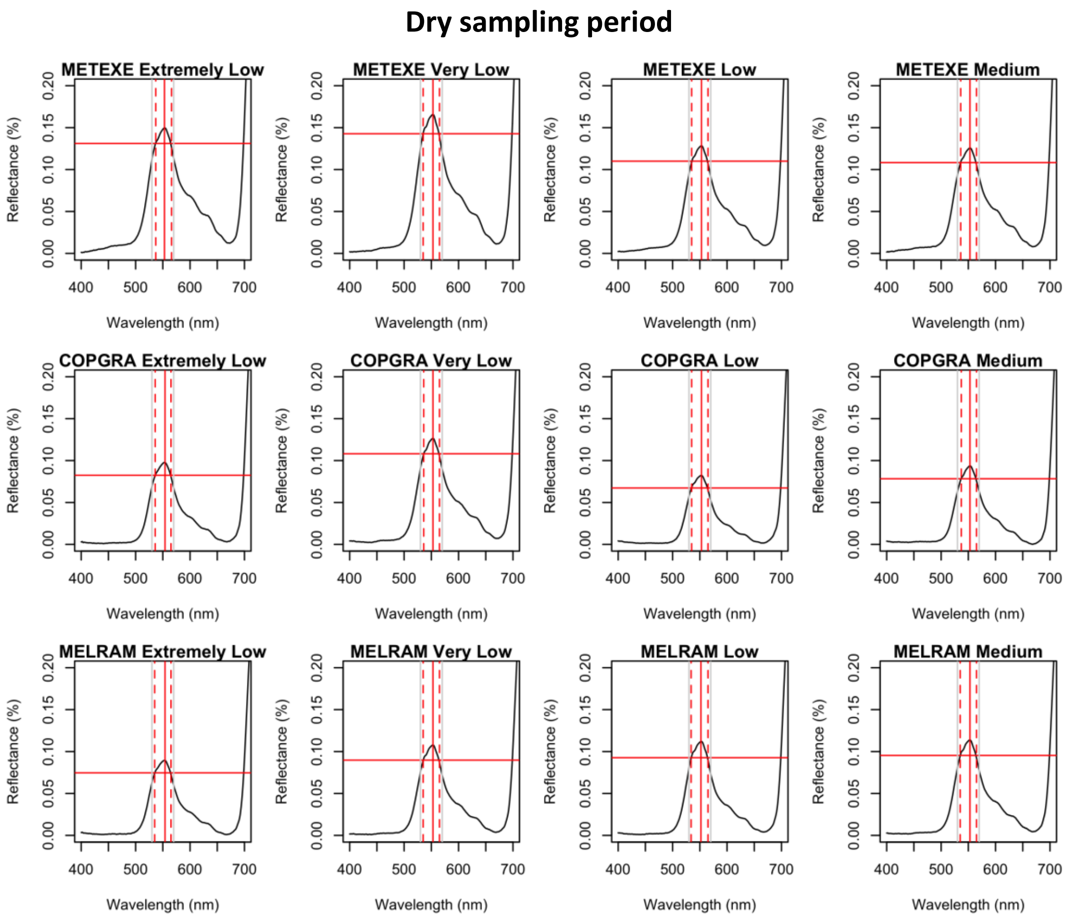

Dry sampling period

Figure 4.9 Spectral reflectance response at the green peak (550nm) for individual species pōhutukawa (METEXE), māhoe (COPGRA), and kanono (MELRAM) from the dry sampling period from the field collection data on Korapuki Islands. The reflectance curves are mean values for each burrow density category; Extremely Low (n=4), Very Low (n=7), Low (n=9), and Medium (n=5) for each species.

Wet sampling period

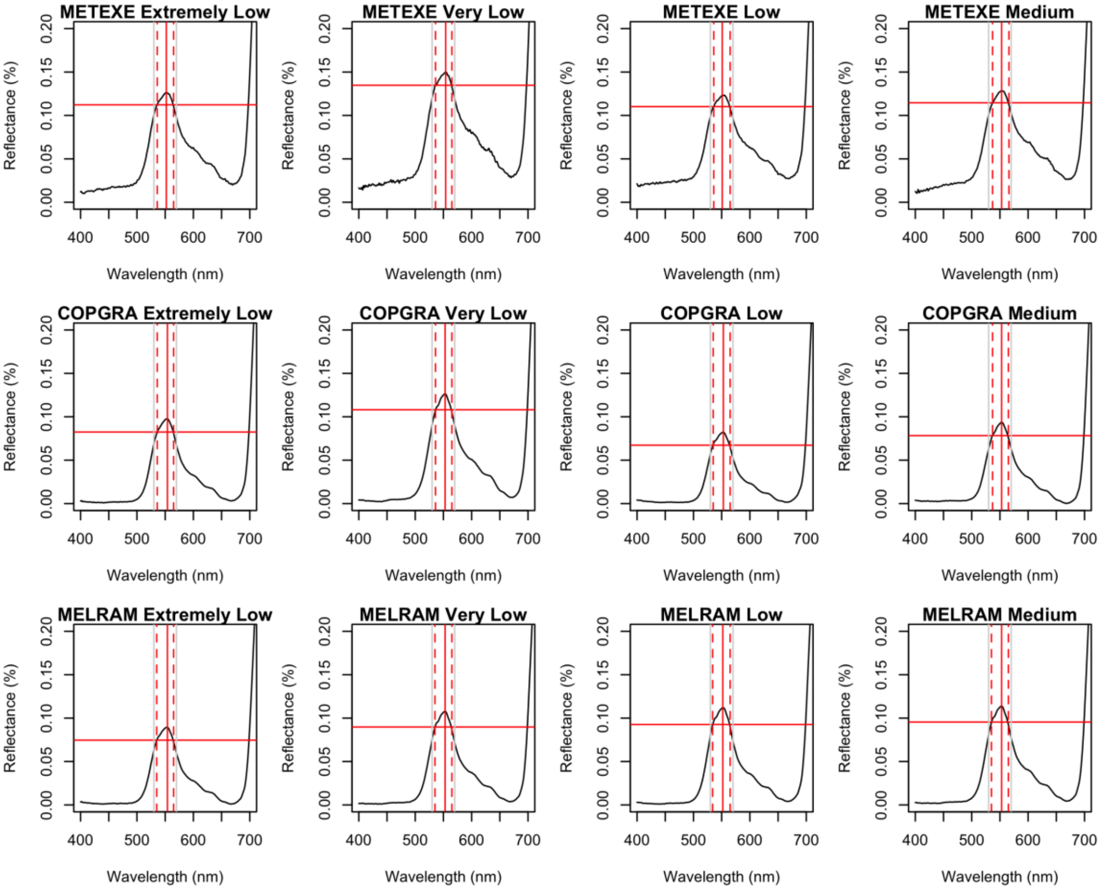


Figure 4.10 Spectral reflectance response at the green peak (550nm) for individual species pōhutukawa (METEXE), māhoe (COPGRA), and kanono (MELRAM) from the dry sampling period from the field collection data on Korapuki Islands. The reflectance curves are mean values for each burrow density category; Extremely Low (n=4), Very Low (n=7), Low (n=9), and Medium (n=5) for each species.

Chapter 5 | Data

Quantifying population impacts of multiple marine threats on data-limited seabirds

5.1 Significance

Seabirds' life-history traits, such as extended immaturity and low reproductive output render them particularly vulnerable to an array of threats on lands and at-sea. We develop an approach to quantify the vulnerability of 81 wide-ranging pelagic seabird species using two readily available life history traits: age of first reproduction and adult survival. We use phylogenetic comparative methods to explore relationships between vulnerability and these life history traits. Additionally, for 14 species, we evaluate the population level impacts from marine threats of fisheries bycatch, plastic pollution and climate change. Our results are congruent with the IUCN Red List threat status and highlight a strong phylogenetic signal emphasising the usefulness of this approach to predict vulnerability of poorly known seabird species from closely related species with sufficient at-sea mortality data.

5.2 Abstract

Seabirds rank among the world's most threatened taxa. The most drastic population declines, nearly 70% in six decades for 20% of species, are occurring in wide-ranging pelagic species. A plethora of agents are responsible for declining populations, and for some taxa, the impact of threats is relatively well understood, such as invasive predators. Yet, there is a paucity of data of at-sea mortality to examine population impacts or risks to multiple intensifying marine threats. Using a demographic modelling approach designed specifically for data-limited species, we calculate the maximum level of annual adult mortality before a decline occurs for 81 wide-ranging pelagic seabirds to anthropogenic sources. Then, using comparative phylogenetic methods we explore the physiological and ecological correlates of vulnerability of seabirds to anthropogenic threats. Finally, for 14 seabird species where terrestrial threats have been eliminated, we use perturbation analyses to explore how the marine threats of fisheries, plastic pollution, and climate change may impact their populations. 38.3% of seabird species have no resilience to any level of anthropogenic mortality under current conditions, congruent with their IUCN Red List threat status. Without intervention, we project intensifying human pressures in the oceans to precipitate into continued population declines. Body mass, range size, and phylogenetic ancestry are strong predictors of the risk to a species to

these threats. Our results suggest that this method may be used to inform vulnerability from closely related species that lack at-sea mortality records.

5.3 Introduction

Most endangered species are stressed by a plethora of agents (*e.g.*, altered habitats, exotic species, pollution; Lawler *et al.* 2002). These agents can act simultaneously (Lawler *et al.* 2002; Barbraud *et al.* 2012), be separated by time and space (Sutherland *et al.* 2012), or target specific stage in the life cycle of a given species (Votier *et al.* 2009). In pelagic seabirds (Order Procellariiforme; albatrosses, petrels, shearwaters, prions, and fulmars), life-history traits, like colonial nesting, extended immaturity, and low reproductive output (Schreiber & Burger 2002), render them particularly vulnerable to predation by invasive mammalian predators at their island breeding sites (Jones *et al.* 2008; Towns *et al.* 2011). However, seabirds are also affected by anthropogenic marine threats, such as pollution, fisheries, and climate change, ultimately reducing adult survival rates (Barbraud *et al.* 2012; Wilcox, Van Sebille & Hardesty 2015). As a consequence, seabirds rank among the most highly threatened marine animals (Paleczny *et al.* 2015; IUCN 2017).

The impacts of multiple threats on seabirds may be interactive or additive (Burthe *et al.* 2014). Indeed, the decline of *Puffinus carneipes* populations is due to fisheries bycatch, and predation pressure at breeding sites (Priddel *et al.* 2006). In New Zealand, many of seabird islands breeding sites have been cleared of introduced predators, but their high annual adult mortality rates due to fisheries are still causing population declines (Richard & Abraham 2013a). Population declines are worsened by the species' high vulnerability to plastic ingestion (Lavers, Bond & Hutton 2014). Quantifying the population-level impacts of single or multiple marine threats is challenging because of limited demographic data, difficulty in detecting at-sea mortality, various demographic factors (*e.g.,* age, breeding success, density dependence), ecological noise (Barbraud *et al.* 2012; Oro 2014), and the manifestation of sub-lethal effects on a species (Tanaka *et al.* 2013).

Here, we expand the demographic invariant method (DIM; Niel & Lebreton 2005), which requires minimal demographic information to estimate the intrinsic annual population growth rate under optimal conditions, to examine the drivers of vulnerability among 81 wide-ranging pelagic species (Order: Procellariiformes;

Figure 5.1). DIM approximates the mortality limit of a species, *i.e.,* the number of individuals that can be removed from the population before a decline occurs (sensu Wade 1998; & Richard & Abraham 2013b; Figure 2.2). We validate our metrics of population performance and vulnerability to at-sea risks against the IUCN Red List categories. Next, we use phylogenetic comparative analyses to explore the morphometric (*e.g.,* body size) and ecological predictors (*e.g.,* foraging strategy, diet, at-sea spatial distribution) of population vulnerability. This approach allows us to quantify the phylogenetic signal of mortality limit, and if high, it will allow managers to infer impacts on a given species, with little to no data based on what is known about closely-related species' demographic parameters and ecological traits. Finally, for a subset of 14 species (Figure 5.1) with at-sea mortality data and where terrestrial threats have been eliminated (predator eradication on their island breeding sites), we implement a perturbation analysis for a finer scale examination of how multiple anthropogenic marine threats may impact these populations.

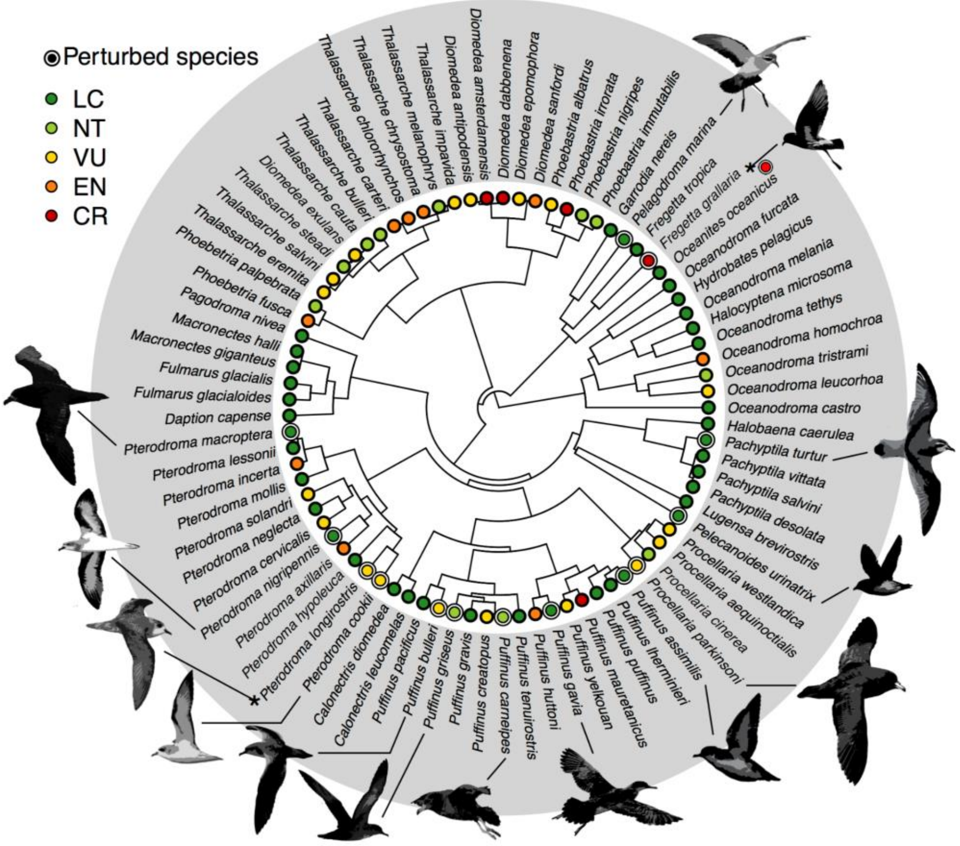


Figure 5.1 Phylogenetic tree of Procelliformes examined in this study (n_{total} = 81) and their corresponding IUCN Red List Threat category. The 14 species used in the perturbation analysis are denoted by a double circle and illustrated pictorially, demographic proxy species are annotated by *; *Pterodroma longirostris* is a proxy species for *P. pycrofti*, and *Fregetta grallaria* is a proxy for *F. maoriana*, which is listed by the IUCN Red List as Critical.

5.4 Methods

5.4.1 Collection of species' data

To calculate the intrinsic population growth rate ($\lambda_{\max}$) and mortality limit (M_{limit}), we collected demographic, morphometric, and ecological information for 81 Procellariiformes (Figure 5.1). The demographic information consisted of: mean age at first reproduction (α) and annual adult survival (s). These variables were obtained from the Biddaba: Bird Demographic Database (Lebreton & Gaillard 2017; unpublished) and the COMADRE Animal Database (Salguero-Gómez *et al.* 2016), as well as from the peer-reviewed literature and online data sources (Birdlife International: birdlife.org/datazone/species and New Zealand Birds Online: nzbirdsonline.org.nz; Table 5.1). The α and s were taken as given in BIDDABA (n=20 species). For species from COMADRE (n=6 species), s was calculated with methods described in Caswell (2001, p 124), whereas α was calculated as the mean column-sums of the sub-matrix of survival-dependent transitions corresponding to adult reproductive stages, weighted by its stable stage distribution (see Salguero-Gómez *et al.* 2016). We used the highest estimate of s, assuming that it was more likely to be a realistic estimate under optimal conditions, *i.e.,* where background mortality is comparable to natural conditions. Where demographic data were incomplete for a given species (*e.g., Pterodroma pycrofti, Puffinus bulleri*), we used data from closely related species as per Penhallurick and Wink (2004). Population size data were obtained from the IUCN Red List (IUCN 2017). Regional population estimates for the subset of 14 species used in the perturbation analysis were obtained from The Northern New Zealand Seabird Trust (Unpublished data; Table 5.7).

The ecological and physiological information of each species was used to correlate key attributes of the species to its vulnerability to at-sea threats. These include foraging strategy (*i.e.*, the primary method of feeding, such as pursuit diving, surface seizing, pattering), primary prey type (*i.e.*, cephalopods, fish) collated from Ashmole (1971), Schreiber and Burger (2002), del Hoyo et al. (2011), and NZ BirdsOnline. Mean (female) adult body mass (B) data were obtained from the CRC Handbook of Avian Mass files (Dunning 2013). At-sea range data were from Birdlife International (2016). We obtained IUCN Red List threatened species ranking and global population estimates for each species (IUCN 2017). We used the IUCN taxonomy and nomenclature for presenting the results, and from Jetz et al. (2012) for the phylogenetic analysis (described below), which differed for some species (Table 5.1)

5.4.2 The Demographic Invariant Method

The Demographic Invariant Method (DIM) combines matrix population models and allometric relationships to calculate important demographic properties such as population growth rate λ (Niel & Lebreton 2005; Richard, Abraham & Filippi 2011; Dillingham *et al.* 2016). Niel and Lebreton (2005) introduced the DIM to approximate the intrinsic annual population growth, $\lambda_{\max}$, for *Thalassarche melanophris,* a data-limited albatross species. This approach relies on the allometric relationship between adult body mass (B) and generation time (T), that is, the weighted mean age of the female at birth in a population (Gaillard *et al.* 2005). Adult body mass is linked to intrinsic annual growth rate $\lambda_{\max}$ and T by a single allometric exponent ~1/4 (Niel & Lebreton 2005). Neil & Lebreton (2005) demonstrated this allometric relationship to be invariant; approximately 1 for 13 bird species across 10 taxonomic families, with adult body mass ranging between 19 and 7,400 g. This correlation is notably tight for Procellaria species (R^2=0.96; Dillingham *et al.* 2016). Consequently, we used this allometric constant ($a_{rT} \approx 1$), for all species in our study.

One of the strengths of the DIM method is that it requires minimal demographic information to produce biologically meaningful metrics of population dynamics. The required demographic information to calculate $\lambda_{\max}$ are age at first reproduction (α), adult survival (s), and the aforementioned allometric constant (a_{rT}) (Niel & Lebreton 2005; Richard & Abraham 2013b). Here we used the maximum value of adult survival reported (s_{opt}), assuming that this value corresponds to adult survival under optimal conditions.

$$\lambda_{\max} = e^{[a_{rT}(\alpha + s_{opt}/(\lambda_{\max} - s_{opt}))^{-1}]} \tag{5.1}$$

The population growth rate above replacement per generation is detailed in equation 2 (Niel & Lebreton 2005; Richard & Abraham 2013b; Table 1):

$$r_{\max} = \log(\lambda_{\max} - 1) \tag{5.2}$$

To calculate the mortality limit (M_{limit}) for a population, an estimation of the minimum number of breeding pairs ($N_{\min}$) is needed. Because census data for seabirds are typically from colony surveys where only breeding adults can be counted, the total population size represented by the census data is often unknown (Richard & Abraham 2013b; Dillingham *et al.* 2016). Indeed, immature birds spending their first few years at sea before returning to the colony to breed, and portions of breeding adults taking sabbaticals from breeding make this accurate calculation challenging (Warham 1990; Richard & Abraham 2013a). Thus, we approximated the minimum breeding population of adults ($N_{\min}$) > 1 year old (assuming adult survival is constant) using the method described by Richard and Abraham (2013b):

$$N_{\min} = \frac{2N_{BP}}{P_B} s^{1-\alpha} \qquad (5.3)$$

where N_{BP} is the estimated number of breeding pairs, P_B is the annual proportion of breeding adults, s is mean adult survival, and α is the mean age at first reproduction (Richard, Abraham & Filippi 2011; Richard & Abraham 2013a).

Next, we calculated the mortality limit M_{limit} of each species using the estimates of maximum population growth rate $\lambda_{\max}$ and $N_{\min}$. Mortality limit corresponds to the maximum number of reproductive individuals in a population that could be removed from it annually, *e.g.*, due to some source of anthropogenic mortality, without causing the population to decline with equation 5.4 (Richard & Abraham 2013b):

$$M_{\text{limit}} = \frac{1}{2}\rho r_{\max} N_{\min} f, \qquad (5.4)$$

where ρ is a calibration factor correcting for overestimation of mortality limits typical of earlier methods (e.g., Wade 1998), particularly among faster reproducing species (*i.e., Pelecanides urinatrix;* Richard & Abraham 2013a; Table 5.1).

A recovery factor (f) is introduced to the calculation of M_{limit} to account for factors that may influence population growth. Here, f=1 is the most optimistic scenario, and f=0 the most pessimistic scenario (Dillingham & Fletcher 2011; Richard & Abraham 2013b). This factor assigned based on population size and trend because smaller populations may be more sensitive to even moderate levels of mortality, particularly if restricted to only a few sites, or for slow-growing species (Lebreton & Clobert 1991; Niel & Lebreton 2005). In addition, the recovery factor accounts for the effect of density dependence on demographic performance (*e.g.,* negative density-dependence effects from environmental stochasticity on breeding phenology, whereby mating efficiency is reduced; Votier *et al.* 2009), undetected mortality (*e.g.*, unidentified oil spills; Votier *et al.* 2005), which may create an imbalance in certain age classes such as the most reproductive adults (Lebreton & Clobert 1991), potential errors in population estimates, or unknown biases (Dillingham & Fletcher 2011; Richard & Abraham 2013a). We used an f value of 0.1 for threatened species (IUCN Red List threat categories; CR, EN, VU), 0.3 for near threatened (NT), and 0.5 for least concern (LC) (Dillingham & Fletcher 2011; Richard, Abraham & Filippi 2011). For the perturbation analyses (n=14), we adjusted the f factor; if the local population was increasing we added 0.1 and subtracted 0.1 if the population was declining (Supporting Information).

Because the recovery factor is informed by the IUCN Red List threat categories, to bypass the circularity in validating the M_{limit} model, we performed a brute force sensitivity analysis by running the M_{limit} model without the recovery factor (f) and validating the output against the IUCN Red List threat categories. Because there was no significant difference between these analyses, we present the results of the validation with the recovery factor included (Figure 5.2.A), and the brute force sensitivity in the Supporting Information (Figure 5.5).

5.4.3 Predictors of risk

Due to shared ancestry, closely related species are expected to share similar trait values (Symonds & Blomberg 2014). To quantify the phylogenetic signal of our traits of interest: body mass, foraging strategy, diet, and at-sea distribution, we estimated Pagel's λ (not to be confused with population growth rate λ), a scaling parameter for the phylogenetic correlation between species that ranges from 0 (no role of phylogeny in determining trait variation) to 1 (trait variation fully explained by phylogeny assuming Brownian motion) (Freckleton, Harvey & Pagel 2002). To do this, we obtained the bird phylogeny by Jetz et al. (2012), which contains time-calibrated phylogenetic relationships from conserved regions of the genomes of 9,993 extant bird species. We manipulated the tree to prune it to our subset of 81 bird species and calculate Pagel's λ using the *R* packages (phytools package; Revell 2012), *ape* (Paradis, Claude & Strimmer 2004), and *caper* (Orme 2013).

To examine the ecological and morphometric metrics that best predict the risk of a species to anthropogenic sources of at-sea mortality, we used phylogenetic generalised least squares (PGLS) regression. We used M_{limit} as our response due to its strong relationship with the IUCN Red List threat criteria (Figure 5.2). Our set of explanatory variables belonged to three broad families: ecology (foraging strategy, prey type, at-sea distribution) and morphometric (mean adult body mass and foraging methods), since evidence exists that these are indicators of species' likelihood to interact with fishing vessels (Genovart *et al.* 2017), ingest plastic pollution (Day, Wehle & Coleman 1985; van Franeker & Law 2015), and/or their overall risk to extinction (*e.g.,* body size; Gaston & Blackburn 1995, foraging method; Ryan, 2016, and spatial distribution; Frederiksen *et al.* 2004).

We used a brute force approach, where we carried out a generalised linear model and then compared the results to the phylogenetically corrected PGLS model (Figure 5.1, Table 5.1). The PGLS were carried out with the function *pgls* of the *caper R* package (Orme 2013), and using the bird phylogeny described above as the backbone.

5.4.4 Marine threat impact simulations

The third step in our approach is to simulate population changes using prospective perturbation analysis (hereafter 'perturbation analysis'; Caswell 2008; Figure 2.3). Perturbation analyses are commonly used in population modelling to simulate future trajectories of population growth rates λ in response to a perturbation of a given vital rate and/or stage (*e.g.,* adult survival; Caswell 2008). We used $\lambda_{\max}$ and M_{limit} (eq. 5.1 & 5.4) for a subset of 14 species from the Northern New Zealand region, for which we obtained accurate regional population estimates (Supporting Information; Table S4). By using this subset, we had greater confidence that the populations were in optimal conditions (*i.e.,* recovering from the pressure of invasive mammalian predators following predator removal, minimal density-dependence effects, no limit of available habitat, and no resource limitations; Niel & Lebreton 2005; Ismar *et al.* 2014; Borrelle *et al.* 2016).

To model the impacts of decreased adult survival due to each of the aforementioned at-sea threats on M_{limit}, we ran perturbation analyses by adjusting adult survival s rates for each of the threats individually and then interactively. The sensitivity of various demographic properties such as $\lambda_{\max}$ and M_{limit} to changes in adult survival; here from the threats of fisheries, plastic pollution, and climate change were then presented along the phylogenetic tree of the 14 species. We also quantified the phylogenetic signal using Pagel's λ. The following details the estimation of changes to s by three key agents in our model:

- Fisheries bycatch: We used the New Zealand fisheries Risk Index data (Richard and Abraham (2013a). The Fisheries Risk Index (FRI) is calculated from bycatch data of four fishing methods; trawl, surface and bottom long-line, and set nets from the New Zealand exclusive economic zone (EEZ) for 2006-07 and 2010-11. FRI provides estimates of annual adult mortality (= 1-s) from fisheries bycatch, which we used to parameterize our perturbation analyses (Supporting Information; Table **5.4**).
- Plastic Pollution: We searched Google Scholar and Web of Science using the terms seabird species + threat (e.g. "*Puffinus carneipes*" and "*plastic* and ingestion*"). Species were categorised into risk from plastic pollution related mortality based on frequency of occurrence of plastic ingestion, (*i.e.,* percentage of individuals found to have ingested plastic rather than mass or volume estimates), using three levels, low: 0-0.004, moderate: 0.004-0.008; and high: 0.008-0.012 (Supporting Information; Table **5.4**). That is, the reduction in annual adult survival (s) due to plastic ingested related mortality per annum.
- Climate change: We searched Google Scholar and Web of Science using the terms seabird species + threat (*e.g.,* "*Puffinus carneipes*" and "*climate change*"). Because few peer-reviewed climate change impacts exist for all 14 species, and to account for the high uncertainty in parameter estimates for effects of climate change on adult survival was estimated to be negative; 0.01, that is, 1% reduction in adult survival due to climate change effects (Table **5.4**).

While some data are reported with uncertainties, much are not. Given this uncertainty, we accounted for variation from the mean based on the data quality, as poor, moderate or high quality and assigned the standard deviation (SD) (Table 5.4). See Supporting Information for further discussion on uncertainty accounting.

5.5 Results

5.5.1 Population growth and mortality limits

Using the DIM approach, the intrinsic population growth rate above replacement r_{max} under non-limiting conditions ranged between r_{max}=0.03, reflecting a 3% population increase for *Puffinus bulleri* and r_{max}=0.17 for *Hydrobates castro* (Table 5.1). Seabirds are expected to have low annual population growth rates, which is a trade-off for longevity and high adult survival (Stearns 1989; Warham 1990).

The M_{limit} was negative, implying species whose populations are already unviable for 38.3% (31) of the 81 examined species (Figure 5.2.A). The highest M_{limit} was 26,653 for *Pelecanoides urinatrix* (Table 5.1), which is expected given their low age of first reproduction (2.5 years), and large population size, and small foraging range close to the highly productive continental shelves (New Zealand Birds Online 2015). Results from our mortality limit (M_{limit}) model are congruent with IUCN Red List threat categories (Figure 5.2.A). As expected, species in the IUCN Red List threatened categories (EN, VU, CR) reflected the lowest mortality limits, although, *Hydrobates leucorhoa* had an unexpectedly high mortality limit (237) compared to other (VU) vulnerable species (Table 5.1). Similarly, several species in the Least Concern IUCN Red List threat category had low (<10) M_{limit} value (Table 5.1).

Mortality limits had a strong phylogenetic signal, particularly for larger bodied species (Figure 5.1 and Supporting Information; Figure 5.7). A phylogenetic signal is considered strongest with a Pagels's lambda value of 1, indicating that traits being evaluated are likely to be observed in closely related species. This means that inferences can be made about a species despite data limitations.

Table 5.1 Demographic parameters and model outputs for 81 Procellariiformes included in the mortality limit, and phylogenetic comparative analyses. The first 14 species in bold are those that are used in the perturbation analyses, see Table 5.7 for regional population estimates. The parameters are: biomass; IUCN Red List category and population trend (↓ decline, → stable, ↑ increase, ? unknown); global population estimate; optimal estimate of adult survival (S_{opt}); age of first reproduction (α); the recovery factor (f; Richard and Abraham 2013b), which accounts for factors that may influence population growth, such as density dependence, environmental stochasticity, undetected mortality, or potential errors in population estimates; calibration factor (ρ) (Richard & Abraham 2013b), which corrects for overestimates of the M_{limit}; minimum population estimate of breeding adults (N_{min}); maximum population growth rate above replacement (r_{max}) in optimal breeding conditions (i.e. without limits on resources or breeding habitat); population increase per year (%); and mortality limits (M_{limit}), that is the number of individuals that can be removed from the population before a decline occurs. The allometric constant (α_{rT}) used in the demographic invariant method for calculating $\lambda_{max} = \sim 1$ was obtained from (Niel & Lebreton 2005). * indicates species demographic information was inferred from the closest phylogenetically related species, as per Penhallurick & Wink (2004).

Species	**Body mass**	**IUCN Red List**	**Trend**	**Breeding pairs**	S_{opt}	a	f	p	N_{min}	r_{max}	**% increase year^{-1}**	M_{limit}
Pachyptila turtur	120	LC	→	222,500	0.947	4.5	0.5	0.32	22,171	0.097	9.68	172
Pelagodroma marina	45	LC	↓	1,780,000	0.94	4	0.4	0.3	290,264	0.111	11.11	1,934
Pelecanoides urinatrix	130	LC	↓	7,120,000	0.947	2.5	0.4	0.17	5,242,245	0.15	14.95	26,653
Pterodroma gouldi	550	LC	↓	667,500	0.98	6.5	0.4	0.41	9,315	0.05	5	38
*Pterodroma nigripennis**	160	LC	↓	4,005,000	0.98	6.49	0.4	0.3	56,452	0.05	5	169
Puffinus assimilis	240	LC	↓	89,000	0.96	5	0.4	0.32	5,453	0.08	7.99	28
Puffinus gavia	365	LC	↓	44,500	0.96	5	0.4	0.41	2,726	0.08	7.99	18
Ardenna carneipes	700	NT	↓	74,000	0.956	6.7	0.1	0.41	1,091	0.068	6.77	2
Ardenna griseus	800	NT	↓	8,900,000	0.98	6	0.2	0.41	204,773	0.053	5.26	442
Ardenna bulleri	420	VU	→	890,000	0.96	6.4	0.1	0.43	13,446	0.067	6.73	19
Procellaria parkinsoni	744	VU	→	720	0.94	6.6	0.1	0.33	101	0.077	7.72	0
Pterodroma cookii	180	VU	↑	298,150	0.98	6.5	0.2	0.32	4,161	0.05	5	7
*Pterodroma pycrofti**	150	VU	↓	13,350	0.98	6.5	0.2	0.3	186	0.05	5	0
*Freggetta maoriana**	35	CR	?	750	0.947	4.5	0.1	0.3	105	0.097	9.68	0
*Aphrodroma brevirostri**	314	LC	→	445,000	0.9609	9	0.5	0.41	500	0.053	5.27	3
*Ardenna gravis**	830	LC	→	6,675,000	0.96	6.7	0.5	0.41	74,709	0.065	6.52	500
Ardenna pacificus	450	LC	↓	2,314,000	0.96	4	0.5	0.41	385,372	0.093	9.34	3,691
Ardenna tenuirostris	550	LC	↓	6,325,000	0.99	7.17	0.5	0.41	119,476	0.035	3.47	425

*Calonectris diomedea**	670.5	LC	↓	178,261	0.9609	10	0.5	0.41	118	0.049	4.9	1
*Calonectris leucomelas**	580	LC	↓	1,335,000	0.9609	9	0.5	0.41	1,499	0.053	5.27	8
*Daption capense**	424.5	LC	→	890,000	0.98	6	0.5	0.32	20,477	0.053	5.26	86
*Fregetta tropica**	52	LC	↓	111,250	0.94	4.5	0.5	0.3	11,003	0.102	10.19	84
Fulmarus glacialis	613	LC	↑	5,918,700	0.98	9	0.5	0.41	15,330	0.04	4.05	64
Fulmarus glacialoides	795	LC	→	1,140,000	0.97	7.6	0.5	0.41	12,779	0.053	5.34	70
*Garrodia nereis**	38.2	LC	↓	89,000	0.94	4	0.5	0.3	14,513	0.111	11.11	121
*Halobaena caerulea**	196	LC	→	445,000	0.947	6.5	0.5	0.32	6,001	0.074	7.44	36
*Halocyptena microsoma**	20	LC	↓	267,000	0.947	3	0.5	0.3	119,234	0.13	13.02	1,165
Hydrbates castro	45	LC	↓	6,008	0.94	2.3	0.5	0.3	5,363	0.169	16.9	68
*Hydrobates furcata**	43	LC	↑	2,670,000	0.94	3.5	0.5	0.3	717,847	0.123	12.26	6,599
*Hydrobates melania**	43	LC	↓	222,500	0.94	4.5	0.5	0.3	22,007	0.102	10.19	168
Hydrobates pelagicus	25.2	LC	↓	687,525	0.947	3	0.5	0.3	307,028	0.13	13.02	2,999
Macronectes giganteus	4395	LC	↑	44,500	0.96	8.5	0.5	0.34	8,200	0.055	5.53	0
Macronectes halli	4185	LC	↑	11,800	0.96	7.33	0.5	0.34	1,799	0.061	6.13	0
*Oceanites oceanicus**	30.45	LC	→	12,460,000	0.947	4	0.5	0.3	2,046,980	0.105	10.54	16,184
*Oceanodroma tethys**	23	LC	↓	22,250	0.94	4.5	0.5	0.3	2,201	0.102	10.19	17
Pachyptila desolata	147	LC	↓	22,250,000	0.947	5.5	0.5	0.32	815,613	0.084	8.38	5,471
*Pachyptila salvini**	159	LC	→	1,780,000	0.947	4.5	0.5	0.32	177,365	0.097	9.68	1,374
Pachyptila vittata	196	LC	↓	6,675,000	0.947	5.4	0.5	0.32	270,417	0.085	8.5	1,838
Pagodroma nivea	268	LC	→	960,000	0.95	8.2	0.5	0.41	8,156	0.062	6.17	52
*Pterodroma hypoleuca**	176	LC	↓	13,350	0.98	6.5	0.5	0.32	986	0.05	5	1
Pterodroma lessonii	704	LC	↓	180,000	0.98	5.5	0.5	0.41	15,024	0.056	5.57	86
Pterodroma mollis	312	LC	→	2,225,000	0.98	6.5	0.5	0.41	31,050	0.05	5	159
*Pterodroma neglecta**	501	LC	↓	77,875	0.98	6.5	0.5	0.41	1,087	0.05	5	6
*Puffinus lherminieri**	168	LC	↓	6,675	0.947	8	0.5	0.32	203	0.064	6.41	0
*Puffinus puffinus**	453.5	LC	↓	445,000	0.99	5.4	0.5	0.41	18,846	0.041	4.14	80
*Oceanodroma tristrami**	83	NT	→	4,450	0.94	6	0.3	0.3	980	0.083	8.27	0
Phoebastria immutabilis	3150	NT	→	377,910	0.962	9	0.3	0.37	1,508	0.052	5.22	4
*Phoebastria nigripes**	3195	NT	→	70,069	0.994	4	0.3	0.43	26,585	0.039	3.93	67
Phoebetria palpebrata	2967.5	NT	↓	26,100	0.973	12	0.3	0.37	9,098	0.038	3.77	0
Procellaria cinerea	1131	NT	↓	178,000	0.97	7	0.3	0.33	4,491	0.056	5.64	4

Thalassarche bulleri	2635	NT	→	32,134	0.99	12	0.3	0.43	6,203	0.025	2.53	0
*Thalassarche cauta**	4025	NT	?	13,662	0.99	5	0.3	0.43	863	0.043	4.34	2
Thalassarche melanophris	3800	NT	↓	700,000	0.962	9.189	0.3	0.43	11.000	0.051	5.14	4
Thalassarche steadi	3940	NT	↓	38,174	0.99	11.9	0.3	0.43	3,403	0.025	2.54	0
*Ardenna creatopus**	740	VU	?	26,320	0.956	6.7	0.1	0.41	1,293	0.068	6.77	0
Diomedea antipodensis	6650	VU	↓	13,350	0.97	11.5	0.1	0.37	897	0.04	4.03	0
Diomedea epomophora	9000	VU	→	8,160	0.97	9	0.1	0.37	209	0.048	4.76	0
Diomedea exulans	8190	VU	↓	4,924	0.968	10	0.1	0.37	345	0.045	4.55	0
*Hydrobates leucorhoa**	44	VU	↓	8,900,000	0.945	6	0.1	0.3	197,460	0.08	7.99	237
*Phoebastria albatrus**	4411	VU	↑	360	0.962	6	0.1	0.43	18	0.069	6.9	0
Procellaria aequinoctialis	1213	VU	↓	1,068,000	0.97	6.49	0.1	0.33	14,900	0.059	5.93	15
Procellaria westlandica	1199	VU	→	3,575	0.96	6.49	0.1	0.33	129	0.067	6.67	0
*Pterodroma cervicalis**	445	VU	↑	66,750	0.98	6.5	0.1	0.41	932	0.05	5	1
Pterodroma solandri	518	VU	↑	44,500	0.98	6.5	0.1	0.41	621	0.05	5	1
*Puffinus yelkouan**	382.5	VU	↓	40,050	0.96	3.5	0.1	0.41	10,997	0.103	10.27	23
Thalassarche eremita	3885	VU	→	4,895	0.98	12	0.1	0.43	354	0.034	3.36	-
Thalassarche impavida	2800	VU	↑	21,648	0.96	9.54	0.1	0.43	1,689	0.051	5.11	0
*Thalassarche salvini**	3795	VU	?	35,596	0.98	12	0.1	0.43	2,340	0.034	3.36	0
Diomedea sanfordi	9000	EN	↓	7,625	0.98	9.5	0.1	0.37	911	0.039	3.91	0
*Hydrobates homochroa**	37	EN	↓	1,535	0.94	4.5	0.1	0.3	152	0.102	10.19	0
*Phoebetria fusca**	2750	EN	↓	4,200	0.95	11.8	0.1	0.43	707	0.048	4.75	0
Pterodroma axillaris	165	EN	↑	623	0.98	5	0.1	0.41	39	0.059	5.93	0
*Pterodroma incerta**	520	EN	↓	382,700	0.98	6.5	0.1	0.41	5,341	0.05	5	5
Puffinus huttoni	364	EN	→	112,500	0.96	5	0.1	0.41	9,706	0.08	7.99	16
Thalassarche carteri	2200	EN	↓	36,490	0.947	8.7	0.1	0.43	5,501	0.06	6.04	0
Thalassarche chlororhynchos	2060	EN	↓	9,345	0.947	9.4	0.1	0.43	700	0.057	5.71	0
Thalassarche chrysostoma	3507.5	EN	↓	93,750	0.96	12.5	0.1	0.43	4,034	0.042	4.22	0
Diomedea amsterdamensis	6270	CR	↓	51	0.977	10	0.1	0.37	-	0.04	4	-
Diomedea dabbenena	7050	CR	↓	1,440	0.99	10	0.1	0.37	187	0.028	2.83	0
*Phoebastria irrorata**	3395	CR	↓	10,408	0.962	5.88	0.1	0.43	983	0.07	6.99	1
*Puffinus mauretanicus**	497	CR	↓	1,398	0.96	3	0.1	0.41	633	0.115	11.48	1

5.5.2 Predictive correlates of species vulnerability

We explored the demographic and ecological traits of body mass, at-sea range, foraging strategy, and diet for predictors of vulnerability to low mortality limits. The phylogenetically corrected generalised least squares models retained body mass, at-sea range, and foraging strategies as predictors of vulnerability (M_{limit}), explaining 54% of variability in risk (Table 5.2). Body mass had a strong phylogenetic signal (Pagel's λ=0.98, 95% CI ± 0.1-0.85, *F-ratio*=7.994, df=66; Table 5.1; Figure 5.2.B) and was the best predictor of M_{limit} for the 81 species in our analysis (p=0.001). Body size tends to strongly co-vary with a number of key biological traits, including reproduction, survival, growth, and extinction risk (Gaston & Blackburn 1995; Hilbers *et al.* 2016; Ripple *et al.* 2017).

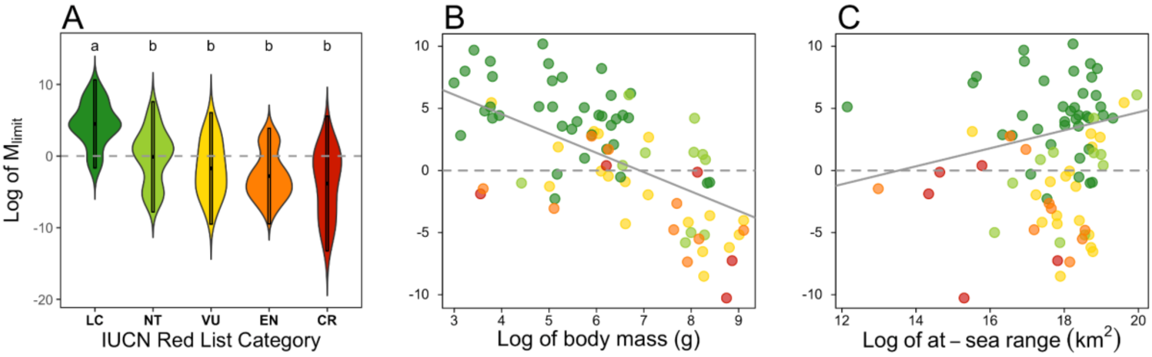


Figure 5.2 Modelled mortality limit's (M_{limit}), that is, the maximum number of breeding adults that could be removed annually from the population without incurring a decline validated against the IUCN Red List threat categories for 81 Procellariiformes. Tukey's groupings for (a) Least Concern [LC] are significantly different ($P \leq 0.0001$) to (b) Near Threatened [NT], Vulnerable [VU], Endangered [EN], and Critical [CR] IUCN Red List threat categories. Phylogenetic generalised least squares (PGLS) for the relationships among demographic traits for seabirds (n=81); B) mortality limit and mean (female) body mass (P=0.001), and; C) mortality limit and at-sea range (P=0.009).

At-sea range was a significant predictor of M_{limit}, although with a less strong phylogenetic signal (M_{limit}: Pagel's λ=0.68, 95% CI ± 0.59-0.93, *F-ratio*=6.642, df=79, P=0.01; Table 5.2; Figure 5.2.C). This finding is in agreement with the inclusion of range size as one of the main metrics of IUCN Red List evaluations of threatened status (IUCN 2017). However, we caution that there are a number of issues in inferring risk from at-sea range alone. For example, Barbraud *et al.* (2011) demonstrated non-linear and variable responses to high and low climate anomalies (*i.e.,* sea surface temperature and sea ice coverage) in breeding success among

Pagodroma nivea, Thalassarche melanophyrs, and *Diomedea amsterdamensis.* Barbraud et al.'s (2011) study suggested that the most southerly distributed species are likely to experience more rapid declines due to changes to prey resources that are driven by sea ice extent. The scale and rate of change to prey distributions due to climatic changes may exert contrasting responses between closely related species depending on their at-sea distributions, including altering temporal breeding phenology (*e.g.,* body condition), and/or resulting in mismatches between prey availability and chick provisioning times (Frederiksen *et al.* 2004). Alternatively, the presence of some threats and species co-occurrence can be predicted. For example, the spatial distribution and abundance of marine litter is strongly linked to plastic ingestion rates for *Fulmaris glacialis* in their foraging areas (van Franeker & Law 2015).

Foraging strategy and diet are expected to have a strong influence on vulnerability given that all of the threats we evaluated are closely related to seabird food resources. The results of the PGLS retained the foraging methods of scavenging (Pagel's λ=0.96, 95% CI ± 0.35-0.86, *F-ratio*=8.919, df=79, p=0.003; 95% CI:), and pursuit diving (Pagel's λ=1; 95% CI ±0.54-0.91, *F-ratio*=5.47, df=79, p=0.04), with strong phylogenetic signals as good predictors of M_{limit}. Indeed, foraging strategy and prey type have been previously linked to seabirds' propensity to ingest plastic (Day, Wehle & Coleman 1985; Ryan 1987b; Provencher *et al.* 2010). Species with generalist prey preferences tend to have the greatest loads of plastic (Ryan 1987b). However, a lack of systematic methodology in plastic ingestion studies means that linking the risk of plastic ingestion to a species is challenging (Provencher *et al.* 2016). A full table of Pagel's λ for all meaningful variables can be found in the Supporting information; Table 5.6).

Table 5.2 Phylogenetic generalised least squares analyses on population growth rate and mortality limits, and the explanatory ecological (at-sea distribution, range, foraging strategy), and morphometric (adult mean body mass) variables retained as significant in the models.

Model	**GLM**	**Phylogenetically corrected *p***	**Pagel's λ** (95% CI)	**LogLink**	**Adjusted R^2**
M_{limit} vs. body mass + at-sea range + foraging strategy		<0.0001			0.54
M_{limit} vs. body mass	<0.0001	<0.0006	0.98 (0.068-0.806)	-65.56	
M_{limit} vs. at-sea range	0.41	0.012	0.68	-135.59	

			(0.528- 0.913)	
M_{limit} vs. foraging strategy	0.15	0.024	1	14.13
- Pursuit Diving	<0.0001	0.004	(0.484- 0.887)	-47.93
- Scavenging	0.004	0.07	0.96 (0.354- 0.866)	-22.15
- Surface filtering			1 (0.480- 0.914)	

5.5.3 Population impact from marine threats

We examined a subset of 14 species, where terrestrial threats were absent for the regional population, *i.e.,* predators have been removed from their breeding sites and habitat is not limited (Ismar *et al.* 2014; Borrelle *et al.* 2016). For these species, we found that the annual mortality limit was nil for half of the regional populations (Table 5.7). For these species, even low levels of adult mortality from one of the marine threats would cause the population to decline. We can attribute the low mortality limits of these species to their small population sizes (Table 5.7), which have been suppressed from predator invasions on many of their breeding islands (Borrelle *et al.* 2016; Brooke *et al.* 2017). Given that at-sea mortality rates for many of these species are expected to be low from each of the examined marine threats (Table 5.3), and the recency of predator eradications in the region (Borrelle *et al.* 2016), some regional populations may still experience population growth in spite of high adult mortality due to marine threats. This result emphasizes that invasive predator eradication at island breeding sites is the most effective form of conservation for the world's seabirds (Jones *et al.* 2016).

Table 5.3 Mortality limit scenarios for the 14 species examined in the perturbation analysis. The table includes M_{limit} for optimal conditions (current population size), and for the individual threats of fisheries, plastic ingestion, and climate change and the mortality limit after accounting for the combined threats. Species with * are those where proxy values of age at first reproduction or adult survival were used from closely related species. Details of the regional populations and model parameters are in Table 5.7.

Species	M_{limit} optimal	M_{limit} fisheries	M_{limit} plastic ingestion	M_{limit} climate change	M_{limit} combined threats
Procellaria parkinsoni	0	0	0	0	0
*Pterodroma nigripennis**	0	0	0	0	0
Ardenna bulleri	0	0	0	0	0

Pelecanoides urinatrix	281	152	147	155	139
Pterodroma cookii	4	4	4	4	3
Pachyptila turtur	23	21	21	21	18
Ardenna carneipes	0	0	0	0	0
Ardenna gavia	14	13	13	14	12
Pterodroma macroptera	9	9	8	9	7
Ardenna assimilis	3	2	2	2	2
*Freggetta maoriana**	0	0	0	0	0
*Pterodroma pycrofti**	0	0	0	0	0
Ardenna griseus	0	0	0	0	0
Pelagodroma marina	57	44	44	44	39

5.6 Discussion and conclusions

We presented a risk assessment tool to explore how marine threats may change the vital rate of a species (*e.g*., adult survival), and thus potentially the population growth rate over time (Caswell 2008). Out of the 81 examined seabird species, *ca.* 38.3% already have no resilience to sustain even moderate levels of anthropogenic sources of at-sea mortality coupled with threats on land. We found that larger species, and those with smaller at-sea ranges, are at greater risk of having no population resilience additional at-sea mortality. The results from the perturbation analyses suggest that marine threats acting individually have variable impacts on a species; however, for species with small populations, or when a species is affected by multiple marine threats, the population impacts could be severe.

Given the high phylogenetic signal, our approach can be used to inform the vulnerability of seabirds without at-sea mortality data. In this way, managers can decide to implement compensatory conservation actions, such as facilitated colony establishment, or the use of social attraction methods (Friesen, Beggs & Gaskett 2017) to improve the resilience of vulnerable colonies.

In theory, long-lived highly mobile species, such as seabirds, should be relatively resilient to natural levels of adult mortality when environmental conditions are poor. This is an idea that has been proposed as a compensatory mechanism for naturally lower population growth rates (Weimerskirch 2001). This is because seabird life history traits, including high adult survival (Weimerskirch 2001), may allow populations to buffer against interannual variation in breeding success and environmental stochasticity (Sæther & Engen 2010). Further, mobile species are able to move to more favourable foraging or breeding grounds when conditions become unfavourable. The compensatory mechanism works in a way that while adult survival remains high, reproductive success may be low and at an individual level or birds may refrain from breeding altogether during these unfavourable periods (Weimerskirch 2001; Giudici *et al.* 2010). This means that in natural conditions (*i.e.,* in the absence of anthropogenic caused mortality), population stochasticity may be high over the short term, but over many generations the population is resilient to environmental stochasticity (Weimerskirch 2001).

However, populations of seabirds are typically sensitive to even slight long-term changes in adult survival (Montevecchi 2002; Barbraud *et al.* 2012; Genovart *et al.* 2017). For example, Genovart *et al.* (2017) found that for *Calonectris diomedea* in the Mediterranean, even if fisheries bycatch mortality was nil, the population would still be in decline due to environmental stochasticity and other sources of adult mortality, such that adult survival would have to be 0.90 yr^{-1} or greater to maintain a viable population. Because most Procellariiformes have high adult survival rates, typically >0.90 (Weimerskirch 2001), if intensifying pressures in the marine environment decrease annual adult survival below a sustainable level, in spite of land-based conservation actions (*e.g.,* predator eradication), these seabirds will continue to experience disproportionate declines, compared to other taxa that have naturally lower adult survival rates (Genovart *et al.* 2017).

Large-bodied bird species have consistently been shown to be more at risk from extinction (Gaston & Blackburn 1995; Ripple *et al.* 2017). Explanations for this include factors such as large-bodied species having generally smaller population sizes, larger range sizes, and lower intrinsic population growth rates (Gaston & Blackburn 1995). Rowe (2010) found albatrosses and large petrels and shearwaters to be at greatest risk from fisheries-related mortality. Similarly, research shows a strong correlation between body size and average mass of plastic ingested, which may be linked to prey size (Ryan 2016). Notably, Lavers *et al.* (2010) found that for larger species of seabirds, increased population growth rate following predator eradication was still insufficient to reverse overall declines, emphasizing the increased risk to larger bodied birds, which generally have lower intrinsic population growth (Table 5.1).

Importantly, the relationship between body size and extinction risk is confounded by additional, negative and positive biological correlates and biomass. For example, although body size weakly and negatively correlates with abundance, abundance is negatively correlated with extinction risk (Gaston & Blackburn 1995).

Alternatively, body size is negatively correlated with environmental stochasticity, which is positively correlated with extinction risk (Gaston & Blackburn 1995; Johst & Brandl 1997). Therefore, a prudent approach is needed when inferring patterns across taxa and the relationship between body size and threat risk for any species.

The risk of exposure to one or more marine threats is likely to be strongly influenced by spatial co-occurrence depending on foraging strategy, behaviour and distribution of both threats and birds (Ryan 1987b, 2016). In the same way that oceanic features vary across latitudes and water masses influencing resource distributions for seabirds, the intensity or existence of a threat is not distributed evenly (Ryan 2016). Species that have large spatial distributions are likely to have variable population level responses to marine threats due to differences in spatial exposure, interspecific phenology, and dispersal patterns (*e.g.,* climate change; Frederiksen *et al.* 2004). While our results indicate a relationship between a species at-sea range and risk, our data lack sufficient detail to explore these patterns adequately. Further research on species behaviour and established associations with threats like fisheries, including tracking data will be a useful tool to further inform how the spatial distribution of seabirds affects risk and exposure to marine threats.

Complicating the strength of range as a risk predictor for seabirds is environmental stochasticity, which is closely linked to demographic stochasticity. That is the random variation of population dynamics due to discrete events (*i.e.,* changes to births and deaths from variable environmental factors), such as climate anomalies, and prey availability (Tuljapurkar 1990). Small populations are particularly vulnerable, where one event has the potential for catastrophic results for a population (Weimerskirch 2001). Although, some species may have naturally low populations, due to density dependence factors or limited breeding site availability (Vermeij & Grosberg 2017; Gaston & Blackburn 1995). Therefore, rarity is not a proxy for extinction, and some populations may remain small but stable despite mortality from low levels of anthropogenic marine threats (Vermeij & Grosberg 2017).

Alternatively, the effects of environmental stochasticity on vital rates for small populations, coupled with anthropogenic sources of adult mortality or reductions in reproductive output due to poor body condition (*i.e.,* plastic ingestion related), may be more pronounced (Lebreton & Clobert 1991). In addition, unpredictable events could be catastrophic for small or spatially constrained populations (*e.g.,* the Tōhoku earthquake-generated tsunami in 2011 inundated the island breeding sites for 14 colonial nesting procellariiformes causing widespread egg and chick losses; Reynolds *et al.* 2017).

Wilcox et al. (2015) found that propensity to ingest plastic was largely explained by body size and foraging strategy, and that species distributed in the southern hemisphere, which include most of the Procellariiformes in our study, were at greater risk. Our results support this assertion. It should be noted, however, that because of the wide range of physiological morphologies between taxa (*i.e.,* gut morphology differs between albatrosses, storm-petrels and other petrels), there is high variability in how a species interacts with marine threats such as plastic ingestion (Ryan 1987b, 2016). This variability may, in reality, attenuate the strength of foraging strategy as a predictor of vulnerability in our model.

The risk of seabirds to marine threats is undoubtedly influenced by multiple demographic and ecological factors, acting in unison, unevenly, and is species-specific. Due to naturally low intrinsic population growth rates of seabirds, even small increases in adult mortality from marine threats have the potential to cause continued population declines affected species. While models such as ours are highly sensitive to parameter uncertainty, and may inadequately account for demographic species-specific variation (Dillingham & Fletcher 2011; Richard, Abraham & Filippi 2011), they remain a useful tool to guide conservation management actions (Niel & Lebreton 2005; Robertson *et al.* 2014). The acknowledgement and quantifications of such uncertainties in any attempt to project the future is vital for informing management decisions and for setting policy.

Predator eradication at seabird breeding sites remains the most effective tool for ameliorating declines in seabird populations (Jones *et al.* 2016). However, our results portend significant conservation challenges for seabirds given the intensifying pressures from anthropogenic activities in the oceans (Croxall *et al.* 2012; Oro 2014; Wilcox *et al.,* 2015). Importantly, conservation solutions to marine threats are not intractable. For example, bycatch mitigation measures that have been adopted internationally have shown to be successful in reducing population declines in albatrosses (Robertson *et al.* 2014). Where data are lacking to evaluate a species risk specifically to marine threats, phylogenetically closely related species can be used to help identifying the relative level of risk to sources of mortality from human activities in the oceans.

5.7 Supporting Information

Our model approach is described in Figure S1:

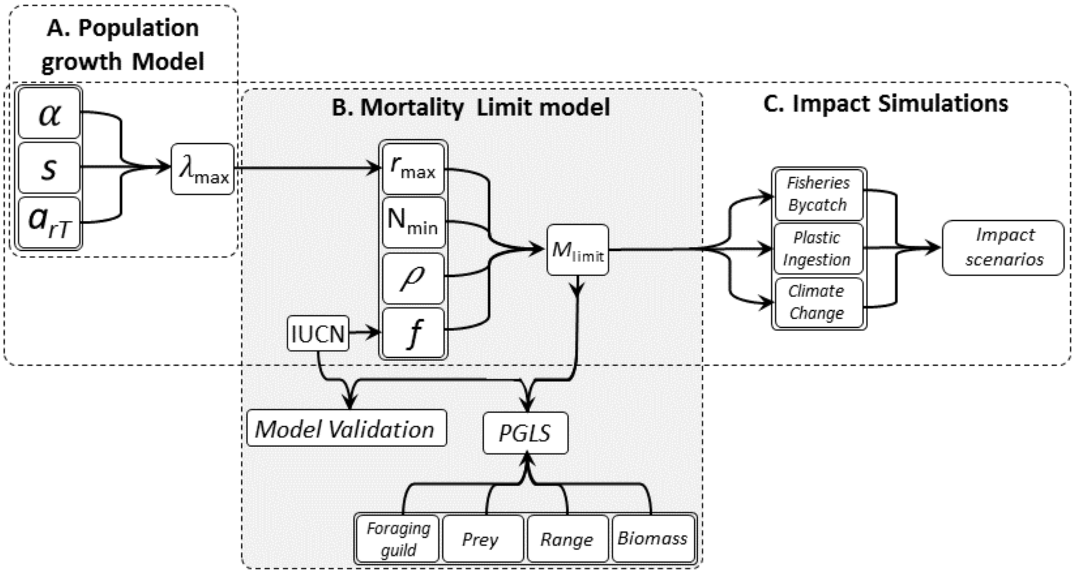


Figure 5.3 Modelling approach to estimate the impact of marine threats on population trends of seabirds. The demographic invariant method (DIM) used here allows us to calculate the asymptotic population growth rate $\lambda_{\max}$, under optimal conditions (A; equation 5.1). Where, *a* is the age of first reproduction, *s* is adult survival, and α_{rT} is the allometric constant (~1; Niel & Lebreton 2005; Dillingham & Fletcher 2011). The allometric constant is based on the relationship between adult body mass to maximum annual growth rate $\lambda_{\max}$ and generation time *T* by a single allometric exponent ~1/4 (Niel & Lebreton 2005). The second step of our approach B) is to calculate the mortality limit, M_{limit}, the maximum number of breeding individuals that could be removed from the population without causing a decline in the population; eq. 5.3). M_{limit} is a function of (i) $r_{\max}$, the annual maximum population growth above replacement ($r_{\max} = \lambda_{\max} - 1$), (ii) $N_{\min}$, the minimum breeding population that is compatible with $r_{\max} \geq$ (eq. 5.2), (iii) a calibration factor, *p*, which accounts for overestimation of M_{limit} (Richard & Abraham 2013b), and (iv) a recovery factor *f*, informed by the *IUCN* Red List listing depending on the threat status. The recovery factor (*f*) accounts for the effect of density dependence on demographic performance (e.g., negative density-dependence effects from environmental stochasticity on breeding phenology, whereby mating efficiency is reduced; Votier *et al.* 2009), undetected mortality (e.g., unidentified oil spills; Votier *et al.* 2005), which may create an imbalance in certain age classes such as the most reproductive adults (Lebreton & Clobert 1991), potential errors in population estimates, or unknown biases (Dillingham & Fletcher 2011; Richard & Abraham 2013a).To validated our model M_{limit} outputs to the IUCN Red List threat categories (Figure 5.2). Next, we used phylogenetic generalised least squares (PGLS) to examine predictors of risk with the ecological variables of foraging strategy, primary prey type, at-sea range, and biomass. In the third step C), using prospective perturbation analyses we simulated impacts on adult mortality from fisheries, plastic pollution, and climate change for a subset of 14 seabird species for which we obtained high-quality threat data. The perturbation analysis adjusts the adult survival rate in response to at-sea mortality, thus $\lambda_{\max}$ and M_{limit}.

5.7.1 Data quality

Parameter estimates for the demographic analysis involving 81 species were form the primary literature, and renowned grey literature (*e.g.,* Birdlife International, and NZ Birds Online websites). Seabirds breed on remote islands, therefore collecting accurate demographic data consistently can be logistically and financially challenging, resulting in large uncertainty of parameter estimates (Richard & Abraham 2013b). Where parameters were missing we used the most closely phylogenetically related species, as per Penhallurick & Wink (2004). Sources of bias and error in the demographic parameters may stem from multiple factors. For example, the estimates of adult survival for most species are likely to underestimate natural rates. This is because it is impossible to remove the effect of anthropogenic sources of mortality from studies that these values are derived from. A brief summary of uncertainties and our approach for data collation is detailed as follows:

Adult survival (s): Most seabirds have an adult survival of more than 90% in optimal conditions, in our analysis, species assigned values at or below 90% may underestimate the maximum potential population growth rate (Richard & Abraham 2013b). We used the mean value of adult survival reported in the literature for the mortality limit model for the 81 species, with the assumption that this estimate was likely to be closest to adult survival in natural conditions, accounting for current sources of mortality in the populations. For the perturbation analyses of the 14 species from the Northern New Zealand region (Figure 5.4), we used the highest estimate of adult survival with the assumption that these regional populations were in optimal conditions, given the available habitat and absence of introduced predators on the islands. This approach allowed us to estimate the potential impacts to a population specifically from the three marine threats evaluated.

Age of first reproduction (a) may be estimated from a small sample size, leading to either an over- or under-estimation. In such cases, this means that the population growth rate (λ_{max}) will over or underestimate growth rate, which will then be carried through the equations. We used the mean value of age of first reproduction (α). Values for α were derived from the mean of all values reported, we then calculated the minimum age of first reproduction by multiplying the mean by 0.75 and the maximum a by 1.25 as per methods described in Richard & Abraham (2013b).

Population size: Estimates of the population size of most species is embedded with bias and uncertainty. This is because many of the population surveys come from data older than eight years, and in most cases, there is a paucity of details about survey methods. Population estimates may come from a one off survey, which may have been a good or bad year for individuals choosing to breed (Frederiksen *et al.* 2004), thereby over- or under-estimating breeding pair numbers. In addition, these counts may not accurately count non-breeding birds (*i.e.,* immature individuals, or those on sabbatical). We used the total population estimates as per the IUCN Red List threat categories (IUCN 2017). If the population was reported as a range, we assume the total population to be the geometric mean of the maximum and minimum values (the square root of the product of a pair of values) (Paleczny *et al.* 2015). For the 14 species included in the perturbation analysis, we used regional population estimates from the Northern New Zealand Seabird Trust (unpublished data). The area where these data are from is shown in Figure 5.4.

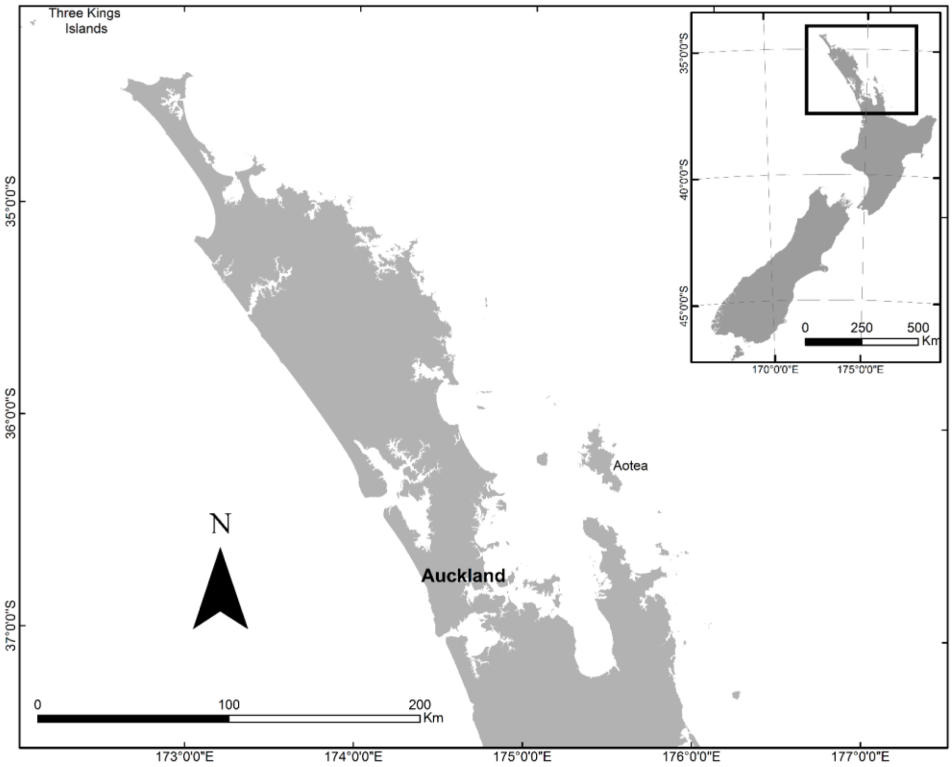


Figure 5.4 The population estimates for the 14 species included in the perturbation analysis are from >100 islands in the wider Hauraki Gulf Region, New Zealand, including the Three Kings Islands (top left).

To calculate the breeding population we used the commonly assumed estimate of ~70% breeders (Karpouzi, Watson & Pauly 2007; Paleczny *et al.* 2015), we calculated the annual breeding population by multiplying the total number of individuals by 0.7. Because we then calculate the mortality limits from an estimate of the minimum breeding population, the M_{limit} results should be considered conservative.

For all of these data, we assigned data a standard deviation as per the quality of data as proportions of the mean of demographic variables; good 0.01, moderate 0.02, and poor 0.03. For assigning an index to the data quality, we used the same methods and categories of poor, moderate and high as Richard and Abraham (2013b). Their assignment was based on the study methodology, and the sample size from the published estimate of each variable. For example, when there were more than 100 individuals included in adult survival from mark-recapture models, the data were categorised as high quality. If there were less than 50 individuals, the data were considered poor quality. The estimates of the proportion of the annual breeding population were unknown for most species (Richard & Abraham 2013b).

Calibration factor ρ: Richard and Abraham conducted a sensitivity analysis to determine ρ, and found overestimations can be corrected based on $\lambda_{\max}$, where for single-egg clutch type species (all of the species in our analysis), the ρ ranged between 0.3 and 0.41 (albatrosses), in the most extreme case, e.g. *Pelecanoides urinatrix* ($\lambda_{\max}$=1.15), it was assigned a value of ρ=0.17 to correct for M_{limit} overestimations (Richard & Abraham 2013b).

Recovery Factor (f): While the recovery factor (f) would account for some of the uncertainty in parameter estimates, it may not account for all factors such as density dependence in both positive and negative directions. Negative density dependence is where λ declines as the population density increases, in this instance it is assumed that fecundity is higher at low densities and decays at a constant rate (Morris & Doak 2002). Although rare, the opposite can also occur, where rapid declines in fecundity occur at low population densities, and then increase at higher densities, given no limiting factors (*e.g.,* no resource or habitat limitations). The magnitude of negative density dependence across a range of densities can vary due to external or internal population level effects (Morris & Doak 2002, pp. 38). Positive density dependence, sometimes referred to as Allee effects, lead to an increase in population as the population increases. Such responses are likely when resources are not limited, mating success is improved, and group defence reduces predation (Morris & Doak 2002).

Determining density dependence extent or type in a population in either direction is inherently difficult due to data limitations (Morris & Doak 2002). Because the current knowledge of processes and effects on population growth rates is lacking, given the long-term and detailed studies required, there is uncertainty in estimating how density dependence may be affecting our results. In relation to these factors, the recovery factor (f) for a species should be evaluated on a case-by-case basis, although a value of 0.5 should be suitable for most stable populations as suggested elsewhere (Richard, Abraham & Filippi 2011; Dillingham *et al.* 2016).

Finally, we did not address the potential carrying capacity of the population, and assumed that the length of time to reach this point for most populations is beyond current temporal management plans (*e.g.,* 200 years; Richard, Abraham & Filippi 2011), also that other threats or changes in levels of mortality from unknown threats (*e.g.,* climate change) will adjust the results of the model considerably.

5.7.2 Marine threat data

Detecting at-sea mortality is inherently challenging because seabirds are scattered widely across their foraging ranges, and carcasses may float just below the surface, sink or be consumed by predators (Laist 1997). Furthermore, the incidence of birds being entangled in fishing ling or ropes may be mistaken for fisheries related bycatch – where animals are incidentally caught in active fishing gear, or in some cases in ghost nets, rather than from mortality from plastic ingestion, although this is likely a very small proportion (Laist 1997). On land many species are understudied, and land-based surveys provide no indication of the number of at-sea mortalities. Therefore, accurately characterising the extent and distribution of plastic ingestion by seabirds is challenging (Laist 1997). As with the demographic parameters, we categorised the quality of the threat mortality data to be poor, moderate or high quality and assigned the standard deviation as 0.03, 0.02, and 0.01 respectively (Table 5.4).

Fisheries: The Fisheries Risk Index (FRI) is expressed as the ratio between annual estimated fatalities and the mortality limit for a population: *Risk Index = Annual mortalities/*M_{limit} (Richard & Abraham 2013b). A ratio of > 1 suggests fishing related mortality exceeds the mortality limit of a species (Richard & Abraham 2013b). FRI does not account for mortality associated with international (beyond the EEZ), illegal and unregulated or recreational fisheries, which may present a significant source of mortality for some species. Furthermore, the estimation of at-sea mortality due to a particular threat typically results in a high degree of imprecision. For example, estimates of adult mortality in a fishery are reported, they are often calculated from a small number (typically < 10%) of ship-board observations (Richard, Abraham & Filippi 2011). In addition, there are a lack of data on cryptic mortalities in commercial fishing operations, that is, when a bird may get caught underwater, but is not brought back on board the vessel.

Although the calculation of the multipliers for cryptic mortalities was improved from Richard et al.'s (2011) seabird mortality estimates, by considering uncertainty, there are no studies of cryptic mortality in New Zealand fisheries that could be used for estimating these multipliers. Estimation of cryptic mortality was primarily based on two studies (Watkins et al. 2008, Brothers et al. 2010) that were conducted in fisheries in South Africa and Australia, respectively. The study of cryptic mortality in trawl fisheries was based on results from a single trip (Watkins et al. 2008), and so is very limited. Moreover, estimation of cryptic mortality only considered birds that were killed but not brought on-board the vessel. It did not include possible problems such as seabird bycatch not being reported when the observer is off duty, or seabird carcasses not being seen by the observer because of the volume of catch. Without a better characterization, it is possible that our anlaysis will either fail to identify seabird species that are at risk or will classify species as being at risk when in fact they are not.

Plastic ingestion: Every year an estimated 4.8 to 12.7 metric tons of plastic pollution enters the oceans (Jambeck *et al.* 2015). The volume of plastic in the ocean poses a threat to all marine life through ingestion, entanglement and toxicity (Ryan 1987a; Vannela 2012). The physiological effects of plastic debris ingestion on seabirds may include; internal and external wounds, skin lesions and ulcerating sores, ingestion causing general debilitation, inhibiting feeding capacity, eventually leading to starvation, reductions in reproductive capacity, drowning, and impairment of predator avoidance (Ryan 1987a; Auman *et al.* 1997; Vannela 2012). Species were categorised into risk from plastic pollution related mortality based on frequency of occurrence of plastic ingestion, (*i.e.,* percentage of individuals found to have ingested plastic rather than mass or volume estimates). While our mortality estimates were conservative, this approach may overestimate the impact of plastic ingestion on adult mortality as there is a lack of understanding about plastic retention in animals and what the long-term impacts may be on adult survival and populations (Rochman *et al.* 2016; Ryan 2016).

Climate Change: Despite impressive research efforts that indicate seabirds are the most vulnerable group of avian fauna to climatic changes (Jenouvrier 2013; Oro 2014), there is high uncertainty in our model to predict adult mortality from climate change pressures. This is due to the difficulty in quantifying how a population is being affected by the complex interactions affecting prey distributions and abundance

(Sæther & Engen 2010; Oro 2014), confounded by the lack of published studies on the effects of climate change for our subset of New Zealand breeding seabird populations.

Vital rates are influenced by energy allocation processes of prey acquisition and energy expenditure (Jenouvrier 2013). Seabirds are marine top predators; as such it is expected that vital rates are affected by climate variability altering prey distributions and temperature-induced phenological changes, such as breeding times, although responses are expected to be delayed and complex (Jenouvrier 2013). The influence of climatic changes on seabird populations may exert either positive or negative changes to vital rates from changes to resource availability and distribution, breeding phenology or impacts on habitat (Jenouvrier 2013; Engen & Sæther 2016). In addition, other factors, such as density dependence, inter- and intra-specific competition, and scale dependent variability in climatic stressors will influence how an individual or population will respond (Jenouvrier 2013; Oro 2014). Thus, attributing changes to adult survival directly to a specific climate driver is complex, and generalising among species can lead to erroneous assumptions (Oro 2014), and until reliable estimates of adult mortality from anthropogenic marine threats to seabirds exist, accurately estimating the population-level effects on seabirds will remain challenging. Because of the high-level uncertainty in the impacts of climate change to seabird adult survival we assigned the data to be of very poor quality, and all species assigned a SD of 0.05 (Table 5.4).

Table 5.4 Parameter estimates for marine threats, including commercial fisheries, plastic pollution, and climate change to seabird population growth. Values are a proportion of the total local population size.

Species	**Regional Population**	**Fisheries mortality (min-max)**	**Fisheries mortality SD**	**Plastic mortality (min-max)**	**Plastic mortality SD**	**Climate (negative)**	**Climate (positive)**	**Climate SD**
Procellaria parkinsoni (Black petrel)	1800	1 (0.743-1.139)	0.01	0.01 (0.008-0.012)	0.02	0.001	-0.001	0.05
Pterodroma nigripennis (Black-winged petrel*)	1000	0.001 (0-0.002)	0.02	0.002 (0.000-0.004)	0.01	0.001	-0.001	0.05
Ardenna bulleri (Buller's shearwater)	20000	0.001 (0-0.002)	0.01	0.010 (0.008-0.012)	0.01	0.001	-0.001	0.05
Pelecanoides urinatrix (Common diving petrel)	60000	0 (0-0.001)	0.01	0.002 (0.000-0.004)	0.02	0.001	-0.001	0.05
Pterodroma cookii (Cook's petrel)	290000	0 (0-0.001)	0.02	0.006 (0.004-0.008)	0.03	0.001	-0.001	0.05
Pachyptila turtur (Fairy prion)	40000	0.001 (0-0.002)	0.01	0.010 (0.008-0.012)	0.01	0.001	-0.001	0.02
Ardenna carneipes Flesh-footed shearwater	12000	0.073 (0.049-0.102)	0.01	0.010 (0.008-0.012)	0.01	0.001	-0.001	0.05
Puffinus gavial Fluttering shearwater	60000	0 (0-0.001)	0.02	0	0.03	0.001	-0.001	0.05
Pterodroma macroptera Grey-faced petrel	300000	0 (0-0.001)	0.02	0	0.03	0.001	-0.001	0.05
Puffinus assimilis (Little shearwater)	10000	0 (0-0.001)	0.02	0.002 (0.000-0.004)	0.02	0.001	-0.001	0.05
Freggetta maoriana (New Zealand storm petrel*)	2000	0 (0-0.001)	0.03	0.010 (0.008-0.012)	0.03	0.001	-0.001	0.05
Pterodroma pycrofti (Pycroft's petrel*)	10000	0 (0-0.001)	0.01	0.006 (0.004-0.008)	0.03	0.001	-0.001	0.05
Puffinus griseus (Sooty shearwater)	5000	0.396 (0.283-0.557)	0.01	0.010 (0.008-0.012)	0.01	0.001	-0.001	0.05
Pelagodroma marina (White-faced storm petrel)	60000	0.001 (0-0.002)	0.02	0.010 (0.008-0.012)	0.01	0.001	-0.001	0.05

5.7.3 Other sources of at-sea mortality not included in the model

In this paper, we address only the impacts of plastic pollution, climate change and commercial fisheries to our seabird populations. We acknowledge that our model does not include the full suite of marine threats that seabirds are exposed to including such as disease, oil-spills, water-bound contaminants, or hunting (Provencher *et al.* 2018). We encourage others to take our model and improve the assessment of species for their region of interest by including additional threats, and updating parameter estimates with the most robust data available.

5.7.4 Mortality limit model validation

We tested the mortality limit model (M_{limit}) with a brute force sensitivity analysis by removing the recovery factor and running the model validation against the IUCN Red List Threat categories. The distribution was the same ($p>0.05$), with lower mortality limits (Figure 5.5) compared to the mortality limit validation including the recovery factor (f) (Figure 5.2). This affirms that the recovery factor is an important inclusion in the model to not underestimate the mortality limits for a species. The brute force sensitivity analysis showed the same pattern but with higher mortality limits, potentially underestimating M_{limit} (Table 5.1; Figure 5.5). An analysis of variance (ANOVA) showed a significant variation among threat categories ($P<0.0001$; Table S3). A post hoc Tukey test showed that species in the IUCN Red List category ‘Least Concern’ have greater mortality limits, that is, the global population can sustain higher levels of mortality before a decline will occur compared to species categorized as NT, VU, EN, and CR, which all had similarly low mortality limits.

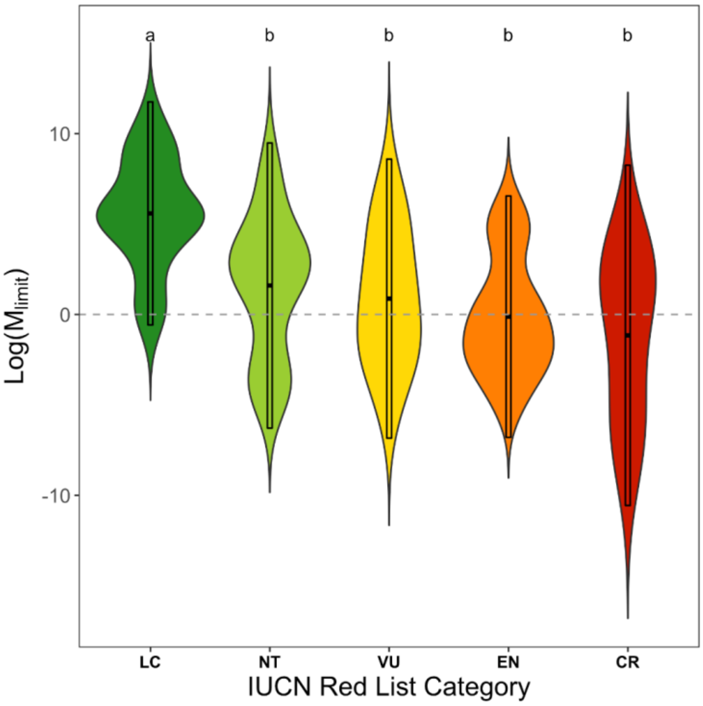


Figure 5.5 The mortality limit (M_{limit}), that is, the maximum number of breeding adults that could be removed annually from the population without incurring a decline validated against the IUCN Red List threat categories for 81 procellariiforme species from the brute force sensitivity analysis without the inclusion of the recovery factor (*f*). Tukey's groupings for (a) Least Concern [LC] are significantly different ($p \leq 0.0001$) to (b) Near Threatened [NT], Vulnerable [VU], Endangered [EN], and Critical [CR] IUCN Red List threat categories (Table 5.5).

Table 5.5 Mortality limit model validation Tukey's Test results (p=0.0001)

IUCN Category	**Means**	**Group**
Least Concern (LC)	4.699	a
Near Threatened (NT)	0.063	b
Vulnerable (VU)	-0.972	b
Endangered (EN)	-2.421	b
Critical (CR)	-3.455	b

We executed correlation analysis to inform our model selection criteria using the *Hmisc* and *corrplot* Packages in R (Harrell Jr & Dupont 2006; R Core Team 2013; Wei & Wei 2016). This was to explore the relationships between all of the variables (ecological and demographic) used in the phylogenetic generalised least squares analysis testing the relative importance of candidate predictor variables in explaining the threat risk of a species to marine threats.

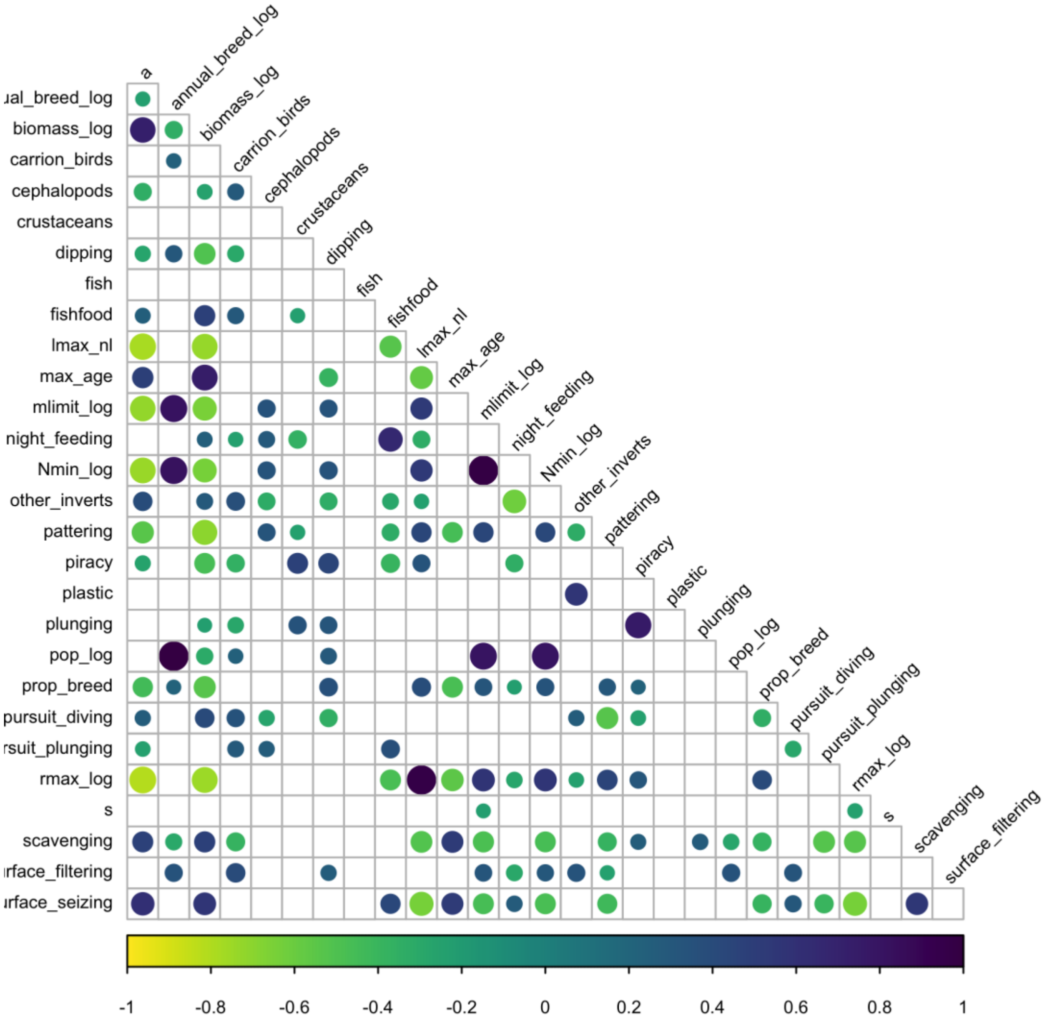


Figure 5.6 Correlation matrix of the variables for model selection criteria for the phylogenetic generalised least squares analysis (PGLS) investigating ecological and demographic predictors of risk. The larger the circle the greater the correlation.

Table 5.6 Pagel's λ for the demographic, ecological and morphometric variables. Presented are variable relationships with the greatest explanatory power for an index $R^2 \leq 0.07$

	Slope	***SD***	***t***	***P***	***Pagel's λ***	***CI***	***R^2***	***P adjusted***
biomass_log ~ scavenging	0.696	0.092	7.604	<0.0001	0.999	0.95	0.423	<0.0001
biomass_log ~ carrion_birds	-0.347	0.052	-6.659	<0.0001	1.000	0.95	0.360	<0.0001
Nmin ~ pursuit_diving	840627.142	135832.256	6.189	<0.0001	0.990	0.95	0.327	<0.0001
mlimit ~ pursuit_diving	7479.212	1281.534	5.836	<0.0001	0.989	0.95	0.301	<0.0001
rmax ~ surface_seizing	-0.026	0.006	-4.486	<0.0001	0.838	0.95	0.203	0.0003
annual_breed_log ~ range_log	0.850	0.207	4.108	0.0001	0.674	0.95	0.176	0.0011
dipping ~ surface_filtering	0.409	0.106	3.860	0.0002	1.000	0.95	0.159	0.0025
biomass_log ~ plunging	0.406	0.109	3.722	0.0004	0.997	0.95	0.149	0.0034
rmax ~ scavenging	-0.023	0.006	-3.697	0.0004	0.835	0.95	0.147	0.0034
biomass_log ~ pattering	-0.504	0.141	-3.565	0.0006	0.979	0.95	0.139	0.0049
rmax ~ pursuit_diving	0.032	0.010	3.289	0.002	0.859	0.95	0.120	0.010
a ~ scavenging	1.104	0.357	3.091	0.003	0.629	0.95	0.108	0.018
surface_filtering ~ pursuit_diving	0.477	0.167	2.849	0.006	1.000	0.95	0.093	0.033
scavenging ~ pursuit_diving	-0.492	0.180	-2.735	0.008	0.956	0.95	0.087	0.041
surface_seizing ~ scavenging	0.170	0.068	2.497	0.02	1.000	0.95	0.073	0.074

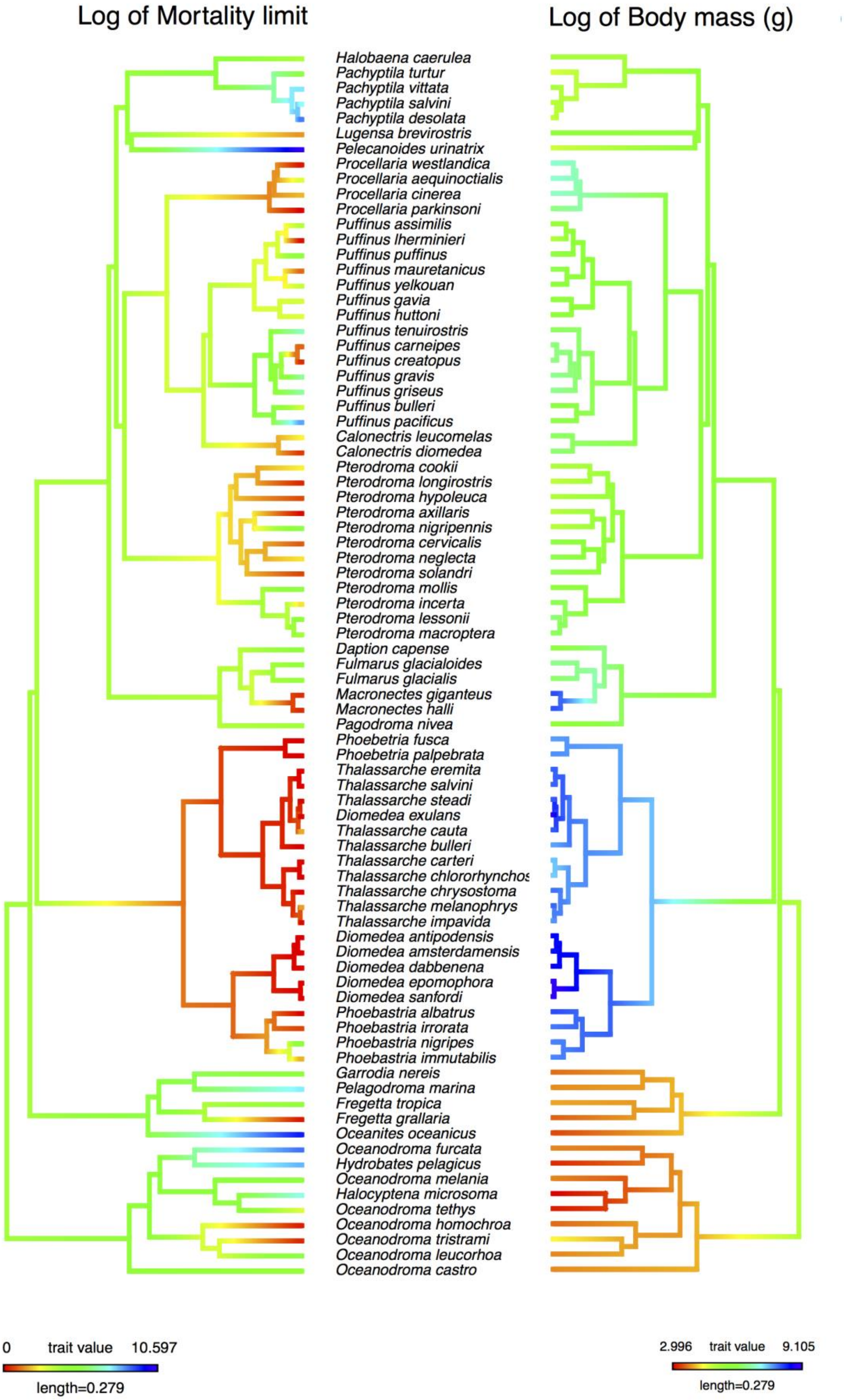


Figure 5.7 Comparison between (log) mortality limit and (log) biomass within the phylogenetic tree.

Table 5.7 Regional population estimates and model parameters for species (n=14) used in the perturbation analysis. The parameters are: biomass; IUCN Red List category and population trend (↓ decline, → stable, ↑ increase, ? unknown); global population estimate; optimal estimate of adult survival (S_{opt}); age of first reproduction (α); the recovery factor (f; Richard and Abraham 2013b), which accounts for factors that may influence population growth, such as density dependence, environmental stochasticity, undetected mortality, or potential errors in population estimates; calibration factor (ρ) (Richard & Abraham 2013b), which corrects for overestimates of the M_{limit}; minimum population estimate of breeding adults (N_{min}); maximum population growth rate above replacement (r_{max}) in optimal breeding conditions (i.e. without limits on resources or breeding habitat); population increase per year (%); and mortality limits (M_{limit}), that is the number of individuals that can be removed from the population before a decline occurs. The allometric constant (α_{rT}) used in the demographic invariant method for calculating λ_{max} = ~1 was obtained from (Niel & Lebreton 2005). * indicates species demographic information was inferred from the closest phylogenetically related species, as per Penhallurick & Wink (2004).

Species	**Biomass (g)**	**IUCN**	**Trend**	**Regional Breeding pop.**	S_{opt}	α	f	ρ	N_{min}	λ_{max}	r_{max}	**% increase year^{-1}**	M_{limit}
Pachyptila turtur	120	LC	→	17,800	0.94	4.5	0.5	0.32	2,571	1.1	0.1	9.68	20
Pelagodroma marina	45	LC	↓	26,700	0.94	4	0.4	0.3	6,310	1.11	0.11	11.11	42
Pelecanoides urinatrix	130	LC	↓	26,700	0.94	2.5	0.4	0.17	8,490	1.15	0.15	14.95	145
Pterodroma gouldi	550	LC	↓	133,500	0.98	6.5	0.4	0.41	12,700	1.05	0.05	5	11
*Pterodroma nigripennis**	160	LC	↓	445	0.98*	6.5*	0.4	0.3	10	1.05	0.05	5	0
Puffinus assimilis	240	LC	↓	4,450	0.96	5	0.4	0.32	395	1.08	0.08	7.99	2
Puffinus gavia	365	LC	↓	26,700	0.96	5	0.4	0.41	2,371	1.08	0.08	7.99	16
Ardenna carneipes	700	NT	↓	5,340	0.96	6.7	0.1	0.41	860	1.07	0.07	6.77	0
Ardenna griseus	800	NT	↓	2,225	0.98	6	0.2	0.41	741	1.05	0.05	5.26	0
Ardenna bulleri	420	VU	→	8,900	0.96	6.4	0.1	0.43	1,949	1.07	0.07	6.73	0
Procellaria parkinsoni	744	VU	→	720	0.94	6.6	0.1	0.33	150	1.08	0.08	7.72	0
Pterodroma cookii	180	VU	↑	129,050	0.98	6.5	0.2	0.32	2,610	1.05	0.05	5	4
*Pterodroma pycrofti**	150	VU	↓	4,450	0.98*	6.5*	0.2	0.3	90	1.05	0.05	5	0
*Freggetta maoriana**	35	CR	↑	750	0.94*	4.5*	0.1	0.3	152	1.1	0.1	9.68	0

5.7.5 Model limitations

Our model is a simplified one, in that it was needed to be general to apply uncertain estimates of mortality from anthropogenic sources, where there are limited or no data available. With a limited number of parameters, we acknowledge that the model doesn’t account for nuances of seabird breeding biology, and transition probabilities, for example, when breeding may be delayed due to the loss of a partner and forming new pair bonds (Richard & Abraham 2013a). Consequently, productivity of some species may have been over- or underestimated. While we attempted to minimise these uncertainties, and included reasonable confidence intervals, attempting to make generalised patterns or predictions across diverse taxa is challenging, given the range of demographic and ecological variability, and spatial distribution among seabird species (Jenouvrier 2013), therefore the results should be interpreted with caution.

There are a number of assumptions in the perturbation model, including: the target species has constant adult survival, operates at low densities, $\lambda_{\max}$ is constant across generations, and female fecundity is constant from age of first reproduction (female offspring per yr^{-1}; Niel & Lebreton 2005; Dillingham 2010; Dillingham *et al.* 2016). Further, our model is unable to capture species specific nuances in behaviour and life-stage, which will likely influence the resilience/risk of a species to a threat. For example, immature birds have a higher probability of dying in fisheries bycatch than breeding adults (Genovart *et al.* 2017). Similarly, young and immature birds are more likely to have higher loads of plastic ingested (van Franeker & Law 2015). Some species are more gregarious when foraging, thus interactions with fisheries operations, or other human activities are likely to cause additional adult mortalities (Genovart *et al.* 2017). Abiotic factors also influence the level of risk at the individual level, for example, different levels of mortality are expected with the type of fisheries gear (Genovart *et al.* 2017). This means that our model may over- or underestimate the impact on a population, because the number of fatalities are for breeding adults only and do not account for the variability in behaviour of individuals.

We also assumed that changes in adult survival from marine threats was only for breeding adults, thus do not account for non-breeding adults in the population (*i.e.,* adults on sabbatical, immature birds). Adult survival was assumed to be equal between sexes and monogamy was assumed (Genovart *et al.* 2017). We did not account for bias in sex and age classes, seasonality and cryptic mortality, which may underestimate the impact of marine threats on some populations (Mills & Ryan 2005), although this was addressed to a degree for fisheries-related mortality in Richard and Abraham's (2013b) model. Because of the level of uncertainty in demographic data and mortality, this method may be useful only to inform a precautionary approach in species management or to assist in prioritizing additional conservation actions following predator eradication for species that may be more at risk from at sea threats.

Conclusion

On a rolling ship in the Southern Ocean, it's hard not to be awe-inspired by the phenomenon of seabirds in flight (Figure 6.1). They are masters of the ocean. Their intrinsic value is reason alone to protect them from continued declines and eventual extinction. From an anthropocentric point of view, in protecting them, we retain eyewitnesses to the condition of the world's oceans. Seabirds are sentinels of the sea, detecting changes in marine foodwebs from climatic oscillations (Barbraud & Weimerskirch 2003), showing changes to fish stock levels (Cury *et al.* 2011), to indicating the extent of marine pollution (Ryan 2016). Their importance as marine top-predators, and ocean sentinels is not diminished by their terrestrial lives. The ecosystem engineering of seabirds renders their island breeding sites unique repositories of biodiversity spanning the globe, from the tropics to the sub-polar regions. However, seabirds are a global conservation priority. Invasive mammalian predators remain a major threat to some seabird populations; and at sea, there is a suite of spatially and temporally varying threats: including pollution, fisheries, and shifts in prey resources due to climate change (Provencher *et al.* 2018).

Figure 6.1 Toroa/Buller's mollymawk *Thallasarche bulleri*, Southern Ocean, 2017. Photo © S. Borrelle.

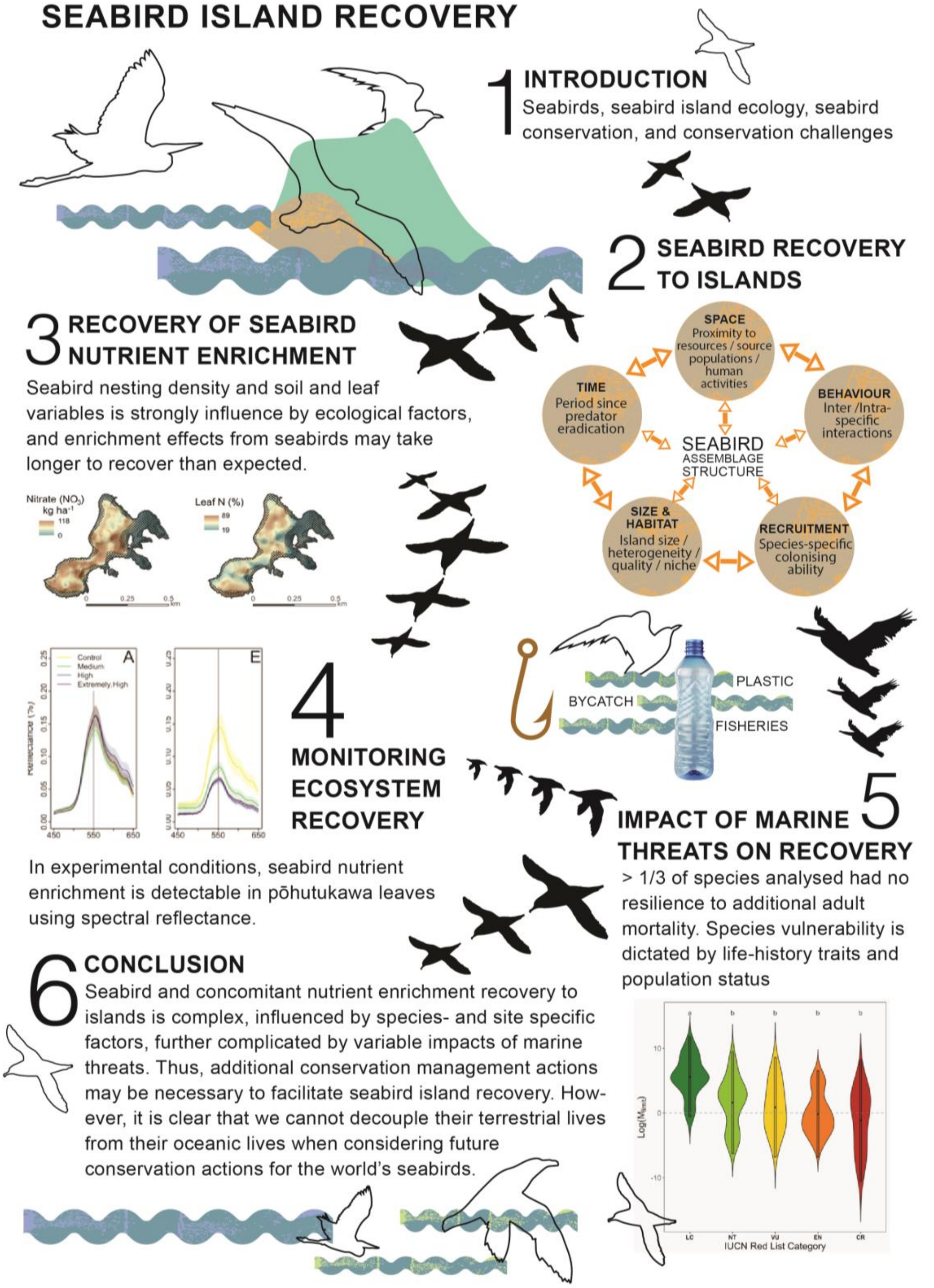
Historically, mammalian predator invasion, and habitat loss have exerted the hardest blows on the world's Procellariiforme seabirds, resulting in severe population declines globally (Paleczny *et al.* 2015). Accordingly, predator eradication is a key conservation action to protect seabirds and their island habitats. An estimated US$21.5

billion is spent annually on conservation worldwide; a large proportion of this is dedicated to offshore islands (Waldron *et al.* 2013; Jones *et al.* 2016), where the impacts of introduced predators have led to a disproportionate number of species declines and even local extinctions, compared to continental ecosystems (Doherty *et al.* 2016). Indeed, conservation actions at the terrestrial breeding sites of seabirds have yielded impressive conservation gains (Jones *et al.* 2016; Brooke *et al.* 2017).

The aim of my doctoral thesis has been to contribute to our understanding about the recovery of seabirds and their ecosystem engineering properties after predator eradication, asking the question: ***'Will invasive predator control deliver enduring benefits for seabird island ecosystems?'*** Specifically, I asked four sub-questions: 1) what are the factors that influence seabirds returning to islands cleared of invasive predators? 2) what are the patterns of recovery of seabird nutrient influences on island ecosystems? 3) are there alternative ways to measure the abundance and recovery of seabirds to islands; and, 4) how do marine threats influence the recovery of seabirds following invasive predator eradication? (Figure 6.2).

To answer *what are the factors that influence seabirds returning to islands cleared of invasive predators?* I used a comparative analysis of 97 islands with three predator histories to investigate the influences on recovery of seabirds to islands post-eradication. I compared seabird assemblages on islands eradicated of introduced predators to islands that have never been invaded by invasive mammals, and islands with invasive predators present, in order to investigate the ecological and demographic factors that influence the recovery and reinstatement of seabird assemblages to islands. I found that islands cleared of predators can show recovery of seabirds over time and interestingly had more unique seabird taxa than islands that never had predators.

The recovery of seabird colonies and recolonisation appears to be influenced by a suite of site- and species-specific factors. While time following the eradication is an important factor, space, demographic traits and population dynamics may have a stronger influence on the passive recovery and recolonisation of seabirds to islands (Figure 6.2). If the aim is restoring seabird islands to a state similar to that of a comparative undisturbed reference site, or if known the state before the invasion of predatory species and modification, then the axiom is to attract seabirds back. Therefore, in cases where seabird recovery may be constrained, additional management actions may be required to meet the long-term restoration goals.



SEABIRD ISLAND RECOVERY

1 INTRODUCTION

Seabirds, seabird island ecology, seabird conservation, and conservation challenges

2 SEABIRD RECOVERY TO ISLANDS

3 RECOVERY OF SEABIRD NUTRIENT ENRICHMENT

Seabird nesting density and soil and leaf variables is strongly influence by ecological factors, and enrichment effects from seabirds may take longer to recover than expected.

4 MONITORING ECOSYSTEM RECOVERY

In experimental conditions, seabird nutrient enrichment is detectable in pōhutukawa leaves using spectral reflectance.

5 IMPACT OF MARINE THREATS ON RECOVERY

> 1/3 of species analysed had no resilience to additional adult mortality. Species vulnerability is dictated by life-history traits and population status

6 CONCLUSION

Seabird and concomitant nutrient enrichment recovery to islands is complex, influenced by species- and site specific factors, further complicated by variable impacts of marine threats. Thus, additional conservation management actions may be necessary to facilitate seabird island recovery. However, it is clear that we cannot decouple their terrestrial lives from their oceanic lives when considering future conservation actions for the world's seabirds.

Figure 6.2 Summary results of the four data chapters and conclusion of this thesis. The introduction provides context for the conservation question of will invasive predator provide enduring benefits for seabirds and their island habitats? In chapter two I found that multiple ecological and demographic factors influence seabird recovery to islands. In chapter 3, I found there is a strong relationship between seabird nesting density and soil and leaf variables, and although seabird influences can be detected relatively quickly, their enrichment effects may take longer to recover. In chapter 4, I found that seabird nutrients are detectable in high concentrations experimentally, but ecological influences attenuate the response of plants in field conditions. In chapter 5, I found that more than one third of Procellariiformes exhibit no demographic resilience to marine threats, potentially thwarting long-term seabird recovery following predator eradication.

Seabird driven systems are naturally in constant flux; a state of stochastic equilibrium, because of the complexity and dynamic nature of ecosystem structure and interactions, which are dependent on species assemblages and their physiology and behaviour, ecological conditions, the history of disturbance, and spatial context. Burrow nesting seabirds, such as many Procellariiformes, exert the greatest influence on the physical and chemical components of island ecosystems through the excavation of burrows and contributing large amounts of guano that can strongly affect soil characteristics, such as porosity, pH, homogenisation and soil hydrology (Ellis *et al.* 2011; Smith *et al.* 2011). When predators are present, ecosystem processes are interrupted or altered (Fukami *et al.* 2006; Mulder *et al.* 2009). When invasive predators are removed, it is possible that seabirds may return, restoring their ecosystem engineering properties (Jones 2010). Thus, seabird recovery greatly influences the recovery trajectories of vegetation, invertebrates and whole island ecological processes (C. G. Jones *et al.* 1994; Smith *et al.* 2011). However, despite the influence of seabird nesting activity over ecosystem community composition and functioning, few studies have quantified the within-island spatial heterogeneity of seabird nutrient recovery after predator eradication.

To answer the question: *what are the patterns of recovery of seabird nutrient influences on island ecosystems?* I conducted a cross-island comparative analysis to quantify soil and foliar nutrients among islands with three predator histories: never invaded by invasive predators, cleared of predators where seabirds are recovering, and one without seabirds, in chapter 3. I explored the ecological drivers of spatial variation in nutrient recovery and used high resolution sampling to create a profile of how seabird density and their nutrient enrichment is distributed in soils and plants after predator eradication. I found that there is a strong relationship between seabird nesting density and the measured soil and leaf variables, but there is variability in ecological influences, at multiple scales on the distribution and accumulation of seabird nutrient enrichment in soils and vegetation. In addition, the severity of historical habitat modification and changes to vegetation communities, including the dominance of weedy ruderal species (Mulder *et al.* 2009), may result in arrested succession, rending restoration islands unable to meet long-term ecological goals. Gaining an understanding of the degree of modification that constrains the recovery of seabird engineering effects on island ecosystems should be a priority, one that requires monitoring of seabird abundance and ecosystem response to seabird recovery.

Monitoring species and ecosystems is widely acknowledged as an essential tool when determining population trends for adaptive conservation management. However, conservation resources are limited, so actions in response to imminent threats to seabirds, such as predator eradication, are often prioritized over long-term monitoring. Because of resource and logistical constraints, we need to identify monitoring tools that are affordable and accessible. In chapter 4, I explored *alternative ways to measure the abundance and recovery of seabirds to islands* by investigating the spectral reflectance response of island plant species to seabird nutrient enrichment in a controlled experiment, and field conditions. Despite the influence of leaf level characteristics, my experiment shows that under high levels of nutrient enrichment and in a limited range of the electromagnetic spectrum (400-700 nm), a spectral response can be detected. Although soil NO_3^- concentrations in the field samples were comparable to the experimental soil NO_3^-, the results from the spectral response of our study plant species suggests the relationship between soil nutrients and spectral reflectance are also confounded by local environmental factors that affect nutrient cycles, in addition to foliar characteristics. While there are many gaps in our knowledge about the relationship between foliar biochemical characteristics and spectral signatures, there is considerable potential for remote sensing to be used as a monitoring proxy for seabird abundance by measuring foliar nutrient content (Asner & Martin 2008; Ramoelo *et al.* 2012; Fretwell *et al.* 2015).

A central question for seabird conservationists is *whether at-sea threats are inflicting a level of mortality that is unsustainable for the long-term population stability or growth of threatened seabirds, i.e.,* is the population being over-harvested by marine threats? In chapter 5, I used a demographic modelling approach to estimate the annual population growth rate and calculate the mortality limits that would allow 81 Procellariiformes to still have viable populations. I found that more than one third of species evaluated are likely to have already depleted their demographic resilience to any additional annual adult mortality. I also explored the impacts of the marine threats of plastic pollution, climate change and fisheries to 14 species from the Northern New Zealand region. The populations in this region are recovering following predator removal from their breeding sites, thus it is possible to evaluate the impacts of marine threats on potential maximum annual population growth. I found that, due to very small population sizes, intrinsic population growth rates, and life-history traits (*e.g.,* fecundity) for some species, even slight increases in adult mortality from marine threats may be enough to cause continued population declines, despite predator removal at their breeding sites. The diversity of impacts of marine threat likely to be sustained by seabirds globally reflects the diversity of seabird species physiology, life history traits, and the specific spatial context for a species. Some will fare better than others under current conditions in the marine environment. Therefore, while predator eradication remains a crucial tool to protect the world's seabirds, consideration of the impacts of marine threats to vulnerable species should be included in developing long-term conservation management strategies.

Ecological models, such as the one I presented in chapter 5, allow us to evaluate whether predator eradication is enough to offset mortality at-sea from anthropogenic sources, but also inform an adaptive conservation management strategy. Despite a lack of data on mortality at-sea, seabird conservation ecologists must make decisions about how to protect species against a range of threats and how those threats might affect a species. However, we need to validate such theoretical models otherwise they serve little conservation value. The inherent uncertainty in any predictive ecological modelling will always limit the forecasting of non-linear biological responses to multiple, stochastic influences (Clark *et al.* 2001). This is an important consideration when modelling seabird species, which operate across a wide range of spatial scales, and where spatial patterns exhibit positive spatial auto-correlation. Acknowledging the limitations of predictive modelling tools, these models can still prove useful for guiding the development of strategic conservation plans for seabirds.

There are no historical analogues to guide us in managing the conservation of seabirds in the face of the increasing pace of global change affecting oceanic resources, intensifying marine pollution, and interactions with human activities. There is an air of hubris in assuming that we will learn how marine threats affect the long-term population stability of seabirds; our knowledge is likely to always be incomplete because of the cryptic nature of seabirds at-sea and the multitude of interacting forces at play. We are in a race to learn what we think we should know, and how to address the issues at hand, while novel challenges continue to emerge.

Challenges for seabird conservation within the context of complex ecological interactions and a rapidly changing environment are to: 1) provide the contextual analyses relevant to past conservation actions; to expand our understanding of how seabirds, and seabird driven ecosystems recover following predator eradication. In this way, conservation practitioners will have knowledge to guide additional management interventions to achieve long-term site- and species-specific restoration goals, whether that may be the return the system to a state comparable to a historical analogue or to a functioning novel ecosystem; and 2) provide more general guidance that can be broadly applicable to a range of spatial contexts to assist in implementing meaningful interventions and monitoring in the face of global scale challenges, such as invasive species, climate change, fisheries in the global commons, and plastic pollution.

Consequently, management actions will have to focus on secondary threats, or compensatory mechanisms, in order to protect global seabird populations until global actions lead to improved conditions in the marine environment, such as a stabilised climate system, and reductions in marine plastic pollution (Seney *et al.* 2013). Action at a global scale is needed to achieve such outcomes. Progress is being made in terms of climate change action, which is recognised in the Paris agreement on Climate Change (2016), which aims to slow rapid warming of the climate to prevent drastic impacts on wildlife, ecosystems and society. Likewise, the Agreement on the Conservation of Albatrosses and Petrels (ACAP) agreement, and Birdlife International provide significant contributions towards reducing seabird fisheries bycatch in international waters (ACAP, 2015). Such actions at the global scale, coupled with continued work towards removing invasive predators from more seabird islands, represent a commitment to address the biggest threats to the world's highly threatened seabirds and their island habitats. On the other hand, the issue of plastic pollution at the global scale is only beginning to be recognised as an urgent environmental challenge to address. While we lack a complete understanding of the population level impacts from plastic pollution to seabirds and all marine wildlife, it is a threat that is unlikely to have *no* impact.

In light of this, for the final part of my conclusion chapter, I discuss the need for an international agreement to address the intensifying problem of marine plastic pollution[3]. The intent of this is to highlight the scale of the problem, not only in the context of seabird conservation, but to the health of marine biodiversity and

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ecosystems worldwide. While local conservation actions, such as predator eradication at seabird island breeding sites, are crucial for the conservation of the world's seabirds, we cannot decouple their marine lives and the threats they face in the oceans. Therefore, the scale of action to address global challenges, such as invasive predators, climate change, fisheries, and plastic pollution and their impacts on seabirds must match the scale of the problem.

6.1 Opinion: Why we need an international agreement on marine plastic pollution[1]

Plastic pollution is strewn across beaches and in oceans, bays, and estuaries. Tiny particles of plastic debris (often called microplastics) are so pervasive in aquatic ecosystems that we find them in seafood (Van Cauwenberghe & Janssen 2014; Rochman *et al.* 2015; Green 2016) and table salt (Karami *et al.* 2017). Marine organisms ingest or are entangled by plastic, sometimes with fatal consequences. Research suggests plastic pollution may impact biodiversity, ecosystem services, food security, and human health. In short, plastic pollution is a global threat.

Despite the ubiquity, persistence, and cross-boundary nature of plastic pollution, stemming it is not an insurmountable task. Motivation for addressing the issue is building at the international level. The time is ripe for the initiation of an international agreement with measurable reduction targets to lessen the plastic pollution in the world's oceans.

6.1.1 Pollution without borders

An estimated 4.4-12.7 million metric tons of plastic are added to the world's oceans annually (Jambeck *et al.* 2015). Like many other contaminants (such as greenhouse gases and ozone-depleting substances), plastic is not constrained by national boundaries, because it migrates via water and air currents and settles in benthic sediments. More than 50% of the ocean's area sits beyond national jurisdiction, including the infamous "garbage patches" in oceanic gyres where plastic accumulates.

Plastic can affect organisms at every level of biological organisation—altering gene expression, cells, and tissues, causing death, and altering population size and community structure (Galloway, Cole & Lewis 2017). Microplastics can impair reproduction and development (Li *et al.* 2015; Sussarellu *et al.* 2016) and alter how species function, disperse, and assemble (Green 2016; Green *et al.* 2016; Rochman *et al.* 2016). These impacts, combined with evidence for accelerating plastic production and emissions into the environment, suggest the international community should come together to limit future emissions of plastic now, before they transform ecosystems irreparably.

6.1.2 The politics of global pollution

Plastic pollution has received little attention in terms of international agreements—a notable contrast to carbon emissions and other global pollutants, such as chlorofluorocarbons (CFCs), and Persistent Organic Pollutants (POPs). There are many regional, national, and international strategies aimed at preventing and mitigating plastic pollution, but none has a level of commitment that scales with the global magnitude and accelerating growth of the problem. Local policies and actions (e.g., bans on microbeads and single-use plastic bags) are spreading across the globe, but there is only a handful of international documents focused on plastic pollution, including MARPOL, the Honolulu Strategy, and the United Nations Environmental Program's (UNEP) new Clean Seas campaign (Figure 6.3). Although these international strategies recognize global contamination, they contain no binding commitment that meets the challenge.

We recognize that the 1973 Annex V of the International Convention for the Prevention of Pollution from Ships, as modified by the Protocol of 1978 (MARPOL), is an international agreement that addresses plastic pollution. MARPOL, which bans ships from dumping plastic at sea, was a great first step. However, since MARPOL entered into force in 1988, the oceans have not benefited from reductions of plastic pollution. Instead, emissions have accelerated at a pace commensurate with plastic production (Jambeck *et al.* 2015). This is because Annex V is limited to maritime emissions, and 80% of plastic enters the ocean from land (Jambeck *et al.* 2015).

Despite the growing problem of plastic pollution in the decades after MARPOL, steps to prevent plastic emissions from land have been voluntary and lack defined reduction targets, methods to monitor progress, and signatories from UN member states. In 2011, the National Oceanic and Atmospheric Administration (NOAA) in the United States and UNEP created the Honolulu Strategy—a planning tool to reduce plastic pollution and its impacts. In 2012, a voluntary commitment of a significant reduction of marine debris was introduced at Rio+ 20 with a deadline of 2025. Similarly, in February 2017, UNEP announced the Clean Seas campaign, asking for individuals, industries, and member states to voluntarily commit to an action of their choice to reduce plastic pollution.

Recent developments in international climate change policy may provide a template for global policy for plastic pollution. Although the pace of the international response to climate change is arguably misaligned with the scale of the problem, the global community has more than 25 years of experience building international agreements to limit carbon emissions.

From the perspective of global policy, international plastic pollution agreements are now where climate change agreements were in 1992, when the UN Framework Convention on Climate Change (UNFCCC) formally recognized the climate change problem and simply encouraged voluntary, undefined support. If policies for plastic pollution maintain the same pace as international carbon emissions deliberations, in terms of crafting international discussions and forging agreements, an effective agreement may not happen until after 2040. By this time, emissions of plastic into the ocean are predicted to increase by an order of magnitude (Jambeck *et al.* 2015). To avoid waiting 25 years for an international plastics agreement with reduction targets, reporting, and signatories, we seek to apply lessons learned from the policy processes related to carbon emissions. The scale and pace of solutions must match the scale and pace of emissions.

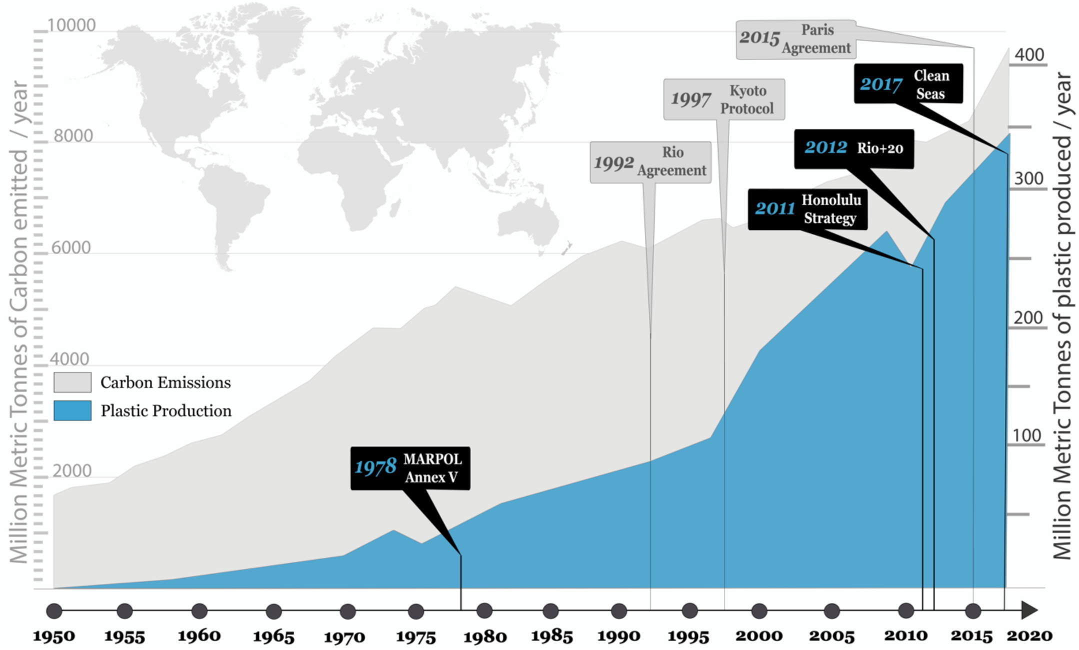

Figure 6.3 Global carbon emissions(data estimated for 2014-2017; Carbon Dioxide Information Analysis Center CDIAC 2016) compared with plastic production (Plastics Europe 2015), since 1950 and when international policy interventions were ratified. If the initiation of international agreements for plastic pollution follows a trajectory and pace similar to the international climate change policy development, an effective international agreement with reduction targets, methods for monitoring progress, and signatories may not happen for plastic pollution until 2040 or later.

6.1.3 Local solutions fall short

Local and national actions have been the primary approach for mitigating plastic pollution, using mechanisms such as bans (*e.g.,* microbeads, plastic bags), maximum daily limits for emissions into watersheds, and incentives for fishing gear retrieval. Positive and measurable progress occurs at these local and national scales. For example, a ban on microbeads in the United States will prevent billions of plastic beads from entering watersheds daily. Still, the pace of this piecemeal progress is not commensurate with the pace of plastic emissions.

Importantly, the ability to prevent and mitigate plastic pollution locally and nationally varies by nation and region because of resource availability for waste management. Many regions receive large imports of single-use plastic products yet have inadequate infrastructure for waste collection and management. This leads to large volumes of plastic litter dumped in the environment, deposited in makeshift landfills, and/or treated by open burning that leads to emissions of hazardous chemicals. This lack of an explicit link between the plastic that is marketed and the capacity for waste management makes it nearly impossible for many local governments to effectively prevent plastic pollution. At an Inter-Parliamentary Union hearing to plan for The Ocean Conference in February 2017, some member states declared they wanted to act but lacked the legislative or infrastructural tools to address marine plastic pollution.

6.1.4 Cross border solutions

The time has come for a meaningful international agreement—one with clearly defined waste reduction targets and a solid foundation to provide all nations with the resources necessary for local reductions to be possible. Successful prevention and mitigation strategies that have already been implemented at national and regional levels are case studies that can be replicated around the world—e.g., beverage container deposit schemes or legislation to eliminate single-use plastic products.

Effective policies must take into account all stages of the lifecycle of plastic—connecting producers to users and ultimately to waste managers. Based on studies from nongovernmental organisations (Ocean Conservancy 2015), industries (British Plastics Federation 2012), scientists (Rochman *et al.* 2013; World Economic Forum, 2017; Worm 2017), consultants (Neufeld *et al.* 2016; Sherrington *et al.* 2016), and policy-makers (UNEP 2012; United Nations 2016, 2017), several steps could be taken to address the plastics problem and provide the starting points for a meaningful international agreement.

Countries should end fossil fuel subsidies. Annually, 4–8% of oil is used to produce raw plastic (Hopewell, Dvorak & Kosior 2009). To reduce production of plastic from raw materials, plastics must be decoupled from fossil fuels (Neufeld *et al.* 2016). Fossil fuel subsidies incentivise the plastic market, allowing the cost of production to be less than production of an alternative.

Countries should come together to establish measurable reduction targets for plastic waste, aimed toward zero-waste, stimulating actions that reduce plastic pollution. These may include container deposit schemes; legislation to reduce single-use plastics; reclassification of plastic pollution (Rochman *et al.* 2013; *e.g.,* to hazardous substance or Persistent Organic Pollutant (POP); Lohmann 2017; Worm 2017) to qualify for funds under existing programs for monitoring, prevention, and clean-up; and mechanisms that incentivize fishers to collect abandoned fishing gear.

Countries should agree on incentives that ensure plastics are produced with a sustainable end of life. To date, 60% of all plastics produced are accumulating in landfills or are in the natural environment (Geyer, Jambeck & Law 2017). An international agreement should work toward achieving a circular economy (Neufeld *et al.* 2016), whereby all plastics produced are recovered and valued. In a waste hierarchy, materials should be first reused, second repurposed for an alternative use, and/or third mechanically recycled into a new product. For some products (e.g., sachets and films for food packaging), truly biodegradable materials may replace oil-based synthetic polymers.

Under this framework, no plastic is sent to landfills and fewer raw materials are needed. Similar to the goals of a "green economy," the plastic economy can be stabilised, becoming more environmentally and socially responsible. To do this, producers and waste managers must work together to produce materials that can be managed sustainably. This should entail incentivizing the production of plastics made from inert chemicals and that can be completely recycled and reused or from truly biodegradable materials that break down completely and assimilate back into the natural carbon cycle (McDevitt *et al.* 2017). This will stimulate innovation and the redesign of materials that are chemically inert, truly biodegradable, 100% recyclable, and/or made from postconsumer recycled material.

Policies could also reward member states that agree to market only plastic products that are recyclable and/or reusable in their region. We recognize that for some countries this will come at an unbearable economic cost. As such, an extended producer responsibility program (Walls 2006) can be implemented to create a global fund that can ultimately be used by member states for waste management infrastructure that is appropriate for them.

Such a global fund is a key measure. Many regions wish to prevent plastic emissions into the environment, but as noted, they lack the means for waste management infrastructure. As the global fund builds, developing economies may access it, much like developing economies can access the UNFCCC's climate fund to combat, mitigate, and prepare for the repercussions of climate change. Solutions for one region may not be appropriate for another, and a global fund should not dictate a specific solution, but it should provide the financial means for each region to flexibly reach an agreement's targets.

6.1.5 Reason to act

If current plastic production and waste management trends continue, roughly 12,000 million metric tons of plastic waste will be in landfills or in the natural environment by 2050 – an order of magnitude above current levels (Geyer, Jambeck & Law 2017). Researchers continue to try to understand how steadily increasing plastic pollution will impact wildlife populations and fisheries stocks. If we continue on our current trajectory, we may not need experiments to determine the answers.

No single solution will stop marine plastic pollution. International collaboration is necessary to reduce the demand for single-use plastic products, shift to a sustainable plastics economy, and improve waste management infrastructure that promotes zero-waste. To do this, the international community must commit to specific, measurable, time-bound targets to reduce plastic emissions into our oceans. By learning from climate change and other global environmental issues (*e.g.,* ozone depletion) (Raubenheimer & McIlgorm 2017), we may be able to fast-track solutions at the global scale.

Nongovernmental organisations, UNEP, and several regional governments have established the groundwork for international policy on plastic pollution. Importantly, there is sufficient evidence to demonstrate that reducing plastic pollution will mitigate impacts on marine ecosystems and the economy. Concerned countries and states should build on current policy and research efforts, pushing for international measures that can stem the rising tide of plastic into the world's oceans.

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Appendices

7.1 Appendix 1: Mercury Islands and their role in understanding seabird island restoration[4]

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[4] Towns, D.R., **Borrelle, S.B.**, Thoresen, J., Buxton, R.T., and Evans, A. 2016. Mercury Islands and their role in understanding seabird island restoration. *New Zealand Journal of Ecology, 40(2): 235-249*

Mercury Islands and their role in understanding seabird island restoration

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Abstract: The progressive removal of invasive mammals from the Mercury Islands has led to over 25 years of field study designed to test the processes of restoration and natural recovery of these seabird-driven island ecosystems. Resulting from this work, four key restoration questions can now be identified as fundamental to designing island restoration programmes. The questions are: what is the regional context of the island (biogeography); how does each island ecosystem operate (ecosystem function); how have invasive species changed the ecosystem (response effects); and how can progress towards a restoration goal be defined (outcome measures)? Examples of how these questions influenced restoration in the Mercury Islands are provided with Korapuki Island as a case study. However, unpredicted and subtle responses can eventuate. In the Mercury Islands these included a hitherto unknown honeydew parasite-bird-gecko food web and subtle effects of rats on plant regeneration. Promising outcome measures of restoration progress are now being developed, including indices of marine influence using stable isotopes of nitrogen and the use of network analysis to analyse the composition of invertebrate food webs.

Keywords: biogeography; species area; colonisation; ecosystem function; eradication; reference sites; Korapuki Island; unknown consequences; New Zealand

Introduction

Islands are not only repositories of disproportionately high numbers of endemic species (e.g. Keitt et al. 2011; Tershy et al. 2015), they have frequently become refugia against the spread of invasive species and habitat loss (Daugherty et al. 1990). For example, although New Zealand has the world's largest number of endemic species of seabirds, the country also has the largest number of threatened seabirds, with most species now confined to offshore islands following the spread of invasive species (Croxall et al. 2012). Only 20 years ago, Duffy (1994) lamented that island ecosystems were becoming so modified, most were unrecognisable. Selected invasive mammals have periodically been eradicated from islands for about 100 years (Bellingham et al. 2010a). However, the eradication of the most pervasive group, introduced rodents (Atkinson 1985; Towns et al. 2011), only became effective and widely applied at the time Duffy was despairing for the future. Today, rodent eradications have been attempted globally on at least 500 islands (Russell & Holmes 2015), with the largest number for a single country conducted in New Zealand (Howald et al. 2007; Keitt et al. 2011). The frequency of eradications in New Zealand began to rapidly increase between 1980 and 1990 (Towns et al. 2013), meaning that the potential to learn from the responses of island ecosystems to comprehensive pest removal covers only 30 years. Attempts to restore islands following eradications of rodents have an even shorter history. Here we review 28 years of restoration activity in the Mercury Islands off northeastern New Zealand. Work in the Mercury Islands developed out of two questions posed in the mid-1980s: can rats be eradicated systematically from islands (Towns 1988), and if they can, is it possible to restore entire ecosystems previously modified by introduced mammals (e.g. Towns et al. 1990; Towns & Atkinson 1991; Towns et al. 1997)?

The developmental history of eradication technology in the context of the Mercury Islands (Towns & Broome 2003) and a summary of achievements that have stemmed from these activities have already been reviewed (Bellingham et al. 2010a; Towns et al. 2013). Instead, we focus on the question of whether entire ecosystems can be restored, since this is often the goal of invasive species eradications (Towns et al. 1990); a goal that may be particularly challenging for island ecosystems penetrated by invasive species (Norton 2009). The first of the Mercury Islands to be cleared of all invasive mammals was Korapuki (Towns & Broome 2003) and an ecological restoration plan for the island was completed 10 years ago (Towns & Atkinson 2004). Here we examine how implementing the Korapuki plan has contributed to the conceptual understanding of island restoration. We aim in particular to address a problem for seabird island ecosystems raised by Duffy (1994): "We cannot put the Humpty Dumpty of an ecosystem back together because we don't know what the original Humpty looked like, nor do we have all the pieces."

This review aims to address the technical issues raised through Duffy's "Humpty Dumpty" problem by using restoration of seabird island ecosystems in the Mercury Islands as a working example. We focus on four key subsidiary questions that are fundamental to understanding the composition and function of island ecosystems: 1) what is the regional context of the island (biogeography); 2) how does each island ecosystem operate (ecosystem function);

3) how did invasive species change the ecosystem and what effects will their eradication have (response effects); and 4) how can progress towards a restoration goal be defined (outcome measures)? The first two questions help to provide the context within which restoration targets can be set, whereas the second two address the progression of an island towards a target and are more site-based. We demonstrate the relevance of context and site-based approaches by using Korapuki Island as a case study.

Biogeography

Study area

The seven Mercury Islands (36.62S; 175.86E) form the largest of four archipelagos from which mammals have been eradicated in their namesake Mercury Islands Ecological District (MIED). The MIED is a biogeographic grouping based on shared geological and biological characteristics (McEwen 1987) and extends from Cuvier Island (36.43S; 175.77E) in the north through to the Aldermen Islands (36.97S; 176.08E) in the south. Cuvier, all Mercury Islands except Great Mercury and the Aldermen are classed as Nature Reserves under the Reserves Act 1977. These are the most highly protected reserves under New Zealand legislation, with access by permit only. Across the MIED, the range of invasive mammals present has included (Atkinson & Taylor 1992): goats (*Capra hircus*), cats (*Felis catus*), ship rats (*Rattus rattus*) and kiore (*R. exulans*) on Great Mercury; goats, cats and kiore on Cuvier; rabbits (*Oryctolagus cuniculus*), kiore and mice (*Mus musculus*) on Ohinau; rabbits and kiore on Stanley and Korapuki; and kiore alone on Double, Red Mercury, and Middle Chain (Supplementary Data). Like most offshore islands, all of the islands in MIED have at some time been modified through burning (Atkinson 2004; Bellingham et al. 2010a).

Two biogeographic concepts discussed below assist with understanding how history influences the way we view restoration of the islands in this district.

Vicariance

The biotic composition of islands in the MIED is largely a function of island origin (e.g. Towns 1994, 2002b; Towns et al. 1997), notably isolation due to sea level rise following the last glaciations (e.g. Hayward 1986). Oceanic islands far from the main islands of New Zealand, such as the Kermadecs (30.37S; 178.48W), were never connected to larger land masses and are colonised by chance, resulting in genetic drift and high levels of endemism of those species that survive (e.g. Carlquist 1965).

In contrast, islands such as those in MIED are within 20 km of the coast (i.e. on the continental shelf) of New Zealand and were part of the mainland during the last glaciation. As sea levels rose, the newly formed islands contained gradually constrained subsets of mainland terrestrial communities. Populations in these subsets were derived from genetically diverse gene pools, so drift was much less likely and thus endemism is relatively uncommon. Furthermore, these islands support many terrestrial species unable to disperse over water, including a great diversity of flightless invertebrates as well as terrestrial reptiles (Daugherty et al. 1990). Bathymetric analyses within MIED indicate that by about 8 000 years ago, Cuvier and the Aldermen had already been separated from the mainland for at least 4 000 years, but the Mercury and Ohinau Islands had only recently lost their dry land connection to the peninsula (Figure 1). At that point, the Mercury archipelago had not formed, but was an extended "Great Mercury super-island". The concept of vicariance applies here: present disjunctive distributions reflecting the fragmentation of contiguous populations by rising sea levels as a geographic barrier (Wiley 1988). Thus, species today confined to individual islands likely once inhabited the whole Great Mercury super-island.

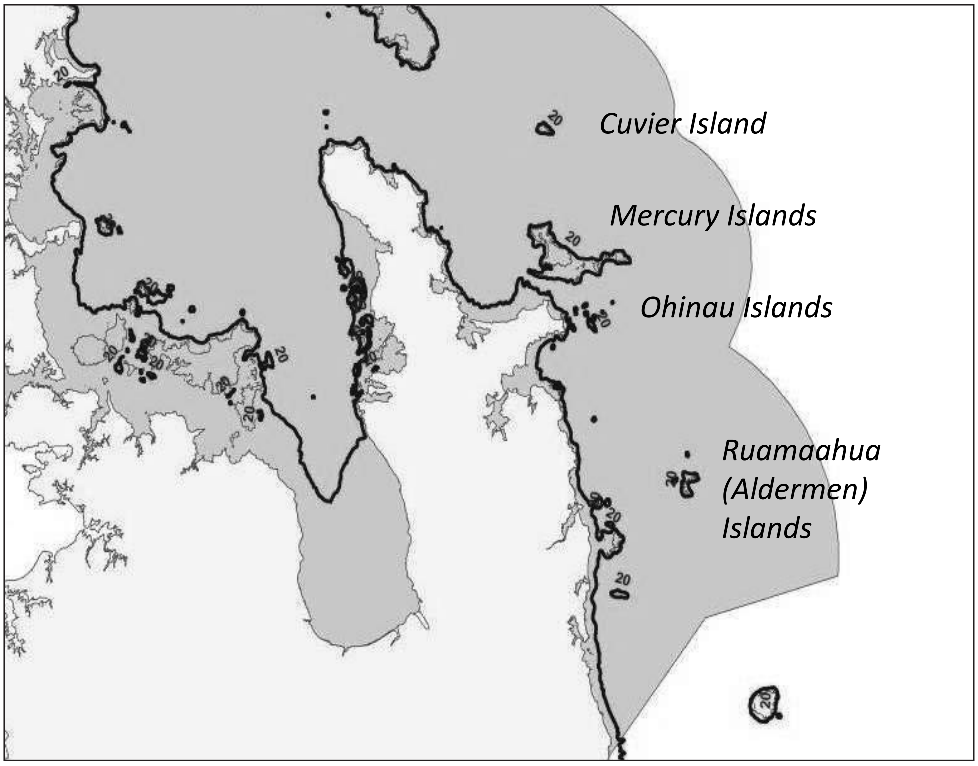

Figure 1. Coastlines around the Coromandel Peninsula at about 8 000 years ago based on the 20 m isobaths (shaded areas are sites within Hauraki Gulf Marine Park) showing four main archipelagos in Mercury Islands Ecological District.

Past connections to the mainland and inclusion within the same ecological district might imply wide application of a variance model. However, the relationship between biota of the Mercury archipelago and others in MIED is not particularly clear. For example, two species of skinks, *Oligosoma whitakeri* and *O. alani,* are present on mammal-free islands in the Mercury Islands but absent from mammal-free islands in the Aldermen. However, a related species, *O. oliveri* is present in both archipelagos (Pickard & Towns 1988). Likewise, the tusked wēta (*Motuweta isolata*), although present in the Mercury Islands, is absent from mammal-free islands in the Aldermen. Subtle differences such as these may reflect differences in isolation history. These differences suggest that for poorly dispersed groups such as flightless invertebrates and reptiles, there has been less unity of distribution than is implied by the vicariance model. Consequently, if high ecological integrity is the restoration goal (see below), the most defensible approach may be to focus within archipelagos; acknowledging that the greatest risk of errors for assumptions about community composition would likely arise from extrapolations between them.

Species-area relationships

A fundamental principle of island biogeography is that, aside from some exceptions, the number of species usually increases in proportion to area (McArthur & Wilson 1967). For example, Whitaker (1978) used this relationship to predict the expected species diversity of reptiles on islands with and without introduced rodents. Although the species-area relationship holds for islands without invasive mammals (e.g. Borrelle et al. 2015), the reverse can develop on islands with invasive vertebrates. As a result, the smallest Mercury Islands, which have not been invaded by mammals, now have more reptile species than larger ones invaded by kiore and rabbits. A similar relationship in response to predation pressure is likely to hold for the large flightless invertebrates.

Species-area relationships are useful because they provide an empirical measure of the proportional reduction of assemblages in the presence of introduced mammals, as well as a basis for predicting the composition of restored assemblages. For example, islands with invasive mammals in the MIED had a 50% reduction in reptile fauna and 75% reduction in wēta fauna (e.g. Towns et al. 1997), which thereby suggests the level of species restoration required for each group.

Ecosystem function

Without detailed understanding of how island ecosystems function when invasive species are absent, it may be difficult to determine how restoration efforts should proceed on islands where invasive species have been present. This understanding can be greatly assisted through the use of reference sites (White & Walker 1997), which are model sites or islands used in order to predict the trajectory or endpoint of an impaired ecosystem after restoration interventions (e.g. Balaguer et al. 2014). Although such sites help with understanding ecosystem function, they do not necessarily indicate the capacity for natural dispersal into previously modified sites. As we discuss below, dispersal ability of some species (particularly plants) often relies on a vertebrate dispersal agent.

Reference sites

Within the MIED, six small islands (3-30 ha) that have never been invaded by introduced mammals can be used as reference sites for restoration of the eight islands (18-1872 ha) from which invasive species have been or are being removed. Five of these reference islands have high seabird abundance and extreme surface fragility due to burrowing by birds. On the larger reference islands (>2 ha), in addition to seabirds, there are dense and diverse reptile populations and numerous species of flightless invertebrates, including wēta, gastropods and spiders (Towns et al. 2009; Bellingham et al. 2010a). These sites indicate the structure and function of seabird driven island ecosystems of different sizes before mammalian predator invasion in the MIED.

Additional reference information can be obtained from invaded islands larger than the uninvaded reference sites. Given their greater area, such islands can have a higher species diversity of plants, which is helpful in identifying species particularly sensitive to browsing (see below). Such sites may only provide fragmentary information, but they extend information available about the composition of local communities as part of an "ecological memory" (*sensu* Balaguer et al. 2014).

Recolonisation potential

When introduced species are removed, many species can return and recover unaided. This recovery is particularly likely for most species of plants, as long as dispersal mechanisms are available and/or local populations remain. For many plants, dispersal is through birds such as kererū or fruit pigeons (*Hemiphaga novaeseelandiae*), which on these islands are the only species capable of long distance seed dispersal of plants with large fruit including kohekohe (*Dysoxylum spectabile*), taraire (*Beilschmedia tarairi*) and tawāpou (*Pouteria costata*; Table 1). Other forms of distribution are less conventional. For example, the seed pods of *Pisonia* are extremely adhesive, potentially as a means of spread between locations by relatively large seabirds, which would explain the wide distribution of the genus throughout the Pacific (e.g. Burger 2005). Given that most islands in the MIED are now free of introduced mammals, it may be possible for natural dispersal through wind and birds to facilitate dispersal of plants.

Despite impressive flight mobility, seabirds still face some barriers to natural dispersal. Studies of seabird colonies have often indicated high philopatry, with birds behaviourally tied to their original birthplace (Warham 1996). A review of colonisation ability of seabirds around New Zealand found more capacity to colonise new islands than had previously been assumed (Buxton et al. 2014). However, frequency of colonisation declined rapidly with distance from source islands, and natural colonisation by most species became unlikely when source populations were >25 km away. Ellipses based on the 25 km radius around uninvaded, densely populated islands in MIED indicate that Mercury, Ohinau and Aldermen archipelagos are all within a 20 km radius (Figure 2). However, Cuvier is between 20 and 25 km from the nearest large uninvaded islands, and still has only been recolonised naturally by three species of Procellariiformes: grey-faced petrel (*Pterodroma macoptera*), fluttering shearwater (*Puffinus gavia*) and diving petrel (*Pelecanoides urinatrix*) (Borrelle et al. 2015).

Table 1. Native species of plants suppressed by kiore as determined from responses of resident species to rodent eradications (from Atkinson 1964; Towns et al. 1997; Campbell & Atkinson 1999, 2002), with canopy species marked*

Species	Study site (s)	Status on reference sites
Kohekohe *Dysoxylum spectabile**	Double, Cuvier, Red Mercury	Locally dominant canopy species on larger islands, rare on Middle, unknown from Green
Parapara *Pisonia brunoniana*	Cuvier, Double, Middle Chain	Subcanopy species capable of forming dense thickets but absent from Middle and Green
Karo *Pittosporum crassifolium*	Double, Red Mercury, Middle Chain	Widespread and common small tree in coastal areas on Middle and Green
Tawapou *Pouteria costata**	Double, Red Mercury, Middle Chain	Often scattered on larger islands but rare on smaller seabird islands such as Middle
Karamu *Coprosma macrocarpa*	Double, Red Mercury	Widespread and common small tree; now widespread on most islands
Taupata *C. repens*	Red Mercury	Coastal shrub now common in coastal areas on all islands
Coastal maire *Nestigis apetala**	Cuvier	Coastal tree absent from Mercury Islands
Nikau *Rhopalostylus sapida*	Cuvier	Palm, which can be locally abundant but absent from Mercury Islands
Houpara *Pseudopanax lessonii*	Double, Cuvier, Middle Chain	Shrub or small tree widespread on Mercury Islands
Milktree *Streblus banksii**	Middle Chain	Small tree with extensive areas as canopy on Middle Island and spreading on Stanley
Hymenanthera *Melicytus novae-zelandiae*	Red Mercury	Shrub widespread in coastal areas on Middle

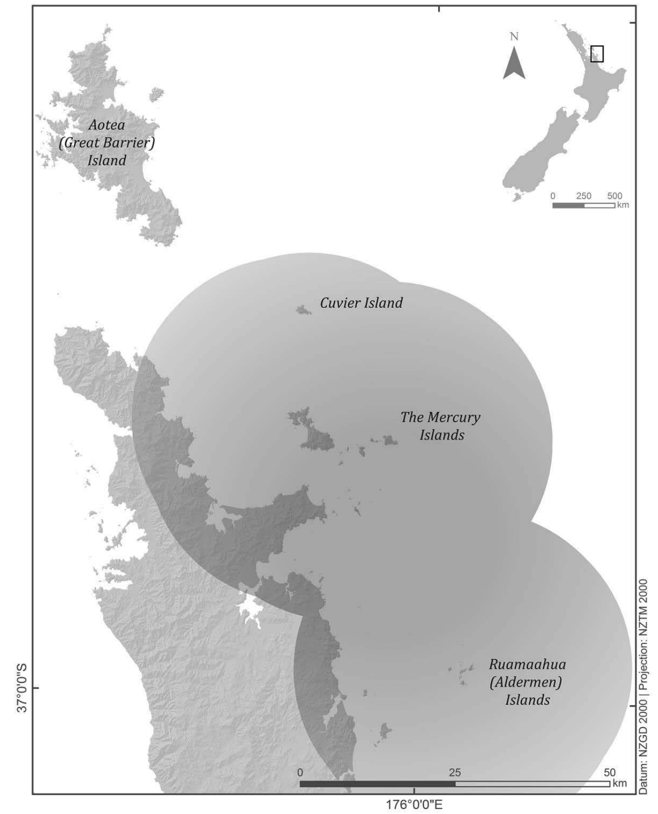

Figure 2. Potential seabird recolonisation ellipses based on 25 km ranges from uninvaded source islands within the Mercury Islands Ecological District.

Effects of invasive species on ecosystem function

Occasionally the effects of invasion are so extreme they are even visible to offshore observers. Examples include extensive vegetation modification and soil loss following decades of browsing by goats (*Capra hircus*) or rabbits (e.g. Merton 1987; Bellingham et al. 2010b). More often the effects are subtle, but even when the invasive species are rodents (e.g. Towns et al. 2006) or ants (e.g. O'Dowd et al. 2003), they can still produce catastrophic changes to ecosystem function.

Studies in New Zealand of the distribution of tuatara (*Sphenodon punctatus*), lizards, invertebrates and plants compared with kiore over a large sample of islands indicate that some species populations are either heavily suppressed by these rats or incompatible with them (Whitaker 1978; Watt 1986; Atkinson 1986; Campbell & Atkinson 1999). A similar comparative approach was used to determine the effects of suppressed seabird populations on island ecosystem function. Nine islands in northern New Zealand (including four in the MIED) with large populations of burrowing seabirds were compared with nine where seabirds were suppressed by introduced rats. On islands with few seabirds, soils had 47% less total C, 45% less total N, 53% less total P and 23% lower marine-derived δ^{15}N than on uninvaded islands (Fukami et al. 2006). Furthermore, on islands with few seabirds, 11 orders of leaf-litter and soil-inhabiting invertebrates were less abundant, foliar and litter N concentrations in several plant species were lower, and litter decomposition rates were slower than on uninvaded islands with large seabird colonies (Towns et al. 2009; Wardle et al. 2009). These studies demonstrate the diverse and subtle effects of seabirds on island ecosystems, and conversely, the extent to which the systems can change when mammalian predators invade. Such studies do not demonstrate cause and effect between mammal invasion and shifts in ecosystem function. They do however, provide a powerful basis for developing hypotheses and conceptual models, which can then be tested experimentally (Veltman 1996; Towns et al. 2009).

Three inferences relevant to islands restoration stem from the above observations. First, introduced species likely have direct negative effects on resident species assemblages. Decades after eradication, the legacy of some invasive mammals, such as kiore, remain on islands, as has been demonstrated by the absence of selected species of seabirds, plants, invertebrates and lizards (Towns 2009). Second, through activities such as burrowing and defecation, seabirds are likely to be one of the most powerful biotic drivers of islands ecosystems around New Zealand (Mulder & Keall 2001) and elsewhere (Mulder et al. 2011). Finally, when invasive species suppress seabird abundance, ecosystem functions engineered by seabirds are suppressed, resulting in a wide range of indirect effects (e.g. Towns & Atkinson 2004; Russell 2011).

Effects of eradicating invasive species

Four sources of information can help us predict the response of native species and ecosystems to the removal of invasive species from islands: 1) studies of the responses of plants and animals after eradication; 2) the use of reference sites that lack invasive species as defined above; 3) using chronosequences of islands from which invasive species have been removed (e.g. Buxton et al. 2016); and 4) paleoecological studies of plant and animal remains in middens, caves, sand-dunes and wetlands (e.g. Towns & Ballantine 1993; Wilmshurst et al. 2014). Direct response studies are most valuable on those islands where a single invasive species was introduced then removed, which avoids complications caused by interactions between invasive species (Towns 2011). An example is provided by tuatara, a species which managed to co-exist with kiore on several islands. In MIED, tuatara were reduced to such low numbers (<20) on kiore invaded islands, their responses to eradication were un-measureable over short timeframes. However, larger numbers of tuatara survived in the presence of kiore in the Marotere Islands, where despite variation between islands, comparisons of recruitment rates of juvenile tuatara before and after kiore eradication demonstrated significant demographic shifts in tuatara populations. Potential competitive effects between kiore and adult tuatara were also revealed by changes in body condition (Towns et al. 2007). Similar comparisons between islands in MIED, using uninvaded islands and those still with kiore, indicated that kiore suppressed 11 of the 17 species of plants studied (Table 1) and that forest composition on the invaded islands had likely been significantly altered (Campbell & Atkinson 2002).

Some apparently extirpated species have reappeared many years after eradications on islands were completed. For example, five populations of geckos and four populations of skinks have reappeared on islands around New Zealand cleared of invasive mammals. One species of gecko, *Dactylocnemis pacificus*, reappeared on at least two the Marotere Islands less than 10 years after the removal of kiore, but the same species has still not been found on any of the Mercury Island Nature Reserves previously inhabited by invasive mammals despite >20 years of monitoring (D. Towns unpublished data).

Restoration goals

All restoration projects require a goal or target (Atkinson 1988). This in itself can be problematic if there is little clarity about what the system previously looked like (Duffy 1994) and since reference sites usually change with time (Simberloff 1990). There are two approaches to defining restoration goals: time or function. A goal could be based on a previous time, such as before the arrival of invasive species, which requires the identification of historic benchmarks (e.g. Atkinson 1988). An alternative is to use ecosystem function as a goal, which does not require the historic reference point, but does require understanding of how key components of ecosystems interact. Such an approach is also greatly assisted if reference sites are available. Now that there is considerable evidence about the engineering role of seabirds (e.g. Mulder et al. 2011), seabird driven island ecosystems as a goal would be a logical option for many islands. This then raises the question of whether intervention is needed.

If the goal is to restore seabird-driven ecosystems, three pieces of evidence suggest that no further manipulation may be required after eradication at many locations (Buxton 2014). First, Jones (2010) analysed marine-derived nitrogen ($\delta^{13}N$) in soils, plants and spiders (as predatory invertebrates) across islands at different stages of recovery after eradication of mammals. She found increasing evidence of a marine seabird-derived signature with time since mammal eradication and predicted that ecosystems with seabird-driven attributes can recover in a few decades. Second, Buxton et al. (2014) found that the rate of seabird recovery on some islands is higher than might be predicted from the breeding success of residents. They found evidence that existing burrowing seabird colonies attract immigrants, which can be conspecifics, but may also be other species. Finally, where suitable habitat is available, and the density of potential source colonies is sufficient, sites can be identified where natural recovery is most likely (Buxton 2014). In MIED, natural seabird recolonisation potential is high in all archipelagos except Cuvier (Figure 2) (Borrelle et al. 2015).

Given that introduced mammals can extirpate a range of species from within these systems (Table 2), a second option is to extend the functional goal of seabird driven ecosystems to include reintroducing species unable to naturally recolonise. For example, since the above biogeographic analyses support an argument for vicariance within the Mercury islands, restoration could aim to restore seabird-driven ecosystems with community composition typical of the Mercury Islands archipelago. The case study outlined below acknowledges the capacity for natural recovery of seabird populations but also the inability of some species of reptile and invertebrate to re-colonize. For other species, such as the tree wēta (*Hemideina thoracica*) and some species of plants, an overlay of data from reference sites combined with knowledge of the effects of invasive species within the archipelago informed the extended restoration goal.

When is the restoration process complete?

The question of when a restoration project has reached a pre-defined target is of particular interest to conservation managers. The range of unpredictable outcomes and uncertainties involved with island restoration are so numerous that predicting an endpoint for such an exercise is complex and could involve timescales beyond the life span of a researcher. For example, the time to reach carrying capacity for Whitaker's skinks (*Oligosoma whitakeri*) reintroduced to Korapuki Island was estimated as at least 140 years (Miller 2009). On other islands in the archipelago, such as Red Mercury Island, which is over ten times larger than Korapuki, the recovery of reintroduced populations of the same species will inevitably take even longer.

The criteria for successful restoration through

Table 2. Status of species of flightless invertebrates and reptiles present on mammal-free Mercury islands but absent from Korapuki Island before removal of introduced mammals and identified as candidates for reintroduction by Towns & Atkinson (2004)

Name	Ecological role	Reintroduction status	Tolerance of invasive predators
Gastropoda *Rhytida greenwoodi*	Predator of gastropods and earthworms	Still to be reintroduced; known only from Green Island	Does not co-exist with kiore on any Mercury Islands, but occasionally does so elsewhere
Arachnida *Cambridgea mercurialis*	Nocturnal predator	Still to be reintroduced; common in seabird burrows on Middle and Green Islands	No data; does not seem to balloon so may have limited dispersal capabilities (M Fitzgerald pers. comm.)
Orthoptera (Stenopelmatidae) *Hemideina thoracica*	Folivore	52 from Double Island (1997) now widespread and abundant (Green 2005)	Co-exists with kiore on some Mercury Islands but not others
Hemiandrus pallitarsus	Predator of invertebrates	Still to be reintroduced; present on Middle and Red Mercury	Co-exists with kiore on some Mercury Islands but not others
Motuweta isolata	Predator of invertebrates	100 captive reared originally from Middle Island (2007) now locally abundant (unpublished report, Department of Conservation)	Does not co-exist with kiore
Coleoptera (Tenebrionidae) *Mimopeus opaculus*	Algal/fungal grazer	100 from Middle Island (2000-2002) now locally abundant (C. Green pers. comm.)	Rarely co-exists with kiore; absent from other Mercury Islands invaded by kiore
Reptilia (Sphenodontidae) *Sphenodon punctatus*	Apex terrestrial predator of invertebrates, lizards and small seabirds	Still to be reintroduced; dense populations on Middle and Green, relict on Stanley and Red	Coexists with kiore on some other Mercury Islands, but with consistent recruitment failure
(Gekkonidae) *Dactylocnemis pacificus*	Omnivore, nectar, fruit and invertebrates	Still to be reintroduced; common in forested areas on Middle	Does not co-exist with kiore in Mercury Islands but does in other archipelagos
(Scincidae) *Oligosoma alani*	Predator of invertebrates and smaller lizards	14 reintroduced (1992-93) from Green; widely dispersed and locally abundant	Does not co-exist with kiore on any islands
Oligosoma oliveri	Predator of invertebrates	25 reintroduced (1992-93) from Green; breeding	Does not co-exist with kiore on any islands
Oligosoma suteri	Intertidal predator of invertebrates	30 reintroduced 1992 from Green; locally abundant	Can co-exist with kiore on islands with appropriate boulder refuges
Oligosoma whitakeri	Predator of invertebrates	28 reintroduced 1988 from Middle; expanding range and locally abundant	Does not co-exist with any mammalian predators on islands

reintroductions are relatively clear (e.g. Towns & Ferreira 2001), and include complete replacement of the release propagule with locally born offspring (Wolf et al. 1996). For some invertebrates, high reproductive output and rapid turnover means that such criteria may be achieved in <10 years. However, for species such as tuatara, adult life spans of up to 100 years mean that monitoring population replacement will require generations of biologists. In contrast to intervention through reintroductions, passive recovery is undirected and process driven. Nonetheless, passive recovery requires monitoring to assess whether hypotheses about ecosystem development are being met. If success is based on changes in ecosystem function, rather than assemblage composition, progress can be estimated in relatively short time scales (Tables 3 and 4). Measures of the recovery of seabird driven ecosystems can include simple measures of burrow density coupled with additional measures of seabird effects. The study of uninvaded islands and those with seabirds suppressed by invasive mammals (e.g. Fukami et al. 2006; Towns et al. 2009) indicated that soil pH strongly reflects seabird activity. Similarly the measures of C:N and $\delta^{15}N$ used by Jones (2010) indicate the rate at which seabird effects can be measured. Analyses of food webs on islands with and without procellariiform seabirds indicate the likely responses of ecosystem processes to predator removal if these seabirds recover (Figure 4). Present indications from work on Korapuki Island are that islands within the colonisation range of seabirds could demonstrate many of the functional attributes typical of uninvaded seabird islands within 50 years. More sophisticated investigations of invertebrate community and food web structure should contribute to methods for verifying these functional changes (e.g. Orwin et al. in press).

Restoration case study: Korapuki Island

Korapuki was the first island in the Mercury archipelago from which all introduced mammals were removed (kiore in 1986, rabbits in 1987), has been the site where the conceptual and practical impediments to restoration have been tested, and is also the only island in the group with a comprehensive restoration plan (Towns & Atkinson 2004). The restoration target initially proposed for Korapuki Island by Towns et al. (1990) was for a seabird-reptile-invertebrate-plant system similar to that of Middle and Green Islands. The subsequent restoration plan expanded on this target by emphasizing features of the Middle and Green reference sites, including coexistence of very dense populations of small seabirds (particularly diving petrels) with a high diversity of reptiles and many invertebrate species (Towns & Atkinson 2004). For extirpated species such as tuatara, five species of lizards and many species of flightless invertebrates, natural recovery is unlikely (Towns 2002b). The restoration plan thus recommends re-introduction of those species likely to have been lost through the action of habitat modification (fire) combined with the previous presence of kiore and rabbits (Table 3). For the purposes of this review, we focus on changes to the biota of Korapuki Island since the removal of mammals in 1986-87 (Tables 2 and 4), restoration activities implemented (Table 3), predicted and unpredicted outcomes, and the many remaining uncertainties in the recovery trajectory of the island (Table 4).

Predicted outcomes

In order to develop hypotheses for the recovery of Korapuki Island after the removal of kiore and rabbits, Towns & Atkinson (2004) constructed conceptual interaction webs. The webs were based on structure of the reference ecosystems of Green and Middle Islands and responses elsewhere in the archipelago to mammal eradications. However, it was not possible at that time to define when various predicted interactions would eventuate, nor were criteria identified as measures of success. Central to the 2004 model was an increasing influence from seabirds adding nutrients to the island's soils, and an increasing density of seabird burrows, which are used as habitat by tuatara and some species of lizards. The speed at which burrow-nesting seabird populations recover was assumed to rest on three aspects of the biology of Procellariiformes: extreme philopatry; low annual reproductive output; and slow development to reproductive maturity (e.g. Warham 1996). In combination with slow population growth by introduced species of reptiles (e.g. Towns 1994), reactivation of the proposed interaction web was assumed to involve timescales of decades or perhaps centuries.

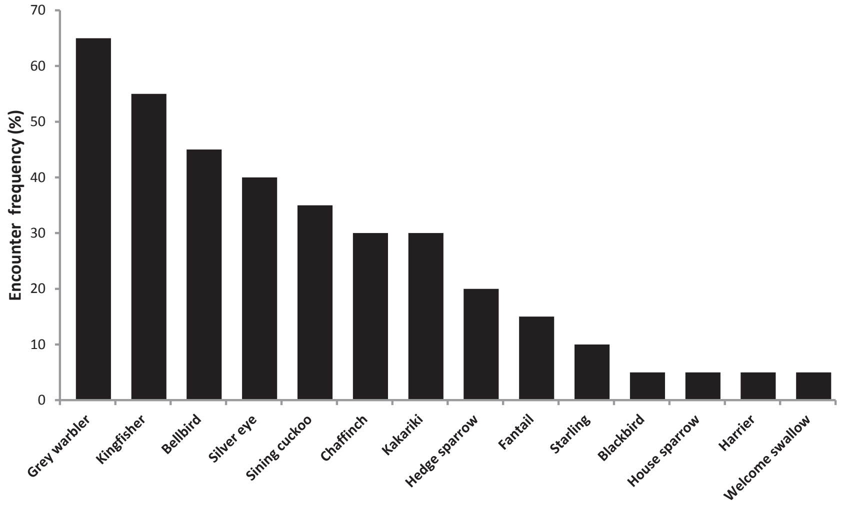

Figure 3. Frequency of forest bird encounters (presence/absence of calls and sightings) at 20 five-minute observation points at 50 m intervals along axial ridges on Korapuki Island in December 2007.

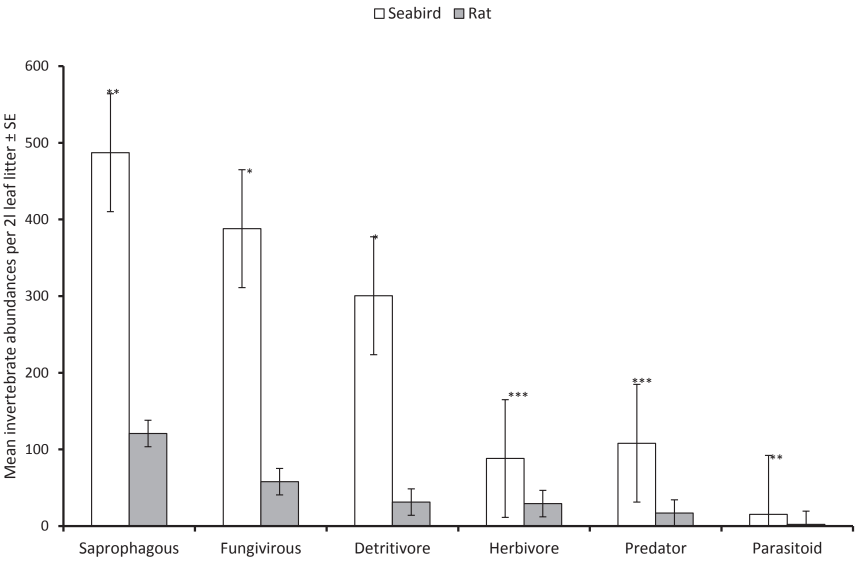

Figure 4. Relative abundance of litter invertebrates from different trophic levels on nine northeastern New Zealand islands invaded by rats and with few seabirds compared with nine islands in the same geographic area never invaded by introduced mammals (for methods and study sites see Towns et al. 2009); Mann-Whitney U Tests were used to compare means with p values identified as * $p<0.05$, ** $p<0.005$, *** $p<0.0005$.

Table 3. Changes to biota of Korapuki Island following the removal of kiore and rabbits.

Species or taxonomic group	Before mammal removal	At least 20 years after mammal removal
Plants	Flora of 96 species (Hicks et al. 1975), with 74% native	Flora of 115 species with 79% native immediately after kiore and rabbit removal (1988); 128 species with 81% native by 2002 (Towns & Atkinson 2004)
Selected woody plants sensitive to kiore	Restricted to <10 known individuals or previously listed as uncommon (a few at one or two locations): *Coprosma repens*; *Corynocarpus laevigatus*; *Melycitus novaezealandiae*; *Myoporum laetum*; *Pouteria costata*; *Streblus banksii* (Hicks et al. 1975)	All species except *C. laevigatus* (spreading but <10 individuals) now present throughout island; *P. costata* with > 80 young plants in some areas (Towns et al. 1997; Towns & Atkinson 2004)
Invertebrates	Few large invertebrates (beetles and millipedes) > 10 mm seen; no other data (Hicks et al. 1975)	Reappearance of three species of native cockroaches, small wēta *Neonetus*? sp. large centipede *Cormocephalus rubriceps* (Towns et al. 1997) and honeydew scale *Coelostomidium zealandica* (Towns 2002b); identification of 24 species of terrestrial molluscs (includes one exotic species of slug) and 70 species of spiders (Towns & Atkinson 2004)
Reptiles	Five species of lizards recorded but only four of these seen by Hicks et al. (1975): *Oligosoma aenea*, not seen; *Woodworthia maculata* and *Hoplodactylus duvaucelii* <10 seen; *O. smithi* and *O. moco*, regarded as common	*O. aenea* trapped in all forest habitats by 1999 (D Towns unpublished data); demographic shifts and habitat changes recorded for *O. smithi* (Towns 1991) and *H. duvacellii* (Towns 1996); increased capture frequencies of all five species (Monks et al. 2014); sighting frequencies of *W. maculata* on coast exceeded Middle Island within 15 years of mammal eradication (Towns 2002b)
Seabirds	Eight species listed, seven of which recorded by Hicks et al. (1975): *Eudyptula minor*, throughout; *Puffinus carneipes*, few seen; *P. griseus*, four seen; *P. gavia*, second-most abundant, <19/ha; *P. assimilis*, scattered burrows <6.8/ha; *Pterodroma macroptera*, most common species <36/ha, 600-700 pairs total; *Pelecanoides urinatrix*, scattered, one site ca 30/ha	*Phalacrocorax varius* observed by Hicks et al. (1975) in coastal waters, but now breeding in pōhutukawa on SW coast
Native land birds	Eleven species of native birds and four exotic species recorded by Hicks et al. (1975), with native species classed as abundant: *Cyanoramphus novaeseelandiae*, *Rhipudura fuliginosa*, *Gerygone igata* and *Zosterops lateralis*. Classed as frequent: *Circus approximans*. Classed as uncommon: *Ninox novaeseelandiae*, *Halcyon sancta*, *Anthornis melanura* and *Prosthemadera novaeseelandiae*	*Hirudo tahitica* not recorded by Hicks et al. (1975), but now seen around the entire coastline (Towns & Atkinson 2004); three species classed as uncommon are now widespread and abundant throughout the island but *P. novaeseelandiae* only reported by A Evans (Unpublished data)

Unpredicted outcomes

Avian predators

Many responses to invasive mammal removals from Korapuki were unpredicted, including the resurgence and recolonisation of two avian predators: the kingfisher (*Todiramphus sanctus)* and the native owl (morepork; *Ninox novaeseelandiae*). Both species were regarded as uncommon by Hicks et al. (1975) and only a single pair of kingfishers was recorded by a survey in 1985 (D. Towns unpublished data). However, in 2007 kingfishers were encountered in over half of the survey sites used (Figure 3).

Moreporks were only occasionally sighted during biennial visits between 1985 and 2009, most likely as visitors from neighbouring islands, as there were no observed territorial calls. By 2009 territorial calls were heard, and in March 2011 moreporks calls were heard across the entire island (D. Towns unpublished data). Moreporks and kingfishers feed on lizards, large invertebrates and small birds (Robertson 1985). Recovery and recolonisation by these two avian predators could thus be an indirect measure of the increased abundance of their prey, one item of which for moreporks is tree wēta reintroduced to Korapuki in 1997 (Table 2).

Insect parasites

Honeydew scale insects are parasites of many forest plant species in New Zealand (Morales 1991). Their role in providing a high energy carbohydrate resource for birds and lizards on islands was unknown until the appearance of coastal forest plants infested by scale insects *Coelostomidia zealandica* on Korapuki (Towns 2002a). As these parasites have gradually spread, the importance of honeydew and other sources of sugar to geckos on these islands has also become apparent. Common geckos (*Woodworthia maculata*) are now common around flax (*Phormium tenax*), where they feed from inflorescences and sap.

Table 4. Chronological measures of progress and success for restoration of communities within a seabird-driven ecosystem of Korapuki Island; with projected measures >25 years.

Years since eradication of invasive mammals	Measure	Comment
10	Dispersal to/within island of key canopy plant species	Dominant species of communities on Middle Island as reference site spreading via bird dispersal (Towns & Atkinson 2004) but likely additional species (e.g. kohekohe) yet to establish (Atkinson 2004)
20	Establishment of selected missing invertebrates and reptiles	Five years for establishment of some invertebrates (e.g. Green 2005) and >8 years for some lizards (Towns & Ferreira 2001)
20-25	Recolonisation of top resident avian predator	Moreporks resident (based on territorial calls), but likely contingent on establishment of large invertebrates including tree wēta
50	Marine signature via seabirds within range of uninvaded islands	C:N and δ^{15}N concentrations in soils and plants equivalent to islands with unsuppressed seabird populations (extrapolated from Jones 2010); high density seabird colonies present but localised (Buxton et al. 2016)
50-100	Complete infestation of potential hosts for honey dew scale; time required to define success for reintroductions of tuatara	About 20% of island with honeydew infested karo or ngaio plants (Evans et al. 2015); successful reintroductions with each population composed of F1 or greater (D. Towns unpublished data)
150	Carrying capacity reached for reintroduced reptiles with low annual reproductive output	Modelled time to carrying capacity for Whitaker's skink (Miller 2009) and likely minimum time for tuatara; density of both species linked to seabird burrow density
>300	Replacement of continuous pōhutukawa canopy by diverse coastal species	Likely gradual change from pōhutukawa to karaka (*Corynocarpus laevigatus*) and kohekohe, but may depend on effects of seabirds

Duvaucel's geckos (*Hoplodactylus duvaucelii*) and common geckos are also found on the host trees for honeydew scale, although Duvaucel's geckos are the more abundant at such sites (Evans et al. 2015). Furthermore, bellbirds (*Anthornis melanura*) are often now seen feeding on the honeydew and vocally defending productive scale-infested karo (*Pittosporum crassifolium*) trees (D. Towns unpublished data).

Seabird recovery and recolonisation

The speed at which seabirds have recolonised and influenced restored island ecosystems in New Zealand has confounded assumptions based on philopatry and low immigration rates (Croxall et al. 2012; Kappes & Jones 2014). Through studies of C:N ratios and the concentration of δ^{15}N in soils, foliage and spiders, Jones (2010) concluded that ecosystem recovery on northeastern New Zealand islands may be achieved in decades. These conclusions were supported by Buxton et al. (2014), who found that on islands <25 km from other dense seabird colonies, intra– and interspecific social attraction can stimulate immigration to previously depleted colonies or establish new ones. These findings were particularly relevant to Korapuki Island, which at the longest time since eradication of mammals (then 22 years) had the highest soil and plant δ^{15}N and lowest C:N of the islands sampled (Jones 2010). In contrast to the scattered low density colonies recorded 10 years before mammal eradication (Hicks et al. 1975), seabird colonies now extend over 70% of surveyed areas on the island (Buxton et al. 2016).

Mysterious declines and disappearances

Surprisingly, we found changes in the abundance and distribution of resident species initially thought to be resistant to the effects of kiore and rabbits. For example, the diurnal shore skink (*Oligosoma smithi*) was regarded as abundant in the presence of kiore and rabbits (Hicks et al. 1975). However, surveys revealed changes in distribution, increases in mean body size, and increased capture frequency soon after mammals were eradicated (Towns 1991, 1996; Monks et al. 2014). Conversely, recent samples indicate declines in the capture rates of shore skinks, while captures of other species of resident and translocated lizards continue to increase at the same sites (D. Towns unpublished data). Whether the current declines of shore skink captures is related to competition or predation from other species of lizards or the increased density of kingfishers as predators remains unclear.

In their early surveys of Korapuki Island, Hicks et al. (1975) observed few large day-flying insects and noted that the only species observed were cicadas and wasps. We assume that the latter were introduced *Vespula* wasps, since these were still present during our visits 10 years later (C. Green pers. comm.). In New Zealand, these wasps compete with birds for honeydew, can kill nestling birds, and prey heavily on spiders and caterpillars, resulting in modified invertebrate community structure (Beggs 2011). Within five years of the mammal eradication these wasps disappeared and have not been seen since (Bellingham et al. 2010a). Similar disappearances have now been observed on other islands after eradication of rats, including very large islands where *Vespula* wasps were once extremely abundant (T. Lovegrove pers. comm.).

Failed colonisations and unknown consequences

Numerous uncertainties remain about the composition and dynamics of communities on Korapuki Island. For example, seed dispersal will inevitably shape forest composition, which for some species requires kererū visiting from neighbouring islands (Towns & Atkinson 2004). The presence of tawāpou and taraire provides evidence of kererū visitation to Korapuki. However, not all species imported by kererū survive. In 1986, three taraire plants appeared to be thriving on the southwestern part of Korapuki; however, all plants succumbed after a drought in the early 1990s and none have been seen since. Other species that are dispersed to the island may germinate only to be destroyed by drought, trampling or clipping by seabirds.

The relatively rapid increase in seabird activity brings additional uncertainties for longer term successional processes. In some areas of Korapuki, seabird burrow density is high under a canopy of 100-year old pōhutukawa (*Metrosideros excelsa*) that developed as a result of burning and the activities of rabbits (Atkinson 2004). Long term, this canopy would likely be replaced by a variety of coastal species, but the intense seabird activity could suppress seedling growth and arrest succession. Because Korapuki has a wide range of habitats and soil depths (Towns & Atkinson 2004) such effects are likely to be localised.

Finally, the recovery trajectory of Korapuki will likely be affected by external influences (Towns 2002b), such as climate change, ocean pollution, and other conservation actions. The latter could include success with mammal eradications on other islands in the archipelago. If the eradication of invasive mammals from Great Mercury in 2014 proves to be successful (Supplementary Data), all Mercury Islands will be free of introduced mammals. It is likely that kererū numbers will correspondingly increase, which in turn will increase the frequency of their movements between islands. The resulting seed dispersal could include species currently absent from islands such as Korapuki, with outcomes that at present are unknown. Another conservation action that may elicit indirect consequences on the recovery trajectory of Korapuki is the protection of New Zealand fur seals (*Arctocephalus forsteri*) following heavy exploitation in the 19th century (Harcourt 2005). The species is now reclaiming its former range, which includes sightings in 2012 of male fur seals ashore on Korapuki Island (A. Evans unpublished data). Rookeries may be established on Korapuki Island at some stage, which could significantly modify coastal vegetation, as well as contribute nutrient subsidies to the ecosystem. How fur seals might influence the function of these warm temperate ecosystems remains unclear.

Discussion

Invasive mammals have been eradicated from seven of the islands in the MIED. These eradications included some of the earliest campaigns against rodents, beginning with kiore (and rabbits) on Korapuki Island in 1986, and eventually leading to cats and rats on the eighth and largest of the islands (Great Mercury; 1872 ha), which began in 2014. With almost 30 years free of introduced mammals, Korapuki Island has been invaluable for testing concepts associated with island restoration as well as methods for species reintroductions. For example, a restoration target to "extend the area of unique seabird-reptile-invertebrate-plant communities" typical of the Mercury Islands was proposed soon after eradications were completed on Korapuki (Towns et al. 1990), but was not developed into a completed restoration plan until much later (Towns & Atkinson 2004). Empirical support for the pivotal role of seabirds, as implied in the restoration target, is even more recent (e.g. Fukami et al. 2006; Mulder et al. 2011). The evolution of ideas and collection of supporting data for restoration of these islands was built around four components: biogeography; ecosystem function; the effects of invasive species; and outcome measures (Figure 5). For example, through testing biogeographic theory, our work suggests that assemblage structure may be most easily predicted on islands previously part of the mainland, but especially those once interconnected.

We have also found that ecosystem function can be determined from two sources: the way resident species respond when invasive species are removed and the use of comparative data from reference sites never occupied by invasive mammals. Reference models are likely to be most instructive when on islands of similar size to the site being restored. As island size increases, reference sites uninvaded by introduced mammals become increasingly rare and for islands >1000 ha do not exist (Parkes & Murphy 2003). However, on some of the larger islands, past assemblage composition can be revealed from the bone fragments, pollen and ancient DNA used for archaeological and palaeoecological studies (Bellingham et al. 2010a; Wilmshurst et al. 2014).

Regardless of the availability of reference sites, the amount of restoration effort required is determined by recolonisation ability; this may vary for seabirds according to the distance from source populations but is consistently poor for reptiles and some terrestrial invertebrates. Finally, restoration endpoints can be defined by combining biogeographic origin, post eradication responses and ecosystem function. For example, a restored seabird-driven ecosystem on Korapuki Island with high ecological integrity typical of the archipelago acknowledges historic vicariance, high rates of natural recolonisation by plants and seabirds, but the extirpation of key reptiles and large flightless invertebrates. However, despite the three decades of reintroductions and recovery on the island, measures of progress towards the restoration endpoints are still in development.

In sum, ecological restoration in the Mercury Islands indicates that the "Humpty Dumpty" problem raised by Duffy (1994) and others who have examined the ambiguity of island restoration (Simberloff 1990) can be addressed within a defensible framework. However, our studies have also revealed many unexpected responses to invasive mammal removal. There are also unpredictable consequences of the previous presence of mammals, responses of species such as kererū to conservation actions elsewhere and the effects of recolonisation of the islands by fur seals. Conversely, there is developing clarity about how these seabird driven systems vary under different climatic and biogeographic regimes and the extent to which they can be modified by introduced animals. Insights have come from comprehensive studies of the general relationships between seabird activity, nutrient subsidy, and vegetation composition beginning in the 1950s (e.g. Gillham 1956a, b), complemented locally by analyses of seabird-soil-plant relationships on Middle Island in the Mercury Group (Atkinson 1964), and extended by studies across islands in northern New Zealand (Fukami et al. 2006) and globally (Mulder et al. 2011). The studies by Jones (2010) and ourselves in the Mercury Islands indicate that removal of predatory mammals can lead to reactivation of the seabird influence on island ecosystems, as long as the birds can recolonise. Furthermore, Buxton et al. (2014) show that there is frequently natural recolonisation of islands <25 km from other large seabird colonies. Collectively, these recent studies indicate that seabird-driven ecosystems in some locations can recover rapidly, but they have also identified markers that can be used to measure the extent of that recovery.

Given that the seabird-driven ecosystem on Korapuki appears to be recovering naturally (Jones 2010; Buxton et al. 2016), is restoration based on pre-determined assemblage composition justified? For example, the ecosystem on Korapuki

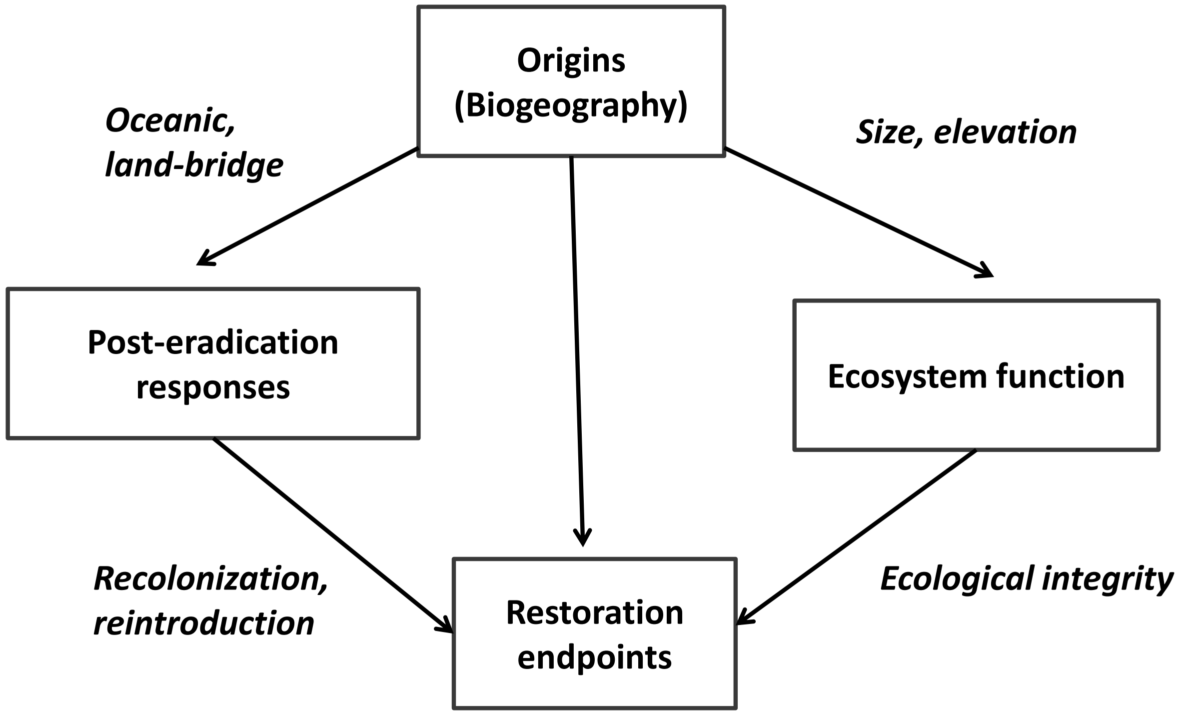

Figure 5. Summary of the relationship between four key components of island restoration.

will not cease to function in the absence of tuatara, which will simply be replaced by Duvaucel's geckos as top reptile predator (Towns 2002b). Furthermore, should we be concerned if ecosystems on islands beyond the natural colonisation range of seabirds enter alternative stable states unlike those with invasive mammals but no longer driven by the engineering effects of seabirds (e.g. Mulder et al. 2009)? Such questions lead us into the realm of value judgements. By phrasing his problem in the context of a children's nursery rhyme, Duffy (1994) implies a social component to restoration, as there is with all conservation biology (e.g. Lawton 1997). One social dimension applied to our study at the outset: a legal framework (i.e. a statutory expression of values) within which to conduct the eradications and attempt ecosystem restoration. Work in the Mercury Islands began on sites administered as Nature Reserves, which mandates the removal of all exotic species where possible (Reserves Act 1977). We therefore assumed that the implicit goal of the reserves is protecting or promoting the highest possible ecological integrity (*sensu* Lee et al. 2005), which on Korapuki includes reintroduction of invertebrates and reptiles (Towns & Atkinson 2004). Nonetheless, even with a legal mandate, when multiple stakeholders are involved there can still be heated debate when invasive species eradications are proposed, as was the case before the removal of kiore from Hauturu (Little Barrier) Island Nature Reserve (Towns et al. 2006). Accordingly, our summary of the essential elements to be considered when undertaking restoration of islands (Figure 5) is a simplified view that excludes the complex regional social issues that may be involved.

Having acknowledged uncertainties about the successional consequences of natural recovery supplemented by reintroductions, our approach on Korapuki has been to allow the ecosystem to develop at its own speed. By facilitating the return of only those components unable to recolonise unaided, we assume that the system will eventually follow a trajectory typical of other regional islands of equivalent size (Simberloff 1990; Towns 2002b). What still remains unclear from the Korapuki study is whether the strong ecosystem engineering effects of seabirds apply on larger islands, or whether such locations develop into more heterogeneous environments than are found on our small reference islands, such as Middle. Consequently, a great deal is still to be learned from the processes of recovery on other Mercury Islands such as Red Mercury, which is over 20 times larger than their available reference sites within the archipelago.

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Location	**Area (ha)**	**Status**	**Date**	**Rodent**	**Other eradications**	**Method used against rodents**	**References**
Korapuki	18	Wildlife Sanctuary (Nature Reserve)	1986	Kiore	Rabbits	Ground-based: kibbled maize in silos; prefeed followed by maize dosed with bromodialone (0.005% by wt)	McFadden & Towns (1991)
Double	8 (West) +19 (East)	Nature Reserve	1989	Kiore	None	Ground-based: kibbled maize in silos; prefeed with aniseed added followed by maize dosed with bromodialone (0.005% by wt) on West Double. Hand broadcast 4 g pellets of STORM containing flocoumafen (0.005% by wt) at 18.5 kg/ha on East Double	McFadden (1992)
Stanley	100	Nature Reserve	1991	Kiore	Rabbits	Aerial spread by helicopter using modified monsoon bucket; 0.8 g cereal pellets of TALON 20 P containing brodifacoum at 20 ppm with follow-up hand spread of TALON 50WB (wax blocks) containing brodifacoum at 50 ppm; total of 17 kg/ha	Towns et al. (1993)
Red Mercury	225	Nature Reserve	1992	Kiore	None	Aerial spread by helicopter using modified monsoon bucket; TALON 20 P with follow-up hand spread of TALON 50WB; 15 kg/ha	Towns et al. (1994)
Middle Chain	23	Nature Reserve	1992	Kiore	None	Aerial spread of TALON 20 P by helicopter using modified monsoon bucket; 15 kg/ha	
Cuvier	170	Nature Reserve	1993	Kiore	None	Aerial spread of TALON 20 P by helicopter using bait spreader; 15 kg/ha	Towns et al. (1995)
Ohinau	43	Iwi (Ngati Hei)	2005	Kiore, mice	Rabbits	Aerial spread of PESTOFF 20R containing brodifacoum in two operations by helicopter using bait spreader; 8+8 kg/ha	R Chappell (pers. comm.)
Great Mercury	1872	Private	2014	Kiore, ship rats	Goats, cats	Aerial spread of PESTOFF 20R containing brodifacoum in two operations by helicopter using bait spreader; 8.8+13.2 kg/ha	P Corson (pers. comm.)

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7.2 Appendix 2: Quantifying ingested debris in marine megafauna: a review and recommendations for standardization[5]

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[5] Provencher, J., Bond, A., Avery-Gomm, S., **Borrelle, S.B**, Rebolledo, E.B., Hammer, S., Kühn, S., Lavers, J., Mallory, M., Trevail, A. and van Franeker, J. 2016. Quantifying ingested debris in marine megafauna: a review and recommendations for standardization. *Analytical Methods.*

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Quantifying ingested debris in marine megafauna: a review and recommendations for standardization†

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Plastic pollution has become one of the largest environmental challenges we currently face. The United Nations Environment Program (UNEP) has listed it as a critical problem, comparable to climate change, demonstrating both the scale and degree of the environmental problem. Mortalities due to entanglement in plastic fishing nets and bags have been reported for marine mammals, turtles and seabirds, and to date over 690 marine species have been reported to ingest plastics. The body of literature documenting plastic ingestion by marine megafauna (*i.e.* seabirds, turtles, fish and marine mammals) has grown rapidly over the last decade, and it is expected to continue grow as researchers explore the ecological impacts of marine pollution. Unfortunately, a cohesive approach by the scientific community to quantify plastic ingestion by wildlife is lacking, which is now hindering spatial and temporal comparisons between and among species/organisms. Here, we discuss and propose standardized techniques, approaches and metrics for reporting debris ingestion that are applicable to most large marine vertebrates. As a case study, we examine how the use of standardized methods to report ingested debris in Northern Fulmars (*Fulmarus glacialis*) has enabled long term and spatial trends in plastic pollution to be studied. Lastly, we outline standardized metric recommendations for reporting ingested plastics in marine megafauna, with the aim to harmonize the data that are available to facilitate large-scale comparisons and meta-analyses of plastic accumulation in a variety of taxa. If standardized methods are adopted, future plastic ingestion research will be better able to inform questions related to the impacts of plastics across taxonomic, ecosystem and spatial scales.

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1 Introduction

Since the invention of plastic in the early twentieth century, it has been polluting the marine environment. Plastic pollution has become one of the largest environmental challenges we currently face. The United Nations Environment Program (UNEP) has listed it as a critical problem, comparable to climate change, demonstrating both the scale and degree of the environmental problem.[1,2] Marine plastic pollution occurs from the Arctic to the Antarctic, with several areas of significant concentrations in regions where ocean currents converge in gyres.[3] Plastic pollution has also been documented in freshwater ecosystems,[4,5] illustrating that few aquatic ecosystems are unaffected. Importantly, plastic pollution impacts wildlife through both entanglement and ingestion. Mortalities due to entanglement in plastic fishing nets and bags have been reported for marine mammals, turtles and seabirds (hereafter referred to as marine megafauna),[6,7] and to date over 690 marine species have been reported to ingest plastics.[8–10]

Over the last few decades, as interest in plastics in marine environments has increased,[2,11] so too has the number of papers documenting plastic ingestion by marine animals. Since 2004, there have been some attempts to introduce standardized methods to plastic ingestion methods and protocols;[12–17] however, a cohesive approach by the scientific community to quantify plastic ingestion by wildlife is lacking. Unfortunately,

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this has undermined attempts to detect spatial and temporal trends in plastic ingestion, or to perform meta-analyses. It may also obscure our ability to fully understand the impacts of plastic ingestion on wildlife. Although it has been shown that plastic ingestion may lead to deleterious effects through a number of physical and biochemical pathways,[18,19] there is a paucity of research rigorously investigating population and ecosystem level effects of plastic ingestion.[20] Improved standardization of sampling for plastic ingestion may help to facilitate an understanding of these higher order effects.

With this lack of framework in mind, the objective of this paper is to help advance the field of marine plastic ingestion. First, we provide a historical overview of the scientific reporting of plastic ingestion in marine megafauna. Second, we present a review of the plastics ingestion literature with a focus on methods of collection, characterization of ingested plastics, the reporting of metrics on ingested plastics and interpretation of results. Most plastic ingestion studies concern marine birds, therefore we use this group as a model to understand patterns in methods and draw lessons that are applicable to plastic ingestion studies in other megafauna groups. Third, we present an example of how employing standardized techniques across oceans enables spatial and temporal comparisons of plastic ingestion and informs science and policy; the seabird Northern Fulmar (*Fulmarus glacialis*). Finally, we offer recommendations for standardized metrics when reporting ingested plastics in marine megafauna, with the aim to harmonize the available data to facilitate large-scale comparisons and meta-analyses of plastic ingestion.

2 Methods and results

2.1 Review of reporting plastic ingestion in marine megafauna

We used the Web of Science search engine and citation index between November 2015 and July 2016 to search for publications using "seabird (or turtle or cetacean or pinniped or fish)* plastic", "seabird (or turtle or cetacean or pinniped or fish)* debris", and "seabird (or turtle or cetacean or pinniped or fish)* pollution". To capture information on plastics from older publications that often reported plastic ingestion in diet studies, we also reviewed several summary papers on the topic including Laist,[8] Kühn *et al.*,[9] Provencher *et al.*,[21] and Ryan.[11] Our literature search spanned records from 1949 to 2015.

We limited our literature search to seabirds as defined by Gaston,[22] which includes penguins (Sphenisciformes), tubenoses (Procellariiformes), cormorants and gannets (Pelecaniformes), tropicbirds (Phaethontiformes), auks, terns, skuas, phalaropes and gulls (Charadriiformes). We included loons (Gaviiformes), and marine sea ducks and mergansers (Anseriformes; Merginae only) as most species spend almost the entire year in marine environments.[22] We also included marine turtles (both Cheloniidae and Dermochelyidae), and mammals, namely cetaceans, sea cows, pinnipeds (sea lions, walruses and seals), otters (Mustelidae; sea otters and marine otters only) and bears (Ursidae; polar bears only) that reside in marine environments. Lastly, we included fish (Agnatha, Chondrichthyes, Acanthodii, and Osteichthyes) using http://fishbase.org to subset only marine species.[9] While we aimed to cover all peer-reviewed literature on plastic ingestion in marine megafauna, the results presented here likely miss some peer-reviewed entries, and do not represent reports from the grey literature or popular media, we feel it is representative of the research field.

Marine megafauna are susceptible to ingesting a range of debris sizes. Although other papers in this special edition focus almost exclusively on microplastics, we include microplastics within a broader category of plastics. For the purpose of this paper, and in line with this special issue, we use the following categories of plastics as defined by Barnes;[23] microplastics (1–5 mm), mesoplastics as (<5–20 mm), and macroplastics (>20–100 mm), while also including megaplastics (>100 mm). While the ingestion of pieces from micro- to macro-plastics has been recorded for many species of marine megafauna, most of these report the range and mean piece size, but do not typically quantify the number of pieces that fall into size categories. As such, we cover plastic ingestion in marine megafauna in general, while recognizing that the plastics reported often span the size categories described above. Additionally, marine megafauna ingest numerous other types of debris such as metal and paraffin wax.[13,24] The majority of the debris found in seabirds is plastics, often >90%.[13,25,26] Therefore, we shape our recommendations for standardization with this in mind. While most papers report plastic ingestion, what is actually measured in almost all papers is the accumulation of ingested plastics. Researchers rarely report birds in the act of ingestion (although see ref. 27 and 28), and more often report the accumulation of ingested plastics found in seabird gastrointestinal tracts but use the term ingestion widely. We recognize the difference between plastic ingestion and accumulation of plastics, but for the purposes of this review we use the term plastic ingestion to refer to the accumulated plastics that can be measured in birds through examination of gastrointestinal contents.

2.2 History of reporting plastic ingestion in marine megafauna

The first scientific publication of marine megafauna ingesting debris was in 1838 with Couch[29] reporting part of a candle stick found in the gut of a Wilson's Storm–Petrel (*Oceanites oceanicus*) and Turner[30] reporting a fish hook found inside a Sperm Whale (*Physeter microcephalus*) in 1895. These early reports illustrate that marine megafauna have always been susceptible to ingesting non-food items. The first reports we found identifying plastic debris specifically as an ingested item in marine megafauna groups was not until the 1960s (Fig. 1). By the 1970s, ingested plastic pollution had been reported in marine birds, mammals, turtles and fish.[8,9,11] Since 1968, there has been an increase in publications related to ingested plastics by marine megafauna, with peaks in both the 1980s and 2000s. This pattern is largely driven by seabird publications (Fig. 1;[11]), likely due to several factors including: (1) numerous long term monitoring studies of seabirds; (2) the relative ease and accessibility of sampling seabirds when they breed on land in large

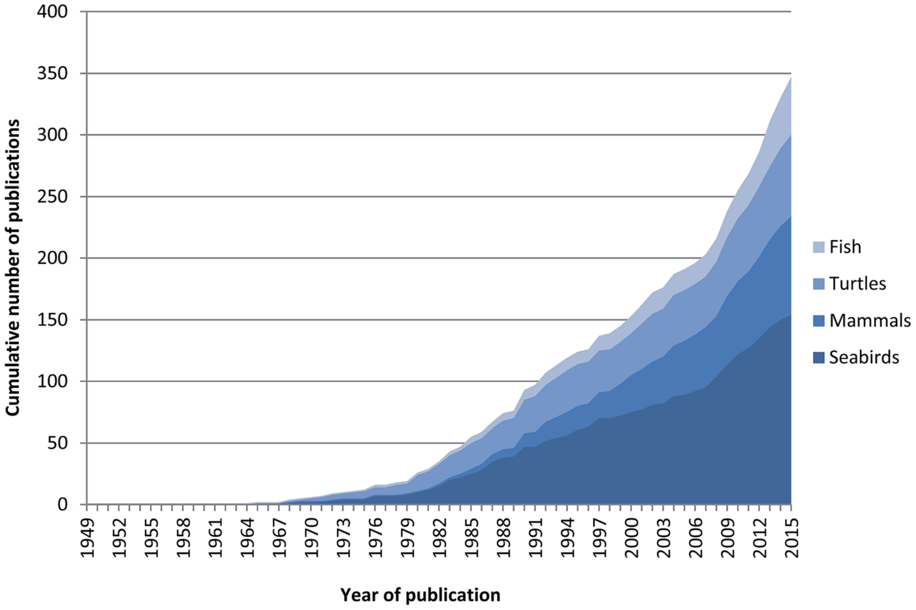

Fig. 1 Cumulative number of publications reporting ingestion of plastic in marine megafauna, including seabirds, mammals, turtles and fish from 1949 to 2015.

colonies; and (3) their general use as biological indicators of the marine environment.[31,32]

In general, while the number of studies varies among the megafauna groups (14–85; Table 1) the types of metrics found in the papers for each group is similar. By far the most often reported metric in literature reporting ingestion in marine megafauna is percentage frequency of occurrence (% FO), also described as incidence or prevalence (Table 1). In all groups, the number of pieces of plastics is the second most reported metric, with mass the third most commonly reported value. Interestingly, median values (of either number or mass) are the least reported measure of central tendency for any metric in all groups. The size and colour of ingested plastics are reported in roughly equal numbers in fish, turtles and mammals, whereas size is reported in marine birds almost 4× more frequently as colour. Importantly in relation to the call for standardized methods, <25% of the papers in all the megafauna groups examined noted the use of a standardized protocol in their methods for reporting plastics (Table 1). Overall this illustrates that studies reporting ingested plastic values for marine megafauna have variable reporting standards, and few use standardized protocols.

2.3 Plastic ingestion in seabirds as a model study group

2.3.1 Historical background on plastic ingestion monitoring in seabirds. Early work on plastic ingestion in wildlife beyond incidental reporting was originally driven not by assessing the biological impacts of plastic pollution, but instead by the need to monitor plastics in the environment in general. In the 1970s legislative attempts were made to reduce the input of debris into the marine environment, including the 1972 London Dumping Convention, the MARPOL Convention 1973/1978, and the 1992 Oslo and Paris Conventions for the protection of the marine environment of the northeast Atlantic (OSPAR). In the absence of significant improvements in the

Table 1 Metrics of ingested plastics reported in peer-reviewed literature from 1949–2015 in marine megafauna. List of papers in each group can be found in the ESI

	Fish	Mammals	Birds	Turtles
Number of studies	43	14	85	34
Frequency of occurrence	72%	64%	89%	100%
Number of pieces	44%	57%	62%	50%
Mass	23%	36%	51%	35%
Mean	11%	29%	47%	35%
Median	2%	0%	4%	9%
Range	4%	29%	24%	38%
Size	25%	57%	36%	35%
Colour	30%	14%	32%	29%
Reference to North Sea standardized protocol	2%	7%	22%	9%

decades following,[33] new policies were created to help reduce plastics and monitor their effect, the most recent being the inclusion of marine debris in the European Marine Strategy Framework Directive (MSFD).[34] Recently, because of the cumulative effects plastics have on the environment and society, monitoring of plastic pollution in the marine environment has become a tool for assessing mitigation strategies and potential impacts of debris.[13] Further, beyond the biological implications of marine debris pollution, there are also economic implications with estimated costs of plastic pollution in some regions to be millions of Euros a year.[35]

To date, OSPAR, in particular the North Sea states, is the only jurisdiction that has implemented regulations aimed to track changes in plastic pollution through an environmental indicator, which is currently followed in all European Commission marine areas.[15,16] The current definition of OSPAR's marine plastics Ecological Quality Objective (EcoQO) is: "there should be less than 10% of Northern Fulmars having 0.1 g or more plastic in the stomach in samples of 50–100 beached Fulmars from each of 5 different areas of the North Sea over a period of at least 5 years".[36] With a lack of policies in other regions, efforts to monitor marine plastic pollution or track ingestion by wildlife, researchers have been left to develop their own framework for studying and reporting plastic ingestion by marine megafauna, often as side projects. Although these various studies clearly add to our knowledge of plastic pollution in the marine environment, this growing field of metric papers without clear standardization of reporting metrics and techniques is not conducive to comparisons across space, time or taxa – or for use in larger meta-analyses and assessments.

2.3.2 Review of methods used for reporting plastic ingestion by seabirds. To identify areas of research that most need coordination, we examined the types of information most often reported in plastic ingestion studies. As the majority of papers on plastic ingestion concerned seabirds, we narrowed our focus to this group to examine the use, or lack of use, of standardized methods, and make recommendations. We restricted our analysis to publications about seabirds found during our literature search (see above) and appearing in primary peer-reviewed sources. Only papers presenting novel data were considered. Articles fell into four broad categories: (1) observational reports (studies of seabirds being exposed to plastic during foraging in the wild); (2) studies that report some metric of plastic ingestion; (3) correlation effect studies; and (4) review and synthesis papers. The first report of plastic ingestion in seabirds was published in 1968,[37] and since that time most publications have reported metrics of ingested plastics (Fig. 2). While the body of literature discussing the effects of plastic ingestion continues to grow, few studies measure these effects in a non-correlative way.[20]

2.3.2.1 Collection techniques. The objective of documenting plastic ingestion is to obtain a representative estimate of plastic ingestion for the wider population. Therefore, it is important to consider whether the collection method for specimens may influence the result. We reviewed 85 publications documenting plastic ingestion in seabirds and found a variety of specimen collection techniques were used. Most data were collected by necropsy of intact birds (70%) and examination of food remains (27%; Table 2), with only a handful (3%) not reporting the collection method. Among the 70% of studies that involved necropsies of intact birds, 5% of studies collected specimens intentionally (*i.e.*, legal and confiscated from illegal hunting), 12% of studies already used carcasses that were in hand (*i.e.*, from rehabilitation centers, fisheries bycatch), and the remaining 21% were collected from beaches following wrecking events (Table 2).

Approximately a quarter ($n = 22$) of the plastic ingestion studies collected specimens using different methods, but only

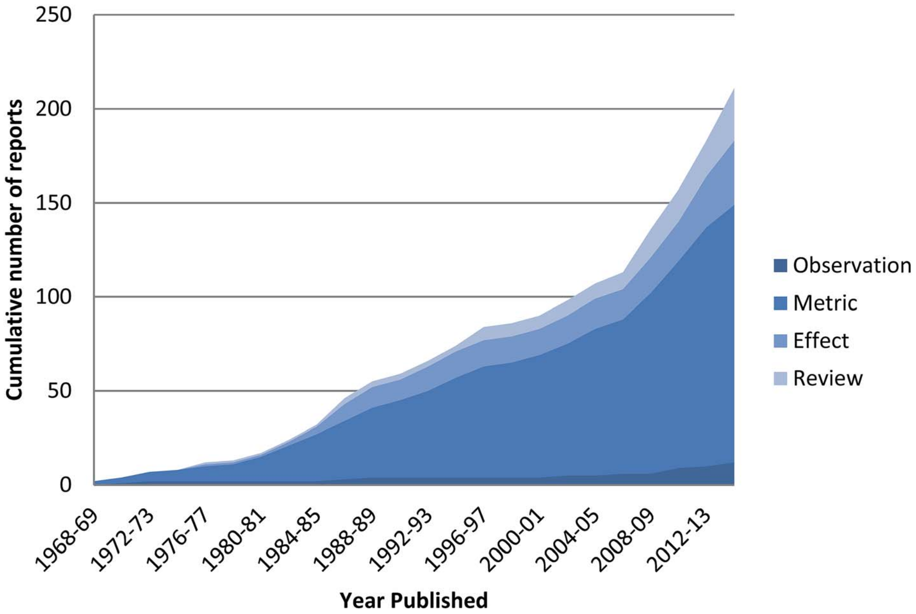

Fig. 2 Cumulative number of published reports in the peer-reviewed literature on ingested plastics in seabirds from 1968 to 2015.

Table 2 Collection methods in 85 peer-reviewed papers examining plastic ingestion in seabirds. As some papers report data from multiple collection techniques, the total of reports by collection method (n = 117) is larger than the number of papers examined (n = 85)

Collection method	N	Percentage of total
Necropsy of stomach contents	82	70%
Beached birds	24	21%
Collected for other research	21	18%
Found dead (*i.e.* predation on colony)	16	14%
Fisheries bycatch	12	10%
Legal hunting	3	3%
Illegal poaching confiscation	2	2%
Killed for plastics work	2	2%
Rehab center	2	2%
Food remains	32	27%
Bolus	12	10%
Regurgitation	11	9%
Water-offloading	8	7%
Emetics	1	1%
Not specified	3	3%
Present data on multiple collection methods	22	26%
Compare between sampling methods	8	9%

a small fraction (9%) compared ingestion results across collection techniques. Among these, we found contradictory results on whether collection methods influence accumulated plastics in seabirds. For example, Van Franeker & Meijboom[38] reported no statistical difference in ingested plastic between fulmars that had died slowly and those that had died instantly (*e.g.*, fisheries or collisions). Similarly, Colabuono *et al.*[39] found no differences in the frequency of occurrence of plastic in eight Procellariiformes between beached birds and those recovered as bycatch by longline fisheries. Conversely, while Ryan[40] found no difference in frequency of occurrence, mass or number of ingested plastics particles in Blue Petrels (*Halobaena caerulea*) either found beached or collected at sea, Ryan did find significantly higher numbers of plastics in beached birds as compared with collected birds in eight species examined. Auman *et al.*[41] found that Laysan Albatross chicks that died naturally had greater masses of ingested plastics as compared with injured chicks. Importantly, these comparison studies represent only a small number of seabird species, suggesting that we know very little about how the collection methods affect ingested plastic detection in other groups. From a comparison of these studies we recommend that a researcher's ability to estimate true population level plastic loads may be influenced by the method of specimen collection, and therefore it is an important variable to consider when comparing results between studies and regions.

A major advantage of collecting data on plastic ingestion through necropsy of whole specimens is that one can examine the entire gastrointestinal tract for plastics, which provides a level of certainty in the findings. For example, in seabirds the proventriculus and gizzard are the main sections examined for accumulated debris. Conversely, in turtles, the entire length of the gastrointestinal tract is examined for plastics, as they frequently have plastics in the intestines as well as the stomach and esophagus.[42] One can also examine different parts of the gastrointestinal tract for plastics, which may help elucidate ingestion and retention times.[43] Importantly, regardless of the section examined, it should be reported to ensure comparability to other studies. A second advantage of examining plastic ingestion *via* necropsies is that the age, sex, possible cause of death and body condition of the birds can be determined. Because many seabirds are externally monomorphic, necropsies can allow an examination of differences between sexes. However, few studies have examined such differences. Only 11 of 85 (13%) studies reported testing for differences in plastic ingestion between sexes, with only one of those reporting a significant difference in just a few of the species examined.[44] We discuss sex differences in plastic ingestion below, as they are related to species' ecology as well as sampling methods. Lastly, necropsies provide an opportunity to examine gastrointestinal contents using a common sized sieve allowing for multiple size classes of plastics to be examined. A 1 mm sieve is commonly used for species that can be examined with the laboratory (*i.e.*, not the large whales), and the widespread uptake of this method will facilitate increased comparability between studies in the future.

For the remaining 27% of the 85 plastic ingestion papers, data on plastic load reviewed involved examination of food items from either live birds (17%) or found boluses (10%) to examine plastic ingestion (Table 2). Sampling of live birds is advantageous because it can be done systematically, although it is unclear whether 100% of the plastic loads can be collected *via* natural regurgitation, or induced regurgitations (*i.e.*, stomach flushing or chemical emetics). Active sampling of live birds can be invasive, and researchers must give careful consideration of the ethical principle underlying the research before using such techniques. Sampling live birds, if complete stomach sampling can be achieved, is advantageous in that it does not rely on ad hoc sampling of birds (*e.g.*, beached birds, although see below). Live birds can generally be sampled using three methods: natural regurgitation, induced regurgitation (*via* stomach pumping, also called lavage or water offloading), and chemical emetics.

Whether it will be possible to sample plastic ingestion from natural or induced regurgitation in a seabird will depend on the species, age class, and time of the year. For most species, natural regurgitations represent chick meals that parents are returning to nest-bound offspring,[45] or occasionally courtship feeding for a prospective mate. Regurgitations are less likely during the non-breeding season (or in non-breeding or pre-breeding individuals), and may also only represent the most recent meal because plastics accumulated previously may remain in the bird. Induced regurgitations *via* stomach pumping, also called lavage or water offloading, involves pumping the bird's stomach with water to induce regurgitation. Unlike natural regurgitations, any individual can be subject to stomach pumping, regardless of breeding status or age class. The technique has been used widely in penguins,[46] fulmarine petrels,[47] and shearwaters.[48] Chemical emetics can also be used to induce regurgitation and obtain dietary samples, including ingested plastics. Emetics are pharmaceutical agents that induce vomiting.[49] However, care must be taken to ensure the correct emetic and dose is chosen. Tartar emetic (antimony potassium tartarate) and apomorphine are more likely to cause adverse reactions than syrup of ipecachuana (ipecac).[50,51] For larger species, the volumes required may be prohibitive,[49] but for smaller species, where stomach flushing may not be recommended, using an emetic may be the best option. In a study of Leach's Storm–petrels (*Oceanodroma leucorhoa*), Bond and Lavers[49] found that of 12 birds subjected to treatment with syrup of ipecac, all experienced complete emesis. Regardless of the technique, the underlying assumption to the approach is that all ingested plastic is available to be enumerated. However, this is likely not the case with most seabirds. For example, stomach pumping may not remove all plastics, with microplastics more likely to be left behind.[52] In flesh-footed Shearwaters (*Ardenna carneipes*), 6% of plastic items in the proventriculus remained after stomach flushing.[52] Plastics in the gizzard are also less likely to be retrieved from live birds given the constriction in the gastrointestinal tract between the proventriculus and gizzard.[53–55] Therefore, stomach pumping and emetics should be used with caution, but particularly when reporting plastics in seabirds.

For species that regurgitate indigestible prey items regularly in the form of boluses, these can also be used to assess plastics (10% of the studies used this technique). Bolus examination is non-invasive, but opportunistic and can be repetitively collected from individuals. Unfortunately, boluses unlikely represent the full plastic load of an individual and caution must be used in assessing plastics when this technique is employed as small pieces of plastics are potentially lost to the environment before collection[56] or *vice versa*, environmental particles sticking to the sample. It must also be recognized that to assign plastic ingestion to a species, year, or individual, particular care must be taken, and potentially the sampling region must be cleared of plastic at the end of each breeding season.

2.3.2.2 Sampling among age classes. We found that numbers of papers reporting plastic ingestion in seabirds equally reported on this phenomenon in adults and juveniles (59% and 53%; $n = 78$ studies reporting some age classification; total greater than 100% as some studies report on both groups). Ingested debris levels in adults may be indicative of individuals' larger range and distribution if ingested plastics accumulate in the gastrointestinal tract of individuals. Breeding stage can influence adult debris loads as adults can regurgitate plastics along with food items to young chicks (inter-generational transfer) resulting in a steady decrease in adult plastic levels over the breeding season.[57] Therefore, when sampling adults it is important to consider annual cycles, migration paths and retention times when interpreting where ingested debris may have been acquired.

Few of the plastic ingestion studies (13%) we reviewed examined differences in plastic ingestion between adults and young birds collected at the same time and location. In general, young birds tended to have higher frequency of occurrence or mass of ingested plastics than adults.[13,54,58–61] Some studies showed that adults had higher levels (mass, number of frequency of occurrence depending on species),[55] while many studies showed no difference in plastic ingestion between age classes.[62–64] Reporting age class and, if applicable, breeding stage are therefore essential to interpreting metrics of plastic ingestion.

Determining the source of plastics in juveniles' stomach contents can also be challenging. Since many species show long term accumulation of plastic debris in their stomachs during chick-rearing, chicks can be fed a mix of distant- and locally-foraged plastics. Adults may have accumulated marine pollution months before the breeding season, which is then fed to the chicks. For example, Wilson's Storm–petrel chicks in Antarctica had higher plastic frequency of occurrence than adults.[60] In fact the plastic levels in chicks was so high that the authors attributed it to sources likely beyond the local foraging ranges.[60] Depending on the species, this can include thousands of kilometers (*e.g.*, albatrosses), or tens of kilometers around the colony (*e.g.*, auklets).

2.3.2.3 Purposeful sampling and reporting. While 73% of the reports that we reviewed included the assessment of plastics as one of the primary objectives of the published work, only 1/85 studies indicated that the findings presented were part of a targeted long-term monitoring effort.[13] All the other papers presented data on plastic ingestion that were collected through either one-time research efforts, or opportunistic sampling of birds collected for other purposes. While this *ad hoc*, opportunistic sampling may pose challenges for rigorously examining broad trends, early data on the presence, or absence, of plastic in seabird gastrointestinal tracts from diet studies are now informing changes in seabird plastic ingestion. For example, an analysis of prey items consumed by short-tailed Shearwaters (*Ardenna tenuirostris*) in Tasmania during 1978–1980 provided some of the first data on plastic ingestion by adults of this species.[65] Recent work found the proportion of adult shearwaters consuming plastic has increased from around 37% of the population in 1978 (ref. 65) to 63% in 2010.[58] Additionally, opportunistic sampling can take advantage of events that can yield large numbers of samples otherwise not available: wreck events where hundreds or thousands of seabirds wash up on beaches provide data on the type or quantity of plastic ingested by a range of species.[58,66] Such surveys are useful as they provide a ‘snap shot’ view of the situation at the time.

Systematic sampling can offer advantages and avoid potential bias (*e.g.*, unequal sampling intensity or preferential sampling of individuals or locations) introduced by the use of a single method, enabling inference of population trends over time as well as identification of variables affecting these parameters that could not be obtained with opportunistic designs alone. Studies that have surveyed individuals systematically over many years have yielded valuable insights into long-term trends in the abundance of plastic in regional waters, as assessed by regular sampling of the stomach contents of wildlife[67,68] (Ryan 2008; Mrosovsky, Ryan & James 2009). Such sampling has contributed significantly to our understanding of patterns and processes over time, and also led to the development of marine pollution management targets, such as the EcoQO for North Sea Northern Fulmars.[13] A combination of systematic and opportunistic sampling is recommended for studies that rely on beach-washed animals. For example, pairing data from beach-washed animals with sampling of live individuals (*e.g.*, boluses or stomach pumping) can overcome any potential bias (due to unknown cause of death; though see above).

2.3.2.4 Types of data in published reports & terminology. There are a variety of metrics used when reporting ingested plastics in marine megafauna with little consistency in how these are interpreted and presented. The most common metric presented in the seabird literature reviewed was the percentage frequency of occurrence (% FO) of ingested plastic (89%; Table 2). This is the most basic information on plastic ingestion: what proportion of the sampled individuals contain plastic? In the ingested plastics literature, the terms prevalence and incidence are often used interchangeably for the % FO, though in other bodies of literature their meanings are quite different.[69] Following diet studies of stomach contents,[70] we therefore recommend to use the term 'Percentage frequency of occurrence (% FO)'. The number of pieces of plastic is the second most often reported metric (62%). The number of plastics can be indicative of how much plastic an individual has consumed. However, it must be considered that as larger plastic items are likely broken down in the stomachs of seabirds the number of pieces accumulated in the stomach may not reflect the number of pieces ingested directly.

Data on the mass of plastics were reported in half of the papers reviewed (51%), though plastic mass is increasingly reported in the seabird literature. While only 21% of the papers published from 1968–1999 reported mass of plastic loads, 64% of those published from 2000–2015 included plastic mass in their results. The mass of accumulated plastics in seabirds is arguably the most important metric from a biological perspective. The mass of plastics relays information on the volume of plastics in an individual, which is important as plastics compete with food for space in the stomach. Many seabirds also rely on reducing wing-loading (body mass to wing size) for flight and diving, therefore adding mass to a seabird gives a plastic-loaded bird a disadvantage. While it is challenging to test for how the mass of plastics may affect seabirds, new research documenting effects of tracking devices attached to birds may provide some insights. Typically, most tracking devices deployed on birds are limited to be <5% of the birds body mass,[71] but research suggests that when devices exceed 2.5% of the bird's body mass, year-to-year survival declines significantly.[72] Therefore, mass of plastics carried by marine birds must be considered on a species-specific basis, and will benefit from applying information gained from the field of seabird science using tracking devices to examining the potential impacts from plastics.

2.3.2.5 Metrics presented in published reports. While there are some standard metrics reported in plastic ingestion studies, the terminology used to quantify the quantity and characteristics of ingested is inconsistent across studies. Though "intensity" is defined as a value derived from only affected individuals (*i.e.* the average mass or number of pieces across only those birds containing plastics), "abundance" is used in the parasitology literature to describe values from all individuals examined (*i.e.*, an average value using all individuals examined[73]). While both intensity and abundance describe plastic burdens for a sample of individuals, their meanings and interpretations differ greatly.[73] Most papers (95% of 85 papers) reported the mean or median abundance (either mass or number of pieces) from all individuals, but a subset actually reported the mean or median intensity (includes only counts from individuals containing plastics). While it can be argued that abundance values contain redundant information partly found in the frequency of occurrence data, it should be noted that abundance values are the most common throughout the literature, and therefore the most comparable among studies. At times, data on plastic debris ingestion can be highly skewed statistically, so reporting intensities can provide key information independent of frequency of occurrence, but this should be in addition to abundance values.

Variable terminology also creates a challenge with the statistical descriptions of metrics of plastic ingestion across studies. Mean values are the most frequently reported, but have the disadvantage of misrepresenting the sample if there are a few individuals with extremely high values, or large numbers of individuals without plastics. Median values are useful for describing ingested plastics data as they are less sensitive to the effects of outliers within the sample, and hence give a more typical value in a skewed dataset. Consequently, mean and median values can differ substantially for the same sample: Provencher *et al.*[74] found a mean mass of 9.5 g plastic ingestion per bird compared to a median of 2 g. Only 40% of the 85 studies reviewed here reported a mean value (for either mass or number of pieces), and only 3% report a median value.

The geometric mean mass is another way of reducing the influence of extreme values on the mean, yet with the advantage of using all of the data points. It calculates the mean of the data following logarithmic transformation.[13] It loses mathematical value when there are many zero values (which some plastics data sets are prone to have), however the geometric mean can provide a good measure for comparing plastic ingestion over time. The disadvantage is that the geometric mean, if read as the 'average', can be misinterpreted as it underestimates the most commonly occurring plastic ingestion metrics. Such an issue is particularly relevant when using seabird ingestion studies to inform policy as it could undervalue the magnitude of marine litter pollution – sometimes we need to know the extreme values. The range and maximum values of plastic ingestion complement presentation of the average by providing context, particularly given the effect of data skew on averages. Only 24% of the published literature presented range values for plastic.

Both standard error and standard deviation are used in the ingested plastics literature. The standard error should be used to indicate the precision of the estimate of the mean, whereas the standard deviation should be used to indicate the dispersion of the sampled data. While plastic ingestion data are unlikely to be normally distributed, few studies treat the data accordingly. Commonly, the number of pieces of plastic is often a Poisson distribution,[75] so the median, inter-quartile range, or 95% confidence intervals are more statistically appropriate. While confidence interval and standard error of the mean both indicate the reliability of the mean, standard error values include only about two-thirds of the values measures, whereas the 95% confidence intervals, by definition, include 95% of the values sampled, giving the reader a better sense of the range of the data.

An important metric that is only reported within the literature for Northern Fulmars is the percentage of birds above or below a certain level (see also Section 3.1).[13] This species-specific approach allows for standard reporting metrics that is straightforward and easy to follow while circumventing some of the more complex idiosyncrasies of data presentation and interpretation as described above. More work is needed to develop such metrics for a broad set of indicator species beyond the Northern Fulmar. Based on our review of the seabird literature we conclude that within the large body of published work there is insufficient information to reconstruct the descriptive statistics and compare findings in meta-analyses.

2.3.2.6 Statistical power. Researchers are often interested in changes in the frequency of occurrence or abundance of ingested plastic over time. Monitoring that change is often challenging given the low sample sizes and low frequency of occurrence or abundance of plastics in most populations. The annual sample sizes required to detect a 20% change in the frequency of occurrence of plastic ingestion in Canadian seabirds ranged from 61 (Thick-billed Murres, *Uria lomvia*) to 193 (Northern Fulmars), depending on interannual variability and frequency of occurrence.[21] Similarly, >600 Laysan Albatrosses (*Phoebastria immutabilis*) would need to be sampled annually to detect a 5% change in the frequency of ingested plastics.[76] In the North Sea, Northern Fulmars have a high frequency of occurrence of plastic, so fewer individuals are required to detect changes over time: evaluation of annual sample variances in Dutch birds[38] indicated that a sample of roughly 30 to 40 birds per year produced reasonably robust figures for frequency of occurrence and average number or mass of plastics. Power analyses of these data produced strongly variable results not only for the different metrics, but also when looking at industrial plastics, user plastics or their combination. Overall, van Franeker & Meijboom[38] concluded that in the order of 4 to 8 years of samples of each around 40 fulmars would be needed to reliably detect changes in ingested plastic mass in the order of 25%. Given that most studies sample few individuals (usually <100), and species often have low frequency of occurrence of plastics, current sampling strategies are often only sufficient to monitor very coarse changes over time.

2.3.2.7 Importance of reporting plastic and non-plastic debris in a common framework for comparisons. The recognition of plastic debris as a threat to marine wildlife has grown over the past five decades,[77] but what has received less attention is a similar treatment for other anthropogenic debris. While foams and rubber materials are often correctly lumped with "plastic", other debris is clearly distinct and often mentioned but not given separate treatment. For example, paper and wood products, and pieces of cardboard are consumed by marine birds, but because they are composed of natural materials and break down (presumably more rapidly than plastic), they are not often reported with the same level of detail as plastics. Non-reporting of non-plastic items is a concern because some recent studies are finding surprisingly high frequency of occurrence of metal debris in some species.[24] We would predict that metals, which presumably sink in water, would not be distributed as broadly as plastics across the ocean, or certainly not be as available to surface feeders. Holland *et al.*[5] have found wax or plastic-coated wrapping papers in coastal marine birds in eastern Canada, and such materials are often grouped with other film-like plastics. Depending on digestion and breakdown rates, this type of product could have similar possibilities of blockage in avian digestive tracts, and would certainly be expected to be more common in scavenging species like gulls. However, in order for researchers to draw sound, statistical comparisons of the frequency of occurrence, abundance, and trends in ingestion of these other types of materials, they require the same rigorous reporting (size, mass, frequency, colour) as for plastic materials.[38]

3 Case study: what can be learned from taking a global standardized approach

3.1 Brief history of Ecological Quality Objective in Northern Fulmars

To meet the emerging need to track and monitor marine litter in the North Sea, the EcoQO was established based on plastic debris found in Northern Fulmar stomachs (both the proventriculus and gizzard), a species known to ingest plastics throughout its range at the time, and often found in beached bird surveys in the North Sea region.[13] Although the initial EcoQO was based on plastic loads found in Northern Fulmars, during the early phases of policy development, working groups of the International Council for the Exploration of the Sea (ICES) and OSPAR worded a preliminary target definition of the proposed EcoQO as plastics in stomachs of 'seabirds' as 'the proportion of birds having 10 or more pieces of plastic in the stomach should be below 2%'.[13,78] This target had no substantiated background of ecological or individual or population health. It represented an arbitrary target considered to reflect 'acceptable ecological quality' as used in policy documents.

After the original level of 2% was determined, the Northern Fulmar became the chosen species for EcoQO monitoring in the policy discussions. At that stage, it was recommended to OSPAR and ICES that the target definition would be more ecologically meaningful in terms of plastic if mass was used instead of number of particles. Early Dutch studies indicated that in terms of 'mass' of plastics in Northern Fulmar stomachs, the critical level of 10 particles equaled to about 0.1 g of plastic.[38] Dutch studies also showed that nearly every Northern Fulmar in the southern North Sea had plastic in the proventriculus, with an average mass of 0.6 g per bird (about 0.1% of the species average body mass) between 1996–2000.[38] Consequently, the policy aim of <2% of Northern Fulmars exceeding 0.1 g of plastic became unrealistic for the foreseeable future. OSPAR and ICES then followed the advice to redefine the less strict target to <10% of beached Northern Fulmars exceeding 0.1 g of plastic in the stomach.

This new target still lacked an ecological background. The arbitrary proportion of 10% of birds was chosen from the definition for the EcoQO on oil pollution, which used Common Murre (*Uria aalge*) as an indicator species with an EcoQO target of <10% of beached guillemots having oil in their feathers.[36] The OSPAR target level is an arbitrary political choice, but was aimed to match pollution levels in environments where anthropogenic influence is expected to be low. Only later, the Northern Fulmar <10% with <0.1 g EcoQO target proved to be somewhat reasonable, when reports for Northern Fulmars in the Canadian high Arctic showed to be close to such a target level.[13,79] The Canadian high Arctic can be viewed as a relatively clean environment, with few local sources of marine pollution, and limited shipping in the region.[40] While it would be unrealistic to have a target below such a level in regions more heavily affected by plastic pollution, aiming at these remote level targets seems reasonable if the goal is to reduce plastics in the environment. Importantly, although the EcoQO target provides no evidence for an acceptable threshold of harm to individuals or negative impacts on populations, it has created a standardized protocol that researchers throughout the northern hemisphere have been able to employ leading to a cohesive approach to monitoring marine plastic pollution, and a framework for similar approaches elsewhere.

3.2 Results from a standardized approach

At a regional level, the standardized approach from the North Sea has allowed temporal trends to be assessed over the last three decades (Fig. 3). Importantly, the framework has allowed researchers to examine patterns in pollution type which has helped to inform policy and mitigation practices as demonstrated by the reduction of industrial plastics in beached birds in the recent decades after industry standards were changed.[13,67] The standardized approaches to assessing the accumulation of plastics in Northern Fulmars has also allowed policies related to target pollution levels to be re-evaluated over time, and reconsidered (Fig. 4; EcoQO change from 2% to 10% and from number to mass metric in 2006;[80]).

While the North Sea Northern Fulmar program has shown great utility in using standardized approaches, the real benefit of the methods were demonstrated when the wider scientific community studying Northern Fulmars adopted the protocol allowing for comparisons among regions at the ocean basin scale. First, as discussed above, the arbitrary target of 10% has since been shown to be realistic in less polluted environments as demonstrated by studies of Northern Fulmars in the Canadian Arctic (Fig. 5). Second, global patterns can also be assessed from the compiled data, allowing us to examine hypotheses developed in earlier studies, for example that the ingestion of plastics decreased with increasing latitude.[81–83] It is only with recent studies of Northern Fulmars throughout their range that this can be tested across multiple sites in two ocean basins (Fig. 6).

While applying the EcoQO to other species is problematic due to its political origins (*i.e.*, lacking known biological level of impact), applying a similar approach to other species could be beneficial. Target levels could, as in the Northern Fulmar, be set at ingestion levels observed in low pollution areas. A wider use of EcoQO may also encourage local governments to adopt similar approaches within their own regions using the species that are present and available for study.

4 Recommendations for plastic ingestion studies in marine megafauna

One of our objectives was to outline a standardized set of methods for measuring and reporting accumulated plastics in marine megafauna to help shape future studies of ingested

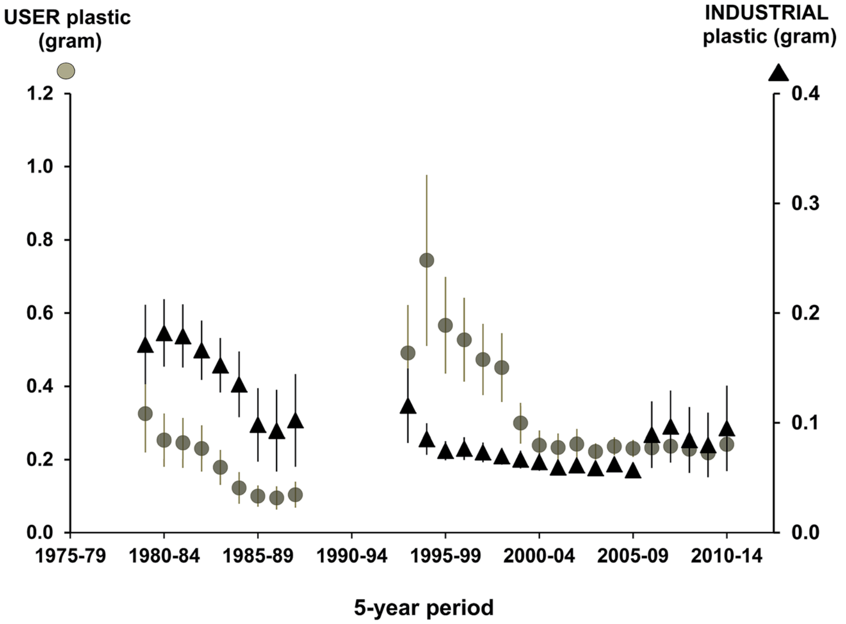

Fig. 3 Five year running arithmetic averages (with standard error bars) for user and industrial plastics (both in grams) in Northern Fulmars (*Fulmarus glacialis*) in the Netherlands collected as part of the standardized 'Save the North Sea' project.[13]

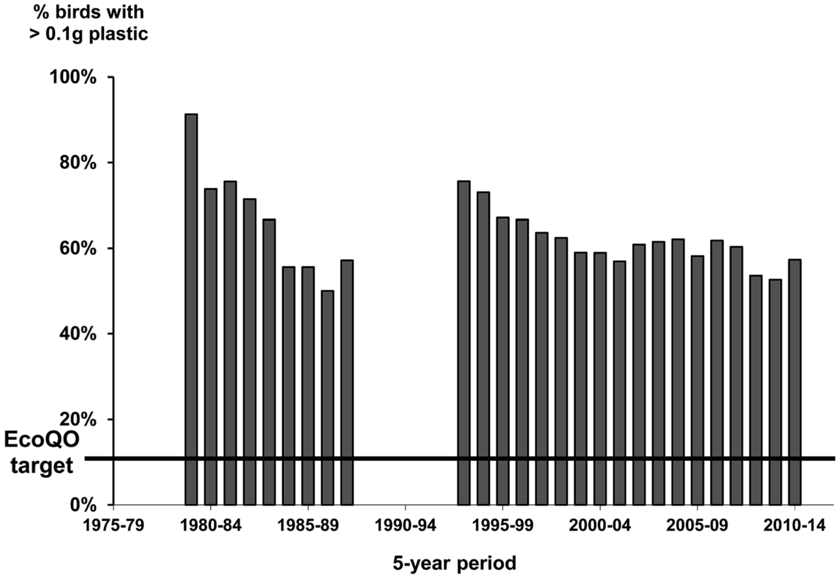

Fig. 4 Percentage of Northern Fulmars with >0.1 g plastic using a running 5 year mean to examine changes in plastic ingestion in the Netherlands collected as part of the standardized 'Save the North Sea' project.[13] The black line represents the Ecological Quality Objective from the North Sea of birds to have 10% or less of >0.1 g of plastic in their stomachs.

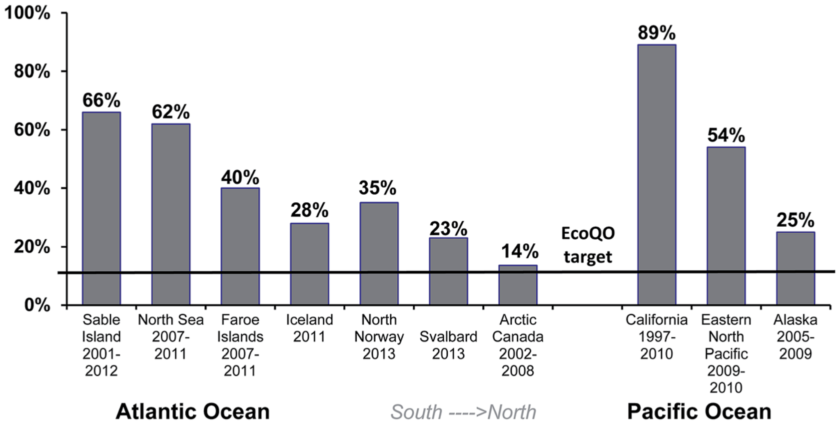

Fig. 5 Percentage of Northern Fulmars (*Fulmarus glacialis*) with >0.1 g of accumulated plastic in their proventriculus/gizzard compared across multiple study regions. The black line represents the Ecological Quality Objective from the North Sea of birds to have 10% or less of >0.1 g of plastic in their stomachs.

plastics, contribute to our global understanding of marine pollution, and facilitate easier comparisons among studies, regions, and species.[84] With this is mind, we make several recommendations here that are specific to seabirds, but useful for all taxonomic groups where ingested pollution is studied.

To this end, standardized methods and metrics should be used across all studies. For seabirds, the methods used by the North Sea Fulmar Study[13,14] have been adopted widely, but not universally. We recommend that all publications reporting ingested plastics in seabirds use this protocol as it offers a comprehensive and flexible framework for the quantification and classification of marine debris. In addition to this method and classification framework, we highly recommend that reporting of data on variables that have been shown to influence plastic accumulation in marine megafauna, and particularly information on collection method, date and location of collection, age, and sex. For other groups of marine megafauna we recommend adopting the North Sea Fulmar Study plastic classification system, which separates debris into user and industrial categories, and then further subtypes (see Section 4.1 below), as well as the same standard minimum metrics outlined above. In a European context such standardization has started with recommended procedures for marine turtle and fish[15] and results for plastic ingestion by seals.[17] Below we present some guidelines for each classification for ingested plastics that will help standardize data reporting and cross-study comparisons.

4.1 Plastic type

Distinction of ingested litter into categories provides an arguably fundamental insight into the source of debris and thus

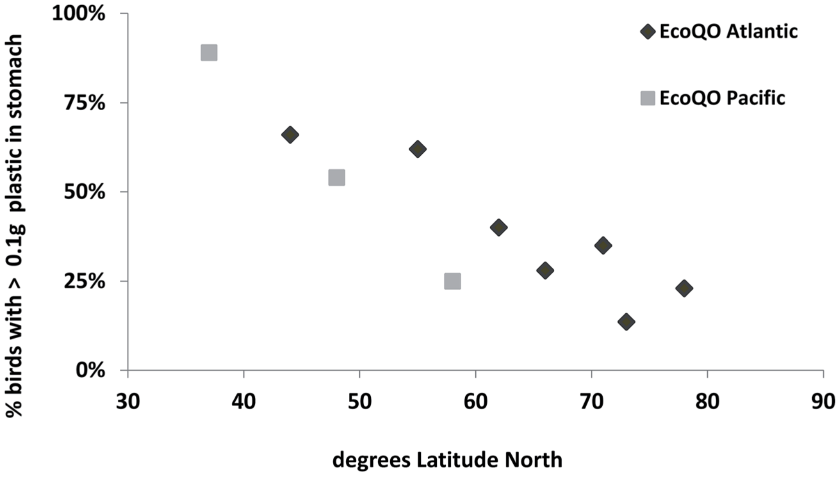

Fig. 6 Ecological Quality Objective performance in Northern Fulmars (*Fulmarus glacialis*) along a gradient of latitude (south to north) in the Atlantic and Pacific Oceans.

required mitigation actions, and is key when using seabirds as indicators of environmental pollution. All plastic items should be broadly categorized as either industrial plastic pellets (or 'nurdles') or user plastic (all non-industrial remains of plastic objects;[85]). Industrial plastic pellets are small, often cylindrical-shaped microplastic granules approximately 4 mm in diameter, but oval, disk-like and rectangular shapes also occur. User plastic includes the following commonly reported categories: sheet plastics (*e.g.*, plastic bags), threadlike plastic (*e.g.*, rope or netting), foamed synthetics (*e.g.*, polystyrene) and hard fragments (from mostly unidentifiable larger objects). A "miscellaneous" category can be used for uncommon items such as cigarette filters, pieces of balloon rubber, *etc.*, however, reports should preferably include specific details of the items included in this category. Online supplemental material or depositing raw data in an online repository is a useful way to include these details if they are not directly relevant to the original study. Such classification has been extensively employed by studies of seabirds, turtles and marine mammals and has enabled valuable studies of long term changes in marine debris composition.[13,67,86] A comprehensive guide to the above categories can be found in the online supplement of Van Franeker *et al.*[13]

Increasingly, there is interest in knowing more about the plastic types in the marine environment.[87,88] If the focus of the study is to provide a baseline for the type of plastics consumed by marine megafauna, or present in the environment, plastic items should be further categorized according to polymer type (*e.g.*, polyethylene) using Fourier Transform Infrared spectroscopy (FT-IR;[89,90]) or Raman Spectroscopy.[91] From a biological perspective, this level of classification of plastics is of particular interest in relation to how different chemical contaminants are associated with marine plastics.

4.2 Plastic size

The most commonly used plastic size classes include mega- (>100 mm), macro- (>20–100 mm), meso- (5–20 mm) and microplastics (<5 mm),[92–94] but no globally accepted definitions exist. As a result, the term "microplastic" has been used to describe plastic particles ranging in size from <1 mm to 20 mm.[95,96] The lack of standardized sizes classifications, and their relevancy to marine biota has been recognized as a research priority.[97,98] While marine megafauna ingest several sizes of plastics, we advocate the use of the categories suggested by Barnes[23] as the most relevant and applicable. This includes megaplastic (>100 mm), macroplastics (>20–100 mm), mesoplastics (>5–20 mm), and microplastics (1–5 mm) as these are the most likely detected in marine megafauna and easily summarized from plastic accumulation studies. We recognize that studies focused on small biota (*e.g.*, plankton, bivalves) may also report smaller plastics (<1 mm), often also referred to as micro-plastic which may be referred to ultrafine-plastics (1 μm to 1 mm), and nanoplastics (1 nm to 1 μm) following the terminology used by the field of nano-ecotoxicology.[99] Specifically, "nano-" refers to particles that have potential to interact with biota at the cellular level, and should be used accordingly. In order to better contribute to the overall assessment of plastics in the environment and biota, we recommend that authors report the percentage of plastics in each of the four size categories.

4.3 Plastic colour

Plastic colour is important to report, but often not reported (only reported in 27% of 85 papers reviewed). First, assessing colour in marine megafauna can give insights into how organisms may select plastics from the environment. Plastic size and colour can influence the chance of being ingested by different animals with different foraging strategies.[100,101] However, to assess selectivity, organismal data needs to be paired with environmental assessments on the availability of different coloured plastics in the environment, which are currently lacking in many regions. Future studies may allow us to hindcast environmental data onto megafauna reports and examine selection of plastics from the environment. Second, plastic colour may also be associated with higher exposure to some chemicals.[102,103]

The specific method of colour determination of plastics particles found ingested by marine megafauna is often not mentioned,[48,58,104] or done by two different observers to confirm the colour;[101] in all these cases it is impossible to compare studies on plastic colours. Ideally, plastic items should be assigned to a colour by comparing individual pieces to a colour wheel or standardized chart. To accurately and consistently report colour across plastic ingestion studies we recommend a two-step colour sorting process. First, a colour wheel (that includes secondary and tertiary colours) should be used to assign plastic pieces to specific colour categories. A Munsell chart or 72-colour wheel can be used for this step (widely available for order online). Second, the specific colour assignments should be grouped into eight broad colour designations; off/white-clear, grey-silver, black, blue-purple, green, orange-brown, red-pink, and yellow.[61] This use of a large colour wheel to assign pieces to a board range of colours, and then collapsing these categories into only broad groupings allows for both observer accuracy (*via* the large initial categories), and systematic presentation of a few comparable groups (the eight broad colour groupings). Distinguishing colour down beyond these categories is likely to lead spurious results due to differences in categorization. Additional scales (*e.g.*, black to grey to white) may also be used, but the source and type of scale should be made clear to the reader to enable comparison. Importantly, plastics, especially white pieces, are frequently discoloured following digestion, so researchers should endeavor to report the likely original colour of each piece.

4.4 Metrics reported

All publications reporting plastic ingestion should report the frequency of occurrence of plastics (with a 95% confidence interval using the Jeffreys interval[105] [also see http://epitools.ausvet.com.au/content.php?page=CIProportion]), sample size and the methods for the collection of the samples. These are the basic components of any study on plastic ingestion in marine megafauna. At a minimum, we also recommend that all authors include data on the mean (with standard deviation), median and range of mass of the ingested plastics per individual, including individuals that contain no plastics (Box 1). Standard Error, as used in Fulmar protocols, can be calculated from standard deviation and sample size, which is critical to ensure future comparisons for this species. Studies should also report the mean, standard deviation, median, and range of all plastic debris metrics (number of pieces, total mass of debris pieces by debris category; see ESI†). All summary statistics should give abundance values (which include all individuals examined not just those containing plastics). Reporting absence data are crucial, as the amount of plastic in the oceans is expected to increase over time.[23,106] For studies examining how the amount and distribution of plastics change over time, authors should include information on temporal trends in the size classes, colour and type of plastics as well. This will be facilitated if data are collected using comparable methods (see above). Data on ingestion of plastics should be reported in tabular form, not graphical form for papers presenting novel plastic ingestion data for marine megafauna. This practice, along with raw data archiving in open access forums, will facilitate spatial and temporal comparisons, without having to guess where bars or points line up with a scantily labeled axis. Luckily the use of online supplemental material makes this practice increasingly easier.

4.5 Future areas of study

4.5.1 Retention times for different species. How long plastic items are retained in an animal's digestive tract has serious implications relating to exposure to plastic co-pollutants, risk of physical injury, and the use of wildlife as sentinels of marine pollution. While retention times of plastic ingestion in marine wildlife are poorly known, some evidence from petrels suggests that plastic loads reflect relatively recent accumulation because 75% of ingested plastic disappears within a month, if no new plastic is ingested.[107] Similarly,

Box 1 – Recommended reporting guidelines for all marine megafauna plastic ingestion studies

As a minimum all studies should report:
- Location and timing of sampling
- Method of sampling
- Sample size
- Frequency of occurrence of ingested plastics (with a 95% confidence interval; Jeffreys interval)
- Mean (with standard deviation and error), median and range of mass of ingested plastics/individual (including all individuals sampled)
- Mean (with standard deviation and error), median and range of all plastics reported by debris category (user/industrial; fragment/foam/sheet/thread/other)

Additional information to be provided:
- Size of plastics reported by size classes (mega/macro/meso/micro/ultra-fine/nano)
- Colour reported in 8 broad colour groups (see text for more details)

a handful of diet studies suggest natural materials (*e.g.*, squid beaks) are eliminated at the same rate of 75% over a month.[43,47,108] However, Ryan[109] argued this may not be the case for all Procellariiformes. Retention time of plastics is almost certainly influenced by a range of other factors such as the size or shape of a plastic item, polymer type, and presence of natural items in the stomach.[109] Microplastics are likely to pass through marine megafauna more quickly than larger pieces that must breakdown before passing through the intestines. Correspondingly, estimates of retention time for ingested hard plastics are highly variable, ranging from as little as 30–50 days in adult birds provisioning chicks,[110] up to 12 months[81,111] with average residence time of around four months.[112,113] Soft plastic items, such as bags and foam, may also reside in the gut of marine wildlife for considerable amounts of time, as latex balloon fragments have been found in the stomach of Green Turtles (*Chelonia mydas*) more than four months post-ingestion.[112]

Votier *et al.*[114] fed six Great Skua (*Stercorarius skua*) breeding pairs fish that contained small numbered plastic markers that were date-stamped inserted within fish heads. From 76 fish fed to the six pairs of skuas, eight (12.3%) of the plastic markers were recovered in pellets. No markers were discovered in faeces, suggesting the birds are unable to pass the plastic items. The bulk of the cast pellets were produced between 6 and 24 hours (53%). Also some species cast pellets, regurgitating indigestible materials such as bones, feathers, or shells. This is particularly the case with gulls and skuas, but occurs in a range of species including albatrosses and shearwaters. Despite this, pellets are unlikely to eliminate plastics completely, though the reasons why only some pieces are regurgitated remain unknown.

Retention times can also be influenced by life history. Adults can have very low frequency of occurrence of debris when feeding chicks, as they offload plastics to their nest-bound young.[57,58,115] These chicks have no mechanism for eliminating plastics fed to them by their parents (though some species can cast pellets to eliminate some items; see above), and consequently fledge carrying the plastics accumulated during the often lengthy chick-rearing period.

4.5.2 Trophic transfer of ingested plastic. One area of emerging research is the mechanisms by which seabirds acquire plastic debris. Of course, the assumed pathway is direct ingestion, with the hypothesis that seabirds mistake plastic particles for food and consume them.[8,28] This seems to be a logical assumption for birds with larger pieces of plastics (>5 mm) in their digestive tracts, as it is difficult to imagine that these could be consumed by accident, or that such large plastic items were inside the bird's prey. However, for microplastics and smaller pieces, marine megafauna may ingest them secondarily by consuming a prey organism which itself has already ingested plastic.

Plastic debris has been found in a variety of marine prey items, either in the wild or with ingestion shown to occur in experimental studies, including zooplankton,[116] sessile molluscs,[117] cephalopods,[118] and large crustaceans like crabs and lobsters.[119] Even among marine megafauna there may be transfer of accumulated plastics. Trophic transfer has been reported between seabirds,[56,120] and an extreme example of this was reported by Perry *et al.*[121] who found marine debris within Dovekie (*Alle alle*), that had been consumed by a Goosefish (*Lophius americanus*). Consequently, researchers have proposed that marine megafauna may in fact acquire plastic debris by consuming prey which themselves have ingested particles.[122,123]

Confirming this hypothesis is challenging. There is no obvious means of distinguishing between directly consumed plastic particles from pieces that were first consumed by fish, which were then eaten and digested by a bird. One way to solve this problem would be to capture and analyze the diet of seabirds that have recently been feeding (*e.g.*, following direct observation). However, this presents another challenge, in that digestion times can be very rapid in seabirds.[124] For example, even when collecting auks which had just been diving for fish and pouring alcohol into their digestive tracts to preserve contents, Provencher *et al.*[125] found that fish which had just been consumed were already partially digested, minutes after capture. Therefore, at present researchers must (safely) assume that plastic in seabird prey becomes plastic in seabirds,[126,127] but distinguishing plastics in species that are directly consumed *versus* consumed through trophic transfer is very difficult to quantify. Given that seabirds accumulate plastics, the source of the plastics (either direct or indirect) is perhaps irrelevant from a toxicological perspective. Therefore, studies interested in the trophic transfer of plastics within the food web should approach this from both a bioaccumulation and a biomagnification standpoint, similar to other ecotoxicology studies interested in biological effects induced from environmental pollution.

4.5.3 Links between microplastics and contaminants. Additives, such as flame retardants and stabilizers (which can contain high levels of heavy metals), that are incorporated into plastic during manufacture have been shown to have harmful effects on organisms, including marine mammals and birds.[48,128] Buoyant plastic debris may be particularly problematic as it is subjected to weathering and becomes porous (as chemical bonds within the plastics degrade), enabling it to both leach additives compounded during manufacture,[129] as well as adsorb high concentrations of contaminants (*e.g.* polychlorinated biphenyls, organochlorides) from the surrounding sea water.[130] These small, weathered plastic particles present potentially the greatest threat of contamination to marine organisms as they have increased surface area to volume ratios compared to larger debris items, and due to their small size, are available for consumption by a vast array of marine life.[106] Correspondingly, the ingestion of plastic has been linked with high concentrations of PBDEs and metals in the tissues of seabirds and marine invertebrates,[131,132] and a corresponding reduction in seabird body condition.[48] Importantly, the sublethal impacts on reproductive condition from contaminants could have ramifications on long term population stability.

5 Conclusions

Over the last 60 years, reporting of plastics ingested by marine megafauna has gone from semi-noteworthy in a report, to a growing body of literature with a rapidly increasing number of publications specifically reporting plastics in marine biota and their potential impacts on the marine environment. While simply reporting plastics within a diet study was once sufficient, the growing interest in marine plastics and their impacts, and purpose-driven publications on plastic accumulation in marine biota now demand a higher standard. Standards for reporting data are required to make studies comparable[84] and to provide data suitable for statistically rigorous meta-analyses. These standards should include consistent reporting of the collection and sampling method, type of debris, the mass, the number, the colour, and the characteristics of the material, as well as the method of sorting and identifying materials. While other metrics and measures should continue to be explored by researchers to ensure creative and novel approaches which will drive researchers to explore new questions, the inclusion of basic metrics as discussed above is critical. The large quantity of data collected in recent years and increased awareness of the problems around marine plastic pollution can enable scientists to answer questions on a larger ecological scale when data are collected and reported using a standardized approach.

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7.3 Appendix 3: Seabirds[6]

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Abstract

Seabirds have a global distribution, are numerous throughout the world’s oceans, and have been used for decades to track and understand changes in the marine environment. Seabirds are dependent on a variety of ecosystems, including terrestrial, coastal, and pelagic, and are thus vulnerable to both marine and terrestrial environmental stressors. This chapter examines impacts on seabird populations that occur in the marine environment and are global in nature (touch more than one ocean basin). Both widespread (i.e., climate change induced alterations to marine food webs and sea level rise), and more point-source impacts (i.e., incidental bycatch in fisheries, hunting) are discussed. Additionally, natural occurrences in marine ecosystems (i.e., oceanographic regime shifts, parasites), and issues related to anthropogenic activities (i.e., plastic and oil pollution) are covered. Lastly, we discuss marine protected areas and other efforts aimed at conserving global seabird populations, including colony restoration, community-based research and international conservation actions.

Keywords

Seabirds, climate change, conservation, cumulative effects, disease, fisheries, hunting, marine protected areas, pollution, populations

Introduction

Seabirds are among the most numerous and widespread of the marine megafauna (Croxall et al., 2012). A single species can range from pole to pole with some having the longest known migrations to date (Fijn et al., 2012). Seabirds are also among the most threatened groups of birds (Croxall et al., 2012), and many populations are in decline (Paleczny et al., 2015), making this group particularly important to consider when examining marine ecosystem structure and condition.

Here, we consider seabirds as defined by Gaston (2004), with some updated classifications as proposed by the International Ornithological Committee World Bird List (http://www.worldbirdnames.org/classification/orders-of-birds-draft-7-1/). This includes gulls, terns, skimmers, skuas, auks and selected phalaropes (Charadriiformes), tropicbirds (Phaethontiformes), penguins (Sphenisciformes), tubenoses (Procellariiformes), cormorants, frigatebirds, boobies, gannets (Suliformes), and pelicans (Pelecaniformes) as the main species. While we focus on ecological issues, the issues impacting seabirds often affect other marine bird groups such as loons (Gaviiformes), sea ducks and mergansers (Anseriformes), as these birds often occupy the same marine habitat. Thus, we present issues that broadly affect birds in the coastal and pelagic marine environment.

As seabirds occupy such a large area of the globe, this chapter includes widespread ecological issues (e.g., sea level rise), and more point source anthropogenic perturbations (e.g., interactions with fishing) affecting seabirds. Beyond the importance of seabird populations to biodiversity, human subsistence hunting (Falk et al., 2006), and as ecosystem modifiers through nutrient subsidies (Honig and Mahoney, 2016), they are recognized as indicators of the condition of the marine environment. The use of seabirds to detect changes in marine ecosystems spans from fish stocks to plastic pollution, from changes in food webs to the global transfer of contaminants (Piatt et al., 2007b). We aim to provide context and background on anthropogenic-related issues that affect seabirds, such as those where the research community has a history of successfully implementing management strategies (e.g., hunting, incidental bycatch). We cannot comprehensively cover all the threats to seabirds as their use of both terrestrial and marine environments make them vulnerable to many different types of ecological issues. For example, the impacts of introduced predators on islands where seabirds breed, while significant and global (Phillips et al., 2016), are not covered here. For further reading on terrestrial ecological issues, see Jones et al. (2015), and Towns et al. (2011b).

Changes in marine prey

Seabirds feed almost exclusively in the marine environment, intrinsically linking seabird survival, reproduction, and condition to marine biota from phytoplankton to fish. Thus, changes in marine biota have direct impacts on seabird individuals and populations, and changes in seabird populations have been detected both under naturally oscillating regimes and in relation to anthropogenically-induced climate change.

Naturally oscillating ocean regimes

Seabird populations are affected by naturally occurring marine regime shifts such as El Niño/La Niña events in the Pacific Ocean. These influence oceanic productivity in the region, and thus many aspects of seabird life history (Ainley et al., 2005). During La Niña events, the sea surface temperature across the equatorial region of the Pacific Ocean is lower than the long-term average, resulting in offshore winds that drive upwelling along the coasts of western South and North America. During these periods, fish, marine mammal, and bird populations can be extremely productive along the west coast of the Americas (Jackson and Domeier, 2003; Marinovic et al., 2002). Conversely, during El Niño years, upwelling slows down along the coast of the Americas, resulting in warmer sea surface temperatures and reduced productivity in the region. These changes can affect seabird diet. For example, both diet composition and prey size differ in Blue-footed Boobies (*Sula nebouxii*) during El Niño years, compared to La Niña oscillations (Ancona et al., 2012). In addition to directly affecting the diet of seabirds, El Niño events are associated with a number of reproductive metrics in seabirds, including increased propensity of female infidelity (Kiere and Drummond, 2016).

The effects of the El Niño/La Niña are not confined to the Southern Hemisphere, but in fact extend into the North Pacific, affecting seabird breeding ecology as far north as Canada and Alaska (Gaston et al., 2009). In the North Pacific, long-term monitoring of marine birds on Triangle Island, Canada has shown that ocean warming during El Niño/La Niña events can lead to changes in both marine prey species, and the seabirds that feed on them (Gaston et al., 2009). During El Niño events, when warmer waters are present in the North Pacific there is a reduction of an important copepod species in the diet of Cassin's Auklets (*Ptychoramphus aleuticus*), which has been linked to poor auklet nestling growth (Bertram et al., 2017). These naturally occurring oscillations, coupled with long-term ocean warming, could eventually affect populations of this species in the region (Bertram et al., 2017). Additionally, declines in annual breeding effort of Black Oystercatchers (*Haematopus bachmani*) have been linked with increasing spring sea-surface temperature in the same region (Hipfner and Elner, 2013). While the mechanisms for this decline are still not clear, Black Oystercatchers were less likely to initiate breeding in warmer sea surface years, and the authors suggested that ocean warming may affect predator-prey interactions in the intertidal zones (Hipfner and Elner, 2013). These studies demonstrate how both pelagic and coastal marine dependent birds can be affected by prey species changing in response to environmental conditions.

Climate change induced alterations in marine prey

Increasing sea surface temperature due to global climate change is altering oceanic current regimes and nutrient movement (Lewandowska et al., 2014). In some regions, this is affecting seabird populations as marine prey species may shift, either in time or space, to stay within their ideal temperature conditions (Crawford et al., 2015). In turn, temporal shifts in the peak of prey abundance close to breeding colonies, mediated through timing of phytoplankton blooms and subsequent fish spawning, have negatively influenced seabird chick growth and survival in the North Atlantic and Norwegian Sea (Scott et al., 2006).

With the increased rate of changing climatic conditions, ecosystems in the polar regions will be altered the most in terms of temperature in the coming decades, most notably due to changes in both sea ice cover and sea surface temperature (AMAP, 2015). This has already led to changes in prey species composition and availability for some seabirds (Provencher et al., 2012; Trivelpiece et al., 2011). The Arctic is a particularly good place to examine these relationships as there are little to no fishery activities, allowing for changes in seabird diet to be directly linked with changes in prey abundance and distributions. Long-term studies in the Canadian Arctic demonstrate how fish and zooplankton may change with environmental conditions, and simultaneously how this influences seabirds. Since the 1970s, the low Arctic regions in Canada have experienced significant declines in summer sea ice cover. During the same period, the dominant prey species of Thick-billed Murres (*Uria lomvia*) has changed from cold-water species (Arctic cod; *Boreogadus saida*) to warmer, more temperate species (capelin; *Mallotus villosus*) (Provencher et al., 2012). Importantly, this change in diet of the birds has also been associated with decreases in chick growth and lower adult body mass (Gaston et al., 2005), suggesting that altered prey species can directly affect seabird condition and reproduction (Elliott et al., 2008). Simultaneously, this shift in prey in the Arctic has also been documented to influence what seabird species utilise the colony. Razorbills (*Alca torda*) attend Thick-billed Murre colonies in the low Arctic only in years when the warm water prey species (sandlance; *Ammodytes* sp.) is in great abundance (Gaston and Woo, 2008). With prolonged changes in prey distribution, these prospecting Razorbills may establish permanent breeding sites, thereby leading to changes in colony species assemblages.

In the Antarctic, changes in sea ice cover are associated with krill productivity, leading to changes in seabird productivity. In the West Antarctic Peninsula and the adjacent Scotia Sea, mean annual air temperature has risen 4ºC since the 1940s, with the area of sea ice in the region decreasing significantly during this time period (Trivelpiece et al., 2011). The main pelagic prey species for penguins in the region is krill, which varies annually with sea ice extent and winter ice duration (Clucas et al., 2015). Declines in the number of breeding pairs and recruitment of both Adélie (*Pygoscelis adeliae*) and Chinstrap penguin (*Pygoscelis antarctica*) populations in the South Shetland Islands indicate that decreases in krill are likely causing the declines rather than species-specific affinity for ice covered habitat (Clucas et al., 2015; Trivelpiece et al., 2011). Importantly, there is variation in how different species respond to changing climatic conditions. While some Antarctic seabird species are arriving more than a week later on their breeding colonies and, on average, laying their eggs a few days later than in the 1950s, this pattern is not universal (Barbraud and Weimerskirch, 2006). Effects of climate change on prey species and seabirds are complex and dependent on species' biology and species interactions.

Climate change induced alterations in prey are not limited to Polar Regions. Warming trends in temperate locations are also linked with changing food webs. In the Benguela ecosystem off southern Africa, a combination of physical changes in the near-shore environment (increased sea-surface temperatures, decreased oxygen concentrations) and fishing pressure have caused eastward shifts in the distribution of the prey of the region's endemic seabird species (Blamey et al., 2015). Breeding populations of Cape Gannets (*Morus capensis*), African Penguins

(*Spheniscus demersus*), and Cape Cormorants (*Phalacrocorax capensis*) were shown to have responded to an altered availability of adult sardine (*Sardinops sagax*) and anchovy (*Engraulis encrasicolus*) west of Cape Agulhas after the late-1990s (Crawford et al., 2016). Gannets showed variation in survival (Distiller et al., 2012), and increased their reliance on sardine and anchovy in response (Green et al., 2015). Numbers of African Penguins breeding in South Africa declined from ~56,000 pairs in 2001 to ~17,000 pairs by 2013, with adult survival, juvenile survival, chick growth, and chick body condition all decreasing concomitantly (Crawford et al., 2015; Sherley et al., 2017b, 2014). In addition, increased upwelling and wind variability in the 1990s contributed to an eastward shift in the abundance of west coast rock lobster (*Jasus lalandii*), the main prey of the endangered Bank Cormorant (*Phalacrocorax neglectus*) in South Africa (Blamey et al., 2012). The cormorant population responded to the changing lobster abundance close to their colonies between 1993 and 2015, declining at breeding sites north of Cape Town and increasing farther east (Sherley et al., 2017a). In some cases, spatial shifts in spawning forage fish in southern Africa have put prey species beyond the foraging range of seabirds during breeding (Durant et al., 2010) and even during non-breeding dispersive phases (Sherley et al., 2017b).

Also of importance for some seabirds is how changes in the environment may lead their predators to change behaviours. For example, Polar Bear (*Ursus maritimus*) predation on seabirds in the Arctic has increased significantly with reduced summer sea ice coverage (Iverson et al., 2014) (Fig 1). How such increased predation will affect seabird populations will depend on the intensity and distribution of depredation, but the consequences may be both at the individual and population level.

Sea level rise

Global sea levels are expected to rise non-uniformly across the oceans (Nicholls and Cazenave, 2010), with estimates ranging from an increase of 26 cm up to ~2 m by the end of the century (Church et al., 2013). As a result, some coastal regions are expecting, and in some cases already experiencing, inundation of sea water. Importantly, groundwater rise is also expected, and the effects will be amplified by storm surges and extreme tides (Reynolds et al., 2015).

Breeding habitat varies among seabird species (e.g., from ground or burrow nesting at low elevations, to trees, cliff-sides, or high elevation forests); therefore, the impact of sea level rise will be species-specific, based on both the exposure of preferred breeding habitats to inundation and the sensitivity of species to both nest losses and habitat damage (Hatfield et al., 2012; Reynolds et al., 2012). For species breeding in low-lying areas, sea level rise in combination with ground water rise, intensified storm surges and extreme tides will lead to salinization and increase land loss from erosion, thereby altering breeding habitat characteristics long term (Wong et al., 2014). More acutely, sudden flooding (or overwash) of breeding colonies can cause direct mortality of juveniles or adults, leading to lower survival or fecundity and possibly to colony losses and species extirpations. The frequency of the sudden flooding is expected to increase, so colony overwash will likely occur more often for species that breed during the typical storm season, and synchronous colonial breeders are more likely to have catastrophic losses from a single event (per breeding season). Lack of dispersal opportunities to predator-free sites at higher elevations creates an ecological trap scenario on the so-called "protected" low elevation islands (Reynolds et al., 2015).

Efforts to quantify how the effects sea level rise at the island and species scale on in the Hawaiian Archipelago suggest that a 1.0 m rise in sea level could leave more than 200,000 tropical seabirds without nesting habitat at French Frigate Shoals, leading to lower carrying capacities of species (Hatfield et al., 2012; Reynolds et al., 2015, 2012). At Midway Atoll, where more extreme projections of + 2.0 m sea level rise is excepted with wave-driven flooding, approximately 60% of albatross and 44% of Bonin Petrel (*Pterodroma hypoleuca*) nests may be flooded with a loss of more than 616,400 breeding albatrosses and petrels. The most vulnerable species to sea-level rise are those with small ranges, specific habitat niche requirements, and are restricted to low elevation islands (Reynolds et al., 2015). However, opportunities exist to adapt seabird conservation efforts to restore breeding colonies to higher elevation habitat using predator removal with other reintroduction techniques to improve the persistence of seabird species vulnerable to sea level rise (Reynolds et al., 2015; Spatz et al., 2017). Other approaches include social attraction techniques such as the placement of decoys or vocalization recordings to attract pre-breeders and displaced adults to new colony sites, or natural colonization may occur with species into areas with higher elevation breeding or nesting habitat after invasive predators have been removed (see Colony restoration section).

Pathogens and parasites of seabirds

Parasites

Seabirds host a diverse range of parasites. This is because of the high densities of seabirds that often characterize their breeding colonies, and by the fact that they tend to be long-lived and highly faithful to their breeding sites and colonies among years. The diversity of endoparasites (parasites living within the body) associated with seabirds is only partially known due to the difficulty in quantifying parasite species; the host generally needs to be necropsied to perform in-depth analyses. Seabird-hosted parasites include both microparasites (bacteria, viruses, protists) and macroparasites (helminths, insects, ticks and mites). Parasites are ubiquitous in seabirds, and their impact depends on the nature of the parasite in question and on interactions with other local environmental factors, such food resources, levels of local pollution, habitat quality, presence of predators, competitors and/or other parasites. Except under extreme conditions where the presence of a parasite or pathogen causes widespread mortality (see Disease section), little is known about how interactions with these organisms alter seabird health, reproductive success, population viability, and evolutionary processes.

The life cycle and transmission pathways of endoparasites (parasites that live internally in the host, e.g., nematodes, cestodes, and trematodes) are often complex, with both direct (i.e., from parent to chick during feeding) and indirect transmission via intermediate hosts or vectors. For example, cestodes and trematodes most often infect seabirds via trophic transmission, where juvenile parasite life stages infect seabird prey items (crustaceans, mollusks, fish, or squid; Galaktionov and Bustnes, 1996). Due to the difficulty in obtaining reliable estimates of parasite diversity and loads, the impact of these species on seabird health and population dynamics has received relatively little attention. However, experimental removals of gastrointestinal nematode parasites were shown to influence both parental condition and reproductive success in wild European Shags (*Phalacrocorax aristotelis*) (Granroth-Wilding et al., 2015, 2014; Reed et al., 2008). Likewise, Provencher et al. (2017) showed a positive effect of parasite removal on the propensity of Common Eiders (*Somateria mollissima*) to breed. However, in both model systems, broad spectrum anti-parasite treatments were used; therefore, the precise impact of specific parasites on reproduction could not be directly measured.

Unlike endoparasites, the diversity and impact of ectoparasites (parasites that live on the external surface of the host) on seabirds is better documented. Common ectoparasites include fleas, lice, mites, and ticks (Fig 2). The overall diversity of these species on seabirds, particularly for lice and mites, is impressive and largely underestimated (Stefan et al., 2013). Ticks and fleas have been more readily studied from a classical taxonomic perspective, but population genetic studies have shown that these organisms repeatedly diverge into local seabird-specific populations (or host races). Therefore, fine scale diversity is important to consider as it can alter infestation probabilities in large multi-specific seabird colonies (McCoy et al., 2013). While the overall impact of fleas, lice, and mites on seabird body condition and overall fitness is still a subject of some debate (Table 1), large populations of ticks within colonies alter seabird body condition (Gauthier-Clerc et al., 1998), reproductive success (Duffy, 1983), and colony selection (Boulinier et al., 2001). This can be due to both direct blood loss and tissue damage inflicted during tick feeding and via the transmission of tick-borne infectious agents. Indeed, seabird ticks are vectors to a large range of bacteria and viruses whose pathogenic effect on the birds is largely unknown (Chambert et al., 2012). Thus, macroparasites can indirectly affect seabird populations by transferring pathogenic microparasites. Given the ubiquitous nature of parasites in seabirds and the wide range of possible impacts, it is clear that more studies are required.

Diseases

Seabirds are potentially exposed to a wide range of pathogens throughout their annual cycles. To date, most work has focused on detection and surveillance, with little work aimed at assessing effects on seabird populations. There are many exceptions, but many diseases found in seabirds are often detected in apparently healthy birds, suggesting that for at least some pathogens, seabirds are carriers, or experience sub-lethal impacts. Work examining potential vectors and transmission routes of infectious agents in seabirds can be particularly informative for understanding both seabird movement and dispersal and for predicting disease emergence (Boulinier et al., 2016; McCoy et al., 2016).

Bacterial pathogens

Avian cholera (caused by *Pasteurella multocida*) is a disease that has spread from poultry to wild animal populations and has recently reached as far as some Arctic wild bird populations (Iverson et al., 2016b; Phillips et al., 2016). In seabirds, there has been minimal reporting of this disease except in Common Eiders (Iverson et al., 2016a) (Fig 3), Common Murres (*Uria aalge*) (Österblom et al., 2004), Cape Cormorants (Waller and Underhill, 2007), and gulls (Wille et al., 2016). Importantly, avian cholera can cause widespread mortality in some populations, especially when the disease is novel (Iverson et al., 2016a) or outbreaks coincide with poor conditions (Waller and Underhill, 2007). A decrease in Cape Cormorants breeding in South Africa's Western Cape in the mid-1990s was attributed, in part, to mortality from avian cholera, potentially triggered by concurrent poor prey availability (Waller and Underhill, 2007). While early analysis of Common Eider populations in an avian cholera outbreak estimated potential rapid population declines (Descamps et al., 2012), more recent work has shown that avian cholera has a high impact on the population initially, with a more moderate effect over time (Iverson et al., 2016b). While avian cholera has become relatively common in seabirds in some regions (e.g., Common Eiders in North America), there are concerns about its potential effects in species that breed in only a limited number of locations, which could be vulnerable to potential outbreaks (Phillips et al., 2016). The threat to small and remote populations of seabirds should be considered severe if avian cholera is found in nearby locations.

Borrelia burgdorferi sensu lato, the causative agent of Lyme disease, has been widely detected in temperate and polar seabird colonies (Schramm et al., 2014). These bacteria circulate in seabirds via the tick, *Ixodes uriae*, and can reach high exposure levels in colonies (Gomez-Diaz et al., 2010; Staszewski et al., 2008). Although no direct effect on seabirds has been documented (Chambert et al., 2012), the same strains that circulate in seabirds are found in terrestrial ecosystems, suggesting that seabirds may be important reservoirs for these bacteria and may circulate them at wide spatial scales (Gomez-Diaz et al., 2011). Other *Borrelia* bacteria may be found circulating in tropical seabird populations, and notably those responsible for relapsing fever and vectored by soft ticks of the genus *Ornithodoros* (Yabsley et al., 2012). However, for now, very little information is currently available on the diversity and distribution of these bacteria or their potential impact on seabirds.

Viruses

While avian influenza in birds has been a global concern for species that come in direct contact with humans on a regular basis, such as poultry, there has been less work on seabirds (Lang et al., 2016). Some seabird species appear to carry the avian influenza virus with little effect, such as Southern Giant Petrels (*Macronectes giganteus*) (de Souza Petersen et al., 2017), Thick-billed Murres (Huang et al., 2014), terns (Lebarbenchon et al., 2015), and gulls (Arnal et al., 2015). Seabirds may therefore represent an important reservoir of influenza diversity. Avipoxviruses are also common in seabird colonies around the globe (Uhart et al., 2017). These double-stranded DNA viruses can be transmitted both directly (via muscosal secretions) or indirectly and primarily affect chicks, often resulting in death. Avipoxviruses have been identified as an important risk factor for the conservation of small and endangered populations, particularly in island species (Gyuranecz et al., 2013). Numerous other viruses have also been documented in seabirds (McCoy et al., 2016; Uhart et al., 2017). For example, a study examining nine species of seabirds from seven islands in the Indian Ocean found that four species regularly tested positive for antibodies against flaviviruses (Jaeger et al., 2016). Flavivirus exposure has also been documented in Yellow-legged Gulls (*Larus michahellis*) in the Mediterranean (Arnal et al., 2014). A flavivirus, an orbivirus, a phlebovirus, and a nairovirus were all isolated from ticks associated with penguins on Macquarie Island (Major et al., 2009). Much work is still required to understand the diversity, transmission, and impact of these viral agents on seabirds.

Hunting of seabirds

Seabird adults, chicks, and eggs are harvested for a variety of reasons, including cultural traditions, food security, recreation, and economy. Hunting takes place both in the marine and terrestrial environments, and thus can affect seabirds at different stages of their life history (e.g., Gilliland et al., 2009; Jones et al., 2015). Today, locally harvested seabirds remain important in some regions of the world, as a subsistence harvest (as food or income), or as a recreational activity. The Common Eider harvest by indigenous peoples in the Arctic (Fig 4), the Northern Fulmar (*Fulmarus glacialis*) and Atlantic Puffin (*Fratercula arctica*) harvest on the Faroe Islands, and the shearwater (*Ardenna* spp.) and petrel (*Pterodroma* spp.) chick harvests in Australia and New Zealand are examples of traditional harvests, which are still important as a supplementary source of nourishment or income, and for maintaining traditional lifestyles and cultural identity (Olsen, 2008; AMAP, 2009; Newman et al., 2009). While the levels of seabird harvest have generally declined since the 20th century, often linked to more restrictive hunting regulations as a result of declining seabird populations, or urbanization and occupational changes towards non-traditional wage economy employment (Frederiksen, 2010), this is not the case universally (Jones et al., 2015; Lyver et al., 2015).

Seabird harvest, in both the marine and terrestrial environments, is a potentially important pressure on seabird populations, which can lead to population declines (Spenneman, 1998) or even extinctions (Crofford, 1989) . Of note, the impacts from present-day harvest can be less obvious (but see Jones et al., 2015; Lyver et al., 2015). Hunting quotas are smaller, and new confounding stressors such as commercial fisheries, bycatch, pollution, and climate change (Croxall et al., 2012), make it challenging to quantify the population-level impact of harvests. Furthermore, international cooperation is needed to assess impacts because many migratory seabirds are harvested during the winter when breeding populations from multiple jurisdictions co-occur (e.g., Frederiksen et al., 2016). The impact of harvest has been clearly demonstrated for the Common Eider in Canada and Greenland, and on Grey-faced Petrels (*Pterodroma macroptera gouldi*) in New Zealand. Before 2001, Common Eider hunting pressure was high and unsustainable in Greenland, but after 2001 the open season was shortened and spring hunting was banned, leading to an approximate 70% reduction in birds harvested. Subsequently, the breeding population increased in Greenland and Canada (by >200% in Greenland by 2007), adult survival rate increased, and there was greater recruitment of first-time breeders (Burnham et al., 2012; Merkel, 2010). In New Zealand, concerns about population declines of Grey-faced Petrels in the 1960s resulted in the cessation of harvesting at some locations. More recently, the combination of traditional knowledge and management practices with demographic modelling has allowed these culturally important traditions to resume (Jones et al., 2015; Lyver et al., 2015).

A similar reduction in hunting pressure on Thick-billed Murres has occurred in Greenland and Canada, the two main hunting regions, but with mixed results (Gaston et al., 2009). While Thick-billed Murre populations in Canada are now stable, the large reduction in hunting pressure did not reverse the declines in Greenland, and nearly two decades later the affected colonies are still declining (Merkel et al., 2014). Other factors may now be equally or more important than harvesting, such as climate-driven oceanographic changes affecting the winter survival of the birds (Merkel et al., 2014). Furthermore, Murre breeding populations mix during the winter in the North Atlantic, and it takes detailed knowledge about migration patterns and timing to evaluate which threats are affecting which populations (Frederiksen et al., 2016). Securing a sustainable harvest for a widely shared migratory species is complex, and working internationally to resolve research questions and management priorities is essential.

A global harvest has not yet been done for seabirds, so the need to identify knowledge gaps about harvest levels and how to secure sustainable harvest practices is urgent (e.g., Madsen et al., 2015). The nature and extent of illegal harvesting also remains largely unknown (Frederiksen, 2010).

Pollutants

Oil in the marine environment

Seabirds can be vulnerable to oiling events in a number of ways. First, direct oiling of seabirds can cause high levels of mortality in exposed populations. There are limitations for calculating accurate numbers of seabird mortalities from oil spills because the number of beach-driven birds can fluctuate considerably, depending on wind direction and ocean currents (Camphuysen and Heubeck, 2001). Seabird carcasses may be blown away from the coastline, resulting in gross underestimates of the number of birds affected. It is generally accepted that collected birds represent an estimated 3-30% of total seabird mortality (Piatt and Ford, 1996). Second, live birds are impacted by oiling of feathers, which can become clumped and sticky, leading to a decline in the insulative properties of feathers, and leaving seabirds vulnerable to hypothermia. This can in turn lead to seabirds being forced to leave cold waters, which can result in dehydration and mobilization of energy stores, and birds can lose up to 13% of their body mass with a week (Morant et al., 1981). Moreover, birds that survive may also try to preen oil off, resulting in significant ingestion and leading to a series of oil-induced diseases, such as aspergillosis, cachexia, haemolytic anemia, ulceration of the stomach, and immuno-suppressant effects (Crawford et al., 2000; Haney et al., 2014).

Three oil spills off South Africa near large colonies of seabirds since 1983 triggered large-scale efforts to relocate and rehabilitate birds, and resulted in a number of studies examining the effects of oil on seabirds. In 1983, 5,000 Cape Gannets were affected when the *MT Castillo de Bellver sank;* in 1994 and 2000, 10,000 and 19,000 African Penguins were oiled after the *MV Apollo Sea* and *MV Treasure* sank, respectively. Large percentages were de-oiled, individually marked, released and monitored for subsequent survival and breeding success. Survival rates of de-oiled gannets were ca. 2% lower than controls and oiling did not affect their probability of breeding (Altwegg et al., 2008). After the *Treasure* spill, ~19,000 oiled penguins were cleaned and 91% were returned to the wild. Another 19,500 unoiled penguins were relocated to unaffected areas, resulting in only ~2,000 individuals dying as a result of the spill. In contrast, approximately 20% of the Bank Cormorants in the region died due to oiling, and the capture and success rate for rehabilitation of this species was low (Crawford et al., 2000). Subsequent survival rates of de-oiled and unoiled penguins were similar in non-breeding individuals for at least 10 years, but an estimated 27% of penguins oiled by the *Apollo Sea* did not breed again. Additionally, those that bred had survival rates 7 to 17% lower than unoiled birds in two years immediately following the spill, and penguins breeding after both spills had lower fledging rates and slower chick growth rates (Barham et al., 2007; Wolfaardt et al., 2008).

The ecological effects of the *MV Exxon Valdez* oil spill in Alaska in 1989 have provided useful insights into how oil pollution can affect seabirds through long-term exposure to oil in the marine environment. Immediately following the spill there was a 25% decrease in Harlequin Duck (*Histrionicus histrionicus*) numbers in the oiled areas, likely due to direct oiling events (Iverson and Esler, 2010). More importantly, long-term studies found that survival rates of Harlequin Ducks were depressed for 6-9 years following the spill and did not fully recover to rates in unoiled areas for 11-14 years. Based on these findings, Iverson and Esler (2010) estimated that the population recovery in the spill regions would take 24 years. Similarly, examination of biochemical indicators of exposure to oil in Barrow's Goldeneyes (*Bucephala islandica*) remained elevated in oiled areas as compared with unoiled areas near the *Exxon Valdez* spill for two decades (Esler et al., 2011). These findings suggest that while the direct and acute effects of oil spills on seabirds are critical to consider, oil spills can negatively affect seabird populations for decades (Iverson and Esler, 2010).

More recently, the *Deepwater Horizon* spill in the Gulf of Mexico has illustrated how oil platforms can also result in large-scale oil spills that have deleterious effects on seabirds. The 2010 oil spill released ~4.9 million barrels of crude oil into the Gulf of Mexico, equivalent to eight *Exxon Valdez* spills (Haney et al., 2014). The slick covered over 100,000 km^2, affected large areas of wetland habitat, and entered the nearshore planktonic foodweb (Haney et al., 2014). Seabird mortality estimates range from 600,000 to 800,000, with the main casualties being Laughing Gulls (*Leucophaeus atricilla*), Royal Terns (*Thalasseus maximus*), Northern Gannets (*Morus bassanus*), and Brown Pelicans (*Pelecanus occidentalis*) (Haney et al., 2014).

In addition to mortality and toxicological impacts of the oil, 7.95 million litres of chemical dispersants were mixed with the oil at the surface (5.05 million litres) and at the well head ~1,300 m deep (2.9 million litres) (Kujawinski et al., 2011). Dispersants are used to break down oil slicks into smaller droplets, with the aim of promoting biodegradation and reducing the impact to coastlines and animals. These dispersants can be highly toxic to marine zooplankton (Almeda et al., 2014). However, it remains unclear how the mixture of chemical dispersants and oil introduced into marine foodwebs, such as in the Gulf of Mexico, will manifest in seabird populations.

In the absence of oil spills, oil exploration activities can also pose a threat to seabird populations. Offshore oil platforms provide enhanced foraging opportunities for seabirds, due to artificial light, and the underwater structures attracting fish schools (Burke et al., 2012). Quantifying patterns of a species' mortality due to oil rig structures, incidental oil pollution, collisions, or flaring is problematic because of the episodic nature of such events (Burke et al., 2012). Evidence of effects from offshore rigs has been poorly reported in the literature to date, primarily because of a lack of robust monitoring programs and a reliance on anecdotal evidence, which is often reported by oilrig workers or temporary observers (Burke et al., 2012). However, Russell (2005) reported on a highly standardised, multi-year survey of the impacts to seabirds of oil and gas platforms in the Gulf of Mexico. He found that the 4,000 oil and gas platforms served as an artificial archipelago for migrating seabirds and nocturnal collisions were a significant source of autumn migration mortalities. Burke et al. (2012) also noted anecdotal reports of storm-petrels and Little Auks (*Alle alle*) flying into oil rig flares. Several thousand individuals are killed annually by offshore oil and gas activities in Canada (Calvert et al., 2013), but there is no global assessment, to date.

Anthropogenic chemicals

It has been known since at least the late 1800s that environmental contaminants (trace elements, various persistent organic pollutants [hereafter POPs], and, most recently, plastic debris) could be taken up by wildlife (Hoffman et al., 2003). However, the recognition of negative effects of this in seabirds began in the 1960s, when POPs were linked to eggshell thinning in some species. Some of the highest levels of polychlorinated biphenyls (PCBs) were found in wild, fish-eating birds, along with plastic debris in albatrosses (Risebrough et al., 1968). Additional research found that certain contaminants (e.g., POPs, mercury [Hg]) biomagnify up food chains while others (e.g., cadmium) do not (Campbell et al., 2005). This, combined with the recognition that many contaminants can end up anywhere in the world through atmospheric and marine transport processes (Beyer et al., 2000), explained why seabirds breeding from the equator to the poles could have high levels of contaminants (Burger and Gochfeld, 2002; Mallory and Braune, 2012).

Research on contaminants in seabirds has progressed along two general lines of investigation. First, studies have examined seabirds for specific, deleterious effects on various species. Research has looked at issues like mortality, deformities, and reduced breeding success directly related to high concentrations of various contaminants (Evers et al., 2008; Verreault et al., 2004), or subtle, behavioural adjustments correlated with higher concentrations of certain contaminants (Bustnes et al., 2001). This work has demonstrated that levels of contamination affect various species quite differently. For example, negative effects of Hg may occur at relatively low concentrations for certain birds, while others tolerate much higher levels (Braune et al., 2012; Shore et al., 2011). Second, seabirds have proven to be exceptionally suitable biomonitors of contaminant levels in the environment because they feed at different trophic levels and are often colonial breeders (Fig 5). Consequently, researchers can sample different tissues from different species, often from a single sampling location, and through time can assess trends in levels of various contaminants in the environment (Elliott and Elliott, 2013; Riget et al., 2011). For broadly distributed seabirds, this has permitted some important regional assessments of marine pollution (Mallory et al., 2004; Riget et al., 2011). In other cases, knowledge of seabird natural history, demography and movement patterns has provided insights into the different seasonal exposure of seabirds to contaminants. For example, Leat et al. (2013) showed that Great Skuas (*Stercorarius skua*) that wintered in different parts of the Atlantic Ocean had markedly different concentrations of POPs in their blood plasma. Monitoring of contaminants in seabird tissues has proven particularly useful for verifying whether international policy implementation on curbing contaminant release has had a direct effect on the environment. For example, Braune et al. (2015) showed that levels of polybrominated diphenyl ethers (PBDEs) declined dramatically in seabird tissues with a short lag after their North American ban.

Across studies, there has been evidence of different contaminants causing impairment or mortality of seabird individuals or their eggs, although these often were the result of point-source contamination (e.g., lead shot at key hunting locations; Franson and Pain, 2011) or effects from POPs before their deleterious effects were well understood (Blus, 2011). Early in the 21st century, few studies were reporting toxic levels and die-offs of seabirds due to contaminants; instead, for many POPs and some trace elements, trends suggest declining environmental concentrations towards background levels, as indexed from seabird tissues (Braune, 2007; Riget et al., 2010). However, the possibility of synergistic, deleterious effects from environmentally-relevant "cocktails" of contaminants cannot be ruled out, and increasingly studies are showing sublethal, negative effects of contaminants associated with seabird reproduction (Provencher et al., 2016), health (Fenstad et al., 2016; Provencher et al., 2016) and even genomes (Crump et al., 2015). Recent advanced genomic techniques to assess how pollutants may cause the up- or down-regulation of genes in seabirds show promise as this allows for a broader approach for assessing cocktails of contaminants than do most traditional methods (Crump et al., 2016, 2015). This is also important when evaluating the impacts of long term exposure to oil pollution (see Oil and Seabirds section).

While research and monitoring continues on many trace elements, legacy POPs, emerging compounds, and plastic ingestion, several areas appear particularly fertile for new scientific developments in this field. First, an emerging concern is that contaminants are leached from plastic debris when they are ingested by seabirds (Lavers et al., 2014; Tanaka et al., 2015; also see Marine Debris and Seabirds section). These concerns extend to DDT and metals that might adsorb to plastic debris, but additionally to plastic-associated contaminants such as plasticizers (Rani et al., 2015). Second, evidence is beginning to accrue that indicates contaminant levels may vary dramatically in seabird tissues through their annual cycle (Fort et al., 2014); this may have implications for how we interpret toxicity thresholds if contaminants potentially have differential impacts on birds as their condition and health fluctuate through the annual cycle.

Radioactivity

The magnitude 9.0 earthquake at Tohuku, Japan and the tsunami that followed on March 11, 2011 inflicted immense damage to the Fukushima Dai-ici nuclear power plant (Kitamura et al., 2013). In response to the nuclear disaster, and to prevent further contamination to the surrounding prefects, the plant's reactor cooling waters were diverted into the Pacific Ocean (Buesseler et al., 2011). This region is a popular foraging area for several seabird species during non-breeding periods because of the high productivity areas driven by Pacific Ocean upwelling currents (Rayner et al., 2011). For example, the trans-equatorial migrant Flesh-footed Shearwater (*Ardenna carneipes*) has been tracked with geolocators and found to feed off the east coast of Japan (Rayner et al., 2011; Reid et al., 2013), within the contaminated marine zone from the Dai-ici nuclear power plant.

The impacts on marine life from radioactive waste being sluiced into the ocean are so far unknown (Buesseler et al., 2011). Being immersed in a salty environment may afford some protection, by preventing the absorption of radioactive ions by marine life (Reardon, 2011). However, other radioactive isotopes, including cesium-137, which has a 30 year half-life, can be incorporated into animal's bodies via the dermis or ingestion and may bioaccumulate in seabird prey (Buesseler et al., 2011; Reardon, 2011). Streaked Shearwater (*Calonectris leucomelas*) chicks from within the affected area had reduced vitamin A levels compared to those breeding at sites unaffected by the accident, though the population effects of the associated radionuclide exposure are unknown (Uematsu et al., 2014).

Measurements of radioactive isotopes in the waters off the coast of eastern Japan indicate that concentrations are elevated many orders of magnitude above baseline measurements (Buesseler, 2014; Buesseler et al., 2011). Further, radioactive concentrations in marine sediments are highly elevated, providing additional pathways for bioaccumulation by filter feeders and marine herbivores through consumption of contaminated brown seaweeds (Buesseler et al., 2011). If there is wide-scale bioaccumulation of radioactive isotopes, the consequences could include reproductive failure, mutations, and stunted growth in seabirds and other marine species (Reardon, 2011).

Marine debris

The first publication of a seabird containing human waste is from 1838 when Couch (1838) reported part of a candlestick found in the gut of a Wilson's Storm-petrel (*Oceanites oceanicus*). Since the middle of the 20th century, plastics have been introduced as waste into the marine environment (Thompson, 2016). While plastic items were first reported in fish in 1949, the first accounts of plastic ingestion by seabirds were not until the 1960s (Provencher et al., 2017). Since this time there have been hundreds of reports of seabirds ingesting plastics across the globe (Provencher et al., 2017; Wilcox et al., 2015) (Fig 6).

The question of *why* seabirds ingest plastics has been addressed by several hypotheses, though the consensus is that they mistake plastics for prey items. There is evidence that seabirds peck at debris in the same fashion as prey (Cadee, 2002), and plastics can absorb dimethyl sulfide (DMS) from the marine environment, which is an olfactory cue for marine predators (Savoca et al., 2016). Many species also likely ingest plastic secondarily by consuming plastic-contaminated prey (Hammer et al., 2016).

Plastic ingestion has been a focus for many studies, but seabirds are also susceptible to entanglement in plastic debris. Some species such as Northern Gannets incorporate debris into their nests (Bond et al., 2012). Though the reasons for this are less studied, these species often use fibrous organic material when building nests, and for some (e.g., kittiwakes), plastic in the nest does not appear to be detrimental, while others, such as Northern Gannets and Bank Cormorants, experience mortality due to entanglement (Votier et al., 2011).

The North Sea is the only region where plastic ingestion is monitored and studied annually in a systematic way (Provencher et al., 2017; van Franeker et al., 2011). Beached Northern Fulmars are collected annually and examined for ingested plastics using a standard protocol developed specifically for monitoring plastics in the marine environment. This approach has allowed marine plastic pollution in the region to be examined over time, and importantly, allowed for adaptive policy decisions (Provencher et al., 2017; van Franeker et al., 2011). The benefit of having such a standardized protocol is also demonstrated by the large-scale comparisons that can be made among sites where the North Sea protocol has been adopted (Provencher et al., 2017). The collective data from a dozen countries (USA, Canada, Iceland, Faroe Islands, Norway, Germany, France, UK, Sweden, Denmark, the Netherlands, and Belgium) clearly show spatiotemporal variation in plastic ingestion within a single species.

Despite a significant body of research, the evidence linking plastic ingestion to population-level parameters, though compelling, is largely correlative (Rochman et al., 2016). There are clear links between ingested plastic and both organic and inorganic contaminants in seabirds (Tanaka et al., 2013), and individual cases of physical damage (Carey, 2011), though plastic was unrelated to nestling growth rates in Laysan Albatrosses (*Phoebastria immutabilis)*, despite the high media attention that this species receives (Young et al., 2009).

While *ad hoc* studies, and those reporting basic mensural data (e.g., frequency of occurrence) have merit, there is a growing push to move beyond reporting to assessing potential impacts and explaining patterns, which need more directed hypothesis-driven studies (Provencher et al., 2017; Rochman et al., 2016). These large-scale studies and syntheses, including meta-analyses of broader trends (Wilcox et al., 2015) can be impeded, however, by inconsistent reporting and heretofore unstandardized sampling. Consistent, standard protocols designed to detect plastics explicitly need to be used so that more high level synthesis research can be undertaken (Provencher et al., 2017). Through such efforts, the key outstanding conservation questions can hopefully be answered, namely, to what degree does plastic ingestion have population-level impacts and through what mechanisms.

Seabird-fisheries interactions

The footprint of industrial fisheries pervades all ocean ecosystems and is arguably one of the greatest current threats to marine biodiversity (Selig et al., 2014). Seabirds interact with fisheries in all ocean basins (Gianuca et al., 2017). These interactions tend to be dominated by the influences of fisheries on birds (but see Montevecchi 2002 for examples of the reverse) and include both direct effects such as incidental bycatch in fisheries (Gianuca et al., 2017), disturbance from or attraction towards fishing vessels (Bodey et al., 2014), and fishery discards as food subsidies (Votier et al., 2004), as well as indirect effects including competition for prey resources (Cury et al., 2011), increases in scavenging and predatory seabirds (Votier et al., 2004), and changes in size-class and/or species-composition of marine communities (Roux et al., 2013). Seabird-fisheries interactions have been reviewed in depth by others including Furness (2003) and Wagner and Boersma (2011), and this chapter focuses on the three areas of greatest contemporary concern, incidental bycatch, competition for prey, and discards.

Incidental bycatch of seabirds in fisheries

Bycatch, the unintentional capture of non-target animals in fisheries, has been a documented issue for seabirds since the 1970s (Tull et al., 1972), though it was likely widespread since the introduction and adoption of nylon gillnets through the 1950s and 1960s (Munilla et al., 2007). Gillnet fisheries were among the first to be recognised as problematic for diving seabirds (Tull et al., 1972), and the high levels of bycatch (of several taxa; Northridge, 1991) in high seas drift gillnets resulted in a global moratorium on this gear in international waters (United Nations, 1991) (Fig 7). Bycatch in longline fisheries, and later trawl fisheries, was implicated in the decline of albatrosses in the late 1980s and early 1990s (Brothers, 1991; Weimerskirch et al., 1997) (Fig 8), though greater research focus on trawl bycatch did not develop until the early 2000s (CCAMLR, 2002; Weimerskirch et al., 2000). In recent years, seabird mortality in purse seine fisheries, particularly of shearwaters, has been recorded (Oliveira et al., 2015; Suazo et al., 2014) and is receiving increased attention.

The impact of bycatch on seabirds is difficult to determine. In Antarctica, the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) demands high levels of observer coverage (CCAMLR, 2016), providing a strong foundation for assessing fisheries impacts (Croxall, 2008). Elsewhere, observer coverage is far lower and understanding the scale of bycatch requires extrapolation from limited data (Richard, Y. et al., 2013). Within Exclusive Economic Zones (EEZs), there is considerable variability among countries and fisheries. This is particularly relevant for gillnet fisheries, frequently composed of smaller-scale operators that are difficult to monitor (due to the size and geographic extent of fleets and/or small vessel size). The relatively recent discovery of seabird bycatch in purse seine fleets indicates that this gear has been subject to little prior monitoring for birds (Suazo et al., 2014).

There are sufficient data to make global estimates of seabird bycatch based on figures or extrapolations for both longline and gillnet fisheries. Anderson et al. (2011) estimated that 160,000–320,000 seabirds were killed in longline fisheries annually, predominantly albatrosses and petrels. This large range in estimates reflects low data reliability from many key fisheries, but the lower estimate is conservative because observed bycatch levels are often underestimated (Gales, 1998). In gillnets, 400,000 seabirds are captured annually, predominantly diving species (Žydelis et al., 2013). There are no global estimates for bycatch in purse seine or trawl fisheries, though observations suggest that bycatch in trawl fisheries, predominantly of albatross and petrels, but also including sulids (Watkins et al., 2008) and penguins (González-Zevallos et al., 2011), may be of a similar order of magnitude to that in longlines (Bartle, 1991; BirdLife International, 2013).

Trawl and longline fisheries have been the focus of most efforts to tackle bycatch, and have well-established ‘best practices’ in mitigating bycatch through the Seabird Bycatch Working Group of the Agreement on the Conservation of Albatrosses and Petrels (e.g., ACAP, 2016). Measures like bird scaring lines, night setting, and line weighting (for longlines) significantly reduce seabird bycatch (Maree et al., 2014). Such measures are built into the strong management of CCAMLR fisheries in the Southern Ocean (CCAMLR, 2016), and are also included in the fisheries regulations of many countries. Beyond national jurisdictions, the five main tuna Regional Fisheries Management Organisations all require vessels to use mitigation measures (Alderman et al., 2011).

Aside from top-down regulatory mechanisms, a bottom-up, grassroots approach can effectively engage industry and reduce bycatch, best exemplified by BirdLife's Albatross Task Force (BirdLife International, 2016). Such an approach has resulted in binding fisheries regulations in several countries (Consejo Federal Pesquero Argentina, 2017; Maree et al., 2014; Republic of Namibia, 2015). These regulations should deliver substantial bycatch reductions if well implemented, a key factor for high seas and national EEZs alike - regulations must be followed by implementation, monitoring, and enforcement. Few fisheries have the competition for licences that permit strong regulations, as in CCAMLR (CCAMLR, 2016), but novel approaches, including electronic monitoring (Papworth, 2013), may help to reduce the dependence on onboard observers. However, there are still many challenges to implementing best practice mitigation in the riskiest longline and trawl fisheries.

Reliable mitigation measures for gillnets or purse seines do not yet exist, though approaches that seek to increase the visibility of nets to birds show initial promise (Martin and Crawford, 2015). While purse seine bird bycatch is a more recent discovery, highly encouraging results exist from experiments to reduce excess netting in Chilean fisheries (Suazo, pers. comm.[1]). Further efforts to identify solutions for these fisheries are required, particularly for gillnets, the most lethal gear type for seabirds.

Competition for prey resources

Seabirds eat ~70–100 million tonnes (Mt) of food annually, the bulk of which is forage nekton like squid, krill, and small schooling fish (Rountos et al., 2015) (Fig 9). Forage nekton are also targeted by industrial fisheries which catch ~20 Mt annually, or ~30% of total global landings (Nicol et al., 2012). These fisheries overlap with seabirds in space, time, size-classes taken, and trophic level of catch (Rountos et al., 2015). Consequently, most efforts to document seabird-fisheries competition focus around forage nekton and implicitly consider that fisheries outcompete seabirds for limited resources (e.g., Hinke et al., 2017), though other forms of competition exist (Sydeman et al., 2017) and seabirds feeding on benthic organisms may also be affected by fishing (Sherley et al., 2017a).

Concerns that forage fisheries were competing with seabirds were first raised in the 1930s (Jaques and Murphy, 1936), but began to receive global attention in the 1970s and 1980s. This increased attention occurred when widespread declines in seabird populations were linked to expansions, shifts, and in some cases collapse (Roux et al., 2013), of large-scale forage-fish fisheries in several ecosystems (MacCall, 1984; Schaefer, 1970). These fisheries have the potential to reduce prey abundance below levels seabirds need to maintain successful reproduction and survival (Cury et al., 2011; Robinson et al., 2015), either through localized prey depletion (Bertrand et al., 2012) or by contributing to broad-scale ecosystem change (Sherley et al., 2017b). Populations of forage nekton vary greatly in response to changing

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environmental conditions (see Changes in marine prey section), even without fishing (Checkley et al., 2017), and seabirds may only react to changes in food resources over long time scales or at the lowest levels of prey abundance (Crawford et al., 2014; Piatt et al., 2007a). Seabird-fisheries interactions are complex, and the evidence that fisheries limit resources for top predators remains equivocal (Hilborn et al., 2017; A D M Smith et al., 2011). Nevertheless, apparent competition between fisheries and threatened marine predators has led to some recent, high-profile conflicts (Cherry, 2014; Mangel, 2010), highlighting the need to better understand when seabird-fisheries competition occurs and how to manage it (Sydeman et al., 2017).

The majority of studies examining seabird-fisheries competition have used long-term monitoring data to relate changes in fisheries landings and/or abundance to seabird numbers (Crawford, 2007), fecundity (Cury et al., 2011), diet composition (Montevecchi et al., 1988), and survival (Robinson et al., 2015). These observational approaches (reviewed by Sydeman et al., 2017) have established important prey abundance thresholds below which seabird performance declines (Cury et al., 2011; Robinson et al., 2015), and provided important baselines for numerical simulations (see below). However, they have little capacity to establish causal relationships.

In recent years, numerical simulations of seabird-fisheries competition have become commonplace (Sydeman et al., 2017). Models used include mass-balance models such as Ecopath and Ecopath with Ecosim (Kaplan et al., 2013; Smith et al., 2011); bioenergetics models of prey consumption (Furness, 1978); individual-based models of foraging ecology and population dynamics (Boyd et al., 2016); system-dynamics models (Weller et al., 2016); end-to-end system models such as Atlantis (Smith et al., 2011); and ecosystem models of intermediate complexity (Punt et al., 2016). While specific conclusions differ, numerical simulations broadly suggest that seabirds can be affected by reductions in prey even in the absence of fishing, that modeled fisheries impacts on seabirds are small relative to natural variation (Kaplan et al., 2013; Smith et al., 2011), but that fishing can accelerate seabird population declines (Punt et al., 2016; Robinson et al., 2015). Several recent studies have also highlighted the importance of the spatial distribution of prey, not just its abundance (Hilborn et al., 2017; Robinson et al., 2015).

Arguably, only field experiments (e.g., time-area fisheries closures) are well placed to demonstrate causal fisheries impacts on seabirds (Sydeman et al., 2017). Field experiments, so far limited to the North Sea (U.K.) and Benguela ecosystem (South Africa), suggest small but measurable impacts on foraging behavior (Pichegru et al., 2010) and reproductive success (Frederiksen et al., 2008; Sherley et al., 2015), which should translate into population-level impacts over time (Sherley et al., 2015). However, these experiments may need decades to account for changing environmental conditions, and not all species, traits or sites studied have responded similarly (Ross-Gillespie and Butterworth, 2016), likely because of species-specific behaviors and differences in local prey fields.

Overall, the importance of the underlying environmental conditions in driving forage fish populations (and, thus, seabird responses) over fisheries impacts are clear in most cases. However, international efforts to implement ecosystem-based fisheries management (Sainsbury et al., 2000), coupled with findings that forage fish stock recovery may be slowed or their declines exacerbated by fishing (MacCall et al., 2016), and that seabirds respond most strongly to the abundance of their prey when it is scarce (Cury et al., 2011), have generated calls to suspend fishing when forage stocks reach critical lower thresholds (Pikitch, 2015). In turn, results from the small number of fisheries experiments indicating measureable impacts on top predators (see above and Conn et al., 2014) make it likely that precautionary implementation of Marine Protected Areas will continue around threatened seabird breeding colonies and at important foraging hotspots (see Marine Protected Areas section below).

Discards

Fisheries produce huge amounts of waste – of approximately 120 million tonnes of global landings, 7.3 million tonnes of discards (8% of total catch) are dumped into the sea each year (Kelleher, 2005). This subsidy attracts large numbers of scavengers including benthic invertebrates, fishes, marine mammals and seabirds (Oro et al., 2013). Discards tend to be relatively predictable in time and space, occur in highly concentrated prey patches and require less energy than diving to depth to catch fish naturally. It is perhaps unsurprising therefore that more than half of seabirds (143 species of 14 families) feed on discards to some degree (Oro et al., 2013), and it is estimated that discards could support approximately 6 million seabirds per annum in the North Sea alone (Garthe et al., 1996). Accordingly, discards can have profound effects on seabirds from individuals to populations.

Many species alter their foraging behaviour in response to discarding vessels. For instance, at the regional level some species alter their movements from super-diffusive to sub-diffusive in the presence of discarding vessels (Bartumeus et al., 2010). Moreover, patterns of activity and distribution strongly influence both the timing and distribution of movements of some species (Cama et al., 2012), with birds responding to the location of vessels at distances of ~11km (Bodey et al., 2014). Discards can also influence prey choice – with spatial and temporal variation in diet being strongly linked with variation in fishing activity (Votier et al., 2008a, 2004). Discard availability may also have important implications for life-history traits. For gulls, fisheries moratoria have led to the production of smaller eggs, lower breeding performance and poorer over-winter condition in relation to periods when discards are available (Oro et al., 2004, 1996). In contrast, the proportion of discards consumed by northern gannets *Morus bassanus* is negatively correlated with adult body condition (Votier et al., 2010) , and Cape gannet chicks grow and survive less well when provisioned on predominately discards (Gremillet et al., 2008).

Discards may also have strong indirect effects on seabirds. Perhaps the most significant effect of discards is attraction leading to entanglement – this ‘incidental’ mortality being probably the single biggest threat to seabird populations worldwide. The provision of discards has tended to favour large generalist species, which have increased in number where fisheries waste is abundant. For instance, a range expansion on northern fulmars *Fulmarus glacialis* can, in part, be attributed to the expansion of fishing fleets in the north east Atlantic (Thompson, 2006). Moreover, populations of large gulls and skuas increased during the latter part of the 20th Century, which coincided with fisheries management that led to the production of large quantities of discards. While these changes cannot be solely attributed to fisheries subsidies, the circumstantial evidence suggests that they have played an important role. However, these increases have also led to problems. Gulls and skuas are important predators, often close to the apex of marine foodwebs, which can exert strong top-down forcing. For instance, in Scotland, great skuas *Stercorarius skua* feed extensively on discards (Votier et al., 2008b), but in years of low discards and forage fish availability they switch to feeding on other seabirds (Votier et al., 2004), leading to declines in some cliff-nesting species (Votier et al., 2008b). Understanding such downstream effects of variation in discard production is challenging and at the heart of an eco-system based approach to fisheries management.

As fisheries change, it seems likely that discard production will decrease, with potential winners and loser among seabird communities (Bicknell et al., 2013). Of particular concern is the impact of prey-switching by generalist predators (Votier et al., 2004). In the short-term this may cause problems, but in the longer-term large populations of generalist predators may diminish, alleviating top-down pressure, but leaving behind very different communities. There may also be negative impacts for large piscivorous species reliant on subsidies. This may impact some components of populations more than others (Patrick et al., 2015), although scavengers do show foraging flexibility (Votier et al., 2013). On the plus side, reducing discards is likely to reduce bycatch in the long-term, although possibly following an initial increase (Soriano-Redondo et al., 2016). Future work should monitor how seabird behaviour and life-history tactics vary in response to fisheries, as well as address the many knowledge gaps about discards, such as the implications for transfer of pollution and parasites, as well as the true demography consequences of this subsidy.

Interactive and cumulative effects

As this chapter has outlined, ecological issues in the marine environment can affect seabirds in a variety of ways. Some threats result in direct mortality, while others are sub-lethal and potentially more difficult to quantify in terms of impact at the population level. Importantly, most species are vulnerable to more than one threat (Bertrand et al., 2012; Croxall et al., 2012), and effects can be cumulative and/or interactive. As described above, because seabirds use both marine and terrestrial habitats throughout their lives, they are vulnerable to environmental threats in both ecosystems (Weller et al., 2016).

As a result, many of the world’s seabirds are experiencing disproportionate population declines compared to terrestrial avian taxa (Paleczny et al., 2015). Penguins, for example, are among the most threatened groups of seabirds, due to cumulative impacts from marine and terrestrial threats (Weller et al., 2016). Similarly, taxa in the order Procellariiformes (petrels, shearwaters, albatrosses, storm-petrels, and diving petrels) are disproportionately exposed to multiple marine threats (Paleczny et al., 2015). For example, Flesh-footed Shearwater populations are declining due to a combination of fisheries bycatch, plastic ingestion, road strikes, and predation pressure (Priddel et al., 2006; Reid et al., 2013). In New Zealand, annual mortality rates of this species from commercial and recreational fisheries (Richard and Abraham, 2013) occur at rates high enough to cause a population decline, while this species is also highly vulnerable to plastic ingestion and its associated sub-lethal effects (Hutton et al., 2008; Lavers et al., 2014). Unfortunately, the consequences of these cumulative, and potentially interactive, effects are unknown for many seabird populations.

In some cases, understanding the relative and cumulative effects of multiple threats can help to manage culturally important species. Wiese et al. (2004) used long-term demographic data for eastern Canadian Arctic populations of Thick-billed Murre to establish that the cumulative impacts of hunting and chronic marine oil pollution were hindering population growth rates and, therefore, increasing the vulnerability of these populations to changes in their environment. This information was used to mitigate illegal behaviour of ship operators and thereby reduce chronic oil-related mortality (Lucas et al., 2012).

Quantifying the effect of direct mortality (e.g., through hunting, oil spills, bycatch or parasite species) is already difficult for wide-ranging populations, but the challenge in evaluating the impacts of sub-lethal effects at the population level is even greater (Oro, 2014). Further complicating efforts to estimate cumulative and interactive effects of multiple threats are the confounding influences of demographic variables (e.g., body size, breeding phenology), and ecological noise (e.g., foraging guild, at-sea distributions, interference competition, predation, and density dependence factors) on population dynamics (Oro, 2014). To determine the relative and cumulative contribution of different pressures on seabird populations, it is usually necessary to have detailed demographic data, as well as information on exposure to each threat. Modelling exercises that use simulation testing, non-informative priors (in a Bayesian context) or expert opinion, such as Models of Intermediate Complexity (MICE; Plagányi et al., 2014) or system-dynamics models (Weller et al., 2016), have been increasingly employed to understand the impact of multiple effects in complex systems.

To meet the ongoing challenge of conserving marine biodiversity, it is important that managers and conservationists remember to consider threats not in isolation, but in the context of how they may act synergistically (or antagonistically) with other threats (Weller et al., 2016). In an ideal situation, estimates of the relative and cumulative effects of multiple threats could inform decisions about conservation actions. Such decisions need to consider the magnitude of each threat, the cost of mitigating the threat, and the probability that the mitigation measure would achieve the intended outcome (Carwardine et al., 2012). When pressing conservation action is needed, but there is data scarcity or uncertainty in our understanding of how population dynamics relate to multiple drivers, models and adaptive management can be used to support decision-making (Weller et al., 2016). Ultimately, tactical decision-making requires continued investment in approaches to disentangling individual and population-level impacts from multiple stressors, as well as continued support for long-term population studies to gather these data.

Marine protected areas

While seabirds are often found thousands of kilometers from land, as immortalized by the albatross in Coleridge's *Rime of the Ancient Mariner* and more recently quantified with tracking technology, there are numerous ecological issues affecting seabirds. As humans have increasingly exploited resources from the oceans, seabirds have come into contact with a variety of ecological stressors. Consequently, consideration of marine protected areas (MPAs) to protect seabirds and other marine life has gained attention in recent decades (Agardy et al., 2011). As top predators in oceans, seabirds tend to congregate in areas at sea that are productive, often with locally high biodiversity. Thus, identifying hotspots at sea for marine birds generally correlates with identifying key sites for conservation of multiple organisms (Lascelles et al., 2012). However, by the very nature of their ability to key into these sites of high productivity, seabirds also tend to come into conflict with locations that are key for human resource extraction, notably fisheries (Brothers, 1991); see Seabird-Fisheries interaction section).

As of 2017, there were 13,674 recognized MPAs, representing 2.98% of the global ocean (Marine Conservation Institute, 2017), although these clearly have varying levels of protection. MPAs are mostly focused along coastal and nearshore areas, with far fewer existing in the pelagic zone (Game et al., 2009). Moreover, the size of MPAs varies greatly, and may not be adequate in many cases to provide suitable protection for seabirds (Thaxter et al., 2012). Increasingly, scientists are realizing that for MPAs to be effective, they must consider the movement of organisms, not just of top predators but also of the prey that attracts them to these sites. Consequently, there are substantial temporal and spatial aspects to effective MPA design (Agardy et al., 2011). Pelagic seabirds may require large MPAs, or carefully placed aggregates of small MPAs, to protect all of their life stages, while other species may benefit from smaller, well-defined areas that protect important resources (Lascelles et al., 2012; Thaxter et al., 2012). However, an overriding consideration is that proper management of MPAs has a greater impact on effectiveness than simply MPA size (Gill et al., 2017).

Although it can be difficult to measure the benefits of MPAs on seabirds, some studies have shown positive effects of MPAs mostly because of the availability of tracking/telemetry devices. The proliferation and miniaturization of telemetry devices has revolutionized our ability to follow almost any seabird (Hart and Hyrenbach, 2009) and now allows us to locate the key foraging areas, migration stopover sites, and wintering areas of birds from the poles to the tropics (Shaffer et al., 2005). With this increased knowledge and ability to define key marine habitats for different species, we are now able to assess temporal and spatial threats to seabirds when they are at sea, such as development of fisheries (Montevecchi et al., 2012), and thereby provide credible scientific data on the need for MPAs and their benefits. For example, Young et al. (2015) found that two large MPAs in the Pacific (Pacific Remote Islands Marine National Monument and Papahānaumokuākea Marine National Monument) effectively contained the majority of foraging habitat for three species of sulids during incubation and early chick rearing. These authors concluded that pelagic MPAs have strong potential to protect relevant habitat for some tropical pelagic seabirds. In another example, experimental fisheries closures in South Africa suggested that even relatively small, no-take zones may reduce foraging effort (Pichegru et al., 2010) and improve chick survival (Sherley et al., 2015) for penguins relying on pelagic prey, with demographic benefits expected to accrue in the long run (Sherley et al., 2015; Weller et al., 2016). This strongly suggests that protection of well-defined areas known for productivity (e.g., fronts) will benefit top marine predators like seabirds. The much greater challenge is generating the collaborative political will to create MPAs, especially in the pelagic zone, given the weight of scientific evidence from multiple taxa showing their long-term benefits for conservation and fishing industries (Agardy et al., 2011; Hart and Hyrenbach, 2009).

Colony restoration

Colony restoration is a leading method to mitigate seabird population declines associated with a variety of anthropogenic impacts, including both marine and terrestrial ecological issues. This chapter defines colony restoration as any action taken to mitigate population declines at a nesting colony and increase populations of nesting seabirds through expanding available nesting habitat, adult survival, and/or fledging success. Colony restoration can be separated into two broad classes of activities: 1) island restoration (e.g., eradication of introduced predators or non-native invasive species) and 2) active seabird restoration (e.g., translocations, social attraction, and colony enhancement).

Introductions of mammalian predators to islands is a significant threat to insular bird populations (Diamond, 1985; Moors and Atkinson, 1984; Towns et al., 2011b) and has been a major focus of colony restoration work. The negative direct and indirect effects of introduced predators on seabirds, particularly rats (*Rattus* spp.) and cats (Jones et al., 2008), and the resultant ecosystem-wide changes that occur when seabird populations are drastically reduced or eliminated (Fukami et al., 2006; Grant-Hoffman et al., 2010) gave rise to the need for island restoration through the eradication of introduced predators. To date, at least 925 islands have had introduced vertebrates successfully eradicated (DIISE, 2017), allowing the islands to revert to a more natural state. The success of these eradication programs can be far-reaching and may result in increased reproductive rates, survival, and re-colonization of seabird species (Ismar et al., 2014; Jones et al., 2016; Towns et al., 2016). Further, the eradication of introduced Arctic foxes (*Vulpes lagopus*) from islands within the Alaska Maritime National Wildlife Refuge resulted in population expansion of Whiskered Auklets (*Aethia pygmaea*) (Williams et al., 2003) and the re-colonization of Amatignak Island by Ancient Murrelets (*Synthliboramphus antiquus*) (Buxton and Jones, 2012). However, predator eradication alone may not be sufficient to facilitate recovery, and islands may become locked into a ‘non-seabird’ state (Jones, 2010).

The propensity of many seabirds to nest among conspecifics and their high rates of philopatry make re-colonization of previously occupied sites unlikely, especially in the short-term (but see Brooke et al., 2007; Jones et al., 2016). Further, given that passive re-colonization tends to occur when a source population is within 25 km (Borrelle et al., 2015; Buxton et al., 2013) and that most seabirds exhibit high survival and low reproductive rates (Weimerskirch, 2002), for many species it may take many decades for a colony to develop (Kappes and Jones, 2014). Thus, active restoration is often desired and an important addition to restoration projects (Fig 10). The best known, and pioneering, active seabird restoration project is Project Puffin. Started by the National Audubon Society in 1973, the goal of this project was to restore breeding Atlantic Puffins to Eastern Egg Rock Island in the Gulf of Maine (Kress, 1998). This work led the way in developing methods to restore seabirds to historically occupied nesting islands using chick translocation and social attraction, including acoustic attraction methods. More recently, Jones and Kress (2012) reviewed global active seabird restoration programs and found that over 128 seabird restoration projects have been implemented in 14 countries with varying success. Moreover, these authors note that methods used to restore seabird nesting colonies need to be implemented in response to specific aspects of the species' life history. For example, chick translocations are often not successful for semi-precocial species (where adults lead chicks to the ocean and provision them on the water), but have a reasonable rate of success in species that are fed at the nest and fledge independent of their parents (Jones and Kress, 2012).

Other restoration activities, such as habitat modification and/or creation of artificial/new habitat, are undertaken to mitigate anthropogenic impacts such as harvesting or oil spills that may occur outside of the breeding period or away from a nesting colony, or to safeguard a population that may occur at a limited number of colonies. For example, Priddel et al. (2006) used nest boxes to create artificial habitat to establish a colony of Gould's Petrels (*Pterodroma leucoptera leucoptera*) on Boondelbah Island in Australia. Prior to this, Gould's Petrels were restricted to one colony on Cabbage Tree Island (Priddel et al., 2006). Predator-proof fences are another technique used to safeguard at-risk colonies against terrestrial predators. Fences, such as the one built at Ka'ena Point, Hawai'i allowed the eradication and control of introduced species within the fence that permitted record numbers of Wedge-tailed Shearwater (*Ardenna pacifica*) and Laysan Albatross (*Pheobastria immutabilis*) chicks to fledge (Young et al., 2013). Overall, there are a large number of activities encompassed in colony restoration and the continual improvement of techniques will continue to benefit global seabird populations.

Community-based seabird conservation work

Community-based outreach and engagement programs are essential components of long-term conservation strategies in places where humans co-exist with wildlife. Until relatively recently, most seabird conservation activities, including invasive species eradications, occurred on remote, uninhabited islands (Towns et al., 2011). These projects have largely been undertaken by government agencies and NGOs, often in the absence of meaningful community involvement (Towns et al., 2013). However, more than half of islands (55%) identified as having high conservation benefits from invasive mammal eradications also have permanent human communities (Brooke et al., 2007). Additionally, seabirds are valued by many indigenous communities across the globe, with seabird populations important to culture and food security (Mallory et al., 2006; Moller, 2009). In this context, the fundamental need for substantive engagement with local communities becomes readily apparent, and without genuine commitments from and active participation by local communities, conservation initiatives are not likely to succeed in the long term.

In some regions there is limited literature available on community participation in seabird and island conservation, likely reflecting the short history of seabird conservation management attempts on inhabited islands (Towns et al., 2011). In other regions, particularly in Canada with the Inuit, and in New Zealand with the Māori, there is more documentation of researchers and indigenous communities working together to direct research questions and achieve successful co-management strategies (Mallory et al., 2003; Moller, 2009). This includes the use of traditional knowledge to identify species in decline (e.g., Mallory et al., 2003; Robertson and Gilchrist, 1998). The importance of cultural inclusion in community-based conservation is a critical component to the long-term sustainability of seabirds and communities, and thus needs to be considered whenever conservation projects are undertaken.

Wider community-based efforts have been successful in many different regions using a variety of different strategies and approaches (Towns et al., 2011). Following are three examples of successful long-term community-focused programs that have advanced seabird conservation. First, efforts led by the Grupo de Ecología y Conservación de Islas (http://www.islas.org.mx/) in México provide compelling examples of innovative engagement with indigenous communities, where both the community and the island's ecosystems and species benefited (Aguirre-Muñoz, et al., 2005; Towns, et al., 2011). Second, on Réunion Island in the Indian Ocean, Life + Petrels (http://www.petrels.re/?lang=en), has used educational initiatives, worked closely with communities on the island on a stranded petrel rescue program, and organized a highly successful "Nights Without Lights" campaign to raise awareness of the status of and engage residents in on-the-ground actions to address the impacts of introduced mammalian predators and light attraction on two endangered endemic petrel species (Pinet and Le Corre pers. comm.). Third, in Chile, Oikonos Ecosystem Knowledge works closely with multiple stakeholder groups, from local communities to federal agencies, and using innovative programs, such as a Shearwater Cup soccer tournament and festival, creative writing and drawing workshops for children, and environmental education programs for schoolchildren (http://oikonos.org/what-we-do/) to achieve seabird conservation goals for the region.

Prior to initiating any conservation or restoration project, the effect of the proposed action/s on human inhabitants and their activities, cultural needs, and relationships need to be considered. This requires clearly defined seabird conservation goals to be agreed upon that integrate local and indigenous knowledge, and community needs (Oppel et al., 2010; Reed, 2008). To ensure conservation is socially-supported, it is important to work with local communities and other stakeholders from the outset. Such an approach to conservation must ensure that there are fair governance and decision-making processes that include and equitably represent all stakeholders, rights-holders and relevant groups, respect cultural heritage, and promote transparency and accountability in conservation processes (Bennett et al., 2017). Successful outcomes require a flexible approach that recognizes that communities possess unique social contexts and are contingent on a project design that is appropriate for the particular local environment, both socio-culturally and technically (Lundquist and Granek, 2005; Towns et al., 2011b). Passionate leadership, the demonstration of a genuine commitment to the community, and regular presence of, and engagement by, conservation scientists and facilitators in local communities build trust and credibility; but also require more time than external agencies and scientists may realize. Ultimately, effective community conservation requires a trans-disciplinary approach that joins conservation professionals and their science, and the needs and aspirations of the indigenous and local community (Towns et al., 2013, 2011a).

International conservation efforts

Throughout their migrations, seabirds frequently occupy waters within the jurisdictions of multiple countries, as well as Areas Beyond National Jurisdiction, in which it is often difficult to take conservation actions (Dias et al., 2017). Consequently, threats in one region may impact a species across a much broader area (Iwamura et al., 2013), and so conservation of marine migratory species requires cooperation by many parties, including national governments, international organizations, and industry regulators. Therefore, seabird conservation poses a challenge to most of the current conservation frameworks as flyway-level study, action, and conservation are often needed.

At present, the widest international focus on seabirds is through the Agreement of Conservation of Petrels and Albatross (ACAP), under the Convention on Migratory Species (CMS), although, this agreement covers only a few groups of seabirds. In the polar regions there is a long history of international cooperation between the Arctic Council's Conservation of Arctic Flora and Fauna's (CAFF), Circumpolar Seabird group (C-bird), and the Scientific Committee's for Antarctic Research's (SCAR) Expert Group on Birds and Marine Mammals (EG-BAMM). These organisations focus on fostering knowledge exchange and research leadership in their respective polar regions. Other groups with large trans-boundary interests in seabirds include the African-Eurasian Waterbird Agreement (AEWA; also under CMS), the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR), and the East Asian Australasian Flyway Partnership (EAAFP). In addition to these inter-governmental organisations, there are numerous non-governmental organisations involved in seabird conservation efforts. While this list is not exhaustive, it illustrates that there are frameworks in place aimed to promote integrated seabird conservation efforts. International scale management and agreements are inherently complex, thus it can take time to achieve meaningful conservation outcomes. Importantly however, these collaborative international initiatives provide a forum for knowledge exchange and scientific cooperation, a co-operative and international approach that is critical to conserving the world's enigmatic seabird species.

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List of Figures

Figure 1 – Due to changing climatic conditions seabirds in some areas are experiencing increased predation. Here a polar bear feeds on thick-billed murres (*Uria lomvia*). The frequency of these events at several colonies in the Canadian Arctic have increased over the last few decades in relation to decreases in summer sea ice which the bears usually use to feed on seals. Photo courtesy of Kyle Elliot.

Figure 2 – A – *Ixodes uriae* ticks; an engorged larva, and engorged nymph and an engorged female. B- engorged tick collected from within a single puffin burrow. Photo credit Karen McCoy.

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Figure 5 – Collection of thick-billed murre (*Uria lomvia*) eggs at Prince Leopold Island, Nunavut Canada for contaminant analysis. This study site has contributed to the long term seabird contaminants study managed by Environment and Climate Change Canada and the Northern Contaminants Program. This work has been critical in such international regulations of contaminants as the Stockholm Convention and the Minamata Convention. Photo credit Mark Mallory.

Figure 6 – A - a Flesh-footed shearwater (*Ardenna carneipes*) fledgling (approximately 90 days old) found on Lord Howe Island, Australia, in May 2012 showing the ingested plastics in its stomach. B – the ingested plastics from the same individual spread out in the lab. Photos courtesy of Jennifer Lavers.

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Figure 8 – Albatrosses and petrels caught as incidental bycatch during a single set by a pelagic longliner in Uruguay. Photo courtesy of Martin Abreu.

Figure 9 – A thick-billed murre (*Uria lomvia*) bringing a capelin (*Mallotus villosus*) back to its chick. Capelin are also a commercially fished species, leading to competition between seabirds and fisheries in some regions for this small forage fish species. Photo courtesy of Kyle Elliot.

Figure 10 – Grey-faced petrel (*Pterodroma macoptera gouldi*) chick being fed at Matakohe Island, New Zealand during a translocation. Photo courtesy of Cathy Mitchell.