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

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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 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.

Introduction

Seabirds are often abundant on islands (Mulder et al., 2011). However, colonial nesting habits, low reproductive output and extended periods of parental care at breeding grounds make

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seabirds vulnerable to predators (here we use the term ‘predator’ to describe only non-native mammalian predator species; Furness & Camphuysen, 1997; Baillie et al., 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 et al., 2006; Jones et al., 2008; Varnham, 2010; 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 (IUCN, 2015; Birdlife International, 2015). Accordingly, predator removal is considered to be one of the most effective seabird conservation strategies (Jones, 2010; Towns et al., 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 (Jones & Kress, 2012; Towns et al., 2006; Towns, 2009; Lavers et al., 2010; 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 (but see: Lavers et al., 2010; Buxton et al., 2014; 2015). Available research has described variable responses among species and islands (Gaze, 2000; Lavers et al., 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 et al., 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 E), 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 (*Pelagodroma albiclunis*; Gaskin, 2012; C. Gaskin, unpublished data).

Twenty-five species of invasive predators of seabirds, have been successfully eradicated from 1016 islands around the world (Island Conservation, 2015; Jones et al., 2016). 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 following predator eradication through space and time 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 diversity maintains a dynamic equilibrium over time, influenced by area and ecological diversity (Preston, 1962; McArthur & Wilson, 1967; Simberloff, 1974). Therefore, we would expect that seabird diversity 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 bigeographical 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.

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 (Fig. 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; Supporting information, Table S2). We excluded islands <1 ha because of the small island effect (Burns et al., 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; Appendix 1). We also excluded islands that have a permanent residential population because of the potential effects of human activities on the establishment of seabird colonies (e.g. land use, presence of domestic animals, light pollution; 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) (Fig. 1; Supporting information, Appendix 2). The climate of the Hauraki Gulf is temperate-humid with a mean annual temperature 16°C, relative humidity of 87% and mean average rainfall 1202 mm (CliFlo, 2016).

Figure 1[Map of spatial data distribution] <<insert here>>

Methods

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 (Fig. 1; Supporting information, Appendix 2). 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 et al., 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 macroptera 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, 2015). We included 16 seabird species in the study: Procellariiformes (n=14), Sphenisciformes (n=1), and Pelecaniiformes (n=1) (Supporting information, Appendix 1, Table S1). 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 (*Sus scrofa;* 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 (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 (Supporting information, Appendix 2).

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 (Okasen, 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 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 1). These sites represent class I and II (pristine and outstanding quality; Taylor, 1989; Supporting information, Appendix 1, Table S2.) because of which, we assumed that there was no limitation of available breeding habitat for seabirds.

Table 1 [Species composition of reference islands] <<insert about here>>

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, Appendix 1). 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 to 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, Appendix 1; Bivand et al., 2013; Paradis et al., 2004; Pebesma, 2004).

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.

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, 2002). 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 (Fig. 3).

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 (Tab. S1) were averaged over all breeding species on a given island.

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; Fig. S1). GLM parameter estimates are presented in Table 2, and model predictions are illustrated in Fig. 2.

Table 2 [GLM parameter estimates] <<insert about here>>

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 (Fig. 2).

Figure 2 [Observed species richness as a function of island area] <<insert about here>>

The largest suite of species included in the analysis was on *cleared* islands, with the smallest on *invaded* islands (Fig. 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 (p = 0.027, standard residual = -1.92). Seven species of seabirds present on *cleared* and/or *uninvaded* islands were absent from *invaded* islands (Fig 3.).

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 3; Fig. S4).

On the reference islands, species composition was stable for up to 85 years (Table 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 1).

Figure 3 [Chi-squared results of expected species richness] <<insert about here>>

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; McArthur & 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 (Fig. 2). This recolonisation result is promising, especially since all of the species absent from invaded islands are now breeding on *cleared* islands (Fig. 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 1.), perhaps as spillover from populations increasing elsewhere as a part of natural assemblage equilibrium processes (C. Gaskin, unpublished data; Simberloff, 1974; Buxton et al., 2015). While differing rates of re-colonisation and local extinction may result in a species richness rebound effect following the removal of predators (Cirtwill & Stouffer, 2015), ecological diversity is likely to exert a strong influence on the return of seabird assemblages to equilibrium on *cleared* islands (Preston, 1962; McArthur & 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 (Fig. 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 4 [Schematic of influences on seabird recovery] <<insert about here>>

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 recolonisation (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; Fig. S1). 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 3, Fig. S4). 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 (Gaskin & Rayner, 2013; Borrelle, 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, Fig. S4). 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 (Fig. 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 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 (2015) 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 2015). 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 4 [Example of pre- and post-predator eradication seabird species assemblage on Burgess Island, Hauraki Gulf] <<insert about here>>

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 et al., 1998; Parejo et al., 2005; 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 et al., 2005). Further, the recruitment of immature individuals is influenced by the availability of suitable habitat and social cues (Danchin et al., 1998; Parejo et al., 2005). 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 et al., 1998; Parejo et al., 2005; 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 (Fig. 3).

Size & Habitat: We found that five of the 16 seabird species included in our analyses are absent from *uninvaded* islands (Fig. 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, 2015), 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 et al., 2003b), 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 (estimated at 286,000 breeding pairs in 2007; Rayner et al., 2007). Similarly, black petrels were once more widely distributed, breeding at five or more sites on the North Island before 1900 (Imber et al., 2003a). Black petrels 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., 2012). For species such as Cook's and black petrels, 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., 2015).

Recruitment: We found that the proportion of islands with fluttering shearwaters was greatest on *uninvaded* islands (Fig. 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

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widely distributed on *cleared* islands, as was found for sooty shearwaters which have an estimated population of less than 800 pairs (Fig. 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 (Dittman et al., 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 (*Pelecanoides urinatrix*) 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 black petrels and Pycroft's petrels with AFR of 5-10 years (New Zealand Birds Online, 2015). 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; Fig. S3a). 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; Fig. S3b). 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 et al., 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 (Schreiber & Burger, 2001; Hamer et al., 2002), although some seabird colonies do show emigration and immigration so are not closed (Igual et al., 2007, Lawrence et al., 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 (e.g. 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.

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Author contributions:

SBB and DRT conceived and designed the study. DRT, CPG provided the data and SBB and PHBS analysed data. SBB, DRT, PHBS, CPG wrote and edited the manuscript.

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Biographical sketches

STEPHANIE BORRELLE's interests include island restoration, and how demography and at-sea threats might be influencing seabird recovery following land-based conservation actions. PHILIPP BOERSCH-SUPAN is a quantitative ecologist focused on marine ecosystems. He is particularly interested in the ecology of oceanic predators and their prey. CHRIS GASKIN conducts surveys and research on seabirds in northern New Zealand. He coordinated the Important Bird Area (IBA) programme for New Zealand's seabirds. DAVID TOWNS's research has been based on understanding the effects of invasive predators on island ecosystems, investigating methods for restoring modified island ecosystems, and the development of biological and social metrics for measuring progress with restoration projects. He is Principal Science Adviser for the New Zealand Department of Conservation and Programme Leader for Applied Conservation at Auckland University of Technology.

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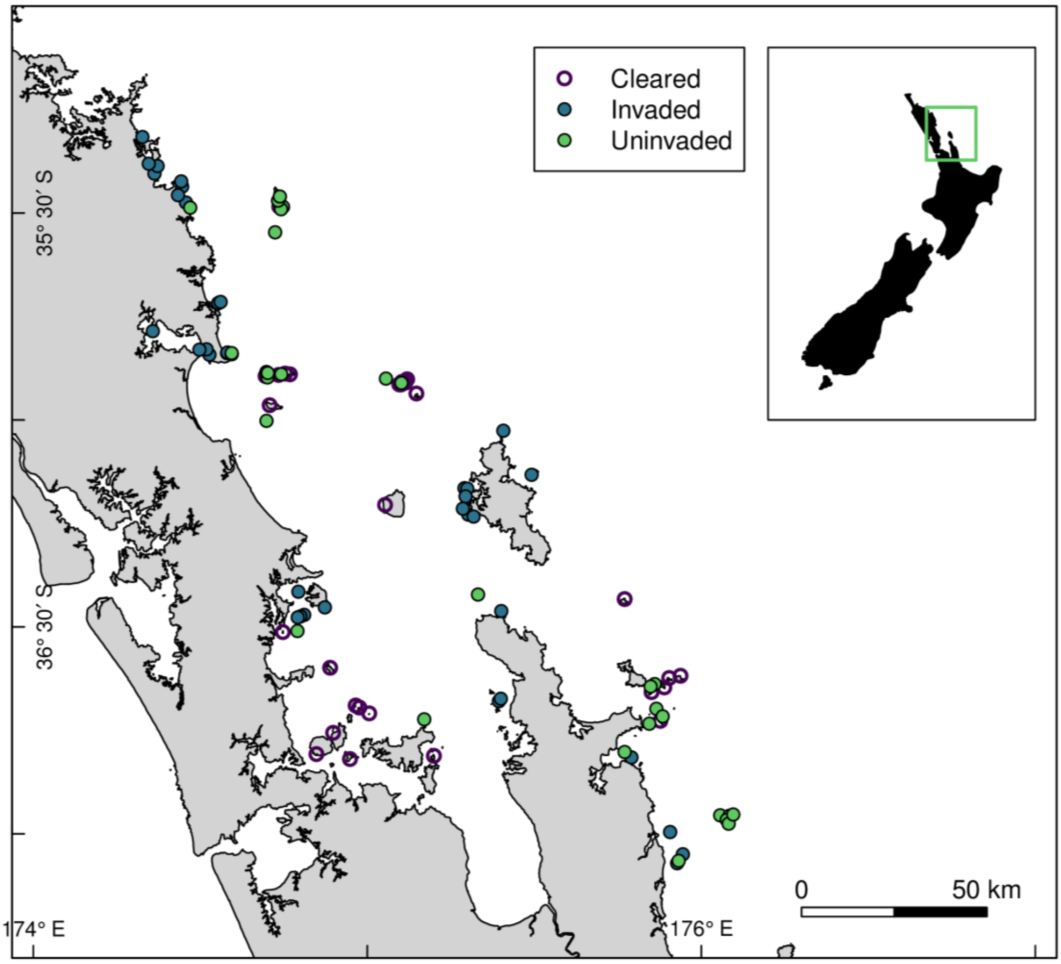

Figure 1: The Hauraki Gulf, New Zealand study area and seabirds presence data locations (n=98).

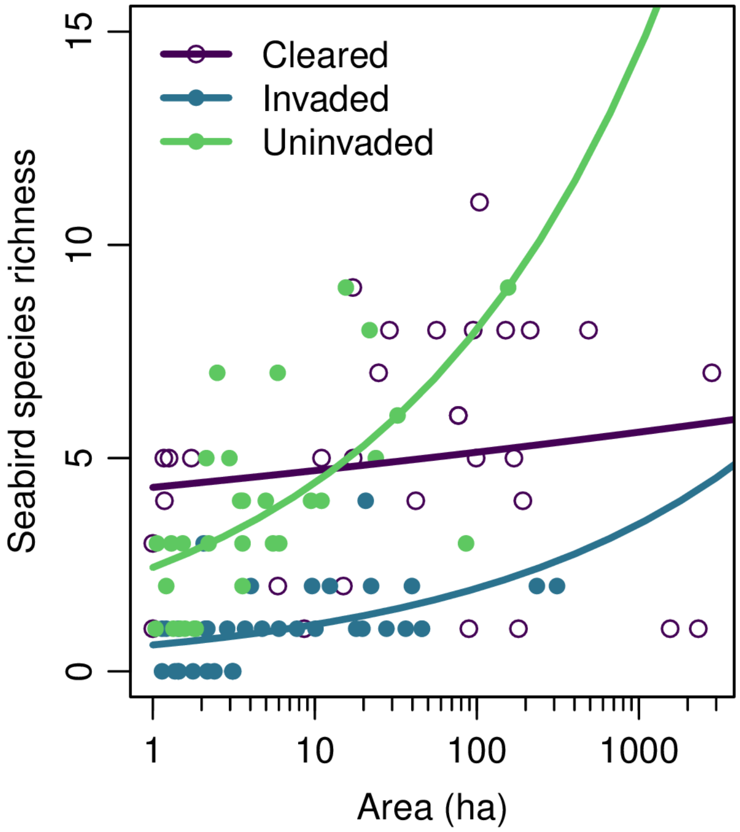

Figure 2: Observed species richness and GLM predictions as a function of island area comparing uninvaded islands (intercept = 2.43, slope = 0.26), cleared islands (intercept = 4.31, slope = n.s.), and invaded islands (intercept = 0.62, slope = 0.25). Model parameter estimates are detailed in Table 2.

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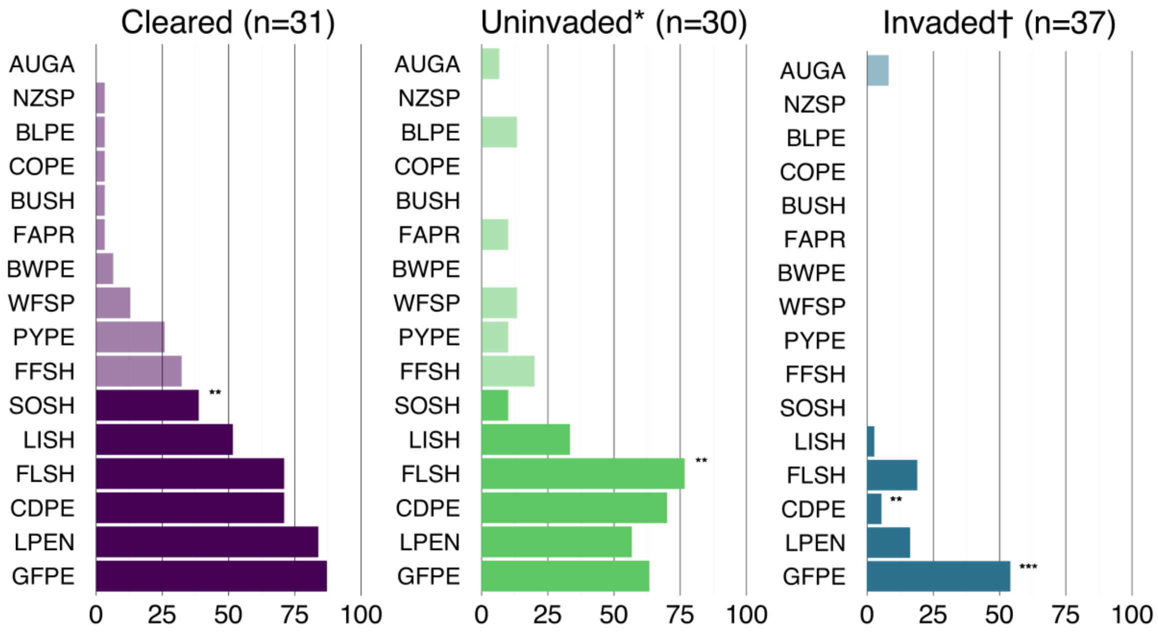

Note: *p<0.1; **p<0.05; ***p<0.01

*Figure 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.*

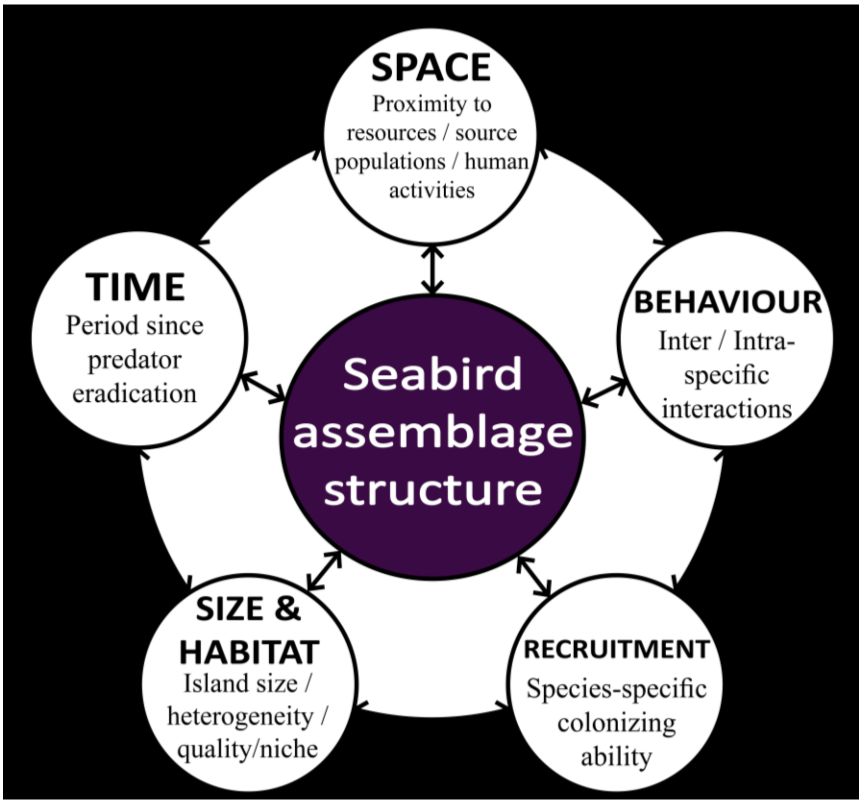

Figure 4. Schematic representation of the key influences on seabird recolonisation to islands cleared of predators.

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Table 1: Species composition recorded over time on reference islands in the Hauraki Gulf, New Zealand that have never had 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]

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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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Table 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
log(ha):Predator_statusCleared	0.038	0.036	0.295
log(ha):Predator_statusInvaded	0.249	0.096	0.009
log(ha):Predator_statusUninvaded	0.259	0.062	< 0.001

Table 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

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Table 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				●

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