ESTIMATING THE IMPACT OF MARINE THREATS TO SEABIRD RECOVERY AFTER PREDATOR ERADICATION

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ABSTRACT

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Pelagic seabirds are one of the most threatened taxa due to sustained and intensifying threats at their breeding sites on land and when foraging at sea. Predator eradication at seabird breeding sites has become a key strategy for the long-term conservation and viability of seabird populations. However, the extent to which increasing marine threats (i.e., those causing excess mortality such as fisheries bycatch, plastic ingestion, climate change/prey depletion) impact recovery remains poorly understood. We used computer simulations to model demographic data obtained from a review of existing databases to explore the impact of direct marine threats to seabird recovery following land-based predator eradication. Using the resulting parameters, we explored the impact of multiple marine threats to the population growth rates of 16 seabird species from 36 colonies worldwide. Next, we tested whether and which seabirds' phylogenetically conserved traits could predict risk to multiple marine threats. The majority (88%) of examined colonies are projected to recover despite multiple marine threats, in the absence of invasive predators. We suggest that phylogenetically conserved traits (e.g., body mass) and species' ecological descriptors (e.g., foraging strategy) are not good predictors of how interacting marine threats may affect population recovery. In the absence of robust at-sea mortality data or reliable predictors of risk from several at-sea sources of mortality, monitoring population recovery for seabirds is a critical element of seabird island restoration projects. Our conclusions can shape how managers implement additional conservation actions for species that fail to recover following predator eradication.

Key words: Climate change, comparative phylogenetic analysis, conservation, fisheries bycatch, plastic pollution, restoration

INTRODUCTION

Human activities exert intensifying and novel destabilizing forces on ecosystems and species. These forces have already led to extinctions and shifts in ecosystems (Ceballos *et al.* 2017). The typically low intrinsic population growth rate (Schreiber & Burger 2002) of pelagic seabirds (order: Procellariiformes) render them particularly vulnerable to sustained incidental mortality due to human activities. These activities include (i) the introduction of invasive mammalian predators at breeding sites (Jones *et al.* 2008, Towns *et al.* 2011) and (ii) anthropogenic marine stressors, such as pollution, fisheries bycatch and competition, and climate change (Provencher *et al.* 2019, Rodríguez *et al.* 2019). These threats can act on a given seabird species simultaneously (Lawler *et al.* 2002, Barbraud *et al.* 2012), they can be separated by time and/or space (Sutherland *et al.* 2012), or they can target different stages in a species' life cycle (Votier *et al.* 2009). Consequently, seabirds are one of the most threatened taxa in the world, with 63 out of the total 147 procellariiform seabird species being currently classified as Vulnerable or worse (IUCN 2021).

Quantifying the population-level impacts of single or multiple anthropogenic marine threats is challenging because we lack detailed demographic information for most of the extant procellariiform seabird species (Dias *et al.* 2019, Rodríguez *et al.* 2019, BirdLife International 2021). Monitoring following predator eradication at breeding sites is sparse or absent (Buxton *et al.* 2014). This limitation belies our ability to accurately assess how at-sea pressures might impact species recovery following predator eradication (Kappes & Jones 2014, Brooke *et al.* 2018). The resulting uncertainty is confounded by (i) the challenges of quantifying at-sea mortality, (ii) the sub-lethal effects of marine stressors on population viability (Lavers *et al.* 2014, Tanaka *et al.* 2015, Clukey *et al.* 2018), and (iii) the lack of knowledge regarding how multiple stressors interact or cumulate to affect seabird population trends (Burthe *et al.* 2014). Such limitations make it challenging to address how current conservation strategies that mitigate one threat intersect with other threats to impact seabird population recovery.

Here, we used a demographic modelling approach to explore the impact of multiple marine threats on the recovery of seabird colonies following invasive predator eradication. Our study tests the following hypotheses: (H1) The expected annual mortality from the interacting marine threats of fisheries bycatch, plastic pollution, and climate change/fisheries depletion will exceed the expected population recovery of a colony after predator eradication;

and (H2) the risk of marine threats for a species can be inferred from phylogenetically shared morphometric and ecological traits. Support for H2 would provide an approach to predict population recovery from closely related seabird species when mortality data from marine threats is lacking.

METHODS

To test H1, we first estimated the annual mortality threshold (AMT) for separate populations of 16 seabird species on 23 widely distributed islands (Fig. 1, Richard *et al.* 2017). AMT is defined as the number of adults in a population that can be removed annually with the population remaining demographically stable (population growth rate $r_{max} = 0$) or increasing ($r_{max} > 0$; Richard *et al.* 2017; Fig. A1 in Appendix 1, available online). This approach is appropriate for petrels and albatross because they tend to be long-lived, with life-history theory predicting that adult survival is a key to their population dynamics (Weimerskirch 2002, Schreiber & Burger 2002). We then calculated the risk ratio of local population extinction to each of the aforementioned marine threats for 16 seabird species from 36 colonies on 23 islands where predators have been eradicated and for which data on demographic rates and population size are available (Table 1, Fig. 1).

To test H2, we used an expanded dataset of 81 procellariiform seabirds for which demographic data were available (Appendix 2). We applied phylogenetic comparative tools to explore whether key morphometric (mean adult body mass) and ecological (primary foraging strategy, primary diet, and at-sea distribution) characteristics predict species' population vulnerability to marine threats, using the AMT approach as a proxy. To validate our metrics of population performance and vulnerability for the 81 species

included in our H2 analysis, we checked them against the IUCN Red List categories (IUCN 2021).

Most procellariiforms breed on remote islands, so collecting accurate demographic data consistently can be logistically and financially challenging, resulting in significant uncertainty of parameter estimates (Richard & Abraham 2013). 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 mortality rates. This is because it is impossible to remove the effect of anthropogenic sources of mortality from studies. Further, natural mortality data are imprecise because dispersal and emigration are rarely investigated. To account for these uncertainties, we applied a Monte Carlo process with 5 000 iterations sampled from distributions identified during data wrangling in which we fitted each parameter estimate (adult survival, at-sea distribution, age at maturity) to multiple distributions and used the most appropriate distribution for each parameter (detailed below).

Statistical methods

To calculate the AMT, we expanded the Demographic Invariant Method (DIM, Niel & Lebreton 2005). The DIM combines matrix population models (Caswell 2001) and allometric relationships to calculate the maximum annual growth rate, λ_{max} (Niel & Lebreton 2005, Dillingham *et al.* 2016, Richard *et al.* 2017). A strength of the DIM over other demographic approaches (e.g., population viability analyses; Chaudhary & Oli 2020) is that it requires minimal demographic information to estimate (i) the intrinsic annual population growth rate of a species' population under optimal conditions and (ii) the AMT for the species. Using the DIM

Fig. 1. Colony locations of the 16 species assessed for impacts of marine threats to colony recovery following predator eradication.

TABLE 1

Model estimates for each colony including population size, annual mortality threshold, and potential mortality from each of the marine threats of fisheries bycatch, plastic ingestion, and climate change/prey depletion, given as the mean and standard deviation (sd) of the mean[a]

Species (IUCN status)	Colony (region)[b]	Population size (sd)	Annual mortality threshold (sd)	Fisheries bycatch mortality (sd)	Plastic ingestion mortality (sd)	Climate change/prey depletion mortality (sd)	Risk ratio (sd)
Calonectris diomedea (LC)	**La Scola (Italy)**	**131 (165)**	**5 (5.8)**	**3.28 (4.61)**	**0.12 (0.02)**	**0.14 (0.02)**	**3.55 (4.62)**
Ardenna carneipes (NT)	**Lady Alice (NZ)**	**3510 (5174)**	**118 (176.0)**	**0.98 (1.49)**	**0.12 (0.02)**	**0.15 (0.02)**	**1.25 (1.50)**
	Ohinau (NZ)	**7367 (10 459)**	**246 (342.1)**	**0.94 (1.38)**	**0.12 (0.02)**	**0.15 (0.02)**	**1.22 (1.38)**
	Whatupuke (NZ)	**4196 (5991)**	**139 (194.8)**	**0.91 (1.26)**	**0.12 (0.02)**	**0.15 (0.02)**	**1.19 (1.26)**
	Coppermine (NZ)	**4723 (6421)**	**185 (258.8)**	**0.81 (1.18)**	**0.10 (0.01)**	**0.13 (0.01)**	**1.04 (1.18)**
Ardenna pacifica (LC)	Oahu (Hawaii)	5811 (9688)	256 (438.8)	0.74 (1.14)	0.05 (0.01)	0.12 (0.02)	0.91 (1.14)
	Kadomo (Fiji)	1377 (20 212)	61 (91.3)	0.73 (1.03)	0.05 (0.01)	0.12 (0.02)	0.90 (1.04)
	Serrurier (Australia)	60 806 (85 885)	2681 (3943.7)	0.71 (1.05)	0.05 (0.01)	0.12 (0.02)	0.88 (1.06)
	Surprise (New Caledonia)	511 (689)	22 (31.4)	0.70 (1.08)	0.05 (0.01)	0.12 (0.02)	0.87 (1.08)
	Monuriki (Fiji)	3505 (4811)	154 (220.2)	0.69 (0.91)	0.05 (0.01)	0.12 (0.02)	0.86 (0.91)
	Jarvis (United States)	167 (223)	7 (10.2)	0.69 (0.87)	0.05 (0.01)	0.12 (0.02)	0.86 (0.88)
Puffinus puffinus (LC)	Lundy (UK)	500 (639)	11 (16.5)	0.00 (0.00)	0.21 (0.11)	0.27 (0.14)	0.49 (0.25)
	Ramsey (UK)	1416 (2155)	33 (56.7)	0.00 (0.00)	0.21 (0.10)	0.27 (0.13)	0.48 (0.24)
Bulweria bulwerii (LC)	Selvagem Grande (Portugal)	1 743 481 (2 401 203)	45 177 (67 917.4)	0.00 (0.00)	0.19 (0.05)	0.20 (0.05)	0.39 (0.09)
Pterodroma pycrofti (VU)	Red Mercury (NZ)	35 222 (54 520)	912 (1443.2)	0.00 (0.01)	0.17 (0.04)	0.20 (0.05)	0.37 (0.09)
	Aorangi (NZ)	133 (178)	3 (4.6)	0.00 (0.01)	0.16 (0.04)	0.20 (0.05)	0.37 (0.09)
Pterodroma cookii (VU)	Hauturu (NZ)	43 165 (58 440)	1095 (1527.3)	0.00 (0.00)	0.16 (0.02)	0.20 (0.03)	0.36 (0.05)
Pterodroma gouldi (LC)	Hauturu (NZ)	98 (125)	3 (3.5)	0.01 (0.01)	0.12 (0.03)	0.20 (0.05)	0.33 (0.08)
	Burgess (NZ)	2562 (3561)	66 94.5)	0.01 (0.02)	0.11 (0.03)	0.20 (0.05)	0.33 (0.08)
	Atihau (NZ)	10 280 (14 348)	266 (358.3)	0.01 (0.02)	0.11 (0.03)	0.20 (0.05)	0.33 (0.08)
	Motuharekeke (NZ)	2571 (3608)	66 (93.3)	0.01 (0.01)	0.11 (0.03)	0.20 (0.05)	0.33 (0.08)
	Otata (NZ)	814 (1045)	21 (26.7)	0.01 (0.02)	0.11 (0.03)	0.20 (0.05)	0.33 (0.08)
	Moutohora (NZ)	69 695 (96 614)	1812 (2641.2)	0.01 (0.02)	0.11 (0.03)	0.20 (0.05)	0.33 (0.08)
Puffinus assimilis (LC)	Burgess (NZ)	1143 (1775)	47 (73.3)	0.00 (0.00)	0.12 (0.02)	0.13 (0.02)	0.24 (0.03)
	Red Mercury (NZ)	3350 (4524)	137 (184.7)	0.00 (0.00)	0.12 (0.02)	0.13 (0.02)	0.24 (0.03)
	Atihau (NZ)	1161 (1607)	48 (67.9)	0.00 (0.00)	0.12 (0.02)	0.12 (0.02)	0.24 (0.03)
Ardenna bulleri (VU)	Aorangi (NZ)	25 261 (33 957)	872 (1201.5)	0.00 (0.00)	0.09 (0.01)	0.15 (0.02)	0.24 (0.03)
Puffinus gavia (LC)	Atihau (NZ)	1055 (1497)	43 (60.5)	0.01 (0.01)	0.11 (0.02)	0.13 (0.02)	0.24 (0.03)
	Hauturu (NZ)	253 (345)	10 (14.5)	0.01 (0.01)	0.10 (0.01)	0.13 (0.02)	0.23 (0.03)
Pterodroma ultima (NT)	Oeno (UK)	22 037 (28 992)	957 (1271.6)	0.01 (0.01)	0.09 (0.01)	0.12 (0.01)	0.21 (0.03)
Ardenna grisea (NT)	Lady Alice (NZ)	95 (117)	5 (5.7)	0.00 (0.00)	0.09 (0.01)	0.11 (0.01)	0.20 (0.02)
Fregetta maoriana (CR)	Hauturu (NZ)	7906 (11 148)	559 (798.7)	0.01 (0.02)	0.05 (0.01)	0.07 (0.01)	0.14 (0.03)
Pelecanoides urinatrix (LC)	Atihau (NZ)	2524 (3141)	205 (256.6)	0.00 (0.01)	0.03 (0.00)	0.06 (0.01)	0.09 (0.01)
	Burgess (NZ)	70 153 (95 301)	5693 (7819.0)	0.00 (0.01)	0.03 (0.00)	0.06 (0.01)	0.09 (0.01)
	Hauturu (NZ)	814 (1004)	66 (83.2)	0.00 (0.01)	0.03 (0.00)	0.06 (0.01)	0.09 (0.01)
Pelagodroma marina (LC)	Burgess (NZ)	43 617 (58 281)	3388 (4562.2)	0.00 (0.00)	0.01 (0.00)	0.07 (0.01)	0.08 (0.01)

[a] The high risk (> 1) for *Calonectris diomedea* and *Ardenna carneipes* was driven predominantly by mortality from fisheries (in bold). The risk ratio was calculated as potential mortalities per year divided by the annual mortality threshold (Richard & Abraham 2013); when this risk ratio is ≥ 1, adult mortality from each of the evaluated threats may impede the recovery of a colony, even after predator eradication. For the remaining 36 colonies of 16 species that we analysed, the risk ratio was < 1, implying that these populations are resilient to marine threats following predator eradication. Colony locations are shown in Fig. 1.

[b] NZ, New Zealand; UK, United Kingdom

approach, we estimated the AMT for 81 seabird species (Fig. A2 in Appendix 1) to test both H1 and H2 with equation 1 (Richard *et al.* 2017):

(1) $AMT = \frac{1}{2} r_{max} N$

where N is the estimated population size and r_{max}, or the population growth rate above replacement per generation, is calculated from equation 2 (Niel & Lebreton 2005, Richard *et al.* 2017):

(2) $r_{max} = \lambda_{max} - 1$

Estimates of mean age at maturation (α), adult survival (s), and population size (N) used to calculate λ_{max} and the AMT are defined by the mean and standard deviation from various data sources. The data for α, s, and N were taken from the Bird Demographic Database (BIDDABA; Lebreton & Gaillard 2012), the COMADRE Animal Matrix Database (Salguero-Gómez *et al.* 2016), peer-reviewed literature, and online data sources (BirdLife International, birdlife. org/datazone/species and New Zealand Birds Online, nzbirdsonline. org.nz); these data are compiled in Appendices A2 and A3.

We used the mean α, which may be estimated from a small sample size, leading to either an over- or underestimation. In such cases, the λ_{max} will be over- or underestimated. Uncertainties in α were incorporated into model outputs using a Monte Carlo process with 5 000 iterations sampled from the gamma distribution and expressed as the mean and standard deviation of the mean. The shape and rate of the sampling distribution, including biologically realistic bounds (e.g., individuals > 1 year) were calculated using the function *gamma.parms.from.quantiles* (Joseph & Bélisle 2012) and the function *rgamma* from the base R package (R Core Team 2013).

Mean adult survival rates for procellariiforms are typically > 90% (Richard & Abraham 2013). For the risk analysis of 16 species, we used the highest value of s reported in the literature. We assumed that this survival estimate was likely to be closest to adult survival in the absence of predators, given the available habitat and absence of introduced predators on the islands (Borrelle *et al.* 2018). We did not account for adult mortality due to other sources of mortality on land. We assumed that this approach allowed us to estimate the potential impacts on a population specifically from the marine threats evaluated. Where data on adult survival for a species were unknown ($n = 3$), we assumed that annual adult survival was 0.93 ± 0.03 (Brooke *et al.* 2010). To account for these uncertainties in adult survival s, the mean and standard error were derived by calculating the logit of the mean using a Beta distribution and then these were back-transformed. The standard deviation (sd) of the logit of the mean for s ($\bar{S}$) was calculated using the Delta method, which is a general method to derive the variance of a function (shown in equation (3), Richard & Abraham 2013):

(3) $sd(\bar{S}) = \dfrac{sd(logit(\bar{S}))}{\bar{S}(1 - \bar{S})}$

The required demographic information to calculate λ_{max} are α, s, and an allometric constant $a_{rT} = 1$ (*sensu* Niel & Lebreton 2005), as shown in equation (4). The allometric constant describes the relationship between the optimal generation time and λ_{max}, which Neil and Lebreton (2005) found to be approximately 1 for 13 bird species.

(4) $\lambda_{max} = e^{[a_{rT}(\alpha + s/(\lambda_{max} - s))^{-1}]}$

We assumed that changes in adult survival from marine threats were influenced mostly by breeding adults, and we thus do not account for effects on adults on sabbatical, immature individuals, or floaters (birds that do not have a nest site). We also assumed adult survival to be equal between sexes and age classes. No seasonality and cryptic mortality was accounted for, which may underestimate the impact of marine threats on some populations (Genovart *et al.* 2017, Gianuca *et al.* 2017).

Population estimates for each colony are needed to calculate the AMT. However, estimates of the population size for most species are associated with high uncertainty. This, in part, is because many of the population surveys we found come from data that is more than eight years old, 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 underestimating breeding pair numbers. In addition, these counts may not accurately tally non-breeding birds (i.e., immature individuals, those on sabbatical, or floaters). Further, accurate calculation is made more challenging by immature birds spending their first few years at sea before returning to the colony to breed and by some adults taking sabbaticals from breeding (Warham 1990, Richard & Abraham 2013). For the phylogenetic comparative analysis, we used the minimum total population estimates as per the IUCN Red List and BirdLife International (BirdLife International 2021, IUCN 2021). When only estimates of breeding pairs were available, we multiplied the breeding pair estimate by 2.3, which includes ~30% for non-breeders ($n = 2$; Slotterback 2020). To account for this uncertainty, we estimated the mean and standard deviation of the population size N using a Monte Carlo simulation with 5000 iterations from a normal distribution at 0.05 intervals.

Marine threat impact

To test H1, we examined 36 colonies spanning 16 species across 23 islands worldwide (Fig. 1) where invasive predators have been eradicated and for which detailed demographic and threat impact data are available. By using this subset, we assumed that the populations were minimally affected by terrestrial threats: 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 (further details in Niel & Lebreton 2005, Ismar *et al.* 2014, and Borrelle *et al.* 2018). To explicitly consider the impacts of this assumption in our outputs, we used the upper bound of adult survival s and the colony size as N. The following sections detail the estimation of annual mortality for the 16 species by three key agents in our model.

Fisheries bycatch

We used the mean annual potential mortality from fisheries from Richard *et al.* (2017) for 12 of the seabird species included in the colony analysis (Appendix 2). The estimates of annual potential fatalities come from the database for Protected Species Bycatch (https://protectedspeciescaptures.nz/PSCv6/, hosted by New Zealand's Ministry for Primary Industries) from four fishing methods: trawl, surface long-line, bottom long-line, and set nets from the New Zealand exclusive economic zone for 2006/07 to 2014/15. Estimates for *Calonectris diomedea* were from Belda & Sánchez (2001). The species *Bulweria bulwerii*, *Pterodroma ultima*, and *Puffinus puffinus* were considered to be at low risk

from fisheries because they are not commonly reported as bycatch in the literature (IUCN 2021). We assumed that the proportion of adults in the total population potentially killed by fisheries would be the same proportion for each colony we evaluated. To account for the uncertainty in these estimates, we sampled the 95% credible intervals from a log-normal distribution using a Monte Carlo simulation of 5000 iterations using the mean reported in the literature (Appendix 3).

Plastic pollution

We calculated the proportion of the population at risk from mortality due to ingesting plastics using the average frequency of occurrence of plastic reported for each species from a literature search (Appendix 2). Because the mortality from plastic ingestion was unknown at the population level, we assumed it was low (i.e., 0.5% of the population), and we sampled the mean and 95% credible intervals from a log-normal distribution with a Monte Carlo simulation of 5000 iterations to generate uncertainty around this estimate. To account for the uncertainty in the estimate of the proportion of individuals killed from ingesting plastic, we tested the sensitivity to 1% and 5% adult mortality rates (Figs. A3 and A4 in Appendix 1). The results presented below are not analytically different from the plastic mortality level detailed above at 0.5%.

Climate change and prey depletion

Prey availability for seabirds is affected by both climatic changes and fisheries (Jenouvrier 2013, Oro 2014, Grémillet *et al.* 2018), which we evaluate together in this scenario. Despite impressive research efforts that indicate seabirds are vulnerable to interannual and episodic climatic changes that affect prey abundance and distribution (Jenouvrier 2013, Oro 2014), there is high uncertainty in our model to predict adult mortality from these pressures. This is due to the difficulty in quantifying adult mortality directly due to the complex interactions affecting prey distributions and abundance (Oro 2014, Sæther & Engen 2010), and it is further confounded by the lack of published studies on the effects of climate change/ prey depletion for the 16 species included in our marine threats risk analysis. In the absence of peer-reviewed estimates of the impact of climate change and prey depletion on mortality in a population (Grémillet *et al.* 2018, Wilcox *et al.* 2018, Dias *et al.* 2019), we explored the effects of prey change on the annual mortality rate. We assumed these impacts would result in 0.5% mortality of the adult population for each colony of the 16 studied species. To account for the high uncertainty in this estimate, we used a Monte Carlo simulation with 5000 iterations drawn from a log-normal distribution, with a mean 0.005 and standard deviation of 0.0005. We also ran scenarios testing adult mortality rates of 1% and 5% of the population for each colony to demonstrate population impacts with greater mortality rates (Figs. A5 and A6 in Appendix 1). As more data become available to better estimate adult survival directly, a more accurate result will be possible. See Appendix 1 for further discussion on uncertainty.

To calculate the proportional per capita mortality rate for each of the colonies evaluated, we used the annual potential mortalities from each of the threats and divided them by the colony population size. We then calculated the risk of a species to each of the above stressors and combined potential mortality from all threats together. The risk ratio is calculated as potential mortalities per year, divided by the AMT (Richard & Abraham 2013). A ratio close to one or

above one means that the species is at high risk of 'over-harvesting' by marine threats. All statistical analyses were carried out in R (R Core Team 2013).

Influence of traits on vulnerability to marine threats

To test H2, we used an expanded dataset that included 81 species in the order Procellariiformes (55% of all procellariiform species) for which demographic data were available (Appendix 3). Here, we used the total global population estimate. We performed phylogenetic generalised least squares (PGLS) regression analysis, using the AMT as the independent variable. Due to shared ancestry, closely related species were expected to share similar trait values (Symonds & Blomberg 2014). Evidence suggests that the key morphometric traits (e.g., mean adult body mass) and ecological characteristics (e.g., foraging strategy, diet, and at-sea distribution, the latter referring to breeding and non-breeding/migration distribution obtained from the Seabird Tracking Database; BirdLife International 2020) are preserved among species. Evidence also suggests that these characteristics are good indicators of a species' likelihood to interact with fishing vessels (Genovart *et al.* 2017), their likelihood of ingesting plastics (van Franeker & Law 2015), and/or their overall risk of extinction (e.g., mean adult body size, Gaston & Blackburn 1995; at-sea distribution, Bærum *et al.* 2019).

A phylogenetic understanding of how different species react to each threat would allow managers to infer risk to a species for which only poor data is available regarding a given variable of interest (e.g., risk ratio) based on available demographic and ecological data from closely related species. We estimated Pagel's λ (not to be confused with population growth rate λ) with PGLS for each of our traits of interest: body mass, foraging strategy, diet, and at-sea distribution. Pagel's λ is a scaling parameter for the phylogenetic correlation between species, and it ranges between 0 (phylogeny plays no role in determining trait variation across the studied species) and 1 (trait variation is fully explained by the structure of the phylogeny, assuming a Brownian motion model of trait evolution; Freckleton *et al.* 2002, Symonds & Blomberg 2014). We obtained the Jetz *et al.* (2012) bird phylogeny, which contains time-calibrated phylogenetic relationships from conserved regions of the genomes of 9993 extant bird species. We manipulated the tree to prune it to our expanded dataset of 81 seabird species to calculate Pagel's λ using the R packages "phytools" (Revell 2012), "ape" (Paradis *et al.* 2004), and the function *pgls* in the "caper" R package (Orme 2018). We used the annual mortality limit for a species as our response due to its strong relationship with the IUCN Red List threat criteria (and thus extinction risk), and our key explanatory variables were the traits described above.

RESULTS

Our first hypothesis, H1, was that expected annual mortality from cumulative marine threats would exceed the expected population recovery of a colony after predator eradication. Under a conservative scenario, where the adult mortality related to climate change/ prey depletion and to the ingestion of plastic pollution for each population are each set to 0.5% per annum and where mortality from fisheries bycatch is estimated from the literature, H1 is false. Instead, we found that 88% (14 out of 16) of the seabird population recoveries in our risk analysis were not significantly impacted by these combined marine threats (Fig. 2). However, for five colonies of two closely related species—*C. diomedea* and *Ardenna*

carneipes—recovery after predator eradication was significantly impeded by marine threats (Table 1; Figs. 2, 3). Moreover, our sensitivity analysis revealed that if mortality from climate change/prey depletion and plastic ingestion affected 1% and 5% of the populations, then 9% and 12% of the colonies, respectively, would experience impeded recovery due to marine threats (Fig. 2, Figs. A3–A6 in Appendix 1).

Our second hypothesis, H2, was that risk from multiple threats can be inferred from closely related species. Our phylogenetic analyses examined species traits that might predict the AMT of the 81 species to test H2; that is, to see whether certain traits make a species more or less vulnerable to marine threats (Fig. 3A). The model retained at-sea distribution and biomass (Fig. 3B), along with the foraging strategies of surface filtering and pursuit diving (Table A2 in Appendix 1). These relationships were weak, suggesting that H2 is also false when using the statistical significance threshold of alpha = 0.05. At the species level (rather than the colony level), the AMT estimates for the 81 species in our analysis were congruent with IUCN Red List threat categories (Fig. 4A). However, our
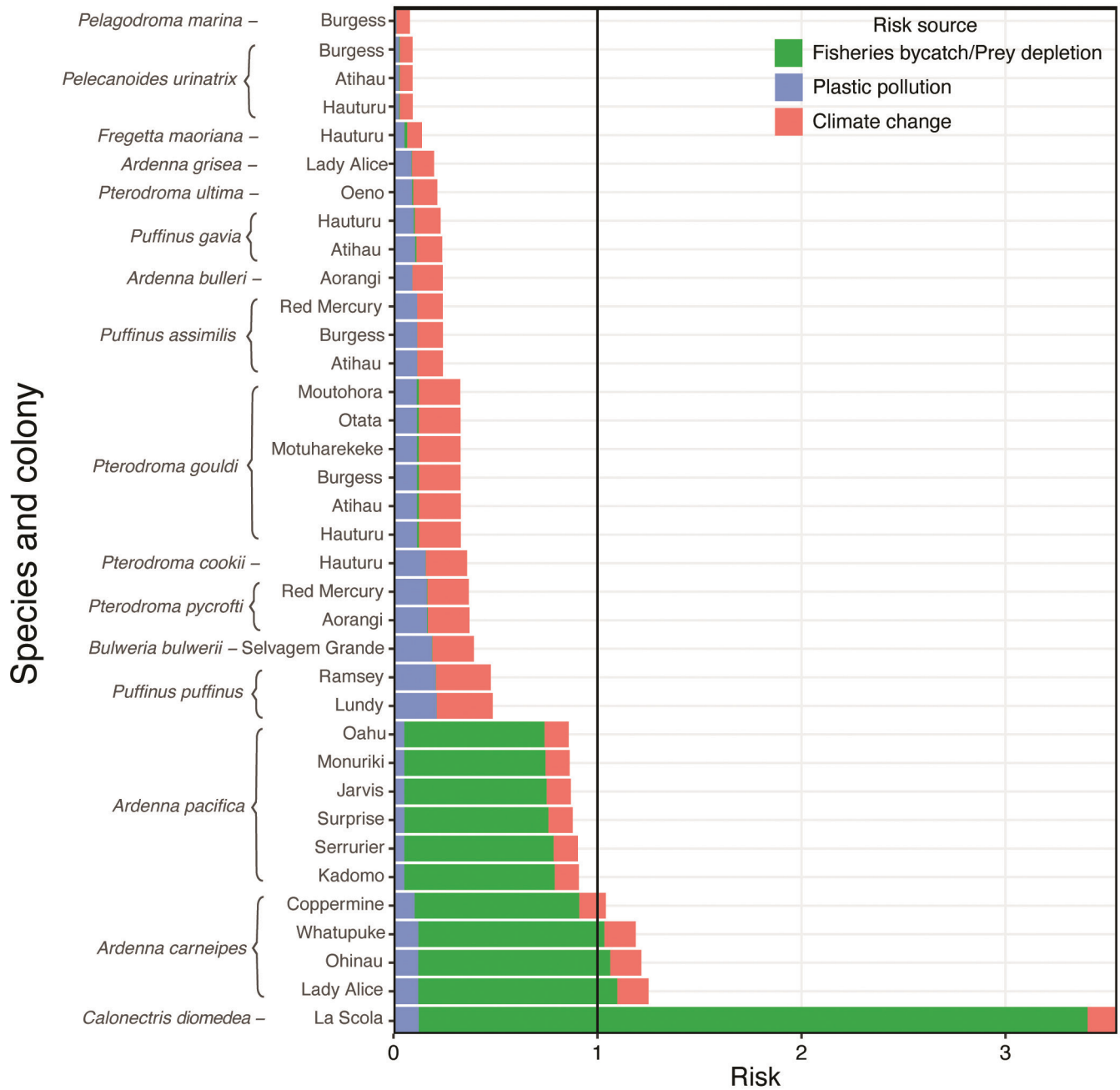

Fig. 2. The relative contributions of the marine threats of mortality from fisheries bycatch/prey depletion (species specific; see Appendix 1, available online), plastic pollution (0.5% annual mortality; *n* = 36), and climate change (0.5% annual mortality) for the colonies of 16 species on 23 islands where predators have been eradicated. The risk ratio was calculated as potential mortalities per year divided by the annual mortality threshold (Richard & Abraham 2013); when this risk ratio is ≥ 1, adult mortality from each of the evaluated threats reduces the resilience of a colony even after predator eradication.

model results indicated that either there are other factors that may more strongly influence a species' risk from marine threats (such as individual behaviour) or that there are multiple factors whose magnitude of impact affects species differently.

Species with smaller at-sea distributions had lower AMTs, although models explained only 14% of the variance. This finding suggests weakly that these species may be more resilient to marine threats than those with larger distributions ($R_{Adj}^2 = 0.14$, $t = 3.7$, $P < 0.001$,
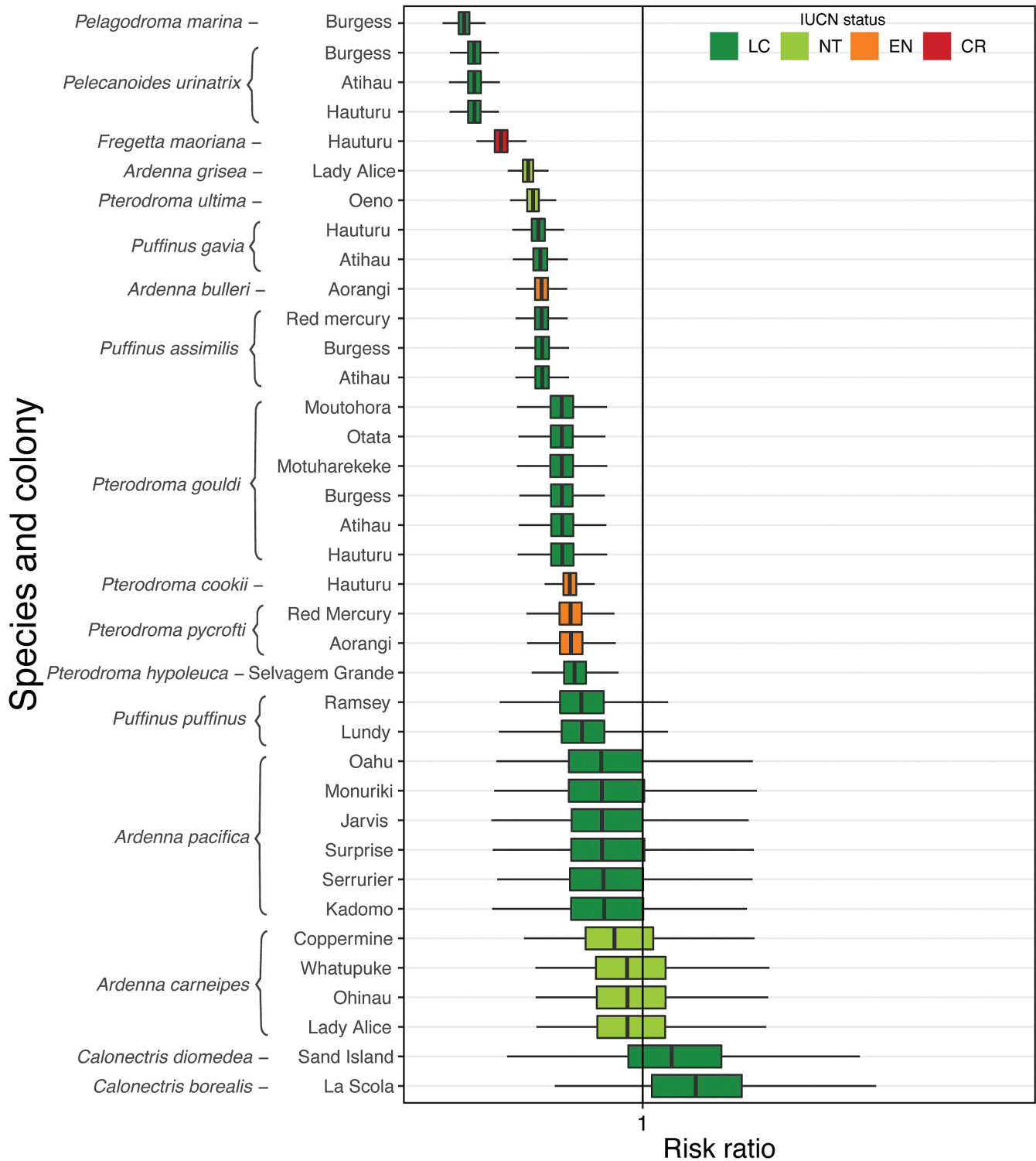

Fig. 3. The risk ratio for the 36 colonies of 16 species, on 23 islands (Fig. 1) where invasive predators have been eradicated. The risk ratio was calculated as potential mortalities per year divided by the annual mortality threshold (Richard & Abraham 2013); when this risk ratio is ≥ 1, adult mortality from each of the evaluated threats may impede the recovery of a colony even after predator eradication. Colours for each species correspond to the IUCN Red List status: Least Concern (LC) is dark green, Near Threatened (NT) is light green, Vulnerable (VU) is yellow, Critically Endangered (CR) is red.

Fig. 4B). The vulnerability of a species and their spatial distribution was strongly conserved among closely related species (Pagel's $\lambda = 0.83$, 0.42–0.97; see Appendices and Table A3). Mean adult body mass explained only 9% of the AMT ($R_{Adj}^2 = 0.09$, $t = -2.8$, $P = 0.02$, Pagel's $\lambda = 0.52$, confidence interval (CI) = 0.06–0.87, $P < 0.001$; Fig. 4C). Surface-filtering and pursuit-diving seabirds were less resilient to marine threats than species with other foraging strategies ($R_{Adj}^2 = 0.24$, $f = 13.18$, $P_{Adj} < 0.001$ for surface-filtering species; $R_{Adj}^2 = 0.18$, $f = 11.18$, $P_{Adj} < 0.001$ for pursuit-diving species; Table A3 in Appendix 1). This relationship was highly preserved among closely related species (Pagel's $\lambda = 1.00$, CI = 0.44–1.00 for surface-filtering species; Pagel's $\lambda = 1.00$, CI =0.64–1.00 for pursuit-diving species).

DISCUSSION

Introduced predators at breeding sites, coupled with sustained and intensifying human pressures in the oceans such as fisheries bycatch, plastic ingestion, and climate change/prey depletion, are responsible for seabird population declines globally (Paleczny *et al.* 2015, Dias *et al.* 2019, Rodríguez *et al.* 2019). We used a population model developed specifically for data-deficient species together with comparative phylogenetic analyses to evaluate the impact of marine threats to the recovery of seabirds after predator eradication, a key conservation strategy that has resulted in the recovery of seabirds worldwide (Jones *et al.* 2016). Specifically, we expected that cumulative mortality from multiple marine threats exceeds population recovery after predator eradication (H1) and that the shared traits between species can inform the risk of a species to multiple marine threats (H2). We suggest that for most seabird colonies examined here (14 out of 16, or 88%), recovery is not expected to be inhibited by cumulative marine threats, thereby disproving H1. Phylogenetic traits may be useful to infer risk from fisheries or plastic ingestion; however, we were not able

to use them to predict the impact of cumulative marine threats on colony recovery in the absence of predation, thereby disproving H2. The impacts of multiple marine threats are likely to occur at the individual level and species level and to be colony-specific (Fig. 2). This means that a more active colony-based conservation approach will be needed to ensure the benefits of predator eradication are maintained in the face of increasing marine pressures.

Mortality from marine threats for the species in our analysis was predominantly driven by fisheries bycatch (Fig. 2). Indeed, all of these species are often reported as bycatch in recreational and commercial fishing activities (Belda & Sánchez 2001, Genovart *et al.* 2017, Richard *et al.* 2017). Globally, long-line and gillnet fisheries are dominant sources of adult mortality for surface-filtering and pursuit-diving species (Bærum *et al.* 2019, Rodríguez *et al.* 2019). There are behavioural influences that impact seabird-fishery interactions, but we were unable to capture them in our model. For example, some species are more gregarious when foraging, so interactions with fisheries operations or other human activities are likely to cause additional adult mortalities (Genovart *et al.* 2017). Likewise, immature birds have a higher probability of dying as fisheries bycatch than breeding adults (Genovart *et al.* 2017). Finally, abiotic factors also influence the level of risk from fisheries interactions at the individual level; for example, different levels of mortality are expected with the type of fishing gear (Genovart *et al.* 2017). *C. diomedea* in the Mediterranean is severely impacted by fisheries (Fig. 2), which contributes the most to its high risk ratio in comparison to other species analysed here.

Theory predicts that species with extensive ranges may be more resilient to environmental stressors and adult mortality (Sæther & Engen 2010, Paniw *et al.* 2018, Cooke *et al.* 2019). Large at-sea distributions mean that when environmental or foraging conditions are poor, highly mobile seabirds are able to move to
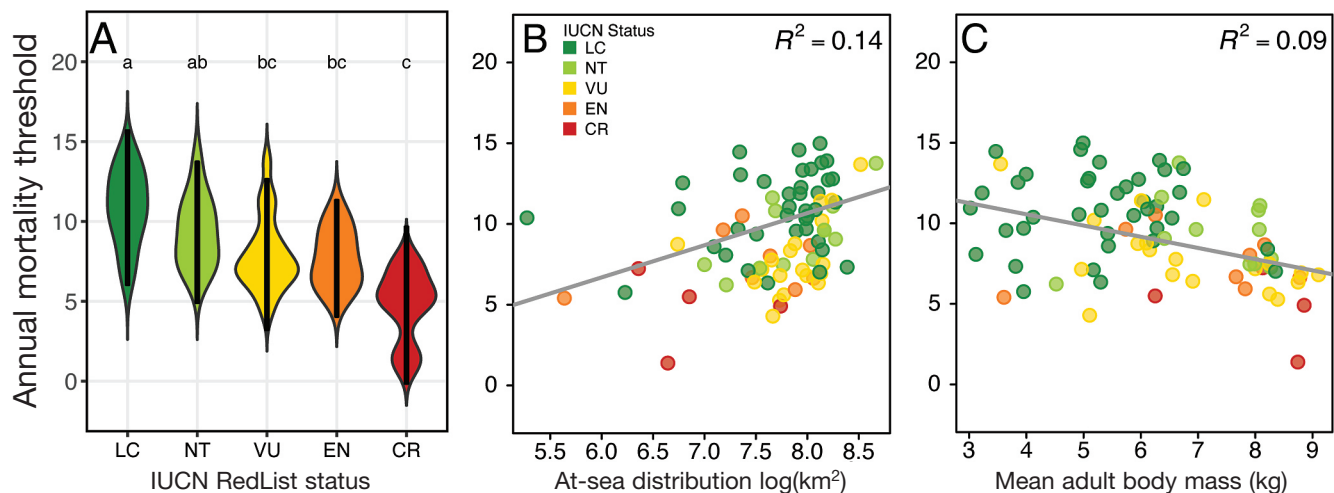

Fig. 4. The log of the annual mortality threshold (AMT) serves as a basis to predict the IUCN RedList status of the examined 81 seabird species (A). The log of the AMT is also predicted by key ecological predictors of the log of at-sea distribution, that is, breeding and non-breeding range (B) and mean adult body mass (C). The AMT is the maximum number of breeding adults that can be removed annually from a population without causing it to decline. Groupings and colours correspond to the IUCN Red List status: Least Concern (LC) is dark green; Near Threatened (NT) is light green; Vulnerable (VU) is yellow; Endangered (EN) is orange; Critically Endangered (CR) is red. Letters on top of each IUCN group in panel A are post-hoc Tukey scores; when two groups do not share the same letter, their annual mortality threshold scores are statistically different at P < 0.05 (see Appendices and Table A2). (B) and (C) contain the phylogenetic generalised least squares for the relationship between the AMT and at-sea distribution (log-scale); Pagel's $\lambda = 0.83$, 95% confidence interval 0.42–0.98, F-ratio = 19.14, $df = 79$, $P < 0.001$), and mean adult body mass (Pagel's $\lambda = 0.52$, confidence interval 0.06–0.87, F-ratio = 4.05, $df = 79$, $P < 0.001$).

more favourable foraging or breeding grounds (Weimerskirch 2002, Giudici *et al.* 2010). However, following predator eradication, the opposite was true here: species in our analysis with large at-sea distributions were less resilient. Three closely related species, all with extensive at-sea ranges, were the least resilient to marine threats following predator eradication: the Mediterranean colony of *C. diomedea* and all four of the Aotearoa New Zealand colonies of *A. carneipes* have range sizes of > 74.3 and 180 million km^2, respectively (Jetz *et al.* 2012, BirdLife International 2020). Other research has found that Mediterranean populations of *C. diomedea* would still be in decline, even in the absence of mortality due to fisheries bycatch or depredation at their breeding sites (Genovart *et al.* 2017). This suggests that marine threats are severely impacting these populations, which is further supported by our results (Fig. 2).

It may be that species with large range sizes have a greater probability of being exposed to multiple, often spatially disparate, stressors compared to species with smaller ranges that may overlap with fewer stressors. The opposite may also be true for specific colonies, as demonstrated by our results with regards to *C. diomedea*, which has a risk ratio three times greater than any other species included in our analysis (Fig. 2).

Species that forage by surface filtering and pursuit diving are thought to be highly vulnerable to fisheries bycatch (Furness 1999, Rodríguez *et al.* 2019) and plastic ingestion (Codina-García *et al.* 2013, Lavers *et al.* 2014). Foraging strategy and prey type have been linked to seabirds' propensity to ingest plastic (Ryan 1987, Provencher *et al.* 2010, Nishizawa *et al.* 2021). All the species in our colony-level analysis are surface foragers or pursuit divers, yet only three species were vulnerable to marine threats in the absence of invasive predators at their breeding sites. While foraging strategy certainly plays a role, mortality from different marine threats is also influenced by spatial co-occurrence, individual behaviour (Krüger *et al.* 2019), and distribution of both stressors and birds (Ryan 1987, 2019). Indeed, the distribution of fishing vessels has been found to alter the foraging behaviour and movement patterns of shearwaters (e.g., *C. diomedea*). This results in greater probability of being caught as bycatch (Bartumeus *et al.* 2010, Weimerskirch *et al.* 2018), which is likely the main threat contributing to population declines.

Larger seabirds appear to be more impacted by marine threats. This is reflected in the lower AMTs, although this relationship is weak, explaining only 9% of the AMT. Mean adult body mass is generally a good indicator of extinction vulnerability for birds (Gaston & Blackburn 1995). For example, larger birds have been found with greater loads of plastics (Wilcox *et al.* 2015, Ryan 2019), and the demographic impact of fisheries bycatch is greater for albatrosses, large petrels, and shearwaters due to their low fecundity, high propensity for interacting with fishing vessels, and greater likelihood of getting caught on baited hooks due to their larger bills (Rowe 2010, Richard *et al.* 2017). Other work has shown large-bodied seabirds still declined following predator eradication (Lavers *et al.* 2010).

If at-sea adult mortality is currently higher than we tested here or if it increases in the future, then vulnerable species will continue to experience disproportionate declines (Genovart *et al.* 2017). Notably, this is the case for *C. diomedea* in this study (Fig. 2). For example, stable isotope analyses suggest either spatial shifts in or reduced availability of prey, indicating the potential for intensifying impacts from climate change (Bond & Lavers 2014) and prey

depletion from fisheries competition (Grémillet *et al.* 2018). Thus, if plastic ingestion or climate change result in higher mortality than we have estimated here, such as 5% annual mortality in the population, declines would likely continue for *A. pacifica*, even after predator eradication (IUCN 2021). This portends significant conservation challenges, even following predator eradication, for seabirds highly impacted by marine threats (Dias *et al.* 2019, Rodríguez *et al.* 2019).

In sum, most seabird populations are expected to recover from the impacts of invasive predators despite adult mortality caused by anthropogenic activities in the oceans. Using phylogenetically shared traits to predict which species are more impacted by multiple marine threats is not straightforward, particularly in the absence of depredation at breeding colonies. While our phylogenetic analysis results align with the consensus on vulnerability, there are colony-level contradictions and species-specific responses to the population impacts of marine threats. Therefore, systematic population surveys after predator eradications to detect both colony recovery rates and how marine threats may be affecting a population are critical elements of a seabird island restoration project.

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In terms of author contributions, SBB, HPJ, RS-G conceived the idea; SBB, YR, RS-G designed the methodology and analysed the data; SBB collected the data; SBB, RS-G led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

REFERENCES

BÆRUM, K.M., ANKER-NILSSEN, T., CHRISTENSEN-DALSGAARD, S., FANGEL, K., WILLIAMS, T. & VØLSTAD, J.H. 2019. Spatial and temporal variations in seabird bycatch: Incidental bycatch in the Norwegian coastal gillnet-fishery. *PLoS One* 14: e0212786. doi:10.1371/journal.pone.0212786

BARBRAUD, C., ROLLAND, V., JENOUVRIER, S., NEVOUX, M., DELORD, K. & WEIMERSKIRCH, H. 2012. Effects of climate change and fisheries bycatch on Southern Ocean seabirds: A review. *Marine Ecology Progress Series* 454: 285–307. doi:10.3354/meps09616

BARTUMEUS, F., GIUGGIOLI, L., LOUZAO, M., BRETAGNOLLE, V., ORO, D. & LEVIN, S.A. 2010. Fishery discards impact on seabird movement patterns at regional scales. *Current Biology* 20: 215–222. doi:10.1016/j.cub.2009.11.073

BELDA, E.J. & SÁNCHEZ, A. 2001. Seabird mortality on longline fisheries in the western Mediterranean: Factors affecting bycatch and proposed mitigating measures. *Biological Conservation* 98: 357–363. doi:10.1016/S0006-3207(00)00178-6

BIRDLIFE INTERNATIONAL. 2020. *Data Zone: Species Distribution Data*. Cambridge, UK: BirdLife International. [Accessed at http://datazone.birdlife.org/species/requestdis on 15 June 2020].

BIRDLIFE INTERNATIONAL. 2021. *Data Zone: Taxonomy, version 6.0*. Cambridge, UK: BirdLife International. [Accessed at http://datazone.birdlife.org/species/taxonomy on 28 March 2021].

BOND, A.L. & LAVERS, J.L. 2014. Climate change alters the trophic niche of a declining apex marine predator. *Global Change Biology* 20: 2100–2107. doi:10.1111/gcb.12554

BORRELLE, S.B., BOERSCH-SUPAN, P.H., GASKIN, C.P. & TOWNS, D.R. 2018. Influences on recovery of seabirds on islands where invasive predators have been eradicated, with a focus on Procellariiformes. *Oryx* 52: 346–358. doi:10.1017/S0030605316000880

BROOKE, M.D.L., BONNAUD, E., DILLEY, B.J. ET AL. 2018. Seabird population changes following mammal eradications on islands. *Animal Conservation* 21): 3–12. doi:10.1111/acv.12344

BROOKE, M.D.L., O'CONNELL, T.C., WINGATE, D., MADEIROS, J., HILTON, G.M. & RATCLIFFE, N. 2010. Potential for rat predation to cause decline of the globally threatened Henderson Petrel *Pterodroma atrata*: Evidence from the field, stable isotopes and population modelling. *Endangered Species Research* 11: 47–59. doi:10.3354/esr00249

BURTHE, S.J., WANLESS, S., NEWELL, M.A., BUTLER, A. & DAUNT, F. 2014. Assessing the vulnerability of the marine bird community in the western North Sea to climate change and other anthropogenic impacts. *Marine Ecology Progress Series* 507: 277–295. doi:10.3354/meps10849

BUXTON, R.T., JONES, C., MOLLER, H. & TOWNS, D.R. 2014. Drivers of seabird population recovery on New Zealand islands after predator eradication. *Conservation Biology* 28: 333–344. doi:10.1111/cobi.12228

CEBALLOS, G., EHRLICH, P.R. & DIRZO, R. 2017. Biological annihilation via the ongoing sixth mass extinction signaled by vertebrate population losses and declines. *Proceedings of the National Academy of Sciences* 114: E6089–E6096. doi:10.1073/pnas.1704949114

CHAUDHARY, V. & OLI, M.K. 2020. A critical appraisal of population viability analysis. *Conservation Biology* 34: 26–40. doi:10.1111/cobi.13414

CLUKEY, K.E., LEPCZYK, C.A., BALAZS, G.H. ET AL. 2018. Persistent organic pollutants in fat of three species of Pacific pelagic longline caught sea turtles: Accumulation in relation to ingested plastic marine debris. *Science of the Total Environment* 610–611: 402–411. doi:10.1016/j.scitotenv.2017.07.242

CODINA-GARCÍA, M., MILITÃO, T., MORENO, J. & GONZÁLEZ-SOLÍS, J. 2013. Plastic debris in Mediterranean seabirds. *Marine Pollution Bulletin* 77: 220–226. doi:10.1016/j.marpolbul.2013.10.002

COOKE R.S., EIGENBROD F. & BATES A.E. 2019. Projected losses of global mammal and bird ecological strategies. *Nature Communications* 10: 2279. doi:10.1038/s41467-019-10284-z

DIAS, M.P., MARTIN, R., PEARMAIN, E.J. ET AL. 2019. Threats to seabirds: A global assessment. *Biological Conservation* 237: 525–537. doi:10.1016/j.biocon.2019.06.033

DILLINGHAM, P.W., MOORE, J.E., FLETCHER, D. ET AL. 2016. Improved estimation of intrinsic growth r_{max} for long-lived species: Integrating matrix models and allometry. *Ecological Applications* 26: 322–333. doi:10.1890/14-1990

FRECKLETON, R.P., HARVEY, P.H. & PAGEL, M. 2002. Phylogenetic analysis and comparative data: A test and review of evidence. *American Naturalist* 160: 712–726. doi:10.1086/343873

FREDERIKSEN, M., HARRIS, M.P., DAUNT, F., ROTHERY, P. & WANLESS, S. 2004. Scale-dependent climate signals drive breeding phenology of three seabird species. *Global Change Biology* 10: 1214–1221. doi:10.1111/j.1529-8817.2003.00794.x

FURNESS, R.W. 1999. Are industrial fisheries a threat to seabird populations? In: ADAMS, N. & SLOTOW, R. (Eds.) *Proceedings of the 22nd International Ornithological Congress, Durban, 16–22 August 1998*. Johannesburg, South Africa: BirdLife South Africa. [Accessed at https://www.internationalornithology.org/PROCEEDINGS_Durban/Symposium/S12/S12.2.htm on 05 April 2022].

GASTON, K.J. & BLACKBURN, T.M. 1995. Birds, body size and the threat of extinction. *Philosophical Transactions of the Royal Society B* 347: 205–212. doi:10.1098/rstb.1995.0022

GENOVART, M., DOAK, D.F., IGUAL, J.-M., SPONZA, S., KRALJ, J. & ORO, D. 2017. Varying demographic impacts of different fisheries on three Mediterranean seabird species. *Global Change Biology* 23: 3012–3029. doi:10.1111/gcb.13670

GIANUCA, D., PHILLIPS, R.A., TOWNLEY, S. & VOTIER, S.C. 2017. Global patterns of sex- and age-specific variation in seabird bycatch. *Biological Conservation* 205: 60–76. doi:10.1016/j.biocon.2016.11.028

GIUDICI, A., NAVARRO, J., JUSTE, C. & GONZÁLEZ-SOLÍS, J. 2010. Physiological ecology of breeders and sabbaticals in a pelagic seabird. *Journal of Experimental Marine Biology and Ecology* 389: 13–17. doi:10.1016/j.jembe.2010.04.002

GRÉMILLET, D., PONCHON, A., PALECZNY, M., PALOMARES, M.-L.D., KARPOUZI, V. & PAULY, D. 2018. Persisting worldwide seabird-fishery competition despite seabird community decline. *Current Biology* 28: 4009–4013.e2. doi:10.1016/j.cub.2018.10.051

ISMAR, S.M.H., BAIRD, K.A., GASKIN, C.P. ET AL. 2014. A case of natural recovery after the removal of invasive predators—community assemblage changes in the avifauna of Burgess Island. *Notornis* 61: 188–195.

IUCN (INTERNATIONAL UNION FOR CONSERVATION OF NATURE). 2021. *The IUCN Red List of Threatened Species*. Version 2021-2. Cambridge, UK: IUCN. [Accessed at https://www.iucnredlist.org on 12 May 2021.]

JENOUVRIER, S. 2013. Impacts of climate change on avian populations. *Global Change Biology* 19: 2036–2057. doi:10.1111/gcb.12195

JETZ, W., THOMAS, G.H., JOY, J.B., HARTMANN, K. & MOOERS, A.O. 2012. The global diversity of birds in space and time. *Nature* 491: 444–448. doi:10.1038/nature11631

JONES, H.P., HOLMES, N.D., BUTCHART, S.H.M. ET AL. 2016. Invasive mammal eradication on islands results in substantial conservation gains. *Proceedings of the National Academy of Sciences* 113: 4033–4038. doi:10.1073/pnas.1521179113

JONES, H.P., TERSHY, B.R., ZAVALETA, E.S. ET AL. 2008. Severity of the effects of invasive rats on seabirds: A global review. *Conservation Biology* 22: 16–26. doi:10.1111/j.1523-1739.2007.00859.x

JOSEPH, L. & BÉLISLE, P. 2012. *Gamma parms from quantiles*. Montreal, Canada: Montreal General Hospital. [Accessed at http://www.medicine.mcgill.ca/epidemiology/joseph/pbelisle/GammaParmsFromQuantiles.html on 15 June 2019.]

KAPPES, P.J. & JONES, H.P. 2014. Integrating seabird restoration and mammal eradication programs on islands to maximize conservation gains. *Biodiversity and Conservation* 23: 503–509. doi:10.1007/s10531-013-0608-z

KRÜGER, L., PEREIRA, J.M., PAIVA, V.H. & RAMOS, J.A. 2019. Personality influences foraging of a seabird under contrasting environmental conditions. *Journal of Experimental Marine Biology and Ecology* 516: 123–131. doi:10.1016/j.jembe.2019.04.003

LAVERS, J.L., BOND, A.L. & HUTTON, I. 2014. Plastic ingestion by Flesh-footed Shearwaters (*Puffinus carneipes*): Implications for fledgling body condition and the accumulation of plastic-derived chemicals. *Environmental Pollution* 187: 124–129. doi:10.1016/j.envpol.2013.12.020

LAVERS, J.L., WILCOX, C. & DONLAN, C.J. 2010. Bird demographic responses to predator removal programs. *Biological Invasions* 12: 3839–3859. doi:10.1007/s10530-010-9776-x

LAWLER, J.J., CAMPBELL, S.P., GUERRY, A.D., KOLOZSVARY, M.B., O'CONNOR, R.J. & SEWARD, L.C.N. 2002. The scope and treatment of threats in endangered species recovery plans. *Ecological Applications* 12: 663–667. doi:10.2307/3060975

LEBRETON, J.-D., DEVILLARD, S., POPY, S., DESPREZ, M., BESNARD, A. & GAILLARD, J.-M. 2012. Towards a vertebrate demographic data bank. *Journal of Ornithology* 152: 617–624. doi:10.1007/s10336-010-0582-0

NIEL, C. & LEBRETON, J.-D. 2005. Using demographic invariants to detect overharvested bird populations from incomplete data. *Conservation Biology* 19: 826–835. doi:10.1111/j.1523-1739.2005.00310.x

NISHIZAWA, B., THIEBOT, J.-B., SATO, F. ET AL. 2021. Mapping marine debris encountered by albatrosses tracked over oceanic waters. *Scientific Reports* 11: 19944. doi:10.1038/s41598-021-90417-x

ORME, D. 2018. *caper: Comparative analyses of phylogenetics and evolution in R.* Version 1.0.1. London, UK: Imperial College.

ORO, D. 2014. Seabirds and climate: Knowledge, pitfalls, and opportunities. *Frontiers in Ecology and Evolution* 2: 79. doi:10.3389/fevo.2014.00079

PALECZNY, M., HAMMILL, E., KARPOUZI, V. & PAULY, D. 2015. Population trend of the world's monitored seabirds, 1950–2010. *PLoS One* 10: e0129342. doi:10.1371/journal.pone.0129342

PANIW, M., OZGUL, A. & SALGUERO-GÓMEZ, R. 2018. Interactive life-history traits predict sensitivity of plants and animals to temporal autocorrelation. *Ecology Letters* 21: 275–286. doi:10.1111/ele.12892

PARADIS, E., CLAUDE, J. & STRIMMER, K. 2004. APE: Analyses of phylogenetics and evolution in R language. *Bioinformatics* 20: 289–290. doi:10.1093/bioinformatics/btg412

PROVENCHER, J., BORRELLE, S.B., SHERLEY, R.B. ET AL. 2019. Seabirds. In: SHEPPARD, C. (Ed) *World Seas: An Environmental Evaluation. Volume III: Ecological Issues and Environmental Impacts. 2nd Edition.* San Diego, USA: Elsevier, Inc. doi:1016/B978-0-12-805052-1.00007-3

PROVENCHER, J.F., GASTON, A.J., MALLORY, M.L., O'HARA, P.D. & GILCHRIST, H.G. 2010. Ingested plastic in a diving seabird, the Thick-billed Murre (*Uria lomvia*), in the eastern Canadian Arctic. *Marine Pollution Bulletin* 60: 1406–1411. doi:10.1016/j.marpolbul.2010.05.017

R CORE TEAM. 2013. R: *A language and environment for statistical computing*. Vienna, Austria: The R Foundation for Statistical Computing.

REVELL, L.J. 2012. phytools: An R package for phylogenetic comparative biology (and other things). *Methods in Ecology and Evolution* 3: 217–223. doi:10.1111/j.2041-210X.2011.00169.x

RICHARD, Y. & ABRAHAM, E.R. 2013. *Application of Potential Biological Removal Methods to Seabird Populations.* New Zealand Aquatic Environment and Biodiversity Report 108. Wellington, New Zealand: Marine Conservation Services, Department of Conservation.

RICHARD, Y., ABRAHAM, E.R. & BERKENBUSCH, K. 2017. *Assessment of the Risk of Commercial Fisheries to New Zealand Seabirds, 2006–07 to 2014–15.* New Zealand Aquatic Environment and Biodiversity Report 191. Wellington, New Zealand: Ministry for Primary Industries, Manatū Ahu Matua.

RODRÍGUEZ, A., ARCOS, J.M., BRETAGNOLLE, V. ET AL. 2019. Future directions in conservation research on petrels and shearwaters. *Frontiers in Marine Science* 6: 94. doi:10.3389/fmars.2019.00094

ROWE, S. 2010. *Level 1 Risk Assessment for Incidental Seabird Mortality Associated with New Zealand Fisheries in the NZ-EEZ.* Wellington, New Zealand: Marine Conservation Services, Department of Conservation.

RYAN, P.G. 1987. The incidence and characteristics of plastic particles ingested by seabirds. *Marine Environmental Research* 23: 175–206. doi:10.1016/0141-1136(87)90028-6

RYAN, P.G. 2019. Ingestion of plastics by marine organisms. In: TAKADA, H. & KARAPANAGIOTI, H.K. (Eds). *Hazardous Chemicals Associated with Plastics in the Marine Environment.* Cham, Switzerland: Springer.

SÆTHER, B.-E. & ENGEN, S. 2010. Population analyses. In MØLLER, A.P., FIEDLER, W. & BERTHOLD, P. (Eds.). *Effects of Climate Change on Birds.* Oxford, UK: Oxford University Press.

SALGUERO-GÓMEZ. R., JONES, O.R., ARCHER, C.R. ET AL. 2016. COMADRE: A global data base of animal demography. *Journal of Animal Ecology* 85: 371–384. doi:10.1111/1365-2656.12482

SCHREIBER, E.A. & BURGER, J. 2002. *Biology of Marine Birds.* Boca Raton, USA: CRC Press.

SLOTTERBACK, J.W. 2020. Band-rumped Storm-Petrel (*Oceanodroma castro*), version 1.0. In: POOLE, A.F. (Ed.). *Birds of the World.* Ithaca, USA: Cornell Lab of Ornithology. doi:10.2173/bow.barpet.01.1

SUTHERLAND, W.J., BELLINGAN, L., BELLINGHAM, J.R. ET AL. 2012. A collaboratively-derived science-policy research agenda. *PLoS One* 7: e31824. doi:10.1371/journal.pone.0031824

SYMONDS, M.R.E. & BLOMBERG, S.P. 2014. A primer on phylogenetic generalised least squares. In: GARAMSZEGI, L.Z. (Ed.). *Modern Phylogenetic Comparative Methods and Their Application in Evolutionary Biology.* Berlin, Germany: Springer-Verlag.

TANAKA, K., TAKADA, H., YAMASHITA, R., MIZUKAWA, K., FUKUWAKA, M. & WATANUKI, Y. 2015. Facilitated leaching of additive-derived PBDEs from plastic by seabirds' stomach oil and accumulation in tissues. *Environmental Science and Technology.* 49: 11799–11807. doi:10.1021/acs.est.5b01376

TOWNS, D.R., BYRD, G.V., JONES, H.P., RAUZON, M.J., RUSSELL, J.C. & WILCOX, C. 2011. Impacts of introduced predators on seabirds. In: MULDER, C.P.H, ANDERSON, W.B., TOWNS, D.R. & BELLINGHAM, P.J. (Eds.). *Seabird Islands: Ecology, Invasion, and Restoration.* New York, USA: Oxford University Press.

VAN FRANEKER, J.A. & LAW, K.L. 2015. Seabirds, gyres and global trends in plastic pollution. *Environmental Pollution* 203: 89–96. doi:10.1016/j.envpol.2015.02.034

VOTIER, S.C., HATCHWELL, B.J., MEARS, M. & BIRKHEAD, T.R. 2009. Changes in the timing of egg-laying of a colonial seabird in relation to population size and environmental conditions. *Marine Ecology Progress Series* 393: 225–233. doi:10.3354/meps08258

WARHAM, J. 1990. *The Petrels: Their Ecology and Breeding Systems*. London, UK: A & C Black.

WEIMERSKIRCH, H. 2002. Seabird demography and its relationship with the marine environment. In: SCHREIBER, E. A. & BURGER J. (Eds.). *Biology of Marine Birds*. Boca Raton, USA: CRC Press.

WEIMERSKIRCH, H., FILIPPI, D.P., COLLET, J., WAUGH, S.M. & PATRICK, S.C. 2018. Use of radar detectors to track attendance of albatrosses at fishing vessels. *Conservation Biology* 32: 240–245. doi:10.1111/cobi.12965

WILCOX, C., HOBDAY, A.J. & CHAMBERS, L.E. 2018. Using expert elicitation to rank ecological indicators for detecting climate impacts on Australian seabirds and pinnipeds. *Ecological Indicators* 95: 637–644. doi:10.1016/j.ecolind.2018.07.019

WILCOX, C., VAN SEBILLE, E. & HARDESTY, B.D. 2015. Threat of plastic pollution to seabirds is global, pervasive, and increasing. *Proceedings of the National Academy of Sciences* 112: 11899–11904. doi:10.1073/pnas.1502108112