INTEGRATED CONSERVATION OF THE WHENUA HOU DIVING PETREL

BY

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Tēnā koutou katoa,

E rere te manu kit e tihi o Puke Hou.

Rere iho te manu mā te awa o Waituna.

Tau ana te manu ki te whenua o Whenua Hou.

Ko Kāi Tahu te mana whenua, te iwi whakaruruhau.

Nō Tiamana ōku tipuna.

Nō Hōrana ahau.

Kei Whanganui-A-Tara taku kāika i nāianei.

Ko Johannes tōku ikoa.

Tēnā koutou, tēnā koutou, tēnā koutou tatou katoa.

Abstract

Seabirds are one of the most threatened taxa on the planet. These species are also considered ecosystem engineers. Therefore, seabirds are of particular conservation interest. One of the most threatened seabirds is the critically endangered Whenua Hou Diving Petrel (*Pelecanoides whenuahouensis*; WHDP). The WHDP is restricted to a minute (0.018 km^2) breeding colony on a single island — Whenua Hou (Codfish Island), Aotearoa (New Zealand). The WHDP population was estimated at 150 adults in 2005. The WHDP is threatened by storms and storm surges, which erode its breeding habitat (fragile foredunes), and potentially by competition for burrows with congenerics.

I aimed to inform suitable conservation strategies for the WHDP. I first quantified the efficacy of past conservation actions (eradications of invasive predators). I compiled burrow counts across four decades to estimate and compare population growth before and after predator eradications. I then investigated offshore threats using tracking data to quantify WHDP offshore distribution, behaviour, and overlap with commercial fishing efforts. Subsequently, I estimated the potential impact and success of WHDP translocations. Specifically, I combined capture-recapture, nest-monitoring, and count data in an integrated population model (IPM) to predict the impact of harvesting chicks for translocations on the source population and to project the establishment of a second population. I then informed future translocation protocols using nest-monitoring data to quantify nest survival and breeding biology. Finally, I tested if WHDP presence had a positive influence on unrelated species groups. I counted two skink species at sites with and without burrows and used occupancy modelling to quantify the influence WHDP burrows had on skink occurrence.

Estimates of population growth before and after predator eradications illustrated that WHDP population growth remained comparatively low and unaffected by this conservation strategy. Therefore, additional interventions are required. WHDP tracking revealed that the non-breeding distribution did not overlap with commercial fishing efforts. However, considerable fishing efforts were present within the breeding distribution. Despite these findings, onshore threats remain present and conservation strategies aimed at addressing terrestrial threats may be more feasible. Results from my IPM showed that translocations could successfully establish a second WHDP population without impacting the source excessively, provided translocation cohorts remain small and translocations are repeated over long time periods (5-10 years). Nest survival was not clearly influenced by interannual variation, distance to sea, and intra- or interspecific competition. Furthermore, I informed future translocation protocols by identifying the preferred harvest window, measurements of ideal translocation candidates, and feeding regimes. Occurrence of one skink species was 114% higher at sites with burrows than at sites without, suggesting that WHDP presence benefits unrelated species.

The information provided in this thesis facilitates the identification of future management strategies for this critically endangered species. However, future conservation management of the WHDP should be based on structured decision-making frameworks that apply iterative adaptive management loops and must acknowledge the unique position of tangata whenua (people of the land). This approach could address the consequences and trade-offs of each alternative, account for uncertainty, facilitate the decolonisation of conservation biology, and would ultimately result in the best potential outcome of the target species in a truly integrated fashion.

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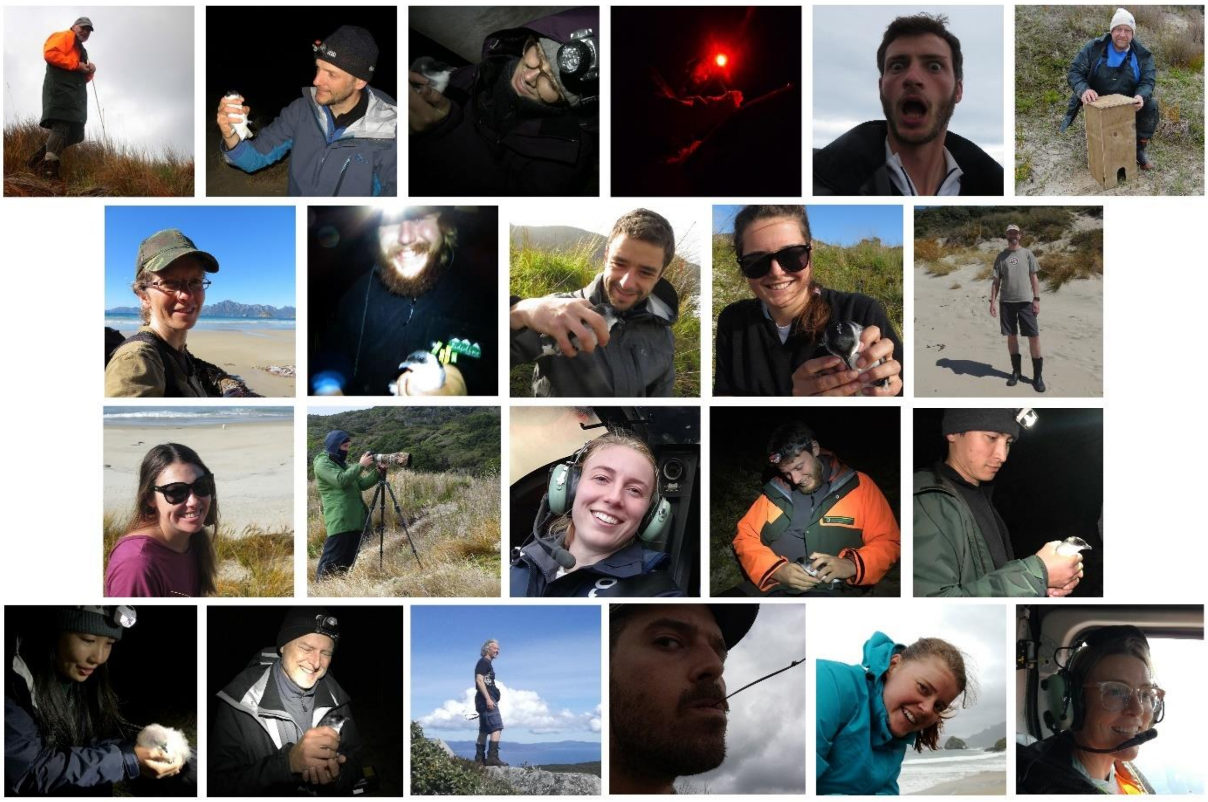

Fig. 1. The Flying Penguin Force. Included here with consent from all members.

The fieldwork on Whenua Hou would not be possible without the support of dozens of amazing people working in the background and I will attempt to thank everyone here. First and foremost, Ros Cole deserves a massive thank you for her ongoing support and guidance. Sharon Trainor has also been a pillar of good spirits through the years and I am very grateful for her support. Brooke Tucker has my deepest gratitude for her archaeological insights and for helping me navigate the complexities of working in and around a field site full of cultural heritage. I am hugely indebted to the entire Kākāpō Recovery whānau for their support and their irreplaceable companionship on Whenua Hou. I will miss you all dearly. The quarantine store team, Rhuaridh Hannan, Janice Kevern, and John Peterson in particular, also played a big role in making this project become reality. I am also indebted to Dominique Filippi (Sextant Technology), James Fox (Migrate Technology), Stu Cockburn and Steve McKevitt (Department of Conservation), Jake Tessler (BDB Enterprises), and Johannes Chambon for their technical support. Finally, Raymond Hector and Bill Moffatt (Stewart Island Flights), Paul Garlick and Fraser Sutherland (Te Anau Helicopters), and Dale Green (Heli My Way) have my everlasting gratitude for facilitating safe passage to and from Whenua Hou for the entire team.

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Contents

List of Figures

List of tables

Ethical statement

All methods were approved by the Whenua Hou Komiti, Kaitiaki Rōpū, the Victoria University of Wellington Animal Ethics Committee (VUW AEC 22252, VUW AEC 23283, and VUW AEC 27621), and the New Zealand Department of Conservation (Wildlife Authority Act 45407-FAU and 45907-FAU, Entry Permit 47920-LND-1516/04, 52029-LND, M1718/01, M1819/01, and M1920/02).

Acronyms

AIC	Akaike information criterion
AM	Adaptive management
BA	Bhattacharyya's affinity
CDP	Common Diving Petrel (*Pelecanoides urinatrix*)
CI	Confidence intervals
CrI	Credible intervals
EEZ	Economic exclusive zone
ENSO	El Niño southern oscillation
GLM	Generalized model
GLMM	Generalized linear mixed effects model
IBA	Important Bird and Biodiversity Area
IPM	Integrated population model
IUCN	International Union for the Conservation of Nature
MCMC	Markov chain Monte Carlo
NSD	Net squared displacement
RVI	Relative variable importance
SDM	Structured decision-making
SE	Standard error
SST	Sea surface temperature
UD	Utilization distribution
WHDP	Whenua Hou Diving Petrel (*Pelecanoides whenuahouensis*)

Chapter 1

General introduction

CONSERVATION IN THE SIXTH MASS EXTINCTION

Biodiversity loss in the last century has been exceptionally rapid and Earth has entered the sixth mass extinction (Pimm *et al.* 1995, Barnovsky *et al.* 2011, Ceballos *et al.* 2015, 2017). The sixth mass extinction is human-induced and driven by the exponentially rising demand for resources (Diaz *et al.* 2019). This planetary devastation is overwhelmingly evident in every indicator of the state of nature including extinction rates, population declines, global biomass allocation, and the integrity of ecosystems worldwide. Since the 15th century, ~700 animal species and ~600 plant species have gone extinct (Diaz *et al.* 2019, Humphreys *et al.* 2019). Extinction rates are now 100 to 1,000 times higher than natural background rates (Pimm *et al.* 1995). An estimated 1,000,000 species are at risk of extinction (Diaz *et al.* 2019). Globally, populations are collapsing, and species ranges are contracting (Ceballos *et al.* 2017). Global plant biomass, and therefore virtually all biomass on Earth, has decreased by ~66% (Bar-on *et al.* 2018, Erb *et al.* 2018). Biomass declines have been equally pronounced in many other taxonomic groups. In the 21st century, biomass of humans outnumbers the combined biomass of all wild mammals and birds by 1:7. In addition, more than 70% of the land surface and more than 80% of the oceans' surfaces has been altered by humans (Watson *et al.* 2016, Kendall *et al.* 2018). The negative trends in these indicators of the state of the planet are projected to worsen (Diaz *et al.* 2019).

While the sixth mass extinction accelerates, conservation efforts can slow the loss of biodiversity (Butchart *et al.* 2006, Hoffman *et al.* 2010, Bolam *et al.* 2020). Conservation biology is the science aimed at halting and reversing current extinction rates, population declines, range contractions, and biodiversity loss (Soulé 1985). Caughley (1994) identified two key paradigms within conservation biology: the declining population paradigm and the small population paradigm. The declining population paradigm is aimed at countering the agents of decline (e.g., invasive species, habitat destruction, overkill, and climate change). The small population paradigm is aimed at addressing the problems arising from the smallness of a population (e.g., inbreeding depression, demographic stochasticity, and environmental stochasticity). Conservation biologists operate in both paradigms, as species recovery is case-specific and complex (Hoffman *et al.* 2010). Conservation efforts have been successful in reducing further escalation of the sixth mass extinction (Butchart *et al.* 2006, Hoffman *et al.* 2010). For example, conservation efforts between 1980 and 2010 have decreased the extinction risk of at least 68 species of birds, mammals, and amphibians (Hoffman *et al.* 2010). Conservation efforts are particularly effective when focused on species at extreme risk of extinction, i.e., those listed as critically endangered on the IUCN Red List (Monroe *et al.* 2019). Conservation efforts have prevented the extinction of 21-32 bird and 7-16 mammal species between 1993 and 2020 (Bolam *et al.* 2020). Without these efforts, extinction rates for birds and mammals would have been at least 2.4-4.2 times higher. Conservation efforts have also ensured that ~15% of the planet's terrestrial surface and ~5% of the oceans' surfaces have received some form of formal protection (Geldman *et al.* 2019, Marine Conservation Institute 2020).

Despite encouraging conservation successes, biodiversity loss continues to accelerate, and conservation efforts must be strengthened, and direct, rapid, and integrated action is required immediately (Butchart *et al.* 2010, Diaz *et al.* 2019). Extinction risks are unequally allocated among conservation paradigms (Caughley 1994), among taxonomic groups (Fig. 2; Hoffman *et al.* 2010, Diaz *et al.* 2019), through space (e.g., habitats and geographic regions; Brooks *et al.* 2002, Butchart *et al.* 2010) and through time (e.g., among life-cycle stages, phenophases, and years; Finkelstein *et al.* 2010, Pardo *et al.* 2017, Robinson *et al.* 2020). Identifying and quantifying threats across this multi-dimensional playing field is complex and relies on long-term monitoring (Willis *et al.* 2007). Designing adequate countermeasures following the identification of threats is equally, if not more, challenging. While lessons can be learned from similar systems and/or species, conservation biology remains reliant on species- or population-specific long-term studies across time and space (Willis *et al.* 2007). Finally, bridging the gap between the identification of adequate conservation measures and the subsequent successful implementation of these measures remains a major challenge in conservation biology (Jarvis *et al.* 2015). Each conservation measure represents a complex decision landscape with a range of consequences and trade-offs, affecting an assemblage of stakeholders, and is often surrounded by considerable uncertainty (Converse *et al.* 2013, Johnson *et al.* 2015). Given these substantial challenges, it is not surprising that conservation biologists have focussed their efforts predominantly on species at the very brink of extinction

(Monroe *et al.* 2019). However, conservation efforts must be further integrated, expanded, and increased around the world to curb the ongoing sixth mass extinction (Diaz *et al.* 2019).

SEABIRD CONSERVATION

Seabird conservation is a striking example of the challenging nature of conservation biology. Seabirds, and Procellariiformes in particular, are one of the most threatened taxa on the planet (Fig. 2; Croxall *et al.* 2012, Dias *et al.* 2019, Rodríguez *et al.* 2019). Of the extant bird species, 13.5% are threatened with extinction (i.e., critically endangered, endangered, or vulnerable; BirdLife International 2020). Seabirds (defined following Dias *et al.* 2019 but including taxonomic updates) are considerably more threatened (31.5%) and seven seabird species are already considered extinct. Procellariiformes (e.g., albatrosses, petrels, and shearwaters) are even more threatened than seabirds in general (46.9%) and two Procellariiformes are already listed as extinct. While the Jamaica Petrel (*Pterodroma caribbaea*) and Guadeloupe Storm Petrel (*Hydrobates macrodactylus*) are listed as critically endangered, both are most likely extinct as well (Tobias *et al.* 2006, BirdLife International 2020). Given the dire conservation status of many seabirds, securing seabird species is of disproportionate conservation interest.

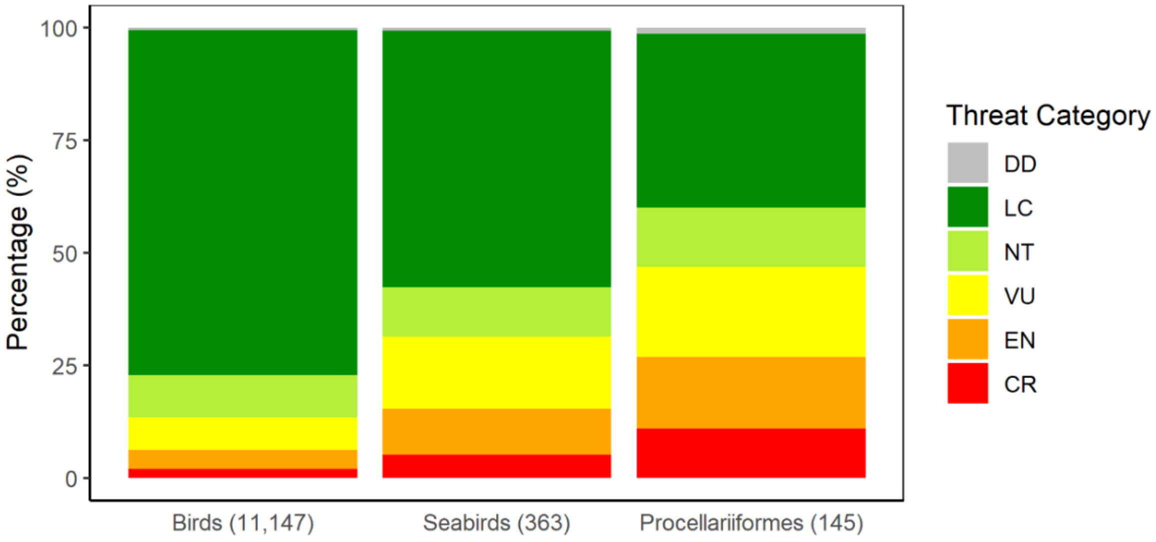

Fig. 2. Threat status of all extant birds, seabirds, and Procellariiformes (*n*). DD = data deficient, LC = least concern, NT = near-threatened, VU = vulnerable, EN = endangered, and CR = critically endangered.

The life history traits of many seabirds, and Procellariiformes in particular, render these birds disproportionately vulnerable. Seabirds are among the most long-lived birds on the planet (Bird *et al.* 2020). The oldest known wild bird is a Laysan Albatross (*Phoebastria immutabilis*) named "Wisdom", which is at least 69 years old (Jensen 2019). In addition to long lifespans, many seabirds exhibit delayed sexual maturity (e.g., Wandering Albatrosses *Diomedea exulans* only start breeding when they are 6–15 years old; Weimerskirch 2018). Seabirds also exhibit low fecundity. Procellariiformes only lay a singular egg per breeding period (Warham 1996) and several species breed only once every two years (Weimerskirch 2018, Taylor *et al.* 2020). Species exhibiting these life history traits are known as *K*-strategists. *K*-strategists are highly vulnerable to extinction drivers, especially those that impact adult survival (Halley *et al.* 2018).

Seabird conservation is also of disproportionate interest because these species are considered ecosystem engineers. Seabirds enable biochemical, biophysical, and biological processes at their breeding colonies that have knock-on effects on species in the surrounding terrestrial and marine ecosystems (Bancroft *et al.* 2005, Graham *et al.* 2018, Otero *et al.* 2018). Seabirds form a crucial link between pelagic and terrestrial ecosystems, as they facilitate nutrient cycling (particularly of nitrogen and phosphorus; Otero *et al.* 2018). The increased nutrient deposition on land also results in increased nutrient deposition in the coastal marine ecosystems surrounding seabird breeding colonies (Lorrain *et al.* 2017, Graham *et al.* 2018). Seabirds consequently increase productivity in terrestrial and marine ecosystems (Bancroft *et al.* 2005, Graham *et al.* 2018). Seabirds provide bioturbation (the movement of soil by organisms e.g., by digging of burrows) which aerates the soil and further enables bottom-up effects (Buxton *et al.* 2016, Orwin *et al.* 2016). Seabirds are also seed dispersers (Ellis 2005). The increased nutrient deposition and subsequent elevation of primary productivity facilitated by seabirds ultimately results in increased diversity and abundance of unrelated species groups on land (e.g., invertebrates; Markwell & Daugherty 2002) and at sea (e.g., reef fish; Graham *et al.* 2018). As such, the decline and extirpation of seabird populations worldwide (Paleczny *et al.* 2015, Dias *et al.* 2019) has wide-reaching implications for the ecosphere.

Seabird conservation at sea

Seabirds face a variety of threats at sea. Accidental bycatch in commercial fisheries is a prominent offshore threat to many seabirds. Hundreds of thousands of seabirds annually succumb to this threat (Phillips *et al.* 2016, Dias *et al.* 2019, Rodríguez *et al.* 2019) which drives some species to the brink of extinction (Oro *et al.* 2004, Genovart *et al.* 2016). Different fisheries affect different seabird species. Albatrosses and larger petrels are particularly affected by long line fisheries (Anderson *et al.* 2011, Dias *et al.* 2019, Rodríguez *et al.* 2019). Pursuit divers such as auks and penguins are especially at risk of becoming bycatch in gill nets (Žydelis *et al.* 2013, Crawford *et al.* 2017). Thousands of seabirds are also killed annually in trawl fisheries, mostly due to collision and entanglement with fishing gear (Sullivan *et al.* 2006, Watkins *et al.* 2008, Maree *et al.* 2014). In addition, deck strikes (caused by artificial lights at sea) is a poorly understood threat which affects smaller seabirds such as diving petrels (Ryan 1991, Black 2005, Glass & Ryan 2013). Another pelagic threat that affects many seabird species globally is environmental pollution (Ryan *et al.* 2009, Wilcox *et al.* 2015). Plastic pollution is especially prevalent, and several trillion pieces of plastic now contaminate the world's oceans (Eriksen *et al.* 2014). Ingestion of plastic can be lethal and virtually all seabird species are expected to suffer from plastic pollution in the near future (Lavers *et al.* 2014, Wilcox *et al.* 2015, Roman *et al.* 2019). Resource competition between humans and seabirds is another widespread threat that continues to impact seabirds, despite global seabird declines (Grémillet *et al.* 2016, 2018). This threat is likely to increase as global fisheries target lower and lower trophic levels (Pauly *et al.* 1998). Finally, climate change and weather extremes also have considerable negative impacts on seabirds at sea (Pardo *et al.* 2017, Piatt *et al.* 2020).

To counter the widespread and disastrous impacts of accidental bycatch on seabird populations, a variety of bycatch mitigation techniques has been developed, many of which show promising conservation outcomes (Agreement on the Conservation of Albatrosses and Petrels 2014, 2017). Refraining from discharging fishery discards has proven to reduce bycatch (Pierre *et al.* 2012). Operating at night further reduces bycatch of diurnal species (Paterson *et al.* 2017). Other, more technical measures have also been developed. Bird-scaring (tori) lines reduce collision and entanglement with trawl fishing gear (Maree *et al.* 2014, Tamini *et al.* 2015). Weighting down long lines reduces the accessibility of hooks and therefore seabird bycatch (Moreno *et al.* 2008, Paterson *et al.*

2017). In addition, more sophisticated methods that shield long line hooks until specific depths are reached are advancing (Sullivan *et al.* 2018, Goad *et al.* 2019). In gill net fisheries, acoustic and visual deterrents are being trialled, although with less promising results so far (Martin & Crawford 2015, Phillips *et al.* 2016, Mangel *et al.* 2018). Each method has advantages and disadvantages, and results appear most beneficial to seabirds when techniques are combined (Domingo *et al.* 2017, Paterson *et al.* 2017).

Another approach to protecting seabirds (and many other wide-ranging pelagic species) is the designation of Marine Protected Areas. When designating Marine Protected Areas, information on the offshore distribution of seabird species is crucial (Delord *et al.* 2014, Lascelles *et al.* 2016). The number of seabird species whose offshore distribution has been identified is growing steadily due to rapidly improving tracking technologies (Phillips *et al.* 2008, BirdLife International Seabird Tracking Database 2020). Consequently, seabird tracking data has been used in an expanding body of literature informing the allocation of candidate Marine Protected Areas on ocean-wide and global scales (e.g., Delord *et al.* 2014, Lascelles *et al.* 2016, Hindell *et al.* 2020). The extent of ocean secured as Marine Protected Areas has increased in the last decade from 2.8% of the world's oceans in 2013 to 5.3% in 2020 (Lascelles *et al.* 2014, Brander *et al.* 2020, Marine Conservation Institute 2020). Yet, one of the targets of the Convention of Biological Diversity was to protect of 10% of the global oceans by 2020 (Convention of Biological Diversity 2010) and thus this goal has not been met.

Seabird conservation on land

Seabirds also face a wide variety of threats on land at their breeding colonies (Dias *et al.* 2019, Rodríguez *et al.* 2019). Habitat destruction is common and widespread and affects a wide range of seabirds, especially those breeding in coastal environments (Bird *et al.* 2014, Raine *et al.* 2017, Rodríguez *et al.* 2019). Light pollution from land-based artificial lights threatens seabirds worldwide by causing disorientation, grounding of fledglings (but also adults), and indirectly, death (Rodríguez *et al.* 2017). Due to the colonial breeding habits of seabirds, environmental stochasticity (e.g., catastrophic weather events) can have a detrimental impact on seabird populations (Cole 2004, Reynolds *et al.* 2017). Human-induced climate change is likely to further exacerbate such stochastic events (Knutson *et al.* 2010, Adam *et al.* 2020). Future sea level rise caused by climate change will further threaten seabirds, especially coastal breeders (Spatz *et al.* 2017).

Predation by, and competition with, native species can cause seabird populations to decline when these population are already under pressure (Gummer *et al.* 2015, Rodríguez *et al.* 2019). Despite impacts from this wide variety of terrestrial threats, predation by invasive species (especially mammals, but also other taxa) forms the most pervasive and devastating terrestrial threat to seabirds (Spatz *et al.* 2014, Dias *et al.* 2019, Rodríguez *et al.* 2019). For example, the four Procellariiformes that are (likely to be) extinct were extirpated by invasive species (Tobias *et al.* 2006, BirdLife International 2020). Especially smaller seabird species, such as petrels, prions, storm petrels, and diving petrels, suffer heavily from predation by invasive mammals (Jones *et al.* 2008). Invasive species also drastically alter habitats that seabirds rely on, which can lead to population declines and extinctions (Taylor 2000ab, Cleeland *et al.* 2020).

Due to the severe impacts of invasive species, eradicating these problematic species from islands is one of the most successful strategies to secure seabird populations on land (Brooke *et al.* 2018a, Rodríguez *et al.* 2019). A disproportionate number of threatened species, including seabirds, are restricted to islands (Tershy *et al.* 2015, Spatz *et al.* 2017). Therefore, island-wide eradication of invasive species is a cost-effective method of conserving global biodiversity (Jones *et al.* 2016). To date > 1,200 island-wide eradications of invasive species have been attempted (Database of Island Invasive Species Eradications 2020). The majority of these eradications were successful (~87%). Island-wide eradications of invasive species have proven extremely beneficial for the recovery of the native flora and fauna, including seabirds, which respond quickly to eradications despite their slow life histories (Jones 2010, Jones *et al.* 2016). Population growth rates of seabirds increased considerably following invasive species eradications (Brooke *et al.* 2018a). A horizon-scanning exercise identified 292 islands on which the eradication of invasive species would result in considerable biodiversity gains, including the conservation of highly threatened seabirds (Holmes *et al.* 2019). Eradications of invasive species have mostly been focussed on uninhabited islands, but this focus is changing towards inhabited islands, which will further benefit seabird populations (Glen *et al.* 2013, Russell *et al.* 2018). The development of mammal-proof fences also allows for small-scale eradications of invasive predators, and consequently the conservation of mainland seabird populations (e.g., Young *et al.* 2013).

Translocating seabirds is another widely used terrestrial conservation strategy. A translocation is defined as the intentional movement of organisms for conservation or restoration purposes (Seddon *et al.* 2007, IUCN 2013, Seddon *et al.* 2014). Translocations are effective conservation strategies if I) suitable habitat is available, II) the species is unlikely to naturally (re)colonize that habitat, and III) the translocation is unlikely to cause negative impacts on source populations. Seabirds are desirable translocation candidates as they are disproportionally threatened with extinction (Fig. 2; Dias *et al.* 2019), but also provide ecosystem functions (e.g., Graham *et al.* 2018, Otero *et al.* 2018). Seabird translocations can be active or passive. Active seabird translocations rely on physically moving individuals to translocation sites. Many seabird species, especially Procellariiformes, exhibit extreme natal philopatry (potentially based on magnetism; Wynn *et al.* 2020). Therefore, translocating chicks prior to fledging is required to ensure imprinting on the translocation site (Miskelly & Taylor 2004, Priddel *et al.* 2006, Miskelly *et al.* 2009). Passive seabird translocations rely on the colonial and social nature of these species and use sensory cues to attract individuals to translocation sites. Sensory cues used in passive translocations can be auditory (e.g., broadcasting of calls), visual (e.g., decoys or mirrors), and olfactory (e.g., scented materials) (Podolsky & Kress 1992, Buxton & Jones 2012, Jones & Kress 2012, Friesen *et al.* 2017). The use of active or passive seabird translocation techniques is often dependent on the habits of the focal species but techniques can be used jointly to increase translocation success (Miskelly *et al.* 2009, Jones & Kress 2012, Friesen *et al.* 2017).

WHENUA HOU DIVING PETREL CONSERVATION

One of the most threatened seabirds in the world is the Whenua Hou Diving Petrel (*Pelecanoides whenuahouensis*; WHDP; Fig. 3). The WHDP is a recently described, nocturnal Procellariiform seabird species that was previously considered conspecific to the South Georgian Diving Petrel (*P. georgicus*). The WHDP was split from the South Georgian Diving Petrel based on preliminary genetic, phenotypic, and ecological differences (Paterson *et al.* 2000, Fischer *et al.* 2018b, Tizard *et al.* 2019). The WHDP was once a widespread and abundant breeder in coastal dune systems throughout southern Aotearoa (New Zealand). WHDP breeding colonies were present on Maukahuka (Auckland Islands, specifically Dundas and Enderby Islands), Rakiura (Stewart Island, specifically Te One Roa/Mason Bay), Muaupoko (Otago Peninsula, specifically Ōrau/Sandfly Bay), and Rēkohu (Chatham Islands) (Fig. 4; Falla *et al.* 1979, Worthy 1998, Taylor *et al.* 2000b, Holdaway *et al.* 2003, Wood & Briden 2008, Wood 2016, Fischer *et al.* 2017b, Tennyson 2020). However, predation and habitat destruction by invasive species (and New Zealand sea lions *Phocarctos hookeri* on Dundas Island) caused multiple local extinctions (Falla *et al.* 1979, Taylor 2000b). One single WHDP breeding colony remains on Whenua Hou (Codfish Island), 3 km west of Rakiura. Here, the WHDP breeding colony is restricted to a small (0.018 km^2) dune system (Fischer *et al.* 2018c) and the global population was estimated at 150 adults in 2005 (Wood & Briden 2008). As such, the WHDP is listed as nationally critical by the threat classification system of Aotearoa (Robertson *et al.* 2017) and as critically endangered on the IUCN Red List (BirdLife International 2020).

Fig. 3. Adult Whenua Hou Diving Petrel. Photo credit: Mithuna Sothieson.

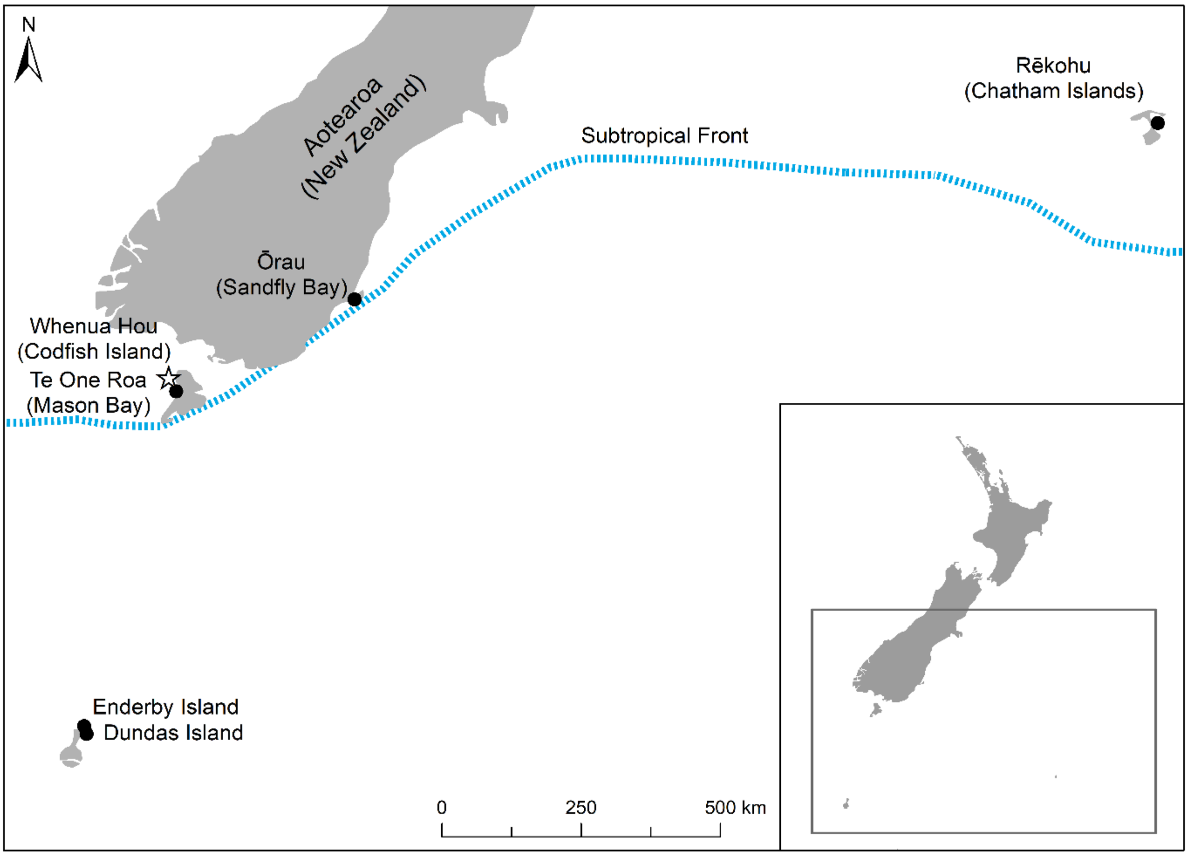

Fig. 4. Extant (white star) and extirpated (black circles) Whenua Hou Diving Petrel colonies. Approximate location of Subtropical Front is based on Harris & Orsi (2006).

Insights into the threats affecting the WHDP remain limited, inhibiting decision-making on adequate conservation measures. Whenua Hou is free of invasive predators following the eradications of Weka (*Gallirallus australis*), brush-tailed possums (*Trichosurus vulpecula*), and kiore (*Rattus exulans*; Brown & Sherley 2002, McClelland 2002, Middleton 2007). Yet, after these eradications, additional threats to the WHDP may remain. The specialization of the WHDP to burrow in steep fragile foredunes < 20 m from the springtide line renders the species vulnerable to erosion caused by storms and storm surges (Fischer *et al.* 2018c). For example, a single storm event in 2003 caused ~40% of all nest attempts to fail and entombed adults, causing adult mortality (Cole 2004). The onset of human-induced climate change will only exacerbate this threat. Stochastic events such as storms and storm surges are expected to increase in severity and frequency (Adam *et al.* 2020). In addition, 30-50% of sandy coastlines in New Zealand are projected to recede by > 100 m in the next century due to increased coastal erosion (Vousdoukas *et al.* 2020). Competition for burrows with the closely related Common Diving Petrel (*P. urinatrix*) may also be a threat to the WHDP (Fischer *et al.* 2017a). No pelagic threats have been identified, but this is most likely due to the lack of knowledge on the offshore distribution and behaviour of the WHDP. Diving petrels are one of the taxa most effected by deck strikes (Ryan 1991, Black 2005, Glass & Ryan 2013). Diving petrels have also been recorded as bycatch in trawl, gill net, and longline fisheries (Žydelis *et al.* 2013, Abraham & Richard 2019, Richard *et al.* 2020). Additionally, diving petrels may be one of the taxa most heavily affected by offshore resource-competition with humans (Grémillet *et al.* 2018). However, these birds are also one of the least-monitored seabirds. This lack of monitoring is also true for the WHDP (e.g., Imber & Nilsson 1980, West & Imber 1989, Fischer *et al.* 2018c). Lack of monitoring prevents the quantification of threats and therefore the evaluation of potential conservation measures (e.g., Sutherland & Dann 2012, Genovart *et al.* 2016, Rodríguez *et al.* 2019). Translocations of WHDPs to a different island may be a suitable conservation strategy to mitigate the impacts from storms, storm surges, climate change, and interspecific competition (Cole 2004, Fischer *et al.* 2017a). However, detailed understanding of WHDP population dynamics are required to quantify the potential impact and success of conservation strategies, including translocations (Panfylova *et al.* 2019).

THESIS STRUCTURE

The objective of this thesis is to facilitate the identification of a suitable conservation strategy to prevent the extinction of the WHDP. This thesis consists of five data chapters. In Ch. 2, I investigate the efficacy of past interventions (eradications of invasive predators) for conservation of the WHDP. I used intermittent burrow counts (1978-2018) with retrospective corrections to estimate population growth before and after predator eradications. In Ch. 3, I investigate pelagic threats to the WHDP by using tracking data (2016-19) to quantify WHDP offshore distribution, behaviour, and overlap with commercial fishing effort. In Ch. 4, I assess the feasibility of WHDP translocations as a conservation strategy by combining intermittent capture-recapture data (2002-19), nest-monitoring data (2017-19), and count data (2002-19) in an integrated population model to quantify population dynamics and simulate the impact and success of a future WHDP translocation. In Ch. 5, I use nest-monitoring data (2017-19) to quantify WHDP nest survival and breeding biology to inform future WHDP translocation protocols. In Ch. 6, I investigate the impact of WHDPs on unrelated species groups. I combined skink counts and occupancy modelling to estimate the influence of WHDP burrows on skink occurrence. Combined these five chapters will inform future conservation management of the WHDP and how management could affect larger dune communities in southern Aotearoa.

This thesis consists of five separate papers which address separate topics relevant to conservation. Addressing these topics does not only benefit WHDP conservation but also contributes to a wider understanding of seabird ecology and conservation globally. Four of these papers (Ch. 2, 3, 5 & 6) have been submitted to or published by peer-reviewed scientific journals prior to the submission of this thesis (Table 1). I am the lead author of all five papers. My supervisors, Heiko U. Wittmer, Doug P. Armstrong, and Igor Debski, are co-author on (almost) all these papers. In addition, Graeme A. Taylor is a co-author on the papers that arose (or will arise) from Ch. 2-5, for providing previously collected data and technical insights. Ros Cole is a co-author on the paper that arose from Ch. 2 for providing previously collected data. Derek Spitz is a co-author on the paper arising from Ch. 3 for assisting with the net squared displacement modelling. Cora F. McCauley is a co-author on the paper that arose from Ch. 6 for covering a substantial amount of fieldwork. All chapters that have been published or submitted are reproduced here with minor modifications, formatting, and inclusion of cross-referencing among chapters. As a consequence, some chapters include te reo Māori abstracts (tuhinga whakarāpopoto), while others do not (yet).

Table 1. Publication status of thesis chapters.

Ch.	Title	Journal	Status	Authors
2.	Population growth estimates of a threatened seabird indicate necessity for additional management following invasive predator eradications*	Animal Conservation	Published, Feb 2020	JH Fischer, GA Taylor, R Cole, I Debski, DP Armstrong & HU Wittmer
3.	Year-round pelagic distribution, behaviour, and overlap with commercial fisheries of a critically endangered small petrel	Marine Ecology Progress Series	Revised and resubmitted, Sep 2020	JH Fischer, I Debski, DB Spitz, GA Taylor & HU Wittmer.
4.	Predicting harvest impact and translocation success in small populations: a case study from a critically endangered petrel	To be decided	In prep.	JH Fischer, HU Wittmer, I Debski, GA Taylor & DP Armstrong
5.	Preparing for translocations of a critically endangered petrel through targeted monitoring of nest survival and breeding biology*	Oryx	Accepted, Jul 2020	JH Fischer, HU Wittmer, GA Taylor, I Debski & DP Armstrong
6.	Contrasting responses of lizard occurrences to burrowing by a critically endangered seabird*	Community Ecology	Published, Apr 2019	JH Fischer, CF McCauley, DP Armstrong, I Debski & HU Wittmer

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Chapter 2

Population growth estimates of a threatened seabird indicate necessity for additional management following invasive predator eradications

ABSTRACT

The eradication of invasive predators from islands is a successful technique to safeguard seabird populations, but adequate post-eradication monitoring of native species is often lacking. The Whenua Hou Diving Petrel (*Pelecanoides whenuahouensis*; WHDP) is a critically endangered seabird, restricted to Whenua Hou (Codfish Island), Aotearoa (New Zealand). Invasive predators, considered the major threat to WHDP, were eradicated on Whenua Hou in 2000. However, estimates of WHDP population size and trends remain unknown, hindering assessments of the success of the eradications. I collated intermittent burrow counts (n = 20) conducted between 1978 and 2018. To estimate the population growth rate (λ) before and after predator eradications, I used log-linear models in a Bayesian hierarchical framework while retrospectively accounting for differences in detection probabilities among burrow counts, due to differences in effort, marking, and timing. The number of WHDP burrows was estimated at 40 (36–46) in 1978 and 100 (97–104) in 2018. The pre-eradication $\hat{\lambda}$ was estimated at 1.023 (0.959–1.088), while the post-eradication $\hat{\lambda}$ was estimated at 1.017 (1.006–1.029). The WHDP population appears to be increasing, yet the rate of increase is low compared to other Procellariiformes following predator eradications. The comparatively low post-eradication $\hat{\lambda}$, combined with an apparent lack of change between pre- and post-eradication $\hat{\lambda}$, indicates that additional threats might be limiting WHDP population growth and that further conservation management is required. The continuation of affordable and simple, albeit imperfect, monitoring methods with retrospective corrections facilitated the assessment of invasive predator eradications outcomes and should guide future management decisions.

TUHINGA WHAKARĀPOPOTO

He tikanga whaihua te whakakorenga o ngā kaikonihi urutomo mai i ngā motu hei tiaki i ngā taupori manu moana, engari i ētahi wā he koretake te aroturuki i ngā momo manu taketake i muri i te whakakore kaikonihi. Ko te kuaka o Whenua Hou (*Pelecanoides whenuahouensis*) he manu moana e noho tata korehāhā ana, kātahi anō ka whakaahuatia, ā, e noho ana anake ki te moutere o Whenua Hou, Aotearoa. Ko ngā tino kaikonihi urutomo o te kuaka i whakawāteahia mai i Whenua Hou i te tau 2000. Engari, kāore i te mōhiotia ngā tatau me ngā ia o te tapori o te kuaka o Whenua Hou, nā reira e whakararurarutia ana ngā aromatawai o te angitu o ngā mahi whakakore kaikonihi. I kohia e mātau ngā tatau tūrua (n = 20 ngā tau) tāmutumutu i waenga i te tau 1978 me te 2018. Hei whakatau tata i te pāpātanga tipu o te taupori (λ) i mua me muri i ngā whakakorenga kaikonihi, i whakamahia e mātau ngā tauira rārangi-pūkōaro i roto i tētahi mahere raupapa Bayes, me te whakauru i muri mai i ngā rerekētanga mō te tautuhi i ngā tūponotanga i roto i ngā tatau tūrua, nā te rerekē o ngā mahi, te waitohu me te wā. Ko te whakatau tata o ngā tūrua o ngā kuaka o Whenua Hou he 40 (36-46) i te tau 1978 me te 100 (97-104) i te tau 2018. Ko te whakatau tata i te $\hat{\lambda}$ i mua i te whakakorenga he 1.023 (0.959-1.088), ā, ko te whakatau tata i te $\hat{\lambda}$ i muri i ngā whakakorenga he 1.017 (1.006-1.029). Te āhua nei kei te piki haere te taupori o te kuaka o Whenua Hou, engari he pāpaku noa iho te pāpātanga o taua piki haere ina ka whakatauritea ki etahi atu Procellariiformes i muri i ngā whakakorenga kaikonihi. Nā te iti o te $\hat{\lambda}$ i muri mai i ngā whakakorenga me te kore rerekēhaeretanga i waenga i te $\hat{\lambda}$ i mua me muri i ngā whakakorenga e tohu ana kei te whakatikia pea e ngā mōrea atu anō te tipuranga o te taupori o te kuaka o Whenua Hou, ā, e hiahiatia ana anō ngā whakahaerenga tauwhiro atu anō. Nā ngā tikanga aroturuki iti te utu me te māmā ukiuki, ahakoa takarepa, me ngā whakatikatanga i muri mai, i āhei te aromatawai i ngā putanga o ngā whakakorenga o ngā kaikonihi urutomo, ā, me ārahi i ngā whakatau whakahaerenga anamata.

INTRODUCTION

Close to two-thirds of all reported extinctions in the sixth mass extinction have occurred on islands, the majority of which have been attributed to predation from invasive species (Tershy *et al.* 2015, Jones *et al.* 2016). To counter the detrimental effects of invasive predators, eradications of these problematic species are attempted on many islands. Native species generally respond positively to eradication efforts. Over 200 native animal species found on islands have benefited from invasive predator eradications through increases in abundance and/or distribution (Jones *et al.* 2016, Brooke *et al.* 2018a). Given these benefits, eradications of invasive predators have become a widespread conservation practise with at least 850 island-wide eradications around the globe between 1950 and 2015 (Database of Island Invasive Species Eradications 2015).

Invasive predator eradications from islands often play a key role in seabird conservation, as many seabird species breed on islands, or are even endemic to them (Taylor 2000ab, Spatz *et al.* 2017, Brooke *et al.* 2018a, Rodríguez *et al.* 2019). Seabirds, and notably members of the order Procellariiformes, are one of the most threatened taxonomic groups on the planet (Fig. 2; Croxall *et al.* 2012, Rodríguez *et al.* 2019). Many Procellariiformes are *K* -strategists (i.e., low fecundity and high longevity). Therefore, these species are highly susceptible to the reduced hatching/fledging success and heightened adult mortality that are typical consequences of invasive predators (Jones *et al.* 2007, Spatz *et al.* 2017, Brooke *et al.* 2018a, Rodríguez *et al.* 2019). Smaller species (< 1 kg) are especially susceptible to invasive predators (Jones *et al.* 2007). While Procellariiformes are *K* -strategists, they can respond surprisingly quickly and positively to invasive predator eradications (Jones 2010, Brooke *et al.* 2018a). However, despite the clear conservation gains of invasive predator eradications, systematic post-eradication monitoring remains rare (Jones *et al.* 2016), hindering the evaluation of success and assessments of complementary threats (Spatz *et al.* 2017, Towns 2018).

Whenua Hou (Codfish Island), Aotearoa (New Zealand), hosts a diverse community of small Procellariiform seabirds and invasive predators were eradicated from the island to restore this seabird community (Middleton 2007). Specifically, Weka (*Gallirallus australis;* a predatory bird species native to Aotearoa but invasive to Whenua Hou; Taylor 2000a) were eradicated in 1984, followed by brush-tailed possums (*Trichosurus Vulpecula*) in 1987, and kiore (*Rattus exulans*) in 2000 (dates here represent the year in which the eradications were completed; Brown & Sherley 2002, McClelland 2002, Middleton 2007). One of the Procellariiform species that breeds on Whenua Hou is the critically endangered Whenua Hou Diving Petrel (*Pelecanoides whenuahouensis*; WHDP). This species faced major range restrictions and population declines due to the impacts of invasive predators and is now restricted to a single colony on Whenua Hou (Fig. 4; Taylor 2000b, Holdaway *et al.* 2003, Fischer *et al.* 2018bc). While invasive predators have been removed from Whenua Hou, little is known about past and contemporary population estimates and trends of the WHDP, hindering any assessment of the population responses to the eradication efforts.

To better understand the effects of the eradications of invasive predators on the WHDP, I collated intermittent WHDP burrow counts (*n* = 20) between 1978 and 2018. I then modelled the annual WHDP population growth rates over two biologically relevant time periods: the pre-eradication period (1978–85) and the post-eradication period (2002–18). I accounted retrospectively for differences in detection probability among burrow counts due to differences in effort, marking, and timing, using expert elicitation and data on patterns of WHDP colony attendance. Finally, I used existing literature to compare the annual WHDP population growth rate post-eradications with the post-eradication growth rates of other Procellariiform species breeding on Whenua Hou.

METHODS

Study species and study area

The Whenua Hou Diving Petrel is a small (~130 g) Procellariiform seabird, which was previously considered conspecific with the South Georgian Diving Petrel (*P. georgicus*; Fischer *et al.* 2018b). Following the designation as a new species, the WHDP has been listed as critically endangered on the IUCN Red List (Fischer *et al.* 2018b, BirdLife International 2020). WHDPs were historically widespread through southern Aotearoa, but predation by invasive species caused local extinctions throughout their range, including Rēkohu (Chatham Islands), Maukahuka (Auckland Islands), Rakiura (Stewart Island), and Muaupoko (Otago Peninsula) (Fig. 4; Worthy 1998, Taylor 2000b, Holdaway *et al.* 2003, Wood & Briden 2008, Fischer *et al.* 2017b). Today, the WHDP is restricted to Whenua Hou (14 km^2; Fig. 5) located circa 3 km west of Rakiura. I conducted my study within the only WHDP colony, which is located in the dunes of Waikoropūpū (Sealers Bay -46.766° S, 167.645° E; Fischer *et al.* 2017a, 2018c). WHDPs breed in burrows in these dunes from early September to late January, but colony attendance varies with breeding stages (i.e., the species' phenology), which complicates burrow counts.

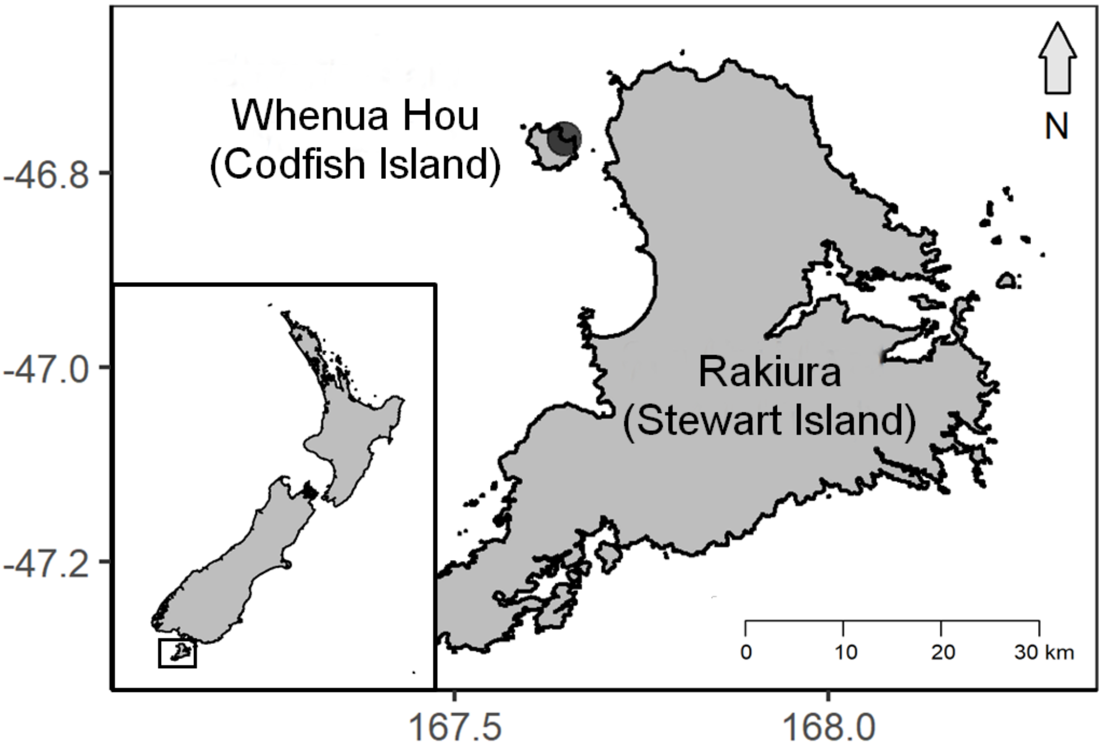

Fig. 5. Location of the study site, Waikoropūpū (Sealers Bay), Whenua Hou (Codfish Island), Aotearoa (New Zealand), as indicated by the dark-grey circle.

Burrow counts

I collated intermittent counts of WHDP burrows based on I) my own WHDP burrow counts (2015–18; reporting the calendar year in which breeding started.), II) the scientific literature, and III) unpublished management reports from the New Zealand Department of Conservation (Table 2). All burrow counts were conducted by walking the entirety of the extremely small (0.018 km^2) breeding colony back and forth (Taylor & Cole 2002, Fischer *et al.* 2018c). After the first count in 1978 (the year in which the colony was discovered; Imber & Nilsson 1980), all detected burrows were marked with stakes during each count (Cox 1991, R Nilsson pers. comm. 2018). When I found more than one count per breeding period in the literature, I used the earlier count. I only considered counts of occupied WHDP burrows, because a small number of Common Diving Petrels (*P. urinatrix*) also breeds in the study area (Fischer *et al.* 2017a). I assessed burrow occupancy through stick palisades, sometimes in combination with playback/human mimics (Imber & Nilsson 1980, Taylor 1991, Taylor & Cole 2002, Fischer *et al.* 2018b). As occupancy assessments require > 1 day, I excluded counts conducted within a single day.

Table 2. Raw Whenua Hou Diving Petrel burrow counts, number of survey days per count (d), marking of burrows, the timing of the count, proportion of attendance ($p_{a,t}$), and corresponding retrospectively corrected estimates ($\widehat{N_t}$; posterior means with 95% CrIs). $\widehat{N_t}$ listed here are based on $\widehat{p_{d,t}}$ informed by all 11 experts.

Year	**Count**	$\boldsymbol{d}$	**Marked**	**Timing in respect to phenology**	$\boldsymbol{p_{a,t}}$	$\widehat{\boldsymbol{N_t}}$	**Reference**
1978	35	2	No	Prospecting-incubation	0.962	40 (36 - 46)	Imber & Nilsson 1980, R Nilsson pers. comm. 2018
1980	32	2	Yes	Incubation	0.962	35 (32 - 39)	West & Imber 1989, R Nilsson pers. comm. 2018
1981	33	2	Yes	Chick-rearing	0.734	45 (38 - 52)	West & Imber 1989, R Nilsson pers. comm. 2018
1983	38	1	Yes	Chick-rearing	0.734	-	West & Imber 1989, A Cox *in lit.* 2018
1985	41	10	Yes	Prospecting	0.902	45 (42 - 50)	West & Imber 1989
1990	42	2	Yes	Prospecting	0.902	48 (44 - 54)	Johnson & Rance 1990
1991	43	3	Yes	Incubation	0.962	45 (43 - 49)	Taylor 1991
1992	41	2	Yes	Incubation	0.962	45 (41 - 49)	Buckingham *et al.* 1995
1993	35	6	Yes	Chick-rearing	0.734	49 (42 - 57)	Cole & Roberts 1994
1998	64	1	Yes	Chick-rearing	0.734	-	Imber 1999
2002	75	5	Yes	Incubation	0.962	78 (75 - 81)	Cole 2004
2003	54	5	Yes	Incubation-chick-rearing	0.962	57 (54 - 60)	Cole 2004
2004	60	10	Yes	Incubation	0.962	63 (60 - 66)	G Taylor unpublished
2005	72	5	Yes	Incubation	0.962	75 (72 - 78)	Trainor 2008
2006	79	7	Yes	Chick-rearing	0.734	99 (90 - 108)	Trainor 2008
2008	76	4	Yes	Chick-rearing	0.734	97 (88 - 106)	Trainor 2009
2015	74	37	Yes	Incubation-chick-rearing-fledging	0.962	78 (74 - 82)	Fischer *et al.* 2018c
2016	78	30	Yes	Prospecting-incubation-chick-rearing-fledging	0.962	82 (78 - 86)	Present study
2017	99	114	Yes	Prospecting-incubation-chick-rearing-fledging	0.962	103 (99 - 107)	Present study
2018	96	102	Yes	Prospecting-incubation-chick-rearing-fledging	0.962	100 (97 - 104)	Present study

Modelling WHDP growth rates

To estimate the yearly rate of WHDP population growth before and after the invasive predator eradications on Whenua Hou while retrospectively correcting estimates of burrow counts, I fitted log-linear models with a Poisson error term in a Bayesian hierarchical framework. Specifically, I fitted the data to:

1. $log(N_t) = \alpha + r_t + \varepsilon_t$

in which N_t is the number of WHDP burrows at year t, α is $log(N_0)$ (the number of WHDP burrows at year 0), r is the log of λ (the finite rate of increase), t is the number of years between 0 and t, and ε_t is random annual variation (Caughley 1977, Caughley & Sinclair 1994). I used log-linear models because I assumed the WHDP population to exhibit exponential growth rates. I considered the number of burrows counted each year (n_t) to be a sampled from a binomial distribution:

2. $n_t \sim Bin(p_t, N_t)$

in which p_t is the probability that a burrow was detected in year t. I modelled the expected variation in p_t as:

3. $p_t = 1 - (1 - p_{d,t})^d \times p_{a,t}$

in which $p_{d,t}$ is the daily probability that a burrow was detected and identified as occupied by WHDPs, d is the number of survey days in year t, and $p_{a,t}$ is the proportion of the WHDP burrows that were attended to at the time of the breeding period that the count was conducted. I thus retrospectively accounted for imperfect detection in WHDP burrow counts by modelling I) the search effort each year, II) the marking of the burrows, and III) the timing of the count in relation to the species' phenology.

To obtain probability distributions for $p_{d,t}$, I designed an expert elicitation based on the Delphi method (Linstone & Turoff 1975, Kuhnert *et al.* 2010, Martin *et al.* 2012). I consulted every living person who had conducted a WHDP burrow count and considered them an expert (*n* = 18). My approach (Delphi method) consisted of two rounds. In round one, I asked experts independently to provide me with a three-point estimate (their best guess, the minimum and the maximum) of p_d, provided the colony is I) marked or II) unmarked. I thus requested separate values for a marked (i.e., after 1978) and an unmarked colony (i.e., 1978) from the experts, allowing me to adjust $p_{d,t}$ according to whether burrows were marked that year. I assumed that $p_{d,t}$ was otherwise constant (e.g., no variation due to learning curves of observers, changes in dune vegetation, or other factors that may have varied among years other than marking). In addition, I assumed that all burrows were equally likely to be detected and that misidentification of WHDP burrows was impossible. The experts were aided in their decision in round one by a graph depicting hypothetical detection probabilities (p_d = 0.1–0.9) as a function over time (Appendix 1). I then compiled responses (n = 11; 61%) and sent anonymous summary statistics to each respondent, allowing them to adjust their initial response (round two; Linstone & Turoff 1975, Kuhnert *et al.* 2010, Martin *et al.* 2012). Only one response (6%) was adjusted in round two (Fig. 6). I obtained beta.PERT distributions (Clark 1962) for $p_{d,t}$ based on the three-point estimates from the expert responses in round two.

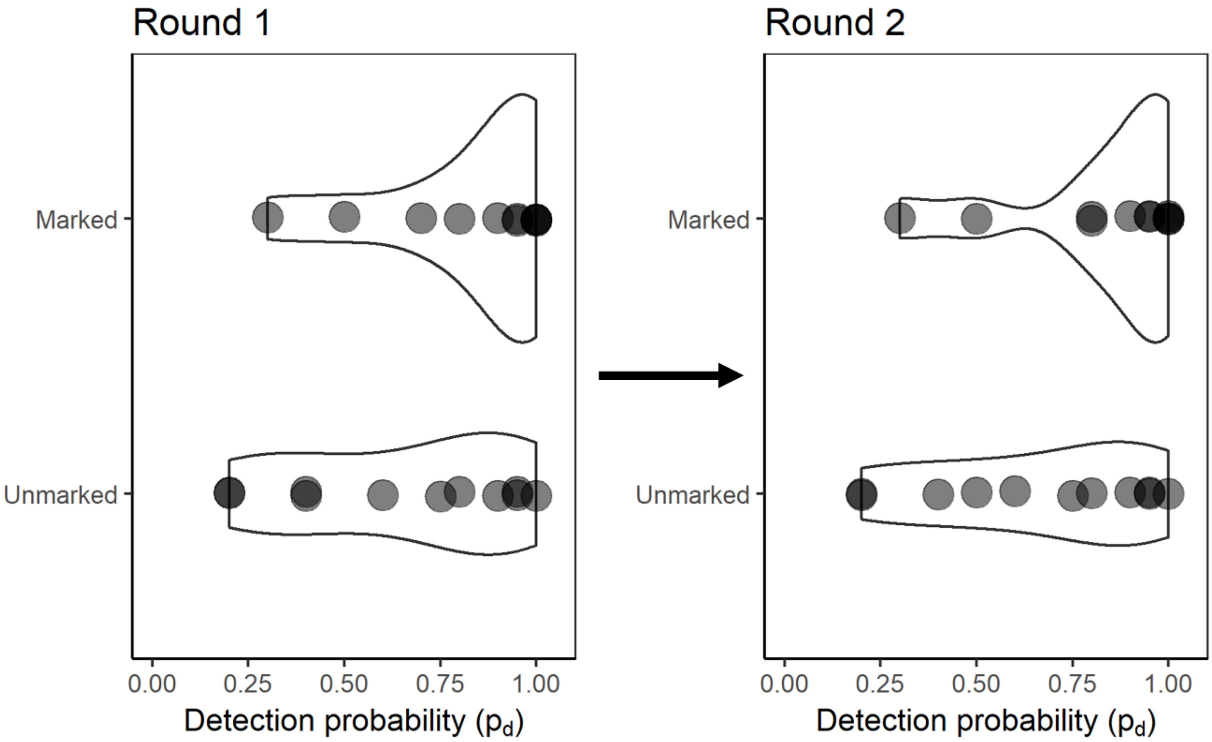

Fig. 6. Violin plots illustrating the distribution of best guesses of detection probabilities (p_d) of Whenua Hou Diving Petrel burrows in marked/unmarked systems, as provided by experts (n = 11) during the two rounds of an expert elicitation following the Delphi method.

To obtain a meaningful numerical value for $p_{a,t}$, I monitored WHDP burrows during the entire 2017 and 2018 period (n = 86 and 81, respectively). Specifically, I monitored the daily activity of these burrows using stick palisades (Imber & Nilsson 1980, Taylor & Cole 2002, Fischer *et al.* 2018c) to create a colony attendance curve throughout the breeding period. At the same time, I monitored a subset of burrows in 2017 and 2018 (n = 29 and 25, respectively) with a burrowscope (Taupe model, Sextant Technologies, Wellington, New Zealand; Lavers *et al.* 2019) to assess mean dates of key phenology events (i.e., lay, hatch, and fledge dates). I summed the daily burrow attendance per week and allocated these into phenologically relevant stages based on the timing of the count (i.e., prospecting, incubation, chick-rearing or fledging). I then obtained $p_{a,t}$ by averaging the weekly values per phenological category. When counts fell into several phenological stages, I allocated the count into the category with the highest $p_{a,t}$. I assumed that the timing of key phenology events during the 2017 and 2018 breeding period were representative off other years.

I used Equation 1–3 to estimate λ for two biologically relevant time periods: before and after the predator eradications. To estimate the λ before the predator eradications, I fitted a model to data between 1978 and 1985. I used the 1978–1985 timeframe because I anticipated a 2-year lag (i.e., expected age at first breeding; Miskelly & Taylor 2004, 2007) of the WHDP population to respond to eradication efforts, in the absence of immigration (Whenua Hou hosts the only WHDP colony). To estimate λ after the predator eradications, I fitted a model to data between 2002 and 2018. In addition, to explore the influence of the expert assessment of $p_{d,t}$on $\widehat{N_t}$ and $\hat{\lambda}$, I repeated my analysis three times using distributions for $p_{d,t}$ that were informed by: I) the average best guess, minimum and maximum from all experts, II) the values provided by the most pessimistic expert, and III) the values provided by the most optimistic expert.

I fitted the models using OpenBugs 3.2.3, which uses Markov chain Monte Carlo (MCMC) algorithms to obtain posterior distributions for parameters, allowing all sources of error to be propagated into those distributions (Lunn *et al.* 2000, Spiegelhalter *et al.* 2014). I used vague priors ($N[mean\ =\ 0, precision\ =\ 0.01]$) for α and r. In most cases I pooled three independent MCMC chains with 100,000 iterations each after a burn-in of 50,000 iterations, resulting in posterior distributions based on 150,000 iterations. Inspection of the Gelman-Rubin statistic ($\hat{R}$) showed slow convergence of chains for the pre-eradication data based on pessimistic values for $p_{d,t}$, so I increased the number of iterations to 2,100,000 with a burn-in of 50,000, giving satisfactory convergence for all estimates ($\hat{R} < 1.05$) (Paxton *et al.* 2016). I report posterior distributions of N_t and λ as means with 95% credible intervals (CrI). The OpenBUGS code of my models can be found in Supplementary Material 1.

Comparison with other Procellariiformes

I compared the λ of the WHDP population after the eradications of invasive predators with the post-eradication λ of other small Procellariform populations breeding on Whenua Hou. Specifically, I used existing literature to source N_t of both Cook's Petrels (*Pterodroma cookii*; ~190 g) and Mottled Petrels (*P. inexpectata*; ~315 g) on Whenua Hou and calculated the λ post eradications using Equation 1 (Marchant & Higgins 1990). When population estimates were reported as a range only, I used the midpoint as N_t. As published estimates of both Cook's and Mottled Petrels lacked detail (e.g., details of historical counts were lost and/or counts were only conducted in small parts of the colonies), I did not apply Equation 2 and 3 to retrospectively correct these estimates.

RESULTS

WHDP population growth rates

A total of 20 raw WHDP burrow counts were collated from 1978 to 2018 (one per breeding period), but two single-day counts were excluded from my analyses (Table 2). The estimates of daily detection probability ($\widehat{p_{d,t}}$) obtained by averaging the data from the 11 experts were 0.83 (minimum = 0.76, maximum = 0.90) in a marked colony and 0.66 (0.58–0.75) in an unmarked colony. The data from the most pessimistic expert produced an $\widehat{p_{d,t}}$ of 0.30 (0.01–0.60) for a marked system and 0.20 (0.01–0.40) for an unmarked system. The data from the most optimistic expert produced an estimate of $\widehat{p_{d,t}}$ of 0.99 (0.97–1.00) for a marked system and 0.99 (0.95–1.00) for an unmarked system. The proportion of attended WHDP burrows ($p_{a,t}$) per phenological stage was as following: prospecting: September - mid October, $p_{a,t}$ = 0.90; incubation: mid-October – late November, $p_{a,t}$ = 0.96; and chick rearing: late November – mid-January, $p_{a,t}$ = 0.73 (Fig. 7). No counts were conducted solely during fledging.

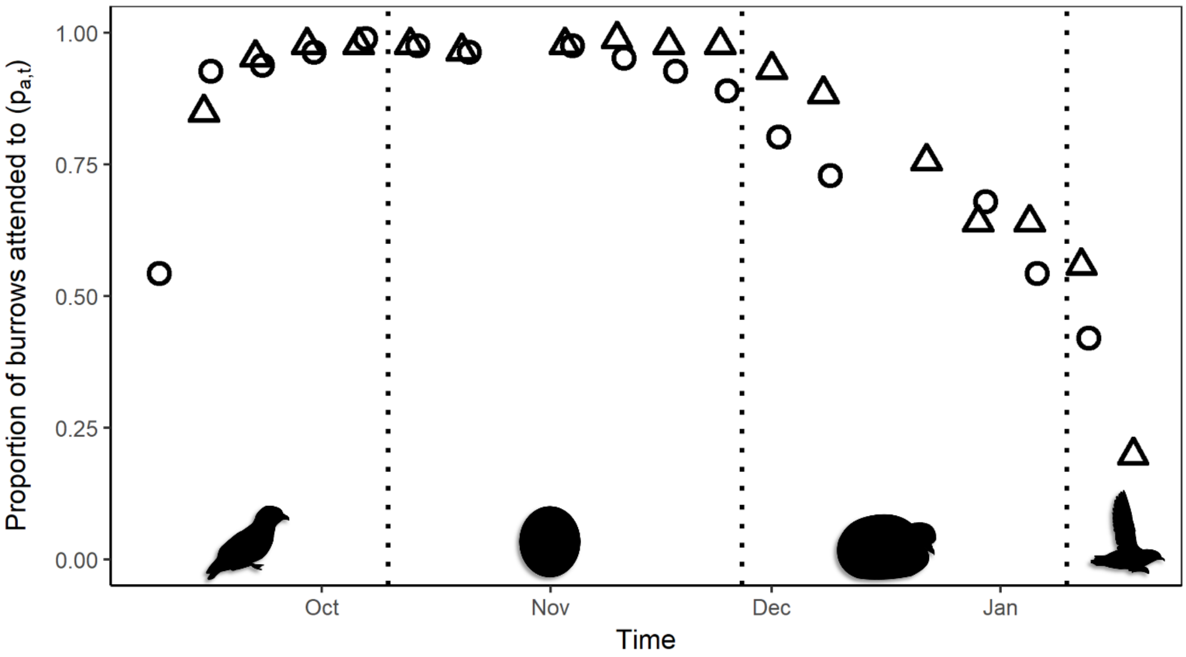

Fig. 7. The proportion of Whenua Hou Diving Petrel burrows that were attended to ($p_{a,t}$) in relation to key phenology events (prospecting, incubation, chick-rearing or fledging) during the 2017 (triangles; n = 86) and the 2018 (circles, n = 81) breeding periods. Dotted lines represent mean lay (09 October), hatch (26 November) and fledge dates (11 January).

When using $\widehat{p_{d,t}}$ informed by the 11 experts, the estimated number of WHDP burrows ($\widehat{N_t}$) varied from 40 (36–46) in 1978 to 100 (97–104) in 2018 (Table 2, Fig. 8), the pre-eradication $\hat{\lambda}$ (1978–85) was estimated at 1.023 (0.959–1.088), and the post-eradication $\hat{\lambda}$ (2002–18) was estimated at 1.017 (1.006–1.029) (Fig. 9). However, when using the $\widehat{p_{d,t}}$ informed by the most pessimistic expert, $\widehat{N_t}$ varied from 59 (48–72) in 1978 to 100 (96–104) in 2018 (Appendix 2), the pre-eradication $\hat{\lambda}$ was estimated at 0.915 (0.833–0.991), and the post-eradication $\hat{\lambda}$ was estimated at 1.014 (1.002–1.026). When using the $\widehat{p_{d,t}}$ informed by the most optimistic expert, $\widehat{N_t}$ varied from 36 (35–39) WHDP burrows in 1978 to 100 (97–104) WHDP burrows in 2018 (Appendix 3), the pre-eradication $\hat{\lambda}$ was estimated at 1.038 (0.975–1.103), and post-eradication $\hat{\lambda}$ was estimated at 1.017 (1.006–1.029).

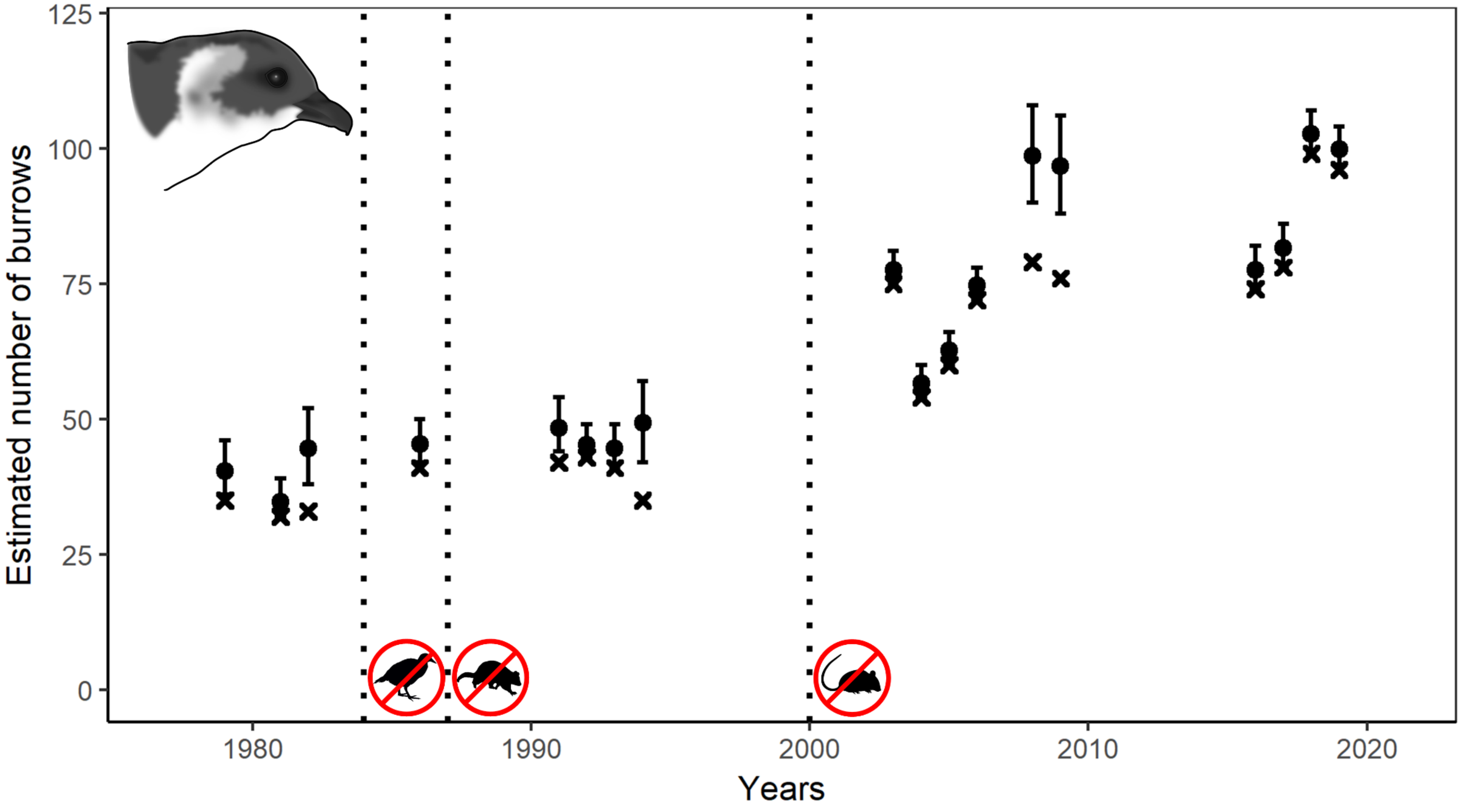

Fig. 8. Raw Whenua Hou Diving Petrel burrow counts (crosses) and retrospectively corrected estimates (filled circles; $\widehat{N_t}$, posterior means with 95% CrIs) based on $\widehat{p_{d,t}}$ informed by all 11 experts, in relation to invasive predator eradications (dotted lines).

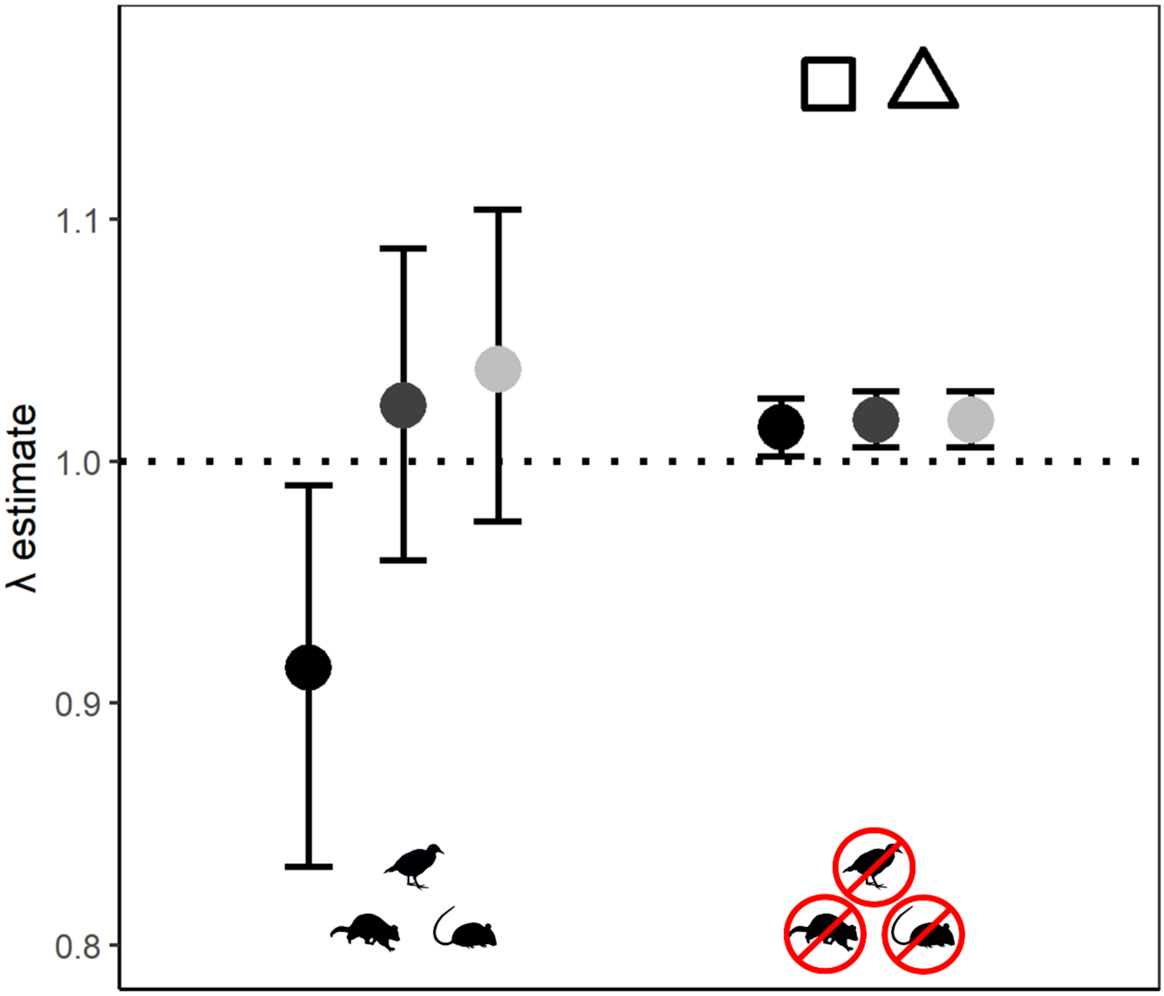

Fig. 9. Estimates of yearly rates of Whenua Hou Diving Petrel population growth ($\hat{\lambda}$), before and after eradications of invasive predators (filled circles; posterior means with 95% CrIs; black = based on $\widehat{p_{d,t}}$ informed by most pessimistic expert, grey = based on $\widehat{p_{d,t}}$ informed by all 11 experts, and light-grey = based on $\widehat{p_{d,t}}$ informed by most optimistic expert), in comparison with estimates of Cook's Petrel (hollow triangle) and Mottled Petrel (hollow square) λ post eradications. Cook's and Mottled Petrel population λ are based on (Robertson & Bell 1984, Taylor 2000a, Imber *et al.* 2003, Rayner *et al.* 2008b).

Comparison with other Procellariiformes

The Cook's Petrel population on Whenua Hou grew from 100 burrows in 1980 to approximately 5,000 (3,500–7,000) burrows in 2007. The λ for this period for Cook's Petrel was 1.156 (Fig. 9). The Mottled Petrel population on Whenua Hou grew from 10,000–50,000 burrows in 1980 to 300,000-400,000 burrows in 1996. The λ for this period for Mottled Petrel was 1.155.

DISCUSSION

I presented WHDP burrow estimates for the last four decades, which ranged from $\widehat{N_t}$ = 40 (36–46) burrows in 1978 to $\widehat{N_t}$ = 100 (97–104) burrows in 2018 (using $\widehat{p_{d,t}}$ informed by all 11 experts). Under the assumption that every burrow was occupied by two adults, these estimates would equate to 80 (72–92) adults in 1978 and 200 (194–208) adults in 2018. These estimates highlighted that the WHDP population slowly increased over the last 40 years but still remained very low. In addition, I also presented the first estimates of the annual population growth rate of the WHDP. The pre-eradication $\hat{\lambda}$ (1978–85) was 1.023, while the post-eradication $\hat{\lambda}$ (2002–18) was 1.017 using $\widehat{p_{d,t}}$ informed all 11 experts. Both $\widehat{N_t}$ and $\hat{\lambda}$ (based on $\widehat{p_{d,t}}$ informed by all 11 experts) indicated that the WHDP population was slowly increasing before invasive predator eradications and still is slowly increasing afterwards.

Comparing raw burrow counts with my estimates derived from retrospective corrections highlighted the importance of accounting for differences in detection probability among burrow counts due to differences in effort and timing. Years in which counts were conducted during chick-rearing (i.e., counts with the lowest $p_{a,t}$) had the greatest difference between the raw burrow counts and $\widehat{N_t}$. Furthermore, burrow counts with a low number of survey days (*d*) resulted in $\widehat{N_t}$ with larger CrIs, highlighting the importance of spending adequate time in the field (MacKenzie *et al.* 2002, 2003). The increased confidence in estimates caused by increased survey effort is also apparent in the $\hat{\lambda}$. The time spent in the WHDP colony after the eradications is considerably higher than before the eradications. Consequently, the $\hat{\lambda}$ post-eradications do not vary, even with different $\widehat{p_{d,t}}$. In contrast, the pre-eradication $\hat{\lambda}$ vary substantially under different $\widehat{p_{d,t}}$. Most noticeably, when using the $\widehat{p_{d,t}}$ informed the most pessimistic expert, the pre-eradication $\hat{\lambda}$ indicated a decreasing WHDP population ($\hat{\lambda}$ = 0.915). However, when compared to detection probabilities of burrows of other Procellariiform species that breed in more vegetated habitats than the WHDP (Barbraud *et al.* 2009, Defos du Rau *et al.* 2015), the $\widehat{p_{d,t}}$ informed by the most pessimistic expert appeared to be underestimates. As such, the $\widehat{p_{d,t}}$ based on values provided by all eleven experts seemed a more realistic estimate.

The post-eradication $\hat{\lambda}$ of the WHDP population contrasted with the λ of other small Procellariiformes post eradications. For example, the population doubling time (t_d) for the Cook's (t_d = 4.49 years) and Mottled Petrels (t_d = 4.52 years) on Whenua Hou was 9.2 and 9.1 times shorter, respectively, than the population doubling time of the WHDP (t_d = 41.18 years) (Caughley & Sinclair 1994). The average population growth rate of 24 Procellariiform populations (17 small, i.e., < 1 kg, species) after invasive predator eradications was $\lambda = 1.079$ (populations established after the eradications were excluded; Brooke *et al.* 2018a). Therefore, the average population doubling time of small Procellariiformes population was t_d = 8.86 years, which is 4.65 times shorter than the t_d of the WHDP. Brooke *et al.* (2018a) highlighted that many seabird species respond rapidly to eradications, potentially due to a pool of immature birds. My intermittent time series did not cover the two years after the eradications (2000-02; the timeframe in which WHDP immatures would have responded; Miskelly & Taylor 2004, 2007), preventing assessments of WHDP responses immediately after the eradications. Regardless of this shortcoming in my study, the population responses of most other Procellariiformes post-eradication efforts were considerably higher than the population response of the WHDP.

The lack of change between the pre- and post-eradication $\hat{\lambda}$ and the low post-eradication $\hat{\lambda}$ indicated that after the invasive predator eradications other factors remained that limit the WHDP population growth and that additional management is required. Various factors could be limiting WHDP population recovery. The distinct preference of the WHDP to only breed in fragile foredunes suggests that the species is extremely vulnerable to storms and storm surges (Fischer *et al.* 2018c). For example, a storm in October 2003 eroded the foredune in which the WHDP breeds, caused nest failures, and increased adult mortality (Cole 2004). Translocations could reduce the vulnerability of the WHDP to these stochastic events (Ch. 4 & 5, Miskelly & Taylor 2004, Miskelly *et al.* 2009). Density dependence could be another explanation to the limited population growth of the WHDP. However, diving petrel colonies have been shown to reach much higher densities (e.g., 6 burrows/m^2; Taylor 2000b) than the current density of the WHDP colony (0.02 burrows/m^2; Ch. 5). Negative interspecific interactions between WHDPs and Common Diving Petrels (Fischer *et al.* 2017a) could also be limiting population growth. While the (meta)population of the Common Diving Petrel within the WHDP colony appeared small (Taylor & Cole 2002, Fischer *et al.* 2018c), measures reducing interspecific interactions (e.g., burrow flaps; Gummer *et al.* 2015) could be considered. Furthermore, no pelagic threats to the WHDP have been assessed to date. Therefore, its pelagic distribution and associated threats, including deck strikes, accidental bycatch in commercial fisheries, or environmental variability, should be investigated (Ch. 3, Taylor, 2000ab, Black 2005, Pardo *et al.* 2017).

While I was unable to identify the factor(s) limiting WHDP population growth, my study illustrated the value of inexpensive and simple, albeit imperfect, field data in combination with retrospective corrections to evaluate the success invasive predator eradications. Eradications of invasive predators from islands have been extremely successful in restoring seabird populations (Jones *et al.* 2016, Spatz *et al.* 2017, Brooke *et al.* 2018a) and the eradications on Whenua Hou clearly were beneficial for the Cook's and Mottled Petrel populations (Fig. 9). Yet, eradications of invasive predators do not exclude the need for follow-up conservation measures (e.g., translocations for WHDPs). Brooke *et al.* (2018a) found that seven seabird populations did not respond to eradication efforts (e.g., Gould's Petrel *Pterodroma gouldii*) and at least 23 seabird populations responded negatively ($\lambda < 1$), suggesting that the limited population response of the WHDP was not an isolated case. Due to the prevalent assumption that native species will be secured following island eradications, monitoring of native fauna post-eradication is rare and thus cases requiring additional management are unlikely to be recognized (Jones *et al.* 2016, Brooke *et al.* 2018ab, Towns 2018). The “unavailability of economical ways to measure change” was listed as another impediment to post-eradication monitoring (Towns 2018). In addition, the allocation of sparse funds towards I) monitoring the responses of native species following eradications or II) future eradications continues to be debated (Brooke *et al.* 2018b). This conundrum is aggravated by the longevity of seabirds (among other long-lived species), as the post-eradication monitoring of these species would ideally span decades, further elevating monitoring costs (Brooke *et al.* 2018ab, Towns 2018). Both Towns (2018) and Brooke *et al.* (2018b) highlight the need for simple, inexpensive monitoring methods that have the potential to assess eradication outcomes over extended time periods. Although detailed (and thus often expensive) monitoring schemes following invasive predator eradications (or even in general) are largely missing (Paleczny *et al.* 2015, Towns 2018), basic, but imperfect data (such as burrow counts) do often exist (e.g., Taylor 2000ab). My results demonstrate that relatively inexpensive monitoring approaches (e.g., burrow-counts), combined with retrospective corrections, can be informative and allow for evaluations of management success across extended time periods, even when monitoring has been intermittent. I thus advocate the use of imperfectly collected historical data and recommend the continuation of similar simple and inexpensive monitoring methods post-eradications to inform outcomes of invasive predator eradications and consequently, future conservation management.

Chapter 3

Year-round offshore distribution, behaviour, and overlap with commercial fisheries of a critically endangered small petrel

ABSTRACT

Year-round offshore distributions, movements, and behaviours of many small (<0.3 kg) seabirds remain largely unknown, despite increasing conservation concern. Without such insights, effective conservation management cannot be applied. The Whenua Hou Diving Petrel (*Pelecanoides whenuahouensis*; WHDP) is a critically endangered small seabird whose offshore habits and threats remain unknown. We tracked WHDPs year-round in 2015/16, 2017/18, and 2018/19 using global location-sensing immersion loggers to identify offshore distribution, movements, behaviour, and overlap with commercial fishing effort. During the breeding period, WHDPs ranged from the south of Aotearoa (New Zealand) to Maukahuka (Auckland Islands). After breeding, WHDPs migrated south-west towards the Polar Front south of Australia, exhibited clockwise movements, and returned to their breeding grounds via the Subantarctic Front. During the non-breeding period, WHDPs exhibited extreme aquatic behaviour and spent up to 99% of their time on, or under, water. Distributions were consistent across years and spatial segregation, either between sexes or between failed and successful breeders, was absent. The core areas used during both breeding and non-breeding periods warrant listing as Important Bird and Biodiversity Areas. Spatiotemporal overlap of commercial fishing effort with breeding distributions was considerable (35%), in contrast with non-breeding distributions (0%). The lack of fishing effort and the extreme aquatic behaviour suggests that WHDPs may be secure from fisheries-related threats during the non-breeding period. Spatial restrictions around the breeding colony during the breeding period could help protect WHDPs. My results illustrate the importance of year-round distributional and behavioural studies to inform the conservation of marine species.

INTRODUCTION

Assessing the threats that species face across their distributions and throughout their annual cycle is crucial for effective conservation management. Seabirds are among the most threatened taxa on the planet and a variety of threats across terrestrial and pelagic ecosystems affect these birds during various stages of their annual cycles (Ch. 1, Dias *et al.* 2019). Offshore threats impacting seabirds during their breeding, migratory, and non-breeding periods include accidental bycatch in fisheries, overfishing, environmental pollution, and attraction to artificial lights at night (Dias *et al.* 2019, Rodríguez *et al.* 2019). The impacts of offshore threats on large seabirds (e.g., albatrosses) are more often quantified than the impacts on smaller seabirds (i.e., < 0.3 kg; Paiva *et al.* 2018, Bolton 2020, Rotger *et al.* 2020). For example, it has been estimated that hundreds of thousands of large seabirds annually are killed as accidental bycatch in commercial fisheries (e.g., Anderson *et al.* 2011). However, small seabird species also suffer from offshore threats throughout their annual cycle, including from bycatch in long-line (Anderson *et al.* 2011), trawl (Rodríguez *et al.* 2019), purse-seine (Oliviera *et al.* 2015), and gill net fisheries (Žydelis *et al.* 2013), as well as from resource competition with humans (Grémillet *et al.* 2018) and deck strikes (collisions with vessels due to disorientation caused by artificial light pollution at sea; Black 2005).

Understanding of the offshore threats affecting smaller seabird species is limited in part by a lack of year-round insights into their offshore distributions, movements, and behaviour. With technological advances in tracking technologies, opportunities to gain insights into offshore distributions and behaviours of small seabirds have increased. Yet, the distributions and behaviours of the smallest seabird species remain poorly understood (e.g., Paiva *et al.* 2018, Rotger *et al.* 2020). For example, only 29% of the smallest Procellariiformes (families Hydrobatidae, Oceanitidae, and Pelecanoididae) have been tracked for a portion of their annual cycles (Adams & Takekawa 2008, Navarro *et al.* 2013, 2015, Rayner *et al.* 2017, Halpin *et al*. 2018, Hedd *et al.* 2018, Paiva *et al.* 2018, Lago *et al.* 2019, Pollet *et al.* 2019, BirdLife International Seabird Tracking Database 2020, Bolton 2020, Dunphy *et al.* 2020, Rotger *et al.* 2020, Wikelski & Keys 2020). Year-round studies covering > 1 annual cycle are virtually absent for any of these species (Pollet *et al.* 2019). Yet, these small Procellariiformes include four data deficient, four vulnerable, four endangered, and two critically endangered species (BirdLife International 2020) and are thus of considerable conservation concern.

Identifying year-round distribution, movements, and behaviour is key to the conservation of small seabird species. If the spatial distribution of species has not been quantified, the threats faced in relevant areas cannot be identified, and conservation management cannot be applied effectively (e.g., Adams & Takekawa 2008, Hedd *et al.* 2018, Bolton 2020). Combining temporal information and spatial insights, increases the efficiency of conservation management. For instance, species may be at risk from certain threats during their breeding period, but not during their non-breeding period, or vice versa (Halpin *et al.* 2018, Clay *et al.* 2019). Such insights are important as migratory bird species are more vulnerable than residents (e.g., Hardesty-Moore *et al.* 2018). In addition, offshore behaviour cannot be ignored when assessing threats. For example, endangered Peruvian Diving Petrels (*Pelecanoides garnotii*) lose their ability to fly during the non-breeding period due to the complete moult of their flight feathers (Murphy & Harper 1921, BirdLife International 2020), potentially rendering them less at risk from deck strikes, but more at risk from bycatch in purse-seine or trawl fisheries and environmental pollution.

Offshore distribution, movements, and behaviour can be subject to variation between demographic groups (e.g., failed and successful breeders or different sexes) and among years (e.g., due to environmental stochasticity) and insights into this variation is crucial when implementing conservation management. If different demographic groups are exposed to annually varying threats, population dynamics could be affected considerably (e.g., Pardo *et al.* 2017, Clay *et al.* 2019). Underlying drivers of offshore distribution and behaviour have been studied extensively in larger seabird species (e.g., Gonzales-Solis *et al.* 2000, Clay *et al.* 2016, Schultz *et al.* 2018). For example, failed breeding Grey-headed Albatrosses (*Thalassarche chrysostoma*) use different, less productive areas during the non-breeding period compared to successful breeders (Clay *et al.* 2016) and male Wandering Albatrosses (*Diomedea exulans*) exploit areas at higher latitudes than females to take advantage of higher winds to offset their larger wing loadings (Clay *et al.* 2020). Such detailed insights for smaller seabird species remain largely absent (Paiva *et al.* 2018), impeding comprehensive assessments of conservation implications.

The Whenua Hou Diving Petrel (*Pelecanoides whenuahouensis*; WHDP) is a small, critically endangered seabird whose offshore distribution, movements, behaviour, and associated threats remain unknown. The WHDP population was once widespread, occupying coastal dunes throughout southern Aotearoa (New Zealand; Fig. 4; Taylor 2000b). However, after humans introduced invasive predators, all breeding colonies except one were extirpated. Now, WHDPs survive in low numbers (182-235 adults; Ch. 4) at one breeding colony on Whenua Hou (Codfish Island; Fig. 5). While Whenua Hou is now free of invasive predators (McClelland 2002), terrestrial threats affecting WHDPs during the breeding period remain (e.g., storms and interspecific competition with Common Diving Petrels *P. urinatrix*; Fischer *et al.* 2017a, 2018c). Due to a lack of data, no offshore threats affecting WHDPs during their breeding and/or non-breeding periods have been identified. Common and South Georgian Diving Petrels (*P. georgicus*) are among the taxa most commonly suffering from deck strikes (Ryan 1991, Black 2005, Abraham & Richards 2019). Diving petrels are also caught as bycatch in trawl, gill net, and longline fisheries, including in waters around Aotearoa (Žydelis *et al.* 2013, Abraham & Richard 2019). As diving petrels are notoriously cryptic, at-sea observations (including records of bycatch events) are often not species-specific (Fischer *et al.* 2018b, Richard *et al.* 2020) and thus of limited use to assess offshore distribution, movements, behaviour, and corresponding threats. Therefore, I tracked WHDPs for three full annual cycles to identify I) offshore distributions, II) movements patterns, III) offshore behaviour, and IV) overlap with commercial fishing effort. In addition, I investigated the effects of potential underlying drivers on distribution, movements, and behaviour (i.e., breeding success, sex, and interannual variation).

METHODS

Deployment and retrieval of geolocators

To investigate WHDP offshore distribution, movements, and behaviour, I deployed global location-sensing immersion loggers (geolocators; Migrate Technology, Cambridge, UK; Table 3) on breeding adults (> 2 years old) at Whenua Hou (-46.766° S, 167.645° E), Aotearoa. I captured WHDPs by hand or with custom-made burrow traps (Fig. 10) and attached geolocators to plastic wrap-around leg bands using cable ties and superglue. The combined weight of geolocators and attachment materials was < 1.5 g, equating to < 1.1% of adult WHDP body weight (average = 133 g), below the commonly accepted 3% threshold (Phillips *et al.* 2003). While I cannot discount potential negative effects (Quillfeldt *et al.* 2012, Bodey *et al.* 2017), WHDPs equipped with geolocators were in good condition upon recapture and had weights that did not clearly differ from individuals without geolocators (I compared 34 WHDPs carrying geolocators with 136 non-equipped WHPDs using a generalized linear model with a Gaussian error distribution and an identity-link function: $\hat{\alpha} = -0.02 \pm 0.09$ SE, $\widehat{\beta_{geolocator}} = 0.07 \pm 0.19$ SE). WHDPs equipped with geolocators also did not show clear deviations from the natural breeding phenology (see results and Ch. 5) or reductions in breeding success (66% of equipped WHDPs fledged a chick, compared to the multi-year average of 55%; Ch. 4).

Table 3. Number of Migrate Technology (Cambridge, UK) geolocators deployed, geolocators retrieved, and year-round data sets obtained.

Year	Model	*n* deployed	*n* retrieved (%)	*n* data sets obtained (%; ♀; ♂)
2015/16	Intigeo-W65A9-SEA	10	7 (70%)	4 (57%; 1; 3)
2017/18	Intigeo-C65-SUPER	26	21 (81%)	20 (95%; 11; 9)
2018/19	Intigeo-C65-SUPER	18	14 (78%)	14 (100%; 9; 5)

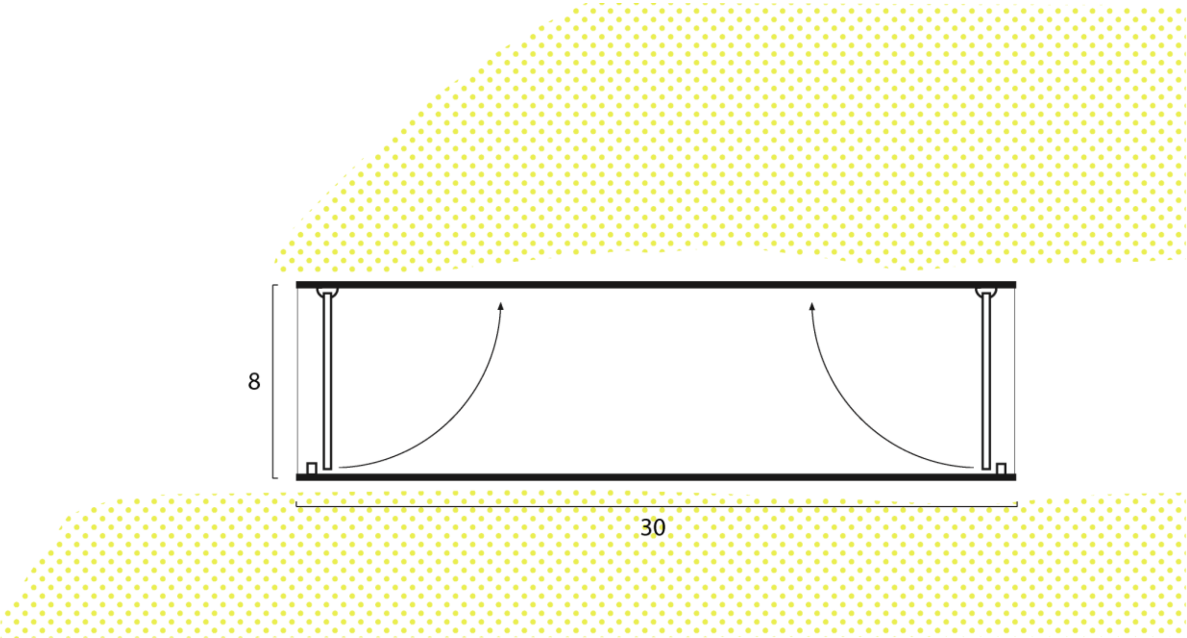

Fig. 10. Custom-made burrow trap to (re)capture Whenua Hou Diving Petrels as they enter/exit their burrow. Dimensions are in cm. The main body of the trap consisted of a polyvinyl chloride piping, while the one-way doors were made of acrylic. Hinges were constructed out of braided stainless-steel wire.

I set geolocators to record light levels (lux) every min and save the maximum value every five mins. I also programmed geolocators to record saltwater-immersion every 30 seconds (0 or 1 which correspond with "dry" or "wet", respectively) and to save the cumulative wet count every 10 min. Recorded values thus ranged from 0 (dry) to 20 (fully immersed). Geolocators deployed after 2015 recorded sea-surface temperature (SST) when immersed in saltwater for > 20 min and saved temperature every eight hours (mean, minimum, and maximum in ° C). Finally, I collected four contour feathers during geolocator attachment and used these for genetic sex determination (using polymerase chain reaction primers specific to the chromodomain-helicase-DNA-binding gene on the W-chromosome; Norris-Caneda & Elliott 1998).

Geolocators are non-transmitting devices and thus I recaptured WHDPs in subsequent years to retrieve devices. I obtained a total of 38 datasets from 24 individuals providing year-round insights (mean geolocator deployment: 317 days).

Light level analyses

To infer offshore locations of WHDPs from recorded light levels, I applied the threshold method to quantify twilight events, followed by an iterative forward step selection to reduce location errors with I) a twilight model, II) a movement model, and III) several spatial masks using the package *ProbGLS* in program R 3.5.3 (Merkel *et al.* 2016, R Core Team 2019). I selected a light threshold of 1.5 for twilight events (Schultz *et al.* 2018) and a solar angle window of -7° to -1° for the twilight model (Taylor *et al.* 2020). I used a bimodal movement model for dry periods (i.e., bird in flight; mean ± σ = 1.4 ± 0.5 m/s, max = 10 m/s) and wet periods (i.e., bird on water; 0.5 ± 0.25 m/s, max = 1.7 m/s) (Rayner *et al.* 2017). I defined wet periods as periods during which the 10-min cumulative wet counts were "wet" for ≥ 1 min. I applied two binary spatial masks: land and sea ice (0.25° × 0.25°; National Oceanographic and Atmospheric Administration high resolution dataset; available at: ftp://ftp.cdc.noaa.gov/Datasets/noaa.oisst.v2.highres/). I thus assumed that WHDPs completely avoided land and sea ice and set the sea ice concentration threshold at 1%. For geolocators deployed after 2015, I also applied a continuous SST spatial mask. Specifically, I cross-referenced the minimum SST values recorded by geolocators with satellite-recorded SST values (daily mean ± SE; 0.25° × 0.25°; National Oceanographic and Atmospheric Administration high resolution dataset; available at: ftp://ftp.cdc.noaa.gov/Datasets/noaa.oisst.v2.highres/; Reynolds *et al.* 2007). I used the minimum SST values recorded by geolocators to avoid artefacts caused by the bird's body temperature and allowed the satellite-derived SST values to differentiate from the geolocator records by 0.5 ° C. I subsequently estimated the median geographic tracks by I) calculating the weighted probability for a cloud of possible locations (1,000 locations per step), II) selecting the most likely location, and III) repeating this process for 100 iterations (Merkel *et al.* 2016). This iterative forward step selection allowed for estimation of locations during the equinox periods. Double tagging with GPS loggers at similar latitudes revealed that locations inferred with this iterative forward step selection had an error of 145 km during the equinoxes (Merkel *et al.* 2016). Using this method, I inferred a total of 22,372 offshore locations of WHDPs from the collected light data. These locations can be accessed at http://www.seabirdtracking.org/.

Spatiotemporal analyses

To objectively identify presence and quantify timing of migratory movements in WHDPs, I fitted a range of models to the net squared displacement (the square of the distance between the starting point and each subsequent point; NSD) of individual WHDPs tracks using the R package *MigrateR* 1.1.0 (Spitz *et al.* 2017, DB Spitz, B Cristescu, CC Wilmers, RE Wheat, T Levi & HU Wittmer unpublished). Specifically, I fitted the NSD of each year-round track to models representing I) residency, II) nomadism, II) dispersal, IV) migration, V) mixed-migration, and VI) multi-range migration (equations are provided in Appendix 4). I compared the fit of these models to the NSD of each track using the Akaike information criterion (Burnham & Anderson 2002) and selected the best supported model. The NSD of all WHDP tracks was best explained by multi-range migratory models (Equation 6 in Appendix 4), which described pronounced migratory movements to and from the breeding distribution and showed additional spatial structures in the non-breeding period. I subsequently used the model-estimated migration phenology to objectively delineate the four annual phenophases for each track: breeding period, outbound migration, non-breeding period, and homebound migration.

I used generalized linear mixed effects models (GLMMs) with a Gaussian error distribution and an identity-link function (Clay *et al.* 2016) within the R package *lme4* (Bates *et al.* 2015) to test for effects of breeding success, sex, and interannual variation on WHDP movements (departure from the breeding distribution, arrival at the non-breeding distribution, departure from the non-breeding distribution, arrival at the breeding distribution, length of the outbound migration, length of the stay at the non-breeding distribution, and length of the homebound migration). I z-transformed all numeric variables. I treated breeding success, sex, and year as fixed effects and individual ID as a random effect in these models.

To quantify year-round WHDP distribution and investigate the underlying drivers, I calculated kernel utilization distributions (UDs) per individual per breeding and non-breeding period using the *adehabitatHR* R package (Calenge 2006). Specifically, to calculate the 50% UDs (core area of use) and the 95% UDs (full extent of distribution), I projected WHDP locations on a 50 km grid using a Lambert Azimuthal Equal Area projection and a kernel smoothing factor (*h*) that corresponded with the geolocator error during the equinoxes (145 km; Merkel *et al.* 2016). As some individuals were recaptured immediately after their return to the breeding colony, I did not calculate UDs for individuals with < 30 breeding distribution locations. Subsequently, to create overall distribution maps, I merged individual breeding and non-breeding UDs into overall UDs which accounted for unequal number of locations among individuals (Clay *et al.* 2017, Schultz *et al.* 2018). I then calculated spatial overlap among individual breeding and non-breeding UDs, overall breeding and non-breeding UDs, UDs of different sexes, and UDs of failed and successful breeders (defined as successfully fledging a chick). Specifically, to quantify spatial overlap, I calculated the Bhattacharyya's affinity (BA), which is a function of the product of two UDs, under the assumption that animals use space independently of each other (BA = 0 equals no overlap, BA = 1 equals complete overlap; Fieberg & Kochanny 2005).

Behavioural analyses

I inferred offshore behaviour of WHDPs using the recorded saltwater immersion records (10 min cumulative wet counts) and the online tool *Actave.net* (Mattern *et al.* 2015). I defined cumulative counts that were "wet" for ≥ 1 min as "on or under water" and counts that were "wet" for < 1 min as "in flight". I quantified time spent "on or under water" per day (24 hours) per individual per phenophase. This allowed me to assess if WHDPs, similar to Peruvian Diving Petrels, exhibited periods of flightlessness (Murphy & Harper 1921). I also quantified the daily number of flight bouts (consecutive data points categorized as "in flight"), duration of flight bouts, and time spent "in flight" per diel category (dawn, day, dusk, and night) per individual per phenophase (Mattern *et al.* 2015). However, I refrained from quantifying flight behaviour during the breeding period, as I could not differentiate between WHDPs in flight and WHDPs on land at the breeding colony (Schultz *et al.* 2018). I then investigated the influence of phenophase, breeding success, sex, and interannual variation on offshore behaviour using GLMMs with a Gaussian error structure and an identity-link function. I z-transformed all numerical variables. I treated phenophase, sex, breeding success, and year as fixed effects and individual ID as a random effect in these models.

Overlap with commercial fishing effort

To infer year-round offshore threats to WHDPs, I quantified the spatiotemporal overlap between the breeding and non-breeding distributions and commercial fishing effort. I sourced data on daily commercial fishing effort (fishing hours at 0.1° cell resolution) from 2012 to 2016 from Global Fishing Watch (dataset available at: https://globalfishingwatch.org/data-download/datasets/public-fisshing-effort-10:v20200316). Global Fishing Watch uses satellite tracking of commercial fishing vessels equipped with automatic identification systems to derive fishing effort (McCauley *et al.* 2016, Kroodsma *et al.* 2018, Taconet *et al.* 2019). This dataset equates to 50-70% of the global fishing effort (*n* > 70,000 vessels; Kroodsma *et al.* 2018). I did not differentiate between vessel types (i.e., based on fishing gear) and summed daily fishing effort from all tracked vessels per breeding and non-breeding period per year. I delineated the breeding and non-breeding periods using the means of the model-estimated migration phenologies (Appendix 4). I then calculated the average fishing effort per breeding and non-breeding period to account for interannual variation. Subsequently, I overlaid the 50% and 95% UDs of WHDP breeding and non-breeding distributions and calculated I) the mean fishing effort per 0.1° cell, II) the sum of fishing effort, and III) the percentage of cells with fishing effort within WHDP breeding and non-breeding distributions during the breeding and non-breeding periods. I conducted these calculations in Program R 3.5.3 (R Core Team 2019) and ArcMap 10.7.1.

RESULTS

WHDP movements

WHDPs showed consistent clockwise migratory movements (Fig. 11 & 12). After the breeding period, WHDPs left Whenua Hou and migrated south-west past Macquarie Island towards the Polar Front (December/January-March). Subsequently, WHDPs moved north-west towards and along the Subantarctic Front (April-June). Ultimately, WHDPs returned to their breeding colony via the Subantarctic Front (July-September). On average, WHDPs departed their breeding distribution on 27 December, spent 8.9 days on their outbound migration, arrived at their non-breeding distribution on 5 January, spent 235.0 days at their non-breeding distribution, departed their non-breeding distribution on 28 August, spent 14.0 days on their homebound migration, and arrived at their breeding distribution on 11 September.

Breeding success influenced WHDP movements. Specifically, failed breeders departed their breeding distribution earlier, arrived earlier at their non-breeding distribution and spent more time at their non-breeding distributions (Table 4). Sex had little influence on WHDP movements, but males exhibited a slightly more prolonged homebound migrations than females. Interannual variation influenced WHDP movements slightly. Birds in 2016 departed earlier from their breeding distribution, exhibited more prolonged outbound migrations, and spent more time at their non-breeding distributions. Additionally, birds in 2019 arrived later at their non-breeding distributions.

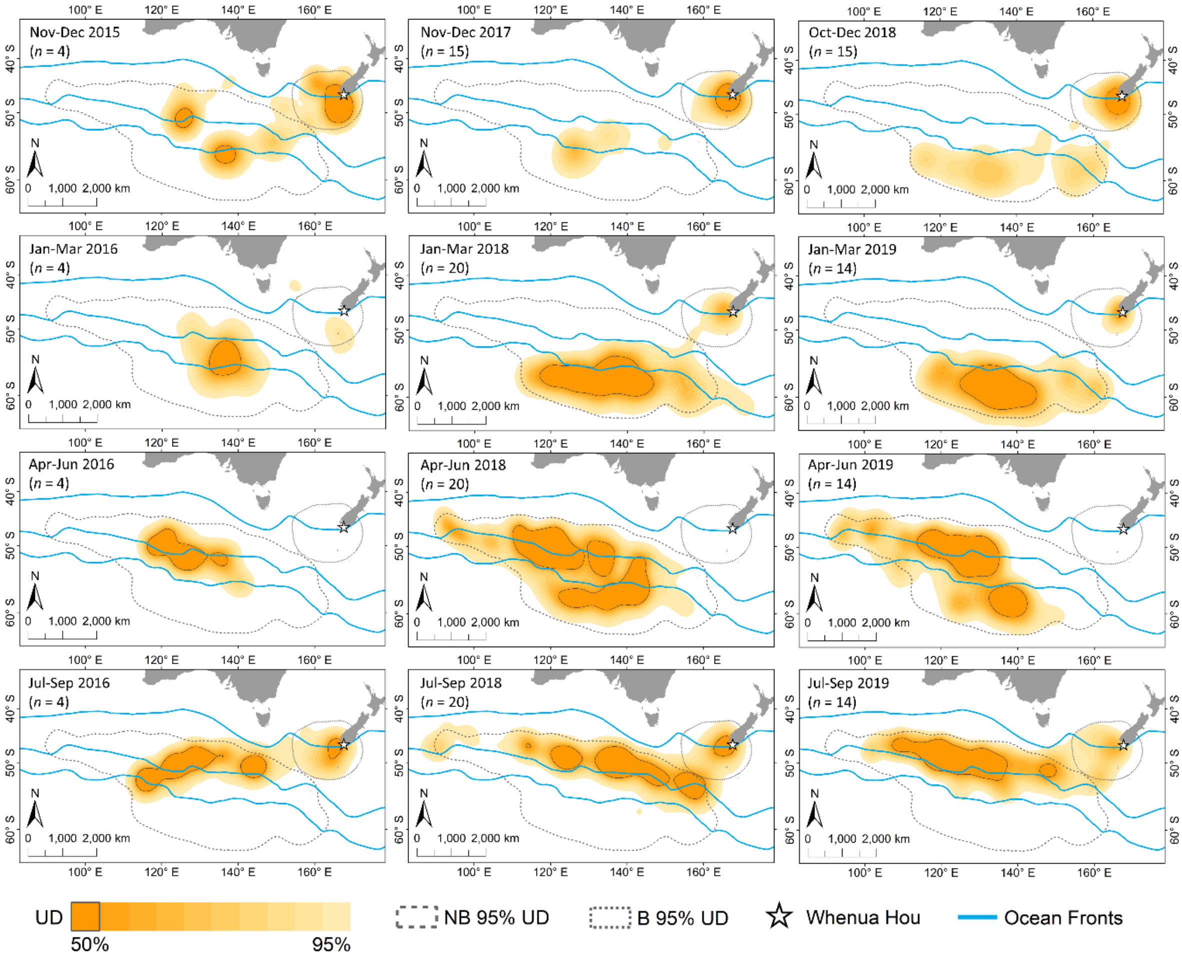

Fig. 11. Year-round movements and distributions of Whenua Hou Diving Petrels during 2015/16, 2017/18, and 2018/19 illustrated by 50% to 95% UDs. NB = non-breeding distribution, B = breeding distribution. Raw data can be accessed at http://www.seabirdtracking.org/. Approximate location of fronts (from north to south: Subtropical Front, Subantarctic Front, and Polar Front) are based on Harris & Orsi (2006).

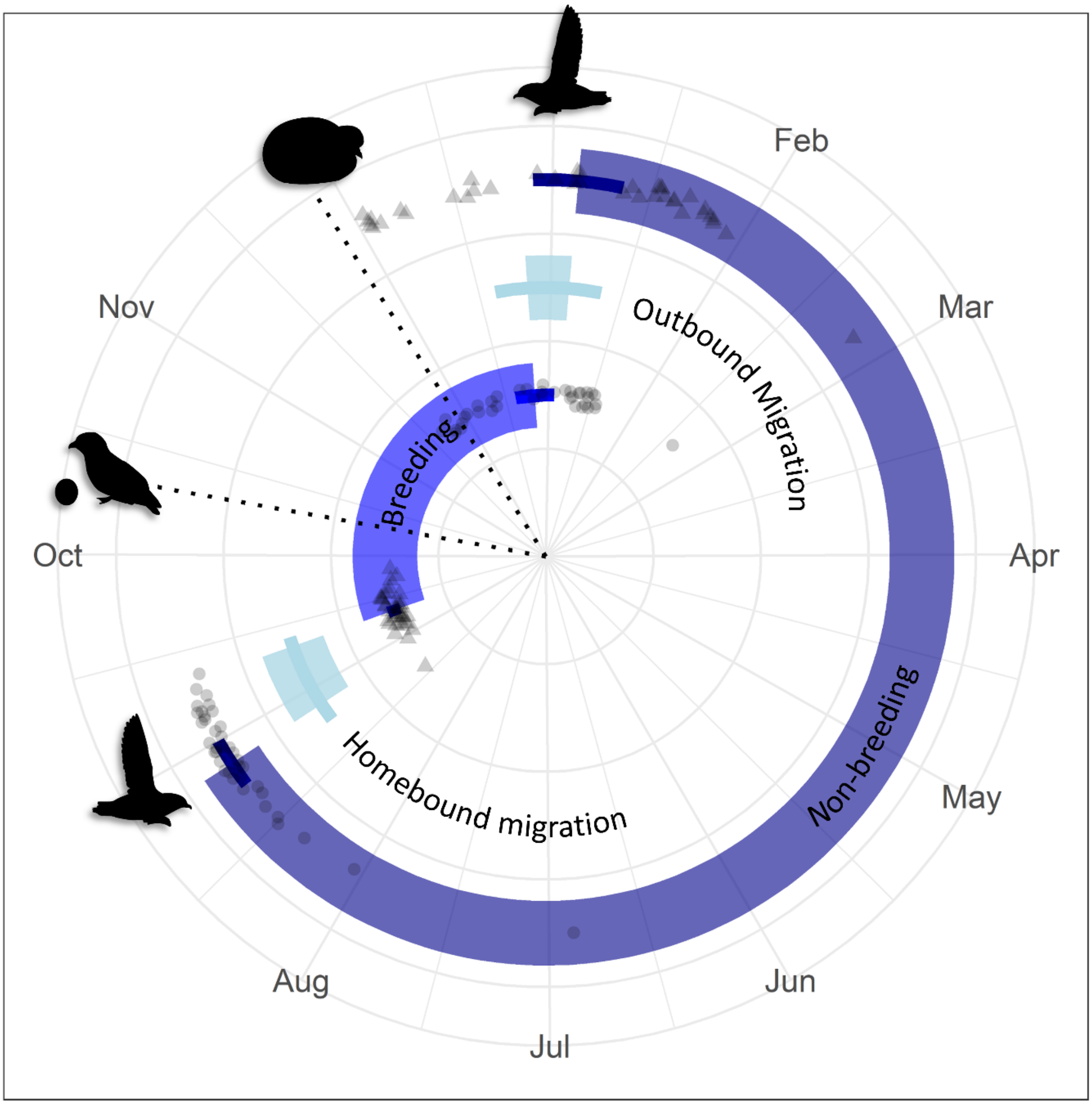

Fig. 12. Estimated year-round Whenua Hou Diving Petrel movement phenology represented by means with 95% CIs. Grey triangles represent individual estimates of arrival dates. Grey circles represent individual estimates of departure dates. Dotted lines represent mean lay (10 October) and hatch dates (27 November; Ch. 5).

Table 4. Estimates of intercepts ($\hat{\alpha}$ ± SE) and fixed effects slopes ($\hat{\beta}$ ± SE) of Whenua Hou Diving Petrel movements. Intercepts and slopes are reported on the link scale. **Bold** indicates that $\beta \pm 2 \times$ SE does not intersect 0.

Movement variable	**Intercept**	**Breeding success**	**Sex**	**Year**
Departure breeding distribution	$\hat{\alpha}$ = -1.89 ± 0.34	$\boldsymbol{\widehat{\beta_{success}}}$ **= 1.61 ± 0.22**	$\widehat{\beta_{female}}$ = -0.31 ± 0.20	$\boldsymbol{\widehat{\beta_{2018}}}$ **= 1.07 ± 0.32** $\boldsymbol{\widehat{\beta_{2019}}}$ **= 1.29 ± 0.35**
Arrival non-breeding distribution	$\hat{\alpha}$ = -1.62 ± 0.36	$\boldsymbol{\widehat{\beta_{success}}}$ **= 1.61 ± 0.23**	$\widehat{\beta_{female}}$= -0.20 ± 0.21	$\widehat{\beta_{2018}}$ = 0.68 ± 0.35 $\boldsymbol{\widehat{\beta_{2019}}}$ **= 0.87 ± 0.37**
Departure non-breeding distribution	$\hat{\alpha}$ = 0.08 ± 0.55	$\widehat{\beta_{success}}$ = 0.16 ± 0.35	$\widehat{\beta_{female}}$= 0.49 ± 0.32	$\widehat{\beta_{2018}}$ = -0.56 ± 0.53 $\widehat{\beta_{2019}}$ = -0.44 ± 0.56
Arrival breeding distribution	$\hat{\alpha}$ = -0.50 ± 0.56	$\widehat{\beta_{success}}$ = 0.30 ± 0.36	$\widehat{\beta_{female}}$= -0.05 ± 0.33	$\widehat{\beta_{2018}}$ = 0.31 ± 0.54 $\widehat{\beta_{2019}}$ = 0.45 ± 0.58
Length outbound migration	$\hat{\alpha}$ = 1.18 ± 0.50	$\widehat{\beta_{success}}$ = 0.001 ± 0.33	$\widehat{\beta_{female}}$= 0.36 ± 0.30	$\boldsymbol{\widehat{\beta_{2018}}}$ **= -1.58 ± 0.48** $\boldsymbol{\widehat{\beta_{2019}}}$ **= -1.52 ± 0.52**
Length of stay at non-breeding distribution	$\hat{\alpha}$ = -1.31 ± 0.42	$\boldsymbol{\widehat{\beta_{success}}}$ **= -1.27 ± 0.28**	$\widehat{\beta_{female}}$= 0.42 ± 0.27	$\boldsymbol{\widehat{\beta_{2018}}}$ **= -0.75 ± 0.37** $\boldsymbol{\widehat{\beta_{2019}}}$ **= -0.91 ± 0.41**
Length of homebound migration	$\hat{\alpha}$ = -043 ± 0.53	$\widehat{\beta_{success}}$ = -0.01 ± 0.34	$\boldsymbol{\widehat{\beta_{female}}}$**= -0.66 ± 0.32**	$\widehat{\beta_{2018}}$ = 0.92 ± 0.49 $\widehat{\beta_{2019}}$ = 0.88 ± 0.53

WHDP offshore distribution

The core breeding distribution of WHDPs (159,497 km^2) ranged from Te Tai-o-Rēhua (Tasman Sea) west and south off Te Waipounamu (South Island) to Maukahuka (Auckland Islands) and appeared concentrated around the Subtropical Front and the Snares Islands shelf (Fig. 11, 13A & 14A). The total breeding distribution (890,632 km^2) extended further northwards in Te Tai-o-Rēhua and further south towards Motu Ihupuku (Campbell Island). The WHDP breeding distribution was consistent among years (BA = 0.92; Fig. 11) and individuals (BA = 0.79). There was no evidence for spatial segregation of WHDPs during the breeding period between sexes (BA = 0.98; Fig. 13A) or failed and successful breeders (BA = 0.99; Fig. 14A).

Both the core area of use (1,521,041 km^2) and the total non-breeding distribution (6,069,461 km^2) encompassed a vast area in the Southern Ocean. The core non-breeding distribution of WHDPs was centred in the Southern Ocean south of Australia and ranged from south of the Polar Front to north of the Subantarctic Front (Fig. 11, 13B & 14B). The total non-breeding distribution ranged from the Polar Front south of Macquarie Island to seas north of the Subantarctic Front west of Western Australia. Average maximum distance from the WHDP breeding colony was 3,791 km. While the number of birds tracked in 2016 (n = 4) appeared insufficient to capture the full extent of the non-breeding distribution (Fig. 11), WHDP non-breeding distribution was highly consistent among years (BA = 0.82) and reasonably consistent among individuals (BA = 0.47). There was no clear evidence for spatial segregation of WHDPs during the non-breeding period between sexes (BA = 0.96; Fig. 13B) or failed and successful breeders (BA = 0.86; Fig. 14B), despite some failed breeders that moved further west.

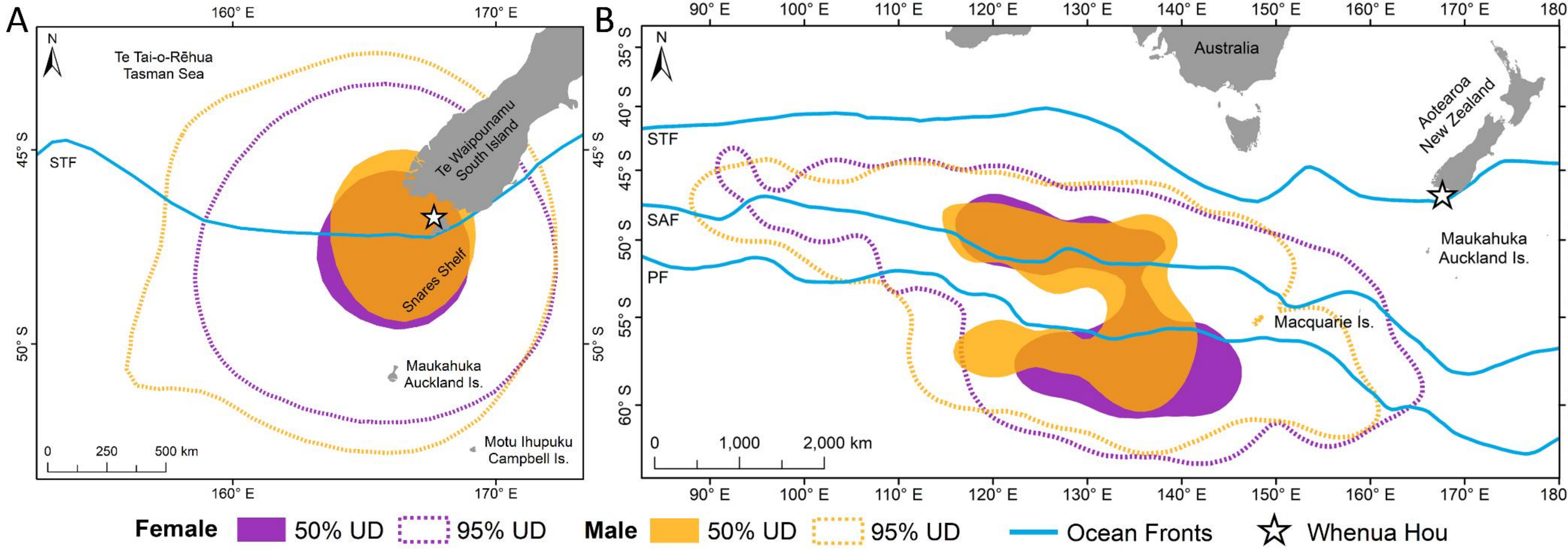

Fig. 13. Breeding (A) and non-breeding distributions (B) of female ($n_{breeding}$ = 25, $n_{non\text{-}breeding}$ = 21) and male ($n_{breeding}$ = 17, $n_{non\text{-}breeding}$ = 17) Whenua Hou Diving Petrels as illustrated by 50% and 95% UDs. Raw data can be accessed at http://www.seabirdtracking.org/. STF = Subtropical Front, SAF = Subantarctic Front, PF = Polar Front; approximate locations are based on Harris & Orsi (2006).

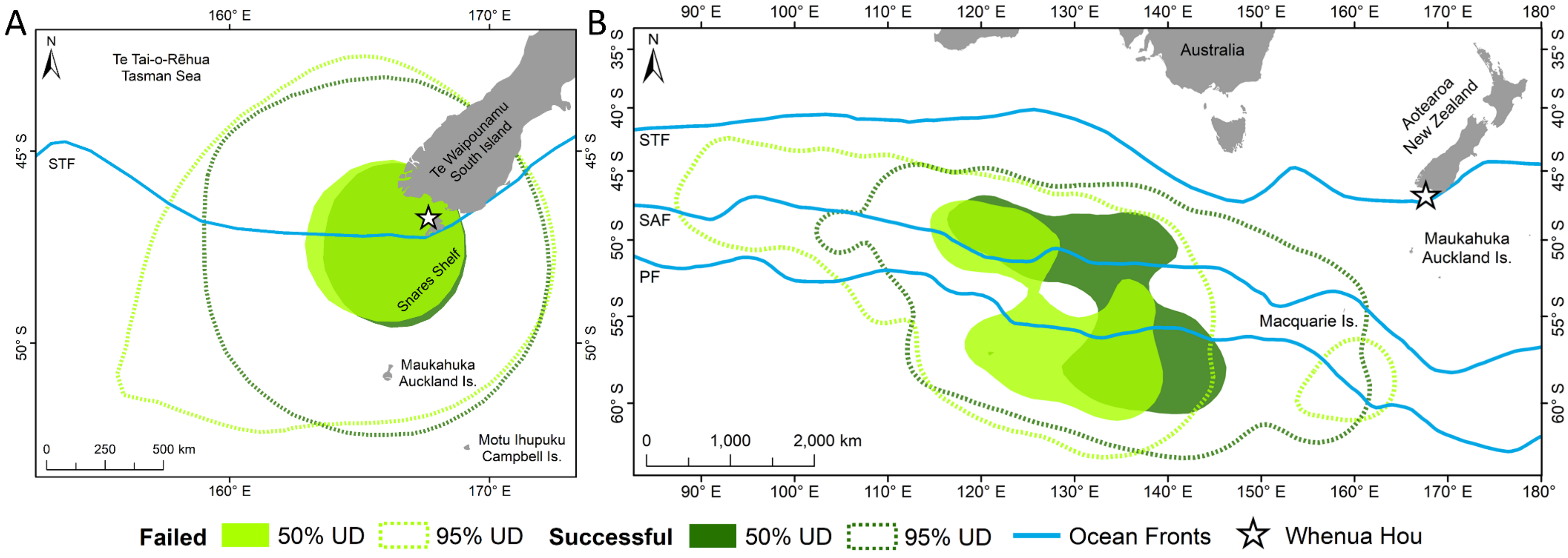

Fig. 14. Breeding (A) and non-breeding distributions (B) of successful ($n_{breeding}$ = 30, $n_{non\text{-}breeding}$ = 25) and failed ($n_{breeding}$ = 13, $n_{non\text{-}breeding}$ = 13) Whenua Hou Diving Petrels as illustrated by 50% and 95% UDs. Raw data can be accessed at http://www.seabirdtracking.org/. STF = Subtropical Front, SAF = Subantarctic Front, PF = Polar Front; approximate locations are based on Harris & Orsi (2006).

WHDP offshore behaviour

At their non-breeding distribution, WHDPs spent on average 95% (22.8 hours/day) and up to 99% (23.7 hours/day) of their time with at least their legs immersed in saltwater (Fig. 15). During the breeding period, WHDPs spent on average 66% (15.7 hours/day) of their time immersed. Thus, phenophase had a considerable influence on offshore behaviour (Table 5, Fig. 16). During the non-breeding period WHDPs exhibited little, predominantly nocturnal, flight activity (2.9 bouts/day lasting 33 min per flight bout). During the rapid outbound migrations, WHDPs exhibited more frequent and more diurnal flight activity (8.7 bouts/day lasting 37 min per flight bout). During the slower homebound migrations, WHDPs did not exhibited such elevated diurnal flight activity, but flight bouts were longer (3.9 bouts/day lasting 46 min per flight bout). Despite their flight efforts during their migrations WHDPs still remained largely on, or under, water. Breeding success had little influence on offshore behaviour, but successful breeders spent more time immersed than failed breeders. Sex had no clear influence on offshore behaviour. Interannual variation had a limited influence on offshore behaviour, but birds in 2019 exhibited fewer and shorter flight bouts and spent less time in flight at night. Additionally, birds in 2016 spent less time flying at dawn.

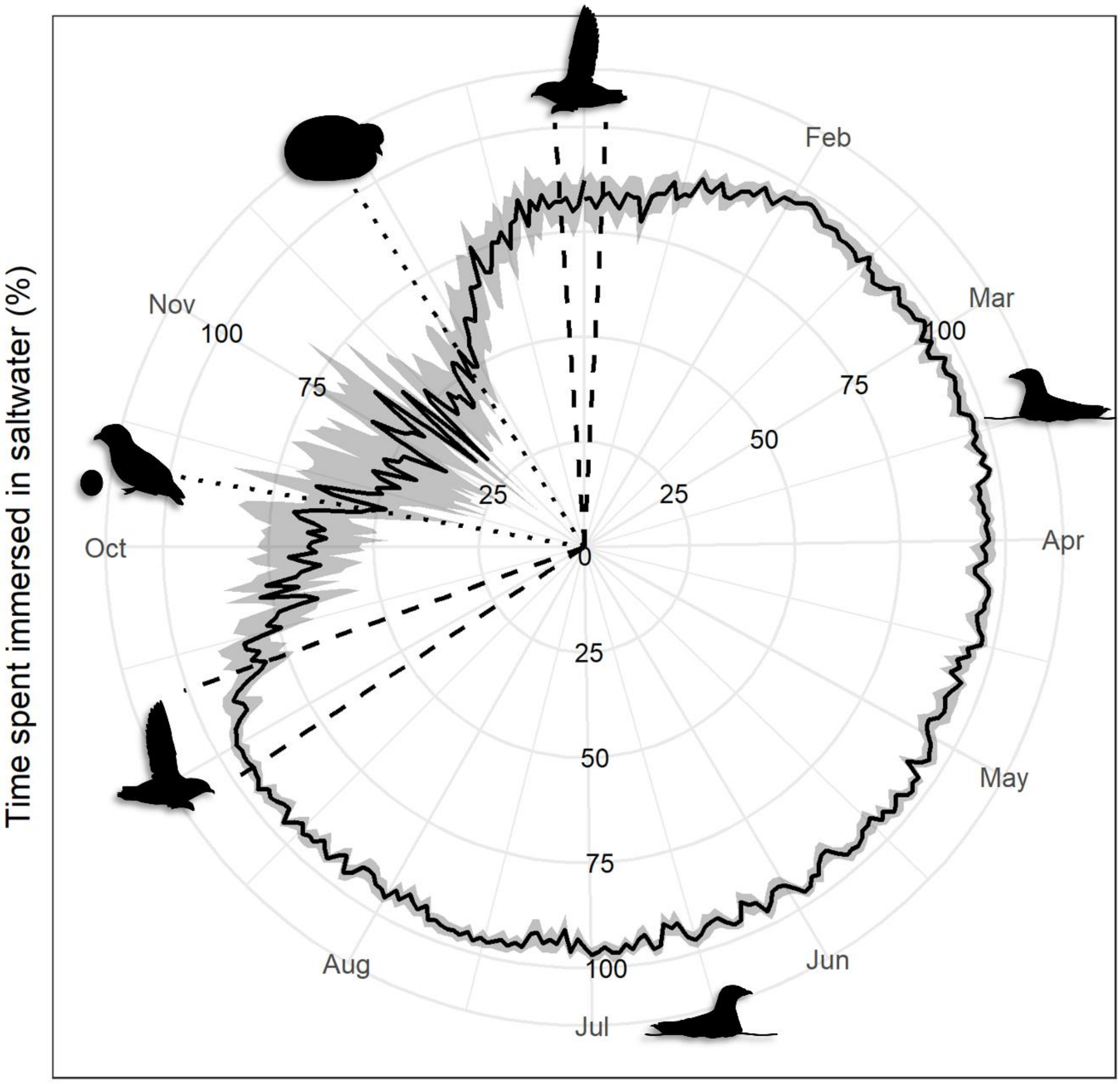

Fig. 15. Proportion of time Whenua Hou Diving Petrels spent immersed in saltwater (% per day; means with 95% CIs). Dashed lines indicate model-estimated means of departure from the breeding distribution (27 December), arrival at the non-breeding distribution (5 January), departure from the non-breeding distribution (28 August), and arrival at the breeding distribution (11 September). Dotted lines represent mean lay (10 October) and hatch dates (27 November; Ch. 5).

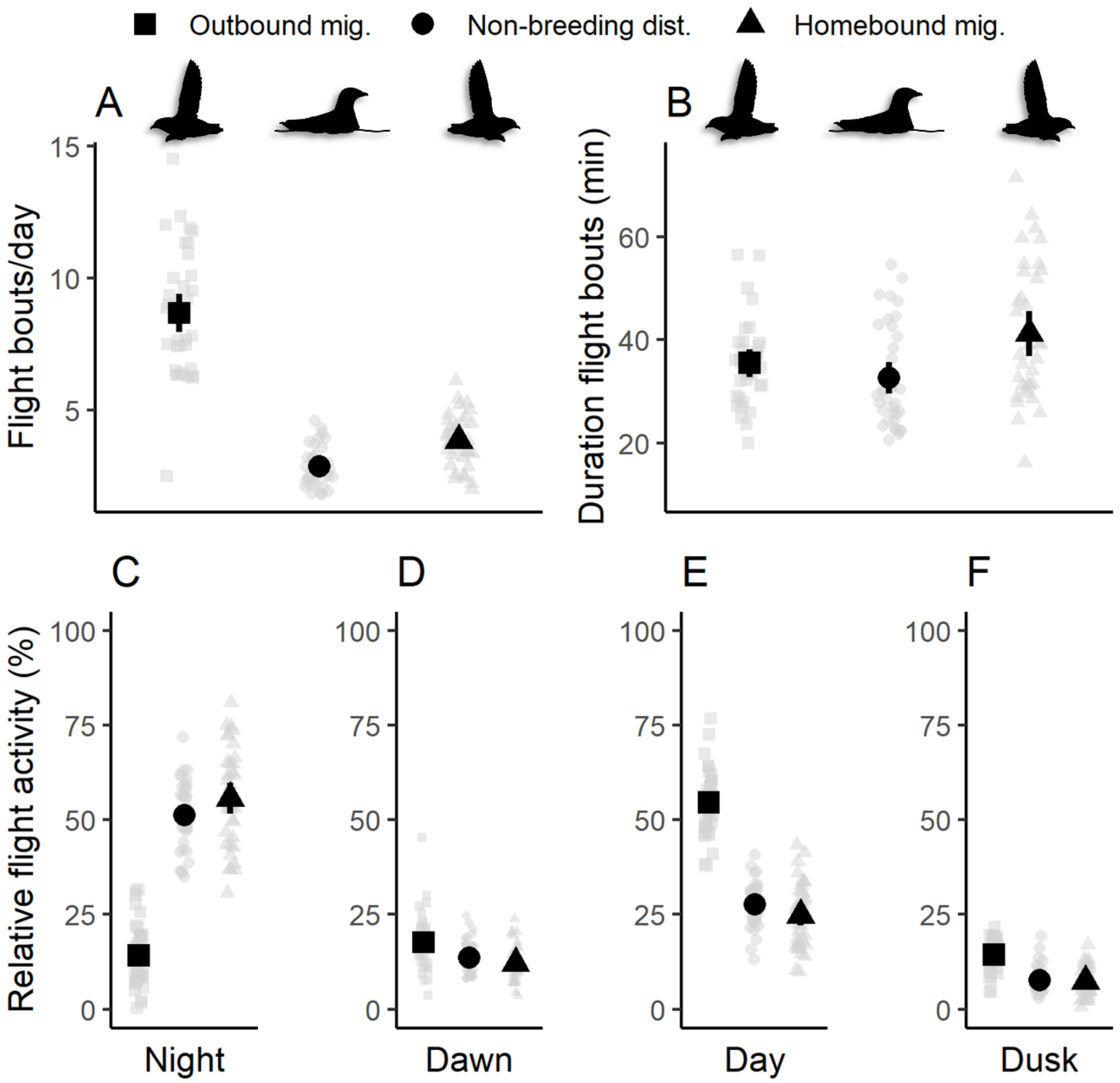

Fig. 16. Number of flight bouts per day (A), duration of flight bouts (B), and relative flight activity per diel category (C-F) per model-estimated phenophase. Black symbols with error bars: means with 95% CIs, grey symbols: raw data.

Table 5. Estimates of intercepts ($\hat{\alpha}$ ± SE) and fixed effects slopes ($\hat{\beta}$ ± SE) of Whenua Hou Diving Petrel offshore behaviour. Intercepts and slopes are reported on the link scale. mig1 = outbound migration, NB = non-breeding distribution, and mig2 = homebound migration. **Bold** indicates that β ± 2 × SE does not intersect 0.

Offshore behaviour variable	Intercept	Phenophase	Breeding success	Sex	Year
Time spent immersed	$\hat{\alpha}$ = -1.29 ± 0.30	**$\widehat{\beta_{mig1}}$ = 0.73 ± 0.14** **$\widehat{\beta_{NB}}$ = 1.87 ± 0.14** **$\widehat{\beta_{mig2}}$ = 1.39 ± 0.14**	**$\widehat{\beta_{success}}$ = 0.26 ± 0.10**	$\widehat{\beta_{female}}$ = -0.13 ± 0.09	$\widehat{\beta_{2016}}$ = 0.35 ± 0.34 $\widehat{\beta_{2017}}$= 0.19 ± 0.32 $\widehat{\beta_{2018}}$= 0.22 ± 0.31 $\widehat{\beta_{2019}}$= 0.59 ± 0.32
Number of flight bouts	$\hat{\alpha}$ = 1.48 ± 0.18	**$\widehat{\beta_{NB}}$ = -1.97 ± 0.11** **$\widehat{\beta_{mig2}}$ = -1.63 ± 0.11**	$\widehat{\beta_{success}}$ = -0.14 ± 0.11	$\widehat{\beta_{female}}$ = 0.08 ± 0.10	$\widehat{\beta_{2018}}$ = -0.14 ± 0.16 **$\widehat{\beta_{2019}}$ = -0.42 ± 0.17**
Duration of flight bouts	$\hat{\alpha}$ = -0.21 ± 0.33	$\widehat{\beta_{NB}}$ = -0.28 ± 0.21 **$\widehat{\beta_{mig2}}$ = 0.54 ± 0.21**	$\widehat{\beta_{success}}$ = 0.07 ± 0.19	$\widehat{\beta_{female}}$ = 0.34 ± 0.18	$\widehat{\beta_{2018}}$ = -0.51 ± 0.29 **$\widehat{\beta_{2019}}$ = -0.73 ± 0.31**
Flight time at night	$\hat{\alpha}$ = -0.96 ± 0.17	**$\widehat{\beta_{NB}}$ = 1.76 ± 0.11** **$\widehat{\beta_{mig2}}$ = 1.98 ± 0.11**	$\widehat{\beta_{success}}$ = -0.09 ± 0.10	$\widehat{\beta_{female}}$ = 0.04 ± 0.10	$\widehat{\beta_{2018}}$ = -0.25 ± 0.15 **$\widehat{\beta_{2019}}$ = -0.37 ± 0.16**
Flight time at dawn	$\hat{\alpha}$ = 0.06 ± 0.35	**$\widehat{\beta_{NB}}$= -0.67 ± 0.20** **$\widehat{\beta_{mig2}}$ = -0.90 ± 0.20**	$\widehat{\beta_{success}}$ = -0.02 ± 0.20	$\widehat{\beta_{female}}$ = -0.27 ± 0.21	**$\widehat{\beta_{2018}}$ = 0.64 ± 0.30** **$\widehat{\beta_{2019}}$ = 0.85 ± 0.32**
Flight time during the day	$\hat{\alpha}$ = 1.06 ± 0.19	**$\widehat{\beta_{NB}}$ = -1.74 ± 0.11** **$\widehat{\beta_{mig2}}$ = -1.93 ± 0.11**	$\widehat{\beta_{success}}$ = 0.11 ± 0.11	$\widehat{\beta_{female}}$ = -0.001 ± 0.10	$\widehat{\beta_{2018}}$ = 0.11 ± 0.16 $\widehat{\beta_{2019}}$= 0.12 ± 0.18
Flight time at dusk	$\hat{\alpha}$ = -0.79 ± 0.29	**$\widehat{\beta_{NB}}$= -1.39 ± 0.16** **$\widehat{\beta_{mig2}}$ = -1.43 ± 0.16**	$\widehat{\beta_{success}}$ = -0.08 ± 0.18	$\widehat{\beta_{female}}$ = 0.02 ± 0.17	$\widehat{\beta_{2018}}$ = 0.13 ± 0.25 $\widehat{\beta_{2019}}$ = 0.41 ± 0.27

Overlap with commercial fishing effort

Considerable commercial fishing effort was present within the breeding distribution during the breeding period (11 September to 27 December; Fig. 17A). Concentrations of commercial fishing effort within the WHDP breeding distribution were evident within the exclusive economic zone (EEZ) south of Aotearoa, along the Snares shelf, and east of Maukahuka. Average fishing effort within the breeding distribution (95% UD) during the breeding period equated to 0.59 hours per 0.1° cell. Average summed fishing effort equated to 4,399 fishing hours. Fishing effort occurred within 10.92% of the WHDP breeding distribution. Average fishing effort within the WHDP core area of use (50% UD) during the breeding period equated to 2.72 hours per 0.1° cell. Average summed fishing effort equated to 2,948 vessel hours. Fishing effort was recorded within 34.51% of the WHDP core area of use during the breeding period.

There was almost no recorded commercial fishing effort within the non-breeding distribution during the non-breeding period (5 January to 28 August; Fig. 17B). The only hotspot of commercial fishing effort within the WHDP non-breeding distribution was near Macquarie Island within the Australian EEZ. Average fishing effort within the WHDP non-breeding distribution (95% UD) equated to 0.004 hours per 0.1° cell. Average summed fishing effort equated to 166 fishing hours per year. Fishing effort was limited to 0.08% of the WHDP non-breeding distribution. No fishing effort was recorded within the WHDP core area of use during the non-breeding period (50% UD).

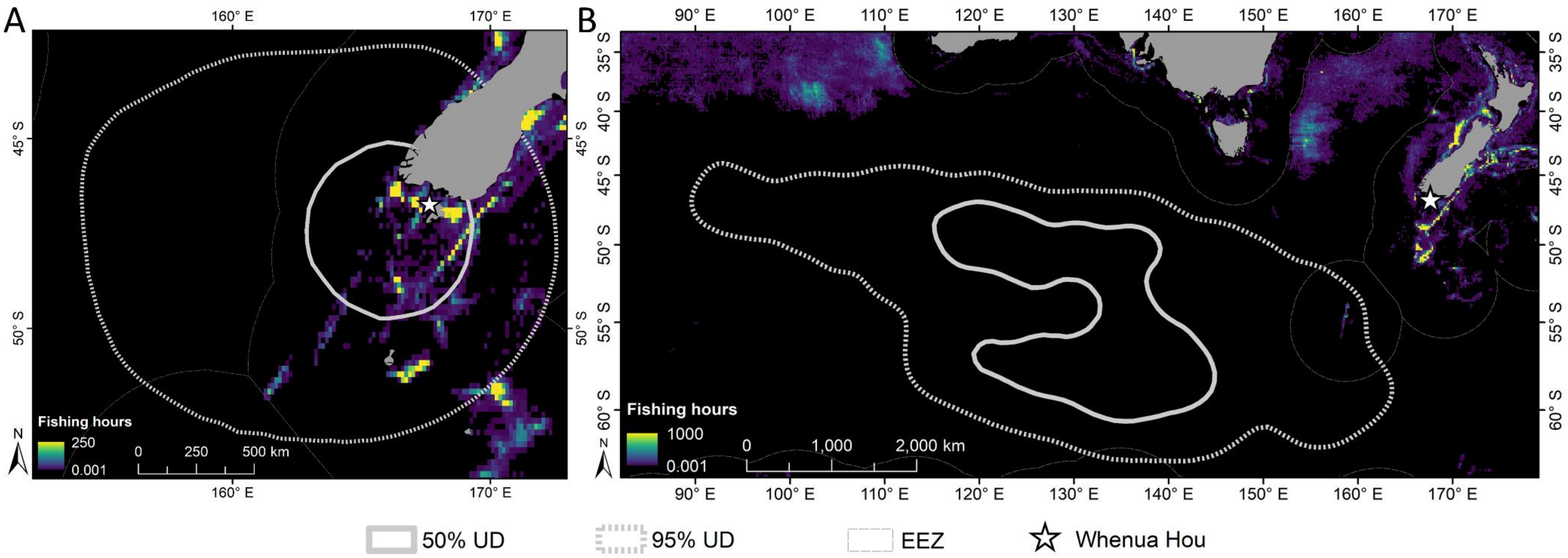

Fig. 17 Spatiotemporal overlap of Whenua Hou Diving Petrel distributions during breeding (A) and non-breeding periods (B) with mean fishing effort. WHDP distributions are illustrated by 50% and 95% UDs and fishing effort in represented by fishing hours per 0.1˚ cell (sourced from Global Fishing Watch https://globalfishingwatch.org/). The model-estimated Whenua Hou Diving Petrel breeding and non-breeding periods lasted from 11 September to 27 December and from 5 January to 28 August, respectively. The displayed fishing effort corresponds with these timeframes.

DISCUSSION

WHDP movements and distribution

WHDPs exhibited a truly pelagic lifestyle and spent the vast majority (> 71%) of their annual cycles at sea. During the breeding period, WHDPs did not range very far from Whenua Hou, as birds were bound by central place foraging, and travelling distances appeared to mirror congeneric species (Zhang *et al.* 2019, Dunphy *et al.* 2020). Rich feeding grounds, characterized by high productivity (chlorophyll-a concentrations), are located relatively close to Whenua Hou (e.g., the Snares shelf, the Subtropical Front, and around Maukahuka; Tréguer & Jacques 1993, Orsi *et al.* 1995). My tracking efforts suggested that WHDP foraged here during the breeding period. These findings aligned with diet analyses, as the presence of larvae of *Histiotheuthis* sp. and *Chirotheuthis* sp. in stomachs suggested that WHDPs feed at the edge of the continental shelf (Imber & Nilsson 1980). WHDPs share these seas with a suite of seabird species including Sooty Shearwaters (*Puffinus griseus*; Shaffer *et al.* 2006), Cook's Petrels (*Pterodroma cookii*; Rayner *et al.* 2008a), Buller's Albatrosses (*T. bulleri*; Waugh *et al.* 2017), and White-headed Petrels (*P. lessonii*; Taylor *et al.* 2020).

After the breeding period, WHDPs spent their time around the Polar and Subantarctic Front. WHDPs migrated towards their non-breeding distributions against the prevailing winds (Young 1999) but completed their migrations rapidly through considerable flying efforts. On their homebound migrations, WHDPs exhibited less concerted flying efforts and probably exploited the prevailing westerly winds and currents. The WHDP non-breeding distribution was, similarly to the breeding distribution, characterized by areas of relatively high productivity. Both the Polar and the Subantarctic Front exhibit heightened concentrations of chlorophyll-a, providing WHDPs with feeding opportunities (Tréguer & Jacques 1993, Orsi *et al.* 1995). Other seabird species, such as White-headed Petrels (Taylor *et al.* 2020) and Grey-headed Albatross (Clay *et al.* 2016), also use these areas.

WHDP offshore behaviour

WHDPs showed extreme aquatic behaviour during the non-breeding period. Even during the breeding period, WHDPs were on, or under, water for two-thirds of their time, while spending considerable amounts of time on land attending their burrows. Despite their predominant aquatic behaviour, WHDPs continued to exhibit flight behaviour throughout the year, indicating they retained flight capability during their non-breeding period, unlike some congenerics (Murphy & Harper 1921). The aquatic behaviour of WHDPs could be explained by their high wing loadings. Diving petrel wings are adapted to wing-propelled diving, allowing relatively deep dives (e.g., 11 and 18 m in Common and South Georgian Diving Petrels, respectively; Navarro *et al.* 2013). Wings adapted to wing-propelled diving, however, have high wing loadings (e.g., 67 and 60 N/m^2 in Common and South Georgian Diving Petrels, respectively; Warham 1977). As such, diving petrels exhibit an energetically costly flight with fast whirring wings low above the sea surface, resembling alcids from the Northern Hemisphere, rather than other Procellariiformes (Rayner *et al.* 2017, Dunphy *et al.* 2020). This flight style may render diving petrels vulnerable to predation by larger seabirds (e.g., skuas), which may explain the largely nocturnal flight activity recorded in WHDPs. However, even compared to alcids, WHDPs are unusually aquatic (Mosbech *et al.* 2012, Dunn *et al.* 2020). Further investigations into the exact behaviour (i.e., resting vs. diving) would allow more detailed insights into the underlying drivers of their extreme aquatic nature (e.g., high daily energy expenditures; Dunn *et al.* 2020).

Conservation implications

The consistent distribution and behaviour of WHDPs has considerable conservation implications, as the regular presence of endangered species is one of the criteria for the designation of protected areas (Delord *et al.* 2014, Lascelles *et al.* 2016). Of the intrinsic factors I investigated, none suggested spatial segregation and WHDP distribution appeared highly consistent. The lack of spatial segregation could indicate an absence of intra-specific competition at sea (e.g., Clay *et al.* 2016, 2020), which could be caused the by the low WHDP population size and/or the lack of sexual dimorphism (Ch. 2, Fischer *et al.* 2018b, 2020a). The consistent use of the same areas by the critically endangered WHDP is a justification to list these regions as Important Bird and Biodiversity Areas (IBAs). IBA criterion A1 requires the regular presence of a threatened species in an area.

Criterion A4ii requires the regular presence of ≥ 1% of the global population of a species in an area (BirdLife International 2010, Delord *et al.* 2014, Lascelles *et al.* 2016). While I did not calculate the true proportion of the WHDP population within these areas (Lascelles *et al.* 2016), I tracked 1.9 %, 9.3%, and 6.7% of the global WHDP population in 2015/16, 2017/18, and 2018/19, respectively (Ch. 4). As such, at least the WHDP breeding/non-breeding core areas of use (50% UDs) warrant listing as marine IBAs following criteria A1 and A4ii (Fig. 18; BirdLife International 2010, Delord *et al.* 2014).

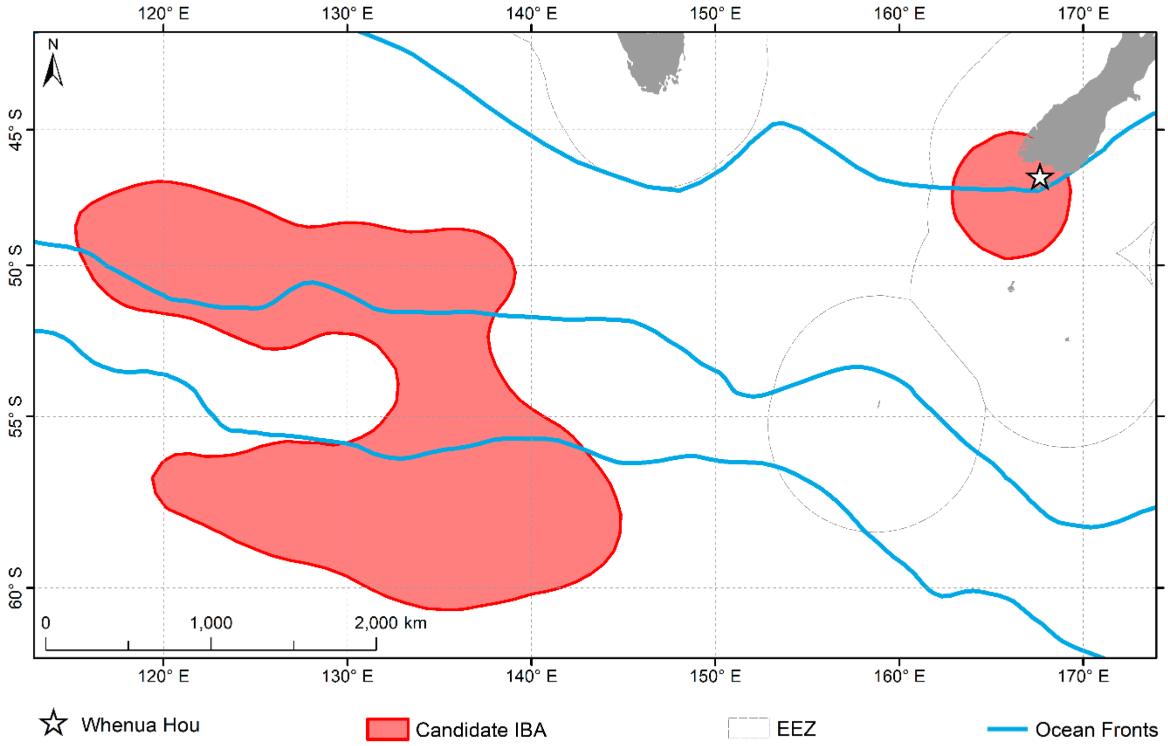

Fig. 18. Candidate marine Important Bird and Biodiversity Areas based on criteria A1 and A4ii triggered by breeding/non-breeding 50% UDs of Whenua Hou Diving Petrels (based on tracking of 1.9 %, 9.3%, and 6.7% of the world population in 2015/16, 2017/18, and 2018/19, respectively). Raw data can be accessed at http://www.seabirdtracking.org/. Approximate location of Ocean Fronts (from north to south: Subtropical Front, Subantarctic Front, and Polar Front) are based on Harris & Orsi (2006).

WHDP non-breeding distribution did not overlap with commercial fishing effort. The non-breeding distribution of WHDPs is located within one of the last stretches of largely untouched ocean on the planet (Kroodsma *et al.* 2018, Taconet *et al.* 2019). The lack of fishing effort recorded by the Global Fishing Watch is mirrored by the lack of marine traffic in this area (Wu *et al.* 2017). This absence of anthropogenic activity could be explained by the remoteness and the challenging conditions (mean wave height > 5 m and mean wind speed > 15 m/s; Young 1999) typical of this stretch of ocean. WHDPs exhibited extremely aquatic behaviour during the non-breeding period. Flight behaviour during this period mostly occurred at night, yet the number and duration of flight bouts remained very limited. The limited flight behaviour combined with a lack of human presence in this region indicated that impacts from anthropogenic threats (e.g., deck strikes) during the non-breeding period were unlikely.

In contrast to the non-breeding distribution, the WHDP breeding distributions overlapped considerably with commercial fishing effort and marine traffic (Wu *et al.* 2017). Several hotspots of commercial fishing effort were located in areas of elevated productivity and these productive areas may be equally attractive to foraging WHDPs (Tréguer & Jacques 1993, Orsi *et al.* 1995). This overlap is indicative of the potential for anthropogenic threats at sea, especially to successful breeders, which stayed longer at their breeding distribution. Accidental bycatch of diving petrels has been recorded within the WHDP breeding distribution (Abraham & Richards 2019). Additionally, the positive correlation between commercial fishing effort and artificial lights at night (Elvidge *et al.* 2015) in combination with increased WHDP flight activity during the breeding period indicated the potential for deck strikes in this area. Indeed, a record of 273 deck-struck diving petrels (all presumed Common Diving Petrels) occurred in this area (Abraham & Richards 2019). A single deck strike event of such a magnitude could be detrimental to WHDP. While deck-struck birds are often released alive, post-release mortality (e.g., due to reduced water-proofing and subsequent hypothermia; Black 2005) is poorly understood.

My results illustrated that offshore conservation measures (during the breeding period) could benefit this critically endangered species. However, the threats posed by commercial fisheries within the WHDP breeding distribution spanned close to 1,000,000 km^2 and managing threats within this vast area appears challenging. Seasonal (i.e., during the WHDP breeding period) restrictions of anthropogenic activity in the direct vicinity of Whenua Hou (i.e., the breeding colony) could be more feasible. Spatial restrictions to protect unique marine communities are in place around other islands, including Maukahuka and Gough and Tristan da Cunha (Chilvers *et al.* 2010, Requena *et al.* 2020). To complement any seasonal spatial restrictions, the following recommendations (Black

2005) to minimize deck strikes should be encouraged: I) alert vessels to the risks of spotlights, II) use black-out blinds, III) minimize external deck lighting, IV) provide protocols on treatment and release of deck-struck birds, and V) keep records of deck strikes (including photographs to aid identification of diving petrels). Glass & Ryan (2013) showed that such measures can reduce deck strikes considerably. I recommend that these measures are implemented throughout the WHDP breeding distribution (at least during the breeding period) as well as around Macquarie Island (at least during the non-breeding period). Improved record keeping and identification (e.g., genetically; Wold *et al.* 2018) of bycaught diving petrels during the WHDP breeding period would further elucidate offshore threats. Finally, higher resolution tracking (i.e., using miniature GPS loggers; Zhang *et al.* 2019, Dunphy *et al.* 2020) during the breeding period would provide more detailed insights into spatiotemporal overlap with offshore threats. The extent to which WHDPs are bound by central place foraging may differ among breeding phenophases, as burrow attendance varies among courtship, incubation, guard, and post-guard phases (Ch. 5). Therefore, quantifying fine scale differences in overlap with offshore threats among breeding phenophases would be of particular interest.

As WHDPs spent a significant amount of time on land during the breeding period, terrestrial threats should be managed concurrently. This is particularly important as the last remaining WHDP breeding colony is restricted to an area of 0.018 km^2 (Ch. 2, Fischer *et al.* 2018c, 2020a). Here, WHDPs nest in fragile foredunes < 20 m from the springtide line and are thus vulnerable to extreme weather events and climate change (Cole 2004). Moreover, close to half of the sandy coastlines on Aotearoa may retreat by > 100 m under the pressure of climate change (Vousdoukas *et al.* 2020). Consequently, while offshore threats during the breeding period should be mitigated, effective year-round conservation of WHDP will rely on managing terrestrial stressors as well.

Chapter 4

Predicting harvest impact and translocation success in small populations: a case study of a critically endangered petrel

ABSTRACT

In small populations, harvesting individuals for translocations could negatively impact source populations and thus, translocation cohorts should remain small, limiting potential establishment of recipient populations. The critically endangered Whenua Hou Diving Petrel (*Pelecanoides whenuahouensis*) could benefit from translocations to mitigate threats (e.g., storms, storm surges, and climate change), but only one small population remains. I used a novel metapopulation approach to an integrated population model to estimate vital rates and source population size, predict harvest impact on the source, and project the establishment of a recipient population under various translocation scenarios, while accounting for the return-to-source probability (juveniles recruiting back to the source post-translocation; ψ_r). I estimated adult survival at 0.868, juvenile survival at 0.772, productivity at 0.548 fledglings per female, population size at 207 adults, and population growth ($\hat{\lambda}$) at 1.023. Scenarios that resulted in establishment of a recipient without excessive impact on the source were harvests of ~10 fledglings/year for five years and ~5 fledglings/year for 10 years. When accounting for $\widehat{\psi_r}$, recipient populations remained ~29% smaller, and harvest regimes had to be increased (~15 fledglings/year for five years or ~10 fledglings/year for 10 years). I illustrate that establishment of new populations from small (seabird) populations can be feasible, but my results also show considerable uncertainty. Therefore, I recommend that translocations of small populations are conducted within an adaptive management framework, incorporating consistent monitoring of source and recipient populations, to evaluate projected impact and success and adjust harvest intensities when required.

INTRODUCTION

Translocations are a powerful strategy to counteract the accelerating biodiversity loss in the current sixth mass extinction (Seddon *et al.* 2014, Parker *et al.* 2020). A translocation can be defined as the intentional movement of organisms from source to recipient populations for conservation or restoration objectives (Seddon *et al.* 2007, IUCN 2013, Seddon *et al.* 2014). Translocations should be considered as a conservation or restoration alternative if: I) suitable translocation sites are available, II) the candidate species is unlikely to naturally colonize these sites, and III) the translocation will not cause negative impacts on the source population (IUCN 2013). Conservation translocations can be used to supplement extant populations (reinforcement), reintroduce the species within their native distribution (reintroduction), or facilitate the colonisation of habitat beyond the species' native distribution (assisted colonisation) (Seddon *et al.* 2014). Restoration translocations can be used to reinstate ecosystem functioning provided by the candidate species within (reintroduction), or beyond the species' native distribution (ecological replacement). Translocations can address conservation and restoration objectives simultaneously (e.g., Miskelly *et al.* 2009).

While translocations are often used to rescue species surviving in small populations from extinction, the harvest of individuals for translocations (i.e., live collection) could have detrimental impacts on source populations (Armstrong & Seddon 2008). Harvest for translocations can impact the viability of the source by lowering genetic diversity, increasing demographic stochasticity, and reducing vital rates (i.e., due to Allee effects; Armstrong & Wittmer 2011). The impact of translocations on genetic diversity on source (and recipient) populations has been studied extensively (e.g., Ramstadt *et al.* 2013, Furlan *et al.* 2020, Hogg *et al.* 2020). However, the demographic impacts of removing individuals on source populations has received less attention (Dimond & Armstrong 2007, Bain & French 2009, Panfylova *et al.* 2019). Translocations of species persisting in small populations are a balancing act between minimizing impact on sources and harvesting sufficient individuals to establish recipient populations. Forecasting the demographic impact on source populations (Dimond & Armstrong 2007) as well as projecting the establishment of recipient populations is therefore crucial to translocation planning (Converse *et al.* 2013, Panfylova *et al.* 2019). Yet, despite their fundamental importance to translocation planning, such dual forecasting exercises are rarely conducted, potentially because available data on endangered species often does not meet the requirements for predictive metapopulation models.

Integrated population models (IPMs) are a powerful tool for conservation management, including translocations, as these models allow for inference and predictions despite the data limitations common in studies of endangered species (Schaub & Abadi 2011, Kery & Schaub 2012, Saunders *et al.* 2018, 2019). IPMs can incorporate incomplete data from a range of studies (e.g., count, capture-recapture, and productivity data) into a single dynamic model (Schaub & Abadi 2011, Kery & Schaub 2012). This unified approach allows for the incorporation of all available information with full expression of uncertainty. IPMs can simultaneously estimate demographic processes and population sizes and project future trends and population viability under various environmental or management scenarios (Oppel *et al.* 2014, Saunders *et al.* 2018). Yet, these models are still infrequently applied in conservation management in general, and translocations in particular (Schaub & Abadi 2011, Saunders *et al.* 2018).

Seabirds are appealing translocation candidates but monitoring of populations is limited and key translocation questions are rarely addressed *a priori* (Armstrong & Seddon 2008, Miskelly *et al.* 2009, Paleczny *et al.* 2015). Seabirds are among the most threatened species groups and are considered ecosystem engineers; thus, these species are suitable for conservation and restoration translocations (Miskelly *et al.* 2009, Jones & Kress 2012, Dias *et al.* 2019, Agreement on the Conservation of Albatrosses and Petrels 2020). The number of seabird translocations is rapidly increasing and > 200 translocations have been attempted to date, despite the challenges that come with seabird translocations (i.e., the reliance on translocating pre-fledging chicks to overcome innate philopatry; Miskelly *et al.* 2009, Jones & Kress 2012, Friesen *et al.* 2017, Zhou *et al.* 2017, Seabird Restoration Database 2020). However, data to evaluate and inform seabird translocations are often limited due to insufficient monitoring (Paleczny *et al.* 2015). Most notably, monitoring of source populations post-translocations is often considered optional (Gummer *et al.* 2014ab). This lack of monitoring could be explained by the sometimes very large population sizes of sources (Miskelly *et al.* 2009), leading to the assumption that source populations may not suffer from translocation harvests. The limited monitoring of sources post-translocations, however, inhibits understanding of the impacts of translocation harvests in small populations. Seabirds are extremely wide-ranging species and thus juveniles could recruit back to the source populations instead of the recipient populations post-translocations (e.g., Miskelly & Gummer 2013, Rowe 2018). Therefore, limited monitoring at source populations also restricts examinations and predictions of translocation success (i.e., establishment of recipient populations).

I constructed an IPM to predict the impact and success of translocations of a critically endangered seabird: The Whenua Hou Diving Petrel (*Pelecanoides whenuahouensis*; WHDP). This species may be a suitable candidate for translocations as I) it is under ongoing pressure at its last remaining breeding colony, II) suitable habitat may be available, and III) the species is unlikely to colonize the suitable habitat on its own (or using acoustic attraction; Fischer *et al.* 2020b). However, the population of the WHDP is extremely small (Ch. 2, Fischer *et al.* 2020a) and thus harvesting individuals for translocations may have negative effects on the source population. Therefore, I formulated an IPM in a novel metapopulation approach to I) estimate vital rates, population size, and growth rate of the source, II) predict the impact of translocation harvest on the source, and III) project the establishment of a recipient population, under various translocation scenarios. In addition, I accounted for the potential of juveniles recruiting back to the source populations post-translocation.

METHODS

Study species

The recently described and critically endangered WHDP once acted as an ecosystem engineer throughout dune systems in southern Aotearoa (New Zealand), but is now restricted to a single colony on one island: Whenua Hou (Codfish Island; -46.766° S, 167.645° E; Fig. 4 & 5; Taylor 2000b, Fischer *et al.* 2018b, 2019, BirdLife International 2020). All invasive predators have been eradicated from Whenua Hou (McClelland 2002). Yet, the WHDP population size remains extremely small (194-208 adults; Ch. 2; Fischer *et al.* 2020a). Based on burrow counts, the population appears to be increasing, but the rate of increase is low compared to other seabirds on the island, indicating ongoing stressors (Ch. 2 & 3). WHDPs only breed in burrows in fragile foredunes < 20 m from the springtide line (Fischer *et al.* 2018c), rendering the species vulnerable to erosion caused by storms, storm surges, and impending climate change (Cole 2004, Vousdoukas *et al.* 2020). Competition for burrows with Common Diving Petrels (*P. urinatrix*) may pose an additional threat (Fischer *et al.* 2017a). WHPDs did not respond to acoustic attraction systems to lure them to more secure breeding sites (Fischer *et al.* 2020b). Consequently, active translocations (i.e., moving pre-fledgling chicks) to another island may be a suitable strategy for to conserve the WHDP and reinstate lost ecosystem functioning.

Life history information is key to the success of translocations (Miskelly *et al.* 2009, Jones & Kress 2012). WHDPs are relatively long-lived animals (> 20 years; pers. obs.). The WHDP breeding period lasts from September to January (Ch. 5). Like all Procellariiformes, WHDPs lay a single egg per breeding period (Warham 1996). After the breeding period, adults migrate to the Polar Front south of Australia (Ch. 3) and juveniles likely spend the first years of their lives entirely at sea. WHDPs mirror other diving petrels and generally start breeding at two years of age (Miskelly & Taylor 2007, Miskelly *et al.* 2009). In addition, all adult WHDPs appear to attend burrows at the breeding colony every year (pers. obs.) and thus, unlike other Procellariiformes (e.g., Weimerskirch 2018), sabbaticals do not seem part of the WHDP life cycle. WHDPs, like other diving petrels (Miskelly & Taylor 2004, Miskelly *et al.* 2009), exhibit an unusually fast life cycle history for a Procellariform seabird, rendering them highly suitable translocation candidates. However, adult survival, juvenile survival, and productivity remain poorly understood, limiting assessments on translocation impact and success.

Capture-recapture data

To quantify WHDP adult survival, juvenile survival, and population size, I used intermittent capture-recapture data of 391 adult and 79 fledgling WHDPs. Specifically, I captured and banded adult WHDPs at their breeding colony on Whenua Hou at night during September-January in 2015-19 (referring to the calendar year in which the breeding period started). I fused this data with pre-existing capture-recapture data of adults from of 2002-04 and 2008 (G Taylor unpublished). I defined adults as birds returning to the colony, as birds cannot be aged phenotypically (Fischer *et al.* 2018b). To reduce capture biases, a variety of capture techniques were applied: I) hand capture, sometimes aided by playback/mimics, II) custom-made burrow traps, and III) spotlighting (Fig. 10; Fischer *et al.* 2017ab, 2018b). In 2015-19, I captured and banded fledglings at their burrows (Ch. 5). I considered each breeding period as a separate sampling occasion to estimate annual survival and detection probabilities. As WHDPs are sexually monomorphic (Fischer *et al.* 2018b), I also collected four contour feathers from 246 adults and 67 fledglings and used these for genetic sex determination (using polymerase chain reaction primers specific to the chromodomain-helicase-DNA-binding gene on the W-chromosome; Norris-Caneda & Elliott 1998). I sexed 116 adult females and 130 adult males, as well as 30 female fledglings and 37 male fledglings.

Productivity data

To inform WHDP productivity, I monitored a total of 204 WHDP burrows for the entire breeding period of 2017-19 (65-79% of all known burrows). WHDP burrows close annually due to the movement of sand dunes and are reopened by birds at the start of every breeding period (Ch. 5 & 6, Fischer *et al.* 2019). I defined a WHDP burrow as a burrow > 60 cm deep and occupied by a WHDP, which I confirmed with a burrowscope (Sextant Technologies, Wellington, New Zealand). I checked burrows at least once per week using a burrowscope (summarized in Ch. 5). The productivity data that I collected consisted of the number of fledglings produced per year in conjunction with the number of burrows surveyed, regardless of whether burrows received an egg. My productivity data thus reflects a product of lay rate and nest success (Ch. 5), allowing me to account for prospecting WHDPs. I assumed that the number of fledglings per burrow was equal to fledglings per female.

Integrated population model

To estimate WHDP vital rates and population size as well as impact and success of translocations, I formulated an age-structured IPM in a Bayesian framework (Schaub & Abadi 2011, Saunders *et al.* 2018). I integrated three subcomponents in my IPM: I) an open-population Cormack-Jolly-Seber model using the annual capture-recapture data, II) a productivity model using the annual productivity data, and III) an abundance model using annual counts of banded and unbanded WHDPs. I used this IPM to simultaneously estimate detection, age-specific survival, productivity, sex ratio, population size, and growth at the source population. Additionally, I included a second (recipient) population in my IPM. Using a novel metapopulation approach, I linked source and recipient populations with vital rates, transition probabilities (harvest rates and return-to-source probabilities), and population estimates of the juveniles arising from translocated fledglings (Fig. 19). Central to my IPM were two age-structured $2 \times 2 \times 2$ Leslie matrices (one each for source and recipient populations; Caswell 2001):

$$1.\quad \begin{bmatrix} N_{juv} \\ N_{ad} \end{bmatrix}_{t+1} = \begin{bmatrix} 0 & f \times pr_{fem} \times \varphi_{juv} \\ \varphi_{juv} & \varphi_{ad} \end{bmatrix}_t \times \begin{bmatrix} N_{juv} \\ N_{ad} \end{bmatrix}_t$$

in which $N_{juv,t}$ is the number of juveniles, $N_{ad,t}$ is the number of adults, f_t is the productivity (fledglings per female), pr_{fem} is the probability of an individual being female, $\varphi_{juv,t}$ is the juvenile survival probability, and $\varphi_{ad,t}$ is the adult survival probability. The matrices for source and recipient populations were identical, apart from variation between productivity at the source ($f_{S,t}$) and the recipient population ($f_{R,t}$).

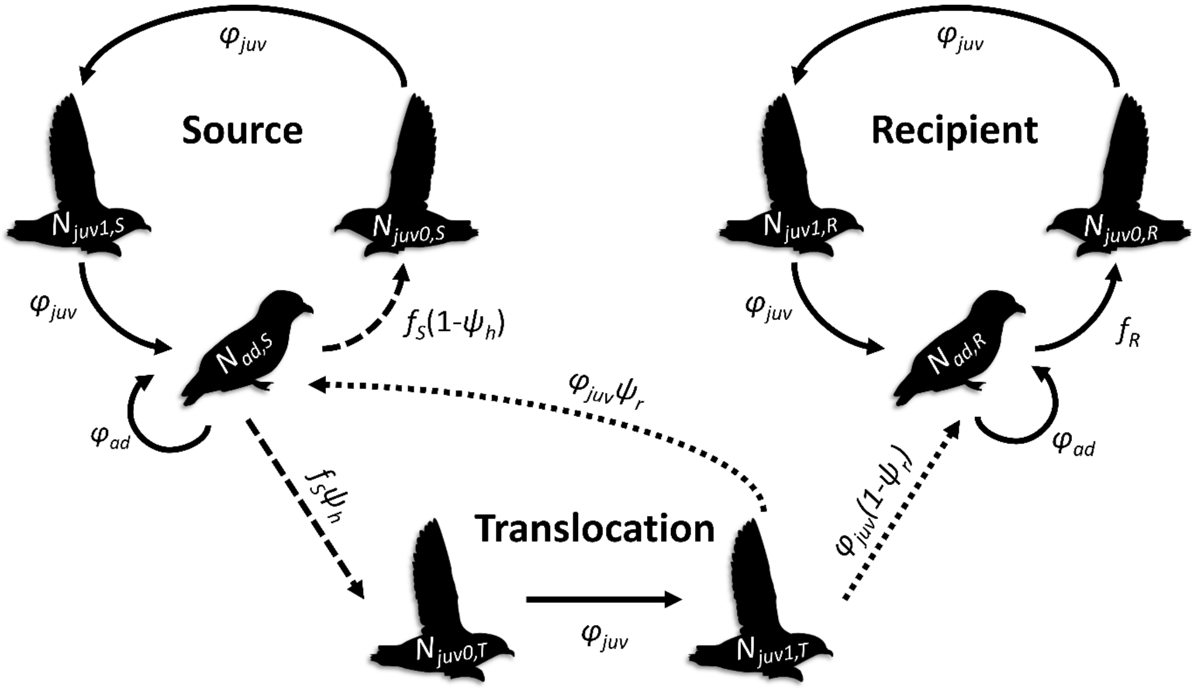

Fig. 19. Conceptual framework of the integrated population model used to estimate Whenua Hou Diving Petrel translocation impact and success. Silhouettes indicate age classes: $N_{ad,S}$ = adults at the source population, $N_{juv0,S}$ = juveniles arising from fledglings at the source population, $N_{juv1,S}$ = 1-year-old juveniles at the source population, $N_{juv0,T}$ = juveniles arising from fledglings from a translocation cohort, $N_{juv1,T}$ = 1-year-old juveniles from a translocation cohort, $N_{ad,R}$ = adults at the recipient population, $N_{juv0,R}$ = juveniles arising from fledglings at recipient the population, $N_{juv1,R}$ = 1-year-old juveniles at the recipient population. Arrows indicate vital rates and transition probabilities: φ_{ad} = adult survival, φ_{juv} = juvenile survival, f_S = productivity at the source population, f_R = productivity at the recipient population, ψ_h = harvest rate, ψ_r = return-to-source probability. Dashed arrows were subjected to scenarios with varying ψ_h; dotted arrows were subjected to scenarios with varying ψ_r.

Estimation of survival

I used an open-population Cormack-Jolly-Seber model (Lebreton *et al.* 1992) in the state-space formulation (Gimenez *et al.* 2007, Kery & Schaub 2012) to estimate annual detection p_t, adult survival $\varphi_{ad,t}$, and juvenile survival probabilities $\varphi_{juv,t}$:

2. $Y_{i,t} \mid X_{i,t} \sim Bernoulli(X_{i,t}, p_{i,t})$
3. $X_{i,t+1} \mid X_{i,t} \sim Bernoulli(X_{i,t}, \varphi_{i,t})$

Equation 2 described the observation process and Equation 3 described the state process. $Y_{i,t}$ equalled 0 if individual *i* was not detected at time *t*, and 1 if it was. $X_{i,t}$ equalled 0 if the individual was dead at time *t*, and 1 if the individual was alive. $p_{i,t}$ is the detection probability of individual *i* at time *t* and $\varphi_{i,t}$ is the survival probability of individual *i* over the time interval *t* to *t* + 1. I estimated $p_{i,t}$ using:

4. $logit(p_{i,t}) = \alpha_p + \varepsilon_{p,t}$

in which α_p is the intercept of the detection equation and $\varepsilon_{p,t}$ is an annual random effect on detection. I used vague priors for α_p $(N[mean = 0, precision = 0.1])$ and $\sigma_{\varepsilon_{p,t}}$ $(U[0, 3])$. I fixed $p_{i,t}$ at 0 for years during which no surveys were conducted (2005-07 and 2009-14) and for one-year-old juveniles, which I assumed to be out at sea (i.e., I fixed age at first return at two years of age). I did not include any age effects on $p_{i,t}$ due to my low sample size of known-age birds. I estimated $\varphi_{i,t}$ using:

5. $logit(\varphi_{i,t}) = \alpha_\varphi + \beta_{juv} \times juv_{i,t} + \varepsilon_{\varphi,t}$

in which α_φ is the intercept of the survival equation, β_{juv} is the age effect on survival, $juv_{i,t}$ is the juvenile status of individual *i* at time *t*, and $\varepsilon_{\varphi,t}$ is an annual random effect on survival. I used vague priors for α_φ $(N[0, 0.1])$, β_{juv} $(N[0, 1])$, and $\sigma_{\varepsilon_{\varphi,t}}$ $(U[0, 3])$. I thus assumed that survival during the first two years of life was different from older birds and estimated annual adult and juvenile survival as:

6. $logit(\varphi_{ad,t}) = \alpha_\varphi + \varepsilon_{\varphi,t}$

7. $logit(\varphi_{juv,t}) = \alpha_{\varphi} + \beta_{juv} + \varepsilon_{\varphi,t}$

Estimation of productivity

I estimated annual productivity (fledglings per female) at the source population $f_{S,t}$ using a generalized mixed effects linear model (GLMM) with a Bernoulli error term:

8. $logit(f_{S,t}) = \alpha_f + \varepsilon_{f_t}$

in which α_f is the intercept of the productivity equation and ε_{f_t} is an annual random effect on productivity. I used a vague prior for α_f ($N[0, 0.1]$), but as I only had three years of data (2017-19), I used a mildly informative prior for $\sigma_{\varepsilon_{ft}}(U[0, 0.2])$. I then estimated the annual productivity at the recipient population $f_{R,t}$ using:

9. $logit(f_{R,t}) = \alpha_f + \beta_{recipient} + \varepsilon_{f_t}$

in which $\beta_{recipient}$ is a fixed effect on the productivity at the recipient site. I assumed that the mean of $f_{R,t}$ will be equal to the mean of $f_{S,t}$, but since I had no data for the recipient population, $f_{R,t}$ could be lower or higher than $f_{S,t}$. As such, I used a mildly informative prior for $\beta_{recipient}$ ($N[0, 2]$) to increase the uncertainty around $f_{R,t}$. I assumed that productivity was the only vital rate that differed between source and recipient populations.

Estimation of population size

Classic IPMs incorporate count data, separate from capture-recapture and productivity data, into the joint likelihood to estimate population sizes (Abadi & Schaub 2011, Saunders *et al.* 2018, 2019). We, however, had no access to separate count data. Therefore, I used the annual counts of banded and unbanded adults (i.e., the number of adults captured for the first time) in conjunction with detection, survival, and productivity estimates to infer adult population size at the source $N_{ad,S,t}$. Specifically, I first estimated the number of 2-year-old juveniles recruiting into the source. I then used this estimate together with the estimated number of surviving undetected adults to estimate the annual pool of unbanded adults available for detection. I then sampled the annual number of captured unbanded adults from this pool using the estimated detection probability. I subtracted the number of the captured unbanded adults from the pool of unbanded adults. Ultimately, I summed the estimated pool of undetected unbanded adults and the sum of the surviving banded adults to infer the population size at the source $N_{ad,S,t}$:

10. $N_{ad.f,S,t} \sim Bin(pr_{fem}, N_{ad,S,t})$
11. $N_{juv0,S,t} \sim Bin(f_{S,t}, N_{ad.f,S,t})$
12. $N_{juv1,S,t} \sim Bin(\varphi_{juv,t-1}, N_{juv0,S,t-1})$
13. $N_{juv2,S,t} \sim Bin(\varphi_{juv,t-1}, N_{juv1,S,t-1})$
14. $N_{ad.unk.surv,S,t} \sim Bin(\varphi_{ad,t-1}, N_{ad.unk,S,t-1})$
15. $N_{ad.unband,S,t} = N_{ad.unk.surv,S,t} + N_{juv2,S,t}$
16. $N_{ad.new,S,t} \sim Bin(p_t, N_{ad.unband,S,t})$
17. $N_{ad.unk,S,t} = N_{ad.unband,S,t} - N_{ad.new,S,t}$
18. $N_{ad,S,t} = N_{ad.unk,S,t} + N_{ad.band,S,t}$

in which $N_{ad.f,S,t}$ is the number of adult females at the source population, pr_{fem} is the probability that an individual is female. I modelled pr_{fem} with a Bernoulli error term and a vague prior ($U[0, 1]$) and assumed pr_{fem} to be constant among years. $N_{juv0,S,t}$ is the number of juveniles arising from fledglings at the source population, $N_{juv1,S,t}$ is the number of 1-year-old juveniles at the source population, and $N_{juv2,S,t}$ is the number of 2-year-old juveniles that recruit into the source population, $N_{ad.unk.surv,S,t}$ is the number of undetected adults surviving from the previous year, $N_{ad.unk,S,t}$ is the number of unknown undetected adults, $N_{ad.unband,S,t}$ is the number of unbanded adults available for detection, $N_{ad.new,S,t}$ is the number of unbanded adults captured for the first time, and $N_{ad.band,S,t}$ is the sum of $X_{i,t}$ (i.e., all banded and surviving adults in year t). For the first year in my study (2002), I used informative priors for $N_{juv1,S,t}$ ($U[0, 60]$) and $N_{ad.unk,S,t}$ ($U[0, 200]$). This approach allowed me to estimate population size for years with capture-recapture data and infer population sizes during years for which no data were collected.

Estimation of population growth rate

I estimated the average finite rate of population growth λ at the source site by solving the quadratic of the matrix in Equation 1, similar to Parlato & Armstrong (2018), which resulted in the following equation:

$$19. \quad \lambda = \frac{\varphi_{ad} + \sqrt{{\varphi_{ad}}^2 + 4 \times f_s \times pr_{fem} \times {\varphi_{juv}}^2}}{2}$$

in which φ_{ad} is the average annual adult survival, f_s is the average annual productivity (fledglings per female) at the source population, and φ_{juv} is the average annual juvenile survival.

Projections of the source population

I projected the size of the source population $N_{ad,S,t}$ under various translocation scenarios, while accounting for juveniles recruiting back into the source post-translocation using:

20. $N_{juv0,S,t} \sim Bin(f_{S,t} \times (1 - \psi_{h,t}), N_{f.ad,S,t})$
21. $N_{juv1,S,t} \sim Bin(\varphi_{juv,t-1}, N_{juv0,S,t-1})$
22. $N_{juv2,S,t} \sim Bin(\varphi_{juv,t-1}, N_{juv1,S,t-1})$
23. $N_{juv2,return,t} \sim Bin(\varphi_{juv,t-1} \times \psi_r , N_{juv1,T,t-1})$
24. $N_{ad,S,t} \sim Bin(\varphi_{ad,t-1}, N_{ad,S,t-1} + N_{juv2,S,t-1} + N_{juv2,return,t-1})$

in which $\psi_{h,t}$ is the annual harvest rate, $N_{juv1,T,t}$ is the number 1-year-old juveniles arising from a translocation cohort, ψ_r is the return-to-source probability, and $N_{juv2,return,t}$ is the number of 2-year-old juveniles that recruit back to the source post-translocation. I did not account for density-dependence in my projections, because diving petrels can breed at very high densities (~6 burrows/m^2; Taylor 2000b) and densities at the WHDP breeding colony are currently comparatively low (0.02 burrows/m^2; Ch. 5).

Projections of the recipient population

I first projected the number of juveniles arising from translocated fledglings using:

25. $N_{juv0,T,t} \sim Bin(f_{S,t} \times \psi_{h,t}, N_{f.ad,S,t})$
26. $N_{juv1,T,t} \sim Bin(\varphi_{juv,t-1}, N_{juv0,T,t-1})$

in which $N_{juv0,T,t}$ is the number of juveniles arising from translocated fledglings. I assumed that translocations would not influence fledgling survival, based on ever-improving seabird translocation and hand-rearing protocols (Miskelly *et al.* 2009, Jones & Kress 2012, Agreement on the Conservation of Albatrosses and Petrels 2020). I then projected size of the recipient population $N_{ad,R,t}$ using:

27. $N_{ad.f,R,t} \sim Bin(pr_{fem}, N_{ad,R,t})$
28. $N_{juv0,R,t} \sim Bin(f_{R,t}, N_{ad.f,R,t})$
29. $N_{juv1,R,t} \sim Bin(\varphi_{juv,t-1}, N_{juv0,R,t-1})$
30. $N_{juv2,R,t} \sim Bin(\varphi_{juv,t-1}, N_{juv1,R,t-1})$
31. $N_{juv2,T,t} \sim Bin(\varphi_{juv,t-1} \times \ (1-\psi_r)\ , N_{juv1,T,t-1})$
32. $N_{ad,R,t} \sim Bin(\varphi_{ad,t-1}, N_{ad,R,t-1} + N_{juv2,R,t-1} + N_{juv2,T,t-1})$

in which $N_{ad.f,R,t}$ is the number of adult females at the recipient population, $N_{juv0,R,t}$ is the number of juveniles arising from fledglings at the recipient population, $N_{juv1,R,t}$ is the number of 1-year-old juveniles at the recipient population, $N_{juv2,R,t}$ is the number of 2-year-old juveniles from the recipient population recruiting into the recipient, and $N_{juv2,T,t}$ is the number of 2-year-old juveniles recruiting into the recipient population post-translocation. My approach thus allowed me to simultaneously project population sizes of source and recipient populations, while accounting for the return-to-source probability.

Estimation of the return-to-source probability

I wanted to investigate the influence of juveniles returning to the source instead of the recipient population post-translocation, on translocation impact and success. I defined the return-to-source probability ψ_r as the proportion of translocated birds returning as adults to the source site relative to the total number of translocated birds surviving to adulthood. I used data published on translocations of members of the family Procellariidae in the scientific literature to inform ψ_r. I searched Google Scholar and Web of Science with the search terms "petrel" OR "shearwater" OR "prion" AND "translocation" and found seven case studies reporting on ψ_r (Table 6). I included one additional report from a seabird translocation practitioner (D Boyle *in lit.* 2020). I then estimated return-to-source probabilities per case study, and ultimately, the overall ψ_r for Procellariidae, as following:

33. $logit(\psi_{r,k}) = \alpha_{\psi_r} + u_{\psi_{r,k}}$
34. $N_{recruit,S,k} \sim Bin(\psi_{r,k}, N_{recruit,tot,k})$
35. $logit(\psi_r) = \alpha_{\psi_r} + u_{\psi_r}$

in which $\psi_{r,k}$ is the return-to-source probability per case study k, α_{ψ_r} is the intercept of the return-to-source equation, $u_{\psi_{r,k}}$ is a random effect per study k, $N_{recruit,S,k}$ is the number of translocated birds returning as adults to the source site per study k, and $N_{recruit,tot,k}$ is the total number of translocated birds surviving to adulthood per study k. I used vague priors for α_{ψ_r} ($N[0, 0.001]$) and $\sigma_{u_{\psi_r}}$ ($U[0, 10]$). I then used $logit(\psi_r)$ to create an informed prior, which I used within my IPM to account for WHDP juveniles returning to the source post-translocations. I assumed that, apart from ψ_r, there was no exchange of juveniles or adults between source and recipient populations.

Table 6. Number of translocated Procellariidae fledglings returning to source ($N_{recruit,S,k}$) and recipient sites ($N_{recruit,R,k}$) post-translocation, the total number of translocated fledglings surviving to adulthood ($N_{recruit,tot,k}$), and the estimated return-to-source probability ($\widehat{\psi_{r,k}}$; posterior mean with 95% CrIs) per case study.

Species	Scientific name	Source site	Recipient site	$N_{recruit,S,k}$	$N_{recruit,R,k}$	$N_{recruit,tot,k}$	$\widehat{\psi_{r,k}}$	Reference
Black Petrel	*Procellaria parkinsoni*	Aotea, Aotearoa	Hauturu, Aotearoa	1	2	3	0.27 (0.03-0.68)	Imber *et al.* 2003
Fluttering Shearwater	*Puffinus gavia*	Te Hoiere, Aotearoa	Kokomohua, Aotearoa	1	32	33	0.06 (0.01-0.15)	Bell *et al.* 2005
Gould's Petrel	*Pterodroma leucoptera*	Cabbage Tree Island, Australia	Boondelbah Island, Australia	2	10	12	0.18 (0.04-0.39)	Priddel *et al.* 2006
Chatham Petrel	*Pterodroma axillaris*	Rangatira, Aotearoa	Rangiaotea, Aotearoa	2	6	8	0.23 (0.05-0.52)	Miskelly *et al.* 2009
Bermuda Petrel	*Pterodroma cahow*	Green Island, USA, Horn Rock, USA	Nonsuch Island, USA	7	17	24	0.28 (0.13-0.46)	Carlile *et al.* 2012
Fairy Prion	*Pachyptila turtur*	Takapourewa, Aotearoa	Mana Island, Aotearoa	25	20	45	0.53 (0.39-0.67)	Miskelly & Gummer 2013
Hutton's Shearwater	*Puffinus huttoni*	Kowhai River, Aotearoa	Te Rai o Atiu, Aotearoa	7	28	35	0.20 (0.09-0.34)	Rowe 2018
Chatham Island Taiko	*Pterodroma magenta*	Tuku Nature Reserve, Aotearoa	Sweetwater Conservation Covenant, Aotearoa	2	41	43	0.06 (0.01-0.15)	D. Boyle *in. lit.* 2020

Translocation scenarios

I projected the source and recipient populations 20 years into the future under varying translocation scenarios. Specifically, I estimated the impact and success of translocations when harvesting 0% to 30% of all fledglings per year (i.e., I varied the annual harvest rate $\psi_{h,t}$ at 0.1 increments). Additionally, I modelled the translocation timeframe as five or 10 consecutive years. I considered a mean estimated decrease of the source population ($\widehat{N_{ad,S,t}}$) to 175 (pre-eradication population estimate; see results) as a cut-off for acceptable impact on the source population. I considered a mean estimate of the recipient population ($\widehat{N_{ad,D,t}}$) > 30 as a successfully established second breeding colony (similar to Dimond & Armstrong 2007).

Model fitting

I fitted my IPMs in the Bayesian modelling program OpenBUGS 3.2.3 (Spiegelhalter *et al.* 2014), which uses Markov chain Monte Carlo (MCMC) algorithms to obtain posterior distributions of all parameters while simultaneously propagating all sources of uncertainty. I fitted 13 versions of my IPM that relate to the decision landscape managers face when considering translocations: a no-harvest scenario, and a scenario for each value of $\psi_{h,t}$, for five or 10 years of harvesting, while either fixing ψ_r at 0 or estimating it. For each IPM, I ran two MCMC chains for 100,000 iterations after a burn-in of 50,000 iterations, which was sufficient to give convergence based on the Gelman-Rubin statistic ($\hat{R}$ < 1.05). I report the mean of posterior distributions with 95% credible intervals (CrI). The OpenBUGS code of my IPM can be found in Supplementary Material 2.

RESULTS

Average adult WHDP survival was estimated at $\widehat{\varphi_{ad}}$ = 0.868 (0.833-0.930), average juvenile survival was estimated at $\widehat{\varphi_{Juv}}$ = 0.772 (0.689-0.878), and average productivity (fledglings per female) at the source population was estimated at $\widehat{f_S}$ = 0.548 (0.481-0.616; Fig. 20). The proportion of females was estimated at $\widehat{pr_{fem}}$ = 0.487 (0.434-0.540). The source population size ($\widehat{N_{ad,S,t}}$) was estimated at 172 (111-232) adults in 2002 and increased to 207 (182-235) adults in 2019 (Fig. 21). Average annual population growth between 2002 and 2019 was estimated at $\hat{\lambda}$ = 1.023 (0.979-1.112). When projecting the source population 20 years into the future without harvesting for translocations, population size was predicted at 255 (27-710) adults in 2039 (Table 7). Estimated study-specific return-to-source probabilities ranged from $\widehat{\psi_{r,k}}$ = 0.06 (0.01-0.15) to $\widehat{\psi_{r,k}}$ = 0.53 (0.39-0.67) (Table 6, Fig. 22). The estimated overall return-to-source probability was estimated at $\widehat{\psi_r}$ = 0.25 (0.01-0.87).

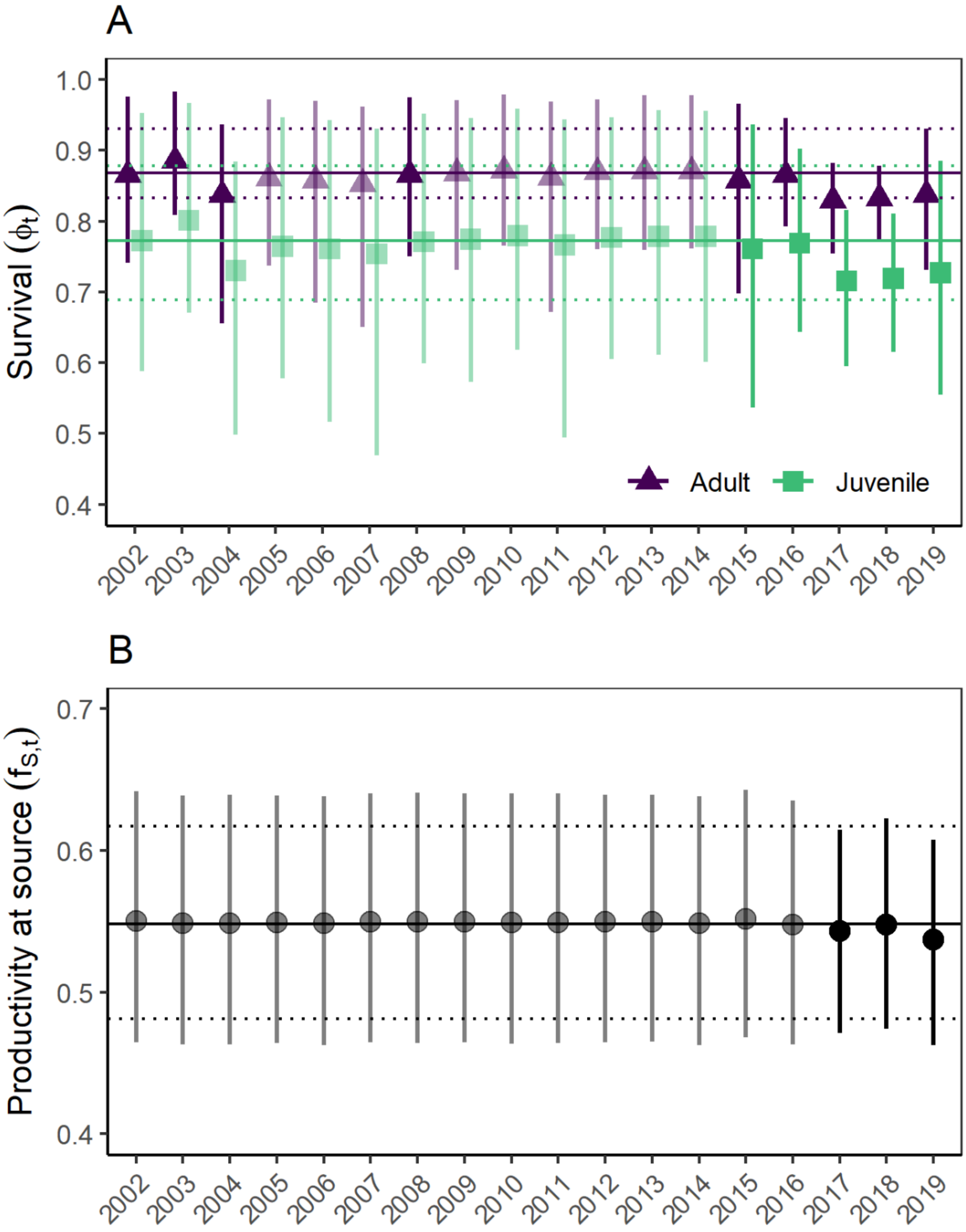

Fig. 20. Annual estimates (posterior means and 95% CrIs) of Whenua Hou Diving Petrel adult and juvenile survival ($\widehat{\varphi_{ad,t}}$ and $\widehat{\varphi_{Juv,t}}$; A) and productivity at source population ($\widehat{f_{S,t}}$; B). Solid and dotted lines indicate average estimates. Solid symbols indicate estimates for years during which surveys took place. Translucent symbols indicate estimates for years without surveys, which were derived using integrated population modelling, fusing inferences of survival, reproduction, and abundance across all years.

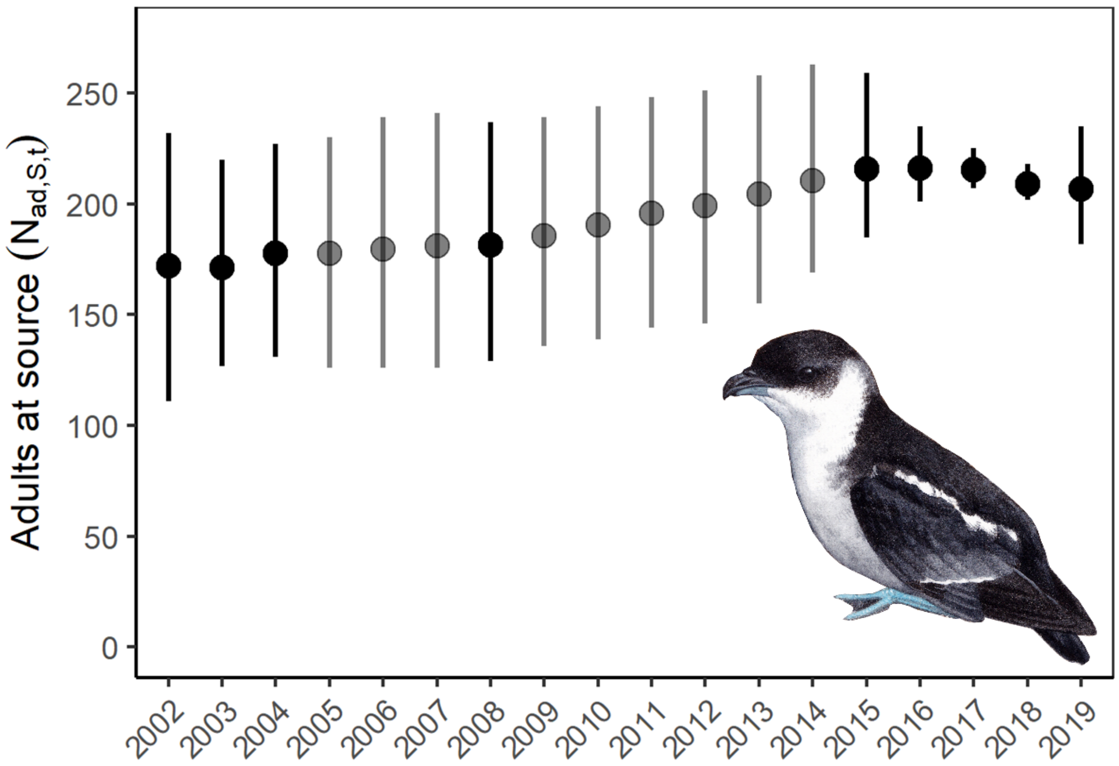

Fig. 21. Estimated Whenua Hou Diving Petrel population sizes at the source site ($\widehat{N_{ad,S,t}}$; posterior means and 95% CrIs). Solid symbols indicate estimates for years during which surveys took place. Translucent symbols indicate estimates for years without surveys, which were derived using integrated population modelling, fusing inferences of survival, reproduction, and abundance across all years.

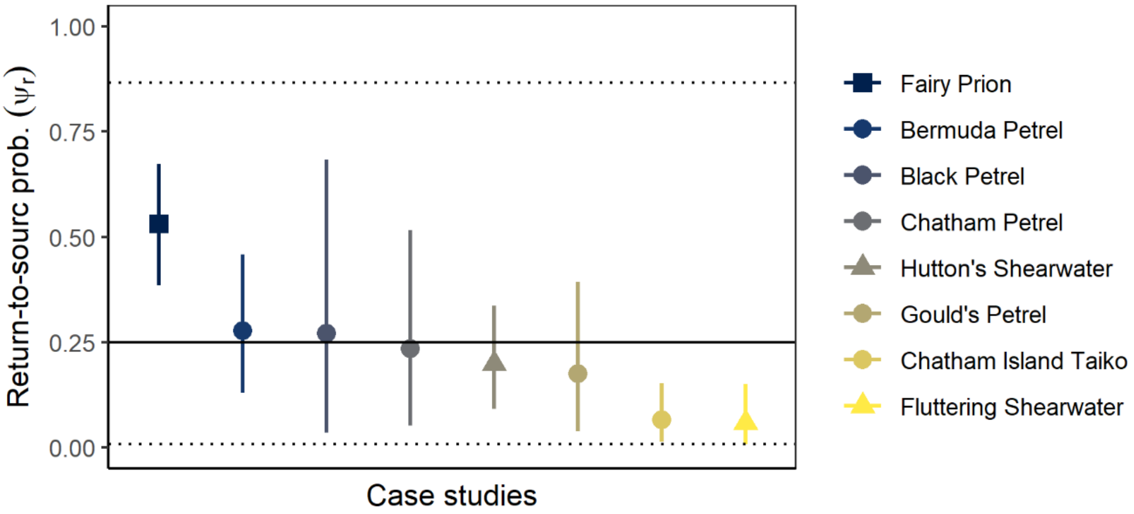

Fig. 22. Study-specific estimates of return-to-source probabilities ($\widehat{\psi_{r,k}}$; posterior means and 95% CrIs), based on case studies of Procellariidae translocations as summarized in Table 6 and overall estimated return-to-source probability ($\widehat{\psi_r}$; solid and dotted lines). Squares represent case studies of prions, circles represent case studies of petrels, and triangles represent case studies of shearwaters.

In all scenarios, translocation harvests caused a temporary reduction at the source population size, but several scenarios resulted in the successful establishment of a recipient WHDP population. When assuming that all juveniles post-translocation recruited to the recipient population (i.e., $\psi_r = 0$), two translocation scenarios met my criteria of success (a mean estimate of the source population of > 175 adults and a mean estimate of recipient population of > 30 adults): harvest of 20% of fledglings (~10 individuals) per year for five years and harvest of 10% of fledglings (~5 individuals) per year for 10 years (Table 7, Fig. 23ABC & 24ABC).

When accounting for juveniles returning to the source population instead of the recipient population post-translocation (i.e., $\widehat{\psi_r} = 0.25$), source populations were less impacted by harvest regimes, but translocations were also less successful at establishing recipient populations. Specifically, when $\widehat{\psi_r}$ was included, source population sizes remained ~2% larger compared to populations under the same translocation scenarios without $\widehat{\psi_r}$ (Table 7). Additionally, when $\widehat{\psi_r}$ was included, recipient population sizes were ~29% smaller compared to populations under the same translocation scenarios without $\widehat{\psi_r}$. Two translocation scenarios that included $\widehat{\psi_r}$ (i.e., more realistic scenarios) met my criteria of success: harvest of 30% of fledglings (~15 individuals) per year for five years and harvest of 20% of fledglings (~10 individuals) per year for 10 years (Fig. 23DEF & 24DEF). However, in all scenarios, regardless of $\widehat{\psi_r}$, the lower 95% CrIs of both source and recipient populations were close to 0, indicating considerable uncertainty.

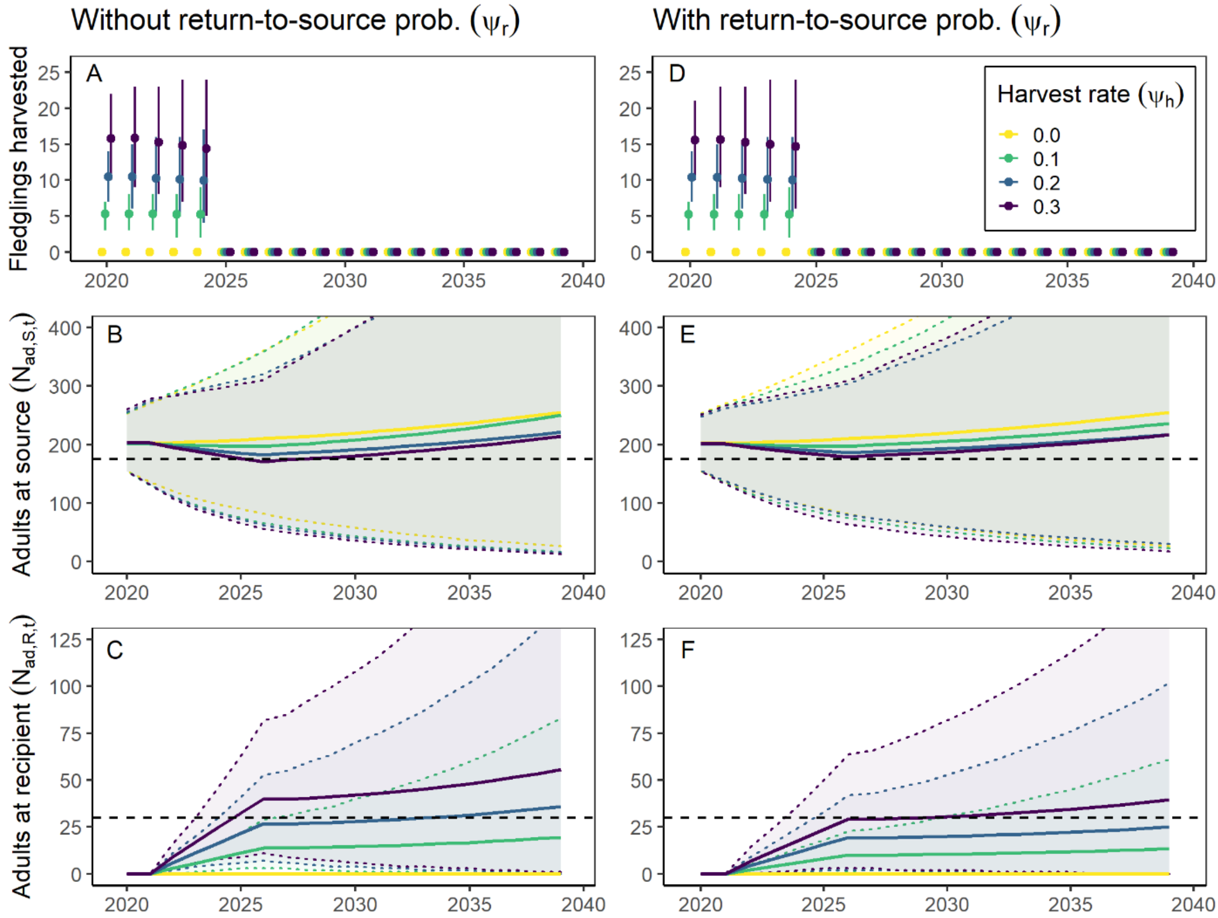

Fig. 23. Projections of Whenua Hou Diving Petrel fledglings harvested for translocation for five years (AD), adults at source ($\widehat{N_{ad,S,t}}$; BE), and adults at recipient populations ($\widehat{N_{ad,R,t}}$; CF) under various translocation scenarios, under the assumption that juveniles either always recruit to recipient populations ($\psi_r = 0$; ABC) or can recruit back to the source populations ($\widehat{\psi_r} = 0.25$; DEF). Solid lines represent posterior means, dotted lines represent 95% CrIs, and dashed lines indicate desired minimum population size at source (175 adults; BE) and recipient populations (30 adults; CF).

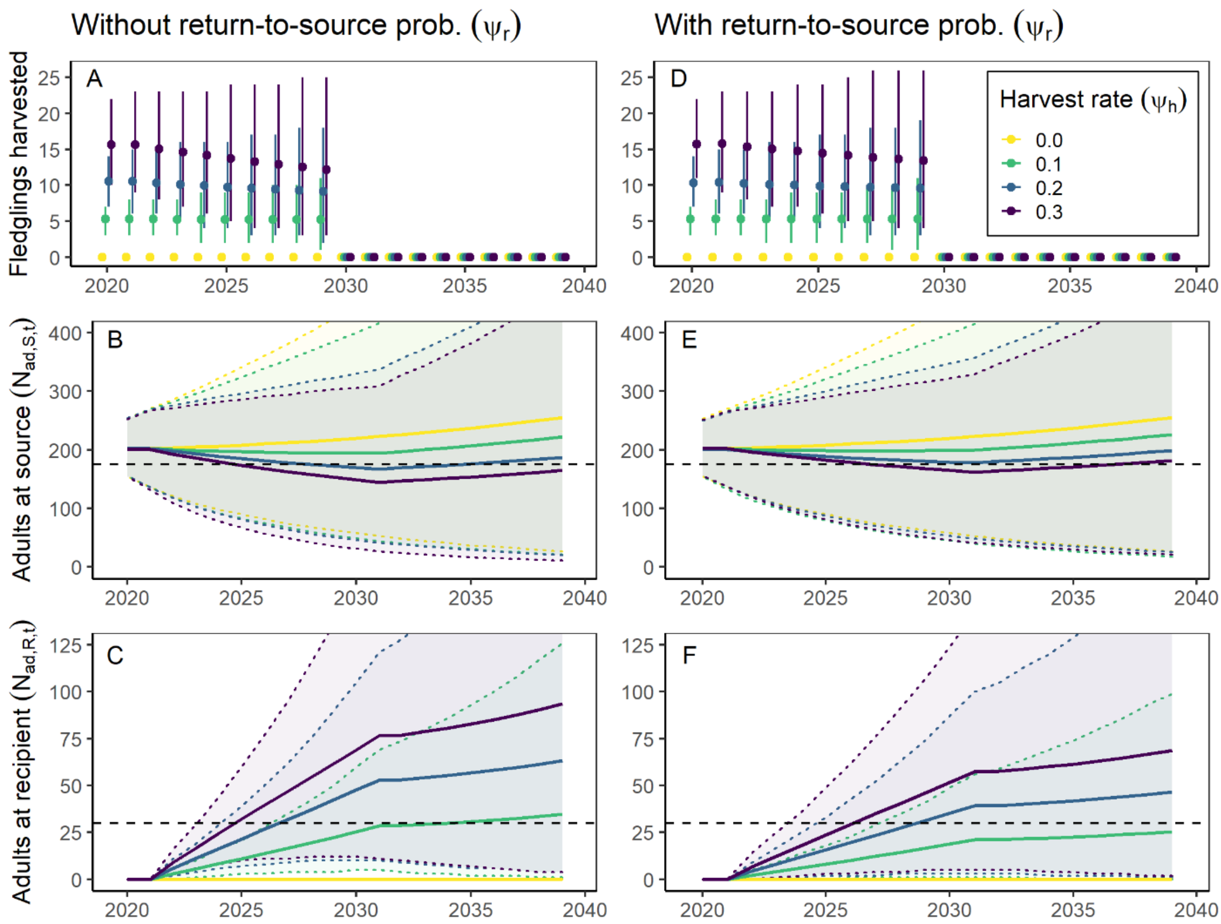

Fig. 24. Projections of Whenua Hou Diving Petrel fledglings harvested for translocation for 10 years (AD), adults at source ($\widehat{N_{ad,S,t}}$; BE), and adults at recipient populations ($\widehat{N_{ad,R,t}}$; CF) under various translocation scenarios, under the assumption that juveniles either always recruit to recipient populations ($\psi_r = 0$; ABC) or can recruit back to the source populations ($\widehat{\psi_r} = 0.25$; DEF). Solid lines represent posterior means, dotted lines represent 95% CrIs, and dashed lines indicate desired minimum population size at source (175 adults; BE) and recipient populations (30 adults; CF).

Table 7. Estimated size of Whenua Hou Diving Petrel source populations at their lowest mean during the 20-year projections ($\widehat{N_{ad,S,t}}$ low) and after 20 years, as well as recipient population sizes ($\widehat{N_{ad,R,t}}$) after 20 years, under varying translocation scenarios (posterior means with 95% CrIs). $\psi_{h,t}$ represents the harvest rate, $\widehat{\psi_r}$ represents the (estimated) return-to-source probability. **Bold** indicates translocation scenarios that do not impact $\widehat{N_{ad,S,t}}$ excessively (i.e., mean > 175) and that result in an acceptable ($\widehat{N_{ad,R,t}}$ low) (i.e., mean > 30).

Harvest years	$\psi_{h,t}$	$\widehat{\psi_r}$	$\widehat{N_{ad,S,t}}$ **low**	$\widehat{N_{ad,S,t}}$ **after 20 years**	$\widehat{N_{ad,R,t}}$ **after 20 years**
0	0	-	-	255 (27-710)	-
5	0.1	0	197 (66-359)	251 (17-775)	20 (0-83)‡
5	**0.2**	**0**	**182 (62-321)**	**221 (16-632)**	**36 (0-140)**
5	0.3	0	171 (56-310)†	214 (13-668)	56 (1-222)
10	**0.1**	**0**	**194 (44-416)**	**222 (21-603)**	**34 (1-126)**
10	0.2	0	167 (41-337)†	187 (20-496)	63 (4-215)
10	0.3	0	144 (27-308)†	165 (11-472)	93 (4-330)
5	0.1	0.25 (0.01-0.87)	197 (75-335)	236 (23-651)	13 (0-61)‡
5	0.2	0.25 (0.01-0.87)	186 (80-304)	217 (30-560)	25 (0-102)‡
5	**0.3**	**0.25 (0.01-0.87)**	**179 (64-309)**	**217 (18-603)**	**40 (0-160)**
10	0.1	0.25 (0.01-0.87)	198 (62-351)	226 (20-756)	25 (0-99)‡
10	**0.2**	**0.25 (0.01-0.87)**	**178 (48-357)**	**199 (26-516)**	**47 (1-170)**
10	0.3	0.25 (0.01-0.87)	162 (41-329)†	182 (21-478)	69 (2-245)

† indicates posterior mean of $\widehat{N_{ad,S,t}}$ below 175.

‡ indicates posterior mean of $\widehat{N_{ad,R,t}}$ below 30.

DISCUSSION

My results indicate that establishing a second WHDP colony through translocations of pre-fledging chicks could be feasible, although small, short-term declines at the source population should be anticipated. Establishing a second WHDP population is highly desirable, as this will reduce the vulnerability of this critically endangered species to storms, climate change, and potentially interspecific competition (Cole 2004, Fischer *et al.* 2017a, 2018b, Vousdoukas *et al.* 2020). Additionally, WHDP translocations would reinstate lost ecosystem functioning (Ch. 6, Fischer *et al.* 2019). The benefits of founding a recipient population appear to outweigh short-term declines at the source population, provided they remain small (i.e., $N_{ad,S,t}$ > 175). Consequently, my projections are encouraging for future WHDP conservation management.

While my results are encouraging, they are based on intermittent (i.e., suboptimal) data and thus continued monitoring to enable more accurate estimates is crucial. My estimates align with estimates of previous analyses, providing confidence in my IPM-derived results. For example, based on burrow counts, WHDP population growth following invasive predator eradications was estimated at $\hat{\lambda}$ = 1.017 (1.006-1.029), aligning with my IPM results (Ch. 2, Fischer *et al.* 2020a). However, the dataset on known-age birds, which provided key information on juvenile survival in my IPM, was limited due to the delayed maturity of WHDPs. Continued monitoring would allow for more accurate estimates of this, and other parameters, and should therefore be considered a priority. Additionally, a sensitivity analysis could facilitate the identification of the parameters with the largest uncertainty and their impact on population growth (Jenouvrier *et al.* 2018). Results from such a sensitivity analysis could help further finetune future monitoring of the WHDP population.

My results highlight the range of considerations conservation practitioners have to make when deciding on strategies for translocations of endangered seabirds, and other species persisting in small populations.

Accounting for juveniles returning to source populations post-translocation appears crucial when planning seabird translocations. I show that failure to account for the return-to-source probability can lead to an overestimation of the recipient population size of ~29%. Simultaneously, harvest impact on source populations may be lower. Therefore, juveniles returning to source populations post-translocation can have profound impacts on the outcome of translocations and higher harvest intensities may be required to successfully establish recipient populations. I used largely anecdotal insights into return-to-source probabilities from the literature (e.g., Imber *et al.* 2003, Priddel *et al.* 2006, Carlile *et al.* 2012) as this parameter remains poorly understood. Most studies investigated the influence of age of translocated fledglings on this parameter and have shown that birds should be harvested 2-6 weeks prior to fledging to reduce the return-to-source probability (e.g., Miskelly *et al.* 2009). However, future seabird translocation efforts will benefit from further investigations into this parameter. Quantifying the influence of I) the number of years spent at sea by juveniles, II) the distance between source and recipient populations, III) the size of source populations, and IV) the use of social attraction systems on return-to-source probabilities should be considered research priorities. I encourage practitioners planning seabird translocations to incorporate thorough monitoring of not just the recipient site, but also the source site, into translocation protocols to gain a more complete perspective of translocation outcomes.

Translocation timeframes and harvest intensities are key to anticipating translocation impact, success, and costs, and should be subjected to structured decision-making (SDM) frameworks (Converse *et al.* 2013, Ewen *et al.* 2014). I illustrate that two approaches can limit impact on source populations, while ensuring adequate establishment of recipient populations: I) higher harvest rates for shorter time frames, or II) lower harvest rates for longer time frames. At first instance, shorter translocation time frames at higher intensities may be most attractive. Many seabird populations only remain on remote islands (Spatz *et al.* 2014, Rodríguez *et al.* 2019). The fixed costs associated with translocations to and from remote islands (e.g., helicopter transfers) are likely to outweigh the costs of hand-rearing individual fledglings at recipient sites (Miskelly *et al.* 2009). Translocations over shorter time frames at higher intensities thus appear a more efficient use of resources. However, for species with low population growth rates, such as the WHDP, the benefits of using resources efficiently should be weighed against the establishment of more robust recipient populations (Panfylova *et al.* 2019). For example, translocations of ~15 fledglings/year for five years resulted in an estimated recipient population of ~40 adults, while translocations of ~10 fledglings/year for 10 years resulted in an estimated recipient population of ~47 adults. With a mean population growth rate of 1.023, it will take close to a decade for a population of ~40 adults to grow to ~47 adults. Lower intensity harvesting for longer time frames at higher costs may thus be more attractive. All translocations are centred around value-based objectives (i.e., saving costs is good, or a bigger recipient population size is good; Parker *et al.* 2020). Therefore, clear articulation of problems, objectives, and management alternatives by key stakeholders within SDM frameworks would improve future translocation planning (Ewen *et al.* 2014, Converse *et al.* 2013, Panfylova *et al.* 2019).

My results show considerable uncertainty in the projections of source and recipient populations, and therefore translocations of species as rare as the WHDP should only be attempted within an adaptive management (AM) framework. AM frameworks involve I) the development of explicit models of a system, II) manipulation of the system and gaining information, and III) the subsequent updating of models to guide management (Armstrong *et al.* 2007, Converse *et al.* 2013). Continued and thorough monitoring is central to AM. Here, I developed the explicit model for WHDP translocations. An AM framework that incorporates monitoring of both source and recipient populations during (and after) translocations, combined with continuous updating of the explicit model would allow for more accurate estimates of impact on the source population, establishment of the recipient population, and the return-to-source probability. This would in turn allow for informed adjustments of translocation protocols (i.e., higher or lower harvest intensities over longer or shorter time frames; Dimond & Armstrong 2007). Furthermore, such an AM framework would also allow for the estimation of demographic parameters currently not included or simulated in my model. Specifically, the estimation of the I) differences in vital rates between source and recipient populations and II) the exchange of adults and juveniles between source and recipient populations (Miskelly & Taylor 2004, Miskelly *et al.* 2009) within an AM framework appears crucial. I therefore recommend, a combination of SDM and AM frameworks for translocations to provide realistic estimates of translocation impact and success, subsequent finetuning of translocation protocols, and ultimately the best possible outcome for the target species.

Chapter 5

Preparing for translocations of a critically endangered petrel through targeted monitoring of nest survival and breeding biology

ABSTRACT

The recently described Whenua Hou Diving Petrel (*Pelecanoides whenuahouensis*; WHDP) consists of ~200 adults that all breed in a single 0.018 km^2 colony in a dune system vulnerable to erosion. The species would therefore benefit from the establishment of a second breeding population through translocations. However, given the small size of the source population, it is essential that translocations are informed by carefully targeted monitoring data. I therefore modelled nest survival at the remaining population in relation to potential drivers (distance to sea and burrow density of conspecifics and a competitor) across three breeding periods. I also quantified breeding phenology, burrow attendance, and chick growth curves. I estimated egg survival at 0.686, chick survival at 0.890, overall nest survival at 0.612, and found no indication that nest survival was affected by distance to sea or burrow density. WHDPs laid eggs in mid-October, eggs hatched in late November, and chicks fledged in mid-January at ~86% of adult weight. Burrow attendance (i.e., feeds) decreased from 0.94 to 0.65 visits/night as chicks approached fledging. WHDP nest survival and breeding biology were largely consistent among years despite interannual variation in climate due to the southern oscillation cycle. Nest survival estimates will facilitate suitability assessments of prospective translocation sites. Breeding phenology will inform the timing of chick harvest (i.e., live chick collection). Burrow attendance combined with growth curves will inform selection of individuals for harvest and subsequent hand-rearing protocols.

TUHINGA WHAKARĀPOPOTO

Kei te pūrei Kūaka Whenua Hou kātahi anō ka whakaahuria (Whenua Hou Diving Petrel - *Pelecanoides whenuahouensis*) ka noho atu ai kia rua rau pakeke ka aitia ki tētahi tāhuna pānekeneke nei 0.018 kiromita pūrua te rahi. Nā reira ka whai hua te momo manu nei i te whakatūtanga o tētahi atu taupori whakatupu mā te nukuhanga kōhanga. Engari, nā te tokoiti kei te taupori matua, me mātua whai i te raraunga ka puta i tā mātou āta aroturuki i ngā kūaka nei. Nō reira, i whakatakune i te oranga tonutanga o ngā kōhanga o te toenga o te taupori e hāngai ana ki ētahi kaupapa ārahi (te tawhiti i te moana, te noho kōpipiri o ngā rua o ngā momo manu ōrite, me ngā hoariri) i ngā tau whakatupu e toru he rerekē te āhuarangi i te hurihanga ngapu o te tonga. I aromatawai hoki mātou i te whakatupuranga āhuarangi, te taenga ki ngā rua, me te tupuranga mai o ngā pīpī. I whakatau tata mātou i te oranga o ngā hua ki te 0.686, te oranga pīpī ki te 0.890, me te oranga tonutanga o te kōhanga ki te 0.612, kīhai i kitea tētahi tohu ka raru te kōhanga i te tawhiti ki te moana, i te kōpipiri rānei o ngā kōhanga. Ka whānau hua mai ngā Kūaka Whenua Hou i te puku o te Oketopa, ka paopao mai ngā pīpī i te whiore o te Noema, ā, ka whai huruhuru ngā pīrere i te puku o te Hanuere e ~86 ōrau o te taumaha o te pakeke. Ko te taenga ki ngā rua (arā ki te kai) ka heke mai i te 0.94 toronga ia pō ki te 0.65 i te pakaritanga o te pīpī ki te taumata pīrere. Ko te oranga tonutanga me te whakatupuranga koiora o ngā Kūaka Whenua Hou, i te rahinga o te wā, kua ū i ngā tau ahakoa te rerekētanga o te āhuarangi. Mā te whakatau tata oranga kōhanga e matapae ai ngā ahunga taupori e haere ake nei me ngā wāhi pai hei wāhi nuku kōhanga. Mā te whakatupuranga āhuarangi e ārahi i te wā kohikohi ai i ngā pīpī (arā te kohinga pīpī ora), ā, mā te taenga atu ki te rua me te tupuranga o ngā pīpī e ārahi ai i ngā tikanga whakatupu pīpī ā-ringa.

INTRODUCTION

Seabirds, and petrels in particular, are among the most threatened taxa on the planet (Fig. 2; Croxall *et al.* 2012, Dias *et al.* 2019). Close to half of all petrel species (i.e., families Procellariidae, Oceanitidae, Hydrobatidae, and Pelecanoididae; *n* = 125 species) are threatened with extinction. Petrel species are affected by a wide range of threats (Dias *et al.* 2019). On land, petrels are threatened by invasive predators (Jones *et al.* 2008, Dias *et al.* 2019), extreme weather events (Cole 2004, Rodríguez *et al.* 2019), and light pollution (Rodríguez *et al.* 2017), among others. At sea, threats include changes in oceanic productivity and climate patterns as well as fisheries impacts (accidental by-catch and overfishing) (Anderson *et al.* 2011, Žydelis *et al.* 2013, Grémillet *et al.* 2018). Various life-history traits render petrels disproportionally vulnerable. Petrels are extremely wide-ranging (i.e., they use entire ocean basins; Shaffer *et al.* 2006), *K*-strategists (i.e., low fecundity, delayed sexual maturity, high longevity; Rodríguez *et al.* 2019), and placed at high trophic levels (i.e., they are top predators; Einoder, 2009). As petrels provide important ecosystem services (e.g., nutrient cycling, bioturbation, and seed dispersal; Ellis, 2005, Orwin *et al.* 2016, Otero *et al.* 2018), their conservation is a priority.

Translocations are an increasingly common conservation strategy (Seddon *et al.* 2007, 2014), including for petrels (Miskelly *et al.* 2009). A translocation entails the intentional movement of animals for species recovery or ecosystem restoration (Seddon *et al.* 2014). Translocations may be effective conservation interventions if habitat is available outside a species' current range, if the species is unlikely to naturally colonize that habitat, and if the translocation is unlikely to cause undesirable impacts (Ch. 4). Translocations may involve supporting existing populations (i.e., reinforcement), reinstating populations within the species' indigenous range (i.e., reintroduction), or creating new populations outside of the species' indigenous range (i.e., assisted colonization) (IUCN 2013). As petrels are often threatened and facilitate ecosystem functioning, petrel translocations can be motivated by both species recovery and restoration goals (Miskelly *et al.* 2009; Jones & Kress 2012). For example, Gould's Petrels (*Pterodroma leucoptera*) have been translocated to Boondelbah Island, Australia, within their indigenous range to strengthen the small existing population (reinforcement; Priddel *et al.* 2006). Common Diving Petrels (*Pelecanoides urinatrix*; CDP) have been translocated to Mana Island, Aotearoa

(New Zealand), to reinstate the ecosystem functions they once provided (reintroduction; Miskelly *et al.* 2009).

Poor understanding of the agents of decline can cause translocation failure, including for petrels (Jones & Kress 2012, Osborne & Seddon 2012). Insights into the drivers of nest survival are key for translocations. Many seabirds, including most petrels, are wide-ranging (e.g., Shaffer *et al.* 2006). Therefore, foraging ranges and associated threats at sea are unlikely to be affected by translocation, as has been shown for Short-tailed Albatrosses (*Phoebastria albatrus*; Deguchi *et al.* 2014, Orben *et al.* 2018). Understanding drivers of nest survival at source sites may thus be key to predicting nest survival potential translocation sites and consequently, translocation success (Osborne & Seddon, 2012). As nest survival in seabirds can be subject to interannual fluctuations driven by climatic conditions (Chastel *et al.* 1995, Quillfeldt *et al.* 2007), multi-year studies of nest survival are critical.

Poor understanding of the breeding biology of the target species is also a potential cause of translocation failure (Jones & Kress 2012). Petrels exhibit high philopatry and their semi-precocial chicks are believed to imprint on their natal colonies prior to fledging (Priddel *et al.* 2006, Miskelly *et al.* 2009). Thus, the use of chicks, 1-6 weeks prior to fledging, is required to successfully translocate these species (Miskelly *et al.* 2009, Jones & Kress 2012). As these chicks then need to be hand-reared at the translocation site, detailed information on the breeding biology of the target species is essential to design protocols. For example, data on breeding phenology (i.e., timing and duration of courtship, incubation, guard, and post-guard stages) will inform translocation timing. Data on feeding regimes and chick growth curves will inform hand-rearing regimes.

The critically endangered Whenua Hou Diving Petrel (*Pelecanoides whenuahouensis*; WHDP) is a recently described burrowing petrel species that could benefit from translocations (Ch. 4, Fischer *et al.* 2018c). These birds were once widespread throughout southern Aotearoa, but following local extinctions caused by invasive predators (e.g., rats; *Rattus spp.*), the species only survives at a single location: Whenua Hou (Codfish Island; Fig. 4 & 5; Worthy 1998, Holdaway *et al.* 2003, Wood & Briden 2008). Here, only 182-235 adults remain in a single colony (Ch. 4). Invasive predators have been eradicated from Whenua Hou (McClelland 2002), but additional threats may still be inhibiting population recovery (Ch. 2 & 3, Fischer *et al.* 2020a). Unlike other petrels, the species breeds exclusively in fragile foredunes < 20 m from the springtide line (Fischer *et al.*

2018c). Erosion caused by storms and storm surges, as well as climate change, may thus be the main threat to this species (Cole 2004, Vousdoukas *et al.* 2020). Competition with the more aggressive CDP for burrow sites may also inhibit population recovery (Fischer *et al.* 2017a). An unsuccessful hybridization attempt between a WHDP and a CDP has been recorded (Fischer *et al.* 2018c), suggesting additional pressures from this closely related species. As CDPs appear to be also attracted to WHDP calls (in contrast to WHDPs), acoustic attraction systems may not be an option to establish new WHDP colonies (Fischer *et al.* 2020b). Therefore, translocations of WHDPs to a more suitable site appears to offer a solution to ensure long-term viability (Ch. 4). Detailed information on the factors affecting nest survival and breeding biology is required to meaningfully assess site suitability and design translocation protocols.

To inform future translocations, I monitored WHDP burrows across three breeding periods (2017–19) with a burrowscope, stick palisades, and nest boxes. I aimed to quantify nest survival and its underlying drivers. Furthermore, I also quantified breeding phenology, patterns of burrow attendance (as a proxy for feeding regimes), and chick growth curves and the influence of interannual variation.

Fig. 25. Distribution of Whenua Hou Diving Petrel (white circles), Common Diving Petrel (black circles), mixed burrows (grey circles), and nest boxes (white squares) 2017-2019.

METHODS

Study area

The entire WHDP colony is restricted to a 0.018 km^2 strip of coastal sand dunes on Whenua Hou (Codfish Island; -46.766° S, 167.645° E; Fig. 25), which is 3 km off the west coast of Rakiura (Stewart Island), Aotearoa. This area holds ~100 WHDP burrows (Ch. 2, Fischer *et al.* 2020a). A small number of CDPs (10-20 burrows) breed within the study area, which sometimes attempt to hybridize with WHDPs (Fischer *et al.* 2017a, 2018c).

Nest survival

To quantify WHDP nest survival (i.e., egg, chick, and overall nest survival), I monitored 62-78 burrows (65-79% of the total population) from early September to late January during the 2017-19 breeding periods (I report the calendar year in which breeding commenced). Monitoring was conducted with a burrowscope (Sextant Technologies, Wellington, Aotearoa; see https://youtu.be/6GGIQ25LTYc). Monitoring included daily checks of the burrows monitored for breeding phenology (see below) and weekly checks of all other burrows that allowed access. Eggs were detected in 48 of the 62 monitored burrows in 2017 (apparent lay rate = 0.77), in 57 of the 64 monitored burrows in 2018 (apparent lay rate = 0.89), and in 62 of the 78 monitored burrows in 2019 (apparent lay rate = 0.79), resulting in 167 WHDP burrows used in subsequent analyses. During each nest check, I recorded the phenological stage (egg, chick, or fledged) and fate (dead or alive). These data were compiled in three capture history matrices showing per day whether each egg had hatched, chick had fledged, and was alive (1 = yes, 0 = no, NA = not checked). I assumed nests to be alive on first detection but otherwise treated the fate of eggs as unknown until a nest was either abandoned or the egg had hatched.

I estimated nest survival using a multi-stage nest survival model within a Bayesian framework (Schmidt *et al.* 2010, Converse *et al.* 2013). My custom-made, multi-stage nest survival model allowed for I) unknown transition and failure dates, II) varying lengths of phenological stages among nests, III) estimation of daily survival rates for two phenological stages (eggs and chicks), and IV) the estimation of fixed and random effects affecting the daily survival rate. Specifically, I fitted the data to a generalized mixed effects model (GLMM) with a Bernoulli error term and a logit-link function:

1) $logit(DSR_{i,j}) = \alpha_{DSR} + \beta_{hatch} \times hatch_{i,j} + \beta_{sea} \times dist_i + \beta_{WHDP} \times WHDP_i + \beta_{CDP} \times CDP_i + u_{year,y})$

where $DSR_{i,j}$ is the survival probability of nest *i* on day *j*, α_{DSR} is the intercept, β_{hatch} is the effect of transitioning from egg stage ($hatch_{i,j}$ = 0) to chick stage ($hatch_{i,j}$ = 1), β_{sea} is the effect of distance to sea ($dist_i$), β_{WHDP} is the effect of WHDP burrow density ($WHDP_i$), β_{CDP} is the effect of CDP burrow density (CDP_i), and $u_{year,y}$ is the annual random effect. I then estimated daily survival rate for the egg ($DSR_{egg,y}$), and chick stage ($DSR_{chick,y}$) per year as:

2) $logit\left(DSR_{egg,y}\right) = \alpha_{DSR} + u_{year,y}$

3) $logit\left(DSR_{chick,y}\right) = \alpha_{DSR} + \beta_{hatch} + u_{year,y}$

Subsequently, I estimated nest survival during the egg ($S_{egg,y}$) and chick ($S_{chick,y}$) stage per year as:

4) $S_{egg,y} = {DSR_{egg,y}}^{T_{inc}}$

5) $S_{chick,y} = {DSR_{chick,y}}^{T_{rear}}$

in which T_{inc} and T_{rear} are the estimated mean durations of the incubation and chick-rearing stages, respectively. Ultimately, I estimated overall nest survival per year (S_y) as:

6) $S_y = S_{egg,y} \times S_{chick,y}$

As I did not know exact dates of phenology events or duration of stages for all nests, missing values for hatching and fledging status were inferred by modelling the duration of each stage for each nest (Miller *et al.* 2017). I assumed these durations were normally distributed among nests with means T_{inc} and T_{rear} and standard deviations σ_{inc} and σ_{rear}. I used mildly informative priors for these parameters: $N[mean = 45, precision = 0.1]$ for T_{inc} and T_{rear}, $U[0, 6]$ for σ_{inc}, and $U[0, 4]$ for σ_{rear}. I based my priors on the breeding phenology of the closely related South Georgian Diving Petrel (*P. georgicus*; Marchant & Higgins 1990). I also used a mildly informative prior for α_{DSR} ($N[5, 1]$) but used vague priors for β_{hatch}, β_{WHDP}, β_{CDP}, and β_{sea} ($N[0, 1]$) and for the standard deviation of the random effect $u_{year,y}$ ($U[0, 1]$).

I measured $dist_i$ as the distance from the WHDP burrow to the highest springtide line per year (m). I measured $WHDP_i$ as the density of other WHDP burrows within a 3-m radius of the burrow (burrows/m^2). Similarly, I measured CDP_i as the density of CDP and mixed (WHDP x CDP) burrows within 3 m (burrows/m^2). I z-transformed these three variables.

I fitted the model using the Bayesian modelling software OpenBugs 3.2.3 (Spiegelhalter *et al.* 2014). The Markov chain Monte Carlo (MCMC) algorithms make it possible to account for multiple sources of uncertainty, such as survival probability, timing, and duration of phenology stages, which are propagated into posterior distributions for parameters. I pooled two MCMC chains of 100,000 iterations, after a burn-in of 25,000 iterations which was sufficient to give convergence based on the Gelman-Rubin statistic ($\hat{R}$ < 1.05). I report the mean of posterior distributions with 95% credible intervals (CrI). The OpenBUGS code of my nest survival model can be found in Supplementary Material 3.

Breeding phenology

To quantify the timing and duration of WHDP breeding phenology, I monitored 25-30 (26-30% of the total population) burrows daily between early September and late January each breeding period. I quantified arrival dates of birds based on when their burrows opened. I quantified the timing of subsequent breeding phenology events, including dates for laying, hatching, commencement of post-guard phase (i.e., the first day a chick was left unattended by an adult), and fledging, using a burrowscope. I monitored burrows daily until I recorded a breeding phenology event, after which I ceased monitoring until a week before the next anticipated event. I initially predicted the timing of these events using published data on the closely related South Georgian Diving Petrel (Marchant & Higgins 1990). I used the timing of phenology events to delineate the phenological stages of courtship, incubation, chick-rearing (consisting of guard and post-guard stages), and the total breeding period, as well as to calculate durations thereof. I assessed the influence of interannual variation on timing and duration of breeding phenology stages using generalized linear models (GLMs) with a Gaussian error distribution and an identity-link function. In these GLMs, I treated initiation date or duration per stage as the response variable and year as the explanatory variable. I transformed initiation dates into a numerical variable first (i.e., days since 01 September) and subsequently z-transformed initiation dates and durations.

Burrow attendance

As a proxy for WHDP feeding regimes, I quantified nightly burrow attendance (i.e., visits/night) per phenological stage (i.e., courtship, incubation, guard, and post-guard stages) using stick palisades. I assessed the influence of interannual variation per stage using GLMs with a quasi-binomial error distribution and a logit-link function. In these GLMs, I treated visits/night per stage as the response variable and year as the explanatory variable. In addition, I assessed how nightly burrow attendance during the post-guard stage changed over time using GLMs with a binomial error distribution and a logit-link function treating visits/night as the response variable and chick age (expressed as days-before-fledging) as the explanatory variable. I could not account for double feeds (i.e., both parents feeding the chick) using my stick palisade method. Thus, burrow attendance should be considered only a proxy for feeding regimes.

Chick growth curves

To quantify WHDP chick growth curves (i.e., wing length and weight), I monitored 10 burrows daily between early December and late January each breeding period. In early September 2017, I installed 10 custom-made, multi-story nest boxes in existing WHDP burrows (Fig. 25 & 26; Fischer *et al.* 2018a). I selected burrows for nest box instalment if I) burrows belonged to successful breeders in 2015 and/or 2016, II) brood chambers had a depth of < 60 cm, and III) burrows were > 10 m from the springtide line. I subjected chicks in nest boxes to daily measurements of weight (g) and wing length (i.e., flattened wing chord; mm) once they reached the post-guard stage until they fledged. Only four chicks fledged from a nest box (most pairs dug new brood chambers behind nest boxes). I increased my sample size by taking measurements from all chicks accessible within natural burrows (*n* = 5). I also took measurements from all chicks caught just before fledging (*n* = 80). I compared chick growth with mean adult weight (127 g; *n* = 136) and mean adult wing length (120; *n* = 111; Fischer *et al.* 2018b).

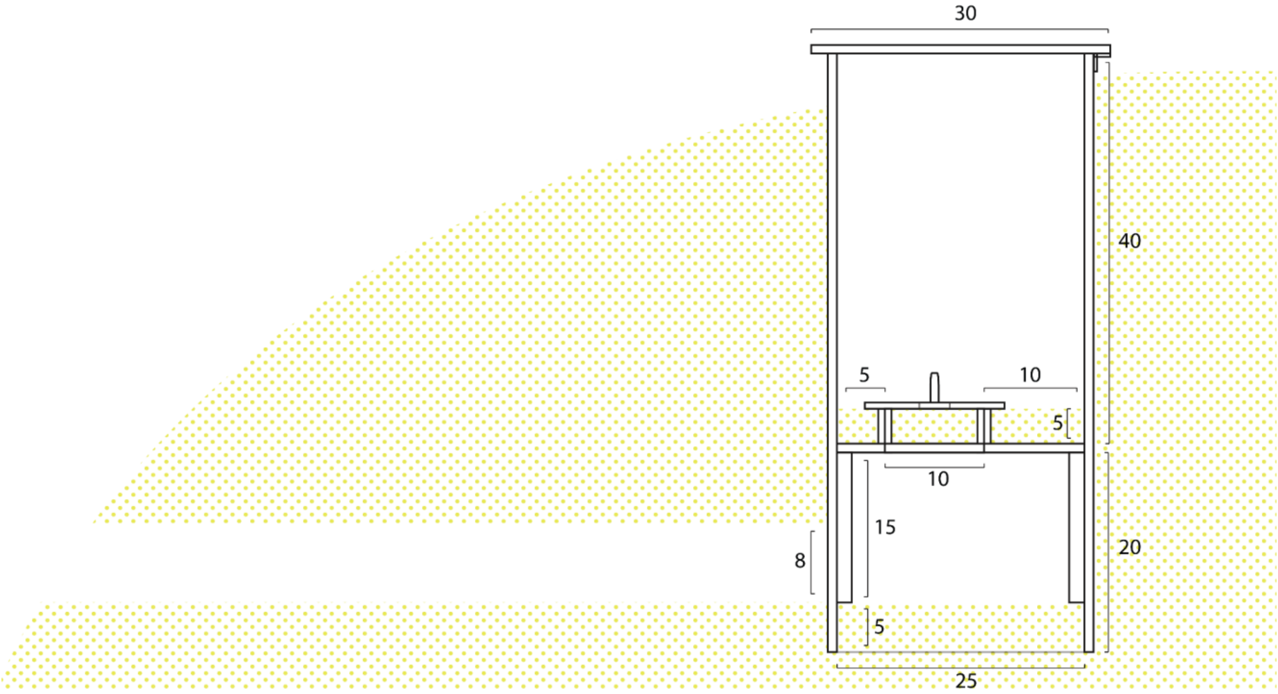

Fig. 26. Design of a Whenua Hou Diving Petrel nest box adopted from Fischer *et al.* (2018a). Dimensions are given in cm.

RESULTS

Nest survival

The daily survival rate of WHDP eggs was estimated at $\widehat{DSR_{egg}}$ = 0.992 (0.988-0.995; Fig. 27A). The daily survival rate of chicks was estimated at $\widehat{DSR_{chick}}$ 0.998 (0.996-0.999). The mean duration of the incubation stage was estimated at $\widehat{T_{inc}}$= 49.1 (48.1-50.0) days and the mean duration of the chick-rearing stage was estimated at $\widehat{T_{rear}}$ = 46.9 (46.5-47.3) days. Egg survival was estimated at $\widehat{S_{egg}}$ = 0.686 (0.551-0.796). Chick survival was estimated at $\widehat{S_{chick}}$ = 0.890 (0.808-0.947; Fig. 27B). Nest survival from laying to fledging was estimated at $\hat{S}$ = 0.611 (0.460-0.738; Fig. 27C). Average distance to sea was 6.7 m (range = 0.1-20.7), average WHDP density was 0.02 burrows/m^2 (0.00-0.11), and average CDP density was 0.01 burrows/m^2 (0.00-0.07). Estimates for the effects of distance to sea ($\widehat{\beta_{sea}}$ = -0.01; -0.29-0.27), density of WHDP burrows ($\widehat{\beta_{WHDP}}$ = -0.01; -0.25-0.25), and density of CDP burrows ($\widehat{\beta_{CDP}}$ = 0.25; -0.03-0.58) did not indicate a clear impact on nest survival (Fig. 27D). There was also no apparent annual variation in survival. Twenty-four abandoned eggs were extracted from burrows to assess fertility, and 16 of these (67%) were found to be infertile.

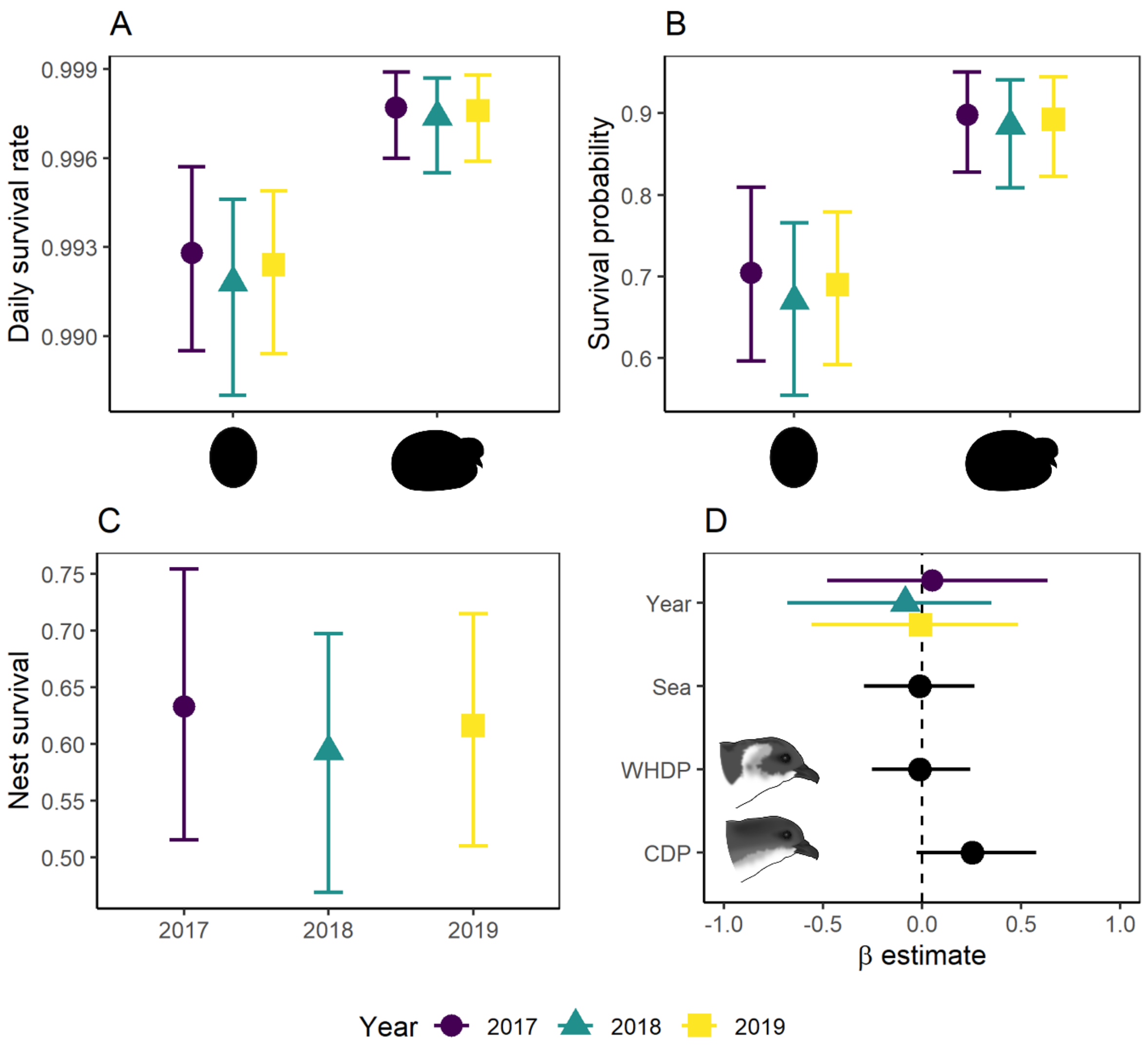

Fig. 27. Estimates of (A) daily survival rates of Whenua Hou Diving Petrel eggs ($\widehat{DSR_{egg,y}}$) and chicks ($\widehat{DSR_{chick,y}}$), (B) probabilities of surviving the egg ($\widehat{S_{egg,y}}$) and chick stages ($\widehat{S_{chick,y}}$), (C) overall nest survival ($\widehat{S_y}$), and (D) slopes ($\hat{\beta}$) of z-transformed covariates affecting the logit daily nest survival (posterior means with 95% CrIs). Sea = effect of distance to sea, WHDP = effect of Whenua Hou Diving Petrel burrow density, and CDP = effect of Common Diving Petrel burrow density.

Breeding phenology

On average, WHDPs arrived at the colony on 13 September, eggs were laid on 10 October, chicks hatched on 27 November, post-guard stage commenced on 4 December, and fledging occurred on 13 January (Fig. 28). Phenology events were protracted and non-synchronous among burrows. Timing of breeding phenology varied slightly among years. Specifically, arrival occurred slightly earlier in 2019 (estimates ± SE: $\widehat{\beta_{2018}}$= -0.50 ± 0.26, $\widehat{\beta_{2019}}$ = -0.80 ± 0.25), laying and hatching occurred slightly later in 2019 ($\widehat{\beta_{2018}}$ = -0.53 ± 0.28, $\widehat{\beta_{2019}}$ = 0.51 ± 0.25 and $\widehat{\beta_{2018}}$ = -0.31 ± 0.30, $\widehat{\beta_{2019}}$ = 0.64 ± 0.28, respectively), post-guard commenced slightly earlier in 2018 ($\widehat{\beta_{2018}}$ = -0.88 ± 0.33, $\widehat{\beta_{2019}}$ = 0.11 ± 0.34), and fledging occurred slightly later in 2019 ($\widehat{\beta_{2018}}$ = -0.49 ± 0.31, $\widehat{\beta_{2019}}$ = 0.81 ± 0.27).

The average duration of breeding stages was as following: courtship: 28.0 days, incubation: 48.2 days, chick guard stage: 8.2 days, and post-guard stage: 39.1 days, resulting in 46.9 days for the total chick-rearing period (Fig. 28). The total breeding period lasted 123.5 days. Duration of courtship stages, incubation stages, and total breeding periods varied slightly among years. The courtship and incubation periods lasted slightly longer in 2019 (estimates ± SE: $\widehat{\beta_{2018}}$ = -0.13 ± 0.28, $\widehat{\beta_{2019}}$ = 0.86 ± 0.25 and $\widehat{\beta_{2018}}$ = -0.04 ± 0.33, $\widehat{\beta_{2019}}$ = 0.76 ± 0.29, respectively), resulting in a longer breeding period ($\widehat{\beta_{2018}}$ = 0.05 ± 0.31, $\widehat{\beta_{2019}}$ = 1.13 ± 0.28). Durations of the guard and post-guard stages were consistent among years ($\widehat{\beta_{2018}}$ = 0.41 ± 0.36, $\widehat{\beta_{2019}}$ = 0.47 ± 0.38 and $\widehat{\beta_{2018}}$ = -0.08 ± 0.38, $\widehat{\beta_{2019}}$ = 0.22 ± 0.39, respectively).

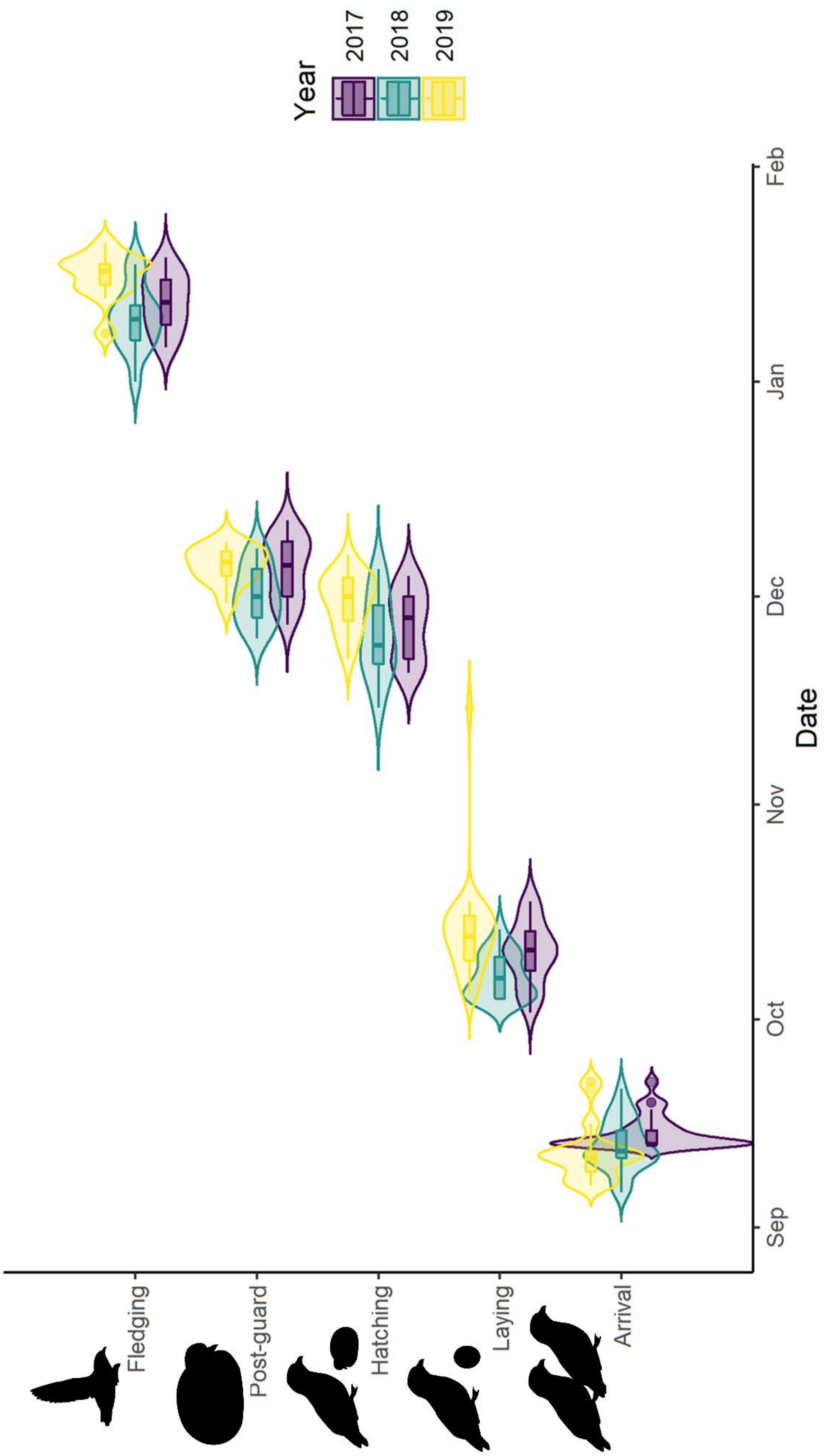

Fig. 28. Whenua Hou Diving Petrel breeding phenology.

Burrow attendance

WHDP burrow attendance was not uniform throughout the breeding period. Burrow attendance was lower during incubation (mean = 0.61 visits/night), compared to burrow attendance during courtship (0.83), guard (0.87), and post-guard (0.85) stages (Fig. 29A). Burrow attendance per stage varied slightly among years. Specifically, burrow attendance during courtship was higher in 2018 (estimates ± SE: $\widehat{\beta_{2018}}$ = 1.04 ± 0.29, $\widehat{\beta_{2019}}$ = -0.32 ± 0.19), burrow attendance during incubation was higher in 2019 ($\widehat{\beta_{2018}}$ = 0.04 ± 0.15, $\widehat{\beta_{2019}}$ = 0.37 ± 0.14), burrow attendance during guard was lower in 2017 ($\widehat{\beta_{2018}}$ = 1.07 ± 0.39, $\widehat{\beta_{2019}}$ = 1.85 ± 0.42), and burrow attendance during post-guard was higher in 2017 ($\widehat{\beta_{2018}}$ = -0.62 ± 0.23, $\widehat{\beta_{2019}}$ = -0.63 ± 0.21). During the post-guard stage, visitation rates decreased over time from 0.94 visits/night in the early post-guard stage (40-20 days-before-fledging) to 0.65 visits/night during the last week before fledging (Fig. 29B). This decrease in visitation rates was more pronounced in 2019 ($\hat{\beta}$ = -0.35 ± 0.05) and 2018 ($\hat{\beta}$ = -0.14 ± 0.02) than in 2017 ($\hat{\beta}$ = -0.03 ± 0.01).

Chick growth curves

Wing lengths of WHDP chicks showed, on average, a gradual and consistent growth from 20 mm at 40 days-before-fledging until approaching a plateau of 111 mm (93% of adult mean) around 7 days-before-fledging (Fig. 29C). Maximum recorded wing length was 119 mm (99% of adult mean). Weight of chicks, on average, increased from 25 g at 40 days-before-fledging to a maximum of 148 g (117% of adult mean) between 20 and 10 days-before-fledging and subsequently decreased to 109 g (86% of adult mean) around fledging (Fig. 29D). Maximum recorded chick weight was 180 g (142% of adult mean).

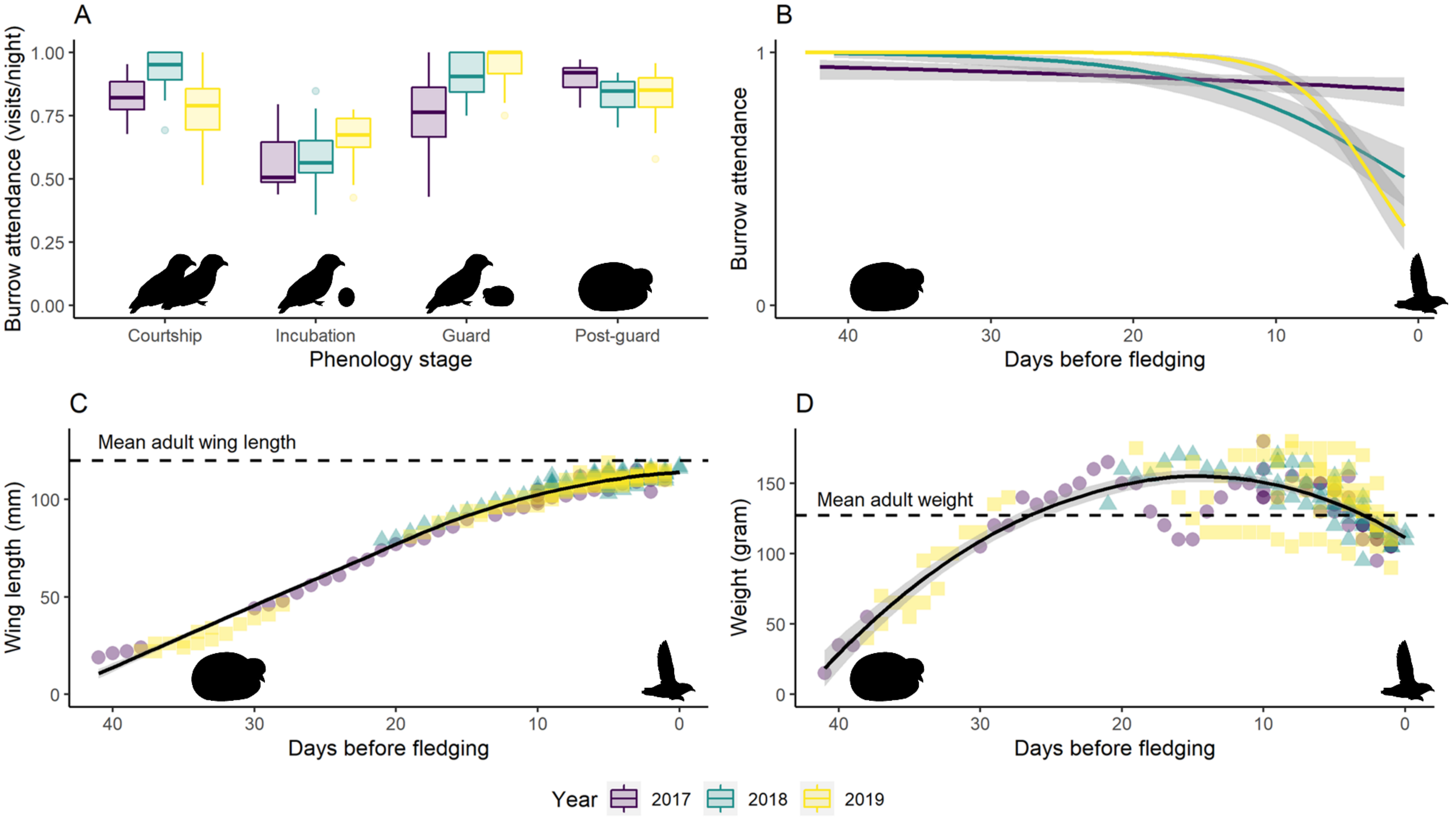

Fig. 29. Whenua Hou Diving Petrel burrow attendance across the entire breeding period (A), burrow attendance changes over time during the post-guard stage illustrated with generalized linear models (B), chick growth curves of wing length (C), and weight (D) as illustrated by locally estimated scatterplot smoother curves.

DISCUSSION

Here I present a detailed nest survival and breeding biology study of a critically endangered petrel species. My results have potential to inform future translocations aimed at establishing a new WHDP breeding colony.

First, by applying a novel Bayesian multi-stage nest survival model, I provide insights into nest survival. Estimates of demographic parameters like nest survival are of vital importance when making structured decisions on conservation management (including translocations) in the face of uncertainty (Panfylova *et al.* 2019). For wide-ranging species like most petrels, differences in nest survival will be a likely driver of translocation success, making nest survival estimates crucial for projecting future population trajectories at translocation sites (Ch. 4). In addition, my estimates of the effects of parameters on nest survival are important to assess the suitability of translocation sites. While no parameters showed a clear impact on nest survival, these may have an influence at different exposure levels (e.g., nest survival may have been influenced at higher CDP burrow densities). As such, these parameters should still be considered when assessing translocation site suitability (Fischer *et al.* 2017a).

Second, my results on WHDP phenology, chick growth, and nest survival help determine the ideal timeframe for chick harvest (i.e., live collection) for translocations. As petrel chicks should be harvested 1-6 weeks prior to fledging to prevent imprinting on the natal colony (Miskelly & Taylor 2004, Miskelly *et al.* 2009), harvesting of WHDP chicks should occur between early December and early January. As chicks reach a weight maximum 20-10 days-before-fledging and may thus be less susceptible to stress associated with translocations, the last week of December appears the ideal timeframe to harvest chicks of this species.

Third, my growth curves will help select the best suited WHDP chicks for future translocations. Wing length combined with weight allows for the estimation of age and condition of chicks (in days-before-fledging; Miskelly & Taylor 2004, Miskelly *et al.* 2009). Chicks selected for translocations should have a wing length of 75-105 mm and a weight of > 140 g, as this combination will ensure the selection of healthy chicks at 20-10 days-before-fledging.

Fourth, while the nest boxes were unpopular with adult WHDPs, four chicks have fledged successfully from these boxes. Nest boxes did not appear to influence nest survival (4/8 nest attempts inside nest boxes were successful). Since these nest boxes are designed specifically for this species (Fischer *et al.* 2018a), chicks can fledge successfully from these nest boxes, and access to chicks is crucial, the use of these nest boxes appears invaluable at future translocation sites.

Fifth, my results on burrow attendance and chick growth can inform feeding regimes for WHDP chicks post translocation. At the translocation site, chicks should be fed daily until 10-7 days-before-fledging to ensure chicks remain above mean adult weight. When translocated chicks approach fledging, feeds should be slowly reduced to every second day, provided chicks are at, or above, mean chick weight (Miskelly *et al.* 2009). I did not provide species-specific information on meal size or diet. However, CDP chicks have been successfully hand-reared using average meal sizes of 25 g (range 10-30; Miskelly *et al.* 2009). As CDPs have similar adult weights (110-150 g), these meal sizes may be appropriate for WHDP chicks as well. Miskelly *et al.* (2009) and Miskelly & Gummer (2013) have shown that many petrel species will thrive on a diet of pureed sardines, regardless of their natural diet, and thus this diet may also be suitable for this species.

WHDP nest survival and breeding biology was largely unaffected by annual variation and therefore varying climatic conditions. The three breeding periods in my study encompassed a range of climatic (El Niño southern oscillation; ENSO) conditions: mean Oceanic Niño Index was -0.79 (La Niña) in 2017, 0.75 in 2018 (El Niño), and 0.43 (approaching ENSO neutral) in 2019 (National Oceanic and Atmospheric Administration Climate Prediction Database repository; available from https://catalog.data.gov/dataset/climate-prediction-center-cpcoceanic-nino-index). The slight differences in timing and duration of phenology appeared unrelated to ENSO conditions. The breeding period under neutral conditions (2019) was delayed and prolonged compared to other breeding periods under more extreme and varying conditions (i.e., La Niña and El Niño). The apparent phenological insensitivity of WHDPs to climatic conditions is not surprising as it mirrors insensitivity observed in many other seabirds (Keogan *et al.* 2018). Climatic variables, however, could have influenced burrow attendance (Quillfeldt *et al.* 2007). In 2017 (La Niña), burrow attendance was higher during the post-guard stage. Food supplies can change with climatic conditions

(Schreiber & Schreiber 1984). Thus, adults in 2017 may have spent more time provisioning their chicks during the post-guard stage (Chastel *et al.* 1995).

The WHDP population is extremely small (182-235 adults; Ch. 4) and room for error in management is slim. Further research is required prior to attempting translocations of this species. The appropriate cohort size and number of cohorts used for translocations should be estimated to minimize risks to the source population while still resulting in the successful establishment of a second population (Ch. 4). Furthermore, infertility appeared a prevalent cause of egg failure. While CDPs can have a similar rate of infertility (Richdale 1945), the current WHDP population likely suffered from a population bottleneck and represents a fraction of the historical genetic diversity (Wood & Briden 2008). As such, the selection of chicks for future translocations may benefit from including a measure of genetic diversity.

Translocations are a useful tool to combat the ongoing sixth mass extinction by restoring species and ecosystem functioning (Seddon *et al.* 2007, 2014). Translocations of petrels fit both conservation and restoration goals (Miskelly *et al.* 2009). I provided the data required to inform future translocations. Such translocations could render this critically endangered species less vulnerable. The WHDP is the only petrel species in Aotearoa that breeds *en masse* in coastal dunes (Worthy 1998) and is thus considered an ecosystem engineer (Ch. 6, Fischer *et al.* 2019). The Predator Free 2050 program (Russell *et al.* 2015) aims to eradicate seven species of invasive mammals from entire Aotearoa by 2050. If this program is successful, more habitat could become available for potential WHDP translocations. The information provided here may facilitate not only the conservation of a critically endangered species, but also the restoration of ecosystem functioning throughout southern Aotearoa.

Chapter 6

Contrasting responses of lizard occurrences to burrowing by a critically endangered seabird

ABSTRACT

Seabirds are considered ecosystem engineers, because they facilitate ecosystem functioning (e.g., nutrient cycling), crucial for other marine and terrestrial species, including reptiles. However, studies of seabird-reptile interactions are limited. Here, I assessed the influence of the critically endangered Whenua Hou Diving Petrel (*Pelecanoides whenuahouensis*; WHDP) on the occurrence of two threatened skinks, Stewart Island green skink (*Oligosoma aff. chloronoton*) and southern grass skink (*O. aff. polychroma*). I surveyed skinks for 26 consecutive days at 51 sites with and 48 sites without diving petrel burrows in the dunes on Whenua Hou (Codfish Island), Aotearoa (New Zealand). I used occupancy modelling to assess the influence of burrows on the occurrence of skinks, while accounting for other factors affecting occupancy (ψ) and detection probabilities (p). Diving petrel burrows had a contrasting effect on the occurrence of skinks. On average, $\hat{\psi}$ of Stewart Island green skinks was 114% higher at sites with burrows compared to sites without, while $\hat{\psi}$ of southern grass skinks was only 2% higher. Occurrence of both skinks was negatively influenced by the presence of the other skink species. On average, $\hat{p}$ were low: 0.013 and 0.038 for Stewart Island green and southern grass skinks, respectively. Stewart Island green skinks appear attracted to burrows, which might facilitate thermoregulation (i.e., shelter from temperature extremes). The larger Stewart Island green skinks may subsequently exclude the smaller southern grass skinks at burrows, causing the contrasting relationships. I suggest that these interspecific interactions should be considered when implementing conservation management, e.g., through the order of species translocations.

INTRODUCTION

Seabirds are considered ecosystem engineers as they have disproportionate impacts on their surrounding environments by providing various biophysical and biochemical ecosystem services (Taylor 2000ab, Şekercioğlu *et al.* 2004, Şekercioğlu 2006). For example, seabirds facilitate nutrient cycling between marine and terrestrial ecosystems through the deposition of their faeces (guano), regurgitated prey items, feathers, and deceased eggs, chicks, and adults at their breeding colonies (Fukami *et al.* 2006, Otero *et al.* 2018). These deposits can even result in the creation of soil (Heine & Speir 1989). In addition, the nutrients deposited at the terrestrial colonies slowly return to the marine ecosystems, increasing productivity in (coastal) marine environments (Lorrain *et al.* 2017, Graham *et al.* 2018). Through the increased nutrient deposition, seabirds also change the terrestrial soil pH (Mulder & Keall 2001, Ellis 2005). Furthermore, the presence of seabirds facilitates terrestrial litter decomposition as well as marine bioerosion rates (Towns *et al.* 2009, Wardle *et al.* 2009, Graham *et al.* 2018). Moreover, many seabirds, small (< 1 kg) Procellariiformes in particular, dig and breed in burrows, facilitating terrestrial bioturbation (i.e., natural soil displacement by burrowing organisms; Buxton *et al.* 2016, Orwin *et al.* 2016).

The biophysical and biochemical ecosystem services provided by seabirds have positive effects on unrelated taxa in both terrestrial and marine environments. For example, seabirds indirectly increase the productivity and seed germination of plants at their terrestrial colonies (Bandcroft *et al.* 2005). In addition, seabirds actively change the vegetation community through trampling and the collection of nesting material (Bancroft *et al.* 2005, Ellis 2005, Lameris *et al.* 2016). Seabirds also facilitate seed dispersal, which can result in remarkable trans-oceanic plant colonisations (Ellis 2005, Cheke & Hume 2008). Furthermore, seabirds indirectly change the composition and boost the diversity and abundance of terrestrial invertebrates (e.g., terrestrial amphipods, spiders, and insects) at their colonies (Markwell & Daugherty 2002, Towns *et al.* 2009, Wardle *et al.* 2009, Orwin *et al.* 2016). In the marine environments near seabird colonies, the presence of seabirds has an indirect positive effect on other species groups. For example, seabird presence is correlated with increases in overall reef fish biomass and growth rates (Graham *et al.* 2018).

Seabirds also have a positive influence on reptiles (Markwell & Daugherty 2002, Corkery *et al.* 2015). Seabird-reptile relationships, however, appear poorly studied. Most investigations into these relationships remain anecdotal (e.g., Walls 1978). As an exception, the large and enigmatic tuatara (*Sphenodon punctatus*) has been shown to profit from co-habiting Fairy Prion (*Pachyptila turtur*) burrows. Tuatara benefitted from warmer internal temperatures when inhabiting prion burrows and fed on prion chicks (Corkery *et al.* 2014, 2015). In addition, lizard communities (Scincidae and Diplodactylidae) were found to be more abundant and diverse on islands inhabited by seabirds than seabird-free islands (Markwell & Daugherty 2002). However, in the latter study, potential biases created by imperfect detections of these small lizards were not accounted for. Accounting for detection probabilities (e.g., through repeat surveys combined with occupancy modelling) is crucial, as non-detection does not indicate that a species is absent (MacKenzie *et al.* 2002, 2003, 2018).

Seabirds and lizards make up a substantial proportion of the native vertebrate fauna in New Zealand (Aotearoa), but both species groups have suffered major population declines following the introduction of invasive predators (Taylor 2000ab, Trewick & Gibb 2010, Hitchmough *et al.* 2016, Jewell 2017). The recently described Whenua Hou Diving Petrel (*Pelecanoides whenuahouensis*; WHDP) is one of the most endangered species in the world. Only one WHDP colony on Whenua Hou (Codfish Island) survived historical extirpations throughout southern Aotearoa caused by invasive predators (Fig. 4; Taylor 2000b, Holdaway *et al.* 2003, Wood & Briden 2008, Wood 2016, Fischer *et al.* 2017b, 2018bc). Furthermore, storms and storm surges threaten the remaining breeding habitat of this species (i.e., fragile foredunes; Cole 2004, Fischer *et al.* 2018bc). Consequently, the WHDP is listed as nationally critical in Aotearoa (Robertson *et al.* 2017) and as critically endangered on the IUCN red list (Fischer *et al.* 2018b, BirdLife International 2020). Two threatened species of skink also occur within the dune in which the WHDP breeds: Stewart Island green skink (*Oligosoma aff. chloronoton*) and southern grass skink (*O. aff. polychroma*). Both are listed as listed as at risk – declining in Aotearoa following considerable range reductions caused by predation by invasive predators and habitat destruction (Hitchmough *et al.* 2016, Jewell 2017). Based on the studies conducted on tuatara (Corkery *et al.* 2014, 2015), I hypothesised that the two threatened small lizard species in the dune of Whenua Hou would occur more frequently at sites with WHDP burrows than at sites without. To test my hypothesis, I used a large number of repeat surveys and occupancy modelling to account for imperfect detection of both skink species.

METHODS

Study area

My study was conducted in the dunes of Waikoropūpū (Sealers Bay; -46.766° S, 167.645° E) on Whenua Hou, located approximately 3 km west of Rakiura (Stewart Island), Aotearoa (Fig. 30). I defined my exact study area (approximately 0.065 km^2) as following: Waikoropūpū beach (north), the coastal shrub, as defined by Wickes & Rance (2010) (east and south), and an unnamed stream (west). My study area encompassed the entire WHDP colony (approximately 100 burrows; Ch. 2, 4 & 5). A small number (10-20 burrows) of Common Diving Petrels (*Pelecanoides urinatrix*) also nests within the WHDP colony (Ch. 5, Cole 2004, Trainor 2008, 2009). Both Stewart Island green skinks and southern grass skinks are common within my study area, but very little is known about their biology, including whether or not they are territorial (Jewell 2017). The southern skink (*O. notosaurus*) also occurs on Whenua Hou (Jewell 2017) but appears absent within the confines of my study area (i.e., the foredunes). The vegetation community within the area is relatively uniform and dominated by native grasses, such as pingao (*Ficinia spiralis*), sand tussock (*Poa billardierei*), and club rush (*Ficinia nodosa*), invasive grasses, such as Yorkshire fog (*Holcus lanatus*) and Cocksfoot (*Dactylis glomerata*), and bidibids (*Aceana novezealandia*) (Wickes & Rance 2010, de Lange *et al.* 2013). However, the vegetation cover within the study area varies considerably.

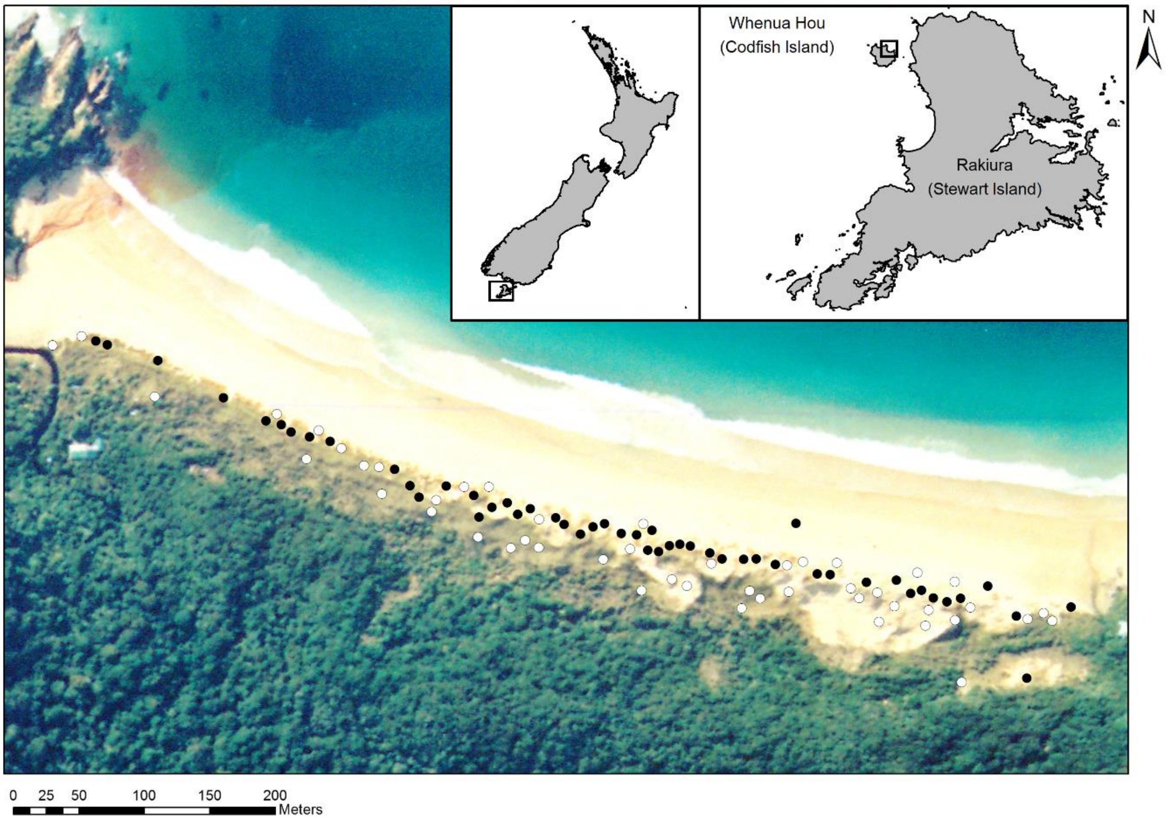

Fig. 30. Skink survey sites (n = 99) in the dunes of Waikoropūpū (Sealers Bay), Whenua Hou (Codfish Island), Aotearoa (New Zealand). Sites with Diving Petrel burrows (n = 51) are represented by black circles and sites without burrows (n = 48) are represented by white circles.

Skink counts

I surveyed the presence of skinks at sites with and without diving petrel burrows. To select sites with diving petrel burrows, I searched the entire study area for burrows by walking back and forth in pairs (Fischer *et al.* 2018c) in September-October 2017. I found a total of 120 diving petrel burrows and included all these sites in my skink surveys. All 120 burrows were active in the 2017 breeding season (assessed using stick palisades; Ch. 5, Cole 2004). Inactive burrows close relatively quickly due to dynamic nature of the dune. To select the sites without diving petrel burrows, I created 59 random points within the study area using ArcMap 10.7.1 and located them within the study area using a handheld GPS. I then physically marked sites with and without diving petrel sites *in situ*, using fibre glass poles and track markers to ensure skinks were surveyed at the exact same site on every occasion.

I surveyed skinks at all sites with (*n* = 120) and without diving petrel burrows (*n* = 59) from mid-November to mid-December 2017 (26 repeat surveys). I considered a circle with an area of 1 m^2 (radius = 56 cm) around each marker pole as the survey site. I alternated surveys between observers (*n* = 2) and visited sites in a pre-defined order to minimise disturbance, but rotated start and end points (i.e., from northeast to southwest or vice versa; Fig. 30). I conducted skink surveys any time between 07:30 and 19:30. I recorded skink sightings as Stewart Island green skink, southern grass skink, or unidentified skink per site per count. Skink identification was based on differences in colouration and size (snout-vent-length of Stewart Island green skinks ≤ 125 mm compared to ≤ 80 mm for southern grass skinks; Jewell 2017).

I ensured independence of my survey sites (i.e., the same individual skink cannot be detected at multiple sites) through retrospective subsampling, as diving petrels can breed in extreme proximity of each other (i.e., up to 6 burrows/m^2 ; Taylor 2000b). For my subsampling, I used data from a closely related skink species (Herbert & Bell 2012). Most (80%) of northern spotted skinks (*O. kokowai*) did not travel further than 4 m over an eight-month study period (Phillpot 2000, Melzer *et al.* 2017). I doubled this travelling distance to get a minimum-distance constraint of 8 m (measured from the centre of each site). I then ran 1,000 iterations of a random subsampling approach. Specifically, I randomly selected the first site to which I applied the minimum-distance constraint. After 1,000 iterations, I selected the subsample with the highest number of remaining sites. After distance-constrained random subsampling, 99 survey sites remained, consisting of 51 sites with burrows and 48 sites without.

I assumed that my ability to identify skinks was equal for both species. I therefore used the naïve occupancy (i.e., number of sites with detected skinks divided by the total number of survey sites) of each species to inform a weighted random allocation to assign unidentified skinks to either of the two species. The naïve occupancy was 0.091 and 0.161 for Stewart Island green skinks and southern grass skinks, respectively. This ratio informed the weighted random allocation of the unidentified skinks (*n* = 9) as following: $P = 0.36$ for Stewart Island green skinks, $P = 0.64$ for southern grass skinks. Ultimately, my approach of random subsampling and random allocation of unidentified skinks resulted in detection histories for each skink species per independent survey site, consisting of 1s (seen) and 0s (not seen), as required for occupancy modelling (MacKenzie *et al.* 2002, 2003).

Occupancy modelling

I fitted single-species, single-season occupancy models to the detection histories of both skink species to assess the influence of diving petrel burrows on the occurrence of skinks, while accounting for imperfect detection (MacKenzie *et al.* 2002, 2003, 2018). I included the effects of potentially important covariates on both occupancy (ψ) and detection probabilities (p) in my models. Specifically, I hypothesized that ψ could be affected by the presence of diving petrel burrows (Walls 1978, Markwell & Daugherty 2002, Corkery *et al.* 2014, 2015), the presence of the other skink species (Petren & Case 1998), the vegetation cover (Berry *et al.* 2005, Seddon *et al.* 2011), and/or the distance to sea (Fischer *et al.* 2018c). Consequently, I modelled the influence of I) the presence of a diving petrel burrow (binomial; denoted as *burrow*), II) the presence of the other skink species (i.e., naïve occupancy; binomial; denoted as *sgs* or *sigs* for southern grass skinks and Stewart Island green skinks, respectively), III) the vegetation cover (m^2 ; modelled as a quadratic function when a concave relationship was detected, or as a linear function when a convex relationship was detected; denoted as veg^2 or *veg*, respectively), and IV) the distance to sea (m from the spring-tide line; denoted as *sea*) on the ψ of both skink species. Additionally, I hypothesized that my ability to detect skinks could be affected by the vegetation cover (Roughton 2005) and/or the time of day (Armstrong 2016). Consequently, I modelled the influence of I) the vegetation cover (m^2 and modelled as a linear function; denoted as *veg*) and II) the timing of each survey (hours after sunrise; denoted as t) on the p of both skink species. I z-transformed all continuous variables (veg^2, *veg*, *sea*, and t) prior to the occupancy modelling (MacKenzie *et al.* 2018).

I used a model-averaging approach informed by the Akaike information criterion (AIC; Burnham & Anderson 2002) to identify the relative importance of covariates affecting ψ and p for Stewart Island green skinks and southern grass skinks. I compared models with all combinations of covariates affecting ψ while retaining p fully parameterized. I included null models, denoted as $(\cdot)$, but excluded interactions. I only included covariates in the same model with a Spearman's correlation coefficient of $r \leq 0.6$. For each model, I generated the -2 × loglikelihood ($-2L$), the logit-transformed estimate of the intercepts ($\hat{\alpha}$) ± standard error (SE), the logit-transformed estimate of the slope per covariate ($\hat{\beta}$) ± SE, and the variance-covariance matrix (Burnham & Anderson 2002, MacKenzie *et al.* 2018). I summed the AIC weights (w) from the models to quantify the relative variable importance (RVI) per covariate. I then used model averaging to obtain a model-averaged

$\hat{\beta}$ ± SE per covariate. I applied the Delta method (Seber 1982; MacKenzie *et al.* 2018) to obtain $\hat{\psi}$ ± SEs at sites with and without diving petrel burrows and p ± SEs per model. When applying the Delta method for $\hat{\psi}$, I used the mean value for *veg* (and veg^2) and *sea* and used 0 (i.e., absence) for *sgs* or *sigs* in models that contained these covariates. When applying the Delta method for $\hat{p}$, I used the mean values of *veg* and t (i.e., between 13:00 and 14:00). Finally, I used model-averaging to obtain model-averaged $\hat{\psi}$ ± SEs for sites with and without burrows per species and model-averaged $\hat{p}$ ± SEs per species.

Statistical analyses were conducted in Program R 3.3.1 (R Core Team 2016) and PRESENCE 2.12.15 (Hines 2006), while data visualisations were created in Program R 3.3.1, using *ggplot2* (Wickham 2009) and *qgraph* (Epskamp *et al.* 2017).

RESULTS

Naïve occupancy at sites with burrows was 0.118 (6/51) for Stewart Island green skinks and 0.216 (11/51) for southern grass skinks (following random allocation of unidentified skinks). Naïve occupancy at sites without burrows was 0.083 (4/48) for Stewart Island green skinks and 0.188 (9/48) for southern grass skinks. Spearman's correlation tests indicated that no covariates were highly correlated ($r \geq 0.6$; Table 8). Summaries of occupancy models for Stewart Island green skinks and southern grass skinks can be found in the Appendix 5 and 6, respectively. A comparison between the ΔAIC and *-2L* did not indicate the presence of any pretender variables (Anderson 2008). Stewart Island green skink occupancy was positively influenced by the presence of diving petrel burrows (RVI = 0.68; model-averaged $\widehat{\beta_{burrow}}$ = 2.11 ± 1.37) (Fig. 31). Southern grass skink occupancy also showed a positive, but considerably weaker, relationship with diving petrel burrows (RVI = 0.28; model-averaged $\widehat{\beta_{burrow}}$ = 0.09 ± 0.68). The model-averaged $\hat{\psi}$ for Stewart Island green skinks was 0.328 (SE = 0.172–0.489) for sites with burrows and 0.153 (SE = 0.092–0.261) for sites without (Fig. 32). The model-averaged $\hat{\psi}$ for southern grass skinks was 0.318 (SE = 0.235–0.415) for sites with burrows and 0.312 (SE = 0.230–0.409) for sites without. Notably, 5.6% of the records of Stewart Island green skinks and 6.1% of the records of southern grass skinks were of communal basking (i.e., two skinks basking within ≤ 50 cm from each other; Fig. 33). Communal basking of both species was only observed at sites with diving petrel burrows.

Table 8. Spearman correlation coefficients (*r*) between covariates included in occupancy models. Covariates included the presence of Stewart Island green skinks (*sigs*), the presence of southern grass skinks (*sgs*), vegetation cover (*veg*), presence of a Diving Petrel burrow (*burrow*), and distance to sea (*sea*).

	sigs	***sgs***	***veg***	***burrow***
sigs				
sgs	-0.09			
veg	0.37	0.22		
burrow	0.06	0.04	-0.07	
sea	0.11	0.09	0.43	-0.39

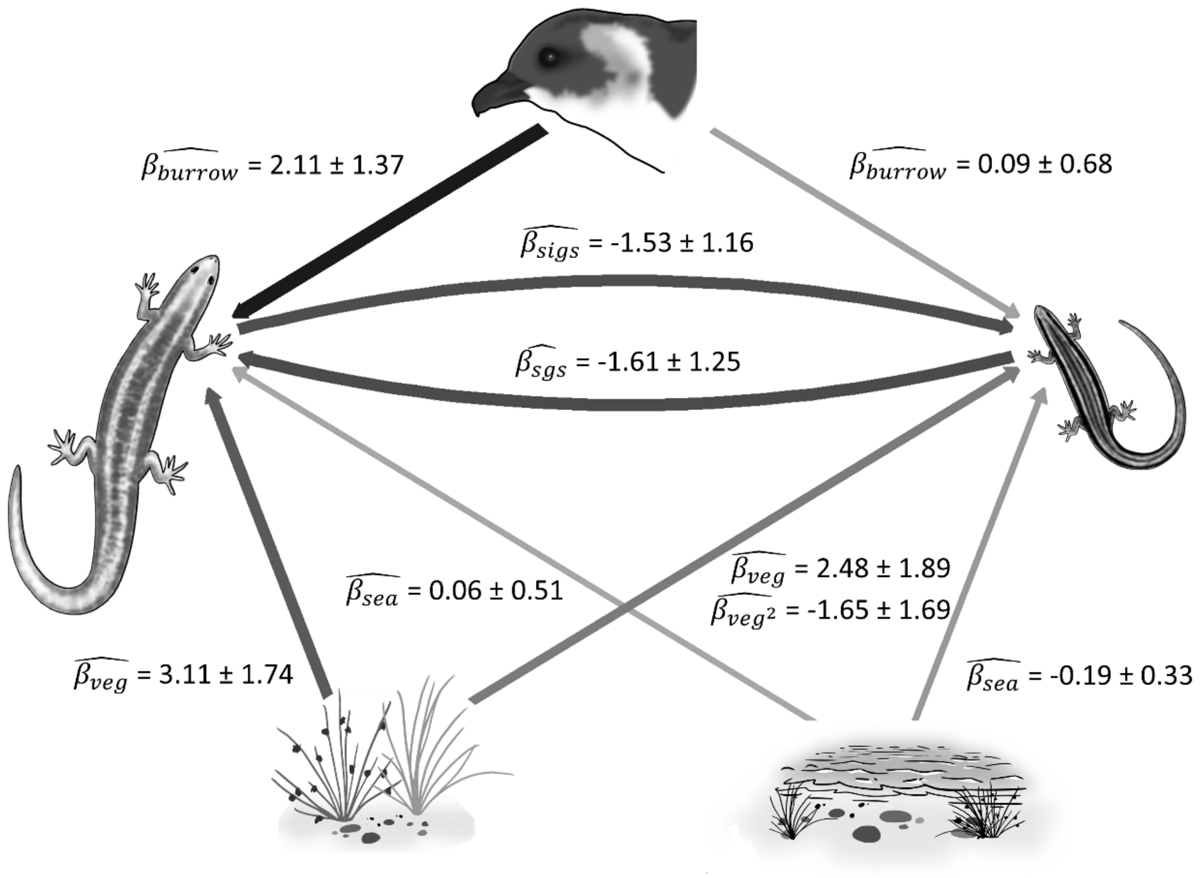

Fig. 31. Relative variable importance (RVI; represented by arrow width and darkness) and model-averaged estimates of logit-transformed slopes ($\hat{\beta}$) ± SE of covariates influencing occupancy probabilities (ψ) in occupancy models for Stewart Island green skinks (left) and southern grass skinks (right).

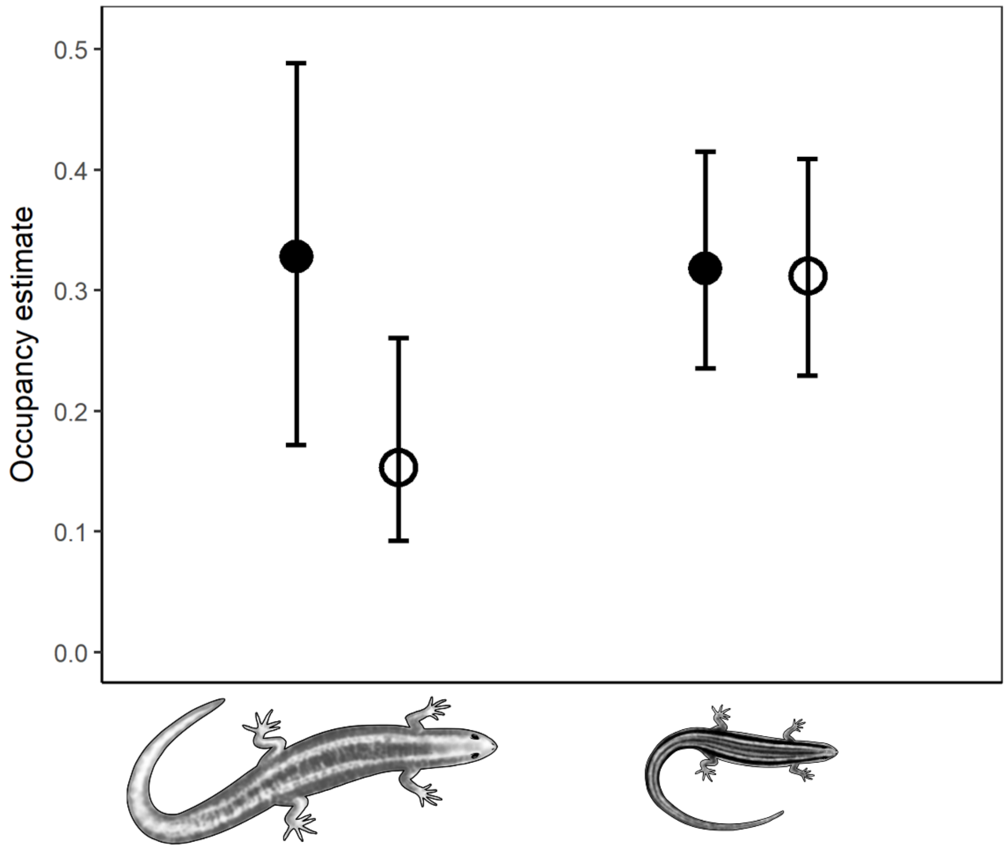

Fig. 32. Model-averaged estimates of occupancy probabilities ($\hat{\psi}$) for Stewart Island green skinks (left) and southern grass skinks (right) at sites with (black circles) and without (white circles) diving petrel burrows, including standard errors.

Fig. 33. Communal basking of Stewart Island green skinks at a Whenua Hou Diving Petrel burrow. Photo credit: Johannes H. Fischer.

Occurrence of Stewart Island green skinks was negatively influenced by the presence of southern grass skinks (RVI = 0.53; model-averaged $\widehat{\beta_{sgs}}$ = -1.61 ± 1.25). Vice versa, southern grass skink occurrence was negatively influenced by the presence of Stewart Island green skinks (RVI = 0.52; model-averaged $\widehat{\beta_{sigs}}$ = -1.53 ± 1.16). Additionally, Stewart Island green skink occurrence was positively influenced by vegetation cover (RVI = 0.49; model-averaged $\widehat{\beta_{veg}}$ = 3.11 ± 1.74). Contrastingly, southern grass skink occurrence indicated an optimum vegetation cover (RVI = 0.39; model-averaged $\widehat{\beta_{veg}}$ = 2.48 ± 1.89; model-averaged $\widehat{\beta_{veg^2}}$ = -1.65 ± 1.69). Furthermore, Stewart Island green skink occurrence was slightly positively influenced by distance to sea (RVI = 0.26; model-averaged $\widehat{\beta_{sea}}$ = 0.06 ± 0.51). Southern grass skink occurrence was slightly negatively influenced by the distance to sea (RVI = 0.31; model-averaged $\widehat{\beta_{sea}}$ = -0.19 ± 0.33).

Detection probabilities of both skink species were low. Model-averaged $\hat{p}$ was 0.013 (SE = 0.003–0.053) for Stewart Island green skinks and 0.038 (SE = 0.028–0.051) for southern grass skinks. Detection of Stewart Island green skinks had a negative relationship with time of day (model-averaged $\widehat{\beta_t}$ = -0.38 ± 0.28), as did detection of southern grass skinks (model-averaged $\widehat{\beta_t}$ = -0.35 ± 0.18). Counts earlier in the day were more likely to detect skinks. In addition, detection of Stewart Island green skinks had a positive relationship with vegetation cover (model-averaged $\widehat{\beta_{veg}}$ = 2.12 ± 1.21). Detection of southern grass skinks was also positively influenced by vegetation cover (model-averaged $\widehat{\beta_{veg}}$ = 0.61 ± 0.31).

DISCUSSION

My results indicate that diving petrel burrows in sand dunes can have a positive effect on the occurrence of Stewart Island green skinks. Despite not testing for the underlying mechanisms driving the elevated skink occurrence at diving petrel burrows, I hypothesise that the burrows offer refugia from heat stress. Previous research has consistently highlighted that lizard habitat selection is influenced by the need to avoid harsh and/or fluctuating environmental temperatures (Downes & Shine 1998, Milne *et al.* 2003, Du *et al.* 2006, Andersson *et al.* 2010, Jewell 2017). To thermoregulate, ectotherms such as lizards, can exhibit a behaviour known as “shuttling”, whereby they use thermal shelters periodically throughout the day to maintain stable internal temperatures (Milne *et al.* 2003, Andersson *et al.* 2010, Corkery *et al.* 2015, Jewell 2017). I thus suggest that diving petrel burrows facilitate "shuttling" behaviour in Stewart Island green skinks, allowing them to shelter from the extreme temperature maxima that are common within dune systems (Fischer *et al.* 2018a).

Predation may be another possible driver of habitat selection in small lizards (Downes & Shine 1998). The dunes of Whenua Hou currently harbour comparatively few diurnal skink predators since the eradication of all invasive predators: Weka (*Gallirallus australis*), brush-tailed possum (*Trichosurus vulpecula*), and kiore (*Rattus exulans*; McClelland 2002, Middleton 2007). However, prior to human colonisation, the avifauna of Aotearoa was more diverse, and many bird species were flightless, terrestrial, and potentially predatory (Duncan & Blackburn 2004, Trewick & Gibb 2010, Wood *et al.* 2017). As such, the use of burrows by Stewart Island green skinks could also be explained by predator avoidance on an evolutionary time scale.

My anecdotal records of communal basking of both skink species, limited to diving petrel burrows, suggest that these burrows may play a role in the skinks' social behaviours (Downes & Shine 1998). Communal basking is rarely documented in the skinks of Aotearoa, and these are the first records of communal basking in both Stewart Island green skinks and southern grass skinks (Jewell 2017, S Herbert *in lit*. 2018). These intraspecific interactions, however, need further investigations (e.g., into the sex and age of communally basking individuals). Alternatively, my records of communal basking in both species of skinks could be explained by coincidental and independent behaviour of individual skinks.

Stewart Island green skinks may exclude southern grass skinks from occupying sites with diving petrel burrows. Both skink species exhibited a negative relationship with the presence of the other skink species, indicating a level of interspecific competition or avoidance (Downes & Shine 1998, Petren & Case 1998). This result is likely due to autocorrelation (i.e., if one species is negatively correlated with the other, then the reverse will be also true). It is probable that the smaller southern grass skink is avoiding the larger Stewart Island green skink, as larger skinks predate on smaller skinks, or consume their autotomized tails (Petren & Case 1998, S Herbert *in lit*. 2018). As such, the larger Stewart Island green skinks are likely to exclude the smaller southern grass skinks from sites with diving petrel burrows, causing the observed difference in occurrence at diving petrel burrows. Perhaps, southern grass skinks show a strong relationship with diving petrel burrows in the absence of Stewart Island green skinks. We, however, cannot assess the relationship between these two skink species in further detail, because I used single-species occupancy models (MacKenzie *et al.* 2002, 2018). Co-occurrence occupancy modelling would allow for detailed assessments of these interspecific relationships (MacKenzie *et al.* 2004, Richmont *et al.* 2010). However, my current approach suggests uncertainty (multiple models with $\Delta AIC < 2.00$ in both model sets). Therefore, it seems ill-advised to elevate the number of estimated parameters from two (ψ and p) to eight (ψ^{A}, $\psi^{B|A}$, $\psi^{B|a}$, p^{A}_{j}, p^{B}_{j}, r^{A}_{j}, $r^{B|A}_{j}$, and $r^{B|a}_{j}$), as would be required for co-occurrence occupancy models (Richmont *et al.* 2010, MacKenzie *et al.* 2018).

The low detection probabilities of both skink species in my study illustrate the importance of repeat surveys in combination with occupancy modelling when studying cryptic species (MacKenzie *et al.* 2002, 2003, 2018). The modelled detection probabilities showed a positive relationship with vegetation cover. This unexpected relationship can be explained by a negative relationship of flight-initiation-distance with vegetation cover (Capizzi *et al.* 2007). In other words, skinks are less likely to flee with more vegetation cover around them, and thus more likely to be detected. The negative relationship of detection probabilities with time of day can be explained by the need to bask and thermoregulate in the morning (Downes & Shine 1998, Du *et al.* 2006, Andersson *et al.* 2010). While I employed visual surveys, detection probabilities of skinks may be higher when other survey techniques were employed (e.g., pitfall traps; Herbert & Bell 2012). These techniques, however, have other drawbacks (e.g., trap-related mortalities; Enge 2001), which cannot be overcome with repeat surveys and occupancy modelling.

Seabirds like the Whenua Hou Diving Petrel would have facilitated “shuttling” behaviour, and potentially social behaviours, in skinks throughout Aotearoa prior to the arrival of invasive predators. It is likely that the interspecific interactions between the WHDPs, Stewart Island green skinks, and southern grass skinks were once widespread throughout the historical range of these three species, but disappeared following local extinctions of the WHDP (Taylor 2000b, Holdaway *et al.* 2003, Wood & Briden 2008, Wood 2016, Fischer *et al.* 2017b, Jewell 2017, Fischer *et al.* 2018bc). For example, both skink species have relict populations on Rakiura, while the WHDP is extirpated from its dune systems (Wood & Briden 2008, Wood 2016, Jewell 2017). Finally, similar interspecific interactions may have occurred between other, closely related skink species (*Oligosoma spp.*) and the WHDP, outside the range of Stewart Island green skinks and southern grass skinks. Such interactions would have equally vanished with the local extinctions of the WHDPs.

Interspecific interactions form crucial parts of ecosystems and conservation management should take such interactions into account (Şekercioğlu *et al.* 2004, Fischer *et al.* 2017c). The WHDPs is the only seabird in Aotearoa that breeds *en masse* in dune systems (Fischer *et al.* 2017ab, 2018abc). Aside from the likely biophysical and biochemical ecosystem services provided by WHDPs across dune systems (e.g., nutrient cycling, bioturbation, seed dispersal; Ellis 2005, Orwin *et al.* 2016, Otero *et al.* 2018), WHDPs may increase the habitat suitability for skinks (Milne *et al.* 2003, Corkery *et al.* 2015). Therefore, this critically endangered species might be a crucial ecosystem engineer within its specific habitat type. All three species clearly merit targeted conservation management, which should take the interactions between these three species into account. One management option for skinks could be to follow Souter *et al.* (2004) and install diving petrel burrow replicas in areas where relict skink populations persist, but WHDPs have been extirpated (e.g., Rakiura; Jewell 2017). Another management strategy would be translocations of WHDPs into a dune system within its natural range (Ch. 4 & 5, Miskelly & Taylor 2004, Miskelly *et al.* 2009, Fischer *et al.* 2018bc). Such WHDP translocations would also benefit any relict skink population. A further option would be to follow WHDP translocations with translocations of skinks. Such multi-stage, multi-species reintroductions may result in better translocation outcomes and the reinstatement of interspecific interactions (Tylianakis *et al.* 2010). Interspecific interactions are lost at higher rates than species, resulting in ecosystem degradation before the extinction of species (Valiente-Banuet *et al.* 2015). Therefore, translocations aimed at reinstating interspecific interactions (next to locally extirpated species) will improve overall ecosystem health and functioning.

Chapter 7

General discussion

DISCUSSION

This PhD thesis is my second thesis on the conservation of the Whenua Hou Diving Petrel (*Pelecanoides whenuahouensis*; WHDP). During my MSc thesis (Fischer 2016), I quantified WHDP nest site selection on Whenua Hou (Codfish Island), resulting in the identification of erosion, caused by storms and storm surges, as a threat to this species (Fischer *et al.* 2018c). I also monitored WHDP burrows using remote cameras, resulting in the identification of competition for burrow sites with Common Diving Petrel (*P. urinatrix*; CDP) as a potential minor threat the WHDP (Fischer *et al.* 2017a). In addition, I quantified phenotypic characteristics of the WHDP and compared these with characteristics of the South Georgian Diving Petrel (*P. georgicus*), which led to the formal description of the WHDP as a new species to science (Fischer *et al.* 2018b).

Following this initial work, I set out to complete this PhD thesis. In Ch. 2, I evaluated the WHDP response to previous management strategies (i.e., invasive predator eradications; McClelland 2002). I found that the WHDP did not respond as anticipated to the eradication of invasive predators (i.e., population growth did not increase and remained low when compared to other seabirds on the island) and concluded that additional management is required to facilitate the recovery of the WHDP (Fischer *et al.* 2020a). In Ch. 3, I quantified WHDP offshore distribution, behaviour, and overlap with commercial fisheries. Results show that WHDPs are exposed to fisheries-related threats during the breeding period but are likely unaffected by these threats during the non-breeding period. While pelagic threats to the WHDP need further quantification and may need to be managed, terrestrial management actions may be more feasible. Consequently, to assess if establishing a second WHDP population through translocations would be a realistic and suitable conservation strategy, I modelled I) the impact of translocation harvest on the source population and II) the prospects of successfully establishing a recipient population (Ch. 4). My results indicated that WHDP translocations could be feasible, provided the number of harvested individuals and the number of years of harvesting are balanced accordingly to minimize the impact on the source while still successfully establishing a recipient population. Since WHDP translocations could be a feasible conservation strategy, I set out to quantify WHDP nest survival and breeding biology to inform translocation protocols (Ch. 5). I attempted to link WHDP nest survival estimates to intra-, interspecific competition, and environmental covariates, but failed to identify clear correlates. As such, future assessments of translocation sites still need to be comprehensive. For example, while my results suggest that interspecific competition does not influence WHDP nest survival, this is based on the CDP density on Whenua Hou. CDPs could influence WHDP nest survival at higher densities and as such CDPs should be surveyed at potential translocation sites. I did, however, identify the ideal harvest window (late December), key measurements of ideal translocation candidates (wing length: 75-105 mm, weight: >140 g), and feeding regimes. In my final chapter (Ch. 6), I investigated the influence of WHDPs (specifically, their burrows) on the occurrence of two threatened skink species. I found that the presence of WHDP burrows elevated the occurrence of the larger skink species, in contrast to the smaller species, indicating competition among skink species. These results indicated that WHDP burrowing activity provides benefits to unrelated species groups (Fischer *et al.* 2019). As such, WHDPs may fulfil an important role in the dune systems of southern Aotearoa and this role should be considered in future management strategies.

The results of my PhD chapters highlight the multidimensional landscape that conservation biologists face in their efforts to reduce ongoing and rampant biodiversity loss (Hoffman *et al*. 2010, Bolam *et al*. 2020). Conservation biology is complex, as threats and corresponding management actions are species-specific, subject to variation across time and space, and can be affected by both small and declining conservation paradigms (Caughley 1994, Dias *et al.* 2019). Ch. 2 highlights that conservation biologists cannot assume that management strategies, such as invasive predator eradications, will automatically result in species recovery, even if most species have responded positively (Brooke *et al.* 2018a). Detailed assessments of outcomes of interventions, based on thorough monitoring, are key to informing the efficacy of conservation management and guiding future strategies (Towns 2018). Ch. 3 highlights that for the conservation of vulnerable migratory species threats should be quantified across their range (Hardesty-Moore *et al*. 2018). In addition, accounting for temporal variation in exposure to these threats is key to effective conservation management (Robinson *et al.* 2020). Ch. 3 also underlines the importance of multi-year approaches to these spatial threat assessments

(Pardo *et al*. 2017). Ch. 4 highlights the small margin of error involved when applying management strategies to small populations. Ch. 4 also highlights the importance of thorough, long-term monitoring in combination with comprehensive modelling approaches to inform conservation management *a priori* while acknowledging uncertainty (Willis *et al.* 2007, Saunders *et al.* 2018). Ch. 5 further illustrates the importance of species-specific information, based on monitoring and subsequent modelling, for planning conservation management. Finally, Ch. 6 highlights that even if a population is small, positive interspecific interactions can be present with unrelated species groups. As such, interspecific interactions should be taken into consideration when applying management, even when management is species-specific (i.e., umbrella species concept; Branton & Richardson 2011). In summary, the conservation of the critically endangered WHDP is a good example of how complex conservation management can be, the variety of threats that should be assessed, the range of conservation strategies that should be considered, and the implications management can have.

OUTLOOK

The aim of this thesis was to facilitate the identification of a suitable conservation strategy for the recovery of the WHDP. The information compiled in this PhD thesis (as well as the information contained in my MSc thesis; Fischer 2016) is of considerable value to the future conservation of the WHDP. Invasive predator eradications were insufficient to stimulate WHDP recovery (Ch. 2, Fischer *et al*. 2020a). Additionally, an attempt to attract WHDPs *in situ* to dunes less vulnerable to storm erosion using an acoustic attraction system did not succeed, as WHDPs were not attracted to the intended site, but CDPs were (Fischer *et al*. 2020b). Therefore, other conservation strategies are required to conserve the WHDP. A potential management action, as outlined in Ch. 3, would be to reduce pelagic threats (e.g., collisions with vessels) by introducing seasonal spatial restrictions of vessels within the direct vicinity of the WHDP colony (i.e., within Waikoropūpū, Sealers Bay, during the WHDP breeding period). An additional benefit of such spatial restrictions would be the reduction of the re-incursion potential of invasive predators (Russel & Clout 2005). Spatial restrictions will, however, will have negative impacts on local stakeholders (i.e., fisheries). Another potential management option would be translocating pre-fledging chicks to establish a second WHDP population at another predator-free dune system in Southern Aotearoa (Ch. 4 & 5). Translocations could render the WHDP less vulnerable to storms, storm surges, future climate change, and potentially competition with CDPs (Cole 2004, Fischer *et al*. 2017a, 2018b, Vousdoukas *et al*. 2020). As a drawback, translocating WHDPs is likely a long-term and costly undertaking (Ch. 4). A third option would be to address putative negative interactions with CDPs (i.e., potential competition and hybridization attempts; Ch. 5, Fischer *et al*. 2017a, 2018b). Specifically, management could involve preventing CDPs from entering WHDP burrows with exclusion devices (e.g., burrow flaps) or more extreme (i.e., lethal) control measures (Gummer *et al*. 2015). WHDP-CDP interactions, however, should be studied in further detail. In Ch. 5, I only investigated CDP impacts on nest survival (showing the absence of direct impacts) and thus impacts on lay rates (e.g., through competition or hybridization attempts) remain unknown. Yet another option would be the *in-situ* management of the dune system on Whenua Hou to render this system less vulnerable to erosion through, for example, ecosystem restoration or physical structures (Coastal Restoration Trust of New Zealand 2011). Nonetheless, the potential short-term benefits of restoring the dune system on Whenua Hou may be undone by the onset of future climate change (Vousdoukas *et al.* 2020). Furthermore, intensive management of the dune on Whenua Hou may not be realistic as it holds several urupā (Māori burial grounds; Middleton 2007). As outlined by the examples above, a range of potential management options exists. However, every decision made in relation to the management of the WHDP should acknowledge I) that every management alternative (i.e., conservation action) will have consequences, not just for the WHDP, but also for a range of stakeholders, II) that considerable uncertainty is present for each management alternative (including doing nothing), and III) the unique status of tangata whenua (people of the land). I will attempt to outline how decisions in (WHDP) conservation management can be made in an appropriate and integrated fashion, while addressing stakeholder interests, accounting for current uncertainty, and acknowledging the unique status of tangata whenua.

Management alternatives are subject to complex, multi-dimensional decision landscapes that should be approached using standardized processes to acknowledge the consequences and trade-offs of each alternative. Structured decision-making (SDM) is a standardized process for making management decisions and is informed by a combination of stakeholder input and modelling (Gregory *et al.* 2012). SDM processes can effectively facilitate decision-making in conservation management (e.g., Gregory & Long 2009, Converse *et al.* 2013, O'Donnell *et al.* 2017). SDM processes consists of six successive stages (Fig. 34): I) defining the problem, II) articulating fundamental objectives, III) identifying potential management alternatives (i.e., conservation actions), IV) predicting consequences of management alternatives, V) weighing trade-offs between the consequences of the management alternatives, and VI) identifying the best options for conservation management (i.e., making a decision). Integral to SDM processes is the involvement of the stakeholders. Problems, objectives, alternatives, and the weighing of trade-offs are based on underlying values of stakeholders. SDM processes are centred around stakeholder meetings during which key stakeholders decide on the first three stages as informed by their underlying values. Subsequently, modelling can predict the consequences of each management alternative. Trade-offs of each alternative can then be weighed during further stakeholder meetings allowing further propagation of the underlying values. Once consequences are estimated and trade-offs are weighed, a management decision can be made. The combination of stakeholder engagement and modelling thus allows for making informed decisions on conservation management. However, SDM typically requires large amounts of data. Both my MSc thesis and this PhD thesis provide this initial data on WHDP conservation. Therefore, a SDM approach to identifying the best course of action for WHDP conservation is now possible and highly encouraged. This process should involve all relevant stakeholders including: Te Rūnanga o Ngāi Tahu, the New Zealand Department of Conservation, and Fisheries New Zealand. It should be noted that Te Rūnanga o Ngāi Tahu (tangata whenua) are more than stakeholders, they are Treaty partners following Te Tiriti o Waitangi (1840; the founding document of Aotearoa that outlines the relationship between Māori and non-Māori people).

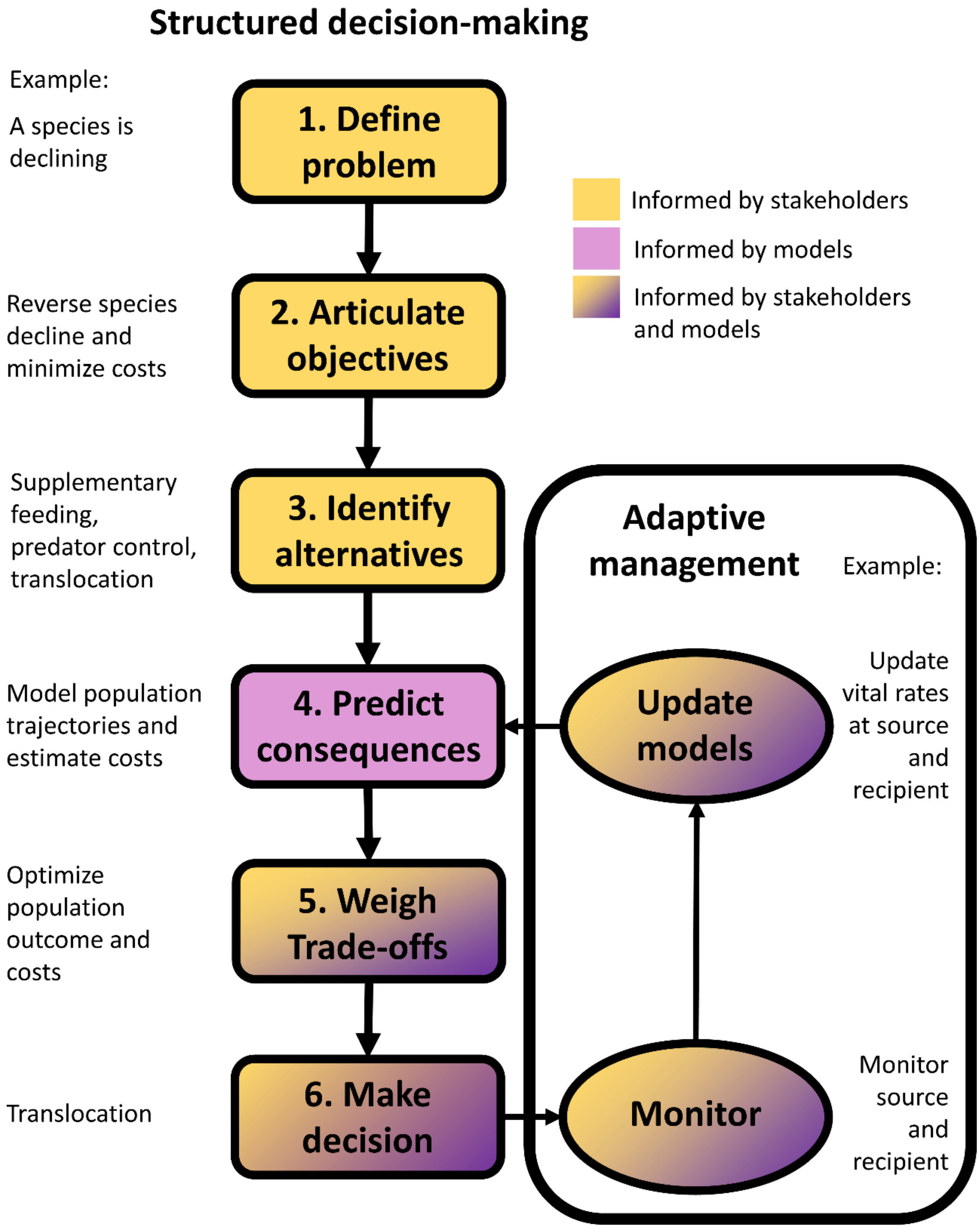

Fig. 34. A simplified diagram (adopted from Gregory *et al.* 2012, Converse *et al.* 2013, and O'Donnell *et al.* 2017) representing the structured decision-making process in combination with an iterative adaptive management loop, including a simplistic example of how this process can be applied to conservation management.

In addition to SDM, future WHDP management should also use adaptive management (AM) approaches to reduce uncertainty surrounding the outcomes of management alternatives. AM approaches consist of iterative feedback loops that involve I) developing models of a system, II) manipulating the system (e.g., by applying management alternatives) and subsequently gaining information, and III) updating the existing models to guide future management (Fig. 34; Armstrong *et al.* 2007, Williams 2011, Converse *et al.* 2013). Continued and thorough monitoring to update understanding of the system (by comparing predicted with observed values) is central to AM approaches. AM can be passive or active (Williams 2011). Active AM revolves around actively (i.e., experimentally) reducing the existing uncertainty, while passive AM reduces the associated uncertainty as a by-product of focusing on management objectives. In other words, the fundamental objectives (as identified, for example, through SDM), determine whether AM is active or passive. As fundamental objectives of conservation management usually involve the recovery of a species (e.g., Fig. 34; O'Donnell *et al.* 2017), rather than reducing existing uncertainty, AM approaches within conservation management are generally passive. AM (most likely passive) could improve WHDP recovery. For example, for WHDP translocations, (passive) AM could be applied to improve management by I) monitoring both source and recipient populations during and after translocations, II) updating the existing estimates of vital rates and projections of population sizes using existing models, and III) and adjusting harvest intensities and timeframes when necessary (Ch. 4). In summary, AM can improve (WHDP) conservation management, as AM allows for alternatives to evolve over time, while uncertainty surrounding consequences and trade-offs is reduced. Consequently, AM enables conservation biologists to move away from potentially detrimental trial-and-error approaches and identify in the most beneficial outcomes for target species.

Finally, future conservation management of the WHDP must acknowledge the unique position of tangata whenua. Indigenous Peoples around the globe exercise traditional rights over vast areas (~38 million km^2 or a quarter of Earth's terrestrial surface; Garnett *et al.* 2018). Furthermore, ~40% of all terrestrial protected areas fall within Indigenous People's lands. As such conservation management around the globe can no longer ignore and must include Indigenous perspectives (Ban *et al.* 2018, Rayne *et al.* 2020). In Aotearoa, conservation management legally must acknowledge the unique status of tangata whenua. Conservation management of the WHDP is no exception to this. Tangata whenua (Ngāi Tahu, specifically) have a deep genealogical, cultural, and spiritual connection to Whenua Hou (Middleton 2007). In fact, Whenua Hou was the site of the first bicultural Māori-Pākehā (non-Māori) settlement in Southern Aotearoa (Smith & Anderson 2009). Additionally, the WHDP is considered a taonga (culturally significant and treasured species) by Ngāi Tahu (New Zealand Government 1998). This connection is signified in both the common name "Whenua Hou Diving Petrel" and the scientific name "*P. whenuahouensis"* which were elected by Ngāi Tahu prior to the formal description of this taxon (Fischer *et al.* 2018b). Consequently, to acknowledge the position of Ngāi Tahu and to uphold agreements made in Te Tiriti o Waitangi (1840) and subsequent settlements (New Zealand Government 1998), Ngāi Tahu must be involved in all phases of future WHDP management.

Conservation biology can be effective and rescue species from extinction (Bolam *et al.* 2020), but more integrative approaches are urgently required to stem the rampant biodiversity loss (Leclère *et al.* 2020). Combining SDM and AM, while acknowledging the unique position of Indigenous Peoples, allows conservation biologists to operate in truly integrated approaches. SDM and AM facilitate informed conservation approaches that acknowledge the complex species-specific nature of species recovery, incorporate stakeholder interests, underline the importance of monitoring and modelling, and allow management to evolve over time as uncertainty is reduced (William 2011, Converse *et al.* 2013). Acknowledging and actively involving Indigenous Peoples in all stages of conservation management will facilitate the much-needed decolonisation of this field (Adams & Mulligan 2003, Smith 2013). The approach outlined here is a way forward for future WHDP management and could be applied to many other conservation projects. As such, I encourage conservation biologists to embrace these points and combat the ever-accelerating sixth mass extinction in truly integrated conservation approaches.

He waka eke noa.

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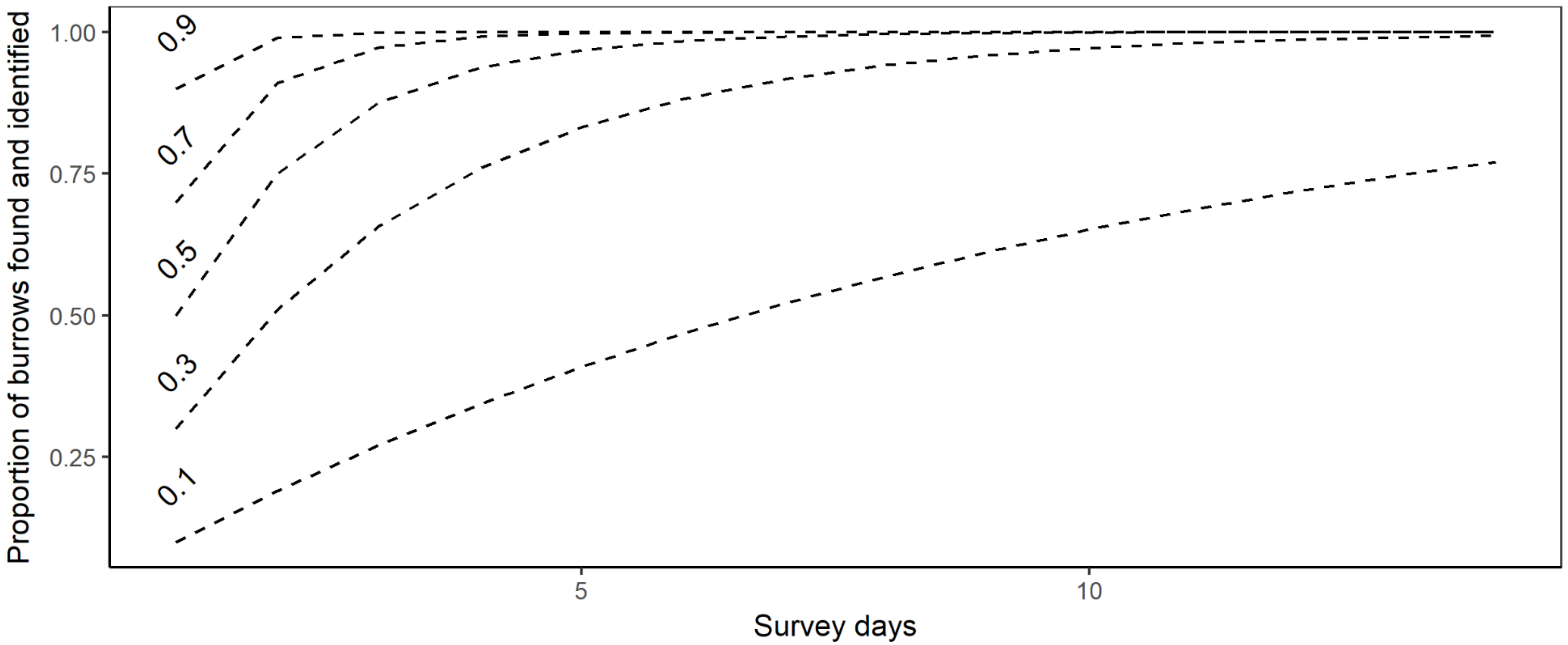
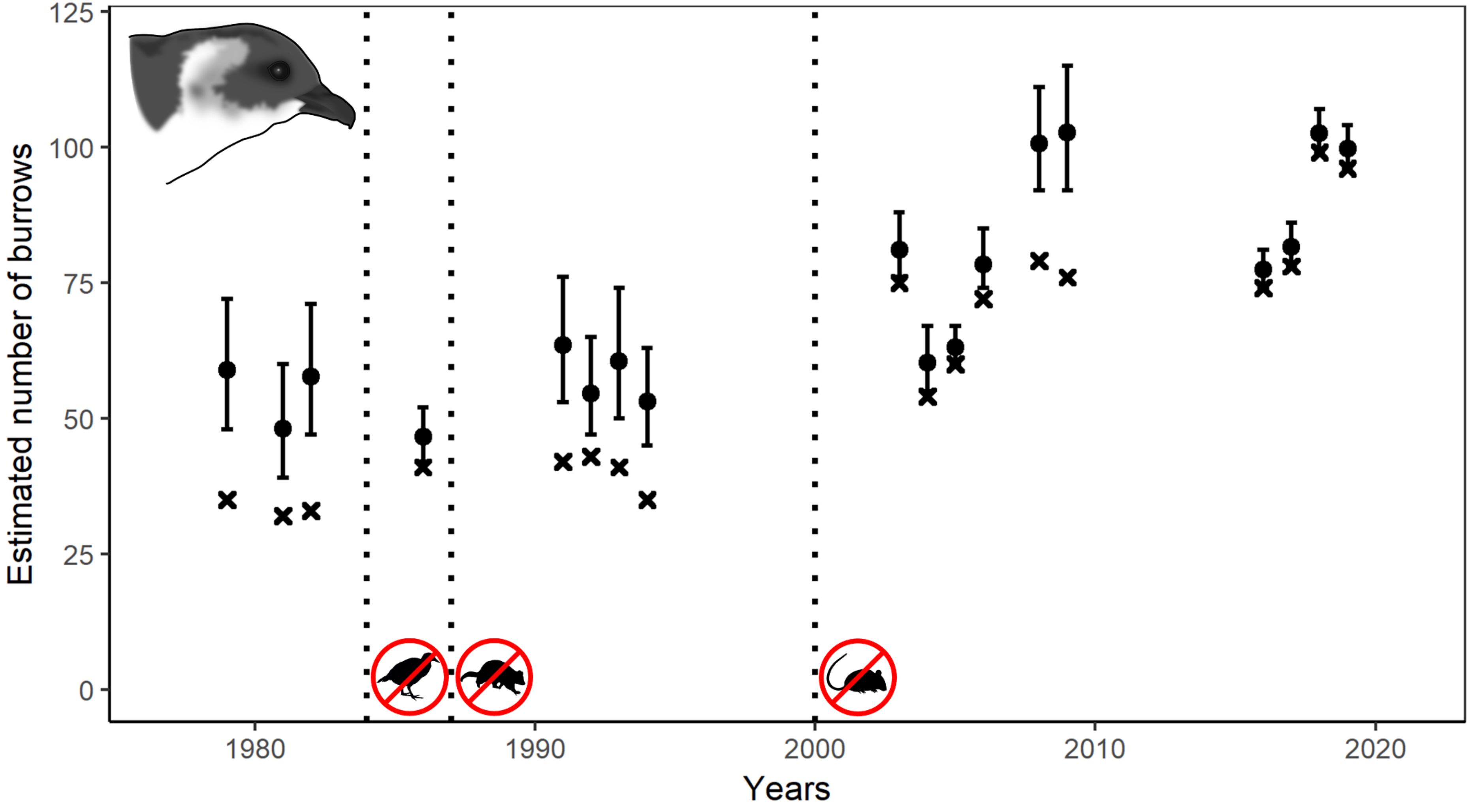
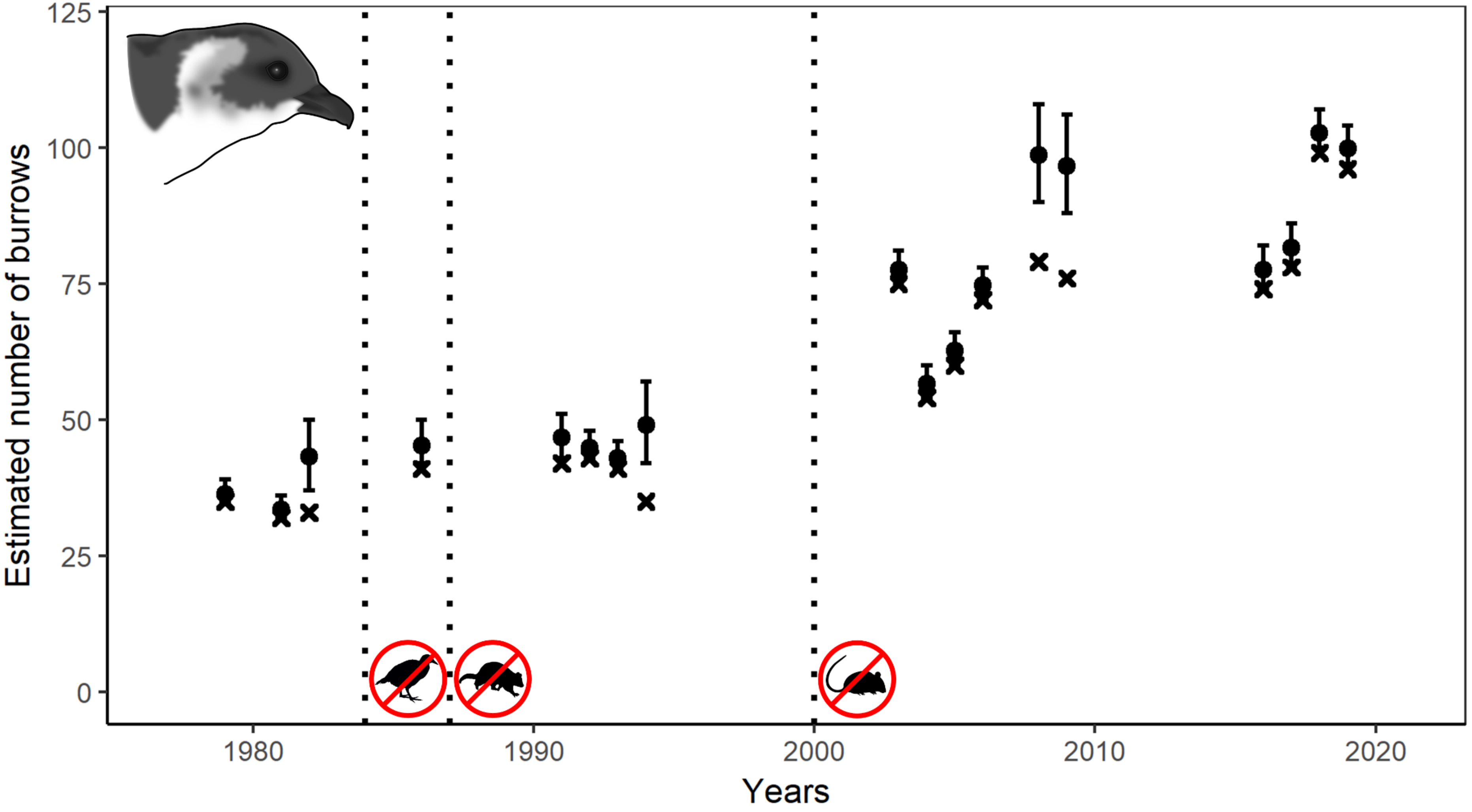
Appendices



Appendix 1. Hypothetical detection probabilities (p_d) with values varying between 0.1 and 0.9 as a function over time to aid experts in their decision-making during an expert elicitation.



Appendix 2. Raw Whenua Hou Diving Petrel burrow counts (crosses) and retrospectively corrected estimates ($\widehat{N_t}$; filled circles, represented by posterior means with 95% CrIs), based on $\widehat{p_{d,t}}$ informed by the most pessimistic expert, in relation to invasive predator eradications (dotted lines).



Appendix 3. Raw Whenua Hou Diving Petrel burrow counts (crosses) and retrospectively corrected estimates ($\widehat{N_t}$; filled circles, represented by posterior means with 95% CrIs), based on $\widehat{p_{d,t}}$ informed by the most optimistic expert, in relation to invasive predator eradications (dotted lines).

Appendix 4

Equations of movement models used in the net squared displacement (NSD) modelling in the R package *MigrateR* (1.1.0; Bunnefeld *et al.* 2011, Spitz *et al.* 2017, DB Spitz, B Cristescu, CC Wilmers, RE Wheat, T Levi & HU Wittmer unpublished), which allowed me to objectively identify presence and quantify timing in migratory movements in Whenua Hou Diving Petrels:

Residency model:

1. $NSD = \gamma \times [1 - \exp(K \ \times t)]$,

in which γ is the mean NSD of all locations, K is the logarithm of the rate constant, and t is the time from start.

Nomadic model:

2. $NSD = \beta \times t$,

in which β is a linear constant.

Dispersal model:

3. $NSD = \frac{\delta}{1 + \exp\left(\frac{\theta_1 - t}{\varphi_1}\right)}$,

in which δ is the distance between the two seasonal distributions, θ_1 is the midpoint of the outbound migration, and φ_1 is the time required to complete 50-75% of the outbound migration.

Migration model:

4. $NSD = \frac{\delta}{1 + \exp\left(\frac{\theta_1 - t}{\varphi_1}\right)} + \frac{-\delta}{1 + \exp\left(\frac{\theta_2 - t}{\varphi_2}\right)}$,

in which θ_2 is the midpoint of the homebound migration and φ_2 is the time required to complete 50-75% of the homebound migration.

Mixed-migration model:

$$5. \qquad NSD = \frac{\delta}{1 + \exp\left(\frac{\theta_1 - t}{\varphi_1}\right)} + \frac{-\delta \times \zeta}{1 + \exp\left(\frac{\theta_2 - t}{\varphi_2}\right)},$$

in which ζ is a factor allowing an individual to return to a breeding distribution different than the original one.

Multi-range migration model:

$$6. \qquad NSD = \sum_{i=1}^{n} \frac{\delta_i}{1 + \exp\left(\frac{\theta_i - t}{\varphi_i}\right)},$$

in which n is the number of range transitions, δ_i is the distance between i seasonal distributions, θ_i is the midpoint of migration i, and φ_i is the time required to complete 50-75% of migration i. The number of range transitions for each individual was determined based on the number of peaks in the moving mean (window width = 3 days) of |ΔNSD| that exceeded the global mean by more than one standard deviation (DB Spitz, B Cristescu, CC Wilmers, RE Wheat, T Levi & HU Wittmer unpublished). To delineate phenophases, I defined the onset of migratory movements when an individual was predicted to exceed 5% of the total distance travelled (δ_i) and the conclusion of migratory movements when an individual was predicted to exceed 95% of the total distance (δ_i).

Appendix 5

Summary of Stewart Island green skink occupancy models, including the number of parameters (K), difference in Akaike information criterion relative to the best performing model (ΔAIC), AIC weights (w), -2 × loglikelihood ($-2L$), logit-transformed intercept estimate for occupancy (ψ) and detection probabilities (p) ($\widehat{\alpha_\psi}$ and $\widehat{\alpha_p}$, respectively, ± SE), and the logit-transformed slope estimate per covariate ($\hat{\beta}$ ± SE). Covariates modelled included the presence of southern grass skinks (sgs), vegetation cover (veg), presence of a Diving Petrel burrow ($burrow$), distance to sea (sea), and time of day (t). AIC of the top performing model was 190.83.

Model	**K**	**ΔAIC**	w	$-2L$	$\widehat{\alpha_\psi}$	$\widehat{\beta_{sgs}}$	$\widehat{\beta_{veg}}$	$\widehat{\beta_{burrow}}$	$\widehat{\beta_{sea}}$	$\widehat{\alpha_p}$	$\widehat{\beta_t}$	$\widehat{\beta_{veg}}$
$\psi(burrow)p(t + veg)$	5	0.00	0.14	180.83	-1.27 ± 0.61			2.35 ± 1.96		-6.90 ± 1.60	-0.35 ±0.27	3.70 ± 1.37
$\psi(sgs + veg + burrow)p(t + veg)$	7	0.24	0.13	177.07	-4.97 ± 2.15	-1.52 ± 1.19	3.44 ± 1.82	1.90 ± 1.01		-3.67 ± 1.48	-0.41 ± 0.29	1.00 ± 1.28
$\psi(veg + burrow)p(t + veg$	6	0.26	0.13	179.09	-5.34 ± 2.19		3.50 ± 1.86	1.91 ± 0.98		-3.68 ± 1.48	-0.40 ± 0.29	1.00 ± 1.28
$\psi(sgs + burrow)p(t + veg)$	6	0.36	0.12	179.19	-0.98 ± 0.64	-1.71 ± 1.36		1.86 ± 1.23		-6.40 ± 1.29	-0.37 ± 0.27	3.32 ± 1.13
$\psi(sgs)p(t + veg)$	5	1.41	0.07	182.24	-0.46 ± 0.54	-1.60 ± 1.18				-5.56 ± 1.05	-0.37 ± 0.28	2.60 ± 0.91
$\psi(\cdot)p(t + veg)$	4	1.69	0.06	184.52	-0.78 ± 0.49					-5.57 ± 1.10	-0.37 ± 0.28	2.61 ± 0.95
$\psi(sgs + burrow + sea)p(t + veg)$	7	1.81	0.06	178.64	-1.56 ± 1.15	-1.71 ± 1.45		2.84 ± 2.11	0.49 ± 0.84	-6.53 ± 1.31	-0.35 ± 0.28	3.41 ± 1.15
$\psi(veg + burrow + sea)p(t + veg)$	7	2.07	0.05	178.90	-5.57 ± 2.31		3.50 ± 1.91	2.21 ± 1.20	0.20 ± 0.44	-3.70 ± 1.54	-0.40 ± 0.29	1.02 ± 1.33
$\psi(sgs + veg + burrow + sea)p(t + veg)$	8	2.17	0.05	177.00	-5.09 ± 2.24	-1.49 ± 1.20	3.42 ± 1.85	2.06 ± 1.21	0.11 ± 0.44	-3.69 ± 1.51	-0.41 ± 0.29	1.02 ± 1.31
$\psi(sgs + veg)p(t + veg)$	6	2.22	0.05	181.05	-2.74 ± 1.54	-1.56 ± 1.16	2.05 ± 1.43			-3.70 ± 1.49	-0.41 ± 0.29	1.00 ± 1.30
$\psi(veg)p(t + veg)$	5	2.56	0.04	183.39	-3.01 ± 1.53		2.00 ± 1.43			-3.69 ± 1.48	-0.40 ± 0.29	0.99 ± 1.30
$\psi(sgs + sea)p(t + veg)$	6	2.99	0.03	181.82	-0.28 ± 0.63	-1.66 ± 1.20			-0.25 ± 0.39	-5.75 ± 1.11	-0.37 ± 0.28	2.76 ± 0.97
$\psi(sea)p(t + veg)$	5	3.36	0.03	184.19	-0.64 ± 0.56				-0.21 ± 0.39	-5.76 ± 1.17	-0.37 ± 0.28	2.76 ± 1.01
$\psi(sgs + veg + sea)p(t + veg)$	7	3.44	0.03	180.27	-2.96 ± 1.59	-1.62 ± 1.16	2.44 ± 1.53		-0.33 ± 0.39	-3.67 ± 1.46	-0.41 ± 0.28	0.98 ± 1.28
$\psi(veg + sea)p(t + veg)$	6	3.94	0.02	182.77	-3.22 ± 1.58		2.35 ± 1.52		-0.29 ± 0.39	-3.67 ± 1.46	-0.40 ± 0.28	0.97 ± 1.27
$\psi(burrow + sea)p(t + veg)$*	6	-	-	-	-			-	-	-	-	-
Model-weighted average					**-2.73 ± 1.32**	**-1.61 ± 1.25**	**3.11 ± 1.74**	**2.11 ± 1.37**	**0.06 ± 0.51**	**5.01 ± 1.40**	**-0.38 ± 0.28**	**2.12 ± 1.21**

* Model failed to converge.

Appendix 6

Summary of southern grass skink occupancy models, including the number of parameters (K), difference in Akaike information criterion relative to the best performing model (ΔAIC), AIC weights (w), -2 × loglikelihood ($-2L$), logit-transformed intercept estimate for occupancy (ψ) and detection probabilities (p) ($\widehat{\alpha_\psi}$ and $\widehat{\alpha_p}$, respectively, ± SE), and logit-transformed slope estimate per covariate ($\hat{\beta}$ ± SE). Covariates included the presence of Stewart Island green skinks (*sigs*), vegetation cover (as linear and quadratic function; *veg* and *veg²*, respectively), presence of a Diving Petrel burrow (*burrow*), distance to sea (*sea*), and time of day (t). AIC of the top performing model was 355.69.

Model	**K**	**ΔAIC**	***w***	***-2L***	$\widehat{\alpha_\psi}$	$\widehat{\beta_{sigs}}$	$\widehat{\beta_{veg}}$	$\widehat{\beta_{veg^2}}$	$\widehat{\beta_{burrow}}$	$\widehat{\beta_{sea}}$	$\widehat{\alpha_p}$	$\widehat{\beta_t}$	$\widehat{\beta_{veg}}$
$\psi(sigs)p(t + veg)$	5	0.00	0.16	345.69	-0.49 ± 0.39	-1.48 ± 1.14					-3.40 ± 0.29	-0.34 ± 0.18	0.81 ± 0.27
$\psi(\cdot)p(t + veg)$	4	0.14	0.15	347.83	-0.70 ± 0.35						-3.33 ± 0.29	-0.35 ± 0.18	0.73 ± 0.27
$\psi(sigs + veg^2)p(t + veg)$	7	0.90	0.10	342.59	-1.07 ± 0.42	-1.56 ± 1.18	2.37 ± 1.81	-1.52 ± 1.61			-3.02 ± 0.32	-0.36 ± 0.19	0.33 ± 0.36
$\psi(veg^2)p(t + veg)$	6	1.08	0.09	344.77	-1.20 ± 0.42		2.73 ± 1.84	-1.98 ± 1.60			-3.03 ± 0.33	-0.36 ± 0.19	0.34 ± 0.37
$\psi(sigs + sea)p(t + veg)$	6	1.68	0.07	345.37	-0.43 ± 0.41	-1.48 ± 1.15				-0.17 ± 0.31	-3.44 ± 0.30	-0.34 ± 0.18	0.85 ± 0.28
$\psi(sea)p(t + veg)$	5	1.78	0.07	347.47	-0.65 ± 0.37					-0.18 ± 0.30	-3.37 ± 0.30	-0.35 ± 0.18	0.78 ± 0.28
$\psi(sigs + burrow)p(t + veg)$	6	1.82	0.06	345.51	-0.62 ± 0.49	-1.51 ± 1.15			0.26 ± 0.62		-3.41 ± 0.30	-0.35 ± 0.18	0.82 ± 0.28
$\psi(burrow)p(t + veg)$	5	2.02	0.06	347.71	-0.81 ± 0.46				0.21 ± 0.59		-3.33 ± 0.29	-0.35 ± 0.18	0.74 ± 0.28
$\psi(sigs + veg2 + sea)p(t + veg)$	8	2.41	0.05	342.10	-1.06 ± 0.42	-1.63 ± 1.19	2.12 ± 1.81	-1.18 ± 1.65		-0.23 ± 0.33	-3.02 ± 0.32	-0.36 ± 0.18	0.33 ± 0.36
$\psi(veg2 + sea)p(t + veg)$	7	2.74	0.04	344.43	-1.19 ± 0.42		2.51 ± 1.84	-1.70 ± 1.64		-0.18 ± 0.32	-3.03 ± 0.33	-0.36 ± 0.18	0.33 ± 0.37
$\psi(sigs + veg2 + burrow)p(t + veg)$	8	2.86	0.04	342.55	-1.14 ± 0.55	-1.61 ± 1.21	2.16 ± 2.09	-1.30 ± 1.93	0.15 ± 0.75		-3.02 ± 0.32	-0.36 ± 0.18	0.33 ± 0.36
$\psi(veg2 + burrow)p(t + veg)$	7	3.05	0.03	344.74	-1.14 ± 0.55		2.89 ± 2.07	-2.15 ± 1.86	-0.12 ± 0.70		-3.03 ± 0.33	-0.36 ± 0.19	0.34 ± 0.37
$\psi(veg2 + burrow + sea)p(t + veg)$	7	3.66	0.03	345.35	-0.49 ± 0.59	-1.49 ± 1.15			0.10 ± 0.74	-0.14 ± 0.37	-3.44 ± 0.30	-0.34 ± 0.18	0.85 ± 0.28
$\psi(burrow + sea)p(t + veg)$	6	3.78	0.02	347.47	-0.65 ± 0.57				0.01 ± 0.73	-0.17 ± 0.37	-3.37 ± 0.30	-0.35 ± 0.18	0.78 ± 0.29
$\psi(sigs + veg2 + burrow + sea)p(t + veg)$	9	4.40	0.02	342.09	-1.03 ± 0.58	-1.60 ± 1.22	2.20 ± 2.06	-1.26 ± 1.91	-0.06 ± 0.82	-0.24 ± 0.36	-3.02 ± 0.32	-0.36 ± 0.18	0.33 ± 0.36
$\psi(veg2 + burrow + sea)p(t + veg)$	8	4.53	0.02	344.22	-1.01 ± 0.59	-1.48 ± 1.14	2.91 ± 2.04	-2.09 ± 1.85	-0.36 ± 0.79	-0.25 ± 0.36	-3.04 ± 0.33	-0.36 ± 0.18	0.34 ± 0.37
Model-weighted average					**-0.80 ± 0.43**	**-1.53 ± 1.16**	**2.48 ± 1.89**	**-1.65 ± 1.69**	**0.09 ± 0.68**	**-0.19 ± 0.33**	**-3.24 ± 0.31**	**-0.35 ± 0.18**	**0.61 ± 0.31**

Supplementary material

Supplementary material 1

OpenBUGS code used to estimate the yearly rate of Whenua Hou Diving Petrel population growth in Ch. 2.

```
Model {

        ### priors ######################################################################
        alpha ~ dnorm(0, 0.01)              # log of intercept (expected n burrows in 1978)
        r ~ dnorm(0, 0.01)                  # log of lambda
        sd ~ dunif(0,20)                    # residual standard deviation in N among years
        tau <- pow(sd,-2)                   # convert standard deviation to precision (i.e. 1/var)

        ### model data ###################################################################
        for (i in 1:n.years) {                                  # for each year
                log(N.mu[i]) <- alpha + r*(year[i]-1978)        # calculate expected N based on log-linear model
                N[i] ~ dpois(N.mu[i])                           # model residual var in N
                P.year[i] <- Pa[phenology[i]]*(1-pow(1-Pd.ave[marked[i]],d[i]))   # calculate detection prob.
                n[i] ~ dbin(P.year[i],N[i])                     # model n burrows based on detection prob.
        }

        ### obtain Beta.PERT distribution for daily detection prob based on expert elicitation ##############
        for (i in 1:2) {                                        # for marked and unmarked burrows

                ### average elicited values across experts #######################################
                Pd.ave.mode[i] <- mean(Pd.mode[i,])             # best guess of daily detection probability
                Pd.ave.min[i] <- mean(Pd.min[i,])               # minimum daily detection probability
                Pd.ave.max[i] <- mean(Pd.max[i,])               # maximum daily detection probability

                ### obtain Beta.PERT distribution with standard parameters ##########################
                mu.Pd.ave[i] <- (Pd.ave.min[i]+Pd.ave.max[i]+4*Pd.ave.mode[i])/6
                v.Pd.ave[i] <- (mu.Pd.ave[i]-Pd.ave.min[i])*(2*Pd.ave.mode[i]-Pd.ave.min[i]-
               Pd.ave.max[i])/((Pd.ave.mode[i]-mu.Pd.ave[i])*(Pd.ave.max[i]-Pd.ave.min[i]))
                w.Pd.ave[i] <- v.Pd.ave[i]*(Pd.ave.max[i]-mu.Pd.ave[i])/(mu.Pd.ave[i]-Pd.ave.min[i])
                p.Pd.ave[i] ~ dbeta(v.Pd.ave[i],w.Pd.ave[i])
                Pd.ave[i] <- Pd.ave.min[i]+p.Pd.ave[i]*(Pd.ave.max[i]-Pd.ave.min[i])
        }

        ### calculate derived parameters ####################################################
        log(N.0) <- alpha                                       # expected no. of burrows in 1978
        log(lambda) <- r                                        # lambda

}       # model end
```

Supplementary material 2

OpenBUGS code of the Whenua Hou Diving Petrel integrated population model in Ch. 4 (including 10 years of harvest of fledglings and accounting for the return-to-source probability).

```
Model {

        ### priors ##########################################################################
        a.p ~ dnorm(0,0.1)                                # logit of mean detection prob
        a.phi ~ dnorm(0,0.1)                              # logit of annual survival prob
        a.fec ~ dnorm(0,01)                               # logit of mean productivity (fledglings/burrow)
        a.psi.r ~ dnorm(-1.548, 0.3412)                   # informative prior for return-to-source probability

        s.t.p ~ dunif(0, 3)                               # SD of among-year var in logit detection prob
        s.t.phi ~ dunif(0,3)                              # SD of among-year var in logit adult survival
        s.t.fec ~ dunif(0, 0.2)                           # SD of among-year variation in logit productivity

        tau.t.p <- pow(s.t.p, -2)                         # convert SD to precision (i.e. 1/var)
        tau.t.phi <- pow(s.t.phi, -2)                     # convert SD to precision (i.e. 1/var)
        tau.t.fec <- pow(s.t.fec, -2)                     # convert SD to precision (i.e. 1/var)
        tau.t.fec.recipient <- pow(s.t.fec.recipient,-2)  # convert SD to precision (i.e. 1/var)

        b.juvi.phi ~ dnorm(0,1)                           # age effect on annual survival probability
        b.newsite.fec ~ dnorm(0,2)                        # fixed effect to increase prod var at recipient

        p.male ~ dunif(0,1)                               # probability of an individual to be male
        p.fem <- 1-p.male                                 # probability of an individual to be female

        ### assign random year effects ####################################################
        for (j in 1:n.year+n.year.trans+n.year.proj+2) {
                re.t.p[j] ~ dnorm(0, tau.t.p)             # random year effect on annual detection prob
                re.t.phi[j] ~ dnorm(0, tau.t.phi)         # random year effect on annual survival prob
                re.t.fec[j] ~ dnorm(0, tau.t.fec)         # assign year effect on productivity
        }

        ### model survival data ###########################################################
        for (i in 1:n.ind) {                              # for each marked individual
                sex[i] ~ dbern(p.male)                    # model sex ratio

                ### construct matrices for counting ###################################################

                # assign "alive" = 0 before first detection in matrices
                for (j in 1:first[i]-1) {
                        alive.a[i,j] <- 0                 # adults
                        alive.Ma[i,j] <- 0                # adult males
                        alive.a.first[i,j] <- 0           # adult first encounter
                        alive.Ma.first[i,j] <- 0          # adult male first encounters
                }

                # assign "alive" = 1 on first detection
                alive[i,first[i]] <- 1
                juvi[i,first[i]] <- age[i]                # juv when enters population if "age" = 1
                alive.a[i,first[i]] <- alive[i,first[i]]*(1-juvi[i,first[i]])
                alive.Ma[i,first[i]] <- alive.a[i,first[i]]*sex[i]
                alive.a.first[i,first[i]] <- alive.a[i,first[i]]
                alive.Ma.first[i,first[i]] <- alive.Ma[i,first[i]]
```

```
    for (j in first[i]+1:n.year) {                      # for each subsequent year

        ### determine age class ##################################################
        juvi[i,j] <- age[i]*step(first[i]-j+1)          # whether a juvenile remains a juvenile at time j

        ### observation equation #################################################
        y[i, j] ~ dbern(psight[i,j])                    # whether individual recorded or not
        psight[i, j] <- p[i,j]*alive[i,j]               # depends on p and whether the individual is alive
        logit(p.hyp[I,j]) <- a.p+re.t.p[j]              # hypothetical detection equation

        p[I,j] <- p.hyp[I,j]*survey[j]*(1-juvi[I,j]) # fix detection at 0 for non-survey years and
                                                        juveniles out at sea

        ### state equation #######################################################
        alive[i, j] ~ dbern(palive[i, j])               # whether individual is alive
        palive[i, j] <- phi[i, j]*alive[i, j-1]         # depends on survival prob and if alive last year
        logit(phi[i,j]) <- a.phi+b.juvi.phi*juvi[i,j-1]+re.t.phi[j]        # survival equation


        ### update count matrices ################################################
        alive.a[i,j] <- alive[i,j]*(1-juvi[i,j])
        alive.Ma[i,j] <- alive.a[i,j]*sex[i]
        alive.a.first[i,j] <- 0                         # adult first encounter
        alive.Ma.first[i,j] <- 0                        # adult male first encounters
    }
}


### model productivity data (whether or not a burrow produces a fledgling) ########################
for (i in 1:n.burrow) {
    fec[i] ~ dbern(p.fec[i])
    logit(p.fec[i]) <- a.fec+re.t.fec[year.fec[i]]      # productivity equation
}

### calculate survival and reproduction rates ##############################################
for (j in 1:n.year+n.year.trans+n.year.proj+2) {
    logit(phi.a.year[j]) <- a.phi+re.t.phi[j]                   # adult survival
    logit(phi.j.year[j]) <- a.phi+b.juvi.phi+re.t.phi[j]        # juvenile survival
    logit(f[j]) <- a.fec+re.t.fec[j]                            # productivity at source pop
    logit(f.recipient[j]) <-a.fec+b.newsite.fec+re.t.fec[j]     # productivity at recipient pop
}

### calculate detection and abundances of banded adults ######################################
for (j in 1:n.year) {
    logit(p.hyp.a.year[j]) <- a.p+re.t.p[j]                     # hypothetical detection probability
    p.a.year[j]<-p.hyp.a.year[j]*survey[j]                      # fix detection at 0 for non-survey years
    Na.banded[j] <- sum(alive.a[,j])                            # no. of banded birds that are alive
    Ma.banded[j] <- sum(alive.Ma[,j])                           # no. of alive male banded birds
    Fa.banded[j] <- Na.banded[j]-Ma.banded[j]                   # no. of alive female banded birds
    Na.banded.first[j] <- sum(alive.a.first[,j])
    Ma.banded.first[j] <- sum(alive.Ma.first[,j])
    Fa.banded.first[j] <- Na.banded.first[j]-Ma.banded.first[j]
}

### model first year counts and abundances ##################################################
Na.unk.c[1] ~ dunif(0, 200)                             # prior for all undetected adults
Na.unk[1] <- round(Na.unk.c[1])
U[1] <- Na.unk[1]+u[1]                                  # no. adults present first year
u[1] ~ dbin(p.a.year[1],U[1])                           # sample count of adults detected first year

Ma.unk[1] ~ dbin(p.male,Na.unk[1])                      # sample no. of undetected adult males
Fa.unk[1] <- Na.unk[1]-Ma.unk[1]                        # sample no. of undetected adult females
N.M[1] <- Ma.banded[1]+Ma.unk[1]                        # add banded and undetected males
N.F[1] <- Fa.banded[1]+Fa.unk[1]                        # add banded and undetected females
N[1] <- N.M[1]+N.F[1]                                   # add males and females
```

```
J0[1] ~ dbin(f[1], N.F[1])                          # no. of juveniles from fledglings produced
J1.c[1] ~ dunif(0,60)                               # prior for no.s of one-year-old juveniles
J1[1] <- round(J1.c[1])

### model subsequent counts and abundances ############################################
for (j in 2:n.year) {

        J0[j] ~ dbin(f[j], N.F[j])                  # no. juveniles from fledglings produced
        J1[j] ~ dbin(phi.j.year[j-1], J0[j-1])      # no. one-year-old juveniles from last year's
        J2[j] ~ dbin(phi.j.year[j-1], J1[j-1])      # no. second-year juveniles from last year's
        Na.surv[j] ~ dbin(phi.a.year[j-1],Na.unk[j-1])  # no. survivors from last year's undetected adults

        U[j] <- Na.surv[j]+J2[j]                    # all unbanded adults available for detection
        u[j] ~ dbin(p.a.year[j],U[j])               # sample count of adults detected
        Na.unk[j] <- max(1,U[j]-u[j])               # no. unknown undetected adults + constraint

        Ma.unk[j] ~ dbin(p.male,Na.unk[j])          # sample no. undetected adult males
        Fa.unk[j] <- Na.unk[j]-Ma.unk[j]            # sample no. undetected adult females
        N.M[j] <- Ma.banded[j]+Ma.unk[j]            # add banded and undetected males
        N.F[j] <- Fa.banded[j]+Fa.unk[j]            # add banded and undetected females
        N[j] <- N.M[j]+N.F[j]                       # add males and females
}

### calculate population growth #########################################################
logit(phi.a.year.ave) <- a.phi                      # average adult survival
logit(phi.j.year.ave) <- a.phi+b.juvi.phi           # average juvenile survival
logit(f.ave) <- a.fec                               # average productivity

f1.ave <- 0                                         # set productivity of juveniles at 0

f2.ave <- f.ave*p.fem*phi.j.year.ave                # sum av. productivity, fem prob., and av. juv surv
s1.ave <- phi.j.year.ave
s2.ave <- phi.a.year.ave

lambda.ave <- (f1.ave + s2.ave + sqrt(pow(f1.ave-s2.ave,2) + 4*f2.ave*s1.ave))/2# population growth
                                                                                  equation

### projections of source population ####################################################
for (j in n.year+1:n.year+n.year.trans+n.year.proj){

        J1[j] ~ dbin(phi.j.year[j-1],J0[j-1])       # 1-year old juveniles at source population
        J2[j] ~ dbin(phi.j.year[j-1],J1[j-1])       # 2-year juveniles at source population
        N.F.surv[j] ~ dbin(phi.a.year[j-1],N.F[j-1])   # survivors from last year's adult fem at source
        N.M.surv[j] ~ dbin(phi.a.year[j-1],N.M[j-1])   # survivors from last year's adult males at source
        J2.F[j] ~ dbin(p.fem, J2[j])                # female 2-year juveniles at source
        J2.M[j] <- J2[j]-J2.F[j]                    # male 2-year juveniles at source
        N.F[j] <- N.F.surv[j]+J2.F[j]+J2.Ft.return[j]  # ad f = surv + recruits from source and transloc
        N.M[j] <- N.M.surv[j]+J2.M[j]+J2.Mt.return[j]  # ad m = surv + recruits from source and transloc
        N[j] <- N.F[j]+N.M[j]                       # add males and females

        ### model translocation cohort ##################################################
        J0.preharv[j] ~ dbin(f[j], N.F[j])          # sample juvs from fledglings pre-harvest
        trans[j] <- round(psi.h[j]*J0.preharv[j])   # remove harvested portion
        J0[j] <- J0.preharv[j]-trans[j]             # no. juveniles left at source
}

### model translocated cohorts ##########################################################
J1.t[19] <- 0             # 1-year juvs from transloc birds (fix to 0 for this year, as no transloc)
for (j in 20:n.year+n.year.trans+1){
        J1.t[j] ~ dbin(phi.j.year[j-1],trans[j-1])  # 1-year old juvs from transloc birds
}

for (j in 30:38){         # 1-year juvs from transloc birds (fix to 0 for these years, as no transloc)
        J1.t[j] <- 0
}
```

```
        for (j in 1:20){                          # 2-year juvs (fix to 0 for these years, as no transloc)
                J2.t[j] <- 0
                J2.Ft[j] <- 0                     # 2nd-year f in transloc cohort
                J2.Mt[j] <- 0                     # 2nd-year m in transloc cohort
                J2.Ft.return[j]<-0                # 2nd-year f in transloc cohort that return to source
                J2.Mt.return[j]<-0                # 2nd-year m in transloc cohort that return to source
                J2.Ft.recruit[j] <- 0             # 2nd-year f in transloc cohort that recruit to recipient
                J2.Mt.recruit[j] <- 0             # 2nd-year m in transloc cohort that recruit to recipient
        }

        logit(psi.r) <- a.psi.r                   # logit transform return-to-source probability

        for (j in 21:n.year+n.year.trans+2){
                J2.t[j] ~ dbin(phi.j.year[j-1],J1.t[j-1])  # 2nd-year juvs in transloc cohort
                J2.Ft[j] ~ dbin(p.fem, J2.t[j])            # 2nd-year f in transloc cohort
                J2.Mt[j] <- J2.t[j]-J2.Ft[j]               # 2nd-year m in transloc cohort
                J2.Ft.return[j] ~ dbin(psi.r, J2.Ft[j])    # 2nd-year f in transloc cohort that return to source
                J2.Mt.return[j] ~ dbin(psi.r, J2.Mt[j])    # 2nd-year m in transloc cohort that return to source
                J2.Ft.recruit[j] <- J2.Ft[j]-J2.Ft.return[j]    # 2nd-year f in transloc cohort that recruit to recipient
                J2.Mt.recruit[j] <- J2.Mt[j]-J2.Mt.return[j]  # 2nd-year m in transloc cohort that recruit to recipient
        }

        for (j in 31:38){                         # 2nd-year birds (fix to 0 for these years, as no transloc)
                J2.t[j] <- 0
                J2.Ft[j] <- 0                     # 2nd-year f in transloc cohort
                J2.Mt[j] <- 0                     # 2nd-year m in transloc cohort
                J2.Ft.return[j]<-0                # 2nd-year f in transloc cohort that return to source
                J2.Mt.return[j]<-0                # 2nd-year m in transloc cohort that return to source
                J2.Ft.recruit[j] <- 0             # 2nd-year f in transloc cohort that recruit to recipient
                J2.Mt.recruit[j] <- 0             # 2nd-year m in transloc cohort that recruit to recipient
        }

        ### projections of recipient population ##############################################################
        N.FT.surv[21] <- 0                                      # ad f at recipient (fix to 0 for this year)
        N.MT.surv[21] <- 0                                      # ad f at recipient (fix to 0 for this year)
        for (j in 22:n.year+n.year.trans+n.year.proj){
                N.FT.surv[j] ~ dbin(phi.a.year[j-1],N.FT[j-1])  # surviving ad f from last year at recipient
                N.MT.surv[j] ~ dbin(phi.a.year[j-1],N.MT[j-1])  # surviving ad m from last year at recipient
        }

        for (j in 21:n.year+n.year.trans+n.year.proj){
                N.FT[j] <- N.FT.surv[j]+J2.Ft.recruit[j]+J2.FT[j]          # ad f = surv + recruits from recipient +
                                                                             transloc cohort
                N.MT[j] <- N.MT.surv[j]+J2.Mt.recruit[j]+J2.MT[j]          # adult m = surv + recruits from recipient
                                                                             + translocation cohort
                N.T[j] <- N.FT[j]+N.MT[j]                       # add ad m and ad f
        }

        for (j in 21:n.year+n.year.trans+n.year.proj){
                J0.T[j] ~ dbin(f.recipient[j], N.FT[j])         # sample juveniles at recipient
        }

        for (j in 22:n.year+n.year.trans+n.year.proj){
                J1.T[j] ~ dbin(phi.j.year[j-1], J0.T[j-1])      # 1st year juveniles at recipient
        }

        J2.FT[21] <- 0                                          # 2nd-year f at recipient (fix to 0 for this year)
        J2.FT[22] <- 0                                          # 2nd-year f at recipient (fix to 0 for this year)
        J2.MT[21] <- 0                                          # 2nd-year m at recipient (fix to 0 for this year)
        J2.MT[22] <- 0                                          # 2nd-year m at recipient (fix to 0 for this year)
        for (j in 23:n.year+n.year.trans+n.year.proj){
                J2.T[j] ~ dbin(phi.j.year[j-1], J1.T[j-1])      # 2nd-year juveniles at recipient
                J2.FT[j] ~ dbin(p.fem, J2.T[j])                 # 2nd-year f at recipient
                J2.MT[j] <- J2.T[j]-J2.FT[j]                    # 2nd-year m at recipient
        }
}       # model end
```

Supplementary material 3

OpenBUGS code of the model used to estimate Whenua Hou Diving Petrel nest survival in Ch. 5.

```
Model {

        ### priors ###################################################################################
        a.s ~ dnorm(5,1)                        # logit(daily survival probability)
        b.hatched ~ dnorm(0,1)                  # fixed effect of hatching on logit(daily survival prob)
        b.WHDP ~ dnorm(0,1)                     # fixed effect WHDP density on logit(daily survival prob)
        b.CDP ~ dnorm(0,1)                      # fixed effect CDP density on logit(daily survival prob)
        b.Dsea ~ dnorm(0,1)                     # fixed effect distance to sea on logit(daily survival prob)

        sd.year ~ dunif(0,1)                    # random effect of year on logit(daily survival prob)
        tau.year <- pow(sd.year,-2)             # convert sd to precision (i.e. 1/var)

        T.inc.mean ~ dnorm(45, 0.1)             # mean incubation period
        sd.T.inc ~ dunif(0,6)                   # standard deviation incubation period
        T.inc.tau <- pow(sd.T.inc,-2)           # convert sd to precision (i.e. 1/var)

        T.rear.mean ~ dnorm(45, 1)              # mean chick-rearing period
        sd.T.rear ~ dunif(0,4)                  # standard deviation chick-rearing period
        T.rear.tau <- pow(sd.T.rear,-2)         # convert standard deviation to precision (i.e. 1/var)

        ### assign random effect ######################################################################
        for (i in 1:3) {
                re.year[i] ~ dnorm(0,tau.year)  # assign random effect for each of 3 years
        }

        ### model data ################################################################################
        for (i in 1:n.burrows) {                        # for each burrow
                d.lay[i] ~ dunif(d.lay.min[i], first[i])        # range of days when egg could have been laid
                T.inc[i] ~ dnorm(T.inc.mean, T.inc.tau)         # sample incubation period
                d.hatch[i] <- d.lay[i]+T.inc[i]                 # calculate hatching day
                T.rear[i] ~ dnorm(T.rear.mean, T.rear.tau)      # sample chick-rearing period
                d.fledge[i] <- d.hatch[i]+T.rear[i]             # calculate fledging day

                alive[i,first[i]] <- 1                          # alive at first detection

                for (j in first[i]+1:last[i]) {                         # for each day
                        p.hatched[i,j] <- step(j-d.hatch[i])*alive[i,j]         # hatched and alive
                        hatched[i,j] ~ dbern(p.hatched[i,j])                    # sample hatched
                        p.fledged[i,j] <- step(j-d.fledge[i])
                        fledged[i,j] ~ dbern(p.fledged[i,j])                    # sample fledged

                        logit(p.surv[i,j]) <-
                        a.s+re.year[year[i]]+b.hatched*hatched[i,j]+b.WHDP*WHDP[i]+b.CDP*CDP[i]+b.Dsea*
                        Dsea[i]                                                 # survival equation
                        p.alive[i,j] <- p.surv[i,j]*alive[i,j-1]
                        alive[i,j] ~ dbern(p.alive[i,j])                        # model survival
                }
        }
```

```
          ### calculate derived parameters ##########################################################
          logit(DSR.egg17) <- a.s+re.year[1]                      # daily survival prob for egg stage in 2017
          logit(DSR.egg18) <- a.s+re.year[2]                      # daily survival prob for egg stage in 2018
          logit(DSR.egg19) <- a.s+re.year[3]                      # daily survival prob for egg stage in 2019
          logit(DSR.chick17) <- a.s+b.hatched+re.year[1]          # daily survival prob for chick stage in 2017
          logit(DSR.chick18) <- a.s+b.hatched+re.year[2]          # daily survival prob for chick stage in 2018
          logit(DSR.chick19) <- a.s+b.hatched+re.year[3]          # daily survival prob for chick stage in 2019
          p.egg.success17 <- pow(DSR.egg17,T.inc.mean)                     # survival during egg stage in 2017
          p.egg.success18 <- pow(DSR.egg18,T.inc.mean)                     # survival during egg stage in 2017
          p.egg.success19 <- pow(DSR.egg19,T.inc.mean)                     # survival during egg stage in 2017
          p.chick.success17<- pow(DSR.chick17,T.rear.mean)                 # survival during chick stage in 2017
          p.chick.success18 <- pow(DSR.chick18,T.rear.mean)                # survival during chick stage in 2018
          p.chick.success19 <- pow(DSR.chick19,T.rear.mean)                # survival during chick stage in 2019
          p.success17 <- pow(DSR.egg17,T.inc.mean)*pow(DSR.chick17,T.rear.mean)      # nest survival in 2017
          p.success18 <- pow(DSR.egg18,T.inc.mean)*pow(DSR.chick18,T.rear.mean)      # nest survival in 2018
          p.success19 <- pow(DSR.egg19,T.inc.mean)*pow(DSR.chick19,T.rear.mean)      # nest survival in 2019

}         # model end
```