



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

Johannes H. Fischer^{1,*}, Igor Debski², Derek B. Spitz³, Graeme A. Taylor²,
Heiko U. Wittmer¹

¹School of Biological Sciences, Victoria University of Wellington, PO Box 600, Wellington 6140, New Zealand

²Aquatic Unit, Department of Conservation, Wellington 6143, New Zealand

³Environmental Studies Department, University of California, Santa Cruz, CA 95064, USA

ABSTRACT: Without insights into the threats affecting species across their distributions and throughout their annual cycles, 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 are poorly understood. 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 southern Aotearoa (New Zealand) to Maukahuka (Auckland Islands). After breeding, WHDPs migrated southwest 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 >95% of their time on, or under, water. The core areas used consistently during breeding and non-breeding periods warrant listing as Important Bird and Biodiversity Areas. Spatiotemporal overlap of commercial fishing effort with breeding distributions was considerable, in contrast with non-breeding distributions. Spatiotemporal management of anthropogenic activity around the breeding colony during the breeding period could help protect WHDPs, but measures should be subjected to a structured decision-making framework. Our results illustrate the importance of year-round studies to inform conservation of marine species.

KEY WORDS: Biologging · Conservation · Global Fishing Watch · Important Bird and Biodiversity Areas · *Pelecanoides whenuahouensis* · Whenua Hou diving petrel

Māori abstract

TUHINGA WHAKARĀPOPOTO: Ki te kore e mātau i ngā āhuatanga mōrearea e pātahi ai ki ngā momo kararehe i ā rātou nohoanga huhua, i ia tau rānei e kore e whakatau ai tētahi ara whakauka e whai hua ana. He manu paku o te moana e ngaro haere ana tōna whare ora te Kuaka Whenua Hou *Pelecanoides whenuahouensis* e kore e mātau pai ana i āna whanonga ki tai, i ngā āhuatanga mōrearea rānei e pātahi ai ki a ia. Nā te pūrere whakaroki-mahi pūoko-wāhi mātou i whāia ai ngā Kuaka i ngā tau 2015/16, 2017/18 me te tau 2018/19 ki te tūtohu i ā rātou hōrapa ki tai, nekehanga, whanonga me tā rātou tūtaki ki ngā pakihi hī ika. I te wā o te whakatipu, i noho ai ngā Kuakas ki te tonga o Aotearoa tae rawa atu ai ki Maukahuka. Ka mutu te whakatipu, i heke whaka-te-māuru-mā-tonga ki te Hauaitū kei te tonga o Ahitereiria, i rere whakatekaraka kia hoki atu ai ki te whenua whānau ai ngā hua kei te Hau-nui-o-Tonga. I te wā kāore rātou i te ai i noho roa ngā Kuaka ki te moana, nui ake i te 95 ōrau o te wā, kei te kawara, kei roto rānei i te moana. Ko ngā wāhi mātua ai te noho, te hokihoki atu ai hoki o ēnei manu ahakoa whakatipu rānei, ahakoa kai rānei me noho ki te rārangi Wāhi Manu, Wāhi Rerenga Rauropi Whakahirahira. He nui hoki tā rātou tūtaki ā wā, ā wāhi ki ngā pakihi hī ika i te wā whakatipu e karekau i te wā kai noa. Ka whai hua pea he herenga a wāhi i te mahi o te tangata ki ō ngā pūrei kōhanga i te wā whakatipu, engari me whai anga whakatau kia whakatauhia ai tēnei. Mātua tohua ai ā mātou putanga i te whakahirahira o te āta whai, i te aromatawai ā-tau kia mātau ai te whakaukahanga o tētahi momo kararehe o te moana.

Resale or republication not permitted without written consent of the publisher

1. INTRODUCTION

Assessing the threats species face across their distributions and throughout their annual cycles 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 (Dias et al. 2019). Offshore threats impacting seabirds during their breeding, migratory, and non-breeding periods include accidental bycatch in fisheries 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 seabirds 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 (Oliveira et al. 2015), and gill net fisheries (Žydelis et al. 2013), as well as deck strikes (collisions with vessels due to disorientation caused by offshore artificial lights at night; Black 2005).

Understanding the offshore threats affecting smaller seabird species is limited in part by a lack of year-round insights into their distributions, movements, and behaviour. With advancing 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 (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, Rayner et al. 2017, Halpin et al. 2018, Paiva et al. 2018, Pollet et al. 2019, Bolton 2020, BirdLife International Seabird Tracking Database 2020, Dunphy et al. 2020, Rotger et al. 2020, Wikelski & Kays 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 4 Data Deficient, 4 Vulnerable, 4 Endangered, and 2 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 (Adams & Takekawa 2008, 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). Therefore, objective and clear delineations of breeding and non-breeding periods and the associated areas of use are crucial to spatiotemporal conservation management (Spitz et al. 2017). However, such delineations are not always straightforward, as seabirds can exhibit exploratory movements prior to actual migrations (Orben et al. 2018). In addition, offshore behaviour (i.e. flying vs. resting or foraging) should also be considered when assessing threats. Such behavioural information adds additional details that are important for conservation management. 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 birds 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. between failed and successful breeders or sexes) and among years (e.g. due to environmental stochasticity), and insight into this variation is crucial when implementing conservation management. If different demographic groups are exposed to annually varying threats, population dynamics could be affected (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. González-Solís 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 (Weimerskirch et al. 2014). Such detailed insight for smaller

seabird species remains largely absent (Paiva et al. 2018), impeding comprehensive assessments of conservation implications.

The Whenua Hou diving petrel *P. 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; Taylor 2000). However, after humans introduced invasive predators, all breeding colonies except one were extirpated. Now, WHDPs survive in low numbers (194–208 adults) at 1 breeding colony on Whenua Hou (Codfish Island; Fischer et al. 2018b, 2020). While Whenua Hou has been free of invasive predators since 2000 (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. 2017, 2018b). 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 southern 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. 2018a, Richard et al. 2020) and are thus of limited use to assess offshore distribution, movements, behaviour, and corresponding threats. Therefore, we tracked WHDPs for 3 full annual cycles to identify (1) offshore distributions, (2) movement patterns, (3) offshore behaviour, and (4) overlap with commercial fishing effort. In addition, we investigated the effects of potential underlying drivers on distribution, movements, and behaviour (i.e. breeding success, sex, and interannual variation).

2. MATERIALS AND METHODS

2.1. Deployment and retrieval of geolocators

We deployed global location-sensing immersion loggers (geolocators; Migrate Technology; Table 1) on breeding adults (>2 yr old) at Whenua Hou

Table 1. Sample sizes of Migrate Technology 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)

(46.766° S, 167.645° E), Aotearoa. We captured WHDPs by hand or with custom-made burrow traps (see Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m660p171_supp.pdf) 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). Geolocators are non-transmitting devices and thus we recaptured WHDPs in subsequent years to retrieve devices. We obtained a total of 38 datasets from 24 individuals providing year-round insights (mean geolocator deployment: 317 d). While we cannot discount potential negative effects (Quillfeldt et al. 2012, Bodey et al. 2018), WHDPs equipped with geolocators were in good condition upon recapture and had weights that did not clearly differ from individuals without geolocators (we compared 34 WHDPs carrying geolocators with 136 non-equipped WHDPs using a generalized linear model with a Gaussian error distribution and an identity-link function: $\hat{\alpha} = -0.02 \pm 0.09$ SE, $\hat{\beta} = 0.07 \pm 0.19$ SE). WHDPs equipped with geolocators also did not show clear deviations from natural breeding phenologies or breeding success (66 % of equipped WHDPs fledged a chick, compared to the multi-year average of 55 %; Fischer 2020).

We set geolocators to record light levels (lux) every min and save the maximum value every 5 min. We also programmed geolocators to record saltwater-immersion every 30 s (0 or 1, corresponding 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 8 h (mean, minimum, and maximum in °C). Finally, we collected 4 contour feathers during geolocator attachment and used these for genetic sex determination (using PCR primers specific to the CHD-W gene; Norris-Caneda & Elliott 1998).

2.2. Light level analyses

To infer offshore locations of WHDPs from recorded light levels, we applied the threshold method to quantify twilight events, followed by an iterative forward step selection to reduce location errors with (1) a twilight model, (2) a movement model, and (3) several spatial masks using the package ‘ProbGLS’ in R version 3.5.3 (Merkel et al. 2016, R Core Team 2019). We 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). We used a bimodal movement model for dry periods (i.e. bird in flight; mean \pm SD = 1.4 ± 0.5 m s $^{-1}$, max = 10 m s $^{-1}$) and wet periods (i.e. bird on water; 0.5 ± 0.25 m s $^{-1}$, max = 1.7 m s $^{-1}$) (Rayner et al. 2017). We defined wet periods as periods during which the 10 min cumulative wet counts were ‘wet’ for ≥ 1 min. We applied 2 binary spatial masks: land and sea ice ($0.25^\circ \times 0.25^\circ$; NOAA OI SST V2 high-resolution dataset, <https://psl.noaa.gov/data/gridded/data.noaa.oisst.v2.highres.html>). We thus assumed that WHDPs completely avoided land and sea ice and set the sea ice concentration threshold at 1%. For geolocators deployed after 2015, we also applied a continuous SST spatial mask. Specifically, we cross-referenced the minimum SST values recorded by geolocators with satellite-recorded SST values (daily mean \pm SE; $0.25^\circ \times 0.25^\circ$; NOAA OI SST V2 high-resolution dataset; Reynolds et al. 2007). We 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 . We subsequently estimated the median geographic tracks by (1) calculating the weighted probability for a cloud of possible locations (1000 locations per step), (2) selecting the most likely location, and (3) 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 this method had an error of 145 km during the equinoxes (Merkel et al. 2016). Using this method, we inferred a total of 22 372 offshore locations of WHDPs from the collected light data (accessible at www.seabirdtracking.org/mapper/index.php).

2.3. Spatiotemporal analyses

To objectively identify and quantify the timing of migratory movements in WHDPs and consequently

delineate breeding and non-breeding periods, we fitted a range of models to the net squared displacement (NSD: the square of the distance between the starting point and each subsequent point) of individual WHDPs tracks using the R package ‘MigrateR’ 1.1.0 (Spitz et al. 2017). Specifically, we fitted the NSD of each year-round track to models representing (1) residency, (2) nomadism, (3) dispersal, (4) migration, (5) mixed migration, and (6) multi-range migration (equations are provided in Text S1; D.B. Spitz et al. unpublished). We compared the fit of these models to the NSD of each track using Akaike’s information criterion (AIC; Burnham & Anderson 2002) and selected the best supported model. The NSD of all WHDP tracks was best explained by multi-range migratory models, and we used the model-estimated migration phenology to objectively delineate the 4 annual phenophases for each track: breeding period, outbound migration, non-breeding period, and homebound migration.

We used generalized linear mixed-effects models (GLMMs) with a Gaussian error distribution and an identity-link function 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). We z-transformed all numeric variables. We 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, we calculated kernel utilization distributions (UDs) per individual per breeding and non-breeding period using the R package ‘adehabitatHR’ (Calenge 2006). Specifically, to calculate the 50% UD (core area of use) and the 95% UD (full extent of distribution), we 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, we did not calculate UD for individuals with <30 breeding distribution locations. Subsequently, to create overall distribution maps, we merged individual breeding and non-breeding UD into overall UD, which accounted for unequal number of locations among individuals (Clay et al. 2017). We then calculated spatial overlap

among individual breeding and non-breeding UD, overall breeding and non-breeding UD, UD of different sexes, and UD of failed and successful breeders (defined as successfully fledging a chick). Specifically, to quantify spatial overlap, we calculated Bhattacharyya's affinity (BA), which is a function of the product of 2 UD, under the assumption that animals use space independently of each other (BA = 0 indicates no overlap, BA = 1 indicates complete overlap; Fieberg & Kochanny 2005).

2.4. Behavioural analyses

We 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). Actave.net provides automatic computation of daily (24 h) aggregates of activity parameters based on time-stamped immersion data. We 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'. We quantified time spent 'on or under water' per day per individual per phenophase. We 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. However, we refrained from quantifying flight behaviour during the breeding period, as we could not differentiate between WHDPs in flight and WHDPs on land at the breeding colony (Schultz et al. 2018). We 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. We z-transformed all numerical variables. We treated phenophase, breeding success, sex, and year as fixed effects and individual ID as a random effect in these models.

2.5. Overlap with commercial fishing effort

To infer the year-round threats from commercial fisheries to WHDPs, we quantified the spatiotemporal overlap between the breeding and non-breeding distributions and commercial fishing effort. We 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/data>

sets/public-fishing-effort-10:v20200316). Global Fishing Watch uses satellite tracking of commercial fishing vessels equipped with automatic identification systems (AIS) 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). We 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. We delineated the breeding and non-breeding periods using the means of the model-estimated migration phenologies. We then calculated the average fishing effort per breeding and non-breeding period to account for interannual variation. Subsequently, we overlaid the 50 and 95 % UD of WHDP breeding and non-breeding distributions and calculated the mean fishing effort per 0.1° cell, the sum of fishing effort, and the percentage of cells with fishing effort within WHDP breeding/non-breeding distributions during the breeding/non-breeding periods. All analyses and calculations were conducted in R 3.5.3 (R Core Team 2019) and ArcMap 10.7.1.

3. RESULTS

3.1. WHDP movements

WHDPs showed consistent clockwise migratory movements (Figs. 1 & 2). After the breeding period, WHDPs left Whenua Hou and migrated southwest 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 d on their outbound migration, arrived at their non-breeding distribution on 5 January, spent 235.0 d at their non-breeding distribution, departed their non-breeding distribution on 28 August, spent 14.0 d on their homebound migration, and arrived at their breeding distribution on 11 September.

Breeding success influenced WHDP movements (Table S1). On average, failed breeders departed their breeding distribution earlier (6 December vs. 7 January), arrived earlier at their non-breeding distribution (15 December vs. 16 January), and spent more time at their non-breeding distributions (255.8 vs. 224.2 d). Sex had little influence on WHDP movements, but males exhibited slightly more prolonged

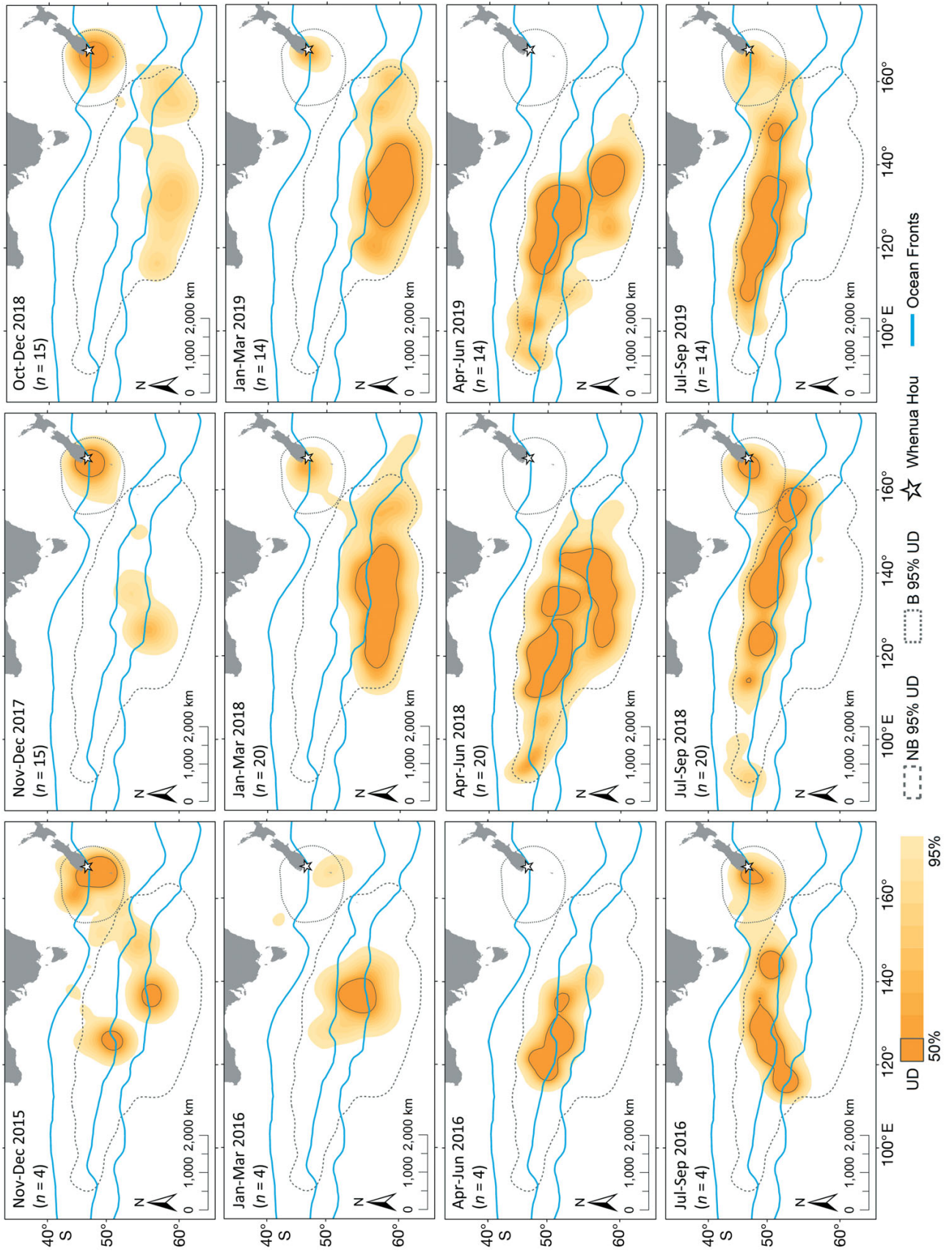


Fig. 1. Year-round movements and distributions of Whenua Hou diving petrels during 2015/16, 2017/18, and 2018/19 illustrated by 50–95% utilization distribution isopleths (UDs). NB: non-breeding distribution; B: breeding distribution. Approximate location of fronts based on Harris & Orsi (2006)

homebound migrations than females (17.1 vs. 11.4 d). Interannual variation influenced WHDP movements, and birds in 2015/16 departed earlier from their breeding distribution (10 December vs. 2 January in 2017/18 and 22 December in 2018/19), exhibited more prolonged outbound migrations (15.9 vs. 7.9 d in 2017/18 and 8.4 d in 2018/19), and spent more time at their non-breeding distributions (249.4 vs. 229.0 d in 2017/18 and 240.7 d in 2018/19). Additionally, birds in 2018/19 arrived later at their non-breeding distributions than birds in 2015/16 (18 January vs. 26 December).

3.2. WHDP offshore distribution

The core breeding distribution of WHDPs (~159 000 km²) 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 Sub-tropical Front and the Snares Islands shelf (Figs. 1, 3A, & 4A). The total breeding distribution (~890 000 km²) extended further northwards in Te Tai-o-Rēhua and further south towards Motu Ihupuku (Campbell Island). The WHDP breeding distribution was consistent among years (95% UD BA = 0.85, 50% UD BA = 0.34; Fig. 1) and individuals (95% UD BA = 0.81, 50% UD BA = 0.31). There was no evidence for spatial segregation of WHDPs during the breeding period between sexes (95% UD BA = 0.92, 50% UD BA = 0.41; Fig. 3A) or failed and successful breeders (95% UD BA = 0.94, 50% UD BA = 0.48; Fig. 4A).

Both the core area of use (~1 521 000 km²) and the total non-breeding distribution (~6 069 000 km²) 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 (Figs. 1, 3B, & 4B). The total non-breeding distribution

ranged from the Polar Front south of Macquarie Island to seas north of the Subantarctic Front southwest of Western Australia. Average maximum distance from the WHDP breeding colony was 3791 km. While the number of birds tracked in 2015/16 ($n = 4$) appeared insufficient to capture the full extent of the non-breeding distribution, WHDP total non-breeding distribution was consistent among years (95% UD BA = 0.72), with some interannual variation in the core area (50% UD BA = 0.24; Fig. 1). The total non-breeding distribution was also reasonably consistent among individuals (95% UD BA = 0.35), but not the core area of use (50% UD BA = 0.06). There was no clear evidence for spatial segregation of WHDPs during the non-breeding period between sexes (95% UD BA = 0.87, 50% UD BA = 0.37; Fig. 3B). There was also no clear evidence for spatial segregation

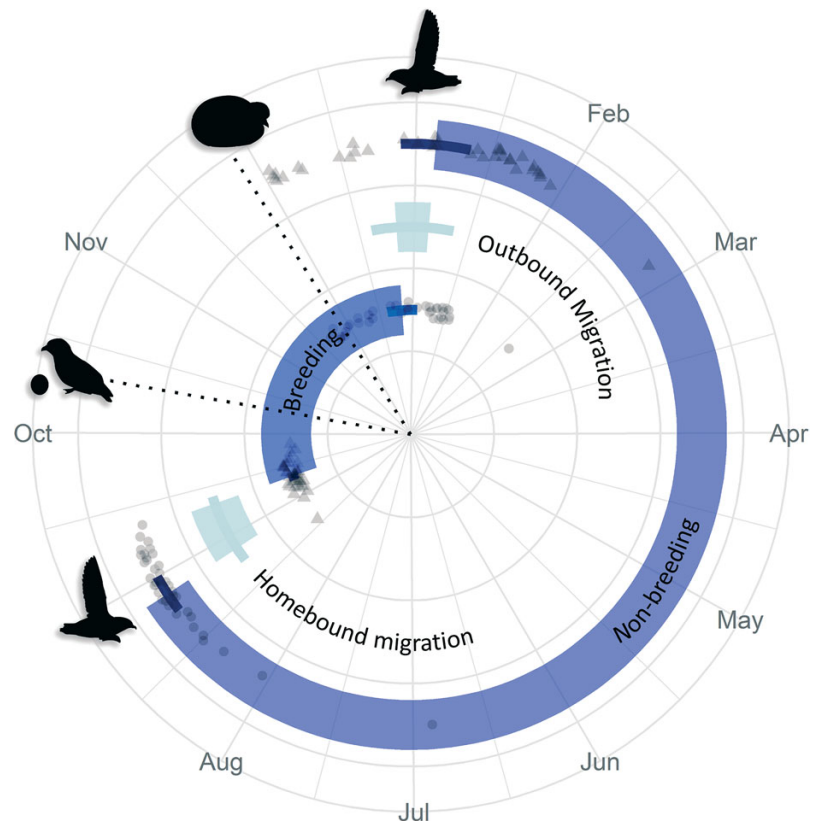
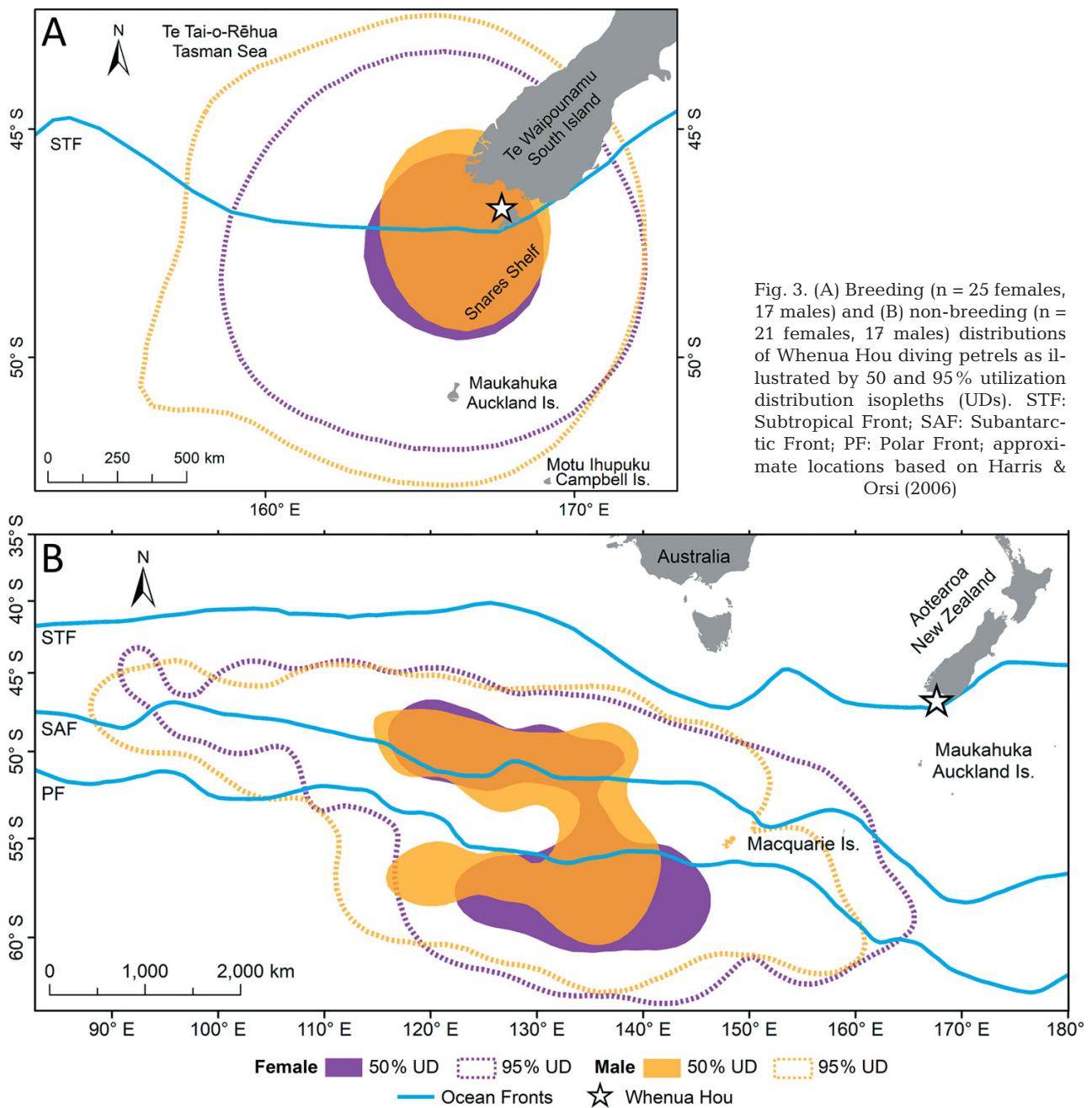


Fig. 2. Estimated year-round Whenua Hou diving petrel movement phenology. Start and end dates of each phase are represented by means \pm 95% CI. Grey triangles represent individual estimates of arrival dates. Grey circles represent individual estimates of departure dates. Dotted lines represent mean lay (10 October) and hatch dates (27 November; Fischer 2020)



between the total non-breeding distributions of failed and successful breeders (95% UD BA = 0.74). However, core areas of use differed somewhat (50% UD BA = 0.25; Fig. 4B) due to failed breeders that moved further west.

3.3. WHDP offshore behaviour

At their non-breeding distribution, WHDPs spent on average 95% (22.8 h d⁻¹) and up to 99% (23.7 h

d⁻¹) of their time, with at least their legs immersed in saltwater (Fig. 5). During the breeding period, WHDPs spent on average only 66% (15.7 h d⁻¹) of their time immersed. Thus, phenophase had a considerable influence on offshore behaviour (Table 2, Fig. 6). During the non-breeding period, WHDPs exhibited little, predominantly nocturnal, flight activity (2.9 bouts d⁻¹ lasting 33 min per flight bout). During the rapid outbound migrations, WHDPs exhibited more frequent and more diurnal flight activity (8.7 bouts d⁻¹ lasting 37 min). During the

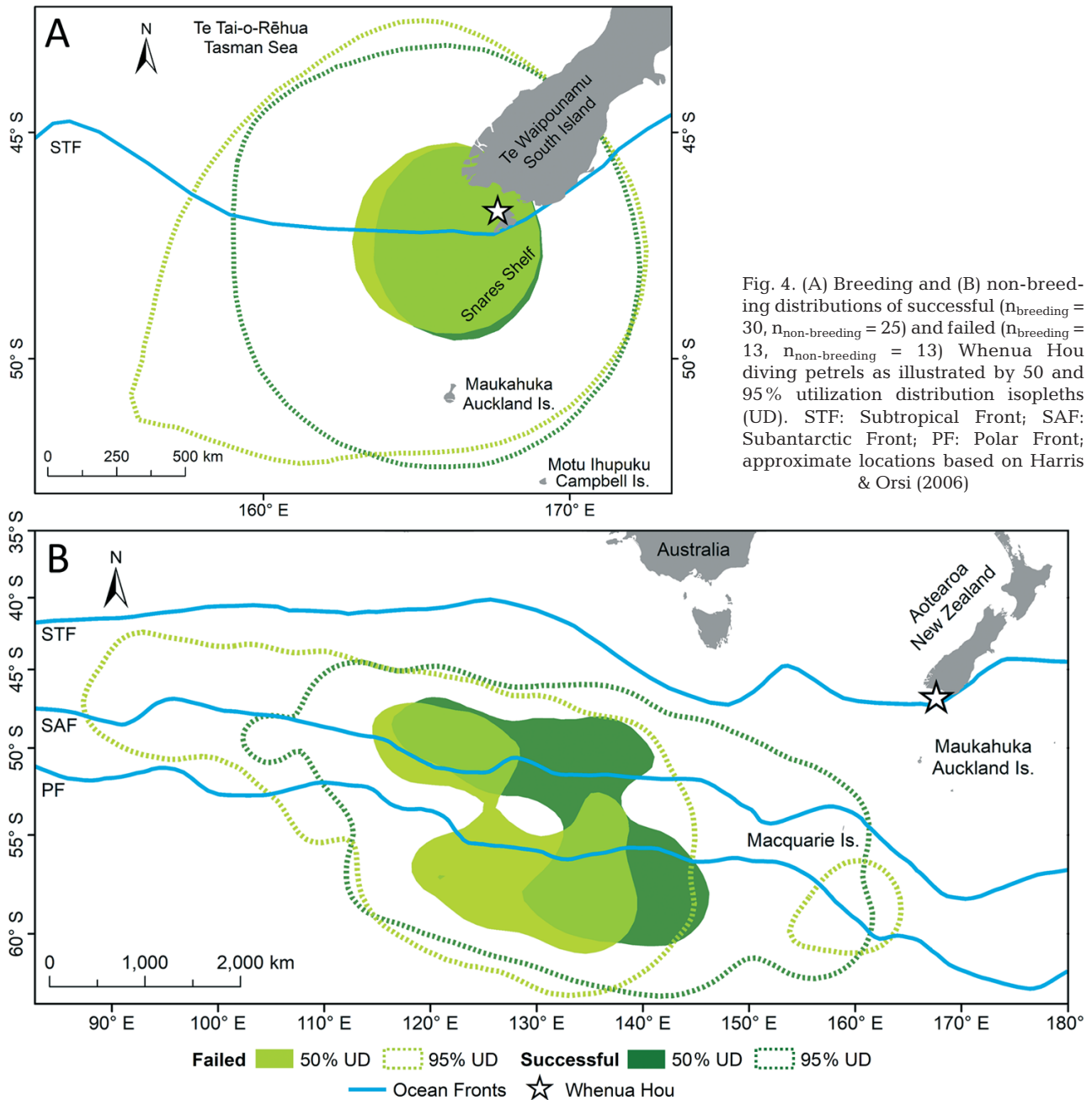


Fig. 4. (A) Breeding and (B) non-breeding distributions of successful ($n_{\text{breeding}} = 30$, $n_{\text{non-breeding}} = 25$) and failed ($n_{\text{breeding}} = 13$, $n_{\text{non-breeding}} = 13$) Whenua Hou diving petrels as illustrated by 50 and 95% utilization distribution isopleths (UD). STF: Subtropical Front; SAF: Subantarctic Front; PF: Polar Front; approximate locations based on Harris & Orsi (2006)

slower homebound migrations, WHDPs did not exhibit such elevated diurnal flight activity, but flight bouts were longer (3.9 bouts d^{-1} lasting 46 min). Despite their flight efforts during their migrations, WHDPs still remained largely on, or under, water. Breeding success had little influence on offshore behaviour, but, on average, successful breeders spent more time immersed than failed breeders (19.4 vs. 18.5 h d^{-1}). Sex had no clear influence on offshore behaviour. Interannual variation had a limited influence on offshore behaviour. Compared to birds in

2015/16, birds in 2018/19 exhibited fewer (5.6 vs. 4.7) and shorter flight bouts (39 vs. 36 min), and spent less time in flight at night (45 vs. 40%). Additionally, birds in 2015/16 spent less time flying at dawn (11 vs. 16% in 2017/18 and 17% in 2018/19).

3.4. Overlap with commercial fishing effort

Considerable commercial fishing effort was present within the breeding distribution during the

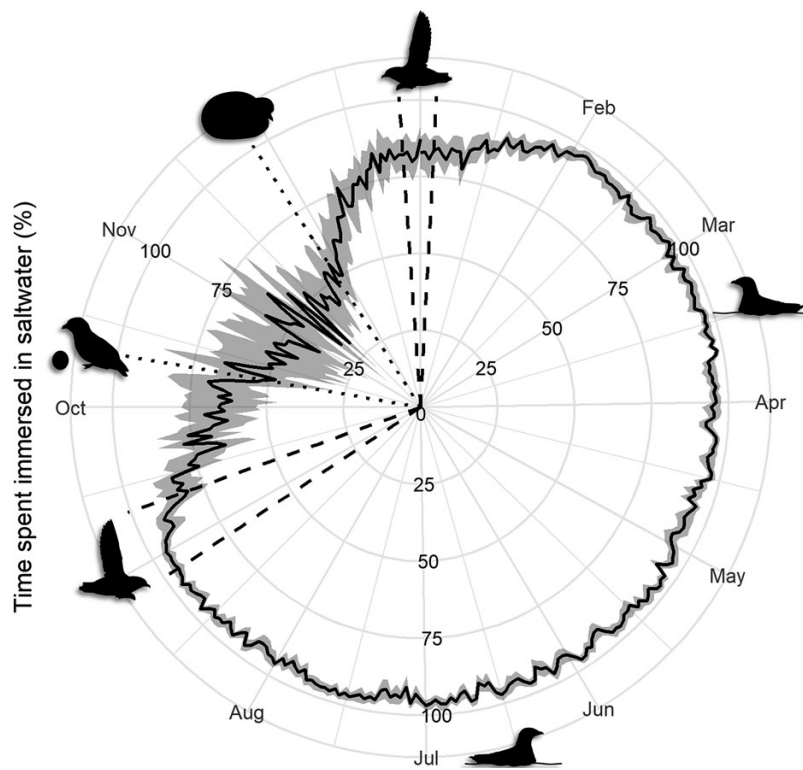


Fig. 5. Time Whenua Hou diving petrels spent immersed in saltwater (% d⁻¹; mean \pm 95% CIs). Dashed lines indicate model-estimated means of departure from the breeding distribution (27 December), arrival at the non-breeding distribution (5 January), departure from the non-breeding distribution (28 August), and arrival at the breeding distribution (11 September). Dotted lines represent mean lay (10 October) and hatch dates (27 November; Fischer 2020)

breeding period (11 September to 27 December; Fig. 7A). 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 fishing hours per 0.1° cell. Average summed fishing effort equated to 4399 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 fishing hours per 0.1° cell. Average summed fishing effort equated to 2948 fishing 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. 7B). The only

Table 2. Estimates of intercepts ($\hat{\alpha} \pm$ SE) and changes of the fixed-effects slopes ($\hat{\beta} \pm$ SE) of Whenua Hou diving petrel offshore behaviour. Intercepts and slopes are reported on the link scale. mig1: outbound migration; NB: non-breeding distribution; mig2: homebound migration. **Bold** indicates that $\hat{\beta} \pm 2$ SE does not intersect 0

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

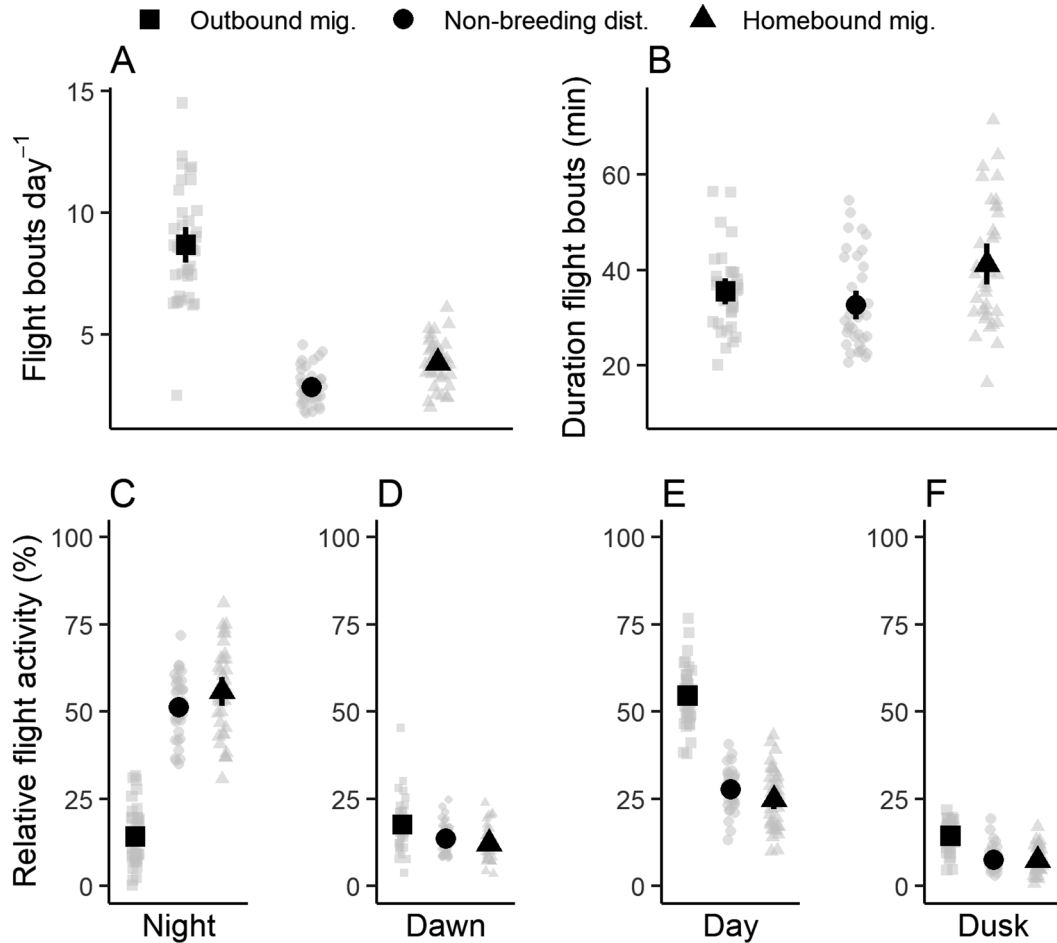


Fig. 6. (A) Number of flight bouts d^{-1} , (B) duration of flight bouts, and (C–F) relative flight activity per diel category per model-estimated phenophase. Black symbols with error bars: mean \pm 95% CIs, grey symbols: raw data

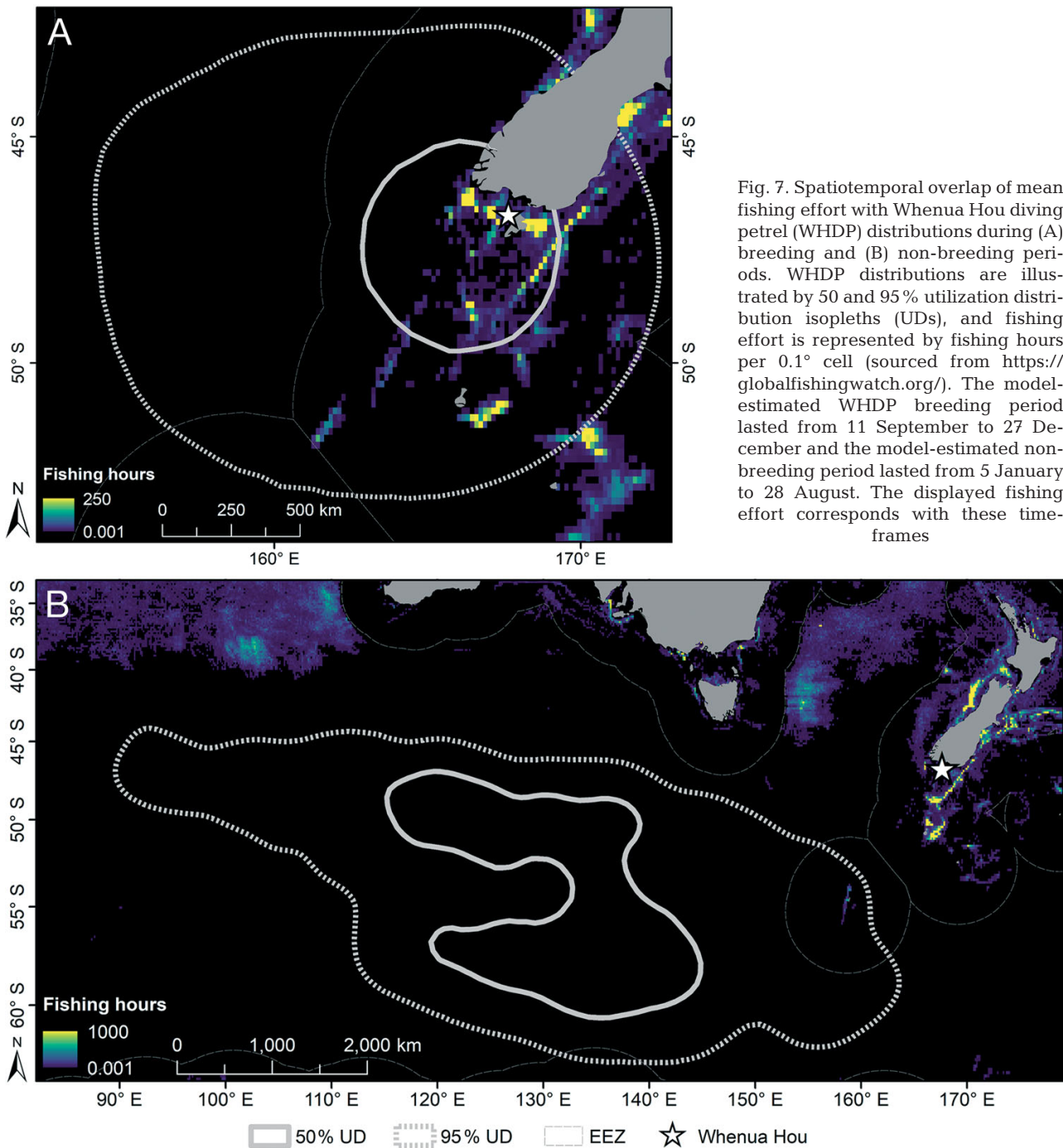
hotspot of commercial fishing effort within the WHDP non-breeding distribution was near Macquarie Island within the Australian EEZ. Average fishing effort within the WHDP non-breeding distribution (95% UD) equated to 0.004 fishing hours per 0.1° cell. Average summed fishing effort equated to 166 fishing hours. 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).

4. DISCUSSION

4.1. 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 far from Whenua Hou, as birds were bound by central place foraging, and travelling distances mirrored 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). Our tracking efforts suggested that WHDPs foraged here during the breeding period. These findings aligned with diet analyses, as the presence of larvae of *Histioteuthis* sp. and *Chiroteuthis* 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. 2008), Buller's albatrosses *Thalassarche 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), also use these areas.

4.2. WHDP offshore behaviour

WHDPs showed extreme aquatic behaviour during the non-breeding period. WHDPs may even be entirely flightless during the non-breeding period, because they may moult all flight feathers simultaneously, as has been observed in congeners (Murphy & Harper 1921). In our study, some WHDP behaviour was classified as 'in flight' throughout the non-breeding period. These classifications, however, may have arisen from birds tucking their legs into their plumage, causing geolocators to log 'dry' records, as has been illustrated for alcids (Linnebjerg et al. 2014). Therefore, WHDPs may be flightless during (part of) the non-breeding period. A more detailed investigation into moult strategies (e.g. through stable isotope analyses) is required to gain deeper insights into the seasonal flightlessness of WHDPs. During the breeding period, WHDPs still showed extreme aquatic behaviour and were on, or under, water for approximately two-thirds of their time, despite spending considerable amounts of time on land attending their burrows.

The aquatic affinity of WHDPs throughout their annual cycles could be explained by their high wing loadings. Wings of diving petrels 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 vs. leg-tucking) would allow more detailed insights into the underlying drivers of their extreme aquatic nature (e.g. high daily energy expenditures; Dunn et al. 2020).

4.3. 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 we investigated, none suggested clear spatial segregation, and WHDP distribution appeared consistent. The lack of spatial segregation could indicate an absence of intra-specific competition at sea (e.g. Clay et al. 2016), which could be caused by the low WHDP population size and/or the lack of sexual dimorphism (Fischer et al. 2018a, 2020). 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 $\geq 1\%$ of the global population of a species in an area (BirdLife International 2010, Delord et al. 2014, Lascelles et al. 2016). While we did not calculate the true proportion of the WHDP population within these areas (Lascelles et al. 2016), we tracked 2.6, 9.7, and 7.0% of the global WHDP population in 2015/16, 2017/18, and 2018/19, respectively (Fischer et al. 2020). 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 (BirdLife International 2010, Delord et al. 2014; Fig. S2).

The WHDP non-breeding distribution did not overlap with commercial fishing effort and thus WHDPs are unlikely to be affected by fisheries-related threats (e.g. deck strikes, by-catch, or oil spills) during the non-breeding period. The non-breeding distribution of WHDPs is located within one of the last stretches of untouched ocean on the planet (Kroodasma et al. 2018, Taconet et al. 2019). The lack of commercial fishing effort recorded is mirrored by a 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 typical of this stretch of ocean (mean wave height > 5 m and mean wind speed > 15 m s⁻¹; Young 1999). When in this area, WHDPs exhibited extremely aquatic behaviour. While flight behaviour during this period mostly occurred at night, 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 fisheries-related threats during the non-breeding period are unlikely. To ensure that WHDPs remain unaffected by anthropogenic threats at their non-breeding distribution, this stretch of ocean should receive formal protection (e.g. through listing as a marine IBA).

In contrast to the non-breeding distribution, the WHDP breeding distribution overlapped considerably with commercial fishing effort and marine traffic (Wu et al. 2017) and thus, WHDPs may be at risk from offshore threats during the breeding period. Our analyses likely underestimated the commercial fishing effort within the WHDP breeding distribution, as the use of AIS technology on vessels has increased considerably since 2012 (Kroodsma et al. 2018, Taconet et al. 2019). Regardless, several hotspots of commercial fishing effort were evident in areas of elevated productivity, and these productive areas may be equally attractive to foraging WHDPs (Tréguer & Jacques 1993, Orsi et al. 1995). The overlap of WHDP breeding distribution with commercial fishing effort 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 & Richard 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 to be common diving petrels) occurred in this area (Abraham & Richard 2019). A single deck strike event of such a magnitude could be detrimental to the 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.

Our results illustrated that offshore conservation measures (during the breeding period) could benefit this Critically Endangered species. However, the potential threats posed by commercial fisheries within the core of the WHDP breeding distribution spanned over 100 000 km², and managing threats within this vast area appears challenging. Seasonal (i.e. during the breeding period) restrictions of anthropogenic activity in the direct vicinity of the breeding colony (Whenua Hou) 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. 2011, Requena et al. 2020). To complement any seasonal spatial restrictions, the following recommendations (Black 2005) to minimize deck strikes should be encouraged: (1) alert vessels to the risks of spotlights and deck lighting, (2) use black-out blinds, (3) minimize external deck lighting,

(4) provide protocols on treatment and release of deck-struck birds, and (5) 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. We recommend that these measures be 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.

Decisions on (offshore) WHDP conservation measures should be subjected to a structured decision-making process. Conservation measures (e.g. seasonal spatial restrictions around Whenua Hou) will have consequences, not just for WHDPs, but also for tangata whenua (people of the land) and stakeholders (e.g. fisheries). This complex, multi-dimensional decision landscape should therefore be approached using standardized processes such as structured decision-making (SDM) (Gregory et al. 2012, McMurdo Hamilton et al. 2020). SDM is informed by a combination of input from tangata whenua and stakeholders and predictive modelling. SDM processes consists of 6 successive stages: (1) defining the problem, (2) articulating objectives, (3) identifying conservation measures, (4) predicting consequences, (5) weighting trade-offs, and (6) identifying the best measure(s). Integral to SDM is the involvement of tangata whenua and stakeholders to propagate underlying values. Modelling can predict the consequences of each conservation measure. Once consequences are estimated and trade-offs are weighted, a well-informed decision can be made. We recommend using the information on offshore threats to the WHDP compiled here, together with information on onshore WHDP threats (Fischer et al. 2018a, 2020), within an SDM process to identify the best conservation measures for this Critically Endangered species.

Acknowledgements. J.H.F. was supported by a Victoria University of Wellington Doctoral Scholarship. Fieldwork was supported by National Geographic Society (grant WW-249C-17), the Birds New Zealand Research Fund (2015, 2017, 2019), the Mohamed Bin Zayed Species Conservation Fund (Project 192520234), the Encounter Foundation, Forest and Bird (JS Watson Trust 2017), an Experiment.com crowdfunder (DOI:10.18258/7331), the Centre for Biodiversity and Restoration Ecology, the Coastal Restoration Trust of New Zealand, IDEA WILD, The Royal Society of New Zealand (Hutton Fund 2017), and the Australasian Seabird Group. We are very grateful to Kāi Tahu, Kaitiaki Rōpū, and the

Whenua Hou Komiti for granting visits to Whenua Hou. We are greatly indebted to the dozens of volunteers for their assistance in the field. We also thank James Fox from Migrate Technology for technical support. Thanks goes to Janne de Hoop and Johannes Chambon for their help with the electronic artwork. We are grateful to Samhita Bose, Thomas Clay, Jacob Fischer, and Hendrik Schultz for their insights into various analyses. We thank Kyle Elliott, Jason Preble, Matt Rayner, Grace Tocker, Karl-Heinz Wunsch, and 2 anonymous reviewers for providing comments on previous versions of this manuscript. All methods and protocols were approved by an institutional animal ethics committee (VUW AEC 22252, 23283, and 27621), the New Zealand Department of Conservation (45907-FAU, 47920-LND, 52029-LND, M1718/01, M1819/01, and M1920/02), the Whenua Hou Komiti, and Kaitiaki Rōpū.

LITERATURE CITED

- Abraham ER, Richard Y (2019) Estimated capture of seabirds in New Zealand trawl and longline fisheries, 2002–03 to 2015–16. Ministry of Primary Industries, Wellington
- Adams J, Takekawa JY (2008) At-sea distribution of radio-marked ash storm-petrels *Oceanodroma homochroa* captured on the California Channel Islands. *Mar Ornithol* 36:9–17
- ✦ Anderson ORJ, Small CJ, Croxall JP, Dunn EK, Sullivan BJ, Yates O, Black A (2011) Global seabird bycatch in longline fisheries. *Endang Species Res* 14:91–106
- ✦ Bates D, Mächler M, Bolker B, Walker S (2015) Fitting linear mixed-effects models using lme4. *J Stat Softw* 67. doi:10.18637/jss.v067.i01
- BirdLife International (2010) Marine Important Bird Areas toolkit: standardised techniques for identifying priority sites for the conservation of seabirds at sea. BirdLife International, Cambridge
- BirdLife International (2020) IUCN Red List for Birds. Species Factsheets. www.birdlife.org (accessed 10 Apr 2020)
- BirdLife International Seabird Tracking Database (2020) Tracking ocean wanderers. www.seabirdtracking.org (accessed 10 Apr 2020)
- ✦ Black A (2005) Light induced seabird mortality on vessels operating in the Southern Ocean: incidents and mitigation measures. *Antarct Sci* 17:67–68
- Bodey TW, Cleasby IR, Bell F, Parr N, Schultz A, Votier SC, Bearhop S (2018) A phylogenetically controlled meta-analysis of biologging device effects on birds: deleterious effects and a call for more standardized reporting of study data. *Methods Ecol Evol* 9:946–955
- ✦ Bolton M (2020) GPS tracking reveals highly consistent use of restricted foraging areas by European storm-petrels *Hydrobates pelagicus* breeding at the largest UK colony: implications for conservation management. *Bird Conserv Int*. doi:10.1017/S0959270920000374
- Burnham KP, Anderson DR (2002) Model selection and multimodel inference: a practical information-theoretic approach. Springer, New York, NY
- ✦ Calenge C (2006) The package “adehabitat” for the R software: a tool for the analysis of space and habitat use by animals. *Ecol Model* 197:516–519
- ✦ Chilvers BL, Amey JM, Huckstadt LA, Costa DP (2011) Investigating foraging utilization distribution of female New Zealand sea lions, Auckland Islands. *Polar Biol* 34: 565–574
- ✦ Clay TA, Manica A, Ryan PG, Silk JRD, Croxall JP, Ireland L, Phillips RA (2016) Proximate drivers of spatial segregation in non-breeding albatrosses. *Sci Rep* 6:29932
- ✦ Clay TA, Phillips RA, Manica A, Jackson HA, Brooke ML (2017) Escaping the oligotrophic gyre? The year-round movements, foraging behaviour and habitat preferences of Murphy’s petrels. *Mar Ecol Prog Ser* 579: 139–155
- ✦ Clay TA, Small C, Tuck GN, Pardo D and others (2019) A comprehensive large-scale assessment of fisheries bycatch risk to threatened seabird populations. *J Appl Ecol* 56:1882–1893
- ✦ Delord K, Barbraud C, Bost CA, Deceuninck B and others (2014) Areas of importance for seabirds tracked from French southern territories and recommendations for conservation. *Mar Policy* 48:1–13
- ✦ Dias MP, Martin R, Pearmain EJ, Burfield IJ and others (2019) Threats to seabirds: a global assessment. *Biol Conserv* 237:525–537
- ✦ Dunn RE, Wanless S, Daunt F, Harris MP, Green JA (2020) A year in the life of a North Atlantic seabird: behavioural and energetic adjustments during the annual cycle. *Sci Rep* 10:5993
- ✦ Dunphy BJ, Vickers SI, Zhang J, Sagar RL and others (2020) Seabirds as environmental indicators: foraging behaviour and ecophysiology of common diving petrels (*Pelecanoides urinatrix*) reflect local-scale differences in prey availability. *Mar Biol* 167:53
- ✦ Elvidge CD, Zhizhin M, Baugh K, Hsu FC (2015) Automatic boat identification system for VIIRS low light imaging data. *Remote Sens* 7:3020–3036
- ✦ Fieberg J, Kochanny CO (2005) Quantifying home-range overlap: the importance of the utilization distribution. *J Wildl Manag* 69:1346–1359
- Fischer JH (2020) Integrated conservation of the Whenua Hou diving petrel. PhD dissertation. Victoria University of Wellington, Wellington
- Fischer JH, Debski I, Taylor GA, Wittmer HU (2017) Assessing the suitability of non-invasive methods to monitor interspecific interactions and breeding biology of the South Georgian diving petrel (*Pelecanoides georgicus*). *Notornis* 64:13–20
- ✦ Fischer JH, Debski I, Miskelly CM, Bost CA and others (2018a) Analyses of phenotypic differentiations among South Georgian diving petrel (*Pelecanoides georgicus*) populations reveal an undescribed and highly endangered species from New Zealand. *PLOS ONE* 13: e0197766
- ✦ Fischer JH, Debski I, Taylor GA, Wittmer HU (2018b) Nest site selection of South Georgia diving-petrels *Pelecanoides georgicus* on Codfish Island, New Zealand: implications for conservation management. *Bird Conserv Int* 28:216–227
- ✦ Fischer JH, Taylor GA, Cole R, Debski I, Armstrong DP, Wittmer HU (2020) Population growth estimates of a threatened seabird indicate necessity for additional management following invasive predator eradications. *Anim Conserv* 23:94–103
- ✦ Glass J, Ryan P (2013) Reduced seabird night strikes and mortality in the Tristan rock lobster fishery. *Afr J Mar Sci* 35:589–592
- ✦ González-Solís J, Croxall JP, Wood AG (2000) Sexual dimorphism and sexual segregation in foraging strategies of northern giant petrels, *Macronectes halli*, during incubation. *Oikos* 90:390–398

- Gregory R, Failing L, Harstone M, Long G, McDaniels T, Ohlson D (2012) Structured decision making: a practical guide to environmental management choices. John Wiley & Sons, Chichester
- Halpin LR, Pollet IR, Lee C, Morgan KH, Carter HR (2018) Year-round movements of sympatric fork-tailed (*Oceanodroma furcata*) and Leach's (*O. leucorhoa*) storm petrels. *J Field Ornithol* 89:207–220
- Hardesty-Moore M, Deinet S, Freeman R, Titcomb GC and others (2018) Migration in the Anthropocene: how collective navigation, environmental system and taxonomy shape the vulnerability of migratory species. *Philos Trans R Soc B* 373:20170017
- Harris U, Orsi A (2006) Locations of the various fronts in the Southern Ocean. Australian Antarctic Data Centre-CAASM Metadata. http://data.aad.gov.au/aadc/metadata/metadata_redirect.cfm?md=AMD/AU/southern_ocean_fronts (accessed 10 April 2020)
- Imber MJ, Nilsson RJ (1980) South Georgian diving petrels (*Pelecanoides georgicus*) breeding on Codfish Island. *Notornis* 27:325–330
- Kroodsma DA, Mayorga J, Hochberg T, Miller NA and others (2018) Tracking the global footprint of fisheries. *Science* 359:904–908
- Lascelles BG, Taylor PR, Miller MGR, Dias MP and others (2016) Applying global criteria to tracking data to define important areas for marine conservation. *Divers Distrib* 22:422–431
- Linnebjerg JF, Huffeldt NP, Falk K, Merkel FR, Mosbech A, Frederiksen M (2014) Inferring seabird activity budgets from leg-mounted time-depth recorders. *J Ornithol* 155:301–306
- Mattern T, Masello JF, Ellenberg U, Quillfeldt P (2015) Actave.net – a web-based tool for the analysis of seabird activity patterns from saltwater immersion geolocators. *Methods Ecol Evol* 6:859–864
- McCaughey DJ, Woods P, Sullivan B, Bergman B and others (2016) Ending hide and seek at sea. *Science* 351:1148–1150
- McClelland PJ (2002) Eradication of Pacific rats (*Rattus exulans*) from Whenua Hou Nature Reserve (Codfish Island), Putauhinu and Rarotoka Islands, New Zealand. In: Veitch CR, Clout MN (eds) Turning the tide: the eradication of invasive species. Proceedings of the International Conference on Eradication of Island Invasives. Occasional Paper of the IUCN Species Survival Commission 27. IUCN, Gland, p 173–181
- McMurdo Hamilton T, Canessa S, Clarke K, Gleeson P and others (2020) Applying a values-based decision process to facilitate comanagement of threatened species in Aotearoa New Zealand. *Conserv Biol*. doi:10.1111/cobi.13651
- Merkel B, Phillips RA, Descamps S, Yoccoz NG, Moe B, Strom H (2016) A probabilistic algorithm to process geolocation data. *Mov Ecol* 4:26
- Mosbech A, Johansen KL, Bech NI, Lyngs P and others (2012) Inter-breeding movements of little auks *Alle alle* reveal a key post-breeding staging area in the Greenland Sea. *Polar Biol* 35:305–311
- Murphy RC, Harper F (1921) A review of the diving petrels. *Bull Am Mus Nat Hist* 44:496–554
- Navarro J, Votier SC, Aguzzi J, Chiesa JJ, Forero MG, Phillips RA (2013) Ecological segregation in space, time, and trophic niche of sympatric planktivorous petrels. *PLOS ONE* 8:e62897
- Norris-Caneda KH, Elliott JD (1998) Sex identification in raptors using PCR. *J Raptor Res* 32:278–280
- Oliveira N, Henriques A, Miodonski J, Pereira J and others (2015) Seabird bycatch in Portuguese mainland coastal fisheries: an assessment through on-board observations and fishermen interviews. *Glob Ecol Conserv* 3:51–61
- Orben RA, Kokubun N, Fleishman AB, Will AP and others (2018) Persistent annual migration patterns of a specialist seabird. *Mar Ecol Prog Ser* 593:231–245
- Orsi AH, Whitworth T, Nowlin WD (1995) On the meridional extent and fronts of the Antarctic Circumpolar Current. *Deep Sea Res I* 42:641–673
- Paiva VH, Ramos JA, Nava C, Neves V, Bried J, Magalhaes M (2018) Inter-sexual habitat and isotopic niche segregation of the endangered Monteiro's storm-petrel during breeding. *Zoology* 126:29–35
- Pardo D, Forcada J, Wood AG, Tuck GF and others (2017) Additive effects of climate and fisheries drive ongoing decline in multiple albatross species. *Proc Natl Acad Sci USA* 114:E10829–E10837
- Phillips RA, Xavier JC, Croxall JP (2003) Effects of satellite transmitters on albatrosses and petrels. *Auk* 120:1082–1090
- Pollet IL, Ronconi RA, Leonard ML, Shutler D (2019) Migration routes and stopover areas of Leach's storm petrels *Oceanodroma leucorhoa*. *Mar Ornithol* 47:55–65
- Quillfeldt P, McGill RAR, Furness RW, Mostl R, Ludynia K, Masello JF (2012) Impact of miniature geolocation loggers on a small petrel, the thin-billed prion *Pachyptila belcheri*. *Mar Biol* 159:1809–1816
- R Core Team (2019) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna
- Rayner MJ, Hauber ME, Clout MN, Seldon DS, Van Dijken S, Bury S, Phillips RA (2008) Foraging ecology of the Cook's petrel *Pterodroma cookii* during the austral breeding season: a comparison of its two populations. *Mar Ecol Prog Ser* 370:271–284
- Rayner MJ, Taylor GA, Gaskin CP, Dunphy BJ (2017) Seasonal activity and unpredicted polar front migration of northern New Zealand common diving petrels (*Pelecanoides urinatrix*). *Emu* 117:290–298
- Requena S, Opper S, Bond AL, Hall J and others (2020) Marine hotspots of activity inform protection of a threatened community of pelagic species in a large oceanic jurisdiction. *Anim Conserv* 23:585–596
- Reynolds RW, Smith TM, Liu C, Chelton DB, Casey KS, Schlax MG (2007) Daily high-resolution-blended analyses for sea surface temperature. *J Clim* 20:5473–5496
- Richard Y, Abraham ER, Berkenbusch K (2020) Assessment of the risk of commercial fisheries to New Zealand seabirds, 2006–07 to 2016–17. Ministry of Primary Industries, Wellington
- Rodríguez A, Arcos JM, Bretagnolle V, Dias MP and others (2019) Future directions in conservation research on petrels and shearwaters. *Front Mar Sci* 6:94
- Rotger A, Sola A, Tavecchia G, Sanz-Aguilar A (2020) Foraging far from home: GPS-tracking Mediterranean storm-petrels *Hydrobates pelagicus melitensis* reveals long-distance foraging movements. *Ardeola* 68:3–16
- Ryan PG (1991) The impact of the commercial lobster fishery on seabirds at the Tristan da Cunha Islands, South Atlantic Ocean. *Biol Conserv* 57:339–350
- Schultz H, Hohnhold RJ, Taylor GA, Bury SJ and others (2018) Non-breeding distribution and activity patterns in

- a temperate population of brown skua. *Mar Ecol Prog Ser* 603:215–226
- Shaffer SA, Tremblay Y, Weimerskirch H, Scott D and others (2006) Migratory shearwaters integrate oceanic resources across the Pacific Ocean in an endless summer. *Proc Natl Acad Sci USA* 103:12799–12802
- Spitz DB, Hebblewhite M, Stephenson TR (2017) 'MigrateR': extending model driven methods for classifying and quantifying animal movement behaviour. *Ecography* 40: 788–799
- Taconet M, Kroodsma D, Fernandes JA (2019) Global atlas of AIS-based fishing activity – challenges and opportunities. FAO, Rome
- Taylor GA (2000) Action plan for seabird conservation in New Zealand. Part B: Non-threatened seabirds. Department of Conservation, Wellington
- Taylor GA, Elliott GP, Walker KJ, Bose S (2020) Year-round distribution, breeding cycle, and activity of white-headed petrels (*Pterodroma lessonii*) nesting on Adams Island, Auckland Islands. *Notornis* 67:369–386
- Tréguer P, Jacques G (1993) Dynamics of nutrients and phytoplankton, and fluxes of carbon, nitrogen and silicon in the Antarctic Ocean. In: Hempel G (ed) *Weddell Sea ecology: results of EPOS European Polarstern Study*. Springer, Berlin, p 149–162
- Warham J (1977) Wing loadings, wing shapes, and flight capabilities of Procellariiformes. *NZ J Zool* 4:73–83
- Waugh SM, Poupart TA, Miskelley CM, Stahl JC, Arnould JPY (2017) Human exploitation assisting a threatened species? The case of muttonbirders and Buller's albatross. *PLOS ONE* 12:e0175458
- Weimerskirch H, Cherel Y, Delord K, Jaeger A, Patrick SC, Riotte-Lambert L (2014) Lifetime foraging patterns of the wandering albatross: life on the move! *J Exp Mar Biol Ecol* 450:68–78
- Wikelski M, Kays R (2020) Movebank: archive, analysis and sharing of animal movement data. www.movebank.org (accessed on 10 April 2020)
- Wold JR, Robertson CJR, Chambers GK, Ritchie PA (2018) Phylogeographic structure and a genetic assignment method for Buller's albatross ssp. (*Thalassarche bulleri* ssp.). *Notornis* 65:152–163
- Wu L, Xu Y, Wang Q, Wang F, Xu Z (2017) Mapping global shipping density from AIS data. *J Navig* 70:67–81
- Young IR (1999) Seasonal variability of the global ocean wind and wave climate. *Int J Climatol* 19:931–950
- Zhang J, Rayner M, Vickers S, Landers T, Sager R, Stewart J, Dunphy B (2019) GPS telemetry for small seabirds: using hidden Markov models to infer foraging behaviour of common diving petrels (*Pelecanoides urinatrix urinatrix*). *Emu* 119:126–137
- Zydalis R, Small C, French G (2013) The incidental catch of seabirds in gillnet fisheries: a global review. *Biol Conserv* 162:76–88

Editorial responsibility: Kyle Elliott,
 Sainte-Anne-de-Bellevue, Québec, Canada
 Reviewed by: M. J Rayner and 2 anonymous referees

Submitted: May 14, 2020
 Accepted: November 17, 2020
 Proofs received from author(s): February 15, 2021