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Diving Ecology of *Procellaria* Petrels Highlights the Necessity of Combining Bird-Scaring Lines, Weighted Branch Lines, and Night Setting in Pelagic Longline Fisheries

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ABSTRACT

Many seabirds are at risk of bycatch including in pelagic and demersal longline fisheries. Bycatch mitigation methods must be informed by seabird foraging behaviour to be effective. Deep-diving seabirds are especially vulnerable to bycatch and also increase risks for less adept divers by bringing baited hooks back to the surface. We deployed time-depth recorders paired with geolocation sensors or GPS loggers in Aotearoa New Zealand to quantify the diving ecology of three *Procellaria* petrel species (combined total number of dives = 12,767), all of which are vulnerable to bycatch in longline fisheries. We present the deepest dives recorded for each species, with Westland Petrels (*Procellaria westlandica*; $n = 32$) reaching 17.3 m, White-chinned Petrels (*P. aequinoctialis*; $n = 14$) reaching 21.7 m, and Black Petrels (*P. parkinsoni*; $n = 10$) reaching 38.5 m, the deepest dive recorded by a *Procellaria* petrel. All species dived faster than the best practice longline sink rate of 0.5 m/s. All dived throughout both day and night, but Black Petrels dived more frequently during the day, while Westland Petrels dived more frequently at night. These results suggest that simultaneous implementation of weighted branch lines, bird-scaring lines, and night setting is necessary to reduce bycatch in pelagic longline fisheries. This integrated approach effectively protects hooks from deep-diving *Procellaria* petrels and prevents them from retrieving hooks and increasing risk to other seabirds. These results also bear direct relevance for custom, target-specific mitigation methods in demersal longline fisheries. Overall, we provide the most in-depth investigation into *Procellaria* petrel diving ecology to date with wide-ranging implications for seabird conservation globally.

1 | Introduction

Seabirds are threatened by a range of anthropogenic threats, including climate change, alien species, and fisheries bycatch, especially in commercial operations (Dias et al. 2019). Bycatch directly increases adult seabird mortality, significantly impacting population abundance and contributing to ongoing declines (Ramírez et al. 2024). Bycatch is estimated to affect 28% of

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seabird species globally (Dias et al. 2019), most pressingly, albatrosses and large petrels. These seabirds are caught in a range of commercial fisheries, including pelagic and demersal longline fisheries. Global bycatch estimates in these (and other) fisheries are highly challenging to derive, but certainly amount to 10,000 s of individuals annually (e.g., Anderson et al. 2011; Abraham et al. 2019; Peatman et al. 2019; Richard and Adasme 2019; CCSBT 2025). In longline fisheries, most bycatch occurs during the setting of hooks, when birds get hooked or tangled in the line as they opportunistically dive after bait and subsequently drown (Gilman et al. 2005).

A range of seabird bycatch mitigation methods has been developed over decades to prevent inadvertent seabird mortalities in longline fisheries (Pierre 2023; Robertson et al. 2006). Mitigation methods in pelagic and demersal longline fisheries include bird-scaring (or 'tori') lines to scare birds away from sinking hooks, weighted branch lines (pelagic) or main lines (demersal) to increase sink rates and reduce the time hooks are available to seabirds, and night setting when many seabirds are less active (Gilman et al. 2005). In addition, more novel methods include hook-shielding (Sullivan et al. 2018) or underwater bait setting devices which prevent access to hooks until a predetermined depth (Ashworth et al. 2018). However, for these methods to be effective, they must be directly informed by seabird diving behaviour (Frankish et al. 2021; Rollinson et al. 2016). For example, seabird dive descent rates can inform the required sink rates of hooks (Gilman et al. 2005), and seabird diving ability can inform depths to which hooks must be protected and thus the aerial extents of bird-scaring lines (Bell 2016). Bycatch can be reduced significantly when appropriate mitigation methods are applied effectively and consistently, allowing populations to recover (Cox et al. 2007; Dasnon et al. 2022), and thus the development and implementation of effective bycatch mitigation methods is a key step in seabird conservation.

Procellaria petrels are particularly susceptible to bycatch in longline fisheries due to their deep-diving capabilities (Bell 2016; Frankish et al. 2021; Rexer-Huber et al. 2025; Rollinson et al. 2016; Waugh and Wilson 2017). These petrels range throughout the Southern Hemisphere, from the Southern Ocean (Delord et al. 2010; Landers et al. 2011; Mischler et al. 2015; Delord et al. 2019) to the tropics (Fischer et al. 2023). The White-chinned Petrel (Karetai kauae mā, *Procellaria aequinoctialis*) is the seabird most frequently killed in longline fisheries in the Southern Ocean and listed as Vulnerable on the IUCN Red List (Rexer-Huber et al. 2025). While the diving behaviour of White-chinned Petrels has been quantified in the Indian (Rollinson et al. 2014) and Atlantic Oceans (Frankish et al. 2021), there are no studies from the Pacific. Variations in foraging behaviour between colonies (Fauchald et al. 2011; Peck and Congdon 2006) highlight the need to study diving behaviour across breeding ranges. Westland Petrels (Tāiko, *P. westlandica*), listed as Endangered, and Black Petrels (Tākoketai, *P. parkinsoni*), listed as Vulnerable, are both Aotearoa (New Zealand) breeding endemics (Bell 2016; Waugh and Wilson 2017) and are among the species most at risk from fisheries bycatch in Aotearoa (Edwards et al. 2023). Despite the vulnerability of these species, only preliminary investigations into Westland and Black Petrel diving behaviour exist to date (Bell 2016; Freeman and Nicholls 1997). The deep-diving abilities of these petrels do not only elevate their own risk of bycatch, but also enable them to retrieve hooks back to the surface, potentially placing other, less adept divers such as albatrosses at additional bycatch risk (Jiménez et al. 2012). Understanding fishing-associated behaviours and subsequent bycatch risk is therefore relevant for preventing bycatch across seabird communities across the Southern Ocean, as all three species range widely.

The aim of our study was to investigate and compare diving behaviour among three of the world's five *Procellaria* petrel species, Westland, White-chinned, and Black Petrels, through the deployment of a range of data loggers including time-depth recorders (TDRs) on 91 individuals across colonies in Aotearoa during 2022–2024. The insights gained from these deployments shed light on the variation in diving behaviour observed within and among these species, have direct relevance to quantifying bycatch risk, and informing seabird bycatch mitigation method requirements in pelagic and demersal longline fisheries globally.

2 | Methods

2.1 | Field Work

We conducted fieldwork on (1) Westland Petrels in their last remaining breeding site near Punakaiki, Te Wai Pounamu, Aotearoa (South Island of New Zealand) (42°08′10.8″ S 171°20′30.2″ E), during their breeding period in the austral winter; (2) Black Petrels at Hirakimata on Aotea (Great Barrier Island) in Northern Aotearoa (36°11′02.4″ S 175°24′36.0″ E): and (3) White-chinned Petrels on Antipodes Island (Moutere Mahue) in Aotearoa's sub-Antarctic (49°41′16.8″ S 178°46′01.2″ E). We deployed data loggers on breeding adults across different stages of the breeding period (incubation, early chick-rearing, late chick-rearing, and non-breeding) during three breeding seasons (2022–2024). Timing and duration of deployments varied among sites and years for logistical reasons. As we did not know hatching dates or specific dates when guard stages ended, the transitions between breeding stages for Westland and Black Petrels were approximated based on field observations and the literature (Bell et al. 2022; Imber 1987; Baker and Coleman 1977; Jackson 1958). All White-chinned Petrel data were collected during the incubation stage.

All fieldwork was carried out with approval from mana whenua mana moana (people of the land and sea; Ngāi Tahu, Ngāti Waiwai, and Ngāti Rehua Ngāti Wai ki te Aotea) to work on their taonga species (treasures), and the Department of Conservation, and with the necessary animal ethics approvals (VUWAEC31247).

2.2 | Data Loggers

We deployed time-depth recorders (TDRs), which record depth (pressure) on 91 breeding adult Westland ($n = 46$), White-chinned (24), and Black Petrels (21) during various phenological stages of the 2022–2024 breeding periods (Table 1). To investigate diurnal patterns in diving behaviour, we paired TDRs with either Global Location Sensing (GLS) or Global Positioning System (GPS) loggers, which approximate

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TABLE 1 | Summaries of TDR deployments, retrievals, and datasets obtained for Westland, White-chinned, and Black Petrels.

			TDR					Paired logger				
									Sampling frequency			
	Location	Year	Type (make; model)	Sampling frequency	No. deployed	Retrieved	With data	Type	Location data	Wet/dry data	Light data	No. with data
Westland Petrel	West Coast	2022	Star-ODDI; DST milli F-TD	2 s	10	9 (90%)	9 (100%)	GLS	—	10 min	5 min	9
	West Coast	2022	CEFAS; CT G5	1–2 s	20	18 (90%)	14 (78%)	GLS	—	10 min (64%) 4 h (36%)	5 min	9
	West Coast	2023	CEFAS; CT G5	1 s	15	12 (80%)	9 (75%)	GLS	—	10 min (86%) 4 h (14%)	5 min	7
					45	**39 (87%)**	**32 (82%)**					**25**
White-chinned Petrel	Antipodes	2022	Star-ODDI; DST milli F-TD	2 s	9	8 (89%)	6 (75%)	—	—	—	—	—
	Antipodes	2022/23	CEFAS; CT G5	1 s	15	12 (73%)	7 (73%)	GLS	—	10 min	5 min	3
					24	**20 (79%)**	**14 (68%)**					**3**
Black Petrel	Aotea	2023	CEFAS; CT G5	1 s	10	9 (90%)	3 (33%)	GLS	—	10 min	5 min	1
	Aotea	2023/24	CEFAS; CT G5	1 s	10	7 (70%)	6 (86%)	GPS	10–15 min	—	—	4
	Aotea	2024	CEFAS; CT G5	1 s	1	1 (100%)	1 (100%)	GPS	10–15 min	—	—	1
					21	**17 (81%)**	**10 (59%)**					**6**

Note: Sampling frequencies of TDRs vary between 1 and 2 s. Totals for each species shown in bold. Also, details on loggers deployed alongside TDRs. Note that all GLS devices sample conductivity every 30 s and light level every 1 min, only the frequency of recording differs (% for each recording frequency is calculated only from GLS loggers retrieved with data). All GLS loggers are Migrate Technology Ltd. Intigeo C330s, and all GPS devices are customised PathTrack GPS nanoFix GEO loggers.

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location via sunrise and sunset times measured with light sensors, and determine geographic position through satellites, respectively. In addition, wet periods (time during which a bird is immersed in seawater) can be attained from conductivity sensors on GLS loggers or, in their absence, from TDR loggers. Wet periods were used to calculate dives per wet hour to provide a metric unaffected by varying times spent in flight or at colonies. All TDRs were housed in custom-made 3D-printed/mould-cast casings which were attached to tarsi using a strip of rubber and superglue. GPS loggers were back-mounted using baseplates, waterproof TESA tape, and dental floss, while GLS loggers were attached to the metal leg band using cable ties. One Westland Petrel had skin abrasions from the TDR but recovered after its removal. For further details on deployment and retrieval of devices, see Bell et al. (2023), Rexer-Huber et al. (2023), Simister et al. (2023), and Bell et al. (2024). From these deployments we recovered 84% of TDR data loggers and obtained 32 TDR datasets for Westland Petrels (25 of which were paired with GLS/GPS loggers), 14 TDR datasets for White-chinned Petrels (3 paired), and 10 TDR datasets for Black Petrels (6 paired).

2.3 | Data Processing

We performed all data filtering and analyses of dive statistics using R Statistical Software v4.4.1 (R Core Team 2024). We extracted and cleaned the dive (pressure) data with the R package *diveMove* (Luque 2024; Luque and Fried 2011). TDR pressure data can drift over the time of deployment, causing records to deviate from true values and to correct for these deviations, we used zero-offset filtering in *diveMove* (Luque and Fried 2011). To exclude residual surface noise, we set the dive threshold at 1 m (Frankish et al. 2021; Navarro et al. 2013; Rollinson et al. 2014). Once the data were filtered, we used *diveMove* to fit each dive into either a unimodal spline model (dives with >5 points) or a smoothing spline model (dives with <5 points), which investigated changes in vertical rates. The derivatives of this model were then used to divide the dive into phases such as descent, ascent, and bottom-phase (Koellmann et al. 2016). We excluded all dives with durations longer than 5 min, descent rates exceeding 4 m/s, and ascent rates exceeding 5 m/s (Frankish et al. 2021). When reporting summary statistics and performing analyses of descent rates, we excluded dives <5 m (Rollinson et al. 2014).

For the paired deployments, we first extracted the time of day from GLS and GPS devices. We used the package *TwGeos* to process GLS light data and extract sunrise and sunset times (Lisovski et al. 2016). Sunrise and sunset times were calculated from GPS time and location data using the *suncalc* package (Thieurmel and Elmarhraoui 2022). We also extracted wet and dry times from GLS loggers, and in the absence of a paired GLS, we used an in-built feature of TDR loggers which records wet periods. Lastly, we used the package *lunar* to retrieve lunar luminance for nighttime dives (Lazaridis 2022).

2.4 | Statistical Analysis

We investigated a range of different dive parameters: dive depths (maximum depth of a dive), durations, ascent rates (depth at the end of the bottom phase/ascent duration), and descent rates (depth at the start of the bottom phase/descent time). The bottom phase duration, that is, the time between descent and ascent phases of a dive, determined the general shape of a dive profile, ranging from V-shape (no bottom phase) to U-shape (bottom phase >0 s). Dive frequencies were calculated as the number of dives per calendar day, only including days with at least one dive to prevent differences in phenology confounding results.

We then compared descent rates for each species with pelagic and demersal longline sink rates from experimental studies or recommended sink rates for reducing bycatch in the Southern Ocean based on the comprehensive literature reviews conducted by Pierre et al. (2015), Frankish et al. (2021), and the Agreement on the Conservation of Albatrosses and Petrels (ACAP) (2023b, 2024). We also included additional references that had specific relevance to sink rates in Aotearoa waters (Goad and Olsen 2022, 2023; Robertson et al. 2008).

We compared diving behaviour among species using general linear mixed-effects models (GLMMs) (Knudson 2024) with species as a fixed effect and individual as a random effect. Model diagnostics were run, and assumptions were checked with R package *DHARMa* (Hartig 2024). All parameters were Gamma distributed except for ascent and descent rates, which were normally distributed; both distributions used a logarithmic link function. To avoid non-positive values, 0.001 s was added to all pre-dive durations and bottom phase durations, allowing data to be fit to a Gamma distribution (Supporting Information 1a–1c). To determine the factors which influence within-species patterns in diving behaviour, we used GLMMs and a model averaging approach providing weighted model summaries and conditional averages. Phenology and sex were fixed effects in Black and Westland Petrel models, but only sex was available for White-chinned Petrels as all data were collected during incubation. Some White-chinned Petrels were of unknown sex, and these were excluded from the sex and phenology analysis (8 of 14 individuals excluded). Westland petrel data consisted of 1 and 2 s sampling frequencies, and we pooled both subsets, as results were consistent between subsets (Supporting Information 2). We defined phenology as an ordered factor, giving output as either linear, quadratic, or cubic depending on the direction of change between subsequent stages. We considered any model significant if $p<0.05$, but we also reviewed AIC values to determine the most parsimonious model if several were significant.

We investigated diurnal trends in diving behaviour using a combination of GLMMs and general additive mixed-effects models (GAMMs). We used GLMMs to compare the frequency of nighttime and daytime dives (only including dates with at least one dive) across all species. We then used GLMMs to determine whether lunar luminance influenced nighttime dive frequencies (local cloud cover was unknown). We used GAMMs to investigate more fine-scale diel patterns in dive depths, durations, ascent, and descent rates for Black Petrel and Westland Petrel. Model diagnostics were run and assumptions were checked with R package *mgcv* (Wood 2017). We excluded White-chinned Petrel from the fine-scale analysis due to our limited sample size of double-tagged individuals (3 individuals, 53 dives). We standardised the time of day for daytime dives and nighttime dives separately by calculating

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the time of day as hours since sunrise or sunset divided by day length, which we then turned into a circular statistic where both 0 and 2 represent sunrise, 0.5 is noon, 1 is sunset, and 1.5 is midnight.

3 | Results

3.1 | Among Species

Diving behaviour varied greatly among species. Black Petrels dived significantly deeper (mean: 5.9 ± 0.2 m) and longer (16.8 ± 1.8 s) than both White-chinned (mean: 2.6 ± 0.5 m, $\beta = -0.773$, $p < 0.001$ and mean: 6.3 ± 0.8 s, $\beta = -0.915$, $p < 0.001$) and Westland Petrel (mean: 2.3 ± 0.1 m, $\beta = -0.902$, $p < 0.001$ and mean: 4.8 ± 0.6 s, $\beta = -1.134$, $p < 0.001$) (Table 2). Westland Petrels reached a maximum dive depth of 17.3 m ($n = 8203$), White-chinned Petrels reached 21.7 m ($n = 618$), and Black Petrels reached 38.5 m ($n = 3855$). Most Black Petrel dives exceeded 5 m, while for both Westland and White-chinned Petrels the majority were shallower than 5 m. Only one White-chinned Petrel dive reached 20 m, while 5.4% of Black Petrel dives exceeded 20 m (Figure 1). Black Petrels also spent significantly longer in the bottom phase of the dive compared to White-chinned ($\beta = 1.104$, $p < 0.001$) and Westland Petrels ($\beta = -1.130$, $p < 0.001$). Westland Petrel descent rates (1.0 ± 0.0 m/s) were significantly faster than Black Petrels (mean = 0.8 ± 0.1 m/s; $\beta = 0.215$, $p = 0.004$) and White-chinned Petrels (0.8 ± 0.0 m/s) (Tables 2 and 3; Figure 2). The frequency of dives also differed among species. Considering days with at least one dive event, Black Petrels dived significantly more frequently (11.8 ± 2.4 dives per day) than White-chinned Petrels with 4.5 ± 0.7 dives per day ($\beta = -0.978$, $p < 0.001$) but not significantly more frequently than Westland Petrels with 8.08 ± 0.65 dives per day (Table 2).

3.2 | Within Species

There is strong evidence for changes in diving behaviour across breeding stages in both Westland Petrels and Black Petrels (Supporting Information 4a, 4b, 6a, 6b). For both species, dive depths, durations, and bottom phase durations increase from incubation to chick-rearing (Figure 3). In Westland Petrels, dive depth, dive duration, and bottom phase duration then decrease into late chick-rearing, and dives also become less frequent (Figure 3). In contrast, Black Petrel depths and both durations continue to increase into late chick-rearing, and then decrease in the non-breeding period (Figure 3). Black Petrels dived most frequently during late chick-rearing and incubation (Figure 3). Lastly, Westland Petrel descent rates increased from incubation to early chick-rearing, and then decreased during late chick-rearing (Figure 3).

There is also evidence for sex-specific foraging behaviours in Westland and White-chinned Petrels (Supporting Information 4a–6b). Male Westland Petrels dived significantly longer than females and spent longer in the bottom phase of the dive (Figure 3), but without evidence of any dive depth difference between sexes. In White-chinned Petrel, we found that males dived significantly deeper than females.

3.3 | Diurnal Patterns

Diurnal patterns in diving behaviour were evident in all species (Supporting Information 7). Foremost, Westland Petrels dived nearly non-discriminatory in light and darkness, with only slightly fewer dives during the day ($\beta = 0.161$, $p = 0.005$). Black Petrel and White-chinned Petrel dived more frequently during the day ($\beta = -1.008$, $p < 0.001$ and $\beta = -0.703$, $p = 0.003$ respectively) (Figure 4). However, with only three White-chinned Petrel individuals with light sensor data, results are not conclusive for this species. Nocturnal Westland Petrel dive frequency increased significantly under increasing lunar luminance ($\beta = 0.363$, $p = 0.001$) (Figure 4). There was a significant effect of time of day on both Westland and Black Petrel dive depths and durations (Supporting Information 8). Smooth terms of the effect of time of day on dive depth for both species show a decreased depth during the night (Figure 4). In Black Petrel this trend was reflected in dive durations, with shorter dives during the night. In Westland Petrel, this trend is not observed in dive durations. There is a small decrease in dive durations at midnight, and a much greater decrease around noon (Figure 4).

4 | Discussion

Our comparative analysis of the diving behaviour of adult Westland, White-chinned, and Black Petrels provides novel information on foraging strategies across these vulnerable species. Specifically, we found that these *Procellaria* petrels dive to considerable depths (> 20 m for all species, and up to 38.5 m in Black Petrel), at high speeds (> 0.5 m/s for all species, and > 1 m/s in Westland Petrel), and during both day and night. We also found significant differences in various aspects of diving behaviour among species, as well as within-species diurnal trends, sex-specific differences, and for Black and Westland Petrels, changes in diving behaviour across the breeding period. Combined, these results highlight the necessity to ensure that bycatch mitigation methods in demersal and pelagic longlines take the strong diving capabilities of these three species of conservation concern into consideration and are implemented accordingly. As these species range widely and can retrieve hooks and thus put other, less adept diving seabirds, such as albatrosses, at risk (Jiménez et al. 2012), this information is not just relevant to the conservation of *Procellaria* petrels but to a wider suite of highly vulnerable seabirds. As such, our study has considerable bycatch mitigation implications around the Southern Ocean and up to the tropics.

4.1 | Dive Depths

We found each species dived to considerable depths, surpassing previously recorded maximum dive depths. Westland Petrels dived on average 2.3 ± 0.1 m, and up to 17.3 m deep, more than twice the previously recorded maximum of 7.6 m (Freeman and Nicholls 1997; $n_{obs} = 3$, compared to $n_{obs} = 8203$ in this study). White-chinned Petrels reached 21.7 m, several metres deeper than the previous record of 16 m (Rollinson et al. 2014; $n_{obs} = 296$, compared to 618). In contrast, we

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TABLE 2 | Summary statistics of diving behaviour for Westland, White-chinned, and Black Petrels, with sex-specific statistics also shown for each dive parameter.

		Depth (m)		Duration (s)		Bottom dur. (s)	Descent rate (m/s)	Ascent rate (m/s)	Dive freq. (n/day)	*n*/wet h
Sex	***n* dives**	**Mean (SE)**	**Max**	**Mean (SE)**	**Max**	**Mean (SE)**	**Mean (SE)**	**Mean (SE)**	**Mean (SE)**	**Mean (SE)**
Westland Petrel										
Female	2261	2.17 (0.12)	12.22	4.17 (0.35)	38	1.78 (0.18)	1.02 (0.07)	1.88 (0.10)	6.49 (0.66)	0.45 (0.06)
Male	5942	2.34 (0.08)	17.31	5.37 (0.25)	65	2.14 (0.10)	1.00 (0.02)	1.77 (0.07)	9.17 (0.92)	0.74 (0.11)
All	8203	2.26 (0.09)	17.31	4.77 (0.60)	65	1.96 (0.18)	1.01 (0.01)	1.82 (0.05)	8.08 (0.65)	0.63 (0.08)
White-chinned Petrel										
Female	60	1.82 (0.11)	13.53	4.96 (1.60)	34	1.75 (0.45)	0.88 (–)	1.72 (0.21)	2.53 (0.53)	0.88 (0.27)
Male	87	3.58 (0.48)	21.72	7.76 (1.57)	52	1.82 (0.29)	0.90 (0.04)	1.90 (0.13)	3.29 (0.68)	0.90 (0.58)
Unkn.	471	2.48 (0.28)	14.19	6.04 (0.91)	42	2.36 (0.19)	0.80 (0.05)	1.48 (0.11)	5.62 (1.07)	0.26 (0.03)
All	618	2.63 (0.51)	21.72	6.25 (0.81)	52	1.98 (0.19)	0.86 (0.03)	1.70 (0.12)	4.52 (0.72)	0.71 (0.20)
Black Petrel										
Female	499	6.08 (1.08)	25.50	18.66 (5.34)	86	5.06 (1.60)	0.78 (0.05)	1.53 (0.18)	7.20 (0.45)	0.92 (0.02)
Male	3356	5.78 (0.90)	38.50	15.00 (2.73)	148	3.89 (0.62)	0.91 (0.04)	1.73 (0.11)	13.13 (2.91)	1.56 (0.27)
All	3855	5.93 (0.15)	38.50	16.83 (1.83)	148	4.48 (0.59)	0.84 (0.07)	1.63 (0.10)	11.95 (2.43)	1.42 (0.22)

Note: Mean is shown with standard errors in parentheses. *n* dives refers to entire datasets, and some values are from subsets of these datasets, as follows. Dive frequencies per day only includes days with at least one dive, and dive frequencies per wet hour includes all wet times across each respective deployment.

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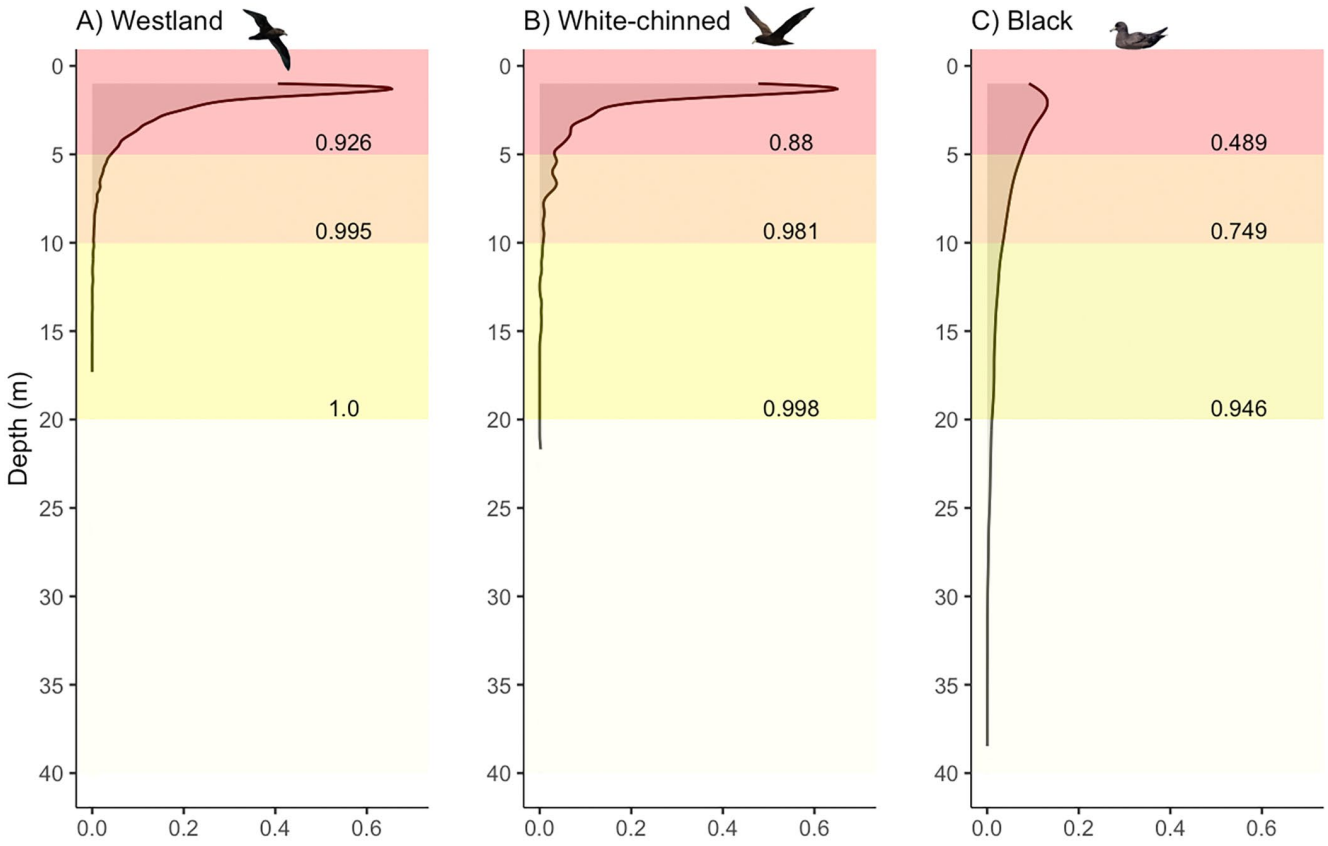


FIGURE 1 | Density plot of maximum dive depths for (A) Westland Petrels, (B) White-chinned Petrels, and (C) Black Petrels. Values on right-hand side of each graph indicate the following: In red sections, the proportion of dives between 0 and 5 m is shown, in orange, the proportion of dives between 0 and 10 m, and yellow, the proportion of dives between 0 and 20 m.

recorded a mean dive depth of 2.5 ± 0.3 m, slightly shallower than the average depth for White-chinned Petrels in the Indian Ocean at 2.9 ± 2.4 m (Rollinson et al. 2014), and the Atlantic Ocean at 3.1 ± 0.2 m (Frankish et al. 2021; $n_{obs} = 895$). Finally, a Black Petrel dive reached 38.5 m, the deepest dive recorded for a *Procellaria* petrel, surpassing the previous maximum recorded depth of 34.3 m (Bell 2016; $n_{obs} = 1706$, compared to 3855). The mean Black Petrel dive depth recorded in our study (5.9 ± 0.2 m) was deeper than the previous mean of 2.6 ± 0.1 m (Bell 2016). Potentially this disparity is due to differing filtering methods whereby this study excluded dives < 1 m while Bell (2016) removed dives < 0.5 m. The dive depths of Westland and White-chinned Petrels are similar to dive depths recorded for Grey Petrels (*P. cinerea*) which exhibit a mean dive depth of 3.2 ± 2.2 m and a maximum dive depth of 22 m (Rollinson et al. 2016; $n_{obs} = 775$). No dive depth studies have been conducted on the Spectacled Petrel (*P. conspicillata*), highlighting a data gap.

4.2 | Differences Among Species

We found considerable differences in diving ecology among Westland, White-chinned, and Black Petrels, potentially due to morphological and environmental differences. Most notably, we observed significantly deeper and longer dives in Black Petrels. Black Petrels have shorter wings and a narrower build than both Westland and White-chinned Petrels (Marchant and Higgins 1990), which may contribute to their diving ability by making them more hydrodynamic and less buoyant (Warham 1977). Thus, their greater dive ability is likely due to dive-specific morphological adaptations. Additionally, Black Petrels forage in warmer, less productive waters than Westland and White-chinned Petrels (Fischer et al. 2023; Delord et al. 2010; Landers et al. 2011), possibly requiring greater diving effort to obtain prey. We also found that though dive ability was similar, White-chinned Petrels made fewer but deeper dives than Westland Petrels. With similar size and build (Marchant and Higgins 1990), this difference in diving behaviour may instead be driven by disparate foraging strategies resulting from prey availability or competition within their respective communities.

4.3 | Diurnal Patterns

Diurnal patterns in the foraging behaviour of seabirds can reveal prey preferences and foraging strategies. A diet study by Imber (1976) showed predominantly bioluminescent prey, particularly ommastrephids, for the *Procellaria* species included in our study, indicating nocturnal feeding (Wilson et al. 1993). We found Westland Petrels preferred nocturnal diving, though dived throughout the day as well. In contradiction to Imber's (1976) expectations, Black Petrels dived mostly during the day, though this does not preclude night-time surface foraging not captured by TDRs. The contrasting diurnal

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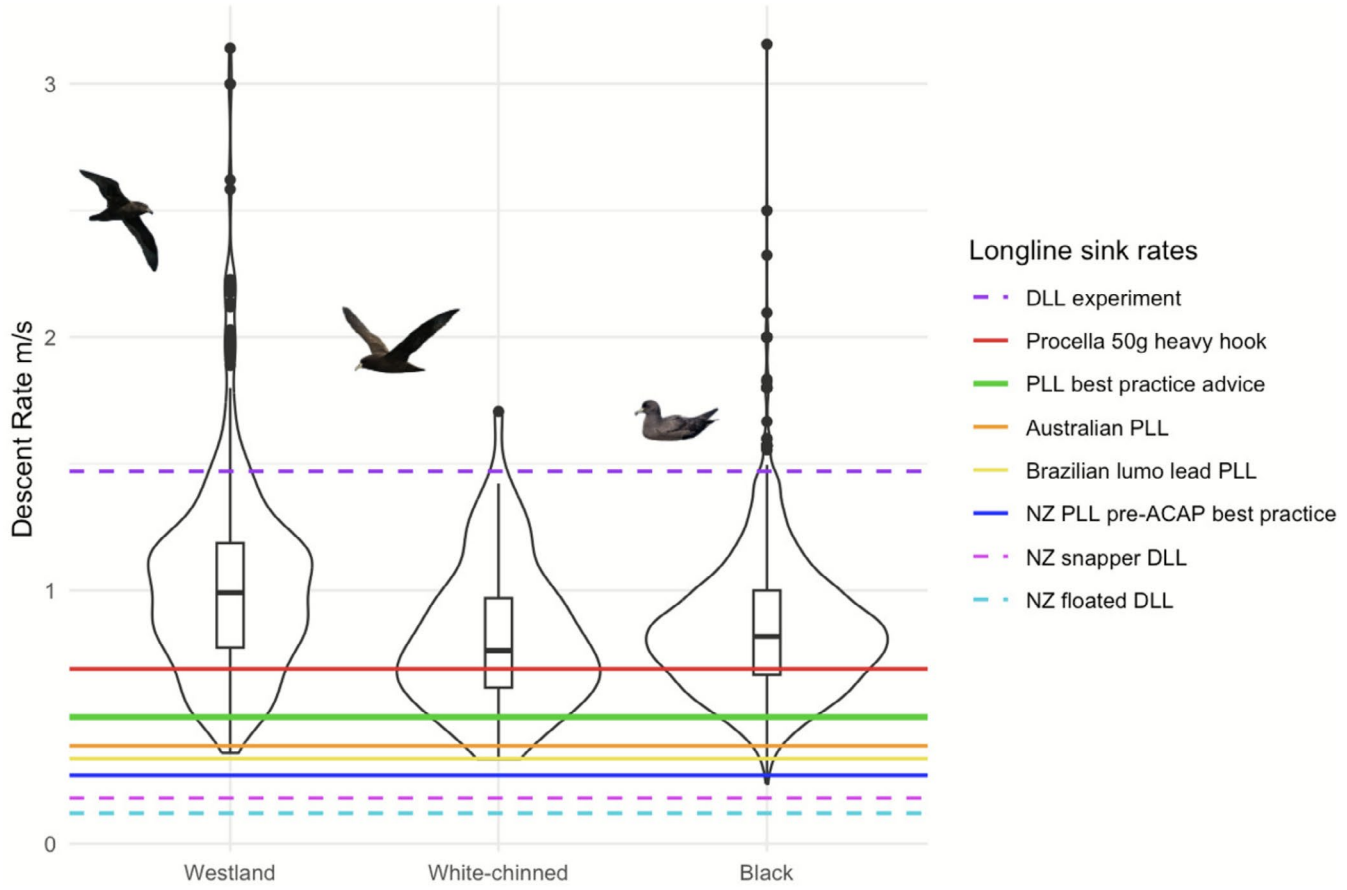


FIGURE 2 | Descent rates of Westland, White-chinned and Black Petrels, excluding dives < 5 m deep. Published and recommended line sink rates for pelagic longline (PLL) are shown with solid lines, while those for demersal longline (DLL) are shown with dashed lines. Citations for sink rates are as follows: DLL experiment (Chilean gear; Robertson et al. 2008); Procella 50 g heavy hook (ACAP 2023a); PLL best practice advice (ACAP 2024); Australian PLL (Robertson et al. 2010); Brazilian lumo lead PLL (Santos et al. 2019); NZ PLL pre-ACAP best practice (Pierre et al. 2015); NZ snapper DLL (Goad and Olsen 2022); NZ floated DLL (Goad and Olsen 2023). The legend follows the order of horizontal lines in the graph.

diving behaviours of Westland and Black Petrels may be due to their distinct diving strategies. Black Petrels dive much deeper with longer bottom phases than Westland Petrels, suggesting active pursuit of prey deeper in the water column, requiring good visibility (Darby et al. 2022). Also, the few dives they perform during the night are much shorter and shallower, indicating they may be limited by sight. Westland Petrels also dive shallower at night, though the difference is less pronounced, and the duration does not change. Westland Petrels dive more frequently on moonlit nights, suggesting some preference for lighter conditions (Regular et al. 2011).

4.4 | Sex Specific Differences

We found all species showed sex-specific foraging behaviours whereby males were the more proficient divers. We found White-chinned Petrels males dived deeper than females, and male Westland Petrels dived faster and for longer durations than females. Male *Procellaria* petrels are generally larger than females (Marchant and Higgins 1990; Mischler 2015; Ryan 1999) thus they may benefit from better oxygen storage/usage (Halsey et al. 2006) when diving. However, male-bias diving proficiency is observed in both sexually monomorphic and dimorphic species (Peck and Congdon 2006; Reyes-González et al. 2021), suggesting sex-specific foraging is not solely a consequence of dimorphism. Potentially, sex-specific foraging allows for niche segregation where resources are limited.

4.5 | Phenology

During the breeding period, resource demand is heightened as birds must accommodate both reproductive costs and provisioning of chicks (Colominas-Ciuró et al. 2022; Gaston et al. 2007). Diving effort is highest during chick provisioning, as birds are spatially constrained (Colominas-Ciuró et al. 2022). As expected, both Westland and Black Petrel dive depths, dive durations, and bottom phase durations increased from incubation to early chick-rearing, suggesting a greater diving effort. Yet Westland Petrel dive depths and durations decreased from early to late chick-rearing, while efforts for Black Petrels continued to increase. This may be indicative of differences in species-specific food availability. For Black Petrel, dive depths became shallower in the non-breeding period as expected when the high resource demands of chick-rearing have ended. It should also be noted that hatching dates and those at the end of guard stage were estimated based on literature and field observations. Future studies may consider candling eggs and weighing chicks to better estimate these dates.

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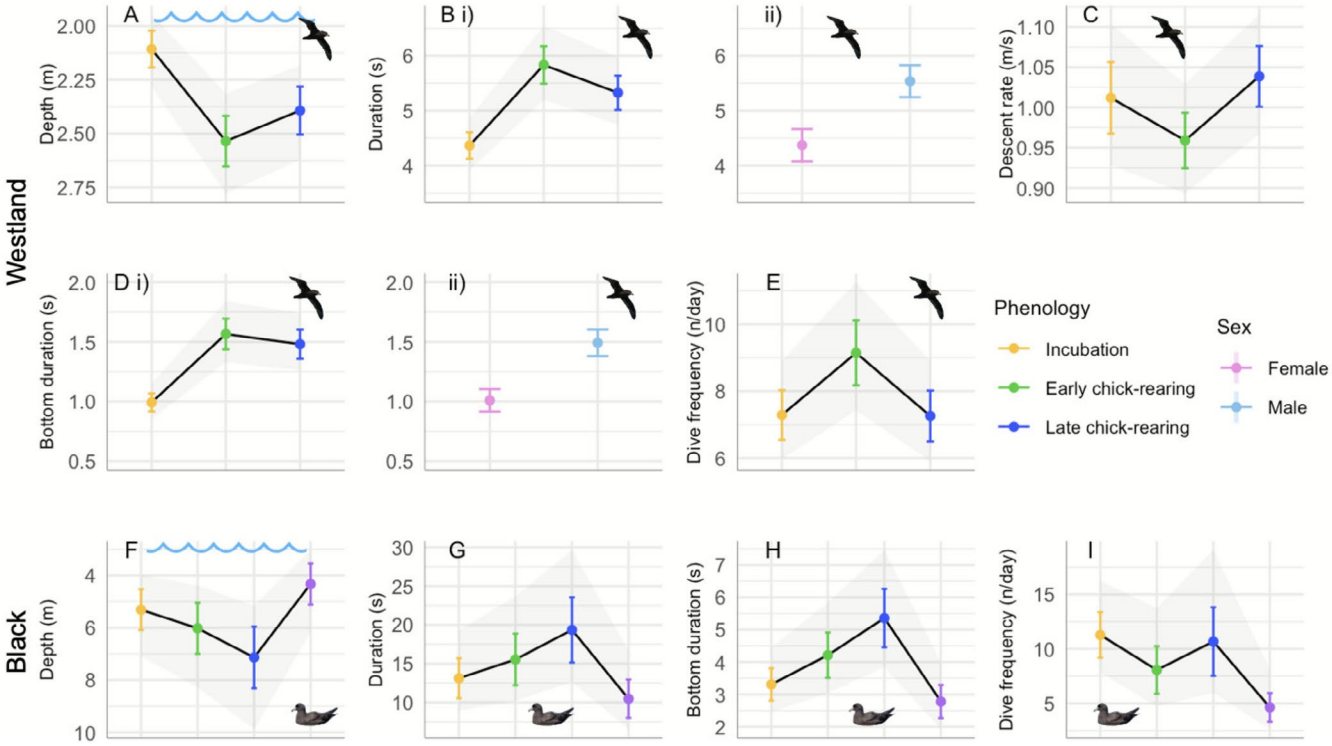


FIGURE 3 | GLMM output of the effect of phenological stage and sex on dive parameters in Westland Petrel (A–E) and Black petrel (F–I). Only significant results are presented.

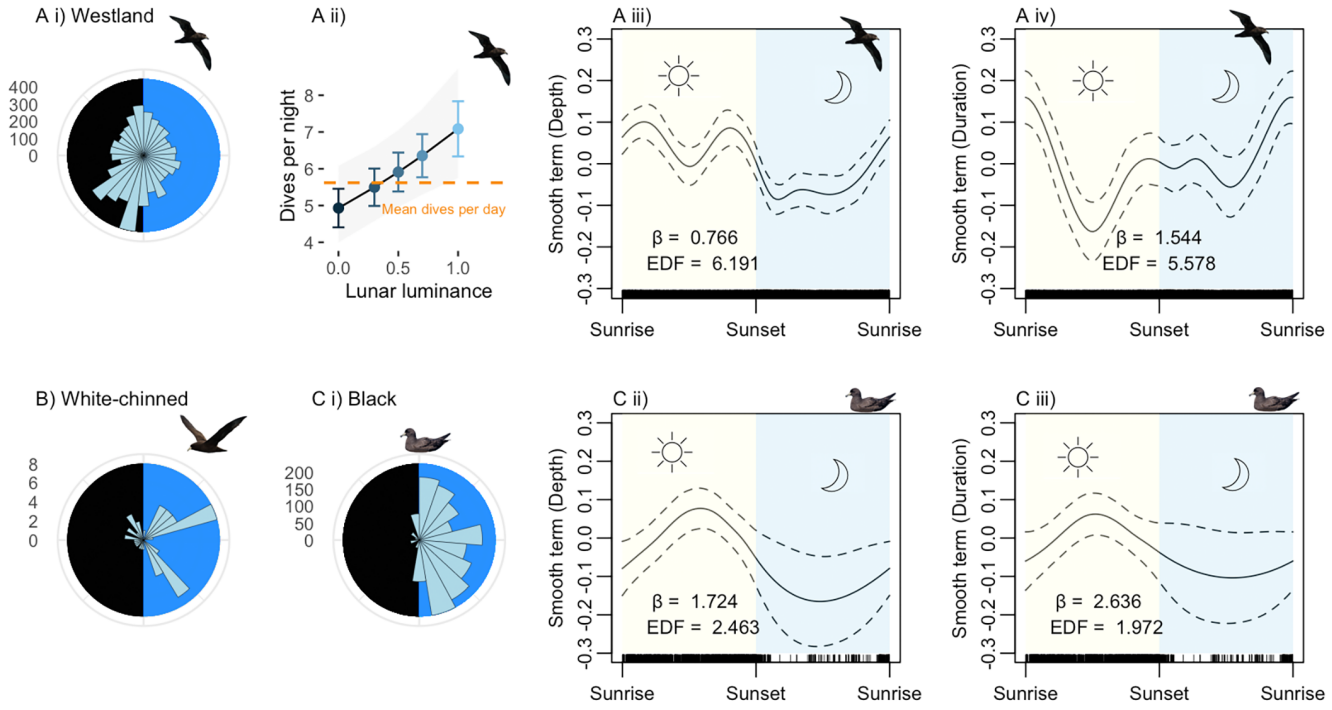


FIGURE 4 | Dive frequencies throughout day and night for (Ai) Westland Petrels, (B) White-chinned Petrels, and (C) Black Petrels. (Aii) shows the effect of lunar luminance on nighttime dive frequency of Westland Petrel. GLMM estimates included for each plot, all of which are significant. Results from GAMMs showing the smooth terms for the effect of time of day (standardised) on (A) Westland Petrel (iii) dive depth and (iv) duration, and (C) Black Petrel (ii) dive depth and (iii) duration.

4.6 | Conservation Implications

Our study captures vital information regarding the bycatch risk of Westland, White-chinned, and Black Petrels, and thus has the potential to guide the essential implementation of bycatch mitigation methods. Most prominently, our results highlight that effectively protecting these highly vulnerable *Procellaria* petrels and other deep diving seabirds from bycatch in pelagic

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and demersal longline fisheries requires simultaneous implementation of weighted branch lines achieving sink rates of at least 0.5 m/s, bird-scaring lines with a minimum 100 m aerial extent, and setting of hooks at night (Melvin et al. 2013).

The dive depths and speeds of *Procellaria* petrels shown in this study indicate current mitigation methods in pelagic longline fisheries are insufficient to prevent bycatch of these species when applied in isolation. The current perception in the Southern Hemisphere is that protecting pelagic longline hooks until hooks have reached a depth of 10 m ensures that they are largely out of range of *Procellaria* petrels. However, all species exceeded this depth, and the Black Petrel regularly does so, with 25.1% of dives deeper than 10 m. We also found descent rates for all species exceeded what is considered best practice sink rates in pelagic longlines (Figure 2) (ACAP 2024). All petrels' mean dive speeds were faster than the recommended hook sink rate of 0.5 m/s (ACAP 2024) and 50 g Procella heavy hook sink rate of 0.69 m/s (ACAP 2023a). With a pelagic longline fishing vessel typically setting at 7 knots (Keith 1999), even with best practice 0.5 m/s sink rates (ACAP 2024) hooks will only be at 13.9 m depth at the end of the 100 m aerial extent of the bird-scaring line (the recommended aerial extent; ACAP 2024), a depth that is well within the range of *Procellaria* petrels. Therefore, it is essential to also set hooks at night when many seabirds including Black Petrels are less active, and dives are shallower. Smaller vessels (e.g., < 35 m in length) may not have the superstructure suitable to accommodate tori lines with a 100 m aerial extent. Consequently, tori lines with a 75 m aerial extent are advised for smaller vessels (ACAP 2024). Even achieving a 75 m aerial extent can be challenging (Ochi 2022), but not impossible (Goad and Debski 2017), and thus these practical considerations further underscore the importance of combining different mitigation methods.

Dive depths from this study also have major implications for the design and implementation of modern mitigation approaches such as hook-shielding devices and underwater bait setters. Hook-shielding devices use pressure sensors to open at 10 m or 20 m depth (Goad et al. 2019; Sullivan et al. 2018). Our results suggest 20 m is the more appropriate threshold. Underwater bait setters are currently limited to 10 m (Ashworth et al. 2018), thus their efficacy would benefit from re-evaluation, particularly within the range of Black Petrels. If these devices alone cannot significantly reduce bycatch, combining them with bird-scaring lines and/or additional weighted branch lines could help protect hooks to 20 m depth.

Our study also has implications for bycatch mitigation methods in demersal longline fisheries. While sink rates in some demersal longline fisheries can exceed the dive speeds of most *Procellaria* petrel dives (e.g., Robertson et al. 2008), sink rates for most fisheries, including those within Aotearoa waters, are often slower than petrel descent rates (e.g., Goad and Olsen 2023). As for pelagic longline fisheries, weighted branch lines must therefore be used in combination with bird-scaring lines and night setting to provide adequate protection from deep diving seabirds such as *Procellaria* petrels. There is also high variability among demersal longline fisheries in target species and associated gear used. Some fisheries may require additional tailored bycatch mitigation methods, such as dropper floats (Goad et al. 2024), which help negate the influence that subsurface floats can have in slowing the sink rate of hooks. The development of custom/target-specific mitigation methods is still subject to ongoing investigations, and our results provide the necessary ecological context in which these methods should be developed.

We provide the most in-depth *Procellaria* petrel diving ecology study to date in which we analysed 12,767 individual dives, and our findings have wide-ranging implications for seabird conservation. As *Procellaria* petrels can expose other seabirds to bycatch by retrieving hooks from depths (Jiménez et al. 2012), tailoring mitigation measures to these deep divers has the potential to protect entire seabird communities from bycatch throughout *Procellaria* petrel ranges, from the Southern Ocean (Delord et al. 2010; Landers et al. 2011; Mischler et al. 2015) to the tropics (Fischer et al. 2023). Our results corroborate ACAP best practice advice for bycatch mitigation for longline fisheries from a behavioural ecology perspective, stipulating the use of three mitigation methods (weighted branch lines, bird-scaring lines, and night setting) in unison. This practice is already mandated in pelagic longline fisheries within the Aotearoa (New Zealand) Economic Zone and should similarly be required across these species' distributions. However, regulations need to be paired with compliance monitoring (e.g., human observers or electronic monitoring systems) to ensure implementation, but coverage is still largely inadequate in the Southern Ocean (e.g., Peatman et al. 2019). Combining effective mitigation requirements with adequate compliance monitoring throughout the range of these species will be required to effectively protect them and wider seabird communities.

Author Contributions

Maria Rosa Düssler, Johannes H. Fischer, Olivia Rowley, Igor Debski, Graeme A. Taylor, and Heiko U. Wittmer conceived the ideas and designed methodology; Maria Rosa Düssler, Johannes H. Fischer, Elizabeth Bell, Matt Charteris, Graeme Elliott, Graham C. Parker, Kalinka Rexer-Huber, Kate Simister, Kath Walker, and Heiko U. Wittmer collected the data; Maria Rosa Düssler and Olivia Rowley analysed the data; Maria Rosa Düssler led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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