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Movements and diving behaviour of white-chinned petrels: Diurnal variation and implications for bycatch mitigation

Caitlin K. Frankish[1,2] | Andrea Manica[2] | Joan Navarro[3] | Richard A. Phillips[1]

[1]British Antarctic Survey, Natural Environmental Research Council, Cambridge, UK

[2]Department of Zoology, University of Cambridge, Cambridge, UK

[3]Institut de Ciències del Mar (ICM-CSIC), Barcelona, Spain

Correspondence
Caitlin K. Frankish, Department of Zoology, University of Cambridge, Cambridge, UK.
Email: cakish36@bas.ac.uk

Abstract

1. Many seabirds dive to forage, and the ability to use this hunting technique varies according to such factors as morphology, physiology, prey availability, and ambient light levels. Proficient divers are more able to seize sinking baits deployed by longline fishing vessels and may return them to the surface, increasing exposure of other species. Hence, diving ability has major implications for mitigating incidental mortality (bycatch) in fisheries.

2. Here, the diving behaviour and activity patterns of the most bycaught seabird species worldwide, the white-chinned petrel (*Procellaria aequinoctialis*), tracked from Bird Island (South Georgia), are analysed. Three data sources (dives, spatial movements, and immersion events) are combined to examine diverse aspects of at-sea foraging behaviour, and their implications for alternative approaches to bycatch mitigation are considered.

3. The tracked white-chinned petrels (*n* = 14) mostly performed shallow dives (<3 m deep) of very short duration (<5 s), predominantly during darkness, but only 7 and 10% of landings in daylight and darkness, respectively, involved diving, suggesting that surface-seizing is the preferred foraging technique. Nonetheless, individuals were able to dive to considerable depth (max = 14.5 m) and at speed (max = 2.0 m·s^{-1}), underlining the importance of using heavy line-weighting to maximize hook sink rates, and bird-scaring lines (Tori lines) that extend for long distances behind vessels to protect hooks until beyond diving depths.

KEYWORDS
behaviour, birds, endangered species, fishing, ocean, tracking

1 | INTRODUCTION

Seabirds vary widely in the manner in which they exploit marine food resources, with diving providing a means of accessing prey at various depths in the water column (Shealer, 2002; Elliott et al., 2008). Knowledge of the diving ability of seabirds was revolutionized by the development of electronic time–depth recorders (TDRs) in the 1970s, which use pressure sensors (Kooyman & Campbell, 1971).

Physiological and anatomical adaptions to pressure, cold temperatures, low light levels, and breath-holding determine the maximum dive capabilities (in terms of depth and duration) of different species (reviewed in Ponganis, 2015). However, diving is energetically expensive in seabirds, and in practice the frequency and characteristics of dives can differ considerably within and among species according to local prey availability and distribution, ambient light conditions, individual energetic requirements, or the degree of inter- and intra-

specific competition for food (Croll et al., 1992; Peery et al., 2009; Regular et al., 2010; Quillfeldt et al., 2011; Navarro, Votier & Phillips, 2014).

Determining the extent of diving behaviour and ability across taxa has major conservation implications, as diving can increase the exposure of seabirds to anthropogenic threats (Waggitt & Scott, 2014; Tavares et al., 2017; Zhou, Jiao & Browder, 2019). In particular, incidental mortality (bycatch) of seabirds in longline fisheries has severely depleted the population sizes of many species, especially wide-ranging and long-lived albatrosses and petrels (Anderson et al., 2011; Phillips et al., 2016). These birds forage behind fishing vessels, attracted by discards (including offal) and baited hooks available during the deployment of longlines. Bycatch occurs when birds seize baits, are hooked and drown as the line sinks; proficient divers are most vulnerable as they are able to access baits at greater depths than surface-feeding species (Brothers, 1991; Rollinson, Dilley & Ryan, 2014; Rollinson et al., 2016). As a result, efforts to reduce bycatch in longline fisheries have focused on modifying gear configuration (e.g. required weight and spacing) to increase the rate at which lines sink, and use of bird-scaring (streamer or Tori) lines to protect baited hooks from attack while they are within seabird diving depths (Løkkeborg, 2011; Melvin, Guy & Read, 2014; Jiménez, Forselledo & Domingo, 2019). Knowledge of diving range and speed is therefore integral to effective mitigation, which, in turn, is key to the recovery of threatened seabird populations and ecosystem-based management of longline fisheries (Ryan & Watkins, 2002; Sánchez & Belda, 2003; Croxall & Nicol, 2004).

Diving ability among procellariform seabirds varies from minimal submersion to deep dives recorded in more specialized species (Prince, Huin & Weimerskirch, 1994; Weimerskirch & Sagar, 1996; Navarro, Votier & Phillips, 2014). Opportunistic *Procellaria* petrels both surface-seize and dive for prey down to 16 m depth; however, it remains unclear whether the latter hunting technique plays a dominant role in their foraging ecology (Huin, 1994; Barnes, Ryan & Boix-Hinzen, 1997; Freeman et al., 1997; Rollinson et al., 2016). In line with optimal foraging theory, animals are expected to favour strategies that maximize net energy gain, thus petrels may increase diving effort (rate, depth or duration) if this improves foraging success (Schoener, 1971). The white-chinned petrels (*Procellaria aequinoctialis*) breeding at South Georgia constitute the largest global population, and compete with a large diversity of sympatric seabirds for resources (Phillips et al., 2008). To co-exist, niche theory stipulates that these species should segregate in spatial, temporal, or trophic axes (Hutchinson, 1957; Schoener, 1974). White-chinned petrels are known to forage to a greater extent over the productive Patagonian Shelf than other seabirds from South Georgia, particularly during the incubation stage (Phillips et al., 2006). Diving may add an additional mechanism resulting in niche partitioning from albatrosses (Diomedeidae) and giant petrels (*Macronectes* spp.) and, combined with their foraging habitat specialization, may help explain the exceptionally high abundance of white-chinned petrels at South Georgia. Diving ability is also of relevance in the context of fisheries interactions, as white-chinned petrels are the most bycaught seabird in the Southern Ocean (Phillips et al., 2016).

In this study, high-resolution dive data (0.5-s sampling interval) were analysed, in combination with movement and immersion data, from incubating white-chinned petrels tracked from South Georgia during the 2009/10 breeding season. The aims were to: (1) build a detailed picture of the foraging behaviour of white-chinned petrels during an energetically expensive period of their annual cycle; and (2) consider the implications for the design and performance of seabird bycatch mitigation measures in longline fisheries. Specifically, the distribution of foraging trips and diving events were mapped to gain an understanding of exposure to fishing vessels, and metrics of foraging behaviour (landing and diving events) were compared between daylight and darkness. In addition, diving descent rates were calculated for comparison with measured and recommended line sink rates for pelagic and demersal longline fishing vessels operating in the Southern Ocean.

2 | METHODS

2.1 | Study area and fieldwork procedure

Fieldwork was conducted on subantarctic Bird Island (54°00′S, 38°03′W), South Georgia, which lies 300 km south of the Antarctic Polar Front in the south-west Atlantic Ocean (Figure 1). Due to high productivity around South Georgia and the Antarctic Peninsula, this island hosts millions of pairs of breeding seabirds in one of the world's densest aggregations (Croxall & Prince, 1980; Atkinson et al., 2001; Clarke et al., 2012). It is a globally important breeding site for many species, including white-chinned petrels, which have been steadily declining since the 1970s due to fisheries bycatch (Martin et al., 2009). Fishing effort is restricted around South Georgia during their austral breeding season (CCAMLR, 2016), but white-chinned petrels forage almost exclusively over the Patagonian Shelf when incubating; where multiple pelagic and demersal fleets have reported high seabird bycatch rates (Phillips et al., 2006; Jiménez et al., 2010; Favero et al., 2013). Illegal, unreported, and unregulated fishing activities may also be high, and these vessels are highly unlikely to use bycatch mitigation (Agnew et al., 2009).

Sixteen incubating adult white-chinned petrels were tracked from Bird Island during the 2009/10 breeding season (3 December 2009–16 January 2010). Birds were fitted with Mk19 geolocator-immersion logger (2.6 g; British Antarctic Survey, Cambridge) attached by cable ties to a plastic leg ring, and a G5 time-depth recorder (TDR; 6.5 g, 12 × 36.5 mm; Cefas Technology Ltd) attached with Tesa® tape to the base of 2–3 tail rectrices. Mean body mass ± standard deviation of tracked white-chinned petrels was 1,364 ± 100 g, and the total mass of devices (geolocators and TDRs) including attachments was therefore far below the 3% threshold of body mass beyond which deleterious effects are more common in pelagic seabirds (Phillips, Xavier & Croxall, 2003). Birds were of unknown sex.
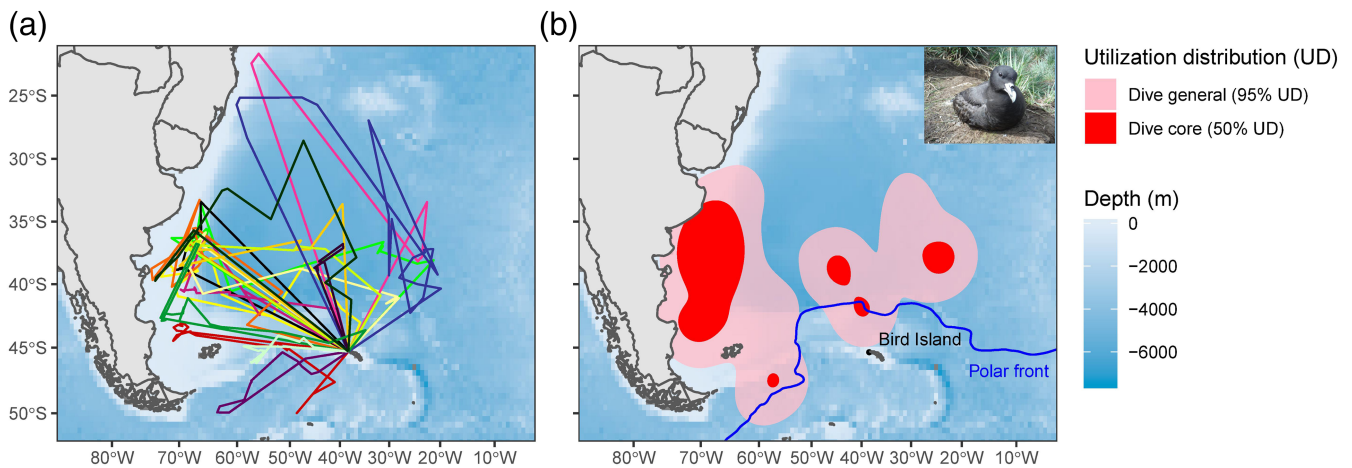
FIGURE 1 (a) Foraging trips of 15 incubating white-chinned petrels tracked from Bird Island (South Georgia) during the 2009/10 breeding season using geolocators. Locations were estimated using the 'ProbGLS' package, and individual foraging trips are represented by different colours. (b) Core (50%) and general (95%) utilization distributions of diving events

2.2 | Tracking data processing

Geolocators were retrieved from 15 of the 16 instrumented birds in December 2009–January 2010. Locations during foraging trips were estimated from the raw light intensities recorded by the geolocator-immersion loggers according to Merkel et al. (2016). Twilight events were first estimated using the function 'preprocessLight' function in the 'TwGeos' package, with a threshold setting of 2 lux, an offset of 12 hours and a maximum light level of 74,418.6 lux. Locations were then computed from the twilight events using the 'prob_algorithm' function in the 'probGLS' package. This function uses an iterative, forward-step-selection, probabilistic algorithm that incorporates information on various sources of uncertainty, the behaviour of the study species, and the characteristics of the environment to generate the most likely movement path (Table S1). Two locations, corresponding to local midday and midnight, were generated per day with a median error of up to 185 km (Merkel et al., 2016). Resulting points were removed if they required unrealistic flight speeds (>35 km·h^{-1} sustained over a 48-h period; Phillips et al., 2004), or for the bird to cross over land. The loggers also tested for saltwater immersion every 3 s, recording the time of transitions between wet/dry states that lasted ≥6 s, providing the timing and duration of flights and landings. White-chinned petrels are burrow-nesting birds, and depart and return to their burrows during darkness, making it difficult to accurately estimate the start and end times of foraging trips. Therefore, foraging trips were trimmed to the first and last-recorded immersion event.

TDRs were retrieved from 14 of the 15 birds recaptured in 2009/10 (one had moulted its tail feathers). TDRs were programmed to record pressure continuously at a low sampling interval (3- and 5-second intervals; see Table S2 for full sampling regime) every day (four birds) or every third day (10 birds). A fast-logging mode was also set to record pressure at a high sampling rate (0.5 s), activated by entry into water. A comparison of the dives identified post-processing

(detailed below) indicated there was little difference between the recording modes in terms of the number and timing of dive events (Table S3). A higher number of dives were identified from the continuous dive recording datasets; however, these dives mostly consisted of a single data point (and were likely to be noise), and the fast-logging mode detected short dives missed by the coarser sampling regime (Table S3). Therefore, to standardize the comparison of diving behaviour across all tracked birds, only the fast-logging data were used for subsequent analyses. Continuous time-series were generated from these data by manually setting depth to 0 m in between the dives (Figure S1). Zero offset correction was then carried out using the function 'calibrateDepth' in the package 'diveMove' (Luque & Fried, 2011). This function uses recursive filtering and a diving threshold to correct for noise and drift in the depth sensor, and to identify diving behaviour. Dive threshold was set at 1 m depth, and dives that lasted <1 s, or were very deep (>10 m) with few data points (<5) were considered to be noise or recording errors and hence removed, resulting in a total sample size of 895 dives from 14 individual birds.

2.3 | Analysis of immersion and dive data

Approximate dive locations were estimated by interpolating the twice-daily geolocator positions, and the core (50%) and general (90%) kernel density distributions of dives generated using the R package 'adehabitatHR' (Calenge, 2006). A grid size of 5 km and a smoothing parameter of 185 km were chosen to account for geolocation error (Merkel et al., 2016). Kernel distributions of dive events were overlaid on the extent of Exclusive Economic Zones (Flanders Marine Institute, 2014), and Statistical Areas, Subareas, and Divisions used by the Convention for the Conservation of Antarctic Marine Living Resources (CCAMLR; https://data.ccamlr.org/dataset/statisticalareassubareasanddivisions (Accessed 27 February 2020)). The kernels were also overlaid on the main areas of operation during

TABLE 1 Dive characteristics of white-chinned petrels tracked from Bird Island (South Georgia) tracked during the incubation period in the 2009/10 breeding season

Ring	Trip	Start trip[a]	End trip[b]	Duration (days)	N days dive data: N days dives	Dives per day Max	Dives per day Mean ± SD
HT65341	1	2009-12-05	2009-12-20	15.13	5: 2	10	8.50 ± 2.12
HT65342	1	2009-12-11	2009-12-25	14.83	5: 4	61	20.75 ± 27.13
HT65343	1	2009-12-07	2009-12-18	11.48	4: 4	4	2.50 ± 1.73
HT65344	1	2009-12-07	2009-12-10	3.55	1:0	-	-
HT65344	2	2009-12-13	2009-12-22	9.44	3:0	-	-
HT65344	3	2009-12-24	2009-12-29	5.66	2: 1	12	-
HT65345	1	2009-12-07	2009-12-19	12.75	4: 2	10	7.50 ± 3.54
HT65346	1	2009-12-19	2009-12-25	6.19	2: 2	96	80.50 ± 21.92
HT65347	1	2009-12-17	2009-12-27	10.26	4: 2	11	7.00 ± 5.66
HT65348	1	2009-12-06	2009-12-19	13.73	5: 4	19	9.00 ± 8.04
HT65350	1	2009-12-06	2009-12-18	12.65	5: 3	16	12.67 ± 3.51
MA13701	1	2009-12-18	2010-01-01	14.40	4: 4	25	14.75 ± 10.08
MA13702	1	2010-01-01	2010-01-14	13.28	14: 10	38	14.50 ± 10.72
MA13703	1	2009-12-26	2010-01-10	15.51	16: 9	8	4.11 ± 3.10
MA13704	1	2009-12-24	2010-01-12	19.35	19: 13	82	17.31 ± 27.90
MA13705	1	2009-12-28	2010-01-08	11.78	12: 7	29	6.14 ± 10.24
MA13706	1	2010-01-03	2010-01-14	11.73	TDR lost		

Note: N days dive data = number of days within the foraging trip with dive data; N days dive = number of days within the foraging trip during which dives took place; SD, standard deviation.

[a]Start of trip corresponds to the first immersion event.

[b]End of trip here corresponds to the last immersion event.

[c]Values exclude all negative descent rates (i.e. when the bird ascended slightly during the descent phase of a dive).

TABLE 1 Continued

Ring	Dive duration (s)			Dive depth (m)			Descent rate (m·s⁻¹)[c]		
	Max		Mean ± SD	Max		Mean ± SD	Max		Mean ± SD
	Daylight	Darkness		Daylight	Darkness		Daylight	Darkness	
HT65341	9.50	14.00	5.38 ± 3.67	4.87	6.87	3.32 ± 1.45	1.50	1.50	0.81 ± 0.53
HT65342	14.00	16.00	5.26 ± 3.59	6.75	8.50	3.71 ± 1.78	1.56	1.68	0.94 ± 0.46
HT65343	23.50	8.00	9.05 ± 7.40	12.21	3.03	5.05 ± 3.90	1.56	0.88	0.88 ± 0.47
HT65344	-	-	-	-	-	-	-	-	-
HT65344	-	-	-	-	-	-	-	-	-
HT65344	20.50	5.00	6.25 ± 5.94	4.21	4.00	3.11 ± 0.87	1.26	1.32	0.80 ± 0.46
HT65345	30.50	23.00	10.57 ± 8.37	8.28	4.09	4.22 ± 1.93	1.50	0.82	1.02 ± 0.34
HT65346	19.00	12.50	3.69 ± 2.64	7.81	5.03	2.23 ± 0.77	1.56	1.26	0.46 ± 0.37
HT65347	2.50	-	1.64 ± 0.66	2.78	-	1.94 ± 0.40	0.32	-	0.21 ± 0.08
HT65348	17.50	13.50	3.07 ± 3.68	6.90	6.68	2.54 ± 1.46	1.32	1.32	0.59 ± 0.57
HT65350	13.00	10.50	5.05 ± 3.43	6.68	4.18	3.21 ± 1.29	1.62	1.38	1.00 ± 0.43
MA13701	22.00	3.50	3.58 ± 4.20	14.5	3.06	3.01 ± 2.32	1.82	1.20	0.85 ± 0.48
MA13702	18.00	23.00	5.03 ± 3.82	8.62	11.40	2.85 ± 1.48	2.00	1.56	0.75 ± 0.53
MA13703	20.00	12.00	6.64 ± 5.29	7.78	5.96	3.33 ± 1.72	1.62	1.56	0.87 ± 0.43
MA13704	12.50	16.00	4.81 ± 3.35	7.06	6.00	2.44 ± 1.09	1.56	1.50	0.68 ± 0.42
MA13705	7.50	13.50	4.33 ± 2.85	3.18	3.37	2.11 ± 0.46	0.94	0.64	0.32 ± 0.21
MA13706									

Note: N days dive data = number of days within the foraging trip with dive data; N days dive = number of days within the foraging trip during which dives took place; SD, standard deviation.

[a]Start of trip corresponds to the first immersion event.

[b]End of trip here corresponds to the last immersion event.

[c]Values exclude all negative descent rates (i.e. when the bird ascended slightly during the descent phase of a dive).

December and January of demersal longline vessels from Argentina and the Falklands Islands from 1997 to 2007, which were the most recent publicly available data by month (Tuck et al., 2016), and of pelagic longline vessels operating under the jurisdiction of the International Commission for the Conservation of Atlantic Tunas (ICCAT) from 2000 to 2010 (Task II catch/effort; https://www.iccat.int/en/accesingdb.html (Accessed 27 February 2020).

To investigate the effects of ambient light levels on at-sea activity (including diving) patterns, immersion (wet) events and dives were assigned to daylight or darkness according to the timing of twilight using the 'TwGeos' package. The following mean activity metrics were calculated separately for the daylight and darkness periods of each foraging trip; (1) proportion of time spent wet; (2) landing rate (wet events, i.e. wet-dry transitions, per hour); (3) wet bout length (minutes); (4) dry bout length (minutes); (5) dive duration (minutes, calculated using function 'divestats'); (6) dive depth (metres, calculated using function 'divestats'); (7) maximum descent rate (m·s^{-1}, calculated as the maximum of speeds travelled by a bird between every consecutive point during the descent phase); (8) dive rate (dives·h^{-1}); and (9) proportion of landings that were dives. One bird completed three foraging trips, but only dived during one of these, and metrics were calculated for this trip only (TRACKID: 19013_3, Table 1). The normality of metrics (1–9) were investigated using the Shapiro–Wilk test, and parametric paired t-tests or non-parametric Wilcoxon signed-rank tests were used, as appropriate, to compare metrics between daylight and darkness.

Finally, every dive was assigned to a maximum depth band (1-m depth intervals; 1–2 m, 2–3 m, etc.), and average descent rates (i.e. diving speeds) of white-chinned petrels over a range of depth bands were compared with longline sink rates measured at sea on pelagic and demersal vessels operating in the Southern Ocean (see Table S4 for references).

All data analyses were conducted with the software R 3.6.2. (R Core Team, 2020). In results, means ± standard deviations are presented, unless indicated otherwise.

3 | RESULTS

3.1 | Overall foraging distribution and diving behaviour

Incubating white-chinned petrels tracked during the 2009/10 breeding season from Bird Island foraged over a large area mainly west and north-west of Bird Island on trips that lasted 3.6–19.3 days (Figure 1a, Table 1). Most birds travelled directly west to the Patagonian Shelf (45–25°S), where most diving events occurred (Figure 1b). A smaller number of birds travelled to the north and north-east of South Georgia, and two to the south-west (~50°S; Figure 1a), resulting in four, more restricted diving hotspots over oceanic waters, around the Antarctic Polar Front, and south-east of the Falklands (Figure 1b). The core diving area (50% kernel polygon) on the Patagonian Shelf occurred largely within the EEZs of Argentina and the Falkland Islands, and overlapped extensively with demersal longline effort in December and January (Figure 2b). The northern portion of this area also overlapped with pelagic longline fleets operating within the jurisdiction of ICCAT (Figure 2c). All diving hotspots occurred outside of CCAMLR subarea 48.3, where demersal longline fishing is prohibited during summer months, when white-chinned petrels are breeding (Figure 2a; CCAMLR, 2016).

Diving behaviour varied considerably among individuals in terms of number of dives per day (range: 0–96), duration (1–30.5 s), maximum depth (1.03–14.46 m), and maximum descent rates
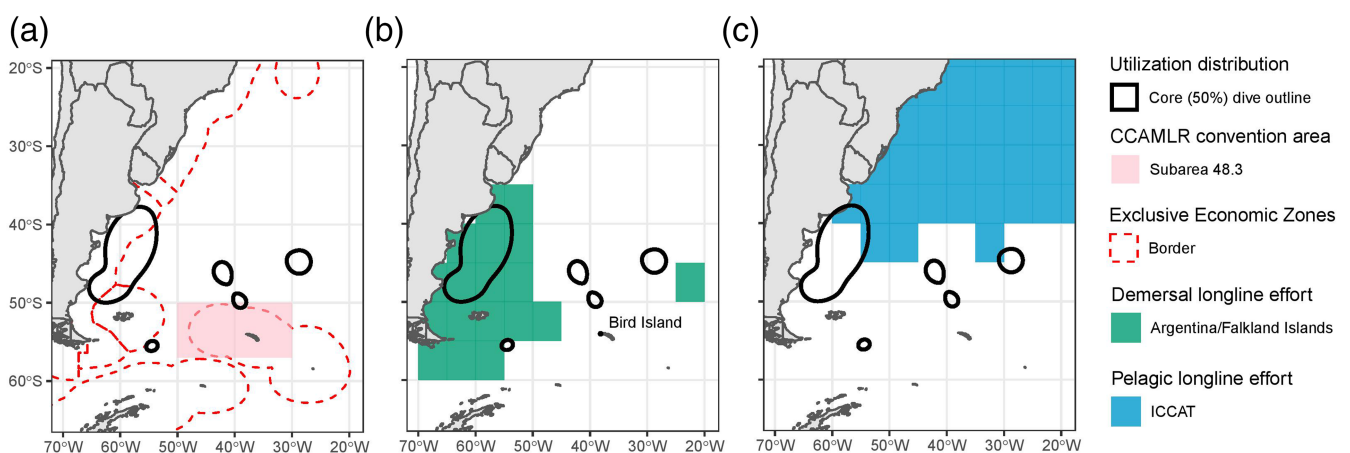

FIGURE 2 Core (50%) utilization distribution of diving events from incubating white-chinned petrels tracked from Bird Island (South Georgia) during the 2009/10 breeding season in relation to (a) Exclusive Economic Zones and Convention for the Conservation of Antarctic Marine Living Resources (CCAMLR) convention subarea 48.3, (b) mean 5 × 5° grid cell distribution of demersal longline fishing for Argentina and the Falkland Islands (averaged for December–January over 1997–2007), and (c) mean 5 × 5° grid cell distribution of pelagic longline fishing of fleets operating under the jurisdiction of the International Commission for the Conservation of Atlantic Tunas (ICCAT) (averaged for December–January over 2000–2010)

(0.06–2.00 m.s^{-1}); however, on average individuals made few (<10 dives·day^{-1}), shallow (<3 m depth), and short dives (<5 s; Table 1 and Figure 3).

3.2 | Diurnal variation in immersion and dive metrics

There was strong evidence for diurnal variation in the diving behaviour and other at-sea activities of tracked white-chinned petrels. Birds were more active during darkness than daylight; they spent a significantly higher proportion of time wet (Figure 4a and Table 2), landed more often on the water (Figure 4b and Table 2), and landing bouts were of shorter duration (Figure 4c and Table 2). Wet and dry bouts were significantly shorter in duration during darkness than daylight (Figure 4c,d and Table 2), suggesting birds both rested and undertook longer transit flights during the day. Birds also dived significantly more often during darkness than daylight (Figure 5d and Table 2), but those dives were significantly less deep (Figure 5a and Table 2), and descent rates were slower (Figure 5c and Table 2). Dives were also shorter on average during darkness than daylight, but this difference was not significant (Figure 5b and Table 2). Only 7 and 10% of landings during daylight and darkness, respectively, were dives (Figure 5e and Table 2), suggesting that

surface-feeding is the dominant foraging strategy regardless of ambient light-levels.

3.3 | Comparison of descent speeds with published longline sink rates

Mean descent rates of white-chinned petrels increased on average with increasing dive depth (Figure 6), and plateaued around the 5–6 m maximum depth band (~1.0 m·s^{-1}, although one bird descended on average >1.5 m·s^{-1} during two separate dives). While descent rates were much slower during the shallow dives (median dive descent rate <0.5 m·s^{-1} for dives up to 3 m depth), birds descended at >0.9 m·s^{-1} during at least one dive in each maximum depth band, suggesting this descent speed can be achieved across all diving depths. This speed exceeds recommended line sink rates for both pelagic and demersal longlines on vessels operating in the Southern Ocean, as well as the fastest sink rate recorded within a pelagic longline fishery sustained over >3 m (0.51–0.61 m·s^{-1} achieved with a 60-g safe-lead swivel placed at the hook; see Figure 6 and Table S4 for full gear configuration and experimental details). The only demersal longline fishery in the Southern Ocean in which a faster sink rate was achieved was in an experiment using the Chilean net-sleeve ('cachalotera') gear configuration, which recorded sink rates of 1.47 m·s^{-1} at 2–5 m depth by
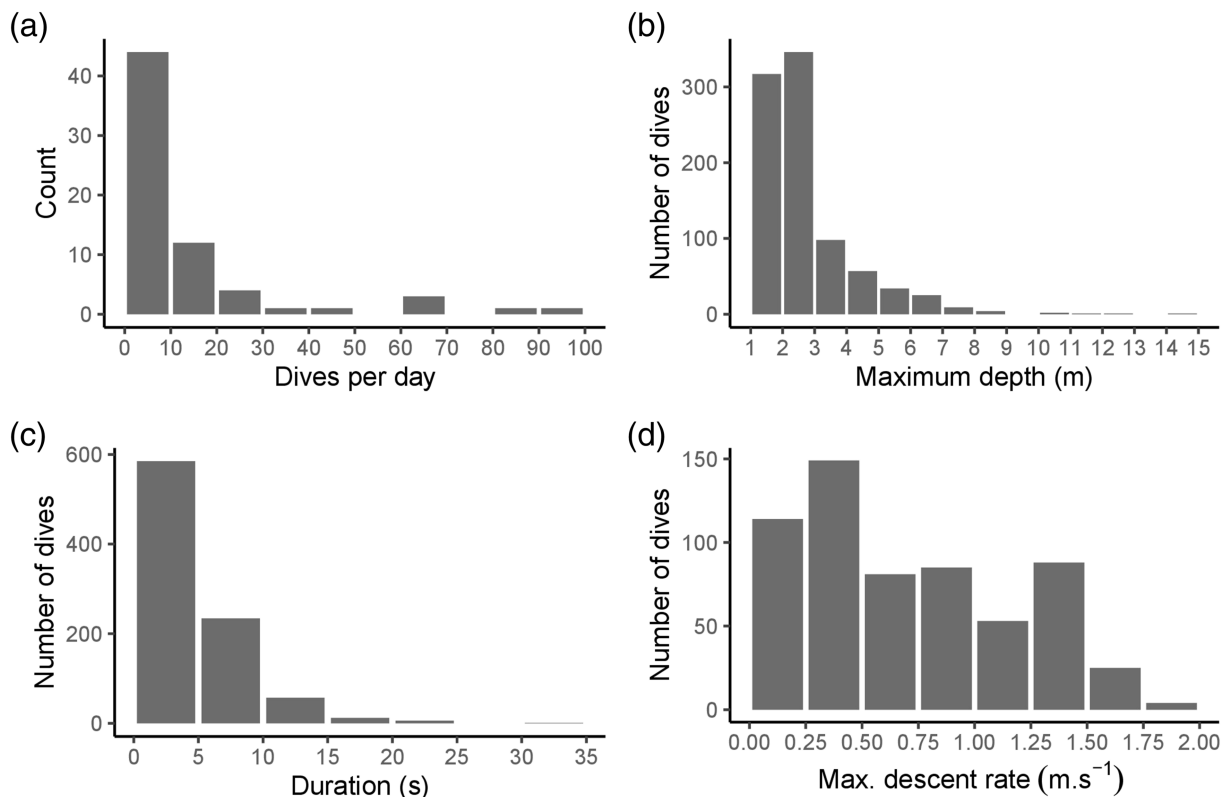

FIGURE 3 Frequency distributions of dive metrics of 14 incubating white-chinned petrels tracked from Bird Island (South Georgia) during the 2009/10 breeding season; (a) total dives per day, (b) maximum dive depths, (c) dive durations, and (d) maximum dive descent rates
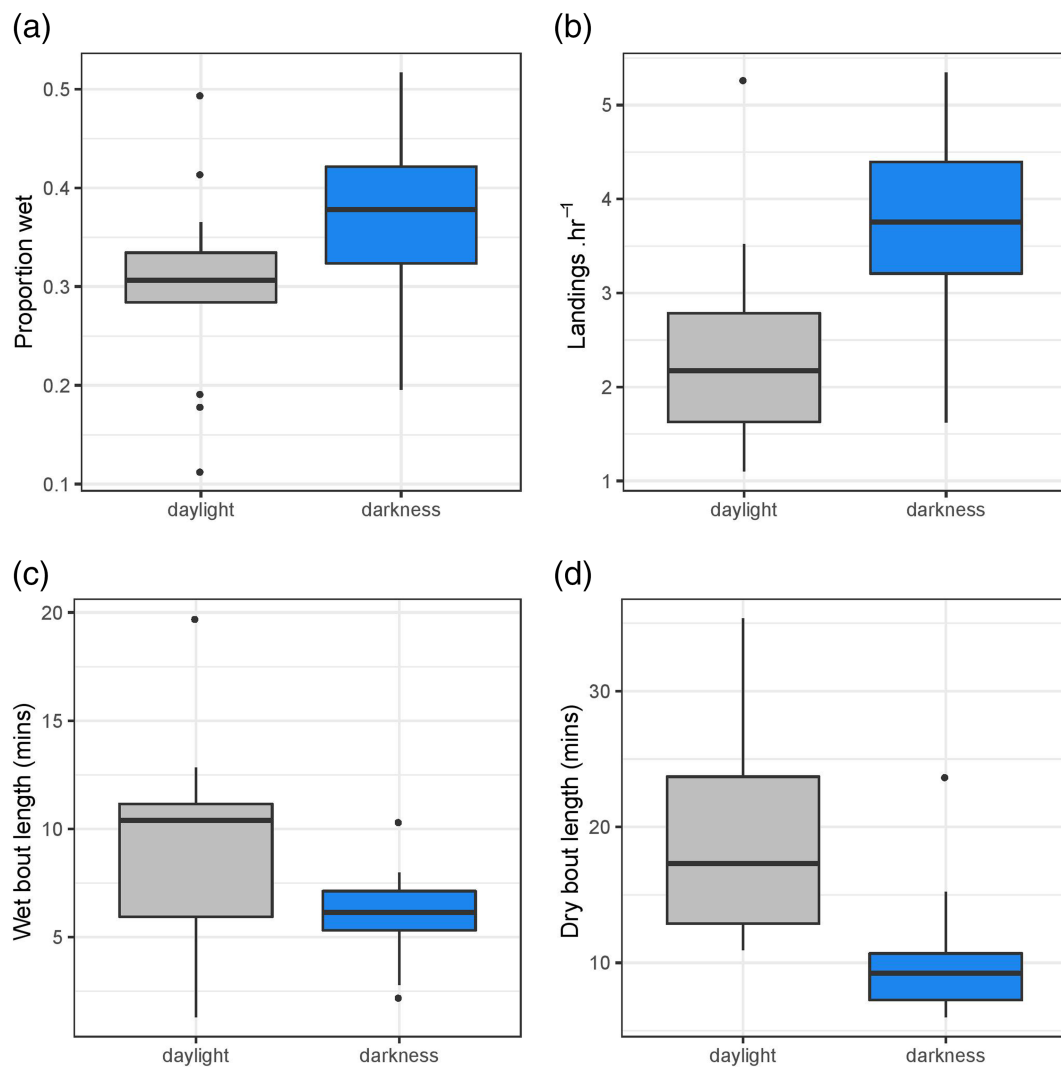
FIGURE 4   Comparison of activity (immersion) patterns between daylight and darkness of 15 incubating white-chinned petrels tracked from Bird Island (South Georgia) during the 2009/10 breeding season

TABLE 2   Comparison of dive and other activity (immersion) metrics between daylight and darkness of white-chinned petrels tracked from Bird Island (South Georgia) during the 2009/10 breeding season

| Metric | Sample size | Sample mean ± standard deviation | | Paired *t*-test/Wilcoxon signed-ranks test |
		Daylight	Darkness	
(1) Proportion wet	15	0.30 ± 0.10	0.36 ± 0.93	t_{14} = −3.310, *P* = 0.005
(2) Landing rate (landings·h^{-1})	15	2.35 ± 1.07	3.68 ± 1.04	t_{14} = −2.337, *P* = 0.013
(3) Length wet bouts (min)	15	9.01 ± 4.65	6.06 ± 1.98	V = 100, *P* = 0.022
(4) Length dry bouts (min)	15	19.10 ± 7.00	10.10 ± 4.55	V = 107, *P* = 0.005
(5) Dive depth (m)	13[a]	3.57 ± 1.18	2.65 ± 0.58	V = 78, *P* = 0.021
(6) Dive duration (s)	13[a]	6.31 ± 2.94	4.60 ± 1.60	V = 115, *P* = 0.124
(7) Max descent rate (m·s^{-1})	13[a]	0.89 ± 0.19	0.67 ± 0.25	t_{12} = 2.756, *P* = 0.017
(8) Dive rate (dives·h^{-1})	13[a]	0.14 ± 0.18	0.42 ± 0.54	V = 11, *P* = 0.013
(9) Proportion landings that were dives	13[a]	0.07 ± 0.05	0.10 ± 0.09	V = 37, *P* = 0.059

Note: Paired *t*-tests or Wilcoxon signed-rank tests used for normal or non-normal data, respectively. Significant differences (*P* < 0.05) are highlighted in bold.

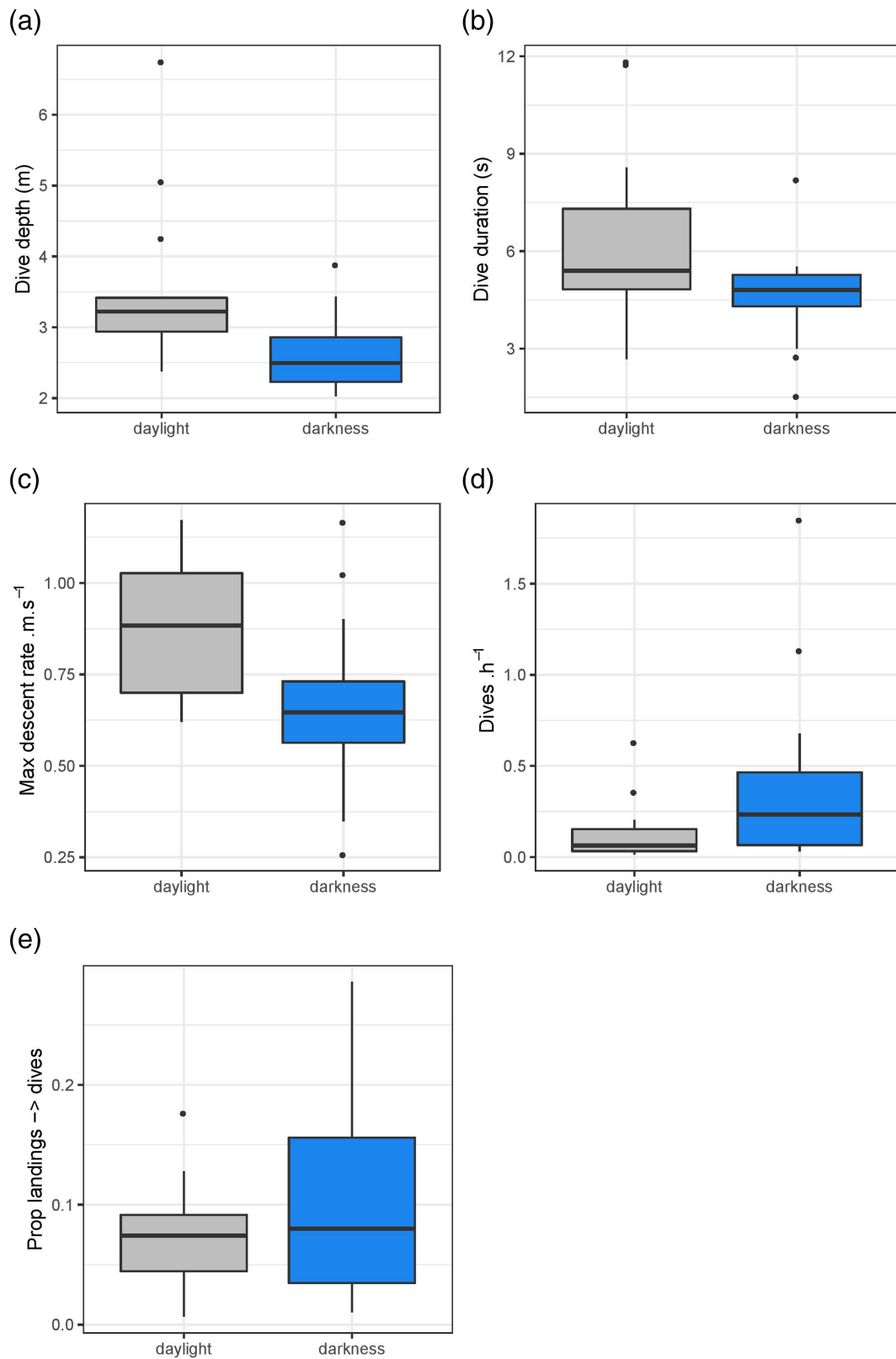[a]One time–depth recorder was not recovered, and one bird did not dive during darkness.

FIGURE 5 Comparison of dive behaviour of 13 white-chinned petrels between daylight and darkness. Fifteen incubating white-chinned petrels were tracked from Bird Island (South Georgia) during the 2009/10 breeding season, Time-Depth Recorders were retrieved from 14 birds, and one bird did not dive during darkness
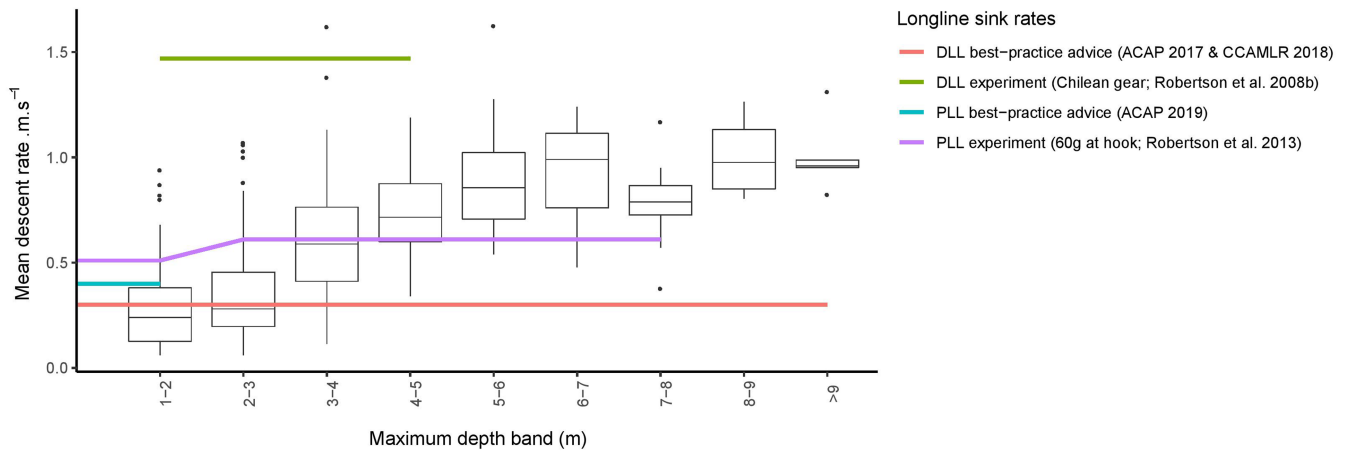
FIGURE 6 Mean diving descent rates in relation to maximum depth achieved by incubating white-chinned petrels tracked from Bird Island (South Georgia) during the 2009/10 breeding season. Fastest published and advised line sink rates for pelagic (PLL) and demersal (DLL) longline fisheries operating in the Southern Ocean are shown for comparison (see Table S4 for full details). Depth range over which line sink rates extend represent the range over which they were measured, or to which best-practice advice extends

attaching 6-kg steel weights at 40-m intervals along longlines (Figure 6 and Table S4).

4 | DISCUSSION

By combining individual movement, immersion, and TDR data, this study confirms that white-chinned petrels dive at the Patagonian Shelf, and provides new insights into their at-sea activity patterns, particularly the importance of nocturnal feeding. These new findings underline the opportunistic foraging abilities of this threatened seabird, and are discussed in the contexts of their foraging ecology and the effective design of bycatch mitigation measures.

4.1 | Insights into the foraging ecology of white-chinned petrels

The diving capabilities of white-chinned petrels from South Georgia were comparable to previous studies in terms of maximum depth, duration, and descent rate; 14.5 m, 30.5 s, and 2 m·s^{-1} (this study) versus 12.8–16.1 m, 22 s, and 1.58 m·s^{-1} (Huin, 1994; Rollinson, Dilley & Ryan, 2014). White-chinned petrels possess ocular and osteological adaptations to aquatic lifestyle (Kuroda, 1954; Martin & Prince, 2001), and are more competent divers than southern hemisphere albatrosses, of which the deepest dive recorded (to 12.4 m, based on a capillary-tube depth gauge) was by a light-mantled albatross (*Phoebetria palpebrata*; Prince, Huin & Weimerskirch, 1994; Hedd et al., 1997; Huin & Prince, 1997). In terms of dive depth, however, the white-chinned petrel is far surpassed in capability by more specialized procellariform species, including the short-tailed shearwater (*Ardenna tenuirostris*; 71 m; Weimerskirch & Cherel, 1998), and also the sympatric South Georgian diving petrel (*Pelecanoides*

georgicus; 18.1 m; Navarro, Votier & Phillips, 2014). Indeed, only a very low proportion (7–10%) of landings by the tracked white-chinned petrels in the study involved diving, implying that surface-seizing of prey is their primary hunting technique. As diving is energetically expensive, especially in shallow waters (Wilson et al., 1992), individuals may only pursue prey underwater when conditions are suitable, or to obtain prey that have a high energy or nutrient content (Peery et al., 2009; Dean et al., 2013).

Regardless of foraging technique, white-chinned petrels are capable of hunting during daylight and darkness (Harper, 1987; Mackley et al., 2011; Rollinson, Dilley & Ryan, 2014). Based on the pattern in landings seen here, birds foraged most actively at night. The extent to which this behaviour is targeted at natural prey versus fisheries discards is unknown. White-chinned petrels from South Georgia overlap in distribution with longline fisheries operating along the Patagonian coast during the breeding and non-breeding season, and may specialize in scavenging behind vessels that set their lines at night (Phillips et al., 2006; Robertson et al., 2006; Laich & Favero, 2007; this study). However, during chick rearing, this species predominantly feeds on Antarctic krill (*Euphausia superba*), squid, and myctophid fish, of which some species vertically migrate to shallower depths during darkness (Roper & Young, 1975; Croxall et al., 1985; Croxall et al., 1995; Berrow & Croxall, 1999; Shreeve et al., 2009). These birds may thus be well-adapted to detecting prey under low light levels, and diving at night may allow individuals to spot prey with ventral bioluminescence from below (Imber, 1976; Young, 1977; Croxall et al., 1995). Deploying stomach temperature loggers would provide additional insight into whether individuals rest on the water during the darkest periods of the night, or whether they continue to feed, potentially using the sit-and-wait method (Wilson et al., 1995; Weimerskirch, Wilson & Lys, 1997; Catry et al., 2004).

In contrast, bouts of flying or sitting on the water were of significantly longer duration during daylight. As these birds are

proficient nocturnal hunters, individuals may choose to rest for long periods during daylight, and avoid competing with large aggregations of diurnal albatrosses and petrels with which they overlap in distribution (e.g. sooty shearwaters, *Puffinus griseus*, or black-browed albatrosses, *Thalassarche melanophris*, from the Falkland Islands; Huin, 2002; Hedd et al., 2014). White-chinned petrels transit rapidly, taking just 1–2 days to move between the colony at South Georgia and their main prey-rich foraging grounds at the Patagonian Shelf, which may account for the long flight bouts. It is unclear why these transit flights would be restricted to daylight, however, as previous research concluded that these birds were just as proficient at flying during darkness (Berrow, Wood & Prince, 2000; Mackley et al., 2011). As individual flight bouts were on average much shorter than in non-breeding white-chinned petrels commuting to their wintering areas (∼19 vs. 107 min), it is possible that the long daylight flights indicate an alternative foraging strategy involving prey searching over larger spatial scales than in darkness (Weimerskirch, Wilson & Lys, 1997; Mackley et al., 2011). This difference would presumably reflect some limitation in their ability to detect more distant prey from the air when light levels are low, which was suggested as the main factor limiting nocturnal foraging of albatrosses (Phalan et al., 2007).

4.2 | Relevance of diving behaviour for the design of bycatch mitigation measures

Demersal longline fishing for Patagonian toothfish (*Dissostichus eleginoides*) historically resulted in high rates of white-chinned petrel bycatch near the colonies at South Georgia (Dalziell & Poorter, 1993). However, seasonal closure of this fishery (in CCAMLR Subarea 48.3; see Figure 2) alongside the implementation of several mitigation measures; prohibition or limiting of offal discharge, use of bird-scaring devices, night-setting, and heavy line-weighting, has drastically reduced bycatch of seabirds, including white-chinned petrels (Croxall, 2008). Birds from the South Georgia population, however, commute to the Patagonian shelf to forage during incubation, where they overlap in distribution with other longline fisheries for which there is recorded bycatch; namely demersal vessels from the Falklands Islands targeting Patagonian toothfish, to a lesser extent vessels from Argentina which also target pink cusk-eel (*Genypterus blacodes*) and yellow-nose skate (*Dipturus chilensis*), and pelagic vessels operating under the jurisdiction of ICCAT targeting tuna, swordfish, and pelagic sharks (Phillips et al., 2006; Otley, Reid & Pompert, 2007; Bugoni et al., 2008; Jiménez et al., 2010; Favero et al., 2013). The major diving hotspot of white-chinned petrels in the study overlapped with these fishing areas, confirming their susceptibility to bycatch during incubation. The majority of the South Georgia population also uses this productive region during the pre-laying exodus and nonbreeding season (Phillips et al., 2006), and so is susceptible to bycatch for much more of the year than other procellariform species from South Georgia (Phillips et al., 2016; Clay et al., 2019; Frankish et al., 2020). Therefore, although dive capabilities (maximum depth and descent

rates) may vary somewhat among seasons (Rollinson, Dilley & Ryan, 2014), recorded dive characteristics in this study provide a relevant baseline for assessing the design and implementation of effective mitigation measures in the south-west Atlantic.

Although white-chinned petrels are far from the deepest-diving of flying seabirds (see review in Navarro, Votier & Phillips, 2014), their mean descent speeds are comparable to those of other bycaught seabird species in the Southern Ocean, including more proficient divers such as the great shearwater (*Ardenna gravis*, >0.9 m·s^{-1}; Hedd et al., 1997; Ronconi, Ryan & Ropert-Coudert, 2010; Quillfeldt et al., 2011; Bell, 2016; Rollinson et al., 2016). As this velocity across dives of varying depth exceeds all but one published line sink-rate (Table S4), it is apparent that white-chinned petrels and other species are capable of reaching sinking longline hooks within their diving range, and facilitate secondary catch of poorer divers such as albatrosses by returning those hooks on long leaders (snoods) to the surface (Jiménez et al., 2012). Maximizing line sink rates is thus an essential mitigation measure as recommended by the Agreement on the Conservation of Albatrosses and Petrels (ACAP, 2017; ACAP, 2019), which can be achieved in pelagic longline fleets by adding sliding leads (recommended minimum standards: ≥4 m·s^{-1} using 40, 60, or 80 g within 0.5, 1, or 2 m of the hook (ACAP, 2019); maximum of 0.51–0.61 m·s^{-1} achieved by using 60 g at the hook (Robertson, Candy & Hall, 2013), and in demersal longline fleets by attaching weights close together on the mainline (recommended minimum standards: >0.3 m·s^{-1} using 5-kg weights at 40-m intervals; ACAP, 2017; maximum of 0.37–0.44 m·s^{-1} achieved in autoline system using 6.5-kg weights at 35-m intervals, and maximum of 0.33–0.80 m·s^{-1} achieved in Spanish system using 8-kg steel weights at 40-m intervals (Robertson, 2000; Robertson et al., 2008)). Alternatively, the Chilean net-sleeve demersal longline system, developed to reduce depredation by killer (*Orcinus orca*) and sperm (*Physeter microcephalus*) whales, has virtually eliminated seabird bycatch as baited hooks are directly above weights, ensuring a very high initial line sink rate (up to 1.47 m·s^{-1}; Moreno et al., 2006; Moreno et al., 2008; Robertson et al., 2008). This gear design has since been used by vessels targeting toothfish in the Falklands, but more research is needed to maximize catch per unit effort, and reduce fish bycatch and scavenging of catch to facilitate its wider implementation (Brown et al., 2010).

To further reduce the impact of longline fisheries on seabirds, ACAP recommends combining appropriate weighting regimes with the use of other best practice mitigation measures; bird-scaring lines and night-setting (ACAP, 2017; ACAP, 2019). Bird-scaring lines are designed to protect baits while they sink; recognized best practice is to deploy one or two lines that reach an aerial extent of >75 or >100 m in small (<24 and <35 m for demersal and pelagic longline vessels, respectively) and large vessels (≥24 and ≥35 m for demersal and pelagic longline vessels, respectively), respectively (ACAP, 2017; ACAP, 2019). It is, however, essential that baits are protected until they sink beyond diving range of white-chinned petrels (c. 15 m depth), requiring the simultaneous use of a suitable weighting regime. For instance, a large demersal longline vessel setting lines at a speed

of 5.5–6.5 knots and using 6.5-kg weights spaced at 35-m intervals with a bird-scaring line providing 100 m of aerial coverage would protect baits until they reach 12 m depth, while a large pelagic longline vessel may protect baits until 15 m depth by setting lines at 9.8 knots using a double-weighted branchline (65–70 g) at 2 m from the hooks with a bird-scaring line providing 100 m of aerial coverage (Robertson, 2000; Melvin, Guy & Read, 2014). Baits can similarly be protected by releasing hooks at depth using underwater setting (funnel, chute, and capsule) or hook-shielding devices (hookpod) (Ryan & Watkins, 2002; Gilman, Boggs & Brothers, 2003; Robertson et al., 2018; Sullivan et al., 2018; Jiménez et al., 2020). Our results underline the importance of attaining a target release depth of c. 15 m. Finally, although night-setting is unlikely to deter white-chinned petrels given the degree of nocturnality and ability to dive deep during darkness (maximum: 11.5 m) indicated in our study, this mitigation method substantially reduces bycatch of diurnal seabirds, and potentially even of nocturnal species under low light conditions if bird-scaring lines protect sinking baits until they are no longer visually detectable (Jiménez et al., 2020). Longlines should therefore be set between the end of nautical twilight and before nautical dawn (ACAP, 2017; ACAP, 2019) and where possible with minimal deck lighting (Weimerskirch, Capdeville & Duhamel, 2000; Bull, 2007; Jiménez et al., 2019).

5 | CONCLUSIONS

White-chinned petrels from South Georgia tracked during the incubation period predominantly landed on the water to forage during darkness, but all birds also fed in daylight, indicating a high degree of flexibility. This array of foraging abilities clearly gives this petrel a competitive advantage over other medium to large flying seabirds feeding within its distribution, and presumably explains its much higher abundance at South Georgia (1 million breeding pairs; Martin et al., 2009). Conversely, these traits render this bird particularly vulnerable to bycatch in longline fisheries, which can only be avoided by effective mitigation measures (in particular heavy line-weighting and bird-scaring lines). This requires monitoring of implementation and bycatch rates, and enforced compliance (Phillips et al., 2016).

CONFLICT OF INTEREST
The authors declare that they have no competing interests.

AUTHORS' CONTRIBUTIONS
R.A.P. conceived the project, and C.K.F. carried out the analyses and wrote the manuscript with support from R.A.P., A.M., and J.N. All authors read and approved the final manuscript.

DATA AVAILABILITY STATEMENT
The datasets supporting the conclusions of this article are available for download from the BirdLife international Seabird Tracking Database (http://seabirdtracking.org/mapper/contributor.php?contributor_id=361); dataset id: 1558.

ORCID
Caitlin K. Frankish https://orcid.org/0000-0002-4930-6153
Andrea Manica https://orcid.org/0000-0003-1895-450X
Joan Navarro https://orcid.org/0000-0002-5756-9543

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of this article.