



Seasonal resource tracking and use of sea-ice foraging habitats by albatrosses and large petrels

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ABSTRACT

The Antarctic seasonal sea-ice zone (SIZ) is one of the most extensive and dynamic habitats on Earth. In summer, increased insolation and ice melt cause primary production to peak, sustaining large populations of locally-breeding seabirds. Due to their hypermobility, large Procellariiformes, including albatrosses, breeding in the subantarctic also have the potential to access the SIZ and track macroscale resource waves over the Southern Ocean but the extent to which they do this is poorly known. Here, we analysed the foraging movements of breeding albatrosses and large petrels (seven species, 1298 individuals) recorded using GPS loggers and satellite-transmitters to quantify their use of sea-ice habitats and test whether they tracked seasonal drivers of primary production. Foraging latitudes of white-chinned petrels *Procellaria aequinoctialis* and black-browed *Thalassarche melanophris*, grey-headed *T. chrysostoma* and wandering albatrosses *Diomedea exulans* varied sinusoidally over the breeding season, presumably in response to lagged effects of solar irradiance on primary production. Foraging latitudes of northern and southern giant petrels (*Macronectes halli* and *M. giganteus*), and light-mantled albatrosses *Phoebastria palpebrata*, exhibited no strong seasonal trend, but the latter two species spent $\geq 20\%$ of their time in the SIZ during incubation and post-brood, prior to or at the time of the spring ice breakup. Southern giant petrels travelled hundreds of km into the pack ice, encountering sea-ice concentrations up to 100%, whereas light-mantled albatrosses remained almost exclusively in open water near the Marginal Ice Zone (MIZ). The remaining species spent up to 15% of their time in the SIZ, typically from 5-7 weeks after breakup, and avoided the MIZ. This supports hypotheses that sea ice presents albatrosses but not giant petrels with physical barriers to flight or foraging, and that open-water-affiliated species use the SIZ only after primary production stimulated by ice melt transfers to intermediate trophic levels. Given that all seven species used the SIZ, it is likely that the phenology and demography of these and many other subantarctic-breeding seabirds are mechanistically linked to sea-ice dynamics. Declines in Antarctic sea ice predicted under climate change could therefore modulate and exacerbate the already unsustainable anthropogenic impacts being experienced by these populations.

1. Introduction

Foraging links the dynamics of consumer populations to the

fundamental mechanisms that regulate food availability and accessibility (Morales, Moorcroft, Matthiopoulos, Frair, Kie et al., 2010). Cyclicity in environmental drivers such as solar irradiance often gives

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rise to predictable resource pulses or waves that foraging animals track in space and time, sometimes with lags due to latency in trophic transfer (Abrahms, Aikens, Armstrong, Deacy, Kauffman & Merkle, 2021; Armstrong, Takimoto, Schindler, Hayes & Kauffman, 2016; Zurell, Gallien, Graham & Zimmermann, 2018). Quantifying spatiotemporal use of habitats, in which production is regulated by particular mechanisms, can provide valuable insights into the dynamics of both consumer populations and the wider ecosystem (Matthiopoulos, Fieberg, Aarts, Beyer, Morales & Haydon, 2015; Morales et al., 2010). In much of the oceans, primary production is highly seasonal (Longhurst, 1998). At mid to high latitudes it is regulated by nutrients, vertical mixing, predator–prey dynamics and especially solar irradiance, giving rise to a poleward advance and retreat of peak production over the annual cycle (Arteaga, Boss, Behrenfeld, Westberry & Sarmiento, 2020; Boyce, Petrie, Frank, Worm & Leggett, 2017; Racault, Le Quééré, Buitenhuis, Sathyendranath & Platt, 2012; Thomalla, Fauchereau, Swart & Monteiro, 2011). In turn, many wide-ranging marine predators undertake meridional (north/south) migrations from lower latitudes in winter to higher latitudes in summer (Abrahms, Hazen, Aikens, Savoca, Goldbogen et al., 2019; Block, Jonsen, Jorgensen, Winship, Shaffer et al., 2011; Murphy, Johnston, Hofmann, Phillips, Jackson et al., 2021). Set within this backdrop is one of the most seasonally dynamic and extensive habitats on Earth – the Antarctic sea ice, which varies in extent over the annual cycle from a maximum of ~ 20 million km² in September, when it covers 40 % of the Southern Ocean, to a minimum of ~ 4 million km² in February (Arrigo, 2014; Gloersen, Campbell, Cavalieri, Comiso, Parkinson & Zwally, 1992). Sea ice has profound biological effects not only in the areas it covers but at all levels of the Southern Ocean food web (Arrigo, 2014; Clarke, 1988; Eicken, 1992; Thomas, 2017). It regulates primary production while intact by attenuating light, concentrating nutrients and acting as a substrate for growth, and following breakup, by releasing nutrients and enhancing stratification (Arrigo, 2014; Taylor, Losch & Bracher, 2013).

Seasonal variation in resource availability is a fundamental driver of migration in marine and terrestrial systems (Aikens, Kauffman, Merkle, Dwinell, Fralick & Monteith, 2017; Alerstam, 1990; Zurell et al., 2018). However, the extent to which land-breeding marine predators track seasonal resource waves during periods of central-place constraint is unclear (Abrahms et al., 2019; Hurme, Fahr, Network, Eric-Moise, Hash et al., 2022). Such behaviour may be most detectable among wide-ranging species, including albatrosses and large petrels, which can cover vast distances rapidly and at relatively low energetic cost, by exploiting the wind (Thorne, Clay, Phillips, Silvers & Wakefield, 2023). The majority of albatrosses and large petrels breed over periods of 7–12 months on subantarctic islands, from where they can commute thousands of km to forage, accessing areas from the subtropics to Antarctic sea-ice zone (González-Solís, Croxall & Wood, 2000a; Péron, Delord, Phillips, Charbonnier, Marteau et al., 2010; Phillips, Silk, Croxall & Afanasyev, 2006; Phillips, Silk, Phalan, Catry & Croxall, 2004; Trebilco, Gales, Baker, Terauds & Sumner, 2008; Xavier, Trathan, Croxall, Wood, Podesta & Rodhouse, 2004).

The use of sea-ice habitats by albatrosses and large petrels has received relatively little attention, perhaps because ship-based studies report these species to be rare within the pack ice (Ainley, And & Boekelheide, 1984; Ainley, Woehler & Lescoërl, 2017; Woehler, Raymond & Watts, 2003). However, many occur in open water within the Seasonal Ice Zone (SIZ; areas that are ice-covered for only part of the year), Marginal Ice Zone (MIZ; areas where waves affect ice structure, resulting in variable but relatively low ice cover), or close to the ice edge, and prey availability in all these zones is affected directly by sea-ice dynamics (Arrigo, 2014; Brierley & Thomas, 2002; Eicken, 1992). Based largely on at-sea surveys, three main seabird assemblages are recognised to use waters south of the Antarctic Polar Front (Ainley et al., 2017): (1) *Ice-affiliated* species that occur within the pack ice; (2) *ice-edge* (or ice-tolerant) species that use the ice edge and adjacent cold waters where icebergs occur regularly but avoid dense pack ice; and (3) *open-water*

species, confined to open, and possibly warmer waters, usually further north. Most ice-affiliates breed on the Antarctic continent and adjacent islands (Woehler et al., 2003), but the origin of southern giant petrels *Macronectes giganteus* seen in these three habitats is uncertain, as they breed both in the Antarctic and on subantarctic islands. The ice-avoiding assemblage is dominated by species that breed only in the subantarctic but migrate into Antarctic waters during the summer months, e.g. black-browed albatrosses *Thalassarche melanophris* (Ainley et al., 1984; Ainley et al., 2017). The ice-tolerant assemblage includes subantarctic breeders, such as light-mantled albatrosses *Phoebastria palpebrata*. However, the age, breeding status or provenance of birds observed during ship-based studies is rarely known.

It remains unclear what factors allow some species to subsist in the pack ice but prevent others from doing so (Ainley et al., 2017). Several processes concentrate euphausiids, cephalopods and fish at shallow depths within or near sea ice (Ainley, Fraser, Sullivan, Torres, Hopkins & Smith, 1986; Bluhm, Swadling & Gradinger, 2016; Brierley, Fernandes, Brandon, Armstrong, Millard et al., 2002; Saenz, Ainley, Daly, Ballard, Conlisk et al., 2020), potentially making them more accessible to albatrosses and large petrels, which have limited diving capabilities (Bentley, Kato, Ropert-Coudert, Manica & Phillips, 2021). In general, prey availability is thought to be high in the pack ice year-round but requires adaptive specialisations to exploit, whereas prey availability outside the pack is seasonally pulsed (Ainley, Ribic & Fraser, 1992; Ainley, Fraser, Smith, Hopkins & Torres, 1991; Ainley, Ribic & Fraser, 1994). Dietary specialisation is not thought to confine ice-affiliated seabirds to the pack ice because their diets are similar in adjacent open waters (Ainley, Ribic & Spear, 1993). Instead, sea ice may physically exclude some species, for example by inhibiting dynamic soaring among albatrosses (Ainley et al., 1984; Griffiths, 1983). If sea-ice cover is complete, seabirds cannot access the water column (Ainley et al., 2017; Jenouvrier, Péron & Weimerskirch, 2015), but some may nevertheless use the ice itself to scavenge or rest (Gilg, Istomina, Heygster, Strøm, Gavrilov et al., 2016; Grunst, Grunst, Grémillet, Sato, Gentès & Fort, 2022). Ice-edge species could specialise on prey or use foraging techniques associated with the edges of floes, or they could prefer water masses in which sea ice occurs (Ainley et al., 2017; Ruhl, Ellena, Wilson & Helly, 2011). Open-water affiliates may simply be attracted to the seasonal pulse in prey in the SIZ that follows sea-ice breakup and the associated phytoplankton bloom (Fauchald, Tarroux, Tveraa, Chere, Ropert-Coudert et al., 2017; Péron et al., 2010; Smith & Nelson, 1985).

Quantifying the seasonal use of sea-ice habitats by different species may help to resolve ambiguities about these causes and constraints. Moreover, use of these habitats would imply mechanistic links between sea-ice dynamics – driven by large-scale climatic processes (Crosta, Etourneau, Orme, Dalaiden, Campagne et al., 2021; Isaacs, Renwick, Mackintosh & Dadic, 2021; Stammerjohn, Martinson, Smith, Yuan & Rind, 2008b) – and the demography of albatrosses and large petrels (Descamps, Tarroux, Lorentsen, Love, Varpe & Yoccoz, 2016; Fraser & Hofmann, 2003; Jenouvrier, Weimerskirch, Barbraud, Park & Cazes, 2005). Impacts of climate change could propagate through or affect such linkages (Bestley, Ropert-Coudert, Bengtson Nash, Brooks, Cotté et al., 2020; Constable, Melbourne-Thomas, Corney, Arrigo, Barbraud et al., 2014; Massom & Stammerjohn, 2010). Although this is already thought to happen in the Arctic, where sea-ice declines have been rapid (Descamps & Ramírez, 2021), overall sea-ice extent in the Southern Ocean has been relatively stable (Fogt, Sleinkofer, Raphael & Handcock, 2022; Turner, Hosking, Bracegirdle, Marshall & Phillips, 2015). However, recent signs are that Antarctic sea ice has begun to decrease overall (Turner, Guarino, Arnatt, Jena, Marshall et al., 2020), and predictions are for this to continue under all realistic future carbon emission scenarios (Eyras, Li, Raphael & Holland, 2021; Roach, Dörr, Holmes, Massonet, Blockley et al., 2020), making it important to understand how this could affect the globally important seabird populations in the region (Bestley et al., 2020). For example, changes in the timing of sea-ice seasonality could lead to deleterious phenological mismatches with

predators (Durant, Ottensen & Stenseth, 2007; McMeans, McCann, Humphries, Rooney & Fisk, 2015). Although theory predicts that avian reproductive phenology is matched to resource pulses (Lack, 1968; Weimerskirch, Zotier & Jouventin, 1989), the extent to which the breeding schedules of albatrosses and large petrels might be synchronised to sea-ice dynamics is unknown.

South Georgia, in the southwest Atlantic Ocean (Fig. 1), holds 10–75% of the global breeding population of seven species of albatrosses and large petrels (Phillips, Gales, Baker, Double, Favero et al., 2016). The SIZ occurs closer to this archipelago than to almost all other subantarctic islands (Gloersen et al., 1992). It is both more extensive and productive than in other sectors (Arrigo, van Dijken & Bushinsky, 2008; Vernet, Geibert, Hoppema, Brown, Haas et al., 2019), and used by a relatively large number of wide-ranging higher predators (Hindell, Reisinger, Ropert-Coudert, Hückstädt, Trathan et al., 2020). The SIZ is well within foraging range of albatrosses and petrels breeding on South Georgia, but we would predict some niche differentiation given these are large, sympatric populations of morphologically similar species (Croxall & Prince, 1980). Indeed, tracking of breeding albatrosses and large petrels from Bird Island, South Georgia since the early 1990s indicates that all these species use the Scotia, Weddell or Bellingshausen Seas – areas that are seasonally ice covered – to some extent, primarily during the latter part of the summer (González-Solís, Croxall & Briggs, 2002; Granroth-Wilding & Phillips, 2019; Phillips, Croxall, Silk & Briggs, 2008; Phillips, Silk & Croxall, 2005a; Phillips et al., 2006; Phillips et al., 2004; Wakefield, Phillips, Trathan, Arata, Gales et al., 2011; Xavier et al., 2004).

Extensive studies of the oceanography, sea-ice dynamics and pelagic ecology of the region have highlighted the key physical and ecological roles of sea-ice dynamics (Lowther, von Quillfeldt, Assmy, De Steur, Descamps et al., 2022; Murphy, Watkins, Trathan, Reid, Meredith et al., 2007; Thorpe & Murphy, 2022; Vernet et al., 2019). The timing of phytoplankton blooming in the Southern Ocean is tightly linked to seasonal cyclicity in irradiance, advancing with decreasing latitude (Ardyna, Claustre, Sallée, D'Ovidio, Gentili et al., 2017; Arteaga et al., 2020). Bloom maxima occur in early September in the subtropical South Atlantic, early October on the Patagonian Shelf, late November-early December in the vicinity of South Georgia, and late December in the Weddell Sea (Ardyna et al., 2017; Borrione & Schlitzer, 2013; Kauko, Hattermann, Ryan-Keogh, Singh, de Steur et al., 2021; Sallée, Llor, Tagliabue & Levy, 2015; Uchida, Balwada, Abernathy, Prend, Boss & Gille, 2019). This macroscale pattern of light control on primary production is modified at finer scales south of the Antarctic Polar Front by iron supply, and within the SIZ by sea-ice retreat (Ardyna et al., 2017; Arteaga et al., 2020). Zooplankton biomass peaks in subantarctic waters in February and in ice-free areas of the SIZ from late summer to early autumn (Cisewski & Strass, 2016; Clarke, 1988). Sea-ice extent and duration, linked to large scale atmospheric processes, affect krill abundance and zooplankton community structure (Atkinson, Siegel, Pakhomov & Rothery, 2004; Loeb, Siegel, Holm-Hansen, Hewitt, Fraser et al., 1997; Loeb & Santora, 2015; Steinberg, Ruck, Gleiber, Garzio, Cope et al., 2015). In turn, these changes are thought to drive decadal changes in flying seabird community structure at South Georgia (Moreno, Stowasser, McGill, Bearhop & Phillips, 2016), but it is unknown whether use of habitats is a mediating mechanism.

Here, our aims were to quantify the use of sea-ice habitats by a sympatric breeding assemblage of subantarctic albatrosses and large petrels, and to test two related hypotheses: (H1) At the macroscale, the meridional movement of the birds tracks variation in solar irradiance, which in turn affects prey availability. If correct, we would expect the median foraging latitude to vary sinusoidally with days elapsed since midwinter because the date of peak primary production in the study area varies sinusoidally with latitude (Ardyna et al., 2017; Arteaga et al., 2020; Cole, Henson, Martin & Yool, 2015). In addition, we would expect a phase lag of the order of weeks to months due to latency in the transfer of primary production to the trophic levels at which seabirds feed

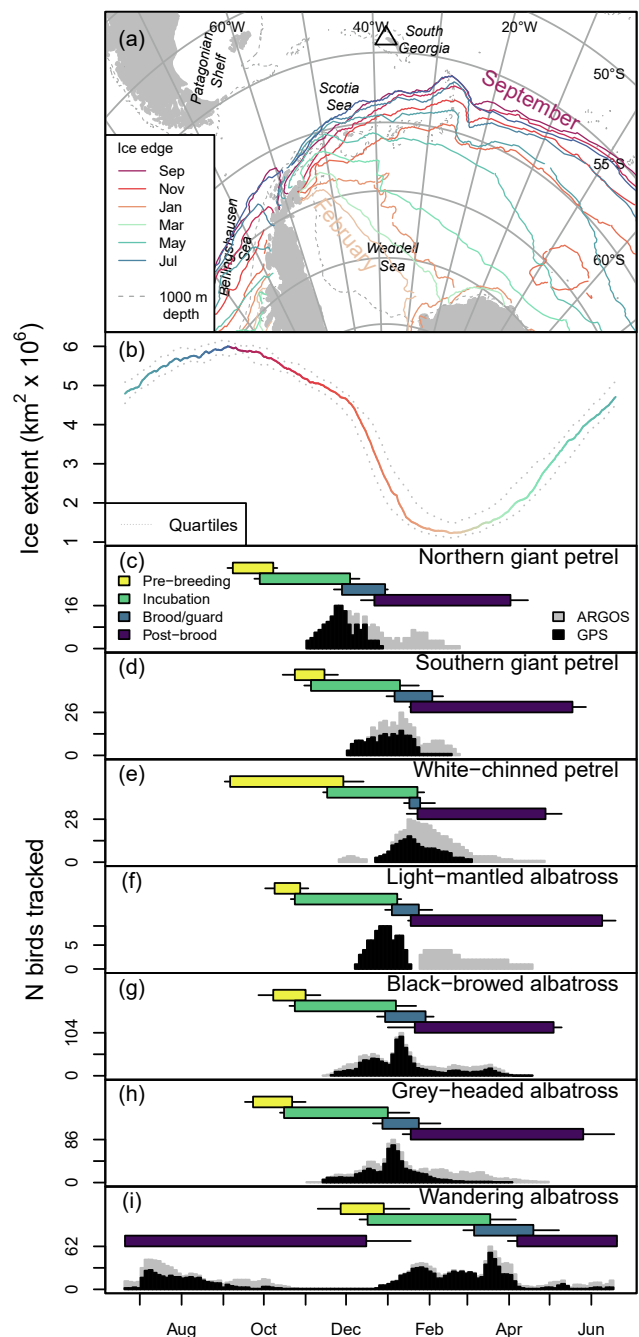


Fig. 1. Seasonality in sea-ice extent and breeding schedules of the study species, and temporal coverage of tracking data. (a) Study area, showing monthly median ice edge over the study period (1990–2023). (b) Median sea-ice extent over the study period within the longitudinal sector used by the study populations during the tracking period (75° W to 5° E). (c–i) Box plots show breeding schedules at Bird Island, South Georgia. Histograms show stacked numbers (summed across years) of individuals tracked within 3-day periods using GPS (black) or ARGOS (grey) devices. Pre-breeding is defined here as the period between first return to the colony and egg laying. Many male southern giant petrels remain in or near the colony for much of the winter (Thiers, Delord, Barbraud, Phillips, Pinaud & Weimerskirch, 2014), so the female pre-breeding period is shown for this species.

(Cisewski & Strass, 2016; Conroy, Steinberg, Thomas & West, 2023; von Berg, Prend, Campbell, Mazloff, Talley & Gille, 2020). (H2) Open-water-affiliated seabirds use locations in the SIZ only after a lag corresponding to the time required for the post-breakup bloom to enhance prey availability in surface waters, whereas ice-affiliated species use the SIZ

before breakup. To test these hypotheses, we analysed breeding-season foraging trips made by black-browed, grey-headed *T. chrysostoma*, light-mantled and wandering albatrosses *Diomedea exulans*, white-chinned petrels *Procellaria aequinoctialis*, and northern *M. halli* and southern giant petrels tracked from Bird Island over three decades, quantifying: (1) seasonal changes in foraging latitude, (2) proportion of individuals that use the SIZ and MIZ, (3) proportion of time spent in the SIZ and MIZ, (4) distribution relative to the ice edge, (5) utilised sea-ice concentrations, and (6) the temporal lags hypothesised above.

2. Materials and Methods

We carried out all analysis in R (R-Development-Core-Team, 2022). Unless otherwise stated, we report means \pm their standard deviations if indices are normally distributed, and medians and the inter-quartile ranges (IQR) otherwise.

2.1. Tracking data and behavioural classification

We analysed the movements of seven species of breeding albatrosses and large petrels tracked from Bird Island (54° 00'S, 38° 03'W) between 1990 and 2023 (Table A1). In most cases, breeding stage (incubation, brood-guard or post-brood chick-rearing) was recorded at the time of tracking, but for white-chinned petrels tracked in 2022, we assigned breeding stage based on the mean timing of hatching and thermal emancipation (i.e., the end the brood-guard period, when chicks are left unattended by their parents) reported by Hall (1987). Within most species, most individuals were tracked during early to mid chick-rearing, followed by late incubation (Fig. 1c-h). Wandering albatrosses were tracked over most of incubation and brood-guard, and in early to mid, but not late, post-brood chick-rearing (mid-October to late December) (Fig. 1i). Across species, tracking data coverage was low or nil during pre-breeding colony attendance, early incubation and late chick-rearing.

The dataset analysed contained 2497 foraging trips made by 1289 birds between 1992 and 2023 (Table A1). Most birds were tracked via GPS (72 %, $n = 924$ birds) and the remainder via the ARGOS satellite system (28 %, $n = 365$; Table A2. for device details). The majority of birds (75 %) were tracked in the latter half of this period but tracking effort was patchily distributed across breeding seasons, with coverage of 1–12 (median 4) breeding seasons per species (Fig. A1). ARGOS has a lower accuracy than GPS, and ARGOS locations have irregular time intervals. We therefore interpolated ARGOS location estimates to 1 h intervals and improved their accuracy as follows: First, using the *argosfilter* package (Freitas, Lydersen, Fedak & Kovacs, 2008), we removed class Z locations and those resulting in speeds > 40 m/s, which we assumed to be unrealistic (Cstry, Phillips & Croxall, 2004). We used default values for spike angles and lengths. In addition, we removed entire trips if they comprised < 3 ARGOS locations, because the next step requires > 2 locations (we define a 'trip' as a bout of movement beginning and ending at the colony). Using the *aniMotum* package (Jonsen, Grecian, Phillips, Carroll, McMahon et al., 2023), we then fitted a simple continuous-time state-space model to observed locations for each trip (or logger deployment if locations had not already been split into trips – see below) and used this to predict hourly locations. We used the 'optim' optimizer, unless this failed, in which case we switched to 'nlminb'. For all other function variables, we used the default settings. We checked goodness of fit by examining one-step-ahead prediction residuals (Thygesen, Albertsen, Berg, Kristensen & Nielsen, 2017). When applied to another seabird species, this approach yielded a median error of 6.0 km (95th percentile 44.0) for data collected before 2011, and 7.5 km (95th percentile 52.6) for data collected thereafter; the difference reflects changes in the way that Collecte Localisation Satellites preprocess the data (Jonsen, Patterson, Costa, Doherty, Godley et al., 2020)). For GPS data, we standardised temporal resolution to 0.5 h by linear interpolation using the *adehabitatLT* package (Calenge, 2006). In

many instances, birds had been tracked over multiple consecutive trips and trip identity was assigned based on visual observations at the colony. When this information was missing, we split GPS tracks into trips by assuming that a trip comprises a bout of contiguous locations spanning > 12 h, of which all but the first and last are > 20 km from the colony. Prior to filtering and interpolation, the median tracking interval within species ranged from 0.9 to 2.2 h (max 6.1) for ARGOS and 0.2 to 1.0 (max 4.1) h for GPS devices (Table A1).

Given that our principal interest was in quantifying the use of sea-ice habitats when birds were foraging or at rest, as opposed to travelling, we discriminated these behaviours using Hidden Markov Models (HMMs; Langrock, King, Matthiopoulos, Thomas, Fortin & Morales, 2012). Models were implemented in the *moveHMM* package (Michelot, Langrock & Patterson, 2016) and fitted to step lengths and turning angles (Bennison, Bearhop, Bodey, Votier, Grecian et al., 2018; Dean, Freeman, Kirk, Leonard, Phillips et al., 2012; Hooten, Johnson, McClintock & Morales, 2017), which we assumed followed von Mises and zero-inflated gamma distributions, respectively. We checked these and other model assumptions via pseudo-residual plots (Michelot et al., 2016). Following McClintock (2021), we did not model individual-level random effects. We specified a realistic range of starting parameter values for each behavioural state within species based on previous studies (Bennison et al., 2018; Clay, Joo, Weimerskirch, Phillips, den Ouden et al., 2020; Dean et al., 2012) and inspection of observed step length and turning angle distributions (Michelot & Langrock, 2022). We then randomly drew parameters from within these ranges and fitted HMMs 25 times, selecting the best starting values as those resulting in the model with the highest likelihood (Michelot & Langrock, 2022). Preliminary analysis showed that only travelling (large steps, concentrated turning angles) vs. not travelling (small steps, dispersed turning angles) could be reliably discriminated for ARGOS-tracked individuals, presumably because HMMs are effective at classifying behavioural states only when location error is negligible compared to the scale of movement characterising the states of interest (Langrock et al., 2012). Moreover, putative foraging (intermediate steps, dispersed turning angles) could not be distinguished from resting or travelling for many GPS-tracked wandering albatrosses and white-chinned petrels. For consistency, we therefore fitted a two-state model for all species and logger types. Unless otherwise stated, we carried out all subsequent analyses using non-travelling locations, assuming these encompasses locations at which birds were either foraging or resting.

2.2. Sea ice data

To quantify sea-ice conditions, we used gridded, daily sea-ice concentrations (SIC), estimated from satellite-borne radiometer measurements. We define the ice edge as the 15 % SIC contour, and the SIZ as the area between the seasonal maximum and minimum sea-ice extents (Taylor et al., 2013). The marginal ice zone (MIZ) is that into which waves penetrate, splitting the pack into floes, and is usually bounded by open water on one side and the inner, closed pack on the other (Dumont, 2022). Here, we follow the common nominal definition of the MIZ as being bounded by the 15 and 80 % SIC contours (e.g. Taylor et al., 2013), noting however that definitions of the MIZ vary widely (Arrigo et al., 2008; Taylor et al., 2013). We refer to SICs > 80 % as the consolidated ice zone (CIZ), which may include areas of seasonal, perennial or fast ice, each of which can foster different ecological conditions (Brierley & Thomas, 2002; Eicken, 1992; Joiris, 1991).

We used two sea-ice datasets, with differing spatial resolutions and temporal coverages. In order to quantify SICs experienced by birds within the MIZ or CIZ, we downloaded ASI (AMSR2/ARTIST Sea Ice algorithm) version 5.4 SIC data on a regular 3.125 km polar stereographic grid (Spreen, Kaleschke & Heygster, 2008) from the Institute of Environmental Physics, University of Bremen (<https://seaice.uni-bremen.de>, accessed March 1st, 2023). These data span June 2002 to October 2011 and June 2012 to the present, a period that excludes

approximately a third of that covered by the seabird tracking data (Fig. A1). Hence, for the remainder of our analyses, which are less sensitive to SIC spatial resolution, we used Sea Ice Index, Version 3 (Fetterer, Knowles, Meier, Savoie & Windnagel, 2017) data, downloaded on a regular 25 km polar stereographic grid from the National Snow and Ice Data Centre (<https://nsidc.org/data/g02135/versions/3>, accessed March 1st, 2023). These data span the entire tracking period. Visual inspection showed that in both datasets, SICs around South Georgia and adjacent subantarctic coastlines were occasionally spuriously high, presumably due to uncorrected land-to-ocean spillover (Meier, Stewart, Windnagel & Fetterer, 2022). Prior to analysis, we therefore set all SICs within 50 km of South Georgia and land masses north of the Antarctic Polar Front, to zero.

2.3. Habitat use

To test whether seabirds shifted their foraging effort meridionally over the breeding season, we first determined the latitude, θ (hereafter, foraging latitude) of the distal location (excluding travelling locations) of each foraging trip. We then used linear models, fitted with the nlme package (Pinheiro, Bates, DebRoy, Sarkar & R Core Team, 2022), to model θ as a function of days, d since austral midwinter. Random intercepts were included for individuals, if necessary nested within breeding seasons. Data from most species covered less than half of the annual cycle, so to test for trends, we first fitted linear and second order polynomial models. When temporal coverage was sufficient, we also fitted a sinusoidal model to test for a phase shift, which we assume reflects any lag between incident solar irradiance and mean foraging latitude. The model took the form

$$\theta = \beta_0 + \beta_1 (\sin(2\pi d/365)) + \beta_2 (\cos(2\pi d/365)) + \epsilon \quad (1)$$

where β_0 is the intercept, β_1 and β_2 are the phase shift parameters estimated from the data and ϵ is the error. We determined the most parsimonious of these models by comparing their AIC.

To model temporal change in use of the SIZ through the breeding season, we classified foraging trips as having used the SIZ if any non-travelling locations overlapped with Sea Ice Index v3 SICs > 15 %. We then used logistic Generalised Additive Mixed-effects Models to model the probability of use of the SIZ as a smooth function of days since midwinter using the mgcv package (Wood 2017). We assigned trip date as the middle day of each trip and structured smooths as cubic regression splines, with shrinkage, using the cyclic form for wandering albatrosses as their breeding season spans a complete annual cycle (Wood, 2017). We specified random intercepts for birds nested within breeding seasons and modelled serial autocorrelation using a first order autoregressive (AR(1)) term. We used logistic Generalised Linear Models to estimate the proportion of non-travelling time spent by birds during each breeding stage within the SIZ, and MIZ or CIZ. We classified locations as being within the MIZ/CIZ using ASI SIC data. We also used kernel density estimation to quantify habitat use in terms of SIC and distance to the ice edge (Péron et al., 2010; Reisinger, Friedlaender, Zerbini, Palacios, Andrews-Goff et al., 2021), limiting these analyses to birds tracked during the period with ASI SIC data coverage (Fig. A1).

Over the study period, sea-ice cover in the longitudinal sector used by albatrosses and large petrels peaked around 14 September (see Results). Following Stammerjohn et al. (2008a) and Kauko et al. (2021), we defined the date of ice breakup (DBU) as the last day after this date on which the mean SIC was < 15 % for the previous five days, with the modification that here SIC is averaged over five days to reduce the effects of intermittent false ice detections (Meier & Stewart, 2019). For each species, i , we defined the date of first use ($DFU_{i,j,k}$), within the j^{th} breeding season, of all grid cells sharing the k^{th} DBU, as the first day on which any of those cells was used by a tracked bird of species i . In order to estimate the approximate lag between sea-ice retreat and the first use of SIZ locations, and to test whether this differed between species, we

modelled $DFU_{i,j,k} - DBU_j$ as a linear function of DBU_j and species, using Generalised Least Squares regression, implemented with the nlme package (Pinheiro et al., 2022). This analysis necessarily excludes regions in which breakup occurred before tracking commenced because within these regions an artificial minimum would be imposed on the lag between DBU and DFU . We used an AR(1) term to model temporal autocorrelation within species and breeding seasons. We started with a model that included interactions between DBU and species, simplifying by backwards selection based on likelihood ratio tests. For illustration, we also fitted the final model rearranged as $DFU_{i,j,k}$ as a function of DBU_j .

3. Results

3.1. Sea-ice and seabird breeding phenology

Between 1998 and 2022, sea ice retreated and advanced along a meridional axis across most of the study area, and a southwest-northeast axis in the eastern Weddell Sea (Fig. 1a). Within the sector used by the tracked albatrosses and petrels, maximum and minimum sea-ice extent occurred on average on 14 September (± 6 days, range 1–28 September) and 22 February (± 4 days, range 14 February – 3 March), respectively (Fig. 1a-b). The minimum distance between Bird Island and the median ice edge averaged 430 ± 90 km in September and 1260 ± 240 km in February. In February, open water extended to the Antarctic continent across most of the study area, but in the western Weddell Sea some fast ice and floes persisted year round.

Colony attendance by all study species except wandering albatrosses begins around the austral spring equinox, coinciding with the sea-ice maximum (Fig. 1c-h). Incubation occurs during the period of most rapid sea-ice retreat and brood-guard just prior to the sea-ice minimum. Post-brood chick-rearing begins around late January, just prior to the sea-ice minimum, and chicks fledge about a month after the autumn equinox, when sea-ice extent has reached around two thirds of its maximum. Wandering albatrosses, which take > 1 year to fledge their offspring, undertake incubation largely within the period of rapid sea-ice retreat and minimum concentration (Fig. 1i). Brood-guard is completed just prior to the most rapid period of autumn ice advance and the remainder of chick-rearing occurs when sea-ice extent is greater than half of its median value.

3.2. Behaviour and seasonal changes in meridional distribution

While at sea, birds spent on average 53–79 % of their time foraging or resting (Table 1). Across species, space use when foraging or resting was high around the latitude of Bird Island, especially during the brood-guard stage. With the exception of southern giant petrels, either the northern, southern or both latitudinal limits of space use shifted south as the breeding season progressed (Fig. 2). Throughout the tracking period, northern and southern giant petrels remained largely north and south of the colony, respectively. A sinusoidal model best described the relationship between the mean foraging latitude and days since midwinter for black-browed, grey-headed and wandering albatrosses, and white-chinned petrels (Fig. 2, Table A3, Table A4). Mean (and 95 % CI)

Table 1

Percentage of locations of albatrosses and petrels tracked from Bird Island, South Georgia, at which behaviour was classified by Hidden Markov Models as travelling.

Species	Median (IQR, range)
Northern giant petrel	20.8 (7.6–44.3, 0.0–98.8)
Southern giant petrel	27.7 (5.8–47.3, 0.0–93.3)
White-chinned petrel	47.4 (42.5–50.8, 26.9–68.7)
Light-mantled albatross	45.6 (39.7–52.3, 22.0–68.5)
Black-browed albatross	31.3 (20.1–43.2, 0.0–85.7)
Grey-headed albatross	41.3 (30.5–51.4, 0.0–82.5)
Wandering albatross	33.8 (22.9–44.1, 0.0–76.1)

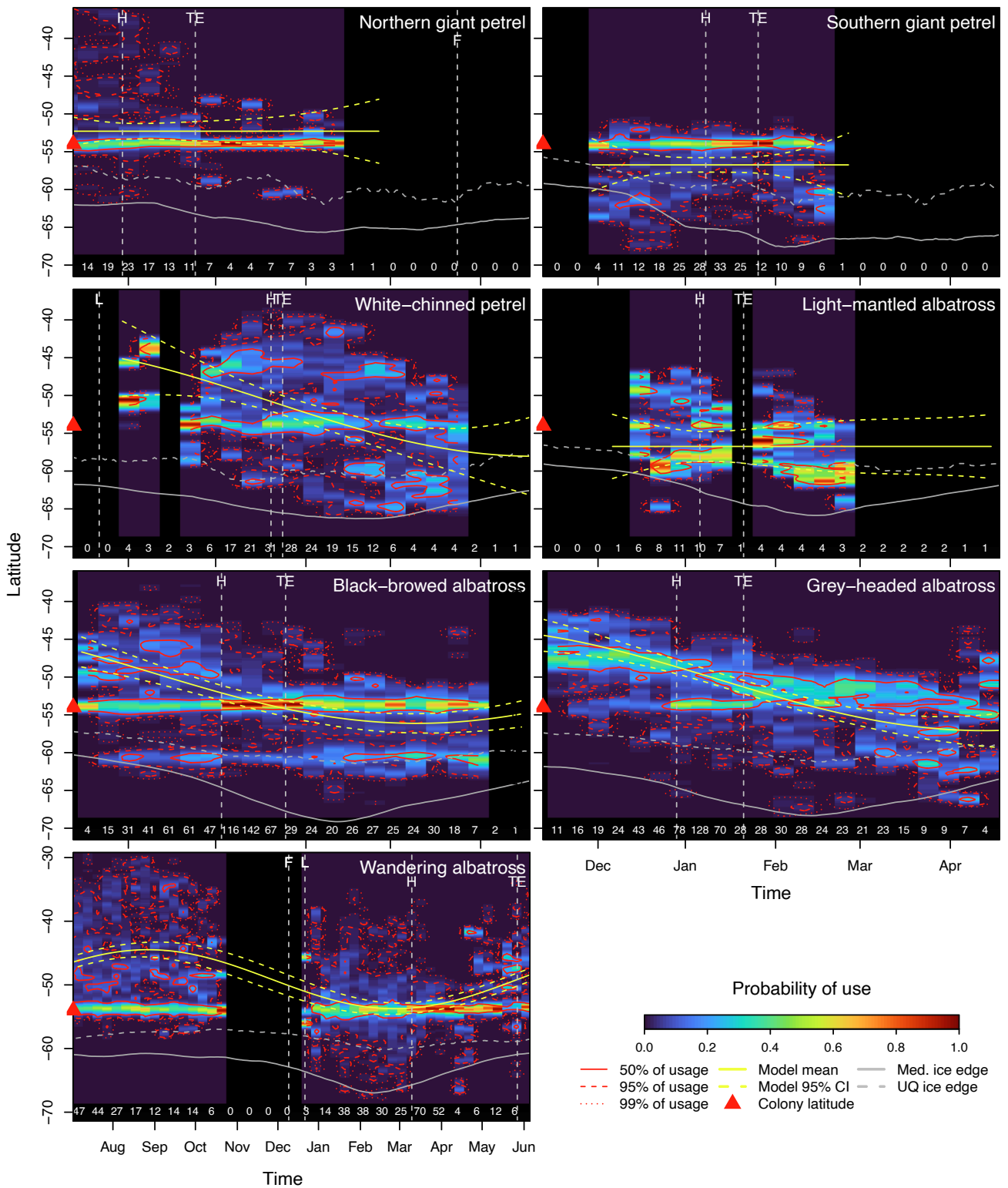


Fig. 2. Temporal variation over the breeding season in the latitudes at which albatrosses and large petrels tracked from Bird Island, South Georgia forage or rest. The y-axis represents latitude, the x-axis time and colour the probability of use. Extents of the axes are wider for wandering albatrosses because they breed over the whole annual cycle and range further than the other species. Utilisation probability is averaged across individuals within weeks during which ≥ 3 birds, pooled across years, were tracked (n birds shown above the abscissa). Red contours encompass 50, 95 and 99 % of usage, respectively. Yellow lines show models of foraging latitude vs. days since austral midwinter (dashed lines are 95 % CIs – see Methods). Grey curves show the median and upper quartile of the latitude of the ice edge in the longitudinal sector used by each species, averaged over study years, weighted by the number of birds tracked in each year. Vertical lines show median dates of laying (L), hatching (H), thermal emancipation (TE), and fledging (F) at Bird Island. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

phase shifts for these species were 82 (70–93), 115 (94–136), 68 (53–83) and 122 (66–178) days, respectively. An intercept-only model (i.e. no significant seasonal trend in mean foraging latitude) was the most parsimonious for the remaining species (Table A4). However, GLMMs (Table A5) showed that the most northerly foraging or resting latitudes reached by northern giant petrels and light-mantled albatrosses were 2.99° (approximate 95 % CI 0.54–12.78°; $p < 0.001$) and 0.90° (0.03–2.77°; $p = 0.039$) further south during chick-rearing than incubation. The mean equivalent difference for southern giant petrels was 0.00° of latitude (–0.26–0.47°, $p = 0.984$).

3.3. Use of sea-ice habitats

Most species remained largely north of the latitude of the median ice edge throughout the breeding season (Fig. 2), but all used the SIZ to some extent, especially to the south and southwest of South Georgia (Fig. 3, Fig. A2). The SIZ near the South Orkney Islands was used very frequently, especially by southern giant petrels and light-mantled,

black-browed and grey-headed albatrosses. The three larger albatross species used the SIZ west of the Antarctic Peninsula; southern giant petrels used the SIZ of the northern Weddell Sea throughout the tracked period; white-chinned petrels, black-browed albatrosses, and wandering albatrosses used the SIZ of the north-eastern Weddell Sea from mid-summer onwards; and light-mantled albatrosses used a wide zonal sector of the SIZ from late spring onwards.

Two broad seasonal trends were evident in the proportion of foraging trips entering the SIZ. Firstly, in most species, the lowest proportion of foraging trips in the SIZ occurred during brood-guard (Fig. 4). This was particularly marked among southern giant petrels, giving rise to a u-shaped seasonal trend in the probability of using the SIZ. Secondly, the probability of entering the SIZ increased from around mid-January in all species except light-mantled albatrosses. White-chinned petrels, black-browed albatrosses and grey-headed albatrosses visited the SIZ more frequently as the summer progressed.

Across species, most birds spent $< 15\%$ of their time in the SIZ, but individual variability was high, with at least one individual within most

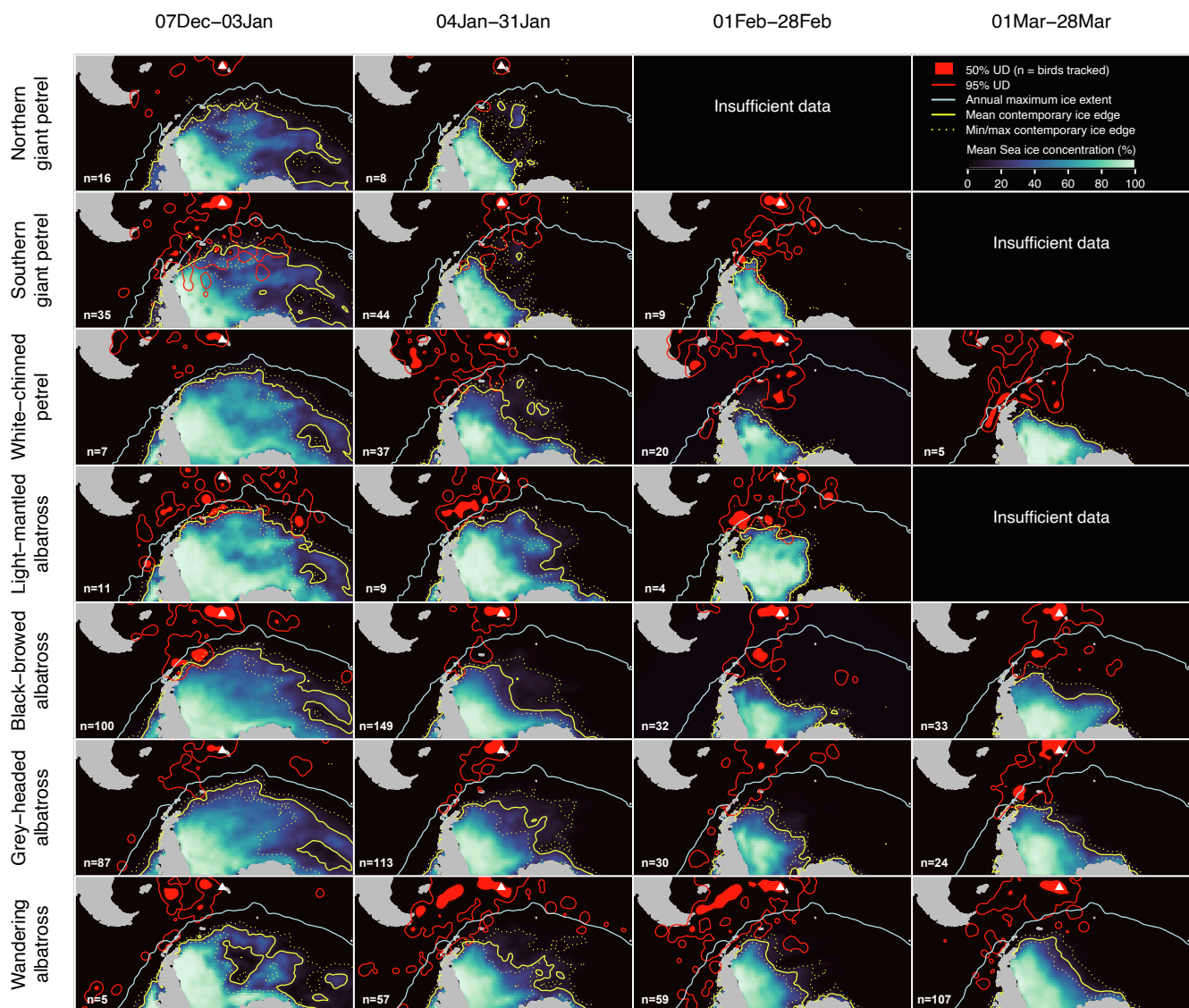


Fig. 3. Seasonal variation in sea ice and the foraging/resting utilisation distributions (UDs) of breeding albatrosses and large petrels tracked from Bird Island, South Georgia (white triangle). Within species (rows), UD were averaged across individuals over each 28-day period (columns) in which ≥ 3 birds, pooled across years, were tracked. For each panel, sea-ice conditions were averaged over years with tracking data, weighted by number of birds tracked in each year. The seasonal and marginal ice zones are the areas south of the blue and yellow lines, respectively. Panel extents and projections as in Fig. 1a. Only the core period of data coverage across species is shown – for the full series for each species, see Fig. A2. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

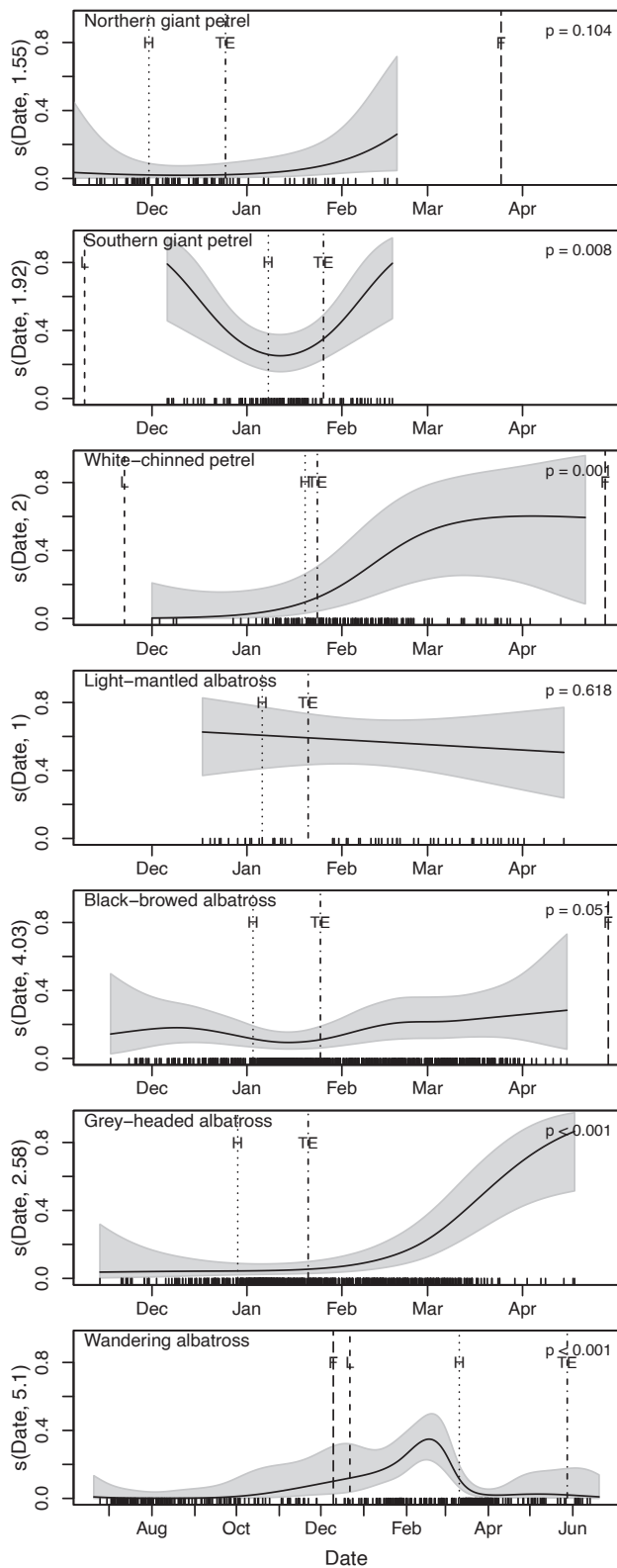


Fig. 4. Generalised Additive Models of the probability of trips made by breeding albatrosses and large petrels tracked from Bird Island, South Georgia, entering the Seasonal Ice Zone vs. time of year. Y axis labels indicate estimated degrees of freedom of smooths, p-values the significance and shaded areas the approximate 95% CIs (note the longer extent depicted for wandering albatrosses, reflecting their longer breeding period). Vertical lines show median dates of laying (L), hatching (H), thermal emancipation (TE), and fledging (F) at Bird Island.

species/stages spending $\geq 70\%$ of its foraging or resting time in the SIZ (Fig. 5). Among northern giant petrels, only females (5 out of 39 cf. 0 of 38 males) used the SIZ – a marginally significant difference (Fisher’s exact test, $p = 0.054$). Similarly, more female southern giant petrels used the SIZ than males (23 of 49 vs. 13 of 49), but this was not significant ($\chi^2(1, N=98) = 0.28, p = 0.596$). Southern giant petrels spent on average 26% (95% CI, 15–40%) and 37% (11–71%) of their foraging/resting time in the SIZ during incubation and post-brood, respectively. Light-mantled albatrosses at these stages, and black-browed albatrosses in post-brood spent $> 25\%$ of their time in the SIZ. Most northern giant petrels and wandering albatrosses spent much less time in the SIZ than the other species. Wandering albatrosses ceased to use the SIZ from mid-March, despite breeding throughout the year (Fig. 4). Use of the SIZ by wandering albatrosses was mainly by males (28 of 177 vs. 5 of 175 females; $\chi^2(1, N=98) = 13.12, p < 0.001$).

On trips that entered the SIZ, southern giant petrels tracked in incubation concentrated their foraging/resting time closer to the ice edge than most other species/stages, whereas light-mantled albatrosses consistently occurred relatively close (< 500 km) to the ice edge across stages (Fig. 6). Wandering albatrosses, black-browed albatrosses and southern giant petrels all concentrated their foraging/resting time closer to the ice edge during incubation than post-brood. Only the latter two species, and light-mantled albatrosses and northern giant petrels, entered the MIZ on more than one occasion (Fig. 7). Southern giant petrels entered the MIZ/CIZ regularly during incubation, spending an average of 8% (95% CI, 2–19%; range 0–75%) of their foraging/resting time there, but the other species spent $< 0.1\%$ of their foraging/resting time in areas where the SIC was $> 15\%$ (Fig. 5). Moreover, in the case of black-browed albatrosses, the majority ($\sim 70\%$) of non-travelling locations in $> 15\%$ SIC, and therefore putatively within the MIZ/CIZ,

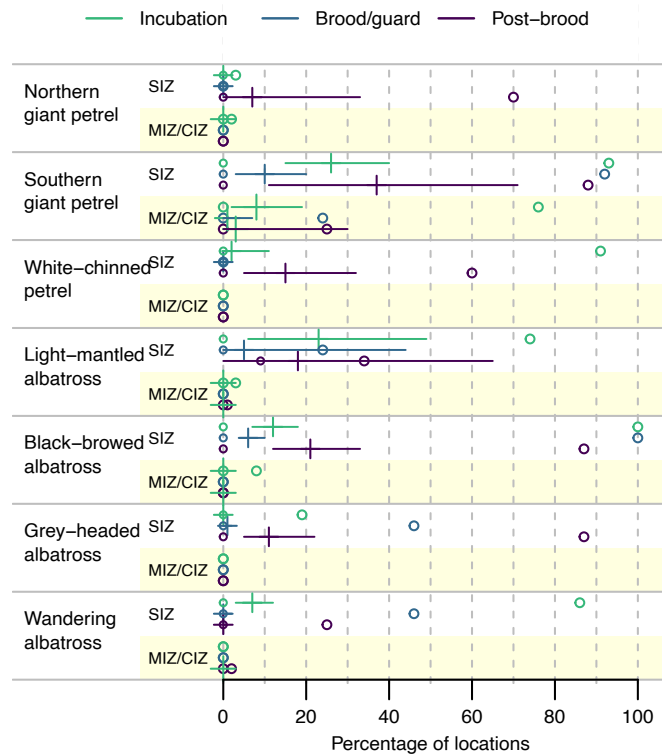
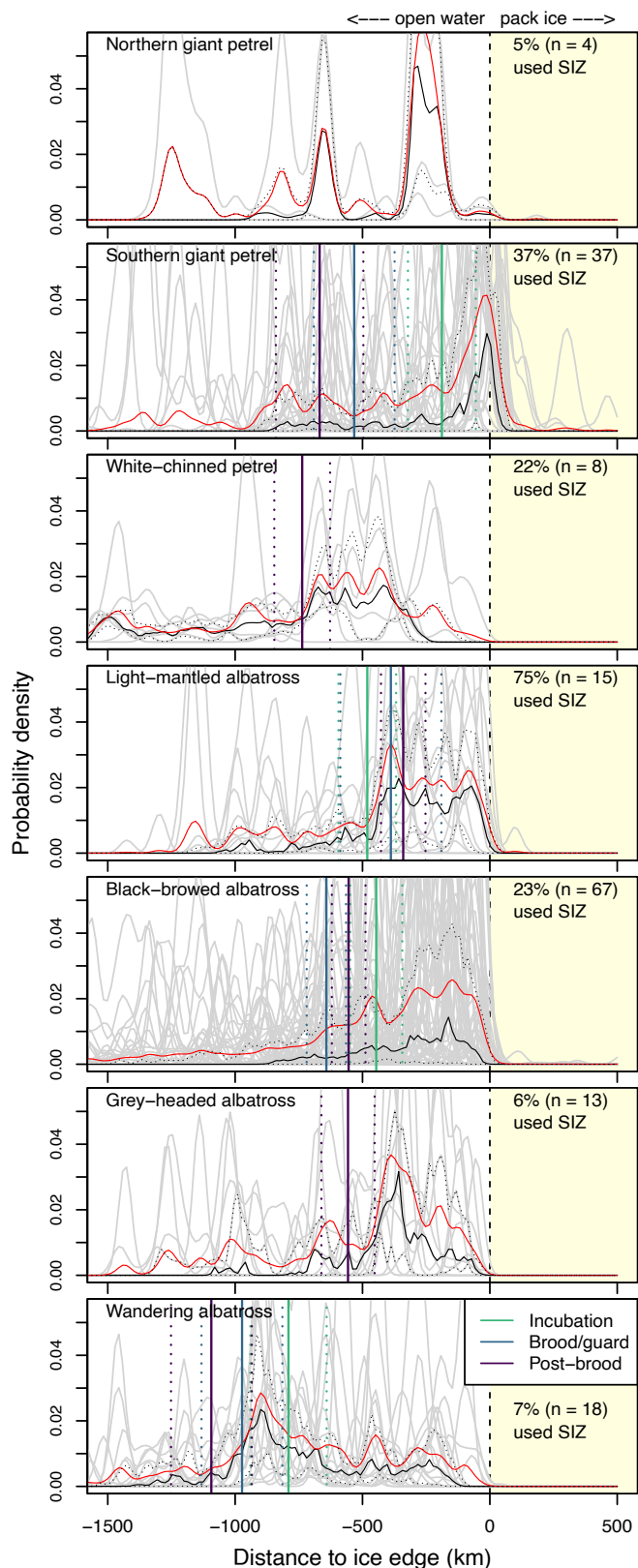


Fig. 5. Variation between breeding stages in the proportion of non-travelling locations of breeding albatrosses and large petrels tracked from Bird Island, South Georgia, in the Seasonal Ice Zone (SIZ) and the Marginal and Consolidated Ice Zones (MIZ/CIZ). Vertical and horizontal lines indicate population-level means and their 95% CIs estimated using logistic Generalised Additive Models fitted separately to each species. Circles indicate minimum and maximum observed values.



(caption on next column)

Fig. 6. Use of space (excluding travelling) relative to distance to the ice edge during all foraging trips by albatrosses and petrels from Bird Island, South Georgia, that entered the Seasonal Ice Zone (SIZ). Positive distances indicate the Marginal or Consolidated Ice Zones (yellow) and negative distances (unshaded) open water. Grey lines show bird-level empirical utilisation distributions (UDs), assuming a kernel bandwidth of 25 km. Red, black and dotted lines are respectively across-individual means, medians, and interquartile ranges of UDUs. Vertical lines are mean (and 95 % CI) ice-edge distances within breeding stages during which ≥ 3 tracked birds used the SIZ, estimated using Generalised Linear Mixed-effects Models fitted to each species. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

were recorded < 12 km from land (Fig. A3). Detailed examination of foraging trips plotted over contemporary SICs (Fig. 8) showed that high SICs encountered by this species occurred close to small Antarctic islands remote from the main ice edge, where SIC estimates can be biased upwards (see Section 4.1). The remaining species encountered SICs > 15 % largely in open water (Fig. 8 and Fig. S2). Of these, light-mantled albatrosses remained almost exclusively on the seaward side of the nominal ice edge (Figs. 6 and 8). In contrast, southern giant petrels travelled up to 530 km into the pack ice, to areas with SICs ranging from 15 to 100 % (Fig. 8). Within species, there were no significant differences in the proportion of females vs. males entering the MIZ/CIZ (Fishers exact tests, $p > 0.05$).

3.4. Lags in use of the seasonal ice zone

There were sufficient data to model the lag between breakup and first use ($DFU - DBU$) of locations in the SIZ for five species (Table 2, Fig. 9). The most parsimonious lag model contained DBU and species but no interactions as explanatory covariates (Table A6). Mean lag between breakup and first use was, respectively, one week for light-mantled albatrosses; ~ 5.5 weeks for black-browed and grey-headed albatrosses; and \sim seven weeks for white-chinned petrels (Fig. 3). There was no significant lag for southern giant petrels. Indeed, they used many parts of the SIZ prior to breakup (Fig. 3, Fig. A2). Across species, the slope $\Delta(DFU - DBU)/\Delta DBU$ did not differ significantly from zero (Table 2), suggesting lag remained constant over the breeding season.

4. Discussion

Although many albatrosses and large petrels that breed on subantarctic islands have previously been tracked to the seasonal and marginal ice zones, most knowledge about their use of sea-ice habitats was hitherto derived from ship-based observations (Ainley et al., 1984; Ainley et al., 2017; Woehler et al., 2003). By analysing their movements in detail, our study provides a new perspective on the extent to which globally important subantarctic breeding populations commute into the SIZ to forage. At the macroscale, most species moved progressively south over the summer, presumably following the southward propagating resource wave driven by solar irradiance and the resulting spring phytoplankton bloom. All species used the SIZ to some extent, but there was substantial variation among species and seasons. Albatrosses and white-chinned petrels largely avoided the pack ice and most used the SIZ only 1–1.5 months after it had become ice free. However, light-mantled albatrosses tracked the receding ice without appreciable delay, using open water relatively close to the ice edge throughout the breeding season. Some southern giant petrels, and to a lesser extent northern giant petrels, used the SIZ and MIZ, but pack ice was only used regularly by the former during incubation.

4.1. Limitations of the study

The tracking data analysed here were collected for a variety of purposes – and the bulk from mid incubation to mid chick-rearing – so

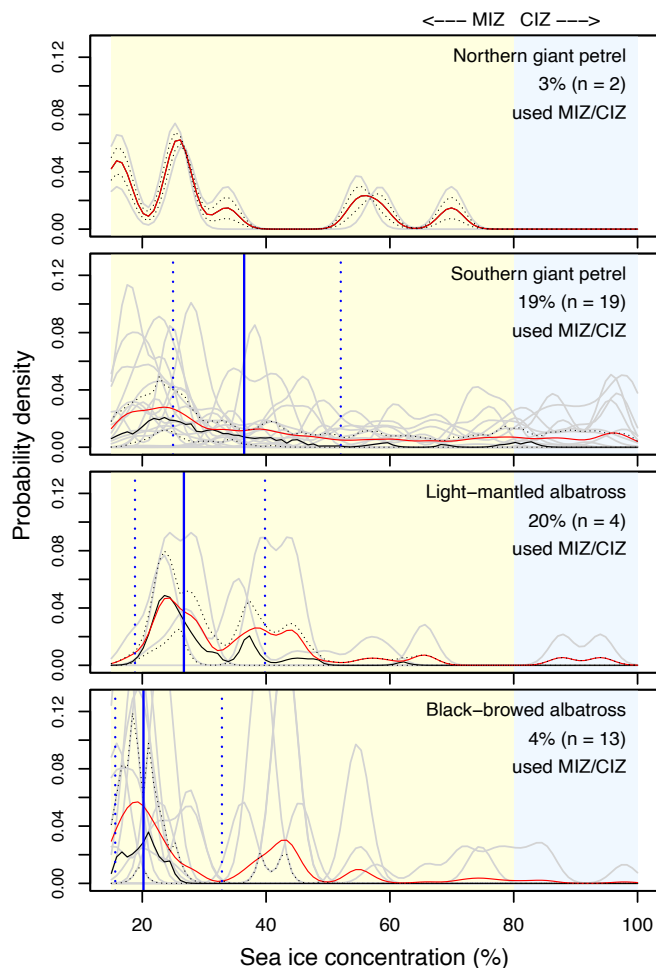


Fig. 7. Sea-ice concentrations at foraging/resting locations used by albatrosses and large petrels from Bird Island, South Georgia, within the Marginal (MIZ, yellow) and Consolidated (CIZ, blue) Ice Zones. Grey lines show bird-level empirical utilisation distributions (UDs). Red, black and dotted lines are respectively across-individual means, medians and interquartile ranges of UD's assuming a kernel bandwidth of 1 %. Blue vertical lines are mean (and 95 % CI) SICs for species where ≥ 3 tracked birds used the MIZ/CIZ, estimated using species-level logistic Generalised Linear Mixed-effects Models. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

coverage was not optimal for quantifying use of sea-ice habitats. Although we cannot therefore directly infer habitat use during other periods, the extent of open water in the SIZ remains near its minimum until after early incubation for all study species except wandering albatrosses (Fig. 1), so it is unlikely that it is used then by the open water affiliates. However, the ice edge at that time is closer to South Georgia, so edge-affiliated light-mantled albatrosses and ice-affiliated southern giant petrels may have used these respective habitats extensively without being observed. Similarly, without tracking data during the autumn, we cannot infer how the study species respond to the formation of new ice. Nor have there been many ship-based studies during this period.

We were also limited in our ability to estimate lags between ice breakup and use of the SIZ, particularly for wandering albatrosses, few of which were tracked in November and December. Our analysis implicitly assumes that sufficient birds were tracked to accurately estimate dates of first use of groups of cells in the SIZ with particular breakup dates (section 2.3). If insufficient birds were tracked, extents of the range margins could have been underestimated (Soanes, Arnould, Dodd, Sumner & Green, 2013), and the dates of first use biased late.

Simulations for albatrosses suggest that at least ~ 30 birds need to be tracked to obtain robust estimates of 95 % utilisation distributions (Gutowsky, Leonard, Connors, Shaffer & Jonsen, 2015). Although our sample sizes for most species were of this order, only 3 – 10 light-mantled albatrosses were tracked at any one time. Moreover, our lag estimate (9 days) was only marginally significant for this species. Hence, light-mantled albatrosses may actually use the SIZ as soon as the ice breaks up, a supposition supported by at-sea observations (Woehler, Raymond, Boyle & Stafford, 2010). Lags for all species could be refined in the future by tracking of many (>30) individuals over the ice-recession period (October-February), or by at-sea surveys, ideally in the same area (Ainley et al., 1993).

Another limitation is the potential mismatch between the spatio-temporal resolution of seabird tracking (typically ≤ 1 location/h, error < 100 m) and the ASI sea-ice data (1 image/d, resolution 3.125 km). For example, a bird location classified as being in 50 % SIC based on ASI data could, at a finer scale, be in a patch of open water or of continuous ice cover up to 1.5 km² in extent, or in a finer mosaic of equal amounts of floes and open water (Kern, Lavergne, Notz, Pedersen, Tonboe et al., 2019; Shi, Su, Heygster, Shi, Wang et al., 2021). Furthermore, sea ice is highly dynamic, moving on average at 0.76 ± 0.54 km/h because of currents, tides, and wind forcing in particular (Kottmeier & Sellmann, 1996; Vihma & Launiainen, 1993), so SIC and the ice edge location can vary markedly in between the daily remotely-sensed images (Kern et al., 2019). Given this and the additional uncertainty associated with localisation of the ice edge, which only nominally coincides with the 15 % SIC contour, our data will contain spurious instances of bird locations within the MIZ and vice versa, and imprecise estimates of distance to the ice edge. Future analyses may resolve these ambiguities using higher-resolution remotely-sensed data or by analysing other properties that structure seabird habitats, such as ice age and thickness (Arrigo, 2014; Eicken, 1992; Flores, Haas, van Franeker & Meesters, 2008). Despite these limitations, summary statistics presented here should be unbiased with the possible exception of SICs for black-browed albatrosses. During at-sea surveys, this species is very rarely recorded in the MIZ (Joiris, 1991; van Franeker, 1993), yet our analysis suggested that four percent of tracked black-browed albatrosses entered the MIZ. We suspect that the latter is spurious because tracked black-browed albatrosses only encountered putative high SICs near Antarctic coastlines and large icebergs, where pixels are often misclassified (see Methods). This methodological issue may affect black-browed albatrosses in particular because they prefer to forage over continental and periinsular shelves (Wakefield et al., 2011), which are relatively narrow around Antarctica.

4.2. Use of sea-ice habitats

Although our results largely conform to the existing three-assemblage paradigm of sea-ice habitat use by seabirds inferred from at-sea surveys (ice-affiliated, ice-tolerant and ice-avoiding species (Ainley et al., 2017; Ainley et al., 1994)), this categorisation of our study species was not exact. Southern giant petrels regularly commuted from South Georgia to both the SIZ and pack ice, highlighting that not all ice-affiliates originate from colonies along Antarctic coastlines (Trebilco et al., 2008). Nevertheless, this species spent most of its time in open-water habitats, or on land (especially males). Among northern giant petrels, only females used the pack ice during the incubation period. These patterns are consistent with previous studies which showed that breeding northern and southern giant petrels generally forage north and south of the Antarctic Polar Front (APF), respectively, and that males spend more time scavenging terrestrially (González-Solís, Croxall & Wood, 2000b; Granroth-Wilding & Phillips, 2019; Hunter, 1983; Johnstone, 1974; Reisinger, Carpenter-Kling, Connan, Cherel & Pistorius, 2020; Thiers, Delord, Barbraud, Phillips, Pinaud & Weimerskirch, 2014).

Previously, immersion data indicated that although breeding giant petrels foraging at sea frequently alight on the water during darkness,

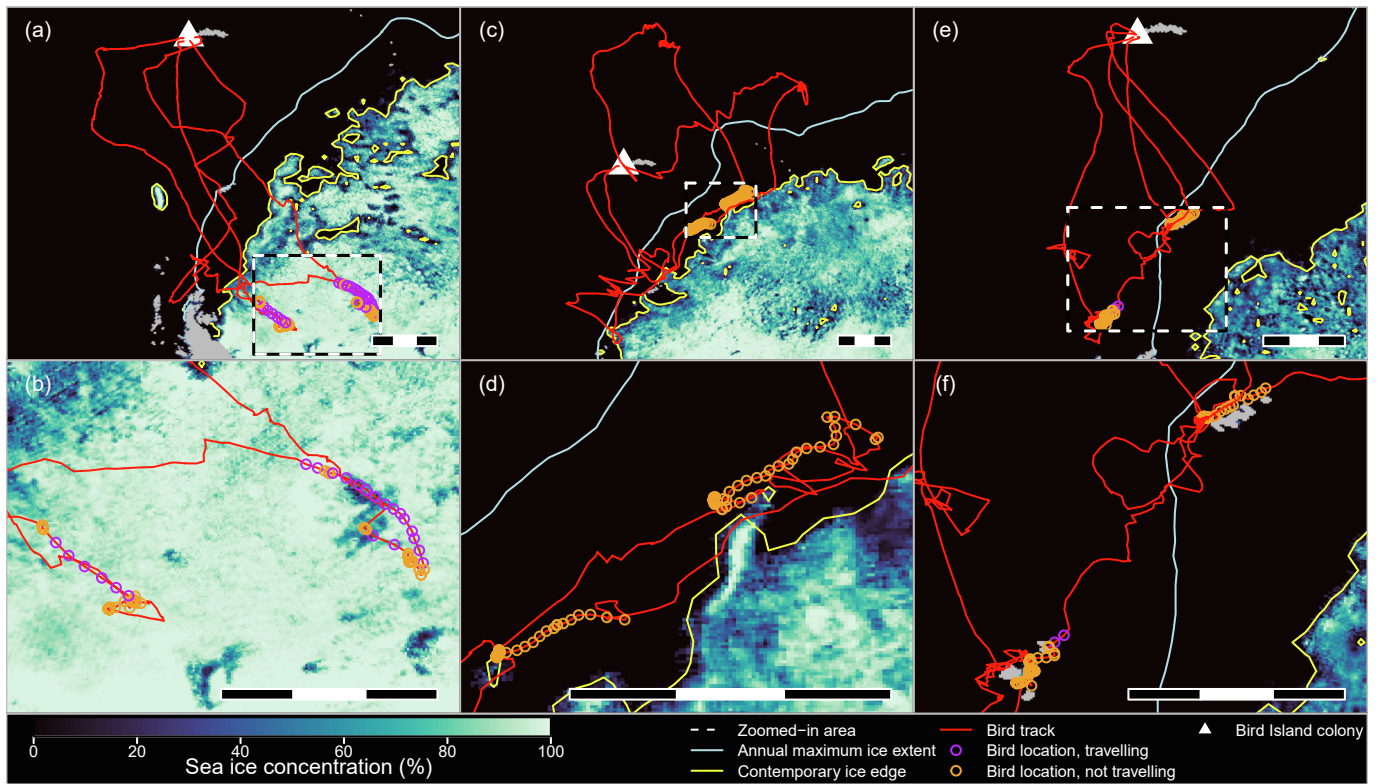


Fig. 8. Examples of typical foraging trips (two per species, each made by a different bird) that entered the Marginal Ice Zone, and corresponding sea-ice concentrations. (a,b) southern giant petrels, (c,d) light-mantled albatrosses and (e,f) black-browed albatrosses. Round symbols highlight half-hourly locations for one focal day for each species – 18 December 2022, 22 December 2014 and 25 December 2021, respectively. Sea-ice concentrations shown in both the top and bottom panels are for those days and the birds’ movements on those days are shown in detail in the bottom panels, zoomed in to the extents shown by the squares in the top panels. Scale bars 300 km.

Table 2

Generalized Least Squares model of the lag between the date of first use (DFU) of regions in the Seasonal Ice Zone and date of breakup (DBU) in those regions as a function of DBU and species.

Species	Parameter	SE	t	p^1	Predicted lag (95 % CI) ¹
All	Slope	-0.2	0.1	-1.63	0.104
Southern giant petrel	Intercept	15.7	15.4	1.01	0.311
White-chinned petrels		68.4	14.8	4.63	<0.001
Light-mantled albatros		32.9	17.0	1.93	0.054
Black-browed albatross		57.5	13.0	4.42	<0.001
Grey-headed albatross		59.6	14.1	4.24	<0.001
					-8.2 (-19.1, 2.8)
					47.9 (33.7, 62.1)
					8.6 (-7.5, 24.7)
					37.9 (28.7, 47.0)
					38.0 (25.1, 50.9)

¹For slope, p indicates the probability that $\Delta(DFU - DBU) / \Delta DBU \neq 0$, and therefore $\Delta DFU / \Delta DBU \neq 1$. p is the probability that the intercept is not zero for southern giant petrels and that it differs from that of southern giant petrels for the other species.

²For each species, this is $DFU - DBU$ predicted for the middle of the observed range of DBU for that species.

individuals travelling 700–1000 km south of Bird Island to areas with no land often spent nights stationary but not immersed (González-Solís et al., 2002). This was tentatively interpreted to arise from roosting on icebergs (Section 4.4) but our analyses show that in at least some of these cases, it is likely due to birds alighting on sea ice to roost or feed.

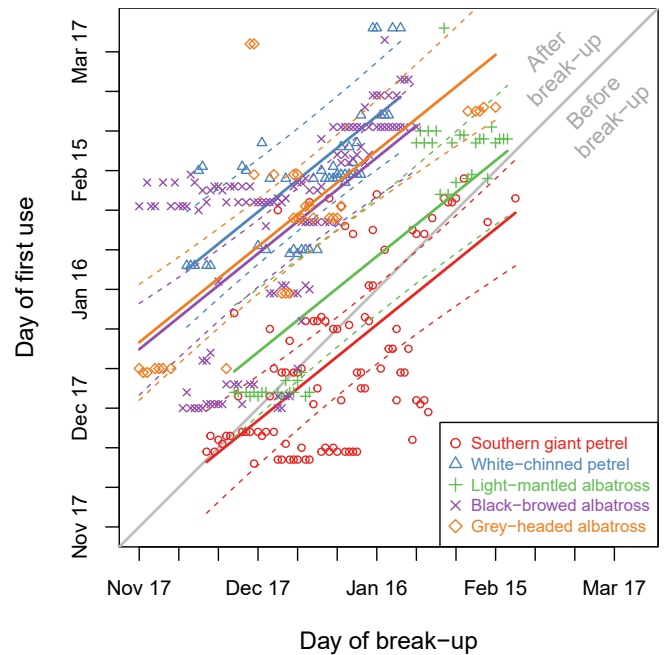


Fig. 9. Date that breeding albatrosses and petrels tracked from Bird Island, South Georgia, first used areas in the Seasonal Ice Zone vs. the day of ice breakup. Coloured lines show species means and their 95% confidence envelopes predicted by a Generalized Least Squares model and the grey line the relationship expected if first use occurred simultaneously with breakup. Points to the right and left of this indicate first use prior to and after breakup, respectively.

Roosting on ice may incur lower thermoregulatory and therefore energetic costs than resting on the sea (Ainley et al., 2017; Grunst et al., 2022). However, giant petrels in our study, and those from Macquarie Island and probably Marion Island (Reisinger et al., 2020; Trebilco et al., 2008), travelled 100 s to 1000 s of km into the pack. Due to the cost of flying such long distances, we assume that this not just to roost but was primarily to forage, for example on carrion associated with pupping of pinnipeds (see Section 4.4). Year-round, southern giant petrels spend more time not immersed at night than northern giant petrels (Thiers et al., 2014), possibly indicating greater use of sea ice by the latter (either to forage or roost) is not just limited to the breeding season. Our findings underline that both species, and particularly southern giant petrels, have the flexibility to forage not only on land and in open water, but also within the ice edge and pack (Ainley et al., 1984; Ainley et al., 1992; Chapman, Ribic & Fraser, 2004; Cline, Siniff & Erickson, 1969; Ryan & Cooper, 1989; Woehler et al., 2003; Zink, 1981). However, we also note that giant petrels breeding in Argentina do not use sea-ice habitats, presumably due to the proximity of more profitable foraging on the Patagonian Shelf (Quintana & Dell'Arciprete, 2002; Quintana, Dell'Arciprete & Copello, 2010).

Light-mantled albatrosses also clearly use some sea-ice habitats for much of the breeding season, but not pack ice. Unlike the other small albatrosses in our study, they do not use oceanic frontal systems extensively (Phillips et al., 2005a). Rather, our results show that they largely remain < 400 km from the ice edge throughout the breeding season, following it south, without appreciable delay, as it recedes in spring and summer. Spatiotemporal distributions of light-mantled albatrosses tracked from other subantarctic colonies (Carpenter-Kling, Reisinger, Orgeret, Connan, Stevens et al., 2020; Cleeland, Alderman, Bindoff, Lea, McMahon et al., 2019; Lawton, Kirkwood, Robertson & Raymond, 2008; Weimerskirch & Robertson, 1994), and observed from ships (Ainley et al., 1984; Hunt, Heinemann, Veit, Heywood & Everson, 1990; Joiris, 1991; Montague, 1988; Orgeira, Alvarez & Salvó, 2022; Ryan & Cooper, 1989; Weimerskirch et al., 1989; Woehler et al., 2010), indicate a similar pattern of habitat use across populations. Indeed, a higher proportion of light-mantled albatrosses (75 %) than other species used the SIZ, so this is arguably the most ice-dependent species in our study.

The remaining species essentially behaved as open-water affiliates but with some important nuances. Black-browed albatrosses foraged within the SIZ for more of the breeding season and in higher SICs than grey-headed albatrosses. This is consistent with occasional records of black-browed, but not grey-headed albatrosses from ships in the outer MIZ (Ainley et al., 1984; Joiris, 1991; Ryan & Cooper, 1989; van Franeker, 1993; Weimerskirch et al., 1989; Woehler et al., 2003). These species are closely related and morphologically very similar, so their different foraging distributions may be a secondary consequence of other habitat or dietary preferences (Phillips et al., 2004; Xavier, Croxall & Reid, 2003). Black-browed albatrosses prefer neritic and shelf-slope waters (Wakefield et al., 2011) in which fast ice may persist late into the summer. In contrast, grey-headed albatrosses select oceanic waters and fronts (Cтры, Phillips, Phalan, Silk & Croxall, 2004; Phillips et al., 2004), mainly frequenting the SIZ late in the summer, when seasonal sea ice has retreated. Tracking suggests that most other black-browed albatross populations also use the SIZ extensively – the exception being the breeding population at the Falkland Islands, which remains on the Patagonian Shelf, presumably due to its proximity and high productivity (Cleeland et al., 2019; Wakefield, Phillips & Matthiopoulos, 2014; Wakefield et al., 2011). Grey-headed albatrosses tracked from colonies in the southern Indian and Pacific Oceans largely avoided latitudes coinciding with the SIZ (Carpenter-Kling et al., 2020; Cleeland et al., 2019; Kroeger, Crocker, Orben, Thompson, Torres et al., 2020; Nel, Lutjeharms, Pakhomov, Anson, Ryan & Klages, 2001; Waugh, Weimerskirch, Cherel, Shankar, Prince & Sagar, 1999). It is unclear whether this reflects a preference for other habitats, or the greater distance of the SIZ from those colonies (1300 and 1100 km, respectively vs. 430 km

from South Georgia).

Wandering albatrosses and white-chinned petrels analysed here both acted as open-water affiliates, predominantly using ice-free areas of the SIZ in late summer. Previous ship-based and tracking observations have reported similar patterns of habitat use in many other areas (Ainley et al., 1984; Carpenter-Kling et al., 2020; Cleeland et al., 2019; Delord, Bost, Cherel, Guinet & Weimerskirch, 2013; Joiris, 1991; Veit & Hunt, 1991; Zink, 1978; Zink, 1981). White-chinned petrels in our study, and those breeding on Crozet and Marion Islands, used the SIZ only during chick-rearing. In contrast, those tracked from Kerguelen additionally did so during incubation (Catard, Weimerskirch & Cherel, 2000; Péron et al., 2010; Rollinson, Dilley, Davies & Ryan, 2018; Weimerskirch, Catard, Prince, Cherel & Croxall, 1999) and foraged much closer to the ice edge than birds from South Georgia (200–300 km vs. 730 km; cf. Fig. 6 & Péron et al., 2010). It is unclear why, given that Kerguelen is ~ 1000 km further from the SIZ than South Georgia, but this may relate to regional differences in the phenology of primary production. During exploratory analysis, we noted that individual variability in use of sea-ice habitats was high among both white-chinned petrels and wandering albatrosses, and some individuals of both species are occasionally recorded far south in the Weddell Sea in late summer (Orgeira et al., 2022; Zink, 1978). Male wandering albatrosses have a more southerly distribution than females, especially during incubation (Froy, Lewis, Cтры, Bishop, Forster et al., 2015; Jiménez, Domingo, Brazeiro, Defeo, Wood et al., 2016; Weimerskirch, Cherel, Delord, Jaeger, Patrick & Riotte-Lambert, 2014; Xavier et al., 2004), so we presume that the use of the SIZ by this species is predominantly by males. The sex of white-chinned petrels in our study was unknown.

Habitat selection is modulated by habitat availability, accessibility and competition, so variation in the relative locations of colonies and resource patches is expected to give rise to geographical differences in habitat use (Matthiopoulos, 2003; Matthiopoulos, Hebblewhite, Aarts & Fieberg, 2011; Wakefield, Bodey, Bearhop, Blackburn, Colhoun et al., 2013). Presumably, this explains why populations of our study species breeding elsewhere, closer to more productive habitats, do not use the SIZ (e.g. Quintana & Dell'Arciprete, 2002; Wakefield et al., 2011). Regardless, our results and those of studies discussed above show that many other albatross and petrel populations breeding on subantarctic islands use the SIZ in a similar manner to those in our study. Habitat use during non-breeding stages, when habitat accessibility is less constraining, is also revealing. Adult southern giant petrels, especially females, tracked from some (Chapman et al., 2004; González-Solís, Croxall & Afanasyev, 2007; Phillips, McGill, Dawson & Bearhop, 2011), but not all colonies (Thiers et al., 2014), used latitudes consistent with foraging in the pack ice during the non-breeding period, as did fledglings (Thiers et al., 2014; Trebilco et al., 2008). Indeed, the majority of southern giant petrels observed from ships in the pack ice in the summer are juveniles (Ainley et al., 1984; Zink, 1981). Non-breeding light-mantled albatrosses tracked from two colonies used latitudes corresponding to the SIZ during the winter (Cleeland et al., 2019; Mackley, Phillips, Silk, Wakefield, Afanasyev et al., 2010). In contrast, non-breeding adults of the open water-affiliated species dispersed well north of the SIZ, often to productive areas, such as upwellings (Cleeland et al., 2019; Delord et al., 2013; Grémillet, Wilson, Wanless & Chater, 2000; Péron et al., 2010; Phillips et al., 2006; Phillips, Silk, Croxall, Afanasyev & Bennett, 2005b; Rollinson et al., 2018). In summary, we are confident that the species-specific patterns of sea-ice habitat use we observed are general, rather than resulting from local circumstances, even though the SIZ occurs closer to South Georgia than to most other subantarctic islands (Gloersen et al., 1992).

4.3. Resource tracking and temporal lags

Our findings point to two distinct seasonal movement patterns, ostensibly reflecting the main mechanisms regulating primary production and inter-specific differences in foraging strategies. First, the mean

foraging latitude of open-water-affiliated species varied sinusoidally, but out of phase by 2–3 months with the sinusoidal variation in incident solar irradiance. This was clearest for wandering albatrosses, because they were tracked over most of their breeding period (which spans a full annual cycle), but was also evident for black-browed albatrosses, grey-headed albatrosses and white-chinned petrels, which were tracked for 5–6 months of their 7–8 month breeding periods. This is likely due to cyclicity in the main drivers of primary production – principally solar irradiance, but also vertical mixing and nutrient availability (Arteaga et al., 2020; Boyce et al., 2017) – which give rise to a meridionally-propagating resource wave (Abrahms et al., 2021), lagged due to the time required for transfer of primary production up to the trophic levels at which seabirds feed (Sommer, Adrian, De, de Senerpont Domis, Elser et al., 2012). Similar seasonal macroscale meridional migrations occur among other wide-ranging higher marine predators (Abrahms et al., 2019; Block et al., 2011). For example, in the North Pacific, blue whales *Balaenoptera musculus* track phytoplankton blooms northwards with a lag of 30 days (Abrahms et al., 2019). However, although it has previously been shown that some post-breeding seabirds migrations track seasonal meridional shifts in production (Egevang, Stenhouse, Phillips, Petersen, Fox & Silk, 2010; Shaffer, Tremblay, Weimerskirch, Scott, Thompson et al., 2006; Thorne et al., 2023), we are not aware of this effect having been quantified among breeding birds. Examination of tracking data for other populations (e.g. BirdLife-International, 2004; Nel et al., 2001; Wakefield et al., 2011) indicates that the pattern is common among albatrosses and petrels breeding at other subantarctic islands. It should be considered as the backdrop to finer scale processes of habitat selection.

The second seasonal pattern was that birds tracked the spring retreat of the ice edge southwards across the SIZ. Open-water species did so with a lag of 1–2 months, whereas ice-edge-affiliated light-mantled albatrosses did so with little or no lag. The most parsimonious explanation for the latter species' behaviour is that sea ice physically impedes their foraging or movement (Ainley et al., 2017) (section 4.4). This could also be the case for the open-water-affiliated species but does not explain their lagged response to the receding ice. Instead, we assume it is due to latency in trophic transfer: Primary production within the pack increases in spring in response to solar irradiance, peaking in late spring or summer, just prior to the breakup (Arrigo, 2014). Melting stimulates primary production in the upper water column by releasing nutrients concentrated in the pack formed the previous winter. It also freshens the water, thereby stabilizing the mixed layer (Smith & Nelson, 1985; Taylor et al., 2013). In addition, zooplankton, including Antarctic krill, respond to increasing photoperiod, plus the altered trade-off between predation risk and foraging reward caused by the burgeoning food supply, by ceasing diel vertical migration and concentrating in surface waters (Ainley, Ballard, Jones, Jongsomjit, Pierce et al., 2015; Cisewski & Strass, 2016; Clarke, 1988; Siegel & Watkins, 2016), making them more accessible to air-breathing predators (Ainley et al., 1986; Beltran, Kilpatrick, Breed, Adachi, Takahashi et al., 2021). Primary production typically peaks 2–6 weeks after break up (Cisewski & Strass, 2016; Conroy et al., 2023; von Berg et al., 2020) and zooplankton abundance 2–3 weeks after that (Conroy et al., 2023) – i.e. 4–9 weeks after break up, which is very similar to the lag we observed for open-water affiliated seabirds first using the SIZ.

We did not detect a clear seasonal shift in latitudes of tracked giant petrels. Potentially, this is because any trend in pelagic distribution is masked by the predominance of terrestrial foraging by males, particularly northern giant petrels, throughout much of the breeding season (González-Solís et al., 2000b; Granroth-Wilding & Phillips, 2019; Hunter, 1983). The southward shift in the northern range limit of northern giant petrels between incubation and chick-rearing implies that seasonal changes in pelagic productivity do nevertheless affect this species (light-mantled albatrosses were likewise affected). Southern giant petrels may be less affected by open-water productivity because they frequently forage terrestrially on carrion, and among pack ice. They

used the SIZ both before and after breakup (large positive and negative residuals in Fig. 5), presumably because they are unimpeded by sea ice (Section 4.4). On average, however, they first used locations in the SIZ around the time of breakup, so the ice edge itself may also be an important habitat. Wandering albatrosses were not tracked during the period of most rapid ice recession but given the overall seasonal trend in their foraging latitude, we hypothesise that their use of the SIZ was lagged similarly to the other open-water affiliates.

While our results are consistent with the hypothesis that wide-ranging marine predators track seasonal pulses in resources (Abrahms et al., 2019; Durant et al., 2007; Lack, 1968), our study was necessarily correlational so it is prudent to consider other potential causes of seasonal meridional movements. For example, seasonal changes in wind could conceivably affect habitat accessibility. However, winds at high latitudes become lighter in summer, which would impede dynamic soaring (Weimerskirch, Louzao, de Grissac & Delord, 2012), having the opposite effect to that observed. Alternatively, birds could move to higher latitudes to increase available daylight for foraging. This too is inconsistent with our results: daylight would be maximised by switching to high latitudes by midsummer, not after a lag that we observed. We also caution that the hypothesised effects of light limitation and ice breakup could be confounded, not least because the former ultimately drives the latter. A more detailed analysis would be required to separate these effects, but we note that ice breakup does not simply proceed along the meridional axis in our study area (Fig. 1a and 3), because it is also caused by wind (Kohout, Williams, Dean & Meylan, 2014; Thorne et al., 2023; Turner, Holmes, Caton Harrison, Phillips, Jena et al., 2022). Future analyses should consider these effects in more detail, as well as those of nutrient supply and stratification, which also regulate local primary production (Ardyna et al., 2017; Arteaga et al., 2020).

Although relatively sparse, other studies largely support the hypothesis that seabirds track resource waves induced by sea-ice dynamics. For example, in Prydz Bay, East Antarctica, seabird assemblages affiliated with the pack ice and ice edge moved meridionally in concert with the seasonal recession and advance of the ice edge (Woehler et al., 2003). In the Weddell Sea, peak seabird diversity and abundance followed the spring retreat of the ice edge but with a spatial lag of ~ 7–10 km (Fraser & Ainley, 1986). Moreover, GPS-tracked Antarctic petrels *Thalassoica antarctica* behaved like the ice-edge affiliates during the spring, targeting waters that had become open 10 days previously, but later in the summer, when sea ice was near its minimum, they behaved like open-water affiliates, selecting areas 50–60 days post-breakup (Fauchald et al., 2017). Notably, these lags are very similar to those we found for these two groups.

4.4. Adaptations to sea-ice habitats

Our study and others support the view that ice- and ice-edge-affiliated species (southern giant petrels and light-mantled albatrosses, respectively) track those habitats year-round, whereas open-water species track seasonal pulses in productivity (Ainley et al., 1994), rather than any particular biophysical niche (Lambert & Fort, 2022). This implies that although prey in open water at high latitudes are seasonally pulsed (section 4.3), they remain relatively abundant throughout the year, albeit not necessarily accessible to non-ice specialists in, and near the pack ice. This prompts the questions: what adaptations facilitate or hinder use of sea-ice habitats, and how do these adaptations maintain niche partitioning?

Several mechanisms have been hypothesised to limit use of pack ice by albatrosses and large petrels. Firstly, dynamic soaring, the principle mode of flight for this group, could be inhibited by sea ice (Ainley et al., 1984; Griffiths, 1983). Of the species tracked during our study, only southern giant petrels flew far (100 s of km) into the pack ice (e.g., Fig. 8). Possibly giant petrels are able to do this because the aspect ratio of their wings is relatively low (Obst & Nagy, 1992; Thorne et al., 2023; Warham, 1977), allowing them to proceed by flapping, rather than

dynamic soaring flight (Ainley et al., 2017; Pennycuik, 2008). However, giant petrels observed from land and sea use flapping flight only marginally more than albatrosses (Obst & Nagy, 1992; Pennycuik, 1982), and we are not aware of any studies that have documented the flight style used by giant petrels when crossing sea ice. Secondly, specialist adaptation could be required to forage on or among ice floes (Griffiths, 1983). Giant petrels are well adapted for bipedal locomotion, (Prince & Morgan, 1987; Warham, 1996), which uniquely among large procellariiforms, allows them to compete for food effectively on land, where both species, and particularly males, frequently consume seal and penguin carrion (Mills, Morley, Votier & Phillips, 2021; Raya Rey, Polito, Archuby & Coria, 2012; Ridoux, 1994). Bipedal proficiency may also allow them to scavenge competitively on ice floes, because they are the only large procellariiform observed to do so (Marchant & Higgins, 1990). Diet within the pack ice is poorly known but is thought to be dominated by carrion (Ainley et al., 1992; Ainley et al., 1993; Conroy, 1972). Indeed, both giant petrel species may use the pack ice more frequently during incubation (Trebilco et al., 2008) because this coincides with pupping by crabeater *Lobodon carcinophaga*, Ross *Ommatophoca rossii* and leopard *Hydrurga leptonyx* seals. These seals give birth on floes between October and November (Würsig, Thewissen & Kovacs, 2017), making placentae and dead pups available. Giant petrels may also scavenge in association with other predators within the MIZ (Ridoux, 1994) and capture live prey from the water near floes (Conroy, 1972).

It is unclear what adaptations facilitate use of the waters adjacent to the ice edge by light-mantled albatrosses. Morphologically, they are very similar to congeneric sooty albatrosses *Phoebastria fusca*, which forage mainly north of the polar front (Bentley, Phillips, Carpenter-Kling, Crawford, Cuthbert et al., 2024). It is unlikely therefore that *P. palpebrata* possess gross morphological adaptations to ice-edge foraging. Both species consume krill, fish, carrion and squid (Cooper & Klages, 1995; Prince & Morgan, 1987; Thomas, 1982). Light-mantled albatrosses are smaller billed (Bentley et al.), so specialisation on prey associated with sea ice could contribute to the observed pattern of habitat use. For example, the commonest squid in their diets at South Georgia are *Galiteuthis glacialis* and *Psychroteuthis glacialis* (Prince & Morgan, 1987). These and other frequently consumed prey, such as Antarctic krill and the Antarctic silverfish *Pleuragramma antarctica* (Thomas, 1982), aggregate at shallow depths under floes and near the ice edge (Brierley et al., 2002; Davis, Hofmann, Klinck, Piñones & Dinniman, 2017; Nesis, Nigmatullin & Nikitina, 1998). Hence, light-mantled albatrosses could occur near but not within the pack ice because they forage at the edges of isolated floes and bergs. Large icebergs enhance local biological production and aggregate zooplankton (Smith, Sherman, Shaw & Sprintall, 2013). They are particularly abundant in the study area due to north-eastward advection out of the Weddell Sea along the so called “iceberg alley” (Stuart & Long, 2011), where light-mantled albatrosses and southern giant petrels have previously been reported associating with 2–39 km long icebergs (Ruhl et al., 2011). During exploratory analysis of our data, we noted that individuals of both species occasionally followed the edges of large tabular icebergs, but data resolution was insufficient to establish whether they were searching for prey or simply avoiding an obstacle. Conceivably, affiliation with the pack ice edge by light-mantled albatrosses could also arise secondarily due to their prey preferring water masses that coincide with the ice edge. Consistent with this hypothesis, the southern limit of light-mantled albatrosses observed in the Ross Sea was not defined by the presence of ice but by the -0.5 °C isotherm (Ainley et al., 1984). Moreover, the prey noted above also occur not only in association with ice but also in open water south of the APF.

Habitat use relative to sea ice by the open-water-associated species is consistent with previous observations (Ainley et al., 2017). We assume they lack the morphological adaptations necessary to forage within the MIZ. Patentley, given their winter distributions (Clay, Manica, Ryan, Silk, Croxall et al., 2016; Mackley et al., 2010; Phillips et al., 2005b),

they are not restricted by dietary specialisation to foraging in high latitude waters. Hence, they use the SIZ only when prey become superabundant following the seasonal breakup of the pack ice, with a lag due to the time required for trophic transfer. This implies another adaptation to sea ice: phenological matching. It has been argued that the breeding schedule of most subantarctic albatrosses and petrels is timed so that brood-guard, when central-place constraint is greatest, coincides with prey abundance near the colony (Lack, 1968; Weimerskirch et al., 1989). Notably, brood-guard of most species in our study occurs approximately a month after the peak phytoplankton bloom around South Georgia (cf. our Fig. 1c-i and Fig. 7 in Borrione & Schlitzer, 2013). During post-brood, both parents can range further from the colony but must feed both themselves and their offspring. Therefore, a refinement to this hypothesis implied by our results is that post-brood (among those species that use the SIZ, other than wandering albatrosses, which have a more protracted breeding period) is timed to coincide with the post-breakup pulse in prey availability in the SIZ.

Differences in phenological matching could also contribute to maintaining niche differentiation among some taxa: For example, the six week earlier breeding of northern vs. southern giant petrels (Fig. 1) is hypothesised to reduce competition between these congeners (Hunter, 1987), with the former timing hatching to coincide with the seasonal peak in availability of Antarctic fur seal *Arctocephalus gazella* carrion at South Georgia (Hunter, 1983). Phenological synchrony between incubation in southern giant petrels and carrion availability within the pack ice could further maintain niche differentiation.

4.5. Connectivity, and implications of climate change

Our results prompt the question of how seabirds breeding in the subantarctic affect ecosystems in the SIZ, and vice versa. Regarding the first part of the question, subantarctic-breeding seabirds may link sea-ice-dominated and subantarctic ecosystems in a similar way to that previously recognised for some pinnipeds (Boyd, Staniland & Martin, 2002; Labrousse, Sallée, Fraser, Massom, Reid et al., 2017). For example, the seasonal influx of seabirds into Antarctic waters exerts top-down control on pelagic ecosystems in the SIZ (Croxall, Prince & Ricketts, 1985; Murphy, Cavanagh, Drinkwater, Grant, Heymans et al., 2016; Warwick-Evans, Kelly, Dalla Rosa, Friedlaender, Hinke et al., 2022), facilitates rapid nutrient recycling (Wing, Gault-Ringold, Stirling, Wing, Shatova & Frew, 2017), and may result in a net flux of biological carbon and nutrients northwards from the SIZ, in some cases across the APF, likely stimulating primary production around subantarctic islands (Otero, De La Peña-Lastra, Pérez-Alberti, Ferreira & Huerta-Diaz, 2018; Shatova, Wing, Gault-Ringold, Wing & Hoffmann, 2016). Our results imply that these processes intensify over the summer as open water affiliates forage in the SIZ more frequently, bolstered by the many smaller but more numerous subantarctic petrels that also exploit the SIZ (Navarro, Cardador, Brown & Phillips, 2015; Ryan & Cooper, 1989; Shaffer, Weimerskirch, Scott, Pinaud, D.R. et al., 2009).

Regarding the second part of the question, seabird populations are regulated in part via the effects of food supply on chick growth and breeding success (Cairns, 1992; Weimerskirch, 2002). Unsurprisingly, there is considerable evidence that sea ice regulates the demography of Antarctic-breeding ice-affiliated seabirds via its effects on prey availability and accessibility (Barbraud, Delord & Weimerskirch, 2015; Labrousse, Fraser, Sumner, Le Manach, Sauser et al., 2021; Trivelpiece, Hinke, Miller, Reiss, Trivelpiece & Watters, 2011). Sea-ice variability is mechanistically linked, mainly via wind, to large scale atmospheric processes such as the El Niño Southern Oscillation and Southern Annular Mode (Crosta et al., 2021; Isaacs et al., 2021; Stammerjohn et al., 2008b), presumably contributing to correlations between the demography of ice-affiliates and indices of these modes (Descamps et al., 2016; Fraser & Hofmann, 2003; Jenouvrier et al., 2005). The demographic rates of subantarctic-breeding albatrosses also correlate with these modes, but the underlying causal mechanisms are poorly understood

(Barbraud, Marteau, Ridoux, Delord & Weimerskirch, 2008; Cleeland, Pardo, Raymond, Tuck, McMahon et al., 2021; Gianuca, Votier, Pardo, Wood, Sherley et al., 2019; Nevoux, Weimerskirch & Barbraud, 2007; Pardo, Forcada, Wood, Tuck, Ireland et al., 2017). Our findings suggest that these could include mechanisms mediated by foraging in the SIZ. For example, open water affiliates would be affected by the impact of sea-ice dynamics on zooplankton abundance and community structure (Arrigo, 2014; Loeb et al., 1997; Murphy et al., 2007), especially during the later part of the summer. Similarly, all of the species might be impacted by the limiting effects of sea-ice extent and persistence on habitat availability (Barbraud et al., 2015). These hypotheses should be considered in future demographic studies, alongside the potentially confounding effects of other mechanisms linked to climatic modes (Lovenduski & Gruber, 2005), and wind-mediated variation in accessibility (Thorne et al., 2023; Weimerskirch et al., 2012). However, even the most ice associated species in our study – southern giant petrels and light-mantled albatrosses – spent only around 20–30 % of their time in the SIZ. Hence, effects mediated via other features, such as water masses, oceanic fronts, and bathymetry (e.g. Ainley, Jacobs, Ribic & Gaffney, 1998; Bost, Cotté, Bailleul, Cherel, Charrassin et al., 2009; Carpenter-Kling et al., 2020; Cleeland et al., 2019; Péron et al., 2010; Reisinger et al., 2020; Ribic, Ainley, Glenn Ford, Fraser, Tynan & Woehler, 2011; Wakefield et al., 2011) may have bigger demographic impacts.

Explaining linkages between demography and sea ice has a growing imperative due to perturbations in sea-ice dynamics expected under climate change (Bestley et al., 2020; Morley, Abele, Barnes, Cárdenas, Cotté et al., 2020). These will be additional to bycatch and other anthropogenic stressors (Cleeland et al., 2021; Gianuca et al., 2019), already causing unsustainable declines among albatrosses and petrels (Phillips et al., 2016). In the Arctic, severe declines in sea ice and changes in its phenology are already negatively impacting seabirds (Descamps & Ramírez, 2021; Hipfner, 2008; Nishizawa, Yamada, Hayashi, Wright, Kuletz et al., 2020; Ramírez, Tarroux, Hovinen, Navarro, Afán et al., 2017). Antarctic sea ice has been relatively stable over the satellite era but in recent summers seasonal sea ice has retreated early and reached record lows (National Snow & Ice Data Center 2023; Raphael & Handcock, 2022; Turner et al., 2020; Turner et al., 2022). Given the use of sea-ice habitats by seabirds in our study, these changes could impact the breeding success and ecosystems roles of substantial populations of subantarctic-breeding seabirds. Ultimately, projected future reductions in the extent of Antarctic sea ice (Eayrs et al., 2021; Roach et al., 2020) is expected to result in large shifts in the breeding distributions of ice-associated species (Ainley, Russell, Jenouvrier, Woehler, Lyver et al., 2010; Ainley et al., 2017; Jenouvrier, Holland, Stroeve, Serreze, Barbraud et al., 2014). More detailed study should be directed to determining how subantarctic breeders will respond (Krüger, Ramos, Xavier, Grémillet, González-Solís et al., 2018) and how this may disrupt the connectivity they provide between Antarctic and global ecosystems (Murphy et al., 2021).

CRediT authorship contribution statement

Ewan D. Wakefield: Writing – original draft, Methodology, Investigation, Formal analysis, Conceptualization. **Erin L. McClymont:** Writing – review & editing, Funding acquisition, Conceptualization. **Ana P.B. Carneiro:** . **John P. Croxall:** Writing – review & editing, Investigation, Funding acquisition. **Jacob González-Solís:** Writing – review & editing, Investigation. **Hannah M.V. Granroth-Wilding:** Writing – review & editing, Investigation. **Lesley Thorne:** Writing – review & editing, Investigation, Funding acquisition. **Victoria Warwick-Evans:** Writing – review & editing, Investigation. **Andrew G. Wood:** . **Jose C. Xavier:** . **Richard A. Phillips:** Writing – review & editing, Investigation, Funding acquisition, Data curation, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

I have shared a link to my data at the attach file step

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Data statement

The tracking data used in these analyses may be downloaded via the BirdLife Seabird Tracking Database (<https://data.seabirdtracking.org/>), using the following dataset IDs: 438, 444, 457, 459, 460, 461, 473, 492, 494, 1382, 1383, 1384, 1385, 1386, 1387, 1392, 1393, 1537, 1885, 1889, 1890, 1891, 1892, 2004, 2005, 2006.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.pocean.2024.103334>.

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