Ecología de forrajeo de pingüinos Pygoscélidos: Ganadores y perdedores frente al cambio global

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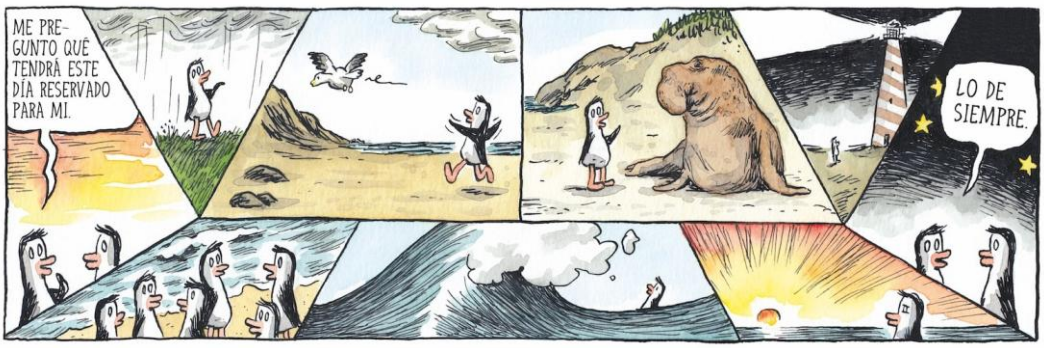

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Resumen

Los rápidos cambios ambientales y la creciente presión antrópica en el océano Austral están transformando profundamente la estructura y funcionamiento de sus ecosistemas. En particular, la región de la Península Antártica (PA) es una de las áreas polares más afectadas por el cambio climático, con un rápido calentamiento atmosférico y de la superficie del mar, reducción de la concentración de hielo marino y aumento de las tormentas, factores que impactan directamente sobre los niveles tróficos inferiores y las poblaciones de los predadores superiores. Las poblaciones de los pingüinos del género *Pygoscelis*, importantes meso-predadores en el océano Austral, han mostrado cambios significativos en sus tendencias poblacionales en la región del oeste de la PA. En general, las poblaciones de pingüinos Adelia (*P. adeliae*) y Barbijo (*P. antarcticus*) han disminuido en esta región mientras que las poblaciones del pingüino papúa (*P. papua*) son estables e incluso están aumentando. Estas especies son consideradas centinelas del ecosistema, dado que ajustan su distribución y comportamiento en respuesta a la variabilidad del océano y los recursos. Comprender cómo los pingüinos ajustan sus estrategias de forrajeo frente a la variabilidad ambiental resulta fundamental para explicar y predecir sus tendencias poblacionales, dado que el éxito en la búsqueda de alimento puede tener importantes implicaciones para la supervivencia y el rendimiento reproductivo de un animal y, en última instancia, determinar las tendencias y características a nivel de población. En este marco, analizar la ecología forrajeo de estos predadores puede ser una herramienta útil para el monitoreo de los ecosistemas y orientar medidas de conservación para la gestión del océano Austral.

El objetivo principal de esta tesis es evaluar los impactos de los cambios globales que afectan al ecosistema marino antártico utilizando a los pingüinos Adelia y papúa como indicadores ecológicos. A partir del análisis integrado de datos de alta resolución de comportamiento de forrajeo, dieta, parámetros poblacionales y condiciones ambientales, esta tesis busca profundizar en la comprensión de las estrategias de forrajeo de ambas especies. Esto busca finalmente aportar información valiosa para evaluar su potencial como indicadores ecológicos del ambiente marino, mejorar la comprensión sobre los mecanismos que subyacen a las tendencias poblacionales divergentes, y contribuir a la generación de medidas de gestión en la región.

En conjunto, esta tesis evidencia que los pingüinos Adelia y papúa responden de manera diferenciada a la variabilidad en la disponibilidad de krill y las condiciones meteorológicas. En el caso de Adelia, se identificaron áreas de alimentación recurrentes próximas a la colonia y un marcado cambio en las estrategias de forrajeo en años con diferentes condiciones en la disponibilidad de presas. En particular, las hembras incrementaron en promedio un 40% su gasto energético diario durante años con menor disponibilidad de krill, lo que podría hacerlas más vulnerables a los efectos negativos de la disminución de presas. Esto podría a su vez comprometer su supervivencia pos-reproductiva y, en consecuencia, afectar la dinámica

poblacional. Asimismo, los análisis de comportamiento de buceo revelaron ajustes en la organización de las secuencias de inmersiones según la abundancia de presas, aportando nuevas perspectivas para interpretar la calidad de los parches de krill a partir de información del comportamiento de sus predadores. Por su parte, el papúa mostró una mayor plasticidad ecológica frente a condiciones ambientales adversas, manteniendo relativamente estable sus estrategias de forrajeo durante diferentes condiciones en la disponibilidad de presas, y un éxito reproductivo elevado incluso tras eventos climáticos extremos. En su conjunto, estos hallazgos contribuyen a una comprensión más profunda de los mecanismos que subyacen a las trayectorias poblacionales divergentes de ambas especies y refuerzan su valor como indicadores ecológicos, a la vez que resaltan la necesidad de incorporar enfoques basados en el monitoreo del comportamiento de forrajeo para fortalecer las estrategias de conservación y el manejo precautorio de los recursos en el océano Austral.

CAPÍTULO 1

Introducción general

1. Introducción

Los ecosistemas marinos están siendo profundamente alterados por los cambios globales, provocando perturbaciones que impactan desde la producción primaria hasta la ecofisiología y distribución de los organismos superiores (Behrenfeld *et al.*, 2006; Poloczanska *et al*., 2013). Dado este contexto, existe una creciente necesidad de comprender cómo estas transformaciones afectan la estructura y funcionamiento de los ecosistemas, y en particular, cómo los organismos que los habitan responden a estos cambios (Huey *et al*., 2012; Buchholz *et al*., 2019). Sin embargo, predecir estas respuestas biológicas resulta complejo, ya que pueden manifestarse en todos los niveles tróficos y variar según condiciones regionales o locales (Rogers *et al*., 2020; Van Moorsel *et al*., 2023). En este contexto, evaluar los efectos de los cambios inducidos por actividades humanas, y distinguirlos de la variabilidad natural, representa un desafío debido a la complejidad inherente de los ecosistemas marinos. Por ello, se considera que el monitoreo de parámetros biológicos y físicos claves puede aportar información crucial sobre los mecanismos que estructuran los ecosistemas y permitir identificar las causas detrás de los cambios observados (Miloslavich *et al*., 2018).

El comportamiento de los animales constituye un factor central en su capacidad de resiliencia frente a los cambios globales (Buchholz *et al*., 2019). Las condiciones ambientales extremas o inusuales ofrecen una oportunidad valiosa para evaluar el rol de la flexibilidad comportamental en la adaptación frente a escenarios cambiantes (Buchholz *et al*., 2019). La adquisición de alimento es un proceso fundamental en todos los animales, que moldea su fisiología, comportamiento y la historia de vida (Kokko y López-Sepulcre 2006; Carter *et al*., 2016). Comprender cómo un animal utiliza su entorno para satisfacer esta demanda, ofrece información valiosa sobre la estructura y dinámica de los ecosistemas. En este contexto, el estudio de la ecología de forrajeo de depredadores marinos, como aves y mamíferos, resulta particularmente útil ya que estos ajustan su distribución y comportamiento en respuesta a la variabilidad del océano, en busca de recursos accesibles y abundantes (Bost *et al.*, 2015). Además, la calidad y cantidad de alimento disponible también puede influir directamente en parámetros como la condición corporal, el éxito reproductivo e incluso la supervivencia (Croxall *et al*., 1999; Lea *et al*., 2006; Ballard *et al*., 2010). De este modo, la relación entre la dieta y estos parámetros puede utilizarse para inferir el efecto de la variabilidad ambiental

sobre la dinámica poblacional (Lescroël *et al.*, 2010; Sherley *et al*., 2013; Russell *et al*., 2013). Este estrecho acoplamiento oceanográfico-ecológico los hace muy valiosos para evaluar el estado de las redes tróficas, pero también muy vulnerables a los efectos del cambio climático, la explotación de recursos o la modificación del hábitat (Masello *et al*., 2021).

La obtención de información detallada sobre la ecología espacial y comportamental de depredadores marinos ha representado históricamente un gran desafío, especialmente debido a su amplia movilidad y al carácter inaccesible del medio marino (Ropert-Coudert y Wilson 2005). Sin embargo, en las últimas décadas, el uso de tecnologías de bio-registro (*biologging*) ha crecido de forma exponencial, revolucionando la capacidad de rastrear la distribución y el comportamiento en el mar a diversas escalas espaciales y temporales (Rutz y Hays 2009; Ropert-Coudert *et al*., 2012; Chung *et al*., 2021). Estos dispositivos que se adhieren a los animales permiten registrar, de manera continua y con alta resolución, variables como posición, profundidad, aceleración, temperatura o presión, brindando acceso sin precedentes al comportamiento, fisiología y características del ambiente en donde se mueven los individuos (Ropert-Coudert *et al*., 2012). En particular, los avances tecnológicos recientes han logrado incorporar a estos dispositivos acelerómetros triaxiales, permitiendo registrar tanto la orientación del animal como la dinámica del movimiento a escala de sub-segundo, revelando detalles finos sobre movimientos como aleteo o intentos de captura de presas (Ropert-Coudert *et al*., 2006; Shepard *et al*., 2008; Brown *et al.*, 2013). En consecuencia, la acelerometría se considera una herramienta poderosa, no solo para estudiar la conducta en detalle, sino también para responder preguntas de conservación en vertebrados superiores, por ejemplo, al combinarse con datos de localización, permite generar mapas de uso espacial, identificando áreas prioritarias para funciones críticas como la alimentación, reproducción o cuidado parental, lo que resulta fundamental para la planificación de medidas de manejo y conservación (Shepard *et al*., 2008).

1.1 La Antártida, el Océano Austral y el cambio global

La Antártida, considerada por el Tratado Antártico como los territorios y barreras de hielo al sur del paralelo 60°S, fue declarada una reserva natural destinada a la paz y a la ciencia, y es gestionada bajo un régimen jurídico especial, en donde ningún país ejerce soberanía sobre este territorio. A su vez, este continente se encuentra rodeado por el océano Austral, definido

como las aguas circumpolares situadas al sur de los 40°S, y constituye aproximadamente el 10% de la superficie de los océanos del mundo (Hindell *et al*., 2020).

A finales de la década de 1970 y principios de los 80, surgió una creciente preocupación en la comunidad científica sobre los efectos perjudiciales que la sobreexplotación de los recursos comerciales podía tener, no sólo sobre las especies capturadas, sino también sobre los depredadores dependientes, y el impacto que podía tener sobre el ecosistema del océano Austral en su conjunto (Clarke y Harris 2003; Miller 2011). Esto fue un catalizador clave para la creación de la Convención para la Conservación de los Recursos Vivos Marinos Antárticos (CCRVMA, o CCAMLR, por sus siglas en inglés *Commission for the Conservation of Antarctic Marine Living Resources*), que entró en vigor en 1982 (CCAMLR 1982). Esta convención desempeña un papel fundamental en la conservación y el uso sostenible de los recursos vivos del océano Austral, mediante un enfoque de la conservación basado en la ciencia, la precaución y el ecosistema, que obliga a tener en cuenta los efectos sobre el ecosistema en la gestión de la explotación de los recursos marinos. Las decisiones de la CCRVMA establecen el marco normativo que rige la gestión de la pesca, abarcando aspectos como los límites de capturas, los cierres estacionales y zonales, medidas para mitigar los posibles impactos sobre las especies no objetivo y los ecosistemas, así como el establecimiento de Áreas Marinas Protegidas (CCAMLR 2023).

La Antártida y el océano Austral brindan una variedad de servicios ecosistémicos esenciales, incluyendo un aporte significativo a la regulación del clima global mediante procesos que impulsan la circulación atmosférica y las corrientes oceánicas, y la absorción de calor y CO2 antropogénicos (Kennicutt *et al*., 2019; Lee *et al*., 2023). Esta región es altamente dinámica, dominada por la Corriente Circumpolar Antártica y sus sistemas frontales, por una marcada estacionalidad con grandes variaciones en la radiación solar y como consecuencia en la temperatura y la luz, y por el avance y retroceso anual del hielo marino (Nicol et al., 2007, Murphy *et al*., 2007; Constable *et al*., 2014). Estas características constituyen un factor ecológico central que condiciona procesos físicos, biológicos y la distribución de muchas especies en este ecosistema (Murphy *et al*., 2007).

Sin embargo, esta región del planeta se encuentra fuertemente presionada por el cambio climático y el impacto de las actividades humanas, que generan pérdida de diversidad

biológica, introducción de especies exóticas, contaminación, sobreexplotación de recursos marinos y cambios fisicoquímicos en el ecosistema marino (Chown y Brooks 2019; Ropert-Coudert *et al*., 2019; Morley *et al*., 2020; Rogers et al., 2020; Cavanagh *et al*., 2021). En particular, la Península Antártica (PA), y específicamente el sector oeste de esta región (OPA), es una de las áreas polares más afectadas por el calentamiento global, mostrando un incremento de la temperatura atmosférica y la superficie oceánica, que ha provocado el retroceso de glaciares, el colapso de plataformas de hielo y la reducción de la duración, extensión y concentración del hielo marino durante el invierno (Stammerjohn *et al*., 2008; Cook *et al*., 2016; Comiso *et al*., 2017, Siegert *et al*., 2019). Además, cambios en la circulación atmosférica han contribuido al aumento de eventos extremos, intensificando la magnitud y frecuencia de las precipitaciones en esta región (Turner *et al*., 2014; Carrasco y Cordero 2020).

Estos rápidos cambios ambientales en el OPA están afectando significativamente la composición y distribución de las comunidades fitoplanctónicas y zooplanctónicas, con un impacto particular sobre especies dependientes del hielo marino, como el krill antártico (*Euphausia superba*) (Atkinson *et al*., 2004, 2019; Lee *et al*., 2010). Esta es una de las especies multicelulares más abundantes del planeta, con una biomasa estimada en aproximadamente 400 millones de toneladas (Atkinson *et al*., 2009). El krill es uno de los principales herbívoros del fitoplancton y presa muy importante para varios depredadores (por ejemplo, peces, pingüinos, focas, ballenas), por lo que desempeña una importante función trófica intermedia, conectando los niveles tróficos inferiores y superiores de la red trófica del océano Austral (Murphy *et al*., 2007; Trathan y Hill 2016). Esta posición central en la red alimentaria, junto con su participación en importantes procesos biogeoquímicos, lo convierte en una especie clave del ecosistema antártico (Trathan y Hill 2016; Cavan *et al*., 2019). Su ciclo de vida está fuertemente controlado por factores ambientales, como temperatura, luz, disponibilidad de alimento y, principalmente, por la dinámica del hielo marino del cual depende directamente para su reproducción, reclutamiento y supervivencia (Murphy *et al*., 2007; Flores *et al*., 2012; Veytia *et al*., 2021). Todas estas características lo convierten en una especie particularmente vulnerable a los efectos del cambio climático (Flores *et al*., 2012; Murphy *et al.,* 2016; Trathan y Hill 2016). Es así que en el OPA se han reportado cambios dramáticos en las poblaciones de krill antártico, incluyendo una disminución en la densidad y el tamaño medio, y una

contracción hacia el sur asociada a mayores condiciones de tiempo cálido, ventoso y nublado, y la reducción del hielo marino (Atkinson *et al*., 2004, 2019).

Además de su rol ecológico, el krill antártico es el principal objetivo de la pesquería en el océano Austral, concentrada actualmente en el área 48 de CCRVMA (Figura 1.1), que abarca el sector occidental de la PA y el Arco de Scotia, donde se encuentra cerca del 70% del stock (Atkinson *et al.,* 2009; Hogg *et al*., 2020). En los últimos años, las capturas comerciales se han incrementado, alcanzando cerca de 620.000 toneladas en la temporada 2024/2025, el valor más alto registrado para el sector (CCAMLR 2025). La actividad pesquera también se ha concentrado espacialmente, con la flota operando de forma recurrente en zonas de alta concentración de krill, particularmente en las proximidades de colonias reproductivas de depredadores en el estrecho de Bransfield y las islas Shetland del Sur (Santa Cruz *et al*., 2018; Trathan *et al*., 2018). En este sentido, Hinke *et al*. (2017) destacan que la superposición directa entre los depredadores dependientes del krill y la pesquería es relativamente frecuente en pequeñas escalas espaciotemporales en toda el OPA, y varios trabajos han señalado la necesidad de una estrategia de ordenación de la pesquería de este recurso que garantice una protección precautoria a pequeña escala para minimizar los efectos negativos sobre los depredadores dependientes de krill (Santa Cruz *et al*., 2018; Watters *et al*., 2020; Trathan *et al*., 2022).

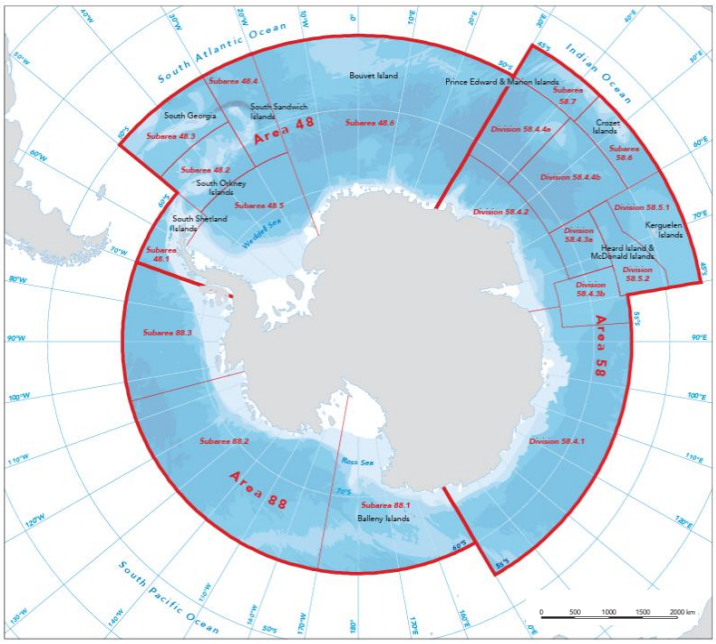

Figura 1.1 Mapa del Área de la Convención de la Convención para la Conservación de los Recursos Vivos Marinos Antárticos (CCRVMA)

Las fluctuaciones en la disponibilidad y abundancia de krill antártico pueden generar efectos bottom-up en la red trófica, impactando directamente sobre las dinámicas poblacionales de los predadores dependientes de este recurso (Fraser y Hofmann 2003; Forcada *et al*., 2006; Murphy *et al*., 2007, Salmerón *et al.,* 2023). En este escenario de rápidos cambios ambientales y creciente presión antrópica, la ecología de forrajeo y tendencias poblacionales de predadores, ofrecen información valiosa sobre el estado del ecosistema, por lo que son ampliamente utilizadas como especies centinelas (Handley *et al*., 2021). Las especies de pingüinos que se reproducen en la Antártida y se alimentan en el océano Austral, son especies ejemplares para comprender la respuesta de las poblaciones a los cambios en el ecosistema marino (Emmerson *et al*., 2015; Hinke *et al.,* 2017; Watters *et al*., 2020).

1.2 Los Pingüinos Pygoscélidos como centinelas del cambio global

1.2.1 Distribución y ciclo de vida

Los pingüinos son aves marinas longevas, con altas tasas de supervivencia en adultos, y si bien pasan la mayor parte de su vida en el océano, dependen de la tierra firme para reproducirse (Ainley y Wilson 2023). Nidifican en colonias por las que presentan una elevada filopatría y, en general, son monógamos (Ainley et al., 1995; Ainley y Wilson 2023). Son particularmente sensibles a cambios en la disponibilidad de presas, especialmente durante la etapa reproductiva, y vulnerables a presiones antrópicas, así como a la degradación de sus hábitats tanto marinos como terrestres (Ropert-Coudert *et al*., 2019). De las 18 especies reconocidas, cinco nidifican en la Antártida, incluyendo al pingüino emperador (*Aptenodytes forsteri*), al macaroni (*Eudyptes chrysolophus*), y a las tres especies del género *Pygoscelis (*Ainley y Wilson 2023).

El género *Pygoscelis* está conformado por tres especies: Adelia (*P. adeliae*); papúa (*P. papua*) y barbijo (*P. antarctica*). En conjunto constituyen cerca del 90% del total de la biomasa de aves en la Antártida, por lo que son considerados importantes consumidores de recursos en el océano Austral (Black *et al*., 2016). Las estimaciones más recientes indican una población aproximada de 3.79 millones de parejas reproductivas de Adelia (Lynch y LaRue 2014), 3.42

millones de barbijo (Strycker *et al*., 2020) y más de 430.000 parejas de papúa (Herman *et al*., 2020). En cuanto a su distribución, los pingüinos Adelia presentan un rango circumpolar, con colonias reproductivas a lo largo de las costas del continente antártico y en islas antárticas y subantárticas, entre los 54° y 77°S. El pingüino papúa se reproduce entre los 46° y 65°S, principalmente en islas subantárticas, pero también en islas antárticas y la Península Antártica, mientras que el barbijo ocupa una posición intermedia, entre los 55° y 67°S aproximadamente, nidificando en la Península Antártica y en islas situadas al sur de la Convergencia Antártica (Borboroglu y Boersma 2013; Humphries *et al*., 2017). Existe cierto grado de solapamiento en su distribución, particularmente en la Península Antártica e islas asociadas donde suelen reproducirse en simpatría, encontrándose áreas donde las especies co-ocurren tanto espacial como temporalmente.

Las tres especies del género *Pygoscelis* presentan patrones de historia de vida similares, aunque con ligeras variaciones en el momento y duración de cada etapa (Ancel *et al*., 2013). Su ciclo reproductivo puede ser dividido en diferentes etapas: arribo a la colonia, incubación, cría de los pichones, formación de guarderías y emplume. Como aves marinas coloniales, regresan cada año a sitios específicos de reproducción, donde la disponibilidad de áreas libres de nieve es crucial para la construcción de nidos en estas tres especies (Borboroglu y Boersma 2013; Ainley y Wilson 2023). En la PA este regreso se da durante la primavera austral, entre finales de setiembre y mediados de octubre (Juáres 2013; Handley *et al*., 2021). Tras el cortejo y cópula, las hembras ponen dos huevos, que son incubados alternadamente por ambos adultos durante 35-38 días. Al eclosionar, comienza la etapa de cría, en la cual los adultos se alternan el cuidado de los pichones y viajes de alimentación en intervalos entre 12 y 24 horas. A las 3-4 semanas de edad, los pichones son mucho más grandes y ya no necesitan el cuidado constante de los adultos, pero también tienen mayores necesidades energéticas. Para satisfacer esta mayor demanda de energía, ambos adultos salen al mar en busca de alimento mientras los pichones se quedan solos en las colonias y se congregan en grupos conocidos como “guarderías”. El emplume, momento en que los pichones mudan el plumón por la pluma, ocurre a diferentes edades según la especie: alrededor de los 50 días en el pingüino Adelia y entre los 75 y 85 días en el papúa (Trivelpiece *et al*., 1987). El ciclo culmina con la emancipación de los juveniles y la posterior muda de los adultos, la cual requiere una intensa fase de acumulación energética previa (Black *et al*., 2016). Los adultos de pingüino papúa

mudan en la colonia donde nidifican, mientras que los adultos de Adelia se van de las colonias para mudar sobre el hielo marino (Korczak-Abshire *et al*., 2021, Zaldúa *et al*., 2024).

Existen otras diferencias entre las especies del género, particularmente en aspectos como la migración invernal y la sincronización del ciclo reproductivo (Black *et al*., 2016). Cuando coexisten en las mismas colonias, generalmente los Adelia son los primeros en llegar al inicio de la temporada, seguidos por los papúas y, más tarde, por los barbijos (Black *et al*., 2016). Sin embargo, los papúas muestran una mayor variabilidad interanual en la fenología reproductiva en comparación con las otras dos especies, mientras que los Adelia presentan una sincronización más predecible (Hinke *et al*., 2012; Juáres *et al*., 2013). Por otro lado, durante el invierno, los Adelia y barbijo migran largas distancias durante el invierno hacia zonas de invernada comunes, mientras que los papúas tienden a permanecer cerca de sus sitios de cría (Hinke *et al*., 2012; 2015; 2019; Korczak-Abshire *et al.,* 2021; Zaldúa *et al*., 2024).

1.2.2 Comportamiento de alimentación

Durante el periodo de reproducción, los pingüinos enfrentan importantes restricciones espaciales y energéticas, ya que deben regresar con frecuencia a las colonias para incubar los huevos o alimentar a sus crías. Esta condición de forrajeadores centrales limita el alcance y la duración de sus viajes de forrajeo, los cuales están condicionados por factores intrínsecos, como el cuidado parental y extrínsecos, como la disponibilidad, accesibilidad y abundancia de presas en el entorno de las colonias (Clarke *et al*., 2006; Emmerson *et al.,* 2015; Ainley y Wilson 2023). En consecuencia, estas aves ajustan su comportamiento de búsqueda de alimento a lo largo de la temporada en respuesta a la variabilidad ambiental, las fluctuaciones en la disponibilidad de presas y las demandas de sus pichones (Clarke *et al*., 2006; Ballard *et al*., 2010; Ainley y Wilson 2023).

Las estrategias de alimentación de los pingüinos del género *Pygoscelis* han sido ampliamente estudiadas en la región del OPA. Durante la temporada reproductiva, las tres especies dependen fundamentalmente del krill antártico como presa principal, aunque se plantea que papúa muestra una mayor flexibilidad trófica, complementando su dieta con peces y otros invertebrados (Kokubun *et al*., 2010; Miller *et al*., 2010; Juáres *et al*., 2016). En cuanto al comportamiento de forrajeo, el pingüino Adelia suele realizar viajes más largos y alejados de la costa, alimentándose en mar abierto y concentrando su actividad de buceo en los primeros

50 metros de la columna de agua (Trivelpiece *et al*., 1987; Wilson 2010; Cimino *et al*., 2016). En contraste, el pingüino papúa presenta un patrón más costero, con viajes de alimentación más cortos, pero buceos más profundos (Kokubun *et al*., 2010; Juáres *et al.,* 2016; Ainley y Wilson 2023). El pingüino barbijo, por su parte, exhibe una estrategia intermedia entre ambas especies. Tiende a alimentarse en aguas oceánicas fuera de la plataforma, realizando inmersiones típicamente pelágicas entre los 15 y 30 metros (Kokubun *et al*., 2010; Miller *et al.*, 2010; Ainley y Wilson 2023).

A pesar de los patrones generales descritos para estas especies, el comportamiento de forrajeo de los pingüinos puede variar considerablemente entre colonias. Factores como la variación regional en las condiciones ambientales (e.g., cobertura de hielo marino o diferentes características batimétricas), la abundancia y distribución de presas, y la competencia intra e interespecífica influyen en la ecología trófica de las distintas poblaciones a lo largo de la PA (Fraser y Trivelpiece 1996; Santora y Reiss 2011; Cimino *et al*., 2016; Nardelli *et al*., 2021). Estas diferencias ponen de relieve la necesidad de incorporar aspectos espaciales y temporales en los esfuerzos de monitoreo (Tierney *et al*., 2009).

1.2.3 Tendencias poblacionales

En la región de la PA, los pingüinos del género Pygoscelis han mostrado cambios significativos en sus tendencias poblacionales. En general, las poblaciones de pingüinos Adelia y barbijo han disminuido en esta región (Trivelpiece *et al*., 2011; Barbosa *et al*., 2012), mientras que las poblaciones del pingüino papúa son estables e incluso están aumentando (Lynch *et al*., 2010; Herman *et al*., 2020). En este contexto, actualmente se considera a los pingüinos papúa como una especie "ganadora", mientras que los Adelia y barbijo se han convertido en "perdedores" frente a estas transformaciones ambientales (Clucas *et al.,* 2014).

Las hipótesis sobre las causas de estos cambios poblacionales han sido intensamente debatidas y han evolucionado en las últimas décadas. Durante la década de los 70, el crecimiento de las poblaciones de pingüino barbijo fue atribuido a un excedente de krill generado por la sobreexplotación comercial de grandes predadores como ballenas y focas, lo que habría reducido la competencia trófica, en la denominada hipótesis del excedente de krill ("*krill surplus hypothesis*") (Laws 1977). Sin embargo, Fraser *et al*. (1992) observaron que las

poblaciones de su congénere Adelia no se comportaban de forma similar. Dado que ambas especies consumen principalmente krill, la competencia por sí sola no podía explicar la disparidad. Propusieron entonces la denominada hipótesis del hielo marino ("*sea ice hypothesis*"), la cual plantea que la reducción del hielo marino invernal provoca directamente el declive de las especies pagofílicas (i.e., dependientes del hielo, como Adelia), mientras que las poblaciones de las especies pagofóbicas (i.e., que evitan el hielo marino, como barbijo y papúa) aumentan (Fraser *et al*., 1992). No obstante, la posterior disminución de las poblaciones de barbijos en un contexto de continua pérdida de hielo marino sugiere que la dinámica es más compleja. Es así que más tarde, Trivelpiece *et al*. (2011) proponen una visión integradora en la que las fluctuaciones en la biomasa de krill, como consecuencia del cambio climático y la presión pesquera, constituyen un eje central para entender las tendencias divergentes observadas en estas poblaciones.

Una comprensión más reciente subraya que los efectos del cambio climático y las actividades humanas pueden tener impactos diferenciales en los pingüinos pygoscélidos, dependiendo de sus estrategias de historia de vida. Diversos estudios plantean que las fluctuaciones en el tamaño poblacional se vinculan con el éxito reproductivo, la supervivencia de adultos o juveniles durante el invierno, en respuesta a factores que operan a una escala local durante la temporada de cría (por ejemplo, disponibilidad de presas o competencia con otras especies o pesquerías), o a gran escala durante la temporada no reproductiva (por ejemplo, extensión del hielo marino en invierno, reclutamiento de krill) (Hinke *et al.,* 2007; Carlini *et al*., 2009; Cimino *et al*., 2023; Salmerón *et al*., 2023). Actualmente el declive de los pingüinos Adelia se asocia con una combinación de factores: baja flexibilidad para ajustar su cronología reproductiva a condiciones locales, disminución en la disponibilidad de krill durante la temporada de cría y efectos negativos sobre la supervivencia de juveniles y adultos durante el invierno (Hinke *et al*., 2007, 2012; Emmerson *et al*., 2011; Cimino *et al*., 2016, 2023). En contraste, el pingüino papúa, con hábitos más costeros, dieta más flexible y residencia invernal cercana a las colonias, parece mostrar una mayor capacidad de adaptación ante un entorno cambiante (Miller *et al*., 2009; Lynch *et al*., 2012; Hinke *et al*., 2012; Juáres *et al*., 2015).

1.3 Área de estudio

La isla Ardley (62°12’ S, 58°55’ O) se ubica en el extremo suroeste de la isla Rey Jorge/Isla 25 de Mayo, en el archipiélago de las islas Shetland del Sur (Figura 1.2). Es designada como Zona Antártica Especialmente Protegida (ZAEP Nº 150) debido a la riqueza y diversidad biológica que alberga. Es además uno de los pocos sitios en la Antártida donde las tres especies de pingüinos del género *Pygoscelis* se reproducen de forma simpátrica. En particular, la colonia posee una importancia especial para el pingüino papúa, ya que más del 1% de su población global nidifica en esta colonia (Braun *et al.*, 2017; Donald *et al.*, 2019). Por este motivo, el área terrestre fue reconocida como Área Importante para la Conservación de las Aves (IBA Nº 48), y el entorno marino adyacente como IBA marina N.º 11 (BirdLife International 2024). Desde 2019, la isla Ardley también forma parte del Programa de Monitoreo del Ecosistema (CEMP) de la CCRVMA, el cual es llevado a cabo de forma conjunta entre Uruguay y Alemania.

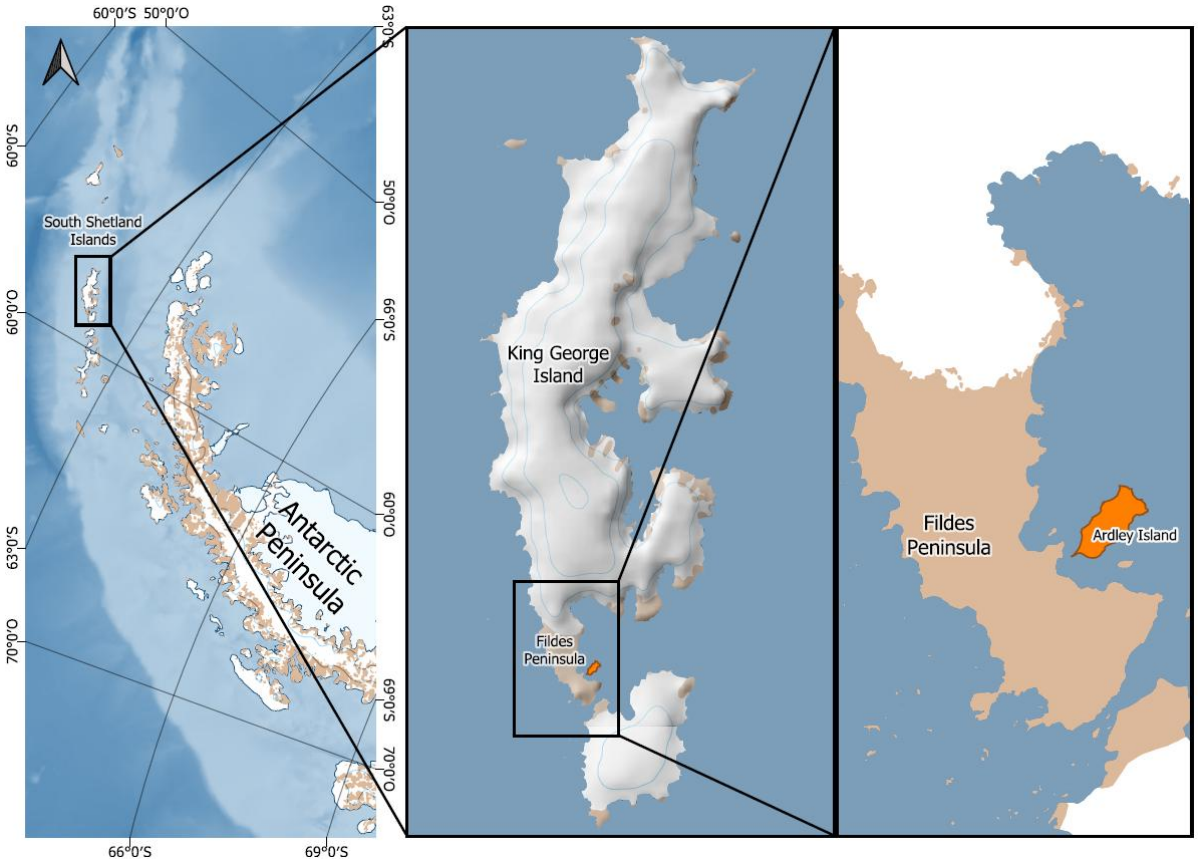

Figura 1.2 Ubicación del sitio de estudio, isla Ardley, en la isla Rey Jorge/Isla 25 de Mayo, islas Shetland del Sur, Antártida.

El monitoreo sistemático del tamaño poblacional y del éxito reproductivo de estas especies en la isla comenzó en la década de 1980 (Braun *et al*., 2025). Desde entonces, se han observado cambios notables en las tendencias poblacionales. En línea con las tendencias registradas en otras colonias de la región, el pingüino Adelia alcanzó su mínimo histórico de 184 parejas en la temporada 2022/23, lo que representa una disminución del 71%. En contraste, la población de pingüino papúa mostró un crecimiento sostenido, alcanzando su máximo histórico con 8808 parejas reproductivas en la temporada 2024/2025, lo que equivale a un incremento de más de un 200% en comparación con los registros iniciales. El pingüino barbijo ha sufrido un colapso poblacional en la isla, con una reducción del 98% desde los primeros conteos, registrándose sólo una pareja reproductiva en la temporada 2024/2025. Por este motivo, es que durante esta tesis sólo se trabajará sobre las colonias de pingüinos Adelia y papúa.

Los muestreos en las colonias de Adelia y papúa se llevaron a cabo durante las temporadas reproductivas 2019/2020, 2020/2021 y 2021/2022. En cada temporada se realizaron monitoreos poblacionales utilizando los métodos estándar de CCRVMA (CCRVMA 2014), registrando el éxito reproductivo utilizando el método estándar A6C y el monitoreo del peso de las crías previo al abandono de la colonia con el método estándar A7A. Por otro lado, aproximadamente 20 individuos adultos de cada especie que se encontraban anidando, fueron equipados con dispositivos Axytrek (Technosmart, Italia) en cada temporada (Figura 1.3). Estos dispositivos combinan un GPS de localización rápida, un acelerómetro de 3 ejes y un registrador de temperatura y profundidad. Las aves fueron capturadas en sus nidos y los dispositivos fueron colocados en la parte inferior-media de la espalda utilizando cinta Tesa® durante un periodo de 5-8 días. Finalmente, los pingüinos fueron recapturados en sus nidos para recuperar los dispositivos, medir la masa corporal y recoger muestras de sangre (1 ml

aprox.) de la vena metatarsiana, utilizada para análisis de isótopos estables, sexado molecular e índices de estrés.

Figura 1.3 Pingüinos papúa (izquierda) y Adelia (derecha) con dispositivos GPS Axytrek colocados.

1.4 Objetivo general y estructura de la tesis

Comprender cómo los pingüinos ajustan sus estrategias de forrajeo frente a diferentes condiciones ambientales y restricciones energéticas resulta fundamental para predecir la dinámica poblacional en un ecosistema antártico cada vez más cambiante (Emmerson y Southwell 2011, 2022). Esta información resulta fundamental para el diseño de herramientas de conservación basadas en evidencia científica, como la planificación de Áreas Marinas Protegidas o la evaluación de riesgos asociados a la pesquería de krill en escenarios de cambio climático (Warwick-Evans *et al.*, 2018; Handley *et al*., 2021). Sin embargo, la información sobre especies clave, como el krill y sus predadores, sigue siendo limitada en un ecosistema tan sensible como la Península Antártica (Chown y Brooks 2019).

En este contexto, el objetivo principal de esta tesis es evaluar los impactos de los cambios globales que afectan al ecosistema marino antártico, utilizando a los pingüinos como indicadores ecológicos, a través del estudio exhaustivo de su ecología de forrajeo y parámetros poblacionales. El conjunto de trabajos que conforman esta tesis busca contribuir con información detallada y actualizada sobre el comportamiento de alimentación de los pingüinos del género *Pygoscelis* en el sector norte del oeste de la Península Antártica.

La tesis se estructura en cinco capítulos principales (capítulos 2 al 6), seguidos de una síntesis general y discusión sobre las implicaciones de estos trabajos en el capítulo 7. De forma general, los capítulos 2 y 3 se centran en la caracterización de los viajes de alimentación de dos especies, Adelia y papúa, durante la etapa de cuidados intensivos de pichones. En particular, en el capítulo 2 se exploran estrategias para incorporar la información sobre el uso del espacio por los pingüinos papúa en las medidas de conservación del Sistema del Tratado Antártico, mientras que en el capítulo 3 se profundiza en la identificación de zonas clave dentro de las áreas de distribución que son utilizadas de manera recurrente como sitios de alimentación de pingüinos Adelia. Para ello, desarrolla un abordaje metodológico que permite identificarlos buceos de alimentación y su localización. En los capítulos 4 y 5 se amplía el análisis de los buceos de alimentación de Adelia y su posible uso como indicadores de la disponibilidad de krill, evaluando cómo varía el comportamiento de forrajeo en respuesta a cambios en la abundancia de presas en las cercanías de las colonias. Asimismo, se analizan las implicancias de estos cambios en términos del gasto energético asociado a los viajes de alimentación y sus consecuencias a nivel individual y poblacional, con énfasis en las diferencias entre sexos. Finalmente, en el capítulo 6 se comparan las respuestas de ambas especies frente a diferentes condiciones meteorológicas y de abundancia de krill, y se discute cómo ciertas características de su historia de vida pueden influir en su capacidad para amortiguar los efectos de condiciones ambientales desfavorables.

CAPÍTULO 2

From spatial prioritization to conservation management in the Southern Ocean using the marine IBAs approach.

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2. From spatial prioritization to conservation management in the Southern Ocean using the marine IBAs approach

2.1 Abstract

Implementing effective conservation action requires spatial prioritization exercises to be functionally integrated with a process for developing an implementation strategy. There is great potential for animal tracking data to inform marine management in the Southern Ocean. Using information on penguin distribution, a set of marine Important Bird Areas (mIBAs) has recently been identified around Antarctica. Large-scale spatial analyses like this are key to guide resources and the attention of decision-makers towards areas of significant value. Yet, protecting marine resources requires translating prioritization exercises into legally-binding conservation measures. Here we use one of the largest gentoo colonies in Antarctica as a case study to explore pathways for the utilization of the mIBAs approach in the design and implementation of conservation measures in the Southern Ocean. For scientists and organizations willing to have a policy impact, there are two main routes to contribute to Antarctic Treaty System (ATS) decision-making: through Parties' National Delegations, or through Experts and Observers. We provide three main recommendations for incorporating the results of spatial prioritization analyses into the agenda of ATS governance bodies using the mIBAs approach: 1. Differentiate the potential contribution of mIBAs to spatial prioritization from the potential contribution to conservation planning, two different stages in the conservation process; 2. Use methods, criteria and data for delineating boundaries of potential conservation areas according to the stage of the conservation process that the outputs are expected to contribute to; 3. Understand how Antarctic mIBAs might fit into the ATS conservation measures framework and ongoing deliberations.

keywords: Ardley Island, King George Island, gentoos, CCAMLR, ASPA

2.2 Introduction

Antarctica and the Southern Ocean provide a variety of ecosystem services of global scope and play an important role in the regulation of climate, sea level, and heat balance (Wauchope et al., 2019). In recent decades, this region has been strongly affected by climate change and pressures derived from human activity, that generate biodiversity loss, alien species introduction, contamination, overexploitation of marine resources, and physicochemical changes in the marine ecosystem (Lee et al., 2022; Wauchope et al., 2019). Due to its remoteness, size and extreme conditions, the identification of ecologically relevant areas in the Southern Ocean depends on the extrapolation of information from spatially scattered data sets (e.g., Hindell et al., 2020). Animal tracking is often the only way to determine species overlap with threats and thus to assess potential impacts of those threats for species that range widely in the oceans (Hays et al., 2019). Thus, there is great potential for animal tracking data to inform marine management (e.g., Bestley et al., 2020; Hindell et al., 2020; Ropert-Coudert et al., 2020). Penguins have been identified as valuable indicators for the identification of areas of ecological relevance in the Southern Ocean (e.g., Handley et al., 2021). Tracking data from *Pygoscelis* penguins have revealed predictable feeding areas and highlighted areas of potential competition with the regional fishery at the Antarctic Peninsula and at nearby archipelagoes (Hinke et al., 2017; Trathan et al., 2018; Watters et al., 2020; Machado-Gaye et al., 2024, among others). For instance, tracking data from Adélie penguins (*Pygoscelis adeliae*) were used to help create the South Orkney Islands southern shelf MPA (Hays et al., 2019; Trathan & Grant, 2020).

The Important Bird and Biodiversity Area (IBA) program was established by BirdLife International in 1979 with the aim of identifying sites of importance for bird conservation at a global scale (note there are also similar proposals for mammals in the Southern Ocean). The Key Biodiversity Areas Programme (KBA) an initiative promoted by a partnership of thirteen global organizations including BirdLife International, IUCN and WWF, among others, takes the concept of “important areas”, and applies it to all taxa, providing common criteria for identifying, mapping, monitoring, and preserving areas that play an important role in the persistence of biodiversity. Given that the designation of KBAs is based on the IBA framework, the latter also constitute KBAs by definition (KBA Programme, 2016). The delimitation of IBAs

was initially focused on terrestrial sites and only began to consider IBAs in marine areas as recently as 2004 (Donald et al., 2018). The identification of marine IBAs (mIBAs) was greatly enhanced by the proliferation of scientific studies providing information about the at-sea distributions of seabirds, especially those based on tracking individual birds (Dias et al., 2018). As a consequence, a standardized method (the mIBA protocol) was developed to define important areas for marine conservation based on tracking data (Lascelles et al., 2016).

A recent study has identified a set of mIBAs around Antarctica that might contribute to marine resources management in the region (Handley et al., 2021). However, to advance in the protection of Southern Ocean resources there is a need for translating prioritization exercises like this into conservation actions. To move from science advice into actual conservation action it is useful to recognize three different stages in the conservation process: 1) conservation assessment (i.e., spatial prioritization), a short-term activity for identifying spatially explicit priority areas for conservation action; 2) conservation planning, a long-term process that complements a conservation assessment with a process for collaboratively developing an implementation strategy; and 3) conservation management, the activities and actions undertaken to achieve the objectives of the conservation initiative (Knight et al., 2006; Moilanen et al., 2011; Tallis et al., 2021). As IBAs boundaries are often identified with the aim of delineating discrete manageable units that are expected to provide the requirements of the trigger species (Donald et al., 2018), there is a risk of confusing the output of a spatial prioritization exercise like this (stage 1), with the output of a planning process (stage 2). Examples abound within the Antarctic Treaty System (ATS) on the challenges for moving from prioritization exercises into the adoption and effective implementation of legally binding conservation measures (e.g., Brooks et al., 2020; Goldsworthy, 2021; Sylvester & Brooks, 2020; Soutullo et al., 2022; Burrows et al., 2023). The geographic areas ultimately affected by these measures result from negotiations and are usually not the ones proposed in the initial conservation assessments.

Spatially explicit conservation measures within the ATS include, among others, MPAs adopted by the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR), and specially protected and managed areas (ASPAs and ASMAs) designated by the Antarctic Treaty Consultative Meeting (ATCM) (Hughes et al., 2023). Here we analyze a case study to discuss

possible pathways towards the translation of large-scale spatial prioritization exercises into local-scale conservation measures that can be adopted and implemented under the ATS legal framework. We focus on two aspects of this process: 1) the need to improve the boundaries derived from coarse, large-scale, spatial analyses, incorporating locally generated information, and 2) the need to complement the spatial prioritization exercise with an implementation strategy that explicitly engages ATS Parties.

The case study focuses on Ardley Island, an ASPA located in the southern tip of King George Island, in the South Shetland Archipelago, which has also been designated as a terrestrial IBA (BirdLife International, 2024; Soutullo et al., 2022) and is surrounded by three mIBAs proposed by Handley et al. (2021). Ardley Island was designated an IBA because it hosts one of the largest breeding colonies of gentoo penguins (*Pygoscelis papua*) in Antarctica, meeting the A4ii IBA criteria, which includes sites that hold ≥1% of the global population of a congregatory species on a regular basis (BirdLife International, 2024). On the West Antarctic Peninsula (WAP), the populations of this species are increasing, while the numbers of the other Pygocelid species are decreasing. The reasons behind these tendencies are still debated, although they are likely associated to life history traits that give gentoo penguins an advantage in changing environments, including a more flexible diet, foraging behavior and phenology, a lower degree of site fidelity, and the ability to relay eggs if they are lost early on in the incubation stage (Miller et al., 2009; Herman et al., 2020; Juáres et al., 2013).

Specifically, here we 1) assess the effects of using locally generated high-resolution data and alternative criteria to estimate individual penguins home ranges, on the boundaries of the conservation proposal; 2) frame the outputs of this analysis as inputs for a planning process to update the ASPA management plan; 3) discuss possible ways of generalizing this case study to other mIBAs in Antarctica. We expect this exercise to shed light on how to move from large-scale prioritization exercises in the Southern Ocean, into the policy process of creating and then implementing spatially explicit conservation measures on smaller scales.

2.3 Material and methods

For this study, we used tracking data from adult gentoo penguins (*P. papua*), collected during the austral summer seasons of 2019/2020, 2020/2021, and 2021/2022 on Ardley Island.

Ardley Island (62°13’ S, 58°56’ W), in the southwest of King George Island/25 de Mayo Island, South Shetland Islands (Fig. 1), is an Antarctic Specially Protected Area (ASPA N°150), a CEMP site (CCAMLR Ecosystem Monitoring Program), and nesting site of one of the largest colonies of gentoo penguins in Antarctica (7704 breeding pairs in the 2023/24 season; this study).

Two main approaches have been used to delineate mIBAs in Antarctica using data on penguins: 1) estimating the at-sea distribution of birds based on the application of a modified foraging radius approach (Handley et al., 2021); 2) using a modified version of the mIBA protocol for its application to penguins (Dias et al., 2018). Following Handley et al. (2021), we focused our analysis on breeding birds during the chick-rearing stage. This is a critical phase of the annual cycle in terms of the requirement of provision to offspring, being the period when birds tend to aggregate most at sea. With a smaller foraging area accessible during that stage, the overlap between different individuals is necessarily higher, facilitating the identification of areas consistently used by a significant fraction of the tracked population (Dias et al., 2018). We studied the colony during three consecutive years, in line with suggestions by Beal et al. (2023). Approximately 20 individuals per season were tagged with Axy-Trek (70 x 40 x 15 mm, 69 g; TechnoSmart, Italy) loggers including GPS and other sensors. The recorders were attached on the birds’ lower back feathers using Tesa® 4651 tape (Wilson et al., 1997). The loggers used represent less than 1% of the body mass of an adult gentoo penguin (mean for Ardley Island 5604 ± 902.1 g; this study). They were programmed to record a position every 5 min. The tagged birds were recaptured in the nest after 5-8 days and the loggers were recovered to access recorded data. All penguin handling procedures were reviewed and approved by the Honorary Commission of Animal Experimentation of Uruguay (CHEA protocol N° 1312).

GPS data was analyzed using the R software (version 4.1.3; R Core Team, 2022). Excessive points recorded before departure and after arrival at the colony were manually removed, retaining only five points located at the colony in each case. To filter possible erroneous location estimates we removed points leading to horizontal speeds above 10 $km.h^{-1}$. This velocity threshold was chosen based on our data: less than 1% of the records were above that value (Appendix S1). We linearly interpolated the raw GPS location data at regular 5 min intervals using the *interpolateTime* function of the 'move' R package.

For each individual, foraging trips were defined from the time birds moved more than 50 m from the colony to the sea until the time they were within 50 m of the colony again. Detailed methods for foraging trips identification are described in Machado-Gaye et al. (2024).

To translate the tracking data into areas delimited by their relevance to the colony, we used the R package 'track2KBA' (Beal et al., 2021), developed to implement the mIBA protocol. The process implies 3 stages: a) estimating individual core areas, b) assessing sample representativeness and c) quantifying spatial overlap among individuals and scaling up to the population level. However, our approach differs from that developed by Lascelles et al. (2016) and the modification introduced by Dias et al. (2018) for its application to Antarctic penguins in two main aspects:

1) As proposed by Lascelles et al. (2016) we used fixed kernel density estimation (KDE) to define an utilization distribution (UD) for each tracked individual. A critical parameter for kernel estimation is its bandwidth, or h-value, which controls the spread of each kernel around each recorded location (Perón, 2019) and hence, reflects the probability distribution of finding individuals in the vicinity of the recorded locations, as the distance from the locations increases. From a biological perspective, it reflects the spatial scales at which individuals interact with their environment (Dias et al., 2018). Here we explore the effect of 4 alternative h-values on the mIBA delimitation: a) we used the 7 km h-value used and suggested by Dias et al. (2018) to delimit mIBAs for penguins in the Southern Ocean; b) we calculated the reference smoothing parameter (href) on the basis of the location of all individuals taken together; the href reflects the number of positions and their spatial variance in longitude and latitude, and is a typical smoother used for identifying important sites for biodiversity (e.g., Beal et al., 2023); c) we calculated a h value using the 'ad-hoc' method (Schuler et al., 2014), which has been suggested to outperform other smoothers, and provide the smallest value for h consistent with a contiguous home-range estimate (Kie, 2013); initial estimation of an UD considering the locations of all individuals together, was calculated using the href value; a sequence of UDs was then calculated by reducing the h-value by 5% in successive steps until the contour fractured into two or more polygons; d) we calculated a h-value estimated on the basis of the maximum horizontal speed of gentoo movements while in water (calculated from our own data), and the average interval between consecutive locations in our study; this value represent the maximum distance the species is able to move in the timespan between two

consecutive locations, thus, the probability of locating an individual beyond that distance from the previous location should be zero; we contend this is a reasonable criterion to define a biologically meaningful h-value that reflects the spatial scales at which individuals interact with their environment at the temporal scale considered in the study.

2) UDs reflect the probability of use throughout an animal's home range, allowing calculation of home-range area within any desired probability contour (i.e. isopleth) (e.g., Gitzen et al., 2006). Börger et al. (2006) have shown that the 90% isopleth can provide unbiased home range estimates even with relatively little data, and that inner isopleths tend to be more biased than outer isopleths. Actually, these authors explicitly caution against the use of home range core areas as a quantitative tool for habitat conservation plans. Therefore, here we opted for using 90% UD when estimating individuals home ranges, instead of the values suggested by Dias et al. (2018). Actually, previous studies in the study area have shown that some of the key foraging sites for penguins in the vicinity of Ardley Island are not located within animals' UD inner isopleths (e.g., Machado-Gaye et al., 2024). This is not surprising, as being central-place foragers, a large proportion of the locations obtained are concentrated around the colony, a sector of the home range consistently used at the beginning and end of the foraging trips, irrespective of where the animals are actually foraging. With central-place foragers, using inner isopleths to identify areas of ecological relevance might restrict the mIBA boundaries to areas regularly used as transit areas, but not necessarily the most relevant ones in terms of food acquisition.

Representativeness of the sample (i.e., the degree to which the tracked animals represent the whole population) was obtained using the function *repAsses* from the 'track2KBA' R package. For the estimates 100 iterations were used, as it is the minimum number recommended by the authors (Beal et al., 2021).

2.4 Results

A total of 301 foraging trips from 60 gentoo penguins were obtained over three breeding seasons between: 2019/2020, 2020/2021 and 2021/2022. Roughly 100 trips per season were recorded, with an average of 5 trips per individual. Trips duration and distances covered are summarized in Table 1. Movements were registered both in a northwest and southeast

direction from the colony (Fig. 1a). For the space use estimation, the value obtained for href was 2.2 km, 2.4 km for h ad hoc, and 0.8 km for the h-value estimated on the basis of the maximum horizontal speed of gentoos. The mean size of the areas obtained for each individual using h ad hoc for the 50, 90, and 95 kernels was 124.7 ± 52.44 km^2, 414.2 ± 163.9 km^2, and 518.1 ± 199.6 km^2, respectively. The href and h ad hoc values obtained were similar to those calculated by Dias et al. (2018) for chinstrap penguin colonies with similar maximum foraging trip distances, calculated from ARS (area-restricted search behavior).

Figure 1b shows the area where the UDs of at least 10% of the colony overlap. Representativeness of the sample was 99.1%. Figure 2 compares the boundaries of the areas used by the gentoo penguin's colony in Ardley Island estimated using different h values, with the boundaries of Antarctic Marine IBAs 9, 11 and 12 proposed by Handley et al. (2021). The size of the estimated areas was 2335.2 km^2 (h = 7km), 910.98 km^2 (h= 2.2 km), 972.56 km^2 (h= 2.4 km) and 524.54 km^2 (h=0.8 km).

Table 1. Summary of the foraging trips (mean ± SD) of gentoo penguins (*P. papua*) breeding in Ardley Island during the 2019/2020, 2020/2021 and 2021/2022 seasons. For each season the following parameters are shown: number of individuals tracked (N), total number of trips (N° trips), trips mean duration (h), maximum distance from colony (km), total distance (km), and 50 and 90 % UDs (h= 2.4 km).

Season	N	N° trips	Duration (h)	Max. distance (km)	Total distance (km)	Home range (50% UD) (km^2)	Home range (90% UD) (km^2)
2019/20	19	102	9.23 ± 3.46	16.3 ± 9.96	37.4 ± 20.3	101 ± 42.5	336 ± 129
2020/21	20	84	13.1 ± 11.8	22.8 ± 11.5	53.1 ± 26.2	138 ± 44.6	457 ± 136
2021/22	21	115	12.1 ± 4.41	18.6 ± 10.9	44.8 ± 23.3	134 ± 61.5	444 ± 195

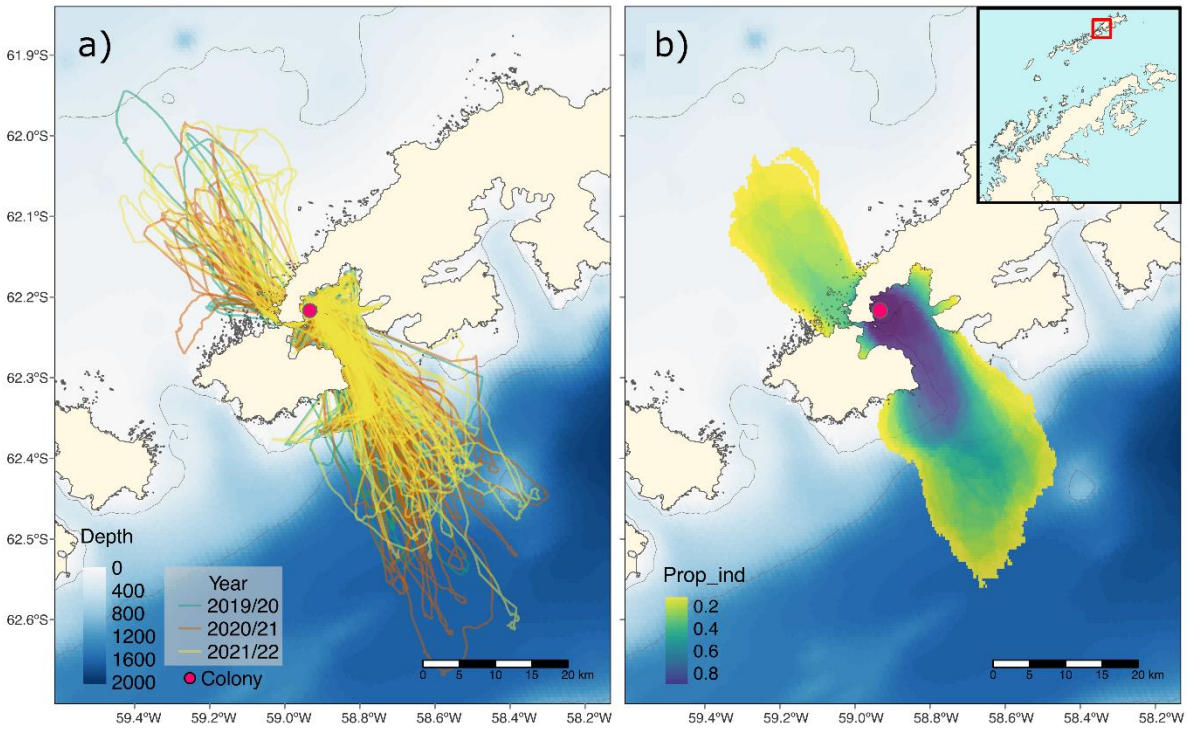

Figure 1. a) Foraging trips of gentoo penguins (*P. papua*) from the colony on Ardley Island (red dot) during the chick-rearing stage of the 2019/2020, 2020/2021 and 2021/2022 breeding seasons; b) marine area used by at least 10 % of the individuals breeding in Ardley Island. Prop_Ind refers to the proportion of the population that used the area across the three seasons. Inset panel in b) shows the location of the study area (red square) in the northwest of the Antarctic Peninsula.

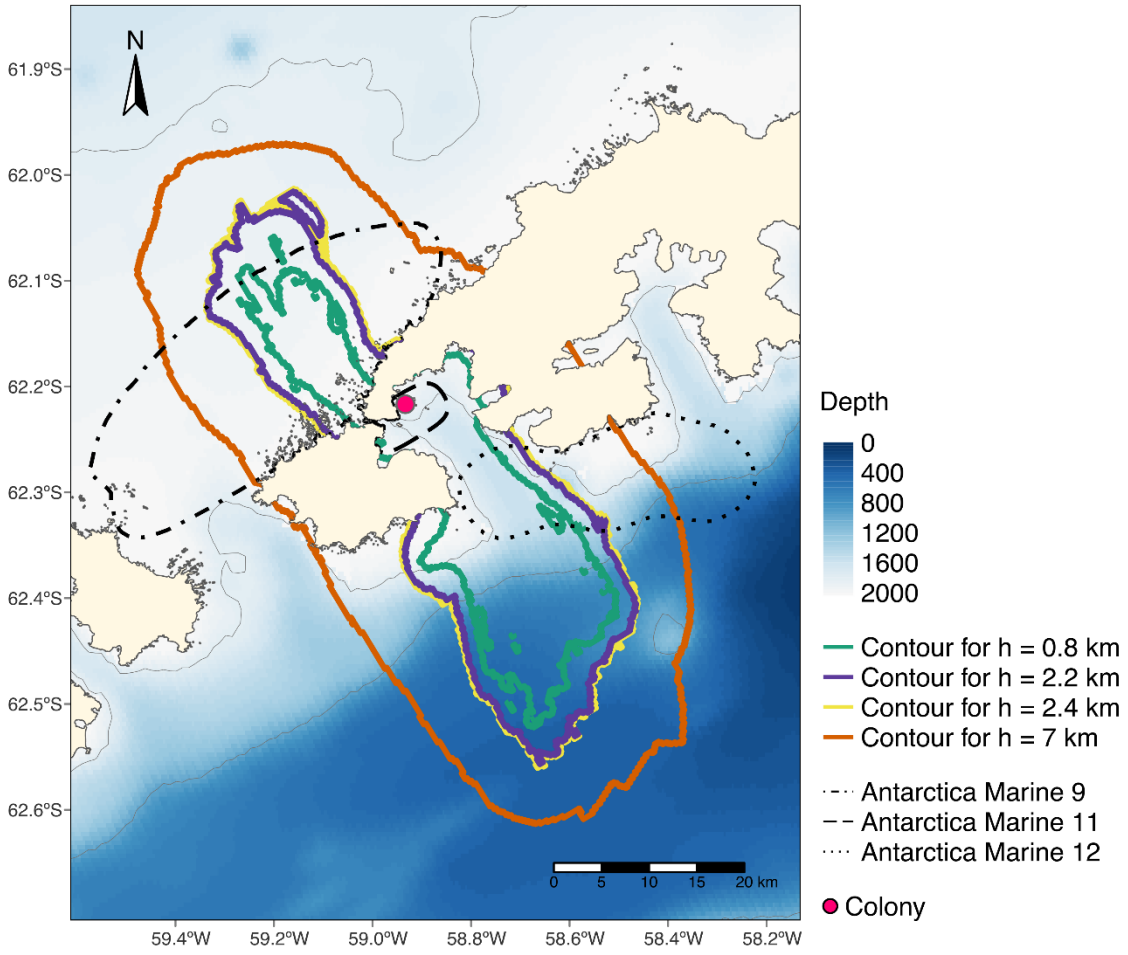

Figure 2. Limits of the area used by the gentoo penguin (*P. papua*) colony in Ardley Island estimated using different h-values: h = 0.8 km, h =2.2km (h ref), h = 2.4 km (h ad hoc) and h = 7km. The limits of the mIBA Antarctica Marine 9, 11 and 12 are also shown.

Rather than contesting the procedures used by Dias et al. (2018) and Handley et al. (2021) to delimit mIBAs, with the adjustments we introduce here we expect to extend the mIBA protocol for its application in the next stage of the conservation process. That is, from using the approach to identify spatial priorities for conservation actions, to produce inputs for a conservation planning process incorporating local-scale data. We understand these modifications better reflect the change of scale of the question at hand and the resolution of the data, while retaining the general approach for the analysis and synthesis of the data. Hence, taking advantage of the widespread use of the mIBAs approach and the experience accumulated with its application across the globe.

2.5 Discussion

We showed how the mIBA approach can be extended to generate inputs for a conservation planning process aimed at providing protection to one of the largest gentoo colonies in Antarctica using high-resolution locally generated tracking data. In doing so we introduce a series of modifications to the approaches used to delineate mIBAs boundaries that we believe can help moving from the spatial prioritization stage into the conservation planning stage of the conservation process. Specifically, when using tracking data to set the boundaries of spatially explicit conservation measures for central-place foragers, we suggest using a 90% UD to define individual home ranges, and a smoothing parameter (h-value) that explicitly considers both the movement characteristics of the species of interest and the study's data acquisition schedule. In the case of Ardley Island, using this approach we identified important areas for gentoo penguins around the island that were not included within the areas proposed by Handley et al. (2021) as mIBAs. This difference is likely a consequence of the different methodological approaches and data resolution used to define the boundaries of the area of interest, highlighting the relevance of considering these differences when using the outputs of spatial analyses for informing policy.

One of the early criticisms to the Key Biodiversity Areas (KBA) approach (also applicable to mIBAs) is that identifying local-scale areas for conserving species using large-scale data sets has the potential to produce significant errors of omission and commission, highlighting the need of incorporating more accurate local-scale data provided by local stakeholders in the analyses (Knight et al., 2007). Actually, it is noteworthy that current estimates of more than 7000 breeding pairs in Ardley Island (Soutullo et al., 2023) more than doubles the median value used by Handley et al. (2021) in their analysis. Coarse analysis for identifying potential areas of conservation value at a continental scale (e.g., using a foraging radius approach) are not meant to provide the detailed information needed for the delimitation of legally binding local-scale conservation measures and hence, the outputs of large-scale and local-scale analyses should not be used interchangeably. Large-scale analyses as Handley et al. (2021)'s are extremely valuable in the Southern Ocean because they help prioritizing funding and research efforts over an extensive area that because of its size and remoteness demands strategic decisions when allocating efforts. This is part of the first stage in the implementation

process described by Knight et al. (2006). Further analysis of these areas to define the spatial extent of the conservation measures is part of the second stage of this process, conservation planning, which requires engaging relevant stakeholders in order to advance towards actual conservation measures on the ground (Knight et al., 2006). The mIBA approach can provide valuable contributions to both stages, but in order to be useful, outputs of the analyses must be used according to the stage they were designed to inform.

Implementing effective conservation action requires spatial prioritization exercise to be functionally integrated with a process for developing an implementation strategy and processes for stakeholder collaboration (Knight et al., 2006). This requires establishing conservation planning capacity in priority regions and engaging local stakeholders (Knight et al., 2007). In the Antarctic Treaty System, key stakeholders include Parties of the Antarctic Treaty (AT) and the CCAMLR, Observers and Expert organizations that provide advice to the governance bodies (Hughes et al., 2023). For scientists and organizations undertaking policy-relevant research willing to have policy impact there are two main routes to contribute to ATS decision-making: either through Parties' National Delegations, or through Experts and Observers officially invited to participate of the ATS fora, including SCAR, the Scientific Committee on Antarctic Research (Hughes et al., 2018, 2022). Conservation measures are adopted by Parties on the advice of the AT Committee for Environmental Protection (CEP) and CCAMLR Scientific Committee (SC-CCAMLR). In order to move from spatial prioritization exercises to concrete conservation proposals, there is a need to incorporate the results of analyses as Handley et al. (2021)'s and ours into the agenda of these governance bodies. That is, there is a need to develop an implementation plan that explicitly involves Parties in the design of an operational model for conservation action.

There are many barriers to using science to inform conservation policy and practice. Yet there is a growing body of evidence on how to better navigate this challenge, including proposals on institutional frameworks that can facilitate science-policy interfaces (Cook et al., 2013; Cvitanovic et al., 2015, 2016; Toomey et al., 2017). Across a range of fields, coproduction has been identified as a promising approach to deliver action based on scientific evidence (Beier et al., 2017; Chambers et al., 2021). Coproduction seeks to connect researchers with other stakeholders to produce knowledge, action and societal change (Chambers et al., 2021).

Within the ATS, advancing in the implementation of conservation measures require integrating spatial prioritization analysis as Handley et al. (2021)'s into the process of creating ASPAs, ASMAs or CCAMLR MPAs, or updating their management plans. Scientists and organizations willing to promote conservation measures on areas identified as mIBAs should actively seek for opportunities to contribute to these processes. Investing time in promoting "spaces" of interactions (*sensu* Toomey et al., 2017) with ATS Parties (especially those conducting operations or with interests in areas close to mIBAs) and building trust are key components for achieving evidence-informed policy (Cvitanovic et al., 2021; Toomey et al., 2017).

In the case of Ardley Island, the current process of updating its management plan (ATS, 2024) provides a unique opportunity for incorporating the results of analyses as the one we present here in a conservation planning process. Ardley Island ASPA boundaries currently encompass most of the island, yet it does not include a marine sector despite penguins being one of the values the ASPA seeks to protect (ATS, 2009). Penguins dependence on marine resources for fulfilling their energetic needs highlight the relevance of incorporating relevant marine sectors in the surroundings of the island for the ASPA to ensure the conditions needed to maintain the breeding colonies. A detailed analysis of animals' distribution at sea, as provided by the mIBA protocol, might provide an initial proposal of new boundaries for discussion. In the lasts ATCM Chile, Argentina, China, Korea, the Russian Federation and Uruguay expressed their will in engaging in the process of upgrading the Management Plan of ASPA N° 150, Ardley Island (ATS, 2024). This seems a perfect opportunity for scientists and organizations willing to advance in the protection of mIBAs to engage in the process.

Overall, we identify three main recommendations for advancing in the incorporation of mIBAs in the design of spatially explicit conservation measures in the Southern Ocean:

1. Differentiate the potential contribution of the mIBAs approach to spatial prioritization from the potential contribution to conservation planning. Large-scale analyses enable identifying potential valuable areas that need to be prioritized in terms of further research to assess their actual value. Yet, systematic conservation planning techniques are needed when aiming at delineating management actions at the local scale (Smith et al., 2019).

2. Use methods, criteria and data for establishing mIBAs' boundaries according to the stage of the conservation process that the outputs are expected to contribute to. We agree with Critchley et al. (2018, 2019) that a foraging radius approach provides a pragmatic and rapid method that can be used as an initial tool to identify important areas for potential protection. Especially in areas with limited data on seabird distributions at sea and limited resources to collect these data. The method predicts a baseline distribution that can be further refined using data on species specific foraging behaviors or other ecological factors. This detailed information is not needed for prioritization at the seascape level, but it is crucial for informing management at a local scale (e.g., Machado-Gaye et al., 2024).

3. Understand how Antarctic mIBAs fit into the ATS conservation measures framework and ongoing deliberations in its governance bodies. Frame the exercise of assessing potential mIBAs within the larger policy and management process: 1) bear in mind extant normative tools (e.g., CCAMLR MPAs or AT ASPAs) and the procedures by which decisions are taken; 2) approach and engage relevant stakeholders, most remarkably those that regularly operate in the surroundings of the mIBAs; 3) seek for ways of integrating the outputs of the analyses in planning process conducted by ATS Parties; 4) maintain long-term commitment with the conservation initiative to ensure approval and, most importantly, effective implementation once approved.

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CAPÍTULO 3

Using latent behavior analysis to identify key foraging areas for Adélie penguins in a declining colony in West Antarctic Peninsula

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3. Using latent behavior analysis to identify key foraging areas for Adélie penguins in a declining colony in West Antarctic Peninsula

3.1 Abstract

Adélie penguins are considered indicators of Antarctic ecosystems. Their populations have declined by more than 50% in the West Antarctic Peninsula, an area strongly affected by global warming, and that concentrates most of Antarctic krill harvesting. The use of high-resolution data to identify foraging areas regularly used by krill predators could provide valuable information for current discussions on the development of small-scale management and conservation measures for this region. We used information on the foraging trips of 57 individuals breeding in King George Island, tracked over 2019/2020, 2020/2021 and 2021/2022 breeding seasons during the chick-rearing stage, to identify their key foraging areas. Using an accelerometry-based latent behavioral analysis approach, we identified an area within 10 km of the colony consistently used by over 60% of the population throughout and between seasons. We also observed that almost 20% of the population uses the area near a seamount located 35 km from the colony for foraging, mainly during the late guarding phase when chick energy demands are highest or the effects of prey depletion might become more evident. The distances and duration of trips and the area explored increased as the season progressed and varied between seasons, consistent with annual differences in krill availability observed in the region. Foraging dives comprise roughly 40% of the dives performed during foraging trips, irrespective of the stage of the chick-rearing period, or the season analyzed. Our results emphasize the need to understand how variability in environmental conditions, prey availability, and energetic demands affect how predators use space, and the role that bathymetric features might play in providing reliable foraging grounds, for penguins, in a rapidly changing region.

Keywords: CCAMLR, Bransfield Strait, bio-logging, Antarctica, Ardley Island, ecosystem management, foraging ecology

3.2 Introduction

Monitoring marine predators at sea, such as penguins, can identify areas of ecological importance. Areas with high concentrations of predators often indicate a high biodiversity and biomass at lower trophic levels and are, therefore, regions that may require special management (Hindell et al. 2020; Ropert-Coudert et al. 2020). With nearly 4 million breeding pairs around Antarctica, Adélie penguins (*Pygoscelis adeliae*) are one of the most important and best studied predators in the Southern Ocean (Ancel et al. 2013; Lynch and LaRue 2014). As a key predator of krill and with a strong dependence on the sea-ice environment, the Adélie penguin has been considered an indicator species, being highly sensitive to changes in the marine ecosystem (Boersma 2008; Hinke et al. 2014; Ropert-Coudert et al. 2018).

In western Antarctic Peninsula (WAP), one of the polar areas most affected by global warming, Adélie penguin populations have declined by more than 50% since the 1970s (Trivelpiece et al. 2011; Lynch et al. 2012). In contrast, East Antarctica has experienced a 1.5% increase in sea-ice extent (Michel et al. 2019), with Adélie penguin populations stable or slightly increasing (Southwell et al. 2015). Penguin population decline in the WAP has been linked to large-scale changes in the biomass of Antarctic krill (*Euphausia superba*; Trivelpiece et al. 2011). Antarctic krill is being affected by ongoing environmental changes, with a decrease in density and mean size, and a southward contraction in the southwest (SW) Atlantic sector associated with warm, windy and cloudy weather, and a reduction in sea ice (Atkinson et al. 2019). This is noteworthy because further environmental changes could cause additional range contractions and decrease in krill biomass along the WAP (Klein et al. 2018; Atkinson et al. 2019), which could lead to a mismatch between peak food availability and breeding season, increasing penguin foraging efforts and decreasing reproductive success (Cimino et al. 2023; Salmerón et al. 2023).

In addition, the commercial catch of krill has increased in recent years in the SW Atlantic sector (FAO statistical Area 48) reaching in the 2019/2020 season the highest level recorded (CCAMLR 2021). Catches are also intensifying, with the fleet repeatedly visiting fishing hotspots, particularly close to predator breeding colonies in the Bransfield Strait and South

Shetland Islands (Santa Cruz et al. 2018; Trathan et al. 2018). Hinke et al. (2017) highlight that direct overlap of krill-dependent predators with the krill fishery on small spatiotemporal scales is relatively common throughout the WAP, and several works have pointed out the need for a krill exploitation framework that ensures small-scale precautionary protection to minimize negative effects on dependent predators (Santa Cruz et al. 2018; Watters et al. 2020; Trathan et al. 2022).

During the breeding season, Adélie penguins are central-place foragers, as they must frequently return to the colony to incubate their eggs or feed their offspring. These seabirds change their foraging behavior in response to environmental variability, fluctuations in prey availability and chick provisioning requirements throughout the season (Clarke et al. 2006; Ballard et al. 2010). The foraging strategies of Adélie penguins have been well studied in the WAP (Wilson et al. 1994; Wilson 2002, 2010; Fraser and Hofmann 2003; Cimino et al. 2016; Hinke et al. 2017; Warwick-Evans et al. 2022). In general, they tend to forage offshore in the upper 50 m of the water column (Trivelpiece et al. 1987; Wilson 2010; Cimino et al. 2016), and unlike colonies in East Antarctica and the Ross Sea, the diet of the colonies in the WAP and the South Shetland Islands is dominated by Antarctic krill throughout the breeding season (Gorman et al. 2014; Negrete et al. 2016; Herman et al. 2017; Juáres et al. 2018; Pickett et al. 2018). However, considerable colony-specific differences are evident in Adélie penguin foraging behavior. The variability in abundance and distribution of prey driven by regional variation in physical and environmental features, such as sea ice cover near the colonies or different bathymetric features (e.g. submarine canyons), influences differences in foraging ecology between penguin populations along the WAP (Fraser and Trivelpiece 1996; Santora and Reiss 2011; Cimino et al. 2016; Nardelli et al. 2021).

Given this scenario of rapid climate change and intensification of krill fisheries in the WAP, monitoring Adélie penguins foraging behavior may improve our understanding on how predators respond to inter-annual variation in krill availability. Furthermore, the use of high-resolution data, such as accelerometers, to identify foraging areas regularly used by these krill predators, could provide valuable information for the development of small-scale management and conservation measures for this region. This is particularly relevant in a warming Antarctic Peninsula scenario (Siegert et al. 2019), where the impacts of ongoing

decrease in sea-ice habitat and southward shifts in marine species distributions are exacerbated by the effects of marine resource extraction.

Thus, the objective of this study is to describe the foraging behavior and identify foraging areas used by Adélie penguins breeding in Ardley Island, in King George Island/Isla 25 de Mayo, South Shetland Islands, an area free of sea-ice throughout the summer. We analyze changes in penguins foraging behavior during the chick rearing stage, a highly demandant period for breeding adults due to the increasing energetic requirements of chicks and foraging constraints as central place foragers (Bevan et al. 2002; Clarke et al. 2006). As chicks grow, the energy needs of adults and the tolerance of chicks to fasting also change, affecting adult foraging behavior throughout the breeding season (Widmann et al. 2015; Riaz et al. 2020; Phillips et al. 2021). To ensure regular feeding of offspring, adults should seek to minimize time away from the colony prioritizing the exploitation of food resources available nearby. However, when prey availability in the vicinity of the colony is low, they have to increase the time away from the colony as they forage in more distant areas (Clarke et al. 2006). Therefore, we expect foraging effort (e.g., trips distances or duration) to increase as the season progresses, or in years with reduced krill availability, with foraging areas' location varying accordingly. Identifying foraging areas that are regularly used by penguin colonies enables adopting spatially explicit conservation measure aimed at avoiding overlap between fisheries and predators during this key stage of the annual cycle.

3.3 Materials and Methods

Study area

Ardley Island (62°13' S, 58°56' W), in the southwest of King George Island/Isla 25 de Mayo, South Shetland Islands (Fig. 1), is an Antarctic Specially Protected Area (ASPA N° 150), a CEMP (CCAMLR Ecosystem Monitoring Program) site, and one of the few areas in Antarctica where the three pygoscelid penguin species breed sympatrically (Braun et al. 2017). Breeding population size and breeding success has been monitored since the 1980s. According to Braun et al. (2017), the numbers of breeding pairs of Adélie penguins have decreased by more than 30% since counts began, reaching the minimum of 184 breeding pairs in the 2022/2023 season (this study). In line with population trends at other colonies in the region, the number

of breeding pairs of chinstrap penguins at Ardley Island has declined by more than 90%, with a total of only six breeding pairs in the 2022/2023 season. In contrast, the number of gentoo penguins increased by over 80% during the same period, with a total of 8763 breeding pairs in the same season (this paper). Other Adélie, chinstrap and gentoo colonies in the vicinity of the study site (i.e., in Maxwell Bay) include: Narębski Point with 2918 chinstrap and 2604 gentoo breeding pairs (Lee et al. 2021); Duthoit Point with 1828 gentoo penguin breeding pairs (Coria et al. 1995); Stranger Point with 3703 Adélie and 5383 gentoo breeding pairs (Juáres et al. 2015, 2020).

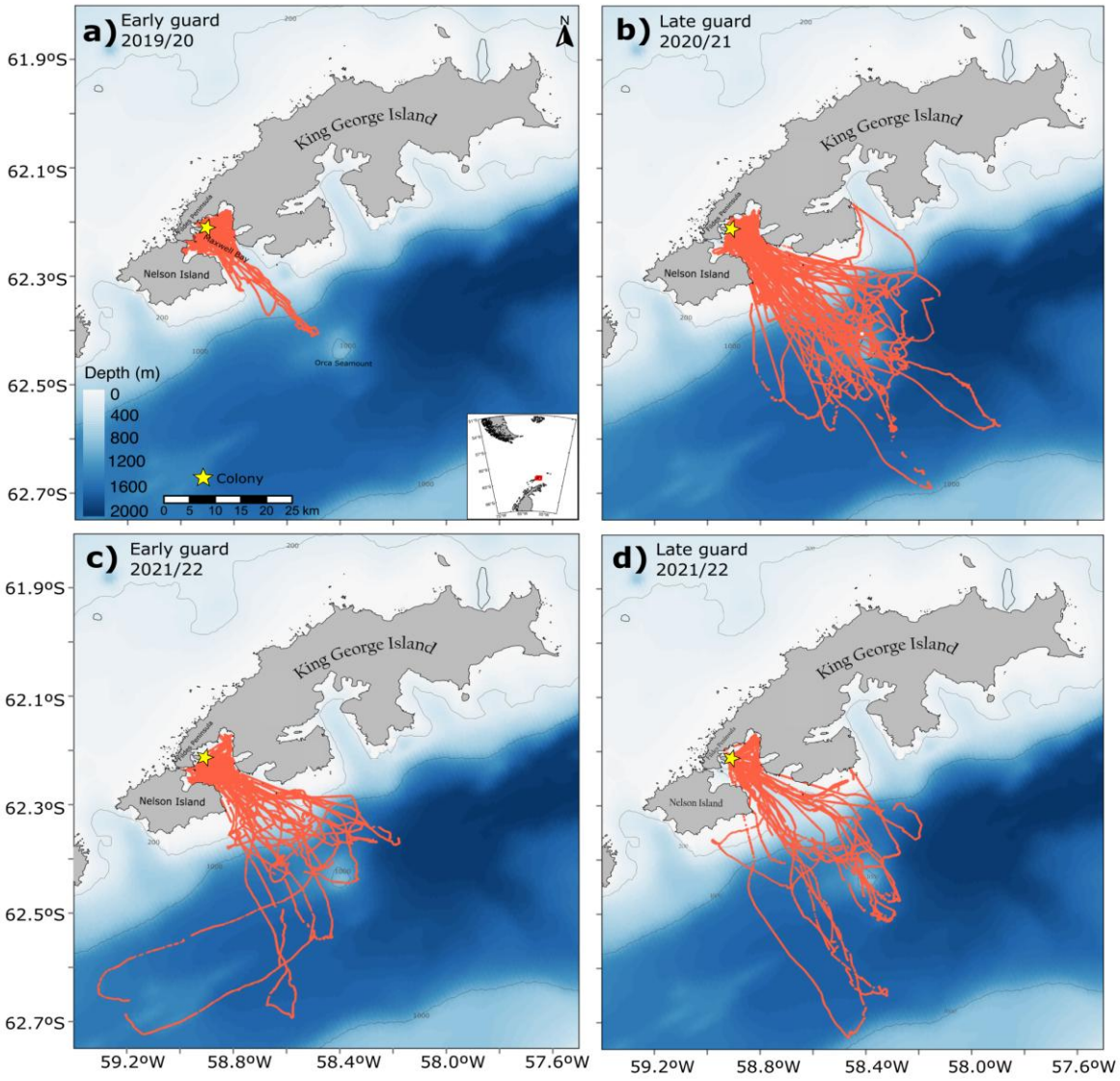

Figure 1. GPS tracks of Adélie penguins breeding in Ardley Island (yellow star), King George Island, South Shetland Archipelago, Antarctica, during the early and late guard over three

seasons (2019/20 – 2021/22). Inset panel in a) shows the location of King George Island (red square) in the northwest of the Antarctic Peninsula.

Field procedure (Deployment of data loggers)

The study was conducted over three breeding seasons: 2019/2020, 2020/2021 and 2021/2022. Axy-Trek (70 x 40 x 15 mm, 69 g; TechnoSmart, Italy) loggers including GPS, accelerometer, and both pressure and temperature sensors were deployed on adult Adélie penguins rearing chicks. To account for the increasing demand for food by chicks as they grow and its possible influence on adult foraging behavior (Widmann et al. 2015), we divided the chick rearing period into two stages: early guard and late guard. Due to logistical limitations, not all stages could be sampled equally in the three years of the study, so data were obtained for early guard stage during 2019/2020 and 2021/2020, and for late guard during 2020/2021 and 2021/2022 breeding seasons (See Table 1). The chick rearing period (i.e., "guard") stage lasts about 22 days (Black 2016), with hatching beginning in late November-early December on King George Island/Isla 25 de Mayo (Juáres 2013; Handley et al. 2021). During the study period, the peak of hatching in the studied colony occurred between December 4 and 6 (this study). Here we defined the early guard stage as approximately the first half of the chick rearing period (between December 6 and 23) and the late guard as the second half of the period and just before the start of crèche (between December 24 and January 6).

We captured only one member of the pair in nests with two chicks, mainly by hand, with the occasional aid of a long-handled net. We also captured chicks during adult handling to protect them from predators and measured their body mass with a Pesola spring balance. We took care to minimize stress to the captured adults by covering the head during handling and ensuring that handling time was always below 20 minutes. The recorders were attached on the birds' lower back feathers using Tesa® 4651 tape (Wilson et al. 1997). The loggers used represent 1.6% of the body mass of an adult Adélie penguin (mean for Ardley Island 3847 ± 392.3 g; this study). The loggers were programmed to record a position every 5 min, pressure (in millibars) at 1 Hz and acceleration along the 3 body axes of the penguins: longitudinal (surge), dorso-ventral (heave) and lateral (sway) at 50 Hz. The tagged birds were recaptured in the nest after 3-7 days and the loggers were removed to access recorded data. After device removal, body mass of the adults and chicks were measured using a Pesola spring balance.

GPS and dive data analysis

GPS data from a total of 205 trips, undertaken by 57 birds with each bird making between two to nine trips, were analyzed using the R software (version 4.1.3; R Core Team 2022). Excessive points recorded before departure and after arrival at the colony were manually removed, retaining only five points located at the colony in each case. To filter possible erroneous location estimates we removed points leading to horizontal speeds above 7 km.h- 1. This velocity threshold was chosen based on our data and less than 1% of the records were above that value (Fig. S1). For each individual, foraging trips were defined from the time the birds moved more than 50 m from the colony to the sea until the time they were within 50 m of the colony again. The number of trips, and the date and time of the start and end of each trip were calculated for each individual. With this, three representative parameters of foraging effort were also calculated for each trip: total trip duration, total trip distance (i.e. the cumulative horizontal distance between all GPS locations per bird per trip), and maximum distance to the colony (i.e. the straight line distance between the colony and the most distal point of a trip).

Dives were analyzed using the software Igor Pro Version 6.37 (Wavemetrics). Pressure (mBar) was converted to water depth (m) as water depth = (pressure – atmospheric pressure)/100.45. Atmospheric pressure is estimated as the mode of the pressure data (around 1000 mBar). The surface line (0m) was visually checked and corrected manually when needed. Dives were defined as the period between the time the birds descended from the water surface and the time when they returned to it. Only dives deeper than 1 m were included due to possible measurement error in instruments and surface waves (Takahashi et al. 2003; Kato et al. 2009). For each dive, different parameters were calculated: dive depth (m) (determined as the deepest point of the dive), total dive duration (s), bottom time duration (s) (start and end of bottom time were defined as the first and last time in a dive when the depth change rate was <0.25 m.s−1) and number of wiggles (number of vertical undulations during the bottom phase, i.e. the point of inflexion in the dive profile). Maximum depth recorded on each trip was also calculated. The grand mean ± SD of these parameters per trip was calculated for each stage and season using the *R effectsize* package (Ben-Shachar et al. 2020).

For each trip we calculated the proportion of trip diving (total time diving divided by trip duration), the proportion of time spent in the bottom phase (total time in bottom diving divided by total time diving), dive frequency (number of dives divided by trip duration) and dive efficiency (total time in bottom diving divided by trip duration). We then matched the dive data with GPS locations, using date and time information. To do this, we allocated a location to each dive by linearly interpolating the timestamp at the beginning of each dive event with the closest GPS locations recorded before and after the dive (Kokubun et al. 2010). The mean time interval between records of GPS locations was 6.9 ± 0.3 min. We used 500-m resolution bathymetry data obtained from the General Bathymetric Chart of the Oceans (GEBCO Compilation Group 2020).

Finally, for each individual we estimated their utilization distributions (UDs) by calculating fixed kernels using the *adehabitatHR* package (Calenge 2006). To calculate h-values, data on all tracks of all individuals monitored during the study period were pooled together. Geographic positions were transformed into stereographic coordinates to calculate the size of UD for different isopleths. We used the 'ad-hoc' method (Schuler et al. 2014) to calculate kernels' bandwidth (h). Initial estimation of the 90% UD was calculated using the reference bandwidth (i.e., the href value, calculated on the basis of the number and spatial variance of all tracking locations, assuming bivariate normality). A sequence of 90% UDs was then calculated by reducing the h-value by 5% in successive steps, until the 90% contour fractured into two or more polygons. The ad-hoc value thus corresponds to the smallest h-value calculated that retains the number of polygons initially calculated using the href value.

Identify key foraging areas

To identify key foraging areas, we use the approach developed by Chimienti et al. (2016, 2022) for characterizing latent behaviors to determine in which dives penguins are attempting to capture prey. Using this approach, we first identify all dives recorded within each foraging trip in which penguins seem to be attempting to catch prey, and then identify the areas where these dives concentrate, integrating information on all trips and individuals studied throughout the whole study period. As a first step for the analysis, accelerometer data were checked and records subsampled at 25 Hz, following Chimienti et al. (2016). We used the depth data to retain only the data during the underwater activity of each individual. Only dives

deeper than 2 m were considered, to avoid measurement errors and behaviors at the sea surface that do not correspond to foraging activities (foraging vs commuting). We then used Chimienti et al. (2016, 2022) method for analyzing accelerometry data to automatically identify behavioral modes and individual behaviors, in species moving in two or three dimensions. The method uses the unsupervised machine learning algorithm Expectation Maximization to find maximum likelihood solutions for mixture models with latent variables, and was implemented using the R package *RMixmod* (Biernacki et al. 2006). Based on the input variables, the model automatically defines clusters without a priori information. The model is tested with different numbers of clusters (from three to eight for the diving part in Chimienti et al. 2022). For the specific case of the Adélie penguins, the optimal number of clusters was four, and was selected as a compromise between ecological meaning of these clusters and model performance (see Chimienti et al. 2022). The ecological meaning of each cluster is inferred by the researcher based on the knowledge of the study species and by visualizing the results of each run. These were: descending phase, deep searching phase, chasing/catching events and ascending phase. As the depth data used to describe the dive profiles were recorded every 1 second, we classified each depth record as corresponding to either a capture attempt or not, based on whether more than 50% of the accelerometer records within that second were classified as chasing/catching events by the model, or not. We then used that information to classify dives as either foraging dives (i.e., where penguins were attempting to capture prey), or not. We aimed to discriminate foraging dives from dives where animals are not hunting, or where the scarce numbers of capture attempts rather reflect casual encounters with prey. We defined foraging dives as those where at least 5 seconds of the diving cycle were classified as capture attempts. The 5 seconds criterion is an arbitrary limit chosen as a rough proxy of the mean number of krills that have to be captured by penguins in foraging dives, to fulfill daily energetic demands. The reasoning supporting this value is as follows: breeding Adélie penguins require approximately 800-1200 grams of krill daily (Watanabe et al. 2013; Warwick-Evans et al. 2022), they capture 300-400 grams of krill in each foraging trip (Watanabe et al. 2013; Juáres et al. 2018), individual krill weight is close to 0.4 g on average (Watanabe et al. 2013; Juáres et al. 2018), Adélie penguins have been observed to capture up to two krill per second in swarms (Watanabe et al. 2013), and our data suggest that in our study area foraging trips last 8-22 hs, diving frequency is close to 30 dives hour-1, and in roughly 50% of the dives penguins do not attempt to capture prey. This suggests

that in all other dives individuals need to devote on average at least 2 to 5 seconds of the dive to food ingestion, if energetic demands are to be met at the end of the day. We thus consider foraging areas as those that concentrate dives that have a potential significant contribution to individuals' energetic demands (i.e., dives where at least 5 seconds of the diving cycle were classified as capture attempts).

For foraging dives the following parameters were determined: dive duration, dive depth, bottom time duration, number of wiggles, foraging frequency (number of dives with at least 5 capture attempts divided by trip duration), and maximum depth recorded per trip. Values per stage and season are presented as grand mean ± SD, and were calculated as described before.

To identify foraging areas we used the *track2KBA* package (Beal et al. 2021) for R. Only positions of foraging dives that met the criterion established in the previous step were included in the analyses (Fig. S3 shows negligible changes in these areas when more restrictive values are used to define foraging dives). For each individual, the 50% isopleth of the UDs were calculated with the h-value calculated using the ad-hoc method described before. To identify foraging areas for the colony, individual UDs overlap was estimated for the whole study period using the package's 'findSite' function. Following Beal et al. (2021), for each 0.16 km2 cell of the study area we calculated the percentage of individuals using that cell (i.e., cells used by an individual are those included within the individuals' 50% isopleth). We estimated the representativeness of our samples with respect to the colony using the function repAssess. The function iteratively selects sub-samples of individual tracks, averages them into a pooled UD and outlines a desired quantile, and then calculates the proportion of out-of-sample tracking locations within the resulting area (i.e., the 'inclusion rate'). This proportion approximates the specified UD quantile when the tracked sample is fully representative (see Beal et al., 2021 supporting information for further details). Representativeness values were estimated after 100 iterations.

Statistical analyses

To test for differences between stages and seasons in the foraging parameters analyzed we used different statistical models, to account for differences in the response variables and their

effects on models assumptions. In each model, the season (early 19/20, early 21/22, late 20/21, late 21/22) or stage (early, late) was considered as an independent factorial variable and the individual (ID) as a random effect to account for repeated measures of the same individual. Season is a combination of year and stage, as it was not possible to sample in both stages during the three breeding seasons as e.g., COVID restrictions precluded early arrival to the study area in 2020. For each model, a residual analysis was performed to test the homoscedasticity and normality of the residuals. When these did not meet models' assumptions, a different model was selected. When significant differences between stages or seasons were detected, we performed Tukey's post hoc tests using the *multcomp* package (Hothorn et al. 2008).

For the only continuous response variable with normal distribution (maximum depth) we used linear mixed models (LMM) implemented in the R package *lme4* (Bates et al. 2015). Continuous response variables that did not present a normal distribution (trip duration, maximum distance from colony, total distance traveled and dive frequency) were log-transformed. For the response variables that did not fit a normal distribution due to a high number of observations with low values (dive duration, depth and bottom time), we compared between seasons and stages using generalized linear mixed models (GLMM) using the Tweedie distribution family (with the index of power variance function selected according to response variable distribution) and a log-link function (Faster and Bravington 2013), implemented in the *lme4* and *statmod* packages. For continuous proportion variables (proportion of bottom time, proportion of trip diving and dive efficiency) we used GLMM with the beta binomial distribution family and for the count response variable (number of wiggles) we used GLMM with negative binomial distribution because of overdispersion, using the *glmmTMB* package (Brooks et al. 2017). In addition, we compared differences in home range area (km2) at 95%, 90%, and 50% isopleths using Analyses of Variance (ANOVA).

For foraging dives we also made comparisons between stage and season. The variables dive duration, depth (log transformed), maximum depth, bottom time and foraging frequency were modeled using LMM and the number of wiggles through a GLMM with negative binomial distribution. In all cases, the season or stage was considered as an independent variable and the individual as a random effect. In all the analyses, when significant differences occurred

between seasons, Tukey's post-hoc tests were performed using the 'glht' function from the *multcomp* package (Hothor et al. 2008), in order to assess whether differences were observed within stages.

3.4 Results

Tracking data from 57 individual birds from Ardley Island over three breeding seasons, provided information on 205 foraging trips, 106 482 dives, and 45 179 foraging dives with at least five capture attempts (Tables 1, 2 and Table S1). We found significant differences in foraging trip characteristics as the season progressed. During the late guard trips lasted longer than during early guard (10.99 ± 0.07 h vs. 19.28 ± 0.09 h; LMM, F=24.38; p<0.001; Fig 2), total distance traveled was more than double during late guard than in early guard (22.41 ± 0.09 km vs. 53.02 ± 0.11 km; LMM, F=34.75; p<0.001; Fig 2), as well as maximum distance to the colony (18.48 ± 0.12 km vs. 7.12 ± 0.10 km; LMM, F=34.95; p<0.001; Fig 2), and the maximum depth recorded was deeper during late guard than in early guard (78.75 ± 2.18 m vs. 90.31 ± 2.61 m; F=11.57; p<0.01; Fig 2). The 50, 90 and 95% UDs were also significantly larger during the late guard (LM, F=45.66; F=45.91; F=45.14; p<0.001, respectively; Fig 2). For these estimates h-value was set at 1.67 km. Finally, the frequency of dives was lower during the late guard (33.74 ± 0.03 vs. 28.94 ± 0.04; LMM, F=7.33; p<0.01; Fig 3). No other dive parameters showed significant differences between stages (Table 1 and S3, Fig 3). The indicated values are the mean and standard error for each parameter.

We also found significant differences in foraging trip characteristics between seasons. During the early guard in the 2019-2020 season, Adélie penguins undertook shorter trips in terms of total distance traveled (16.08 ± 0.11 km vs. 33.75 ± 0.12 km; LMM, F=22.88), maximum distance (5.23 ± 0.13 km vs. 10.45 ± 0.14 km; F=18.38; p<0.001) and duration (8.04 ± 0.07 h vs. 16.04 ± 0.08 h; LMM, F=26.83; p<0.001) than at the same stage in the 2021-2022 season (Fig 2). Similarly, the 50, 90 and 95% UDs were smaller (LM, F=22.23; F=28.56; F=28.75; p<0.001, respectively), and the maximum depth recorded was shallower (75.52 ± 2.64 m vs. 86.66 ± 2.97 m; LMM, F=8.90; p<0.001; Fig 2). There were no significant differences between the same stage in different seasons for the other parameters (Table 1 and S3, Fig 3). The indicated values are the mean and standard error for each parameter.

Table 1. Trip and dive characteristics (mean ± SD) of Adélie penguins breeding in Ardley Island during early and late guard between 2019 and 2022. The (*) indicates that there are significant differences between early and late guard. Significant differences between seasons within the same guard period are shown in bold. UDs were calculated using h-value=1.67 km.

	Early Guard		**Late Guard**	
Season	2019/2020	2021/2022	2020/2021	2021/2022
Date of sampling	06 dec-15 dec	09 dec-23 dec	24 dec-02 jan	24 dec-06 jan
Trip parameter				
N° Trips (N° ind)	67 (19)	52 (15)	59 (16)	27 (7)
Trip duration (h)*	**8.63 ± 3.66**	**18.26 ± 11.26**	20.85 ± 11.01	22.55 ± 11.44
Max. distance from colony (km)*	**6.6 ± 5.42**	**15.21 ± 14.76**	25.16 ± 17.92	23.77 ± 19.00
Total distance traveled (km)*	**19.33 ± 12.33**	**43.33 ± 36.26**	64.66 ± 40.40	62.47 ± 42.23
Max. trip depth (m)*	**73.14 ± 17.24**	**86.35 ± 19.95**	90.85 ± 14.73	85.50 ± 21.03
Home range (95% UD) (km2)*	**126.25 ± 61.68**	**361.58 ± 270.51**	587.78 ± 215.56	580.40 ± 231.62
Home range (90% UD) (km2)*	**100.69 ± 51.48**	**293.36 ± 226.59**	490.67 ± 185.41	482.65 ± 198.17

Home range (50% UD) (km2)*	**31.59 ± 15.99**	**80.40 ± 75.91**	149.65 ± 66.88	150.59 ± 72.24
Dive parameter				
N° of dives	20342	31625	37119	17396
Dive duration (s)	54.89 ± 6.13	61.86 ± 7.23	71.79 ± 7.73	63.26 ± 7.01
Depth (m)	18.84 ± 5.28	21.50 ± 6.66	25.03 ± 6.42	21.45 ± 6.03
Bottom time (s)	28.36 ± 3.10	33.20 ± 2.99	36.50 ± 3.16	34.91 ± 4.21
N° of wiggles	4.67 ± 0.58	5.10 ± 0.59	5.47 ± 0.67	5.25 ± 0.94
Proportion of bottom time	0.52 ± 0.07	0.55 ± 0.08	0.52 ± 0.07	0.56 ± 0.04
Dive frequency*	35.90 ± 9.34	34.06 ± 10.74	30.58 ± 9.63	29.16 ± 10.16
Proportion of dives	0.53 ± 0.09	0.55 ± 0.12	0.58 ± 0.14	0.49 ± 0.15
Dive efficiency	0.27 ± 0.06	0.30 ± 0.08	0.30 ± 0.09	0.28 ± 0.09

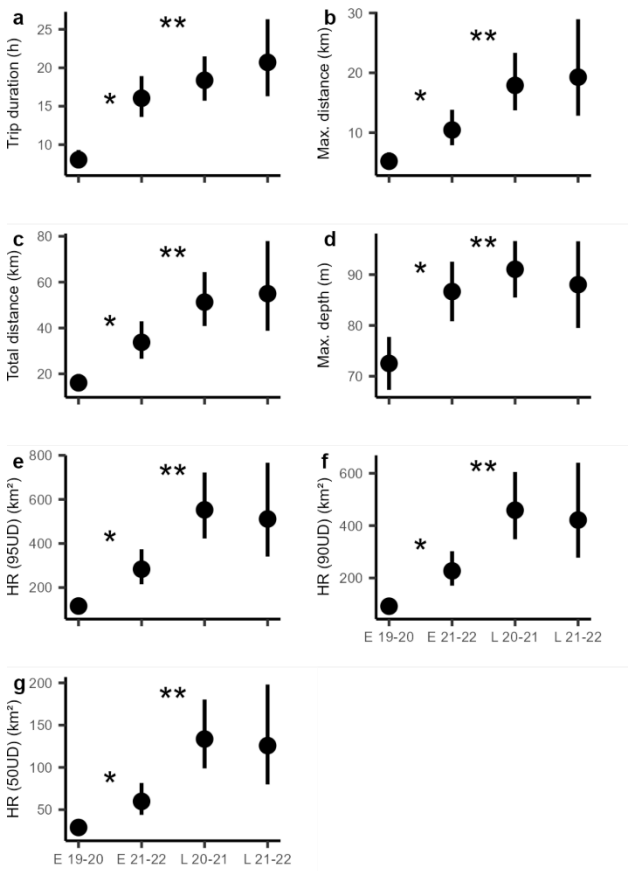

Figure 2. Characteristics of the foraging trips of Adélie penguins breeding in Ardley Island, King George Island, during early and late guard between 2019 and 2022 (e.g. early guard 2019-2020 and 2021-2022: E 19-20, E 21-22; late guard 2020-2021 and 2021-2022: L 20-21, L 21-22. Mean and SE (standard error) calculated from model outputs: a) Trip duration (h), b) maximum distance from colony (km), c) total distance traveled (km), d) maximum trip depth (m), e-g) Home Range (HR). The (*) indicates significant differences between seasons and (**) indicates significant differences between stages

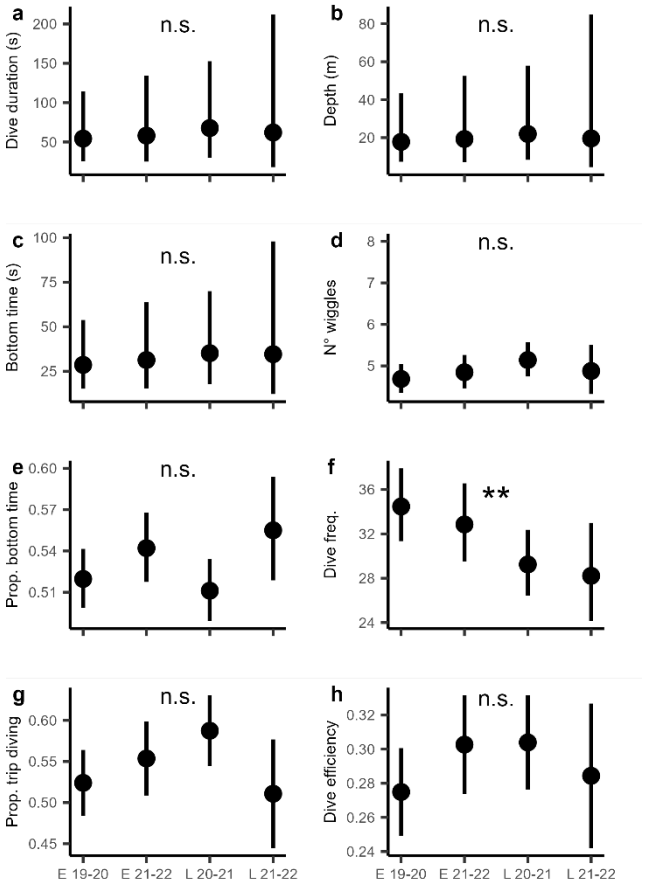

Figure 3. Diving behavior of Adélie penguins breeding in Ardley Island, King George Island, during early and late guard between 2019 and 2022 (e.g. early guard 2019-2020 and 2021-2022: E 19-20, E 21-22; late guard 2020-2021 and 2021-2022: L 20-21, L 21-22. Mean and SE (standard error) calculated from model outputs: a) dive duration (s), b) depth (m), c) bottom time (s), d) number of wiggles, e) proportion of bottom time, f) dive frequency g) proportion of the trip diving, h) dive efficiency. The (*) indicates significant differences between seasons, (**) indicates significant differences between stages and "n.s." indicates no significant differences.

Foraging dives of Adélie penguins were restricted to the vicinity of Ardley Island and comprise roughly 40% of the dives penguins perform during their foraging trips (Fig 4 and Table 2). Figure 5 shows the areas of overlap of the 50% UD of all the individuals tracked during the study period (for the whole colony h-value=1.67 km). Representativeness of these individuals with respect to the whole colony was estimated in 98%. Only 0.16 km2 cells where the 50% UD of at least 10% of the individuals studied overlap are shown.

Table 2. Foraging dives characteristics (mean ± SD) of Adélie penguins breeding in Ardley Island during early and late guard between 2019 and 2022.The (*) indicates that there are significant differences between early and late guard. Significant differences between sampling seasons within the same guard period are shown in bold.

	Early Guard		**Late Guard**	
Season	2019/2020	2021/2022	2020/2021	2021/2022
N° of dives	8246 (40.5%)	13708 (41.3%)	17124 (46%)	6101 (35%)
Dive duration (s)*	**85.12 ± 6.44**	**96.63 ± 6.50**	100.25 ± 5.73	106.52 ± 8.71
Depth (m)*	34.04 ± 5.13	36.73 ± 6.06	39.71 ± 4.62	44.72 ± 5.23
Max.trip depth (m)*	**73.07 ± 17.31**	**85.99 ± 19.77**	90.85 ± 14.73	85.50 ± 21.03
Bottom time (s)*	**41.85 ± 2.98**	**49.94 ± 2.95**	48.23 ± 2.75	51.75 ± 5.06
N° of wiggles	7.41 ± 0.60	7.77 ± 0.66	7.95 ± 0.58	8.54 ±1.12
Foraging frequency	15.00 ± 4.61	16.08 ± 5.66	**15.27 ± 4.75**	**11.42 ± 5.60**

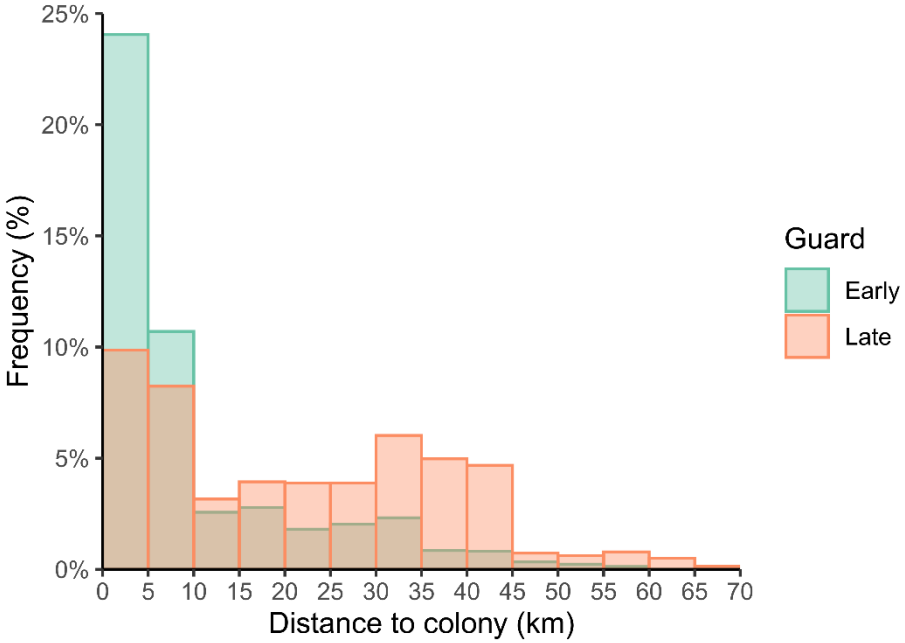

Figure 4. Frequency distribution of distance of foraging dives to the colony (km) of Adélie penguins breeding in Ardley Island, King George Island, during early guard (green) and late guard (pink)

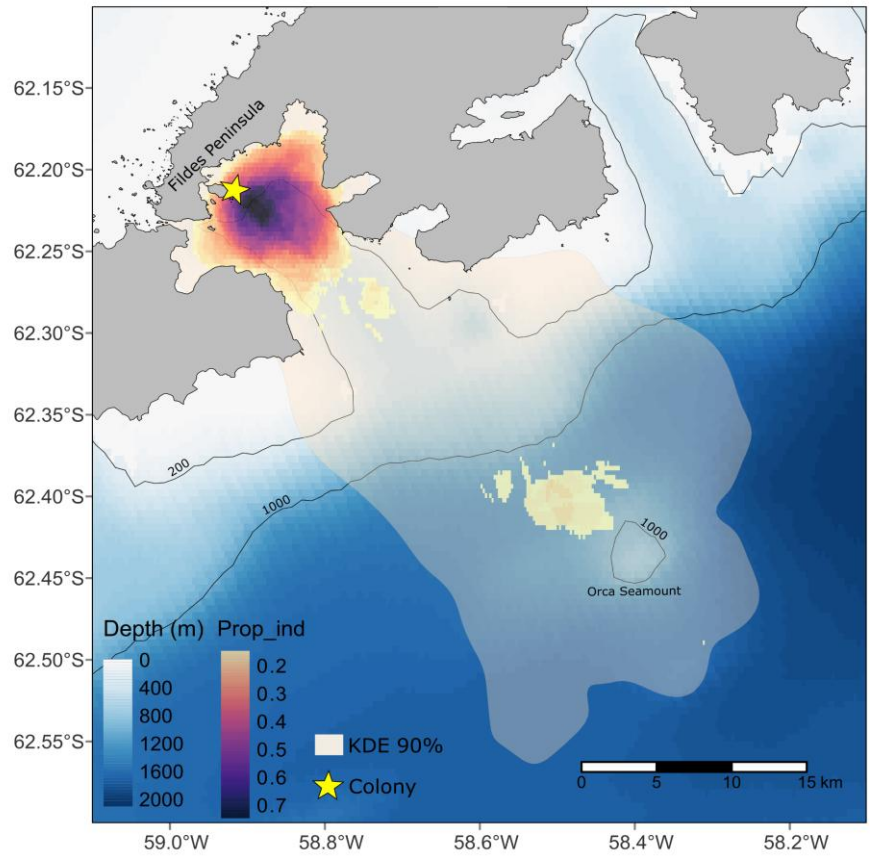

Figure 5. Key foraging areas of Adélie penguins breeding in Ardley Island. Proportion of individuals (Prop_ind) foraging in each 0.16 km2 cell is shown. Only cells where the 50% UD of at least 10% of the population overlaps are shown. KDE 90% indicates the isopleth of the 90% kernel density of all locations recorded during the study.

There were significant differences between foraging dive characteristics during the early and late stages. During the late guard foraging dives were deeper (26.56 ± 0.04 m vs. 33.07 ± 0.05 m; LMM, F=12.26; p<0.001), the maximum depth was deeper (78.54 ± 2.14 m vs. 90.28 ± 2.57 m; LMM, F=12.28; p<0.001), lasted longer (89.62 ± 2.08 s vs. 102.72 ± 2.52 s; F=13.71; p<0.001) and bottom time was longer (45.88 ± 1.07 s vs. 49.67 ± 1.29 s; LMM, F=5.11; p<0.05) than during the early guard (Fig 6). There were also differences between seasons. During the early guard in the 2021-2022 season, dive duration (83.42 ± 2.44 s vs. 97.38 ± 2.73 s; LMM, F=11.9) and time spent at the bottom lasted longer (42.29 ± 1.21 s vs. 50.35 ± 1.35 s; F=9.91; p<0.001), and maximum depth was deeper (72.46 ± 2.61 m vs. 86.28 ± 2.94 m; LMM, F=9.05; p<0.001) than at the same stage in the 2019-2020 season (Fig 6). On the other hand, during the late guard the only variable that showed significant differences between seasons was foraging frequency, which was higher during the 2020-2021 season (15.21 ± 0.77 vs. 11.31 ± 1.18; LMM, F=3.78; p<0.05) (Table 2, S4 and Fig 6). The indicated values are the mean and standard error for each parameter.

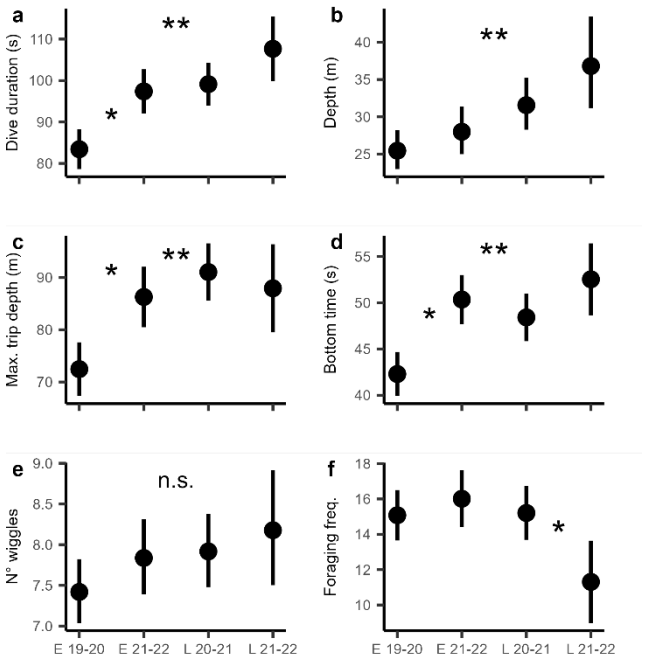

Figure 6. Characteristics of foraging dives of Adélie penguins breeding in Ardley Island, King George Island, during early and late guard between 2019 and 2022 (e.g. early guard 2019-2020 and 2021-2022: E 19-20, E 21-22; late guard 2020-2021 and 2021-2022: L 20-21, L 21-22. Mean and SE (standard error) calculated from model outputs: a) dive duration (s), b) depth (m), c) maximum trip depth (m), d) bottom time (s), e) number of wiggles, f) foraging frequency. The (*) indicates significant differences between seasons, (**) indicates significant differences between stages and "n.s." indicates no significant differences.

3.5 Discussion

In this study, we integrated spatial location, dive, and accelerometry data from Adélie penguins rearing chicks in Ardley Island, King George Island/Isla 25 de Mayo, to characterize their foraging behavior and identify key foraging areas regularly used by a declining colony in an area free of sea-ice throughout the austral summer. During the chick-rearing period, both early and late guard, and across seasons, Adélie penguins breeding in Ardley Island forage in the vicinity of the colony, within Maxwell Bay. Foraging dives comprise roughly 40% of the dives penguins perform during their foraging trips, irrespective of the stage of the chick-rearing period, or the season analyzed. Our results add relevant information on Adélie penguin foraging behavior in a rapidly changing region and to the current debate on small-scale management units for the krill fishery, for which the identification of foraging areas used by predators represents critical information to mitigate potential competition between predators and fisheries (Hinke et al. 2017; Trathan et al. 2022).

Distances covered during the trips, trips duration and area explored changed throughout the breeding season, increasing as the season progressed, with average duration of trips changing from mean values of 8.6-18.3 h in the early guard to 20.9-22.5 h in the late guard, and mean maximum distance to the colony changed from 6.6-15.2 km in the early guard to 23.8-25.2 km in the late guard. Dive frequency was higher and maximum depth was shallower during the early guard. All other dive parameters did not show any differences between stages, suggesting that trip distance and duration are the key parameters adjusted to account for differences in prey availability or energetic demands as the season progresses. The same was observed when seasons were compared. During the early guard in the 2019-2020 season, Adélie penguins undertook shorter trips, with maximum depth being the only other

parameter where differences between seasons was observed. No significant difference was observed between late stages in any parameter. We found no differences between dive characteristics, such as dive duration, time spent at the bottom or number of wiggles, parameters often used to infer foraging effort and success (e.g., Bost et al. 2007; Riaz et al. 2020, 2023).

However, when only foraging dives were considered, we observed differences in dive characteristics, with penguins diving deeper, and dive durations and time spent at the bottom lasting longer during the late guard. We also found differences between seasons, with higher maximum dive depth and duration and time spent at the bottom lasting longer during the early guard of 2021-2022 and foraging frequency being smaller during the late guard of 2021-2022. These differences might reflect differences in prey abundance, quality and/or availability (e.g., Riaz et al. 2023), and/or penguin energetic demands as seasons progress. The use of video data in combination with GPS accelerometer tags could help validate behaviors estimates and the number of prey captured, clarifying energetic demand (Watanabe et al. 2013).

In general, the characteristics of Adélie foraging trips during chick-rearing in Ardley Island are comparable to other studies on this species in the early 90s at the same colony and other colonies in the WAP more recently, with maximum distance from the colony of less than 40 km and trip duration of less than 24 hours (Wilson 2002; Oliver et al. 2013; Oosthuizen et al. 2022). When compared to other colonies around Antarctica, values of maximum distance and trip duration in Ardley Island are lower than those reported for colonies in Adélie Land (range values from 6 to 89 km and from 16 to 96 h, Widmann et al. 2015; Michelot et al. 2021), Béchervaise Island (trip duration between 25 and 73 h, Clarke et al. 1998; Riaz et al. 2020), Prydz Bay (mean trip duration of 64 h, Watanuki et al. 1997) and in Ross Island (maximum distance values from 25 to 35 km and mean trip duration between 24 and 84 h, Ainley et al. 1998; Lescroël et al. 2010, 2020). Differences might reflect different environmental conditions between colonies, since both East Antarctica and the Ross Sea region have sea-ice cover near the colonies during the breeding season, whereas Ardley Island has no sea-ice cover at any time during the season. This would be supported by reported values of maximum distance and trip duration similar to those reported in our study, at colonies in East Antarctica during

seasons with low sea ice concentration records (Ito et al. 2020; Michelot et al. 2021). Differences could also be due to colony size, given that at small colonies, like Ardley Island, individuals tend to forage closer to the colony than those in larger colonies (Ballance et al. 2009; Patterson et al. 2022). Also, note that several studies have documented that penguins, including *pygoscelid*, may exhibit sex-specific differences in their foraging behavior (Clarke et al. 1998; Beaulieu et al. 2010; Riaz et al. 2020). Yet, sex was only determined for some of the individuals tracked, therefore precluding statistical comparisons due to the small sample size in each season. Hence, there are some behavioral differences that may influence our results that have not been considered in this study.

During the breeding season parents must meet the increasing energetic demands of chicks by increasing foraging effort (Kato et al. 2003; Ainley et al. 2004; Clarke et al. 2006; Kokubun et al. 2010). In Narębski Point (Barton Peninsula), located 10 km away from Ardley Island, Kokubun et al. (2010) shown that, during chick rearing, both chinstrap and gentoo penguins (*Pygoscelis antarcticus* and *P. papua*) move away from the colony as the season progresses, and attributed this to a reduction in prey availability around the colony. Competition for food resources has been proposed as a regulating mechanism of pelagic seabird populations by prey depletion near the colony ('Ashmole's halo'), forcing individuals to forage further (Birt et al.1987; Ballance et al. 2009; Patterson et al. 2022). Although the Adélie penguin colony in Ardley Island is small, many other penguins nesting on the same island and in nearby colonies may contribute to prey depletion within Maxwell Bay. The increase in foraging distance as the season progresses observed in our study might be reflecting this process.

On the other hand, the differences in foraging behavior observed between seasons might reflect inter-annual variability in krill availability. In the vicinity of our study area Salmerón et al. (2023) reported direct evidence of lower krill abundance in 2021-2022 than in 2019-2020. They showed that chinstrap penguins breeding less than 20 km away from our study area, in Nelson Island, substantially increased their foraging effort during the year of low krill availability, supporting our interpretation that the differences observed in the foraging behavior of Adélie penguins in Ardley Island also reflects variations in prey availability during the study period. Our observations have also been also evidenced for Adélie penguins in different colonies around Antarctica which in response to changes in energy demand and/or

prey availability/size tend to modify the distance and duration of foraging trips (Watanuki et al. 1993; Fraser and Hofmann 2003; Ainley et al. 2015; Lescroël et al. 2020), the depth of dives (Lescroël et al. 2023; Ainley et al. 2015) and/or the type of prey (Cherel 2008; Jarman et al. 2013; Ainley et al. 2018).

Our accelerometry-data-based approach showed that the core foraging area of the colony is located within Maxwell Bay, 10 km off the colony, with this area being systematically used by more than 60% of the population throughout the seasons and across seasons. We also observed that nearly 20% of the population uses the area close to Orca Seamount for foraging (35 km from the colony), mainly during the late guard stage or during periods of low prey availability. Lee et al. (2021) report similar observations for the gentoo and chinstrap colonies breeding in Ardley Island. Both species foraged in the vicinity of the colony, within the Maxwell Bay, evidencing a clear overlap of foraging area of three species of *pygoscelid* penguins breeding in the island. They also reported, as did Kokubun et al. (2015), that the Orca Seamount area is a foraging hotspot used by Narębski Point's chinstrap and gentoo populations. Studies on Adélie penguins at Anver Island report similar behavior: short foraging trips (8-25 km) associated with a submarine canyon near the colony (Oliver et al. 2019; Nardelli et al. 2021). This kind of bathymetric features, such as submarine canyons and seamounts appear to increase zooplankton availability through physical processes that affect the vertical distribution of nutrients, such as upwelling, thus, constituting important areas for marine predators (Clarke et al. 2006; Santora and Reiss 2011).

Understanding the predator-prey interactions at small scales is critical for ecosystem conservation planning and resource management (Watters et al. 2020; Trathan et al. 2022). As krill catches intensify in the Western Antarctic Peninsula, particularly in coastal areas, there is an increasing need for ecological data at small spatial and temporal scales to inform potential overlap and conflicts. Although fishing in Maxwell Bay is not currently significant, King George Island is located within one of the regions that concentrates most of the krill fishing activity (e.g., Hinke et al. 2017). Identifying relevant foraging areas in the vicinity of other penguin colonies in the northern shelf of the South Shetland Islands and Bransfield Strait, where krill fishery currently concentrates, would enable small-scale conservation measures for implementing small-scale management of the krill fishery in the region, as well

as other conservation measures (e.g., Hogg et al. 2020). Here, we propose an accelerometry-data-based approach to identify these areas. Implementing conservation measures aimed at avoiding additional pressures on the main foraging areas, or the areas to which colonies resort when the availability of prey decreases, might play a key role in diminishing the potential impact of fisheries on predator populations.

Under current environmental changes in the WAP, southward contraction and krill biomass reduction trends are expected to continue, linked to positive trends in Southern Annular Mode (SAM) anomalies, which are associated with warm, windy and cloudy weather and reduced sea ice (Atkinson et al. 2019). With reduced prey availability, changes in foraging behavior and reproductive success of penguins are expected, such as those already observed by Cimino et al. (2023) on Anver Island in years with early sea ice retreat and by Salmerón et al. (2023) associated with winter sea ice scarcity and likely deepening of the mixed layer resulting from stronger winds. Recently, it has been suggested that the coupling of climatic events and fisheries may exacerbate local effects on krill availability, affecting penguin breeding populations (Watters et al. 2020; Krüger et al. 2021). Thus, in the WAP, identifying local foraging hotspots for krill-dependent predators, might be crucial for determining areas of ecological importance that require consideration in management measures.

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CAPÍTULO 4

Energy expenditure of Adélie penguins during the breeding season: females pay the cost in years of low food availability

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4. Energy expenditure of Adélie penguins during the breeding season: females pay the cost in years of low food availability

4.1 Abstract

Changes in prey availability can lead to mismatches between consumers and resources, decreasing the fitness of consumers, especially during periods of high energy demand such as reproduction. We investigated inter-seasonal variations in the foraging behaviour of chick-rearing Adélie penguins (*Pygoscelis adeliae*) in a declining colony in the West Antarctic Peninsula to assess the impact of changes in prey abundance. Specifically, we analysed how these changes affect the energetic cost of males and females during the breeding season. Using information from foraging trips, diet, body condition, and daily energy expenditure of 38 Adélie penguins breeding in Ardley Island, King George Island, in 2019/20 and 2021/22, we found that during low food availability conditions, penguins were forced to increase their foraging effort, and the body mass was lower. Specifically, females extended their foraging trips, resulting in 40% higher energy expenditure compared to a year with high prey availability. We observed no significant changes in physiological condition, breeding success, or trophic niche. The lower fat reserves and higher energy expenditure of females during the breeding season with low food availability may render them more vulnerable to the challenging conditions of the winter season, with potential negative consequences on population trends.

Keywords: Accelerometry; Ecosystem management; Foraging ecology; Trophic ecology

4.2 Introduction

Behaviour is a key determinant of the resilience of animal species to a rapidly changing climate (Buchholz et al., 2019). Unusual weather conditions provide valuable opportunities to understand the role of behavioural flexibility in the ability of animals to cope with novel conditions and hence, the role of behaviour in buffering the impacts of climate change on population persistence. The annual cycles of seasonally breeding birds involve key life history events such as reproduction, migration and winter survival, shaped by fluctuating resources and environmental conditions (Buehler and Piersma, 2008). To cope with the challenge of seasonal survival, animals must adjust their behaviour and balance their energy acquisition and expenditure (Karasov, 1986; Dunn et al., 2020). At high latitudes, the temporal window for the breeding season is limited and often strongly coupled with seasonal peaks in food availability (Forcada and Trathan, 2009; Chapman et al., 2010). The match-mismatch hypothesis predicts that predators breed more successfully in years in which the most energetically demanding phase of their breeding cycle overlaps extensively with the seasonal peak in prey availability (Cushing, 1990; Durant et al., 2007). This means that a temporary mismatch between food supply and energy demand must be addressed by parents, affecting foraging costs and individual fitness (e.g., Nicol et al., 2008; Forcada and Trathan, 2009; Chapman et al., 2010; Joly et al., 2022).

Biparental care is essential for offspring success and is widespread among birds. Parental investment is often not equally shared, with sex-related differences in foraging and provisioning behaviour (Lack, 1968). These differences are particularly pronounced in sexually dimorphic species, yet sex-specific foraging patterns have been widely reported in monomorphic or slightly size-dimorphic seabird species (e.g., Gray and Hamer 2001; Lewis et al., 2002; Welcker et al., 2009). Sex-specific foraging behaviours are generally considered to result from different energetic or nutritional needs between the sexes (Gray and Hamer 2001; Lewis et al., 2002; Welcker et al., 2009); from intersexual competition, causing one sex to be spatially displaced or to forage in different niches (González-Solís et al., 2000; Miller et al., 2018); and differences in nest attendance rhythms (Aguilera, 1990).

Reproduction is an energetically costly period for central-place foragers, such as seabirds (Ellis and Gabrielsen, 2002; Dunn et al., 2018). During this time, they must frequently return to the colony to incubate their eggs or to feed their offspring. Their movements are thus spatially and temporally restricted to exploit resources within a given range around the colony (Orians and Pearson, 1979). Therefore, parents incur high values of energy expenditure by making physiological and behavioural adjustments to maintain their body condition while meeting the increasing energetic requirements of their chicks (Drent and Daan, 1980; Dunn et al., 2020). In a context of global environmental changes, understanding animals' capability to modify their trophic niche or foraging behaviour in response to changes in food availability, while meeting parental energy demands, is essential to assess the potential impact of these changes on populations. Here we assess the impact of changes in food availability on the trophic niche and foraging behaviour of one of the most widespread vertebrates of Antarctica, in one of the regions of the globe most affected by climate change: Adélie penguins (*Pygoscelis adeliae*) in the Antarctic Peninsula.

The Adélie penguin is a migratory and pagophilic species (Ainley, 2002), considered an indicator species as it is highly sensitive to changes in the ecosystem (Boersma, 2008). In western Antarctic Peninsula (WAP), a large decline in their breeding populations had been reported at several colonies and linked to rapid environmental changes in the region (Trivelpiece et al., 2011; Fraser et al., 2013; Lynch and LaRue, 2014; Juáres et al., 2015). Climate change have profound effects on both marine and terrestrial environments, impacting penguins' overwinter pack-ice habitat, food resources, and physical conditions of nesting sites (Massom et al., 2006; Hinke et al., 2007, 2012, 2017; Trivelpiece et al., 2011; Fraser et al., 2013; Cimino et al., 2023; Salmerón et al., 2023). Overall, the limited flexibility of Adélie penguins to adapt their breeding chronology according to local conditions, the decline in prey availability during the breeding season, and overwintering processes affecting the survival of juveniles and adults have been proposed as the main factors determining such declines (Hinke et al., 2007, 2012; Emmerson et al., 2011; Lynch et al., 2012; Juáres et al., 2013; Cimino et al., 2016).

The Antarctic krill (*Euphausia superba*) currently constitutes the main prey for Adélie penguins breeding populations of the northern WAP (Trivelpiece et al., 2011; Negrete et al., 2016;

Juáres et al., 2018). In this region, Antarctic krill is being affected by ongoing environmental changes, with a decrease in recruitment and abundance, and a southward contraction associated with the continuous decline in the winter sea-ice extent, increase in the sea surface temperature and decline in marine primary production (Montes-Hugo et al., 2009; Hill et al., 2019; Atkinson et al., 2019, 2022). Furthermore, in recent years, Bransfield Strait and the South Shetland Islands have become a hotspot for the krill fishery (Santa Cruz et al., 2018), leading to interference competition with krill predators (Watter et al., 2020). Coupled climate events and fisheries may exacerbate local effects on krill abundance (Watters et al., 2020; Krüger et al., 2021), highlighting the urgent need to understand how fluctuations in krill abundance may impact on dependent marine predators in this region (Hogg et al., 2020; Watters et al., 2020; Krüger et al., 2021; Trathan et al., 2022). Chapman et al. (2011) also postulates that the absence of Antarctic silverfish (*Pleuragramma antarctica*) in the diet of Adélie penguins in the Antarctic Peninsula may have resulted in lower quality (energy content) chick diets, making it difficult for adult Adélie penguins to produce chicks that will recruit. Under current and projected climate change scenarios in the WAP, Adélie penguins, as a species with limited flexibility in the timing of breeding and high dependence on Antarctic krill provide an exceptional case study to understand the potential consequences on populations persistence of climate-driven mismatches between the periods of highest energy demand and maximum food availability (Chapman et al., 2010; Cimino et al., 2023).

Adélie penguins show considerable foraging behavioural flexibility in response to fluctuations in food availability, modifying the distance and duration of foraging trips (Watanuki et al., 1993; Nicol et al., 2008; Lescroël et al., 2020) and the depth of dives (Ainley et al., 2015; Lescroël et al., 2023). With a slight sexual size dimorphism (Ainley and Emison, 1972) their feeding ecology also shows sex-specific differences. Females tend to forage farther, longer, and dive shallower, while males exploit waters closer to the colony and dive deeper (Clarke et al., 1998; Watanuki et al., 2002; Ballard et al., 2010; Lescroël et al., 2010; Widmann et al., 2015). These differences have been attributed to the different energetic needs of females (Chappell et al. 1993a; Clarke et al. 1998; Colominas-Ciuró et al., 2018), differences in diving capacity and to intra-specific competition for segregation in foraging habitats or diet (Widmann et al., 2015; Massaro et al., 2020). In some colonies, foraging success has been suggested as a determinant factor of their survival and reproductive success (Ballard et al.,

2010; Lescroël et al., 2010), with episodes of total breeding failure or low offspring survival linked to poor foraging conditions (Emmerson and Southwell, 2008; Ropert-Coudert et al., 2015; Cimino et al., 2023).

Some studies have analysed the energetic cost of changes in foraging behaviour in response to fluctuations in krill availability for Adélie penguins (e.g., Nagy and Obst, 1992; Chapell et al., 1993; Ballance et al., 2009; Watanabe et al., 2020), however, none of them address how changes in prey availability affect the energy cost of males and females. Therefore, the main objective of our study is to analyse differences in energy expenditure during the breeding season of Adélie penguins from a colony in King George Island/Isla 25 de Mayo in two seasons with large differences in krill availability (Salmerón et al., 2023). We also explore whether this energetic cost differs between males and females. We combined information from previous work on the characteristics of their foraging trips (Machado-Gaye et al., 2024), diet (based on stable isotope analysis), body condition, and daily energy expenditure derived from accelerometry data. The findings reported for the same colony showed differences in foraging behaviour between seasons with differences in prey availability, so here we aim to test the following hypotheses: a) changes in foraging behaviour due to reduced food availability increases the energy expenditure of Adélie penguins, b) Adélie penguins modify their trophic niche to buffer the effects of differences in krill availability, and c) the increase in energy expenditure associated with increased foraging effort exhibits sex-specific differences.

4.3 Materials and Methods

Field work

Fieldwork was conducted at Ardley Island (62°13’ S, 58°56’ W), in the southwest of King George Island/Isla 25 de Mayo, South Shetland Islands, within the Antarctic Specially Protected Area (ASPA) N°150, during the early guard stage of the 2019/20 and 2021/22 breeding seasons (Fig. 1). Between December 6th and 24th, a total of 38 breeding Adélie penguins (19 in 2019/20; 19 in 2021/22) were equipped with data-loggers (Axy-Trek, 70 x 40 x 15 mm, 69 g; TechnoSmart, Italy) including GPS, accelerometer, and both pressure and temperature sensors. We captured only one member of the pair in nests with two chicks, mainly by hand, with the occasional aid of a long-handled net. We also captured chicks during

adult handling to protect them from predators. The recorders were attached on the birds' lower back feathers using black Tesa® 4651 tape (Wilson et al., 1997). The loggers used represent about 1% of the body mass of an adult Adélie penguin (mean for birds in this study 5112 ± 1431 g). The loggers were programmed to record positions every 5 min, pressure (in millibars) and temperature at 1 Hz and acceleration along the 3 body axes of the penguins: longitudinal (surge), dorso-ventral (heave) and lateral (sway) at 50 Hz. After the deployment procedure and immediately before the release of the adult bird, we returned the chicks to the nest, and released the adults some 10 m from their nests. All birds returned to their nests and attended their chicks shortly after being released.

Individuals were recaptured in the nest to recover the devices after 3-7 days and the body mass was weighed. Blood samples were collected immediately after capture via a peripheral foot vein using a sterilized needle and heparinized capillary tubes and five body feathers were plucked from the belly. A small amount of blood was collected in FTA cards for molecular sex determination and one drop of blood was smeared on microscope slides, air-dried and fixed in 96% ethanol for 5 min for measurement of body condition estimates. Remaining blood was preserved in ethanol for subsequent $\delta^{13}C$ and $\delta^{15}N$ analyses. During the study seasons, we also counted the number of active nests at the end of November (before hatching) and the number of surviving chicks in early January (in the crèche stage close to fledging), to calculate the breeding success of the colony (defined as the number of fledglings divided by the number of active nests).

Finally, in order to describe differences in prey abundance in the area, we used the information on krill acoustic reported by Salmerón et al. (2023) in the surroundings of Nelson Island. In the study, the authors conducted acoustic transects between December 2019 and January 2020, and during January 2022. Although the transect analysed by these authors slightly differs with foraging area used by the penguins tagged in Ardley Island, we assume it reasonably reflects krill abundance in our study area (Fig. 1; but also see Fig. 1 in Salmerón et al. (2023)). The authors found that in 2019/20 krill were more abundant but also more available to penguins, as swarms were found at a shallower depth than in 2021/22.

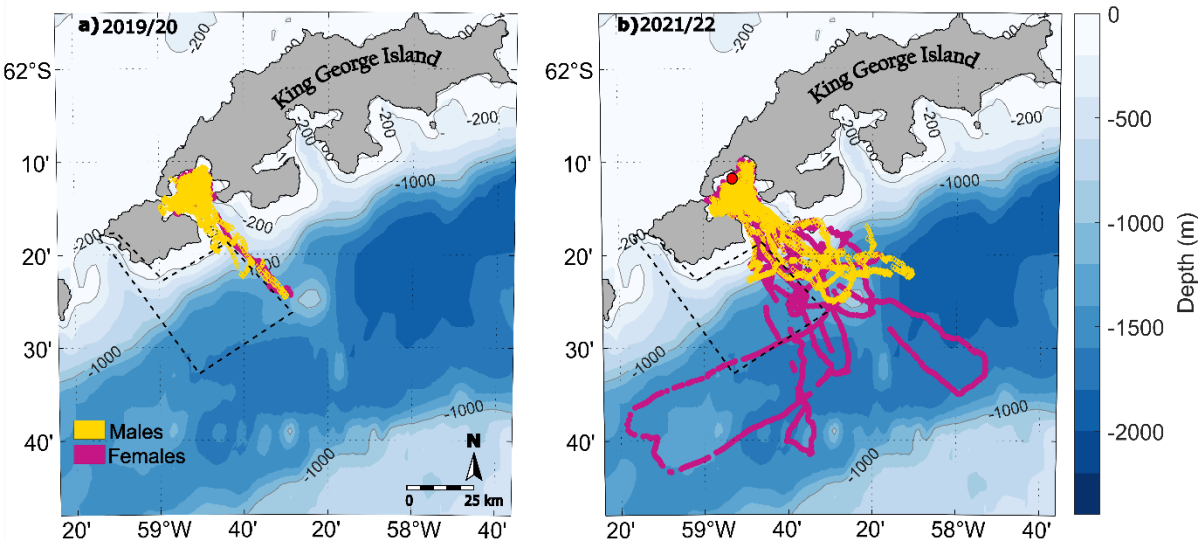

Figure 1. Tracking locations of Adélie penguins breeding in Ardley Island (red dot) (King George Island/Isla 25 de Mayo) during early guard stage in 2019/20 and 2021/22 seasons. The black dotted line represents the area of the krill acoustic transects carried out in both seasons, modified from Salmerón et al. (2023).

Data processing

From 38 deployments, we obtained 33 complete sets of GPS and dive data, comprising location, time, and dive depth, which we used in the following analyses. GPS data were analysed using the R software (version 4.1.3; R Core Team 2022). A speed filter set to 7 $km.h^{-1}$ was applied to remove unrealistic velocity, and foraging trips were defined from the time the birds moved more than 50 m from the nest to the sea until the time they were within 50 m of the nest again. For each individual, we calculated total trip duration, total trip distance as the cumulative horizontal distance between all GPS locations per bird per trip, and maximum distance to the colony as the straight line distance between the colony and the furthest point of a trip. Dives were analysed using the software Igor Pro Version 6.37 (Wavemetrics). Pressure (mBar) was converted to water depth (m), surface line (0 m) was visually checked and corrected manually when needed. Only dives deeper than 1 m were included due to possible measurement error in instruments and surface waves (Takahashi et al., 2003; Kato et al., 2009). For each dive, we calculated the dive depth (m) (determined as the deepest point of the dive), total dive duration (s), bottom time duration (s) (start and end of bottom time were defined as the first and last time in a dive when the depth change rate was < 0.25 $m.s^{-1}$). Maximum dive depth recorded on each trip was also calculated.

Calculation of energy expenditure

Energy expenditure is classically measured in relation to the activity level of an animal. At the organismal level, field metabolic rate (FMR) is the total sum of energy that a free-ranging animal metabolizes over a specified period of time (Dunn et al., 2018). Average FMR per 24 hr-period is also routinely used to calculate daily energy expenditure (DEE; Grémillet et al., 2018). To calculate DEE (KJ g^{-1} day^{-1}) during at sea foraging trips, we used the existing DEE vs activity-specific dynamic body acceleration (DBA) relationship built and validated for Adélie penguins (Hicks et al., 2020).

Accelerometry data were analysed using the software Igor Pro Version 6.37 (Wavemetrics). DBA was calculated by smoothing data for each axis across a 1-s period to calculate the static acceleration, and then subtracting the static acceleration from the raw acceleration values. As a metric for bird activity levels, we calculated the vectorial dynamic body acceleration (VeDBA) as the square root of the sum of the squares of dynamic body acceleration in the three axes: $VeDBA = \sqrt{(A^2_X + A^2_Y + A^2_Z)}$ where Ax, Ay and Az are the derived dynamic accelerations at any point in time corresponding to the three orthogonal axes of the accelerometer (Hicks et al., 2020). For all individuals, we calculated the proportion of time spent on land and in water during a foraging trip (time budget) and the mean VeDBA value for each. We also calculated total VeDBA as the mean behavioural DBA value multiplied by the duration of time spent in that behaviour per day. To calculate the DEE we used the calibrated equation (4) for Adélie penguins proposed by Hicks et al. (2020): $DEE = (4.54 \times 10^{-1} \pm 4.09 \times 10^{-2}) + (1.93 \times 10^{-5} \pm 1.76 \times 10^{-6}) VeDBA_{Water} + (-1.16 \times 10^{-5} \pm 5.25 \times 10^{-6}) VeDBA_{Land} + (-3.08 \times 10^{-2} \pm 2.09 \times 10^{-2})$ Sex.

Stable isotope analysis

The stable isotope value in a tissue reflects the diet composition and foraging habitat of seabirds during the time of synthesis. The analysed carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) stable isotope values of whole blood allowed us to compare the diet the penguins fed their chicks during the study period, as whole blood provides dietary information integrated of approximately 20 days (Barquete et al., 2013; but also see Bearhop et al., 2000). Isotope analyses were performed at the LIttoral ENvironnement et Sociétés (LIENSs) laboratory, La Rochelle University, with a mass spectrometer (Delta V Plus with a Conflo IV interface, Thermo

Scientific, Bremen, Germany) coupled to an elemental analyser (Flash 2000, Thermo Scientific, Milan, Italy). Prior to analyses, blood samples were freeze-dried for 24 h, homogenized to powder and aliquots between 0.1 to 0.5 mg were weighed into tin capsules (8 × 5 mm, Elemental Microanalysis Ltd, Okehampton, United Kingdom) using an analytical balance. Stable isotope values were conventionally expressed as δ values in ‰, using the following equation: $\delta X = ([R_{sample}/R_{standard}]-1 \times 1000)$, where R_{sample} is the ratio of the heavy to light isotope for either $^{13}C/^{12}C$ or $^{15}N/^{14}N$, and $R_{standard}$ is the heavy to light isotope ratios for international standards - Vienna PeeDee Belemnite for carbon (VPDB), and atmospheric nitrogen (Air-N_2) for nitrogen. Quality control was done using reference materials USGS-61 and USGS-63 (US Geological Survey, Reston, VA, USA) based on their assigned carbon and nitrogen isotope-delta values and standard uncertainties (i.e., -35.05 ± 0.04 ‰ and -1.17 ± 0.04 ‰ for carbon, respectively, and -2.87 ± 0.04 ‰ and +37.83 ± 0.06 ‰ for nitrogen, respectively). The uncertainty of the reported isotope values was evaluated as the standard deviation of repeated (n = 8) measurements of each reference material (i.e., USGS-61 and USGS-63) within a single group of analyses. Uncertainty does not exceed 0.06 ‰ for $\delta^{13}C$ values and 0.12 ‰ for $\delta^{15}N$ values.

Finally, intact specimens of 3 to 4 whole adult *Euphausia superba* were taken from regurgitate samples collected during the season 2020/21, to represent the sources for analysis. Lipids were removed from prey samples using a 2:1 chloroform:HCl mixture solution. Isotope analyses were performed at the Center for Stable Isotopes, University of New Mexico. We calculated the trophic position for each individual following the model proposed by Post (2002) $TP = \boldsymbol{\lambda}\ (\delta^{15}N_{secondary\ consumer} - \delta^{15}N_{base})/\Delta n$, where $\boldsymbol{\lambda}$ is the trophic position of the organism used to estimate $\delta^{15}N_{base}$ (e.g., $\boldsymbol{\lambda} = 1$ for primary producers), $\delta^{15}N_{secondary\ consumer}$ is measured directly, and Δn is the enrichment in $\delta^{15}N$ per trophic level. We assumed that diet tissue fractionation factors (Δn) for $\delta^{15}N$ was + 2.7 ‰ between lipid-free prey and penguin whole blood (Cherel et al., 2005).

Body condition parameters

The blood smeared on microscope slides was stained with Giemsa pH 7.2 (Masello et al., 2021). Areas of blood smear where the blood cells had separated in a monolayer with similar density of cells were analysed from the x and y axes under light microscope. For each smear

we obtained (1) the White Blood Cells (WBC) total count, and (2) the heterophils and lymphocytes ratio (H/L) as physiological health and stress status. The total count of WBC provides information about the general level of immune response of the individual. It was performed counting the number of WBC in 10 visual fields at x400 magnification as a standardized method (Menéndez-Blázquez et al., 2021). The differential leucocyte profile was calculated as the percentage of the difference of WBC of a total of 100 at x1000 amplification (oil immersion). From this profile, we evaluated the H/L ratio, which has been successfully applied as an indicator of physiological status and effort (high ratio = high stress) (Davis and Maney, 2018). Smears analysis was made by the same observer in order to reduce variability and biases derived from identification.

As a proxy for body condition, we also measured adult body mass, considering it as an indicator of the energy reserves for the chick rearing period. Body mass of adult penguins were measured using a Pesola spring balance after recapture and tracking devices removal.

Sex determination

Molecular methods were employed for sex determination using blood and feather samples. DNA was extracted from blood using the DNA Blood and Tissue Kit (QIAGEN, Germany), performed in the laboratory of the Museo Nacional de Ciencias Naturales (Spain), and from feathers using the PrepGem Universal kit (MicroGem; Southampton, UK) performed at Instituto de Investigaciones Clemente Estable (Uruguay), both according to the manufacturers' instructions. The latter was used when blood samples were unavailable or insufficient. Sex identification was performed via PCR using primers P2 and P8 (Griffiths et al., 1998) in a 20 µL reaction containing 1x Platinum Multiplex Master Mix (Invitrogen Life Technologies, Carlsbad, California), 0.5 µL of each primer, and 50 ng of genomic DNA. The P2 primer was labeled with FAM to facilitate fragment size analysis by capillary electrophoresis. The PCR profile included an initial denaturation at 94°C for 10 min, followed by 35 cycles of 94°C for 30 sec, 47°C for 1 min, and 72°C for 1 min, with a final extension at 72°C for 10 min. Both positive and negative controls were included in each PCR run, using known sex samples of *Gubernatrix cristata*. The PCR products were verified by 1% agarose gel electrophoresis, and those from feather analysis, sent to the *Unidad de Secuenciación* at *Hospital de Clínicas, Dr. Manuel Quintelas* (UdelaR, Uruguay), for fragment analysis. Genotype assignment was conducted using

GeneMarker 2.4.0 (Softgenetics LLC, State College, Pennsylvania), identifying males as homozygotes (370/370 bp) and females as heterozygotes (370/388 bp).

Statistical analyses

To test for differences between seasons and sexes in the variables analysed we used different statistical models, to account for differences in the response variables and their effects on models assumptions. For each model, a residual analysis was performed to test the homoscedasticity and normality of the residuals. When these did not meet models' assumptions, a different model was selected. When significant differences between seasons and sex were detected, we performed Tukey's post hoc tests using the *multcomp* package (Hothorn et al., 2008). In each model, the season and sex were considered as an independent factorial variable and the individual as a random effect to account for repeated measures of the same individual. For the only continuous response variable with normal distribution (maximum dive depth per trip) we used linear mixed models (LMM) implemented in the R package *lme4* (Bates et al., 2015). Continuous response variables that did not present a normal distribution (trip duration, maximum trip distance and total trip distance) were log-transformed. For the variables that did not have repeated measures by individual (adult body mass, daily energy expenditure and isotopic values of $\delta^{13}C$ and $\delta^{15}N$) we used two-way analysis of variance (ANOVA), with the season and sex as factors. For the response variables that did not fit a normal distribution due to a high number of observations with low values (dive duration, depth and bottom time), we compared between seasons and sexes using generalized linear mixed models (GLMM) using the Tweedie distribution family (with the index of power variance function selected according to response variable distribution) and a log-link function (Foster and Bravington, 2013). implemented in the *lme4* and *statmod* packages. Variation in breeding success between seasons was evaluated with X^2-tests.

Ethical Note

All penguin handling procedures were reviewed and approved by the Honorary Commission of Animal experimentation of Uruguay (CHEA protocol N° 1312). We were always careful to minimize the stress of the captured individuals by covering their eyes during handling and

ensuring that handling time was always less than 15 minutes. After the birds were released, we always made sure that they returned to their nests and attended to their chicks.

4.4 Results

Though breeding success did not differ significantly between the two seasons (Chi-square test: X2=0.11, df= 1, p=0.7), foraging behaviour of Adélie penguins varied substantially between breeding seasons (Table 1 and Fig. 1). The interaction between season and sex was not significant. We found significant differences between seasons, with longer foraging trips during 2021/22, in terms of duration (LMM: F= 22.40, p<0.001) and the maximum and total distance reached (LMM: F= 11.10, p<0.01; LMM: F= 17.08, p<0.001, respectively). In addition, we found differences between sexes, with female Adélie penguins making longer trips in terms of duration (LMM: F= 4.50, p<0.05). Maximum dive depth per trip was deeper in 2021/22 compared to 2019/20 (LMM: F= 6.89, p<0.05), and no differences were found between sexes (LMM: F=0.68, p=0.41). There were no significant differences between seasons and sexes for other dive parameters.

Table 1. Foraging and breeding performance of male and female Adélie penguins breeding in Ardley Island (King George Island/Isla 25 de Mayo) in 2019/20 and 2021/22 seasons. Values shown are the mean ± SD. The (*) indicates that there are significant differences between seasons and (**) indicates that there are significant differences between seasons and between sexes.

	2019-2020		**2021-2022**	
Breeding success (N° BP)	1.16 (303)		1.11 (202)	
Sex	Male	Female	Male	Female
N° Trips (N° birds)	52 (14)	12 (4)	32 (10)	20 (5)
Trip duration (h)**	8.91 ± 4.67	10.31 ± 5.03	14.98 ± 7.15	23.38 ± 14.61

Max. trip distance (km)*	6.55 ± 4.95	7.38 ± 7.70	11.72 ± 11.52	20.76 ± 17.78
Total trip distance (km)*	19.03 ± 11.12	20.91 ± 17.38	35.31 ± 25.72	56.03 ± 46.67
Max. dive depth per trip (m)*	73.96 ± 18.18	73.08 ± 9.44	89.05 ± 20.77	82.05 ± 18.25
Dive duration (s)	53.19 ± 39.56	52.87 ± 37.26	59.52 ± 49.51	52.13 ± 44.66
Dive depth (m)	18.21 ± 20.12	15.92 ± 17.15	20.18 ± 24.43	17.07 ± 20.87
Bottom time (s)	27.22 ± 19.98	30.42 ± 21.15	32.40 ± 25.97	27.98 ± 23.31
Adult body mass (kg)**	6.78 ± 0.62	5.74 ± 0.28	4.09 ± 0.20	3.56 ± 0.24

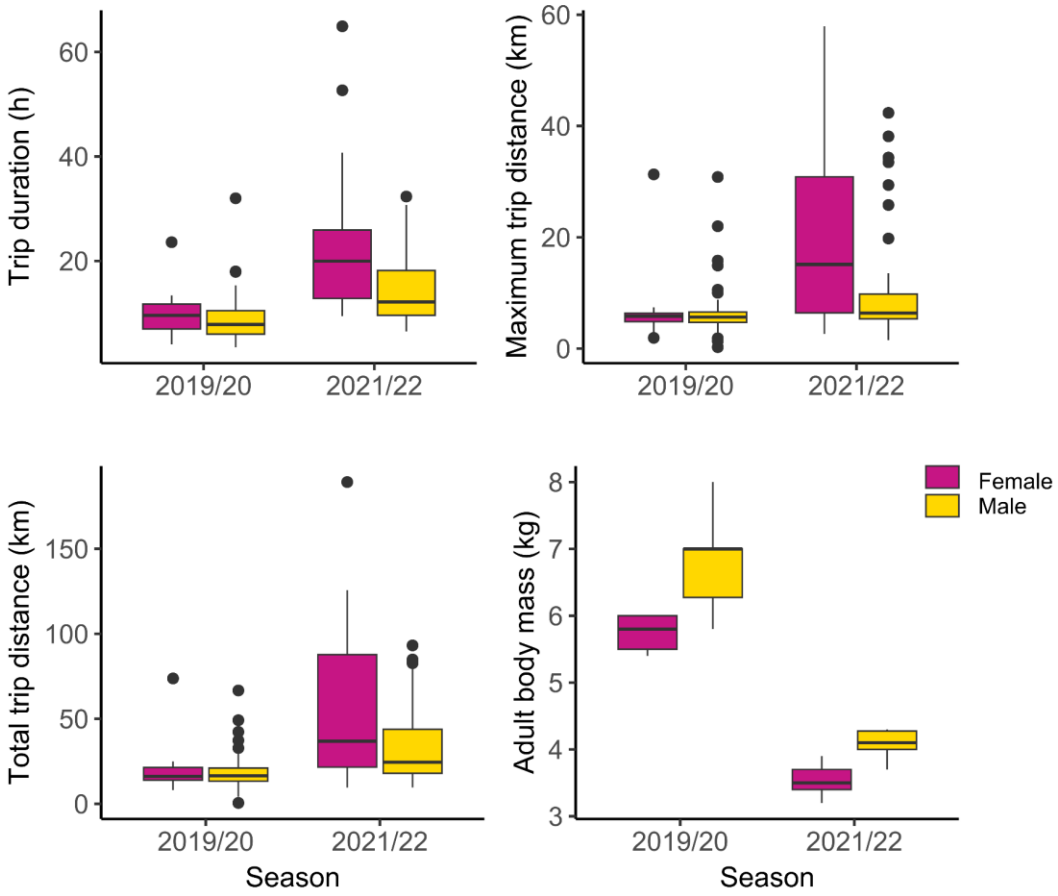

Figure 2. Foraging trip characteristics and adult body mass (kg) of male and female Adélie penguins breeding in Ardley Island (King George Island/Isla 25 de Mayo), during early guard phase in 2019/20 and 2021/22 seasons.

For the analyses of energy expenditure based on accelerometer records, the interaction between season and sex was significant (LM: $F_{1,40}$= 7.97, p<0.01, fig. 3). During the 2021/22 breeding season, both males and females incurred in higher DEE than in 2019/20 (Fig. 3). In particular, females showed 40% higher DEE values than females in 2019/20 season and males 16% higher values than in 2019/20. Furthermore, during 2021/22 females showed DEE values 20% higher than males in the same season. During 2019/20 the DEE did not differ between males and females.

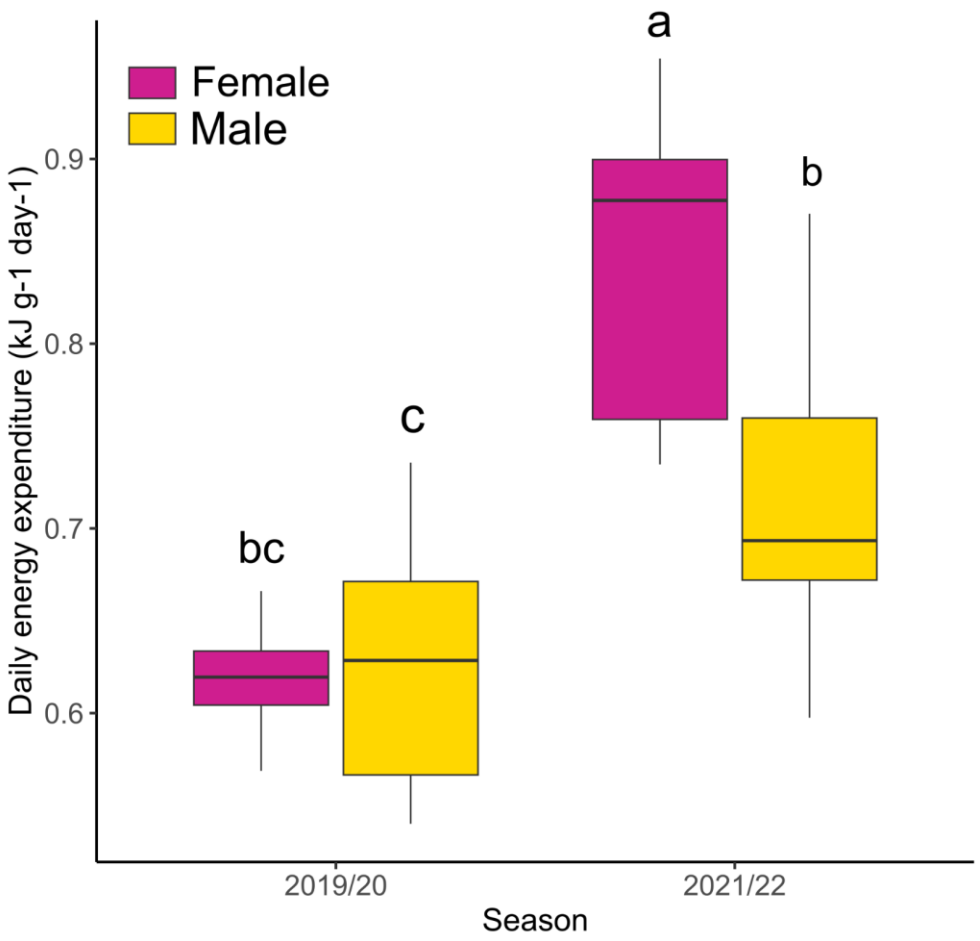

Figure 3. Daily energy expenditure (DEE; mean ± SD) of male and female Adélie penguins breeding at Ardley Island (King George Island/Isla 25 de Mayo), during the early guard stage of the 2019/20 and 2021/22 breeding seasons. Different letters indicate significant differences between groups.

The blood stable isotope values of Adélie penguins at Ardley Island significantly differ between seasons (Fig. 4; Table S2). During 2019/20, $\delta^{13}C$ values were significantly higher than in 2021/22 (LM: $F_{1,34}$= 20.71, p<0.0001), but we did not find significant differences in mean $\delta^{13}C$ values between sexes (LM: $F_{1,34}$= 2.55, p=0.12). For $\delta^{15}N$, we found significant differences between seasons (LM: $F_{1,35}$= 5.58, p<0.05) and sexes (LM: $F_{1,35}$= 24.19, p<0.0001). We found higher mean values during 2021/22 than in 2019/20 and higher values for males than females (Table S2). The mean $\delta^{13}C$ and $\delta^{15}N$ values for Antarctic krill were -25.21 ± 0.30 ‰ and 4.44 ± 0.22 ‰, respectively. Trophic position according to the model proposed by Post, (2002) was 2.28 ± 0.05 and 2.37 ± 0.07 for females in 2019/20 and 2021/22, respectively. For males, the trophic position was 2.44 ± 0.07 in 2019/20 and 2.47 ± 0.08 in 2021/22.

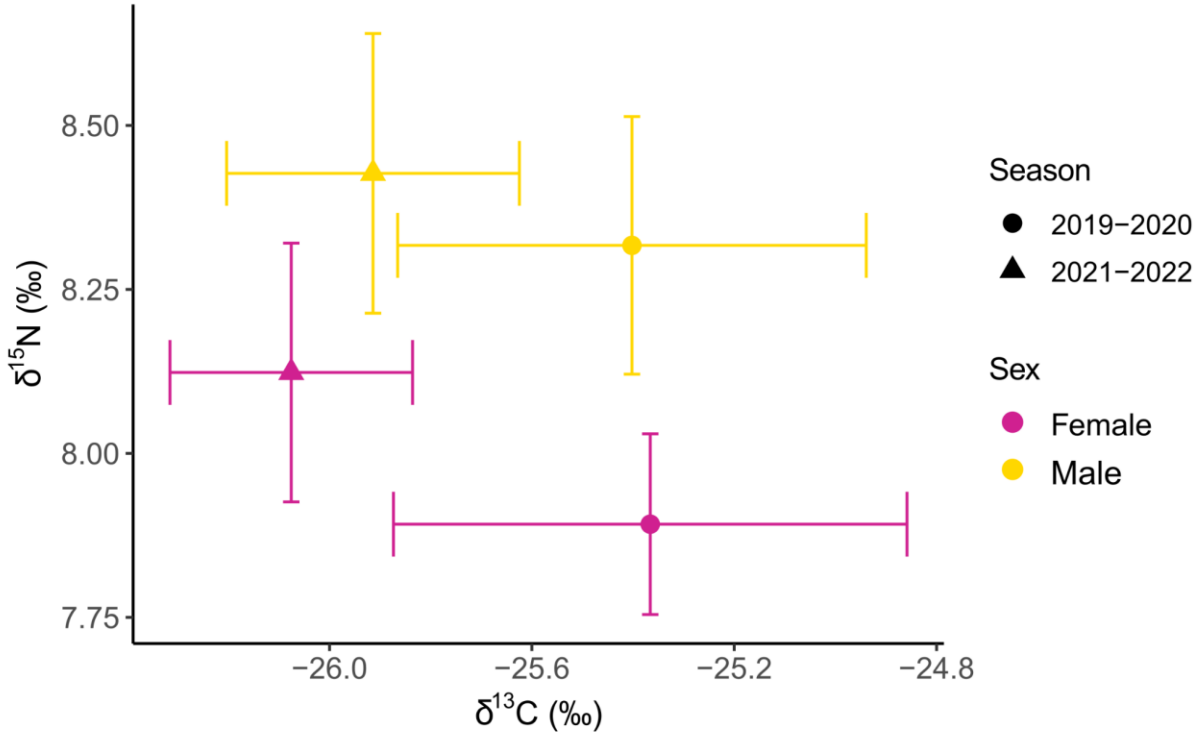

Fig. 4 Biplot of Isotopic $\delta^{13}C$ and $\delta^{15}N$ values (‰) of whole blood from male and female Adélie penguins breeding in Ardley Island (King George Island/Isla 25 de Mayo) in the early guard stage of the 2019/20 and 2021/22 breeding seasons.

Body condition parameters

Differences in adult body mass between seasons was statistically significant, being birds heavier in the 2019/20 season than in 2021/22 (LM: $F_{1,29}$= 256.20, p<0.0001), and males being heavier than females in both seasons (LM: $F_{1,35}$= 31.11, p<0.0001). Comparisons of the H/L ratios as a stress measures revealed no differences between sex during the same breeding season [season 2019/20 - females mean ± SD: 1.28 ± 0.97 (n = 4), males: 1.31 ± 0.94 (n = 13); Wilcoxon rank sum exact test: W = 125, p = 0.1048. Season 2021/22 - female: 1.23 ± 0.76 (n = 14), males: 0.93 ± 0.66 (n = 14); W = 0.213, p = 0.834]. There were no differences between the same sex in different seasons either [females: W = 23, p = 0.632; males: W = 32.5, p = 0.670]. Similarly, no significant differences were found in WBC in 10 optical fields between sexes within the same season [season 2019/20 – females: 29.25 ± 9.81, males: 37.00 ± 10.02; W = 11.5, p = 0.112. Season 2021/22 - female: 32.57 ± 25.57, males: 33.35 ± 12.67; W = 70.5, p = 0.213] and also between the same sex in different seasons [females: W = 32.5, p = 0.670; males: W = 124.5, p = 0.107] (Fig. S1).

4.5 Discussion

Our results support two of our hypotheses: 1) Adélie penguins modify their foraging behaviour and energy expenditure to account for differences in prey availability, and 2) there are differences between sexes on how they respond to differences in prey availability. During a breeding season with low food abundance, female Adélie penguins rearing chicks, extended both the distance and duration of their foraging trips, resulting in higher energy expenditure compared to males (yet, no sex-differences in diving behaviour were observed). Regarding our second hypothesis, we only found minor changes in trophic niche in response to differences in prey availability.

Sex-based differences in investment in foraging and breeding efforts are widespread in seabird species, related to divergent parental roles, foraging niche partitioning, sex-specific nutritional requirements or anatomy (e.g., body size). Several studies have shown these differences in different species, with females usually making a greater foraging effort during chick-rearing period (Lewis et al., 2002; Miller et al., 2017; Reyes-González et al., 2021; among others). In contrast, Raya-Rey et al. (2013) found an opposite pattern for two penguin species (*Spheniscus humboldti* and *S. magellanicus*), with males making longer foraging trips than females. For Adélie penguins, this sex-specific foraging behaviour has also been reported. In general, females forage longer distances and during more time, while males make shorter trips to closer foraging grounds throughout the guard period in East Antarctica (Clarke et al., 1998; Watanuki et al., 2002; Clarke et al., 2006; Widmann et al., 2015; Riaz et al., 2020), in the Ross Sea (Ballard et al., 2010; Lescroël et al., 2010; 2020) and in the Antarctic Peninsula (Chappell et al., 1993a). In the Ardley Island colony, we also showed that females made significantly longer trips in both breeding seasons. However, in a season with low food abundance, although both parents increased their foraging effort, the difference between males and females became more pronounced, and females made a higher foraging effort, with trips about 50% longer in duration and distance than males. This is consistent with other seabird species, with females showing a higher increase in foraging effort when food becomes scarce (Raya-Rey et al., 2012; Paiva et al., 2017; Reyes-González et al., 2021).

Food availability plays an important role in regulating adult energy expenditure in seabirds by directly affecting energy acquisition, foraging efficiency, and adult body condition (Jodice et

al., 2006). Theoretically, food availability may affect energy expenditure through two different processes: DEE may be forced to increase by low food supply (Kitaysky et al., 2000; Regular et al., 2014) or may increase by high levels of food availability (Jodice et al., 2006; Kahane-Rapport et al., 2022). Studies on energy expenditure associated with fluctuations in food availability in Adélie penguins are scarce, but they have reported that under conditions of low prey availability during breeding, they increase their energy expenditure associated with higher foraging effort (Nagy and Obst, 1992; Ballance et al., 2009). Our results are consistent with these observations, as we found that both males and females Adélie penguins increase their foraging effort and DEE in the season with low krill abundance. Furthermore, our results show that the energetic costs of foraging is approximately 20% higher for females than for males in the years of low krill abundance, with no differences between sexes in good years. We also show that females increase their energetic expenditure by about 40% in the year with poor foraging conditions. It is noteworthy that DEE values reported here are within the range of values reported by Hicks et al. (2020) for a colony near Dumont d'Urville station in East Antarctica, where environmental conditions differ significantly from those in Ardley Island (e.g., there is sea ice around the colony throughout the summer).

Different foraging strategies have been also related to body conditions of parents during the brooding stage. Some seabird species are known to adopt a bimodal foraging strategy, alternating between frequent and short trips for chick provisioning with long trips for self maintenance (Clarke, 2001; Ropert-Coudert et al., 2004; Welcker et al., 2009; Carpenter-Kling et al., 2017). To explain this, it has been suggested that long trips are triggered by a threshold in the body mass of the individuals, below which they decide to go on a long self-maintenance trip to restore body reserves, implying that foraging decisions result from a trade-off between the allocation of food to chicks and self-maintenance (Weimerskirch, 1998; Clarke, 2001). For seabirds foraging in areas of low productivity or prey availability, this threshold may be easier to reach (Carpenter-Kling et al., 2017). For Adélie penguins, Ballard et al. (2010) demonstrated that they start the breeding season with an energy cushion, which they subsequently lose as they raise their chicks, and observed that parents that had lost more than ~8% of their body mass made longer foraging trips, gaining mass for themselves while bringing their chicks less food. Our results are in line with these findings, although we did not specifically analyse this alternating bimodal strategy of long and short trips. We observed that during a season with

prey scarcity and longer foraging trips, the body mass of Adélie penguins was about 40% lower compared to that in a good year. Also, these longer trips have a cost for the offspring and ultimately on breeding success (Ballance, 2009; Ballard et al., 2010; Salmerón et al., 2023). Yet, we found no differences in breeding success between seasons, suggesting that despite the decrease in prey abundance Adélie penguins were able to rear their chicks successfully. However, we did not measure the body mass of fledglings during these seasons. Hence, we do not know if the increased foraging effort of the adults affected the body condition of the chicks, as was reported for other colonies (Cimino et al., 2014; Ainley et al., 2018).

Considering the H/L ratios and WBC as estimates of immune system and body conditions, we found no differences between sexes or breeding seasons. Several studies indicate that the H/L ratio rises in response to increased breeding efforts (Davis et al., 2008), but, although we observed a higher foraging effort in females during 2021/22, we cannot assume that this sex difference is due to a poorer physiological condition associated with higher reproductive costs for females, as proposed by Colominas-Ciuró et al. (2017). These H/L ratios were similar to another colony in the Antarctic Peninsula (Colominas-Ciuró et al. 2017), but lower than in a colony in the Ross Sea (Olmastroni et al., 2019),which could suggest a higher breeding effort in this area compared to the study area. In general, similar WBC levels were previously reported for other Adélie colonies in the Antarctic Peninsula and Ross Sea (Olmastroni et al., 2019, 2024; Menéndez-Blázquez et al., 2021).

Lower $\delta^{13}C$ values typically indicate offshore/pelagic foraging habitats (Cherel and Hobson, 2007). As expected, $\delta^{13}C$ values during the 2021/22 season were lower compared to 2019/20, reflecting the increased distance of foraging trips. However, we did not find significant differences between sexes, also reflecting what was observed in the tracking data, with both foraging in more coastal areas during 2019/20 and more offshore/pelagic in 2021/22. Sex-specific foraging strategies have also been linked to differences in diet, which might facilitate sexual segregation particularly when resources are limited (Clarke, 2001; Tierney et al., 2009; Widmann et al., 2015; Massaro et al., 2020). For Adélie penguins in East Antarctica and Antarctic Peninsula it has been proposed that females tend to consume larger quantities of krill and males consume more fish (Clarke et al., 1998; Beaulieu et al., 2010; Colominas-Ciuró et al., 2018). Colominas-Ciuró et al. (2018) proposed that given the higher reproductive costs

incurred by females, observed in lower antioxidant capacity and higher oxidative damage and stress (Colominas-Ciuró et al., 2017), higher krill consumption allows them to recover to some extent from this reproductive effort, since krill has a higher antioxidant content than fish and is a rich source of high quality protein and omega-3 fatty acids (Beaulieu et al., 2010). According to our results, the diet was dominated by Antarctic krill in both sexes, however, males showed slightly higher $\delta^{15}N$ values than females in both seasons, suggesting that they might have incorporated a larger proportion of higher trophic level prey. Furthermore, we also found that both sexes showed slightly higher $\delta^{15}N$ values in 2021/22 than in 2019/20, which suggest that both sexes might have had slightly higher levels of supplementation by secondary prey items (e.g., fish, squid) to compensate for low krill abundance. Prey switching during poor seasons was previously reported by Nicol et al. (2008), who found that the diet of Adélie penguins in the Mawson region consisted about 50% of fish during a season with low krill availability. However, we observed that there were no remarkable changes in trophic position in both sexes or between years (2019/20: 2.44 ± 0.07 and 2.28 ± 0.05; 2021/22: 2.37 ± 0.07 and 2.47 ± 0.08, males and females, respectively), indicating that, even under conditions of low krill abundance, they did not substantially modify their trophic niche. Although it had been proposed that fish consumed by Adélie penguins (*P. antarcticum, Electrona antarctica*) have a higher calorific content compared to krill (Ainley et al., 2003) the fact that these components were low in the diet when krill were scarce suggests that prey switching was not possible, probably due to scarcity of other prey options.

Here we deepen current understanding on how Adélie penguins respond to mismatches with their main prey during the breeding season. We have shown that under low krill abundance conditions, female Adélie penguins incur a higher energy expenditure than males. This sex-based variability in foraging effort could have implications for the effect that environmental or fisheries impacts have at different times on different components of the population and, consequently, may require management plans that incorporate these differences. This is particularly relevant in the northern WAP, considering the ongoing discussions on small-scale management of krill fisheries in the region, which concentrate more than 30% of the total krill catch in Antarctica (CCAMLR, 2024). Understanding the sex-specific responses to changes in prey availability and the identification of key foraging areas, as predictable areas of food availability at times of high energy demand (Cresswell et al., 2007; Machado-Gaye et al., 2024)

is essential for the design of appropriate conservation measures in a region undergoing significant changes. In addition, it may be relevant to understand how these effects propagate beyond the breeding season. Morandini et al. (2024) reported reduced survival of females once birds become breeders in the Ross Sea, and Hinke et al. (2007) found that for Adélie penguins in the WAP, the spatio-temporal reduction in sea ice during winter negatively impacts juvenile and adult survival. Therefore, the poorer body condition and higher energy expenditure of females during the breeding season may render them more vulnerable than males to changes in food availability, affecting their survival during winter, as they start this challenging stage of their annual cycle with less body reserves. Birds that finish breeding in poor condition may be less likely to successfully complete the molt or may finish molting with low energy reserves (Chappell et al., 1993b), hence impacting on wintering survival or in body conditions and the onset of the next breeding season, with negative effects on population trends.

Overall, the study of the processes underlying Adélie penguin population declines in the WAP provide valuable insights on some of the potentially diverse and subtle factors affecting populations persistence under climate-change scenarios, and the role of behavioural flexibility in buffering some of the impacts of these changes. In the specific case of Adélie penguins breeding in Ardley Island, observed population trends are likely consequence of a range of ecological process acting at different spatial and temporal scales. For example, the marked decline in breeding pairs between 2019/20 and 2021/22 might be linked to unusually harsh breeding conditions during 2020/21 (Machado-Gaye, pers. comm.). Although the breeding success or body condition of the fledglings has no effect on the breeding population size in the following season, since juveniles recruit as breeding adults 3-4 years later (Ainley and Schlatter, 1972), poor conditions during the season may have an effect on the number of breeding pairs that attempt to reproduce in the following year. Factors operating on the overwintering survival of breeding adults cannot be ignored either. This might be linked to the poor body condition in which they finish the breeding season, as we suggest here, but also to adverse conditions during the non-breeding season, miles away from the breeding grounds. Despite no evident effects on breeding success, low krill availability might have subtle effects on adult survival that are difficult to properly assess. Although not decisive on their own, these effects might contribute to an accumulation of subtle impacts that taken together can have a

significant impact on the fate of these populations, highlighting the importance of implementing efforts aimed at minimizing any manageable impact (e.g., fisheries). Also, the need for holistic approaches when planning the management of marine living resources in the Southern Ocean (Zaldúa et al., 2024).

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CAPÍTULO 5

Bout time for krill- contrasting Adélie penguin foraging behaviour during years of high and low krill availability

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5. Bout time for krill - contrasting Adélie penguin foraging behaviour during years of high and low krill availability

5.1 Abstract

Understanding how marine predators structure and adjust their foraging in response to prey field characteristics is a longstanding objective in marine ecology. This is particularly challenging in Southern Ocean ecosystems, where logistical and financial constraints hinder assessment of predator foraging and prey field information at relevant spatial and temporal scales. Here, we examine how Adélie penguins, *Pygoscelis adeliae*, a key Southern Ocean indicator species, perform and organize their foraging behaviour during two contrasting years of krill (*Euphausia superba*) abundance. Using multiyear krill acoustic data from King George Island in the West Antarctic Peninsula (WAP), we assess broad seasonal conditions in krill availability. We also analyse a suite of penguin biologging data (spatial location, dive and accelerometry-derived activities) during the same period to identify broad behavioural differences in their bout-diving activity, a classical measure of the temporal organization of foraging in diving predators. During years of high krill abundance and availability, penguins performed shorter dive bouts (consisting of shallower and shorter-duration dives), which were more concentrated in time and space. Despite these differences in bout structure, prey capture attempts occurred at the same rate within bouts. These findings challenge traditional interpretations assuming that increased bout durations (and related proxies of prey capture effort) signal increased krill patch abundance and profitability. Although additional data are required to understand the full scope of penguin bout diving and krill prey field associations, our work improves understanding of penguin behavioural variation and provides insights into how foraging behaviours could potentially be used to interpret krill availability at predator- and management-relevant scales.

Keywords: bout, dive, foraging, krill, penguin

5.2 Introduction

Ecosystem sentinels are species that respond rapidly to environmental fluctuations, providing insights into ecosystem status and environmental change (Hazen et al., 2019). Knowledge of how predator sentinel species structure and adjust their foraging in response to prey field characteristics can yield critical information regarding the balance and health of ecological communities (Clark-Wolf et al., 2024). However, these insights are challenging to obtain in marine ecosystems, where predator–prey interactions occur in a dynamic three-dimensional environment. In these systems, prey resources are often patchily and hierarchically distributed, with high-density prey patches nested within larger-scale low-density patches (Benoit-Bird et al., 2013; Carroll et al., 2018; Fauchald et al., 2000; Watanabe et al., 2014). In response to prey field heterogeneity, marine predators must adapt their foraging behaviours and strategies to ensure adequate rates of prey encounter and consumption (Chimienti et al., 2017; Guinet et al., 2001; Sommerfeld et al., 2015; Weimerskirch et al., 2005).

For diving seabirds and marine mammals, foraging activity is constrained by the need to regularly return to the surface to replenish oxygen stores. Individual dives can be reflective of short-term and fine-scale prey availability, whereas larger-scale prey patches are exploited through diving bouts, consisting of distinct and rapid sequences of multiple dives (Austin et al., 2006; Foo et al., 2016; Ramasco et al., 2014; Watanabe et al., 2014). Aggregating and adapting dive-scale effort into dive bouts may be a mechanism in which marine predators maximize prey encounter rates and energy acquisition, while minimizing energy loss associated with finding forage opportunities (Mori & Boyd, 2004; Ramasco et al., 2014; Stephens & Charnov, 1982). However, understanding these complex and scale-dependent predator–prey interactions is generally hampered by difficulties in obtaining and linking predator foraging and prey field information at relevant spatial and temporal scales (Benoit-Bird et al., 2013).

Adélie penguins, *Pygoscelis adeliae*, are a key indicator species under the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) Ecosystem Monitoring Program (CEMP). This programme seeks to monitor predator parameters that can signal fluctuations in the

availability of Antarctic krill, *Euphausia superba* (hereafter 'krill'), which dominate many Southern Ocean ecosystems and energy pathways (Agnew, 1997). Adélie penguin movement and dietary data collection has therefore been a central theme in Antarctic research (Ratcliffe & Trathan, 2012). Their foraging ecology has been extensively investigated, including diet composition (e.g. Ainley, 2002; Cherel, 2008; Juáres et al., 2018), spatiotemporal distribution (e.g. Clarke et al., 2006; Widmann et al., 2015) and diving behaviour (e.g. Le Guen et al., 2018; Lescroël et al., 2020; Watanuki et al., 1993) and how these foraging components relate to marine environmental conditions (e.g. Ainley et al., 1998; Emmerson et al., 2015; Nicol et al., 2008; Watanabe et al., 2020). Yet, there remains a limited understanding of how Adélie penguins structure and adjust these foraging components in response to prey field characteristics and variability (i.e. periods of high and low krill availability) (Ainley et al., 2015; Ford et al., 2015; Lescroël et al., 2021; Riaz et al., 2023).

In the horizontal dimension, extended Adélie penguin foraging trips during the breeding period have been shown to indicate low krill availability and foraging success (Machado-Gaye et al., 2024; Nicol et al., 2008). In the vertical dimension, where foraging actually occurs, bout-diving organization is expected to reflect krill patch availability (Watanabe et al., 2014). However, the functional relationship between diving bouts and krill availability is not well resolved. Distance and duration of the interbout period (i.e. between-bout metrics) have been linked to patch level encounter rates and availability (Watanabe et al., 2014). The number of dives performed in a bout and bout duration (i.e. within-bout metrics) are also assumed to indicate prey patch size and profitability (Boyd, 1996; Le Guen, 2018; Lescroël et al., 2021). These inferences follow the assumption that each bout corresponds to foraging in a single prey patch (Dunn et al., 2024; Foo et al., 2016; Mori & Boyd, 2004), and animals should maximize time spent in patches of high energetic gain (Stephens & Charnov, 1982). But few studies have quantitatively assessed how these bout diving dynamics vary with direct measurements of prey field conditions (Watanabe et al., 2014), limiting our understanding of how bout activity should be interpreted in the context of krill availability.

In the West Antarctic Peninsula (WAP), Adélie penguin populations predominantly feed on

Antarctic krill during the breeding season (Herman et al., 2017; Juáres et al., 2018; Negrete et al., 2017; Pickett et al., 2018). Broad-scale changes in the biomass of Antarctic krill (Forcada et al., 2006; Trivelpiece et al., 2011) has coincided with significant (~50%) Adélie penguin population declines across the region, highlighting the need for an improved understanding of penguin–krill relationships. At Nelson Island, located in the WAP, Salmerón et al. (2023) conducted local-scale krill acoustic surveys in the austral summer of 2019/2020 and 2021/2022, reporting markedly different krill biomass between years, characterized as relatively high and low krill abundance, respectively. Coupling survey-scale krill biomass estimates with demographic and biologging data (spatial location and dive) from a local chinstrap penguin, *Pygoscelis antarcticus*, colony, they found individuals increased their foraging effort (i.e. trip distance and duration) in the year of low krill abundance and also had a lower breeding success. During the same 2-year period, Adélie penguin monitoring efforts were coincidentally being conducted at the adjacent King George Island (Machado-Gaye et al., 2024, 2025). Interannual comparison of these data similarly demonstrated chick-rearing Adélie penguins performed more extensive foraging trips (distance and duration) and increased time allocation within a dive (interpreted as a measure of vertical foraging effort) during the low krill abundance year, although no significant differences in breeding success were observed. With these predator biologging and prey acoustic data sets, there is a unique and valuable opportunity to improve our understanding of bout-diving activity, a fundamental component of penguin foraging behaviour and penguin–krill dynamics.

In this study, we capitalize on a rare and valuable research opportunity to examine how Adélie penguins perform and structure their bout dive behaviour during 2 years where there were contrasting conditions of krill abundance and availability (considering distance to the colony and/or swarm depth). We expand upon the survey-scale krill biomass findings reported in Salmerón et al. (2023), examining the spatial characteristics of krill swarm abundance during 2019/2020 and 2021/2022 at a scale more relevant to the penguin populations at King George Island. We then separately examine yearly and spatial differences in how penguins organize their foraging activity into dive bouts using a suite of biologging data (spatial location, dive and accelerometry) collected in the same area and over the same chick-rearing period. We expected

that penguins would show markedly different bout-diving dynamics between the two years, with differences linked to prey abundance and availability. Specifically, in response to high krill abundance and availability, we expected (1) shorter distance and duration (i.e. interbout period) between bouts, indicative of increased krill availability/prey patch encounters, and (2) increased duration and number of prey capture attempts (derived from accelerometers) within bouts to maximize patch-scale prey intake.

Through this work, we aim to develop a broad-scale understanding of penguin bout-diving dynamics and how krill availability could potentially be signalled through the patch-scale foraging behaviour of this important indicator species.

5.3 Methods

Krill Data: Acoustic Surveys and Processing

Acoustic surveys were carried out in the waters adjacent to King George Island/Isla 25 de Mayo, South Shetland Islands, on the Chilean Antarctic Institute research vessel *RS Karpuj* during the austral summer of 2019/2020 (27–30 December) and 2021/2022 (5–6 January) (Fig. 1, Supplementary Fig. S1). This region is ice-free during the summer period. The full acoustic surveys in 2019/2020 and 2021/2022 spanned approximately 1560 km and 264 km, respectively. In this study, we use a spatial subset (387 km) of the 2019/2020 acoustic data to more accurately represent the spatial distribution of chick-rearing Adélie penguins at our King George Island study site (see Fig. 1, Supplementary Fig. S1 and Penguin Data: Study Site, Tagging Procedure and Movement Analyses below).

Acoustic data were recorded using a SIMRAD EK60 multifrequency echo-sounder equipped with 38, 120 and 200 kHz split-beam transducers. Data collection range was set from 5 to 500 m depth and recorded only during daylight hours. Full details of acoustic calibration and data collection are provided in Salmerón et al. (2023), using the same acoustic data collected in 2019/2020 and 2021/2022, albeit with a slightly different spatial subset to what is presented here to better reflect the distribution of their chinstrap penguin data set.

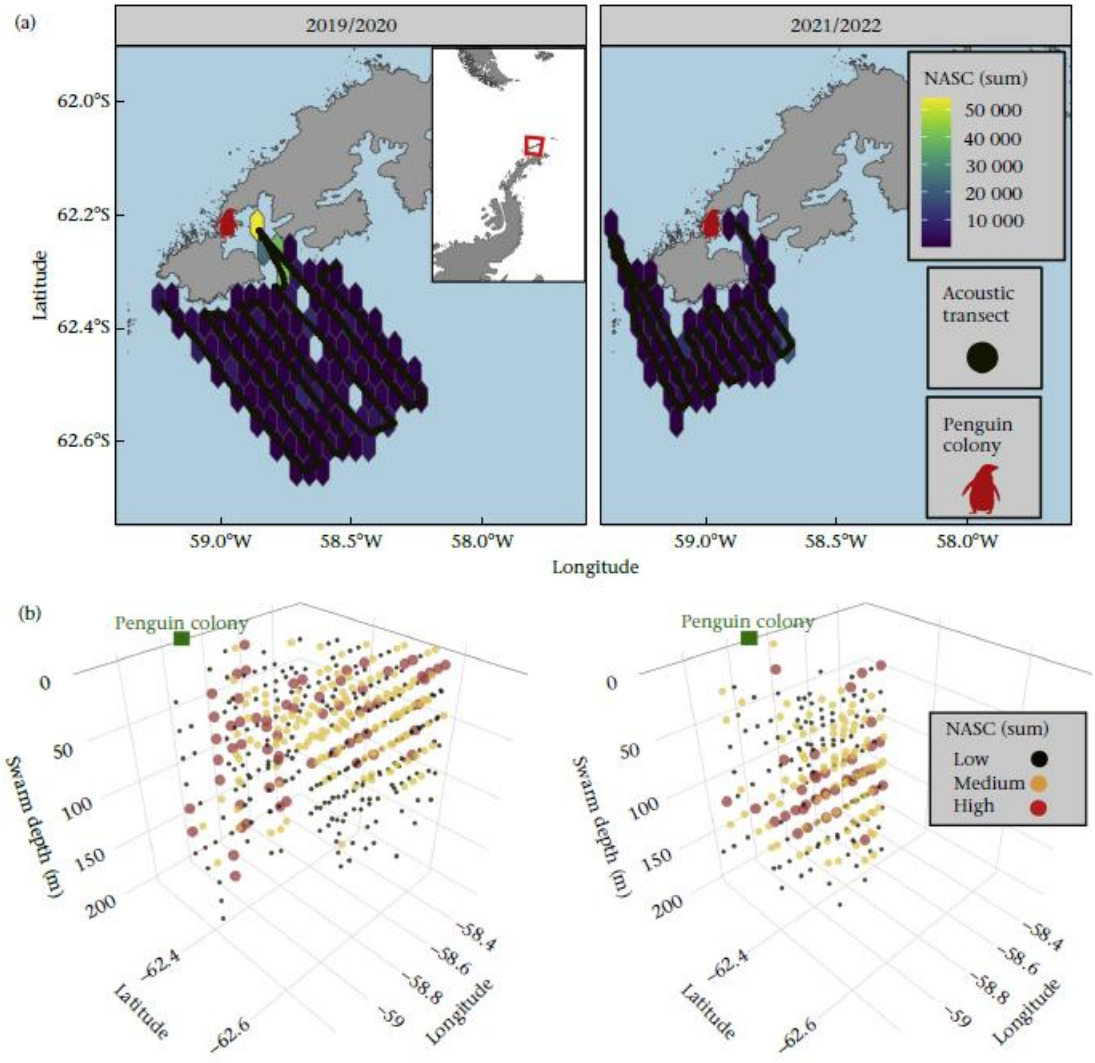

Figure 1. Spatial distribution of krill acoustic transects and the nautical area scattering coefficient (NASC; m^2/nautical $miles^2$), summarized (a) in the horizontal dimension at a 0.05 × 0.05° resolution and (b) in the horizontal and vertical (depth) dimensions. To aid visual presentation in (b), NASC is summarized in 20 m depth bins and grouped into three categories based on quantiles: low (<0.50); medium (>0.50 and <0.85); high (>0.85). Inset panel of the broader study region is displayed in the corner of the first facet in (a), with the red box displaying the King George Island study site.

Acoustic records were postprocessed using Echoview 9.1 (Echoview Software, Battery Point, Australia). A semi-automatic user-independent algorithm was used to remove electrical

interference, mechanical noise, bubble-attenuated pings and double-bottom echoes (Alegría et al., 2017). Acoustic records within the transducer near-field were also removed to avoid ringdown effect produced by vibrations (Riquelme-Bugueño et al., 2020). From cleaned echograms, Antarctic krill swarms were identified and selected following the CCAMLR methodology for the identification and integration of krill swarms (SG-ASAM-17). Acoustic information was echo-integrated into basic sampling units (BSUs) of 0.5 m by 5 m depth, then converted to a nautical area scattering coefficient (NASC, m^2/nautical $miles^2$), a widely used proxy of potential krill abundance in the water column (Klevjer et al., 2010; Riquelme-Bugueño et al., 2020).

Penguin Data: Study Site, Tagging Procedure and Movement Analyses

Adélie penguin tagging efforts were conducted at the Ardley Island colony (62°13'S, 58°56'W), an Antarctic Specially Protected Area (ASPA), located in the southwest of King George Island during the early guard stage of the 2019/2020 and 2021/2022 breeding seasons. A total of 46 adult Adélie penguins (19 in 2019/2020; 27 in 2021/2022) were equipped with data loggers (Axy-Trek, 70 × 40 × 15 mm, 69 g; TechnoSmart, Colleverde, Italy) including GPS, accelerometer and both pressure and temperature sensors. Full details of animal handling and tag deployment procedures are provided in Machado-Gaye et al. (2024) and the Supplementary Material.

From 46 deployments, we obtained 41 complete sets of GPS and dive data, comprising location, time and dive depth, which we used in the following analyses. In the remaining five cases, some loggers failed, while others recorded incomplete trips with very few locations, preventing their use in the analysis. GPS data were cleaned and quality-controlled using R software (version 4.1.3; R Core Team, 2022). In brief, excessive location fixes recorded before departure and after arrival at the colony were manually removed. A speed filter set to 7 km/h was also applied to remove unrealistic travel rates. Foraging trips were defined from the time the birds moved more than 50 m from the colony to the sea until the time they were within 50 m of the colony again. Dives were analysed using the software Igor Pro Version 6.37 (Wavemetrics, https://www.wavemetrics.com/). Only dives >2 m were included due to possible measurement error in instruments and surface waves. Technical details of GPS and dive data processing are also

provided in Machado-Gaye et al. (2024) and the Supplementary Material. All subsequent analyses were performed using R statistical software. Dive data were matched with GPS locations, using date and time information. In brief, we allocated a location to each dive by linearly interpolating the time stamp at the beginning of each dive event with the closest GPS locations recorded before and after the dive.

To detect foraging dives, we used the approach developed by Chimienti et al. (2016, 2022). This method characterizes latent behaviours from accelerometry data to determine when penguins were performing prey capture attempts (PCAs); using the expectation maximization unsupervised machine-learning algorithm to find maximum likelihood solutions for mixture models with latent variables. Accelerometer records were subsampled at 25 Hz. As the depth data used to describe the dive profiles were recorded every 1 s, we classified each depth record as corresponding to either a capture attempt or not, based on whether more than 50% of the accelerometer records within that second were classified as chasing/catching events by the model. Chasing/catching events are defined as the period during which an individual displays sharp body movements and high acceleration, indicative of targeted prey pursuit. While there is currently no validation for foraging success in this data set, similar accelerometer-derived signals were associated with prey capture events in Magellanic penguins, *Spheniscus magellanicus* (Del Caño et al., 2021). Our modelling approach produced a numerical value for each dive corresponding to the total duration (s) of prey capture attempts recorded. Foraging dives were then defined as any dive where at least 5 s of the dive cycle were classified as capture attempts. Technical details of this method are provided elsewhere (see Chimienti et al., 2022; Machado-Gaye et al., 2024).

Bouts are defined as periods of high-intensity and sustained dive effort with relatively short postdive/surface rest intervals (Luque et al., 2008). In this study, we classified bouts using only foraging dives. This provides an opportunity to infer krill availability (e.g. spatial structure and distribution) from penguin foraging behaviour. Across all individuals, we classified foraging dives into foraging bout activity using the 'segmented' package (Muggeo, 2017). This approach uses a log survivorship analysis to quantify a BEC, clustering all foraging dives performed within a given postdive interval as a single bout (Sibly et al., 1990). Because nonforaging dives were excluded

from our analysis, we refer to postdive intervals as the period between foraging dives. To summarize our BEC approach, the relationship between the cumulative frequency of postdive intervals were plotted on a logarithmic scale in relation to postdive intervals on a natural scale. Two breakpoints in the log survivorship curve were then identified at 40 s and 90 s. Consistent with other seabird bout studies, we identified the second breakpoint (90 s) to likely indicate the end of an intensive diving period, with the first breakpoint likely representing brief periods of recovery between dives (Le Guen et al., 2018; Dunn et al., 2024). Using this 90 s BEC threshold applied across all individuals, dives were then grouped into dive bouts (refer to Fig. 2 for an example). Only bouts consisting of three or more dives were considered as valid bout events (Kato et al., 1991; Viviant et al., 2014). To validate our chosen BEC approaof threepared our BEC value with three different bout-analysis techniques commonly used and executed using the 'divemove' package (Luque 2007). In brief, this included fitting nonlinear least squares regression and maximum likelihood models to postdive interval data (refer to the Supplementary Material for details). The broad consistency between all population level BEC values across the different approaches provided us with confidence in our quantitative BEC threshold (refer to the Supplementary Material for details).

With all foraging dives clustered into foraging dive bouts, we calculated a range of metrics reflective of patch-scale foraging activity. These metrics were examined at the between-bout and within-bout scale. Between-bout metrics examined were (1) interbout duration (min) and (2) interbout distance (km); and within-bout metrics included (3) bout duration (min), (4) mean maximum dive depth (m) and (5) PCA rate, calculated as total PCAs per bout divided by bout duration (PCAs/min).

Statistical Analyses

Given the slight temporal mismatch (1–2 weeks) in predator–prey data streams for both years (Supplementary Fig. S1), we did not attempt to statistically link penguin foraging and krill acoustic measures. Instead, we examined these data separately and made broad temporal and spatial associations between krill swarm dynamics and penguin bout parameters. By doing so, we

assumed that the snapshot of krill abundance provided by the surveys were representative of local-scale prey field characteristics through the duration of the Adélie penguin tracking period (Supplementary Fig. S1) (e.g. Nicol et al., 2008; Riaz et al., 2023). Similarly, we also assumed that the penguin tracking data recorded during both years were broadly representative of foraging behaviour over the early guard period (Supplementary Fig. S1).

To characterize spatial differences in the krill prey field between the 2 years, we fitted a generalized additive model (GAM), examining how NASC (response variable) varied in relation to distance from the Adélie penguin breeding colony (km). In this model, sampling year (2019/2020 and 2021/2022) was configured as a factor smooth term ('mgcv' package; Wood, 2023) and fitted with a thin plate smoothing spline. To optimize model fit and comparison between the 2 years, we truncated acoustic data exceeding 38 km distance from the colony in 2019/2020, which was the maximum distance from the colony for which data were recorded in 2021/2022.

We then separately examined how Adélie penguins structured their bout level dive behaviour within these two periods to infer how foraging dive bouts are performed in relation to the contrasting patterns in krill abundance and availability. To do this, we fitted a range of generalized linear mixed effects models (GLMM). For each of the five bout level diving response variables (two between-bout and three within-bout metrics), we fitted independent GLMMs with year (2019/2020 and 2021/2022) configured as a categorical predictor variable ('glmmTMB' package; Brooks et al., 2017). Each GLMM was also configured with penguin identity (ID) as a random effect to allow relationships to vary among individuals.

To better understand spatial dynamics in bout activity, we also fitted a generalized additive mixed model (GAMM) ('mgcv' package) examining interbout duration as a function of distance from the colony. This GAMM framework included a thin plate smoothing spline and penguin ID as a random effect. Similar to our krill prey field GAM, we optimized the model smooth and statistical comparison between years by examining bout records at an equal spatial distribution. This meant that bout records exceeding 31 km distance from the colony in 2021/2022 (i.e. the maximum distance recorded in 2019/2020) were truncated.

All penguin bout models (except bout duration and interbout duration) were considered to have serial nonindependence within the time series and were therefore configured with an Ornstein–Uhlenbeck (ou) covariance structure (i.e. temporal autocorrelation parameter). All krill and penguin models were either fitted with a Gaussian or gamma distribution (refer to Supplementary Tables S1–S3). All model covariates were considered significant at $P < 0.05$.

Ethical Note

All penguin handling procedures were reviewed and approved by the Honorary Commission of Animal Experimentation of Uruguay (CHEA protocol number 1312). To tag chick-rearing adult penguins, we randomly selected only one member of the adult pair in nests that had two chicks present. Individuals were primarily caught by hand, with the occasional aid of a long-handled net. During adult handling, we also captured chicks to protect them from predators. We took care to minimize stress to the captured adults by covering the head during handling and ensuring that handling time was always below 20 min. The devices were attached to the birds' lower back feathers using black Tesa4651 tape. The devices represented approximately 1% of the body mass of an adult Adélie penguin (mean for birds in this study 4954 ± 1377 g). After release, we carefully observed the birds to confirm they returned to their nests and continued attending to their chicks. To recover the devices, individuals were recaptured in the nest after 3–7 days.

5.4 Results

Krill Prey Field Characteristics

Between the 2 years, acoustic surveys showed contrasting conditions of krill abundance (Figs 1, 3, Supplementary Table S1). During 2019/2020 and 2021/2022, a total of 311 672 and 111 602 NASC (m^2/nautical $miles^2$) were recorded during acoustic transects spanning a maximum of 51 km and 38 km away from the Adélie penguin colony at King George Island, respectively. Over an equal spatial extent (38 km from the penguin colony), the 2019/2020 year recorded 264 569 NASC; 58% more than the NASC recorded in 2021/2022. Across both sampling years, krill swarms were recorded throughout the survey area and detected at broadly similar depth ranges (5–210

m and 5–170 m in 2019/2020 and 2021/2022, respectively) (Fig. 1).

Our GAM results showed there was a significant relationship between krill NASC and distance from the Adélie penguin colony at King George Island in 2019/2020 ($F_{13.78}$= 47.76, P < 0.001; Fig. 3, Supplementary Table S1). During this year, krill abundance was particularly pronounced within the first 15 km from the colony (53% of the total survey NASC). However, the largest krill swarms were concentrated in waters immediately adjacent to the penguin colony (<5 km), accounting for 16% of the total survey NASC. At distances greater than 15 km, krill NASC was reduced and more uniform across the survey area (Figs 1, 3).

In contrast, krill aggregations in 2021/2022 had substantially lower NASC values, which were also more evenly distributed across the survey area (Figs 1, 3, Supplementary Table S1). During this year, there was no relationship between krill NASC and distance to colony ($F_{2.56}$ = 0.84, P = 0.36; Fig. 3, Supplementary Table S1). Krill aggregations in 2021/2022 were more patchily distributed across the survey area, particularly 8–18 km from the penguin colony, where relatively low NASC values were recorded (Figs 1 and 3).

Penguin Foraging Characteristics

Our penguin dive data set comprised 69 363 dives across 41 individuals (N = 19 and N = 22 in 2019/2020 and 2021/2022, respectively). Of these dives, 27 909 (40%) were considered as foraging dives. There were 2079 bouts recorded across all individuals, which comprised 23 912 foraging dives. The proportion of foraging dives structured in foraging bouts ranged from 45% to 99% across individuals, averaging 85% in both years.

In 2019/2020, individuals performed bouts at a maximum of 31 km away from the colony (based on the start location of bouts) (Fig. 4, Supplementary Figs S1 and S3). The vast majority of these bouts (92%) were performed within the first 10 km from the colony. In contrast, penguin bouts in 2021/2022 were spread out over a greater area. Bouts were performed at a maximum distance of 61 km away from the colony, almost double the maximum distance observed in 2019/2020 (Fig. 4, Supplementary Figs S1 and S3). Approximately half of all bouts (49%) were performed

within the first 10 km of the colony, after which, bouts became more evenly dispersed over the length of the spatial distribution (Supplementary Fig. S3).

Penguin foraging bout metrics showed different within- and between-bout patterns between the 2 years. In 2019/2020, penguins exhibited shorter mean interbout durations and distances compared to 2021/2022. The interbout models estimated mean interbout durations of 22 min (95% CI: 19.8–24.6) and interbout distances of 0.9 km (95% CI: 0.7–1.1) in 2019/2020, whereas in 2021/2022, interbout durations increased to 26 min (95% CI: 23.5–28.7) and interbout distances to 1.3 km (95% CI: 1.1–1.6) (Fig. 5, Supplementary Table S2). Within-bout model results indicated that, in 2019/2020, dives were generally shallower in depth and shorter in duration, averaging 33.4 m (95% CI: 30.3–36.5) and 14.5 min (95% CI: 13.0–16.3). In contrast, dives in 2021/2022 averaged 38.9 m (95% CI: 36.7–41.0) and 18.3 min (95% CI: 16.4–20.7). However, there was no significant difference in PCA rates between the 2 years (Fig. 5, Supplementary Table S2). Our GAMM showed interannual differences in the spatial distribution of interbout durations (Fig. 5, Supplementary Table S3). In 2019/2020, interbout durations were notably shorter within ~10–25 km of the colony ($F_{3.68}$ = 2.86, P < 0.05). In contrast, during 2021/2022, there were no statistical differences in the spatial distribution of interbout durations ($F_{3.65}$ = 1.47, P = 0.26; Fig. 5, Supplementary Table S2).

5.5 Discussion

In this study, we couple 2 years of krill acoustic survey records with Adélie penguin spatial location, dive and accelerometry (i.e. prey capture) data to broadly assess how foraging activity is organized within dive bouts during krill-rich and krill-poor conditions. Our findings show that when krill abundance and availability were high, individuals performed shorter-duration feeding bouts, which were more concentrated in time and space. Despite these structural differences in how dive bouts were organized, the rate of prey capture attempts did not vary with krill conditions. Our findings reiterate the complexity of marine predator patch-scale foraging dynamics and challenge traditional interpretations of bout-diving metrics, which often assume that increased bout effort and structure (i.e. bout duration and number of dives) reflect increased

foraging success, efficiency and profitability (Mori & Boyd, 2004; Le Guen et al., 2018). Although additional years of data and a finer-scale integration of predator–prey data streams are required to provide a more robust understanding of patch-scale foraging dynamics, the research presented here can influence how we interpret penguin dive effort in the context of krill abundance and availability, a topic of longstanding relevance to ongoing Southern Ocean monitoring programmes (Constable et al., 2023; Trathan et al., 2022).

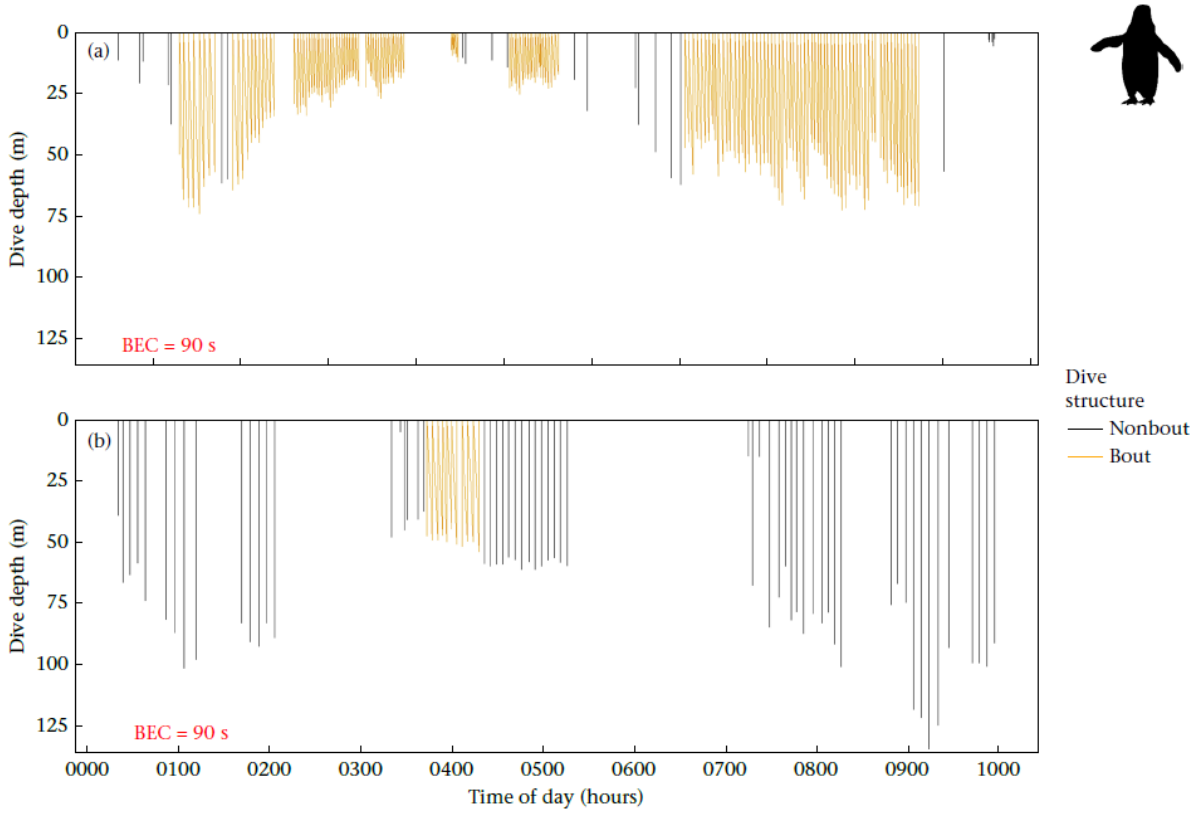

Figure 2. Example of dive profiles for two Adélie penguin individuals in (a) 2019/2020 and (b) 2021/2022. Dive profiles are categorized into bout and nonbout diving behaviour using the 90 s bout-ending criteria (BEC). Refer to Methods for details.

Seasonal Characteristics of the Krill Prey Field

Prey field acoustic surveys are a valuable tool for observing the distribution and abundance of krill, an integral component of Southern Ocean ecosystems (Cox et al., 2010; Jarvis et al., 2010; Tarling et al., 2009). Our krill acoustic findings extend the work of Salmerón et al. (2023) by

providing a spatial context to krill swarm abundance observations. This spatial context is essential for disentangling complex spatiotemporal predator–prey relationships (Reisinger et al., 2022; Santora et al., 2011; Watters et al., 2020). It is also particularly relevant in the case of breeding Adélie penguins, where the distribution and aggregation of krill swarms has been identified as an important prey field characteristic (Ainley et al., 2015; Riaz et al., 2023).

We found contrasting conditions in both krill swarm abundance and availability (i.e. distance from the colony and depth) between the two survey years. In 2019/2020, the krill abundance was primarily concentrated in waters immediately adjacent to the Adélie penguin breeding colony at King George Island. In contrast, the krill prey field in 2021/2022 was markedly different. In this year, krill abundance was substantially lower and less spatially concentrated across the survey area. Importantly, from the perspective of breeding Adélie penguins at King George Island, krill abundance was particularly low and patchily distributed in waters directly adjacent to the penguin breeding colony. While we show clear differences in both kill abundance and availability between the sampling years, these surveys provide only a snapshot of the krill prey field in time. Consistent with numerous studies examining predator–prey relationships (e.g. Benoit-Bird et al., 2013; Phillips et al., 2022; Riaz et al., 2023), we rely on the assumption that these prey field snapshots are spatiotemporally representative of our predator tracking data. Spatial advection rates of krill and the structural persistence of krill swarms through time remain key areas of uncertainty, influenced by numerous factors, including the active swimming of krill (Richerson et al., 2015), oceanographic conditions (Bestley et al., 2018; Nardelli et al., 2021) and predation pressure (Ainley et al., 2015). Although we could not ascertain localized changes in prey field conditions throughout the study period, our prey field seasonal assumptions are supported by the spatial differences in Adélie penguin foraging trips between the 2 years. Individuals in 2019/2020 (putatively high krill availability year) restricted their foraging activity to waters immediately adjacent to the colony at distances of less than ~30 km, while individuals in 2021/2022 (putatively low krill availability years) ranged approximately double the distance to locate prey and satisfy their energetic requirements. Similarly, Salmerón et al. (2023) also found that chick-rearing individuals at a nearby chinstrap penguin colony (~25 km away) displayed the

same contrasting patterns in foraging trip distribution between the two survey years. Taken together, these findings align with numerous studies demonstrating a relationship between penguin foraging distribution and prey availability during the chick-rearing period, specifically, that localized foraging corresponds to high krill availability whereas more extended foraging trips correspond to low krill availability (Ainley et al., 2015; Lescroël et al., 2020; Nicol et al., 2008; Watanuki et al., 1993).

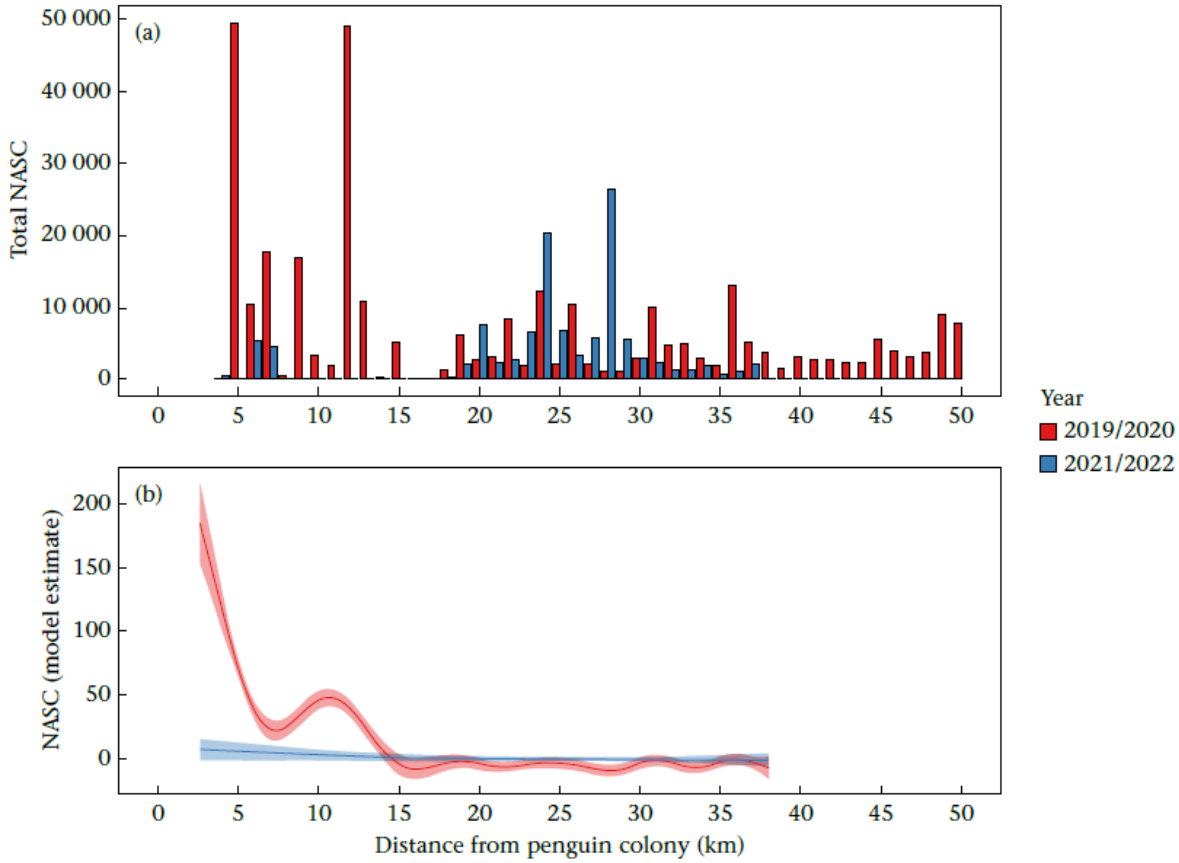

Figure 3. The relationship between the total nautical area scattering coefficient, NASC (m^2/nautical $miles^2$), and the distance to the Adélie penguin colony at King George Island (km). (a) NASC data are summarized into 1 km units across the entire survey area for both years (2019/2020 and 2021/2022). (b) Results from the fitted generalized additive model (GAM). Darker red and blue lines indicate the modelled relationship between individual krill swarm NASC and the distance to the penguin colony, and lighter shaded areas represent 95% confidence intervals (refer to Methods for full details on model configuration and Supplementary Table S1 for model

coefficients).

Penguin Foraging Bout Behaviours and Strategies

In this study, we leveraged accelerometer data to fine-tune our discrimination of Adélie penguin foraging dive activity. Traditionally, these classifications are inferred using more indirect behavioural measures within dive profiles (e.g. dive depth, bottom time and wiggles) (Cimino et al., 2016; Ford et al., 2015; Lescroël et al., 2021). Through our accelerometry-based approach, we found that individuals primarily structured prey capture attempt activity within dive bouts. These findings reinforce the idea that analysing bout-diving behaviour is fundamental to understanding how Adélie penguins perform and structure their foraging activity (Le Guen et al., 2018; Watanuki et al., 2010).

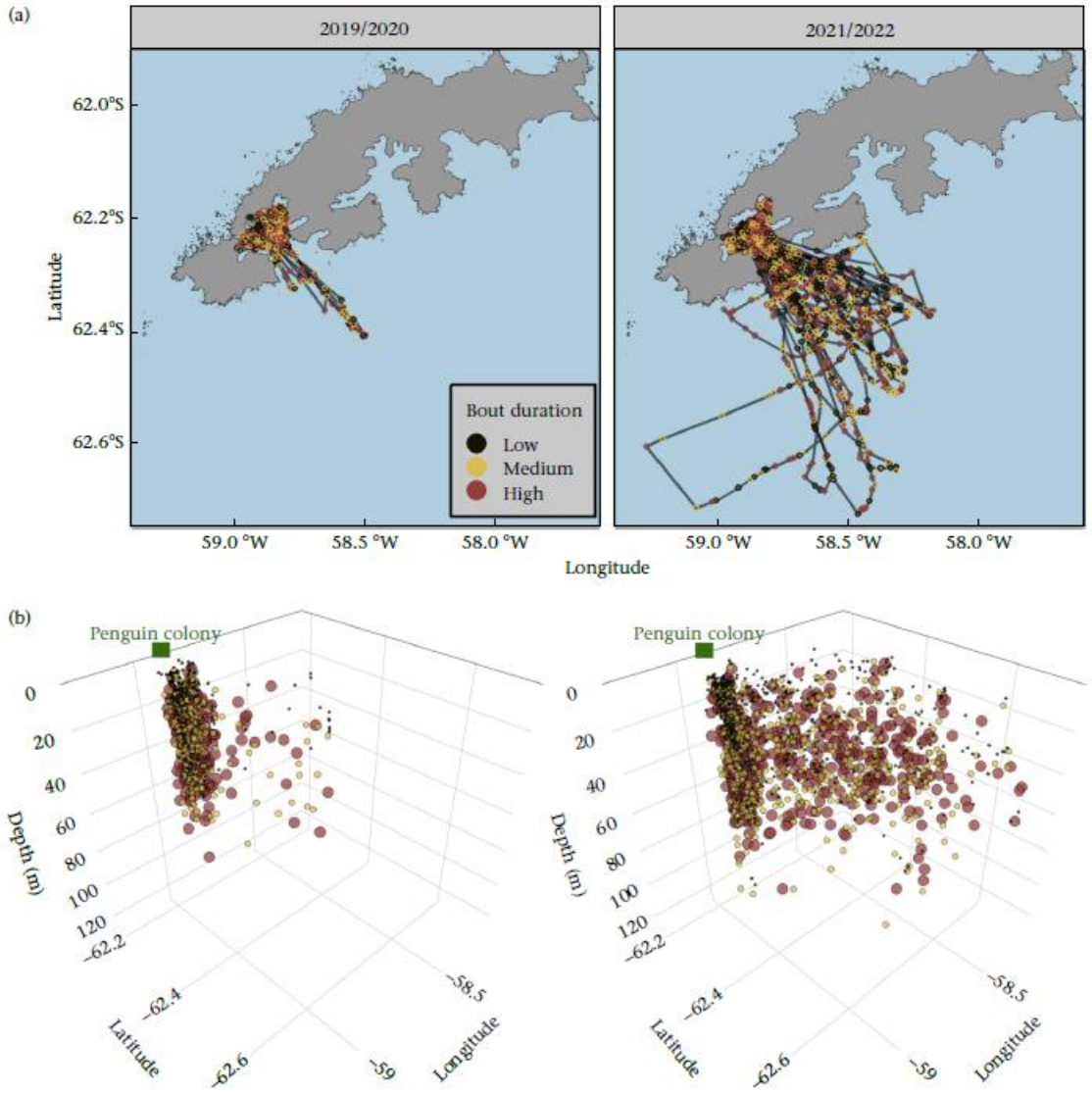

Figure 4. Spatial distribution of Adélie penguin bout-diving activity across both years (2019/2020 and 2021/2022) at the King George Island study site. (a) Horizontal distribution of bout activity. (b) Dive activity over three dimensions (latitude, longitude, depth). To aid visual presentation, bout duration values are grouped into three categories based on quantiles for each individual: low (<0.33), medium (>0.33 and <0.66) and high (>0.66). Penguin colony mapping features displayed as for Fig. 1.

In this study, we demonstrate how Adélie penguin foraging bout activity can vary with krill abundance and availability. In 2019/2020, when krill abundance and availability were high,

foraging dive bouts were highly concentrated both in time and space. In comparison, foraging bouts were more scattered in 2021/2022, likely indicative of a more patchy and dispersed krill prey field. These results lend support to the idea that interbout periods (both distance and duration) are useful and predator-relevant proxies of prey aggregation and availability (Luque et al., 2008; Sutton et al., 2021). While these between-bout results align with our initial expectations, interestingly, our within-bout results were contrary to expectations. Our results show that bouts in 2019/2020 were actually shorter in duration, with no between-year differences in the rate of prey capture attempts within bouts. It is commonly assumed that increased bout duration corresponds to increased size and quality of prey patches encountered (Le Guen et al., 2018; Lescroël et al., 2021; Sommerfield et al., 2015). This is based on the idea that patch residence time should increase in more productive prey patches as individuals make foraging decisions based on dive-scale assessments of patch quality (Foo et al., 2016). However, our results demonstrate that shorter and more discrete bouts can be a functional response to increased krill abundance and availability. This provides broad support for the marginal value theorem (MVT) branch of optimal foraging theory, which asserts that increased time at depth may not provide the most efficient foraging strategy and that patch residency decisions (i.e. bout duration) are mediated by a longer-term and bout-scale assessment of habitat quality (i.e. profitability of neighbouring prey patches) (Watanabe et al., 2014). The application of MVT in penguin–krill systems is likely influenced by the spatial structure and distribution of the krill prey field, affecting how penguins assess bout-scale patch quality during foraging trips (Watanabe et al., 2014). Our bout-diving findings suggest that MVT predictions in penguin–krill systems may apply during times of high krill abundance and availability, particularly when large aggregations of krill are spatially concentrated and distributed close to the colony at relatively shallow depths. Conversely, during times of low krill availability when krill swarms are more patchily distributed, there may be a limited capacity to conduct a broader-scale and longer-term assessment of habitat quality, resulting in extended bout durations and the overuse of poor krill patches (Chimienti et al., 2017; Esposito et al., 2010).

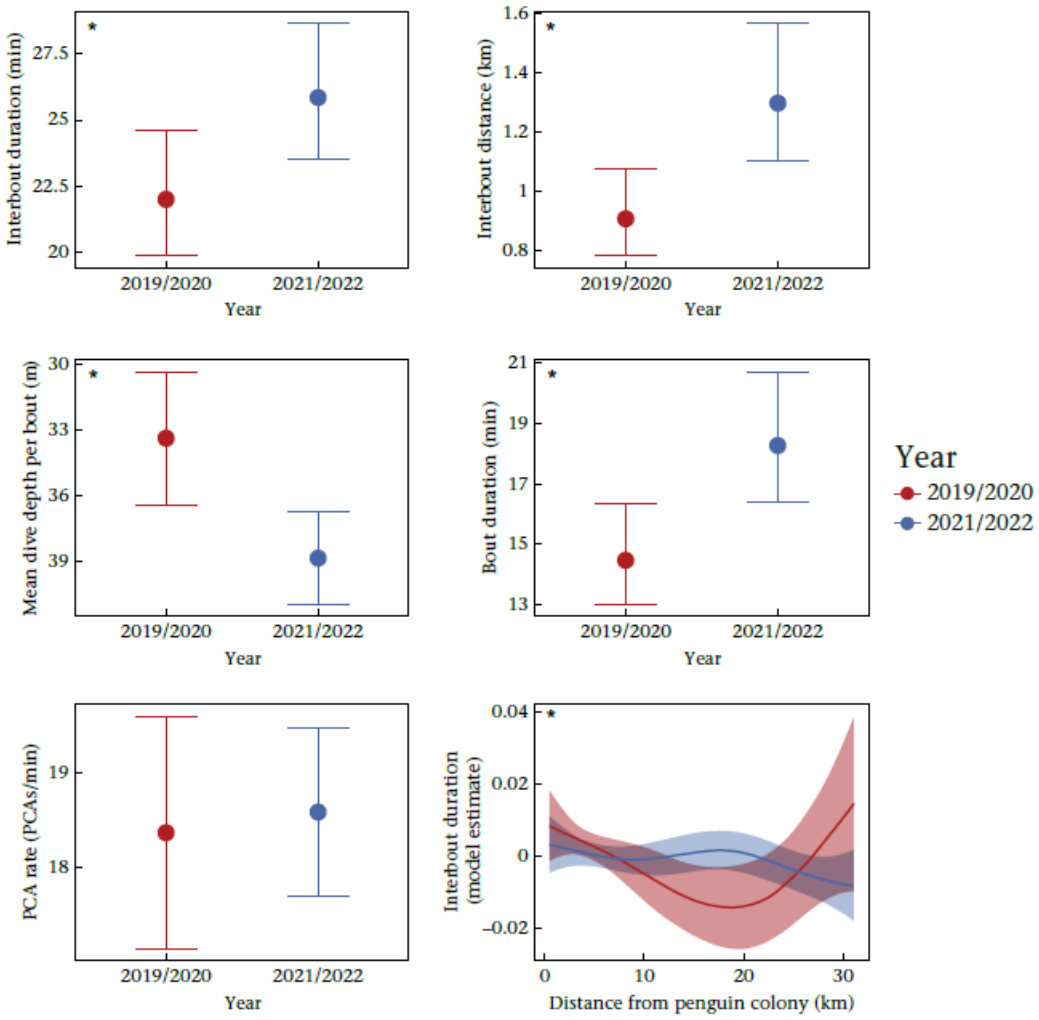

Figure 5. Results from penguin bout generalized linear mixed effects models (GLMM) and generalized additive mixed models (GAMMs). GLMM results display the estimated mean and 95% confidence intervals across both years (2019/2020 and 2021/2022). GAMM results display model estimates of interbout duration and distance to colony for both years, with shaded areas illustrating 95% confidence intervals. Statistically significant models ($P < 0.05$) are indicated by a black asterisk in the top left corner of plots. Full model coefficients are provided in Supplementary Table S2 (GLMM) and Table S3 (GAMM). Refer to Methods for further details on model configuration. PCA: Prey capture attempts.

With the marked differences observed in krill abundance and availability between 2019/2020 and 2021/2022, it is somewhat surprising that we observed no differences in the rate of prey capture

attempts between years. It is plausible that, within a prey patch, the quantity of krill available is sufficient relative to a penguin's rate of consumption (Ford et al., 2015), with increased energetic costs during times of low krill availability primarily related to the distance and duration between patch encounters. However, the quality (e.g. krill size) and predator-relevant density of krill patches, which we were unable to resolve in this study, may affect krill ingestion rates and thus may have influenced our within-bout model results (Sutton et al., 2021). Individual krill weigh 0.4 g on average, and approximately 800–1200 g of krill are required to meet the daily energetic demands of breeding individuals (Juáres et al., 2018; Southwell et al., 2015; Watanabe & Takahashi, 2013). Inevitably, these estimates will vary based on the energetic costs of foraging trips (longer trips require more energy), the energetic demand of chicks (larger chicks demand more energy) and the energetic contribution of each prey item (larger individual krill provide more energy). During Adélie penguin foraging dives, individual prey capture attempts (i.e. head jerks, as detected by accelerometers) have been shown to reflect up to two individual krill captures (Watanabe & Takahashi, 2013). So, during periods of high krill availability, when resources are densely aggregated in time and space, penguins may be able to increase the efficiency in their energy acquisition by ingesting multiple and/or larger krill per foraging attempt in a dive (Benoit-Bird et al., 2013; Watanabe & Takahashi, 2013). Similarly, when krill availability is low, there may be a greater proportion of unsuccessful PCAs during foraging dives. Based on this notion of predator-relevant krill availability, previous studies have suggested that threshold dynamics may be an applicable conceptual framework, whereby foraging efficiency varies with specific tipping points of krill availability, rather than overall krill abundance (Fraser & Hofmann, 2003). Finer-scale and more direct measures of penguin foraging activity (i.e. through the complementary use of video data) are required to empirically test and disentangle the complex patch level dynamics within penguin–krill systems (Schoombie et al., 2024; Sutton et al., 2021; Watanabe et al., 2014; Watanabe & Takahashi, 2013).

Moving Beyond the BEC Approach for a Dynamic Detection of Animal Decision Making

Bout-ending criteria are widely used to classify marine predator dive effort into distinct bout dives (Luque et al., 2008; Mori & Boyd, 2004; Viviant et al., 2014). Numerous studies have used this

technique to calculate a population level BEC, by applying a single numeric value across the dive profiles of all individuals (Lescroël et al., 2021; McInnes & Pistorious, 2019; Weimerskirch et al., 2012; this study). However, it is well established that there can be significant individual variability in marine predator dive data associated with various intrinsic (i.e. energetic capacity, age, foraging experience and preferences) and extrinsic (i.e. spatial or temporal changes in the prey field, resource competition) factors (Ainley et al., 2015; Emmerson et al., 2015; Lescroël et al., 2020; Zimmer et al., 2011). Therefore, a population level BEC may not be representative of individual level foraging trip dynamics and may over- or underestimate an individual's bout-diving behaviour. Across the different BEC approaches we tested, we found that Adélie penguins showed a high degree of interindividual variability in BEC, ranging from 24 s to 406 s. This individual level BEC variability is consistent with other Adélie penguin bout-diving studies (Watanuki et al., 2010). But importantly, and consistent with other BEC comparison studies, we found that individual BEC values were highly variable based on subjective decisions of modelling parameters (Luque & Guinet, 2007). Nevertheless, our results lend support to the idea that individual level bout criteria should be developed and considered in future marine predator bout-diving investigations (Gutowsky et al., 2014; Luque et al., 2008).

More flexible modelling techniques may provide novel and promising approaches to identify drivers of bout-diving structures. Even if BEC values are calculated across all individuals, modelling approaches currently available are not flexible to time-varying bout-diving strategies or decisions that would inevitably occur during penguin foraging trips. One possible solution to this issue is the use of hidden Markov models (HMMs), which are capable of quantifying the probability of switching between behavioural states given intrinsic and/or extrinsic variables (Carter et al., 2020; McClintock, 2021). Previous studies have demonstrated how HMMs can be used to determine discrete behavioural classes (i.e. short–shallow versus long–deep) within dive profiles and also how behaviours can be hierarchically nested, yielding powerful insight into complex time series data (Hart et al., 2010; Photopoulou et al., 2020). Further integration of high-resolution biologging technology (i.e. dive, accelerometer, camera) with prey availability and abundance data has the potential for signal validation of prey capture events and more precise time-varying

discrimination of how foraging activity is clustered into dive bouts.

Conclusion

Despite the wealth of behavioural information generated by marine predator dive data and its widespread use in Adélie penguin monitoring programmes around Antarctica, the signals of foraging success within these complex time series can be difficult to identify and interpret (Le Guen et al., 2018; Lescroël et al., 2021). This is because linkages between predator dive structure/organization and the hierarchical distribution of prey are still largely unknown. Understanding these decision-making processes and their drivers and how the information is hidden behind what we measure is key for assessing the application and validity of ecological foraging theory and providing useful metrics for conservation and management. Contemporaneous predator–prey data are ultimately required to test these theoretical frameworks and ascertain the drivers of at-sea foraging decisions, but this is notoriously difficult to achieve in Southern Ocean ecosystems and is rarely undertaken (but see Cimino et al., 2016). By capitalizing on the unique research opportunity to examine the associations between krill acoustic data and penguin foraging behaviours, our findings improve understanding of how Adélie penguin bout-diving behaviours and strategies may be used to interpret krill availability.

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CAPÍTULO 6

Divergent responses of *Pygoscelis* penguins to unfavourable weather conditions in the South Shetland Islands.

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6. Divergent responses of *Pygoscelis* penguins to unfavourable weather conditions in the South Shetland Islands

6.1 Abstract

Pygoscelis penguins are valuable indicators of the effects of rapid warming in the Antarctic Peninsula (AP). In the western AP, Adélie penguins show a declining population trend, while gentoos are expanding. The notably low reproductive success of Adélie but not gentoo penguins at Ardley Island during the 2023/2024 breeding season, provided an opportunity to explore the potential effects of weather conditions and food availability as possible determinants of reproductive output. We explore associations between reproductive output, air temperature, wind speed, wind chill temperature, and accumulated rain and snow. As a proxy for food availability, we used data of penguins' foraging trips, which reflects krill abundance. A late-winter storm at the end of October 2023 led to a record low wind chill temperature and sustained snow cover, negatively affecting the number of eggs that hatched successfully and/or the number of chicks that survived the first days after hatching. The effects were similar for both species, yet for gentoo penguins, chick survival in the late stage of the chick-rearing phase was remarkably higher, possibly due to high food availability and a longer nestling period. As previously suggested, the greater plasticity of gentoo penguins may allow them to mitigate the negative effects of environmental variability, potentially explaining the divergent breeding success despite unusually harsh meteorological conditions.

Keywords: Breeding phenology, Foraging trips, King George Island, *Pygoscelis adeliae, Pygoscelis papua*

6.2 Introduction

Antarctic Peninsula warming in the late 20th century was greater than anywhere else in the Southern Hemisphere (Turner et al. 2005; Siegert et al. 2019). The surrounding waters of the Southern Ocean have become warmer and fresher, resulting in changes in oceanic circulation (e.g., Haumann et al. 2016; Pellichero et al. 2017; Armour et al. 2016; Chown et al. 2022); changes in the duration and extent of sea ice (e.g., Comiso et al. 2017) and the acceleration of breaking of ice shelves (e.g., Liu et al. 2015). Under a 1.5°C global warming scenario, Antarctic Peninsula temperatures are expected to increase by 1-2°C in winter and 0.5-1.0°C in summer, with up to 130 days per year above 0°C, leading to increasing rain, snow, and ice melt and surface run-off (Siegert et al. 2019). Sea ice extent is expected to be highly variable in the Western Antarctic Peninsula (WAP), and southward shifts in marine life distribution are expected to continue (Atkinson et al. 2019). The WAP is also one of the regions in Antarctica with the highest human footprint (Pertierra et al. 2017), mostly because of the accumulation of research and logistical infrastructures, and the concentration of touristic activities and krill fisheries (Hogg et al. 2020).

All these changes have noticeable impacts on diverse biological processes (Ducklow et al. 2007; McClintock et al. 2008; Convey & Peck 2019; Schofield et al. 2024). However, understanding and predicting biological responses is complex, as they may occur in all trophic levels and vary according to different regional or local conditions (Clarke et al. 2007; Trathan et al. 2007; Rogers et al. 2020). *Pygoscelis* penguins are often considered valuable indicators of the impact of these changes on Antarctic ecological communities (Ainley 2002; Boersma 2008). Particularly interesting are the sympatric populations of the three species across the WAP, which already show contrasting trends in response to climate change impacts in this region. Overall, while Adélie (*Pygoscelis adeliae*) and chinstrap (*P. antarctica*) penguins show a decreasing trend in population size, gentoo penguins (*P. papua*) are expanding both in number and spatial extent (Lynch et al. 2012; Herman et al. 2020).

Human and climate-induced changes may have differential effects on *Pygoscelis* penguins depending on their life-history strategies. Population size fluctuations have been linked to breeding success, the survival rate of adults or juveniles, and factors operating both at a local scale during the breeding season (e.g., prey availability or competence with other species or

fisheries), and at large-scale during the non-breeding season (e.g., sea-ice extent in winter, krill recruitment) (Hinke et al. 2007; Carlini et al. 2009; Cimino et al. 2023; Salmerón et al. 2023). In general, the population decline of Adélie and chinstrap penguins has been closely related to large-scale changes in the biomass of Antarctic krill, their main prey. In contrast, gentoo penguins are considered to have more generalist foraging strategies and a flexible trophic niche, although they also predominantly feed on krill during the austral summer in the WAP (Polito et al. 2015; Herman et al. 2017; McMahon et al. 2019). Additionally, migration during non-breeding months has been proposed as an important factor in the population trends of these species. Gentoo penguins are a non-migratory species and remain close to their breeding colonies during the winter, allowing them a timely assessment of local environmental conditions at the breeding site, and thus greater flexibility to adjust their chronology to these conditions (Hinke et al. 2012; Juáres et al. 2013; Korczak-Abshire et al. 2021). In contrast, Adélie and chinstrap penguins migrate long distances to their wintering habitats, which precludes an adequate phenological response to changing local conditions at breeding sites (Hinke et al. 2012; Zaldúa et al. 2024).

However, while most of the research in the WAP has focused on the potential effect on population trends of prey availability during the summer season (due to differences in penguins' trophic-niche and dietary flexibility) (Hinke et al. 2007; Trivelpiece et al. 2011; Juáres et al. 2013; Cimino et al. 2016; Salmerón et al. 2023), other factors, such as the effects of weather conditions on breeding success have been studied only in a limited number of colonies. These studies have shown that local weather conditions may directly influence the timing of reproduction in penguins, the brood survival, and the chick mass at fledging (Lynch et al. 2009, 2012; Hinke et al. 2012; Fraser et al. 2013; Cimino et al. 2014; Juáres et al. 2015). For example, it has been suggested that cold spring air and severe snowstorms that prevent snow melt at the beginning of the breeding season can delay clutch initiation dates, given the need for these species to find snow-free areas for nest building (Hinke et al. 2012; Lynch et al. 2012; Cimino et al. 2019). The accumulation of snow may also cause early nest desertion or reduce the survival of eggs or chicks due to nest flooding (Trivelpiece & Fraser 1996; Cimino et al. 2014; Juáres et al. 2015). Precipitation, strong winds, and low air temperatures during critical periods such as hatching may also be a factor in reducing chick survival, as new hatchlings and young chicks are ectothermic and are particularly vulnerable to hypothermia

during this period (Moreno et al. 1995; Olmastroni et al. 2004; Demongin et al. 2010; Chapman et al. 2011; Smiley & Emmerson 2016).

Recently, Salmerón et al. (2023) proposed that a combination of low sea-ice in winter and weather conditions during spring and summer have a significant impact on krill abundance, and as a consequence of limited food availability, on the breeding success of chinstrap penguins breeding in the South Shetland Islands region. In contrast, Machado-Gaye et al. (2025) did not find differences in breeding success of Adélie penguins between years for the same period and area. Scarcity in food availability was however reflected in the foraging behaviour of both species, which made longer foraging trips during the chick-rearing stage in years with low krill abundance (Salmerón et al. 2023; Machado-Gaye et al. 2024, 2025). Therefore, the observations of extremely low reproductive success in Adélie but not gentoo penguins in the colonies of Ardley Island (King George Island) during the 2023/24 breeding season, provide a unique opportunity to explore the relative contribution of the effects of weather conditions and prey abundance on the breeding success of these colonies.

To identify putative determinants of this low reproductive success, here we explore associations between the breeding output of the two species during five breeding seasons (2019/20 - 2023/24), and a set of weather conditions that have been suggested as potential determinants of egg failure or chicks' mortality. Specifically, we explore potential links with i) air temperature, ii) wind speed, iii) wind chill, iv) rain, and v) snow cover in the area during October-November-December (the incubation and chick-rearing stages in Ardley Island). We also explore associations with characteristics of their foraging trips as indicators of food availability. By integrating data on adult foraging behaviour, chick survival rates throughout the chick-rearing stage, and weather conditions, we aim to identify the ecological mechanisms underlying the unusual and contrasting breeding outputs observed during 2023/24. We specifically explore the following alternative hypothesis: 1) higher snow accumulation at the beginning of the breeding season (November) decreased egg success and/or hatchlings survival due to eggs freezing/cracking or chicks hypothermia caused by nest flooding (late November/early December); 2) higher wind intensity and lower air temperature (low wind chill), and higher rainfall during the chick-rearing period (December) decreased chicks survival due to hypothermia; and 3) reduced food availability during the chick-rearing period

decreased the amount of food delivered to the chicks, causing higher mortality due to starvation.

6.3 Methods

Study area

Field studies were conducted from November to February in Ardley Island (62°13' S, 58°56' W), in the southwest of King George Island/Isla 25 de Mayo, South Shetland Islands, an Antarctic Specially Protected Area (ASPA N°150), during five breeding seasons (2019/2020 to 2023/2024) (Fig. 1). This colony is one of the few sites where Adélie, gentoo, and chinstrap penguins breed sympatrically (Braun et al. 2017). The colony holds special importance for gentoo penguins, as >1% of the global population nests there (Braun et al. 2017; Donald et. 2019). Consequently, the terrestrial area is designated as an Important Bird Area (IBA) No. 48, and part of the surrounding marine area is recognized as a marine IBA No. 11 (BirdLife International 2024). Since 2019, the Ardley Island colony is also a designated site under the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) Ecosystem Monitoring Program (CEMP). Breeding population size has been monitored since the 1980s for the three species present. According to Braun et al. (2017), the number of breeding pairs of chinstrap penguins has declined by more than 90% since the 1980s. However, this decline occurred mainly during that decade, when the population dropped from ~240 to fewer than 20 nests, remaining relatively stable thereafter. In contrast, Adélie penguins exhibited marked variability from the 1970s to the 1990s, followed by a sharp decline in the early 2000s, and a further decrease to <200 nests between 2018 and 2022. In contrast, Gentoo penguins increased over the same period by more than 80% (Humphries et al. 2017).

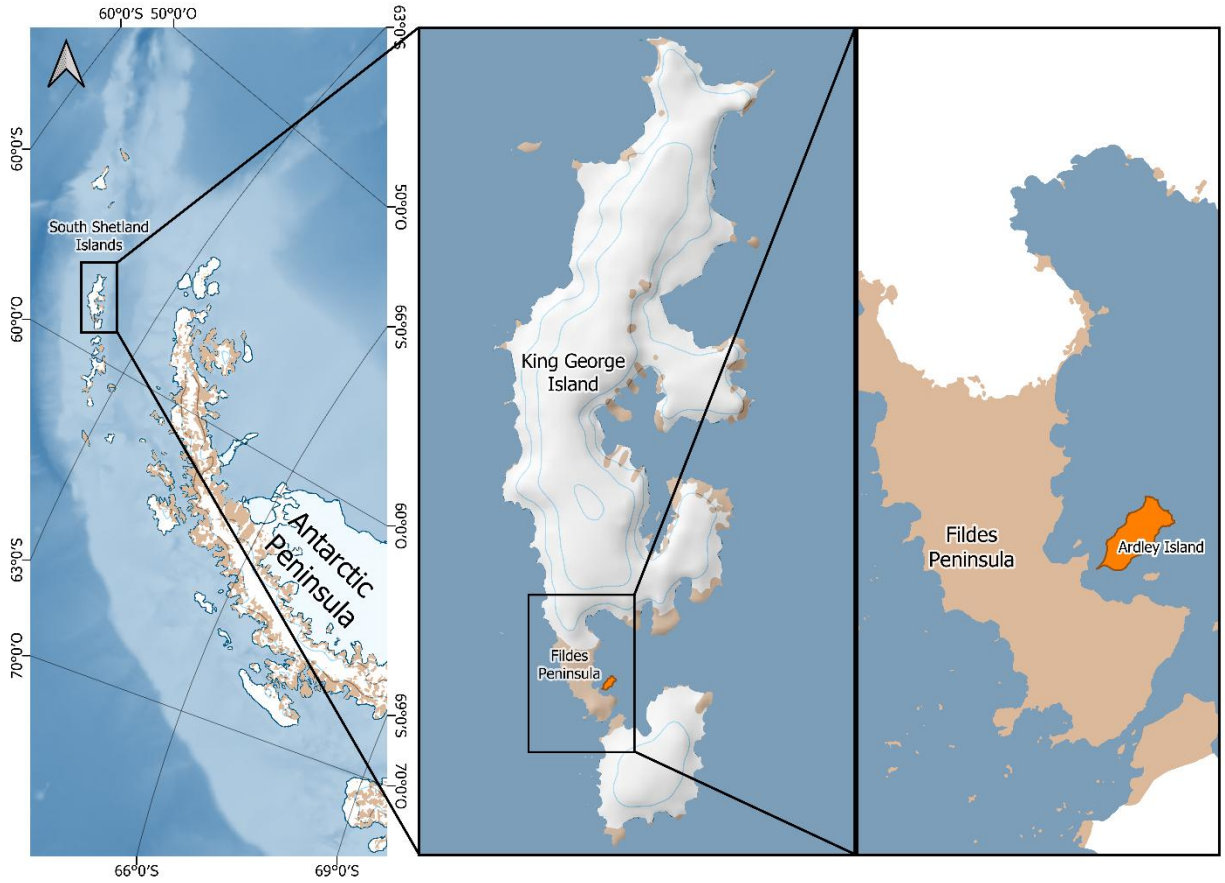

Figure 1. Location of Ardley Island colony in King George Island/Isla 25 de Mayo, South Shetland Islands, Antarctica.

Breeding parameters

Following the standard methods of CCAMLR (2014), we defined reproductive success based on three counts conducted in different stages of the breeding seasons (Method A6C): (a) the number of nests with eggs; (b) the number of nests with chicks when hatching was complete; and (c) the number of chicks in crèche. For each count (a, b and c) three separate counts on the same day were performed by independent researchers for the entire colony of Adélie and gentoo penguins, and mean values were calculated (Table 1). The mass of fledgling chicks of gentoo penguins was measured during three periods of five days of duration each following the CCAMLR protocol Method A7A (CCAMLR 2014) (i.e., chick weight was measured in three consecutive periods of five-days of duration each, with the first period beginning when the first fledglings appear on the beach). This enables recording differences in weight of early vs late fledglings. Fledgling chicks of Adélie penguins were weighed on a single day once they left

their natal colonies and were on the beach (CCAMLR protocol Method A7B; CCAMLR 2014). It is worth noting that, since the Adélie colony on Ardley Island is very small, fledglings depart within a narrow window of only 1–2 days, which often limits the possibility of conducting timely weight measurements. During this period, chicks of both species were captured near the water with a long-handled net and weighed with spring scales to the nearest 50 g. Only Adélies and gentoos were considered in this study due to the low number of chinstrap breeding pairs in Ardley Island. Due to logistical limitations (including those due to the COVID pandemics), not all stages could be sampled equally in the five years of the study.

We calculated three indices of breeding success to account for variations in each stage throughout the season. For each season we calculated: 1) breeding success (number of chicks in crèche divided by the number of nests with eggs); 2) proportion of hatched nests (number of nests with chicks divided by the number of nests with eggs); 3) hatchlings survival (number of chicks in crèche divided by the number of nests with chicks).

Penguin foraging characteristics

Along the five breeding seasons, 88 Adélie and 101 gentoo adult penguins rearing chicks were equipped with data-loggers (Axy-Trek, 70 x 40 x 15 mm, 69 g; TechnoSmart, Italy). Recorders were attached to only one member of the pair in nests with two chicks, using black Tesa® 4651 tape (Wilson et al. 1997). The tagged birds were recaptured in the nest after 3–8 days and the loggers were removed to access recorded data. From 189 deployments, we obtained 839 complete foraging trips, analysed using the R software (version 4.1.3; R Core Team 2022). Excess points recorded at departure and arrival were manually removed, retaining five points at the colony for each event. Unrealistic positions indicating speeds were filtered out (>7 $km \cdot h^{-1}$ for Adélies and >10 $km \cdot h^{-1}$ for gentoo penguins). Foraging trips were defined from the time the birds moved more than 50 m from the nest to the sea until the time they were within 50 m of the nest again. For each individual, we calculated total trip duration, total trip distance (as the cumulative horizontal distance between all GPS locations per bird per trip), and maximum distance to the colony (as the straight-line distance between the colony and the furthest point of a trip). Further details on field procedures and location analyses are provided in Machado-Gaye et al. (2024) and Soutullo et al. (2024).

Meteorological data

To describe weather conditions in the colony we used *in situ* measured meteorological data at the Chilean base Frei station at King George Island, about 4 km from the study colonies, between 1994 and 2023, covering a 30-year period. The variables used were daily values of: mean temperature, accumulated rainfall, and mean wind speed. Accumulated snow was also used, but it is only available since 2012. Wind chill was calculated using air temperature and wind speed, following Osczevski & Bluestein (2005). Anomalies were calculated by substracting the mean value of the respective day or month in the 30-year period. Finally, NCEP reanalysis data (Saha et al. 2010) was used to study the large-scale weather situation that generated a 30-year record-low wind chill anomaly at Frei station during the penguin breeding season (October to December) the 28 of October 2023.

Statistical analyses

Variation in breeding success, proportion of hatched nests, and hatchling survival between seasons was evaluated with X^2-tests. To test for differences in foraging trip characteristics between seasons, we used linear mixed models (LMM) implemented in the R package *lme4* (Bates et al. 2015). For each model, a residual analysis was performed to test the homoscedasticity and normality of the residuals. Since the variables analysed for Adélie penguins did not present a normal distribution, they were log-transformed. Season was considered an independent factor variable and individual (ID) a random effect to account for repeated measures of the same individual. For the variable that did not have repeated measures by individual (fledgling body mass), we used a one-way analysis of variance (ANOVA), with the season as a factor. When significant differences between seasons were detected, we performed post-hoc Tukey tests using the *multcomp* package (Hothorn et al. 2008).

To test alternative hypotheses that could explain the observed low breeding success in Adélie penguins, but not in gentoo penguins during the 2023/24 breeding season, we conducted a series of analyses. First, we identified whether November 2023 had high accumulated snowfall for the study period by ranking the accumulated values for each year along the 30 years with weather data. Second, we examined whether, during December 2023, wind intensity was

higher, air temperature was lower, and as a consequence wind chill was lower, or accumulated rainfall was greater compared to other seasons, also using a comparative ranking of mean/accumulated values. Finally, we analysed foraging behaviour data to determine whether the duration, total distance, or maximum distance of foraging trips differed significantly in 2023/24 relative to the other years with tracking data.

Finally, to explore the relationship between breeding success and weather conditions, we performed a Principal Coordinates Analysis (PCoA) based on the meteorological variables included in hypotheses 1 and 2 (i.e., snow accumulation in November; wind speed, air temperature, wind chill and rainfall in December). Study years were ordered according to their position along the two main PCoA axes, providing a composite gradient of environmental severity to assess potential associations with breeding outcomes.

6.4 Results

Breeding parameters

Although we acknowledge gaps in some variables and years, we observed that the breeding population of Adélie penguins on Ardley Island declined by more than 30% during the study period. In contrast gentoo penguin breeding pairs increased by 17% (Table 1 - N° nest with eggs). Throughout the five years of this study, significant differences were found in the breeding success of both Adélie (X^2=13.51, df= 3, p=0.003) and gentoo penguins (X^2=157.01, df= 2, p<0.001), with 2023/24 being the year with the lowest breeding success for Adélie penguins but not for gentoos (Table 1). For both species, we also found significant differences in the number of nests with eggs that hatched successfully and had chicks that survived the first few days after hatching (X^2=7.78, df= 3, p=0.05 and X^2=99.12, df= 1, p<0.001, for Adélies and gentoos respectively). In particular, we observed that the 2023/24 breeding season had the highest rate of egg failure at hatching and/or hatchling mortality for both species (Table 1). In contrast, survival rate of chicks to crèche did not show significant differences between seasons for Adélie penguins (X^2=3.58, df= 4, p=0.5), while for gentoo penguins the maximum value recorded for the study period occurred in 2023/24 (X^2=758.69, df= 3, p<0.001). In summary, our results showed that the 2023/24 season had the lowest hatching and early chick survival rates, as well as the lowest overall breeding success for Adélie penguins, while in

gentoo penguins, only hatching and/or early chick survival was reduced. The weight of fledglings varied significantly during the study period for both Adélies (ANOVA: $F=36.79$, $p<0.001$) and gentoos (ANOVA: $F=137.7$, $p<0.001$), with 2023/24 being the season in which the highest chick mass was recorded for Adélie penguins, and the second highest for gentoos (Table 1). Although sample sizes were relatively small in some seasons for Adélies, they represent a substantial proportion of the colony's fledglings. Yet, results should still be interpreted with due caution.

Table 1. Measures of breeding parameters of Adélie and gentoo penguins breeding in Ardley Island (King George Island/Isla 25 de Mayo) during five breeding seasons (2019/20 - 2023/24). "-" indicates unavailable data.

	2019/20	2020/21	2021/22	2022/23	2023/24
Adélie					
N° nest with eggs	303	-	202	184	209
N° nest with chicks	262	353	162	168	129
N° chicks in crèche	350	408	224	235	163
Breeding Success (n° chicks in crèche/n° nest with eggs)	1.16	-	1.11	1.28	0.78
Proportion of hatched nests (n° nest with chicks/n° nest with eggs)	0.86	-	0.80	0.91	0.62
Hatchling survival (n° chicks in crèche/n° nest with chicks)	1.34	1.16	1.38	1.40	1.26
Chick mass at fledging (g)	-	2905 ± 402 (n=79)	2800 ± 465 (n=14)	3700 ± 449 (n=80)	3780 ± 390 (n=22)
Gentoo					
Nest with eggs	6695	-	7083	-	7846
Nest with chicks	5768	6107	-	8763	5255
Chicks in crèche	8903	7720	7906	8914	9650
Breeding Success (n° chicks in crèche/n° nest with eggs)	1.33	-	1.12	-	1.23
Proportion of hatched nests(n° nest with chicks/n° nest with eggs)	0.86	-	-	-	0.67
Hatchling survival (n° chicks in crèche/n° nest with chicks)	1.54	1.26	-	1.02	1.84

Chick mass at fledging (g)	5183 ± 189 (n=120)	4151 ± 211 (n=300)	4785 ± 240 (n=280)	4900 ± 554 (n=260)	5070 ± 540 (n=270)

Penguin foraging characteristics

Our dataset consisted of 345 trips for Adélie and 494 trips for gentoo penguins (Table 2). Over the five seasons of study, Adélie penguins exhibited significant differences in their foraging trip characteristics. We found significant differences in foraging trip duration (LMM: $F=16.26$, $p<0.0001$), maximum distance (LMM: $F=11.19$, $p<0.0001$) and total distance travelled (LMM: $F=14.93$, $p<0.0001$) in the 2019/20 and 2023/24 seasons compared to the other seasons, but not between them. During these two seasons the lowest values for the three parameters were recorded, suggesting high food availability (Fig 2a). Foraging trip characteristics of gentoo penguins showed slight variations between seasons (Fig. 2b). Trip duration during 2019/20 did not differ significantly from those of summer 2023/24, though it did significantly differ from other seasons (LMM: $F=4.43$, $p<0.01$). Regarding maximum and total distance, trips made by gentoo penguins during 2019/20 and 2023/24 showed the lowest values, with significant differences compared to the 2020/21 season (LMM: $F=3.01$, $p<0.05$; LMM: $F=2.93$, $p<0.05$, respectively).

Table 2. Summary of the foraging trips (mean ± SD) of Adélie and gentoo penguins breeding in Ardley Island (King George Island/Isla 25 de Mayo) during five breeding seasons (2019/20 - 2023/24). For each season the following parameters are shown: total number of trips (N° trips), number of individuals tracked (N° individuals), trips duration (h), maximum distance from colony (km), total distance travelled (km).

	2019/20	2020/21	2021/22	2022/23	2023/24
Gentoo					

N° trip	100	83	115	122	74
N° individuals	19	20	21	21	8
Trip duration (h)	9.39 ± 3.31	11.94 ± 4.26	12.07 ± 4.41	12.09 ± 4.84	10.85 ± 3.41
Max. distance (km)	16.54 ± 9.85	22.85 ± 11.55	18.55 ± 10.89	17.48 ± 11.32	15.43 ± 10.32
Total distance (km)	38.07 ± 19.89	51.97 ± 24.40	44.80 ± 23.28	42.10 ± 26.07	36.79 ± 21.03
Adélie					
Nº trip	67	59	98	86	35
Nº individuals	19	16	24	10	6
Trip duration (h)	9.07 ± 4.67	20.85 ± 11.01	19.31 ± 10.98	16.73 ± 11.11	10.92 ± 6.28
Max. distance (km)	6.60 ± 5.42	25.15 ± 17.92	16.95 ± 16.30	19.25 ± 16.95	10.30 ± 11.67
Total distance (km)	19.33 ± 12.33	64.66 ± 40.39	46.95 ± 37.94	47.80 ± 41.21	25.43 ± 27.00

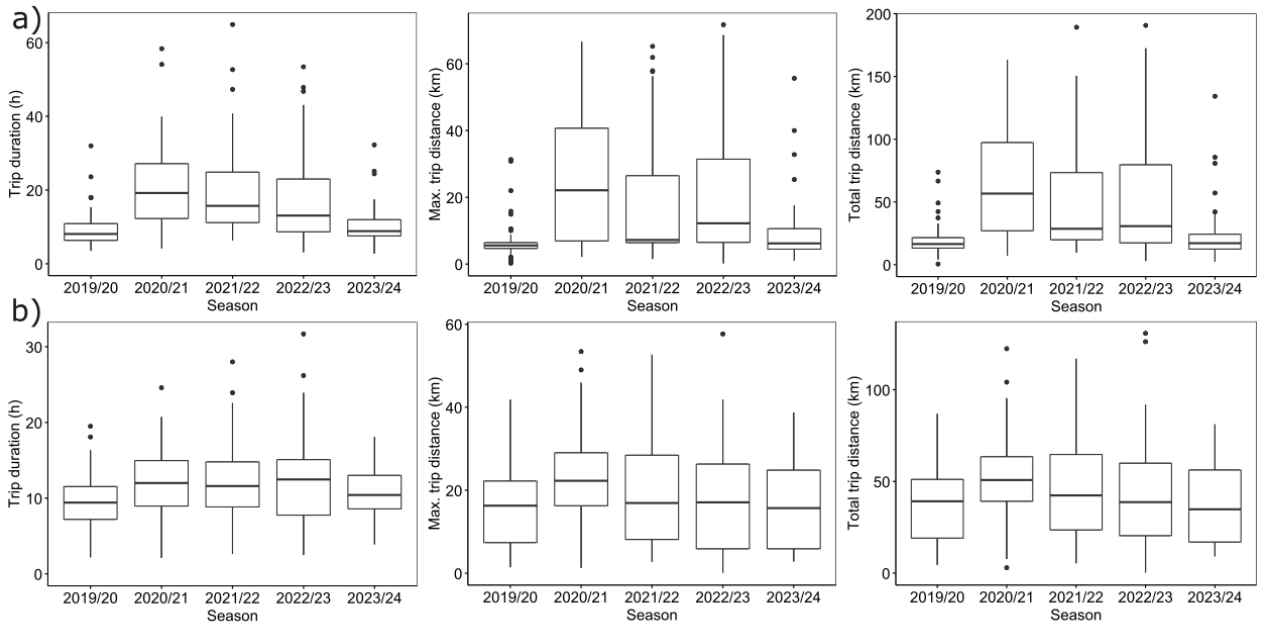

Figure 2. Foraging trips characteristics of a) Adélie penguins and b) gentoo penguins, breeding in Ardley Island (King George Island/Isla 25 de Mayo) between 2019/20 and 2023/24 seasons.

Meteorological conditions during the breeding seasons

Meteorological data from the Chilean Weather Service at Frei station showed large seasonal and interannual variability. Accumulated snow shows a clear seasonal cycle, decreasing from 77 ± 66 cm in October to 41 ± 31 cm in November and 17 ± 17 cm in December, while rainfall follows a similar pattern, decreasing from 53 ± 45 mm to 43 ± 24 mm and 35 ± 19 mm, respectively. These patterns coincide with increasing temperatures as the season progresses. While air temperature and windchill are primarily driven by the seasonal cycle, wind speed is influenced mainly by high-frequency variability (Figure 3).

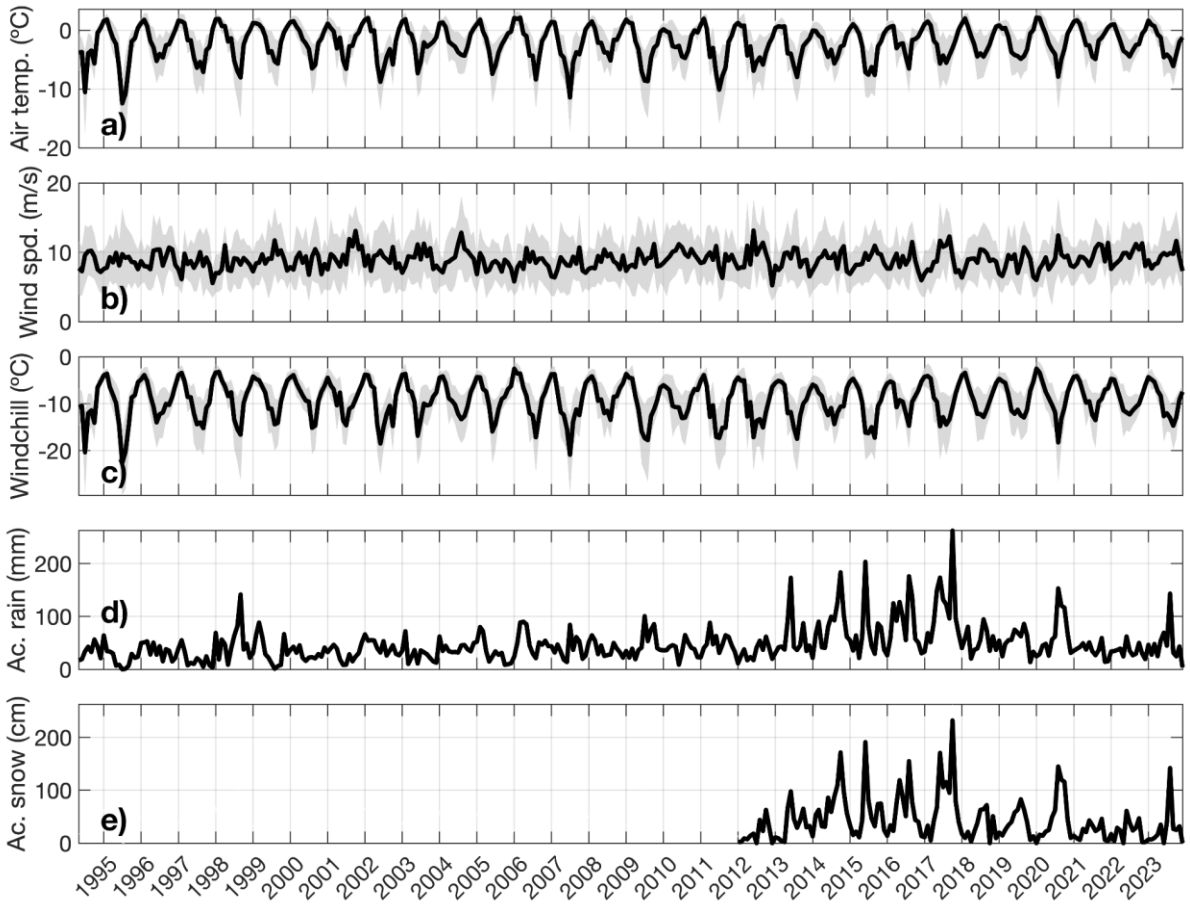

Figure 3. 30 years of in situ meteorological conditions at Frei station in King George between 1994 and 2023. Black lines show monthly means of a) Air temperature (°C), b) Wind speed (m/s), c) Windchill (°C), d) Accumulated rain (mm) and e) Accumulated snow (cm). Panels a), b) and c), also show the standard deviation of the variables as grey shades.

Meteorological data during the five years with overlapping penguin data (Oct-Dec 2019 to 2023) showed large season to season variability, registering both seasons with values close to the 30-year average like 2022, and very anomalous seasons like 2021 and 2023. In particular, 2023 was the coldest and windchillest season. October 2023 recorded the second-highest average wind speed and the third-lowest windchill temperature for any October in the 30-year record. November 2023 recorded the highest accumulation of snow and rain among all Novembers with breeding data, excluding 2020, which had higher values but breeding output data is not available as the island was inaccessible due to COVID-19 restrictions. December

2023 was the driest in the 30-year period, with the second-lowest windchill and the third-coldest air temperature on record (Table S1).

During most days across all breeding seasons, wind chill temperatures remained above -15°C (Fig. 4c). Temperatures below -15°C were only recorded during Octobers. Of the three events where wind chill dropped below -20°C during the five years with overlapping breeding data, two occurred in 2023 and one in 2019. The sharpest decline in wind chill was observed on October 28, 2023, primarily due to an anomalous low-pressure system in the Drake Passage (marked with L in Fig. 4d) and a relatively high-pressure system centered in the Weddell Sea which brought strong, cold southeasterly winds to Ardley Island. This weather pattern was also observed during the other extreme wind-chill events. October 28, 2023 marked the lowest wind chill anomaly (-14,77°C indicated by an arrow in Fig. 4c3b) in the 30- years analysed of the Frei meteorological station, which corresponds with an absolute value of windchill of -23.4°C. NCEP reanalysis shows that King George Island experienced a reverse in the prevalent westerly winds with velocities up to 18 m/s due to a very low-pressure system centered in the Drake Passage, producing an advection of very cold air from the Weddell Sea, dropping temperatures 8°C below the expected climatological values on 28 October 2023 (Fig. 4d and 4e).

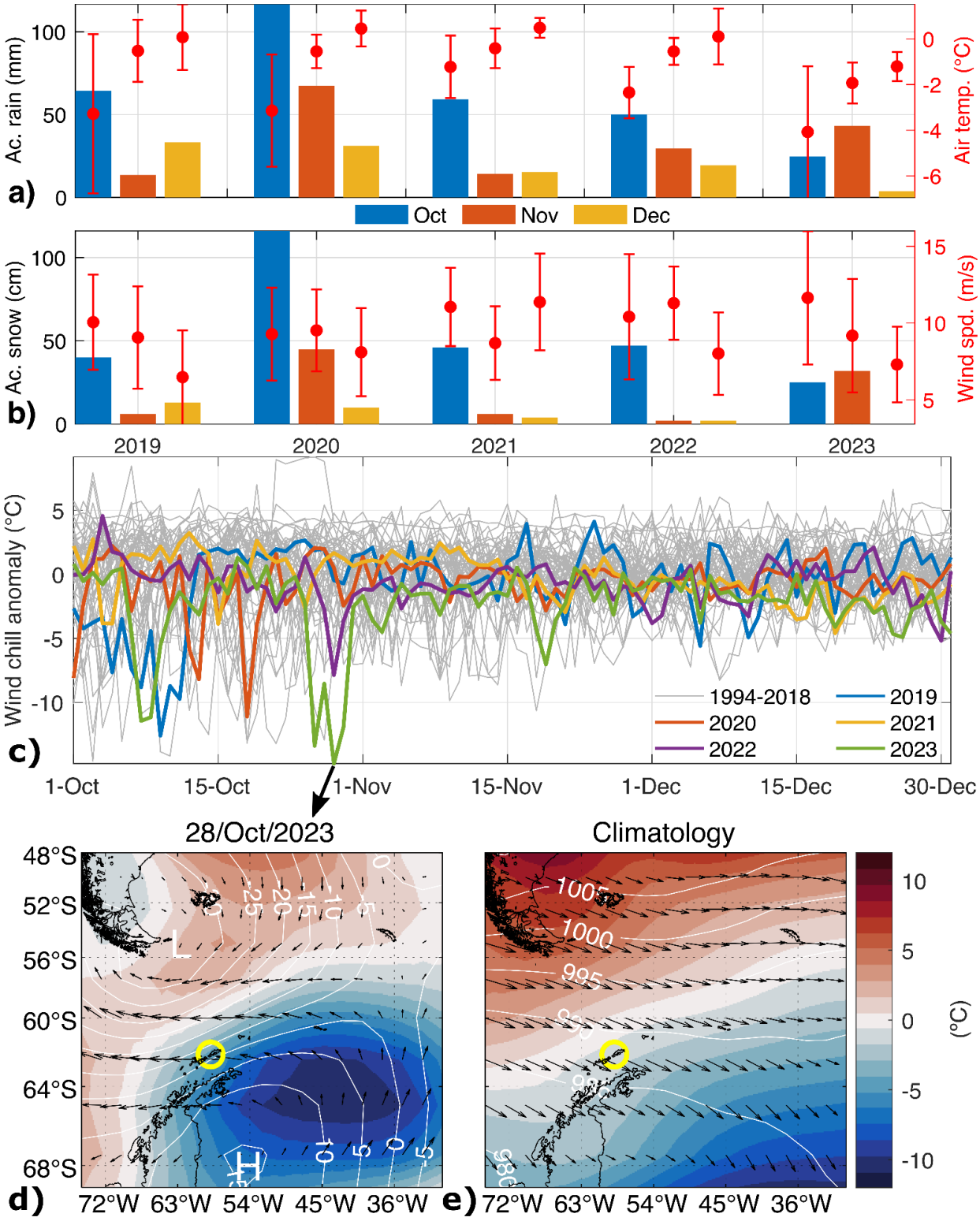

Figure 4. Meteorological conditions at King George Island during the breeding season 2019/20 to 2023/24. a) Monthly accumulated rain (mm, bars) and mean air temperature (ºC, dots). b)

Monthly accumulated snow (cm, bars) and mean wind speed (m/s, dots) at Frei meteorological station for October, November, and December between 2019 and 2023. c) Daily average of wind chill temperature (ºC) at Frei meteorological station for October, November, and December between 2019 and 2023. d) Composite of 10m mean wind (m/s, black vectors), mean sea level pressure (hPa, white contours), and 2m air temperature anomaly (shades) for NCEP reanalysis in the Antarctic Peninsula for the 28 of October for d) 2023 and e) climatology. The yellow circle shows the location of the study site.

Principal Coordinates Analysis (PCoA) performed to explore the inter-annual variability of weather conditions and their possible relationship to Adélie penguin breeding success showed that 2023 was anomalous year when in addition to December temperature, wind and windchill, a) November accumulated snow and b) December rainfall were considered (Fig 5). This analysis also showed that the lowest breeding success coincided with years positioned near extreme weather conditions, especially in 2023.

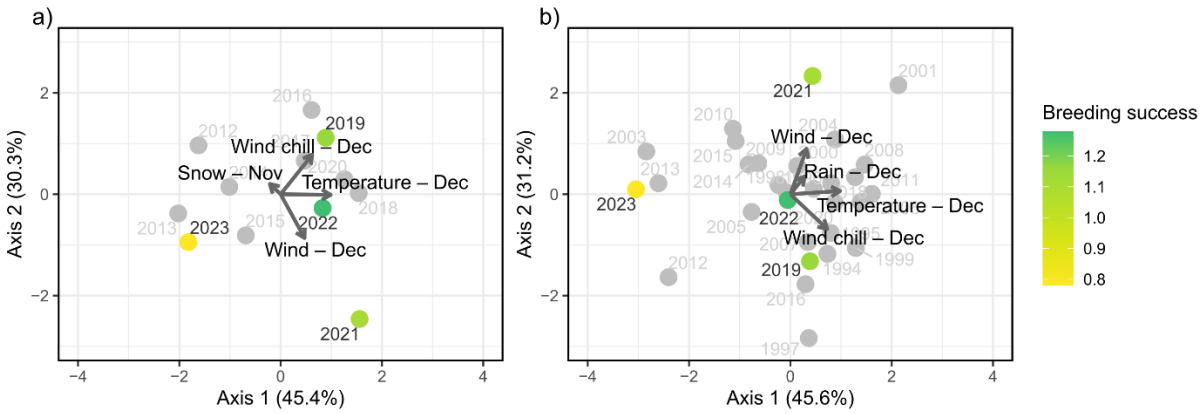

Figure 5. Principal Coordinates Analysis (PCoA) of meteorological variables and breeding success. Breeding success of Adélie penguins is shown as an example. a) PCoA of meteorological variables for the period 2012–2023 (temperature, wind, wind chill and snow) and b) PCoA including variables for the period 1994-2023 (temperature, wind, wind chill and rain).

6.5 Discussion

The main drivers of population changes in *Pygoscelis* penguins in the WAP have been widely debated. Overall, the differential ability of these species to adapt their breeding chronology

according to local conditions, the availability of prey during the breeding season, and overwintering factors affecting the survival of juveniles and adults have been the main proposed modulating factors (Hinke et al. 2007, 2012; Emmerson et al. 2011; Lynch et al. 2012; Juáres et al. 2013; Cimino et al. 2016). Our results, combining data on population parameters of Adélie and gentoo penguins nesting on Ardley Island, and the characteristics of their foraging trips over five breeding seasons, add evidence to the reports on the differential response of these species to meteorological conditions during the breeding season in the WAP. In particular, our observations strongly support the hypothesis that unusual weather conditions during the early breeding season may have a significant impact in population trends of Adelie penguins in the WAP, irrespective of food availability

Weather conditions at the beginning of the breeding season, specifically mean October temperatures and snow accumulation at nest sites, have been proposed as relevant factors affecting breeding success (Lynch et al. 2009, 2012; Hinke et al. 2012; Juáres et al. 2013). The main mechanism proposed to explain this process is that increased snow accumulation and low temperatures that prevent early melting may lead to loss of breeding habitat early in the season, as well as increased egg failure and loss of chick due to late melting soaking chicks, leading to hypothermia. In eastern Antarctica, it has been reported that the peak of Adélie penguin nest failure occurred in the first few days after hatching, as chicks do not yet fully regulate their body temperature, being especially vulnerable to unfavourable environmental conditions (Olmastroni et al. 2004; Smiley & Emmerson 2016). Conversely, for gentoo penguins it has been suggested that the increased ability to alter their breeding chronology by delaying the timing of egg-laying under unfavourable local conditions, or even re-laying after early failure of nests, allows them to buffer impacts in their reproductive success under changing conditions (Lynch et al. 2009, 2012; Hinke et al. 2012, Juáres et al. 2015). In Ardley Island, during the 2023/24 season we observed the lowest breeding success for Adélie penguins in the 5 years analysed, while for gentoos this value was within the observed range of previous seasons. The observation of an extreme event of high wind intensity and low temperature at the end of October 2023 which caused an anomalous drop in wind-chill temperature, and also an above-average snow accumulation during November 2023, may explain the low breeding success observed in Adélies. Furthermore, although we did not record colony arrival dates or egg-laying dates, field observations of the colonies at the end of

November allow us to assume that during 2023/24 the gentoo penguins began laying eggs several days later than observed in previous seasons.

Moreover, for both species we observed a high rate of nest loss between the first count of nests with eggs and the count of nests with chicks about 15 days later. Thus, we infer that for both species there was a high rate of egg-hatching failure and/or a high rate of hatchlings mortality in this season, probably related to the late winter extreme storms registered during October, and the consequent delay in the early snow melt, but also colder conditions throughout the whole trimester. Rain events were rather limited during December in 2023, so nests flooding due to rain cannot be considered a plausible explanation. Yet, this does not fully explain the contrasting reproductive success of Adélies and gentoos during 2023/24. Interestingly, in 2023/24 the chick survival rate, considered in this study as the number of chicks that reached the crèche over the number of nests with chicks, was the highest recorded for gentoo penguins in the analysed period, while for Adélie it was slightly lower compared to other seasons. We suggest that these differential responses reflect species phenological differences and high food availability during the chick-rearing stage in the 2023/24 season, as inferred from penguins foraging behaviour and chicks' weight.

Prey abundance and quality may have a strong influence on breeding chronology and success (Ballard et al. 2010; Lescroël et al. 2010; Cimino et al. 2014; among others). During breeding season, *Pygoscelis* penguins are central-place foragers and hence depend on local food resources for the daily provisioning of chicks. Foraging trip characteristics have been proposed as good predictors of food availability in the vicinity of the colony (Carpenter-King et al. 2017; Salmerón et al. 2023; Machado-Gaye et al. 2024). Previous studies of foraging behaviour on Adélie and chinstrap penguins in the South Shetland Islands showed that shorter foraging trips in both duration and distance during 2019/20 breeding season reflected high krill abundance assessed by acoustic monitoring (Salmerón et al. 2023; Machado-Gaye et al. 2024). Thus, given that Adélie penguin foraging trips during the 2023/24 breeding season were similar in duration and distance to trips made during 2019/20, being the shortest trips in the five years of study, we infer that there was a high availability of krill in the area during the 2023/24 season. Furthermore, the masses of fledglings during 2023/24 were the highest recorded for Adélie and the second highest for gentoo penguins, consistent with conditions of high food

availability during chick-rearing. Thus, low food availability appears an unlikely explanation for the low reproductive success of Adélie penguins in Ardley Island during 2023/24 breeding season, in agreement with Machado-Gaye et al. (2025) observations. However, it may have been an important factor in the reproductive success of gentoo penguins, since the high survival rate of chicks to crèche may actually be a consequence of high food availability. Gentoo penguin chicks require a greater amount of food compared to chicks of Adélie penguins and exhibit lower growth rates, typically fledging after an average of 72 days, whereas Adélie penguin chicks fledge after 52 days (Trivelpiece et al. 1987). Delayed laying (or even re-laying after failure) and a larger chick-rearing stage with high food availability might have provided gentoo penguins the opportunity to recover from an exceptionally harsh onset of the breeding season.

It is worth noting that our study has some limitations in the amount of population parameter data collected in the five seasons. Such is the case for the 2020/21 season, during which an extreme weather event also occurred at the beginning of the breeding season with high snow accumulations and precipitation during October and November. Furthermore, considering the foraging trip characteristics of both species and chicks' weight, it would also appear to have been a season of low food availability. However, given the logistical restrictions caused by COVID-19 during that season, we were unable to record the number of nests with eggs and therefore the breeding success or the rate of successfully hatched eggs.

In summary, our results suggest that the breeding success of Adélie and gentoo penguins nesting in Ardley Island is influenced by a combination of characteristics of their life-history, weather conditions, and food availability during the breeding season. These observations warn against the risks of misleading conclusions derived from considerations of only some of these factors and highlight the need for integrated monitoring programmes that simultaneously record information on all these dimensions. Current climate projections for the Antarctic Peninsula project a continued shift towards warmer conditions, along with an increase in precipitation, wind speed and the length of the snow melt season (Siegert et al. 2019; Bozkurt et al. 2021). This could reduce food resources and affect weather conditions during the breeding season, directly influencing the reproductive success and population trends of *Pygoscelis* penguins. Furthermore, there are other key factors in interpreting

population trends for these species such as those operating during the non-breeding season. Overwinter conditions faced by juveniles and adults may affect their survival, with consequences for recruitment and the conditions under which potential breeders initiate the next breeding season, hence affecting the size of breeding populations (Hinke et al. 2007, 2012). For this, it is also essential to consider how factors such as food availability during the breeding season determine the body condition at which juveniles and adults begin the wintering season. The high energetic costs faced by adults to meet the energetic demands of their offspring during seasons of low food availability may result in poorer adult body condition to face the winter season (Machado-Gaye et al. 2025), while for fledglings, the first weeks of independence imply a bottleneck stage in their survival, also related to their body condition (i.e., body mass; Hinke et al., 2007).

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7. Síntesis y discusión general

El objetivo general de esta tesis fue comprender cómo los pingüinos del género Pygoscelis, en particular *P. adeliae* y *P. papua*, responden a las crecientes presiones de los cambios globales en el noroeste de la Península Antártica. A partir del análisis integrado de datos de alta resolución de comportamiento de forrajeo, dieta, parámetros poblacionales y condiciones ambientales, esta tesis contribuye a una comprensión más profunda sobre las estrategias de forrajeo de ambas especies. Esto busca finalmente aportar información valiosa para evaluar su potencial como indicadores ecológicos del ambiente marino, mejorar la comprensión sobre los mecanismos que subyacen a las tendencias poblacionales divergentes, y contribuir a la generación de medidas de gestión en la región.

A lo largo de esta tesis, se caracterizaron en detalle los viajes de alimentación de pingüinos Adelia y papúa durante la etapa reproductiva, generando una valiosa línea de base para comprender cómo ambas especies ajustan sus estrategias de forrajeo frente a las restricciones impuestas por la reproducción y la variabilidad ambiental. Se identificaron áreas de uso recurrente, incluyendo áreas clave de alimentación para Adelia ubicadas dentro de los 10 km de la colonia. Asimismo, mostramos que estas aves ajustan su esfuerzo de forrajeo frente a variaciones en la disponibilidad de krill, especialmente las hembras de Adelia, que en años desfavorables invierten mayor energía que los machos, lo que podría tener implicancias en su supervivencia post-reproductiva y, en consecuencia, en la dinámica poblacional. Por otro lado, el análisis de la organización de los buceos en ráfagas ("*bouts*") reveló que, durante temporadas con alta abundancia de krill, los pingüinos Adelia realizaron inmersiones más concentradas en el espacio y tiempo, mientras que en temporadas de baja disponibilidad los bouts fueron más largos y dispersos, aunque la tasa de intentos de captura se mantuvo constante, cuestionando la interpretación clásica de la rentabilidad de los parches de krill. Finalmente, se evaluaron los efectos de condiciones meteorológicas extremas sobre el éxito reproductivo de ambas especies, encontrando que condiciones desfavorables redujo la eclosión y supervivencia temprana de los pichones en ambas especies; sin embargo, papúa logró mantener un alto éxito reproductivo al final de la temporada, mientras que Adelia no logró recuperarse, incluso con buena disponibilidad de alimento, reflejando una menor capacidad de respuesta frente a perturbaciones ambientales.

7.1 Valor relativo de *P. adeliae* y *P. papua* como indicadores ecológicos

La utilidad de las especies de nivel trófico superior como indicadores del ecosistema está determinada por nuestra capacidad para relacionar los cambios en sus parámetros de respuesta con las fluctuaciones en los niveles tróficos inferiores (Reid *et al*., 2005). En el marco del enfoque ecosistémico adoptado por la CCRVMA, los pingüinos del género *Pygoscelis* han sido seleccionadas como especies indicadoras dentro del Programa de Seguimiento del Ecosistema (CEMP), el cual busca detectar cambios en el ecosistema mediante el uso de estas especies y determinar si estos cambios se atribuyen a factores pesqueros o ambientales (Agnew 1997). Para ello, se han definido parámetros críticos que reflejan respuestas a corto plazo (e.g., duración de los viajes de alimentación) y largo plazo (e.g., éxito reproductivo) frente a variaciones en la disponibilidad de presas (Agnew 1997; Trathan *et al*., 2021). Sin embargo, para maximizar su valor como indicadores, resulta esencial una comprensión exhaustiva de cómo sus estrategias de forrajeo reflejan la abundancia/disponibilidad de presas e influyen sobre diferentes parámetros demográficos (Emmerson *et al*., 2015).

Diversos estudios han demostrado que los pingüinos ajustan su comportamiento de forrajeo para amortiguar los efectos de una disminución en la disponibilidad de alimento, ya sea extendiendo la duración de sus viajes o aumentando la frecuencia de alimentación, incluso a costa de su propia condición corporal (Watanuki *et al*., 1993; Clarke 2001; Nicol *et al*., 2008; Ballard *et al*., 2010; Salmerón *et al*., 2023). Nuestros resultados muestran que en general los pingüinos Adelia que anidan en isla Ardley ajustan sus estrategias de forrajeo en función de la disponibilidad de krill, alimentándose principalmente en zonas cercanas a la colonia o en un monte submarino próximo. Durante temporadas favorables, con buena abundancia de alimento, realizaron viajes más cortos en tiempo y distancia (capítulos 3 y 4), la secuencia de buceos de alimentación en ráfaga (*bouts*) fueron más cortos y agrupados (capítulo 5) y tanto el peso de adultos como de pichones en la etapa de emplume fue mayor (capitulo 5 y 6). Por el contrario, en años de escasez de krill, los viajes de alimentación se incrementaron tanto en duración como en distancia, los *bouts* fueron más largos y dispersos tanto espacial como temporalmente, y el peso de adultos y pichones fue menor (capítulos 3-6). En contraste, los pingüinos papúa mostraron una mayor estabilidad en la duración y distancia de los viajes de alimentación entre temporadas con diferente disponibilidad de krill, siendo ligeramente

menores en años con buena disponibilidad de presas (capítulos 2 y 6). En la misma línea que los Adelia, tanto el peso de los adultos (Figura 7.1) como de los pichones al emplume (capítulo 6) varió en concordancia con la disponibilidad de alimento en las diferentes temporadas reproductivas. Cuando analizamos su comportamiento de buceo observamos algunas diferencias entre las temporadas con diferente disponibilidad de krill. Al igual que Adelia, durante la temporada con mayor disponibilidad de krill los pingüinos papúa realizan bouts más cortos y agrupados. Sin embargo, a diferencia de Adelia, las inmersiones dentro de los *bouts* fueron significativamente más profundas durante temporadas con baja disponibilidad de presas (Figura 7.2).

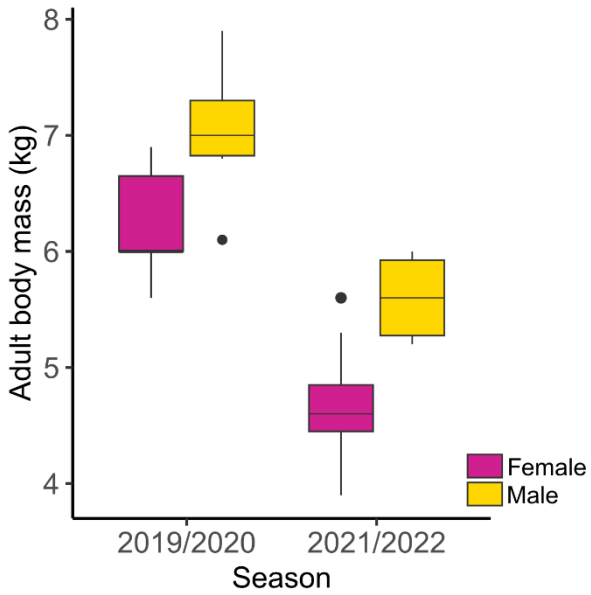

Figura 7.1 Masa corporal (kg) de pingüinos papúa adultos machos y hembras que se reproducen en la isla Ardley (isla Rey Jorge/Isla 25 de Mayo), durante las temporadas de cría 2019/2020 y 2021/2022.

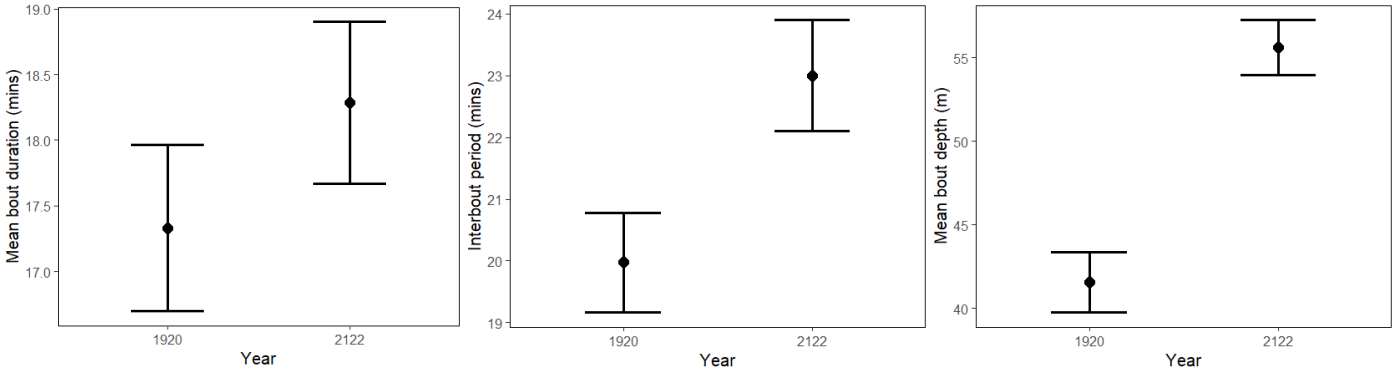

Figura 7.2 Métricas del comportamiento de buceos de alimentación en ráfaga "bouts" de los pingüinos papúa durante las temporadas de cría 2019/2020 y 2021/22

Si bien la disponibilidad de alimento suele estar asociada al éxito reproductivo en aves marinas, nuestros resultados no evidencian una relación directa entre la abundancia de krill y el éxito reproductivo de Adelia y papúa. Esto sugiere que el éxito reproductivo no responde únicamente a la disponibilidad de presas, sino que está mediado por múltiples factores, incluyendo condiciones meteorológicas extremas, características del sitio de nidificación y particularidades de la historia de vida de cada especie. Esta complejidad resalta la importancia de programas de monitoreo integrados que incluyan múltiples dimensiones para interpretar adecuadamente los cambios observados en el ecosistema.

Por otro lado, destacamos el valor de distintos aspectos del comportamiento de forrajeo y del peso de los pichones al emplume de ambas especies como indicadores sensibles de la disponibilidad de presas. En particular, el uso de características de los viajes de alimentación de los pingüinos Adelia, como la duración y distancia de los viajes, parecería ser un indicador robusto para detectar variaciones en la abundancia de krill a escala local, que ha sido evidenciado anteriormente por diversos autores (Watanuki *et al.,* 1993; Fraser and Hofmann 2003; Ainley *et al*., 2015; Lescroël *et al*., 2020). Asimismo, el análisis del comportamiento de buceo, especialmente su organización en bouts, permite incorporar una dimensión adicional en la evaluación de la disponibilidad de presas, al considerar no solo su abundancia, sino también su accesibilidad en la columna de agua para las distintas especies. Este enfoque cobra especial relevancia en el contexto de las discusiones actuales del Grupo de Trabajo sobre Monitoreo y Gestión de Ecosistemas (WG-EMM) de la CCRVMA sobre la revisión de los métodos estándar del programa CEMP y la necesidad de identificar nuevos indicadores más sensibles y específicos.

7.2 Tendencias poblacionales

Los factores que determinan las tendencias poblacionales en pingüinos del género Pygoscelis en la Península Antártica occidental han sido ampliamente debatidos. Mediante la integración de información sobre distintos parámetros poblacionales, comportamiento de forrajeo y condiciones ambientales locales, esta tesis aporta evidencia para comprender los mecanismos que subyacen a las trayectorias contrastantes observadas entre Adelia y papúa.

La tendencia poblacional de estas especies suele evaluarse a partir de los cambios interanuales en el número de parejas reproductivas presentes en una colonia al comienzo temporada, un indicador que refleja la influencia de procesos de largo plazo y es, en parte, una medida de supervivencia durante el invierno precedente (Fraser *et al*., 1992; CCRVMA 2004). En especies altamente filopátricas como los pingüinos, el éxito reproductivo condiciona el reclutamiento de nuevos individuos, influyendo directamente en las tendencias poblacionales a mediano plazo (Hinke *et al.,* 2007), que a su vez, suele estar modulado por factores locales y puntuales que operan durante la temporada de cría, como la disponibilidad de alimento y la calidad del sitio de nidificación (Trathan *et al*., 1996). En este contexto, se propone que los principales moduladores de las tendencias poblacionales incluyen la capacidad diferencial de las especies para ajustar su cronología reproductiva a las condiciones locales, la disponibilidad de alimento durante la temporada de cría y factores invernales que afectan la supervivencia de juveniles y adultos (Hinke *et al*., 2007, 2012; Emmerson *et al*., 2011; Lynch *et al.,* 2012; Juáres *et al*., 2013; Cimino *et al*., 2016).

7.2.1 Pygoscelis adeliae

En el caso del pingüino Adelia, el análisis de cinco temporadas en Isla Ardley mostró variaciones en el número de parejas reproductivas y en el éxito reproductivo, influenciadas por una combinación de factores ecológicos que operan en distintas escalas temporales y espaciales. En cuanto a la disponibilidad de alimento, observamos que en años con baja abundancia o disponibilidad de krill se producen cambios en las estrategias de forrajeo tanto en machos como en hembras. En particular, las hembras incrementaron significativamente la duración y distancia de sus viajes de alimentación, con un esfuerzo de forrajeo aproximadamente un 50% mayor, lo que se tradujo en un costo energético un 20% más alto.

Este patrón ha sido interpretado como una respuesta a un umbral crítico de masa corporal, en el que, al alcanzar un peso corporal mínimo, los adultos priorizan su propia condición corporal mediante viajes más largos para recuperar reservas. Estos viajes más largos pueden tener un costo para las crías y, en última instancia, en el éxito reproductivo (Ballance 2009; Ballard *et al*., 2010; Salmerón *et al*., 2023).

Nuestros datos muestran que la masa corporal de los pingüinos Adelia fue aproximadamente un 40% menor en años de baja abundancia, en comparación con temporadas de buena disponibilidad de krill, lo que sugiere que en particular las hembras alcanzaron una masa corporal que las llevó a realizar viajes más largos para recuperar reservas. Aun así, no se observaron diferencias significativas en el éxito reproductivo entre temporadas con distinta disponibilidad de krill, lo que sugiere que los pingüinos Adelia lograron amortiguar la baja disponibilidad de alimento y criar a sus pichones. Sin embargo, la cantidad y calidad de alimento aportado durante la etapa de cría puede ser determinante, ya que la condición corporal de los pichones al momento de la emancipación influye en su supervivencia durante el primer invierno (Ainley *et al*., 2018; Cimino *et al*., 2014). En otras regiones, como la Antártida este (Nicol *et al*., 2008; Tierney *et al.*, 2009; Beaulieu *et al*., 2010) y el mar de Ross (Olmastroni *et al*., 2020; Jafari *et al*., 2021) se ha documentado que los pingüinos Adelia pueden modificar su dieta ante la escasez de krill, incorporando una mayor proporción de peces (en particular *Pleuragramma antarctica*), consideradas presas de mayor valor energético, lo que les permite mantener un buen éxito reproductivo (Nicol *et al.,* 2008; Beaulieu *et al*., 2010). Sin embargo, nuestros análisis de isótopos estables no evidenciaron cambios significativos en la posición trófica entre temporadas con alta o baja abundancia de krill, lo que indica que los pingüinos en Isla Ardley no modificaron sustancialmente su dieta. Esto sugiere que, a diferencia de lo observado en otras colonias, el cambio de presa no fue una opción viable en nuestra área de estudio, probablemente debido a la disminución reportada en la abundancia de peces en la región (Mintenbeck y Torres 2017; Corso et al., 2022). Así, aunque el éxito reproductivo no se vio afectado, el menor peso de los pichones en años de escasez de krill puede ser un reflejo de las limitaciones por la ausencia de presas alternativas de alto valor energético.

En cambio, durante la temporada 2023/24, los pingüinos Adelia de Isla Ardley registraron el éxito reproductivo más bajo de todo el período analizado. Sin embargo, los parámetros asociados a la duración de los viajes de alimentación y al peso de los pichones al emplume sugieren que la disponibilidad de krill fue elevada, por lo que es probable que la causa principal de esta baja productividad esté vinculada a factores meteorológicos adversos ocurridos al inicio de la temporada. A fines de octubre se registró un evento extremo caracterizado por vientos muy intensos y temperaturas inusualmente bajas, lo que provocó una fuerte caída en la sensación térmica. A esto se sumó una acumulación de nieve por encima del promedio durante noviembre, retrasando el derretimiento temprano y manteniendo condiciones frías durante todo el trimestre. Este tipo de eventos han sido señalados como determinantes en el éxito reproductivo (Lynch *et al*., 2009, 2012; Hinke *et al.,* 2012; Juáres *et al*., 2013). En nuestra colonia, estas condiciones coincidieron con una marcada pérdida de nidos entre el conteo inicial de parejas con huevos y el recuento de nidos con pichones unas dos semanas después, lo que indica una elevada mortalidad temprana de pichones y/o fallas en la eclosión.

Entonces, la variabilidad ambiental tanto en el medio marino como en el terrestre puede impactar fuertemente la dinámica poblacional de *P. adeliae*, dada su limitada capacidad para amortiguar fluctuaciones modificando aspectos de su ecología. Aunque registramos cierta flexibilidad en el comportamiento de alimentación que probablemente permitió enfrentar en parte la variabilidad en la disponibilidad de presas, la disminución local de krill puede impactar en otros aspectos demográficos. En particular, la mala condición corporal de las hembras en años de baja disponibilidad de alimento podría incrementar su vulnerabilidad y reducir su supervivencia invernal, disminuyendo así el número de adultos que retornan a reproducirse la temporada siguiente. Este efecto puede potenciarse con otros factores invernales, como la reducción del hielo marino y la escasez de alimento en las áreas de invernada. Un ejemplo de esto fue la temporada 2022/23, cuando se registró el menor número de parejas reproductivas de la serie, posterior a un año en que las hembras mostraron baja condición corporal y alto gasto energético asociado a la escasez de krill.

Por otro lado, su escasa plasticidad en la fenología reproductiva, condicionada por limitaciones fisiológicas y comportamentales, restringe su capacidad para ajustar el inicio de

la reproducción a condiciones locales (Hinke *et al*., 2012). El arribo a la colonia desde las áreas de invernada lejanas, seguido de un período de ayuno implica un límite energético que dificulta retrasar la puesta para evitar efectos negativos de las condiciones ambientales. Así, la acumulación de nieve excesiva en los sitios de nidificación puede reducir marcadamente el éxito reproductivo, independientemente de la disponibilidad de alimento. Por último, si bien la menor condición corporal de los pichones o un bajo éxito reproductivo no afectan el tamaño de la población reproductiva en la temporada inmediata siguiente, dado que los juveniles reclutan como adultos reproductores entre 5-6 años después, sí pueden influir en las tendencias poblacionales a mediano plazo.

En resumen, factores como la declinación de la biomasa de krill antártico, incremento en tormentas tardías al comienzo de la temporada y la poca plasticidad ecológica de los pingüinos Adelia, generarían en conjunto factores negativos que impactan sobre la tendencia poblacional. Además, esta tendencia poblacional negativa parecería estar determinada por factores que operan tanto durante el período invernal como durante el período reproductivo.

7.2.2 Pygoscelis papua

En el caso del pingüino papúa, se registró un incremento sostenido en el número de parejas reproductivas a lo largo de las temporadas estudiadas, mientras que el éxito reproductivo se mantuvo relativamente estable, incluso en la temporada 2023/24, cuando Adelia registró su menor valor en cinco años, lo que sugiere que existen algunas características que le confieren la capacidad de amortiguar las condiciones cambiantes.

Por un lado, a diferencia de su congénere, papúa es una especie no migratoria y no presenta un período de ayuno previo a la puesta de huevos, lo que le permite evaluar tempranamente las condiciones locales y ajustar el inicio de la reproducción bajo escenarios desfavorables (Forcada y Trathan 2009; Hinke *et al*., 2012; Juáres *et al*., 2013; Korczak-Abshire *et al*., 2021). Esta plasticidad incluye la posibilidad de retrasar la puesta, realizar una segunda puesta tras un fallo temprano, o incluso relocalizar nidos, lo que le permite amortiguar los efectos de eventos adversos y sostener su éxito reproductivo (Lynch *et al*., 2009, 2012; Hinke *et al*., 2012; Juáres *et al*., 2015). Si bien durante nuestro periodo de estudio no registramos las fechas de llegada a la colonia ni de puesta de huevos, las observaciones de campo a finales de noviembre

sugieren que durante la temporada 2023/24, los pingüinos papúa iniciaron la puesta varios días más tarde que en temporadas previas. Sin embargo, al igual que Adelia, se registró una elevada mortalidad temprana de pichones y/o fallas en la eclosión al comienzo de la temporada, lo que indica que, a pesar de su capacidad de retrasar la puesta, los papúas también sufrieron el impacto de las malas condiciones ambientales en los sitios de nidificación. Entonces, sugerimos que otros factores adicionales pudieron influir en su capacidad para sostener un elevado éxito reproductivo.

En las altas latitudes, la ventana temporal para la reproducción suele estar estrechamente sincronizada con los picos estacionales de disponibilidad de alimento (Chapman *et al.*, 2010; Forcada y Trathan 2009), de modo que cualquier cambio en la fenología reproductiva puede generar desajustes entre depredadores y presas (Durant *et al.*, 2007; Boersma 2008). No obstante, nuestras observaciones durante la temporada 2023/24 muestran que un inicio tardío en la reproducción no afectó negativamente el éxito reproductivo de papúa, sugiriendo que una alta disponibilidad de alimento durante el periodo de cría pudo compensar el retraso. Esto probablemente se deba al ciclo reproductivo más prolongado de esta especie, con un periodo de cría cercano a 72 días (Trivelpiece *et al.*, 1987), que bajo condiciones de alta disponibilidad de presas le permitió recuperarse de un comienzo de temporada desfavorable.

Por otro lado, considerando su comportamiento de forrajeo, esta especie mostró una mayor estabilidad en la duración y distancia de los viajes de alimentación entre temporadas con distinta disponibilidad de krill. Esta estabilidad podría estar asociada a su plasticidad en la dieta y comportamiento de forrajeo (Miller *et al.*, 2009). Si bien en la región de la PA el krill antártico es su principal recurso, estudios previos han reportado que los peces constituyen un componente importante en su dieta (Miller *et al.*, 2009, 2010), lo que potencialmente les permitiría amortiguar fluctuaciones interanuales en la disponibilidad de krill. Sin embargo, a partir de análisis isotópicos en Isla Ardley, observamos que papúa mantuvo una posición trófica relativamente estable a lo largo de las temporadas, sin evidencias claras de un cambio marcado en la dieta entre años de distinta abundancia de krill (Figura 7.3). Esto sugiere que, durante nuestros años de estudio, al igual que Adelia, la dieta potencial de papúa podría estar limitada por la oferta local de presas alternativas. No obstante, su capacidad de bucear a mayores profundidades, posiblemente asociada a su mayor tamaño corporal, le permitiría

explotar un nicho inaccesible para su congénere (Trivelpiece *et al*., 1987). Durante la temporada de baja abundancia de krill (2021/22), Salmerón *et al*. (2023) reportaron mediante sondeos acústicos, que tanto la abundancia como la disponibilidad del recurso eran menores para los pingüinos, ya que los parches se encontraban a mayores profundidades. En este contexto, el registro de buceos de alimentación más profundos en papua durante esa temporada podría haberle permitido alcanzar parches de krill más profundos y mantener así relativamente estable la duración de sus viajes de alimentación.

En resumen, características de su historia de vida como su mayor flexibilidad fenológica, ciclo reproductivo más largo y ser una especie residente durante el período no reproductivo parecería conceder ciertas ventajas frente a condiciones ambientales cambiantes de la PA.

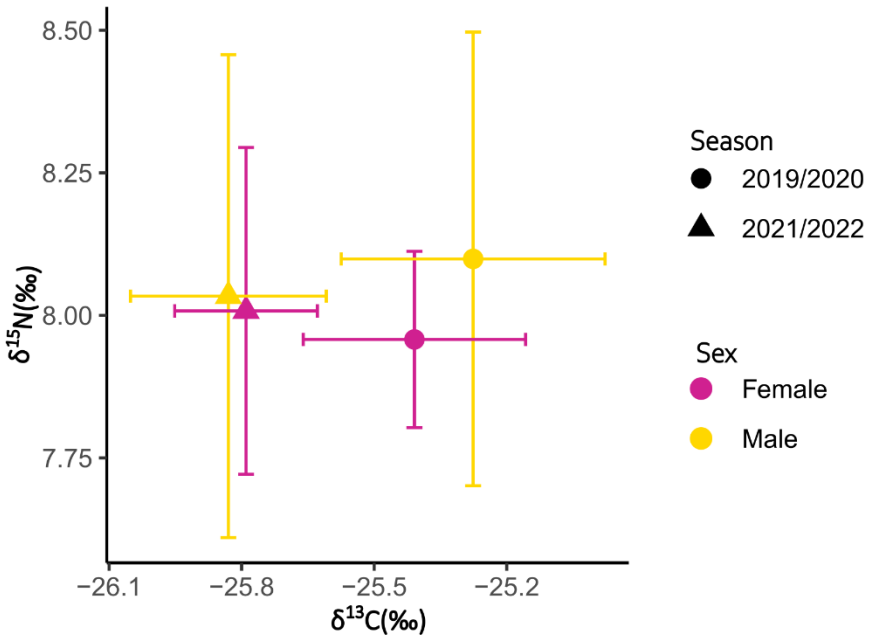

Figura 7.3 Biplot de los valores isotópicos $\delta^{13}C$ y $\delta^{15}N$ (‰) de sangre de pingüinos papúa adultos machos y hembras que se reproducen en la isla Ardley (Isla Rey Jorge/25 de Mayo) durante las temporadas 2019/2020 y 2021/2022.

7.3 Aportes para la gestión del océano Austral

En el sector norte de la PA existe una necesidad creciente de contar con más y mejores datos ecológicos que sustenten decisiones para la conservación del ecosistema y la gestión de la pesquería. La información sobre la distribución en el mar de los predadores tope es clave para comprender la dinámica del ecosistema y constituye un insumo fundamental para las medidas

de manejo espacial que buscan identificar regiones de importancia para la conservación. En este sentido, Trathan *et al.* (2022) destacan que, ante el aumento de la presión pesquera, la recuperación de mamíferos marinos y el acelerado cambio climático, el monitoreo detallado sobre los cambios en las poblaciones de krill, sus depredadores dependientes y su entorno oceanográfico resulta esencial para una gestión ecosistémica efectiva.

Para conservar el ecosistema marino ante este escenario de cambios, la CCRVMA debería adoptar una estrategia de gestión precautoria para la pesca de krill que ajuste de manera flexible los límites de captura. Sin embargo, la estrategia actual utiliza límites de captura fijos, que no se han actualizado en más de una década (Watters y Hinke 2022). Dos medidas de conservación (CM por sus siglas en inglés) definían hasta el momento la estrategia de gestión del krill en el norte de la PA y el mar de Escocia. La primera, la CM 51-01, establece un límite de captura de 5,61 millones de toneladas en cada temporada de pesca para el área 48, pero que, hasta que la CCRVMA haya definido una asignación de este límite de captura total entre unidades de gestión más pequeñas (*small-scale management units*, SSMUs), la captura total combinada en todas las subáreas se limita a 620.000 toneladas por temporada de pesca (conocido como "*trigger level*"). Esto fue definido con el fin de restringir la posibilidad de que todas las capturas se realicen en puntos específicos del área total. Sin embargo, con el aumento de la pesquería desde la década de 2000, surgió la preocupación de que capturas concentradas en áreas pequeñas podrían afectar a depredadores dependientes del krill. Para mitigar estos riesgos, se adoptó la medida de conservación CM 51-07, que subdividió espacialmente el *trigger level* entre las subáreas 48.1 a 48.4, asignando capturas máximas por subárea.

Sin embargo, debido a la falta de consenso en la última reunión de la CCAMLR (2024), la CM 51-07 expiró, generando gran preocupación al representar un retroceso en las políticas precautorias de conservación (Trathan *et al*., 2025). Su vencimiento implica que ahora es posible alcanzar el *trigger level* en cualquiera de las subáreas del área 48, lo que podría tener un impacto significativo en las especies dependientes de krill, especialmente si el esfuerzo pesquero se concentra en el tiempo y el espacio, como se ha observado recientemente en el Estrecho de Bransfield y las Islas Shetland del Sur (Santa Cruz *et al*., 2018; Watters *et al*., 2020). En este contexto, comprender las interacciones predador-presa a pequeña escala es

fundamental para el diseño de estrategias de conservación y gestión sostenible de recursos en esta región (Watters *et al*., 2020; Trathan *et al*., 2022; Warwick-Evans *et al*., 2022). En particular, la generación de mapas a escala detallada del consumo de presas por parte de los predadores proporciona un mecanismo para informar la evaluación de riesgos e identificar las áreas y los momentos de interacción que pueden utilizarse para fundamentar las decisiones de gestión sobre la asignación de capturas (Warwick-Evans *et al*., 2022).

En el norte de la PA, aunque existen antecedentes que describen la distribución espacial y el hábitat de pingüinos reproductores y no reproductores (Wilson 2002; Kokubun *et al*., 2010; Lee *et al*., 2021; Oosthuizen *et al*., 2022; Salmerón *et al*., 2023), así como su solapamiento con la pesquería (Hinke *et al*., 2017; Krüger *et al*., 2021; Watters *et al*., 2020), la información detallada, actualizada y de alta resolución sobre su comportamiento de forrajeo en el mar continúa siendo escasa. En este sentido, esta tesis aporta información valiosa para mejorar la comprensión de cómo los pingüinos utilizan su hábitat marino tridimensional y cómo ajustan sus estrategias de forrajeo ante variaciones en la disponibilidad de krill.

En particular, proponemos la aplicación de un enfoque novedoso de alta resolución basado en acelerometría para la identificación de comportamientos específicos de capturas presas. Mediante esta aproximación, es posible mapear las áreas clave de alimentación de los predadores, pudiendo generar información relevante para la planificación de la gestión espacial de la subárea 48.1. De hecho, el uso de datos de seguimiento ha sido clave para respaldar la creación de Áreas Marinas Protegidas (AMP), como en la plataforma sur de las islas Orcadas del Sur (2009) y en el Mar de Ross (2016) (Warwick-Evans *et al*., 2018; Brooks *et al*., 2021). En esa misma línea, los resultados de esta tesis pueden contribuir de forma sustantiva a fortalecer la propuesta de un AMP en el oeste de la Península Antártica, actualmente en discusión en el seno de la CCRVMA (Hogg *et al*., 2020).

Finalmente, una línea clave para fortalecer el rol del monitoreo de depredadores en la gestión ecosistémica de la pesquería de krill es avanzar hacia estimaciones más precisas y espacialmente explícitas de las necesidades de consumo de krill por parte de los predadores. Este enfoque permitiría mejorar las evaluaciones de riesgo previas a la toma de decisiones de manejo (Warwick-Evans *et al*., 2022). En este contexto, el uso de acelerómetros para identificar comportamientos específicos de captura de presas representa un avance

metodológico significativo frente a los métodos tradicionales basados en detección de *wiggles* en los perfiles de buceo (Oosthuizen *et al*., 2025). Recientemente, se ha demostrado que la detección de eventos de alimentación a partir de acelerometría proporciona estimaciones más precisas y confiables del esfuerzo de búsqueda y de la tasa de captura (Schoombie *et al*., 2024), lo que permite inferir con mayor certeza cuándo, dónde y con qué intensidad los pingüinos están accediendo a sus presas. Este tipo de información resulta clave para modelar la demanda energética de los predadores y establecer límites de captura precautorios en escalas coherentes con las interacciones predador-presa.

7.4 Conclusiones generales

En conjunto, esta tesis contribuye sustancialmente al entendimiento de cómo los pingüinos del género *Pygoscelis* responden a la variabilidad ambiental en la Península Antártica Occidental. Al integrar información espacial, fisiológica y poblacional, ofrece una visión más completa de los mecanismos detrás de sus respuestas ecológicas. Este conocimiento es estratégico para apoyar medidas de manejo ecosistémico, tales como la planificación de Áreas Marinas Protegidas o la regulación espacial de la pesquería de krill, especialmente en zonas como el estrecho de Bransfield y las islas Shetland del Sur, que concentran más del 30% de la captura total de krill en el continente antártico.

A lo largo de este trabajo se caracterizó en detalle cómo estas especies ajustan sus estrategias de alimentación frente a restricciones energéticas y ambientales, identificando áreas clave de alimentación y revelando diferencias relevantes entre sexos, años y especies. Se observó que *P. adeliae* responde de forma más marcada a variaciones en la disponibilidad de krill, mostrando mayor sensibilidad en sus parámetros de comportamiento y gasto energético, lo que lo posiciona como un indicador particularmente informativo sobre las condiciones del ecosistema marino. En contraste, *P. papua* exhibe una mayor flexibilidad conductual y en su fenología, que podría explicar en parte su éxito reproductivo más estable y sus tendencias poblacionales positivas en la región.

Los resultados de esta tesis no sólo profundizan el conocimiento ecológico sobre estas especies, sino que también ofrecen insumos concretos para la gestión basada en evidencia. El uso de herramientas novedosas como los acelerómetros permitió identificar zonas de

alimentación recurrentes, información crucial para la planificación de Áreas Marinas Protegidas y para el manejo espacial de la pesquería de krill. Por lo tanto, este trabajo destaca la relevancia de los enfoques integrados y la necesidad de continuar generando datos de alta resolución que permitan monitorear el ecosistema antártico en un escenario de cambios sin precedentes.

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