Assessing the adequacy of a novel fisheries no-take zone around a major African penguin (Spheniscus demersus) colony, Dyer Island, South Africa

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Assessing the adequacy of a novel fisheries no-take zone around a major African penguin (*Spheniscus demersus*) colony, Dyer Island, South Africa

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Abstract (English version): Assessing the adequacy of a novel fisheries no-take zone around a major African penguin (*Spheniscus demersus*) colony, Dyer Island, South Africa.
Camille Van Landuyt, 2025 – 2026, BirdLife South Africa; Supervisors: Alistair McInnes & Eric Parmentier

The African penguin is the most threatened penguin species globally and could become extinct in the wild by 2035. One of the main threats facing this species is a lack of prey: mostly anchovy and sardine. The causes of the reduced availability of prey are complex but competition with the purse-seine fishery is partly responsible as this fishery targets the same species as the penguins. To mitigate resource competition, the South African government implemented no-take zones around six of the largest African penguin colonies in 2022, forbidding catches of small pelagic fish (sardine, anchovy and round herring) in these zones, although the extent of the majority of these closures was assessed as not being representative of important penguin foraging areas. After a court order in March 2025, improved no-take zones were implemented around four of the six colonies. However, the zone around the colony at Dyer Island remained unchanged. This thesis focuses on the specific case of the no-take zone around Dyer Island, which, unlike other no-take zones that involve a total fishing ban, includes a fully restricted zone inside of a broader vessel-size restricted zone, prohibiting vessels equal to or greater than 26 meters long to enter the zone – a design aiming to allow local vessels to continue fishing, while excluding the larger vessels from more distant ports. Hence, this work aims to assess the adequacy of this novel no-take zone configuration around the Dyer Island colony through a comparative study of different penguin path metric parameters before and after the closure was implemented in 2022. This work also assesses how the general trend of fishing catches changed after the implementation of this zone, and assesses whether the current no-take zone configuration has the potential to alleviate competition between local vessels and those from elsewhere. There was no evidence of significant differences in the maximum distance penguins travelled from the colony, total distance travelled per trip and trip duration between the period preceding and following the implementation of the no-take zone. Fishing trends within the no-take zone perimeter appeared to be driven primarily by imposed fishing quotas rather than the no-take zone itself. Specifically, fishing trends and fishing effort from vessels frequently operating in the area remained similar within the closure area after its implementation, suggesting the no-take zone did not have an impact on the local fishing vessels. Overall, results of this assessment suggest that the current configuration of the no-take zones around Dyer Island is likely insufficient to reduce resource competition on African penguins and highlights the need to explore alternative fishing closure regimes for this important colony.

Résumé (version en français): Évaluation de la pertinence d'une nouvelle zone de non-prélèvement halieutique atour d'une colonie majeure de manchots du Cap (*Spheniscus demersus*), Dyer Island, Afrique du Sud.
Camille Van Landuyt, 2025 – 2026, BirdLife South Africa; Promoteurs: Alistair McInnes & Eric Parmentier

Le manchot du Cap est l'espèce de manchots la plus menacée au monde et pourrait se retrouver éteint en milieu naturel d'ici 2035. L'une des principales menaces à laquelle l'espèce fait face est le manque de proies, principalement des anchois et sardines. Les raisons de ce manque de disponibilité en proies sont complexes, mais la compétition alimentaire avec la pêche à la senne coulissante est en partie responsable, car elle vise les mêmes espèces que le manchot. Afin d'atténuer la compétition pour ces ressources, le gouvernement sud-africain a mis en œuvre en 2022 des zones de non-prélèvement autour des six plus grandes colonies de manchots du Cap, y interdisant le prélèvement de petits poissons pélagiques en leur sein (sardines, anchois et harengs), bien que l'étendue de la majorité de ces fermetures ait été jugée comme non-représentative des zones de recherche de nourriture importantes du manchot. Suite à une décision de justice rendue en mars 2025, des zones de non-prélèvement améliorées ont été mises en place autour de quatre de ces six colonies. Cependant, la zone autour de la colonie de Dyer Island est restée inchangée. Ce mémoire porte sur le cas spécifique de la zone de fermeture autour de Dyer Island, qui, contrairement aux autres zones de non-prélèvement qui interdisent totalement la pêche, comprend une zone de fermeture totale à l'intérieur d'une zone plus large de restriction de taille des navires, interdisant l'accès aux navires de 26 mètres de long et plus – une configuration ayant pour objectif de permettre aux navires locaux de continuer à pêcher, tout en excluant les navires plus grands provenant de ports plus éloignés. Ce travail vise ainsi à évaluer la pertinence de cette nouvelle configuration de zone de non-prélèvement autour de la colonie de Dyer Island par une étude comparative de différentes métriques de déplacement des manchots avant et après la mise en œuvre de la fermeture en 2022. Cette étude évalue également l'évolution des tendances des captures de pêche dans cette zone après sa mise en place, et évalue si la fermeture actuelle a la capacité d'atténuer la compétition entre les navires de pêche locaux et ceux venant d'ailleurs. Aucune différence significative n'a été observée concernant la distance maximale parcourue en mer par les manchots depuis la colonie, la distance totale parcourue par sortie et la durée des sorties entre les périodes précédant et suivant la fermeture. Les tendances de pêche au sein du périmètre de fermeture sont apparues comme étant principalement imposées par les quotas de pêche plutôt que par la fermeture elle-même. En particulier, les tendances de pêche ainsi que l'effort de pêche des navires opérant fréquemment dans la zone sont restés similaires au sein de la zone après sa mise en place,

suggérant que la fermeture n'a pas eu d'impact sur les navires de pêche locaux. Globalement, les résultats de cette évaluation suggèrent que la configuration actuelle de la fermeture autour de la colonie de manchots de Dyer Island est probablement insuffisante pour réduire la compétition alimentaire qui pèse sur le manchot du Cap, et soulignent la nécessité d'explorer d'autres régimes de fermeture pour cette colonie majeure.

Table of abbreviations:

AIC: Akaike Information Criterion

CI: Confidence Interval

DFFE: Department of Forestry, Fisheries and the Environment

EAFM: Ecosystem Approach to Fisheries Management

GLM: Generalized Linear Model

GLMM: Generalized Linear Mixed Model

ICE: Island Closure Experiment

LMM: Linear Mixed Model

MPA: Marine Protected Area

OBM: Opportunity-Based Model

OMP: Operational Management Procedures

TAB: Total Allowable Bycatch

TAC: Total Allowable Catch

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INTRODUCTION

A) ECOLOGY OF THE AFRICAN PENGUIN

1) GEOGRAPHICAL DISTRIBUTION AND HABITAT

The African penguin (*Spheniscus demersus*), previously named Black-footed penguin or Jackass penguin because of its donkey-like braying (Hockey et al., 2005), is a flightless seabird species endemic to the greater Benguela Upwelling Ecosystem, off the coasts of Namibia and South Africa (Kemper et al., 2001; Crawford et al., 2006a). Historically, African penguins have been found breeding between Hollams Birds Island (Namibia) and Bird Island in Algoa Bay (South Africa), although non-breeding birds have been recorded up to Sette Cama (Gabon) and Inhaca Island (Mozambique) (Shelton et al., 1984). During pre- and post-moult, adult penguins can range up to 600 km away from their colony (Carpenter-Kling et al., 2022). Nonetheless, breeding African penguins are invariably restricted to within 50 km of their breeding sites (Shelton et al., 1984). African penguins occur in cold upwelling ecosystems, typically in shallow coastal waters not exceeding 200 meters in depth (Carpenter-Kling et al., 2022). Breeding colonies, which are also used for the moulting stage, are established on coastal habitats, mostly islands, generally characterised by low-lying and rock-strewn terrain, with almost no vegetation (Frost et al., 1976a; Martínez et al., 2020). To cope with the heat of their terrestrial environment, they have several adaptations, such as a crepuscular lifestyle and a preference for the shelter of a rock or bush as breeding sites (Frost et al., 1976a).

2) PHYSICAL CHARACTERISTICS

Adult African penguins are 55 to 65 cm tall, with black and white feathers and a patch of naked pink skin above the eyes (Hockey et al., 2005). They have a characteristic black band on the breast and a black and white pattern on the face (BirdLife International, 2024). Mean body mass of an adult is 3.2 kg, with females having a significantly lower body mass than males (Nagy et al., 1984; Hockey et al., 2005). Their longevity can exceed 27 years (Hockey et al., 2005).

3) DIET AND FORAGING ACTIVITY

African penguins primarily feed on anchovy (*Engraulis capensis*) and sardine (*Sardinops sagax*) as well as other pelagic fish, the vast majority of their fish prey being

between 50 mm and 115 mm long (Crawford et al., 2011; Wilson, 1985a). Although anchovy is predominant in the African penguins' diet, especially during the breeding season, sardine (*Sardinops sagax*) can also constitute a significant part of their diet, especially during the non-breeding season (Crawford et al., 2011; Robinson et al. 2015). Local variations also include other types of prey, such as chokka squid (*Loligo reynaudii*) in Algoa Bay, or pelagic gobies (*Sufflogobius bibarbarus*) in Namibia, largely due to the collapse of small pelagic species (Connan et al., 2016; Ludynia et al., 2010; Crawford et al., 1985)

There is a positive correlation between the distance travelled at sea and the amount of food gained (Wilson, 1985b). The swimming speed, duration and distance travelled at sea depend on the availability of food as well as the type of activity at sea (i.e. commuting, foraging or resting) (Heath & Randall, 1989; Petersen et al., 2006). The duration of foraging trips also depends on the individual experience and the nutritional demands of the chicks (Heath & Randall, 1989). Although usually lasting less than a day, the foraging duration during the breeding season can last between one and ten days, depending on the abundance and the proximity of prey to the breeding sites, and the foraging range generally extends from 5 to 30 km from the colonies, with a mean dive depth of 14 m (Pichegru et al., 2010; Heath & Randall, 1989; Ryan et al., 2007).

During the breeding season, African penguins generally leave the colony early in the morning (Petersen et al., 2006). They mainly dive during the day and then usually return to the colony in the afternoon or at night (Ryan et al., 2007; Heath & Randall, 1989). Penguins are visual hunters, explaining why they dive during daylight, although they are able to use olfactory cues such as dimethyl sulphide to locate their prey (Cunningham et al., 2008; Wright et al., 2011).

African penguins frequently forage in groups and are highly cohesive and synchronized when diving (Siegfried et al. 1975; Ryan et al., 2012). Group foraging on schooling prey enhances prey capture where they circle schools of pelagic fish, disrupt their schooling behaviour and sometimes force them to come up to the surface in a so-called bait-ball (McInnes et al. 2017; Ryan et al., 2012).

4) Reproduction and social structure

There are currently 26 breeding localities dispersed throughout South Africa and Namibia (7 in Namibia and 19 in South Africa) (Sherley et al., 2024). Colony populations vary over time, depending on several factors such as prey biomass (Crawford et al. 2011).

African penguins are monogamous, and can exhibit high partner fidelity (Randall, 1983). The main breeding season occurs from February to September and the breeding peak varies between colonies but invariably occurs in the winter months, likely mediated by seasonal variation in food availability (Crawford & Dyer, 1995; Wilson, 1985a). Incubation duties are shared between both adults with incubation shifts that are typically one to two days long but can last for more than five days (Williams & Cooper, 1984; Randall, 1983). Clutch size varies between one and two eggs, although it can go up to three eggs. Depending on the breeding colony, a second clutch can occur during the same year, rarely a third one (Cock & Cooper, 1987; Crawford et al., 1999). Fledging success is related to prey biomass with high inter-annual and inter-colony variation (Crawford et al., 1999). Food availability on a regional or local scale has an influence on the number of birds that will breed, and breeding success is highly dependent on the availability of pelagic prey within a 20 - 30 km radius of their breeding sites (Crawford et al., 1999; Crawford & Dyer, 1995; Pichegru et al., 2009). During the chick-guarding phase, this spatial constraint is exacerbated, as pairs alternate nest attendance, with one individual attending the nest while the other undertakes foraging trips at sea (Nagy et al., 1984).

Historically, African penguins predominantly nested in guano burrows which afforded them protection from solar radiation and offered a more favourable microclimate, with less variations in temperature, higher humidity and less wind (Frost et al., 1976a). Nests can also be found under rocks, under bushes, exposed or, in rare occasions, in caves (Frost et al., 1976a; Loutit & Boyer, 2024).

5) Moulting

African penguins undergo an annual moult where their old feathers are rapidly replaced by new ones. This period is also referred to as “catastrophic moulting” as it includes a rapid replacement of all feathers, lasting only 13 to 34 days, and occurs on land. The moulting period is critical as penguins undergo thermoregulatory deficits and a loss of their waterproof feathers,

which prevents them from feeding during this phase (Welman et al., 2024; Beltran et al., 2018). The moulting period generally takes place between September and January in South Africa, when prey is generally less abundant (Crawford et al., 2006b; Wolfaardt et al., 2009). Prior to moult, birds spend an uninterrupted period at sea lasting over a month, during which time they build fat reserves (Randall, 1983). During the moulting period, individuals lose approximately 47% of their body mass (Wilson, 1985b).

6) THREATS

The population decline of the African penguin is the result of cumulative historical pressures and ongoing threats, which collectively maintain the population on a downward trajectory. Historical threats included egg collecting for human consumption, with over 13 million eggs collected between 1900 and 1930, and guano mining as a source of fertilizer (Frost et al., 1976b; Frost et al., 1976a). Guano mining during the 19th and 20th centuries destroyed most of the African penguin's natural nesting habitat, forcing individuals to nest more in surface nests rather than burrows, increasing their vulnerability to heat stress and predation (Frost et al., 1976a). The extent of this habitat loss is exemplified by the colony of Bird Island, where, in 2012, less than 1% of the birds were able to breed in natural burrows in guano (Lei et al., 2014). As a result, various types of artificial nests have been developed on colonies since 2001 (Pichegru et al., 2024). Although these two practices are now banned, a number of additional pressures are currently taking place. The most central pressure on the African penguin is food depletion, resulting from a combination of two factors: shifts in prey biomass and competition for food with industrial fishing. Due to climate change and localized overfishing, the biomass distribution of sardines and anchovies has shifted from the west coast to the south and east coasts of South Africa (Ramírez et al., 2022; Coetzee & de Moor, 2024). However, commercial fishing, historically concentrated on the west coast, maintains higher levels of exploitation in that area than on the south coast for logistical reasons (Coetzee & de Moor, 2024). This mismatch between prey distribution and areas of intensive fishing creates food-depletion hotspots to which penguins, as central-place foragers, are exposed (Ramírez et al., 2022). Predation also constitutes a threat for penguins, both at sea and on land, as they are preyed upon by caracals (*Caracal caracal*), leopards (*Panthera pardus*), domestic dogs (*Canis lupus familiaris*), Cape grey mongooses (*Galerella pulverulenta*), feral cats (*Felis catus*), and Cape fur seals (*Arctocephalus pusillus*) (Vanstreels et al., 2019; Borboroglu & Boersma, 2013; Makhado et al., 2013). Marine traffic further drives species decline, with a demonstrated link

between increased noise generated by maritime traffic and a decrease in breeding pairs, as well as through oil spills (Ludynia et al., 2026; Pichegru et al., 2022). Avian Influenza H5N8 also contributes to the threats, amongst other factors (Roberts et al., 2023).

B) Fisheries in South Africa

The small pelagic sector is the largest fishery by volume extracted in South Africa, and is regulated by the Department of Forestry, Fisheries and the Environment of the South African Government (DFFE). In 2021, the wholesale value of the sector was estimated at ZAR 5.5 billion (290 million €), providing approximately 5 800 jobs (Department of Forestry, Fisheries and the Environment, 2021). Anchovy and sardine together account for 80% of the average annual catches. The most commonly used catch method is purse-seining, which is selective in targeting small pelagic fish (Department of Forestry, Fisheries and the Environment, 2021). Fish caught by purse-seine vessels can be frozen, canned, used as bait or reduced into fishmeal or fish oil, the latter being mostly exported for use as aquafeeds (FAO, 2018; Statistics South Africa, 2021). Management of the industrial or commercial purse-seine fishery is critical to ensure sustainability of small pelagic fish stocks, such as sardine and anchovy, and is based on the resource status determined by annual recruitment and spawner biomass surveys. Critical levels of anchovy and sardine biomass are set and, if the biomass of these species is estimated to be below this threshold, a reduction in the catches is applied. This procedure, developed under the management strategy evaluation, is referred to as Operational Management Procedures (OMP). The OMP is based on an algorithm approach, involving testing a set of rules or formulas through simulation in order to issue management recommendations (Moloney & Johnston, 2002; de Moor et al., 2011). When selecting a management model, the OMP applies a precautionary principle to uncertainties related to the managed resource (de Moor et al., 2011). The resulting candidate OMP must then be agreed on between the management sector, the fishing industry and scientists (FAO, 2018). In South Africa, it is used for the management of sardine, anchovy, hakes (*Merluccius capensis* and *Merluccius paradoxus*), round herring and west coast rock lobsters (*Jasus lalandii*) in the major commercial fisheries (Geromont et al., 1999; FAO, 2018).

The management of small pelagic fisheries in South Africa has changed over time. Total Allowable Catches (TACs) were implemented in 1971. TACs are defined as the "maximum quantity of fish of individual species or groups of species made available annually, or during such other period of time as may be prescribed, for combined recreational, subsistence,

commercial and foreign use" (Marine Living Resources Act, 1998). TACs were then refined in 1983 by introducing species-specific TACs to encourage diversification, protect sardines, and prevent the overexploitation of anchovies. From 1991, a management procedure for directed sardines and directed anchovies was established, and three years later, the management of these two species was combined. This joint management of anchovies and sardines is necessary as the anchovy fishery targets juveniles, and sardine and anchovy juveniles school together (Coetzee & de Moor, 2024). Bycatch of juvenile sardines is therefore unavoidable, which negatively impacts the sardine fishery, primarily targeting adults for canning (de Moor et al., 2011). There is therefore a trade-off in resource use, and the TACs for sardines and anchovies are set interdependently. For sardines, a TAB (Total Allowable Bycatch) is also implemented. The TACs and TABs are determined at the beginning of the year using the biomass surveys from the previous November spawner survey (biomass of fish aged one year and older) (Coetzee & de Moor, 2024; de Moor et al., 2011). The TACs for anchovies and TABs for sardines are then revised mid-year based on the recruit survey conducted in May/June (Coetzee & de Moor, 2024).

Alongside managing fisheries through quotas, Marine Protected Areas (MPAs) have also been established as a conservation framework to maintain and protect marine life. Defined broadly as legally protected marine and coastal habitats than enjoy a higher level of protection than their surroundings, South African MPAs are managed by the Government (OECD, 2017; Western Cape Government, 2018). In 2019, 20 new MPAs were declared in the country, increasing protected area coverage in South Africa's exclusive economic zone from 0.4% to 5.4% (Department of Environmental Affairs, 2019). There are also other area-based management interventions that restrict purse-seine fishing, distinct form MPAs in their legal basis, notably purse-seine no-take zones around seabirds colonies; these are implemented through the provisions of the Marine Living Resource Act.

C) PROBLEMATIC

In the most recent global assessment of seabirds, 31% of 359 seabird species were classified as threatened, primarily due to impacts from alien invasive mammal species, fisheries bycatch, and climate change but also hunting/trapping and overfishing. Half the penguin species are threatened by problematic native species, pollution, invasive alien species, overfishing and hunting/trapping, making it the second most threatened seabird group after albatrosses. Even though overfishing is the seventh most impactful ongoing threat on seabird

species, it is among the top four threats causing the highest average impact (Dias et al., 2019). Overfishing therefore affects less seabird species but with a greater impact, associated with depletion of food resources around colonies as well as bycatch (Dias et al., 2019; Crawford et al., 2017). Declining small pelagic fish stocks are known to have negative impacts on Benguela endemic seabird species that specialize on these preys in South Africa, including the African penguin (Crawford, 1979, Crawford et al. 2022).

African penguins are endemic to the Benguela Upwelling Ecosystem off south-western Africa and they mainly feed on small pelagic preys, primarily sardine and anchovy. In the early 2000's, there was a shift in sardine and anchovy distribution to the east which resulted in a mismatch between the location of breeding colonies and prey biomass. This was exacerbated by ongoing competition with the commercial purse-seine fishery (Coetzee et al., 2008; Crawford et al., 2011). Between 1993 and 2023, the African penguin population declined from ~ 44 300 to ~ 9 900 breeding pairs, representing a decrease of 77.8% within three generations. The current decline of the African penguin is not a novel phenomenon, as the population has been decreasing for over 70 years (Sherley et al., 2024). African penguins were uplisted to Critically Endangered in 2024 and could be extinct in the wild by 2035 if the ongoing trend persists (BirdLife International, 2024; Sherley et al., 2024). The sensitivity of seabirds to prey depletion can be further understood through a critical ecological threshold of prey abundance: if the biomass of fish targeted by seabirds falls below one third of its maximum observed value, the reproductive success of seabirds drops accordingly, and becomes more variable (Cury et al., 2011). When prey biomass drops below this critical threshold, colonies decrease in number and become fragmented. This leads to risks associated with the allee effect, meaning the loss of advantages linked to living in large numbers. This can manifest itself in a reduction of the benefits of group foraging, a diminished role of colonies as information centers, and an increase in the number of nests on the periphery, consequently increasing the risk of predation on eggs and chicks. It is therefore imperative that the size of these birds' colonies does not fall below the threshold at which the allee effect becomes exacerbated (Crawford et al. 2022).

It is in this context that an Island Closure Experiment (ICE) was implemented between 2008 and 2021 around four South African colonies (Robben Island, Dassen Island, St. Croix Island and Bird Island) and included purse-seine fishery no-take zones (Punt et al., 2023). While the design of the ICE was limited in its ability to quantify the benefits of survival, the no-take zones showed benefits on the population growth rates deduced from breeding success

parameters, with an increase of 0.71 – 1.51% per year, compared to a scenario without closures (Punt et al., 2023). In September 2022, following failed negotiations between the conservation sector and the purse-seine fisheries stakeholder groups, the DFFE established interim no-take zones which were not endorsed by the conservation sector around six colonies (McInnes et al., 2024). A year later, the DFFE endorsed the principle of purse-seine fishery no-take zones, the extents of which should maximise benefits to the penguin population while minimizing losses to the fisheries (McInnes et al., 2024). In order to resolve this issue, the government designed a panel of six international expert scientists to provide an external, independent and objective review of the situation. The panel has now established criteria and approaches for evaluating trade-offs between benefits to penguins and costs to fishery, and recommendations regarding monitoring and other methods to evaluate the effectiveness of no-take zones. A settlement agreement was reached in March 2025 between the fishing industry and the conservation organizations BirdLife South Africa and the Southern African Foundation for the Conservation of Coastal Birds (SANCCOB). The agreement consists of no-take zones (hereafter referred as "closures") for a 10-year period around Dassen Island, Robben Island, Stony Point, Dyer Island, St Croix Island and Bird Island, with a fully restricted closure regarding the use of purse-seine nets. The closure around the colony at Dyer Island however shows a specific configuration, as only a small portion of the closure is a fully restricted closure. The rest of the closure of the area is a vessel-size restricted closure, which only prohibits vessels equal to or greater than 26 meters long (Figure 1). This partial closure was put in place in order to avoid significant losses for the local fishing company, which owns smaller vessels and is therefore considered as more dependent on the area due to fewer resources. The fully restricted closure currently covers only 20.8 % of the core foraging area (mIBA-ARS) (McInnes et al., 2024).

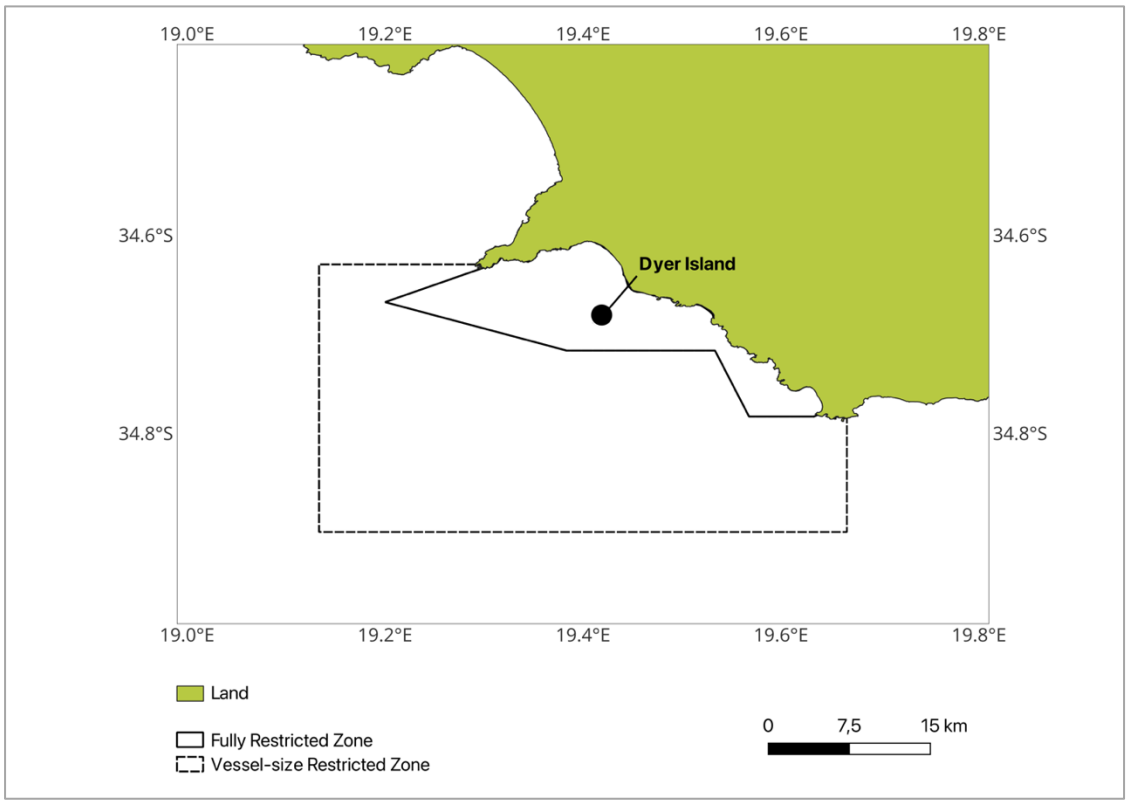

Figure 1: Dyer Island closure configuration. No fishing vessels are allowed inside the fully restricted zone (solid black line). Vessels smaller than 26 meters long are allowed to fish inside the vessel-size restricted zone (between the dashed and solid lines). The African penguin colony at Dyer Island lies at the centre of the fully restricted zone.

A period of 6 to 10 years after the establishment of fishing closures was established by the evaluation panel to assess the effectiveness of the designated closed areas. This timeframe is necessary to account for the effects of the closures on the penguins' key biological processes and thus obtain reliable results. The ongoing monitoring system and assessment programme includes an evaluation of many penguin parameters. Population monitoring focuses on counting individuals, adult survival, and juvenile recruitment. During the breeding season, several parameters are monitored: breeding success, weight of adults at the beginning and end of the breeding season, as well as chick condition, their survival, growth, fledging success and fledging weight. Pre-moult weight is also recorded. Foraging efficiency and body condition of adult penguins are also being monitored, currently measured through the deployment of loggers on breeding birds, and automatic weighbridges, which record individual weights of birds in transit to and from the colonies (Punt et al., 2023).

D) Objectives and hypotheses

To understand the impacts of fishing closures on African penguins, it is important to understand how fish schools move through the ecosystem and how African penguins adapt

themselves to those natural variations in food availability. By understanding the penguin path metrics (maximum distance from the colonies, trip length and trip duration), it is then possible to understand how fishing disturbs natural variations in food availability. This type of method will allow to define African penguin thresholds on the South African colonies, after which they will not have enough food to maintain their own body condition as well as their chicks'. Given the novelty of the partial closure around the colony at Dyer Island, implemented in 2022, this master's thesis aims to assess if the current closure configuration is indeed effective in reducing significant catches and improving the foraging performance of penguins. It is expected that the current configuration of the island closure may not have a positive enough impact on the foraging behaviour of the penguins for it to be sustainable.

In particular, this thesis aims to:

1) Analyze and compare the penguins' path metrics before and after the closure around Dyer Island, namely maximum distance travelled from the colony, path length and trip duration at sea. If the island closure is adequate, a reduction in the maximum distance travelled, the path length and the trip duration at sea is predicted after its implementation, translating to an improvement in the foraging efficiency of penguins.
2) Quantify and compare the fishing catches within the closure perimeter, before and after its implementation, as a proxy of fish pressure inside the closure area. If the closure is effective, a reduction in catches within the closure perimeter is expected following its implementation, reflecting restricted access for larger vessels.
3) Quantify the impact of the closure on the local fishery company by analysing catches and fishing effort of the frequent fishing vessels within the closure area, before and after its implementation. Because the identity of the local fishing company could not be disclosed, frequent vessels in the perimeter were used as a proxy for local fishing activity, in order to assess whether the behaviour of the local fishing company changed following the closure. It is expected that the current configuration of the island closure will not lead to significant changes on the frequent vessels' behaviour.

MATERIALS AND METHODS

A) STUDY SITE

Dyer Island is a small island located off the south-western coast of South Africa, about 10 km south-east of Gansbaai, within the Benguela Upwelling Ecosystem. The island has a surface of 20.77 ha. The site was designated as a Ramsar wetland in March 2019, and is now designated as the "Dyer Island and Geyser Island Provincial Nature Reserve". Managed by CapeNature, the site covers a surface of 288 ha and comprises two islands, Dyer and Geyser. According to BirdLife International 2026, Dyer Island is considered one of the 90 Important Bird Areas in South Africa. The island hosts around 48 bird species, including 21 species breeding on the island. The site is limited to boat-based recreational activities and scientific research. Dyer Island is home to one of the 26 current African penguin colonies and used to be the largest colony in 1979 with 22 655 breeding pairs. It then declined to fewer than 1 500 breeding pairs in 2013 and to 884 pairs in 2023 (Sherley et al., 2024).

B) DATA AND PATH METRICS ANALYSIS OF THE PENGUINS

1) DEPLOYMENT PROCEDURES

This study focuses on the African penguin colony at Dyer Island (34.682009°S 418972°E). Biologgers were deployed between May and August during two distinct periods: 2010 – 2012, and 2021 – 2025, on chick-rearing adults (n = 4 - 15 per year), over deployment periods of one to six days to study their foraging behaviour. Two biologger types were fitted to adult penguins: 1) Pathtrack loggers, Otley, UK; L x W x H = 60 x 22 x 15 mm, mass = ~ 30 g for birds deployed between 2010 and 2012, and 2) GPS-TD loggers (GPS with a time-depth recorder, 45 g, LXWXH: 65 x 40 x 15 mm, Axy-Trek Marine HD TechnoSmArt) were deployed between 2021 and 2025. Biologgers were fitted using waterproof tape (Tesa tape #4651, Beiersdorf AG, Hamburg, Germany; Wilson et al., 1997) on the penguins' lower back feathers. The biologgers recorded latitude and longitude every 30 seconds, with an accuracy of 10 meters. The devices weighed < 3% of the adult penguin body mass in order to avoid increasing and biasing the trips of the birds (Phillips et al., 2003). The loggers were retrieved when the adult returned to the nest site. Deploying and retrieving the biologgers on each individual lasted less than 6 minutes, according to the methods approved by University of Cape Town's animal ethics committee.

2) DATA CLEANING

The tag identifier, date, time, latitude and longitude were retrieved from the devices. Data were then analysed in the program R studio (R version 2025.05.1+513) (Posit team, 2025). Locations on the island were excluded using a shapefile layer of the island to only keep the data points at sea. If the speed between two GPS locations was >12.4 km per hour (the penguins mean maximum speed), the second point was considered as invalid and removed. Obvious erroneous data points were manually removed using a map point visualisation. Data were then split into trips using the R function "tripSplit" from the package track2KBA (Beal et al., 2021). The function identified foraging trips, and a buffer of 0.5 km around the center of the colony was established to make sure the birds were at sea during their trips. A return buffer of 1.5 km around the colony was established to consider incomplete trips where birds did not come back to the colony perhaps due to device failure. The minimum duration of a trip to be allocated as a foraging trip was two hours. Trips with less than five GPS coordinates were removed as they contained too little information. Trips starting inside the foraging zone, characterized by area-restricted search behaviour (increased sinuosity), were excluded to minimize potential inaccuracies in the dataset. An artificial starting point was imputed within the 0.5 km buffer to the incomplete trips that started during the commuting phase to mitigate signal acquisition lag during porpoising behaviour. The location of the starting point was defined as the center of the colony, as imputing a starting point on the 500 m buffer would have introduced an arbitrary directional bias as the initial direction of travel was unknown. The date and time of this supplementary point was estimated using linear interpolation, considering the transit speed at 1.33 m/s. 16 trips out of the 87 final trips were reconstructed, with the artificially injected phase representing a mean of 5.15% (range: 1.24 % – 22 %) of the total path length and 3.28% (range: 0.64% - 10.42%) of the total trip duration. To avoid pseudo-replication, data were only recorded for a single foraging trip per bird and, when multiple trips were recorded for individuals, only the first trip was retained. As some GPS segments generated paths intersecting the peninsula in the area near the colony, the locations were manually re-routed to ensure ecological validity. Using a waypoint at the tip of the peninsula and a shapefile of the South African coastline, terrestrial intersections were identified and rerouted through the waypoint, while maintaining temporal continuity between data points.

3) PATH METRICS ANALYSIS

To assess the potential effect of the closure implementation on the penguins' foraging behaviour, proxies of foraging effort were estimated through maximum distance travelled from the colony (km), foraging path length (km) and trip duration (hrs). Individual path metrics were calculated for each bird. The maximum distance from the colony was calculated in kilometers using the Vincenty formula, which measures the shortest distance between two points along the surface of a sphere (great-circle distance). The Vincenty formula was implemented via the R function "distVincentySphere()" from the geosphere package (Vincenty, 1975; Hijmans et al., 2026). The total path length represents the cumulated distance travelled per individual, in kilometres. It was obtained by summing the Vincenty distances between each successive GPS point of the path. Finally, the trip duration, in hours, was calculated as the time difference between the last and the first data point of each trip. The interquartile range (IQR) method was then applied to identify and remove outlying trips based on these three path metrics, which resulted in a final dataset of 87 trips. As path length and trip duration showed bimodal distributions, trips were categorized as short trips or long trips by identifying the local minimum of the density curve of both metrics (path length = 76.5 km; duration = 23 hrs). The two trip classifications were then compared, and trips overlapping both categories were removed from the dataset for the analysis of path length and duration (n = 85 trips). Each trip was then assigned a "before" or "after" association depending on when it took place relative to the closure implementation on 1st September 2022.

Prior to modelling, the three path metrics pre- and post-closure periods were assessed using Mann-Whitney tests. Metrics with a bimodal distribution (path length and duration) were also tested separately for short and long trips. The three path metrics values from trips that occurred before and after the closure implementation were then analysed through generalized linear mixed effect models. For each model, several predictors were considered: the closure status, the deployment year, the Julian day and the cumulated catches before each trip. The deployment year was included to account for inter-annual variability in natural processes, such as prey abundance and oceanographic conditions. Julian day accounted for the intra-annual variability, as all the deployments were not carried out at the same time during the year, and was standardized (mean = 0; sd = 1) to facilitate the convergence of the models. Cumulative fishing catches were included as co-variables to quantify the direct food competition for fish inside the closure area between the penguins and the fisheries. Each trip was assigned cumulative catches (in tonnes) for anchovy, sardine, and their combination, over 60- and 90-

day periods prior to each trip, counted inside the closure perimeter, and scaled using the z-score method due to large isolated quantities. The cumulative catches were compiled using small pelagic fisheries catch data obtained from the South African government's Department of Forestry, Fisheries and the Environment (DFFE). Sardine catches were defined as the sum of bycatch and directed sardine, and combined catches as the sum of anchovy and sardine catches. Despite being part of the African penguin's diet in smaller proportions (Randall & Randall, 1986), round herring was excluded from the analyses, as fishing surveys showed a disproportionate peak in round herring catches in the closure perimeter in 2022 that was inconsistent with the national fishing trend, likely reflecting fishers' behaviour rather than a biological signal, and therefore introducing a confounding effect. A 30-day window could not be included, as the cumulative catches for anchovy and sardine over that period of time were all null after the closure implementation, making it impossible to distinguish their effect from that of the closure due to perfect collinearity. Given the high collinearity between each catch variable, models were fitted separately for each type of cumulated catches (species and timescales). Hereafter, cumulative catches of anchovy, sardine and their combination over 60- and 90- days periods are referred to as anchovy(60), anchovy(90), sardine(60), sardine(90), total(60), and total(90). Models including cumulative catches as a co-variable were run on smaller datasets, as fishing data were available on a smaller time window (from 2012 to 2024) and as a 90-day truncation was applied after the first fishing haul to avoid skewing the first cumulative catches.

As all the path metrics were continuous positive variables with right skewed distributions (Figure 2 - 4), generalized linear models (GLM) and generalized linear mixed models (GLMM) were fitted using a Gamma family and a Log link function. For the duration of long trips specifically, several families were compared (Gamma, log link; Lognormal, log link; Gaussian, identity link) and the model with the lowest AIC was selected (Gamma, log link; Table S1 – supplementary). Due to the small size of the dataset, interaction models were not included in the analyses.

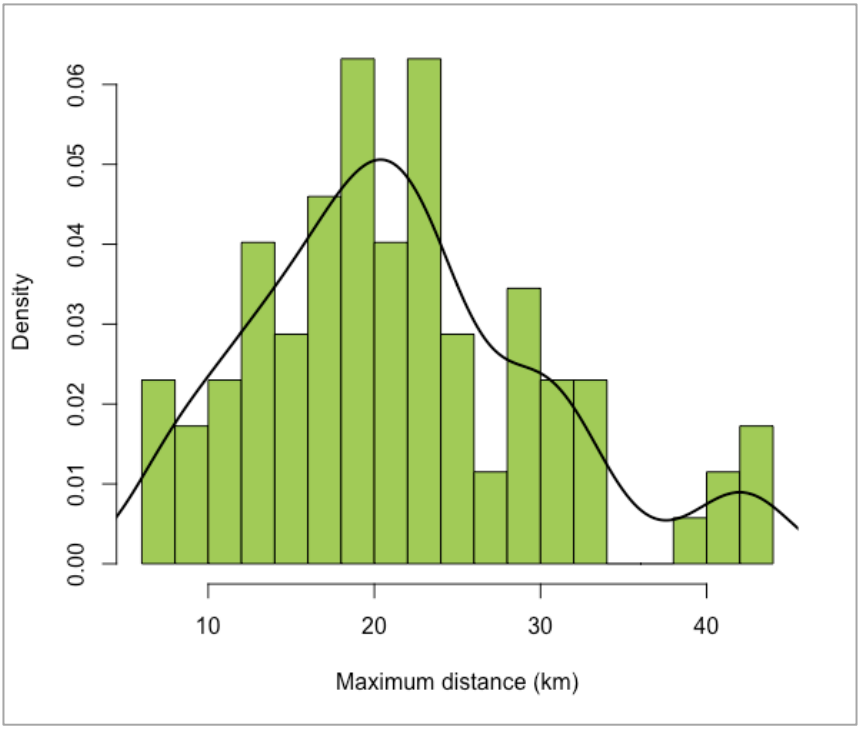

Figure 2: Density histogram of the maximum trip distance (km) of African penguin foraging trips from Dyer Island colony (n = 87). The curve represents the kernel density estimation. The distribution is right-skewed, justifying the use of a Gamma family in subsequent models.

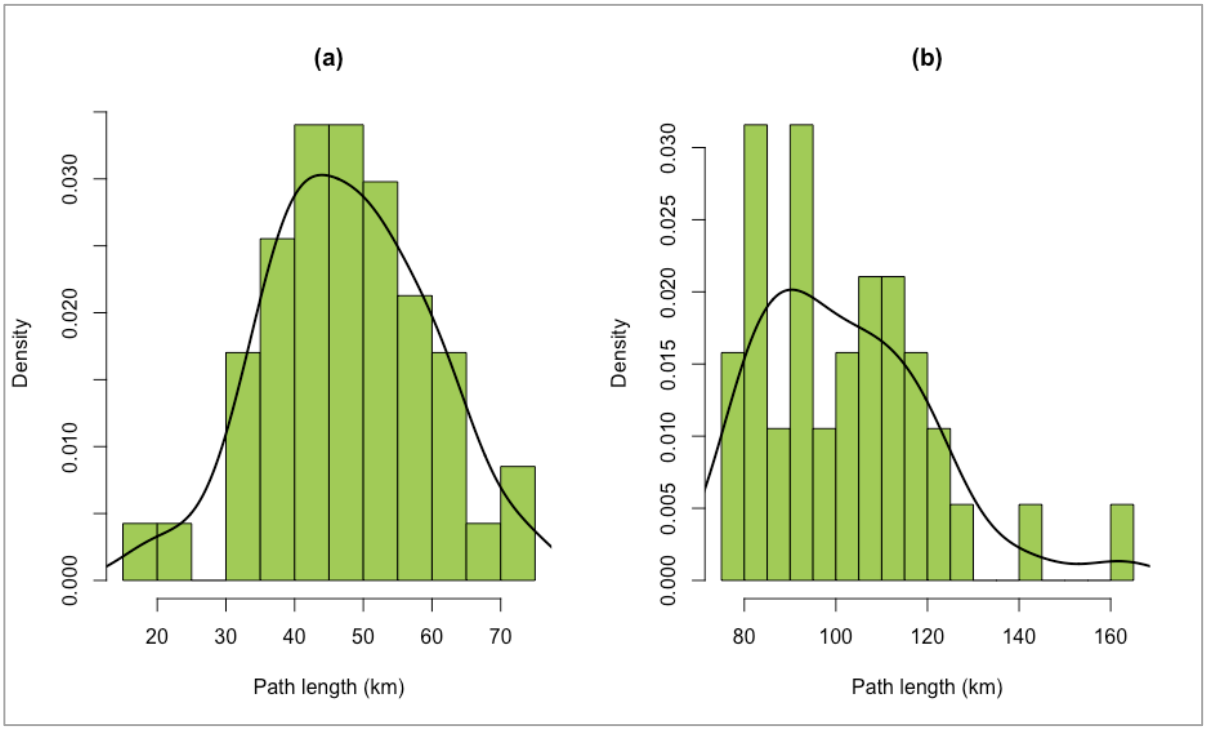

Figure 3: Density histograms of the total path length (km) of African penguin foraging trips from Dyer Island colony, for a) short trips (n = 47) and b) long trips (n = 38). The curve represents the kernel density estimation. Distributions are right-skewed, justifying the use of a Gamma family in subsequent models.

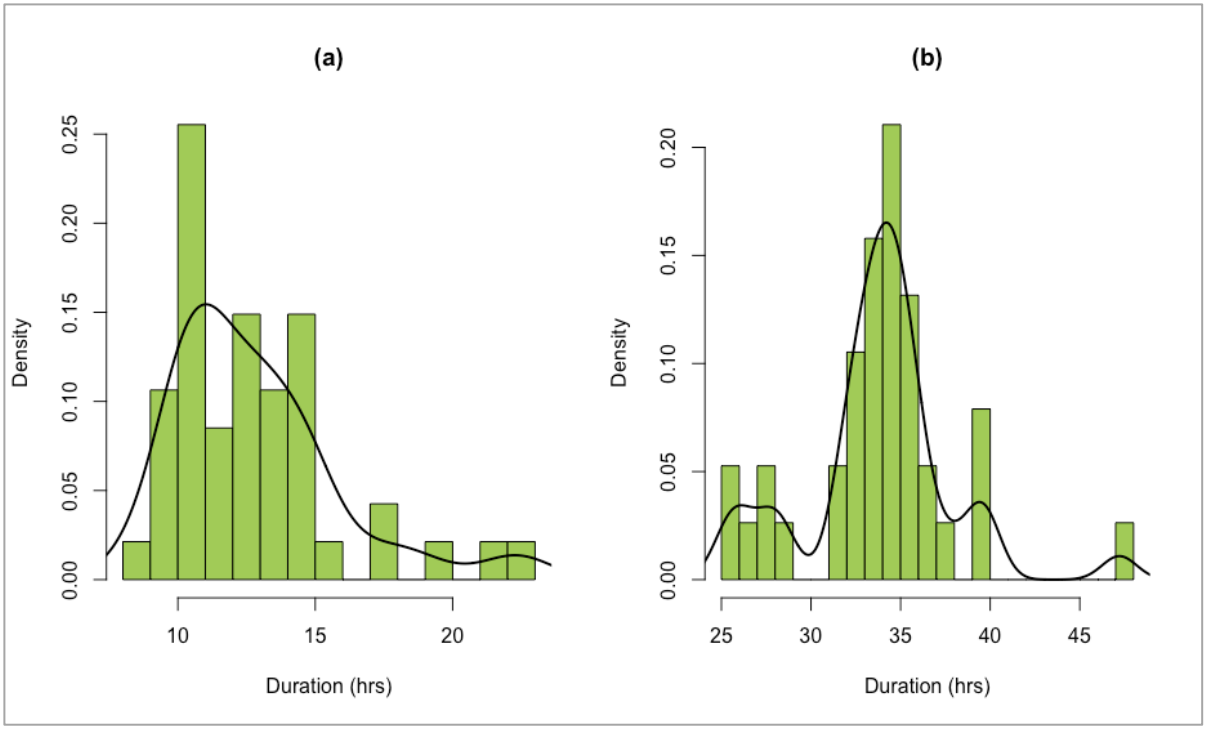

Figure 4: Density histograms of trip duration (hrs) of African penguin foraging trips from Dyer Island colony, for a) short trips (n = 47) and b) long trips (n = 38). The curve represents the kernel density estimation. The distribution of short trips is right-skewed, justifying the use of a Gamma family in subsequent models. As the distribution of long trips does not show a clear skew, the model family selection was performed via AIC comparison (Table S1, supplementary).

For each metric, three candidate models (gamma family, log link) with increasing complexity were compared: 1) a baseline GLMM with the closure status as a fixed effect alone, 2) a GLMM adding the deployment year as a random effect, and 3) a GLMM also including Julian day as a continuous covariable. The selection of models was performed using the Akaike Information Criterion, and the principle of parsimony was applied to select the simplest model when $\Delta AIC < 2$. Each selected model was then verified by performing a residual analysis (DHARMa R package) (Hartig et al., 2024). The model structure was then re-evaluated on restricted datasets (n = 50 trips for maximum distance; n = 29 trips for short trip path length and duration; n = 20 trips for long trip path length and duration) reflecting the shorter time window of fishing data and a 90-day truncation following the first recorded haul, prior to assessing the effect of cumulative catches on the metrics. The same three candidate models were evaluated, and a reference model was selected using the AIC, and verified by performing a residual analysis (DHARMa). Each reference model was then compared to six GLMMs including anchovy(60), anchovy(90), sardine(60), sardine(90), total(60), and total(90), following the same AIC-based selection and DHARMa residual verification procedure as described above.

C) Analysis of the fishing effort and catches within the closure

1) Data acquisition and compilation

To study the impact of the closure implementation around the Dyer Island colony on fisheries, small pelagic fisheries catch data between January 2011 and December 2024 were obtained from the DFFE. This data included the vessel name, vessel size, catch date, catch location, and catch weight (t) of directed anchovy catch, sardine bycatch and directed sardine catch. For the purpose of this study, sardine catches were defined as the sum of bycatch and directed sardine, and total catches as the sum of anchovy and sardine catches. Simultaneous zeros between the anchovy and sardine catches (total catch = 0) were removed. Each haul was attached to an identifier "before" or "after" the closure, as well as "in" or "outside" the closure perimeter (including the fully restricted plus size-restricted zones).

However, catch data alone may not reflect the true impact of the closure, as variations in catches could result from variations in TACs set each year. To disentangle the effect of the closure from that of TACs-driven constraints on fishing activity, TACs were also used, with TACs for anchovy and sardine being respectively retrieved for 2011 to 2024, and 2015 to 2024 (DFFE data). TACs are set by DFFE's Fisheries Management Branch. Anchovy TACs covered the whole South African coast, while sardine TACs covered the waters west of Cape Agulhas. This geographical discrepancy is a consequence of the acknowledgement of two distinct stocks within the South African sardine population (Coetzee & de Moor, 2024). The timescale of the TACs for sardines is therefore more restricted, reflecting the division of the sardine population between the western and eastern regions (Coetzee & de Moor, 2024).

To further contextualize the catch trends in relation to fisheries management, pelagic recruit and spawner biomass were retrieved from the annual surveys of small pelagic fish biomass conducted by the Fisheries Management Branch of DFFE. Spawner biomass refers to the total biomass of reproductively capable individuals. The purpose of the associated surveys is to provide estimates of the reproductive potential of populations of exploitable small pelagic fish species to inform the allocations of catches by the purse-seine fishing industry. These surveys were conducted annually (except for the recruit survey in 2018) over a period of 51 days, between mid-October and mid-December. Note that the 2023 and 2024 pelagic spawner biomass surveys were conducted late due to a vessel mechanical failure (respectively in February/March 2024, and in March/April 2025). Surveys took place in transects perpendicular

to the South African coast, from Hondeklip Bay to Port St Johns, using a scientific echosounder system and including hydrographic and fish trawl sampling. Fish trawl sampling was conducted in the mid-water to identify fish species quantified in the echosounder data. Recruit biomass refers to the individuals resulting from the spawner population, joining the exploitable phase of a stock. The recruit surveys were conducted within a 43-day period between mid-May and early July. In this study, spawner and recruit biomass for anchovy and sardine between Cape Point and Cape Agulhas (the region which includes Dyer Island) were retrieved, for a period covering 2011 to 2024.

2) FREQUENT VESSELS SELECTION

To evaluate the closure impact on the local fishing activity, vessels frequently operating within the closure perimeter prior to its implementation were used as a proxy for local fishing activity. An elbow threshold determined the minimum number of visits from which a fishing vessel was considered frequent inside the closure area (≥31 visits inside the closure perimeter, before 1st September 2022) (Figure 5). 14 vessels were selected out of the 82 that recorded fishing activity within the perimeter before the closure. 17 vessels were initially selected, however three had ceased their activity before the closure and were therefore excluded from the analysis of the frequent vessels.

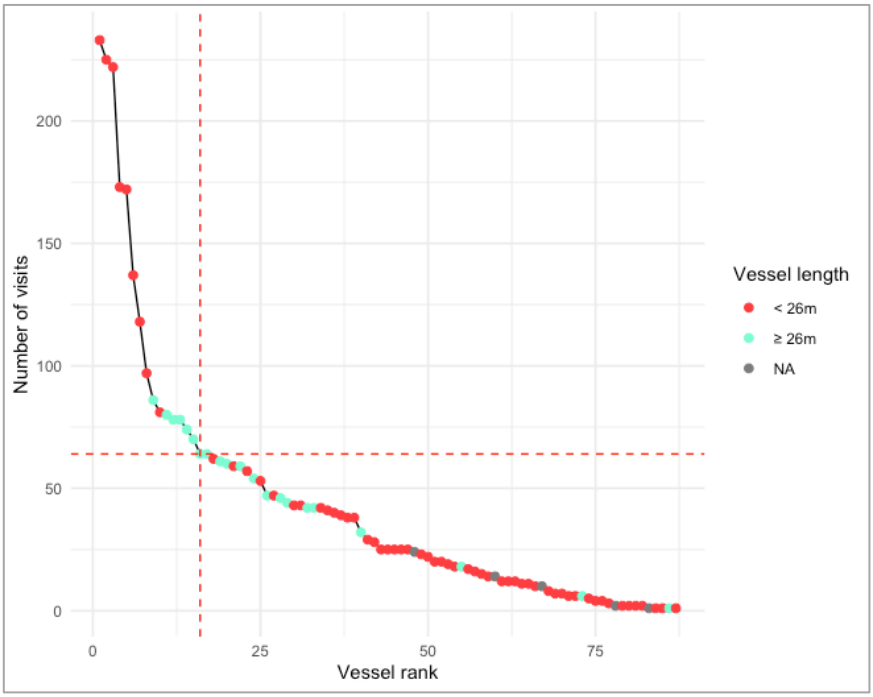

Figure 5: Ranking of vessels by the number of visits within the closure perimeter prior to its implementation (elbow method). Dashed red lines represent the elbow threshold, set at ≥31 visits (17 vessels). Red dots: vessels unaffected by the closure size restriction (< 26 m). Blue dots: vessels excluded from the size restricted closure perimeter (≥26 m). Grey dots: vessels with no length data available. The elbow threshold was used to define the minimum number of visits within the closure perimeter for a vessel to be classified as frequently operating inside the closure perimeter.

3) ANALYSES

The following analyses aim to answer two questions: 1) Have the total fishing catches in anchovy, sardine and both combined (hereafter referred as "total catch") within the closure perimeter significantly changed after the closure implementation, and 2) Has the closure significantly impacted frequent fishing vessels? Due to absence of vessels ≥ 26 meters in the closure perimeter after its implementation, this size category was omitted from the analysis.

First, Poisson rate ratio tests were performed to assess whether the number of fishing hauls with catches containing anchovy, sardine and total catches differed significantly before and after the closure. For each species category and vessel category (all vessels, vessels < 26 m, frequent vessels) within the closure perimeter, the number of hauls containing the target species was compared pre- and -post closure period using the poisson.test R function. The time-window for the tests containing haul events from all vessels and vessels under 26 meters was defined as 68 active fishing days recorded within the closure perimeter, before and after the closure implementation (1st September 2022), across an 800-day window on each side of the closure date. The time-window regarding the frequent vessels' tests was defined as 65 active fishing days, across an 810-day window on each side of the closure date. These standardised timescales ensure that the Poisson test is balanced in terms of sampling effort before and after the closure implementation, and were defined based on the available data after the closure. Total catches in tonnes of each species from each type of vessels, over the same periods, were descriptively reported alongside the Poisson tests.

Second, to assess the impact of the closure on the catch volumes, catch data for anchovy, sardine and total catches were aggregated at a month resolution. Monthly catches were preferred for this analysis over annual catches, as including annual catches would have required removing the year of the closure from the analysis, since it was implemented in September. To disentangle the effect of the closure from that of large-scale fisheries dynamics, the analysis was conducted at two spatial scales: 1) catches within the closure perimeter, and 2) catches at a national level. The analyses were conducted for all vessels, vessels under the size restriction of the closure, and for the frequent vessels. Differences between monthly catches before and after the closure implementation were then assessed. The normality of the monthly catch distributions was assessed using Shapiro-Wilk tests, separately for each species category (anchovy, sardine, total), each vessel category (all vessels, vessels < 26m, frequent vessels), and at both spatial levels (within closure, national level). Since the assumption of normality

was rejected for all tests, Mann-Whitney tests were used to compare catches before and after the closure. A Bonferroni correction was then applied to control for the increase in type I errors due to multiple comparisons. Bonferroni correction was applied separately for each spatial level for the analyses on all vessels and < 26m vessels (n = 6 tests; three catch categories: anchovy, sardine, total; two vessel types: all vessels, < 26 m vessels), and for the frequent vessel analysis (n = 3 tests; three catches categories: anchovy, sardine, total; one vessel type). To investigate whether local catch trends were reflected at the national level, Spearman correlation tests were performed between local and national levels for monthly catches of anchovies, sardines, and total catches. For all vessels and vessels < 26 meters, correlations were calculated between catches within the closure and national catches. For the frequent vessel groups, the correlation compared local and national catches from the frequent vessels. Finally, a Bonferroni correction was applied (n = 3 tests) to control for the increase in type I errors due to multiple comparisons. A significant correlation between the national and local trends was interpreted as reflecting a large-scale dynamic, rather than a direct effect of the closure implementation.

To further contextualise catch trends (of all vessels and frequent vessels) in relation to fisheries management, Spearman rank correlations were used to assess relationships between annual catches (at closure and national levels), TACs, spawner biomass, and recruit biomass for both anchovy and sardine. Spawner biomass was lagged by one year to reflect the management procedure, as TACs are set at the beginning of the year based on the previous November spawner surveys. Recruit biomass was considered for the same year as TACs as it informs the mid-year revision of TACs. Anchovy TACs were available from 2011 to 2024, and sardine TACs from 2015 onwards. Biomass survey were available from 2010 to 2024, with three years missing in recruit biomass (2010, 2011 and 2018). Because the closure was implemented in September 2022, the year 2022 was removed from this analysis to avoid artefacts. A Bonferroni correction was applied to account for multiple comparisons (n = 6 tests per species and per vessel category). A significant correlation between catches and TACS or biomasses was interpreted as reflecting national or regional fisheries management effects, rather than a direct effect of the closure implementation.

Finally, models were built to investigate a potential difference in the quantities of fish (anchovy; sardine; total) caught before versus after the closure, inside the closure area, by all vessels and by frequent vessels. Using a dataset excluding zero catches of the target species,

linear mixed models (LMM) were built with the log-transformed haul size of anchovy, sardine, and total catch as the response variable. For all models, the primary variable of interest was the closure status (open or closed). The month covariate, reflecting the seasonality of pelagic species, was treated as a cyclic variable (month(sine) = sin(2*π*month/12); month(cosine) = cos(2*π*month/12)) to ensure continuity between December and January. The year of the haul was included as a random effect to account for unexplained annual variation, and the vessel name was included as a random effect to account for variation between vessels. The biomass survey data could not be considered as covariates in the fishing models because the spatial resolution was too coarse, failing to reflect local biomass conditions and thus creating too much noise in the models. For each model, an AIC comparison was performed between the model as presented above and one with the month covariates removed. When significant outliers were detected, they were individually inspected to determine if they represented errors or legitimate catches. If the outliers were legitimate data, they were retained in the dataset. However, to ensure a robustness in this approach, alternative models excluding the outliers were tested to assess their influence on the models.

Lastly, regarding the study of the impact of the closure on frequent vessels within the closure perimeter, relative fishing effort was examined. Relative fishing effort per month was calculated as the number of hauls by each vessel multiplied by the ratio of vessel length to the average length of all vessels. It was then compared among frequent vessels, within the closure area and at the national level, as well as for all vessels within these same two zones. The standardised fishing effort for vessel i in month t was calculated as follows:

$$E_{i,t} = H_{i,t} \times (L_i \div L)$$

where $H_{i,t}$ = the number of hauls recorded for vessel i in month t; L_i = the length of vessel i; L = mean length of frequent vessels. This standardisation weights each vessel's contribution by its size, relative to the mean fleet, reflecting different fishing capacities due to different vessel lengths. Standardized fishing effort was compared before and after the closure within two areas (closure area and national) for both frequent vessels and all vessels. Normality of monthly effort distribution by vessel category and by area, before and after closure, was rejected for each distribution (Shapiro-Wilk tests: $p < 0.05$), and differences in fishing effort between the two periods were tested using Mann-Whitney tests. A Bonferroni correction was then applied (n = 2 tests). To account for a potential seasonal effect in the comparison of fishing effort, a paired Wilcoxon test was performed, comparing mean fishing effort in equivalent

months before and after the closure. To further distinguish closure specific effects from broader national trends, the ratio of frequent vessels' monthly effort within the closure perimeter to the national monthly effort of all vessels was compared before and after the closure using a Mann-Whitney test. If a closure specific effect exists, the ratio is expected to drop or increase after closure.

RESULTS

A) PATH METRICS RESULTS

Table 1 summarises the path metrics recorded across the nine deployment years. Median maximum distance from the colony ranged from 12.15km (2022) to 33.43 km (2023), median path length from 39.66 km (2024) to 112.17 km (2023) and median trip duration from 11.14 hrs (2022) to 34.79 hrs (2023). Metrics from 2022 and 2024 consistently contained the lowest values across the three metrics. Note that the 2022 deployments happened before the closure of the area. Metrics from 2023 consistently showed the highest values, although they should be interpreted with caution since only four trips were recorded for that year. The spatial distribution of individual foraging trips can be visualised in Figure 6.

As a first assessment, the three penguins path metrics were compared pre- and post-closure periods using Mann-Whitney tests on the complete dataset (n = 87 trips; 3 tests) and separately on short and long trips (n = 47 short trips and n = 29 long trips; 2 tests each). On the complete dataset, results revealed no significant difference between before and after the closure implementation for all three metrics. When separating short trips from long trips, the results were not significant for all three metrics as well, although the path length of short trips showed a significant decrease after the closure implementation (median before = 48.28 km; median after = 43.03 km; original p-value = 0.04), which did not reach significance after correction (adjusted p-value = 0.28). These preliminary results are further explored through the following models accounting for seasonality, inter-annual variability and the influence of the fisheries.

Year	N (trips)	Maximum distance (km)	Path length (km)	Trip duration (hrs)
2009	13	22.21 [11.62 - 33.35]	76.06 [33.78 - 96.11]	27.58 [9.83 - 34.32]
2010	8	20.24 [17.64 - 29.44]	72.76 [47.81 - 122.45]	21.66 [10.79 - 35.12]
2011	3	29.12 [19.81 - 41.76]	96.13 [52.89 - 121.91]	34.49 [12.26 - 39.55]
2012	15	23.66 [13.07 - 32.12]	89.09 [40.3 - 141.45]	32.25 [9.38 - 39.57]
2021	5	24.35 [19.04 - 38.53]	74.8 [58.29 - 162.63]	19.13 [11.24 - 47.21]
2022	14	12.15 [7.14 - 19.17]	46.71 [32.98 - 84.3]	11.14 [9.36 - 27.91]
2023	4	33.43 [23.42 - 43.12]	112.17 [102 - 119.76]	34.79 [33.23 - 36.69]
2024	9	14.3 [8.18 - 17.45]	39.66 [23.49 - 92.91]	14.56 [10.24 - 33.46]
2025	16	22.52 [7.99 - 42.66]	70.52 [18.28 - 114.04]	21.76 [8.06 - 39.64]

Table 1: Summary of foraging path metrics of African penguins at Dyer Island colony across nine deployment years. Metrics reported are maximum distance from colony (km), foraging path length (km) and trip duration (hrs). Values are median [min – max]. N: number of trips recorded per deployment year.

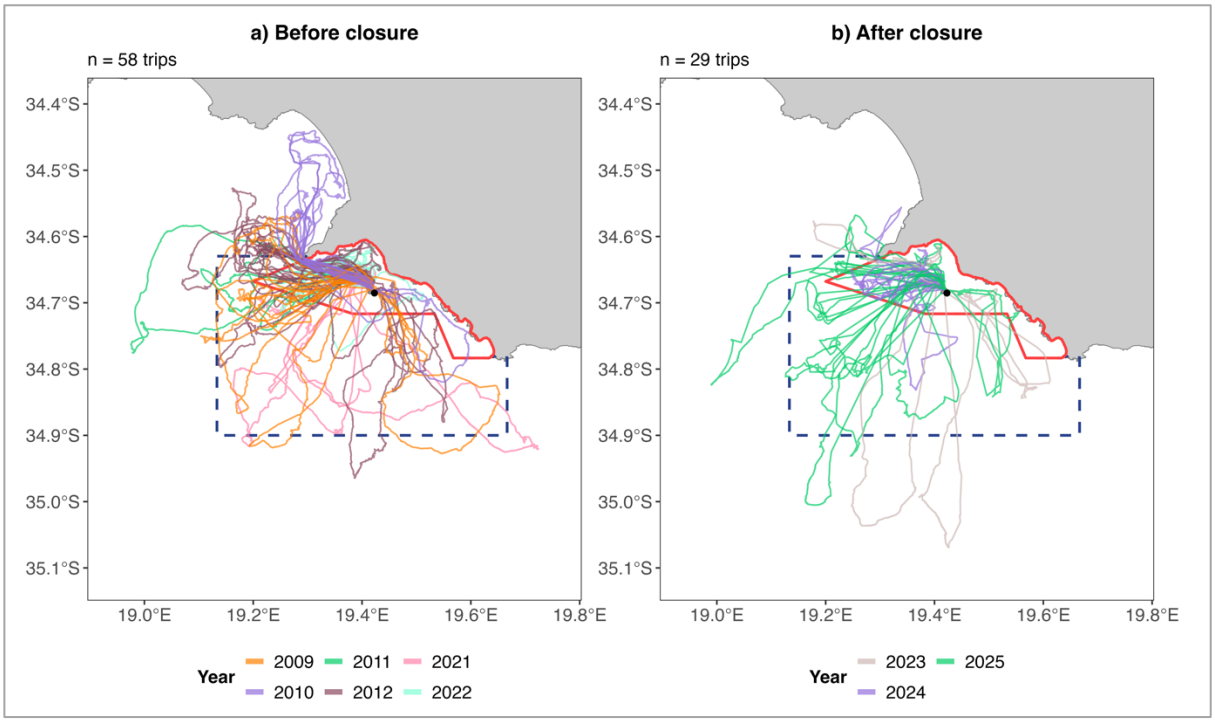

Figure 6: African penguin rerouted foraging trips from Dyer Island colony, a) before (n = 58 trips) and b) after (n = 29 trips) the purse-seine fishery closure implemented on 1st September 2022. Trips are coloured by year. The solid red line represents the outline of the fully-restricted zone, the dashed blue line represents the size-restricted zone, prohibited to fishing vessels ≥26 m in length. The black dot indicates the colony location.

1) IMPACT OF THE CLOSURE ON MAXIMUM DISTANCE FROM THE COLONY

For maximum distance, the selected model was a GLMM (gamma function, log link) including closure status and Julian day as fixed effects and deployment year as a random effect (n = 87 trips; ΔAIC = 3.64 with the second-best model; Table S2, Figure S1 – supplementary). No models with cumulative catches outperformed the selected model on the restricted dataset (Table S3, S4 – supplementary). The closure did not significantly affect the penguins' maximum distance travelled from the colony. Julian days were a significant positive predictor of the maximum distance (β = 0.11; p-value = 0.02), indicating that the penguins travelled further away from the colony as deployment period progressed within the year (Table 2). 57.2% of the variance was explained by the model, with the closure and days effects accounting for only 6.1% of the variance, suggesting that the deployment year accounted for half (51.1%) of the variance in the maximum distance from the colony travelled by penguins (Figure 7). These results indicate a strong inter-annual variability.

Fixed effects	β	SE	z-value	p-value
Intercept	3.09	0.14	22.80	<2 e-16 ***
Closure	-0.02	0.24	-0.08	0.94
Julian day	0.11	0.05	2.40	0.02 *
Random effects	Variance		SD	
year	0.10		0.31	
Model fit				
Marginal R^2	0.061			
Conditional R^2	0.572			

Table 2: Results of the GLMM (gamma function, log link) modelling breeding African penguins maximum foraging trip distance (km) from Dyer Island colony. Closure status and Julian day account for fixed effects. Deployment year is included as a random effect. The pre-closure period is the reference category for the closure status variable. N = 87 trips, 9 deployment years. *p < 0.05; ***p < 0.001.

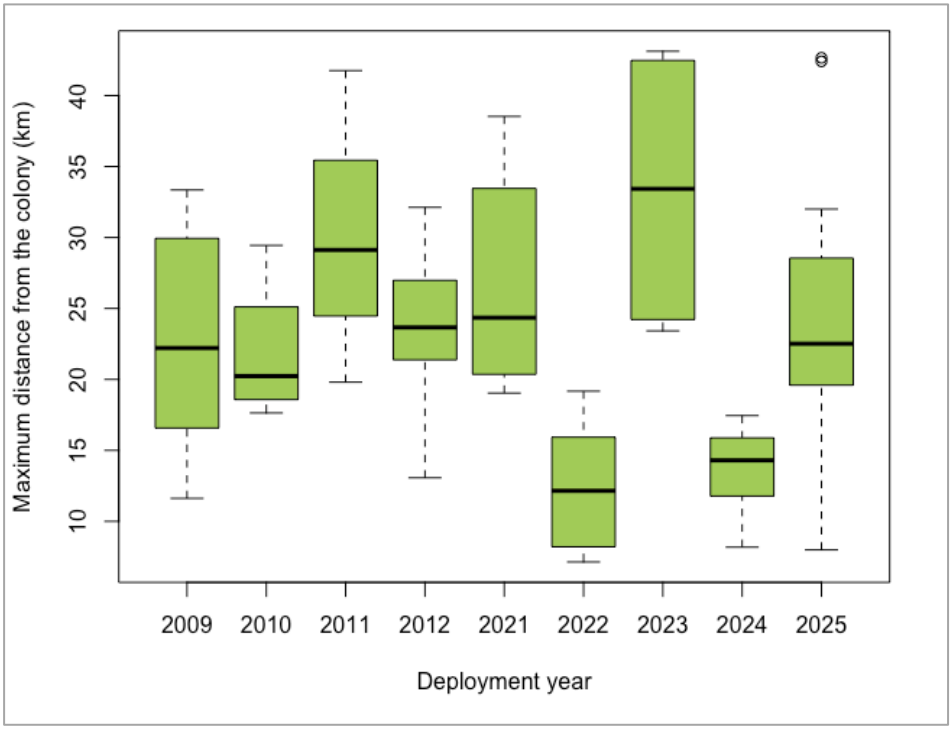

Figure 7: Boxplots of the maximum foraging trip distance (km) of African penguin from the colony at Dyer Island per deployment year (n = 87 trips). The black line represents the median, the boxes are the inter-quartile range, the whiskers extend to 1.5x the IQR, and dots represent the outliers.

2) IMPACT OF THE CLOSURE ON PATH LENGTH

For path length of short trips, while the principle of parsimony led to the GLMM including closure status only, the selected model also included deployment year as a biologically justified element (n = 47 trips; Table S5, Figure S2 – supplementary). The model only considering the closure status and the deployment year showed a significant effect of the closure on the short trips path length, with trips associated with shorter distances after the closure implementation (β = -0.22; p-value = 0.04) (Table 3; Figure 8). Model-predicted mean path length of short trips decreased from 51.5 km (95% CI: 45.8 – 58.0) to 41.4 km (95% CI: 34.6 – 49.4) after the closure. This represents a decrease of 12.65 km (-19.71 %) in the short trips path length. These results are consistent with raw data (before: 50.4 +/- 11.2 km; after: 41.6 km +/- 11.5 km). 28.7% of the variance was explained by the model, with the closure effect accounting for 15.2% of the variance. The remaining variance attributed to the inter-annual variability was low, explaining only 13.5% of the variation in the short trips path length.

On the restricted dataset, the model accounting for closure status, cumulative anchovy catches over 90 days and deployment year was selected (n = 29 trips; Table S6, S7, Figure S3 – supplementary). In this model, closure was no longer a significant predictor, whereas an

increase in anchovy catches 90 days prior to each foraging trip was significantly and positively associated with path length of short trips (β = 0.18; p-value < 0.01) (Table 3), suggesting that prey availability was a better predictor of the penguins' behaviour than closure itself. Model-predicted mean path length of short trips increased from 39.7 km (95% CI: 35.8 - 43.9) at one standard deviation below the mean catch level (437.54 tonnes) to 56.8 km (95% CI: 47.1 - 68.6) at one standard deviation above (2082.46 tonnes). This represents an increase of 43.07 % across this range. The marginal R^2 indicated that the closure and anchovy catches accounted for 43.7 % of the variance of the model, while the conditional R^2 was not estimable. Although the variance attributed to the deployment year was negligible on this restricted dataset, it was retained in the model structure as a biologically justified term. Due to strong collinearity between cumulative anchovy catches over 90 days and the closure implementation, the two predictors could not be included simultaneously in the same model. Two models were then fitted separately using the same dataset (n = 29 trips): a closure-only model and an anchovy(90)-only model, both including the deployment year as a random effect. The AIC comparison favoured the anchovy(90)-only model (ΔAIC = 5.1). The model also explained a greater proportion of the variance (marginal R^2 = 0.438 vs. 0.322), suggesting that prey availability was a stronger predictor of path length of short trips than the closure status. The statistical separation between the two variables was limited, and their individual contribution on path length could therefore not be determined. Full model outputs are provided in Table S8 to S11 (supplementary).

	Model 1	Model 2
Fixed effects	β (SE)	β (SE)
Intercept	3.94 (0.06) ***	3.85 (0.05) ***
Closure	-0.22 (0.11) *	0.03 (0.14)
Anchovy(90)	/	0.18 (0.06) **
Random effects	Variance (SD)	Variance (SD)
Year	0.01 (0.10)	1.36 e-10 (1.18 e-05)
Model fit		
Marginal R^2	0.152	0.437
Conditional R^2	0.287	/

Table 3: Results of GLMMs (gamma function, log link) modelling breeding African penguins path length (km) of short foraging trips. Model 1 includes closure status only (N = 47 trips, 8 deployment years). Model 2 includes closure status and anchovy catches 90 days prior to each trip (anchovy(90)) (N = 29 trips. 5 deployment years). Both models include deployment year as a random effect. The pre-closure period is the reference category for the closure status variable. *p < 0.05; ***p < 0.001.

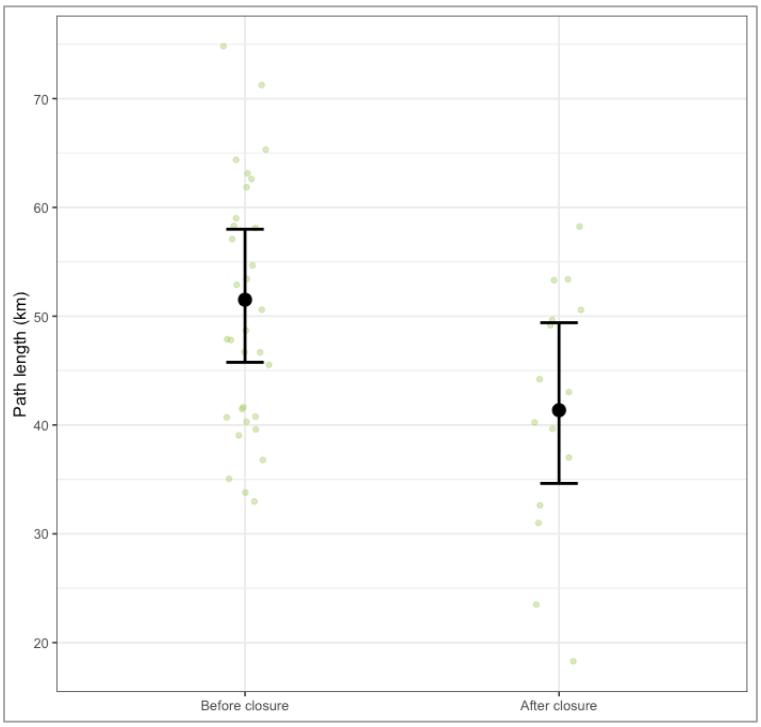

Figure 8: model-estimate mean path length (km) of short trips of African penguins before and after the closure implementation, with 95% confidence interval (black lines). Green points represent individual observations.

For path length of long trips, the model structure accounting for closure status and deployment year was selected (n = 38 trips: ΔAIC = 1.56 with the second-best model; Table S12, Figure S4 – supplementary). In this model, closure status was not significantly associated with path length (Table 4), and did not appear to be the main explanatory variable of the variance (R^2 marginal < 0.01). The random effect of the deployment year accounted for the majority (54%) of the variance explained by the model, suggesting the deployment year was the main source of variability in long trips length (Figure 9). These results contrast with those observed for short trips, for which closure was a significant predictor of the path length. Models with cumulative catches as covariates were excluded due to convergence issues, likely due to the small sample size.

Fixed effects	β	SE	z-value	p-value
Intercept	4.62	0.09	50.22	<2e-16 ***
Closure	- 0.01	0.11	- 0.08	0.93
Random effects	Variance		SD	
year	0.02		0.14	
Model fit				
Marginal R^2	< 0.01			
Conditional R^2	0.54			

Table 4: Results of the GLMM (gamma function, log link) modelling breeding African penguins path length (km) of long foraging trips. Closure status accounts for the only fixed effect. Deployment year is included as a random effect. The pre-closure period is the reference category for the closure status variable. N = 38 trips. 9 deployment years. *p < 0.05; ***p < 0.001.

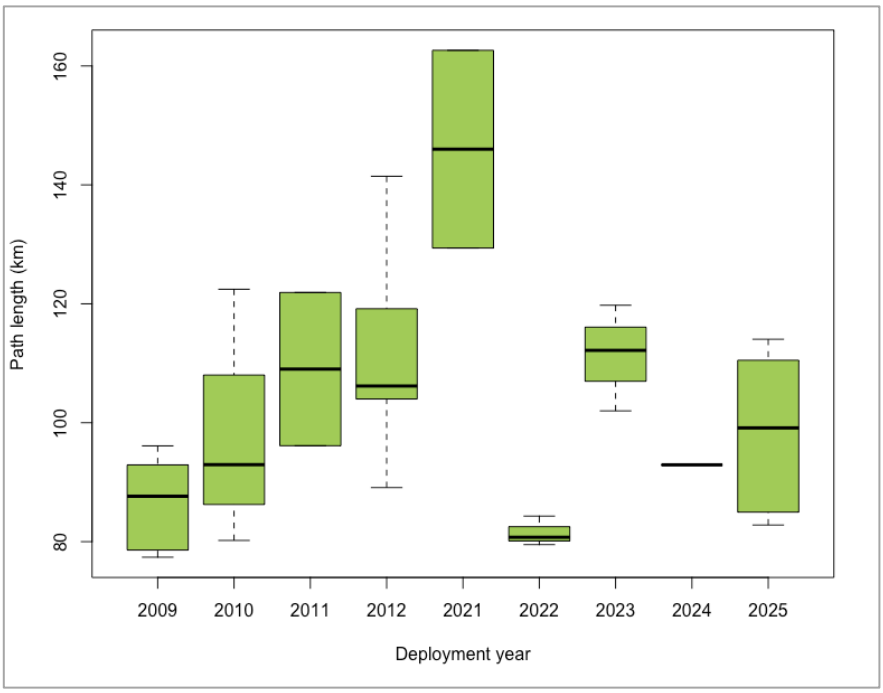

Figure 9: Boxplots of the path length (km) of long foraging trips of African penguins per deployment year (n = 38 trips). The black line represents the median, the boxes are the inter-quartile range, the whiskers extend to 1.5x the IQR, and the dots represent the outliers.

3) IMPACT OF THE CLOSURE ON TRIP DURATION

The selected model for short trip duration included closure status and deployment year, which, despite year-to-year variability having no significant effect on the model results, was kept as a biologically justified element (n = 47 trips; Table S13, Figure S5 – supplementary). Similarly to the short trip path length model, the conditional R^2 of short trip duration model was not estimable due to the negligible variance attributed to the random effect of the deployment year. However, in contrast to path length, the closure status was not a significant predictor of the duration of short trips, and only explained 1.8 % of the variance of the model (Table 5). No model accounting for the cumulative catches outperformed the reference model on the restricted dataset (Table S14, S15 – supplementary).

For duration of long trips, the selected model included closure status and deployment year (n = 38 trips; Δ AIC = 1.97 with the second-best model; Table S16, Figure S6 – supplementary). The results of the selected model were consistent with those of the path length model: the closure status was not a significant predictor of long trip duration (Table 5), and the model was mostly (53 %) explained by inter-annual variations (Figure 10). These results mirror the pattern observed for the path length metric. Finally, likely due to the small sample size (n = 20 trips), the selected cumulative catches model for duration of long trips failed to converge

and was therefore discarded (Table S17, S18 – supplementary). Full model outputs are provided in Table S19 and S20 (supplementary).

	Model 1: short trips	Model 2: long trips
Fixed effects	β (SE)	β (SE)
Intercept	2.53 (0.04) ***	3.54 (0.06) ***
Closure	0.06 (0.07)	0.02 (0.08)
Random effects	Variance (SD)	Variance (SD)
Year	8.91 e-11 (9.44 e-06)	0.01 (0.10)
Model fit		
Marginal R^2	0.018	< 0.01
Conditional R^2	/	0.53

Table 5: Results of GLMMs (gamma function, log link) modelling breeding African penguins' duration (hrs) of 1) short (N = 47 trips. 8 deployment years) and 2) long (N = 38 trips. 9 deployment years) foraging trips. Closure status accounts for the only fixed effect. Deployment year is included as a random effect. The pre-closure period is the reference category for the closure status variable. ***p < 0.001.

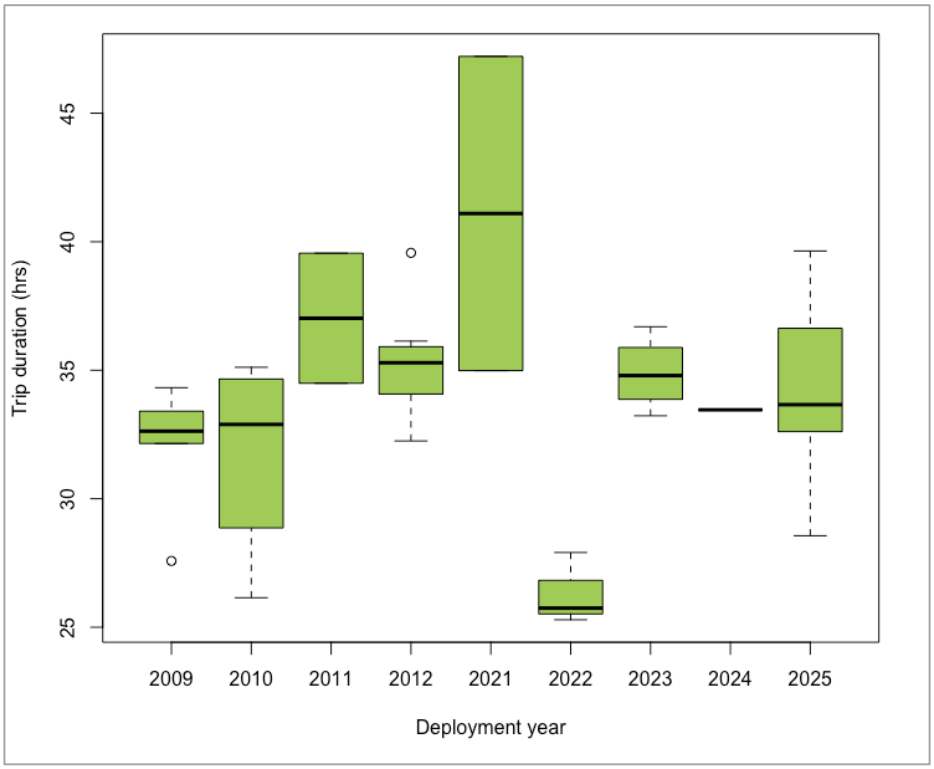

Figure 10: Boxplots of the duration of long foraging trips (hrs) of African penguins per deployment year (n = 38 trips). The black line represents the median, the boxes are the inter-quartile range, the whiskers extend to 1.5x the IQR, and the dots represent the outliers.

B) FISHERIES RESULTS

1) IMPACT OF THE CLOSURE ON FISHING CATCHES WITHIN THE CLOSURE PERIMETER

Poisson rate ratio tests, performed to assess whether the number of fishing hauls differed after the closure, revealed significant reductions in the number of hauls within the closure perimeter following the closure implementation, for most species and for both vessel categories (Table 6). Anchovy haul counts decreased significantly across both vessel categories and, for all vessels combined, the number of anchovy hauls declined by 63% (p-value < 0.001). Anchovy catches over the same period decreased following the closure. A similar pattern was observed for vessels < 26m, with a 57.6% decline in the number of hauls (p-value < 0.001) and a decrease in anchovy biomass caught. Regarding sardine hauls, a significant reduction was only observed for all vessels, with a 35.7% decline (p-value < 0.001). Despite fewer hauls, the biomass of sardine catches increased over the period following the closure. Sardine haul counts of vessels under the size restriction within the closure perimeter did not significantly change following the closure implementation. Finally, total catch haul counts for all vessels and vessels < 26m significantly decreased (48% and 39% decline respectively, p-values < 0.001). The combined biomass of catches over the same periods roughly halved (Table 6, Figure 11).

Haul category		Fishing hauls (n)		Poisson test		Catch (t)	
		before	after	rate ratio (95% CI)	p-value	before	after
Anchovy	All	219	81	2.7 (2.09 – 3.53)	< 0.001 ***	10 596.3	2 194.2
	< 26 m	191	81	2.36 (1.81 – 3.1)	< 0.001 ***	9 584.0	2 194.2
Sardine	All	157	101	1.55 (1.2 – 2.02)	< 0.001 ***	2 812.5	3 010.8
	< 26m	124	101	1.23 (0.94 – 1.61)	0.142	1 819.3	3 010.8
Total	All	268	139	1.93 (1.57 – 2.38)	< 0.001 ***	13 408.8	5 205.0
	< 26m	228	139	1.64 (1.32 – 2.04)	< 0.001 ***	11 403.4	5 205.0

Table 6: Results of Poisson rate ratio tests comparing fishing haul counts within the closure perimeter before and after the closure implementation, for all vessels and vessels under the size restriction (< 26m). The comparison time-window was defined as 68 active fishing days distributed over an 800-day period, on each side of the closure date. Total catches (tonnes) are reported for the same period. Rate ratio >1 indicates a decrease in haul frequency after the closure. ***p < 0.001.

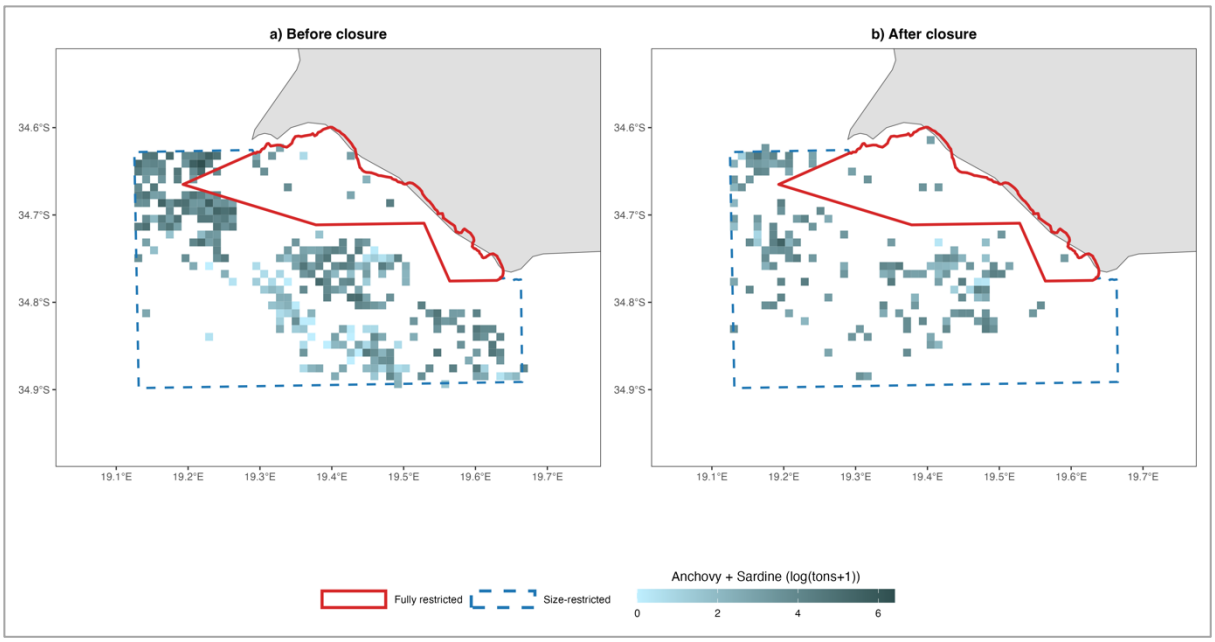

Figure 11: Spatial catch intensity maps of total catches (anchovy + sardine) of all vessels on 63 active fishing days a) before and b) after the closure implementation. Catches are in log+1 tonnes. Grids: 1 × 1 km^2.

Mann-Whitney tests assessed whether the fish biomass removed from the closure perimeter changed after its implementation, and contextualised the locally observed trends to broader tendencies. The tests revealed significant reductions in monthly catch volumes for anchovy and total catches, from all vessels, at both closure and national levels, while sardine catches remained unaffected. For vessels under the size restriction, only anchovy catches were marginally affected at closure level, and significantly affected at the national level. Sardine and total catches did not change significantly (Table 7). For the "all vessels" category, median monthly anchovy catch volume decreased significantly after closure within its perimeter (median monthly catch volume: before closure = 85.17 t, after closure = 8.32 t, original p-value = 0.004, adjusted p-value = 0.02), as well as at the national level (median monthly catch volume: before = 9 951.38 t, after closure = 508.06 t, original p-value = 0.002, adjusted p-value = 0.01). The same trend was observed for the total catches within the closure perimeter (median monthly catch volume: before closure = 732.17 t, after closure = 187.61 t, original p-value = 0.002, adjusted p-value = 0.01), which was similarly reflected at the national level (median monthly catch volume: before = 1 5748.84 t, after = 4 856.47 t, original p-value = 0.004, adjusted p-value = 0.02). Sardine catches were not significantly impacted by the closure, at either spatial level. Regarding vessels ≥26 m, Mann-Whitney tests revealed a marginal reduction in anchovy median catch volume within the closure perimeter (median monthly catch volume: before closure = 56.38 t, after closure = 8.32 t, original p-value = 0.01, adjusted p-value = 0.08.), which was significantly reflected at the national level (median monthly catch

volume: before closure = 6086.65 t, after closure = 440.22 t, original p-value = 0.002, adjusted p-value = 0.01). Neither sardine nor total catches significantly changed after closure, at either spatial level.

	Species	Level	Median Before (t)	Median After (t)	Original p-value	Adjusted p-value
All vessels	Anchovy	closure	85.17	8.32	0.4 e-02 **	0.02 *
		national	9 951.38	508.06	0.2 e-02 **	0.01 *
	Sardine	closure	149.49	90.03	0.38	1.00
		national	3 573.49	3 415.03	0.86	1.00
	Total	closure	732.17	187.61	0.2 e-02 **	0.01 *
		national	15 748.84	4 856.47	0.4 e-02 **	0.02 *
< 26m vessels	Anchovy	closure	56.38	8.32	0.01 *	0.08 ·
		national	6 086.65	440.22	0.2 e-02 **	0.01 *
	Sardine	closure	82.59	90.03	0.53	1.00
		national	1 717.64	2 727.77	0.23	1.00
	Total	closure	318.79	187.61	0.06 ·	0.37
		national	8 704.08	3 922.70	0.02 *	0.12

Table 7: Results of Mann-Whitney tests comparing median volume of monthly catches of anchovy, sardine and total catch, before and after the closure. Tests were conducted at two spatial levels (catches within the closure perimeter and national catches) and for two vessels categories (all vessels and vessels under the size restriction of 26 meters). Medians are expressed in tonnes. A Bonferroni correction was applied separately for each spatial level (n = 6 tests). ·p < 0.1; *p < 0.05; **p < 0.01.

To investigate whether local catch trends of all vessels were reflected at the national level, Spearman correlation tests were performed between local and national levels for monthly catches of anchovies, sardines, and total catches. The tests revealed a significant positive correlation between monthly catches at closure level and national level, for anchovy catches ($\rho = 0.43$, $p < 0.05$) and sardine catches ($\rho = 0.51$, $p < 0.05$), suggesting that catch trends at the closure level were driven by large-scale fisheries dynamics, rather than by the closure implementation itself. In contrast, total catches at the closure level were not significantly correlated to those at the national level ($\rho = 0.20$, $p = 0.084$) (Table 8).

Species	rho	Original p-value	Adjusted p-value
Anchovy	0.43	7.57 e-07 ***	2.27 e-06 ***
Sardine	0.51	1.35 e-09 ***	4.04 e-09 ***
Total	0.20	2.80 e-02 *	0.08 ·

Table 8: Results of Spearman rank correlations between monthly catches at closure level and national level, for anchovy, sardine and total catches, from all vessels. ρ: Spearman rank correlation coefficient. A Bonferroni correction was applied for multiple comparisons (n = 3 tests).
·p < 0.1; *p < 0.05; **p < 0.01; ***p < 0.001.

To determine whether fishing trends of all vessels within the closure perimeter were driven by broader factors, relationships between annual catches, recruit and spawner biomass, and TAC were investigated. Spearman correlations did not reveal any significant correlation between annual anchovy catches and anchovy TACs, spawner biomass or recruit biomass for anchovy, at either spatial level (closure and national). Regarding sardine, annual catches at closure level were significantly positively correlated with both sardine spawner biomass (ρ = 0.80, p-value = 0.01) and sardine TACs (ρ = 0.97, p-value = 0.13 e-03). At the national level, annual sardine catches remained correlated to spawner biomass (ρ = 0.77, p-value = 0.01), while the correlation with sardine TACs was only marginal (ρ = 0.80, p-value = 0.06). No significant correlation was observed between sardine annual catches and recruit sardine biomass (Table 9; Figure 13).

Species	Catch level	Correlated with	n	rho	Original p-value	Adjusted p-value
Anchovy	Closure	Recruit	11	0.06	0.85	1.00
		Spawner	13	0.25	0.41	1.00
		TAC	13	-0.06	0.83	1.00
	National	Recruit	11	0.29	0.38	1.00
		Spawner	13	0.18	0.55	1.00
		TAC	13	0.32	0.292	1.00
Sardine	Closure	Recruit	11	0.69	0.02 *	0.11
		Spawner	13	0.80	0.1 e-02 **	0.7 e-02 **
		TAC	9	0.97	2.15 e-05 ***	0.13 e-03 ***
	National	Recruit	11	0.56	0.07 ·	0.43
		Spawner	13	0.77	2.11 e-03 **	0.013 *
		TAC	9	0.80	9.63 e-03 **	0.058 ·

Table 9: Results of Spearman rank correlations between annual catches of sardines and of anchovy (closure level and national level, for all vessels), and total allowable catches (TACs), recruit biomass and spawner biomass. Spawner biomass was lagged by one year to reflect the management procedure. The year 2022 was excluded for all test to avoid artefacts from the mid-year closure implementation. n: number of years accounted. ρ: Spearman rank correlation coefficient. A Bonferroni correction was applied for multiple comparisons (n = 6 tests). ·p < 0.1; *p < 0.05 ; **p < 0.01; ***p < 0.001.

Three LMM were then fitted to assess the haul-sizes of different fish species (anchovy, sardine, total) caught inside the closure area by all vessels before versus after the closure. The best AIC output was always that of the model including the closure status and haul month as

fixed effects, and the haul year and vessel name as random variables. The residuals of each model were then explored using the DHARMa package (Hartig et al., 2024) (Table S21 to S23, Figure S7 to S9 – supplementary). The models demonstrated that month had a significant impact on the haul-size, with a peak of anchovy hauls in March / April, a peak in sardine hauls in November / December and in total hauls in March / April. The closure did not have a significant effect on the size of anchovy hauls, and only a marginal effect on the size of sardine hauls (with a decrease in haul size after the closure). For total catches, the closure had a significant positive impact on haul-size, with an increase of the haul-size by 49% after the closure ($\beta = 0.67$, p-value = 0.02; Figure 12). Models explained 47.6 to 57% of the total variance, with closure status and months accounting for only 2.2 to 3.4%. Inter-annual variance and inter-vessel variance accounted for approximately half of the total variance. Tables of models estimates for haul sizes are detailed in Table 10. Full model outputs are provided in Table S24 to S26 (supplementary). Regarding model validation, KS tests were significant across all models, likely due to a large sample size. Dispersion tests were all non-significant. Outliers tests were significant for the LMM models of sardine catches and total catches. Outliers revealed respectively 4 and 29 extremely low haul-sizes, corresponding to legitimate fishing events, which were therefore retained in the analysis. For sardine catches, removing the outliers did not improve the model diagnostic. Regarding the total catches, removing the outliers improved the model diagnostic but altered the significance of the effect of the closure. These models should therefore be interpreted with caution.

Term	Anchovy (β)	Sardine (β)	Total (β)
Intercept	2.16 (0.57) ***	2.85 (0.44) ***	4.31 (0.31) ***
Closure	0.08 (0.53)	-0.82 (0.43) ·	0.67 (0.29) *
Month (sine)	0.38 (0.08) ***	-0.13 (0.06) *	0.16 (0.03) ***
Month (cosine)	-0.51 (0.08)***	0.40 (0.08) ***	0.02 (0.04)
Random effects	Variance (SD)	Variance (SD)	Variance (SD)
Year	1.17 (1.08)	0.58 (0.76)	0.46 (0.68)
Vessel	2.13 (1.46)	1.15 (1.07)	0.37 (0.60)
Model fit			
Marginal R^2	0.022	0.034	0.023
Conditional R^2	0.570	0.476	0.513
N hauls	1 533	1440	2 104
N years	14	14	14
N vessels	78	83	85

Table 10: Results of the LMM modelling the log-transformed positive haul size of anchovy, sardine and total catches within the closure perimeter (all vessels). Fixed effects include closure status and seasonality (modelled via cyclic sine and cosine transformations of the month). Random effects include haul year and vessel name, accounting for inter-annual and inter-vessels variability. The pre-closure period is the reference category for the closure status variable. Model were fitted using restricted maximum likelihood (REML). *p < 0.05; **p < 0.01, ***p < 0.001.

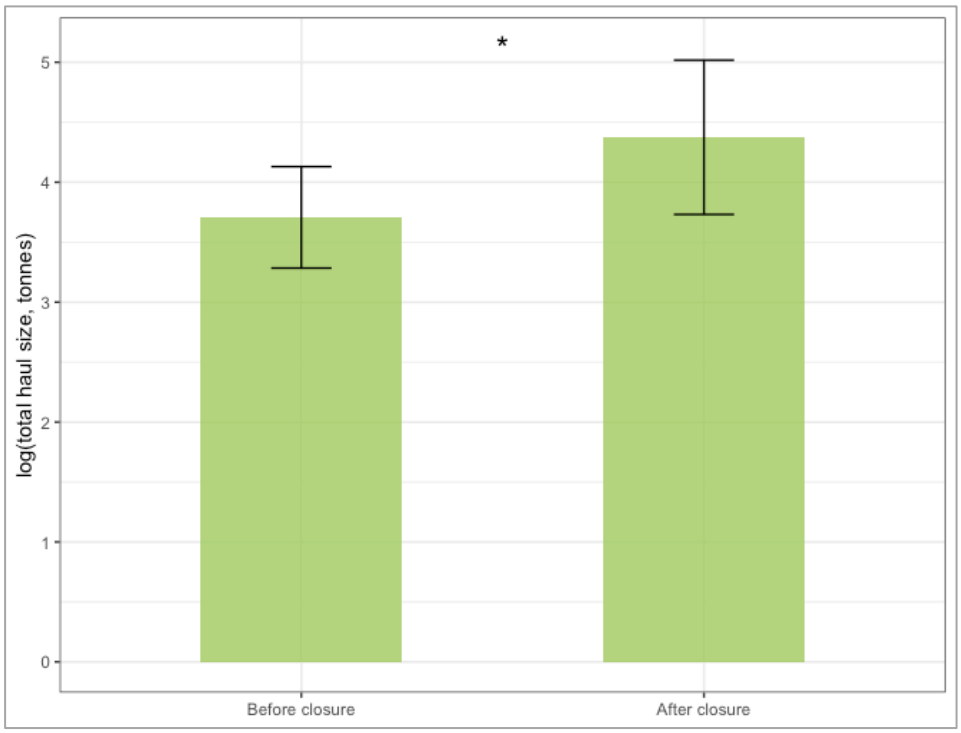

Figure 12: Estimated marginal means of the log-transformed total catch volume per haul (anchovy + sardine, in tonnes) before and after the closure implementation. Bars: 95% confidence interval. The change in haul volume is significant (p-value < 0.05).

2) IMPACT OF CLOSURE ON FREQUENT VESSELS

Within the frequent vessels, 10 out of the 14 vessels (71.4%) were under the size restriction of 26 meters. Following the closure, the four frequent vessels that were affected by the size-restriction left the area, proving that the closure changed the composition of the fishing vessels within its perimeter.

Poisson rate ratio tests were performed on frequent vessels to test whether the number of fishing hauls differed significantly after the closure. Results showed a significant decrease of anchovy and total haul counts after the closure implementation, for all frequent vessels and frequent vessels under the size restriction. Anchovy haul count decreased significantly, across all frequent vessels (55.1% decline; p-value < 0.001), and frequent vessels under the size restriction (52.7% decline; p-value < 0.001). The compiled biomass of anchovy catches over the same period declined after the closure was implemented. In contrast to anchovy, sardine haul counts within the closure perimeter did not significantly change following the closure implementation, neither for all frequent vessels, nor for frequent vessels under the size restriction. The compiled biomass of catches over the same periods increased after the closure implementation. Finally, total catch hauls showed similar results to anchovy hauls, with a post-

closure decline of 35.3% for all frequent vessels (p-value < 0.001), and 31.2% for frequent vessels under the size restriction (p-value = 0.001). The combined biomass of catches over the same periods roughly halved after the closure was implemented for both vessel categories (Table 11).

Haul category		Fishing hauls (n)		Poisson test		Catch (t)	
		before	after	rate ratio (95% CI)	p-value	before	after
Anchovy	All	176	79	2.23 (1.7 – 2.94)	< 0.001 ***	8 322.3	1 980.6
	< 26 m	167	79	2.11 (1.61 – 2.8)	< 0.001 ***	7 871.4	1 980.6
Sardine	All	109	95	1.15 (0.86 – 1.53)	0.36	1 635.4	2 885.0
	< 26m	100	95	1.05 (0.79 – 1.41)	0.77	1 196.1	2 885.0
Total	All	204	132	1.55 (1.24 – 1.94)	< 0.001 ***	9 957.7	4 865.6
	< 26m	192	132	1.45 (1.16 – 1.83)	0.001 **	9 067.5	4 865.6

Table 11: Results of Poisson rate ratio tests comparing fishing haul counts within the closure perimeter before and after the closure implementation, for frequent vessels. The comparison time-window was defined as 65 active fishing days distributed over an 810-day period, on each side of the closure date. Total catches (tonnes) are reported for the same period. Rate ratio >1 one indicates a decrease in haul frequency after the closure. **p < 0.01; ***p < 0.001.

Mann-Whitney tests assessed whether the fish biomass removed from the closure perimeter changed after its implementation, and contextualised the locally observed trends to broader tendencies. The tests did not reveal any significant reduction in monthly catch volume (for anchovy, sardine and total catch) within the closure perimeter after its implementation. In contrast, monthly catches of the frequent vessels at a national level significantly decreased for anchovy and total catches (anchovy: before closure = 2 271.59 t, after closure = 98.18 t, original p-value = 0.5 e-03, adjusted p-value = 0.0014; total catch: before closure = 3 851.49 t, after closure = 1 182.41 t, original p-value = 0.5 e-03, adjusted p-value = 0.0014). Monthly sardine catches were not significantly impacted at either spatial level (Table 12).

To investigate whether catch trends of frequent vessels within the closure perimeter were reflected at the national level, Spearman correlation tests were performed between local and national levels for monthly catches of anchovies, sardines, and total catches. The tests revealed a significant positive correlation between monthly catches at closure level and national level, for anchovy catches ($\rho = 0.46$, p-value < 8.12 e-07) and sardine catches ($\rho = 0.53$, p-

value < 2.93 e-09), suggesting that catch trends at the closure level were significantly associated with large-scale fisheries dynamics, rather than by the closure implementation itself. Total catches at the closure level were not significantly correlated to those at the national (Table 13; Figure 13).

Species	Group	Median Before (t)	Median After (t)	original p-value	Adjusted p-value
Anchovy	Closure	50.98	8.32	0.05 ·	0.15
	National	2 271.59	98.18	0.5 e-03 ***	0.14 e-02 **
Sardine	Closure	72.60	121.60	0.34	1.00
	National	1 059.41	866.30	0.52	1.00
Total	Closure	353.00	193.21	0.19	0.57
	National	3 851.49	1 182.41	0.5 e-03 ***	0.14 e-02 **

Table 12: Results of Mann-Whitney tests comparing median monthly catches of anchovy, sardine and total catches before and after the closure. Tests were conducted at two spatial levels (catches within the closure perimeter and national catches), for frequent vessels. Medians are expressed in tonnes. A Bonferroni correction was applied separately for each spatial level (n = 3 tests). ·p < 0.1; **p < 0.01; ***p < 0.001.

Species	rho	Original p-value	Adjusted p-value
Anchovy	0.46	2.71 e-07 ***	8.12 e-07 ***
Sardine	0.53	9.78 e-10 ***	2.93 e-09 ***
Total	0.16	0.10	0.30

Table 13: Results of Spearman rank correlations between monthly catches at closure level and national level, for anchovy, sardine and total catches, from frequent vessels. ρ: Spearman rank correlation coefficient. A Bonferroni correction was applied for multiple comparisons (n = 3 tests). ·p < 0.1; *p < 0.05; **p < 0.01; ***p < 0.001.

To determine whether fishing trends of frequent vessels within the closure perimeter were driven by broader factors, relationships between annual catches and recruit biomass, spawner biomass, and TAC were investigated. Spearman correlations did not reveal any significant correlation between anchovy catches and anchovy TACs, spawner or recruit biomass of anchovy, at either spatial level (closure and national). Regarding sardine, annual catches at both closure and national levels were significantly positively correlated to sardine spawner biomass (closure level: $\rho = 0.81$, p-value = 0.004; national level: $\rho = 0.79$, p-value = 0.008) and sardine TACs (closure and national level: $\rho = 0.92$, p-value = 0.003). No correlation was found between sardine annual catches (within the closure perimeter and at national level) and recruit sardine biomass (Table 14; Figure 13).

Species	Catch level	Correlated with	n	rho	Original p-value	Adjusted p-value
Anchovy	Closure	Recruit	11	-0.12	0.73	1.00
		Spawner	13	0.28	0.35	1.00
		TAC	13	-0.15	0.61	1.00
	National	Recruit	11	0.35	0.30	1.00
		Spawner	13	0.27	0.37	1.00
		TAC	13	0.15	0.63	1.00
Sardine	Closure	Recruit	11	0.68	0.02 *	0.12
		Spawner	13	0.81	0.7 e-03 ***	0.4 e-02 **
		TAC	9	0.92	0.5 e-03 ***	0.3 e-02 **
	National	Recruit	11	0.62	0.04 *	0.26
		Spawner	13	0.79	0.1 e-02 **	0.8 e-02 **
		TAC	9	0.92	0.5 e-03 ***	0.3 e-02 **

Table 14: Results of Spearman rank correlations between annual catches of sardines and of anchovy (closure level and national level, for frequent vessels), and total allowable catches (TACs), recruit biomass and spawner biomass. Spawner biomass was lagged by one year to reflect the management procedure. The year 2022 was excluded for all tests to avoid artefacts from the mid-year closure implementation. n: number of years accounted. ρ: Spearman rank correlation coefficient. A Bonferroni correction was applied for multiple comparisons (n = 6 tests). ·p < 0.1; *p < 0.05; **p < 0.01; ***p < 0.001.

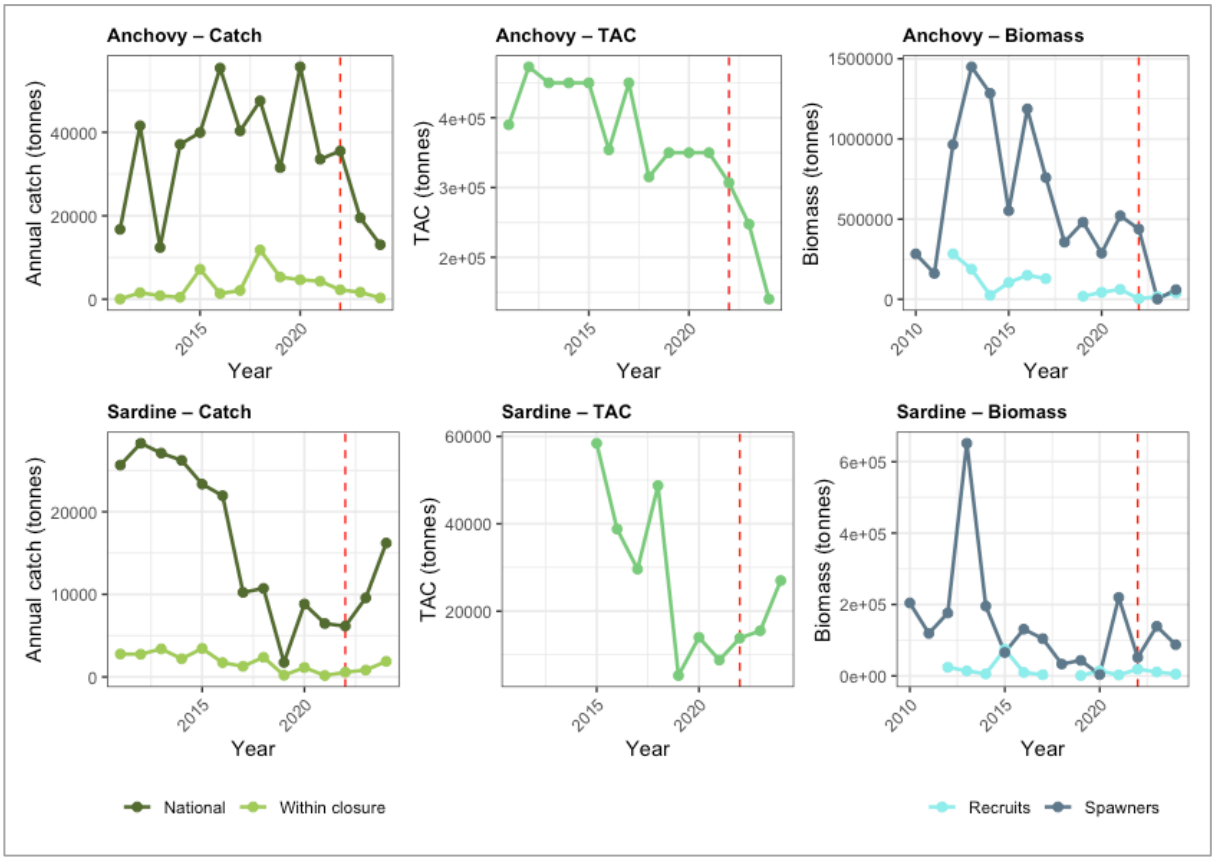

Figure 13: Annual trends in fishery catches, total allowable catch (TAC) and biomass (spawner and recruit). Left panels: annual catches of anchovy (top row) and sardine (bottom row) by frequent vessels at closure and national level. Middle panels: annual anchovy (top row) and sardine (bottom row) TACs.

Anchovy TACs apply for east and west Cape Agulhas regions, sardine TACs only apply for west Cape Agulhas. Right panels: annual anchovy (top row) and sardine (bottom row) recruit and spawner biomass between Cape Point and Cape Agulhas.

Three LMM were then fitted to assess the haul-sizes of different fish species (anchovy, sardine, total) caught inside the closure area by frequent vessels before versus after the closure. The best AIC output was always that of the model including the closure status and haul month as fixed effects, and the haul year and vessel name as random variables. The residuals of each model were then explored using the DHARMa package (Hartig et al., 2024) (Table S27 to S29, Figure S10 to S12 – supplementary). For all fish species, month had a significant impact on the haul-size, with a peak of anchovy in hauls in March / April, a peak in sardine in November / December and in total catch in March / April. The closure did not have a significant effect on the haul-size containing anchovy nor total catch, and it only had a marginal effect on the size of sardine hauls (with a downward tendency after closure). Models explained 36 to 63% of the total variance, with closure status and months only accounting for 0.6 to 4.2%. Inter-annual variance and inter-vessel variance accounted for approximately a third to a half of the total variance. Tables of models estimates for species presence are detailed in Table 15, and full model outputs are provided in Table S30 to S32 (supplementary). Regarding model validation, KS tests were significant across all models, likely due to a large sample size. Dispersion tests were all non-significant. Outliers tests were significant for the LMM of total catches (28 extremely low haul-sizes), and corresponded to legitimate fishing events, which were therefore retained in the analysis. Removing the outliers improved the model diagnostic but altered the significance of the effect of the closure. These models should therefore be interpreted with caution. Last, a convergence warning was noted for the LMM model of anchovy catches.

To assess whether the fishing effort of frequent vessels was affected by the closure, fishing effort was compared before and after the closure implementation. Two spatial scales and vessel fleets were considered: frequent vessels within the closure area and all vessels at a national level. A second comparison was conducted to account for confounding effects of seasonality on the fishing effort. The fishing effort of frequent vessels within the closure perimeter before and after its implementation did not differ significantly. In contrast to this result, all vessels at a national level marginally decreased their standardised fishing effort after the implementation of the closure (p-value = 0.09) (Figure 14). These patterns remained unchanged when controlling for seasonality: neither the frequent vessels, nor all vessels showed a significant difference in fishing effort after the closure implementation (Table 16).

Term	Anchovy (β)	Sardine (β)	Total (β)
Intercept	1.42 (0.64) *	3.20 (0.45) ***	3.77 (0.18) ***
Closure	0.51 (0.50)	-0.76 (0.38) ·	0.06 (0.25)
Month (sine)	0.23 (0.10) *	-0.18 (0.08) *	0.11 (0.04) **
Month (cosine)	-0.37 (0.10)***	0.25 (0.10)**	-0.01 (0.05)
Random effects	Variance (SD)	Variance (SD)	Variance (SD)
Year	1.08 (1.04)	0.36 (0.60)	0.18 (0.42)
Vessel	2.08 (1.44)	0.88 (0.94)	0.25 (0.50)
Model fit			
Marginal R^2	0.020	0.042	0.6 e-02
Conditional R^2	0.627	0.438	0.357
N hauls	770	713	1 072
N years	14	14	14
N vessels	14	14	14

Table 15: Results of the LMM modelling the log-transformed positive haul size within the closure perimeter (frequent vessels). Fixed effects include closure status and seasonality (modelled via cyclic sine and cosine transformations of the month). Random effects include haul year and vessel name, accounting for inter-annual and inter-vessels variability. The pre-closure period is the reference category for the closure status variable. Models were fitted using restricted maximum likelihood (REML). *p < 0.05; **p < 0.01, ***p < 0.001.

Statistical approach	Group	Median before	Median after	W	Original p-value	Adjusted p-value
Overall comparison (Mann-Whitney tests)	Frequent vessels (closure level)	9.33	8.59	867.5	0.73	1.00
	All vessels (national level)	567.59	310.50	2 428.0	0.05 ·	0.09 ·
Seasonal comparison (paired Wilcoxon tests)	Frequent vessels (closure level)	16.33	8.92	39	0.05 ·	0.11
	All vessels (national level)	772.76	282.37	65	0.04 *	0.08 ·

Table 16: Statistical comparison of standardised monthly fishing effort before and after closure implementation (1st September 2022). Standardised fishing effort was defined as: $E_{i,t} = H_{i,t} * (L_i / L)$ ($H_{i,t}$: the number of hauls recorded for vessel i in month t; L_i : the length of vessel i; L : mean length of frequent vessels). Monthly effort was calculated across frequent vessels at the closure level, and all vessels at the national level. Medians are expressed in standardised haul units. A Bonferroni correction was applied for multiple comparisons (n = 2 tests per approach). For each month in the seasonal approach, mean effort was calculated across all years pre- and post-closure, and paired comparisons were performed on monthly effort to account for seasonal variations in fishing effort. ·p < 0.1; *p < 0.05.

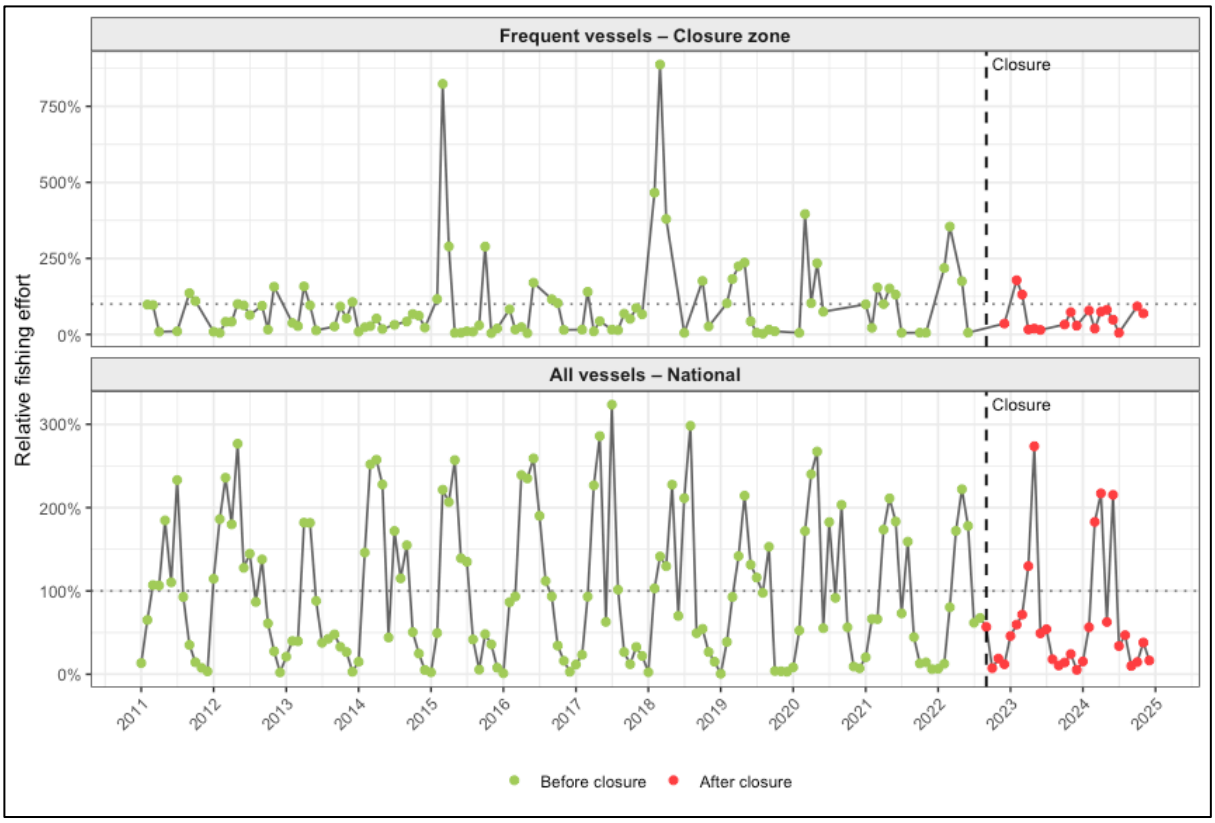

Figure 14: Relative monthly fishing efforts of frequent fishing vessels within the closure area and all vessels at a national level. Standardised fishing effort was defined as: $E_{i,t} = H_{i,t} * (L_i / L)$ ($H_{i,t}$: the number of hauls recorded for vessel i in month t; L_i : the length of vessel i; L : mean length of frequent vessels). Effort is expressed relative to the mean monthly effort before the closure implementation (= 100%). Values above 100% indicate months where the average effort was higher than the average effort before closure. Black dashed line represents the date of the closure implementation.

Finally, the ratio of monthly effort of frequent vessels within the closure perimeter to the national monthly effort of all vessels did not change significantly after the closure (median ratio before closure = 0.017; median ratio after closure = 0.033; p-value = 0.41), suggesting the closure did not have a specific effect on the monthly effort of frequent vessels.

DISCUSSION

This study aimed to investigate the effectiveness of the purse-seine fishery closure around the African penguin colony at Dyer Island by assessing its impact on penguins' foraging behaviour and on fishing activity within its perimeter. Overall, the closure did not show any significant improvement on the penguins' foraging performance. No effects were detected on the maximum distance of foraging trips from the colony, nor on the foraging trip duration, although the total path length of short trips appeared to be shorter after the closure. However, this effect could not be distinguished from that of a variation in prey availability. Regarding

fishing activity, even though the global fishing activity declined within the area after the closure, this decline mirrored broader fisheries and stock dynamics than the closure itself. As intended by the closure design, frequent vessels within the closure perimeter appeared to be unaffected by its implementation.

A) Lack of effect of the closure on the penguins' foraging metrics in the absence of reduced fishing pressure

First, the closure did not bring any significant isolated changes to the fishing activity within the closure perimeter. While haul counts decreased significantly after closure, this reduction was observed for both all vessels and vessels unaffected by the size restriction, suggesting it is not a direct consequence of the closure, but rather driven by broader factors such as a decrease in prey availability. These results align with the observation that the decrease in monthly catch volume for anchovy and for total catches was correlated to broader dynamics. In contrast, the closure appeared to have negatively impacted the sardine haul counts within its perimeter, which decreased significantly for all vessels after the closure, while remaining unchanged for the vessels unaffected by the size restriction. However, monthly sardine catch volumes inside the closure remained unaffected, and sardine annual catches were correlated to TACs and spawner biomass, further reinforcing the hypothesis that fishing trends in the area were driven by broader dynamics rather than the closure itself. The only closure-driven result was a 49% increase in total haul volume, although the closure only explained less than 3% of the variance. These results suggest that the observed variations in fishing activity within the closure perimeter reflected broader national dynamics, and were not a direct consequence of the closure itself.

These fishing trends provide useful contextual information to help explain the lack of any significant difference in African penguin path metrics before and after the implementation of the closure around Dyer Island: neither on the maximum distance, nor the total distance, nor the duration showed significant improvement post-closure, suggesting the penguins' foraging performance was not improved by the closure. The effect of the closure on the path length of short trips was no longer significant when cumulative anchovy catches over the previous 90 days of each trip were added. The high collinearity between the closure and the anchovy catches over the previous 90 days did not allow to statistically distinguish if the detected effect reflected the effect of the closure implementation itself, a response to changes in prey availability, or

both. These results were nonetheless consistent with the fisheries analyses, where the significant decrease of monthly anchovy catch volume within the closure perimeter was also reflected at the national level, which suggests that this decrease mirrors broader dynamics than the closure itself. Because the shape of the residuals impacted the model explaining the maximum distance, these results must be interpreted cautiously.

In addition to the challenge of isolating confounding ecological trends, the current use of biologgers presents limitations to accurately reflect the trips themselves. For example, trips are highly dependent on individuals, who vary considerably. However, individual identity was not tracked across all deployments. Furthermore, the loggers only represent a short window of an individual's lifespan. For instance, a bird might expend more or less energy depending on the length of its trips, and thus adjust its trip frequency accordingly. Therefore, we would only have part of the story (Pinaud et al., 2005). It is also important to note that the metrics data are limited due to restricted biologger deployments. This limitation extends to the time period, with no data available between 2012 and 2021, but also to the number of deployments permitted per year because of the species' protected status, with only 20 deployments allowed per colony and per year. Furthermore, only three years of deployments were considered after the closure implementation, creating asymmetry in the metric data between before and after the closure, further limiting the comparative data. Note that the data was collected only during the breeding period and not throughout the year, which therefore only reflects penguins' condition during this specific period, leaving out other key life history stages such as the pre- and post-moulting periods. It would also have been beneficial to link these results to chick survival. These methodological limitations are factors that can create a lack of power in the path metrics analyses. Furthermore, anchovy and sardine biomasses could not be included in the models due to their spatial resolution being too large compared to the local conditions of the studied area, creating a significant mismatch. Future work, particularly with a larger amount of data and finer-scale resolution biomass data, would facilitate a more robust assessment. Despite these limitations, these preliminary results suggest that the closure configuration does not conform to its intended benefits in alleviating resource competition for African penguins.

Research into the effects of purse-seine fishing no-take zones during the ICE have demonstrated small but meaningful benefits to African penguin conservation, such as Sherley et al. (2018) who demonstrated that chick survival and chick condition improve when fishing is excluded around penguin colonies, with a 2 to 11% increase in chick survival (Sydeman et

al., 2021). This increase in chick survival and condition is likely to translate into a global improvement in the growth rate of the population (Punt et al., 2023). Punt et al. (2023) also raises the point that closures offer substantial relief in food competition, potentially facilitating reduction in foraging effort during critical non-breeding periods as well. Indeed, such mitigation of energy constraints outside of breeding or moulting seasons triggers positive carryover effects, which optimise resources accumulation ahead of a highly demanding life event. Pichegru et al. (2010), on the St. Croix colony, highlighted a 25-30% reduction in foraging effort and significant energy savings just a few months after the closure was implemented around the island. Trips also increased from 75% concentrated outside the closure to over 70% concentrated within the closure the year following the closure implementation. However, these results need to be interpreted with caution, as the colony's health deteriorated a year later following the closure, suggesting that the closure perimeter was too small. This decline in performance was linked to increased fishing pressure on the closure's boundaries that year (a fishing practice called "fishing the line"), suggesting, among other things, the implementation of buffer zones around closures and locally reduced fishing quotas to decrease food competition with penguins (Pichegru et al., 2011). This demonstrates that even in favourable studies, the effects of closures on penguins' health are difficult to isolate. Increased fishing on the boundaries of closures is not uncommon around MPAs, because it allows for the exploitation of resources leaving the protected area ("spillover effect") (Bucaram et al., 2018; Franceschini et al., 2024). However, this effect is not universal as it can depend on factors such as the distance and travel time between the port of fishing vessels and the target area (Sultan, 2020). If this phenomenon were to be observed around the Dyer Island closure, it would be beneficial to study its effects on the desired efficiency of the area. A second limitation concerns the economic model, i.e. the Opportunity-based models (OBM), used to evaluate the economic costs of these closures to fisheries. The international review panel identified several aspects of the OBM model that are likely to overestimate catch losses (Punt et al., 2023). The results observed for the fisheries within the closure area were consistent with this declaration: neither catches of all vessels, nor fishing effort of local vessels were impacted by the Dyer Island closure. If the actual cost of the closure is lower than the estimated cost by the OBM, the justification for the closure's perimeter, which was maintained unchanged after the March 2025 court order for economic reasons, is therefore weakened and the closure boundaries should be revised.

While the closure area studied here is static, dynamic area-based management tools can potentially help to better accommodate the dynamic nature of marine habitat conditions and associated prey availability (Klerk et al., 2024). For instance, a dynamic approach has been modelled for the little penguin in Australia, where dynamic areas are adjusted according to foraging distributions. Although the system relies on accurate predictions of environmental conditions and reproductive success before the breeding season, it would be more space-efficient and more acceptable to fishers (Venegas-Li et al., 2023). Another method for managing dynamic MPAs is to adapt the size of the no-take zones during years where pelagic prey biomass is scarcer. This method is based on the overlap intensity between penguins and fishing vessels. Considering this pressure would allow for fishing restriction zones to be adapted to the real-time needs of penguins, while minimizing losses for fishers (Glencross et al., 2025). However, deploying such a dynamic closure that is reliant on continuous monitoring would be impractical with the conservation status of the African penguin. Automated Penguin Monitoring System (APMS) records penguin activity at a colony using PIT tags and weighbridges, and constitutes an alternative to a monitoring system reliant on more invasive techniques such as the deployment of biologgers. APMS can be used to obtain proxies of foraging success, by continuously logging foraging trip duration and body mass change at each crossing (Afanasyev et al., 2015). APMS therefore provides individual-proxies of foraging effort throughout the year, without requiring the birds to be handled. These data can then be synchronized to real time fisheries data, for adaptive closure management, allowing restrictions to be adapted to real-time penguin foraging performance. This system is currently deployed in five penguin colonies in South Africa, including at Dyer Island.

Finally, it should be kept in mind that despite their conservation value, closures alone are unlikely to reverse the decreasing population trajectory of the African penguin. At the current rate of decline of the species – estimated at around 8% per year since 2005 – the closure types implemented in 2022 were assessed as providing “little benefit to the African penguin” in their configurations (Punt et al., 2023; McInnes et al., 2024). The island closure around Dyer Island, which remained unchanged following the March 2025 court order, falls within this assessment. Moreover, the effectiveness of a closure area is contingent on the broader health of the ecosystem within which it lies, and its success is therefore questioned when the prey abundance has collapsed around the closure area (Cury et al., 2011; Frederiksen et al., 2008). Beyond fisheries management, facilitating the creation of new colonies to offset the mismatch

between colonies and preys has been proposed as a complementary conservation tool (Punt et al., 2023).

Taken together, these perspectives suggest that the African penguin's survival will not only depend on these closures, but on a series of coordinated adaptive measures, in terms of spatial management of their preys and assisted range adjustments.

B) Stability of local vessel activities post-closure

Regarding the impact of the closure implementation on the local vessels, vessels frequently active in the closure area – serving as a proxy for local fishing activity – appeared to be unaffected by its implementation. While the fishing haul counts significantly decreased for anchovy and total catches, monthly catches as well as haul sizes remained unaffected, indicating a dissociation between the frequency of hauls and catch volumes. The high correlation between local and national catches suggests that local fishing conditions are a reflexion of broader fishing trends. Regarding the fishing effort of local vessels, it remained stable before and after the closure, while national effort showed a marginal decrease. These results mirror those of the monthly catches, which despite decreasing at a national level, did not significantly change within the closure. The two possible explanations for this behaviour are: 1) that the post-closure period is currently too short (2 years and 4 months) to identify a clear trend, or 2) that local vessels maintained their effort, possibly by concentrating it inside the closure area, taking advantage of the absence of competition with longer vessels – a dynamic that would undermine the conservation purpose of the closure.

The overall findings from the fisheries analyses are nonetheless subject to several limitations. The most significant limitation is the timeframe of the study, with 11 years and 8 months of data before the closure, compared to 2 years and 4 months of data after. This temporal imbalance reduces the power of the statistical tests and increases type II errors. Furthermore, the Bonferroni correction is inherently conservative, and combined with the limited data, can possibly mask significant results. The second bias in this analysis concerns the differences between geographical scales. Biomass surveys were concentrated between Cape Point and Cape Agulhas, TACs for sardines covered the region west of Cape Agulhas, and those for anchovies covered national waters. This spatial mismatch is difficult to transpose to

the small scale of the closure, and can therefore introduce biases into the correlations. Third, local-scale fishing surveys could have more easily distinguished the effect of the closure, particularly within models where local biomass could have been a discriminating effect. Fourth, the gap that leaves the biggest question mark concerns the internal decision-making factors of fishing companies, such as business decisions, available equipment, economic priorities, etc. Finally, the interpretation of the fishing models was impacted by several statistical limitations highlighted through the residual diagnostics. First, the Kolmogorov-Smirnov test was significant for all models, indicating that the residuals were not uniformly distributed, suggesting potential misspecification of the models. However, KS tests can become highly sensitive with large sample size and therefore reject normality more easily. Over-dispersion does not always indicate a poor model fit and can be due to the nature of the data, such as an excess of zeros or over-dispersion, common with count data in ecology (Harrison, 2014). Second, the models were highly sensitive to small catch data, with the significant effect of the closure on total catches disappearing when the outliers were removed from the data, which suggests that the signal was driven by boats bringing in very small quantities.

Fishing data could have also been investigated with more sophisticated evaluation methods, proposed in the 2023 panel report. These methods can be divided into two approaches: an ex-ante analysis and an ex-post analysis (Punt et al., 2023). The first consists of a random utility model that predicts future behaviour of fishers after the closure of the area. The second approach evaluates the impact of the closure after its implementation, by comparing a control group (vessels that do not fish in the closure area) to a treated group (vessels that fish in the closure area). It can be executed through three different methods: 1) the difference-in-difference method, which determines the impact of the closure by comparing all the vessels together, 2) the propensity score matching method, a more refined method which associates an affected vessel to an unaffected one with similar characteristics, and 3) the synthetic control method, which is also more refined, as it mathematically constructs an artificial comparative group that weights the characteristics of unaffected vessels so that they closely resemble the affected ones (Punt et al., 2023). Although these approaches would have offered a higher resolution, implementing them was outside of the scope of this study, mainly due to a lack of access to vessel-level data.

Beyond methodological limitations of this study, its findings must be contextualised within the broader African penguin conservation and fisheries management framework in

South Africa. Although the Ecosystem Approach to Fisheries Management (EAFM) is recognised by the South African government, notably through the Marine Living Resources Act (Marine Living Resources Act, 1998), its implementation in practice is limited. In the context of small pelagic fisheries, the EAFM takes two different forms: a) area-based measures, such as the penguin closures, and b) an ecological reference point in the OMP, to monitor the impact of catches on non-target species. In the specific case of penguins, they are held as a key predator species in the EAFM, as they predominantly prey on anchovy and sardine, and because of their Critically Endangered status (DFFE, 2025). In particular, a reference point of 25% of the sardine historical maximum biomass from west Cape Agulhas is presented in the 2018 OMP, below which the mortality rate of adult penguins would be accelerated (Robinson et al., 2015). In practice, this reference point has never been implemented, as a state of exceptional circumstances was declared in 2019, after the sardine stocks fell below the range of scenarios simulated by the OMP. The March 2025 court order represented a step forward in conservation for the implementation of long-term closures. However, the situation of Dyer Island remains an unresolved case, and the only closure with a split configuration, standing as a compromise between penguin conservation and local economic sustainability. Results of this preliminary research, despite its limitations in sample size and post-closure data availability, suggest little to no measurable effect of the closure on both penguins' foraging performance and fisheries effort. Altogether, this assessment highlights the gap between intent legislation and its implementation in practice.

CONCLUSION AND PERSPECTIVES

This study investigated the effectiveness of a novel split-zone fisheries closure around Dyer Island in reducing resource competition between the purse-seine fishery and African penguins. The study provides little evidence of a significant effect of the closure on the penguin's foraging performance, and the fishing activity within the zone appeared to be driven by broader fisheries and stock dynamics rather than the closure itself. These results therefore suggest a lack of detectable effect under the current closure configuration. Fishing effort by frequent vessels remained unchanged, suggesting that the closure did not significantly impact local fishing activity, as intended by the closure design. Although the study had several limitations, the area does not appear large enough to reverse the decline of the African penguin population at the Dyer Island colony. These results were consistent with other assessments stating that the configuration of the Dyer Island closure provides only little benefits to the

penguins, and the international panel review's finding that economic costs of the closure implementation were likely overestimated. The urgency for effective conservation measures around this colony stems from the 8% annual decline of the African penguin, while the current closure configuration – the only split-closure among the six closures – has remained unchanged despite its proven ineffectiveness. Exploring alternative closure regimes for this important colony before the 6-year scheduled review, with finer-scale data, is urgently needed in order to improve the conservation measures while redefining a sustainable compromise with the local fishing economy.

USE OF ARTIFICIAL INTELLIGENCE TOOLS

The use of AI tools (Claude, Anthropic) was limited to debugging and correcting R codes used for statistical analyses and figures generation.

CONTRIBUTIONS

The penguin GPS tracking data were collected by Lauren Waller and Deon Geldenhuys between 2009 and 2012, and by Tegan Carpenter-Kling, Alistair McInnes, Eleanor Weideman and Philip Faure for the deployments of 2021 to 2025. The fisheries data, including small pelagic fisheries catch data, total allowable catches and biomass surveys were obtained through the DFFE's Fisheries Management Branch. All data processing and analyses were conducted by the author.

REFERENCES

Afanasyev, V., Buldyrev, S. V., Dunn, M. J., Robst, J., Preston, M., Bremner, S. F., Briggs, D. R., Brown, R., Adlard, S., & Peat, H. J. (2015). Increasing Accuracy: A New Design and Algorithm for Automatically Measuring Weights, Travel Direction and Radio Frequency Identification (RFID) of Penguins. *PLoS ONE*, *10*(4), e0126292. https://doi.org/10.1371/journal.pone.0126292

Beal, M., Oppel, S., Handley, J., Pearmain, E. J., Morera-Pujol, V., Carneiro, A. P. B., Davies, T. E., Phillips, R. A., Taylor, P. R., Miller, M. G. R., Franco, A. M. A., Catry, I., Patrício, A. R., Regalla, A., Staniland, I., Boyd, C., Catry, P., & Dias, M. P. (2021). track2KBA: An R package for identifying important sites for biodiversity from tracking data. *Methods in Ecology and Evolution*, *12*(12), 2372–2378. https://doi.org/10.1111/2041-210X.13713

Beltran, R., Burns, J., & Breed, G. (2018). Convergence of biannual moulting strategies across birds and mammals. Proceedings of the Royal Society B: Biological Sciences, 285, 20180318. https://doi.org/10.1098/rspb.2018.0318

BirdLife International. (2024, July 4). IUCN Red List of Threatened Species: Spheniscus demersus. IUCN Red List of Threatened Species. https://www.iucnredlist.org/en

BirdLife International. (2026). *Country factsheet: South Africa*. Downloaded from https://datazone.birdlife.org/country/factsheet/south-africa on 22/05/2026

BirdLife International. African Penguin Spheniscus Demersus Species. BirdLife DataZone. Retrieved February 22, 2025, from https://datazone.birdlife.org/species/factsheet/african-penguin-spheniscus-demersus

Borboroglu, P. G., & Boersma, P. D. (2013). Penguins: Natural history and conservation. University of Washington Press.

Bucaram, S. J., Hearn, A., Trujillo, A. M., Rentería, W., Bustamante, R. H., Morán, G., Reck, G., & García, J. L. (2018). Assessing fishing effects inside and outside an MPA: The impact of the Galapagos Marine Reserve on the Industrial pelagic tuna fisheries during the first decade of operation. *Marine Policy*, *87*, 212–225. https://doi.org/10.1016/j.marpol.2017.10.002

Carpenter-Kling, T., de Blocq, A., Hagen, C., Harding, C., Morris, T., Pichegru, L., Roberts, J., Ryan, P. G., Wanless, R. M., & McInnes, A. (2022). Important marine areas for endangered African penguins before and after the crucial stage of moulting. Scientific Reports, 12(1), 9489. https://doi.org/10.1038/s41598-022-12969-w

Cock, G. D. L., & Cooper, J. (1987). The breeding frequency of Jackass penguins on the West Coast of South Africa.

Coetzee, J.C., & de Moor, C. L. (2024). *A summary of the South African sardine fishery*. https://doi.org/10.25375/uct.27908280.v1

Coetzee, J. C., Van Der Lingen, C. D., Hutchings, L., & Fairweather, T. P. (2008). Has the fishery contributed to a major shift in the distribution of South African sardine? ICES Journal of Marine Science, 65(9), 1676–1688. https://doi.org/10.1093/icesjms/fsn184

Connan, M., Hofmeyr, G. J. G., & Pistorius, P. A. (2016). Reappraisal of the Trophic Ecology of One of the World's Most Threatened Spheniscids, the African Penguin. PLOS ONE, 11(7), e0159402. https://doi.org/10.1371/journal.pone.0159402

Crawford, R. J. M. (1979). Implications of recruitment, distribution and availability of stocks for management of South Africa's Western Cape purse-seine fishery [PhD dissertation]. University of Cape Town.

Crawford, R., Altwegg, R., Barham, B., Barham, P., Durant, J., Dyer, B., Geldenhuys, D., Makhado, A., Pichegru, L., Ryan, P., Underhill, L., Upfold, L., Visagie, J., Waller, L., & Whittington, P. (2011). Collapse of South Africa's penguins in the early 21st century. African Journal of Marine Science, 33, 139–156. https://doi.org/10.2989/1814232X.2011.572377

Crawford, R., Goya, E., Roux, J.-P., & Zavalaga, C. (2006a). Comparison of assemblages and some life-history traits of seabirds in the Humboldt and Benguela systems. African Journal of Marine Science, 28, 553–560. https://doi.org/10.2989/18142320609504205

Crawford, R., Hemming, M., Kemper, J., Klages, N. T. W., Randall, R. M., Underhill, L., Venter, A. D., Ward, V. L., & Wolfaardt, A. (2006b). S24-2 Molt of the African penguin, Spheniscus demersus, in relation to its breeding season and food availability. Acta Zoologica Sinica, 52.

Crawford, R. J. M., Cruickshank, R. A., Shelton, P. A., & Kruger, I. (1985). Partitioning of a goby resource amongst four avian predators and evidence for altered trophic flow in the pelagic community of an intense, perennial upwelling system. South African Journal of Marine Science, 3(1), 215–228. https://doi.org/10.2989/025776185784461252

Crawford, R. J. M., & Dyer, B. M. (1995). Responses by four seabird species to a fluctuating availability of Cape Anchovy Engraulis capensis off South Africa. Ibis, 137(3), 329–339. https://doi.org/10.1111/j.1474-919X.1995.tb08029.x

Crawford, R. J. M., Shannon, L. J., & Whittington, P. A. (1999). Population dynamics of the African Penguin Spheniscus demersus at Robben Island, South Africa.

Crawford, R. J. M., Sydeman, W. J., Tom, D. B., Thayer, J. A., Sherley, R. B., Shannon, L. J., McInnes, A. M., Makhado, A. B., Hagen, C., Furness, R. W., Carpenter-Kling, T., & Saraux, C. (2022). Food limitation of seabirds in the Benguela ecosystem and management of their prey base. *Namibian Journal of Environment*, *6*, A-13. https://doi.org/10.64640/ft3yd661

Cunningham, G., Strauss, V., & Ryan, P. (2008). African penguins (Spheniscus demersus) can detect dimethyl sulfide, a prey-related odour. The Journal of Experimental Biology, 211, 3123–3127. https://doi.org/10.1242/jeb.018325

Cury, P. M., Boyd, I. L., Bonhommeau, S., Anker-Nilssen, T., Crawford, R. J. M., Furness, R. W., Mills, J. A., Murphy, E. J., Osterblom, H., Paleczny, M., Piatt, J. F., Roux, J.-P., Shannon, L., & Sydeman, W. J. (2011). Global seabird response to forage fish depletion -one-third for the birds. *Science*, *334*(6063), 1703–1706. https://doi.org/10.1126/science.1212928

de Moor, C. L., Butterworth, D. S., & De Oliveira, J. A. A. (2011). Is the management procedure approach equipped to handle short-lived pelagic species with their boom and bust dynamics? The case of the South African fishery for sardine and anchovy. *ICES Journal of Marine Science*, *68*(10), 2075–2085. https://doi.org/10.1093/icesjms/fsr165

Department of Environmental Affairs. (2019, May 28). *Environmental Affairs on Operation Phakisa Oceans Economy Marine Protected Areas*. South African Government. https://www.gov.za/news/media-statements/environmental-affairs-operation-phakisa-oceans-economy-marine-protected-areas

Department of Forestry, Fisheries and the Environment. (2021). *Policy on the Allocation and Management of Small Pelagic Commercial Fishing Rights: 2021* (Government Gazette No. 45504). South African government. https://faolex.fao.org/docs/pdf/SAF210239.pdf

DFFE (Department of Forestry, Fisheries and the Environment). (2025). *Status of the South African marine fishery resources 2025*. Cape Town: DFFE. https://doi.org/10.15493/DFFE.10000008

Dias, M. P., Martin, R., Pearmain, E. J., Burfield, I. J., Small, C., Phillips, R. A., Yates, O., Lascelles, B., Borboroglu, P. G., & Croxall, J. P. (2019). Threats to seabirds: A global assessment. Biological Conservation, 237, 525–537. https://doi.org/10.1016/j.biocon.2019.06.033

FAO. (2018). Profils FAO de la pêche et de l'aquaculture par pays: Afrique du Sud [Profils FAO Pêche Afrique du Sud.]. Pêche et Aquaculture. https://www.fao.org/fishery/fr/facp/zaf?lang=en

Franceschini, S., Lynham, J., & Madin, E. M. P. (2024). A global test of MPA spillover benefits to recreational fisheries. *Science Advances*, *10*(29), eado9783. https://doi.org/10.1126/sciadv.ado9783

Frederiksen, M., Jensen, H., Daunt, F., Mavor, R. A., & Wanless, S. (2008). Differential effects of a local industrial sand lance fishery on seabird breeding performance. *Ecological Applications: A Publication of the Ecological Society of America*, *18*(3), 701–710. https://doi.org/10.1890/07-0797.1

Frost, P. G. H., Siegfried, W. R., & Burger, A. (1976a). Behavioural adaptations of the Jackass Penguin, Spheniscus demersus to a hot, arid environment. *Journal of Zoology*, *179*, 165–187. https://doi.org/10.1111/j.1469-7998.1976.tb02289.x

Frost, P. G. H., Siegfried, W. R., & Cooper, J. (1976b). Conservation of the jackass penguin (*Spheniscus demersus* (L.)). *Biological Conservation*, *9*(2), 79–99. https://doi.org/10.1016/0006-3207(76)90042-2

Geromont, H. F., De Oliveira, J. A. A., Johnston, S. J., & Cunningham, C. L. (1999). Development and application of management procedures for fisheries in southern Africa. ICES Journal of Marine Science, 56(6), 952–966. https://doi.org/10.1006/jmsc.1999.0536

Glencross, J. S., Glencross, A. J., Grigg, J. L., Lang, S. D. J., Makhado, A. B., Upfold, L., Russell, D. J. F., Brierley, A. S., & Sherley, R. B. (2025). Spatial overlap alone downplays the level of interaction between a central place forager and the local fishery. *Journal of Applied Ecology*, *62*(12), 3277–3287. https://doi.org/10.1111/1365-2664.70199

Harrison, X. A. (2014). Using observation-level random effects to model overdispersion in count data in ecology and evolution. *PeerJ*, *2*, e616. https://doi.org/10.7717/peerj.616

Hartig, F., Lohse, L., & leite, M. de S. (2024). *DHARMa: Residual Diagnostics for Hierarchical (Multi-Level / Mixed) Regression Models* (Version 0.4.7) [Computer software]. https://cran.r-project.org/web/packages/DHARMa/index.html

Heath, R. G. M., & Randall, R. M. (1989). Foraging ranges and movements of jackass penguins (Spheniscus demersus) established through radio telemetry. Journal of Zoology, 217(3), 367–379. https://doi.org/10.1111/j.1469-7998.1989.tb02496.x

Hijmans, R. J., Karney (GeographicLib), C., Williams, E., & Vennes, C. (2026). *geosphere: Spherical Trigonometry* (Version 1.6-5) [Computer software]. https://cran.r-project.org/web/packages/geosphere/index.html

Hockey, P., Dean, W., & Ryan, P. (2005). Roberts birds of southern Africa (7th edn). John Voelcker Bird Book Fund.

Kemper, J., Roux, J.-P., Bartlett, P. A., Chesselet, Y. J., James, J. A. C., Jones, R., Wepener, S., & Molloy, F. (2001). Recent population trends of African Penguins Spheniscus demersus in Namibia. South African Journal of Marine Science, 23, 429–434. https://doi.org/10.2989/025776101784528728

Klerk, B. E., Heinrich, K., & Primicerio, R. (2024). Beyond equilibrium thinking: Dynamic area-based management tools in a changing ocean. *Frontiers in Marine Science*, *11*. https://doi.org/10.3389/fmars.2024.1418435

Lei, B. R., Green, J. A., & Pichegru, L. (2014). Extreme microclimate conditions in artificial nests for Endangered African Penguins. *Bird Conservation International*, *24*(2), 201–213. https://doi.org/10.1017/S0959270913000671

Loutit, R., & Boyer, D. (2024). Mainland Breeding by Jackass Penguins Spheniscus Demersus in South West Africa / Namibia. Marine Ornithology, 13(1). https://digitalcommons.usf.edu/marine_ornithology/vol13/iss1/4

Ludynia, K., Roux, J.-P., Jessica, K., & Underhill, L. G. (2010). Surviving off junk: Low-energy prey dominates the diet of African Penguins Spheniscus demersus at Mercury Island, Namibia, between 1996 and 2009. https://doi.org/10.2989/1814232X.2010.538151

Ludynia, K., Stassen, M., Fearon, G., & Pichegru, L. (2026). Evaluation of risks of oil contamination in endangered seabirds in Algoa Bay, South Africa, linked to ship-to-ship bunkering and anthropogenic maritime activities. *Marine Pollution Bulletin*, *224*, 119089. https://doi.org/10.1016/j.marpolbul.2025.119089

Makhado, A., Crawford, R., Waller, L., & Underhill, L. (2013). An assessment of the impact of predation by Cape fur seals Arctocephalus pusillus pusillus on seabirds at Dyer Island, South Africa. *Ostrich: Journal of African Ornithology*, *84*, 191–198. https://doi.org/10.2989/00306525.2013.863234

Marine Living Resources Act, Pub. L. No. No. 18 of 1998, No. 18930 Government Gazette (1998). https://sapfia.org.za/wp-content/uploads/2022/11/Marine-Living-Resources-Act-1.pdf

Martínez, I., Christie, D., Jutglar, F., & Garcia, E. (2020). African Penguin (Spheniscus demersus), version 1.0. Cornell Lab of Ornithology, Ithaca, NY, USA. https://birdsoftheworld.org/bow/species/jacpen1/cur/introduction

McInnes, A. M., McGeorge, C., Ginsberg, S., Pichegru, L., & Pistorius, P. A. (2017). Group foraging increases foraging efficiency in a piscivorous diver, the African penguin. Royal Society Open Science, 4(9), 170918. https://doi.org/10.1098/rsos.170918

McInnes, A., Weideman, E., Carpenter-Kling, T., Barham, P., Christian, M., Day, K., Glencross, J., Hagen, C., Kock, A., Lawrence, C., Ludynia, K., Makhado, A., Pichegru, L., Shannon, L., Sherley, R., Smith, C., Steinfurth, A., Stander, N., Upfold, L., & Waller, L. (2024). Commercial fishery no-take zones for African penguins minimize fisheries losses at the expense of conservation gains. ICES Journal of Marine Science, 1–15.

Moloney, C. L., & Johnston, S. J. (2002). Using decision analysis to evaluate candidate OMPs for the South African west coast rock lobster fishery. South African Journal of Science, 98(9), 461–464.

Nagy, K. A., Siegfried, W. R., & Wilson, R. P. (1984). Energy Utilization by Free-Ranging Jackass Penguins, Spheniscus Demersus. Ecology, 65(5), 1648–1655. https://doi.org/10.2307/1939143

OECD. (2017). *Marine Protected Areas: Economics, Management and Effective Policy Mixes*. OECD Publishing. https://doi.org/10.1787/9789264276208-en

Petersen, S. L., Ryan, P. G., & Gremillet, D. (2006). Is food availability limiting African Penguins Spheniscus demersus at Boulders? A comparison of foraging effort at mainland and island colonies. Ibis, 148(1), 14–26. https://doi.org/10.1111/j.1474-919X.2006.00459.x

Phillips, R. A., Xavier, J. C., & Croxall, J. P. (2003). Effects of Satellite Transmitters on Albatrosses and Petrels. The Auk, 120(4), 1082–1090.

Pichegru, L., Grémillet, D., Crawford, R. J. M., & Ryan, P. G. (2010). Marine no-take zone rapidly benefits endangered penguin. Biology Letters, 6(4), 498–501. https://doi.org/10.1098/rsbl.2009.0913

Pichegru, L., Ryan, P. G., van Eeden, R., Reid, T., Grémillet, D., & Wanless, R. (2011). Industrial fishing, no-take zones and endangered penguins. *Biological Conservation, Seabirds and Marine Protected Areas Planning*, *156*, 117–125. https://doi.org/10.1016/j.biocon.2011.12.013

Pichegru, L., Ryan, P., Le Bohec, C., van der Lingen, C., Navarro, R., Petersen, S., Lewis, S., Westhuizen, J., & Grémillet, D. (2009). Overlap between vulnerable top predators and fisheries in the Benguela upwelling system: Implications for marine protected areas. *Marine Ecology-Progress Series - MAR ECOL-PROGR SER*, *396*. https://doi.org/10.3354/meps08283

Pichegru, L., Sherley, R. B., Malan, T., Barham, B. J., Ludynia, K., Geldenhuys, D., Amos, K., Barham, P. J., Drost, E., Hahndiek, V., Hufke, A., Hugo, C., Lawrence, C., McGeorge, C., McInnes, A. M., Makhado, A. M., Mashau, M., Milne, R., Purves, A., … Waller, L. (2024). Decades of artificial nests towards African penguin conservation—Have they made a

difference? *Ecological Solutions and Evidence*, *5*(4), e12388. https://doi.org/10.1002/2688-8319.12388

Pichegru, L., Vibert, L., Thiebault, A., Charrier, I., Stander, N., Ludynia, K., Lewis, M., Carpenter-Kling, T., & McInnes, A. (2022). Maritime traffic trends around the southern tip of Africa – Did marine noise pollution contribute to the local penguins' collapse? *Science of The Total Environment*, *849*, 157878. https://doi.org/10.1016/j.scitotenv.2022.157878

Pinaud, D., Cherel, Y., & Weimerskirch, H. (2005). Effect of environmental variability on habitat selection, diet, provisioning behaviour and chick growth in yellow-nosed albatrosses. *Marine Ecology Progress Series*, *298*, 295–304. https://doi.org/10.3354/meps298295

Posit team (2025). RStudio: Integrated Development Environment for R. Posit Software, PBC, Boston, MA. URL http://www.posit.co/.

Punt, A., Furness, R., Parma, A., Plagányi-Lloyd, E., Sanchirico, J., & Trathan, P. (2023). Report of the International Review Panel regarding fishing closures adjacent to South Africa's African Penguin breeding colonies and declines in the penguin population. DFFE. https://www.dffe.gov.za/sites/default/files/Reports/penguinbreeding_coloniesreport.pdf

Ramírez, F., Shannon, L. J., van der Lingen, C. D., Julià, L., Steenbeek, J., & Coll, M. (2022). Climate and fishing simultaneously impact small pelagic fish in the oceans around the southernmost tip of Africa. *Frontiers in Marine Science*, *9*. https://doi.org/10.3389/fmars.2022.1031784

Randall, R. M. (1983). Biology of the Jackass penguin Spheniscus demersus at St. Croix island, South Africa [PhD dissertation]. University Port Elizabeth.

Randall, R. M., & Randall, B. M. (1986). The diet of jackass penguins *Spheniscus demersus* in Algoa Bay, South Africa, and its bearing on population declines elsewhere. *Biological Conservation*, *37*(2), 119–134. https://doi.org/10.1016/0006-3207(86)90087-X

Republic of South Africa. (2019). *Government Gazette, Vol. 647, No. 42478* (No. 42478). https://cer.org.za/wp-content/uploads/2019/05/MPA-declarations.pdf

Roberts, L. C., Abolnik, C., Waller, L. J., Shaw, K., Ludynia, K., Roberts, D. G., Kock, A. A., Makhado, A. B., Snyman, A., & Abernethy, D. (2023). Descriptive Epidemiology of and Response to the High Pathogenicity Avian Influenza (H5N8) Epidemic in South African Coastal Seabirds, 2018. *Transboundary and Emerging Diseases*, *2023*(1), 2708458. https://doi.org/10.1155/2023/2708458

Robinson, W. M. L., Butterworth, D. S., & Plagányi, É. E. (2015). Quantifying the projected impact of the South African sardine fishery on the Robben Island penguin colony. *ICES Journal of Marine Science*, *72*(6), 1822–1833. https://doi.org/10.1093/icesjms/fsv035

Ryan, P., Edwards, L., & Pichegru, L. (2012). African Penguins Spheniscus demersus, Bait Balls and the Allee Effect. Ardea, 100. https://doi.org/10.5253/078.100.0113

Ryan, P., Petersen, S., Simeone, A., & Grémillet, D. (2007). Diving behaviour of African penguins: Do they differ from other Spheniscus penguins? African Journal of Marine Science, 29(2), 153–160. https://doi.org/10.2989/AJMS.2007.29.2.1.184

Shelton, P. A., Crawford, R. J. M., Cooper, J., & Brooke, R. K. (1984). Distribution, population size and conservation of the jackass penguin Spheniscus demersus. South African Journal of Marine Science, 2(1), 217–257. https://doi.org/10.2989/02577618409504370

Sherley, R. B., Barham, B. J., Barham, P. J., Campbell, K. J., Crawford, R. J. M., Grigg, J., Horswill, C., McInnes, A., Morris, T. L., Pichegru, L., Steinfurth, A., Weller, F., Winker, H., & Votier, S. C. (2018). Bayesian inference reveals positive but subtle effects of experimental fishery closures on marine predator demographics. *Proceedings of the Royal Society B: Biological Sciences*, *285*(1871), 20172443. https://doi.org/10.1098/rspb.2017.2443

Sherley, R. B., Makhado, A. B., Crawford, R. J., Hagen, C., Kemper, J., Ludynia, K., Masotla, M. J., McInnes, A., Pichegru, L., Tom, D., Upfold, L., & Waller, L. J. (2024). The African Penguin Spheniscus demersus should be considered Critically Endangered. Ostrich, 95(3), 181–187. https://doi.org/10.2989/00306525.2024.2355618

Siegfried, W. R., Frost, P. G. H., Kinahan, J. B., & Cooper, J. (1975). Social Behaviour of Jackass Penguins at Sea. Zoologica Africana, 10(1), 87–100. https://doi.org/10.1080/00445096.1975.11447495

Statistics South Africa. (2021, May 18). The most important products in our ocean fishing industry | Statistics South Africa. https://www.statssa.gov.za/?p=14327

Sultan, R. M. (2020). Modelling fishing location choice and spatial behaviour of fishers near a marine protected area. *Marine Economics and Management*, *4*(1), 1–22. https://doi.org/10.1108/MAEM-10-2019-0009

Sydeman, W. J., Hunt, G. L., Jr, Pikitch, E. K., Parrish, J. K., Piatt, J. F., Boersma, P. D., Kaufman, L., Anderson, D. W., Thompson, S. A., & Sherley, R. B. (2021). South Africa's experimental fisheries closures and recovery of the endangered African penguin. *ICES Journal of Marine Science*, *78*(10), 3538–3543. https://doi.org/10.1093/icesjms/fsab231

Vanstreels, R. E., Parsons, N. J., McGeorge, C., Hurtado, R., Ludynia, K., Waller, L., Ruthenberg, M., Purves, A., Pichegru, L., & Pistorius, P. A. (2019). Identification of land predators of African Penguins Spheniscus demersus through post-mortem examination. *Ostrich - Journal of African Ornithology*, *90*(4), 359–372. https://doi.org/10.2989/00306525.2019.1697971

Venegas-Li, R., Chiaradia, A., Schinagl, H., Kato, A., Ropert-Coudert, Y., Possingham, H., & Reina, R. D. (2023). *Integrating animal tracking data into spatial conservation prioritisation for seabirds during their breeding season*. 2023.12.14.571606. https://doi.org/10.1101/2023.12.14.571606

Vincenty, T. (1975). Direct and inverse solutions of geodesics on the ellipsoid with application of nested equations: No. 176. *Survey Review*, *Vol. XXII*. https://www.ngs.noaa.gov/PUBS_LIB/inverse.pdf

Welman, S., Green, J. A., Ryan, P. G., Parsons, N. J., & Pichegru, L. (2024). Body temperature and thermoregulatory behaviour in the Endangered African Penguin *Spheniscus demersus*. *Bird Conservation International*, *34*, e29. https://doi.org/10.1017/S095927092400025X

Western Cape Government (2018, October 12). Overfishing. Retrieved May 13, 2025, from https://d7.westerncape.gov.za/general-publication/overfishing

Williams, A. J., & Cooper, J. (1984). Aspects of the breeding biology of the Jackass Penguin Spheniscus demersus. *Proceedings of the Fifth Pan-African Ornithological Congress*, 841–853.

Wilson, R. P. (1985a). Seasonality in diet and breeding success of the Jackass PenguinSpheniscus demersus. Journal Für Ornithologie, 126(1), 53–62. https://doi.org/10.1007/BF01640442

Wilson, R. P. (1985b). The Jackass Penguin (Spheniscus demersus) as a pelagic predator. Marine Ecology-Progress Series - MAR ECOL-PROGR SER, 25, 219–227. https://doi.org/10.3354/meps025219

Wilson, R. P., Pütz, K., Peters, G., Culik, B., Scolaro, J. A., Charrassin, J.-B., & Ropert-Coudert, Y. (1997). Long-term attachment of transmitting and recording devices to penguins and other seabirds. *Wildlife Society Bulletin*, *25*, 101–106.

Wolfaardt, A. C., Underhill, L. G., & Visagie, J. (2009). Breeding and moult phenology of African penguins Spheniscus demersus at Dassen Island. African Journal of Marine Science, 31(2), 119–132. https://doi.org/10.2989/AJMS.2009.31.2.1.873

Wright, K., Pichegru, L., & Ryan, P. (2011). Penguins are attracted to dimethyl sulphide at sea. The Journal of Experimental Biology, 214, 2509–2511. https://doi.org/10.1242/jeb.058230

SUPPLEMENTARY MATERIAL

Model	K	AIC
Gamma	4	215.9513
Lognormal	4	216.8123
Gaussian	4	217.3656

Table S1: Selection of the best model to analyse duration of long trips based on the AIC. K: number of parameters in the model. The model with the lowest AIC was selected (gamma distribution, AIC = 215.9513).

Model	K	AIC	ΔAIC
closure + Julian day + deployment year	5	586.09	0.00
closure + deployment year	4	589.73	3.64
closure	3	620.29	34.19

Table S2: Model selection for the effect of closure status on the maximum trip distance from the colony. All models use a gamma distribution with a log link function. Closure status and Julian day account for fixed effects. Deployment year is included as a random effect. Models are ranked by AIC. K: number of parameters in the model. ΔAIC: the difference in AIC with the best model. N = 87 trips, 9 deployment years. The model accounting for closure status, Julian day and deployment year was selected.

Model	K	AIC	ΔAIC
closure + Julian day + deployment year	5	331.47	0.00
closure + deployment year	4	331.73	0.26
closure	3	361.91	30.44

Table S3: Model selection for the effect of closure status on the maximum trip distance from the colony. All models use a gamma distribution with a log link function. Closure status and Julian day account for fixed effects. When mentioned in the models, deployment year is included as a random effect. Models are ranked by AIC. K: number of parameters in the model. ΔAIC: the difference in AIC with the lowest AIC model. N = 50 trips, 6 deployment years. The model accounting for closure status and deployment year was selected.

Model	K	AIC	ΔAIC
closure + anchovy(60)	5	331.56	0.00
closure	4	331.73	0.17
closure + total(90)	5	333.01	1.44
closure + sardine(90)	5	333.06	1.50
closure + total(60)	5	333.21	1.65
closure + anchovy(90)	5	333.61	2.04
closure + sardine(60)	5	333.73	2.17

Table S4: Model selection for the effect of closure status on the maximum trip distance from the colony. All models use a gamma distribution with a log link function. Closure status and cumulative catches account for fixed effects. Deployment year is included in all models as a random effect. Models are ranked by AIC. K: number of parameters in the model. ΔAIC: the difference in AIC with the lowest AIC model. N = 50 trips, 6 deployment years. The model accounting for closure status and deployment year was retained.

Model	K	AIC	ΔAIC
closure + deployment year	4	368.18	0.00
closure	3	368.20	0.03
closure + Julian day + deployment year	5	369.12	0.95

Table S5: Model selection for the effect of the closure status on short trips' path length of the penguins. All models use a gamma distribution with a log link function. Closure status and Julian day account for fixed effects. When mentioned in the models, deployment year is included as a random effect. Models are ranked by AIC. K: number of parameters in the model. ΔAIC: the difference in AIC with the lowest AIC model. N = 47 trips, 9 deployment years. The model accounting for closure status and deployment year was selected.

Model	K	AIC	ΔAIC
closure + Julian day + deployment year	5	222.15	0.00
closure + deployment year	4	223.19	1.04
closure	3	224.14	1.99

Table S6: Model selection for the effect of the closure status on short trips' path length of the penguins. All models use a gamma distribution with a log link function. Closure status and Julian day account for fixed effects. When mentioned in the models, deployment year is included as a random effect. Models are ranked by AIC. K: number of parameters in the model. ΔAIC: the difference in AIC with the lowest AIC model. N = 29 trips, 5 deployment years. The model accounting for closure status and deployment year was selected.

Model	K	AIC	ΔAIC
closure + anchovy(90)	5	220.00	0.00
closure	4	223.19	3.20
closure + total(90)	5	223.42	3.42
closure + anchovy(60)	5	224.39	4.40
closure + sardine(90)	5	225.05	5.05
closure + sardine(60)	5	225.14	5.15
closure + total(60)	5	225.18	5.18

Table S7: Model selection for the effect of closure status on the total path length of short trips. All models use a gamma distribution with a log link function. Closure status and cumulative catches account for fixed effects. Deployment year is included in all models as a random effect. Models are ranked by AIC. K: number of parameters in the model. ΔAIC: the difference in AIC with the lowest AIC model. N = 29 trips, 5 deployment years. The model accounting for closure status, cumulated anchovy catches over the 90 days prior to deployment, and deployment year was retained.

Fixed effects	β	SE	z-value	p-value
Intercept	3.94	0.06	65.23	<2 e-16 ***
Closure	-0.22	0.11	-2.01	0.04 *
Random effects		Variance		SD
year		0.01		0.10

Table S8: Results of the GLMM (gamma function, log link) modelling breeding African penguins path length (km) of short foraging trips. Closure status accounts for the only fixed effect. Deployment year is included as a random effect. The pre-closure period is the reference category for the closure status variable. N = 47 trips. 8 deployment years. *p < 0.05; ***p < 0.001.

Fixed effects	β	SE	z-value	p-value
Intercept	3.85	0.05	78.25	< 2e-16 ***
Closure	0.03	0.14	0.20	0.84
Anchovy(90)	0.18	0.06	3.06	0.2 e-02 **
Random effects		Variance		SD
year		1.36 e-10		1.18 e-05

Table S9: Results of the GLMM (gamma function, log link) modelling breeding African penguins path length (km) of short foraging trips. Closure status and anchovy(90) account for fixed effects. Deployment year is included as a random effect. The pre-closure period is the reference category for the closure status variable. N = 29 trips. 5 deployment years. *p < 0.05; ***p < 0.001.

Fixed effects	β	SE	z-value	p-value
Intercept	3.98	0.08	51.86	< 2e-16 ***
Closure	-0.35	0.15	-2.29	0.02 *
Random effects		Variance		SD
year		0.01		0.11

Table S10: Results of the GLMM (gamma function, log link) modelling breeding African penguins path length (km) of short foraging trips. Closure status accounts for the only fixed effect. Deployment year is included as a random effect. The pre-closure period is the reference category for the closure status variable. N = 29 trips. 5 deployment years. *p < 0.05; ***p < 0.001.

Fixed effects	β	SE	z-value	p-value
Intercept	3.85	0.04	106.61	< 2 e-16 ***
Anchovy(90)	0.17	0.04	4.76	1.96 e-06 ***
Random effects		Variance		SD
year		1.24 e-10		1.11 e-05

Table S11: Results of the GLMM (gamma function, log link) modelling breeding African penguins path length (km) of short foraging trips. Anchovy(90) accounts for the only fixed effect. Deployment year is included as a random effect. N = 29 trips. 5 deployment years. ***p < 0.001.

Model	K	AIC	ΔAIC
closure + deployment year	4	324.61	0.00
closure + deployment year + Julian day	5	326.16	1.56
closure	3	332.37	7.76

Table S12: Model selection for the effect of the closure status on long trips' path length of the penguins. All models use a gamma distribution with a log link function. Closure status and Julian day account for the fixed effects. When mentioned in the models, deployment year is included as a random effect. Models are ranked by AIC. K: number of parameters in the model. ΔAIC: the difference in AIC with the lowest AIC model. N = 38 trips, 9 deployment years. The model accounting for closure status and deployment year was selected.

Model	K	AIC	ΔAIC
closure	3	235.46	0.00
closure + deployment year	4	237.46	1.99
closure + deployment year + Julian day	5	237.47	2.01

Table S13: Model selection for the effect of the closure status on short trips' duration of the penguins. All models use a gamma distribution with a log link function. Closure status and Julian day account for fixed effects. When mentioned in the models, deployment year is included as a random effect. Models are ranked by AIC. K: number of parameters in the model. ΔAIC: the difference in AIC with the lowest AIC model. N = 47 trips, 9 deployment years. The model accounting for closure status and deployment year was selected.

Model	K	AIC	ΔAIC
closure	3	153.20	0.00
closure + deployment year	4	155.20	1.99
closure + deployment year + Julian day	5	155.83	2.63

Table S14: Model selection for the effect of closure status on the short trips' duration. All models use a gamma distribution with a log link function. Closure status and Julian day account for fixed effects. When mentioned in the models, deployment year is included as a random effect. Models are ranked by AIC. K: number of parameters in the model. ΔAIC: the difference in AIC with the lowest AIC model. N = 29 trips, 5 deployment years. The model accounting for closure status and deployment year was selected.

Model	K	AIC	ΔAIC
Closure	4	155.2	0.00
closure + anchovy(90)	5	155.51	0.31
closure + total(90)	5	156.25	1.05
closure + anchovy(60)	5	156.66	1.47
closure + sardine(60)	5	156.83	1.63
closure + sardine(90)	5	156.87	1.67
closure + total(60)	5	157.13	1.94

Table S15: Model selection for the effect of closure status on the short trips' duration. All models use a gamma distribution with a log link function. Closure status and cumulated catches account for fixed effects. Deployment year is included in all models as a random effect. Models are ranked by AIC. K: number of parameters in the model. ΔAIC: the difference in AIC with the lowest AIC model. N = 29 trips, 5 deployment years. The model accounting for closure status and deployment year was retained.

Model	K	AIC	ΔAIC
closure + deployment year	4	215.95	0.00
closure + deployment year + Julian day	5	217.92	1.97
closure	3	220.59	4.63

Table S16: Model selection for the effect of closure status on the long trips' duration. All models use a gamma distribution with a log link function. Closure status and Julian day account for fixed effects. When mentioned in the models, deployment year is included as a random effect. Models are ranked by AIC. K: number of parameters in the model. ΔAIC: the difference in AIC with the lowest AIC model. N = 38 trips. 9 deployment years. The model accounting for closure status and deployment year was selected.

Model	K	AIC	ΔAIC
closure + deployment year + Julian day	5	117.25	0.00
closure + deployment year	4	117.42	0.18
closure	3	124.41	7.16

Table S17: Model selection for the effect of closure status on the long trips' duration. All models use a gamma distribution with a log link function. Closure status and Julian day account for fixed effects. When mentioned in the models, deployment year is included as a random effect. Models are ranked by AIC. K: number of parameters in the model. ΔAIC: the difference in AIC with the lowest AIC model. N = 20 trips. 6 deployment years. The model accounting for closure status and deployment year was selected.

Model	K	AIC	ΔAIC
closure + anchovy(60)	5	112.82	0.00
closure	4	117.42	4.60
closure + total(90)	5	118.64	5.82
closure + total(60)	5	118.69	5.87
closure + sardine(90)	5	118.85	6.03
closure + anchovy(90)	5	119.29	6.47
closure + sardine(60)	5	119.36	6.54

Table S18: Model selection for the effect of the closure status on long trips' path length of the penguins. All models use a gamma distribution with a log link function. Closure status and cumulated catches account for fixed effects. When mentioned in the models, deployment year is included as a random effect. Models are ranked by AIC. K: number of parameters in the model. ΔAIC: the difference in AIC with the lowest AIC model. N = 20 trips, 6 deployment years. The model accounting for closure status, cumulated anchovy catches over the 60 days prior to deployment and deployment year was retained.

Fixed effects	β	SE	z-value	p-value
Intercept	2.53	0.04	64.85	<2e-16 ***
Closure	0.06	0.07	0.91	0.36
Random effects		Variance		SD
year		8.91 e-11		9.44 e-06

Table S19: Results of the GLMM (gamma function, log link) modelling breeding African penguins duration (hrs) of short foraging trips. Closure status accounts for the only fixed effect. Deployment year is included as a random effect. The pre-closure period is the reference category for the closure status variable. N = 47 trips. 8 deployment years. ***p < 0.001.

Fixed effects	β	SE	z-value	p-value
Intercept	3.54	0.06	54.89	<2e-16 ***
Closure	0.02	0.08	0.32	0.75

Random effects	Variance	SD
year	0.01	0.10

Table S20: Results of the GLMM (gamma function, log link) modelling breeding African penguins duration (hrs) of long foraging trips. Closure status accounts for the only fixed effect. Deployment year is included as a random effect. The pre-closure period is the reference category for the closure status variable. N = 38 trips. 9 deployment years. ***p < 0.001.

	df	AIC	Δ AIC
closure + month	7	6039.43	0.00
closure	5	6095.03	55.60

Table S21: Model selection for the log-normal LMM of positive anchovy haul size, within the closure perimeter (all vessels). Fixed effect includes closure status. Random effects include haul year and vessel name, accounting for inter-annual and inter-vessel variability. When mentioned in the model, seasonality (modelled via cyclic sine and cosine transformations of the month) is included as a fixed effect. Models are ranked by AIC. K: number of parameters in the model. ΔAIC: the difference in AIC with the lowest AIC model. N = 1 533 hauls, 14 years, 78 vessels. The model accounting for seasonality was retained.

	df	AIC	Δ AIC
closure + month	7	5331.41	0.00
closure	5	5369.75	38.34

Table S22: Model selection for the log-normal LMM of positive sardine haul size, within the closure perimeter (all vessels). Fixed effect includes closure status. Random effects include haul year and vessel name, accounting for inter-annual and inter-vessel variability. When mentioned in the model, seasonality (modelled via cyclic sine and cosine transformations of the month) is included as a fixed effect. Models are ranked by AIC. K: number of parameters in the model. ΔAIC: the difference in AIC with the lowest AIC model. N = 440 hauls, 14 years, 83 vessels. The model accounting for seasonality was retained.

	df	AIC	Δ AIC
closure + month	7	5790.46	0.00
closure	5	5809.42	18.96

Table S23: Model selection for the log-normal LMM of positive anchovy plus sardine cumulated haul size, within the closure perimeter (all vessels). Fixed effect includes closure status. Random effects include haul year and vessel name, accounting for inter-annual and inter-vessel variability. When mentioned in the model, seasonality (modelled via cyclic sine and cosine transformations of the month) is included as a fixed effect. Models are ranked by AIC. K: number of parameters in the model. ΔAIC: the difference in AIC with the lowest AIC model. N = 2 104 hauls, 14 years, 85 vessels. The model accounting for seasonality was retained.

Term	β	SE	df	t-value	p-value
(Intercept)	2.16	0.57	52.43	3.82	3.56 e-04***
Closure	0.08	0.53	93.72	0.15	0.88
Month (sine)	0.38	0.08	1462.00	4.45	9.25e-06 ***
Month (cosine)	-0.51	0.08	1456.60	-6.10	1.37e-09 ***
Random effects		Variance		SD	
Year		1.17		1.08	
Vessel		2.13		1.46	

Table S24: Results of the LMM modelling the log-transformed positive anchovy haul size within the closure perimeter (all vessels). Fixed effects include closure status and seasonality (modelled via cyclic sine and cosine transformations of the month). Random effects include haul year and vessel name, accounting for inter-annual and inter-vessels variability. The pre-closure period is the reference category for the closure status variable. The model was fitted using restricted maximum likelihood (REML). N = 1 533 hauls, 14 years, 78 vessels. ***p < 0.001.

Term	β	SE	df	t-value	p-value
(Intercept)	2.85	0.44	43.72	6.47	7.14e-08 ***
Closure	-0.82	0.43	58.19	-1.92	0.06 ·
Month (sine)	-0.13	0.06	1380.55	-2.31	0.02 *
Month (cosine)	0.40	0.08	1375.16	5.27	1.59e-07 ***
Random effects		Variance		SD	
Year		0.58		0.76	
Vessel		1.15		1.07	

Table S25: Results of the LMM modelling the log-transformed positive sardine haul size within the closure perimeter (all vessels). Fixed effects include closure status and seasonality (modelled via cyclic sine and cosine transformations of the month). Random effects include haul year and vessel name, accounting for inter-annual and inter-vessels variability. The pre-closure period is the reference category for the closure status variable. The model was fitted using restricted maximum likelihood (REML). N = 1 440 hauls, 14 years, 83 vessels. ·p < 0.1; *p < 0.05; ***p < 0.001.

Term	β	SE	df	t-value	p-value
(Intercept)	4.31	0.31	13.77	18.13	3.02e-16 ***
Closure	0.67	0.29	116.5	2.33	0.02 *
Month (sine)	0.16	0.03	2 048	4.81	1.60e-06 ***
Month (cosine)	0.02	0.04	2 035	0.55	0.58

Random effects	Variance	SD
Year	0.46	0.68
Vessel	0.37	0.60

Table 26: Results of the LMM modelling the log-transformed positive total catch haul size within the closure perimeter (all vessels). Fixed effects include closure status and seasonality (modelled via cyclic sine and cosine transformations of the month). Random effects include haul year and vessel name, accounting for inter-annual and inter-vessels variability. The pre-closure period is the reference category for the closure status variable. The model was fitted using restricted maximum likelihood (REML). N = 2 104 hauls, 14 years, 85 vessels. *p < 0.05; ***p < 0.001.

	df	AIC	Δ AIC
closure + month	7	2801.55	0.00
closure	5	2818.35	16.80

Table S27: Model selection for the log-normal LMM of positive anchovy haul size, within the closure perimeter (frequent vessels). Fixed effect includes closure status. Random effects include haul year and vessel name, accounting for inter-annual and inter-vessel variability. When mentioned in the model, seasonality (modelled via cyclic sine and cosine transformations of the month) is included as a fixed effect. Models are ranked by AIC. K: number of parameters in the model. ΔAIC: the difference in AIC with the lowest AIC model. N = 770 hauls, 14 years, 14 vessels. The model accounting for seasonality was retained.

	df	AIC	Δ AIC
closure + month	7	2513.98	0.00
closure	4	2527.17	13.19

Table S28: Model selection for the log-normal LMM of positive sardine haul size, within the closure perimeter (frequent vessels). Fixed effect includes closure status. Random effects include haul year and vessel name, accounting for inter-annual and inter-vessel variability. When mentioned in the model, seasonality (modelled via cyclic sine and cosine transformations of the month) is included as a fixed effect. Models are ranked by AIC. K: number of parameters in the model. ΔAIC: the difference in AIC with the lowest AIC model. N = 713 hauls, 14 years, 14 vessels. The model accounting for seasonality was retained.

	df	AIC	Δ AIC
closure + month	7	2860.50	0.00
closure	5	2863.54	3.05

Table S29: Model selection for the log-normal LMM o positive total catch haul size, within the closure perimeter (frequent vessels). Fixed effect includes closure status. Random effects include haul year and vessel name, accounting for inter-annual and inter-vessel variability. When mentioned in the model, seasonality (modelled via cyclic sine and cosine transformations of the month) is included as a fixed effect. Models are ranked by AIC. K: number of parameters in the model. ΔAIC: the difference in AIC with the lowest AIC model. N = 1 072 hauls, 14 years, 14 vessels. The model accounting for seasonality was retained.

Term	β	SE	df	t-value	p-value
(Intercept)	1.42	0.64	46.92	2.22	0.03*
Closure	0.51	0.50	85.91	1.01	0.31
Month (sine)	0.23	0.10	754.51	2.32	0.02 *
Month (cosine)	-0.37	0.10	750.17	-3.85	1.26 e-04 ***
Random effects		Variance		SD	
Year		1.08		1.04	
Vessel Name		2.08		1.44	

Table S30: Results of the LMM modelling the log-transformed positive anchovy haul size within the closure perimeter (all vessels). Fixed effects include closure status and seasonality (modelled via cyclic sine and cosine transformations of the month). Random effects include haul year and vessel name, accounting for inter-annual and inter-vessels variability. The pre-closure period is the reference category for the closure status variable. Model were fitted using restricted maximum likelihood (REML). N = 770 hauls, 14 years, 14 vessels. *p < 0.05; ***p < 0.001.

Term	β	SE	df	t-value	p-value
(Intercept)	3.20	0.45	39.81	7.17	1.12 e-08 ***
Closure	-0.76	0.38	33.25	-1.97	0.06 ·
Month (sine)	-0.18	0.08	697.24	-2.35	0.02 *
Month (cosine)	0.25	0.10	689.02	2.64	8.47 e-03 **
Random effects		Variance		SD	
Year		0.36		0.60	
Vessel Name		0.88		0.94	

Table S31: Results of the LMM modelling the log-transformed positive sardine haul size within the closure perimeter (frequent vessels). Fixed effects include closure status and seasonality (modelled via cyclic sine and cosine transformations of the month). Random effects include haul year and vessel name, accounting for inter-annual and inter-vessels variability. The pre-closure period is the reference category for the closure status variable. Model were fitted using restricted maximum likelihood (REML). N = 713 hauls, 14 years, 14 vessels. ·p < 0.1; *p < 0.05; **p < 0.01; ***p < 0.001.

Term	β	SE	df	t-value	p-value
(Intercept)	3.77	0.18	21.39	20.83	1.09e-15 ***
Closure	0.06	0.25	28.90	0.22	0.83
Month (sine)	0.11	0.04	1058	2.59	9.83 e-03**
Month (cosine)	-0.01	0.05	1056	-0.147	0.88

Random effects	Variance	SD
Vessel name	0.25	0.50
Year	0.18	0.42

Table S32: Results of the LMM modelling the log-transformed positive total catch haul size within the closure perimeter (frequent vessels). Fixed effects include closure status and seasonality (modelled via cyclic sine and cosine transformations of the month). Random effects include haul year and vessel name, accounting for inter-annual and inter-vessels variability. The pre-closure period is the reference category for the closure status variable. Model were fitted using restricted maximum likelihood (REML). N = 1 072 hauls, 14 years, 14 vessels. ***p < 0.001.

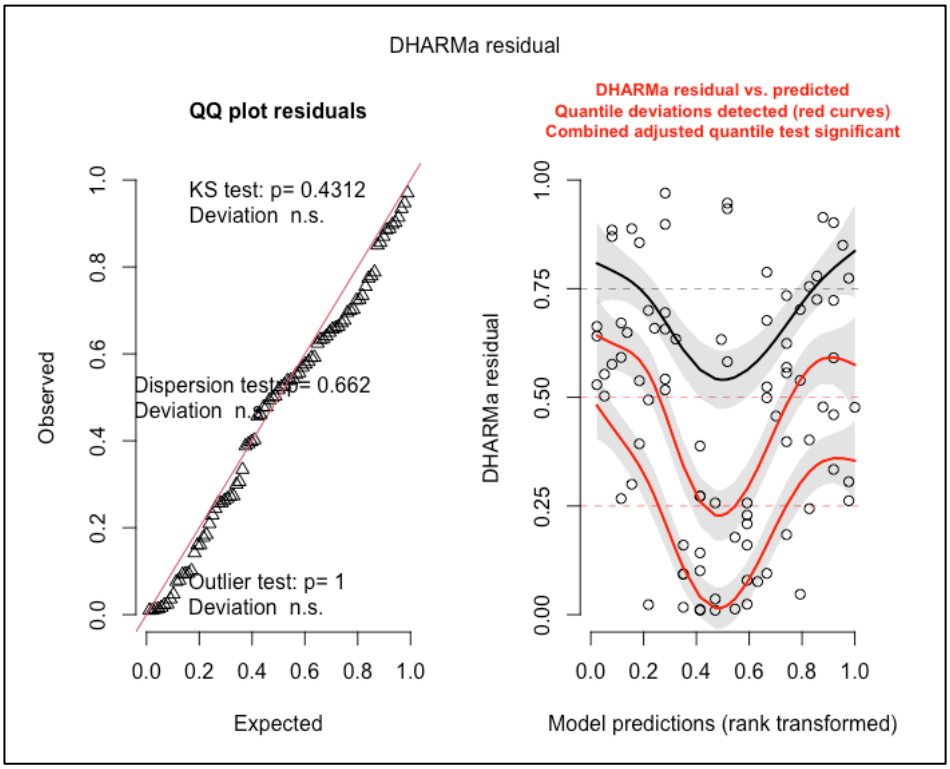

Figure S1: DHARMa residual diagnostic for the selected GLMM (closure + Julian day + deployment year) assessing maximum trip distance from the colony. The QQ-plot (left) showed no significant violation of model assumption (KS: p = 0.43; dispersion test: p = 0.66; outliers test: p = 1). Residual vs. predicted values plot (right) showed a significant deviation in the lower quantile and the median of the distribution from the expected distribution. The model was considered acceptable.

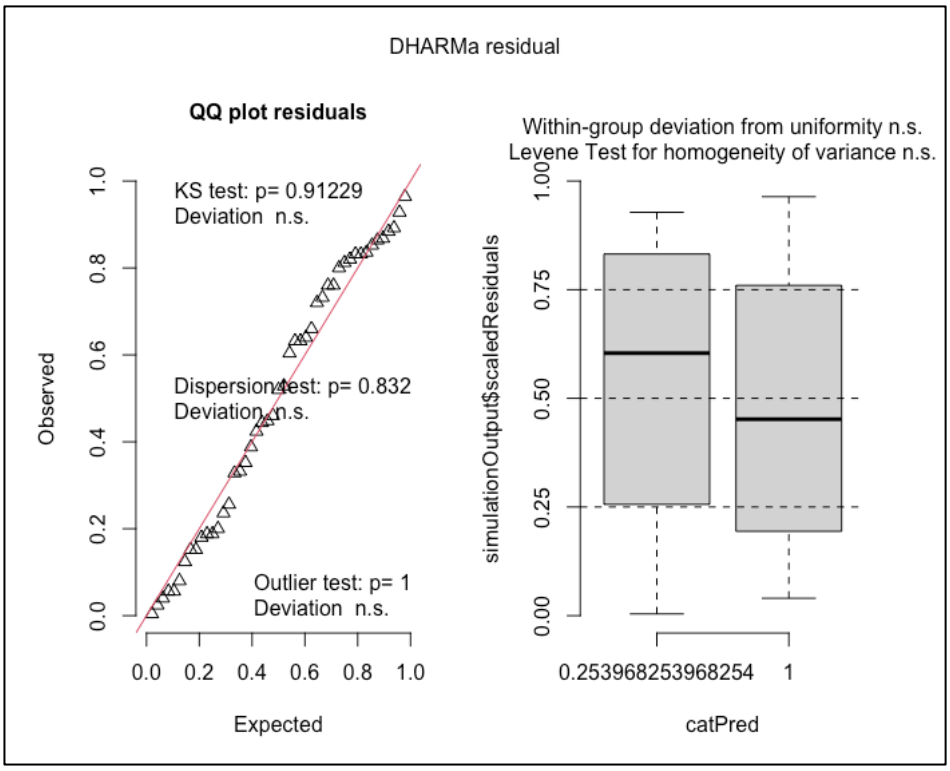

Figure S2: DHARMa residual diagnostic for the selected GLMM (closure + deployment year) assessing short trips' path length. No significant violation of model assumptions was detected. The model was considered acceptable.

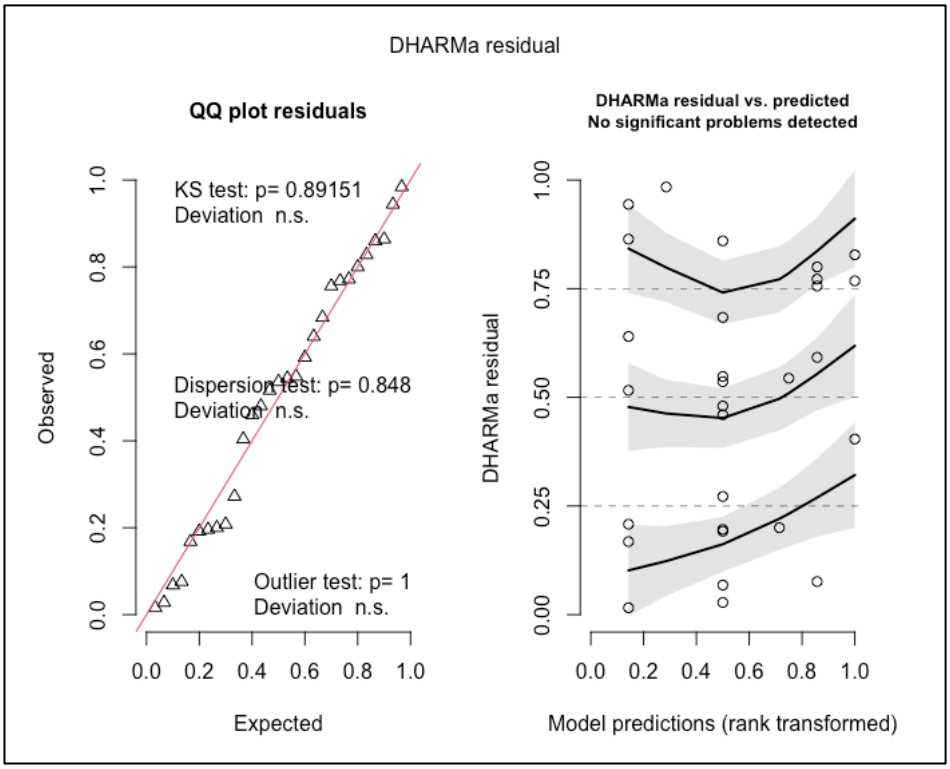

Figure S3: DHARMa residual diagnostic for the selected GLMM (closure + anchovy(90) + deployment year) assessing short trips' path length. No significant violation of model assumptions was detected. The model was considered acceptable.

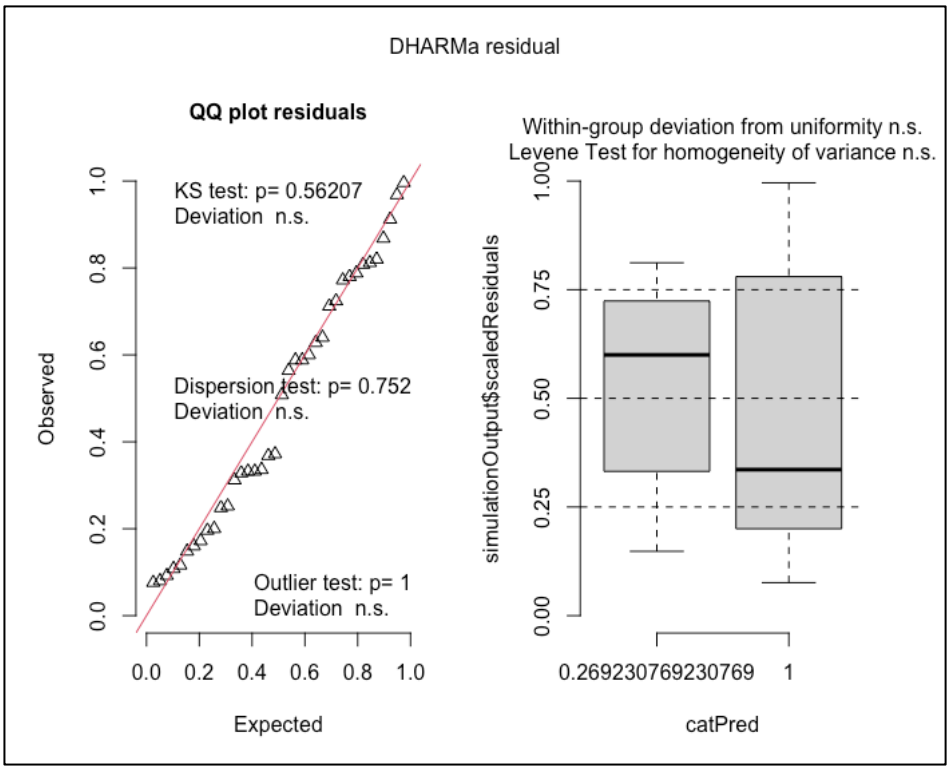

Figure S4: DHARMa residual diagnostic for the selected GLMM (closure + deployment year) assessing long trips' path length. No significant violation of model assumptions was detected. The model was considered acceptable.

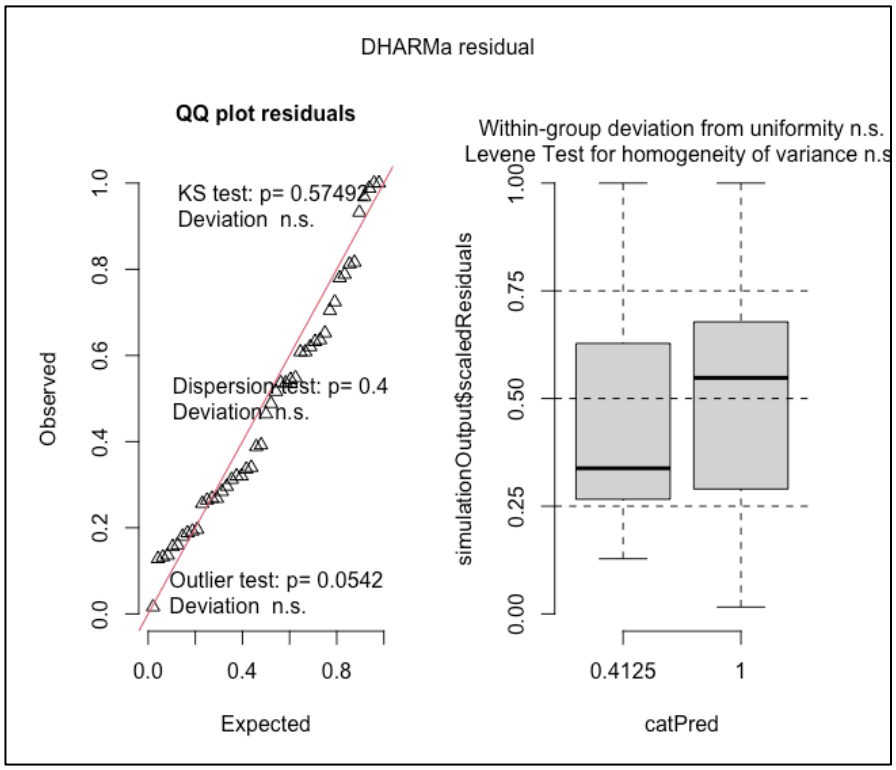

Figure S5: DHARMa residual diagnostic for the selected GLMM (closure + deployment year) assessing short trips' duration. No significant violation of model assumptions was detected. The model was considered acceptable.

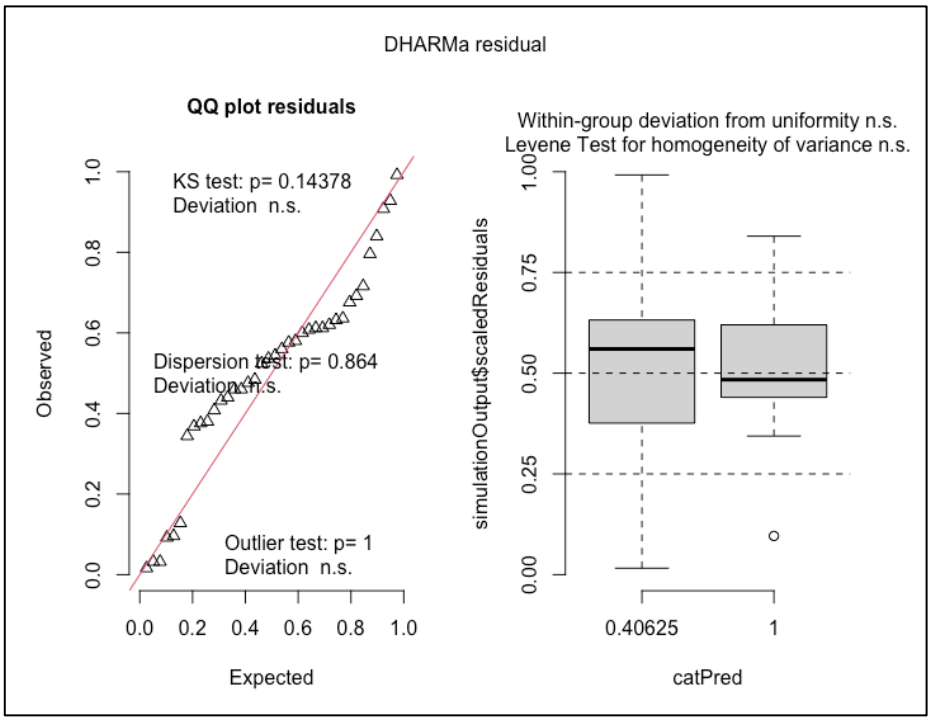

Figure S6: DHARMa residual diagnostic for the selected GLMM (closure + deployment year) assessing long trips' path duration. No significant violation of model assumptions was detected. The model was considered acceptable.

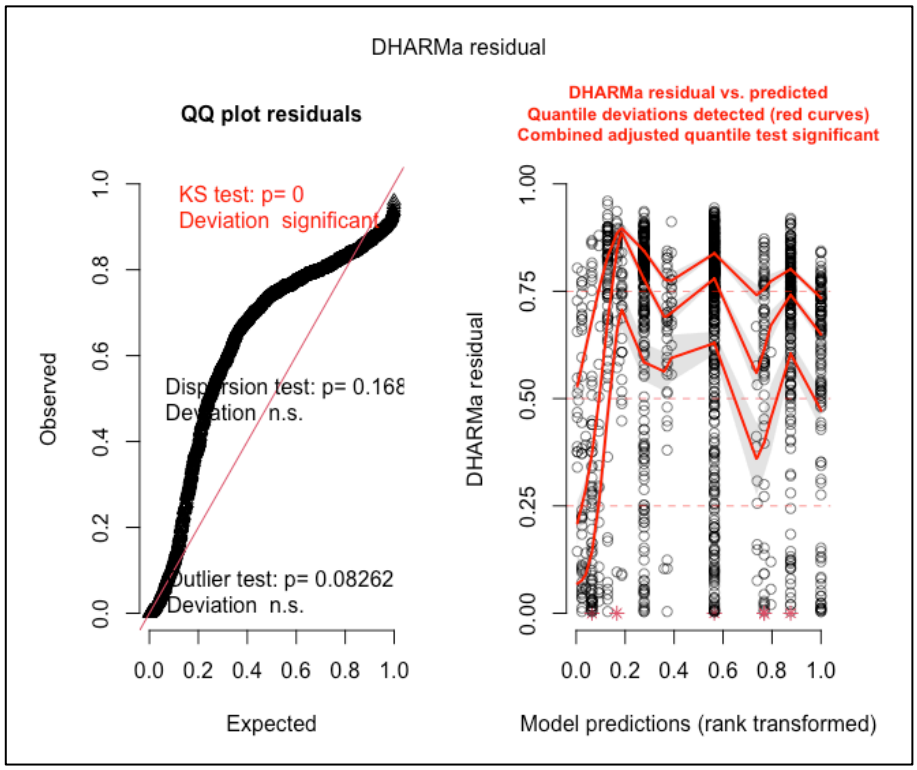

Figure S7: DHARMa residual diagnostic for the LMM model on log-transformed anchovy haul size within the closure perimeter (all vessels, positive catches only). The QQ-plot (left) showed a significant KS test ($p < 0.001$), attributable to the large sample size ($n = 1\,533$ hauls). Dispersion test: $p = 0.168$. Outliers test: $p = 0.08$. Residual vs. predicted values plot (right) showed quantile deviation. The model was considered acceptable.

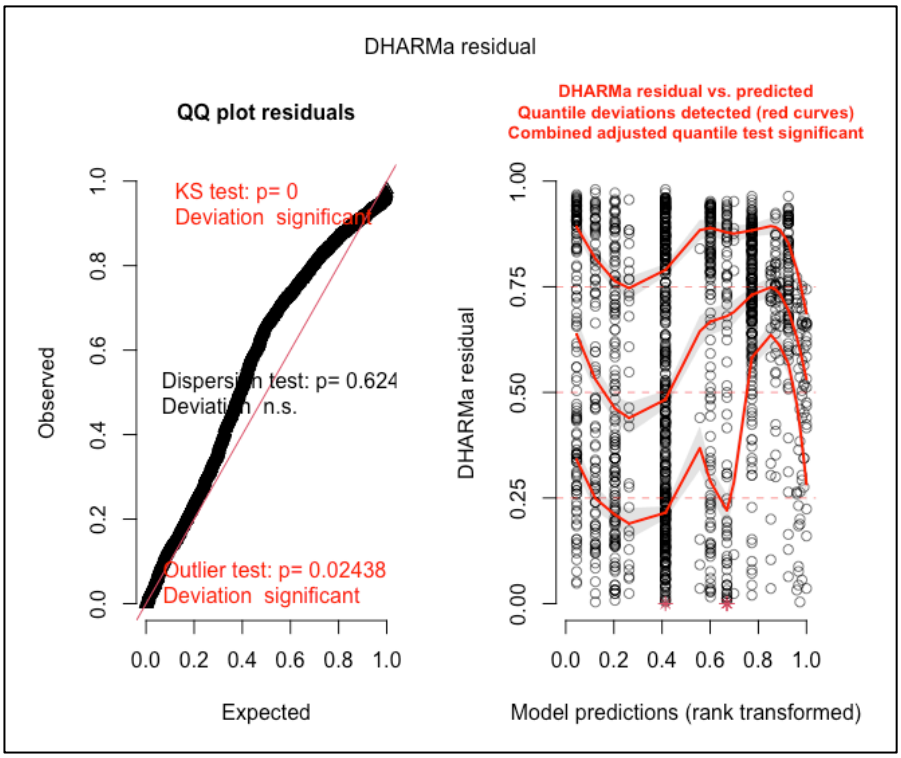

Figure S8: DHARMa residual diagnostic for the LMM model on log-transformed sardine haul size within the closure perimeter (all vessels, positive catches only). The QQ-plot (left) showed a significant KS test ($p < 0.001$), attributable to the large sample size ($n = 440$ hauls). Dispersion test: $p = 0.62$. Outliers test: $p = 0.02$ (significant). Inspection of the 4 flagged observations revealed legitimate haul sizes. Residual vs. predicted values plot (right) showed quantile deviation. Results should be interpreted with caution.

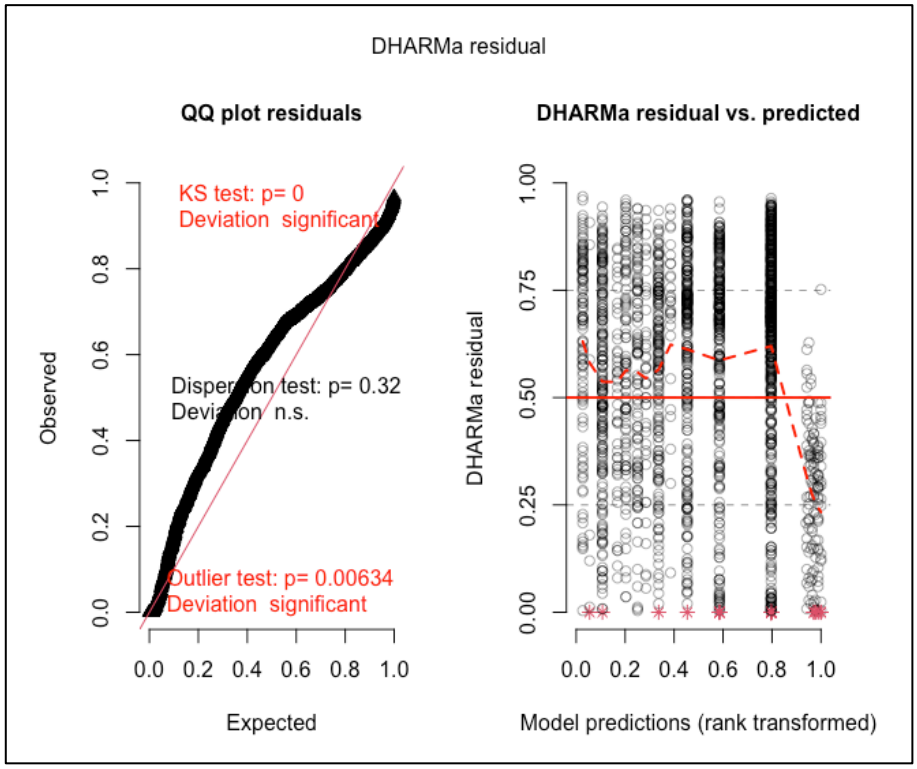

Figure S9: DHARMa residual diagnostic for the LMM model on log-transformed total catch haul size within the closure perimeter (all vessels, positive catches only). The QQ-plot (left)

showed a significant KS test ($p < 0.001$), attributable to the large sample size (n = 2 104 hauls). Dispersion test: $p = 0.32$. Outliers test: $p = 0.006$ (significant). Inspection of the 29 flagged observations revealed legitimate haul sizes. Residual vs. predicted values plot (right) showed slight quantile deviation. Results should be interpreted with caution.

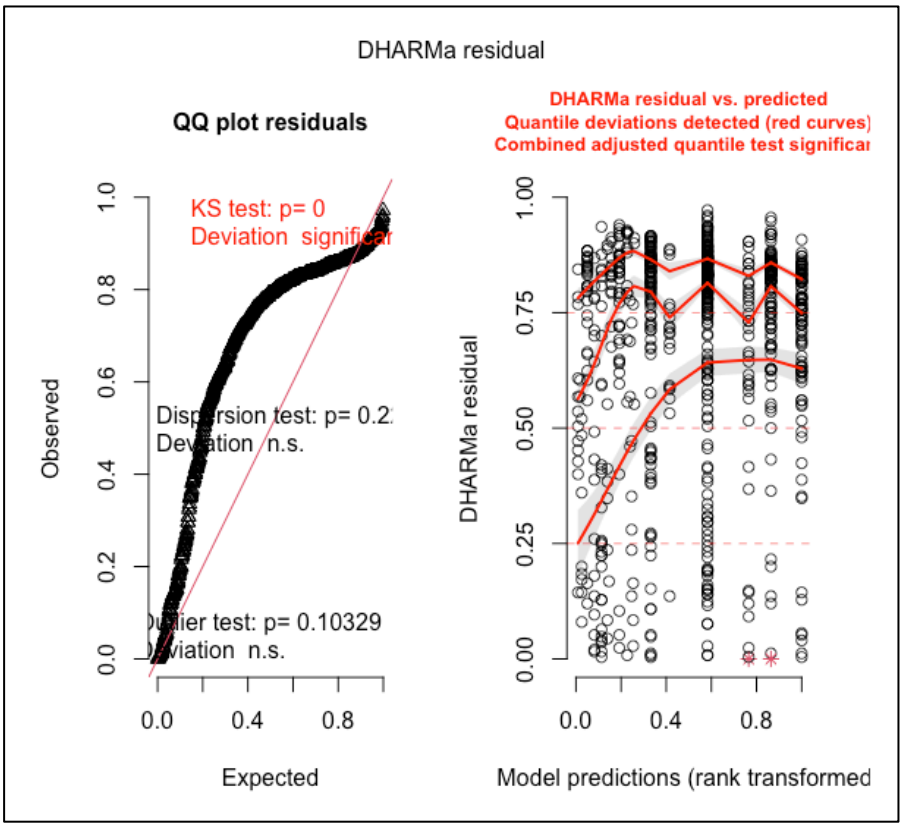

Figure S10: DHARMa residual diagnostic for the LMM model on log-transformed anchovy haul size within the closure perimeter (frequent vessels, positive catches only). The QQ-plot (left) showed a significant KS test ($p < 0.001$), attributable to the large sample size (n = 770 hauls). Dispersion test: $p = 0.22$. Outliers test: $p = 0.10$. Residual vs. predicted values plot (right) showed quantile deviation. The model was considered acceptable.

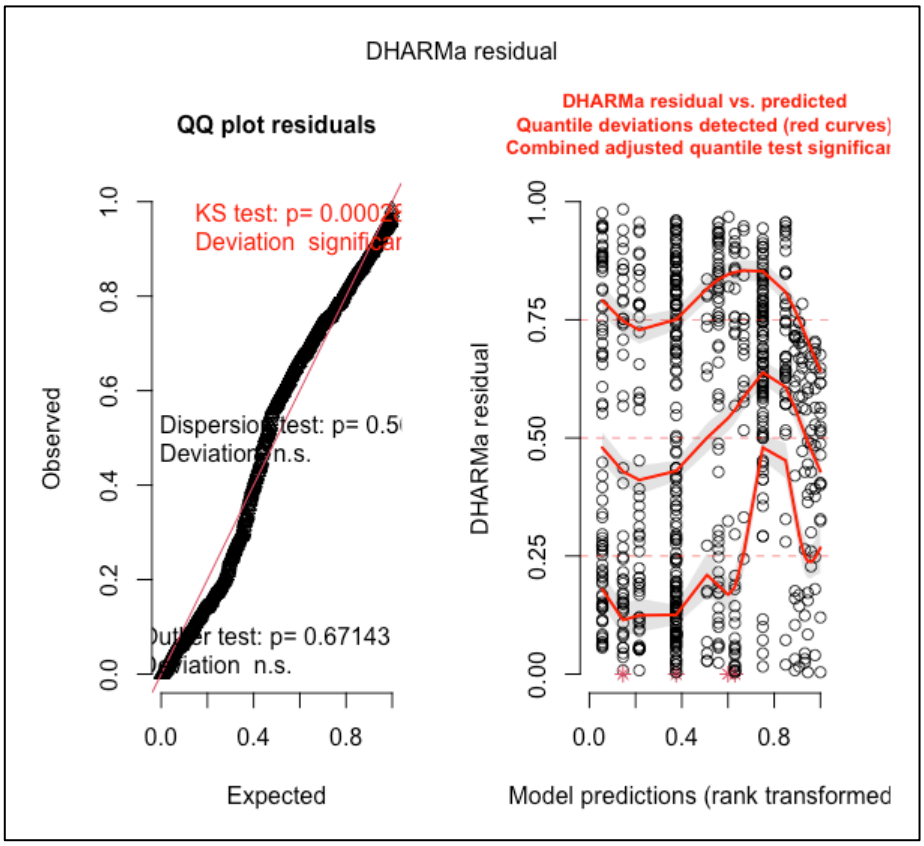

Figure S11: DHARMa residual diagnostic for the LMM model on log-transformed sardine haul size within the closure perimeter (frequent vessels, positive catches only). The QQ-plot (left) showed a significant KS test ($p < 0.001$), attributable to the large sample size ($n = 713$ hauls). Dispersion test: $p = 0.57$. Outliers test: $p = 0.67$. Residual vs. predicted values plot (right) showed quantile deviation. The model was considered acceptable.

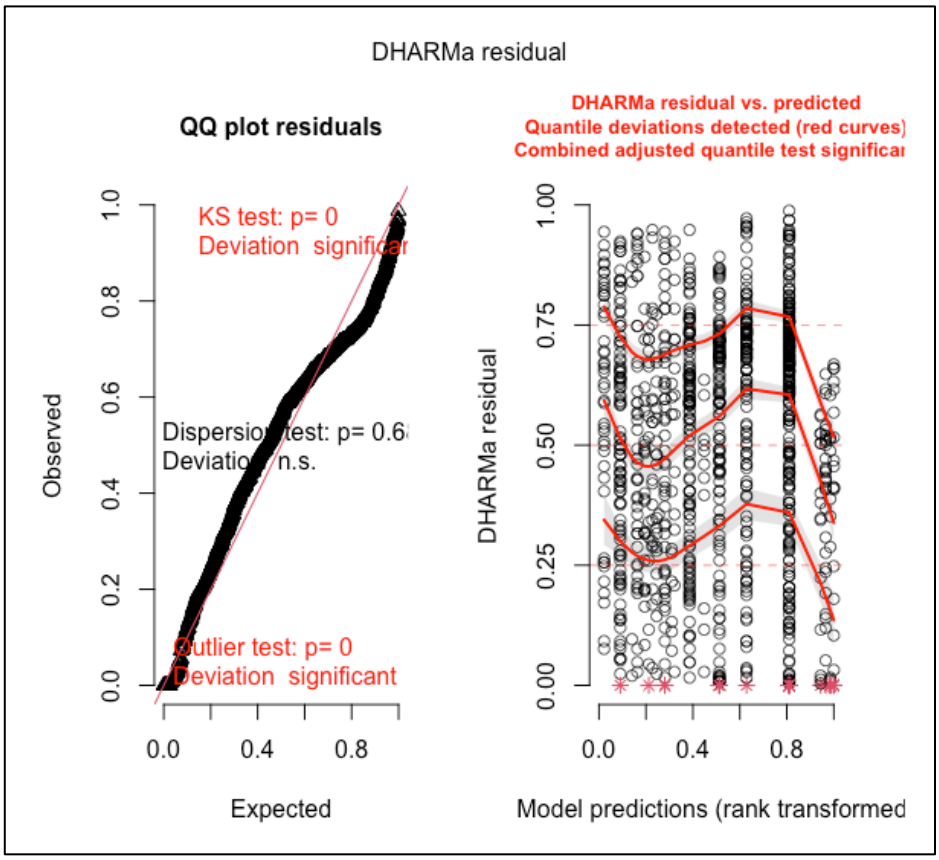

Figure S12: DHARMa residual diagnostic for the LMM model on log-transformed total catch haul size within the closure perimeter (frequent vessels, positive catches only). The QQ-plot (left) showed a significant KS test ($p < 0.001$), attributable to the large sample size ($n = 2\,104$ hauls). Dispersion test: $p = 0.69$. Outliers test: $p < 0.001$ (significant). Inspection of the 28 flagged observations revealed legitimate haul sizes. Residual vs. predicted values plot (right) showed quantile deviation. Results should be interpreted with caution.