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Spatial overlap between South American fur seal foraging effort and commercial trawl fisheries in the Falkland Islands

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A B S T R A C T

Interactions between seals and commercial fisheries can pose a significant threat to the conservation status of seal populations. In the Falkland Islands, home to over 50 % of the global South American fur seal (SAFS) population, there has been a dramatic (~ 900 %) increase in the number of SAFS-fishery interactions in recent years. However, significant knowledge gaps regarding SAFS spatiotemporal foraging behaviour and habitat use hinders our capacity to assess the ecological mechanisms underpinning these interactions. In this study, we investigate the spatial overlap between SAFS foraging effort and commercial squid and finfish trawl fisheries in the Falkland Island Exclusive Economic Zone (EEZ). By spatially integrating two years of SAFS horizontal and vertical movement data with contemporaneous trawl-by-trawl information from the Falkland Islands fishing fleet, we examine whether SAFS concentrate their foraging effort in areas associated with greater squid and finfish catch quantities. Our findings reveal a marked spatial overlap between SAFS foraging effort and commercial trawling activity within the Falkland Islands EEZ, particularly in areas associated with Patagonian longfin squid (*Doryteuthis gahi*) and common hake (*Merluccius hubbsi*). Across the various metrics of foraging effort (summarised dive activity) examined, we found SAFS performed a greater number of dives, travelled greater vertical distances and performed deeper dives in intensively fished areas. These results suggest SAFS forage in the same habitats targeted by commercial squid and finfish fisheries, where they compete for demersal resources by performing a high frequency of deep dives. The implications of our findings are discussed within the broader context of local prey-field dynamics and fisheries-management. This study represents one of the most comprehensive investigations of SAFS movement ecology and advances our understanding of seal-fishery interactions in the Falkland Islands EEZ – a topic of increasing management concern. Importantly, this work can support conservation efforts for this globally significant SAFS population and contribute to long-term marine management objectives of the Falkland Islands fishery.

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1. Introduction

Interactions between marine mammals and commercial fisheries are one of the key threats to marine mammal populations worldwide, and are the focus of significant conservation and management efforts (Read et al., 2006; Lewison et al., 2014; Jog et al., 2022). Both direct interactions (i.e. entanglement, bycatch and depredation) and indirect interactions (i.e. spatial and trophic overlap) between marine mammals and fisheries can have significant implications for foraging success and individual survival, ultimately affecting population-level trends and characteristics (Trites et al., 1997; DeMaster et al., 2001; Tuck et al., 2001; Matthiopoulos et al., 2008; Jog et al., 2022). These interactions can also have a substantial economic cost to fisheries, through for example, damage to fishing gear, catch loss, closure of fishing areas, or changes in fishing gear (Lent and Squires, 2017; Nelms et al., 2021). Given the potential ecological and economic impacts, understanding the particular animal behaviours or fishing operations driving marine mammal-fishery interactions can facilitate mitigation measures and ecosystem-based management approaches aimed at reducing interactions (Hazen et al., 2018; Nelms et al., 2021).

The South American fur seal (*Arctocephalus australis;* hereafter 'SAFS') is a high-order marine predator, distributed almost continuously throughout the eastern South Pacific and western South Atlantic coast of South America (i.e. Peru to southern Brazil) (Vales et al., 2015; Baylis et al., 2019b; Milano et al., 2020; Vales et al., 2020; Sepúlveda et al., 2023). The global population is estimated to be ~ 400,000 individuals (Crespo and Oliveira, 2021). SAFS-fisheries interactions occur throughout the species' geographic range. Interactions include depredation, bycatch and incidental mortality in fish farm, gillnet, longline, purse-seine and trawling (pelagic, mid-water and bottom) operations; although the nature and magnitude of these interactions varies spatially across different fisheries, habitats and fishing jurisdictions (Crespo and Oliveira, 2021; Sepúlveda et al., 2023). Despite the SAFSs abundance, extensive breeding range and relatively frequent interactions with commercial fisheries (Crespo and Oliveira, 2021), remarkably little is known about many aspects of the species' foraging ecology. Few studies have examined SAFS at-sea movement behaviour using biologging and telemetry devices (Thompson et al., 2003; Franco-Trecu, 2015; Baylis et al., 2018b, 2018a; Cárdenas-Alayza et al., 2022) and consequently, there are substantial knowledge gaps about their foraging strategies and habitat use. This ultimately hinders our capacity to assess the frequency and extent of SAFS interactions with fisheries at large spatiotemporal scales in which SAFS foraging decisions occur (Thompson et al., 2003).

The Falkland Islands are located in the South Atlantic Ocean on the Patagonian Shelf, approximately 500 km east of the South American coast. They are home to over 50 % of the SAFS population (Baylis et al., 2019a). The Falkland Islands also have one of the most productive marine ecosystems in the world due to upwelling fronts bringing cold, nutrient-rich waters from depths onto the continental shelf (Belkin et al., 2009; van der Grient et al., 2023). Commercial fisheries are central to the Falkland Islands' economy, comprising up to 60 % of the annual Gross Domestic Product (GDP) (Augé et al., 2018; Baylis et al., 2021). This includes a highly lucrative squid-fishery accounting for a significant proportion of the global supply (Ospina-Alvarez et al., 2022), one of the few targeted commercial skate fisheries in the world (Winter, 2015; Winter and Arkhipkin, 2023), and a productive year-round multi-species finfish fishery (Arkhipkin et al., 2012; Fisheries Department Fishery Statistics, 2022). Annual commercial catch within the Falkland Islands Exclusive Economic Zone (hereafter referred to as 'EEZ', but locally known as the Falkland Islands Conservation Zones) can exceed 460,000 t (Fisheries Department Fishery Statistics, 2022). While SAFS dietary studies are limited, there appears to be trophic overlap with commercial fisheries within the Falkland Islands EEZ. For example, commercially exploited squid and finfish species recorded in SAFS diet include Patagonian longfin squid (*Doryteuthis gahi;* hereafter 'Loligo'), southern blue whiting (*Micromesistius australis australis*), red cod (*Salilota australis*), common hake (*Merluccius hubbsi*) and longtail southern cod (*Patagonotothen ramsayii*; locally and hereafter referred to as 'rock cod') (Baylis et al., 2014).

Despite trophic overlap with commercial fisheries, direct seal-fishery interactions in Falkland Islands waters have historically been low and an uncommon occurrence (only 13 incidental moralities reported between 1998 – 2016) (Iriarte et al., 2020). However, a marked increase (~ 900 %) has been observed within the Loligo trawl fishery in recent years. Specifically, in 2017, seal bycatch dramatically increased with mortalities peaking at 140 seals in a single season (Iriarte et al., 2020). While Seal Exclusion Devices (SEDs) have become mandatory across the entire Loligo-fishery since 2017 (see Iriarte et al., 2020 for details), frequent seal-fishery interactions remain an ongoing and evolving problem, with increased levels of interaction also being reported in the finfish trawl fishery (Fisheries Department Fishery Statistics, 2022). SAFS-fishery interactions in the Falkland Islands is of particular interest because of the dual ecological and economic ramifications. Changes in survival rates and demographic parameters for SAFS breeding in the Falkland Islands will impact the global conservation status of this species (Baylis et al., 2017, 2019a). Additionally, increased seal-fishery interactions in the Falkland Islands can disrupt fishing operations through the enforcement of temporary mitigation measures (i.e spatial closures and fishing restrictions), as was the case in 2017 (Fisheries Department Fishery Statistics, 2017; Iriarte et al., 2020).

Developing a mechanistic understanding of increased seal-fishery interactions requires an understanding of both the spatial and temporal associations between predator foraging effort and commercial fishing activity (Zador et al., 2008; Hindell et al., 2022). A preliminary assessment of SAFS-fisheries overlap in the Falkland Islands was conducted by Baylis et al. (2018b). To broadly assess spatial overlap, this study used relatively coarse-scale (hourly spatial locations) horizontal movement information from four male SAFS; and integrated this with daily summaries of vessel movement and inferred fishing activity (obtained from the Global Fishing Watch database) (Kroodsma et al., 2018). Using these heuristic approaches, results suggested significant (43 %) spatial overlap between SAFS habitat and fishing activity within the Falkland Islands EEZ. However, this study was not able to consider fine-scale horizontal-vertical movement behaviour, which provides information on where SAFS dive effort is concentrated along their movement trajectories. Furthermore, the vessel monitoring data used relied upon machine learning techniques to detect areas indicative of fishing activity, which may not accurately reflect how catch quantities are spatially structured across the EEZ.

Here, we further examine the seal-fishery spatial overlap in the Falkland Island EEZ by integrating fine-scale spatial location and dive behaviour from SAFS with spatially-explicit trawl-by-trawl catch data across the entire squid and finfish trawling fishing fleet. We examine horizontal-vertical movement behaviour of lactating adult female SAFS over two consecutive seasons (2018 and 2019) using GPS devices with in-built Time-Depth Recorders (TDRs). Our study focusses on female SAFS because, like other otariid species, females play a critical role in sustaining populations through pup provisioning (Page et al., 2005). To investigate the spatial associations between seal foraging effort and commercial fishing activity, we examined fisheries catch data throughout the EEZ over the same time period. We test whether seal dive effort (summarised dive activity) increased in areas associated with high levels of fishing yield (summed catch quantity). We describe SAFS fine-scale foraging behaviour and habitat use, and provide information about the spatial overlap with Falkland Islands fisheries, which will support the development of long-term marine management objectives aimed at achieving sustainable and holistic marine management.

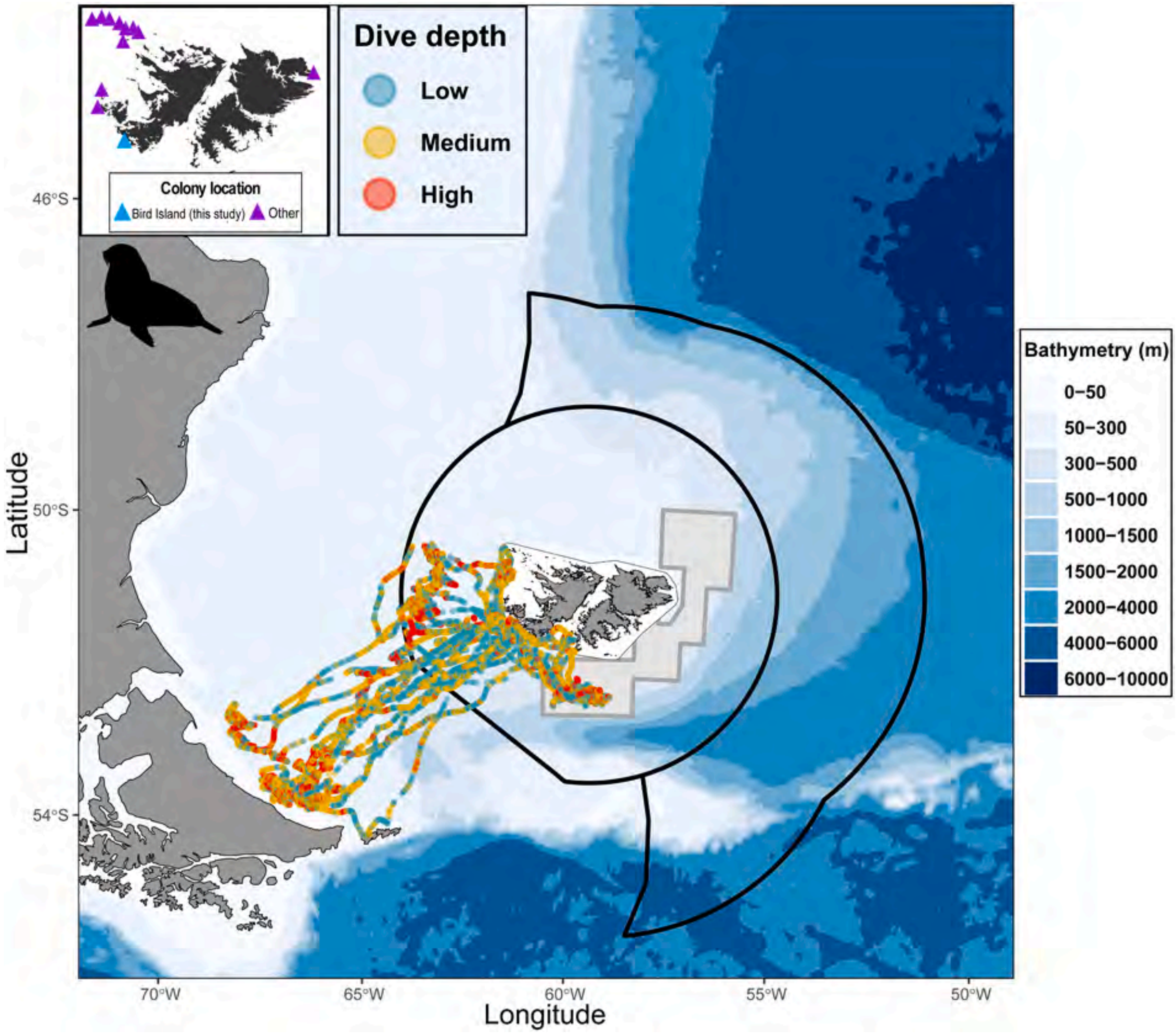

Fig. 1. State-space model location estimates for SAFS (n = 18) from the Bird Island colony integrated with dive data (dive depth presented here as an example) to provide horizontal-vertical foraging information (see *Methods* for details). To aid visual presentation and standardise across individuals, dive depth (i.e. summed vertical distance) values are presented relative to each individual, where shallow, medium and deep categories based on < 0.33, 0.33 – 0.66 and > 0.66 quantiles, respectively. Thick solid lines: EEZ of the Falkland Islands. Light grey shaded area: Loligo Box. Thin solid maritime boundary adjacent to the Falkland Islands coastline: fishing closure area. Inset panel, top left corner: location of the Bird Island colony (blue triangle) and all other Falkland Islands SAFS colonies (purple triangles). Bathymetric gradients displayed were created using the '*ggOceanMaps*' package (Vihtakari, 2022). Refer to Fig. S1 for a zoomed-in display of SAFS data adjacent to the Bird Island colony and within the Falkland Islands EEZ.

2. Materials and methods

2.1. SAFS spatial location and dive data

The SAFS movement data examined in this study was from the Bird Island colony (52º17 S, 60º92 W) (one of the Falkland population's 12 colonies), located in the south-west Falkland Islands (Fig. 1). While this colony is relatively small (< 2 % of the population), it is located in close proximity to commercial squid and finfish fishing operations. Data-archiving GPS location and dive tags (TDR-10-F; Wildlife Computers; approximately 300 g) were deployed on lactating adult female SAFS during July and August over the years 2018 and 2019. This dataset provided horizontal and vertical movement information for 18 SAFS ranging from 19 July to 14 August in 2018 (n = 9) and 20 July to 15 August in 2019 (n = 9).

To limit disturbance, adult female SAFS associated with a pup were selected at random and lightly immobilised through a remotely administered chemical restraint (Zoletil, Virbac; 1.5 mg kg^{-1}) using 0.5 cc darts (Pneu dart) and a CO_2-powered tranquiliser gun (Dan Inject JM Standard) (Baylis et al., 2015). Females were then masked and anaesthesia was induced or maintained using a portable gas anaesthetic machine and isoflurane (VOC Rota Flush, Medical Developments International) (Baylis et al., 2018a). Re-capture to retrieve tags followed the same procedure as capture. Using a 2-part epoxy glue (Devcon 5-minute epoxy), individuals were equipped with archival Fastloc-GPS tags (Wildlife Computers TDR10-F) that were programmed to collect GPS data at 10-minute intervals. These devices also had an integrated Time-Depth Recorder (TDR), recording depth at 1 s intervals with a ± 0.5 m resolution. Location and dive data were downloaded using Wildlife Computers software, and all subsequent processing and analyses were performed using R statistical software (version 4.3.1; R Core Team, 2022).

Location data for the 18 SAFS were assembled (n = 19,616 GPS locations), plotted and visually inspected. Foraging trip start and end times were identified using dive data. Data were then subjected to quality-control checks to ensure the removal of near-duplicate (< 10 s) location estimates and unrealistic travel speeds (> 4 m s^{-1}). This left us with a dataset of 19,580 GPS locations. With the quality-controlled SAFS data, we fitted a continuous-time correlated random walk (CRW) State-Space Model (SSM) using the '*fit_ssm*' function in the '*aniMotum*' package (Jonsen et al., 2023). We interpolated tracks to 15-minute time steps, which was roughly the mean sampling interval between raw GPS locations. In some cases, predicted location estimates fitted by the CRW model were positioned on land, creating unrealistic locations. This is because the SSM implementation does not have information about potential barriers to animal movement along movement trajectories (Jonsen et al., 2023). To address this, we re-routed land-based predicted locations back to the water using the '*route-path*' function. With the predicted and corrected re-routed movement trajectories, we assessed predictive performance by comparing location estimates with the fitted irregular location estimates for each individual. Our final SSM dataset containing tracks regularised at 15-minute intervals comprised 24,125 SAFS location estimates (Fig. 1).

To process SAFS dive data, we first applied a zero-offset correction to depth profiles. To account for surface noise, dives < 3 m were excluded from our analyses, analogous with other seal diving studies (e.g. Lea et al., 2002, Augé et al., 2011). All subsequent processing and analysis of dive data were performed using the '*divemove*' package (Luque, 2007). For each dive, various dive metrics were calculated. These included: (1) maximum depth (m); (2) dive duration (s); (3) bottom duration (s) (the period after descent and before the ascent phase; and (4) wiggle distance (m), which refers to vertical undulations in the bottom phase, commonly used to infer prey capture attempts (Dragon et al., 2012). Each dive was also assigned a solar position value using the '*maptools*' package (Lewin-Koh, 2010) based on the sun position at Bird Island. Solar position values < -12°, between -12° and 12°, and > 12° were assigned as night, crepuscular (i.e. dawn and dusk) and day, respectively. Dive data for the 18 individuals were collated and binned into 15-minute time periods corresponding to predicted SSM locations. To examine total dive effort, we calculated the sum of the maximum depth (i.e. vertical distance) (m), dive bottom duration (s), wiggle activity (m) and number of dives (#) performed every 15-minutes across the duration of horizontal movement trajectories (Fig. 1). Because total number of dives performed and total vertical distance may be related (i.e. total depth covered will necessarily increase with more dives), we also calculated mean dive depth (m); as a way to understand the spatial distribution of relatively deep/shallow dives. By summarising each of the five dive parameters in this way, we quantified how different metrics of dive effort were spatially distributed along horizontal trajectories.

2.2. Fisheries data

Location and catch quantity information from all trawl operations within the Falkland Islands EEZ, corresponding to SAFS data (July and August in 2018 and 2019), were requested and obtained from the Falkland Islands Fisheries Department (FIFD). This fishery predominately consists of bottom-trawl operations, which is most effective for catching target squid and finfish species (i.e. demersal assemblages). The EEZ covers 453,897 km^2 of ocean around the Falkland Islands, beyond the 3 nautical mile fishing closure area (mandated by the FIFD) (Fig. 1). Within the EEZ, extending south to north-east of the Falkland Islands is the Loligo Box, which is the only area in which target trawling for Loligo is permitted (Arkhipkin et al., 2004a) (Fig. 1). Fisheries data incorporated catch quantity (kg) from ten main catch groups: Loligo, Southern blue whiting, red cod, hake, rock cod, Patagonian grenadier (*Macruronus magellanicus*), kingklip (*Genypterus blacodes*), Illex squid (*Illex argentinus*), Patagonian toothfish (*Dissostichus eleginoides*) and skates (Rajidae spp.). Using these data, total catch quantity for an entire trawl was calculated. Trawl location data for each vessel was provided as a start and end location and timestamp. To examine the spatial distribution of trawl efforts at-sea, we applied a linear interpolation at 10-minute intervals using the '*adehabitatLT*' package (Calenge, 2011). This approach is commonly used to examine vessel movements trajectories in the absence of high-resolution vessel monitoring data (Stelzenmüller et al., 2008; Cardiec et al., 2020; Joo et al., 2021; Kroodsma et al., 2023).

2.3. SAFS-fisheries data integration

To examine the spatial overlap and relationship between commercial fishing catch effort and seal foraging effort, we integrated the horizontal-vertical movements of SAFS with total trawl catch quantity recorded across the same time period (July and August) for the two consecutive years of data (2018 and 2019). We first partitioned total catch quantity by trawl length (28 km ± 16 km), which equally distributed catch values across 10-minute interpolated vessel locations (mean trawl durations were 5 hrs ± 2 hrs). To identify the spatial organisation of fishing activity within the EEZ, we then summarised total catch quantity at a 0.1° latitude × 0.1° longitude resolution (approximately 10 × 10 km). Although it is impractical to assume fishing catch is evenly distributed across the length of trawls, our approach of dividing catch values in this manner ensured that information were not duplicated across multiple adjacent grid cells when trawls straddled or exceeded 0.1° latitude × 0.1° longitude bins.

Gridded fishing catch quantity were overlaid with the horizontal-vertical movements of SAFS individuals tagged at Bird Island. We spatially binned SAFS metrics of foraging effort into corresponding 0.1° latitude × 0.1° longitude grid cells. For each SAFS individual, we calculated: (1) total vertical distance, (2) total bottom duration, (3) total wiggle distance, (4) total number of dives and the (5) mean dive depth occurring within each grid cell. Gridding data in this way can reduce spatial autocorrelation within high-resolution animal or vessel movement data (Warwick-Evans et al., 2022; Riaz et al., 2023).

2.4. Statistical analysis

Using the spatially integrated SAFS-fisheries dataset, we examined the spatial relationship between SAFS dive effort and fisheries catch quantity. We tested these spatial associations using generalised linear mixed effects models (‘*glmmTMB*’ package; Brooks et al., 2017). Using each of the five SAFS diving response variables (total vertical distance, bottom duration, wiggles, number of dives and mean dive depth), we fitted five independent models with catch quantity as a single predictor variable. Each of the five models were configured with individual seal ID nested within year (i.e. Year/Seal ID) as a random effect to allow relationships to vary among individuals and sampling years. Through our modelling approach, we assume our sample of female lactating SAFS (n = 18 individuals) are representative of the entire cohort for this particular age/sex class at the Bird Island colony. To deal with overdispersion and right skew in the SAFS dive data, we configured vertical distance, wiggles, bottom duration and mean dive depth models with a gamma distribution (log link function), while the number of dives (count data) model was fitted with a negative binomial distribution (log link function). To aid model convergence, catch quantity values exceeding the 99 % quantile range were revalued to the 99 % quantile value. This capped a small number (n = 10, equating to < 1 % of data) of catch quantity values > 1,745,012 kg in grid cells to this value. This quantile-based approach for dealing with outliers is analogous with various other studies using fisheries and environmental datasets (Donovan et al., 2018; Robinson et al., 2019; Lester et al., 2020). Catch quantity values inputted into the model were also scaled and centred (‘*datawizard*’ package; Patil et al., 2022), which is a common approach to aid model convergence (Zuur et al., 2009). Model covariates were considered significant at p-values < 0.05.

3. Results

3.1. SAFS movement characteristics

From the 18 SAFS individuals (n = 20 foraging trips), we recorded 97,117 dives across 24,125 GPS locations. Seal movements were widely distributed in all directions north to south-west of the Bird Island colony (Fig. 1; Fig. S1). On average, individuals ranged 270 km away from the colony on foraging trips that lasted 14 days (see Table 1 for means and standard deviations [SD]). However, some individuals ranged up to 459 km away from the colony towards the southern coastline of Tierra del Fuego, Argentina (Fig. 1; Table 1). The number of dives performed during foraging trips was highly variable between individuals. The mean number of dives performed was 4099, although some individuals performed over twice this amount (see Table 1 for means ± SD and range foraging trip

Table 1
Summary statistics of SAFS foraging trip and dive behaviour. Mean values are calculated per individual and then averaged across individuals. Mean values are presented alongside standard deviation. See *Methods* for dive metric definitions.

SAFS		
(n = 18 individuals)		
Trip characteristics (n = 20)	Mean ± SD	Range
Foraging trip		
Duration (days)	14 ± 5	5 – 22
Maximum distance from colony (km)	270 ± 139	77 – 459
Number of dives	4099 ± 2716	758 – 9888
Dive data		
Depth (m)	36 ± 25	3 – 334
Duration (s)	71 ± 33	2 – 445
Bottom duration (s)	23 ± 8	1 – 205
Wiggles (m)	12 ± 5	1 – 132

statistics). Individuals generally travelled to a mean depth of 36 ± 25 m. However, during a single dive, the maximum dive depth was 334 m, and the longest dive performed lasted 7 mins in duration. On average, bottom durations lasted 23 ± 8 s and 12 ± 5 m of wiggles were performed during this time (Table 1).

The mean time seals spent inside the EEZ was 64 %, and 16 % of this time was recorded in the Loligo Box area. While there was notable individual variability, mean dive activity (depth, duration, bottom duration, wiggles and number of dives) within the EEZ and Loligo Box ranged between 60 – 66 % and 13 – 17 %, respectively (95 % CIs provided in Table 2). Of all locations in the EEZ, large amounts of dive activity (mean values ranging between of 21 – 27 %) also occurred within the fishing closure area immediately adjacent the Bird Island colony (see Table 2 for means and 95 % CIs).

Within the fishing closure area, the Loligo Box and the remaining area of the EEZ, dives were performed at a variety of different depths throughout the day (Fig. 2). Based on visual assessment, marginally deeper dives were performed during crepuscular and day light hours in all three areas, although deep dives were also performed during night hours. SAFS travelled to the greatest depths in the Loligo Box and EEZ, frequently performing dives > 100 m (Fig. 2).

3.2. *Fisheries data*

During the study period there were 4831 trawls within the EEZ from 29 vessels (Fig. 3). Total catch quantities ranged from 52 – 112,833 kg per trawl. The mean catch quantity of trawls was 10,449 kg, with 1 % of hauls being over 50,000 kg. Within the spatial extent of SAFS foraging distribution at Bird Island (Fig. 1; Fig. 3), 2418 trawls were recorded. This meant 50.1 % of trawling fishing effort spatially overlapped with the foraging areas of lactating SAFS females originating from Bird Island (Fig. 3). Of these trawls, 1090 (45 %) occurred in the Loligo Box (Fig. 3).

The proportion of catch across the spatial bounds of SAFS foraging activity was similar between both years (Table 3). Catch composition was dominated by Loligo. In total, > 6,000,000 kg of Loligo were caught by commercial trawl fishing, which accounted for 86 – 88 % of total catch quantity. Catch effort were primarily from the southern Loligo Box (Fig. 4; Table 3). Hake was the second most exploited species, accounting for 10 – 13 % of the total catch across the SAFS spatial domain. Hake catches were largely concentrated in the habitat west of the Bird Island colony (Fig. 4; Table 3). All other commercially caught species made up < 1 % of total catch (Fig. S2; Table 3).

3.3. *SAFS-fishery spatial relationship*

When binned at a 0.1° latitude × 0.1° longitude spatial resolution, SAFS foraging effort (beyond the fishing closure area) extended across 420 grid cells (Fig. 5). The spatial distribution of all five metrics of dive effort examined in models (total vertical distance, bottom duration, wiggles, number of dives and mean dive depth) varied. However, in general, all five foraging effort parameters were consistently high in the southern Loligo Box and the boundary of the EEZ west of the colony. All parameters, except for mean dive depth, also demonstrated an increased pattern in the nearshore habitat immediately adjacent to Bird Island (Fig. 5). The mapped distribution of fishing effort corresponding to these 420 grid cells showed trawl fishing catch quantities were also concentrated broadly over the western boundary of the EEZ and in a small area in the southern Loligo Box (Fig. 4).

Model results showed that the total vertical distance and number of dives seals performed were greater in areas associated with a greater catch quantity. Mean dive depth was also greater in areas of high fishing catch (Table 4; Fig. S3). In contrast, total wiggles and bottom duration was not significantly related to areas of increased fishing activity (Table 4).

4. Discussion

This study provides one of the most comprehensive and detailed analyses of SAFS movement behaviour and is the first to report how dive behaviours are spatially distributed along horizontal movement trajectories. By spatially integrating fine-scale horizontal-

Table 2
Mean and 95 % CI of horizontal and vertical movement characteristics from SAFS recorded from the Bird Island colony in different management zones around the Falkland Islands. This includes the Falkland Islands EEZ, Loligo Box (management area for Loligo target trawling) and fishing closure area (encompasses the entire area around the Falkland Islands coastline within 3 nautical miles of the baseline). Values are calculated across all individuals. Mean Loligo Box and fishing closure area values are calculated based on movement data from within the EEZ.

SAFS			
(n = 18 individuals)			
Habitat zones Movement characteristics	EEZ Mean (95 % CI)	Loligo Box	Fishing closure area
Spatial locations (#)	64 % (44 – 85 %)	16% (0 – 33 %)	20 % (7–32 %)
Number of dives (#)	65 % (44 – 86 %)	15% (0 – 32 %)	25 % (11–38 %)
Depth (m)	60 % (37 – 84 %)	17% (0 – 36 %)	21 % (6–35 %)
Duration (h)	63 % (41 – 85 %)	16% (0 – 33 %)	24 % (9–38 %)
Bottom duration (h)	66 % (45 – 86 %)	13% (0 – 28 %)	26 % (13–40 %)
Wiggles (m)	63 % (41 – 85 %)	14% (0 – 28 %)	27 % (13–41 %)

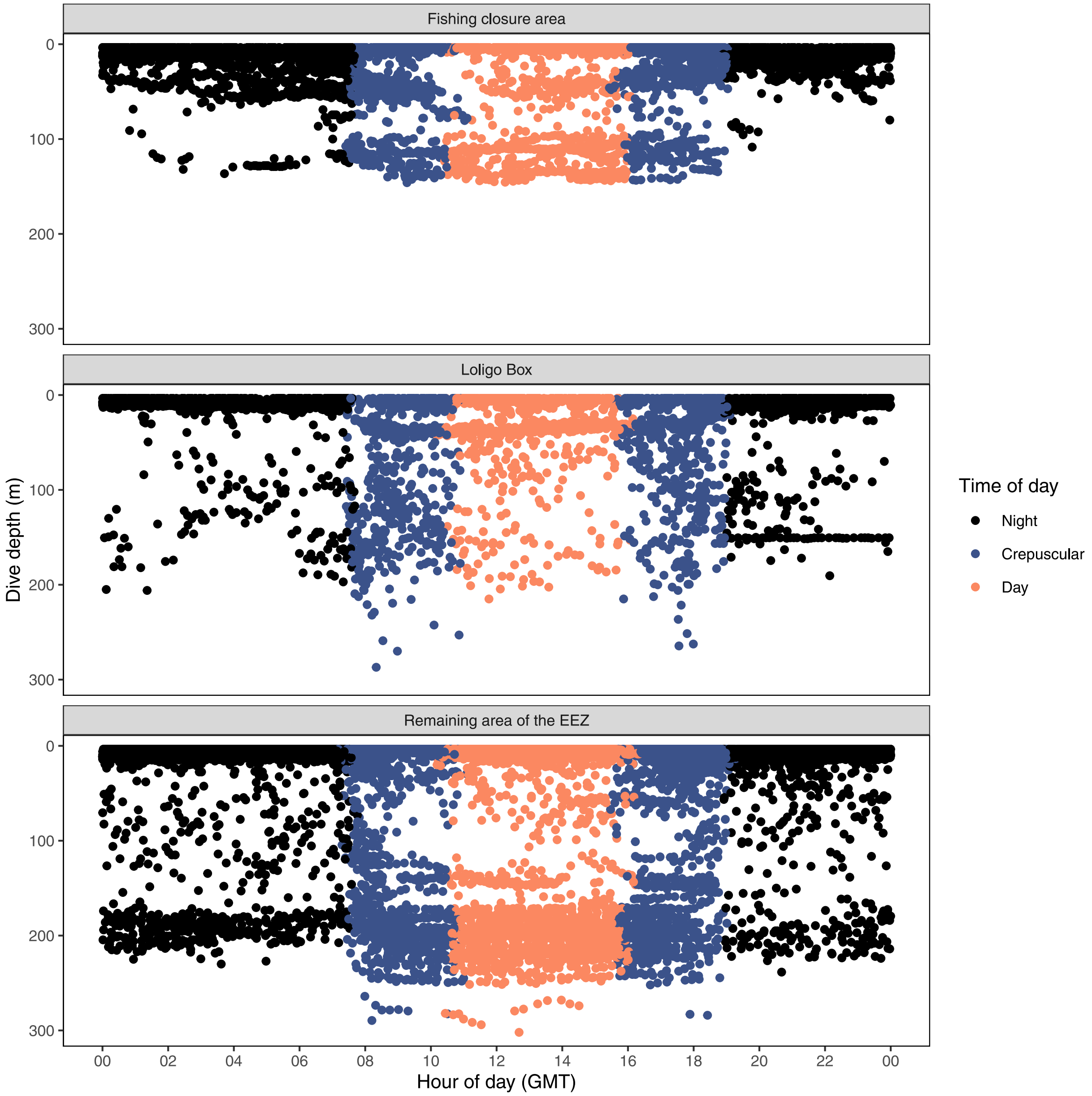

Fig. 2. Time-series of SAFS (n = 18) dive data. Maximum dive depth (m) of each dive performed is plotted in relation to the hour of day (GMT). Each panel represents the region within the EEZ dives occurred, including the nearshore fishing closure area, Loligo Box and the remaining area of the EEZ. Dives are also coloured by the time of day they occurred (day, crepuscular or night), based on solar position values (see *Methods* for details).

vertical movements with the distribution of fishing effort throughout the Falkland Islands EEZ, our findings improve understanding of seal-fishery interactions within the Falkland Islands trawl fishery – a topic of increasing management concern. Our results indicate a distinct spatial overlap between female SAFS foraging effort and fishing activity in the Falkland Islands EEZ. We found SAFS increased their dive effort (total number of dives, vertical distance and mean dive depth) in areas associated with increased catches, likely driven by a trophic overlap for demersal Loligo and hake resources. The results of this study can support spatial conservation and fisheries management aimed at mitigating seal-fishery interactions in the Falkland Islands, which is home to the largest breeding population of SAFS in the world.

4.1. SAFS distribution and movement

During the study period, we found female SAFS travelled to multiple discrete foraging habitats over the Patagonian Shelf. Some individuals ranged over 450 km away from their colonies towards the southern tip of Argentina. These maximum distances are

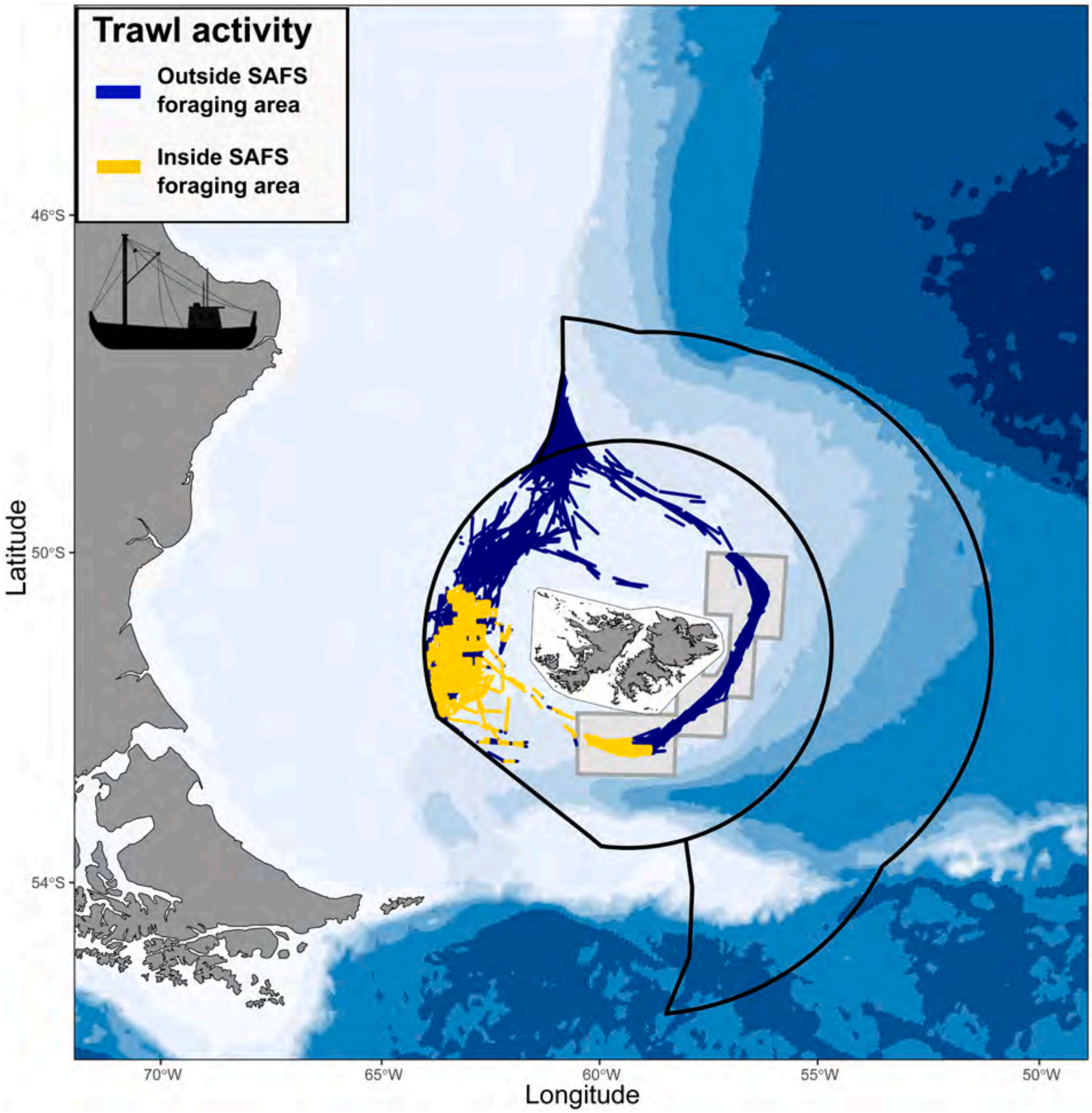

Fig. 3. All trawl-by-trawl data within the Falkland Islands EEZ for the years 2018 and 2019. Trawls inside (yellow) and outside (blue) the spatial bounds of female SAFS foraging distribution from animals originating at Bird Island are displayed. Map features and boundaries displayed as for Fig. 1.

comparable to records of lactating female SAFS at other colonies around the Falkland Islands (Baylis et al., 2018a). However, we found the greatest proportion of their time at-sea and foraging activity occurred within the Falkland Islands' EEZ, including the Loligo Box. The nearshore fishing closure area also appeared to be an important foraging area for SAFS, providing an additional layer of support to the current Marine Managed Area (MMA – equivalent to a marine protected area) proposal; which is based on the area's significant biodiversity value and proximity to land-based breeding colonies (Baylis et al., 2021). The habitat use findings of this study are consistent with previous winter observations for SAFS breeding in the Falkland Islands, which show that individuals utilise a range of foraging strategies, including short and long foraging trips (Thompson et al., 2003; Baylis et al., 2018a). Importantly, our findings demonstrate SAFS foraging trips and dive effort occur within multiple different management zones within the Falkland Islands EEZ. Additionally, within these areas, dives were performed during all times of the day. This is likely an artefact of female SAFS foraging continuously at-sea over multiple days to meet the energy demands of pups (Lea et al., 2002; Hoskins and Arnould, 2013). Understanding these horizontal and vertical components of SAFS foraging is critical to develop knowledge of priority habitats and the extent

Table 3
Total fisheries catch quantity of the ten main species groups within the spatial bounds of SAFS foraging in the Falkland Islands EEZ. Summed values and proportions are separated by year. Hake and Loligo species groups highlighted in bold text represent major catch quantities.

Catch Species	2018 (n vessels = 24) (n trawls = 1256) Sum (kg)	2019 (n vessel = 27) (n trawls = 1162) Sum (kg)
Loligo	**6,366,634 (88 %)**	**6,143,306 (86 %)**
Hake	**739,939 (10 %)**	**906,249 (13 %)**
Kingklip	29,542 (< 1 %)	21,298 (< 1 %)
Red cod	25,242 (< 1 %)	19,868 (< 1 %)
Skates	21,313 (< 1 %)	17,960 (< 1 %)
Rock cod	29,676 (< 1 %)	8042 (< 1 %)
Toothfish	4693 (< 1 %)	2489 (< 1 %)
Grenadier	1503 (< 1 %)	129 (< 1 %)
Blue Whiting	1028 (< 1 %)	11 (< 1 %)
Illex	8 (< 1 %)	80 (< 1 %)
Total	**7,219,578**	**7,119,432**

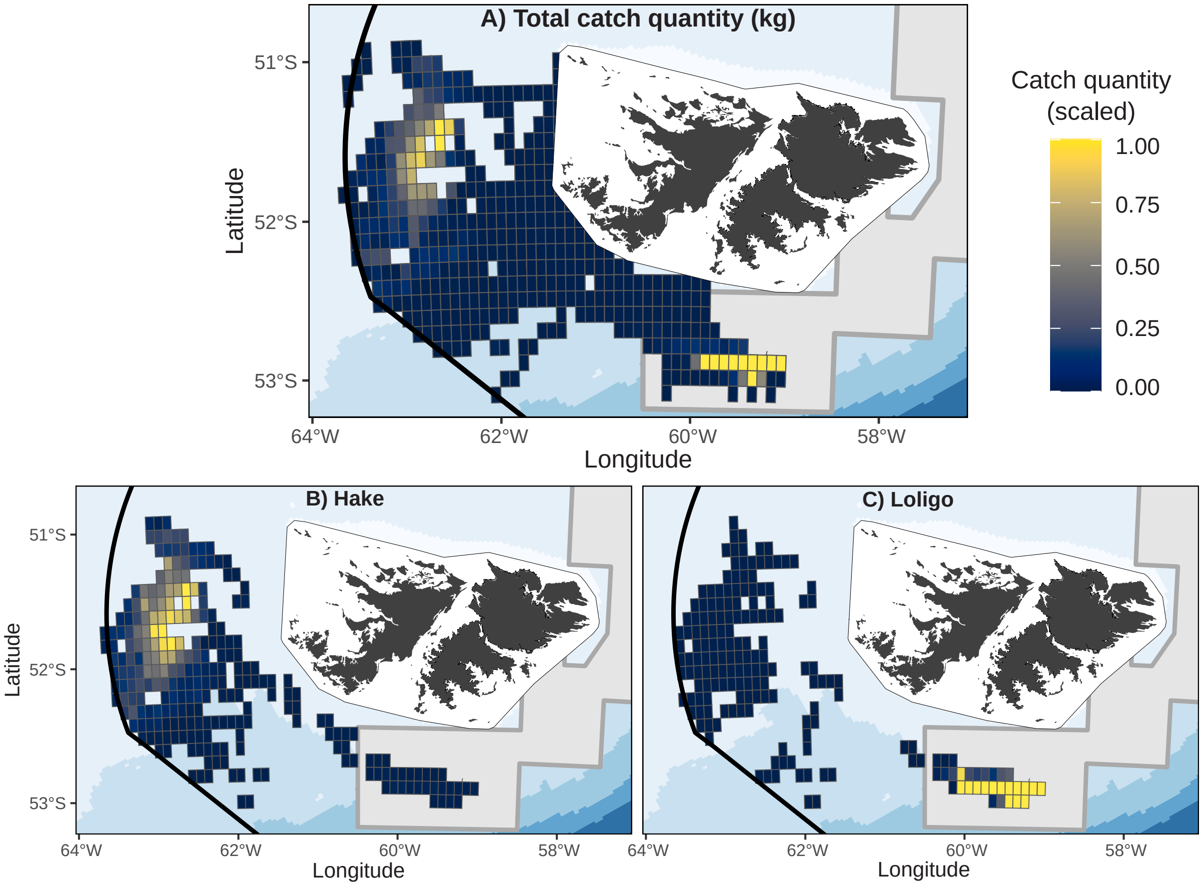

Fig. 4. Total catch quantity of all ten species combined (A) and the two dominant catch species, Hake (B) and Loligo (C), from the trawl fishing fleet operating within the spatial bounds of SAFS foraging effort over the study period. Fishing data are spatially gridded to 0.1 × 0.1° resolution. Map features and boundaries displayed as for Fig.

in which individuals may be exposed to fishing activity while foraging at-sea (Queiroz et al., 2019; Clay et al., 2019; Reisinger et al., 2022), which can ultimately inform spatially-explicit conservation guidelines for this globally significant population (Baylis et al., 2021).

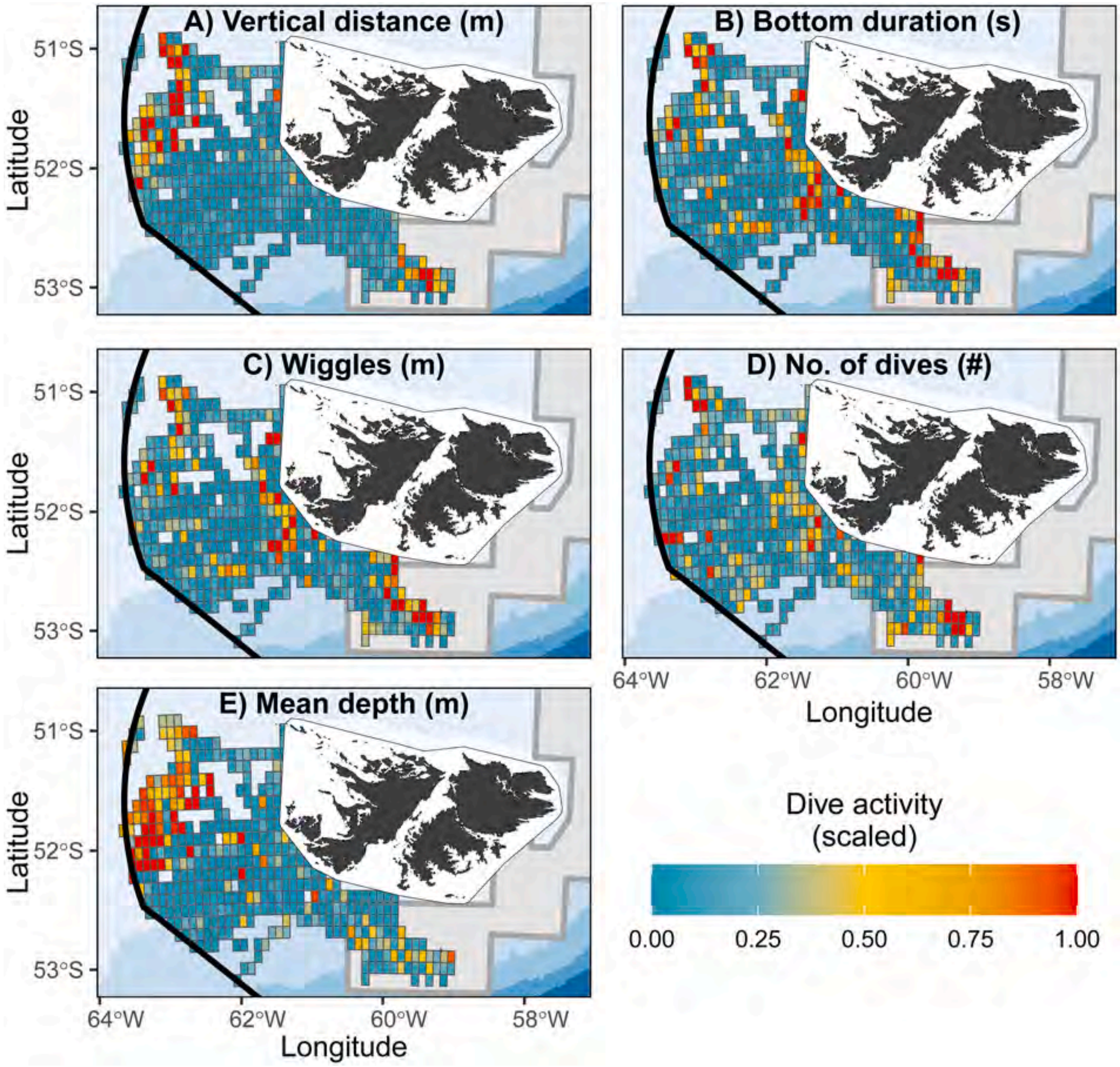

Fig. 5. Spatially gridded summaries (0.1 × 0.1° resolution) of all five SAFS foraging metrics examined (A – E). To aid visual presentation, gridded seal dive metrics are scaled (0 – 1) across the spatial domain. Mapping features and boundaries displayed as for Fig. 1.

4.2. Spatial overlap with the Falkland Islands trawl fishery

Our results suggest fishing catch was concentrated in the southern Loligo Box and western boundary of the Falkland Islands EEZ. The southern Loligo Box accounted for the vast majority (~ 85 %) of all catch quantity (by mass) recorded over the study period, where > 12,000,000 kg of Loligo were caught. This area is characterised by a consistently high density of Loligo (Agnew et al., 2005; Fisheries Department Fishery Statistics, 2017) and is a focal area of squid fishing effort. In the other intensively fished region over the western boundary of the EEZ, hake were the dominant catch species and accounted for ~ 10 % of the total catch recorded. Both of the areas represent highly productive fishing grounds, likely due to frontal features and strong upwelling (Arkhipkin et al., 2004a, 2013).

In these areas of increased fishing activity, we found SAFS also increased their dive effort. Seals performed an increased number of dives and travelled a greater vertical distance in the water column. These two metrics of dive effort have also been linked with increased prey abundance for other fur seal species (Georges et al., 2000; Skinner et al., 2014; Kuhn et al., 2015). Combined with our results showing a positive relationship between mean dive depth and catch quantity, our study suggests SAFS perform a greater frequency of deep dives in productive bottom-trawl fishing grounds. In contrast, we found SAFS did not increase wiggle activity or time spent in the bottom phase in areas associated with higher catch quantity. These results were somewhat surprising because it is widely assumed that seals and other marine predators search for and acquire food during these parts of the dive cycle (Thompson and Fedak,

Table 4
Results of the five generalised linear mixed effects models for each dive metric in relation to fisheries catch quantity. Model coefficients for predictor variables and random effects (Year/ID) are displayed. Statistically significant *p*-values are displayed in bold text.

Response variable	Model variables	Coefficients				
		Est	Variance	SE	z-value	*p*-value
Vertical distance	Intercept	6.19		0.22	27.94	<0.0001
	Catch quantity	0.25		0.05	4.65	**<0.001**
	Seal ID:Year		0.68	0.83		
	Year		0.02	0.13		
Bottom duration	Intercept	6.10		0.14	44.72	<0.0001
	Catch quantity	0.04		0.06	0.68	0.48
	Seal ID:Year		0.21	0.46		
	Year		0.01	0.01		
Wiggles	Intercept	5.06		0.14	37.00	<0.0001
	Catch quantity	0.06		0.06	0.99	0.30
	Seal ID:Year		0.28	0.53		
	Year		0.01	0.01		
No. dives	Intercept	3.12		0.13	23.34	<0.0001
	Catch quantity	0.13		0.04	3.04	**<0.001**
	Seal ID:Year		0.30	0.54		
	Year		0.01	0.01		
Mean depth	Intercept	3.43		0.23	15.24	<0.0001
	Catch quantity	0.10		0.04	2.70	**<0.001**
	Seal ID:Year		0.38	0.62		
	Year		0.05	0.24		

2001; Austin et al., 2006; Kuhn et al., 2009; Hanuise et al., 2010; Iwata et al., 2012; Gallon et al., 2013). However, our results are consistent with studies examining the dive behaviour and prey consumption of northern fur seals (*Callorhinus ursinus*) (Skinner et al., 2014). Using direct measures of feeding activity (via in-situ stomach temperature sensors), Skinner et al. (2014) found wiggles and bottom duration did not reflect mass gain or prey capture, and total vertical distance and dive frequency were better descriptors of foraging effort. It is important to note that in the absence of real-time prey-field information, we cannot exclude the possibility that increased dive effort is actually associated with low prey availability and decreased foraging success (Womble et al., 2014; Viviant et al., 2016; Florko et al., 2023). However, our interpretation that increased dive effort is a proxy for greater rates of foraging and prey encounter is supported by our results, which show SAFS increased dive effort and performed deeper dives in the same areas associated with productive and prey-rich areas of demersal assemblages, as evidenced by fisheries activity. While further work is needed to understand which components of an individual SAFS dive are measures of foraging effort and success, our findings support the idea that dive profiles and indices of dive effort can vary between marine predator species based on local prey-field characteristics (i.e. distribution, structure and abundance in the water column) (Fuiman et al., 2007; Viviant et al., 2016).

The SAFS behavioural findings presented here can be explained by the vertical distribution of Loligo and hake prey items and the physiological constraints of SAFS as an air-breathing marine predator. Loligo occupy habitat over the continental shelf around the Falkland Islands (20 – 350 m deep) (Roa-Ureta and Arkhipkin, 2007). In the southern Loligo Box, research surveys have shown Loligo occur in the greatest concentrations at depths of 100 – 140 m (Arkhipkin et al., 2004b). Similarly, over the western boundary of the EEZ, the majority of hake biomass are located at depths of 100 – 250 m (Arkhipkin et al., 2015). Within these two areas, we found SAFS frequently travelled to these depths in the water column. To reach these depths, SAFS would be required to perform relatively deep dives (this study, Baylis et al., 2018a,b), which necessarily take more time and oxygen (Roncon et al., 2018). By travelling to greater depths and performing an increased number of dives, less oxygen (and therefore time) is available to spend in the dive bottom phase (Carbone and Houston, 1996; Mori, 1999). Numerous studies on other seal species have demonstrated that prey distribution and depth in the water column are key determinants of dive behaviour (Womble et al., 2014; Kuhn et al., 2015). The SAFS behavioural findings presented in this study are important in helping us understand the vertical foraging strategies employed within the southern Loligo Box and western boundary of the Falkland Islands EEZ, particularly given evidence that both areas may be important foraging grounds for the broader Falklands SAFS population (Baylis et al., 2018a,b).

4.3. Implications for fisheries management

Within the southern Loligo Box, there has been a dramatic increase in direct seal-fishery interactions in recent years (i.e. since 2017) (Fisheries Department Fishery Statistics, 2022). Since 2017, the total annual catch of Loligo has been consistently high, with the fishery achieving record high catch quantities across multiple successive years (refer to Fisheries Department Fishery Statistics, 2022 for data summaries). The Loligo fishery is responsibly managed, adopting conservative escapement biomass thresholds (i.e. minimum biomass limits allowed to escape and spawn) and in-season real-time management using depletion models to ensure the risk of overfishing is negligible (Agnew et al., 2002, 2005; Fisheries Department Fishery Statistics, 2022). Therefore, greater catch yields and increased seal-fishery interactions could be an artefact of the higher abundance of Loligo in the region, consistent with the global proliferation of cephalopod stocks in recent years (Arkhipkin et al., 2021). Increased prey abundance can influence the spatial distribution of seal foraging effort, resulting in increased seal density and resource competition in particular habitats (Ramasco et al., 2017). It is also plausible the increase in seal-fishery interactions is related to the expanding population of SAFS breeding in the Falkland Islands, which has increased dramatically in both population size and number of breeding colonies since at least the 1980s (Baylis et al., 2019a). These kind of changes in fur seal population dynamics can drive increased intra-specific competition for resources and influence the foraging strategies individuals employ (Kuhn et al., 2014). In the case of SAFS in the Falkland Islands, this may translate to greater interaction or spatial overlap with commercial trawl operations, which can spatially retract and aggregate prey in the water column, providing a foraging advantage to marine predators (Hamer and Goldsworthy, 2006).

High rates of SAFS bycatch and mortality have been reported in hake trawl fisheries elsewhere throughout the species' geographic range, likely driven by spatiotemporal and trophic overlap (Sepúlveda et al., 2023). There is evidence that SAFS incidental capture and mortality is becoming an increasing issue in the Falkland Islands trawl finfish fishery (Fisheries Department Fishery Statistics, 2022). Our findings showing a marked spatiotemporal overlap between female SAFS originating from Bird Island and the commercial hake fishery presents a partial explanation for this. Furthermore, hake fishing effort is concentrated to the west of the Falkland Islands, and given the trip distances observed in this study, is likely within the foraging range of an additional 10 colonies and > 90 % of the SAFS population (Baylis et al., 2019a).

The rapid increase in seal-fishery interactions has also coincided with ecosystem shifts in finfish composition and abundance in the Falkland Islands EEZ. Southern blue whiting were once the most abundant finfish species on the Patagonian Shelf, however sustained overfishing (spanning > 10 years) caused the stock to decline, and ultimately collapse between 2004 – 2007. This niche was overtaken by rock cod, which experienced a dramatic increase in abundance and became the dominant species exploited by the finfish fishery (Laptikhovsky et al., 2013). However, rock cod abundance and biomass also declined precipitously (Gras et al., 2017; Fisheries Department Fishery Statistics, 2022). Since 2015, hake has emerged as the primary target of the Falkland Islands fishery, accounting for the vast majority of all finfish catch (91.1 % in 2022) (Fisheries Department Fishery Statistics, 2022). It is possible these changes in finfish assemblages and community structure may have impacted the foraging behaviour and success of SAFS, potentially increasing competition and interaction with commercial fisheries.

Most finfish species found with the Falkland Islands EEZ are straddling stocks which pass through multiple jurisdictions across the annual cycle. Understanding the drivers of population dynamics for Falkland Island finfish assemblages is an extremely challenging task (van der Grient et al., 2023). Furthermore, there are no regional or multilateral fishing arrangements in place to manage the exploitation of straddling finfish stocks (Barton et al., 2004; Villasante and Sumaila, 2008; Arkhipkin et al., 2023). Currently, Falkland Islands finfish fisheries are managed using Total Allowable Effort (TAE) (Ramos and Winter, 2022). However, with substantial knowledge gaps about the population dynamics of these straddling finfish stocks, it is difficult to ascertain whether allocated TAE quotas are conservative and sustainable (Mainardi, 2021). Further work is needed to disentangle the precise environmental and operational mechanisms underpinning the increased levels of seal interactions with the Falkland Islands finfish fishery, and how these interactions can be mitigated in future.

4.4. *Future research direction*

Our study used fine-scale horizontal and vertical movement behaviour of 18 female SAFS at a single colony to infer the degree of spatial overlap with commercial trawl fisheries in the Falkland Islands. Despite being a small dataset compared to other fur seal species (Lea et al., 2010; Arthur et al., 2015), it is one of the largest datasets compiled on the movement ecology of SAFS. This highlights the paucity of SAFS movement data available. However, consistent with other fur seal species (Boyd et al., 1998; Knox et al., 2017), SAFS exhibit marked sex-specific differences in foraging behaviour driven by life history constraints (Baylis et al., 2018b). Furthermore, there are substantial inter-colony differences (Baylis et al., 2018a), likely associated with spatial variability in local-scale prey-field characteristics, environmental features and resource competition (Robson et al., 2004; Lundström et al., 2010). Further research is therefore needed to obtain data which are more representative of population-level foraging behaviours and habitat use within the Falkland Islands EEZ. This includes investigating how fishing interactions may vary in relation to different intrinsic factors (i.e. sex, age and breeding status) and extrinsic factors (i.e. colony location, time of year and prey abundance/availability) (Lundström et al., 2010; Cronin et al., 2012). Acquiring these larger datasets can also facilitate more sophisticated modelling efforts, where interactions between different behavioural and demographic parameters are examined and different random effects configurations explored to improve understanding of population-level seal-fishery interactions (Kuhn et al., 2015).

Our study provides an important advancement to understanding SAFS spatiotemporal and trophic overlap with commercial fishing operations in the Falkland Islands. Without information on real-time predator-prey interactions or predator diet at relevant temporal scales (Ainley et al., 2015; Goulet et al., 2019), spatially-explicit catch data from contemporaneous fishing operations can provide a useful proxy for predator diet composition (Cronin et al., 2012). However, efforts to understand the nature and magnitude of seal-fishery interactions requires a comprehensive understanding of SAFS diet and energetic needs. To date, only one study has quantitatively assessed SAFS diet in Falkland Islands waters (Baylis et al., 2014). Population-level inferences are restricted by the limited temporal coverage and the widely accepted limitations of traditional scat analysis techniques (Yonezaki et al., 2003; Tollit et al., 2009). Furthermore, recent evidence of ecosystem shifts in finfish assemblages and increased seal-fishery interactions in the Falkland Islands EEZ suggests these dietary findings may be outdated, warranting renewed investigations of diet and trophic overlap with commercially harvested species. A greater understanding of energy flow and trophic pathways within the Falklands Islands ecosystem can ultimately inform trophodynamics models and facilitate ecosystem-based management of seal-fishery interactions.

The integration of GPS and dive data in this study generates important fine-scale information about how and where SAFS dive effort is spatially distributed. A natural extension of this work is to assess real-time seal-fishery interactions to examine what factors lead to these interactions (Orben et al., 2021) and how SAFS behave around commercial fishing operations (Hamer and Goldsworthy, 2006).

These insights can reveal the nature of seal-fishery interactions, and the utility of different mitigation strategies, including technical (i.e. SEDs, acoustic deterrents, altered mesh sizes on nets) and non-technical (i.e. spatial closures and discard management/retention) approaches (Nelms et al., 2021).

Animal ethics statement

All handling and tagging of SAFS was conducted under research permits issued by the Falkland Islands Government (R19/2018 and R19/2019).

Declaration of Competing Interest

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

Data Availability

Data will be made available on request.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2023.e02615.

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