

Seal-fishery interactions in the Falkland Islands—operational and environmental factors drive resource competition

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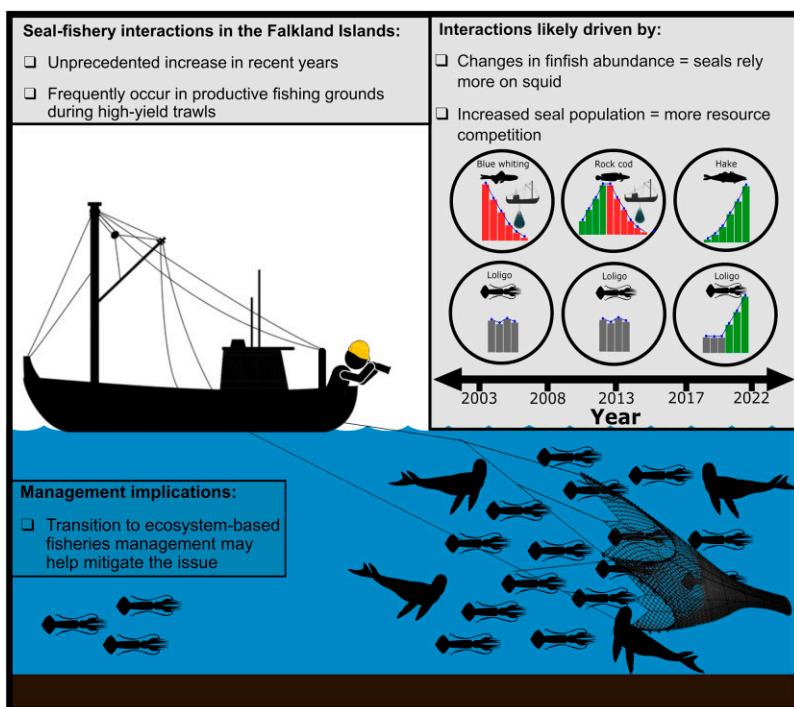
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Abstract

Direct interactions between marine mammals and commercial fisheries are a worldwide conservation challenge. Observer programmes remain the most effective and reliable method for collecting data on these interactions. In the Falkland Islands—home to globally significant seal populations and commercial squid fisheries, seal-fishery interactions have escalated in recent years, prompting management concerns. Complete observer coverage within the squid fishery presents a valuable opportunity to investigate the nature, extent, and drivers of these interactions. Integrating multi-year observer records with extensive ancillary (i.e. vessel logbook and oceanographic) datasets, we examine the operational and environmental factors influencing the occurrence of seal-fishery interactions. Our findings show interactions most frequently occur in the main squid fishing grounds during trawls associated with high catch quantities. Assessment of long-term catch data (both finfish and squid) also suggests the increase in seal-fishery interactions may be caused by collapses in dominant finfish stocks over the past 20 years, constricting foraging resources available to seals. Taken together, our findings indicate resource competition may be a mechanism of interactions. To help mitigate this issue, we advocate for the development of ecosystem-based fisheries management, which considers the trophic effects of fishing practices and the energetic requirements of local marine predator populations.

Keywords: bycatch; interactions; fisheries; seal; Falkland Islands

Graphical abstract



Introduction

Interactions between marine mammals and commercial fisheries are a key threat to marine mammal populations worldwide. The incidental capture and entanglement of marine mammals during commercial fishing operations is regarded as a significant cause of mortality in global marine ecosystems (Avila et al. 2018, Nelms et al. 2021). Various marine mammal populations have experienced dramatic declines as a result of sustained interactions and competition with fisheries (Nelms et al. 2021, Jog et al. 2022). Notable examples include North Atlantic right whales (*Eubalaena glacialis*) (Kenney 2018); vaquita (*Phocaena sinus*) (Jaramillo-Legorreta et al. 2019); monk seals (*Monachus monachus*); and Australian (*Neophoca cinerea*) and New Zealand (*Phocarctos hookeri*) sea lions (Hamer et al. 2013, Chilvers and Meyer 2017). These potential population- and ecosystem-level impacts of fisheries represent a fundamental challenge to ecosystem-based fisheries management (Jog et al. 2022).

Fisheries observer programmes are the most effective means of understanding the frequency and extent of interactions between marine mammals and fisheries (Lewison et al. 2004, Gilman et al. 2017). These programmes involve the deployment of trained scientific observers on fishing vessels to monitor and quantify direct interactions with non-target species during fishing operations. Observer surveys are a valuable source of data, generating reliable and accurate information about the nature of marine mammal interactions with fisheries, which can be used to inform marine conservation and management efforts (Hazen et al. 2018, Roda et al. 2019). However, observer programmes are also both logistically and financially intensive to run, precluding their widespread implementation (Gilman et al. 2014). As a consequence, many observer programmes are constrained by low observer coverage (i.e. the proportion of fishing effort monitored by trained personnel), which hampers the utility and application of these data (Wakefield et al. 2018, Mannocci et al. 2020). Insufficient observer coverage across fishing fleets can result in significant data gaps and blind spots, potentially yielding inaccurate or misleading estimates of marine mammal interactions with fisheries. This ultimately affects modelling efforts that seek to quantitatively assess the ecological factors underpinning marine mammal-fishery interactions (Gilman et al. 2014).

The Falkland Islands, located in the South Atlantic Ocean over the Patagonian Shelf, are a hotspot for marine biodiversity and considered to have one of the most productive marine ecosystems in the world (Belkin et al. 2009, van der Grient et al. 2023). For example, the Falkland Islands are home to a diverse range of higher-order marine predators, including a globally significant (> 50%) South American fur seal (*Arctocephalus australis*; hereafter ‘SAFS’) population and other resident pinniped species (i.e. South American sea lions; *Otaria flavescens*; hereafter ‘SASL’) (Baylis et al. 2017, 2019a, b). Patagonian longfin squid (*Doryteuthis gahi*; hereafter ‘Loligo’) are a regionally dominant species that play a fundamental role in the Falkland Islands ecosystem structure and composition (van der Grient et al. 2023, Büring et al. 2024). As a key prey item for the Patagonian Shelf pinniped and seabird community (Thompson et al. 1998, Putz et al. 2001, Baylis et al. 2014, Kuepfer et al. 2023, Büring et al. 2024), Loligo supports a significant predator biomass (Baylis

et al. 2021). Additionally, Loligo resources within the Falkland Islands form the basis of a substantial squid fishery (Arkhipkin et al. 2015b, 2021). In this highly productive and lucrative commercial bottom trawl fishery, catch can exceed 90 000 t annually (Fisheries Department Fishery Statistics 2022). These fishing efforts play a major role in sustaining global squid markets (Ospina-Alvarez et al. 2022), and in turn, comprise a substantial proportion of the Falkland Islands’ GDP (Arkhipkin et al. 2021, Fisheries Department Fishery Statistics 2022).

Despite the trophic overlap between seals and the commercial Loligo fishery in the Falkland Islands, historically, seal-fishery interactions have been regarded as a rare and uncommon occurrence (only 13 mortalities recorded between 1998 and 2016) (Iriarte et al. 2020). However, in recent years, there has been a sudden and unprecedented increase in seal-fishery interactions. In 2017, seal bycatch dramatically increased by ~900% ($n = 140$ seal mortalities recorded in a single year) (Iriarte et al. 2020). In response to this conservation and management concern, the Falkland Islands Government and the fishing industry implemented a raft of monitoring and mitigation measures. All trawl vessels operating within the Falkland Islands Loligo fishery are now required to have seal exclusion devices (SEDs) fitted to nets. The SEDs comprise an additional section of netting between the trawl lengthener and cod-end, with an angled metal grid designed to prevent seals from entering the cod-end, and instead, redirecting them to an open escape hatch at the top of the net (Iriarte et al. 2020). Additionally, observer coverage on these trawl vessels increased from ~10% to 100% in 2018, making it the only bottom-trawl fishery in the Southwest Atlantic with full observer coverage (Iriarte et al. 2020, Arkhipkin et al. 2021). While the introduction of SEDs has significantly reduced the number of seal mortalities within the Loligo fishery, seal-fishery interactions remain at high levels today. Evidence suggests interactions are also an emerging issue in the finfish trawl fishery, which currently has a low (~10%) observer coverage (Fisheries Department Fishery Statistics 2022). The ecological mechanisms driving this sudden increase in seal-fishery interactions remain a mystery. However, data available from complete observer coverage of the Loligo fishing fleet presents a valuable research opportunity to examine the mechanisms associated with high rates of seal-fishery interactions.

In this study, we investigate the factors underpinning seal-fishery interactions in the Falkland Islands bottom trawl fishery within recent years. We utilise fisheries observer data collected over a 5-year period (2018–2022) from the Loligo trawl fishery, documenting the occurrence, location, and nature of seal-fishery interactions. Observer records are integrated with trawl-by-trawl data from vessel logbooks and remotely sensed environmental information to quantitatively examine the spatiotemporal, operational, and oceanographic factors associated with seal-fishery interactions. We also compile long-term (> 20 years) fisheries catch data from both the Loligo and finfish trawl fishery to assess spatial patterns in fishing activity and stock dynamics, which may have influenced the sudden increase in seal-fishery interactions. Through this research, we provide an improved understanding of the mechanisms driving seal-fishery interactions in the Falklands Islands, supporting long-term sustainability and marine management objectives of the Falkland Islands fishery.

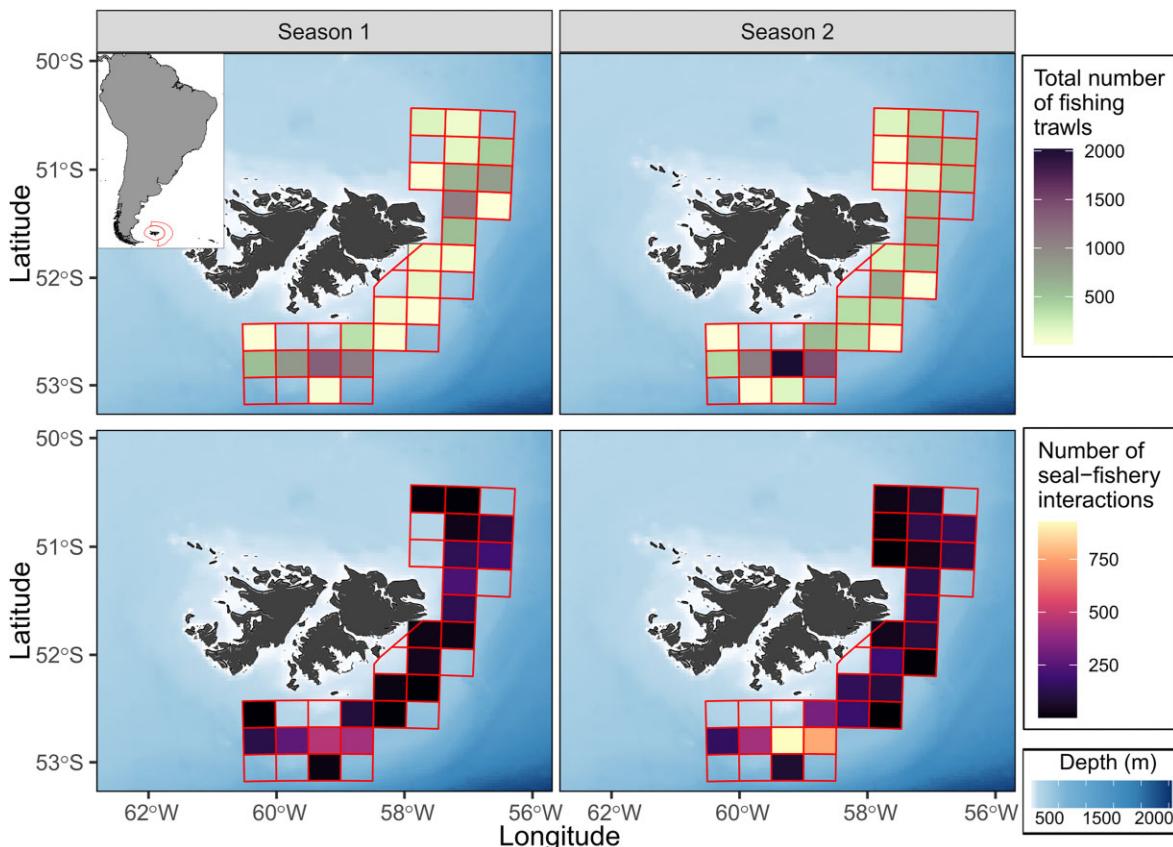


Figure 1. Spatial summary of seal-fishery interactions in the Loligo Box (red boundary of main panels) derived from observer records. To aid visual presentation, data are gridded at a 0.25° latitude \times 0.50° longitude resolution. Data over the 5-year period (2018–2022) are aggregated and displayed separately for season 1 (February–May) and season 2 (July–October). Inset panel in the top left displays the Falkland Islands and the Exclusive Economic Zone (red) boundary within the region.

Materials and methods

Study area and fishery description

Loligo is a small and abundant demersal squid species that inhabits waters around the Falkland Islands. Their population dynamics are influenced by a suite of complex oceanographic features (Arkhipkin et al. 2004b, 2006, 2013). Juveniles use shallow inshore areas as nursery grounds and migrate to deeper offshore waters at the shelf edge to feed. Upon maturation, adults return to inshore waters to spawn and eventually die. While in offshore feeding grounds, Loligo form dense aggregations, particularly in the Loligo Box—the designated Loligo fisheries management area extending south to northeast of the Falkland Islands ($\sim 18\,000\text{ km}^2$) where target trawling for Loligo is permitted in the Falklands Exclusive Economic Zone (hereafter ‘EEZ’, but locally known as the ‘Conservation Zone’) (Fig. 1) (Arkhipkin et al. 2004b, van der Grient et al. 2023). Waters in the Loligo Box are predominately associated with the eastern branch of the northward-flowing Falkland Current, which is derived from the Antarctic Circumpolar Current flowing through the Drake Passage. The Falklands Current is comprised of Subantarctic Surface (SAWS; $< 300\text{ m}$ depths) and Antarctic Intermediate Water Mass (AAIW; $> 300\text{ m}$ depth), which deliver cold water onto the Falklands Shelf. Mixing between the SASW and shelf waters forms cyclonic and anticyclonic eddies around the Falkland Islands, which intensify and weaken over the summer and winter months, respectively. The upwelling associated with

these eddies brings nutrient-rich deep waters to the surface and creates seasonal mesoscale fronts with strong temperature gradients (Arkhipkin et al. 2013, Song et al. 2016, van der Grient et al. 2023). These factors contribute towards the Loligo Box being a critical foraging habitat for Loligo, which in turn, supports resident pinniped populations and a thriving Falkland Islands squid fishery (Arkhipkin et al. 2004b, Agnew et al. 2005, Baylis et al. 2014, Fisheries Department Fishery Statistics 2017, Riaz et al. 2023).

The Loligo fishery dominates trawl activity within the Falkland Islands EEZ. It is characterised by two fishing seasons that occur between February and May (season 1) and July and October (season 2). The timing of these two fishing seasons corresponds with the seasonal migration patterns of the two different Loligo spawning cohorts (Autumn and Spring, respectively) during their short 1-year life span (Patterson 1988, Arkhipkin et al. 2004a, van der Grient et al. 2023).

In contrast, the finfish trawl fisheries operate year-round and are comprised of both resident and straddling stocks (i.e. shared distribution with neighbouring South American jurisdictions). A diverse range of species are caught in the finfish trawl fisheries, including but not limited to southern blue whiting (*Micromesistius australis australis*), red cod (*Salilota australis*), hake (common: *Merluccius hubbsi* and southern: *Merluccius australis*), and longtail southern cod (*Patagonotothen ramsayi*; hereafter ‘rock cod’) (Fisheries Department Fishery Statistics 2022). Finfish trawl operations are largely

Table 1. Summary of operational, spatiotemporal, and environmental predictors corresponding to the date and location of each trawl that recorded seal-fishery interactions.

Covariate type	Predictor	Description
Operational	Catch quantity	Total catch quantity (kg) of <i>Loligo</i> recorded for each trawl
	Trawl duration	Total duration (mins) of each trawl occurring within the <i>Loligo</i> Box
	Catch per unit effort (CPUE)	Catch quantity \div Trawl duration
Spatiotemporal	Trawl location	Latitudinal coordinates of the end trawl position. Latitude was considered an appropriate metric of trawl location given the north-south geometry of the <i>Loligo</i> Box positioned over the shelf-break
	Vessel clustering (near-real-time)	For each trawl, we calculated how many other trawling operations occurred within a 20 km distance and a 5-h window
	Vessel clustering (time lag)	As for the near-real-time clustering, although within a 24-h time window
	Distance to land	Vessel straight-line distance (km) to nearest land feature, indicative of possible seal resting area
	Time of year	Calendar month (1–12) vessel trawl activity occurred
	Sea surface temperature (SST)	Measured daily ($^{\circ}$ C) at a 0.01 $^{\circ}$ spatial resolution
Environmental	Sea surface height (SSH)	Measured daily (m) at 0.25 $^{\circ}$ spatial resolution
	Bathymetry (BATH)	Sea floor depth (m) at a 0.02 $^{\circ}$ spatial resolution
	Bathymetry slope (BSlope)	Gradient ($^{\circ}$) of the sea floor calculated from bathymetry data (0.02 $^{\circ}$ spatial resolution)

concentrated in the western area of the Falklands Islands EEZ (Riaz et al. 2023), influenced by complex frontal features detailed elsewhere (Arkipkin et al. 2013).

Fisheries observer data

Data on seal-fishery interactions from all trawl operations within the EEZ were obtained from observer data provided by the Falkland Islands Fisheries Department (FIFD). These data were recorded over a 5-year period from 2018 to 2022. Since 2018, the Falklands Islands *Loligo* fishery has had 100% observer coverage (i.e. 1 observer deployed on each vessel in the fleet) as part of the FIFD's Marine Mammal Observer Programme. Observers are trained to record and broadly describe the occurrence of seal-fishery interactions during trawl operations. Due to low observer coverage (~10%) across the finfish trawl fleet, observer records from this fishery were excluded from our analysis.

To ensure our dataset was restricted to records of direct seal interactions within the *Loligo* fishing fleet, we retained records indicative of bycatch and net entanglement (i.e. incidental capture); foraging from or around the net and discard chute; and actively following trawl nets or vessels during trawl operations. Hereafter, we collectively refer to these as 'seal-fishery interactions'. All subsequent data processing and analyses were performed using R statistical software (R Core Team 2022). We matched observer records of seal-fishery interactions with vessel logbook records, which contained trawl-by-trawl information detailing trawl start and end locations and times. Logbook records also included information on the total duration (mins) and catch quantity (kg) of each trawl. All trawls over the 5-year period were marked with either 1 or 0 based on the presence or absence of a direct seal-fishery interaction event. This presence–absence approach was considered pragmatic for our purposes to broadly explore mechanisms underpinning direct seal-fishery interactions. Species-level identification of seals were not available for all types of documented seal-fishery interactions, and consequently, our study focused on broadly assessing the drivers of all pinniped interactions with the *Loligo* trawl fishery.

Modelling variables

To examine the influence of different parameters on seal-fishery interaction events, we extracted and calculated a range of variables associated with trawl activity (Table 1). Broadly, we sought to obtain a suite of explanatory variables that could be reasonably expected to influence seal foraging behaviour and at-sea decisions to interact with trawl operations. Operational variables included total catch quantity of trawls (kg), trawl duration (mins), and catch per unit effort (CPUE; see Table 1 for details). Spatiotemporal variables included trawl location (latitudinal position), distance to land and month of year. These spatiotemporal variables were all based on the trawl end location and timestamp—which was considered practical given that (i) observer data did not pinpoint precise space-time detail during trawls and (ii) seal-fishery interactions often occur during haul operations at the end of trawls (Iriarte et al. 2020).

Additionally, we calculated two vessel clustering indices, which included the number of trawl operations occurring within a 20 km radius of any given trawl location within a time period of (i) 5 h and (ii) 24 h. The purpose of these clustering indices was to assess whether seals were attracted to aggregations of vessel activity in near-real time and with a time delay. Our 5-h time threshold was based on the mean duration of trawls across the fishing fleet ($5 \text{ h} \pm 2 \text{ h}$). Our 20 km clustering distance was chosen as a reasonable measure of proximity to vessels based on SAFS foraging trip characteristics and localised foraging behaviour (Thompson et al. 2003, Riaz et al. 2023). In addition to these operational and spatiotemporal variables, we also compiled a suite of environmental parameters associated with each trawl using the 'raad-tools' package (Sumner 2020). We extracted sea surface temperature (SST), sea surface height (SSH), bathymetry (BATH), and bathymetric slope (BSlope) (refer to Table 1 for details). These environmental variables have previously been used to predict species distribution of Falkland Islands pinniped populations (Baylis et al. 2019b) and are also variables known to mediate prey availability and influence the movement and foraging behaviour of air-breathing marine predators (Bost et al. 2009, Wakefield et al. 2011, Scales et al. 2014, Massie et al. 2016, Reisinger et al. 2018, Green et al. 2020).

Statistical analysis

Using the full integrated dataset (presence–absence of seal interactions based on observer data integrated with operational, spatiotemporal, and environmental information), we examined the relationship between the occurrence of seal-fishery interaction events (1 = seal-fishery interaction event or 0 = no seal-fishery interaction event) and the full suite of predictor variables compiled using generalised additive mixed models (GAMMs). Models were fitted with a binomial distribution using the ‘mgcv’ package (Wood 2023). We considered GAMMs to be an appropriate modelling approach to account for the complex (non-linear and linear) relationships expected between seal foraging behaviour and the suite of spatial, environmental, and fisheries operational variables examined (Bradshaw et al. 2004). To explicitly examine season-specific relationships, we configured separate models for seal-fishery interactions occurring between the two different fishing seasons.

Before modelling the data, we first inspected correlation coefficients of all predictor variables to assess collinearity issues. Across both fishing seasons, there was a consistent and strong correlation (correlation coefficient > 0.70) between several operational and spatiotemporal predictor variables (Fig. S1) (Wei et al. 2017). Consequently, we decided to exclude the near-real-time (< 5 h) clustering metric, distance to land, and CPUE from our analysis, which were highly correlated with the delayed (< 24 h) clustering metric, latitude, and catch quantity, respectively. The decision to retain total catch quantity within the model configuration was based on the fact that seal-fishery interactions occur during haul operations at the end of trawls (Iriarte et al. 2020), where nets represent a dense aggregation of catch accumulated over space and time.

For both seasons separately, we then fit GAM models with the selected predictor variables. Our spatial vessel clustering metric and both operational variables (catch quantity and trawl duration) were fit as linear parametric terms based on expectations that seals would increase foraging effort in areas associated with increased fishing effort and activity (Allen et al. 2014, Riaz et al. 2023). Both operational variables were also scaled to aid model convergence (‘datawizard’ package; Patil et al. 2022). All other spatiotemporal and environmental variables were configured as non-parametric smooth terms to account for non-linear expectations (Žydelis et al. 2011, Santora et al. 2014, 2017, Baylis et al. 2019b, Carpenter-Kling et al. 2020). Month and SST were configured as a tensor product, fit with a cyclical spline basis function to account for their inherent temporal interaction (Pedersen et al. 2019). All other smooth terms were configured with thin plate regression splines. Models were fitted with a REML estimation method with shrinkage and null space penalisation (Marra and Wood 2011). We also configured each combination of vessel ID and Year as a random effect to account for variability between inter-annual trawling operations.

With these season-specific model fits, we then assessed issues of multicollinearity among parametric variables and concurvity among non-parametric variables. Parametric terms in both models (catch quantity, trawl duration, and vessel cluster) were deemed to have collinearity issues [variance inflation factors (VIF) > 5]. Dropping single parametric model terms (i.e. one of the three terms) and refitting the model did not resolve collinearity issues. Therefore, trawl duration and the vessel clustering metric were both dropped from the models.

The decision to retain catch quantity was based on previous work linking this variable with seal foraging effort in the Falkland Islands EEZ (Riaz et al. 2023). Following inspection of model concurvity estimates among non-parametric environmental variables, we also decided to drop bathymetry (concurvity > 0.6), which was approximated by latitude and BS-slope. For the two final model configurations, covariates were considered significant at P -values < 0.05 .

Spatial changes in fishing effort

Effective management of seal-fishery interactions at the Falkland Islands requires an understanding of the root causes, particularly given the rapid onset of the problem since 2017. Therefore, we also investigated long-term patterns of fishing operations within the Falkland Islands EEZ to identify factors that may have influenced the dramatic increase in seal-fishery interactions. Spatially gridded catch data of all bottom trawl fishing operations (Loligo and finfish) within the Falkland Islands EEZ were obtained from FIFD between the years 2003–2022. Catch data were provided at 0.25° latitude $\times 0.50^\circ$ longitude resolution—which is the spatial resolution of management units used by FIFD. To assess changes in fisheries catch composition and the spatial distribution of trawl operations over time, we calculated the annual total fishing catch quantity for Loligo and the dominant finfish catch species that have historically comprised the Falkland Islands finfish fishery. This includes southern blue whiting, rock cod, and hake (Fisheries Department Fishery Statistics 2022)—all of which play an important role in SAFS and SASL diet (Baylis et al. 2014). Although southern blue whiting and hake are straddling stocks with multi-jurisdictional annual cycles, trends in fisheries catch data within the Falkland Islands EEZ are expected to provide a broad indication of fishing patterns and overall stock dynamics (Laptikhovsky et al. 2013, Arkhipkin et al. 2015a, Fisheries Department Fishery Statistics 2022). To visualise long-term trends and patterns in the Falkland Islands fishery, we aggregated catch data into 4-year time blocks. This temporal aggregation was considered robust in capturing broad spatiotemporal patterns within the time series when visually compared to shorter time scales (i.e. 1 and 2-year blocks).

Results

Loligo fishery characteristics

Over the 5-year period, 21 097 individual trawls were recorded in the Loligo Box, with Loligo total catch quantity exceeding 320 000 t. Trawl activity was recorded throughout the spatial extent of the Loligo Box, but was most pronounced in the southern-most area (Fig. 1; Fig. S2). Operational variables marginally differed between seasons. Trawls in season 1 and season 2 accounted for 42% ($n = 8878$) and 58% ($n = 12 219$) of all trawl activity recorded, respectively. On average, trawls during season 1 recorded higher catch quantities than season 2 trawls (20 192 and 11 916 kg, respectively). Similarly, CPUE was also substantially greater in season 1, recording 92 kg/min compared to the 41 kg/min recorded in season 2 (Table 2 for means \pm SD).

All spatiotemporal and environmental variables were broadly similar between both Loligo fishing seasons, except SST, which displayed a marked seasonal variation consistent

Table 2. Summary statistics of the various operational and environmental variables examined.

Predictor variable	Season 1		Season 2	
	Range	Mean \pm SD	Range	Mean \pm SD
Operational				
Catch quantity (kg)	1–94 130	20 192 \pm 12 423	1–112 833	11 916 \pm 10 229
Trawl duration (min)	35–820	247 \pm 100	35–1165	347 \pm 146
CPUE (kg/min)	0.1–983	92 \pm 71	0.01–1277	41 \pm 55
Environmental				
SST (°C)	6.7–11.4	8.7 \pm 0.8	4.5–6.7	5.6 \pm 0.4
SSH (m)	0.2–0.5	0.4 \pm 0.04	0.2–0.5	0.3 \pm 0.04
BATH (m)	-85 to -406	-203 \pm 62	-77 to -445	-219 \pm 63
BSlope (°)	0–0.03	0.01 \pm 0.005	0–0.03	0.01 \pm 0.005

Range and mean \pm SD values over the 5-year period (2018–2022) are provided for season 1 and season 2 separately.

Table 3. Summary of bycatch events across the 5-years (2018–2022) examined.

Year	No. of capture and releases (live)			Mortalities		
	SAFS	SASL	SXX	SAFS	SASL	SXX
2018	71	18	2	16	8	0
2019	27	3	6	7	1	1
2020	50	9	1	17	2	0
2021	114	3	1	36	3	14
2022	61	4	5	13	4	9
Total	323	37	15	89	18	24

Number of live capture and releases and seal mortalities are displayed separately for each seal species. SAFS: South American fur seal; SASL: South American sea lion; SXX: Seal species not identified by observer.

with temperature changes during the autumn and spring periods (mean and range values displayed in **Table 2**).

Nature and extent of seal-fishery interactions

Across the 5 years of data, 6799 (32%) trawls were associated with seal interaction events (**Fig. 1**). A total of 2413 seal-fishery interactions were recorded in season 1, while 4386 were recorded during season 2 (27% and 36% of trawls, respectively). The occurrence of seal-fishery interaction events was consistent with this spatial pattern of fisheries trawl effort, with the southern Loligo Box being a particularly high-interaction area (**Fig. 1**; **Fig. S2**). Of all trawls recorded, 417 (2%) had reported cases of seal bycatch events, comprising of 375 live capture and releases and 131 mortalities (**Table 3**). SAFS were the main bycatch species group affected (81% of bycatch records), although there were also some records of SASL capture events (11%). The number of bycatch events varied across the 5 years examined, peaking in the year 2021 with 36 mortalities and 114 live captures and releases.

Modelling results

In both seasons, we found that a consistent set of operational, spatiotemporal, and environmental factors played a significant role in explaining the occurrence of seal-fishery interactions (**Fig. 2**; **Table 4**). In the first season, our final model configuration revealed that the probability of seal-fishery interaction events increased during trawls, which recorded higher catch quantities. These interaction events were more pronounced in the southern area of the Loligo Box between -53 and -52° . Generally, the probability of interaction events decreased with increasing latitude, albeit for a

small spike in interactions in the northeast of the Falklands at around -51° . We also found interactions were more likely to occur during trawls conducted over steeper bathymetric gradients and tended to occur more frequently during the middle of the fishing season (March–April) when SST ranged between 7°C and 11°C (**Fig. 2**; **Table 4**).

In the second season, the likelihood of a seal-fishery interaction was influenced by the same spatial and operational predictors as the first season (**Fig. 2**; **Table 4**). However, in the second season, the latitudinal gradients associated with seal-fishery interactions were more pronounced, occurring most notably over a narrow latitudinal bound at approximately -52.5° . Additionally, in the second season, SSH was deemed to be a significant predictor of seal-fishery interactions, with the probability of interactions increasing in areas characterised by low SSH. Our results indicated seals generally interact with trawl operations throughout the latter half of the second season, albeit in areas of relatively high (6°C – 6.6°C) and low (4.5°C – 5°C) SST (**Fig. 2**, **Table 4**).

Spatiotemporal trends in catch

Assessment of spatiotemporal patterns in fishing activity over a 20-year period (2003–2022) showed a relatively consistent distribution of *Loligo* catch. Across the two decades, fishing operations have primarily been concentrated in the southern (-53 to -52°) and northern (approximately -51°) areas of the Loligo Box. However, between 2018 and 2022, *Loligo* catch markedly increased (**Fig. 3**; **Fig. 4**). Our results also show evidence of dramatic changes within the Falkland Islands finfish fishery, with each 4-year time period showing differing patterns in species catch composition (**Fig. 4**; **Figs S3–S5**). Blue whiting catch was distributed in the western area of the EEZ and throughout the Loligo Box until 2012. Then finfish catch was dominated by rock cod between 2013 and 2016, primarily concentrated in the western area of the EEZ with some catch also recorded in the Loligo Box. Low rock cod catches were recorded from 2018, with finfish operations trawl effort becoming hake-dominated.

Discussion

Leveraging a unique dataset of seal-fishery interactions derived from a dedicated fisheries observer programme, we quantitatively examine the spatiotemporal, environmental, and operational factors underpinning seal-fishery interactions within the Falkland Island *Loligo* squid fishery. Importantly,

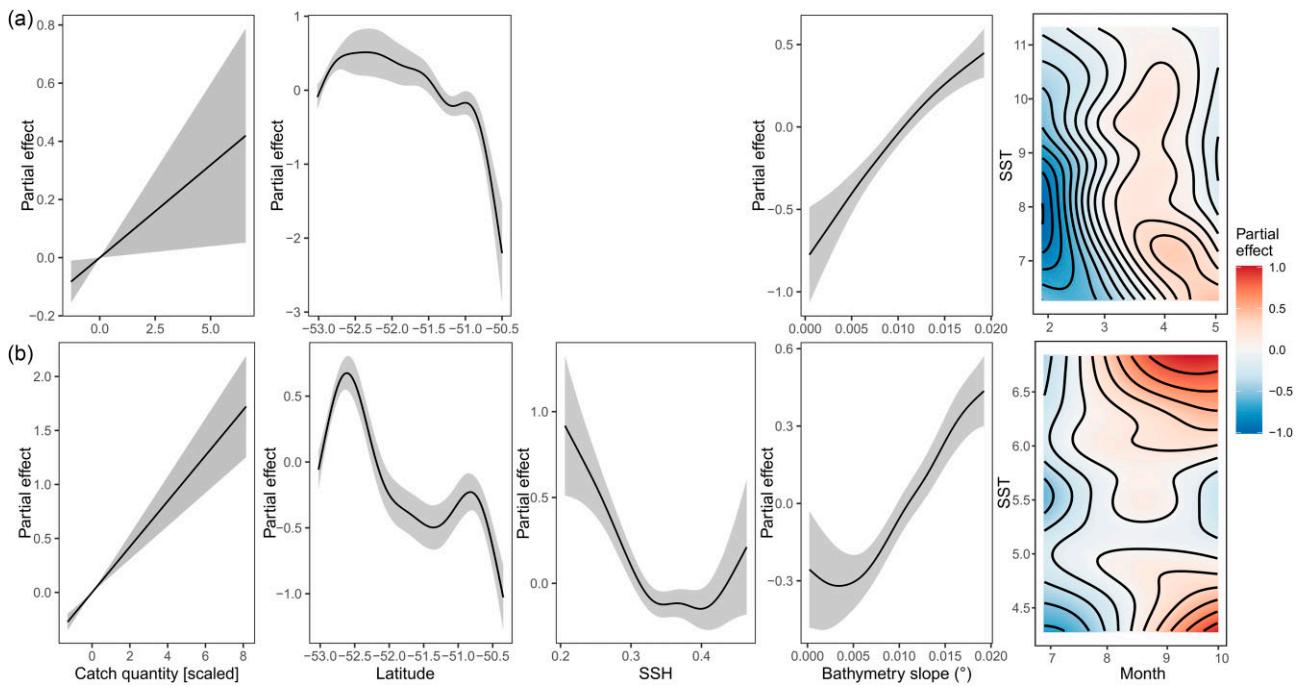


Figure 2. Partial residual plots showing the smooths of significant model terms from seal-fishery interactions GAMM configurations. Panels (A) and (B) represent model results for the first and second seasons, respectively. See Table 4 for full model results. The far-right panels display partial effects of SST in relation to month of year (configured as a tensor product in models). All other panels display partial effects in relation to model smooth terms (model fit and 95% confidence interval displayed by thick black lines and grey shading, respectively).

Table 4. Summary output final GAMMs for season 1 and season 2 seal-fishery interaction models.

Model formula	Parametric and Non-Parametric Coefficients				
		Est	SE	z-value	P-value
$\sim \text{Catch quantity} + s(\text{Latitude}) + te(\text{Month}, \text{SST}, bs = c('cc', 'tp')) + s(\text{SSH}) + s(\text{BathySlope}) + s(\text{YearID}, bs = 're'), \text{method} = \text{'REML'}, \text{family} = \text{'binomial'}, \text{knots} = \text{list}(\text{Month} = c(0, 4)), \text{select} = \text{TRUE})$	Intercept	-1.26	0.13	-9.97	<.0001
	Catch quantity	0.08	0.03	2.64	<.01
	EDF		RefDF	Chi.SQ	P-value
	s(Latitude)	6.05	9	177.64	<.0001
	te(Month, SST)	13.35	36	316.13	<.0001
	s(SSH)	0.01	11	0.01	0.44
	s(BathySlope)	1.13	9	96.27	<.0001
s(YearID)	57.54	67		541.59	<.0001
		Est	SE	z-value	P-value
	Intercept	-0.77	0.15	-5.09	<.0001
	Catch quantity	0.19	0.03	6.39	<.0001
	EDF		RefDF	Chi.SQ	P-value
	s(Latitude)	6.78	9	814.5	<.0001
	te(Month, SST)	12.77	39	163.1	<.001
s(SSH)	4.20	9		176.8	<.0001
	s(BathySlope)	2.73	9	122.8	<.0001
	s(YearID)	73.97	79	1364.6	<.0001

Predictor variables with significant P-values are displayed in bold text.

the work presented here underscores the value of extensive and well-coordinated observer programmes in supporting quantitative modelling of interactions between fisheries and non-target species. Our study demonstrates seal-fishery interactions are a common and significant management challenge for the Loligo fishery. The spatial and operational components of the Loligo fishery play a key role in influencing seal-fishery interactions, with interactions most frequently occurring in the southern Loligo Box (i.e. where fishing activity is primarily concentrated) and during trawls associated with

high catch quantities. Compiling long-term fisheries catch data, our study suggests a significant increase in Loligo catch yield, in conjunction with successive collapses in other mid-trophic level finfish stocks (i.e. blue whiting and rock cod). This may have increased pinniped reliance on Loligo resources, resulting in resource competition and increased seal-fishery interactions. An increased seal population in the Falkland Islands (compared with historical population surveys) lends support to this hypothesis. In this context, a transition from single-species stock assessments

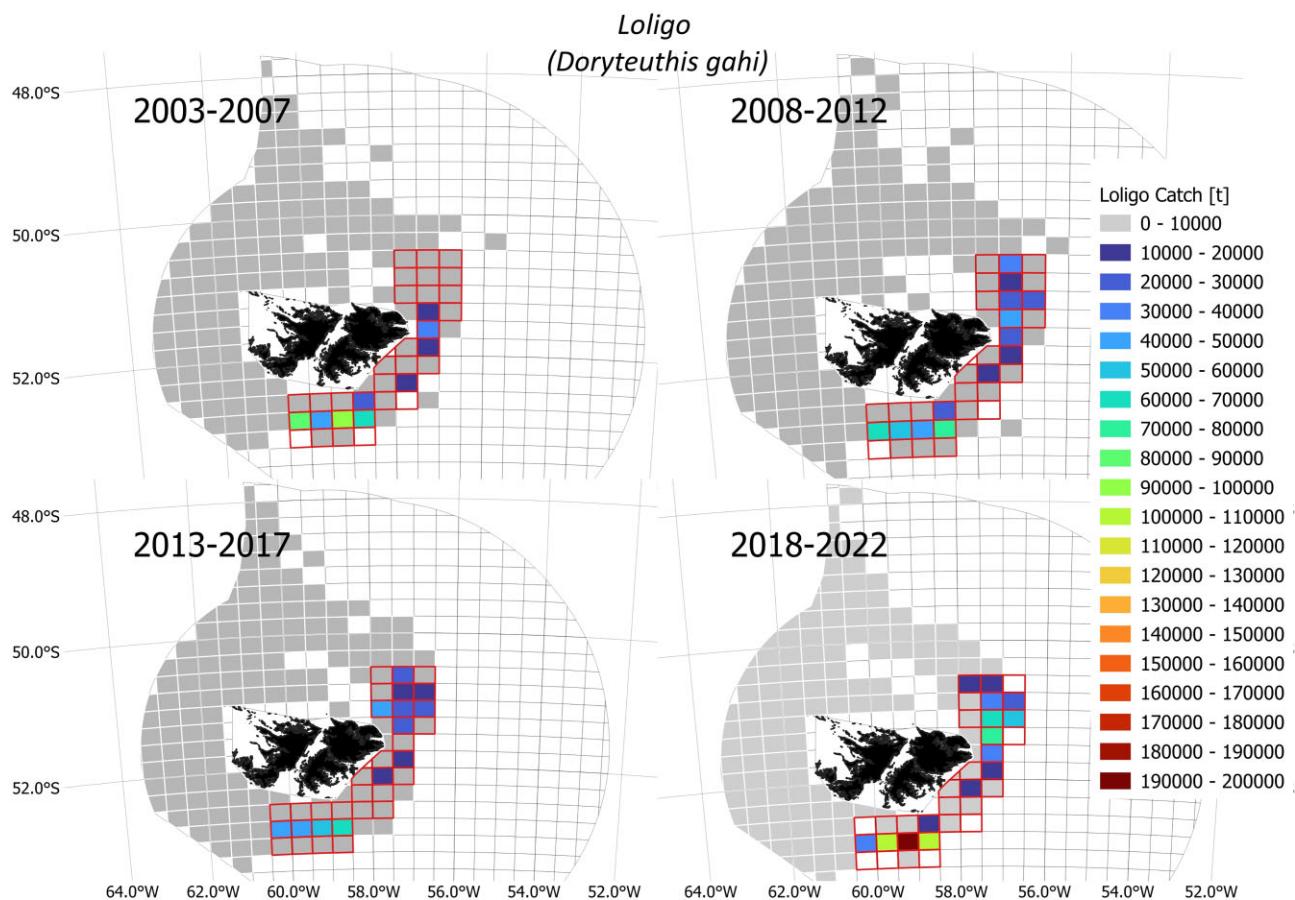


Figure 3. Spatial distribution of total Loligo catch quantity over time (2003–2022). To aid interpretability of long-term trends in historical catch records, data were aggregated and summarised into 4-year bins at a 0.25° latitude \times 0.50° longitude resolution. Refer to the ‘Materials and methods’ section for further details.

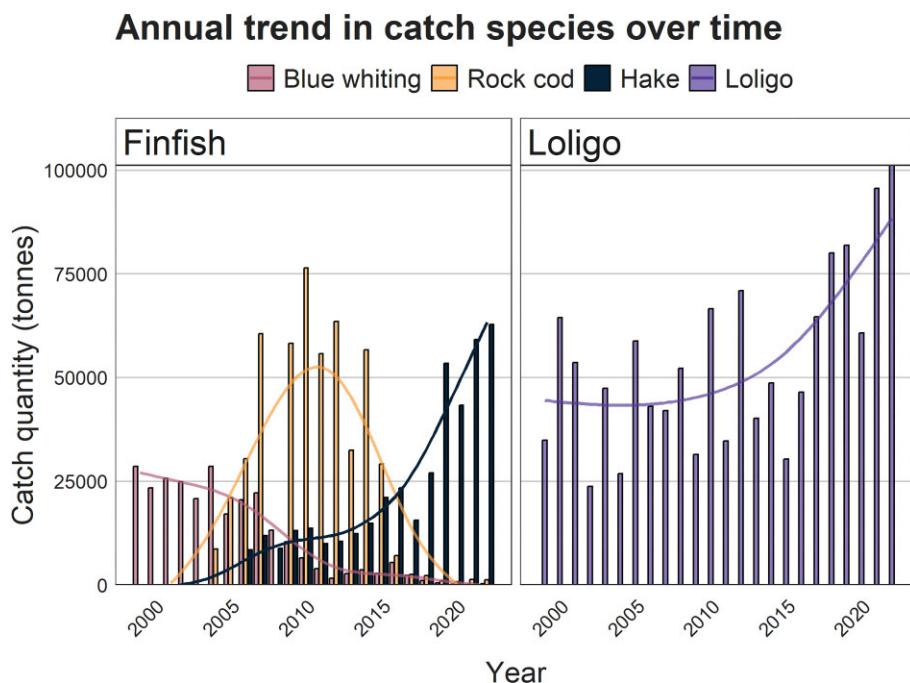


Figure 4. Annual trend in catch quantity over time for the Falkland Islands Loligo and finfish fishery. Finfish species presented comprise the three main catch groups—blue whiting, rock cod, and hake. A cubic spline trend line is co-plotted with annual catch data (vertical bars).

and harvesting frameworks to ecosystem-based fisheries management—which considers the trophic effects of fishing practices and enables consideration of bioenergetics—may be an essential tool in mitigating seal-fishery interactions.

Extent of seal-fishery interactions

Seal-fishery interactions are a prevalent issue within the *Loligo* fishery. Direct interactions between seals and fishing vessels were relatively common (i.e. foraging from the net or actively following the vessel), occurring in 32% of trawls. Of these, more than 500 bycatch events (mortality and net captures) were recorded over a 5-year period between 2018 and 2022, primarily involving SAFS. However, these seal bycatch events were relatively infrequent (2% of all trawls). These findings indicate SEDs, which were introduced in 2017, are effective in reducing bycatch and associated mortality events within the Falkland Islands *Loligo* fishery (compared to pre-SED bycatch rates presented in Iriarte et al. 2020). However, importantly, seal mortality still occurs, and other forms of seal-fishery interactions remain a significant and consistent problem. This potentially indicates an issue of underlying resource competition between seals and the *Loligo* fishery. While seal-fishery interactions could also be prevalent within the finfish fishery, limited observed coverage (~10%) across the finfish fleet hinders our quantitative and risk assessment capacity. Greater observer coverage and reporting precision across all bottom-trawl fishing operations (*Loligo* and finfish) within the Falkland Islands EEZ is required for a more integrated and holistic understanding of this conservation and management issue.

Predictors of seal-fishery interactions

Across both seasons, we found interactions were most pronounced in the southern *Loligo* Box. This area is regarded as one of the most productive regions of the Patagonian Shelf, hosting predictable aggregations of macrozooplankton and newly recruited fish and squid (Croxall and Wood 2002, Agnew et al. 2005, Lee et al. 2021, Fisheries Department Fishery Statistics 2022). It is also a critical foraging habitat for SAFS at the Falkland Islands and a focal area of *Loligo* fishing activity where disproportionately high catch yields occur (Riaz et al. 2023). The spatiotemporal and trophic overlap between SAFS foraging effort and commercial fishing activity in the southern *Loligo* Box likely plays a key role in influencing seal-fishery interactions. Spatially concentrated fishing activity in this area may also explain why the probability of seal-fishery interactions was greater during high catch quantity trawls performed over steeper bathymetric gradients. This is because of the steep shelf slope over the southern *Loligo* Box, which drives strong upwelling of nutrient-rich waters, creating enhanced primary productivity and attracting dense aggregations of *Loligo* (Arkhipkin et al. 2013).

Although there were consistent spatial and operational predictors of seal-fishery interactions across both seasons, our model results suggest a complex seasonal influence of SST. During season 1, seal-fishery interactions appeared to be largely influenced by time, occurring with the greatest frequency during the middle of the fishing season (March–April). In contrast, during season 2, seal-fishery interactions occurred throughout the second part of the fishing season (August–October) in waters associated with high and low SST. These results may be explained by complex and seasonally variable oceanographic drivers governing *Loligo* abundance and dis-

tribution around the Falkland Islands. Throughout the year, the 5.5°C isotherm marks the limit of *Loligo* distribution into deeper waters. During the first fishing season (February–April), squid stay shallower at temperate (9°C–10°C) surface waters of the Transient Zone, located at 50–125 m depth in summer, with mixing of pre-mature individuals from the autumn spawning cohort and juvenile individuals of the spring spawning cohort (Arkhipkin et al. 2004b). In contrast, during the second fishing season, warm intermediate near-bottom waters (~150–250 m) limit *Loligo* distribution within the water column, with colder water layers above and below restricting their vertical movements (Arkhipkin et al. 2004b). These water layers during winter might also be a refuge for prey species of *Loligo* (Büring et al. 2021, 2023). The temporal- and temperature-mediated aggregations of *Loligo* during both fishing seasons may result in profitable foraging conditions for seals, and in turn, may be an important factor influencing seal-fishery overlap, interaction, and competition.

Similarly, our model results found low SSH was an important predictor of seal-fishery interactions during the second fishing season. As a proxy for shifting frontal systems (Sokolov and Rintoul 2007) and nutrient upwelling (Moore and Abbott 2000), SSH is commonly used to infer regions of high biological activity (Moore and Abbott 2000, Bost et al. 2009). Both negative and positive SSH anomalies can be signs of eddies (Liu et al. 2021). The Falklands Current, mesoscale eddies, and other frontal features are thought to influence *Loligo* distribution patterns—particularly within the southern *Loligo* Box, where there is a high degree of inter- and intra-annual variability in the position and intensity of these oceanographic features (Arkhipkin et al. 2004b, Belkin et al. 2009, van der Grient et al. 2023). Several pinniped species in the Southern Ocean are known to forage in close association with mesoscale eddies and frontal features (Bost et al. 2009). In this context, it is somewhat surprising SSH was not a significant predictor of seal-fishery interactions during the first fishing season as well. This may be an artefact of seasonal variation in the position and intensity of the Falklands Current (van der Grient et al. 2023). In the absence of fine-scale information about eddy formations and primary productivity at the Falkland Islands and the subsequent effect on *Loligo* cohorts, it is unclear which biophysical and time-varying features of SSH influence the occurrence of seal-fishery interactions within the *Loligo* Box. Further research is required to improve understanding of the oceanographic drivers of *Loligo* abundance and availability between fishing seasons, which in turn, can be used to support inferential and predictive seal-fishery interaction modelling efforts.

Long-term ecosystem trends and implications for management

The findings of this study have important management implications and can help to support the long-term sustainability objectives of the Falkland Islands pertaining to fisheries and the marine environment. Our results illustrate commercial fisheries have likely played a pivotal role in shaping and changing the Falkland Islands ecosystem over the past 20 years (Fig. 4; Figs S3–S5). The spatial changes in finfish structure and composition showcased here (Fig. 4; Figs S3–S5) may have had a significant impact on SAFS and SASL foraging success, acting as a driver of competitive interactions

between seals and commercial trawl operations in the Loligo Box.

The Loligo fishery is managed using in-season/real-time depletion models, which ensures at least 10 000 t of Loligo are allowed to escape capture and spawn. While this escapement biomass threshold has limited biological justification, it has been used for over 20 years and has proven to be highly effective in managing the Loligo stock (as evidenced by the increasing trend in Loligo stock abundance and biomass) (Fig. 4). However, challenges in managing mixed fishery assemblages and obtaining accurate discard data have resulted in the over-exploitation of blue whiting and rock cod within the Falkland Islands EEZ (straddling and resident stocks, respectively). As planktivorous mid-trophic level keystone species, integral to the Falkland Islands' wasp-waist (i.e. middle-out ecosystem control mediated by a few species) ecosystem dynamics (Laptikhovsky et al. 2013, Ricciardelli et al. 2020, van der Grient et al. 2023, Büring et al. 2024), stock reductions have caused radical changes in ecosystem structure and functioning in recent years (Laptikhovsky et al. 2013, Fisheries Department Fishery Statistics 2022, Riaz et al. 2023). Blue whiting and rock cod stocks were depleted in ~2007 and ~2016, respectively—the latter coinciding with the rapid onset of seal-fishery interactions within the Falkland Islands. Both finfish species were regarded as important components of SAFS diet (Baylis et al. 2014). Declines in their abundance may be constraining the availability of mid-trophic level foraging resources (Büring et al. 2024), forcing high-order marine predators like SAFS and SASL to rely more heavily on other mid-trophic level resources, such as Loligo squid. Further, the sequential decline in blue whiting and rock cod abundance may be allowing short-lived, adaptable species like Loligo, to expand into the niche previously held by these finfish species (Doubleday et al. 2016). While hake have dramatically increased in abundance since the collapse of rock cod stocks in ~2016, they are likely not an equivalent dietary substitute because they (i) are a predator species occupying a higher trophic position; (ii) are generally larger and more mobile, meaning they are more challenging to predate on; and (iii) are migratory and not always available as local foraging resources (Arkhipkin et al. 2013, 2015a, Laptikhovsky et al. 2013).

Because SAFS and SASL diets have been poorly studied in the Falkland Islands, we are unable to assess how diets have shifted in response to changes in ecosystem structure and composition. This data gap also means there is limited opportunity to integrate seal energetic requirements into Falkland Islands fisheries management. Quantitative food-web and energetic analyses are urgently required to better understand the relative importance of Loligo to SAFS and SASL diet, and importantly, how this may change over time in the context of continued fishing pressure, ecosystem change, and broad-scale projected reductions in Loligo habitat suitability (Guerreiro et al. 2023). These trophodynamic modelling efforts may support the re-evaluation of current Loligo escapement biomass thresholds using an ecosystem-based fisheries management approach that considers the energetic requirements of pinnipeds and other marine predators (Craig and Link 2023).

In addition to these mid-trophic level ecosystem changes within the Falkland Islands, it is important to consider how pinniped population dynamics may be contributing to seal-fishery interactions. Recent archipelago-wide surveys have found a 4-fold increase in SAFS population size since the last surveys conducted in the 1980s (Baylis et al. 2019a). Simi-

larly, there is evidence to suggest a gradual population growth of SASL in recent years after catastrophic population declines in the mid-1900s (Baylis et al. 2015). Local-scale expansion of pinniped populations can act as a key driver of resource competition, which may influence changes in individual-level foraging decisions and strategies (Kuhn et al. 2014). At the Falkland Islands, increased SAFS and SASL populations (compared to historical values) coupled with collapses of other mid-trophic level resources (i.e. rock cod) may be contributing to heightened resource competition with the Loligo fishery. Tracking work conducted in 2018 and 2019 demonstrated SAFS may be competing with the Loligo fishing fleet for resources (Riaz et al. 2023), but unfortunately no long-term datasets are available to examine how trends in finfish and Loligo stock dynamics have affected SAFS spatial distribution and habitat use. A key limitation of the inferential modelling framework used in this study was the absence of intrinsic (i.e. energetic requirements, sex, age, breeding status) and extrinsic (i.e. local-scale prey-field dynamics, inter- and intra-specific competition) pinniped parameters. These additional layers of model complexity are constrained by significant data and knowledge gaps regarding SAFS and SASL ecology and behaviour in the Falkland Islands. Ongoing pinniped tracking and population monitoring will be critical in further efforts to understand the nature, extent, and drivers of seal-fishery interactions at the Falkland Islands.

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Author contributions

J.R. and A.M.M.B. conceived the study; J.R. designed and performed the research; J.R. and T.B. analysed the data; J.R., T.B., and J.vd.G. wrote the paper; A.W., B.L., A.M.M.B., and P.B. provided input and comments on manuscript drafts. A.M.M.B. secured funding to support this research.

Supplementary data

Supplementary data is available at *ICES Journal of Marine Science* online.

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Data availability

All R code used in this study is publicly available at <https://github.com/Javedmoves/>. The data used in this study are available from the corresponding author and the Falkland Islands Fisheries Department upon request.

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