Male Antarctic fur seals: neglected food competitors of bioindicator species in the context of an increasing Antarctic krill fishery

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The fishery for Antarctic krill is currently managed using a precautionary, ecosystem-based approach to limiting catch, with performance indices from a long-term monitoring program focused on several krill-dependent predators that are used to track ecosystem health. Concerns over increased fishing in concentrated areas and ongoing efforts to establish a Marine Protected Area along the Peninsula, a key fishing region, is driving the development of an adaptive management system for the fishery. The cumulative effects of fishing effort and interactions among krill-dependent predators and their performance is at present neglected in the CCAMLR Ecosystem Monitoring Program. However, we show considerable overlap between male Antarctic fur seals and the krill fishery in a complex mosaic, suggesting potential for cumulative impacts on other krill dependent predators. A holistic view is required as part of future efforts to manage the krill fishery that incorporates various sources of potential impacts on the performance of bioindicator species, including the fishery and its interactions with various krill dependent predators.

Climate modifications to marine ecosystems continue unabated, accompanied by pressures to maintain ecosystem services such as fishing. This challenging combination has led to considerable concern as to how to balance resource exploitation and ecosystem resilience and health. Marine ecosystems must ideally support the needs of the guild of marine predators that rely on a resource and predation by commercial fisheries which target the same resource. Knowledge regarding the spatial and temporal overlap between natural predators and fisheries is a precursor to determining the degree and significance of any functional overlap, which can then be prioritised for management and mitigation measures, forming the basis of Ecosystem Based Fisheries Management (EBFM)1,2.

In the western Antarctic Peninsula (WAP) and Scotia Sea the diet of upper trophic marine predators is heavily dominated by Antarctic krill *Euphausia superba*, a keystone species in a short-chain food web typical to polar regions1. Historically, this region has undergone substantial modification to the food web, with uncontrolled harvesting of krill-eating whales, seals and mesopelagic fishes throughout the Southern Ocean during the nineteenth and early twentieth century. While upper trophic harvesting ended by the latter half of the twentieth century, the impacts on the WAP and Scotia Sea ecosystem from the extreme and rapid depletion and subsequent variable levels of recovery are unknown. The WAP is also undergoing rapid and nonlinear restructuring due to the impacts of a warming environment, with areas responding differently contingent on the interaction between large scale and fine scale processes interlinking meteorological, hydrographic, sea ice and primary productivity variability (e.g. Schofield et al.4). Amidst this incredibly complex and altered marine ecosystem operates the largest volume fishery in the Southern Ocean. The fishery for Antarctic krill, henceforth krill, is a mid-water trawl fishery with a catch that has increased recently to approximately 300,000 tonnes per annum. The fleet used traditional (TR) trawl gear exclusively until 2006, whereupon a continuous pumping (CP) system initially tested by Vanuatu in 2004 was introduced into the fishery by Norway5. The more modern CP trawlers are thought to be more efficient and some believe that they have a lower ecological impact than TR trawling due to their smaller ecological footprint, though this has not been empirically demonstrated5. The Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) manages the fishery in a precautionary fashion, by setting a

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Total Allowable Catch Limit of 5.6 million tonnes. However, a trigger level of 620,000 t has been set because of a lack of scientific data to ensure the fishery is precautionary. In 2009, CCAMLR introduced measures designed to reduce the spatial concentration of the catch by allocating a percentage of the trigger level to different Subareas. Furthermore, CCAMLR has mandated that the trigger level will remain in place until such time that ecosystem-based fisheries management (EBFM) strategies can be employed that will avoid harvest levels that might impact the predator-prey balance and cause irreversible damage to the marine ecosystem. Efforts to characterise the spatial footprint of the fishery have been limited to kernel density summaries of summed fishing effort over decadal time periods (e.g.67) with the exception of one study that identified temporally persistent fishing hotspots over six consecutive seasons8. Interestingly, this study proposed that the fishery should be considered another member of the krill predator guild.

Juxtaposed with efforts to achieve EBFM is the recent development of a proposal for a Marine Protected Area9 in the WAP region, comprising a suite of statically-bounded zones with a variety of different management measures. Integrating the two strategies presents a complex managerial challenge for CCAMLR; efforts to develop EBFM for the krill fishery have been underway for over 2 decades, with little progress in achieving a viable, practical solution. Several approaches have been proposed previously, all of which rely to some extent on performance signals derived from a 30+ year time series of krill predator monitoring that was initiated by CCAMLR in 198797.

The CCAMLR Environmental Monitoring Program (CEMP) currently monitors breeding krill-dependent predators, with efforts in the western Antarctic Peninsula being dominated by penguin studies. CEMP monitoring studies on Antarctic fur seals (AFS: Arctocephalus gazella) focus exclusively on adult females and their pups, on populations in the South Shetlands and South Georgia Islands. However, male AFS are a numerically abundant krill predator that is likely capable of significant competitive pressure with respect to CEMP monitored species such as chinstrap penguins. Male AFS provide no parental care to their offspring and move southwards to the South Orkney Islands, presumably to access higher quality foraging grounds once mating is complete at South Georgia11. Indeed, census data from the South Orkney Islands as far back as the late 1970’s describe a rapid increase in numbers of juvenile, subadult and nonbreeding adult male AFS12 during late January. The seasonal influx of potentially vast numbers of spatially unconstrained krill predators that are unaccounted for in current assessments could have implications for disentangling the key drivers of ecosystem processes. In the context of the WAP, these processes are often characterised by models linking predator performance indices, large-scale climate processes and fishing effort13-16, with many being underpinned by model parameter estimates that neglect male AFS below reproductive age17.

On the other hand, breeding pygoscelid penguins, such as chinstrap penguins Pygoscelis antarcticus are at their most spatially and temporally constrained in terms of at-sea foraging behavior between mid-January and mid-March. Adults must return to land frequently in order to feed growing chicks. For penguins, that must feed their young with prey items directly, this means foraging trips that last only a few hours, with adults often traveling less than 50 km to find food18.

Our study aims to characterise the four-dimensional movement characteristics of a three-predator guild of unconstrained male AFS, CP and TR trawlers. Specifically, we quantify the overlap between this predator guild in relation to potential cumulative impacts on a representative CEMP monitored predator, chinstrap penguins. We hypothesise that male AFS overlap in both time and space with the fishery and that the two fishing gear types have different spatiotemporal patterns, resulting in a mosaic of potential competitive pressures. Finally, we discuss these competitive pressures in the context of interpreting performance indices of CEMP monitored predators as bioindicators of fishing pressure.

Materials and methods

Field work for our study was conducted at Powell Island in the South Orkney Islands during the austral summer of 2015–2016 (henceforth 2016, Fig. 1). Twenty juvenile, subadult and adult male AFS were instrumented with either Sea Mammal Research Unit (SMRU) low-profile satellite relayed data loggers (SRDL, N = 18) that transmitted 6 hourly summary dive data in addition to locations, or SMRU Conductivity, Temperature and Depth loggers (CTD-SRDL, N = 2), which in addition to dive summary data also sent randomly selected CTD profiles daily19. Individual male AFS were remotely injected with an intramuscular anaesthetic (Zoletil®) at a dosage of 1.48 mg/kg estimated body mass, using a Paxarms modified 0.22 LR dart gun. Individuals who were not sufficiently drugged for safe handling were treated with a gaseous anaesthetic (Isofluorane®) at a 5% induction/0.5–1.5% maintenance level via a portable closed-circuit anaesthetics’ machine (Stinger, Advanced Anaesthesia Specialists, Sydney Australia). Electronic tags were attached on the dorsal pelage at a point midway between the foreflippers, using a two-part epoxy resin (Araldite 2012®).

Male AFS instrumentation data. Both electronic tag variants were set to transmit a signal to the ARGOS CLS satellite constellation every 40 s while at sea, providing a doppler-based estimate of location post-processed by a Kalman filter by the data provider to accuracies ranging from 250 m—10’s of km20. When tags were dry (for a predetermined period of greater than 4 h), transmission rates shifted to every 80 s for two of every 5 h, until it was again immersed in seawater, thus providing the means to partition the location data temporally for each individual between at-sea and hauled out on land. Each tag variant also recorded data on each dive performed, then processes these data onboard and transmitted 6 h summaries. Summary data included the number of dives conducted (a dive being defined as deeper than 2 m and longer than 8 s), mean and maximum dive depths and dive time (the time taken from departing the surface until returning to it). Only days with complete summary data available (i.e. four consecutive six hourly summaries) were used for further analysis.
Figure 1. (A) Argos satellite telemetry data from 20 adult male Antarctic fur seals between 1st January and 8th December 2016 tagged at Powell Island, South Orkney Islands. The seals were fitted with either low profile Satellite Relay Data Loggers (SRDL) with incorporated dive loggers (N = 18) or Conductivity-Temperature-Depth SRDL (N = 2). Two animals ranged as far as the eastern Ross Sea and east of Bouvetøya in the Atlantic, though the remaining 18 individuals remained within the Scotia Sea and western Antarctic Peninsula. Our study focussed on the 18 animals that remained in the key krill fishing grounds (white dashed box) within CCAMLR Statistical Subareas 48.1 and 48.2 (shown in red). (B) The most probable at-sea locations from each animal were interpolated every 2 h within a continuous state space movement model framework for each animal. Filtered location data were then subsequently fitted with a Biased Random Bridge to estimate the 95% Utilisation Distribution (UD) across the entire dataset. Data are presented as a heatmap of intensity distribution reflecting the average time spent by animals in 5 km resolution grid cells. The figure was prepared using Quantarctica 3.12 (www.npolar.no/quantarctica)59.
The seals ranged in body length from 127 to 184 cm (mean 160.9 ± 3.71 cm; Supplementary Table 1), reflect-
visualized with Ocean Data View 4.7.823 using the Data Interpolating Variational Analysis (DIVA) gridded
Spatio-temporal water temperature profiles derived from the temperature sensors on each instrument were
at Deception Island (60.57° W, 62.95° S) was calculated for each day of tracking using the R package “solarPos”.
context, environmental data in the form of daylight length and water temperature were used. Daylight length
periods in a 24 h period) as a fixed effect and each individual animal as a random effect. To place dive data into
Additive Mixed Models (GAMM), with time period nested within Julian Day (to account for multiple time
by calculating the mean cell values across all 20 individuals.

Antarctic krill fishery data. The Antarctic krill fishing season starts and ends in November and thus spans
parts of two calendar years—we henceforth refer to the fishing season by the year in which it closed. We used
the CCAMLR C1 Antarctic krill Catch and Effort dataset to summarize catch distribution for continuous pump-
ing (CP) and traditional (TR) trawlers for the 2016 fishing season and over the combined dataset spanning
2009–2018.

Statistical analyses. Male AFS instrumentation data processing. Raw telemetry data were handled in two
stages. Firstly, locations recorded by the instruments during haulout (i.e. on land) were removed so that the
remaining telemetry data represented only at-sea bouts for each individual. These locations were subsequently
processed using a continuous-time correlated random walk model21, using empirically derived error estimates
for each Argos CLS location class to create a continuous movement path model, from which location predictions
were made at 2 h intervals. Given that telemetry processing methods still have a level of uncertainty regard-
ing the true location of an individual, we choose to characterise marine habitat usage by constructing Utilisa-
tion Distributions (UD) of home range (95%) and core areas (25%). We applied Biased Random Bridges to the
modelled, predicted locations to account for serial temporal autocorrelation inherent in movement paths22 at
a resolution of 5 km to account for the remaining, post-processed uncertainty in animal locations23. We then
visualized habitat UD as a function of Intensity Distribution (the residency time in hours within 5 km grid cells)
by calculating the mean cell values across all 20 individuals.

Dive data summarized at six-hourly intervals were used as dependent variables in a series of Generalised
Additive Mixed Models (GAMM), with time period nested within Julian Day (to account for multiple time
periods in a 24 h period) as a fixed effect and each individual animal as a random effect. To place dive data into
context, environmental data in the form of daylight length and water temperature were used. Daylight length

Antarctic krill fishery data. To spatially represent the fishery, we used the reported location at which each tow
was set and assumed that this represented the true location (that is, without spatial error). We first applied a
95% Gaussian kernel weighted by catch (in tonnes) at a 5 km resolution with a 10 km search range, representing
the approximate distance of a TR trawler haul and matching the resolution of the male AFS treated telemetry
data24. As the fishery changed its location throughout the season and given that the fishery in Subareas 48.1 and
48.2 is orientated broadly along an east–west axis, we characterized its temporal evolution by the longitudinal
movement of the two fishing gear types over time. Finally, to facilitate comparison with the vertical exploitation
of habitat by male AFS, we describe the temporal change in reported trawl depths for each gear type over the
season.

Spatio-temporal overlap between male AFS, fishing gear types and chinstrap penguins. Using the generated 5 km
resolution rasters for the 2016 season fishing catch and male AFS distribution, we calculated the area (km²) and
proportional overlap of UD between male AFS at 25% (core areas) and 95% (home range) with the 95% kernel
of gear types. Information on the modeled distribution of chinstrap penguin foraging habitat throughout the
study area is available in6,7 which, when placed into the context of our study, suggests there is considerable spatial
overlap across the male AFS—gear type—chinstrap penguin predator guild. To extend this understanding, we
incorporated the level of temporal overlap among the various krill fishers by comparing the longitudinal displace-
ment of individual male AFS and each fishing gear type over time to the median fledging date of chinstrap
penguins5,26. All analyses were conducted in R and are presented as mean (± Standard Error) unless otherwise
stated.

Ethical statement. All experimental research was carried out in accordance with the guidelines and regu-
lations and permitted by the British Antarctic Survey Animal Welfare and Ethical Review Body (2015).

Results
Male AFS instrumentation data. Induction times for immobilisation of male AFS ranged between 6 and
29 min; once induced all procedures were completed within 23 min (18.8 ± 0.78 min) (Supplementary Table 1).
The seals ranged in body length from 127 to 184 cm (mean 160.9 ± 3.71 cm; Supplementary Table 1), reflect-
ing an age range from 3–8 year of age27. Instrumented individuals provided telemetry data for between 37.5
and 260 days (mean 166 ± 16.54 days), with a mean 1119 ± 172 raw location estimates over 2–23 at-sea bouts of
4–60 days duration, interspersed with haulouts that were less than 3 days long (mean 0.6 ± 1 day; Table 1. Adult
Table 1. Summarised deployment, movement and dive data for 20 adult male Antarctic fur seals instrumented with either low profile Satellite Relay Data Loggers (SRDL) with integrated dive loggers (N = 18) or Conductivity-Temperature-Depth SRDL (N = 2) between 5th and 26th January 2016 at Powell Island, South Orkney Islands. Dashed lines represent instruments that failed to collect dive data.

| ID      | Date      | Deployment (d) | Trips (N) | Duration (days) | Foraging trip ± SD | Haulout ± SD | Dives (N) | Dive depth (m) | Duration (min) |
|---------|-----------|----------------|-----------|-----------------|--------------------|--------------|-----------|---------------|---------------|
| ag01-01-15 | 05/01/2016 | 127.2          | 9         | 12.76           | 22.24              | 0.7          | 10,282    | 18.393        | 215           |
| ag01-02-15 | 06/01/2016 | 163.7          | 8         | 18.68           | 24.11              | 0.56         | 155       | 16.45         | 7.93          |
| ag01-03-15 | 06/01/2016 | 191.7          | 23        | 4.06            | 6.21               | 2.6          | 22.24     | 18.393        | 215           |
| ag01-04-15 | 07/01/2016 | 171.8          | 9         | 25.1            | 20.14              | 0.49         | -         | 18.393        | 215           |
| ag01-06-15 | 08/01/2016 | 126.9          | 13        | 6.98            | 9.97               | 0.83         | -         | 18.393        | 215           |
| ag01-07-15 | 08/01/2016 | 225.3          | 12        | 21.34           | 44.83              | 0.56         | -         | 18.393        | 215           |
| ag01-08-15 | 09/01/2016 | 254.8          | 15        | 20.69           | 33.24              | 0.55         | -         | 18.393        | 215           |
| ag01-09-15 | 09/01/2016 | 37.5           | 2         | 15.64           | 0.19               | 0.45         | -         | 18.393        | 215           |
| ag01-10-15 | 10/01/2016 | 127.7          | 2         | 59.81           | 59.81              | 0.41         | -         | 18.393        | 215           |
| ag01-11-15 | 10/01/2016 | 172.1          | 7         | 46.66           | 55.27              | 0.6          | -         | 18.393        | 215           |
| ag01-12-15 | 11/01/2016 | 171.5          | 7         | 36.96           | 48.16              | 0.45         | -         | 18.393        | 215           |
| ag01-13-15 | 11/01/2016 | 200.6          | 11        | 21.63           | 31.49              | 0.53         | -         | 18.393        | 215           |
| ag01-14-15 | 11/01/2016 | 54             | 2         | 15.65           | 3.03               | 0.96         | -         | 18.393        | 215           |
| ag01-16-15 | 21/01/2016 | 213.5          | 7         | 36.9            | 68.35              | 0.45         | -         | 18.393        | 215           |
| ag01-17-15 | 21/01/2016 | 169.4          | 7         | 12.08           | 10.89              | 0.47         | -         | 18.393        | 215           |
| ag01-18-15 | 21/01/2016 | 223.1          | 12        | 25              | 39.94              | 0.6          | -         | 18.393        | 215           |
| ag01-19-15 | 23/01/2016 | 119.2          | 11        | 9.5             | 6.5                | 0.79         | -         | 18.393        | 215           |
| ag01-20-15 | 23/01/2016 | 169.2          | 10        | 14.81           | 24.26              | 0.41         | -         | 18.393        | 215           |
| ag01-244g-14 | 26/01/2016 | 260.6          | 10        | 13.13           | 15.86              | 0.86         | -         | 18.393        | 215           |
| ag01-273-14 | 26/01/2016 | 98.9           | 13        | 18.57           | 21.25              | 0.67         | -         | 18.393        | 215           |

| ID      | Date      | Deployment (d) | Trips (N) | Duration (days) | Foraging trip ± SD | Haulout ± SD | Dives (N) | Dive depth (m) | Duration (min) |
|---------|-----------|----------------|-----------|-----------------|--------------------|--------------|-----------|---------------|---------------|
| ag01-26-15 | 26/01/2016 | 260.6          | 10        | 13.13           | 15.86              | 0.86         | -         | 18.393        | 215           |
| ag01-273-14 | 26/01/2016 | 98.9           | 13        | 18.57           | 21.25              | 0.67         | -         | 18.393        | 215           |

male AFS ranged over large distances, reaching as far west as the eastern Ross Sea and east to Bouvetøya, though most individuals stayed between the South Orkney Islands and the Gerlache Strait (Fig. 1). While some males stayed resident around the South Orkneys throughout the entire study, many moved into the Bransfield Strait in late January/early February, with some remaining in the strait until just before the subsequent breeding season on South Georgia (Fig. 2).

Instruments from three of the seals failed to provide meaningful dive data, but from the other 17 individuals a total of 266,189 dives were collected (range 3817–31,819 dives per individual, mean 13,365 ± 2068) (Table 1). Mean maximum and average dive depths were 166 m (± 53.9 range 90–280 m) and 166.6 m (± 8.1 range 3.9–43.8 m), respectively. Average dive duration was 1.6 min (± 0.52, range 0.44–2.81 min) (Table 1). At the start of the instrumentation period, average and maximum dive depths were shallow (100 m and 110 m, respectively), despite near-constant daylight, with dives to only 50 m or less being common in February and March (Supplementary Fig. 2). As autumn progressed into winter and day length decreased, dives became deeper with animals diving to maximum depths of 200 m regularly (Supplementary Fig. 2). These patterns are supported by the smoothed response of dive parameters as the study period progressed, characterizing a trend of increased number of dives as well as increased average depth and duration, particularly from dawn to late evening though between midnight and early morning these patterns were reversed (Fig. 3). This progression to deeper diving at the onset of winter was matched by the behaviour of both fishing gear types, which also shifted to deeper fishing within the same vertical range as the male AFS (Supplementary Fig. 3). The change in exploitation depth matched changes in the physical structure of the water column, with temperature profiles from male AFS SRDL showing the upper 100 m of the water column to be between 0° and + 1 °C during the summer, cooling down to below zero during the winter (Supplementary Fig. 4).

**Spatio-temporal overlap between male AFS, fishing gear types and chinstrap penguins.** Some male AFS dispersed over vast oceanic areas, though most of the animals remained within the WAP and Scotia Sea (Fig. 1). Typically, male AFS remained at Powell Island for up to two weeks after instrumentation, though some stayed within the South Orkneys until the end of June. They were likely forced away from the islands by thickening sea ice. However, most of the instrumented animals moved into the Bransfield Strait by late January and remained there until the transmitters stopped functioning in late winter/early spring.

The 95% UD of all males (derived from Biased Random Bridges) covered an area an order of magnitude greater than the fishery in 2016 and more than twice the size of the area exploited by trawlers between 2009 and 2018 (Table 2). The areas exploited by both gear types occupied less than 6% of male AFS home range during the study, though up to 18% of the recent historical area of the fishery (Table 2). Conversely, the majority of the area exploited by both fishing gear types was within the range of the male AFS. The core 25% UD of male AFS was focused in the southern central Bransfield Strait, the southern aspect of Elephant Island, and around the South Georgia.
Orkney Islands coastal shelf (Figs. 1b, 3a; Table 2), overlapping between 25 and 28% of fished areas depending on fishing gear type (Table 2).

In contrast to male AFS, the fishery displayed different movement strategies that appeared to be related at least in part to gear type, though experience and choices made by the vessel Masters’ undoubtedly also play a role. CP trawlers alternated between the W AP and South Orkney Islands and most TR trawlers remained within the W AP but started the season much later (Fig. 4). Thus, while spatial overlap was apparent between male AFS and the fishery (and by extension, chinstrap penguins), the movement strategies of the fishery reduced temporal overlap. At the South Orkney Islands, the CP trawlers and male AFS overlapped temporally with almost the entire breeding season of chinstrap penguins, with fishing vessels leaving at the median date of chinstrap penguin fledging (Figs. 2, 4D). Temporal overlap in the W AP was more complex, with CP trawlers leaving and both male AFS and TR trawlers entering the area in mid-January (Fig. 4D). However, both fishing gear types and the majority of instrumented male AFS temporally and spatially overlapped the median chinstrap penguin fledging date (Figs. 2, 4D).

Discussion

We provide the most detailed characterization of the spatiotemporal movements of male AFS and their overlap with the commercial krill fishery to date. While the seals occupied vast ranges compared to the fishery in 2016, areas used most intensively by male AFS overlapped with the fished areas. There was substantial temporal variability in the distribution of the two fishery predators, with the CP trawlers fishing off the western coast of the South Orkney Islands between January and March while the TR trawlers season started in mid-January and went through until June (Supplementary Fig. 1). In excess of 32,000 adult and subadult male AFS arrive in late January at Signy and Laurie Islands in the South Orkney Islands with recorded numbers decreasing throughout April29,30. The diet of male AFS at the South Orkney Islands is dominated by krill31; assuming an average age of 4 year32 and using the estimated amount of Antarctic krill consumed for this age class at South Georgia (3 t/year)33, the number of male AFS recorded at just these two sites in two months would consume approximately 24,000 t or 70% of the total recorded catch in Subarea 48.2 in 201634. Areas intensively used by both male AFS and the fishery around the South Orkney Islands overlap in space and time with the late stages of chinstrap penguin breeding35.
and numerous large penguin colonies occur along the western coastlines of the islands. Importantly, the true number of male AFS arriving at the South Orkney Islands is likely to be substantially higher than that recorded at Signy and Laurie Islands alone, though abundances will likely vary considerably interannually.

Our study shows that the spatial and temporal nature of potential resource competition between male AFS and the fishery and between both these groups and centrally foraging, krill dependent chinstrap penguins is likely to be complex. The male AFS study we conducted was concurrent with the second season of a similar tracking study on chinstrap penguins at the same location, during one of the strongest El Nino seasons on record. Lowther et al. showed pronounced differences in chinstrap penguin foraging behaviour attributed to El Nino-driven coastal downwelling, forcing penguins to forage farther from shore in search of food presumably due to krill movement away into the open ocean. How similar events impact unconstrained predators such as male AFS is unknown, but even assuming that the patterns of space use we describe are consistent across years, the cumulative impacts of male AFS and fisheries on the foraging behaviour and reproductive success of chinstrap penguins at the South Orkney Islands is unlikely to be consistent because of the variability in numerical abundance of male AFS as well environmental stochasticity similar to that described by Lowther et al. Importantly, the degree and significance of the cumulative impacts of these various krill predators on each other is unknown, yet this understanding is important for appropriately interpreting the demographic trends of krill-dependent centrally foraging penguins. Presumably, the greatest impacts of competition on chinstrap penguins would be constrained to the western coastline of the South Orkney archipelago given the restricted foraging range of penguins during breeding. Owing to the inaccessibility and lack of infrastructure in this area, there have been no meaningful population surveys of penguins in the last 40 years. However, future monitoring efforts should concentrate here given the potential for studying the direct impacts of fishing on centrally foraging penguins.

In the Bransfield and Gerlache Straits, the potential for resource competition and cumulative impacts of male AFS and the fishery on chinstrap penguins is even more complex. The core fishing area for both fishing gear types fish at similar depths. Additionally, CP trawlers deploy and leave fishing gear deployed for prolonged periods away into the open ocean. How such events impact unconstrained predators such as male AFS is currently impossible to estimate impacts on younger birds because the ontogeny of foraging behaviour both horizontally and vertically in fledgling pygoscelid penguins is poorly understood, though a pattern of progressively improving diving capabilities has been described for fledglings of other penguin species such as the Emperor penguin Aptenodytes forsteri and King penguin A. patagonicus. Chinstrap fledglings depart their natal colonies in late February—early March and assuming they are initially shallower divers than adults, cumulative population declines. Adult pygoscelid penguins typically forage at shallow depths (30–40 m) during summer breeding but they can dive to depths in excess of 100 m which during the summer coincides with foraging depths used by male AFS in our study. After breeding, adult chinstrap penguins undertake large migrations away from breeding areas releasing them from trophic competition with male AFS and the fishery. However, it is currently impossible to estimate impacts on younger birds because the ontogeny of foraging behaviour both horizontally and vertically in fledgling pygoscelid penguins is poorly understood, though a pattern of progressively improving diving capabilities has been described for fledglings of other penguin species such as the Emperor penguin Aptenodytes forsteri and King penguin A. patagonicus. Chinstrap fledglings depart their natal colonies in late February—early March and assuming they are initially shallower divers than adults, cumulative competition with male AFS and the fishery could impact their foraging efficiency and thus survival. However, such interference competition would be conditional on spatial overlap between fledglings, male AFS and the fishery, the degree of which is currently unknown. Importantly though, in the context of interpreting penguin population demographic decline through reduced survival of a key life history stage, consideration should also be given to the likely nonlinear increase in potential competitive interactions, particularly given the rapid increase in male AFS abundance in recent decades. Additional factors not directly related to this study should also be considered, such as the direct mortality of fledglings by male AFS with several studies highlighting the impact even of few penguin-eating seals can be.

Through the treatment of fishing gear types as individual predator groups, our study also revealed very different spatiotemporal behaviours within the krill fishery. Continuous pumping trawlers occupied almost half of the fishing area used by TR trawlers between 2009 and 2018 (Table 2) yet caught between 56 and 66% of the catch over this period. Our analysis of trawl depths over the season seems to indicate that CP trawlers target slightly deeper depths during the summer than their traditional counterparts until the onset of winter when both gear types fish at similar depths. Additionally, CP trawlers deploy and leave fishing gear deployed for prolonged periods and can maintain fishing effort at relatively low densities of krill. Conversely, TR trawlers repeatedly target shallower depths.
Figure 3. Smoothed responses from Generalised Additive Mixed Models of the (A) average dive depths, (B) dive time and (C) number of dives within 6 h time periods (00:00–06:00, 06:00–12:00, 12:00–18:00, 18:00–00:00) each day across all individuals. There was a consistent trend of increased average dive depth and dive time between April and August and a concomitant decrease in the number of dives between 0000 and 06:00.
set and haul trawl nets and try to fish in high densities to maintain production rates in the onboard factories\textsuperscript{52}. Presumably the differences in operating depths, densities of krill and the level to which swarms can be economically depleted and duration that gear is deployed, particularly during the key summer breeding season for krill dependent predators, adds an additional (though currently unincorporated) layer of complexity to disentangling these interactions. Importantly, if CP trawlers are selected for in the future, there is currently no ability to predict how a shift in the dominant fishing gear type will change the impacts on the current suite of bioindicators such as those included in CEMP.

While the difference in core areas may reflect to some degree the different numbers of vessels operating each gear type and thus operational issues of safety leading to a spreading of vessel effort, the catch levels as a function of overlap with male AFS core range, suggesting that while they utilised a much broader home range than the fishery, the same areas were preferred by both.

Studies examining the response of fisheries to management actions are limited, even though the impact of measures will profoundly affect how this “predator” adapts\textsuperscript{53,54}. In the context of the krill fishery, a reduction in available fishing area may elicit a switch to more efficient gear such as continuous pumping, which in turn could increase the risk of localized depletion\textsuperscript{43}. However, managing the fishery adaptively at the scale at which it operates is feasible, given that a substantial portion of the vessels within the krill fishing fleet are fitted with scientific-quality acoustic echosounders that have proven capable of providing near-real-time estimates of krill abundance and distribution in an area being fished\textsuperscript{50-57}. Incorporating such information into fisheries assessments might provide an opportunity to adaptively scale catch to local krill availability, preventing localized depletion.

We demonstrate that male AFS, whose abundance has increased rapidly throughout the lifetime of the Antarctic krill fishery, and on which monitoring effort is lacking, overlaps in all four dimensions (horizontal, vertical and temporal) with the krill fishery in a complex mosaic. We show that the fishery itself is comprised of two distinct predator types, with the more modern and efficient CP trawlers possibly being selected for in the future should static management efforts constrict the area over which the fishery can operate, fueling concerns over localized depletion. Together, male AFS and the krill fishery likely contribute to cumulative impacts on centrally foraging predators monitored in CEMP. A holistic view will provide not only a more detailed understanding of the impact of the fishery, but also its interaction with species on the breeding and recruitment success of CEMP monitored species.

However, sophisticated, spatially resolved modelling approaches have already been proposed to evaluate the demographic trends of penguins throughout the WAP and Scotia Sea. These models are better equipped to capture the complexity of cumulative, spatially heterogeneous competitive interactions between species and the nonlinear effects of climate change\textsuperscript{58}, and may lead to a more transparent and implementable EBFM system for the Antarctic krill fishery.

| Area and the proportional overlap between the 95% Utilisation Distributions (UD) of male Antarctic fur seals (male AFS), continuous pumping (CP) and traditional trawling (TR) in 2016 and across the entire 10 year dataset (2009–2019) and the combined efforts of the fishing fleet for 95% UD. Numbers in parentheses represent similar comparisons of areal size and proportional overlap at the 25% UD core range of mAFS. Data above the diagonal are overlaps of column-within-row and vica versa for below the diagonal; for example 74% of the continuous pumping trawl home range were contained within that of male AFS home range, yet only 5% of male AFS home range fell within areas exploited by the pump trawlers. Note the disproportionate levels of overlap with male AFS core range, suggesting that while they utilised a much broader home range than the fishery, the same areas were preferred by both. |
|---|
| **95% (25%) area (km\(^2\))** | **Proportional overlap 95% (25%) UD** |
| | Male AFS | CP (2016) | TR (2016) | CP (all years) | TR (all years) | Fishery (all years) |
| Male AFS | 194,225 (22,250) | – | 0.74 (0.26) | 0.69 (0.28) | 0.7 (0.24) | 0.51 (0.14) | 0.53 (0.15) |
| CP (2016) | 12,375 | 0.05 (0.14) | – | 0.27 | 0.34 | 0.14 | 0.16 |
| TR (2016) | 18,250 | 0.06 (0.23) | 0.4 | – | 0.31 | 0.25 | 0.22 |
| CP (all years) | 32,938 | 0.11 (0.36) | 0.91 | 0.56 | – | 0.38 | 0.42 |
| TR (all years) | 69,554 | 0.18 (0.43) | 0.79 | 0.95 | 0.8 | – | 0.77 |
| Fishery (all years) | 72,704 | 0.19 (0.51) | 0.92 | 0.89 | 0.92 | 0.8 | – |
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**Author contributions**

A.L., I.J.S.T., C.L. and K.M.K. conceived the project. A.L. and I.J.S.T. conducted fieldwork. A.L. wrote the initial manuscript draft and prepared the figures. All authors reviewed the manuscript.

**Competing interests**

The authors declare no competing interests.

**Additional information**

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