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The ecosystem approach to management of the Antarctic krill fishery - the ‘devils are in the detail’ at small spatial and temporal scales

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ABSTRACT

Fishery demand for Antarctic krill is increasing, and projected to continue increasing into the future. Krill has the potential to contribute approximately 10% to all future marine landings, adding significantly to global food security. However, the fishery is effectively data-limited so is currently managed using precautionary assessments that relate to large spatial and temporal scales that preclude the need for fine-scale ecological data.

To respond to recent changes in fishery operation and to mitigate possible ecological impacts, the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) plans to revise its management strategy so that it takes into account ecosystem operation at smaller spatial and temporal scales, such as those relevant to krill-dependent predators.

Here, we consider how catches in coastal areas potentially present challenges for these predators, where cumulative catches over the fishing season can sometimes be greater than local consumption by predators, and sometimes greater than the standing stock of krill within an area because of krill transport and replenishment by ocean currents. Protecting feeding areas used by land-based predators such as penguins and seals, whilst also offering a high level of protection for pelagic predators such as some species of fish and recovering populations of cetaceans, will require innovative solutions.

We highlight critical ecological research needed to reduce management uncertainty. This is important as we demonstrate that krill consumption by predators in near-shore coastal habitats relies absolutely upon krill movement and oceanographic transport. We also highlight the need to improve understanding about krill behaviour, especially in relation to observed seasonal changes in krill biomass. Finally, we highlight that without up-to-date data about changes in krill, krill-dependent predator populations and their oceanographic environment, management will remain challenging in the context of increasing fishing pressure, recovering populations of marine mammals and a changing climate.

1. Introduction

Globally, under-fished marine stocks account for less than 7% of all stocks assessed (FAO, 2018). Of these, Antarctic krill (*Euphausia superba*) has the potential to become a major source of marine protein (Everson, 1977, 1992). Estimates of the total annual production in the Southern Ocean vary, but range from 340 to 540 Mt. (Atkinson et al., 2009). Two products are likely to be of importance; krill oil, intended for direct human consumption, and krill meal, which is most likely destined for aquaculture feeds (FAO, 2018), pet foods and supplements (www.akerbiomarine.com/; accessed 18 May 2021). Currently, catches can only be taken from the southwest Atlantic and the southern Indian Ocean; the precautionary catch limit for these two areas sums to 8.6 Mt., contrasting with current catches that now approach 450,000 t. In comparison, the total existing global marine capture of all harvested species is 79.3 Mt., whilst production from global aquaculture is 80.0 Mt. (FAO, 2018). Thus, krill has the potential to contribute around 10% to all future marine landings, adding significantly to global food security. With the global human population at 7.8 billion and expected to reach 9.8 billion in 2050, food security is a pressing need.

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1.1. *The fishery for Antarctic krill*

The Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) is responsible for managing the krill fishery (see Supplementary Information). The CAMLR Convention requires an ecosystem approach, including consideration of the needs of krill-dependent predators. This is because krill is an important dietary item for many species, including fish, squid, penguins, flying seabirds, seals and baleen whales (Trathan and Hill, 2016). Competition with these predators is a major consideration for managers, although concerns still exist about the validity of meal production from krill (e.g. Jacquet et al., 2010) and about the impacts of climate change (e.g. Flores et al., 2012).

Since the fishery began, CCAMLR has recognised that krill catches have become increasingly concentrated (e.g. SC-CAMLR-XXXV, 2016, paragraph 3.47), with the fleet now repeatedly visiting a small number of fishing hotspots. In the southwest Atlantic (Fig. 1), where over 99% of harvesting takes place, such hotspots occur to the northeast of South Georgia, to the west of the South Orkney Islands, within the central Bransfield Strait, and in the northern Gerlache Strait. As catches have become more concentrated, particularly near to predator breeding colonies, CCAMLR has agreed that it needs an appropriate management framework (SC-CAMLR-38, 2019). In particular, CCAMLR has recognised the need for a framework that ensures precautionary protection at small scales; that is at scales typical of those used by predators and now by the fishery (scales <50 to 100 km).

1.2. *Updating the management framework for krill*

Given CCAMLR's ecosystem-approach, a fundamental understanding of ecosystem operation should underpin any proposed revisions to krill fisheries management. Therefore, in this context, we consider some of the challenges now facing CCAMLR, including the movement of krill in ocean currents, issues related to predator consumption, and the behaviour and standing stock of krill itself. We focus on Subarea 48.1 (Fig. 1), as an exemplar of issues prevalent across the southwest Atlantic.

Krill are a micro-nektonic species and move with ocean currents, albeit with some behavioural control (Marr, 1963; Mackintosh, 1972; Nicol, 2006; Thorpe et al., 2007). Consequently, detailed understanding about the potential for krill redistribution is vital for management, especially at small spatial and temporal scales. Such movement is fundamental for understanding where and when krill spawn, how they are replenished within the foraging ambit of a given predator colony, and how fishing hotspots recover after intensive extraction. Krill flux has therefore been a major concern for CCAMLR (e.g. SC-CAMLR-XIII, 1994), but understanding about the ecological consequences, and how to incorporate these into management across a range of spatial and temporal scales, remains unresolved.

One important consequence of krill flux coupled with behaviour, is that catch limits that are set for large geographic areas can increase the risks of ecological impacts at smaller scales. This is because krill may concentrate in preferred habitats (for spawning, for feeding, etc.) which the fishery will inevitably always seek out as the most profitable areas, leading to concentration of catch and effort. Such concentrations by the fishery could impact the stock itself (in spawning areas), or have consequences for dependent predators that habitually use the same habitats. However, setting catch limits at smaller scales relevant to predator foraging, or fishery concentration, potentially requires a great deal of ecological information, much of which is never likely to be available.

Krill exists across diverse habitats (e.g. Atkinson et al., 2008; Schmidt et al., 2011), where they are preyed upon by many species (Trathan and Hill, 2016). Recent work by Warwick-Evans et al. (2021) has explored the energetic requirements of some of these predators, assuming a diet based largely upon krill, apportioning consumption according to modelled foraging distributions. Amongst others, Warwick-Evans et al. (2021) considered species known to be major krill consumers (Croxall et al., 1985; Reilly et al., 2004); these included the *Pygoscelis* penguins (*P. adeliae*, Adélie; *P. antarctica*, chinstrap; *P. papua*, gentoo) and humpback whales (*Megaptera novaeangliae*), a species that is now rapidly

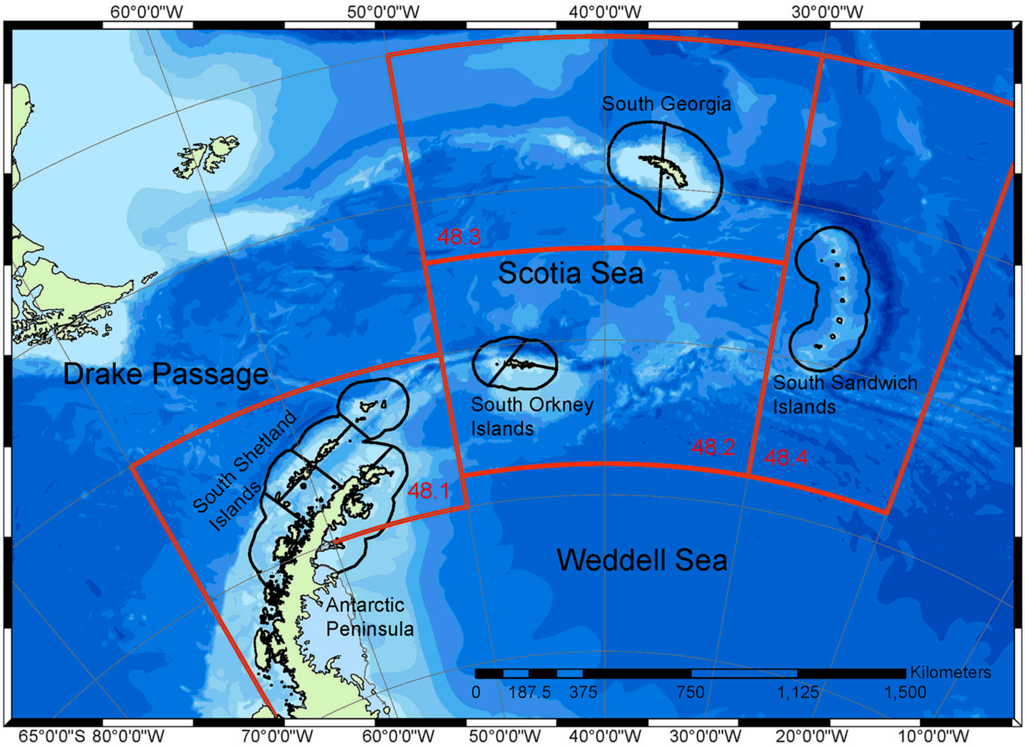

Fig. 1. The southwest Atlantic showing the main Subareas of Area 48 (identified in red) where the fishery for Antarctic krill operates. Proposed Small Scale Management Units (identified in black) for the krill fishery (Hewitt et al., 2004) are highlighted. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

recovering (Clapham et al., 1999; Matsuoka et al., 2006; Herr et al., 2016; Branch, 2011). Characterising the dietary demands of such species is vital for understanding the spatial and temporal operation of marine foodwebs, as well as for understanding areas of increased risk from commercial harvesting, given knowledge of krill biomass (Kinzey et al., 2015; Hill et al., 2016; Reiss et al., 2008, 2017).

A new krill management framework is also now needed as seasonal sea-ice in Subarea 48.1 has decreased over the past decades in response to regional warming (e.g. Stammerjohn et al., 2008; Turner et al., 2016). This has created new opportunities for the fishery, which has now shifted southwards (Silk et al., 2014). Future southward movement of the fishery is probable, which means that the development of complex infrastructure to manage the fishery is unlikely to be long lasting, or cost-effective.

Understanding the present situation in Subarea 48.1 will not only increase understanding about other areas where the fishery operates, but also help inform the future. Therefore in this paper, we consider the major oceanographic flows that supply krill into the Bransfield Strait - the plausible sources of krill that replenish removals taken by both natural predators and the fishery. We also consider the levels of krill consumed by *Pygoscelis* penguins and humpback whales, demonstrating how oceanographic complexity and krill behaviour are key to understanding ecosystem operation, and therefore management.

CCAMLR has recognised the need to offset risks associated with the concentration of catches, particularly during predator breeding (SC-CAMLR-XXXV, 2016, paragraph 3.110). As such in 2019, CCAMLR endorsed a plan for the revision of management, including how to apportion catch limits spatially and temporally at smaller spatial scales in order to avoid negative impacts on predators, (SC-CAMLR-38, 2019, paragraph 3.31 to 3.36). Here, we show that the devil is in the detail, especially for those parts of the ecosystem only rarely evaluated, including coastal areas where the fishery now increasingly operates. We recommend that incremental revision of any management solution must occur, wherever, and whenever adequate data are forthcoming. CCAMLR must find a pragmatic solution, offering the best compromise between adequate data and sufficient precaution.

2. Methods

2.1. Catch and effort data from the fishery for Antarctic krill

Every year, CCAMLR compiles haul-by-haul catch and effort data from the fishery. We use these data for Subarea 48.1 until the end of the 2017/2018 fishing season (CCAMLR C1 Catch and Effort Data, 2019), throughout referring to each CCAMLR fishing season (December to November) by the end date, so 2018 = 2017/2018.

We used ArcGIS (ESRI Version 10.4.1) to collate catch (tonnes) and effort (hours fished) at a spatial resolution of 10 × 10 km and at a temporal resolution of 1 calendar month (Supplementary Tables 2, 3, 4 and 5). We collated catch and effort during the *Pygoscelis* penguin breeding season (October to March) and post breeding (April to September). Penguin settlement occurs in October to November, while fledging occurs in February to March (Black, 2016; Warwick-Evans et al., 2018). Black (2016) reports chick departure dates prior to the middle of March for all three *Pygoscelis* species.

Recognizing recent concentration of harvesting in coastal habitats, we also considered catches from those areas within the coastal voluntary buffer zones (VBZ) (Fig. 2) proposed by the krill fishing companies that form the Association of Responsible Krill harvesting companies (ARK; www.ark-krill.org/ark-voluntary-measures; accessed 18 May 2021). The VBZ close coastal areas to krill fishing during the summer, in the proximity of important *Pygoscelis* penguin breeding sites. The VBZ have been maintained by the entire international krill fishing fleet since 2018 (Fig. 2), they are:

(i) Gerlache Strait - within 30 km of gentoo penguin colonies, in an area where gentoo and chinstrap penguin colonies dominate, and gentoo populations have been increasing and extending their geographic range southwards (Lynch et al., 2012; Humphries et al., 2017; Trathan et al., 2019). This is also an area where

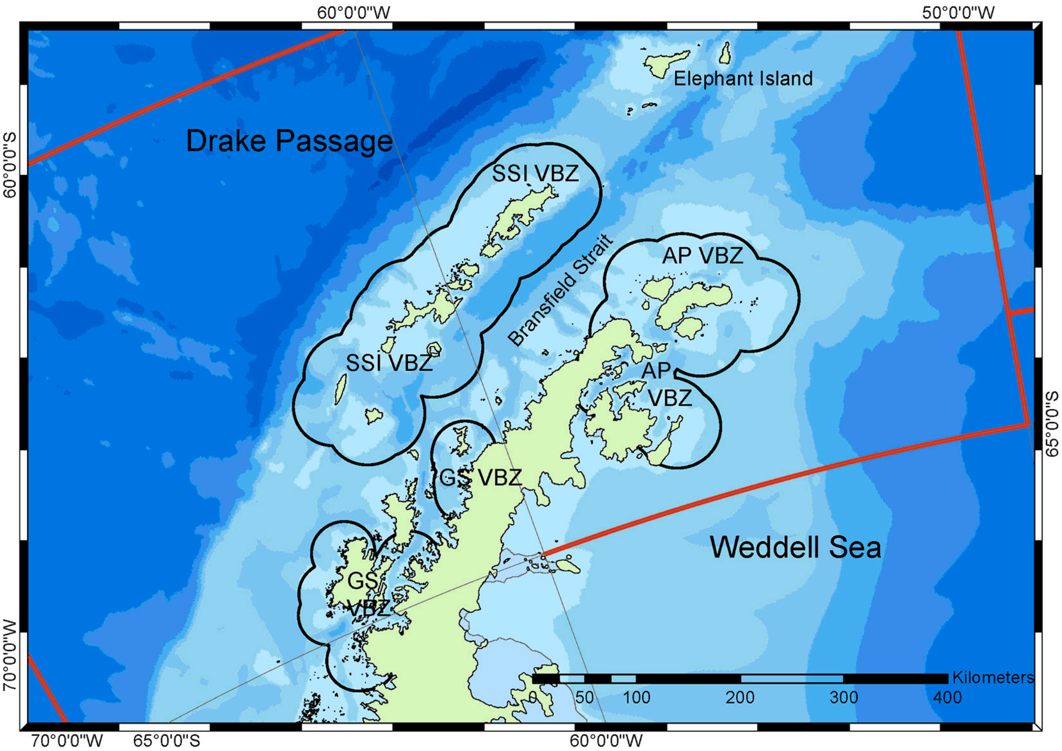

Fig. 2. Association of Responsible Krill harvesting companies (ARK) voluntary coastal buffer zones (VBZ). GS VBZ: Gerlache Strait; SSI VBZ: South Shetland Islands; AP VBZ: Antarctic Peninsula.

humpback whales are repeatedly sighted (e.g. Nowacek et al., 2011);

(ii) South Shetland Islands - within 40 km of chinstrap penguin colonies, in an area where chinstrap penguins dominate, and where gentoo populations are known to be increasing and chinstrap populations decreasing (Lynch et al., 2012; Humphries et al., 2017; Trathan et al., 2019); and,

(iii) Antarctic Peninsula - within 40 km of Adélie colonies, in an area where Adélie penguin colonies dominate and are stable (Humphries et al., 2017; Borowicz et al., 2018).

2.2. *Consumption of krill by selected predators*

We considered spatially explicit estimates of krill consumption developed by Warwick-Evans et al. (2021) for all *Pygoscelis* penguin colonies and humpback whales feeding in Subarea 48.1 (see Supplementary Information). Specifically, we explored how consumption was distributed, and how it varied inside and outside the VBZ. We used ArcGIS to collate the estimates of consumption (Warwick-Evans et al., 2021) at a spatial resolution of 10 × 10 km.

2.3. *Oceanographic connectivity and krill flux*

We explored oceanographic connectivity within the area used by the krill fishery in Subarea 48.1 (see Supplementary Information) using the NEMO high-resolution model described by Trathan et al. (2018). Predicted flows from this model were used to drive an Individual Based Model (IBM) to simulate Lagrangian transport of individual ‘krill’ released in different patches at the three major oceanographic gateways into the Bransfield Strait; these are (i) the Weddell Sea inflow near the tip of the Antarctic Peninsula, (ii) the Gerlache Strait, and (iii) the shelf edge to the west of the South Shetland Islands. For these simulations, we released 100,000 model particles on 1st December 2010 at a depth of 50 m. After release, particles moved according to the 3-dimensional 5-day mean flows, with vertical distribution restricted to between 1 and 100 m. Tides were not resolved and no particle behaviour was included; in reality, krill might disperse less, due to swarming behaviour.

3. Results

3.1. *Catch and effort data from the fishery for Antarctic krill*

We focused on krill harvesting since the 2012 fishing season (CCAMLR C1 Catch and Effort Data, 2019), but prior to the establishment of the VBZ. Gridding data at a spatial resolution of 10 × 10 km shows how catches have aggregated in the recent past (Supplementary Information Table 6; Supplementary Information Fig. 1). In most cells, the mean annual catch was less than 650 t y^{-1}; however, a small number of cells showed high catches (>10,000 t y^{-1}). Over the fishing seasons 2012 to 2018, approximately half the catch from Subarea 48.1 (494,371.8 t of 985,164.9 t) was taken from a restricted area. In any given year, fewer than 350 cells were fished (Fig. 3), with approximately 50% of the catch coming from just ~50 cells; (Supplementary Information Table 6). Some cells provided high catch levels in multiple years (Supplementary Information Fig. 1).

Harvesting is further summarised in Supplementary Information Table 7, with catch data tabulated separately for summer (October to March) and winter (April to September), corresponding to our definition of the *Pygoscelis* penguin breeding season, which cross CCAMLR fishing seasons. The highest catches are in March, April and May (see Supplementary Information Tables 2, 3, 4 and 5), with over half of all harvesting in winter (Supplementary Information Table 7). In the years prior to the establishment of the VBZ, approximately 13% of total annual sum of catches occurred during the penguin breeding season within the foraging ambit of penguins, with a further ~21% taken close to land after most penguins had finished breeding (Supplementary Information Table 7). In general, of catch in summer, and of catch in winter, around one third of harvesting was close to penguin breeding sites (Fig. 4; Supplementary Information Table 7). The estimates of harvesting are highly variable with high estimated standard deviations (Supplementary Information Tables 6 and 10).

3.2. *Consumption of krill by selected predators*

Krill consumption by the four krill predators considered here was highly concentrated and not equally distributed (Fig. 5), highlighting the importance of the coastal ecosystems targeted by these species during the main breeding period for penguins, and the summer feeding period for humpback whales (Fig. 6).

The VBZ (Fig. 2) include the majority of the penguin foraging habitat during breeding for colonies within Subarea 48.1, encompassing approximately 74.3% of chinstrap, 97.5% of gentoo and 91.4% of Adélie penguin colonies. Thus, the VBZ include large tracts of foraging habitat around penguin colonies totalling approximately 74,160.8 km^2: 13,131.9 km^2 within the Gerlache Strait; 37,055.6 km^2 around the South Shetland Islands; and 23,973.3 km^2 around the tip of the Antarctic Peninsula.

The average daily demands from breeding gentoo, chinstrap and Adélie penguins across the whole of Subarea 48.1 range from 0.4 to 6.3 kg km^{-2} d^{-1} (Supplementary Information Table 8); however, local

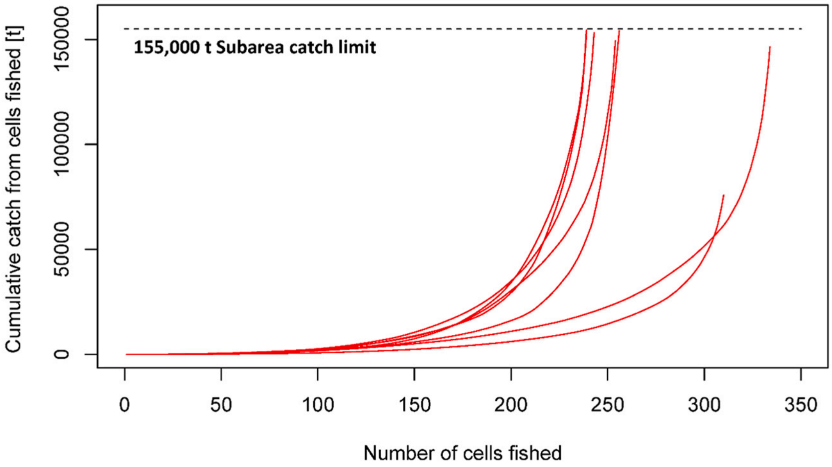

Fig. 3. Krill catch characteristics for Subarea 48.1 after gridding CCAMLR C1 catch data into 10 × 10 km cells. Lines show cumulative catch from the cells fished for the fishing seasons between 2011/2012 and 2017/2018. In this period, 1875 different cells were fished. See Supplementary Information, Table 6.

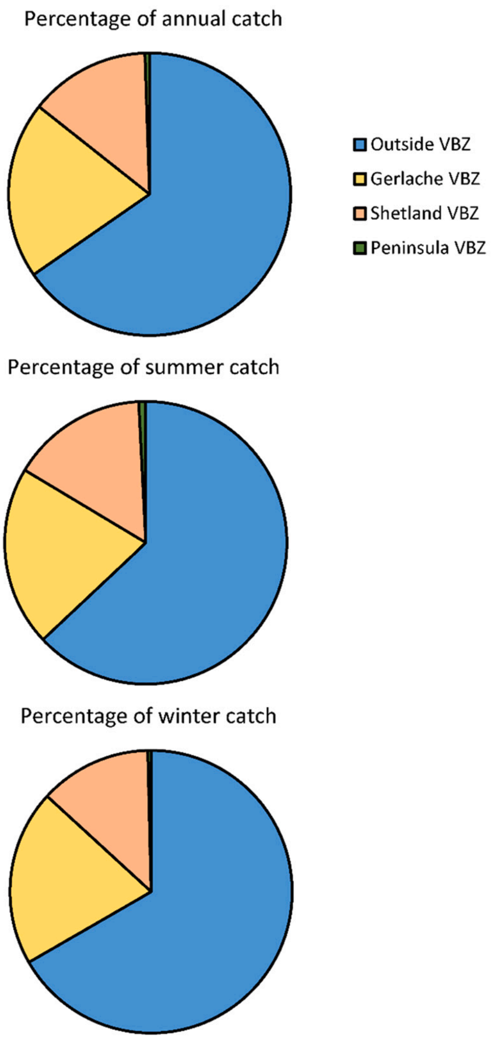

Fig. 4. Percentage krill catches for Subarea 48.1 after gridding CCAMLR C1 catch data into 10 × 10 km cells. Pie charts show the average catch from cells fished for the fishing seasons between 2011/2012 and 2017/2018 for summer (October to March) and winter (April to September); note difference to CCAMLR fishing seasons. Catches for the voluntary coastal buffer zones (VBZ) around major penguin colonies in the Gerlache Strait, the South Shetland Islands and the northern Antarctic Peninsula are shown. See Supplementary Information, Table 7.

consumption levels within the VBZ are much higher, and probably more representative of penguin needs. In the Gerlache Strait VBZ, mean levels of consumption by chinstrap penguins reach 3.1 kg km^{-2} d^{-1}; in the South Shetlands VBZ, mean levels of consumption by chinstraps reach 52.2 kg km^{-2} d^{-1}; whilst mean levels of consumption by Adélie colonies at the tip of the Peninsula VBZ can reach 72.0 kg km^{-2} d^{-1}. Maximum levels of consumption close to colonies are very much higher.

Penguin breeding lasts approximately 95, 85 and 95 days, respectively for gentoo, chinstrap and Adélie penguins (Croll and Tershy, 1998). Within the VBZ, average seasonal krill consumption by penguins ranges from 0.7 t km^{-2} y^{-1} in the Gerlache VBZ, to 7.1 t km^{-2} y^{-1} in the tip of the Peninsula VBZ, although maximum rates close to colonies are significantly higher (Supplementary Information Table 8). Thus, the seasonal consumption directly adjacent to the largest colonies can be as much as 44.9 t km^{-2} y^{-1}, but decreases with increasing distance from the colonies.

The humpback whale population that feeds along the west Antarctic Peninsula (nominally breeding stock G) is increasing rapidly (Branch, 2011; Jackson et al., 2015). Scaling population estimates from surveys undertaken in 2000 (Reilly et al., 2004) with a fixed population increase per annum (4.6%, 95% CI: −3.4% to 12.9%; Branch, 2011) suggests that whale numbers may now be such that they consume very significant amounts of krill (Supplementary Information Table 8). The average daily demand from humpback whales can range up to 59.1 kg km^{-2} d^{-1}, with an average of 20.9 kg km^{-2} d^{-1} across the whole of Subarea 48.1 (Supplementary Information Table 8). Assuming that humpback whales remain in their summer feeding grounds for approximately 120 days (Lockyer, 1981), annual krill consumption equates to approximately 2.5 t km^{-2} y^{-1} on average, but reaching a maximum of 7.1 t km^{-2} y^{-1} in some areas; consumption is highly concentrated and not evenly distributed (Fig. 5).

The estimates of consumption for both penguins and humpback whales are highly variable, with high estimated standard deviations (Supplementary Information Tables 8). Other uncertainties are also present and must be considered when making comparisons, but which remain challenging to estimate (Supplementary Information Tables 10).

3.3. *Oceanographic connectivity and krill flux*

Our oceanographic model reproduces the primary persistent flows (Fig. 7) to the north of the South Shetland Islands and inside the Bransfield Strait (Thompson et al., 2009; Sangrà et al., 2011; Dotto et al., 2016; Trathan et al., 2018; Moffat and Meredith, 2018). Weddell Sea shelf water contributes to the Coastal Current, which transports krill into the Bransfield Strait from the east, whilst there are western inputs of krill from the Bellingshausen Sea, the Gerlache Strait and the southern Antarctic Circumpolar Current. The mean oceanographic flows are generally invariant between seasons, (Supplementary Information Fig. 3), suggestive of strong topographic steering, including the dominant Antarctic Slope Front in the east of the region.

Fishing is congruent with the shelf-edge current to the northwest of the South Shetland Islands, the Bransfield Current, and the Coastal Current to the north and west of the Antarctic Peninsula, although the presence of sea ice in winter affects fishing locations (Supplementary Information Fig. 3).

Our simulation of individual ‘krill’ released in a patch at the eastern end of the Bransfield Strait shows how local currents widely disperse seeded patches (Fig. 9; release point within an ellipse at 56.75°W, 62.55°S with major and minor axes of 25 km and 10 km respectively, oriented 30° north of east). Individual particles move considerable distances, including to the north of the South Shetland Islands. Some particles remain close to the Peninsula as the complex flows in and around the canyons retain particles. Our simulation for a similar ‘krill’ patch released at the western edge of the South Shetland Islands (Fig. 9; release point within a circle at 61.00°W, 62.35°S with axes of 10 km), shows how local currents widely disperse particles seeded in proximity to one of the other important oceanographic gateways. Finally, our simulation for a patch released at the third major gateway, to the north of the entrance to the Gerlache Strait (Fig. 9; release point within a circle at 61.25°W, 63.75°S with axes of 10 km) similarly shows a complex pattern of dispersal and persistent circulation around the South Shetland Islands.

4. Discussion

Our results highlight the complexity and magnitude of data required for an ecosystem approach to management at small spatial and temporal scales, especially in coastal areas. Throughout, we have used the most up-to-date sources of data available, yet we highlight that important data gaps remain. The krill fishery has existed for almost five decades, and in that time major advances in the ecosystem approach to management have been achieved, but krill fishery management essentially remains data-limited (see Trathan et al., 2021). Currently therefore, management progress is most likely to be made through modelling and other approaches that support decision making when data are less than

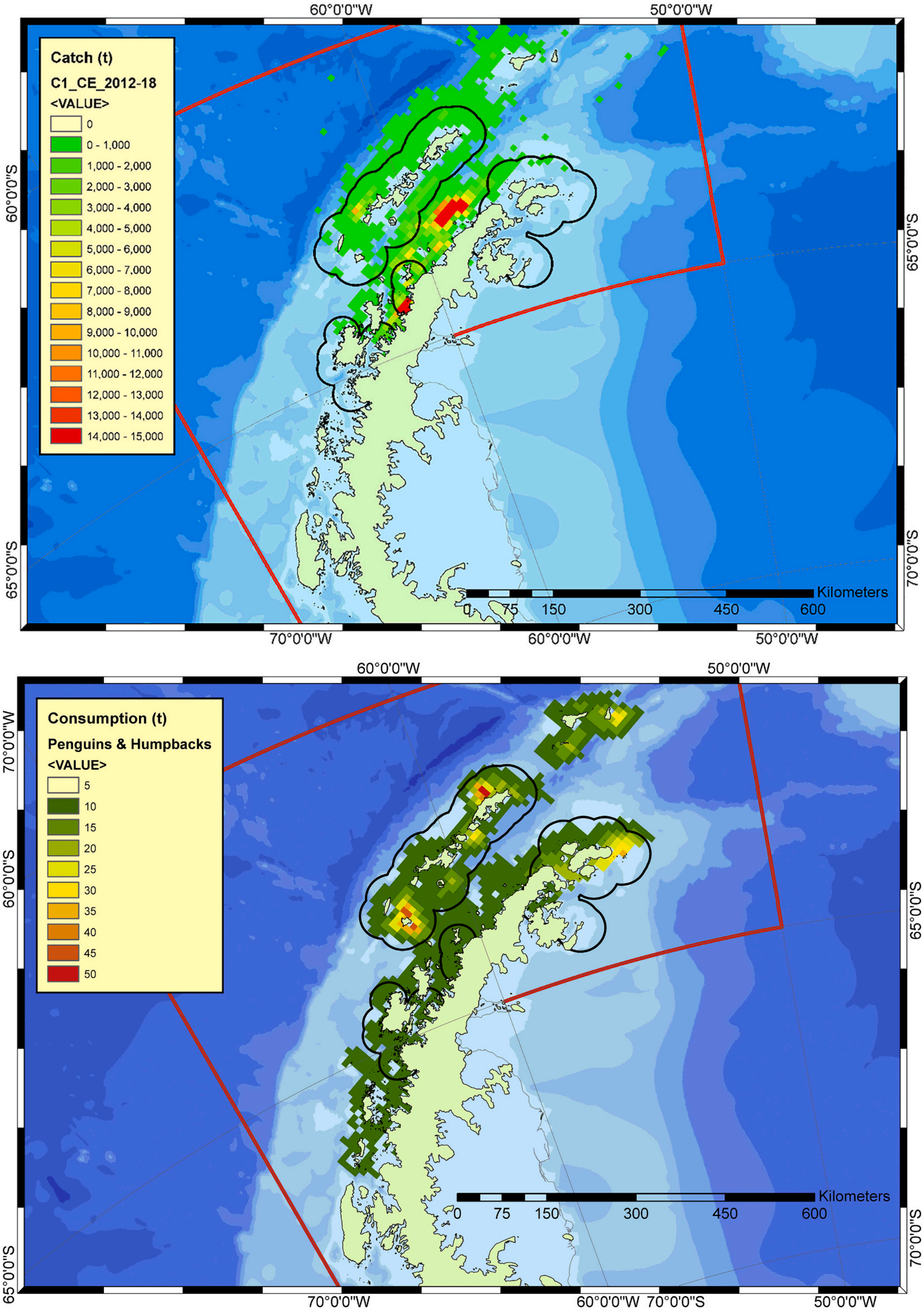

Fig. 5. (a) Catch distribution for Subarea 48.1 after gridding CCAMLR C1 catch data into 10 × 10 km cells (t cell^{-1} y^{-1}). Data show catches between 2011/12 and 2017/18 (see Supplementary Information Fig. 1. (b) Estimates of krill consumption (t km^{-2} y^{-1}; to convert to t cell^{-1} y^{-1} multiply by 100) for *Pygoscelis* penguins (gentoo, chinstrap and Adélie penguins, with respective breeding periods of 95, 85 and 95 days) combined with humpback whales (120 days feeding) in CCAMLR Subarea 48.1.

perfect (Carruthers et al., 2014).

The ARK VBZ were developed in response to the lack of data amidst increasing concerns about potential competition between the krill fishery and breeding penguins constrained to return to land to provision their offspring. The VBZ also provide protection for important whale feeding areas. Here, we have focused our analyses on the VBZ in order to highlight a number of ecological issues that have relevance to coastal locations near to other krill fishing hotspots, as well as in other ecosystems that depend upon forage fish species (e.g. Pichegru et al., 2010, 2012; Bertrand et al., 2012; Sherley et al., 2015; Barbraud et al., 2018).

Our analyses demonstrate the complexity and magnitude of data required for an ecosystem approach to management and show that

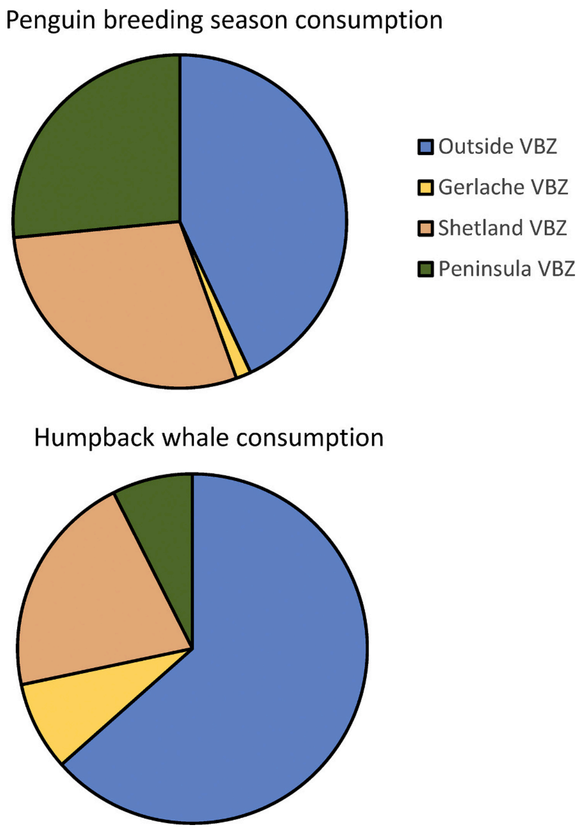

Fig. 6. Percentage krill consumption (t km^{-2} y^{-1}) for penguins and humpback whales in Subarea 48.1 after gridding consumption data into 10 × 10 km cells. Pie charts show the consumption in the voluntary coastal buffer zones (VBZ) around major penguin colonies in the Gerlache Strait, the South Shetland Islands and the northern Antarctic Peninsula. See Supplementary Information, Table 8. Seasonal krill consumption assumes a breeding season of 95, 85 and 95 days, respectively for gentoo, chinstrap and Adélie penguins, based on Croll and Tershy (1998), and a feeding season of 120 days for humpback whales, based on Reilly et al. (2004) and Lockyer (1981).

different geographic areas have local ecological complexities, each with differing levels of consumption by our four study species (Fig. 5). Consideration of other krill-dependent species (e.g. Santora et al., 2017; Forcada et al., 2012; Warwick-Evans et al., 2021), though not included in our study, would add greater levels of complexity.

We demonstrate that the krill harvest also varies in different areas (Supplementary Information Table 6 and Supplementary Information Table 7), but is concentrated in preferred areas. Such concentration also has implications for predators, but in the absence of monitoring, it remains uncertain whether the magnitude of impacts are ecologically important (see Watters et al., 2020). Our results suggest that one location is not necessarily a good proxy for all locations (Supplementary Information Table 8), and that management might need to be location specific (Trathan et al., 2021). Our krill consumption analyses reflect how species have preferred habitats and that not all habitats are equal (Supplementary Information Table 8). Finally, our oceanographic analyses (Fig. 9) highlight how different sources of krill might replenish krill consumed by predators, or removed by harvesting.

The complexity of Subarea 48.1 indicates the need for additional ecological data (or models. e.g. Carruthers et al., 2014) to inform management, if it is to identify absolute risks to the ecosystem. Such information is necessary across wide areas, given that the fishery is not restricted in space or time, but only by catch limit. The fishery can operate anywhere in Subarea 48.1, but it preferentially operates within a relatively small number of 10 × 10 km cells (Supplementary Information Table 6). Consequently, CCAMLR now faces a dilemma if it is ever to facilitate increased catch limits, whilst also minimizing any risk of ecological damage (see Supplementary Information). As krill catches increase, particularly in coastal areas, there is an increasing need for ecological data at small spatial and temporal scales. Furthermore, information about krill movement and behaviour, both within and between key foraging locations is vital at these scales. At present, CCAMLR's proposed management approach does not incorporate such data. Currently, CCAMLR has no means of identifying absolute risk, so relies upon a precautionary approach. If catches are to increase, CCAMLR will need to better understand ecosystem operation and absolute risk.

4.1. *Predator requirements*

Different predators have different habitat requirements and different demands for krill (e.g. Supplementary Information Table 8). Therefore, understanding the temporal and spatial demand for krill by predators at small scales is vital for management, especially where predator demand overlaps with fisheries. Overlap is especially important where predator or fishery requirements are conditioned by similar habitat quality, based on krill availability (Supplementary Information Tables 6, 7 and 8; see also e.g. Weinstein and Friedlaender, 2017; Weinstein et al., 2017, 2018; Warwick-Evans et al., 2018; Trathan et al., 2018), or on swarm size, structure and distribution. However, in reality, levels of complexity are likely to be greater. This is because we do not account for juvenile and non-breeding penguins, although we do include the energetic demands of pre-fledged chicks. Non-breeding penguins that are not constrained to provision offspring may use the same foraging areas, but they may also use areas not used by breeding adults. Indeed, recent evidence suggests that post-breeding penguins and fledglings do use coastal areas at least some of the time (Hinke et al., 2019).

The analyses of Warwick-Evans et al. (2021), and hence, also ours, are based upon the best available telemetry data. However, we recognise that penguin foraging is most constrained during brood and to a lesser extent during crèche, with less constraint during incubation and premoult. This will have implications for our habitat models. Nevertheless, gentoo penguins are coastal and resident, so their foraging is generally near-shore (Ratcliffe et al., 2019). For chinstrap penguins, 60% of all incubation foraging trips are within 40 km, whilst over 80% of brood trips and almost 75% of all crèche trips are within 40 km (Warwick-Evans et al., 2018; Trathan et al., 2018). For Adélie penguins, as for chinstraps, most foraging is constrained during breeding. New telemetry data could therefore improve spatial estimates of distribution, especially if collected from sites where no tracking data exist (see Trathan et al., 2018).

Further complexity in management occurs because of historical harvesting of fish, seals and krill-dependent baleen whales in the Antarctic. For example, historically, different species of cetacean were heavily exploited and reduced to very low population numbers, including blue (*Balaenoptera musculus*) and fin (*Balaenoptera physalus*) whales which are still very much below historical pre-exploitation levels (e.g. Matsuoka et al., 2006). As these population recover, changes in the marine ecosystem should be anticipated (Murphy, 1996 c.f. Dewar et al., 2006), challenging krill management frameworks. Surveys to estimate baleen whale abundance have been undertaken in Subarea 48.1, but spatial and temporal coverage are not currently optimal (Warwick-Evans et al., 2021).

4.2. *Potential for the fishery to compete with predators*

Populations of krill-dependent penguins respond to changes in their environment, including prey availability (e.g. Cury et al., 2011). However, lags in ecological processes can introduce complexity in attributing cause to observed changes (Trathan et al., 2006, 2007; Forcada and Trathan, 2009). Predator life-history processes also operate over multiple scales (Horswill et al., 2014), again underscoring that management

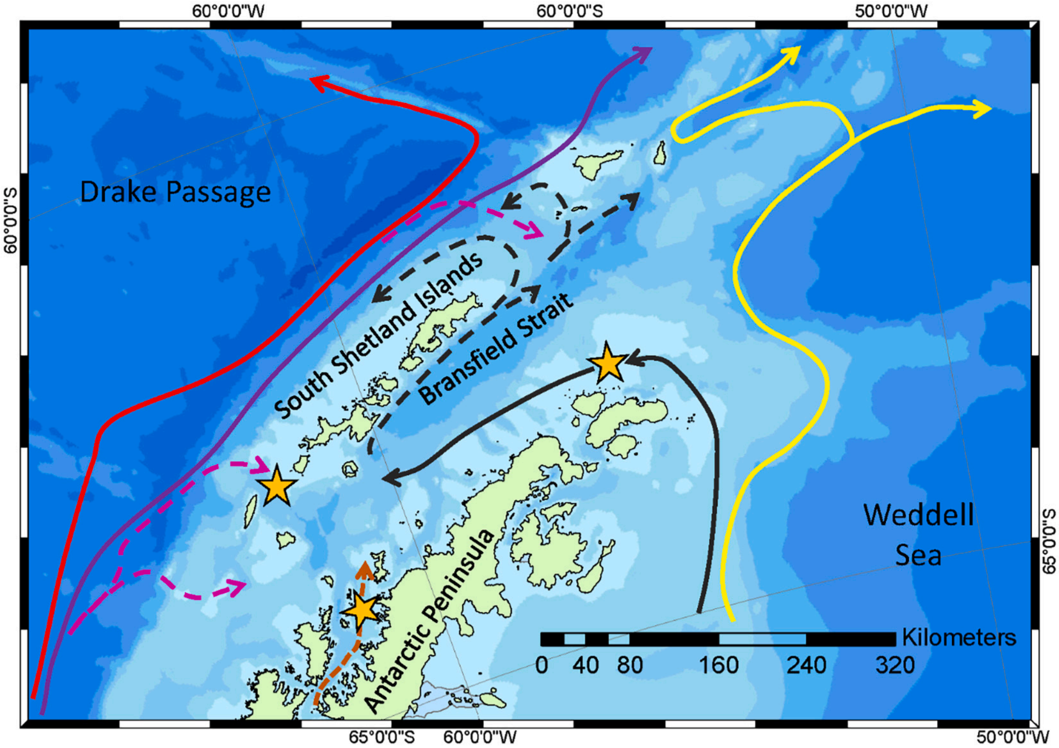

Fig. 7. Schematic of the currents near the Antarctic Peninsula following Thompson et al. (2009) and Dotto et al. (2016); see also Trathan et al. (2018) and Moffat and Meredith (2018). The positions of the South Shetlands shelf-edge current and Bransfield Current (Black dashed), Coastal Current (Black), the Antarctic Slope Front (Yellow), the Antarctic Circumpolar Current (ACC) Southern Boundary (Purple) and Southern ACC Front (Red) are shown. Weddell Sea shelf water contributes to the Coastal Current from the east whilst surface water originating from the Bellingshausen Sea, Circumpolar Deep Water (Mauve dashed) and the outflow from the Gerlache Strait (Rust dashed) enter the Bransfield Strait from the west. The major oceanographic gateways into the Bransfield Strait are identified by orange stars. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

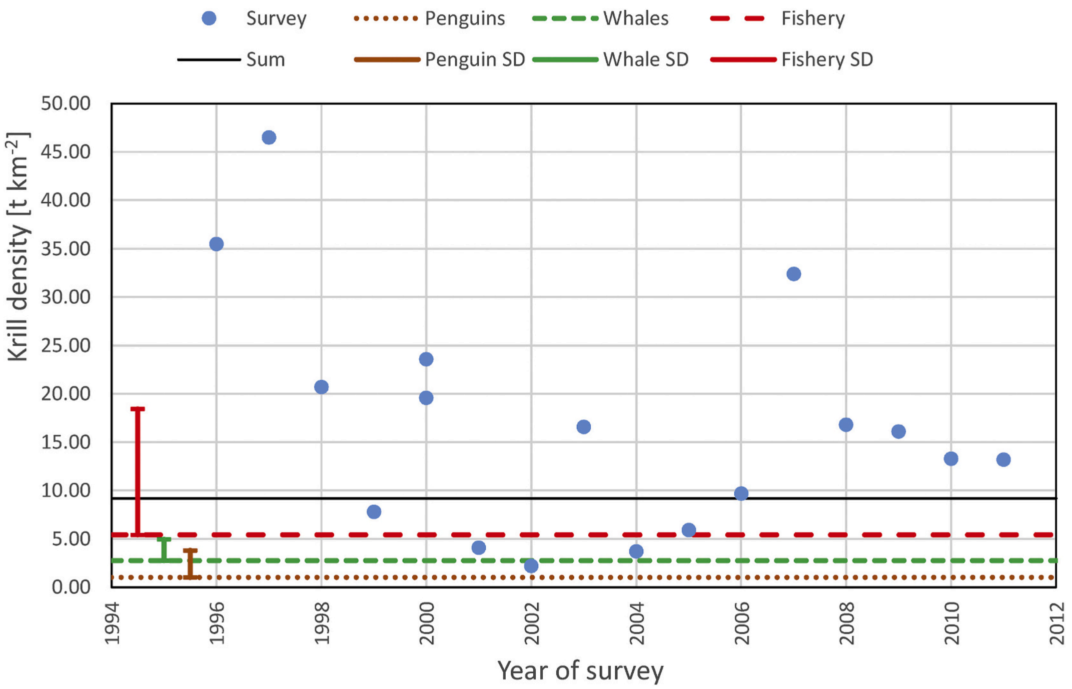

Fig. 8. Estimated average biomass of Antarctic krill (t km^{-2}) from a series of bio-acoustic surveys [blue] within Subarea 48.1 (see Kinzey et al., 2015, and Supplementary Information Table 9). Average krill consumption (t km^{-2}) by penguins [orange] and humpback whales [green] in Subarea 48.1 (see Supplementary Information Table 8), and average extraction (t km^{-2}) by the commercial krill fishery [red] (see Supplementary Information Table 6 – mean across 2012 to 2018). Also shown are estimates of the standard deviation associated with the spatial distribution of consumption and harvesting. See Supplementary Information Table 10 for other aspects related to uncertainty. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

at small temporal or spatial scales requires detailed consideration. Nevertheless, it is generally accepted that depleted prey during breeding can result in irregular provisioning for penguins which may then lead to chick failure (e.g. Lynnes et al., 2004; Cresswell et al., 2008; Cury et al., 2011; Oro, 2014; Pichegru et al., 2010, 2012; Sherley et al., 2015, 2018; Watters et al., 2020).

Our results show that in some areas, the average annual resource requirements from a 10 × 10 km^2 cell for penguins (Supplementary Information Table 8; e.g. 1.0 t km^{-2}) and for humpback whales (Supplementary Information Table 8; e.g. 2.5 t km^{-2}), are comparable to the average level of standing stock in some years (Fig. 8). This suggests that in years with a low biomass, the fishery has the potential to compete with penguins and whales, especially where catches are large (Watters et al., 2020). In a number of years, the summation of the average penguin demand for krill, the average humpback demand and the average fishery demand exceeds the estimate of the krill standing stock (Fig. 8). Naturally, caution is required as all estimates have high standard deviations, whilst spatial and temporal averages mask variation which may be important to predators (Supplementary Information Table 10). It is also well established that predators do not range equally across coastal areas and neither does the fishery (e.g. Trathan et al., 2018; Warwick-Evans et al., 2018). However, if catch limits were to increase in the future, then the potential for competition would be much greater, especially in any future years with a low standing stock.

Understanding ecosystem impacts of fishing will be challenging, especially at the scale of the individual penguin colony, that is at foraging scales of 10 to 40 km. This is because the majority of colonies are not monitored, and combined standardised indices (Boyd and Murray, 2001) derived from monitored colonies show little congruency between sites (CCAMLR Secretariat, 2016, 2017, 2018). Analyses also show that inter-annual changes in penguin indices show decreases in correlation between sites as the duration of the data series increases, and that there is little evidence of a simple (linear) relationship related to distance between sites (CCAMLR Secretariat, 2016). Such lack of congruency supports the assertion that management at small scales is likely to be both complex and data intensive. This is particularly important for assessment of fisheries impacts, and disentangling such impacts from changes brought about by other ecosystem processes, such as regional environmental, or climate change (Trathan and Reid, 2009).

Prey depletion, or prey disturbance during humpback whale foraging is unstudied, and is likely to be difficult to study. Humpback whales remain on their feeding grounds for 120 days (Lockyer, 1981), but individuals are not completely synchronous (Weinstein and Friedlaender, 2017). Some whales may also remain on the feeding ground over winter (Širović et al., 2004). Tracking individuals and relating possible interference competition to future calving performance, will require novel approaches.

Consideration of overlap between the fishery and predators during winter is not feasible, as data to develop preferred habitat models and consumption estimates are not available. Thus, though predators are less constrained in winter, this period remains a key gap in our understanding of predator overlap with krill fisheries. In the future, knowledge about the winter will become more important as the fishery now preferentially operates in the autumn (Supplementary Tables 2, 3, 4 and 5) when krill are oil rich. Further, Trathan et al. (2021) also report how ecological states in the winter can carry-over into subsequent seasons, suggesting that future models should best consider the dynamics of the ecosystem, rather than representing the ecosystem as a simple snapshot in time.

4.3. Oceanographic connectivity and krill flux

Duffy and Schneider (1994) highlight various metrics of predator-fishery overlap. However, calculation of these metrics requires knowledge about the residence time of krill. Therefore, it remains challenging to calculate metrics of overlap without knowledge about regional oceanography and krill movement. The relationship between standing stock (Supplementary Information Table 9), predator consumption (Supplementary Information Table 8) and harvesting (Supplementary Information Tables 6 and 7) highlights the importance of the dynamic operation of the Antarctic marine ecosystem, something CCAMLR has recognised (SC-CAMLR-XIII, 1994), but has yet to address. True metrics of predator-fishery overlap will be needed if CCAMLR is to understand the magnitude of real risks to the ecosystem.

Acoustic surveys that estimate krill standing stock have restricted spatial and temporal coverage (e.g. Reiss et al., 2008; Kinzey et al., 2015), particularly in near-shore waters where penguins and humpback whales forage, and where the fishery operates. Improved understanding about the availability of krill in these areas is now vital. In particular, data are necessary that describe coastal levels of standing stock, rates of krill flux, and the retention time of krill. Having such information at comparable spatial and temporal scales (including for predators, their prey and for the fishery) is important for developing plausible management options.

Krill harvesting generally aligns with the dominant oceanographic flows where mean current speeds are in the range 0.08 m s^{-1} to 0.18 m s^{-1} (Supplementary Information Fig. 3). These flows are such that the linear movement of a parcel of water is likely to lead to turnover rates of between 2.6 and 5.8 days over a distance of 40 km, approximately equivalent to the foraging radius of chinstrap and Adélie penguins. Such calculations make no assumptions about variability in flow, tidal forcing, or relationships with sea ice. Interestingly, such estimates correspond with observations that catch rates per hour in fishing hotspots gradually decline over periods of 4 or 5 days, until fishing vessels move elsewhere (SC-CAMLR-XXXV, 2016 Annex 6, paragraphs 2.215 to 2.221). Santa Cruz et al. (2018) reported similar results, showing that hotspots last for between 3 and 17 days, depending upon the number of vessels present and the scale of a fishing hotspot.

The Coastal Current and the Bransfield Current are key components of the clockwise circulation pathway within the Bransfield Strait (Fig. 7). Assuming linear transport and flow speeds of between 0.08 and 0.18 m s^{-1}, the transport of krill around a clockwise path of some ~760 km could take between 49 and 110 days, providing many opportunities for the fishing fleet to target the same patches of krill. However, some areas within the Bransfield Strait have slower flow speeds (Supplementary Information Fig. 3), so krill transport is likely to be spatially and temporally variable, and transport around the Bransfield Strait could take considerably longer. In addition, complex topography and current flows in the region mean transport pathways are unlikely to be linear, allowing further opportunities for repeated fishing on the same krill.

The time taken for passive particles ('krill') to enter the Bransfield Strait, and move around the clockwise circulation pathway (Fig. 9) is comparable to critical time-periods for predators. Respectively, gentoo, chinstrap and Adélie penguins require 95, 85 and 95 days to raise their chicks, whilst cetaceans remain to feed during the summer for 120 days. This highlights that significant depletion of krill at the scale of an individual colony might take 4 or 5 days to replenish and that significant depletion at the scale of the Bransfield Strait itself, could take 3 or 4 months to recover.

The mean flow field from our oceanographic model highlights the fundamental physical properties of the ecosystem. Different sources of krill supply the Bransfield Strait, whilst mixing inside the Bransfield Strait is variable; this mean that the abundance of krill could depend upon prevailing conditions; e.g. if one flow dominates, or dominates under particular environmental conditions (e.g. Naganobu et al., 1999). Consequently, further work to reduce levels of uncertainty about sources of krill in the area fished, would enhance management information. Recent analyses of krill length frequency highlight the potential for different sources (Reiss et al., 2020). Other, minor oceanographic gateways also exist, for example between the islands of the South Shetland Islands. Tidal dynamics, including in these channels, are important and could influence krill movement (c.f. Bernard and

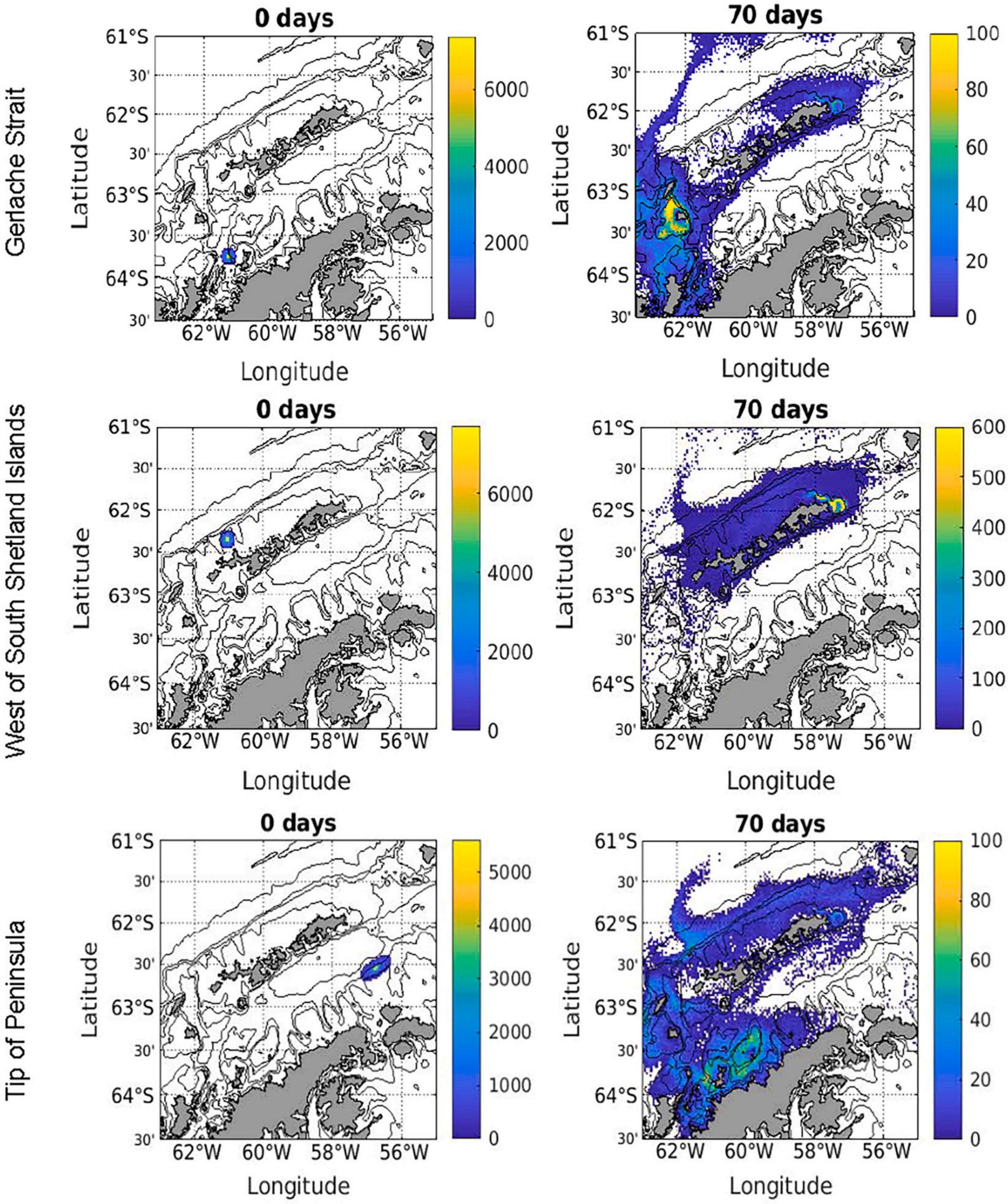

Fig. 9. The number of particles within each oceanographic model grid cell after 70 days following release of 100,000 particles on 1st December 2010 near each of the major oceanographic gateways to the Bransfield Strait; release was at 50 m, particles moved according to the 3-dimensional 5-day mean flows, with vertical distribution restricted to between 1 and 100 m. Tides were not resolved and no particle behaviour was included (see Fig. 7, and Supplementary Information). Note different colour scales in plots.

Steinberg, 2013; Bernard et al., 2017).

Several studies have previously considered krill movement in relation to local oceanography in the Antarctic Peninsula region, including aspects that will be important for managing the krill fishery. For example, Capella et al. (1992) concluded that the Bransfield Strait and the South Shetland Islands receive krill larvae from the Bellingshausen Sea to the west, the Weddell Sea to the east and from north of the South Shetland Island arc. Capella et al. (1992) also identified the anticyclonic circulation around Elephant Island we find in our model. Subsequently, Piñones et al. (2011, 2013a), used a Lagrangian model to calculate residence times for biological hotspots, and inferred that certain physical features aided retention, including proximity to deep depressions and shelter from wider shelf circulation, something highlighted in our results (e.g. Supplementary Information Fig. 4).

4.4. *Krill behaviour*

Complexity associated with krill behaviour will also be important, but necessitates major assumptions about daily and seasonal behavioural patterns (e.g. Thorpe et al., 2007). Recently, Reiss et al. (2017) reported that the median krill abundance in the Bransfield Strait during winter was generally an order of magnitude higher (8 krill m^{-2}) than in summer (0.25 krill m^{-2}), and that the same pattern occurred in all winters regardless of ice cover. Reiss et al. (2017) also observed that acoustic estimates of krill biomass were an order of magnitude higher in winter (e.g. ~5,500,000 t in 2014), compared with the 15 year mean in summer (e.g. 520,000 t). Reiss et al. (2017) suggested that such observations were consistent with the hypothesized shelf-ward seasonal movement of krill from offshore waters during autumn and winter

(Siegel, 1988; Trathan et al., 1993). However, other explanations are also plausible, but remain untested. For example, during the summer, large numbers of land-based central-place predators forage within shelf waters. Given their breeding constraints, such predators may differentially target krill swarms with mature animals, given their greater energy content, particularly females (Hill et al., 1996; Reid et al., 1996). This could result in a reduction of the numbers of mature krill over such areas. As autumn approaches and spatial constraints on central-place predators decrease, or as predators leave the area, inflow of krill via the local oceanographic gateways may lead to an apparent increase, or recovery, in average krill size. In addition, winter krill biomass might also increase if predators are feeding elsewhere. Such an alternative hypothesis would be plausible, and consistent with Reiss et al. (2017).

Determining the reasons behind elevated winter biomass will be important, as such biomass could be vital for predators in the following year, for example during the ensuing spring and early summer (Trathan et al., 2021). Consequently, seasonal behaviour coupled with movements of krill may be critically important at scales relevant to both predators and the fishery. The consequences of behavioural aspects are not only important within Subarea 48.1, but also more broadly. For example, Piñones et al. (2013b) and Capella et al. (1992) noted that predictions of off-shelf transport from the west Antarctic Peninsula, support the hypothesis that spawning contributes to populations downstream across the Scotia Sea. Further, age-dependent sea ice associated behaviour may be important in the transport and distribution of krill populations (Thorpe et al., 2007), with subsequent impacts on geographically-constrained foragers.

Other aspects of krill behaviour, including swarm formation in response to potential biological and physical processes, is a precursor for understanding which swarms are targeted by predators and the fishery alike, and as such, Lagrangian models (e.g. Hofmann et al., 2004) incorporating neighbour-neighbour interactions, random diffusion, proximity to food and predation can help identify ecological uncertainties for management. Diel vertical migration (DVM) over a 24 h cycle may also have implications for krill availability to some predators (including the fishery), although, Piñones et al. (2013b) noted that DVM made little (<10%) difference in the horizontal and vertical dispersion of particles.

4.5. *Future management options for krill*

At present, all management approaches are severely data-limited with respect to krill movement, krill behaviour and predator demand. This is because the complex ecosystem structure and biological diversity within the southwest Atlantic arises from the combination of numerous biological and physical interactions. In this area, not only are there populations of krill-dependent predators that are decreasing, for example chinstrap penguins (e.g. Lynch et al., 2012; Strycker et al., 2020), but there are also populations that are now recovering following previous unsustainable exploitation of, for example, fish and marine mammals (e.g. Kock, 1992; Reilly et al., 2004; Branch, 2011). Climate change (Stammerjohn et al., 2008; Vaughan et al., 2013; Larsen et al., 2014; Cook et al., 2016) is also leading to significant alteration, with consequences reported at the base of the foodweb (Moline et al., 2004) and for mid-trophic levels (Atkinson et al., 2004, 2019; Flores et al., 2012; Kawaguchi et al., 2013; Freer et al., 2019). Given this complexity, the data and management infrastructure required to manage the krill fishery at small spatial and temporal scales appears daunting.

Improved understanding requires data if such processes are to be modelled and eventually disentangled from any impacts from harvesting. Management might eventually involve compromises that may disadvantage certain ecosystem components over others, albeit within the context of CCAMLR's management objective, depending upon the location, timing and intensity of harvesting. Without adequate data, such compromises are likely to be arbitrary and may have unintended consequences.

For the fishery to comply with CCAMLR's objective (see Supplementary Information) whilst catches concentrate in coastal areas, a number of big changes are likely to be necessary. Key information gaps need to be addressed, and can be summarised as the need to improve understanding about:

- the movement and retention of krill in ocean currents (e.g. Capella et al., 1992; Piñones et al., 2013b);
- the consequences of krill behaviour on abundance and distribution (e.g. Hofmann et al., 2004; Meyer et al., 2017);
- the drivers of seasonal patterns of krill abundance and distribution (e.g. Siegel, 1988);
- the spatial distribution and consumption requirements of krill-dependent predators (e.g. Warwick-Evans et al., 2021); and,
- the consequences for the ecosystem of marine mammal recovery and climate change (e.g. Branch, 2011).

In near-shore areas where ecological dynamics vary between years (e.g. Fraser and Hofmann, 2003), and evolve over days to weeks (Fig. 9), management is likely to remain challenging. As such, a pragmatic and effective management solution is necessary for near-shore areas. Trathan et al. (2021) suggest a prioritisation of information gaps for krill fisheries operating at South Georgia (Subarea 48.3), with the highest priority proposed as improved estimates of the local standing stock of krill biomass in each area used by the fishery, preferably with surveys prior to the start of fishing and after fishing is complete. Without an improved understanding of seasonal population abundance, management will need to remain highly precautionary. Such information would help facilitate development of a krill stock hypothesis accounting for movement, behaviour and abundance.

In the mean time, the simplest method to ensure precautionary management in near-shore areas during critical ecological time-periods is to limit catch concentrations within sensitive areas. This could be implemented using move-on rules and catch limits based on local ecological properties, and would best be parameterised using up-to-date ecological data for all parts of Subarea 48.1, given that all locations vary (Supplementary Information Table 8). However, given the scientific infrastructure needed to determine relevant local ecological properties, rules based on a fixed harvest limit for each grid cell (pragmatically greater than 10 × 10 km; Supplementary Information Table 6) might be more feasible.

Alternatively, maintenance of seasonally closed coastal buffers, such as the VBZ, during critical ecological time-periods (Supplementary Information Table 8) could be used to manage coastal catch limits; however, improvements to the VBZ will be needed. For example, the transition date from open to closed might usefully be reviewed, especially as peak harvesting now occurs in March to May (Supplementary Information Tables 2, 3, 4 and 5), overlapping in space and time with resident gentoo penguins and some naïve, recently fledged chinstrap penguins (Hinke et al., 2019). Whether closed areas are seasonal or year round, and the date of transition from closed to open, creates different levels of fishery displacement (Supplementary Information Table 7), and thus different concerns for the ecosystem and for the fishery. The VBZ might also be extended to include other near-shore areas in Subarea 48.1 (e.g. Elephant Island) and around coastal areas at the South Orkney Islands (Subarea 48.2), particularly where whales (Viquerat and Herr, 2017) and chinstrap penguins (Warwick-Evans et al., 2018) occur in abundance.

Options that would eventually allow the fishery to develop in some near-shore areas include adaptive-management based on an agreed experimental framework (see SC-CAMLR-XXXVI, 2017 paragraphs 3.17 to 3.22; SC-CAMLR-XXXVII, 2018 paragraphs 3.27 to 3.28). This should be designed to provide new understanding about krill-predator-fishery interactions, including within coastal areas.

4.6. *Important research topics especially within coastal areas during critical ecological time-periods*

In Subarea 48.1, harvesting traditionally occurred between December and June, making it feasible to undertake regular acoustic surveys using the fishing fleet to estimate krill standing stock (Godø et al., 2014). Autonomous survey platforms such as gliders and moorings may offer future opportunities (Guihen et al., 2014), though these can be compromised by ice. To understand the dynamic nature of the ecosystem and the natural cycle of krill (e.g. Siegel, 1988; Trathan et al., 1993), acoustic surveys should take place each month, at least until such a time that we understand seasonal changes in biomass (c.f. Reid et al., 2010; Saunders et al., 2007). These surveys should extend into all areas where harvesting occurs, including coastal locations where fishing is concentrated (Trathan et al., 2018; Supplementary Information Fig. 1). Small-scale before-and-after acoustic surveys to determine the degree of stock depletion (and recovery) by the fishery will also be key.

Fishing vessels also offer opportunities to use modern drone technology (e.g. Korczak-Abshire et al., 2019) to update penguin colony population estimates, and undertake cetacean sightings. Collaboration and joint endeavours between CCAMLR, ARK and the International Whaling Commission, will therefore be important, including to better understand compensatory competition for krill amongst different predator species (e.g. Laws, 1977; Ballance et al., 2006; Trathan et al., 2012).

5. Conclusion

An effective ecosystem approach to management at small spatial and temporal scales demands a fundamental understanding of basic ecology, and therefore the necessary integration of critical data layers. At present, the required ecological data are not available for managing at these scales across the wider area used by the fishery, but especially in Subarea 48.1, and as previously identified, Subarea 48.2 (Trathan et al., 2016).

Implementing a staged approach to management for the most ecologically complex areas, that is near-shore areas, is a pragmatic management option. Better ecological understanding of the spatial and temporal distribution of non-target life stages (Perry et al., 2019) or species (Rombolá et al., 2019) of krill, as well as of larval and juvenile fish (Everson et al., 1992), will provide further confidence of fishery sustainability (See Supplementary Information). Cetaceans are key consumers of krill, but CCAMLR has so far not considered this major gap in ecosystem understanding.

Pressures on the Antarctic are likely to increase over the 21st century (Rintoul et al., 2018). Maintaining CCAMLR is therefore vital, and necessitates that any future management approach reflects the prevailing operation of the fishery. Finding a pragmatic solution to management is key, balancing the need for data with adequate levels of precaution.

Declaration of Competing Interest

None.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jmarsys.2021.103598.

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