ICES Journal of
Marine Science

International Council for the Exploration of the Sea
Conseil International pour l'Exploration de la Mer

ICES Journal of Marine Science (2021), doi:10.1093/icesjms/fsab092

Enhancing the ecosystem approach for the fishery for Antarctic krill within the complex, variable, and changing ecosystem at South Georgia

P. N. Trathan *, S. Fielding, P. R. Hollyman , E. J. Murphy, V. Warwick-Evans , and M. A. Collins

British Antarctic Survey, NERC, High Cross, Madingley Road, Cambridge, CB3 0ET, UK

**Corresponding author: tel: +44(0)1223 221602; e-mail: pnt@bas.ac.uk.*

Trathan, P. N., Fielding, S., Hollyman, P. R., Murphy, E. J., Warwick-Evans, V., and Collins, M. A. Enhancing the ecosystem approach for the fishery for Antarctic krill within the complex, variable, and changing ecosystem at South Georgia. – ICES Journal of Marine Science, doi:10.1093/icesjms/fsab092.

Received 8 September 2020; revised 29 March 2021; accepted 30 March 2021.

The objective of the ecosystem approach to fisheries management is to sustain healthy marine ecosystems and the fisheries they support. One of the earliest implementations was in the Southern Ocean, where decision rules and stock reference points were developed for managing the Antarctic krill fishery, together with an ecosystem-monitoring programme intended to aid management decisions. This latter component has not been incorporated directly into management, so here, we consider variability in the krill fishery at South Georgia, relating it to physical and biological monitoring indices, finding sea surface temperature to be a key correlate with both annual catch and long-term biological indices. Some indices from krill predators showed significant positive relationships with krill harvesting in the preceding winter, presumably indicative of the importance of winter foraging conditions. We explore how ecological structure affects results, examining two monitoring sites 100 km apart. Results suggest different biological conditions at the two sites, probably reflecting different scales of ecosystem operation, emphasizing that an appreciation of scale will enhance krill fishery management. Finally, in reviewing different drivers of ecological change, we identify important additional monitoring that would help better reflect ecosystem status, improve the utility of CEMP, providing information necessary for the ecosystem approach at South Georgia.

Keywords: Antarctic krill, CCAMLR, ecosystem approach to fisheries management, ecosystem change, ecosystem monitoring, ecosystem variability, environment drivers, South Georgia

Introduction

To move beyond single-species fisheries management, the ecosystem approach [Early on, Garcia *et al.* (2003) recognized that the lexicon of terms associated with the ecosystem approach was not universally defined but was progressively evolving (see also Trochta *et al.*, 2018). Now, as the terminology matures, we follow definitions used by Patrick and Link (2015), who define the ecosystem approach (typically for a single species) as having a stock focus in order to enhance understanding about fishery dynamics ensuring stock-focused management decisions are better informed through the inclusion of ecosystem factors (see also Link and Browman, 2014).] incorporates ecosystem considerations to ensure sustainable utilization of marine resources (e.g. Garcia *et al.*, 2003; Pikitch *et al.*, 2004). The approach is now widely used across a growing number of states and a wide range of fisheries, recognizing local context, definitions, and meaning (e.g. Pitcher *et al.*, 2009). Considerations of the ecosystem approach are of particular interest for all fisheries, but increasingly in relation to fisheries for forage species where competition with dependent predators is a major concern (e.g. Cury *et al.*, 2011;

Pikitch *et al.*, 2014, 2018; Hilborn *et al.*, 2017; Sydeman *et al.*, 2017). One of the earliest attempts at developing the approach was in the Southern Ocean in the early 1980s, when at that time it was an entirely new concept for any management convention (Agnew, 1997). The approach became enshrined in Southern Ocean management, such that the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) agreed to limit harvesting in order to maintain ecological relationships and prevent changes to the marine ecosystem that might result from fishing, and which might take longer than two or three decades to reverse.

CCAMLR is the major governance structure for managing Southern Ocean fisheries, providing opportunities for stakeholder engagement amongst the 26 Members, and with Observers. CCAMLR's Scientific Committee and its subsidiary Working Groups provide opportunities for management debate, including about relevant ecosystem processes. CCAMLR utilizes the precautionary approach using the best available data. Fisheries are each the subject of a detailed fishery report. CCAMLR's Commission agrees Conservation Measures that impose legally binding quotas, management measures, and other fishery-related requirements based on the Scientific Committee's advice on stock attributes, decision rules and reference points, and ecosystem considerations.

The implementation of the ecosystem approach, in particular for the harvesting of Antarctic krill (*Euphausia superba*), a key forage species in the Southern Ocean, required CCAMLR to develop novel techniques and new ideas. Key was the development of a yield model that considers the status of the krill stock including growth, recruitment, and mortality, etc., and which for a number of decades, has been successfully combined with precautionary decision rules and stock reference points (Constable, 2001, 2011; Constable *et al.*, 2000). CCAMLR also implemented an Ecosystem Monitoring Programme (CEMP) with the express aim of detecting ecosystem change and determining whether observed changes are due to natural environmental events, or fishing (Agnew, 1997).

CEMP focusses on high-trophic level species, primarily seabirds and marine mammals, as these are believed to integrate ecosystem variability (e.g. Boyd and Murray, 2001), with predator performance reflecting ecosystem status throughout the year (e.g. Trathan *et al.*, 2006; Boersma, 2008; Cury *et al.*, 2011), contrasting with shipboard measurements that generally only provide a temporal snapshot of the ecosystem. Based on such assumptions, Bengston (1984) and Green-Hammond *et al.* (1984) developed the objectives of CEMP but recognized that monitoring of all species was not practical (Bengston, 1984). Consequently, CCAMLR identified a suite of indicator species that now form the core of CEMP. CEMP does not consider pelagic predators such as finfish or whales, and all monitoring metrics are land-based. As such, the CEMP standard methods (CCAMLR, 2014) mostly relate to performance parameters for krill-eating penguins, albatrosses, and seals.

CCAMLR has generally considered CEMP to be an extremely powerful tool for understanding and managing the Antarctic marine ecosystem (Agnew, 1997). This is because harvesting could lead to competition for krill, a key trophic link, or to disturbance of krill swarms, thereby leading to impacts on krill-dependent predators. However, identifying positive or negative impacts on predators beyond a reasonable doubt requires statistical power, and this may only become evident over long timescales (e.g. Henson *et al.*, 2016). In 2003, CCAMLR recognized that at current harvesting levels, with the existing design of CEMP monitoring, and with the data duration available, it was unlikely that managers could distinguish between ecosystem changes resulting from harvesting, and changes due to environmental variability, whether physical or biological (CCAMLR, 2003). Moreover, CCAMLR also recognized that with the existing design of monitoring, it might never be possible to distinguish between these different and potentially confounding causal factors (CCAMLR, 2003).

CEMP has provided data and understanding in support of various management measures; however, CCAMLR has never incorporated CEMP directly into management processes. Importantly, CCAMLR has not used CEMP to set objectives for predator populations (Constable, 2011). The development of CEMP has proved challenging. Perhaps, partly because of low fishery demand for krill products; partly because of the large spatial scales of the region fished (the krill fishery operates across the Scotia Sea, from the west Antarctic Peninsula to South Georgia; Figure 1); and, partly because of the complexity of ecosystem interactions, including foodweb connections with numerous predators dependent upon krill. Indeed, the data currently available from monitoring krill and its predators and for determining the abundance of predator populations remain insufficient to reduce large uncertainties, and hence identify potential fishery impacts on the ecosystem; moreover, given existing research activities, these uncertainties are unlikely to be resolved quickly (Constable, 2011).

The role of indicators (of both the stock and the ecosystem) is central to a decision framework in the ecosystem approach (Link, 2005), as they permit assessment of the status of a system and because they can form the basis for developing or testing both empirical and theoretical reference and/or limit values (e.g. Sainsbury and Sumaila, 2001). The challenge is to establish ecosystem control rules that prescribe particular management actions if the indicator-based thresholds are exceeded (Sainsbury and Sumaila, 2001). CCAMLR has already developed stock reference and limit values, and a set of CEMP indices, but has no clarity about whether CEMP indices provide robust indicators for management, or how they might react as krill catches approach the CCAMLR reference points.

Recently, CCAMLR has sought to reduce perceived ecosystem risks across the southwest Atlantic (Figure 1), by spatially allocating catch in a manner that not only minimizes risks to predators, but also to the krill stock itself and to the fishery (CCAMLR, 2019a). The revised CCAMLR approach now under development focuses on three priority elements:

(i) Regular updates of biomass estimates for krill, initially at the Subarea scale, but potentially at multiple scales;
(ii) A stock assessment to estimate precautionary krill harvest rates; and
(iii) A risk assessment framework to inform the spatial allocation of krill catch.

Part of the impetus for CCAMLR to develop the new management framework was the recognition that krill catches have become increasingly concentrated (e.g. CCAMLR, 2016), with vessels now repeatedly visiting a small number of fishing hotspots. Management at these smaller scales has important implications for data collection to inform management decisions.

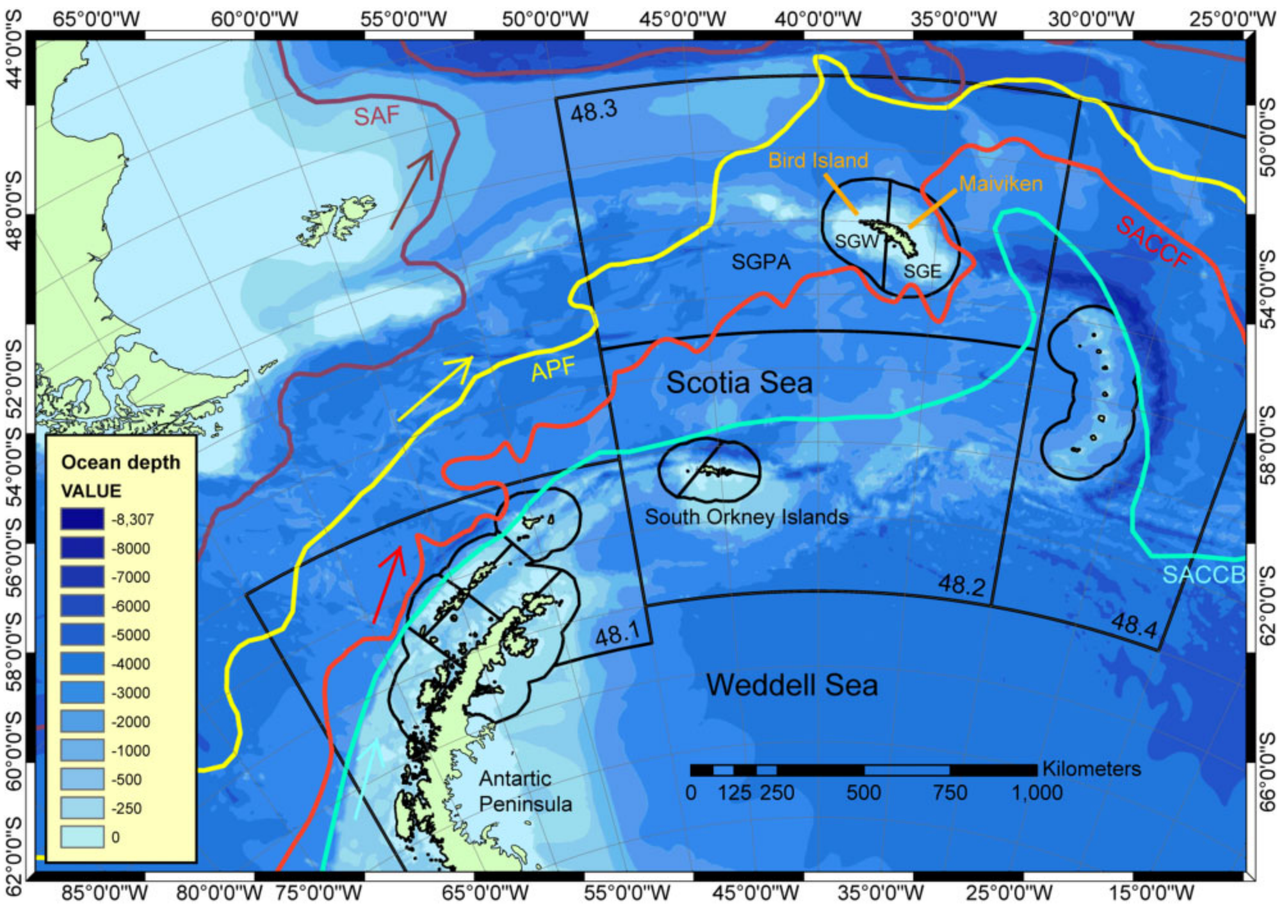

Figure 1. The Scotia Sea showing the location and direction of flow for the major fronts in the Antarctic Circumpolar Current (ACC)—Brown: Sub-Antarctic Front (SAF); Yellow: Antarctic Polar Front (APF); Red: Southern ACC Front (SACCF); Blue: Southern ACC Boundary (SACCB). The locations of Bird Island and Maiviken are indicated. The krill fishery Small Scale Management Units are shown (Hewitt *et al.*, 2004), with South Georgia West (SGW), South Georgia East (SGE), and South Georgia Pelagic (SGPA) identified.

Assessments of krill fisheries management have considered harvesting to be precautionary (Hill *et al.*, 2016); however, as catches increase and continue to concentrate in space and time, indicators of ecosystem status will become increasingly important for ensuring CCAMLR is meeting its obligations to maintain ecological interactions. Here, we consider the management implications at one of the important hotspots for the krill fishery, South Georgia, where catches are now increasing and becoming increasingly aggregated.

Management at South Georgia incorporates all measures agreed internationally through CCAMLR, as well as additional domestic measures designed to reduce further risks to the krill-based ecosystem. Local regulations include a seasonal prohibition on krill fishing during the summer months when many krill predators are provisioning offspring, coupled with coastal no-take fishery exclusion zones that protect near shore communities throughout the year (Trathan *et al.*, 2014).

Despite such precautions, risks may remain, particularly given regional climate change, together with observed variability in local oceanographic conditions (e.g. Trathan and Murphy, 2003; Whitehouse *et al.*, 2008). Further, biological change is also taking place across the Scotia Sea with reported changes in krill abundance and distribution (Atkinson *et al.*, 2019, but see also Cox *et al.*, 2019). Similarly, the major mammalian and avian consumers of krill at South Georgia are known to be changing (Boyd, 2002; Trathan *et al.*, 2012; Zerbini *et al.*, 2019), as are populations of krill-eating finfish, as they recover from historical over-exploitation (e.g. Kock, 1992; Kock and Jones, 2005; Belchier, 2013; Hollyman *et al.*, In Review). These changes in the physical environment and in the populations of krill and its predators (whales, seals, penguins, and finfish) now result in an increased urgency for improved understanding about ecosystem status and relationships between CEMP monitoring data and fishery harvest. Whilst catches remained low in relation to both krill biomass (CCAMLR, 2010) and predator demands (Boyd, 2002), CCAMLR had time to develop its management approach; however, increasing catches now require that all available monitoring indices are subject to detailed study.

Therefore, our primary goal for this article was to examine the utility of CEMP at South Georgia, exploring available monitoring data in relation to the annual catch of krill. In addition, we sought to provide further insights into whether CEMP data also show relationships with aspects of the changing environment. A further goal for this article was to identify any additional data necessary to help implement the three priority elements of CCAMLR's new strategy at South Georgia, in particular, to identify important data that would enhance the utility of CEMP to better reflect ecosystem status. Finally, some key management data are not currently available for South Georgia but are vital for continued precautionary management; developing a broad scope for a fisheries risk assessment (e.g. Sainsbury and Sumaila, 2001) should help identify key missing data that will enhance sustainable management.

Methods

A comprehensive assessment of the krill fishery at South Georgia, and at other fishery hotspots, requires a considerable body of work. Background information that underpins our initial analysis in respect of physical variability, biological variability, and krill fishery catch variability are included in Supplementary Material SA–SC, respectively.

Statistical analyses

We used R version 3.2.2 (2015-08-14; The R Foundation for Statistical Computing Platform: i386-w64-mingw32/i386 [32-bit]) and RStudio (version 1.0.136; RStudio, Inc.) to develop statistical analyses. We used ArcGIS (ESRI version 10.4.1) for all spatial analyses.

Variability in the krill fishery

CCAMLR collates reports of krill catch and effort from the commercial fishery, with data available upon request from the CCAMLR Secretariat. The spatial resolution of early records is less precise than of later data; early records combine data spatially (e.g. 0.5° lat × 1.0° long) and temporally (e.g. 5-day or 10-day), whilst later data are at the resolution of the individual haul. The data we used included haul-by-haul data until the end of the 2017/2018 fishing season (CCAMLR C1 Catch and Effort Data 2019). Throughout, we refer to each CCAMLR fishing season, December to November, by the year of the end date, thus 2018 = 2017/2018.

We used ArcGIS to sum all hauls for catch (tonnes) and effort (hours fished). We considered all hauls from all CCAMLR Members, whether conventional mid-water trawls, or those using the continuous fishing system (Nicol *et al.*, 2012). To document krill fishing activity at South Georgia, we considered the period from the 1980 fishing season, with a greater focus on the years of overlap with krill-dependant predator monitoring (especially since 2009).

In addition, we undertook analyses of annual catch in relation to various physical and biological monitoring indices. For these analyses, we focused upon the most recent years (from 2006 onwards; see Supplementary Material SC) as the fishery had by that time settled into a regular pattern of operation. In exploring whether physical indices are related to catch variability (c.f. Fedulov *et al.*, 1996), we considered the Southern Oscillation Index (SOI), the El Niño-Southern Oscillation (ENSO), the Southern Annular Mode (SAM), and local sea surface temperature (SST); these analyses, methods, and results are described in Supplementary Material SC.

CEMP data

Monitoring of various predator indices (e.g. penguin arrival weight, fledging weight, and breeding success; see Supplementary Material SB) takes place at Bird Island, South Georgia (Figure 1) where data on four krill-eating CEMP species are collected; black-browed albatross (*Thalassarche melanophrys*), gentoo penguins (*Pygoscelis papua*), macaroni penguins (*Eudyptes chrysolophus*), and Antarctic fur seals (*Arctocephalus gazella*). Other predator species are also monitored at Bird Island but are not part of CEMP. Here, we focus on the three diving CEMP species as these are most heavily constrained during the summer breeding season; these species are limited in their foraging range, unlike black-browed albatross that can forage far beyond the South Georgia archipelago. Moreover, black-browed albatross population declines are ongoing and largely influenced by mortality in long-line fisheries (Pardo *et al.*, 2017).

Gentoo penguins and Antarctic fur seals are also monitored at a second site at South Georgia, Maiviken (Figure 1), but data are of shorter duration. All CEMP data are short by meteorological standards, where climatological standards indicate the need for averages of climatological data computed for consecutive periods of 30 years (www.wmo.int/datastat/wmodata_en.html; accessed 10 May 2021). Throughout, we refer to each penguin or seal breeding season by the year that offspring become independent, thus 2018 = 2017/2018.

There are nine other CEMP sites across the Scotia Sea, including at the Antarctic Peninsula and the South Orkney Islands. The maximum number of monitored CEMP species at any of these sites is three, either three penguin species, or two penguin species plus Antarctic fur seals. CEMP monitoring at South Georgia is therefore representative of all other sites near to krill fishing areas.

To explore long-term variability in the predator monitoring indices from Bird Island, we carried out multivariate analyses of the CEMP data, relating the output to known drivers of ecosystem variability. We considered SOI, ENSO, SAM, as well as local SST (e.g. Trathan and Murphy, 2003; Trathan *et al.*, 2006; Whitehouse *et al.*, 2008; Fielding *et al.*, 2014). In addition, we also related the output from the multivariate analyses to local extraction by the commercial krill fishery (Trathan *et al.*, 1998). These analyses and results are reported in Supplementary Material SB.

We also evaluated differences in predator monitoring indices between Bird Island and Maiviken, using regression to detect whether there were consistent trends between the two sites. These analyses and results are also described in Supplementary Material SB.

Monitoring of gentoo penguins began at Bird Island in the early 1980s. Breeding phenology is determined each year across two colonies, based on the date that the first egg appears and the date by when 75% of monitored nests have eggs. In our analyses, we related these dates to the number of days before or after 1 October. Based on this chronology, the timing of all other monitoring indices are determined. Indices include the number of nests, chicks hatched, breeding success (chicks fledged per nest), and chick fledging weight. Monitoring of gentoo penguins at Maiviken, ~100 km to the southeast of Bird Island, began in the 2009 breeding season, with more complete monitoring from the following year. Methods are the same as at Bird Island, but using just one chronology colony.

As part of our comparison between sites, we also considered Antarctic fur seal pup mass gain. At the Bird Island special seal study beach, fur seal breeding phenology is determined each year (Doidge *et al.*, 1984; Forcada *et al.*, 2005; Forcada and Hoffman, 2014). Based on this, a random selection of pup weights are recorded from nearby Freshwater Bay; this takes place annually in January, February, and March, at standard times beginning one month after peak pupping. On each occasion, more than 100 pups are weighed (male pups tend to be heavier, so samples include approximately equal sex ratios), with approximately half taken from the beach and half from the surrounding tussac grass. At Maiviken, peak pupping is also determined, with pups also weighed in January, February, and March. To explore variability in pup mass between sites, we created box plots for each site for each year and evaluated differences between Bird Island and Maiviken with an analysis of variance. To explore possible environmental relationships with different parts of the seasonal cycle leading up to the breeding season, we compared pup mass with indices of SST from the closest area of the ocean (see Supplementary Material SA for SST data sources).

Results

Variability in the krill fishery

The krill fishery at South Georgia is currently a winter-only fishery, though in earlier years it also operated during the summer. The switch to winter occurred in 1990; initially through vessel choice, but later under domestic legislation that prohibited krill fishing during the predator summer breeding season. Although never achieved, the current CCAMLR allowable catch limit for the Subarea (South Georgia lies with FAO Subarea 48.3) is 279000 t; this was first set in 2009. The level of harvest varies inter-annually (Figures 2 and 3), with the highest-ever catch in the 1987 fishing season, when 312134 t was taken.

Early exploitation occurred across a broad region to the north of South Georgia, including oceanic offshore areas. However, harvesting rapidly aggregated in preferred areas, focussing along the northern shelf (Figure 2). The spatial distribution of catches varies between years and over longer time scales, with lower catches to the north of Bird Island in recent years (Figure 2). Of the total catch at South Georgia between 2002 and 2018, more than 76% (559964 t) was taken to the northeast of Maiviken, with only 24% (175725 t) taken to the west (Figure 2). Currently, the preferred area of operation is close to the northern shelf edge, over a series of submarine banks and gullies (see Trathan *et al.*, 1998) with a preference for the edge of the banks and gullies in water depths of 180 to 280 m (Figure 2; Supplementary Figure S14). More than 63% of catches have come from within this depth stratum since the fishery began.

From 1991, when the catch was 87898 t, until 2020 when the catch was 115268 t, catches have remained below 75500 t. Since 1991, the lowest catches were in 1993 (13776 t), 1999 (0 t), 2000 (19346 t), 2006 (14901 t), 2009 (1 t), 2010 (8834 t) and 2017 (18558 t). Annual catches (t) relate to effort (h) in a linear manner, for both traditional mid-water trawls and for the continuous fishing method (Supplementary Figure S15). In years when the annual catch was high, catches from both traditional mid-water trawls and from the continuous fishing method increased (Supplementary Figure S16).

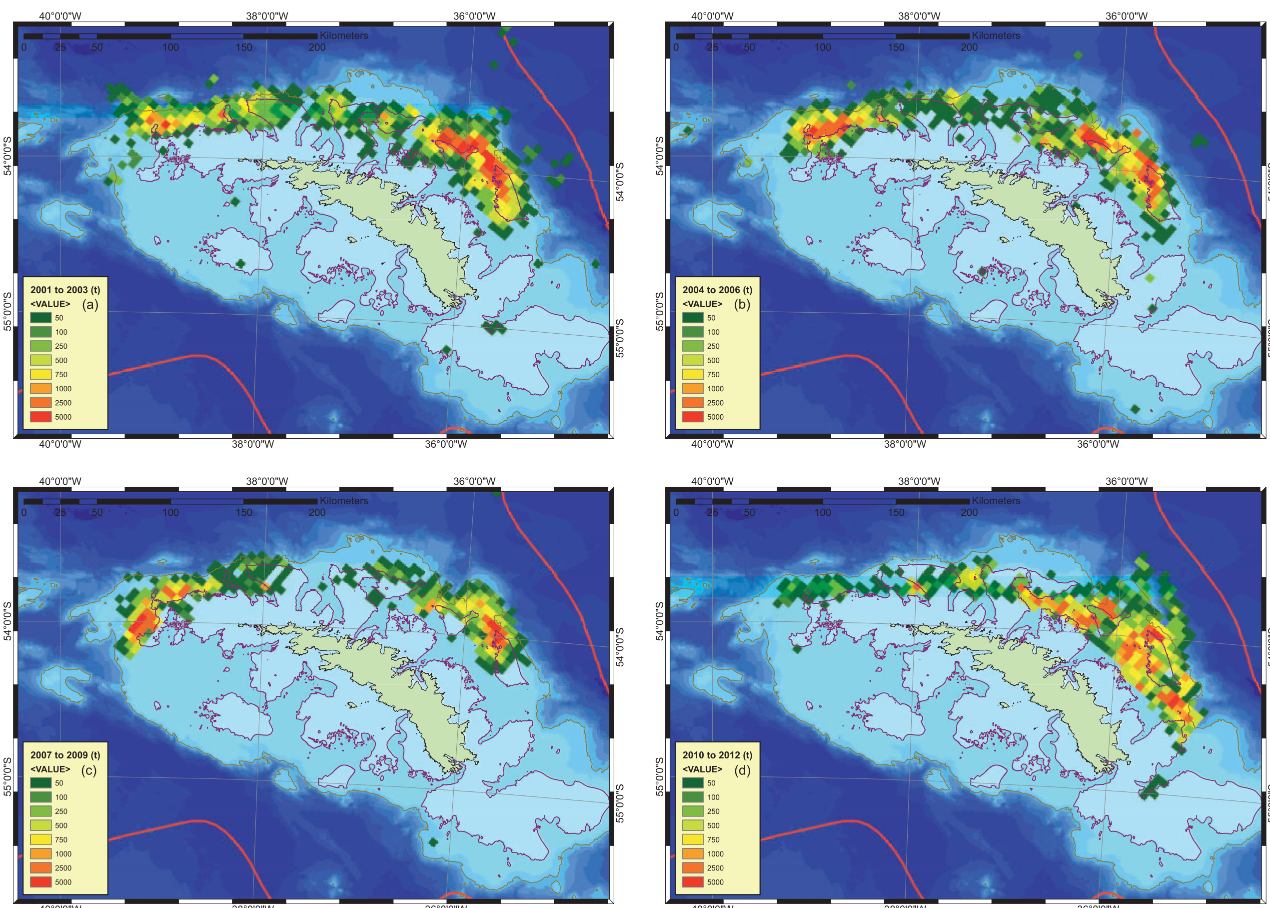

Figure 2. Distribution of winter krill catches at South Georgia; shown in red is the location of the Southern ACC Front (Figure 1). (a) 2001–2003; (b) 2004–2006; (c) 2007–2009; (d) 2010–2012; (e) 2013–2015; (f) 2016–2018; (g) Proportion of catches in pelagic (SGPA), western (SGW), and eastern (SGE) waters (see Figure 1 and Hewitt *et al.*, 2004).

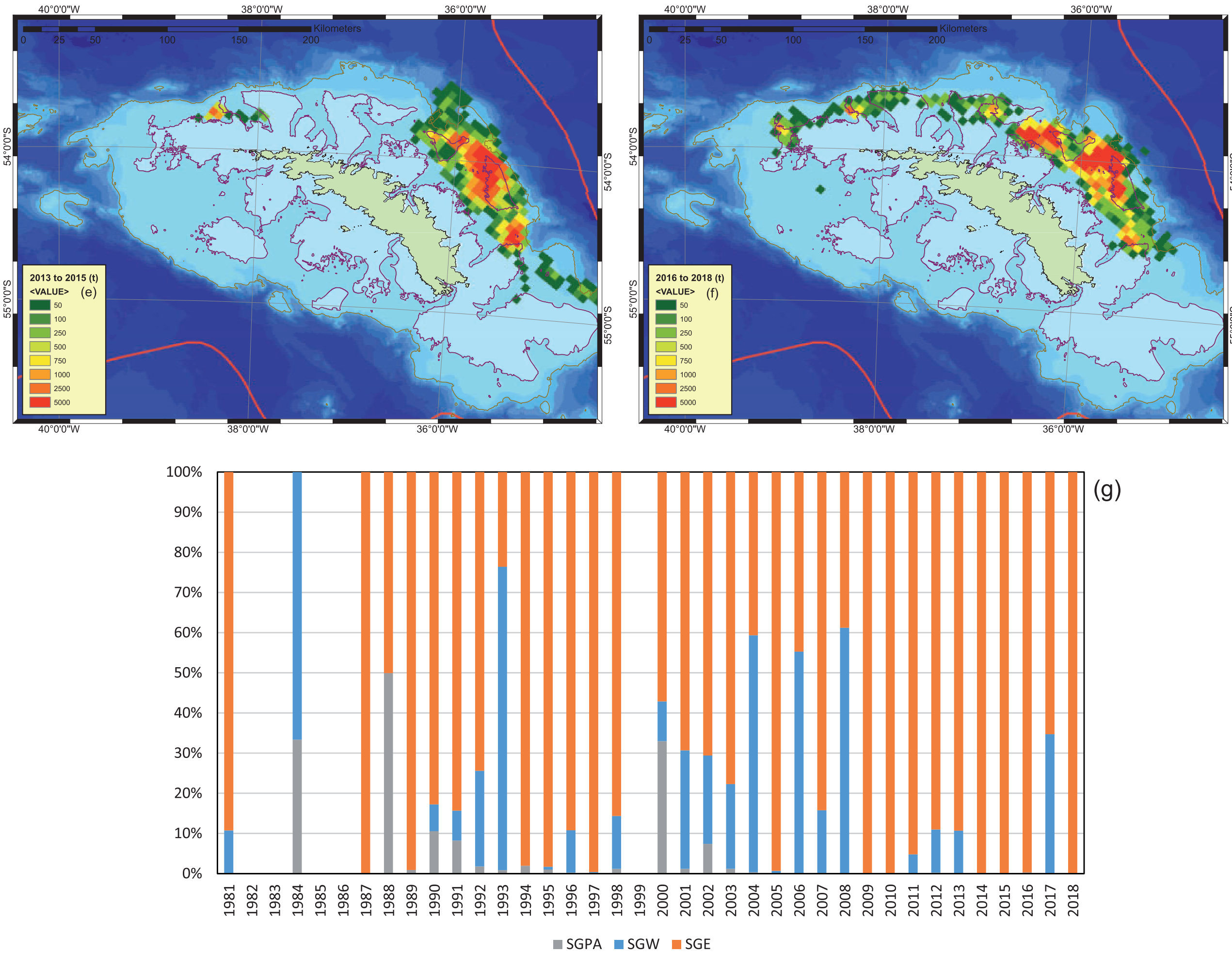

Figure 2. Continued.

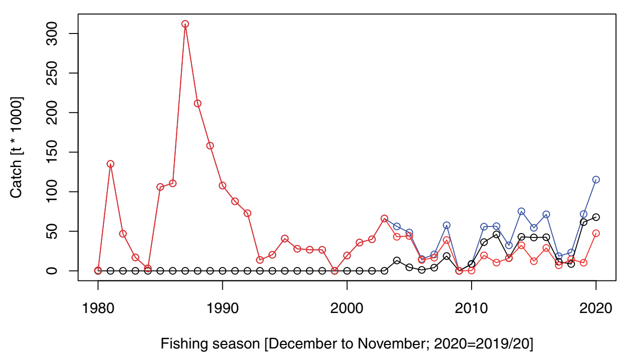

Figure 3. Annual krill catch ($t \times 10^3$) at South Georgia; blue is total catch, red is catches made with traditional mid-water trawls, and black is catches made with the continuous fishing system. Some early catches (before 1988) cannot be attributed in space or time. The local interim catch limit is 279000 t.

Analyses for the full duration of the catch history showed no relationships between annual catch and SST; this was the case for temperatures for any month in the preceding year from either the west or east of South Georgia (maximum Pearson correlation coefficient was −0.2). However, some of the years with low catches occurred just before or just after warmer ocean conditions; for example, mid-late 1993, early 2000, mid-2006, early 2009, late 2010, and late 2017. In these years, catch (<20000 t) was low. In contrast, analyses of annual catches from 2006 onwards did reveal a significant relationship with SST during the early part of the fishing season ($F = 5.258$, df = 1, 13, Adj $R^2 = 0.233$, $p < 0.039$; Figure 4; see also Supplementary Figure S17).

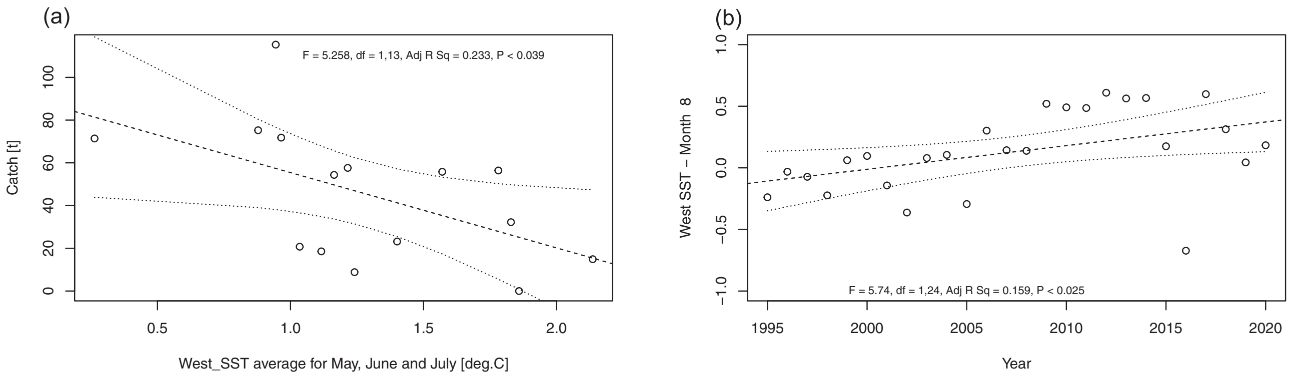

Figure 4. (a) Annual krill catches ($t \times 10^3$) at South Georgia from 2006 onwards in relation to sea surface temperature averaged across May, June, and July (see also Supplementary Figure S17). (b) Sea surface temperature trend in August over the period since 1995.

CEMP monitoring indices for gentoo penguins—comparison between sites

The monitoring metrics for gentoo penguins at Bird Island and Maiviken showed consistent significant relationships between sites (Table 1), good years and poor years were consistent between sites with no lag. For chick fledging mass, no weights were available in years with complete breeding failure and in general, fledging mass was greater at Bird Island than at Maiviken.

Gentoo penguins experienced reduced reproductive performance in 1990, 2004, and 2005 and major breeding failures (<0.5 chicks per nest) in 1991, 1994, 1998, 2009, and 2016 (Figure 5). Some, but not all of these failures followed major warming events (Figure 7); we found no significant relationships with SST.

The number of nests at Bird Island (linear regression F = 13.05, df = 1, 30, Adj $R^2 = 0.280$, $p < 0.001$) and at Maiviken (linear regression F = 3.10, df = 1, 10, Adj $R^2 = 0.160$, $p = 0.109$) indicated a possible relationship with the krill catch level in the preceding winter. Seasons of fewer nests followed less productive fishing seasons, potentially indicative of carryover effects following from winter-feeding conditions. No other gentoo penguin monitoring indices showed a significant relationship with krill catch.

CEMP monitoring indices for Antarctic fur seals—comparison between sites

Variability in the numbers of fur seal males, females, and pups showed no correlation between Bird Island and Maiviken (maximum Pearson correlation coefficients <0.57). The numbers at Bird Island have been decreasing at a significant rate over the period 2002 to 2020, whereas the numbers at Maiviken are either

Table 1. Relationship between various gentoo penguin monitoring indices at Bird Island and at Maiviken.

Property	Linear regression
Number of nests	F = 10.72, df = 1, 10, Adj $R^2 = 0.469$, $p < 0.005$
Date first egg appeared	F = 36.64, df = 1, 9, Adj $R^2 = 0.781$, $p < 0.001$
Date of peak egg laying	F = 45.98, df = 1, 9, Adj $R^2 = 0.\ 818$, $p < 0.001$
Number of chicks per nest	F = 7.17, df = 1, 10, Adj $R^2 = 0.359$, $p < 0.023$
Breeding success	F = 27.46, df = 1, 10, Adj $R^2 = 0.359$, $p < 0.001$
Chick fledging mass	F = 8.27, df = 1, 8, Adj $R^2 = 0.447$, $p < 0.021$

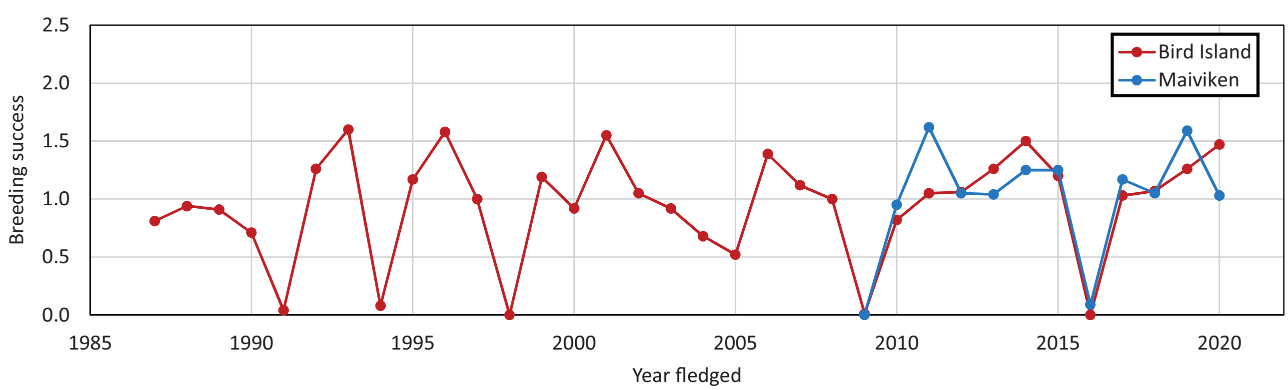

Figure 5. Breeding success (chicks per nest) for gentoo penguins at Bird Island (1987–2020) and at Maiviken (2009–2020).

stable or increasing (Supplementary Figures S9–S13). There was considerable interannual variation and the linear regressions were not statistically significant over the recent period since 2009. However, a loess local polynomial regression with variability bands set at ± 1 standard deviation (Supplementary Figure S11) shows evidence of the continuing decrease at Bird Island and increase at Maiviken since 2009, though the number of pups at Maiviken was at its highest around 2016. Note that the decreases reported here do not reflect a population demographic assessment, as in Forcada and Hoffman (2014), rather simple decreases in the numbers observed on the beach.

Antarctic fur seal pup mass indices from Bird Island and Maiviken showed considerable variation (Figure 6). During each of January, February, and March, there were statistically significant differences between the two sites (Table 2). In January, pups born at Bird Island were always on average smaller just after birth than those born at Maiviken (Figure 6). However, average pup mass apparently increased more rapidly at Bird Island than at Maiviken, and in many years, pups at each site were on average closer in mass by March (Figure 6). However, it is unclear whether the apparent growth rate at Bird Island was the result of differential mortality of smaller pups or better provisioning opportunities. In March, there were significant differences between years (Table 2).

Years when the mean pup mass at Bird Island remained lower than at Maiviken in March, included 2009, 2013, 2016, and 2018 (Figure 6). Pup mass at Bird Island was also low in January 1991 and 1994, but no comparable data exist for Maiviken. Some, but not all years of low pup mass at Bird Island followed warmer ocean temperatures; for example, in mid-late 1993, early 2009, and late 2017 (Supplementary Figure S2). However, no detectable warming was evident before other low pup mass events.

Cross-correlation analyses for pup weights at Bird Island and local SST in the west (Supplementary Figure S1) showed a significant negative correlation. A regression model with the greatest level of significance (lowest p-value) using R library *olsrr* to add and subtract monthly temperature series in a stepwise manner, established August as the single most influential month. High temperatures in the preceding August were associated with lower pup weights in January over the period 1989–2020 (acf = −0.39, confidence limits assume white noise with $p < 0.05$, $n = 32$; linear regression F = 5.959, df = 1, 30, Adj R^2 = 0.138, $p < 0.020$). Pup weights in February and March also showed similar negative correlations with temperatures in the preceding August (respectively, acf = −0.47; linear regression F = 8.399, df = 1, 30, Adj R^2 = 0.193, $p < 0.007$, and acf = −0.35; linear regression F = 3.967, df = 1, 30, Adj R^2 = 0.087, $p < 0.056$). Cross-correlation analyses for pup weights at Maiviken and SST (either in the west or the east; Supplementary Figure S1) showed no significant correlations.

Despite the consistent aggregation of krill catches and the proximity of harvesting to Maiviken, no significant relationships were evident between the magnitude of the catch and the number, or mass of fur seal pups at Maiviken in the following January. However, relationships between the level of catch and the number of pups did suggest that as catches increased, the number of pups at Maiviken also increased (Catch: F = 3.898, df = 1, 10, Adj R^2 = 0.209, $p < 0.077$). This suggests that the fishery and fur seals may benefit from years with higher krill availability. No significant relationships were evident between fur seals at Bird Island, and catch levels.

CEMP data—ecosystem status

Results from a Principal Component Analysis (Supplementary Material SB) highlight that CEMP data from Bird Island show long-term change, with the most important changes related to indices that better reflect winter conditions (Supplementary Figure S5).

To further explore temporal variability at South Georgia (Figure 7), we plotted years with warmer ocean temperatures (Supplementary Figures S2–S4), years with poor gentoo breeding success (<0.5 chicks; Figure 5), years with low fur seal pup mass

Table 2. Analysis of variance of Antarctic fur seal pup weights in January, February, and March at Bird Island and Maiviken, South Georgia for the breeding seasons between 2009 and 2020.

	df	Sum Sq	Mean Sq	*F*	*p*
January					
Site	1	333	332.8	109.4	<0.001
Year	1	3	3.4	1.1	
Residuals	2424	7375	3.0		
February					
Site	1	441	440.9	85.0	<0.001
Year	1	11	10.9	2.1	
Residuals	2417	12545	5.2		
March					
Site	1	253	252.5	37.3	<0.001
Year	1	28	27.7	4.1	<0.050
Residuals	2404	16 280	6.8		

See Figure 6.

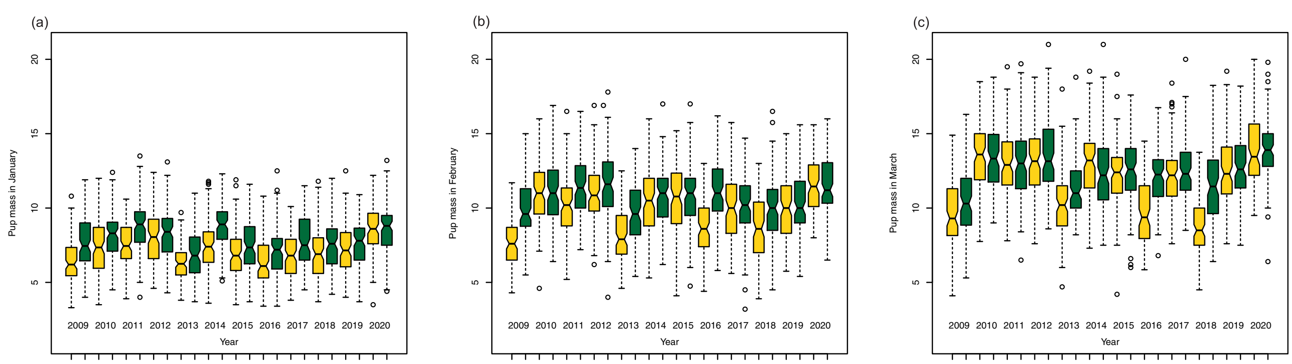

Figure 6. Antarctic fur seal pup weights in (a) January, (b) February, and (c) March at Bird Island (yellow) and Maiviken (green), South Georgia for the breeding seasons between 2009 and 2020. See also Table 2.

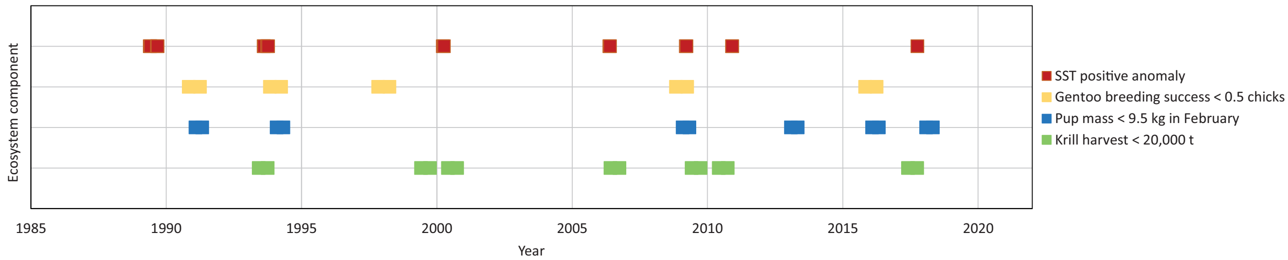

Figure 7. Temporal relationships between extreme SST events at South Georgia in the west (see Supplementary Figure S1), gentoo penguin breeding success <0.5 chicks per nest at Bird Island and Maiviken (see Figure 5), fur seal pup mass below 9.5 kg in February at Bird Island (Figure 6), and years with krill harvests below 20000 t (see Figure 3).

in February (<9.5 kg; Figure 6), and years with poor krill harvests (<20000 t catch; Figure 3), to show their relative alignment. We used a fixed harvest level of 20000 t per annum, as catch per unit effort (CPUE) varied spatially (Supplementary Figure S14), as well as temporally. In general, the results from gentoo penguins and fur seals highlight years with extreme low values, more than they do years with extreme high values.

Discussion

In the context of the ecosystem approach to fisheries management at South Georgia, we explored variability in the Antarctic krill fishery, and how krill-dependent predators are responding to variability in their local ecosystem, including in relation to the local fishery. Although we considered CEMP data for all diving predators (penguins and seals), we focused on two species, gentoo penguins and Antarctic fur seals, for which monitoring occurs at two sites. Our results reflect some of the longest consistently maintained time series of CEMP predator monitoring anywhere in the Southern Ocean.

We focus our discussion on three issues: firstly, patterns and variability in the krill fishery at South Georgia. Secondly, whether existing CEMP data have utility, at least in part, to inform management of the krill fishery by reflecting ecosystem status. Finally, whether other monitoring data will increase the utility of CEMP and better facilitate the identification and attribution of ecosystem change. In addressing this latter issue, we also consider the new management framework recently agreed by CCAMLR (CCAMLR, 2019a), and how this may be implemented at South Georgia. We also consider the wider suite of risks beyond those included in CCAMLR's current agreed management framework, to advance further the ecosystem approach (Table 3).

Variability in the krill fishery

Krill catches at South Georgia vary between years, with annual catches in the early years being much greater than in recent years (Figure 3). Links between SST and krill abundance exist over the northwest shelf, north of Bird Island, at least during summer (e.g. Whitehouse *et al.*, 2008; Fielding *et al.*, 2014). As such, variability in ocean temperatures might drive relationships with krill abundance and therefore harvesting success. However, when considering the full duration of the catch history, we found no such relationships. Only in years of extreme krill fishery failure was there a suggestion that ocean temperatures might be linked (Figure 7; Fedulov *et al.*, 1996). Analyses of a shorter time series since 2006 are more informative (Supplementary Material SC), as they do provide evidence of a relationship between annual catch and SST (Figure 4), but not other environmental indices. From this, we hypothesis that the high availability of krill biomass in a given year is probably associated with cold temperatures (with temperature plausibly acting as a proxy for improved habitat availability within the Antarctic Circumpolar Current). Vessels therefore have good catches in years of colder temperatures, exert greater effort, and have increased harvests. Further studies about variation in how krill arrive, or are retained along the northern shelf, are now needed (Table 3, Row 4). We also suggest that further work is necessary to explore environmental links, including for krill demography, distribution, and abundance (Table 3, Row 5), because if larger krill catches are apparently restricted to years with colder temperatures, then warming oceans (Figure 4; Supplementary Figure S4) are likely to have important consequences for the krill fishery (Trathan and Agnew 2010).

Over time, there have been major changes in fishery operations, including a switch to winter harvesting in 1990, the cessation of former Soviet fishing interests in 1991 (the USSR was the major krill fishing nation during the 1970s and 1980s), and the introduction of the continuous fishing method in 2004. Since 2006, the fishing fleet has been relatively stable, and our analyses support the suggestion that the level of krill harvesting at South Georgia in any given year reflects a combination of factors including links with the environment. However, at times these environmental relationships are not evident, probably in part because of the changing composition of the fleet, seasonal timing of vessel-days, the number of continuous fishing vessels present, local management arrangements, and other socio-economic factors (Nicol *et al.*, 2012). Additionally, harvesting at South Georgia might also reflect conditions and catch rates at other favoured fishing grounds further south. Hence, whether favoured southern grounds are open or closed (either by sea ice or by catch limit), will determine whether South Georgia becomes a target for harvesting (Everson and Goss, 1991).

Krill catches are concentrated to the northeast of Maiviken and along the northern shelf break (Figure 2). Kemp and Bennett (1932), and subsequently Everson (1984), reported that historical whale catches at South Georgia between 1923/1924 and 1930/1931 for both blue (*Balaenoptera musculus*) and fin (*Balaenoptera physalus*) whales were focused in a similar location, indicating putative predictably located "aggregations of krill." This suggests that such areas were historically important for krill and krill-dependent predators, and are likely to remain important into the future as blue and fin whale populations recover. Interestingly, the preferred seabed depth range used by the fishery (180–280 m; Supplementary Figure S14) also includes habitats utilized by nearshore or land-based predators (e.g. Trathan *et al.*, 2006),

Table 3. Selected information requirements needed to enhance the ecosystem approach for the krill fishery at South Georgia; prioritized requirements are in Rows 1, 2, and 3, which map to the endorsed CCAMLR approach (CCAMLR, 2019a).

Row	Requirement	Current status	Desirable status	Work needed
1	Estimates of the local standing stock of krill biomass in each area used by the fishery, either in the WCB or the ECB, or both (Figure 8)	No data in winter at the time that the fishery operates; summer data in the WCB (Fielding *et al.*, 2014) and ECB (Trathan *et al.*, 2003)	Calibrated acoustic surveys prior to the start of fishing and after fishing is complete, see Figure 8 for plausible transects, including a reduced subset for fishing vessel occupation	Initiate acoustic surveys in May and September
2	Estimates of ecosystem risk arising from fishing	No data	Spatial and temporal estimates of krill consumption by marine predators in order to compare with estimates of available krill biomass and estimates of fishery removals; assessment of other risks from this paper	Estimate predator abundance and distribution, including fish, at the time that fishing takes place; estimate fraction of krill in the diet; consider depletion effects of krill for predators in the subsequent season; ecosystem models
3	Catch limits based on the estimate of local standing stock in each area used	CCAMLR Yield Model in connection with decision rules and stock reference points (Constable, 2001, 2011; Constable *et al.*, 2000)	Yield model parameterized for local conditions at South Georgia	Analyse catch, research net and predator diet data to determine recruitment frequency
4	Estimates of krill movement and retention so management can move beyond the use of local standing stock estimates and towards a dynamic stock estimate	Young *et al.* (2014)	Understanding about how krill move and are retained by local mesoscale eddies, including rates; understand how krill arrive at South Georgia	General circulation models; ecosystem models
5	Development of a geographically focused demographic model for krill	No data	Understanding of local demographic process in relation to growth and reproduction	Demographic models; ecosystem models; general circulation models
6	Estimates of carryover effects of winter fishing mortality on the availability of krill in the following summer, and effects on dependent species	This paper	Understanding whether harvesting impacts particular predator species in the following breeding season	Analyses of predator monitoring data, fishery catch data and movement and retention of krill in oceanographic models
7	Estimates of whether particular types of krill swarms are targeted by the fishery and by predators	No data	Understanding about swarm characteristics and target preferences	Analysis of fishery data in relation to available krill swarms; analysis of predator tracking data
8	Estimates of incidental mortality and bycatch of non-target species	CCAMLR CM 51-01 requires marine mammal exclusion devices to prevent seal bycatch; CCAMLR CM 25-03 prohibits net monitoring cables to prevent seabird mortality	Understanding of bycatch of fish and non-target crustacean species; improved understanding of trawl warp bird strike occurrence	Electronic monitoring of net cables; enhanced analysis of net bycatch

Continued

Table 3. continued

Row	Requirement	Current status	Desirable status	Work needed
9	Consideration of the consequences of cetacean recovery for fishery management	Zerbini *et al.* (2019), Calderan *et al.* (2020)	Projections of krill consumption by all marine mammal populations; consideration of cetacean ship strike by fishing vessels	Analyses to explore cetacean rates of recovery, diet and consumption; studies on phenology and feeding period; analyses of vessel speed and cetacean ship strike frequency
10	Consideration of climate change	Knowledge of warming ocean temperature, and changes in climate indices (e.g. Trathan *et al.*, 2006, 2007; Whitehouse *et al.*, 2008; Fielding *et al.*, 2014; Forcada and Hoffman, 2014)	Understanding of how climate change interacts with marine mammal recovery and krill fishing	Identification of reference areas to help partition impacts of fishing and climate

although risks to predators are reduced through spatial and temporal fisheries closures (Trathan *et al.*, 2014).

Even with low exploitation rates (Hill *et al.*, 2016), and with catches almost negligible in relation to the levels of krill consumed by predators (Boyd, 2002; Trathan *et al.*, 2012), it remains possible that the spatial and/or temporal concentration of catches (Figure 2) could lead to adverse ecosystem effects. Maintaining monitoring at Maiviken is therefore vital, especially as catches are increasing (CCAMLR, 2019a; Figure 3). Predator data from this site could provide indicators about harvesting impacts, particularly as monitoring datasets increase in duration. Near Bird Island, where local catches are lower, predator success might not be so sensitive. Nevertheless, co-location of monitoring sites close to the fishery should help alert managers to changes in the ecosystem, including potential impacts from the fishery. Therefore, limiting the fishery to operate only in those areas where monitoring occurs would be precautionary. Monitoring in locations not influenced by the fishery would also be informative, given the continued requirement for separating fishery from climate effects.

CEMP data—monitoring indices for gentoo penguins

Gentoo penguins show consistent patterns of breeding behaviour at Bird Island and Maiviken. Years of almost complete breeding failure (Figure 5) occurred at both locations, readily distinguished by breeding success (chicks per nest) values below 0.1. In most years, breeding success was greater than 0.8, suggestive of a near binary response. Thus, gentoo penguins were able to produce chicks in most years but failed when conditions fell below some ecological threshold. This may be because gentoo penguins have a varied diet (Waluda *et al.*, 2017) and are therefore able to utilize alternate prey species, except in extreme years. Gentoo breeding failure events did not always coincide with periods with warmer SST, or with years of reduced (or elevated) krill catches.

Interestingly, years with high levels of gentoo nest initiation, followed years with high krill catches, suggesting that winter conditions are important to gentoo penguins. Ecological carryover effects from the winter into the summer are clearly important but require further exploration. Seasonal variation in krill acoustic density between summer and winter (based on a single mooring over a 3-year period) suggests elevated biomass in summer, with potentially a second smaller peak in winter (Saunders *et al.*, 2007). Understanding the relative importance of these peaks is now important, as well as the potential for these to vary or change and influence gentoo penguin (and other predator) population processes.

CEMP data—monitoring indices for Antarctic fur seals

Our results support earlier evidence that Antarctic fur seals are decreasing at Bird Island (Forcada and Hoffman, 2014), whilst they are either stable or possibly increasing at Maiviken (Supplementary Figures S9–S13). Data series are probably too short at Maiviken to determine the precise nature of the trend, but they appear to differ from those at Bird Island.

Pups born at Bird Island are on average significantly smaller just after birth than are those at Maiviken (Figure 6). This difference is consistent for each year that data are available. By March, Bird Island pups have on average reached a similar weight to those at Maiviken (Figure 6), suggesting that pup mortality and/or growth rates differ between the two sites. This result suggests that local biological conditions differ in the foraging areas utilized by female fur seals from the two sites and that management cannot rely on monitoring results from a single site or a single species when assessing ecological change at South Georgia.

Interestingly, pup weights at Bird Island in January showed a significant relationship with SST during the preceding winter, again highlighting the importance of understanding carryover effects from the winter into the summer. However, not all warm events resulted in low pup mass; for example, no detectable warm period occurred before or during the 2016 low pup mass event (Figure 6), although an unusually low temperature was evident prior to this event (Supplementary Figure S2). Thus, a better understanding of the complexity within the ecosystem (e.g. Murphy *et al.*, 2007a, b) that leads to anomalous events is almost certainly important for an ecosystem approach to management.

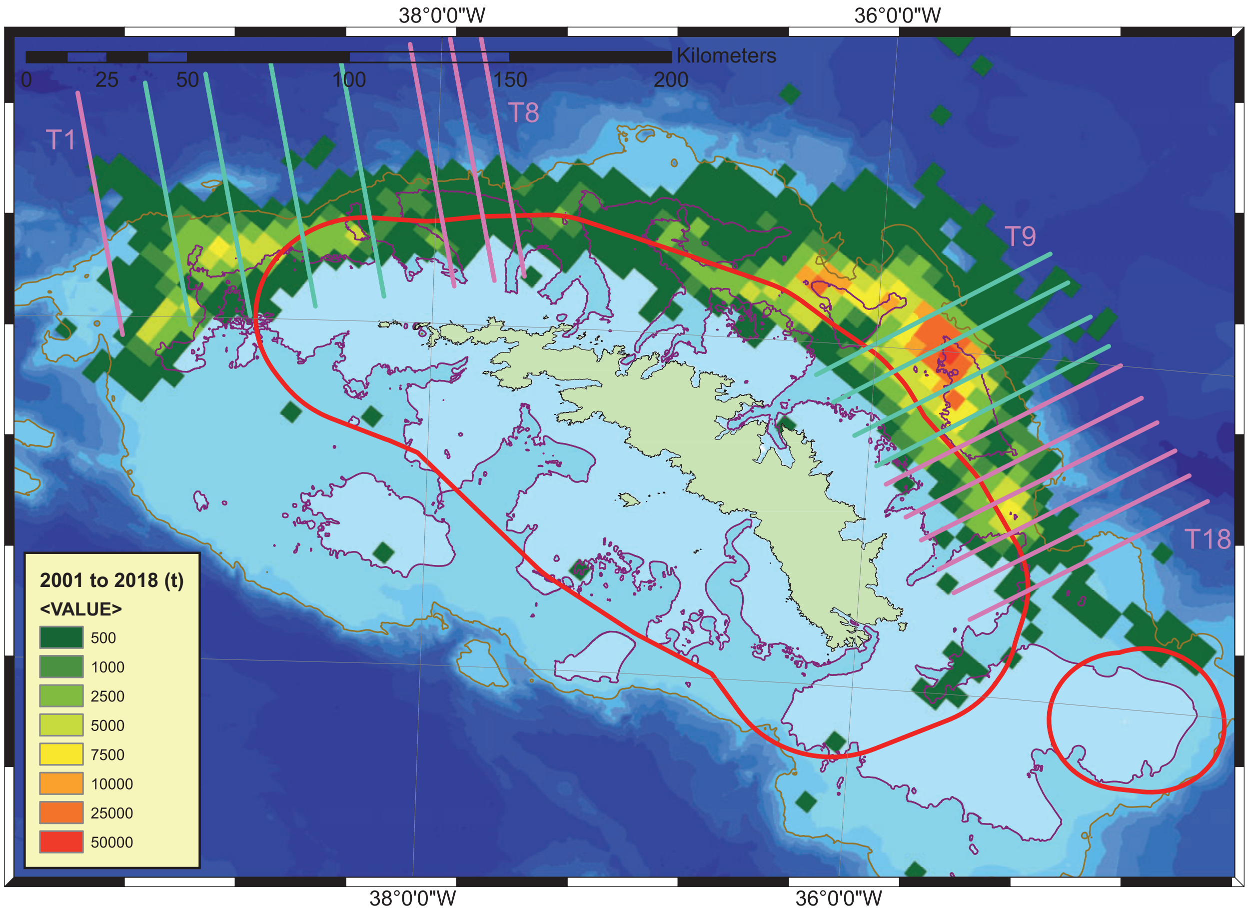

Figure 8. The cumulative krill fishery catch (t) at South Georgia for the period 2001 to 2018; no-take zones are shown in red (see text), with proposed acoustic transects for monitoring krill status with the Western Core Box (T1 to T8) and the Eastern Core Box (T9 to T18); transects suitable for repeated fishery occupation are shown in turquoise (see text).

CEMP data—ecosystem status

Analyses of CEMP data from Bird Island indicate that the marine ecosystem at South Georgia is changing (Supplementary Figures S5 and S6), with changes most evident in winter (Supplementary Figures S7 and S8). Relationships with SST and SAM are significant. Management of the krill fishery in the context of a warming ocean (Supplementary Figure S4) and changing predator population processes (Supplementary Figure S5) requires robust indicators to inform management options. However, gentoo penguins and Antarctic fur seals provide contrasting signals of ecosystem status at South Georgia. Gentoo penguins show broadly similar responses across the island, yet provide little discrimination between years, except in bad years. Antarctic fur seals show different responses between sites. This means that both species present different challenges when considering their use as indicators of ecosystem status. Anomalous years for each index do not necessarily align, highlighting the complexity of using simple metrics to reflect ecosystem status (Figure 7).

Plausibly, our CEMP monitoring data might be more difficult to interpret because our study location is recovering from significant levels of historical over-harvesting. Seals (Payne, 1977), whales (Laws, 1977), and fish (Kock, 1992; Kock and Jones, 2005; Belchier, 2013) are now recovering, with changes in the relative abundance of different predators still ongoing (Trathan and Reid, 2009; Trathan *et al.*, 2012; Zerbini *et al.*, 2019). Conceptual models of ecosystem interactions at South Georgia (Murphy, 1995) have hypothesized that populations of krill, penguins, seals, and whales should change following the cessation of marine mammal harvesting in the 1960s. Such models suggest that penguin numbers will decrease after initial population expansion; subsequently that fur seal numbers will also decrease and that cetaceans will eventually recover.

Understanding if the hypothetical model proposed by Murphy (1995) is supported by evidence is important, as management must understand the relative significance of all forcing factors, or drivers of change that are acting on the ecosystem. Indeed, any such understanding should be able to explain the differences in predator monitoring observed at both Bird Island and Maiviken, two locations ~100 km apart.

Increasing the utility of CEMP to facilitate the ecosystem approach to fisheries management

Various studies have suggested general approaches for determining fisheries catch levels for forage species so as not to disproportionately affect different components of the marine ecosystem (e.g. Cury *et al.*, 2011; Smith *et al.*, 2011). However, identifying an appropriate catch level for krill based on CEMP data, including the questions of when, and by how much catch should be increased or decreased, and when and from where catch can be taken (e.g. Hewitt *et al.*, 2004), has not been achieved. Moreover, evaluation of ecological connectivity at relevant scales (Murphy *et al.*, 1988) still remains to be achieved. Although attempts have been made to integrate different CEMP indices (e.g. de la Mare and Constable, 2000; Boyd and Murray, 2001; Reid *et al.*, 2005, 2007), none have been adopted by CCAMLR.

At Bird Island, multiple species are monitored (including species that are not part of CEMP), with fewer monitored at Maiviken. With multiple monitoring parameters, some might be changing in different ways, so a combined standardized index (CSI) has been suggested (e.g. Boyd and Murray, 2001; Reid *et al.*, 2005, 2007). The CSI was developed to reflect ecosystem status; however, without the inclusion of pelagic predators, which are also known to be changing and are major krill consumers, it remains unclear whether this concept still has relevance for management. For example, perciform fish take as much krill as do whales, penguins, and fur seals combined, whereas myctophid fish may take double that amount (Hill *et al.*, 2007). Our results confirm that different species respond differently (Figure 7; see also Supplementary Material SB), whilst the same species may respond differently at different sites (Figure 6; see also Murphy *et al.*, 2013), adding further to the challenges (and complexity) of translating CEMP into management action. An important question remains—whether, and if so, how can different species responses be rationalized against each other, or combined, to facilitate management decisions. The translation is made even more complex as CEMP was designed to include parameters that vary over different time scales (e.g. over multiple years—penguin population size, between years—penguin breeding success, and within years—penguin body mass). Rationalizing the spatial and temporal scales (Murphy *et al.* 1988) implicit in these different indices presents challenges. Moreover, the statistical power needed to determine ecological change points may not be available (CCAMLR, 2003; Reid *et al.*, 2007). Translation will also be made complex should the ecosystem become more productive as whales recover (Dewar *et al.*, 2006; Nicol *et al.*, 2010), which they now are within the Scotia Sea (Zerbini *et al.*, 2019; Calderan *et al.*, 2020). The approach reported in Supplementary Material SB, could be enhanced with additional monitoring data, including from krill-eating fish (Main *et al.*, 2009; Hollyman *et al.*, In Review) and cetaceans (Zerbini *et al.*, 2019).

Thus, although CEMP includes numerous species and indices, management does not directly use the outputs of monitoring. CCAMLR was innovative in attempting to achieve this, but to date, has not managed to close the loop between monitoring and management action. An important indirect benefit of CEMP has been the realization that management of the krill fishery at small spatial and temporal scales requires an assessment of risk at these smaller scales, something now recognized by CCAMLR (CCAMLR, 2019a). Recent work has reiterated the need to define safe ecological limits for predators, coupled with a method to adjust fishing activities in response to the state of the predator population (Hill *et al.*, 2020). However, where multiple predators depend upon a fished target species, reference points will need to be clearly articulated so that they do not have unintended consequences elsewhere in the ecosystem. Ultimately, reference points for predators need to reflect management objectives. For CCAMLR, the management objective expresses the need to maintain ecological relationships and prevent changes that are irreversible except over short timescales. Operationalizing this has engendered intense debate within CCAMLR (often unresolved with strongly voiced opposing views about data sufficiency and ecosystem processes) and is likely to remain challenging for an ecosystem that is dynamic and evolving and where predator indices are changing in relation to one another (e.g. Supplementary Figures S5 and S6), confirming the complexity of utilizing marine predators as indicators of ecosystem status (Tett *et al.*, 2013).

Moving towards management at smaller spatial and temporal scales

Recognizing the challenges associated with using CEMP data, CCAMLR is now pursuing a new framework (CCAMLR, 2019a). At South Georgia, the greatest data requirement under CCAMLR's new approach will be to develop acoustic estimates of krill density and biomass (Table 3, Row 1; Figure 8), including krill distribution and swarm structure at relevant times of the year. Further, it will be necessary to consider scales of ecosystem operation in order to assess risks from fishing (Table 3, Row 2). Assessment of risk should provide critical ecosystem information at appropriate spatial and temporal scales to match the footprint of the fishery and key foraging areas of not only land-based predators but also selected pelagic predators.

There is a long history of estimating krill biomass (c.f. Table 3, Row 1) at South Georgia (Brierley *et al.*, 1997; Fielding *et al.*, 2014), including at different times of year (Reid *et al.*, 2010) and in areas used by the krill fishery (Trathan *et al.*, 2003). However, surveys at the time of year that the fishery takes place have never been undertaken, as most surveys were designed to address ecological questions about predator–prey dynamics, rather than about fisheries management. Nevertheless, the survey transects used in the past (Figure 8) have the potential to provide information about both the stock and predator–prey interactions if they are carried out in winter as well as in summer, also providing increased understanding about winter carryover effects. Some transects could be repeated during the course of the fishing season to explore whether depletion of krill is detectable (Figure 8). Co-location of CEMP monitoring would allow fishery impacts to be most easily determined, suggesting that the fishery should be restricted to the northern shelf of South Georgia (Figure 8), at least until more information is available.

At South Georgia, the seasonal closure of the krill fishery and coastal no-take buffers (Trathan *et al.*, 2014; Figure 8) minimize risks to predators (c.f. Table 3, Row 2), in a manner consistent with the new CCAMLR approach (CCAMLR, 2019a). Coastal buffers protect the foraging areas of marine predators such as gentoo penguins, cormorants, petrels and prions, and spawning aggregations of various fish species. A recent review of the buffers (see www.gov.gs/wp-content/cache/all/32110-2/index.html; accessed 10 May 2021), extended coastal protection to 30 km, to reduce further any likelihood of spatial overlap with the winter krill fishery. An important consideration was that the buffers should be consistent with the voluntary buffers at the Antarctic Peninsula (Handley *et al.*, 2021). Further refinement of the seasonal closure of the krill fishery and coastal no-take buffers might be valuable as more information about the winter distribution of predators becomes available (e.g. Bamford *et al.*, 2021).

The data to support CCAMLR's new approach (Table 3, Rows 1, 2, and 3) are not part of CEMP, but combining the new approach with CEMP has the potential to enhance understanding about the performance of different predators, providing an ecosystem status report, or ecosystem health check. For example, understanding spatial and temporal variation in krill biomass could help inform predator functional responses, which are likely to be variable and complex (e.g. Koehn *et al.*, 2017). More information to inform about krill movement in ocean currents (flux) would enhance understanding about the stock itself (e.g. Meyer *et al.*, 2020) and about krill–predator interactions (Trathan and Hill, 2016).

Until winter carryover effects are better understood, the krill catch limit within the area regularly fished at South Georgia (Figures 2 and 6) should be closely regulated, particularly as the fishery is so spatially concentrated and the climate is changing (Figure 4). An interim catch limit below the CCAMLR interim catch limit (279000 t) for Subarea 48.3, specific to the area fished would be precautionary, at least until data are available to estimate the winter biomass of krill at South Georgia, including information about krill recruitment periodicity, and retention and replenishment rates (Table 3, Rows 3, 4, and 5).

The median (summer) density of krill within the area covered by Transects 1 to 8 (Figure 8) is $\sim$48.925 g m^{-2} over the period 1996/97 to 2012/13 (Fielding *et al.*, 2014), extrapolating to almost 1250000 t in the area currently used by the winter fishery (Figure 8). The harvest rate of 0.093 currently used by CCAMLR (CCAMLR, 2010; see also Table 3, Row 3), indicates that an annual catch limit of $\sim$114500 t could be considered precautionary. A further priority should be the development of an appropriate local parameterization of CCAMLR's yield model (Constable *et al.*, 2000; Constable, 2001) based on local estimates of growth, recruitment, and natural mortality, but also consideration of krill flux (Table 3, Rows 3, 4, and 5).

Utilizing new technologies to reduce any limitations with future monitoring would be sensible. An important trade-off towards improved ecosystem monitoring is likely to be the tension between what parameters are measured and how broadly measurements can be made. In this respect, unoccupied aerial vehicles (UAVs or drones), autonomous survey vehicles (gliders and sailbuoys), and moorings should be considered. Similarly, individual fishery quotas could be used to help encourage fishing vessels to participate in data collection, whilst reducing the negative effects of Olympic fishing (e.g. Aranda, 2009).

Thus, instigating annual biomass estimates for use in combination with the CCAMLR yield model, decision rules, and stock reference points (Constable, 2001; 2011; Constable *et al.*, 2000) should ensure the continuation of precautionary catch limits for South Georgia. This, used in combination with an assessment of the ecological structure, should further reduce risks to the ecosystem. Exploring CEMP data in relation to available krill biomass (in winter and summer) then has the potential to inform on ecosystem status and change. Enhancing the framework proposed by CCAMLR (CCAMLR, 2019a; Table 3 Rows 1, 2, and 3) to incorporate krill movement and retention has the potential to improve management options, including by increasing catch limits. Moving towards a dynamic understanding of the stock would enhance the ecosystem approach for krill fishery management.

Other management actions that would enhance the ecosystem approach at South Georgia include mitigation measures appropriate to reduce incidental mortality of seabirds and marine mammals, or bycatch of fish (Table 3, Rows 8 and 9). Seal exclusion devices are already mandatory across the krill fishery including at South Georgia (CM 51-01; www.ccamlr.org/en/measure-51-01-2010; accessed 10 May 2021) and are generally effective (CCAMLR, 2018); however, efforts to minimize incidental mortality of seabirds during the course of trawl fishing (CM 25-03; www.ccamlr.org/en/measure-25-03-2020; accessed 10 May 2021) almost certainly still require revision, including consideration of warp strike (ACAP, 2017; Kuepfer *et al.*, 2018). Ship strike may become important as cetacean populations recover. Many fisheries include the use of move-on rules for bycatch mitigation, but these have never been considered for krill, so should be more fully evaluated (e.g. Everson *et al.*, 1992). Appropriate mitigation of incidental mortality and bycatch is dependent upon a better understanding of fishery operations. Therefore, in addition to full scientific observer coverage (CM 51-06; www.ccamlr.org/en/measure-51-06-2019; accessed 10 May 2021), electronic monitoring (Ewell *et al.*, 2020), coupled with proposed best practice (ACAP, 2017) should be considered mandatory for the krill fishery. Scientific observation should of course be in accordance with the CCAMLR Scheme of International Scientific Observation (CCAMLR, 2019b).

In the longer term, krill management should consider the utility of climate change reference areas (Table 3, Row 10). Krill catches are focused to the north of South Georgia, while the southern shelf remains free of any fishery influence (apart from extraction much further south at the Antarctic Peninsula and at the South Orkney Islands). As such, the south-eastern shelf at South Georgia might be a suitable reference area, having the potential to help partition impacts of fishing and climate and assist in attributing cause the for observed change.

Conclusion

Fisheries management includes consideration of trade-offs, which for the ecosystem approach includes considerations about the ecosystem. We emphasize that monitoring to understand ecosystem operation and change requires different information to that required for fisheries management, but the former should inform the latter. Here, we report important relationships between krill catches and the environment and between predators and the environment, which now warrant further investigation. Enhanced monitoring of krill in particular is likely to increase the probability of detecting changes in the ecosystem, and correctly attributing cause. A key trade-off now will be about how much investment in monitoring is necessary, and who pays, to prevent potential fisheries impacts in biodiverse ecosystems where predators that compete with the fishery are abundant. Before catches increase, a reliable ecosystem health check will be necessary. Our work shows that carry-over effects from winter are important for predators in the following summer, emphasizing that risks in time and space need to be better understood. Development of the analyses presented here could help provide an annual ecosystem status report.

Setting or changing krill fishery catch limits by use of predator monitoring data without the availability of an independent stock assessment is challenging. Monitoring of krill in winter and summer would enhance the utility of CEMP for providing an ecosystem health check. CEMP data provide a useful means to assess ecosystem status, but regular stock assessments at the scale of fishery operation are now necessary for the management of the krill fishery at South Georgia.

Our findings have relevance to the other krill fishery hotspots that occur elsewhere in the Scotia Sea, at the Antarctic Peninsula, and at the South Orkney Islands. Table 3 highlights gaps that remain to be addressed under the ecosystem approach, not just at South Georgia, but also at other hotspots used by the fishery.

Data availability

The CEMP monitoring data from Bird Island underlying this article are available from the UKRI/BAS Polar Data Centre:

Macaroni penguin arrival weights—https://doi.org/gb69.
Macaroni penguin fledging weight—https://doi.org/gb7c.
Macaroni penguin breeding success—https://doi.org/gb7k.
Gentoo penguin nesting chronology—https://doi.org/gb78.
Gentoo penguin fledging weight—https://doi.org/gb7n.
Gentoo penguin breeding success—https://doi.org/gb7v.
Antarctic fur seal special study beach summary counts—https://doi.org/gb79.
Antarctic fur seal fur seal pup weight—https://doi.org/gb72.

The CEMP monitoring data from Maiviken underlying this article are available from the UKRI/BAS Polar Data Centre:

Gentoo penguin fledging weight—https://doi.org/gb7q.
Gentoo penguin breeding success—https://doi.org/gb7x.
Antarctic fur seal summary counts—https://doi.org/gb77.
Antarctic fur seal fur seal pup weight—https://doi.org/gb76.

The krill fishery catch and effort data underlying this article were made available by the CCAMLR Secretariat. These data can be shared on reasonable request to CCAMLR.

Acknowledgements

There are no conflicts of interest with publication of this article. It is a contribution to the BAS Ecosystems ALI-Science programme, which provides the UK contribution to the CCAMLR Ecosystem Monitoring Program. We thank CCAMLR Members for providing krill catch and effort data, and Chris Darby for helpful discussions during manuscript preparation. We also thank two anonymous referees and the editor, Jason Link, who greatly helped us during the development of this article.

Funding

This work was supported by UKRI/BAS Ecosystems. VWE was supported by Darwin Plus grant DPLUS072 and Pew Charitable Trusts grant 00034295.

Supplementary material

Supplementary material is available at *European Journal of Preventive Cardiology* online.

References

ACAP. 2017. ACAP Review and Best Practice Advice for Reducing the Impact of Pelagic and Demersal Trawl Fisheries on Seabirds, Reviewed at the Tenth Meeting of the Advisory Committee Wellington, New Zealand, 11–15 September 2017. www.acap.aq/en/bycatch-mitigation/mitigation-advice; accessed 10 May 2021.

Agnew, D. J. 1997. The CCAMLR ecosystem monitoring programme. Antarctic Science, 9: 235–242.

Aranda, M. 2009. Developments on fisheries management in Peru: the new individual vessel quota system for the Anchoveta fishery. Fisheries Research, 96: 308–312.

Atkinson, A., Hill, S. L., Pakhomov, E. A., Siegel, V., Reiss, C. S., Loeb, V. J., Steinberg, D. K., *et al.* 2019. Krill (*Euphausia superba*) distribution contracts southward during rapid regional warming. Nature Climate Change, 9: 142–147.

Bamford, C. C. G., Warwick-Evans, V., Staniland, I. J., Jackson, J., and Trathan, P. N. 2021. Wintertime overlaps between female Antarctic fur seals (*Arctocephalus gazella*) and the krill fishery at South Georgia, South Atlantic. PLoS One, 16: e0248071.

Belchier, M. 2013. Decadal Trends in the South Georgia Demersal Fish Assemblage. CCAMLR WG-FSA-13/26. CCAMLR, Hobart, Australia.

Bengston, J. L. 1984. Monitoring indicators of possible ecological changes in the Antarctic marine ecosystem. Scientific Committee for the Conservation of Antarctic Marine Living Resources, Selected Scientific Papers, 1982-1984, Part 11: 43–153. CCAMLR, Hobart, Australia.

Boersma, P. D. 2008. Penguins as Marine Sentinels. BioScience, 58: 597–607.

Boyd, I. L. 2002. Estimating food consumption of marine predators: antarctic fur seals and macaroni penguins. Journal of Applied Ecology, 39: 103–119.

Boyd, I. L., and Murray, A. W. A. 2001. Monitoring a marine ecosystem using responses of upper trophic level predators. Journal of Animal Ecology, 70: 747–760.

Brierley, A. S., Watkins, J. L., and Murray, A. W. A. 1997. Interannual variability in krill abundance at South Georgia. Marine Ecology Progress Series, 150: 87–98.

Calderan, S. V., Black, A., Branch, T. A., Collins, M. A., Kelly, N., Leaper, R., Lurcock, S., *et al.* 2020. South Georgia blue whales five decades after the end of whaling. Endangered Species Research, 43: 359–373.

CCAMLR. 2003. Report of the Twenty-second Meeting of the Scientific Committee, SC-CCAMLR-XXII. CCAMLR, Hobart, Australia.

CCAMLR. 2010. Report of the Fifth Meeting of the Subgroup on Acoustic Survey and Analysis methods, SC-CCAMLR-XXIX Annex 6, Paragraph 3.30. CCAMLR, Hobart, Australia.

CCAMLR. 2014. CCAMLR Ecosystem Monitoring Program Standard Methods. CCAMLR, Hobart, Australia.

CCAMLR. 2016. Report of the Thirty-fifth Meeting of the Scientific Committee, SC-CCAMLR-XXXV, Paragraph 3.47. CCAMLR, Hobart, Australia.

CCAMLR. 2018. Krill Fishery Report. CCAMLR, Hobart, Australia. www.ccamlr.org/en/document/publications/krill-fishery-report-2018.

CCAMLR. 2019a. Report of the Thirty-eighth Meeting of the Commission, CCCAMLR-38, Paragraphs 5.8 to 5.9 and Paragraphs 5.17 to 5.20. CCAMLR, Hobart, Australia.

CCAMLR. 2019b. CCAMLR Scheme of International Scientific Observation. CCAMLR, Hobart, Australia. www.ccamlr.org/en/document/publications/text-ccamlr-scheme-international-scientific-observation.

Constable, A. J. 2001. The ecosystem approach to managing fisheries: achieving conservation objectives for predators of fished species. CCAMLR Science, 8: 37–64.

Constable, A. J. 2011. Lessons from CCAMLR on the implementation of the ecosystem approach to managing fisheries. Fish and Fisheries, 12: 138–151.

Constable, A. J., de la Mare, W. K., Agnew, D. J., Everson, I., and Miller, D. 2000. Managing fisheries to conserve the Antarctic marine ecosystem: practical implementation of the Convention on the Conservation of Antarctic Marine Living Resources (CCAMLR). ICES Journal of Marine Science, 57: 778–791.

Cox, M. J., Candy, S., de la Mare, W. K., Nicol, S., Kawaguchi, S., and Gales, N. 2019. No evidence for a decline in the density of Antarctic krill *Euphausia superba* Dana, 1850, in the Southwest Atlantic sector between 1976 and 2016. Journal of Crustacean Biology, 38: 656–661.

Cury, P. M., Boyd, I. L., Bonhommeau, S., Anker-Nilssen, T., Crawford, R. J. M., Furness, R. W., Mills, J. A., *et al.* 2011. Global seabird response to forage fish depletion – one-third for the birds. Science, 334: 1703–1706.

de la Mare, W. K., and Constable, A. J. 2000. Utilising data from ecosystem monitoring for managing fisheries: development of statistical summaries of indices arising from the CCAMLR Ecosystem Monitoring Program. CCAMLR Science, 7: 101–118.

Dewar, W. K., Bingham, R. J., Iverson, R. L., Nowacek, D. P., St. Laurent, L. C., and Wiebe, P. H. 2006. Does the marine biosphere mix the ocean? Journal of Marine Research, 64: 541–561.

Doidge, D. W., Croxall, J. P., and Baker, J. R. 1984. Density-dependent pup mortality in the Antarctic fur seal *Arctocephalus gazella* at South Georgia. Journal of Zoology (London), 202: 449–460.

Everson, I. 1984. Marine interactions. *In* Antarctic Ecology, Vol. 2. Ed. by R. M. Laws. Academic Press, London.

Everson, I., and Goss, C. 1991. Krill fishing activity in the southwest Atlantic. Antarctic Science, 3: 351–358.

Everson, I., Neyelov, A., and Permitin, Y. E. 1992. Bycatch of fish in the South Atlantic krill fishery. Antarctic Science, 4: 389–392.

Ewell, C., Hocevar, J., Mitchell, E., Snowden, S., and Jacquet, J. 2020. An evaluation of Regional Fisheries Management Organization at-sea compliance monitoring and observer programs. Marine Policy, 115: 103842.

Fedulov, P. P., Murphy, E. J., and Shulgovsky, K. E. 1996. Environment–krill relations in the South Georgia marine ecosystem. CCAMLR Science, 3: 13–30.

Fielding, S., Watkins, J. L., Trathan, P. N., Enderlein, P., Waluda, C. M., Stowasser, G., Tarling, G. A., *et al.* 2014. Interannual variability in Antarctic krill (*Euphausia superba*) density at South Georgia, Southern Ocean: 1997–2013. ICES Journal of Marine Science, 71: 2578–2588.

Forcada, J., and Hoffman, J. I. 2014. Climate change selects for heterozygosity in a declining fur seal population. Nature, 511: 462–465.

Forcada, J., Trathan, P. N., Reid, K., and Murphy, E. J. 2005. The effects of global climate variability in pup production of Antarctic fur seals. Ecology, 86: 2408–2417.

Garcia, S. M., Zerbi, A., Aliaume, C., Do Chi, T., and Lasserre, G. 2003. The ecosystem approach to fisheries. Issues, terminology, principles, institutional foundations, implementation and outlook. Fisheries and Aquaculture Management Division Serial Title: FAO Fisheries Technical Paper Series Number, 0429–9345.

Green-Hammond, K. A., Ainley, D. G., Siniff, D. B., and Scott-Urquhart, N. 1984. Selection Criteria and Monitoring Requirements for Indirect Indicators of Changes in Availability of Antarctic Krill Applied to Some Pinniped and Seabird Information. Scientific Committee for the Conservation of Antarctic Marine Living Resources, Selected Scientific Papers 1982-1984, Part 11: 295–339. CCAMLR, Hobart, Australia.

Handley, J., Rouyer, M.-M., Pearmain, E. J., Warwick-Evans, V., Teschke, K., Hinke, J., Lynch, H., *et al.* 2021. Marine important bird and biodiversity areas for penguins in Antarctica, targets for conservation action. Frontiers in Marine Science, 7: 1–17.

Henson, S. A., Beaulieu, C., and Lampitt, R. 2016. Observing climate change trends in ocean biogeochemistry: when and where. Global Change Biology, 22: 1561–1571.

Hewitt, R. P., Watters, G., Trathan, P. N., Croxall, J. P., Goebel, M. E., Ramm, D., Reid, K., *et al.* 2004. Options for allocating the precautionary catch limit of krill among small-scale management units in the Scotia Sea. CCAMLR Science, 11: 81–97.

Hilborn, R., Amoroso, R. O., Bogazzi, E., Jensen, O. P., Parma, A. M., Szuwalski, C., and Walters, C. J. 2017. When does fishing forage species affect their predators? Fisheries Research, 191: 211–221.

Hill, S. L., Atkinson, A., Darby, C., Fielding, S., Krafft, B. A., Godø, O. R., Skaret, G., *et al.* 2016. Is current management of the Antarctic krill fishery in the Atlantic sector of the Southern Ocean precautionary? CCAMLR Science, 23: 31–51.

Hill, S. L., Hinke, J., Bertrand, S., Fritz, L., Furness, R. W., Ianelli, J. N., Murphy, M., *et al.* 2020. Reference points for predators will progress ecosystem-based management of fisheries. Fish and Fisheries, 21: 368–378.

Hill, S. L., Reid, K., Thorpe, S. E., Hinke, J., and Watters, G. M. 2007. A compilation of parameters for ecosystem dynamics models of the Scotia Sea – Antarctic Peninsula region. CCAMLR Science, 14: 1–25.

Hollyman, P. R., Hill, S., Laptikhovsky, V. V., Belchier, M., Gregory, S., Clement, A., and Collins, M. A. In Review. A long road to recovery: dynamics and ecology of the marbled rockcod (*Notothenia rossii*) at South Georgia, 50 years after over-exploitation. ICES Journal of Marine Science.

Kemp, S., and Bennett, A. G. 1932. On the distribution and movements of whales on the South Georgia and South Shetland whaling grounds. Discovery Reports, 6: 165–190.

Kock, K.-H. 1992. Antarctic Fish and Fisheries. Cambridge University Press, Cambridge, UK.

Kock, K.-H., and Jones, C. D. 2005. Fish stocks in the southern Scotia Arc region - a review and prospects for future research. Reviews in Fisheries Science, 13: 75–108.

Koehn, L. E., Essington, T. E., Marshall, K. N., Sydeman, W. J., Szoboszlai, A. I., and Thayer, J. A. 2017. Trade-offs between forage fish fisheries and their predators in the California Current. ICES Journal of Marine Science, 74: 2448–2458.

Kuepfer, A., Crofts, S., Tierney, M., Blake, D., and Goyot, L. 2018. Falkland Islands National Plan of Action for Reducing Incidental Catch of Seabirds in Trawl Fisheries, 2019 (FI NPOA-S-T-2019). Stanley, Fisheries Department, Directorate of Natural Resources, Falkland Islands Government.

Laws, R. M. 1977. Seals and whales of the Southern Ocean. Philosophical Transactions of the Royal Society of London, Series B, 279: 81–96.

Link, J. S. 2005. Translating ecosystem indicators into decision criteria. ICES Journal of Marine Science, 62: 569e576.

Link, J. S., and Browman, H. I. 2014. Integrating what? Levels of marine ecosystem-based assessment and management. ICES Journal of Marine Science, 71: 1170–1173.

Main, C. E., Collins, M. A., Mitchell, R., and Belchier, M. 2009. Identifying patterns in diet of mackerel icefish (*Champsocephalus gunnari*) at South Georgia using bootstrapped confidence intervals of a dietary index. Polar Biology, 32: 569–581.

Meyer, B., Atkinson, A., Bernard, K. S., Brierley, A. S., Driscoll, R., Hill, S. L., Marschoff, E., *et al.* 2020. Successful ecosystem-based management of Antarctic krill should address uncertainties in krill recruitment, behaviour and ecological adaptation. Communications Earth & Environment, 1: 1–12.

Murphy, E. J. 1995. Spatial structure of the Southern Ocean ecosystem: predator – prey linkages in Southern Ocean food webs. Journal of Animal Ecology, 64: 333–347.

Murphy, E. J., Hofmann, E. E., Watkins, J. L., Johnston, N. M., Piñones, A., Ballerini, T., Hill, S. L., *et al.* 2013. Comparison of the structure and function of Southern Ocean regional ecosystems: the Antarctic Peninsula and South Georgia. Journal of Marine Systems, 109-110: 22–42.

Murphy, E. J., Morris, D. J., Watkins, J. L., and Priddle, J. 1988. Scales of interaction between Antarctic krill and the environment. *In* Antarctic Ocean and Resources Variability. Ed. by D., Sahrhage Springer, Berlin, Heidelberg.

Murphy, E. J., Trathan, P. N., Watkins, J. L., Reid, K., Meredith, M. P., Forcada, J., Thorpe, S. E., *et al.* 2007a. Climatically driven fluctuations in Southern Ocean ecosystems. Proceeding of the Royal Society, Series B, 274: 3057–3067.

Murphy, E. J., Watkins, J. L., Trathan, P. N., Reid, K., Meredith, M. P., Thorpe, S. E., Johnston, N. M., *et al.* 2007b. Spatial and temporal operation of the Scotia Sea ecosystem: a review of large-scale links in a krill centred food web. Philosophical Transactions of the Royal Society Series B, 362: 113–148.

Nicol, S., Bowie, A., Jarman, S., Lannuzel, D., Meiners, K. M., and van der Merwe, P. 2010. Southern Ocean iron fertilization by baleen whales and Antarctic krill. Fish and Fisheries, 11: 203–209.

Nicol, S., Foster, J., and Kawaguchi, S. 2012. The fishery for Antarctic krill – recent developments. Fish and Fisheries, 13: 30–40.

Pardo, D., Forcada, J., Wood, A. G., Tuck, G. N., Ireland, L., Pradel, R., Croxall, J. P., *et al.* 2017. Additive effects of climate and fisheries drive ongoing declines in multiple albatross species. Proceedings of the National Academy of Sciences, 114: E10829–E10837.

Patrick, W. S., and Link, J. S. 2015. Myths that continue to impede progress in ecosystem-based fisheries management. Fisheries, 40: 155–160.

Payne, M. R. 1977. Growth of a fur seal population. Philosophical Transactions of the Royal Society, Series B, 279: 67–79.

Pikitch, E. K., Boersma, P. D., Boyd, I. L., Conover, D. O., Cury, P., Essington, T. E., Heppell, S. S., *et al.* 2018. The strong connection between forage fish and their predators: a response to Hilborn et al. (2017). Fisheries Research, 198: 220–223.

Pikitch, E. K., Rountos, K. J., Essington, T. E., Santora, C., Pauly, D., Watson, R., Sumaila, U. R., *et al.* 2014. The global contribution of forage fish to marine fisheries and ecosystems. Fish and Fisheries, 15: 43–64.

Pikitch, E. K., Santora, C., Babcock, E. A., Bakun, A., Bonfil, R., Conover, D. O., Dayton, P., *et al.* 2004. Ecosystem-based fishery management. Science, 305: 346–347.

Pitcher, T. J., Kalikoski, D., Short, K., Varkey, D., and Pramod, G. 2009. An evaluation of progress in implementing ecosystem-based management of fisheries in 33 countries. Marine Policy, 33: 223–232.

Reid, K., Croxall, J. P., Briggs, D. R., and Murphy, E. J. 2005. Antarctic ecosystem monitoring: quantifying the response of ecosystem indicators to variability in Antarctic krill. ICES Journal of Marine Science, 62: 366–373.

Reid, K., Croxall, J. P., and Murphy, E. J. 2007. The power of ecosystem monitoring. Aquatic Conservation: Marine and Freshwater Ecosystems, 17: S79–S92.

Reid, K., Watkins, J. L., Murphy, E. J., Trathan, P. N., Fielding, S., and Enderlein, P. 2010. Krill population dynamics at South Georgia: implications for ecosystem-based fisheries management. Marine Ecology-Progress Series, 399: 243–252.

Sainsbury, K., and Sumaila, U. R. 2001. Incorporating ecosystem objectives into management of sustainable marine fisheries, including "best practice" reference points and use of marine protected areas. *In* Responsible Fisheries in the Marine Ecosystem, pp. 343–361. Ed. by M., Sinclair and G., Valdimarsson FAO and CAB International, Rome, Italy, and Wallingford, UK.

Saunders, R. A., Watkins, J. L., Reid, K., Murphy, E. J., Enderlein, P., Bone, D. B., and Brierley, A. S. 2007. Intra-annual variability in the density of Antarctic krill at South Georgia, 2002–2005: within year variation provides a new framework for interpreting previous 'annual' variation. CCAMLR Science, 14: 27–42.

Smith, A. D. M., Brown, C. J., Bulman, C. M., Fulton, E. A., Johnson, P., Kaplan, I. C., Lozano-Montes, H., *et al.* 2011. Impacts of fishing low–trophic level species on marine ecosystems. Science, 333: 1147–1150.

Sydeman, W. J., Thompson, S. A., Anker-Nilssen, T., Arimitsu, M., Bennison, A., Bertrand, S., Boersch-Suppan, P., *et al.* 2017. Best practices for assessing forage fish fisheries-seabird resource competition. Fisheries Research, 194: 209–221.

Tett, P., Gowen, R. J., Painting, S. J., Elliott, M., Forster, R., Mills, D. K., Bresnan, E., *et al.* 2013. Framework for understanding marine ecosystem health. Marine Ecology-Progress Series, 494: 1–27.

Trathan, P. N., and Agnew, D. 2010. Climate change and the Antarctic marine ecosystem: an essay on management implications. Antarctic Science, 22: 387–398.

Trathan, P. N., Brierley, A. S., Brandon, M. A., Bone, D. G., Goss, C., Grant, S. A., Murphy, E. J., *et al.* 2003. Oceanographic variability and changes in Antarctic krill (*Euphausia superba*) abundance at South Georgia. Fisheries Oceanography, 12: 569–583.

Trathan, P. N., Collins, M. A., Grant, S. M., Belchier, M., Barnes, D. K. A., Brown, J., and Staniland, I. J. 2014. The South Georgia and the South Sandwich Islands MPA: protecting a biodiverse oceanic island chain situated in the flow of the Antarctic Circumpolar Current. *In* Marine Managed Areas and Fisheries. Advances in Marine Biology, 69. Ed. by M. L. Johnson and J.. Sandell pp. 15–78.

Trathan, P. N., Everson, I., Murphy, E. J., and Parkes, G. 1998. Analysis of haul data from the South Georgia krill fishery. CCAMLR Science, 5: 9–30.

Trathan, P. N., and Hill, S. L. 2016. The importance of krill predation in the Southern Ocean. *In* Biology and Ecology of Antarctic Krill (Advances in Polar Ecology). Ed. by V. Siegel Springer International Publishing, Switzerland. pp. 321–350.

Trathan, P. N., and Murphy, E. J. 2003. Sea surface temperature anomalies near South Georgia: relationships with the pacific El Niño regions. Journal of Geophysical Research, 108, NO. C4, 8075, 1–10.

Trathan, P. N., Murphy, E. J., Forcada, J., Croxall, J. P., Reid, K., and Thorpe, S. E. 2006. Physical forcing in the southwest Atlantic: ecosystem control. *In* Top Predators in Marine Ecosystems. Ed. by I. L. Boyd, S. Wanless, and C. J.. Camphuysen Cambridge University Press, Cambridge, UK.

Trathan, P. N., Ratcliffe, N., and Masden, E. A. 2012. Ecological drivers of change at South Georgia: the krill surplus, or climate variability. Ecography, 35: 983–993.

Trathan, P. N., and Reid, K. 2009. Exploitation of the marine ecosystem in the sub-Antarctic: historical impacts and current consequences. Papers and Proceeding of the Royal Society of Tasmania, 143: 9–14.

Trochta, J. T., Pons, M., Rudd, M. B., Krigbaum, M., Tanz, A., and Hilborn, R. 2018. Ecosystem-based fisheries management: perception on definitions, implementations, and aspirations. PLoS One, 13: e0190467.

Waluda, C. M., Hill, S. L., Peat, H. J., and Trathan, P. N. 2017. Long-term variability in the diet and reproductive performance of penguins at Bird Island, South Georgia. Marine Biology, 164: 39.

Whitehouse, M. J., Meredith, M. P., Rothery, P., Atkinson, A., Ward, P., and Korb, R. E. 2008. Rapid warming of the ocean around South Georgia, Southern Ocean, during the 20th century: forcings, characteristics and implications for lower trophic levels. Deep Sea Research I, 55: 1218–1228.

Young, E. F., Thorpe, S. E., Banglawala, N., and Murphy, E. J. 2014. Variability in transport pathways on and around the South Georgia shelf, Southern Ocean: implications for recruitment and retention. Journal of GeophysicalResearch, Oceans, 119: 241–252.

Zerbini, A., Adams, G., Best, J., Clapham, P. J., Jackson, J. A., and Punt, A. E. 2019. Assessing the recovery of an Antarctic predator from historical exploitation. Royal Society Open Science, 6: 190368.

Handling editor: Jason Link