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RESEARCH ARTICLE

Antarctic krill fishery effects over penguin populations under adverse climate conditions: Implications for the management of fishing practices

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Abstract Fast climate changes in the western Antarctic Peninsula are reducing krill density, which along with increased fishing activities in recent decades, may have had synergistic effects on penguin populations. We tested that assumption by crossing data on fishing activities and Southern Annular Mode (an indicator of climate change in Antarctica) with penguin population data. Increases in fishing catch during the non-breeding period were likely to result in impacts on both chinstrap (*Pygoscelis antarcticus*) and gentoo (*P. papua*) populations. Catches and climate change together elevated the probability of negative population growth rates: very high fishing catch on years with warm winters and low sea ice (associated with negative Southern Annular Mode values) implied a decrease in population size in the following year. The current management of krill fishery in the Southern Ocean takes into account an arbitrary and fixed catch limit that does not reflect the variability of the krill population under effects of climate change, therefore affecting penguin populations when the environmental conditions were not favorable.

Keywords Antarctic Peninsula · Chinstrap penguin · Gentoo penguin · Population growth rate · Southern annular mode

INTRODUCTION

The western Antarctic Peninsula (WAP) is one of the areas most affected by climate change. Fast warming in the last decades (Cook et al. 2016; Moffat and Meredith 2018) and the southward input of warmer waters are decreasing the seasonal sea ice extent and duration (Stammerjohn et al. 2008; Moffat and Meredith 2018). Climate change effects have also been observed in different macro-scale atmospheric phenomena, such as the southern oscillation index (SOI) and the Southern Annular Mode (SAM; Stammerjohn et al. 2008; Moffat and Meredith 2018). Specifically, warming in the WAP has been related to strengthening a positive trend in the SAM, which describes atmospheric circulation patterns associated to the belt of westerly wind surrounding Antarctica (Clem et al. 2016). The SAM has a strong influence in the inter-annual variability around the WAP, driving changes in sea ice formation and melting and the injection of meteoric water (combination of glacial discharge and precipitation) to the Southern Ocean (Moffat and Meredith 2018).

Current climate change has had significant effects in the Antarctic ecosystem, particularly for sea ice-dependent species, such as the Antarctic krill *Euphausia superba*. Several studies have shown dramatic changes in Antarctic krill populations, including distributional range contraction (Atkinson et al. 2019), size reduction (Tarling et al. 2016), decreased recruitment (Atkinson et al. 2019; Perry et al. 2019), and decreased density (Atkinson et al. 2009; Flores et al. 2012). Variability in regional sea ice has been identified as an important limitation for krill abundance (Flores et al. 2012). Sea ice cover can affect the survival of krill larvae, due to their reliance on sea ice to feed and for shelter during winter (Meyer 2012). Predicted future environmental changes are expected to produce further changes associated with seawater warming and reduced sea ice cover having an impact on krill distribution and biomass (Piñones and Fedorov 2016; Atkinson et al. 2019).

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Krill is a keystone species in the Antarctic marine food web (Hofmann et al. 2011; Ballerini et al. 2014) and hence, it is expected that any negative effects on krill will not only affect its direct predators but also will produce a cascade effect on the entire ecosystem. If climate-based reductions in krill density continue at the predicted rate (Atkinson et al. 2009), it is expected that krill predator populations will follow a steep decline (Trathan and Reid 2009). There have been widespread decreases of penguin populations over the Antarctic Peninsula with climate change recognized as the main driver (Lynch et al. 2012; Casanovas et al. 2015). The population trends in these species seem to be related to a reduction in sea ice cover and krill abundance (Forcada et al. 2006; Trivelpiece et al. 2011). Some authors have supported the hypothesis that there is a direct relationship between the sea ice variations and the penguin abundance, including contrasting trends for "ice-loving" and "ice-avoiding" species (Forcada et al. 2006). In this sense, it would be expected that sea ice retreat and the resulting access to ice-free foraging areas should benefit both chinstrap (*Pygoscelis antarcticus*) and gentoo (*P. papua*) penguins, which have been identified as "ice-avoiding" species. However, although this is consistent with the gentoo penguin global population trends (yet local decreases of gentoo penguin abundance exist in the South Shetland Islands; i.e., Petry et al. 2016, 2018), the evidence pointing to a decline of chinstrap penguin populations throughout the WAP suggests that reduction in krill availability could be playing a critical role to explain the population dynamics of this species (Trivelpiece et al. 2011; Lima and Estay 2013).

The Antarctic krill is target of an important fishery in the Southern Ocean, occurring mainly in the Atlantic sector (FAO statistical subareas 48.1, 48.2 and 48.3). The Commission for the Conservation of Marine Living Resources (CCAMLR) is the international organization responsible for the management of the krill fishery and has successfully managed fishery based on a precautionary approach since its creation in the early 1980s (Constable 2011). In recent years, there has been increasing concerns on how climate-based changes and the current-concentrated behavior of the krill fishery (Santa Cruz et al. 2018; Krüger 2019) can affect synergistically the penguin colonies over the WAP. Moreover, krill catches have been reaching values like those recorded in the 1990s before the adoption of a fixed catch (CCAMLR 2018). Although catches are considered to be low compared to the krill abundance (catch limit is < 1% of the total estimated biomass ≈ 60 million tons on Antarctic Peninsula alone, CCAMLR 2019), catch is expected to keep increasing in the future with the development of new technologies and changes in both fishing technologies and Antarctic environment. Contrasting to what fisheries did back in the 1990s, now the whole krill catches are concentrated on relatively small spots on the WAP and the South Orkney Islands (Santa Cruz et al. 2018; Krüger 2019). While CCAMLR performance has been considered a successfully sustainable managed practice (Nicol et al. 2012), under the current climate changes, it is likely that this may change (Hill et al. 2016) as signs of krill fishery decreasing performance of penguins are becoming evident (Watters et al. 2020). This study aimed to evaluate the risk of the krill fishery to populations of Pygoscelid penguins, testing if the population changes are proportional to changes in the distribution of catches in WAP, and their synergistic relation with climate variability. We used 38 years of fishing data to evaluate risk for both chinstrap and gentoo penguins and used mixed models to test how population growth could have responded to the fishing pressure under contrasting SAM conditions.

MATERIALS AND METHODS

Penguin population data

All data on populations of chinstrap (*P. antarcticus*) and gentoo (*P. papua*) penguins breeding in the WAP area available at the Mapping Application for Penguin Populations and Projected Dynamics MAPPPD (penguinmap.com, Humphries et al. 2017) between 1980 and 2017 were downloaded (Fig. 1, chinstrap = 197 colonies, gentoo = 78 colonies). MAPPPD is a penguin population databank, which puts together all available information about population counts of penguins on their breeding colonies. Counts include different type of data: breeding pairs, adults, and chicks. Only pair counts made in November and December, matching the early breeding season and providing a better picture of actual population size, were used. Temporal variation in colony-level population growth rate was expressed as follows:

$$\lambda_{\text{std}} = ((n_b/n_a)/\text{years}_{b-a}) - 1,$$

where n is the number of breeding pairs counted in November or December of a given year (b) and the number of breeding pairs counted in a previous year (a), divided by the number of years in between b and a. This procedure allowed us to deal with differences in sampling size by smoothing any too steep values resulting from a too large temporal gap in data, at the same time, providing population-level temporal variability of each penguin colony. From this value 1 was subtracted, so that the result varied from − 1 (population extinction) to ∞, with positive values representing population increase. Each colony was classified based on CCAMLR Small-Scale Management Units: Elephant Island, Drake East, Drake West, Bransfield East, Bransfield West, and Antarctic Peninsula West,

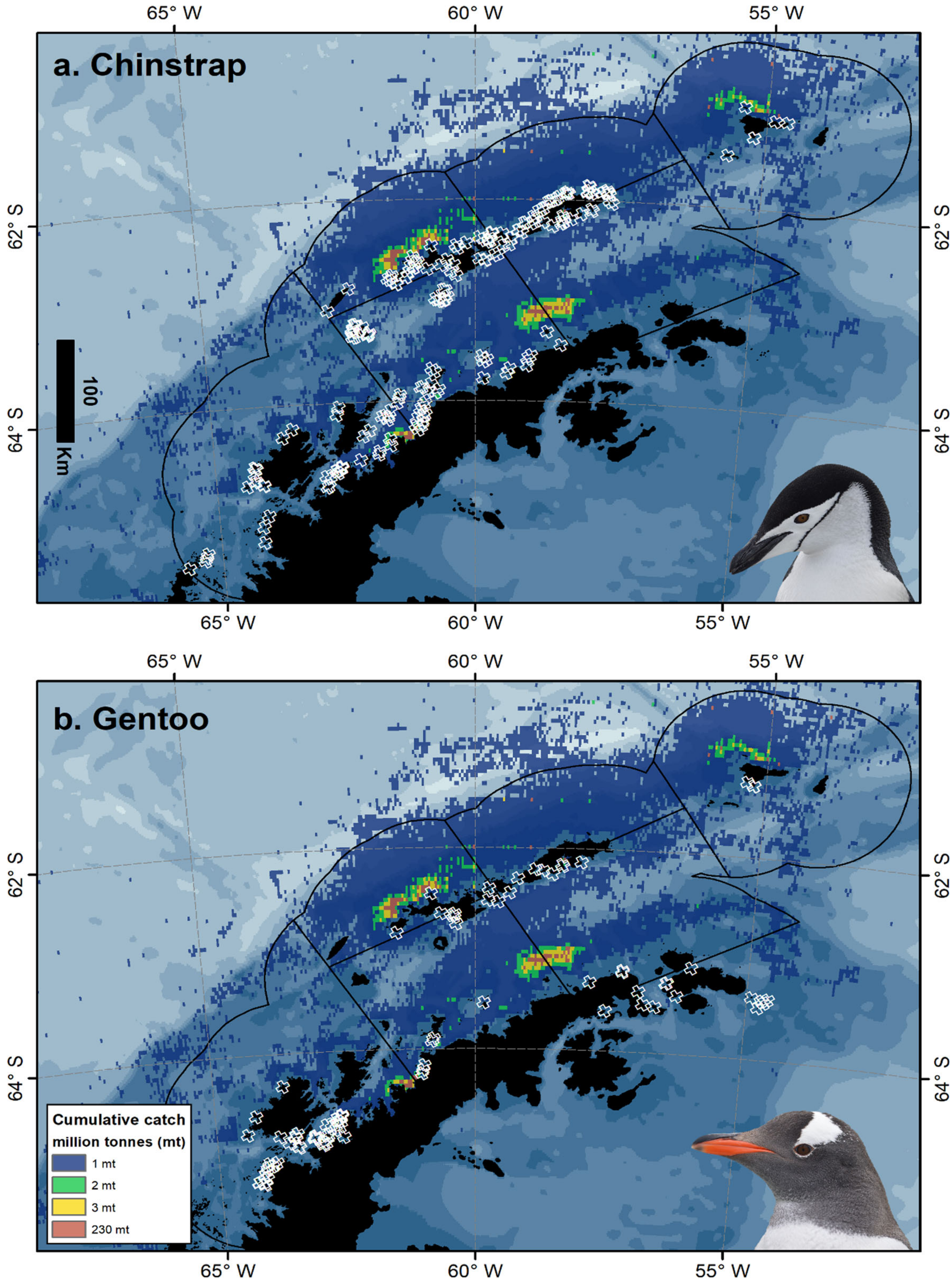

Fig. 1 Distribution of chinstrap *Pygoscelis antarcticus* (**a**) and gentoo *P. papua* (**b**) penguins breeding colonies (white crosses) along the western Antarctic Peninsula, overlapped with the Antarctic krill accumulated fishing catch. Data on fishing catch represent all the catch in the area accumulated between 1980 and 2017. It is all the krill that were extracted from a given spatial cell in 38 years. Penguin data from MAPPPD (penguinmap.org; Humphries et al. 2017)

which we will refer as Gerlache Strait because fishing in this area concentrated within the strait (Fig. 1). Small-Scale Management Units are zones proposed in order to be a spatial tool for local monitoring of the krill fishery and krill predators and devised for spatially subdividing the krill catch limits (Constable and Nicol 2002). Most penguin colonies did not have data on the whole 38 years considered; majority of colonies had less than 10 counts, while 38 chinstrap and 45 gentoo colonies had at least 2 counts (enough for calculating the λ_{std}) (Appendix S1).

Krill fishery data

Haul-by-haul data of the fleet operations were obtained from the CCAMLR Secretariat database for the period between 1980 and 2017 (38 years). The accumulated catch within a 30-km radius of each colony was used to evaluate the risk of exposition of each colony to the changes in catch distribution. During breeding season (when counts were made), foraging of pygoscelid penguins is more probable within 30 km of the colonies (Warwick-Evans et al. 2018). We, therefore, assumed this to be the distance where krill availability would be more important during key periods of the year cycle and competition with fisheries would be more impacting. Each fishing event was classified based on important period of the penguin intra-annual life cycle: chick-rearing (January to March), non-breeding (April to September), and early breeding (October to December). Catch was accumulated within those periods for each year (Appendices S2, S3) in order to better describe the periods when penguin are more at risk to experience impacts from fishery, but catch was accumulated throughout the whole year to test statistically the response of populations (below).

Climate data

The southern annular mode SAM is the main large-scale pressure system driving climate in Antarctica (Kwok and Comiso 2002; Doddridge and Marshall 2017). SAM is defined as the difference of the normalized zonally mean sea-level pressure of 40° S and 65° S (see Gong and Wang 1999 for details). As SAM indicates differences, it can have negative and positive values: negative values mean air pressure in Antarctica (65° S) is higher than in the subantarctic (40° S); positive values mean air pressure is higher in subantarctic (40° S) than in Antarctic (65° S). Pressure differences reflect the large-scale movements of air masses. By examining SAM values, it is possible to infer whether warmer currents from the north intruded areas further south; therefore, SAM can accurately indicate trends of sea ice and temperature anomalies in Antarctica (Marshall and Bracegirdle 2014; Doddridge and Marshall 2017). Penguins (Forcada et al. 2006) and Antarctic krill (Flores et al. 2012; Meyer 2012) are knowingly responsive to abrupt changes on temperature and ice conditions during winter. SAM monthly data were downloaded from NOAA Earth System Research Laboratory ESRL (esrl.noaa.gov). Data on Fractional Sea Ice Cover, Surface Level Temperature, and Open Water Sensible Heat Flux were downloaded from NASA Giovanni data browser (giovanni.gsfc.nasa.gov) per month.

Penguins, fishery, and climate

Considering the high correlation of the climate variables in WAP (Appendix S4), and correlation of climate variables with SAM variability with a temporal lag from 0 to 3 months (Fig. 2), we used SAM during the non-breeding period together with accumulated catch within each year in a binomial Generalized Linear Mixed Model using the 'lmerTest' R package (Kuznetsova et al. 2018) and the 'sjPlot' R package (Lüdecke et al. 2019) to plot models:

$$\text{bin}\lambda_{std} \sim \text{catch}_y * \text{SAM} + (1|\text{ colony ID}),$$

where $\text{bin}\lambda_{std}$ is a binary estimate of the standardized growth rate λ_{std} (positive values = 0, negative values = 1) understood as the probability of population decreasing in a given year. Catch_y is the accumulated year krill catch, and SAM is the southern annular mode during winter (non-breeding season). We used mixed models which allows to control for the effects of lack of independence and sample size differences within the structure of the data. We used the colony ID as a random term in the formula accounting for the colony-level differences on the intercept of the response to the explanatory variables. The effect of the random term was tested with a likelihood ratio test using the function 'ranova'. All data processing and analysis were done in R environment (R Development Core Team 2014) using 'raster' (Hijmans 2013), 'plyr' (Wickham 2020), and 'ggplot2′ (Wickham and Chang 2015) packages. Maps were produced using ArcGis 10.4.

RESULTS

Changes of spatial catches distribution

Krill catches within the 30 km radius from colonies of both species occurred predominantly during chick-rearing and non-breeding periods (Fig. 3). Although, catches after the mid-1990s decreased or remained stable in Elephant Island and Drake Passage sectors, respectively (Fig. 3), catches in the Bransfield Strait increased near colonies of both penguin species (Fig. 3). During the last decade, fleets started to operate more intensively in the Gerlache Strait,

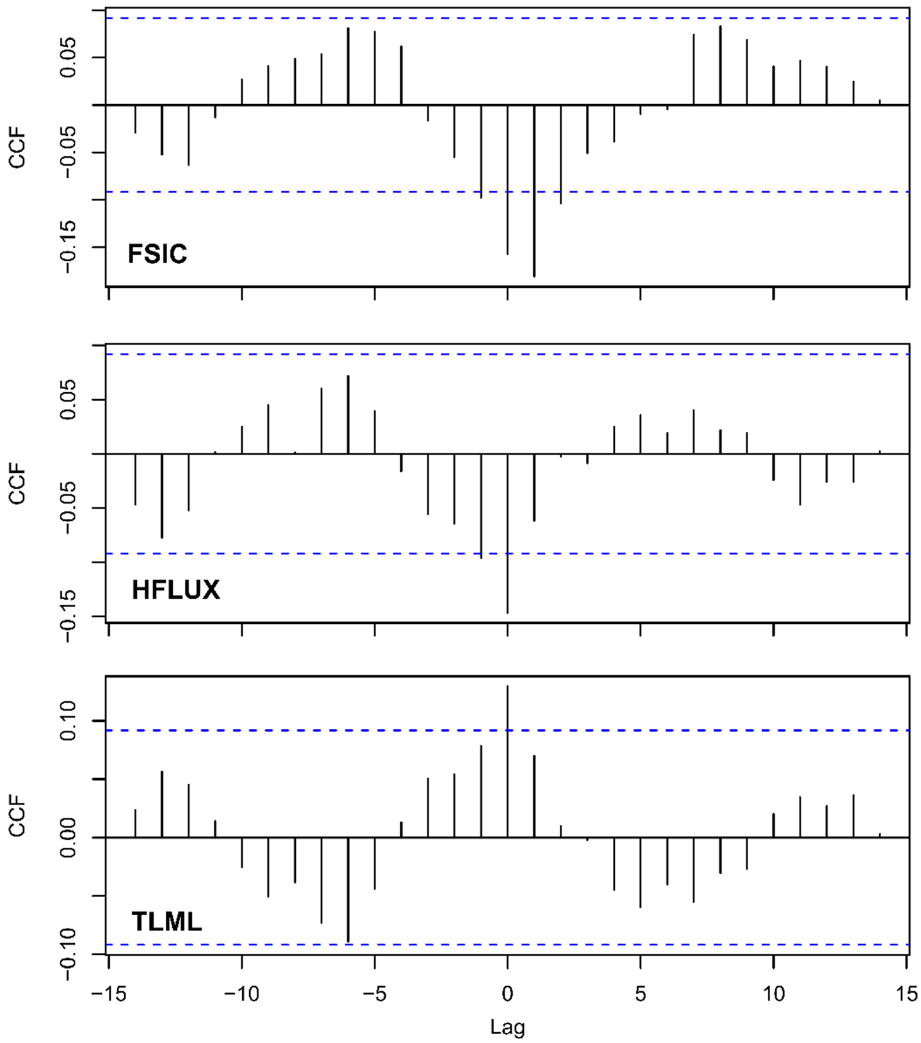

Fig. 2 Lagged regression model (cross correlation function CCF) testing the temporal response of fractional sea ice cover (FSIC), open water sensible heat flux (HFLUX), and sea-level air temperature (TLML) at the Western Antarctic Peninsula to the variation of the Southern Annular Mode (SAM). Lag interval is in months. Dashed blue line indicates where the correlation is significant at the $P < 0.05$ level. Analysis was done in the 'astsa' R package (Stoffer 2008)

increasing catches during both chick-rearing and non-breeding periods near chinstrap colonies (Fig. 3).

Trend of the penguin populations

Most of the λ_{std} values for chinstrap penguins were negative (58.78% of cases) in the WAP (Appendix S5). Gentoo penguins presented a mean growth trend bordering the stability (Appendix S5) with 50.72% of negative cases of λ_{std}.

Probability of chinstrap population decrease was related to catch$_y$ ($F_{155,3} = 2.96$, $z = 2.65$, $P = 0.008$) and to the interaction catch$_y$ * SAM ($F_{155,3} = 1.72$, $z = -1.63$, $P = 0.055$), but not to SAM alone ($F_{155,3} = 1.17$, $z = 1.50$, $P = 0.133$). Random factor was not significant for chinstrap penguins (LRT = 0.15, $P = 0.910$), meaning population-level response was homogeneous throughout the WAP. For gentoo populations, the probability of decrease was marginally related to catch$_y$ ($F_{251,3} = 0.76$, $z = 1.47$, $P = 0.090$) and catch$_y$ * SAM interaction ($F_{251,3} = 1.70$, $z = -1.75$, $P = 0.085$), but not to SAM alone ($F_{251,3} = 0.11$, $z = 0.74$, $P = 0.461$), and random effects were significant (LRT = 5.95, $P = 0.014$); therefore, population-level variability is important in the response of gentoo penguins to fishing catches (Appendix S6). For both chinstrap (Fig. 4a) and gentoo (Fig. 4b), probability of decrease in a given year (λ_{std}) was constant with increasing fishing catch during years of positive SAM, but increased with increasing catch during years of negative SAM. In extreme negative SAM, fishing catches above ≈5000 tons meant a mean estimated probability of decrease above 75% for both species (Fig. 4).

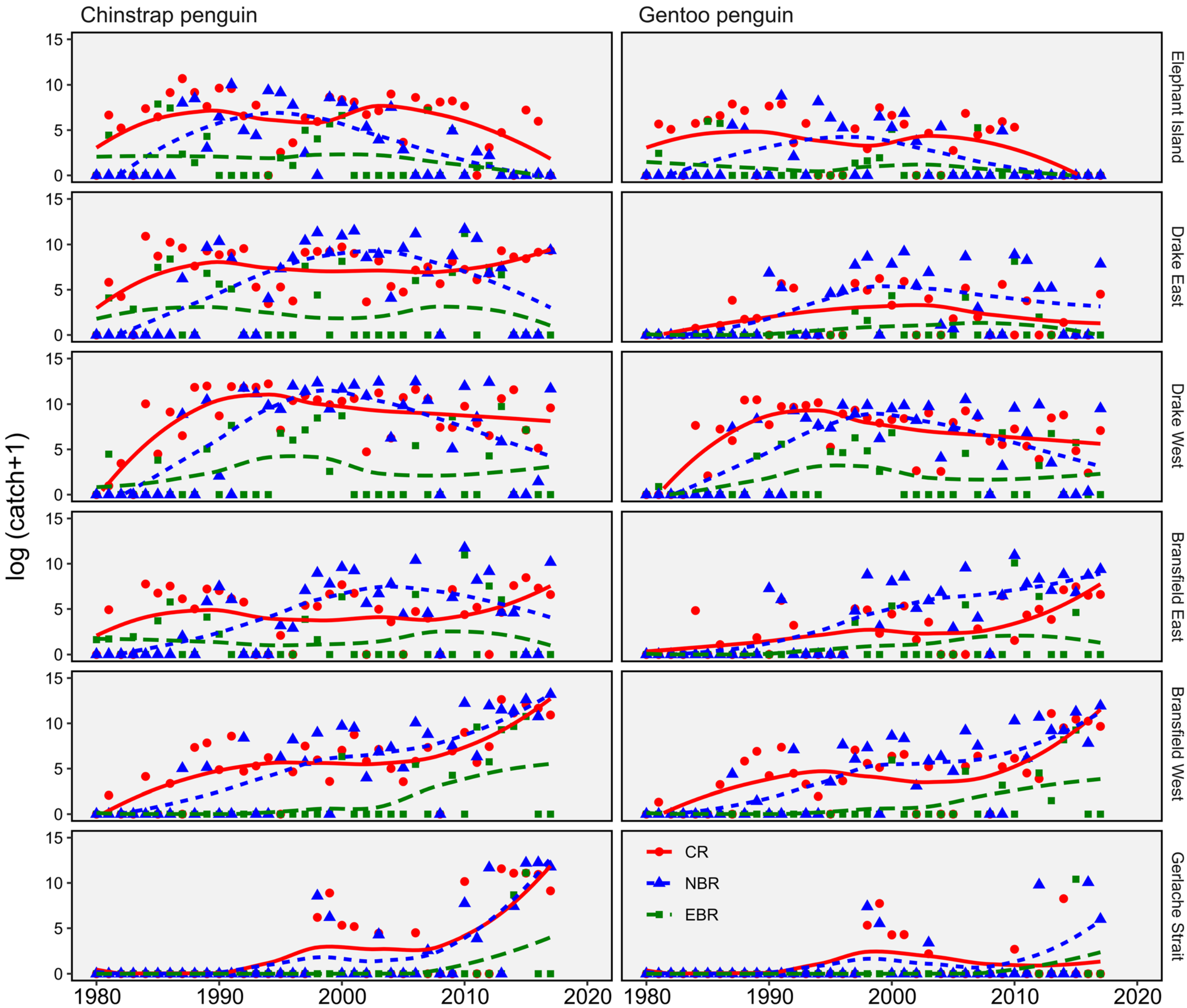

Fig. 3 Seasonal accumulated catch within 30-km radius around each breeding colony of chinstrap (*Pygoscelis antarcticus*) and gentoo (*P. papua*) penguins during chick-rearing CR (January–March), non-breeding NBR (April–September), and early breeding EBR (October–December) periods classified according to small-scale management unities SSMUs: Elephant Island, Drake Passage East and West, Bransfield Strait East and West; Gerlache Strait. See also Fig. 1

DISCUSSION

In the last two decades, krill catches have increased consistently near penguin colonies in the Bransfield and Gerlache Straits during chick-rearing and non-breeding periods, whereas in the Drake Passage and Elephant Island catches have remained stable or mostly decreasing. These patterns reflect the southward expansion experienced by the fleet during the last decade, mentioned by previous works (Nicol et al. 2012; Santa Cruz et al. 2018; Krüger 2019). Our findings also indicated that the relation between the standardized penguin growth rate and cumulative fishing catch was contrasting depending on SAM conditions. In this manner, in positive SAM values, the range of the probability of decreasing varied largely, while in negative SAM values, there was a consistent rise in the probability of decreasing for both chinstrap and gentoo penguins when fishing catches near colonies was very high ($> \approx 5000$ tons). Moreover, the additional effect over krill recruitment caused by the decrease in sea ice coverage, due to the key role played by this factor for the development of krill larvae, coupled with the increase in krill catches in the areas near penguin colonies, could generate a much more vulnerable scenario for these species during the breeding season (i.e., Trivelpiece et al. 2011). Recovery of baleen whale populations also have been suggested out as a potential explanation for current observed trends in penguin populations, as whaling in the last century would have

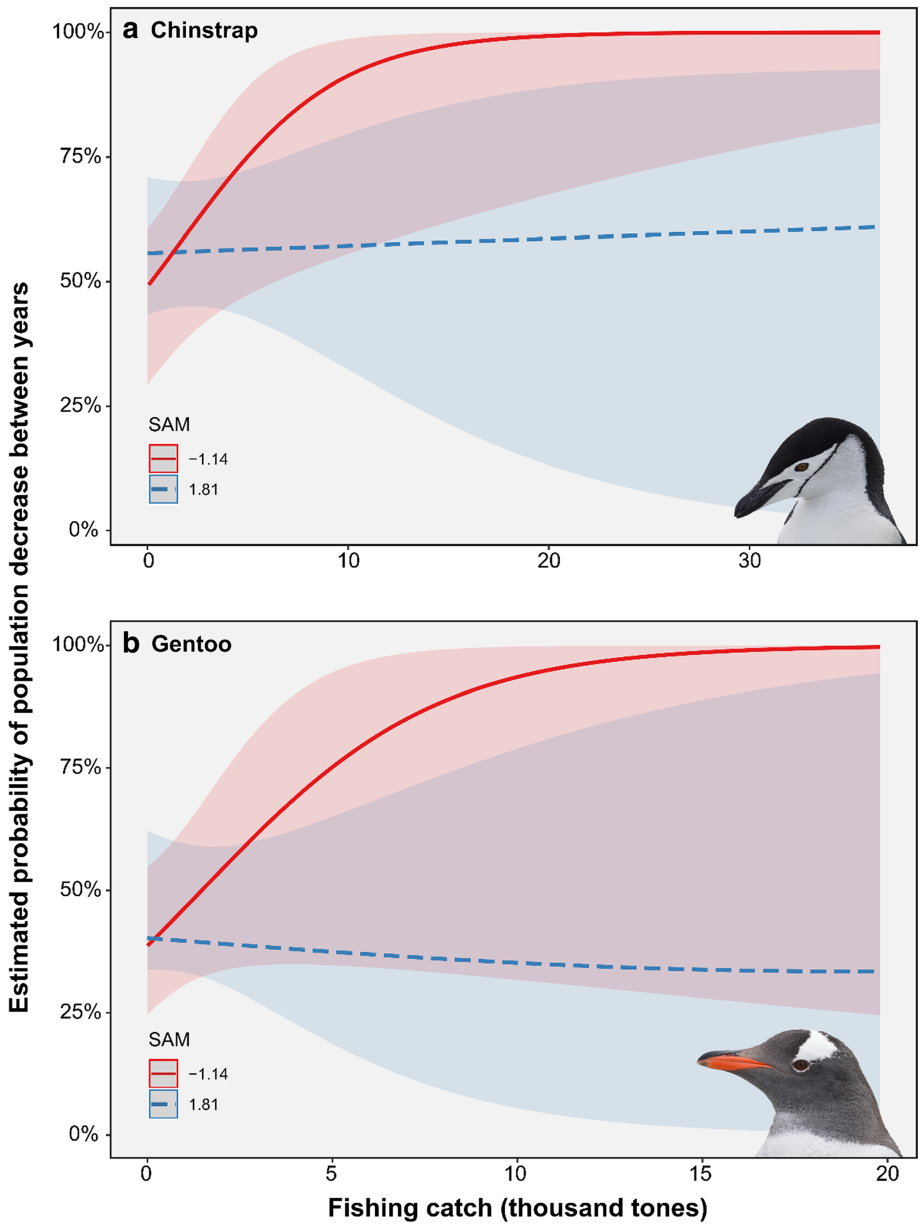

Fig. 4 Estimated probability (trend lines) ± standard deviation (shaded area) of chinstrap *Pygoscelis antarcticus* (**a**) and gentoo *P. papua* (**b**) penguins having a negative standardized population growth rate as a response to fishing catch within 30-km radius around colonies during years of contrasting Southern Annular Mode SAM values: negative (solid red line) and positive (dashed blue line). The 'sjPlot' R package through the function 'plot_model' allows visualizing the estimated mean response to the extreme values of the interacting variable, in this case maximum and minimum SAM values

allowed for an increase in krill availability, the krill surplus hypothesis, but so far, studies dealing with that hypothesis did not find solid evidences and suggested environmental variability as more important to changes in krill biomass (Fraser et al. 1992; Surma et al. 2014). Previous studies mentioned potential impacts of krill fishery on penguin populations (i.e., Trivelpiece et al. 2011), and a recent paper (Watters et al. 2020) reached conclusions similar to ours by applying a different method and evaluating population data at two sites. Our study, to our best knowledge, is the first to reveal the effect of climate change and krill fishery on penguin population declines looking explicitly at multi-population trends on the scale of the whole Antarctic Peninsula. It is worth mentioning that a previous work by Che-Castaldo et al. (2017) tested whether krill fishery could have an effect on Adelie penguin population dynamics; however, the spatial scale of the fishing data used was too coarse to allow detecting strong local effects.

Considering what it is mentioned above, the next step from now on would be to move towards the implementation of a new krill fishery management strategy (see further below), which could consider new elements that are not currently included. Elements such as regular biomass estimations and identification of the spatial scales of the impact of krill fishery on penguins, thus, identifying where higher catches would have higher impact on penguins and other predators, and distributing catches accordingly.

Risk of competition with krill fishery

Recent changes of the spatial distribution of the krill fishing fleet in the WAP (Santa Cruz et al. 2018; Trathan et al. 2018; Krüger 2019) can be linked to the general trend of decreasing winter sea ice extent and duration that has been reported for the area (Parkinson 2019). Increased ice-free conditions allowing trawlers to continue their activities after the end of the Austral summer (Nicol et al. 2012) explains the increasing catches near penguin colonies during the non-breeding season. While sensibility of penguins to climate change is well known (Casanovas et al. 2015; Che-Castaldo et al. 2017), the interaction of climate change with increasing catches may have a synergistic detrimental effect on penguins. According to Doddridge and Marshall (2017), negative SAM anomalies precede higher temperatures, low sea ice, and low krill productivity in the Southern Ocean, particularly in Antarctic Peninsula, with effects being cascaded throughout the whole food web (Dahood et al. 2019).

Carry-over effects of the potential competition of penguins with the krill fishery during the non-breeding season are still unknown, but given our results, cumulative catches within 30 km from colonies seemed to impact negatively both *Pygoscelis* species in years when sea ice was low. Although chinstrap penguins tend to disperse from breeding grounds, it is evident that there is a large variability and part of the population may remain nearby the breeding area (Trivelpiece et al. 2007; Hinke et al. 2015, 2017). On the other hand, gentoo penguins tend to remain closer to the breeding grounds during winter (Wilson et al. 1998; Thiebot et al. 2011; Hinke et al. 2017). Winter distribution of fledgling and immature stages of both penguin species is still unknown for most populations, but evidence suggests penguin recruitment is an important population parameter explaining penguin population decrease in the WAP, which has been also linked to decreased recruitment of krill (Hinke et al. 2007; Trivelpiece et al. 2011; Atkinson et al. 2019). Penguin populations have been potentially affected by the krill fishery (this study, Watters et al. 2020) in zones where intense fishing occurred in recent years (i.e., Santa Cruz et al. 2018) which overlapped with important krill nursery and krill recruitment areas (Perry et al. 2019) in the Bransfield and Gerlache Straits.

We propose two hypotheses to explain our findings. Firstly, krill densities are declining and their distributions are contracting southward (Atkinson et al. 2019); therefore, increased fishing activities in areas with reduced krill availability increase competition between penguins and fishery, particularly in periods of low productivity. Secondly, increased catches on years with low krill productivity decrease availability of krill to penguin populations. Krill population rises and falls from year to year, with potential recruitment cycles lasting 5 to 6 years (Reiss et al. 2008), mostly driven by food competition (Ryabov et al. 2017; Walsh et al. 2020). Summer melting of sea ice accumulated during winter can boost local productivity in the WAP (Eveleth et al. b, 2017a); therefore, during years of negative SAM (when winter sea ice cover is lower), krill could experience population limitation due to low availability of food and consequently low recruitment (i.e.,Flores et al. 2012; Meyer 2012). Under this scenario, increased fishing catches could mean a krill shortage for penguins in the next breeding season if the krill caught is not recovered. The fishery would be extracting biomass cumulatively from the same population before new adults arrive, temporarily depleting resources for penguins.

Management consequences

CCAMLR manages the krill fishery following the principle of rational use of the marine living resources, which implies both the precautionary and ecosystem-based approach. Since 1991 CCAMLR has established catch limits for area 48 (WAP and Southern Scotia Arc), oftentimes updated depending on the availability of new biomass estimations. So far, the current catch limit for area 48 is 620 000 tons (known as the trigger level, a value adopted entirely based on the previous highest catches). Thereafter, trying to avoid potential concentration of the catches in small areas, and based on the biomass distribution, the trigger level was split proportionally among the subareas, setting 155 000 tons for area 48.1 and 279 000 tons for subarea 48.2 (further details of this process see Nicol and Foster 2016). Unfortunately, the catch limit is fixed and does not vary according to the variability of the krill population, being particularly problematic in years of low productivity (i.e., environmentally-impacted krill recruitment, Thorpe et al. 2019). Catch limits should be established based on seasonal krill abundance estimates that also must include predator demands. For instance, CCAMLR is pursuing a feedback management of krill fishery that would be achieved through an ecological risk assessment (i.e.,Trathan et al. 2018; Warwick-Evans et al. 2018; Lowther et al. in review) quantifying the amount of krill required from top-predators on a spatial grid; fisheries would use that information plus continuously updated information on krill density to guide when, where, and how much they should fish. Our results support the need for implementing such kind of management approach, meaning that in years when krill density is lower, catch limit should be lower than the currently being used. In addition, an increasing concern is that precautionary catch limit was calculated for a regional scale, but our results as many others (Hill et al. 2016; CCAMLR 2018; Santa Cruz et al. 2018; Krüger 2019) demonstrated that the fishery is not a randomly distributed activity, rather catches occurs in a highly concentrated manner, especially in Bransfield and Gerlache Straits. This, coupled with the new evidences of the impacts produced by climate change and krill fishery on penguin populations (Watters et al. 2020, this study), creates concerns about whether the precautionary catch limit is still precautionary under the current scenario.

CCAMLR is pursuing the implementation of a Marine Protected Area Network as a tool to protect Antarctic marine ecosystems and manage human activities, including fisheries (Brooks et al. 2016; Coetzee et al. 2017). In this regard, a large MPA in the Domain 1 (WAP) was proposed recently by Argentina and Chile parties (https://www.ccamlr.org/en/ccamlr-38/25-rev-1) aiming to provide extra protection for several conservation objectives, including krill; however, despite many countries have strongly supported the proposal, a few have expressed their concerns voting against its adoption since decision-making in the Commission is based on consensus, the proposal has not been adopted. The current proposal includes general protection zones that precisely encompass the major locations of the synergistically climate and fishery affected penguin colonies (and other krill predators). Particularly, around SOI, South Shetland Islands and the Gerlache Strait, where evidences support that closures to krill fishing would be beneficial for krill predators if fishing pressure increases (Klein and Watters 2020). Examples of MPAs that allowed for increases in stocks of harvested species are abundant (Duffy et al. 2016; Chirico et al. 2017; Sala and Giakoumi 2018), even producing better fishing yields (Lynham et al. 2020). Therefore, it is a strategy with potential to not only protect top-predators and its resources, but also to allow for a long-term fishery in the WAP.

CCAMLR has recognized the need for a more precautionary and dynamic approach taking into account contemporary changes in the WAP, and its currently working on the development of a new approach of the management of the krill fishery (CCAMLR 2019). Evidence such as the presented here along with other new research and new monitoring plans will be crucial for implementation of a more dynamic management strategy of the krill fishery that ensures the protection of krill dependent predator under a changing environment in this unique ecosystem.

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