Environmental drivers of the physiological condition of mature female Antarctic krill during the spawning season: implications for krill recruitment

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ABSTRACT: Southern Ocean pelagic productivity relies on the abundance of Antarctic krill *Euphausia superba*, which fluctuates on a 5–7 yr cycle and is driven by interannual variability in recruitment. The western Antarctic Peninsula (wAP) is home to a significant proportion of the circum-Antarctic krill biomass and is the focus of the krill fishery. The wAP is warming at a rate quicker than most other places on Earth, with notable regional changes in the pelagic ecosystem. There is a major gap in our understanding of how environmental variability affects the reproductive success of krill. We used historical krill population data collected at the wAP (January 1993–2008, Palmer Antarctica Long Term Ecological Research) to assess the effects of environmental variability on the condition of mature female krill during the spawning season and its relationship with krill recruitment. Mature female krill condition during the spawning season was positively correlated with recruitment the subsequent year. Results of generalized additive models indicated that the predominant drivers of krill condition during the spawning season were climatological (Southern Annular Mode and Multivariate El Niño Southern Oscillation Index), though the timing of sea ice advance and retreat, and diatom concentrations were also important. Gaining a better understanding of the oceanographic and climatological factors that affect the physiological condition of mature female krill is critical for predicting future demographic patterns and responses to change. Results from our study emphasize the importance of including the effects of climate change in the management models for the Antarctic krill fishery.

KEY WORDS: Antarctic krill · Physiological condition · Recruitment · Reproduction · Climate drivers

1. INTRODUCTION

Antarctic krill *Euphausia superba* are an essential component of the western Antarctic Peninsula (wAP) ecosystem, serving as the predominant prey item for predatory megafauna (Laws 1977, Croxall & Prince 1980) and facilitating carbon export and sequestration (Atkinson et al. 2012). Antarctic krill are also the focus of the largest fishery in the Southern Ocean, with approximately 313 000 tons harvested in 2018 (Nicol et al. 2012, Commission for the Conservation of Antarctic Marine Living Resource [CCAMLR] 2018). The wAP is warming at a quicker rate than most other places on

Earth, with a 6°C increase in mean annual air temperature observed in the northern region over the past 60 yr (Vaughan et al. 2003). Warmer temperatures have led to a reduction in sea ice extent and duration, accelerated sea ice retreat, intensified winter surface ocean mixing and increased oceanic heat uptake (Stammerjohn et al. 2008a, Venables & Meredith 2014). These changing environmental conditions have resulted in an up to 2-fold decrease in krill recruitment at the wAP since the 1970s (Atkinson et al. 2019). The reduction in krill recruitment throughout the wAP has been linked to a positively trending Southern Annular Mode (SAM) index and associated increased temper-

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atures (Atkinson et al. 2019). Krill are an ecologically and economically valuable species and understanding how warming affects their population dynamics is critical for interpreting the resilience of Antarctic ecosystems and for the future management of the krill fishery (Meyer et al. 2020).

The population dynamics of krill at the wAP have fluctuated over the past 40 yr, with some years exhibiting stronger cohorts than others (Siegel 2005, Fielding et al. 2014). Peaks in krill biomass occur every 5–7 yr in response to strong year classes that were produced during years of high krill recruitment (Quetin & Ross 2003, Ryabov et al. 2017), which is calculated as the proportion of young-of-year, or age-class 1, krill to the total krill population. High levels of krill recruitment are coupled with positive chlorophyll *a* (chl *a*) anomalies and high winter sea ice cover at the wAP (Siegel & Loeb 1995, Saba et al. 2014, Steinberg et al. 2015). Further, Quetin & Ross (2001) found that the timing of sea ice retreat is correlated with the percentage of female krill that are reproductively active. Saba et al. (2014) found that positive chl *a* anomalies and high winter sea ice cover are associated with a –SAM phase in the winter and spring. Siegel & Loeb (1995) suggested that high sea ice concentrations throughout the winter promote an early initiation of the spawning season, which is correlated with higher levels of krill recruitment. While these studies have worked to establish a better understanding of the climatological and environmental drivers of variability in krill recruitment success, none have explicitly resolved the mechanisms by which these drivers affect krill recruitment. Recently, Ryabov et al. (2017) proposed a possible mechanism, suggesting that intraspecific competition for food controlled krill recruitment success, with climatological variability acting as a modulating factor.

Krill recruitment is primarily driven by the degree of reproductive output by mature female krill during the spawning season and the subsequent survival of larvae during the winter (Quetin & Ross 2003). Larvae must consistently feed throughout the autumn and winter, principally on sea ice algae, in order to survive (Meyer & Teschke 2016). While the mechanism behind the success of larval survival has been identified, it is less certain what the mechanism behind successful reproductive output is. In general, years with elevated recruitment typically follow those with high reproductive output, which can be achieved as a result of (1) a longer spawning season, (2) larger batch sizes per female at each spawning event, (3) more mature females in the population, (4) larger (in length) and older mature females in the population, or (5) a combination of these (Siegel & Loeb 1995, Quetin & Ross

2001). The first 2 factors, length of the spawning season and number of eggs produced per female, are of relevance to our study. The length of the spawning season is influenced, in part, by the timing of initiation of the first spawning event in a given spawning season, which is determined by the timing of gonad maturation (Ross & Quetin 2000). During sexual development, female krill produce oocytes to be used during reproduction, and the number of oocytes produced is dependent on the amount of energy that the female can obtain from its environment (Cuzin-Roudy & Labat 1992). The number of spawning events during a single spawning season will also influence the length of the spawning season. Both the number of spawning events and the size of the egg batches are primarily dictated by the number of oocytes produced by the female prior to the spawning season during the early stages of gonad maturation (Cuzin-Roudy 2000, Ross & Quetin 2000). Thus, timing and degree of gonad maturation are important for reproductive output. Because changes in reproductive output reflect changes in an organism's physiological condition (Ricklefs & Wikelski 2002), the factors that affect the condition of mature female krill may be a driving mechanism for high reproductive output and subsequent recruitment success. The physiological condition of an organism reflects its feeding history at timescales greater than days or weeks. Thus, by examining the physiological condition of mature female krill during their spawning season, we can start to understand how environmental variability, which affects food availability, leading up to and throughout the spawning season drives the reproductive output and recruitment of Antarctic krill.

Typically, female krill produce 3–9 batches of eggs per spawning season, each batch consisting of 100–8000 individuals (Cuzin-Roudy 2000, Ross & Quetin 2000). The number of spawning events in a given spawning season is dependent on the quantity and quality of food available to krill in the environment (Quetin & Ross 1991). Ovarian maturation typically occurs in the spring (September–November), and an early initiation of the spawning season is more likely to occur when environmental conditions favor a high quality and ready availability of food at the wAP during the sexual maturation period, increasing the rate of reproductive development in female krill (Quetin & Ross 2001). If resources remain plentiful during the spawning season, mature female krill will undergo several cycles of egg production and will exhibit higher levels of reproductive output with each spawning event (Quetin & Ross 1991, Siegel & Loeb 1995). Thus, it is probable that female krill that are in better physiological condition, as a result of plentiful

resources prior to and throughout the spawning season, will lead to higher levels of krill recruitment success through the introduction of greater numbers of larvae into the population.

The connection between mature female krill condition, reproductive output and recruitment serves as the impetus for our study. We examine these relationships and their environmental drivers, which encompass both climatological and oceanographic drivers, along the wAP from 1993 to 2008 using data collected during the Palmer Long Term Ecological Research (PAL LTER) summer cruises. We hypothesize that the physiological condition of mature female krill during the spawning season will be positively correlated with krill recruitment the following year. Further, we hypothesize that seasonal fluctuations in climatological and oceanographic parameters will affect the physiological condition of mature female krill during the spawning season either directly through changes in their food supply, or indirectly through mechanisms that alter their food supply. Gaining a better understanding of the environmental factors that affect the physiological condition of mature female krill is crucial for predicting future demographic patterns and responses to continued climate change. Identifying the factors that result in successful recruitment in krill populations is critical

when developing population models and when making ecosystem-based management decisions regarding the future of the krill fishery (Meyer et al. 2020).

2. MATERIALS AND METHODS

2.1. Study region

Data used in this study were collected during the PAL LTER austral summer (January) cruises aboard the MV 'Polar Duke' from 1993 to 1997 and from the ARSV 'Laurence M. Gould' from 1998 to 2008. The sampling area spanned from just south of Anvers Island (65.05°S) to just south of Marguerite Bay (68.16°S) along the wAP (Quetin & Ross 2003; our Fig. 1). The PAL LTER sampling grid consists of gridlines that are spaced 100 km apart and run perpendicular to shore. Sampling stations, spaced 20 km apart, are located along each gridline, extending from near-shore to approximately 200 km offshore (Waters & Smith 1992). In 1997, 3 stations inside Marguerite Bay were added along the 200 km gridline. The sampling stations varied annually based on the ship schedule, weather and sea ice conditions (Ross et al. 2014).

Climate variability at the wAP is primarily driven by fluctuations in SAM and the Multivariate El Niño Southern Oscillation Index (MEI) (Thompson & Wallace 2000, Loeb et al. 2009). Through alterations in atmospheric and oceanic circulation patterns, these climate oscillations can directly impact sea surface temperatures (SSTs), sea ice, and water column dynamics at the wAP (Stammerjohn et al. 2008b). SAM and MEI can indirectly affect the amount of primary productivity at the wAP by altering the depth of the Winter Water Layer (WWL) and the Surface Mixed Layer (SML), 2 water masses that are critical in establishing the magnitude and frequency of phytoplankton blooms (Park et al. 1998, Massom et al. 2006, Stammerjohn et al. 2008a). The depth of the WWL is dependent on the degree of mixing that occurs in response to changes in the magnitude and frequency of winter winds, while the depth of the SML fluctuates primarily in response to warming in the spring and summer that results in an influx of freshwater via the melting of sea ice

Fig. 1. Palmer Long Term Ecological Research region along the western Antarctic Peninsula (inset) used in this study from 1993 to 2008. Sampling gridlines were spaced 100 km apart, with the 200 km gridline being the southern boundary and the 600 km gridline being the northern boundary of the sampling area. Black dots: sampling stations used in this study

(Park et al. 1998). The depth of the remnant WWL and SML in the spring and summer is associated with different levels of primary production, depending on either the retention of phytoplankton within, or the dispersion of phytoplankton out of, the surface ocean based on the level of water column stability. A shallow and more stable remnant WWL and SML throughout the spring and summer results in more favorable conditions for phytoplankton growth (Vernet et al. 2008).

2.2. Krill collection

Antarctic krill were collected during the austral summer from 1993 to 2008 for abundance and biomass estimates, length-frequencies, sex, and maturation stage. Krill were collected using a 2 × 2 m square fixed-frame net (700 µm stretch mesh, 500 µm cod end) that was towed obliquely between the surface and 120 m depth. The depth of the tow was collected with either a benthos-time-depth recorder or a pressure sensor at the end of the tow cable. The volume of water filtered during each net tow was measured using a General Oceanics flowmeter attached to the center of the net frame (Ross et al. 1998, 2014, Quetin & Ross 2003). The tow depth of 120 m was used based on evidence that krill were not likely to be found below that depth in the summer time (Ross et al. 1996).

Euphausia superba were enumerated and measured on board the research vessel after each net tow. The total abundance of krill at each station was estimated based on the size of the catch and the volume of water filtered, yielding a value for the number of krill present per 1000 m³. A random subsample of ~100 individuals (or all individuals if catch size < 100) were measured using Standard Length 1 (SL1), which is the length from the tip of the rostrum to the end of the uropod (Mauchline 1980). Larger krill were given a sexual category based on their external characteristics. Mature female krill were identified as having a fully mature thelycum that was either clear or red in color. To determine wet weight, krill were frozen at –80°C in pre-weighed vials and weighed at Palmer Station within a week of the end of each cruise (Quetin & Ross 2001). Excess water was removed from the krill by gently rolling each individual in a bed of Kimwipes, paying attention to the ventral side where water may have collected in the feeding and swimming appendages. This technique effectively wicks the water off the krill prior to obtaining their wet weight. Data on the wet weight of krill were not collected during the January cruise in 1998; therefore we were unable to calculate mature

female krill condition factors for that year. Krill recruitment was calculated for the wAP as the proportion of young-of-year krill, defined in this study as krill <30 mm in total length, to the total number of krill in the region. This is referred to as the krill recruitment index.

2.3. Calculation of mature female krill condition factor

Spawning at the wAP takes place throughout the spring and summer, initiating as early as November, and often extending through mid-February (Ross & Quetin 1986, Spiridonov 1995). The height of the spawning season usually occurs from late January to early February; however, there is interannual variability in the spawning intensity and season duration that has been correlated with changing sea ice dynamics at the wAP (Ross & Quetin 1983, Spiridonov 1995). In the present study, krill condition during the ‘spawning season’ refers to krill collected in January: a month in which spawning intensity is typically at its peak. The physiological condition of mature female krill in this study was calculated using an empirical formula derived from parameters estimated through an ordinary least-squares regression (Cone 1989). Other commonly applied methods for estimating an organism’s condition factor (also referred to as condition index in the literature) include Fulton’s *K* (Fulton 1904) and Le Cren’s relative condition factor (Le Cren 1951). However, Cone (1989) pointed out that Fulton’s *K* assumes isometric growth, which is not an appropriate assumption for organisms where growth is allometric and/or where it changes with ontogeny. For instance, as mature female krill develop their ovaries, their body size swells outward under their carapace (Cuzin-Roudy & Amsler 1991), resulting in an increase in weight without necessarily a corresponding increase in length; in other words, they become ‘plumper’. While Le Cren’s relative condition factor attempts to remove the assumption of isometric growth, it is only useful for within-sample comparisons since it relies on using the sample mean. The ordinary least-squares regression recommended by Cone (1989) simplifies the procedural estimation of condition factor and prevents unnecessary assumptions that can result in incorrect conclusions.

The condition of mature female krill during the spawning season from 1993 to 2008 was thus calculated according to Cone (1989) as: $CF = \frac{W}{L^b}$, where

CF is the condition factor, W is the wet weight (μg) of mature female krill, L is the total length of mature female krill (mm) and b is the slope of the relationship between length and wet weight, determined from the ordinary least-squares regression of log-transformed data. The slope, b , was 3.71 for mature female krill at the wAP from 1993 to 2008, thus $\text{CF} = \frac{W}{L^{3.71}}$. In order

to ensure that b did not change with region, we incorporated spatial interactive terms into our ordinary least-squares regression analysis and found that there were no significant slope differences by region.

2.4. Statistical analyses

A 1-way ANOVA and a post hoc Tukey test were implemented to examine the interannual variability in mature female krill condition during the spawning season from 1993 to 2008 at the wAP. We used a linear regression model to examine the relationship between mature female krill condition during the spawning season and krill recruitment the following year. The average annual values for mature female krill condition during the spawning season and krill recruitment at the wAP were calculated for each year from 1993 to 2008 and from 1994 to 2009, respectively. To maintain normal distributions for the data, krill recruitment values were square-root-transformed prior to running the linear model. The average annual values for mature female condition during the spawning season were normally distributed, so they remained non-transformed for the linear model.

To assess the environmental drivers of the interannual variability in mature female krill condition during the spawning season from 1993 to 2008 at the wAP, we ran generalized additive models (GAMs) using the 'mgcv' package in RStudio (v. 1.3.959) (Wood 2011, RStudio Team 2020). We chose a suite of climatological and oceanographic predictors for these models (Table 1). For further details on the rationale for using each predictor variable and for how those data were acquired, see Text S1 in the Supplement at www.int-res.com/articles/suppl/m669p065_supp.pdf.

Prior to running statistical analyses, univariate relationships between mature female krill condition and each predictor variable were examined using the 'ggplot' package in RStudio (Wickham 2016). GAMs were chosen as an apt statistical model given the observed nonlinear relationships between the

Table 1. Predictor variables incorporated into the generalized additive models (GAMs): seasonal Southern Annular Mode (SAM) and Multivariate El Niño Southern Oscillation Index (MEI), sea surface temperature (SST), depths of Winter Water Layer (WWL) and Surface Mixed Layer (SML), stratification index, anomalies for the day of sea ice advance and retreat, and sea ice season duration, integrated chlorophyll a (chl a ; mg m^{-2}), integrated fucoxanthin (mg m^{-2}), and ratio of integrated fucoxanthin to chl a . *Predictor variables significantly related (at $p < 0.05$) to mature female krill *Euphausia superba* condition factor ($\mu\text{g mm}^{-3.71}$) during the spawning season. To achieve normality in the data, mature female krill condition, integrated chl a and integrated fucoxanthin were log-transformed and the stratification index was square-root-transformed

Model	Predictor variables
Climatological GAM	Autumn SAM*, Winter SAM*, Spring SAM*, Summer SAM*, Autumn MEI, Winter MEI, Spring MEI*, Summer MEI
Oceanographic GAM	SST, WWL Depth, SML Depth, Stratification Index, Sea Ice Advance*, Sea Ice Retreat*, Sea Ice Season Duration
Phytoplankton Biomass GAM	Chl a , Fucoxanthin*, Fucoxanthin:Chl a
Full GAM	Autumn SAM*, Winter SAM*, Spring SAM*, Summer SAM*, Spring MEI*, Sea Ice Advance, Sea Ice Retreat
Reduced GAM	Autumn SAM*, Winter SAM*, Spring SAM, Summer SAM, Spring MEI, Sea Ice Advance*, Sea Ice Retreat*, Fucoxanthin

predictor variables and krill condition (Wood 2017). The number of potential predictor variables ($n = 18$) was large, which negatively affects the efficacy of GAMs. Thus, we first grouped the potential predictor variables into 3 categories (Climatological, Oceanographic, and Phytoplankton Biomass) and ran separate GAMs using the set of variables within each category (see Table 1 for the full list of predic-

tor variables). In this way, we identified the climatological, oceanographic and phytoplankton biomass predictor variables that had the strongest effects on mature female krill condition during the spawning season. Annual anomalies were used for sea ice data, seasonal indices were used for SAM and MEI, and data for oceanographic and phytoplankton biomass parameters were obtained for each station. Mature female krill condition was averaged for each station. For a detailed description of model construction and selection criteria, see Text S1 in the Supplement.

After running every predictor combination for each model, the best iterations from the Climatological, Oceanographic, and Phytoplankton Biomass Models were identified (Table S1 in the Supplement, see also Text S1). The significant predictor variables in the best Climatological and Oceanographic Models (autumn, winter, spring, and summer SAM, spring MEI, and the anomalies for the day of sea ice advance and retreat) were subsequently combined into one Full Model to identify the predominant environmental drivers of mature female krill condition during the spawning season at the wAP from 1993 to 2008 (Table S2). Covariates from the Phytoplankton Biomass Model (integrated chl *a*, integrated fucoxanthin and the proportion of integrated fucoxanthin to chl *a*) were not considered for the Full Model because, unlike the covariates in

the Climatological and Oceanographic Models, they did not contain data from 2002 and 2005. The best performing Full Model was subsequently identified along with the predominant drivers of mature female krill condition during the spawning season at the wAP from 1993 to 2008 (Table 2, see also Table S2).

We constructed a Reduced Model with the predictor variables in the best Climatological, Oceanographic, and Phytoplankton Biomass Models in order to include integrated fucoxanthin, which was the only significant driver in the Phytoplankton Biomass Model, into the combined model formulation (Table S2, see also Text S1). This was a Reduced Model because it was a more limited sampling time-frame, as it did not include data from 2002 and 2005. The best performing Reduced Model was identified along with its predominant drivers of mature female krill condition during the spawning season at the wAP from 1993–2008 (Table 2, see also Table S2). Integrated fucoxanthin was not a significant predictor variable in the Reduced Model; therefore, the remainder of our paper will focus on the results from the Full Model because it incorporates more data from the time series. For a closer look at the regional drivers of mature female krill condition during the spawning season that were identified in the Oceanographic and Phytoplankton Biomass GAMs, see Text S2.

Table 2. Models used to identify, for *Euphausia superba* at western Antarctic Peninsula from 1993 to 2008, (1) relationship between log-transformed mature female krill condition factor during the spawning season (cf; $\mu\text{g mm}^{-3.71}$) at year = y and square-root transformed krill recruitment index (lag_KR) at year = $y + 1$; (2) relationships between non-transformed mature female krill condition factor during the spawning season (CF; $\mu\text{g mm}^{-3.71}$) at year = y and significant predictor variables in the best performing Full Model: autumn (SAMAUT), winter (SAMWIN), spring (SAMSPR), and summer (SAMSUM) Southern Annular Mode (SAM) and spring Multivariate El Niño Southern Oscillation Index (MEISPR); and (3) relationships between CF and significant predictor variables in the best performing Reduced Model: SAMAUT and SAMWIN, and anomalies of the day of sea ice advance (IceAdv) and retreat (IceRet). NS: north/south; AIC: Akaike information criterion score; GCV: generalized cross-validation score; Dev. exp.: percentage of deviance explained by the model

Model	Type	Formulation	AIC	GCV	R ²	Dev. exp. (%)
1. Krill Condition and Recruitment	Linear	cf ~ lag_KR	–191.24	1.52×10^{-7}	0.247	30.1
2. Full	GAM	CF ~ factor(NS) + s(SAMAUT, k = 3) + s(SAMWIN, k = 3) + s(SAMSPR, k = 4) + s(SAMSUM, k = 3) + s(MEISPR, k = 3)	–564.38	0.007	0.397	42.0
3. Reduced	GAM	CF ~ factor(NS) + s(IceAdv, k = 4) + s(IceRet, k = 4) + s(SAMAUT, k = 4) + s(SAMWIN, k = 3)	–388.17	0.007	0.31	33.4

3. RESULTS

3.1. Interannual variability in mature female krill condition and recruitment

There was significant interannual variability in mature female krill condition during the spawning season from 1993 to 2008 at the wAP ($F_{14,279} = 14.58$, $p < 0.001$). The average condition of mature female krill during the spawning season in 1995–1996 and 2000–2002 was $0.64\text{--}0.66 \mu\text{g mm}^{-3.71}$, significantly higher than the average condition in other years, e.g. $0.55\text{--}0.60 \mu\text{g mm}^{-3.71}$ (Fig. 2a). The krill recruitment index fluctuated from 1993 to 2008, with first-year recruits ($<30 \text{ mm}$) making up $>25\%$ of the population at the wAP in 1996–1997, 2002–2003 and 2007–2008 (Fig. 2b). Mature female krill condition during the spawning season from 1993 to 2008 had a positive linear relationship with krill recruitment the subsequent year (1994–2009) at the wAP (Fig. 2c, $R^2 = 0.25$, $p = 0.03$). Typically, new krill recruits made up $>25\%$ of the observed Antarctic krill population at the wAP (krill recruitment index ≥ 0.25) when mature female krill condition during the spawning season was at least $0.64 \mu\text{g mm}^{-3.71}$ the preceding year (Fig. 2). The highest level of krill recruitment was observed in 2002 when new recruits made up $\sim 68\%$ of the Antarctic krill population at the wAP.

3.2. Seasonal SAM and MEI as large-scale drivers of mature female krill condition

The predominant climatological drivers of mature female krill condition during the spawning season at the wAP from 1993 to 2008 were the autumn, winter, spring and summer SAM as well as the spring MEI (Table 1, see also Table S1). These combined climate variables explained 42% of the deviance in the Full Model (Table 2, see also Table S2). Mature female krill condition during the spawning season had a positive relationship with autumn SAM from the preceding year (Fig. 3a), plateauing once the autumn SAM index reached $\sim +0.5$. There was a negative relationship between mature female krill condition during the spawning season and winter SAM from the preceding year (Fig. 3b). Mature female krill condition during the spawning season was high when spring SAM was < -1 and $> +1$ and spring MEI was < -0.5 and $> +0.5$ (Fig. 3c,d). Summer SAM had a negative relationship with mature female krill condition during the spawning season (Fig. 3e).

Fig. 2. *Euphausia superba* at the western Antarctic Peninsula from 1993 to 2008: (a) Interannual variability in mature female krill condition factor (CF) during the spawning season. Pink shading: years with a high mature female CF that corresponded with a high krill recruitment the subsequent year; bold line: median CF; upper and lower limits of the box: third and first quartile, respectively; whiskers: data range; dots: outliers. (b) Krill recruitment index (see Section 2.2 for definition). Pink shading: years with high krill recruitment that corresponded with high mature female CF the previous year. (c) Relationship between average mature female krill CF during the spawning season at year = y and square-root-transformed krill recruitment index at year = $y + 1$. Dotted lines: 95% CI; solid line: linear regression; dots: observed values

Fig. 3. Relationship between the anomaly of mature female krill *Euphausia superba* condition factor (CF) during the spawning season and (a) autumn Southern Annular Mode (SAM), (b) winter SAM, (c) spring SAM, (d) spring Multivariate El Niño Southern Oscillation Index (MEI), and (e) summer SAM at the western Antarctic Peninsula from 1993 to 2008 as determined by the best performing Full generalized additive model. Seasonal SAM and MEI were calculated based on average values observed during austral autumn, winter and spring for 1992–2007 to correspond with summers of 1993–2008, and during summer values from December the prior year were averaged with those from January and February in the year of each survey (see Text S1 in the Supplement). Red dashed line: zero anomaly; dots: model residuals; solid line: model regression; shaded areas: 95% CI

4. DISCUSSION

Antarctic krill is a critical component of the wAP ecosystem, and the reasons for the orders of magnitude changes between years in their population size and in the recruitment of their young have been the focus of numerous studies (see e.g. Quetin & Ross 2003, Steinberg et al. 2015, Conroy et al. 2020). However, although several studies have demonstrated how climatological and oceanographic parameters influence krill recruitment and thus population size

(see e.g. Quetin & Ross 2003, Saba et al. 2014), the mechanisms behind this are not well understood. For instance, while there is an established relationship between the degree of reproductive output during the spawning season and krill recruitment the subsequent year (Quetin & Ross 2001), an understanding of the factors that impact the reproductive output of mature female krill has been lacking. Our study is the first, to our knowledge, to demonstrate that changes in mature female krill physiological condition are linked to changes in krill recruitment and

that climatological and oceanographic variability influences the condition of mature female krill.

We found that the condition of mature female krill during the spawning season was positively related to krill recruitment the subsequent year, likely through changes in the degree of reproductive output, which is affected by (1) a longer spawning season, (2) larger batch sizes per female at each spawning event, (3) more mature females in the population, (4) larger (in length) and older mature females in the population, or (5) a combination of these (Siegel & Loeb 1995, Quetin & Ross 2001). This suggests that there is a relationship between mature female krill condition during the spawning season and reproductive output. Mature female krill condition was tied to both proximal and distal mechanisms of krill foraging at the wAP through fluctuations in environmental conditions and food availability, respectively.

Our study indicates that large-scale climate variability is the predominant driver of mature female krill condition during the spawning season. Specifically, we found that SAM and MEI were important climatological drivers of mature female krill condition at the wAP from 1993 to 2008. While climate variability during the spawning season can impact the condition of mature female krill, the results from our study suggest that climate variability prior to the spawning season is also critical in shaping the physiological condition of mature female krill during the spawning season. In addition to long-term warming, seasonal variability in SAM and MEI can alter environmental conditions along the wAP and can lead to changes in sea ice dynamics and food availability (Ducklow et al. 2013, Saba et al. 2014), which can have implications for mature female krill condition and subsequent krill recruitment at the wAP.

Historically, +SAMs and -MEIs, or La Niñas, have been thought to negatively affect krill populations at the wAP through changes in weather patterns and atmospheric-ocean dynamics that lead to warmer conditions at the wAP (Quetin & Ross 2003, Atkinson et al. 2019). Positive phase (+SAM) and negative phase (-MEI) move strong, warm air across the wAP, resulting in increased atmospheric and sea surface temperatures that are correlated with a later sea ice advance, an earlier sea ice retreat and a shorter sea ice season (Stammerjohn et al. 2008a). These changes in sea ice dynamics can affect the amount of food available to krill, as less sea ice at the wAP has been linked to changes in the phytoplankton community, favoring smaller phytoplankton over the larger diatoms that krill feed on both pelagically and in the sea ice (Moline et al. 2004, Montes-Hugo et al.

2008, Schofield et al. 2017). However, our study reveals that the relationship between climate and mature female krill condition is not entirely straightforward, in that, depending on the time of year, both negative and positive phases of SAM and MEI can result in high observed condition in mature females during the spawning season. Below, we explain these relationships in further detail.

4.1. Interannual variability in mature female krill condition and relationship with krill recruitment

Mature female krill condition during the spawning season at the wAP varied substantially from year to year between 1993 and 2008, with peaks observed in 1995–1996 and 2000–2002. Similarly, the krill recruitment index fluctuated from 1993 to 2008, with first-year recruits making up >25% of the population at the wAP in 1996, 1997, 2002, 2003, 2007 and 2008. Krill recruitment is primarily driven by the winter survival of larvae and the degree of reproductive output by mature female krill during the spawning season (Quetin & Ross 2003). Here, we focused on the relationship between mature female krill condition and krill recruitment, assuming that changes in the physiological condition of female krill could lead to changes in their reproductive output. We found that the condition of mature female krill during the spawning season was positively correlated with krill recruitment success the subsequent year. The condition of mature female krill during the spawning season not only affects their degree of reproductive output, but it can also affect their offspring's physiology (Siegel & Loeb 1995, Yoshida et al. 2011). Mature females that have access to more food resources prior to and throughout the spawning season will undergo multiple spawning cycles and produce more eggs in a single brood than females that have fewer food resources (Cuzin-Roudy 2000, Ross & Quetin 2000). Krill larvae themselves are more likely to be in better condition upon hatching if the females that spawned them were in good condition (Yoshida et al. 2011), and will be more likely to survive their first winter (Meyer et al. 2009).

However, our observations did not hold true in all years. The higher-than-average condition of mature female krill during the spawning season in 2000 did not translate into high krill recruitment in 2001, suggesting that other factors influenced krill recruitment success that year. The high mature female krill condition we observed in 2000 coincides with a

positive anomaly in larval krill abundance along the wAP the same year (Conroy et al. 2020), suggesting that reproductive output was high and that the low krill recruitment observed in 2001 may have been caused by reduced overwinter survival of larval krill (Siegel & Loeb 1995). Larvae need to feed consistently throughout the autumn and winter in order to survive, relying on ice algae when food in the water column is scarce (Daly 2004). In 2000, sea ice advanced later than average at the wAP, and the sea ice season was anomalously short (Stammerjohn 2020). Sea ice supports communities of microscopic algae, and delayed sea ice formation results in a lower biomass of sea ice algae available for larval krill to feed on (Fritsen et al. 2008). Therefore, it is possible that a low food availability during the winter of 2000 may have negatively affected the overwinter survival rate of krill larvae, causing the mismatch between mature female krill condition in 2000 and krill recruitment in 2001.

Advection of larval krill into or out of the wAP region could also explain this mismatch. The Antarctic Circumpolar Current (ACC) flows in a northeasterly direction along the wAP, while a cross-shelf current works to transport oceanic waters of the ACC to the wAP shelf (Nowlin & Klinck 1986, Martinson & McKee 2012). Regional circulation patterns have been observed to retain larval krill inshore of the area where they were spawned; however, if spawning occurs near the ACC, a proportion of larval krill would be transported northward, outside of the region in which they were spawned (Piñones et al. 2013). This theory is further supported by the findings from Conroy et al. (2020), who found a positive correlation between the krill larval abundance at the wAP and the total number of recruits at the northern Antarctic Peninsula the subsequent year.

We also observed high krill recruitment in 2007 and 2008 at the wAP that did not follow years of high mature female krill condition. Despite this apparent mismatch, we believe that the peaks in krill recruitment in 2007 and 2008 could still be attributed to a higher krill population fecundity in 2006 and 2007, respectively, but for different reasons. On average, ~47% of the krill population observed at the wAP from 1993 to 2008 was composed of mature females (R. M. Ross & L. B. Quetin unpubl. data). In 2006, mature female krill made up ~70% of the total krill population at the wAP, corresponding to an average density of ~11 ind. 1000 m⁻³ (R. M. Ross & L. B. Quetin unpubl. data). Despite the high contribution of mature female krill to the total population in 2006, their average density was considerably less than that

observed in other years during our study. However, the mature females present in 2006 were relatively large, with an average total length >47 mm. Larger female krill are capable of producing greater egg batch sizes than their smaller counterparts (Siegel & Loeb 1995). Indeed, female krill produced an average of 5300 eggs per batch in 2006, which was greater than the average egg batch size of 3890 eggs per batch observed at the wAP from 1993 to 2008 (Table S3 in the Supplement). These factors suggest that reproductive output in 2006 was high, despite the low densities and average physiological condition of mature females that year. It is thus plausible that the high level of krill recruitment observed in 2007 was a result of the higher-than-average population fecundity observed in 2006. In addition to a high reproductive output, krill recruitment in 2007 could have been supported by a higher proportion of larval krill surviving through the winter. This theory is supported by the fact that sea ice advanced earlier than average and persisted for longer than normal in 2006, which would have favored the growth of sea ice algae, an enhanced foraging effort by larval krill, and a greater chance of surviving the winter (Lowe et al. 2012, Stammerjohn 2020).

In 2007, mature female krill made up ~57% of the total krill biomass at the wAP, with an average density of 62 ind. 1000 m⁻³, ~6× that observed in 2006 (R. M. Ross & L. B. Quetin unpubl. data). The average density of mature females in 2007 was greater than what was annually observed at the wAP from 1993 to 2008, with the exception of 1993 and 1996 (R. M. Ross & L. B. Quetin unpubl. data). More mature females in the population can lead to a higher level of reproductive output (Quetin & Ross 2001), and could be one of the primary reasons why krill recruitment was high in 2008, despite the fact that their physiological condition appeared within the normal range. It is likely that the high level of krill recruitment observed in 2008 was driven primarily by high reproductive output, rather than by a higher-than-average overwinter survival of larval krill, because in 2007, sea ice advanced later than average, retreated earlier than average, and the sea ice season duration was anomalously short at the wAP (Stammerjohn 2020), encouraging unfavorable conditions for the winter survival of larval krill. Piñones et al. (2013) used Lagrangian particle tracking to model the advection of krill embryos from the Bellingshausen Sea to the wAP, where they settled as late-stage furcilia larvae. Thus, it is possible that the high krill recruitment observed in 2008 could have also been due in part to larval krill advection into the region.

While there are several factors that can affect the degree of krill recruitment success, results from our study suggest that the physiological condition of mature female krill during the spawning season can impact the number of first-year recruits in the Antarctic krill population the subsequent year. Below, we discuss the drivers of mature female krill condition.

4.2. Effects of autumn SAM on mature female krill condition during the spawning season

We found that the autumn SAM was positively correlated with the condition of mature female krill during the spawning season. A predominantly +SAM in autumn can lead to a delayed sea ice advance at the wAP as the northerly winds strengthen and move warm air across the peninsula, resulting in increased atmospheric temperatures and SST (Stammerjohn et al. 2008b). Furthermore, we found that the day of sea ice advance was positively correlated with the condition of mature female krill during the spawning season (Fig. S1a, see also Text S2). While autumn diatom blooms have been observed at the wAP (Comiso et al. 1990, Vernet et al. 2012), pelagic phytoplankton concentrations begin to decrease later in the season in response to lower light levels and a deepening of the mixed layer (Vernet et al. 2012). This, in combination with a delayed sea ice advance and ice algae formation (Fritsen et al. 2011), may result in higher levels of autumn carnivory by krill (Atkinson et al. 2002).

In addition to feeding on diatoms and autotrophic dinoflagellates, krill feed on zooplankton, such as copepods and protozoans (Price et al. 1988, Atkinson & Snýder 1997, Cripps & Atkinson 2000, Haberman et al. 2003, Schmidt et al. 2006, 2014). Zooplankton are high in triacylglycerols, and feeding on them may be beneficial for krill in the late summer and throughout autumn, as doing so would increase lipid stores that krill survive on during winter starvation (Hagen et al. 2001, 2007, Schmidt et al. 2014). Indeed, seasonal changes in preferential fatty-acid absorption are pronounced in adult krill, with higher proportions of carnivory biomarkers (20:1 + 22:1 and 18:1(*n*-9c)/18:1(*n*-7c)) in autumn in relation to the rest of the year, indicating a greater prevalence of zooplankton in their diet from late summer to autumn (Ericson et al. 2019). As autumn transitions into winter, light levels decrease and winds intensify, reducing the amount of food available for krill to feed on at the wAP (Ashjian et al. 2004, Vernet et al. 2012).

Adult krill that feed carnivorously in the autumn will thus likely be in better condition through the winter when food supplies are low and they must suppress their metabolism and survive on lipid reserves (see discussion on winter conditions in Section 4.3). K. S. Bernard et al. (unpubl. data) found that krill feeding on a mixed zooplankton assemblage in autumn were in better condition than krill feeding solely on diatoms, likely due to the higher accumulation of lipids that is characteristic of a carnivorous diet. Therefore, when autumn SAM is positive at the wAP and sea ice advances later than average, mature female krill are more likely to feed carnivorously, as primary production is limited and krill often feed on the most prevalent food source (Schmidt & Atkinson 2016). A carnivorous diet in late summer and throughout autumn would result in mature female krill being in better condition at the onset of, and throughout, the subsequent spawning season (Fig. 4). Further, our results suggest that there is a threshold autumn SAM value of $\sim +0.5$ where mature female condition begins to plateau.

4.3. Coordinated effects of winter and spring SAM and spring MEI on mature female krill condition during the spawning season

Results of our analyses indicate that a -SAM during the winter corresponded with a higher observed condition in mature female krill at the wAP during the spawning season. A -SAM phase results in cooler conditions over the Antarctic Peninsula, reduced wind speeds and greater sea ice concentrations (Stammerjohn et al. 2008b). Greater first-year sea ice coverage is correlated with higher concentrations of ice-associated algae that is typically dominated by diatoms (Fiala et al. 2006). In addition to serving as a habitat for phytoplankton, sea ice acts as a physical barrier to strong winter winds and prevents the mixing of the WWL with deeper waters. When sea ice concentrations are low, the WWL is deepened and phytoplankton are dispersed to greater depths via wind-induced mixing of the surface waters, resulting in delayed blooms and an overall reduction in diatom biomass (Venables & Meredith 2014, Schofield et al. 2017). In contrast, high sea-ice concentrations would support earlier and larger pelagic diatom blooms at the wAP (Smith et al. 2008), fueling the reproductive development of female krill and increasing their physiological condition (our Fig. 4).

Fig. 4. Seasonal environmental conditions correlated with a high condition in mature female krill during the spawning season (January). Autumn: A positive phase Southern Annular Mode (+SAM) can result in the Surface Mixed Layer (SML) falling below depth of irradiance necessary for photosynthesis (I_D). As this could result in lower phytoplankton biomass, higher levels of carnivory by krill are expected (see Section 4.2 for details). Winter: A negative phase SAM (-SAM) promotes greater sea ice growth that can lead to a shallow Winter Water Layer (WWL) and high ice algae concentrations, thus enhancing foraging activity by krill at the end of winter (see Section 4.3 for details). Spring: A -SAM and a positive phase Multivariate El Niño Southern Oscillation Index (+MEI) encourages ice algae growth and seeds the SML with algae, preconditioning the water for an early phytoplankton bloom, resulting in increased foraging activity by krill, both synergically and pelagically. A +SAM and -MEI can lead to an overall lower abundance of krill, and with less krill in the environment intraspecific competition is reduced and individual krill are able to forage at a higher rate (see Section 4.4 for details). Summer: A -SAM supports a highly productive ecosystem with plentiful resources available to enhance maturation and spawning in krill (See Section 4.5 for details).

*Timeframe in which sexual maturation typically occurs. **Timeframe in which spawning typically occurs

When the spring SAM was ≤ -1 and $\geq +1$ and the spring MEI was ≤ -0.5 and $\geq +0.5$, we found that mature female krill condition during the spawning season was high. A +SAM is correlated with an earlier sea ice retreat, while a -SAM is correlated with a delayed retreat (Stammerjohn et al. 2008b). A -MEI (La Niña) results in warmer conditions, high wind speeds and an earlier sea ice retreat, while a +MEI (El Niño) results in cooler conditions, reduced wind speeds and a later retreat (Stammerjohn et al. 2008b, Loeb et al. 2009). The timing of sea ice retreat is critical for establishing phytoplankton blooms in the marginal ice zone (MIZ) (Smith et al. 2008, Vernet et

al. 2008, Montes-Hugo et al. 2009, Venables et al. 2013). When sea ice retreats prior to the weakening of the winter winds, phytoplankton may be dispersed below the depth of irradiance as the SML mixes with deeper waters. However, if sea ice retreats after the winds have died down, the freshwater influx from the melting of the sea ice stabilizes the water column, creating a shallow SML where phytoplankton are retained above the depth of irradiance. Thus, a later sea ice retreat has been linked with greater levels of primary production in the spring and early-season phytoplankton blooms (Vernet et al. 2008). Greater sea ice concentrations enhance water column stratifi-

cation in the MIZ as the magnitude of freshwater melt during sea ice retreat increases (Vernet et al. 2008). This would not only create a more stable SML, but would also seed the surface ocean with ice algae, promoting dense phytoplankton blooms (Ackley & Sullivan 1994, Garibotti et al. 2003).

Spring phytoplankton blooms and a prolonged primary productivity season could explain why mature female krill condition during the spawning season was positively correlated with a $-SAM$ and a $+MEI$ (Fig. 4). If resources are abundant enough in the spring for female krill to fully mature and carry out reproduction, they can spawn as early as November in the lower latitudes of the peninsula (Spiridonov 1995). Overall, we found a positive relationship between the day of sea ice retreat and mature female krill condition during the spawning season (Fig. S1b, see also Text S2), which corroborates with the observation of increased mature female krill condition during a $-SAM$ and $+MEI$. While a later sea ice retreat can establish the conditions necessary for spring phytoplankton blooms at the MIZ, if sea ice retreats too late, primary production can be delayed, as sea ice acts as a physical barrier and prevents light from traveling into the surface waters (Arrigo et al. 2008). Quetin & Ross (2001) found that when sea ice retreat was anomalously late ($\sim$ November), annual primary production was lower and female krill did not have enough time to build up sufficient lipid reserves prior to the spawning season, negatively affecting krill reproduction.

Contrary to the negative impacts of a $+SAM$ and $-MEI$ on krill populations found in previous studies (e.g. Saba et al. 2014, Atkinson et al. 2019), we found that a $+SAM$ ($\geq +1$) and a $-MEI$ (≤ -0.5) in the spring were correlated with elevated mature female krill condition during the spawning season. Years with a high mature female krill condition were also observed when SAM and MEI were in opposing phases (i.e. when SAM was $+$ and MEI was $-$): a situation that is known to result in amplified warming conditions over the wAP (Stammerjohn et al. 2008b). These conditions would have resulted in reduced food availability for krill in the spring, as an early sea ice retreat would restrict phytoplankton growth in the MIZ (Quetin et al. 1996, Vernet et al. 2008). It is thus perhaps surprising that these years corresponded with elevated mature female krill condition. In 1999 and 2000, when spring SAM and MEI were in strongly opposing warm phases, krill population numbers were low along the wAP, measuring 1–2 magnitudes less than peak years in krill biomass from 1993 to 2008 (Ryabov et al. 2017). Fewer krill in

the environment would result in reduced intraspecific competition for resources (Ryabov et al. 2017) and, consequently, higher individual mature female krill condition (our Fig. 4). Our models suggest that positive anomalies in mature female krill condition were occasionally observed when sea ice retreated early, even as early as 60 d in some cases (Fig. S1b). This corresponds with the observation of increased mature female condition during a spring $+SAM$ and $-MEI$. These positive anomalies in mature female condition that corresponded with early sea ice retreat could reflect the response of increased food availability as a result of lowered intraspecific competition suggested above. Our study shows that both cool and warm spring conditions can co-occur with elevated mature female krill condition during the summer spawning season.

With high concentrations of ice algae and early spring pelagic phytoplankton blooms at the MIZ, female krill would have plentiful resources to feed on towards the end of the winter starvation period. When there is enough food available to support growth, female krill will undergo reproductive development in preparation for the upcoming spawning season, a process that requires substantial energy reserves (Ross & Quetin 2000). Thus, higher concentrations of food available to krill throughout winter and spring would encourage early initiation of krill maturation and a longer spawning season (Siegel & Loeb 1995, Kawaguchi et al. 2007). Additionally, female krill that have access to more resources during the time of their sexual development are more likely to produce more and larger broods during the spawning season (Ross & Quetin 2000), which could be reflected in their condition (our Fig. 4).

4.4. Effects of summer SAM on mature female krill condition during the spawning season

The summer SAM at the wAP was negatively correlated with mature female krill condition during the spawning season from 1993 to 2008. The coastal waters of the wAP are characterized by large diatom blooms in the summer (Prézelin et al. 2000, Smith et al. 2008) and the magnitude and frequency of the blooms are determined by light and nutrient availability, which is modulated by the depth of the SML (Mitchell & Holm-Hansen 1991, Venables et al. 2013). Environmental and climate variability throughout the winter and spring can precondition the water column in the summer for diatom blooms (Saba et al. 2014). Winter sea ice extent and the tim-

ing of sea ice retreat are critical factors in determining the depth of the remnant WWL and the SML in the summer. Greater sea ice formation in the winter and a later sea ice retreat (typical of a –SAM) create a highly stratified surface ocean, with a shallow SML and a shallow WWL beneath it, in the spring and summer (Smith et al. 2008, Vernet et al. 2008). During summer, there are ~18–22 h of daylight at the wAP that provide phytoplankton with the energy needed for photosynthesis. Solar heating of the surface ocean increases the stratification of the SML (Vernet et al. 2008). Additionally, summers that are characterized by low wind speeds, typical of a –SAM, at the wAP have been linked with greater levels of primary production as wind-induced mixing of the SML is limited (Stammerjohn et al. 2008b, Schofield et al. 2017). The combination of solar heating, freshwater input from melting sea ice and reduced wind speeds, creates a more stable water column that favors the presence of diatom blooms throughout the summer (Vernet et al. 2008), which would enhance the physiological condition of mature female krill (our Fig. 4).

Abundant diatom concentrations at the wAP have been linked with greater Antarctic krill biomass and heightened levels of reproductive success and recruitment (Siegel & Loeb 1995, Quetin et al. 1996, Ducklow et al. 2007, Schmidt et al. 2014). Therefore, we were surprised when we found that the relationship between mature female krill condition during the spawning season and summer diatom concentrations was weaker than expected (Fig. S2, see also Text S2). However, it is important to note that our fucoxanthin measurements were recorded at a single time point in the summer, offering only a snapshot of the seasonal primary productivity at the wAP. Both Ross et al. (2000) and Atkinson et al. (2006) found that the growth rate of krill is driven by food availability over longer time scales. It is probable, therefore, that the condition of mature female krill is impacted more by average summer diatom biomass and the interannual variability thereof, rather than by the concentrations recorded at a single space in time (Alonzo et al. 2005).

In addition to the abundance of diatoms in the water column, the size of diatoms within the phytoplankton community can control the dynamics of diatom blooms at the Antarctic Peninsula (Costa et al. 2020). Large diatoms (>20 µm) are correlated with high chlorophyll biomass, more efficient filter-feeding by krill, and higher krill recruitment, while smaller diatoms (<20 µm) are associated with low chlorophyll biomass, less efficient filter-feeding by

krill, and lower krill recruitment (Meyer & El-Sayed 1983, Quetin & Ross 2003, Rozema et al. 2017). In an attempt to examine the correlation between diatom size and mature female krill condition during the spawning season, we incorporated both the integrated chl *a* and the proportion of integrated fucoxanthin to chl *a* into our Phytoplankton Biomass Model. However, we did not find any significant correlations between either integrated chl *a* or the proportion of integrated fucoxanthin to chl *a* and mature female krill condition. It is likely, though, that the occurrence of large diatoms at bloom concentrations is advantageous to mature female krill, because blooms dominated by large diatom species have been shown to be correlated with higher levels of female krill reproductive output (Quetin & Ross 2001).

4.5. Conclusions and implications

The reproductive success of Antarctic krill is determined in part by the physiological condition of mature females in the population. We have shown that krill recruitment success is correlated with the condition of mature female krill in the year prior, which is determined largely by seasonal variability in SAM and MEI. The relationship between mature female krill condition and krill recruitment is likely driven by changes in the length of the reproductive season, reproductive output, and the physiology of offspring upon hatching (Siegel & Loeb 1995, Quetin & Ross 2001, Yoshida et al. 2011). Fluctuations in SAM and MEI influence the proximal and distal mechanisms of krill foraging by altering oceanographic conditions that can impact the quality and type of food available at the wAP (Ducklow et al. 2013, Saba et al. 2014). When female krill experience optimal climatological and oceanographic conditions from autumn to spring, they are more likely to be in better physiological condition at the onset of their spawning season in response to the better quality and quantity of food resources available to them during this time. Similarly, if environmental conditions are favorable in the summer, mature female krill will likely maintain a high physiological condition throughout the duration of the spawning season.

Successful krill recruitment is important in maintaining krill populations at the wAP (Quetin & Ross 2003, Ryabov et al. 2017). Long-term warming at the wAP has led to significant regional changes in the pelagic ecosystem, including decreases in krill abun-

dance and recruitment (Ducklow et al. 2012, Siegel et al. 2013, Atkinson et al. 2019). Lower levels of krill recruitment at the wAP are primarily a result of a positively trending SAM (Atkinson et al. 2019). While there are natural climate fluctuations at the wAP associated with SAM and MEI (Turner et al. 2016), studies have shown that there has been an aberration from normal variability as SAM has been steadily shifting towards a positive phase since the 1950s (Swart & Fyfe 2012). Moreover, model reconstructions of SAM variability over the last millennia suggest that the recent shift in SAM lies outside of the pre-industrial range for natural variability (Dätwyler et al. 2018) due to anthropogenic greenhouse gas emissions and ozone depletion (Sexton 2001, Thompson & Solomon 2002, Arblaster & Meehl 2006).

As SAM moves toward a more positive phase and temperatures continue to rise at the wAP, sea ice extent and duration are predicted to decline (Stammerjohn et al. 2008b), and diatom blooms are projected to decrease, both in magnitude and frequency (Montes-Hugo et al. 2009, Rozema et al. 2017, Schofield et al. 2017). A significant proportion of the circum-Antarctic krill biomass is concentrated at the wAP, and this region is the center of the Antarctic krill fishery (CCAMLR 2018). Population models required for the effective management of the krill fishery rely on knowledge of krill fecundity. Our study suggests that krill fecundity is variable and negatively affected by warming conditions. The CCAMLR, the body responsible for managing the Antarctic krill fishery, currently does not include climate change effects in their population models for Antarctic krill (Hill et al. 2020, Meyer et al. 2020). Our findings suggest that by not incorporating climate change impacts into krill population models, CCAMLR may be severely overestimating krill fecundity in years where conditions are unfavorable. Future studies should examine the effects of a positively trending SAM and continued warming on the fecundity of Antarctic krill.

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