KRILL GROWTH AND CLIMATE CHANGE IN THE PRESENCE OF INTERNAL CLIMATE VARIABILITY IN THE SOUTHERN OCEAN

by

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ABSTRACT

Climate change is rapidly altering the habitat of the most abundant keystone species of the Southern Ocean food web, Antarctic krill (*Euphausia superba*). Krill support a growing commercial fishery, however, there remains limited understanding of how krill habitat is impacted by changing oceanic conditions. In addition to trends forced by global-scale, human-driven warming, the Southern Ocean is highly dynamic, displaying large fluctuations in surface climate on interannual to decadal timescales. The dual roles of forced climate change and natural variability affecting Antarctic krill productivity complicate interpretation of observed trends and contribute to uncertainty in future projections. This research uses the Community Earth System Model Large Ensemble (CESM-LE) coupled with an empirically-derived krill growth model to detect and attribute trends in krill growth to the forced trend of human-driven climate change superimposed on natural variability within the system. Our findings indicate that the forced trend in krill growth habitat is characterized by a poleward contraction of optimal krill growth conditions and an overall reduction in Southern Ocean krill habitat. However, the natural climate is dynamic, such that these trends cannot be formally distinguished from natural variability over much of the Southern Ocean by 2100. Our results illustrate how natural variability can strongly modulate regional trends in krill growth and can mask the forced trend from detection until late in the 21st century. This research demonstrates an approach for determining ecosystem impacts from climate change and variability that can be used to inform krill management in the Southern Ocean.

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Introduction

The Southern Ocean, which surrounds Antarctica, is a critical component of the Earth system and supports a marine ecosystem of immense economic and intrinsic value. It is also among the most sensitive areas to climate change (Hagen et al., 2007) and has already experienced physical changes in ocean temperature, sea-ice dynamics, stratification, and currents (Flores et al., 2012). The cumulative impact of these changes on the marine ecosystem and its primary keystone species, Antarctic krill (*Euphausia superba*), is predicted to increase considerably during the present century (Doney et al., 2012; McBride et al., 2014). However, in addition to trends forced by global-scale, human-driven warming, the Southern Ocean is also subject to highly-dynamic natural climate variability, which can exert important influence on the system on interannual to multi-decadal timescales. This research presents an analysis of the superposition of forced climate change and natural variability on Antarctic krill habitat. In the context of climate change and the highly dynamic Southern Ocean, the framework we present provides insights that are important for decision makers to consider in the context of climate change adaptation strategies.

Antarctic krill (hereafter krill) are at the center of the Southern Ocean food web as well as the target of the largest commercial fishery in the Southern Ocean (Nicol et al., 2012). Krill are a large bodied (up to ~6 cm), fast swimming, aggregating, zooplankton known as a dominant species in the food web and in biogeochemical cycles (Tarling and Fielding, 2016; Trathan and Hill, 2016; Cavan et al., 2019). Krill are one of the most abundant species on Earth, with a biomass estimated between 300 and 500 million tonnes (Nicol and Mangel, 2018). The rate at which krill biomass is produced, or productivity, is central to the success of the ecosystem; thus, changes in krill distribution and abundance have ramifications across the ecosystem (Murphy et

al., 2012; Constable et al., 2014; Larsen et al., 2014). A wide variety of Antarctic species feed on krill and they are the main energy pathway connecting primary producers to higher order predators (Quetin and Ross, 2003; Atkinson et al., 2009; Schmidt et al., 2011). Localized industrial fishing efforts, however, are growing rapidly (Nicol et al., 2012) and remove krill biomass in direct competition with krill-dependent species. These ecological and economic activities, however, are situated in the context of a highly dynamic climate system. Climate variability and change has the potential to drive important fluctuations in krill biomass, yielding widespread ecological impacts and causing variations in the definition of sustainable catch. Prediction of climate variability and change is therefore of high importance for effective long term management of the ecosystem.

Concerns over the ecosystem impacts of growing commercial fishing interest for krill in the 1980's spurred the creation of the Convention on the Conservation of Marine Living Resources, or CAMLR Convention, the arm of the Antarctic Treaty System which governs the Southern Ocean. Since the early 2000's human interest in krill has been rising and now represents the largest fishery, by biomass, in the Southern Ocean (Nicol et al., 2012). The krill fishery is managed under a mandated precautionary, ecosystem-based approach - including managing for environmental change, and based on the best available science. Fishing activities in the Southern Ocean are regulated by the multi-national Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR, pronounced 'cam-ah-lar'), which implements the CAMLR Convention (CCAMLR, 1980). The ecosystem-based management dictates that the "ecological relationships between harvested, dependent and related populations must be maintained and the risk of changes in the marine ecosystem which are not potentially reversible over two or three

decades' must be minimized" (CCAMLR, 1980 Article II para 3). Under CCAMLR, fishery management objectives are designed to be precautionary for fished populations themselves and the wider ecosystem, including predators that feed on fished populations. Currently, krill are managed with catch limits that are deemed to be precautionary, however, these limits are set using a stock assessment that does not account for environmental variability or climate change impacts(Constable and Kawaguchi, 2018; Watters et al., 2020). The Commission has noted that understanding the effects of climate change is important in delivering the objective of the Convention. Yet despite acknowledging the rapid climate change observed in the Atlantic sector, CCAMLR has not endorsed management actions, including prioritizing gathering data to inform climate-ready management. Fisheries compete with natural predators for krill biomass, making coordinated management critical for sustaining the Antarctic marine ecosystem. Variation in climate, however, independently affects krill productivity, yielding bottom-up fluctuations in krill biomass. Effective management of the krill fishery, therefore, depends on sound understanding of climate-driven variations in krill populations. This research is thus motivated to inform this critical gap in management regarding the impacts of natural variability and climate change.

Climate affects krill through direct impacts (e.g., physiological thresholds, habitat use) and indirect impacts such as ecosystem interactions, including impacts on food supply and predation. As a stenothermic crustacean, krill can only survive in a very narrow range of temperature (–1-5°C) and are strongly influenced by environmental variables (Atkinson et al., 2008). Many studies have stated that the influence of natural climate variability is a large factor in understanding krill abundance, distribution, and productivity. For example, changes in

phytoplankton community production drive seasonal production of krill (Siegel and Loeb, 1995) and the synergy of temperature and food availability have been shown to be important in determining growth and reproduction in Antarctic krill (Kawaguchi et al., 2007; Wiedenmann et al., 2009). However, accurate measurements of krill biomass are sparse, making it difficult to develop mechanistic connections between possible environmental drivers and krill production. The lack of a definitive observational constraint has left the subject of climate impacts on krill open to debate (Quetin et al., 2007; Schmidt et al., 2011; Cox et al., 2018; Atkinson et al., 2019). In spite of uncertainty regarding specific mechanistic connections, there is broad consensus that krill populations are likely to be impacted by future changes in climate (Murphy et al., 2012; Constable et al., 2014; Rogers et al., 2020). However, attributing trends in krill production to anthropogenic climate change is challenged by the confounding influence of natural variability on top of limited observational data. The Southern Ocean's natural system is sufficiently dynamic such that important environmental fluctuations are likely even in the absence of human-driven warming.

In the context incorporating climate information into fisheries management, it is critical to recognize that "climate" is not static, but rather manifests as a superposition of naturally-driven variability and human-driven trends (Hawkins and Sutton, 2009; Deser et al., 2012). Natural climate variability is an intrinsic feature of the coupled atmosphere-ocean-land system; it is attributable to nonlinear dynamical processes and interactions between climate system components that integrate information over different timescales (Hasselmann, 1976). Anthropogenic forcing from human-driven trends, like emissions of heat-trapping gases, externally forces the climate system. The characteristics of the superposition of internal

variability on anthropogenic forcing in the Southern Ocean are illustrated by the Westerly Winds that drive the Antarctic Circumpolar Current (Allison et al., 2010) (For reference, see Figure 1). The strength and position of the Westerlies naturally fluctuate in association with the Southern Annular Mode (Rogers and van Loon, 1982; Thompson and Wallace, 2000). Human-driven trends are superimposed on this variability: ozone depletion, followed by CO_2-driven warming has resulted in an intensification of the SAM index, a trend that is projected to continue over the next several decades (Fogt and Marshall, 2020). Understanding the how, where, and by how much the fluctuations of natural variability may obscure observed trends in anthropogenic climate change on different timescales is highly important for effective and long term resource management (Ryabov et al., 2017).

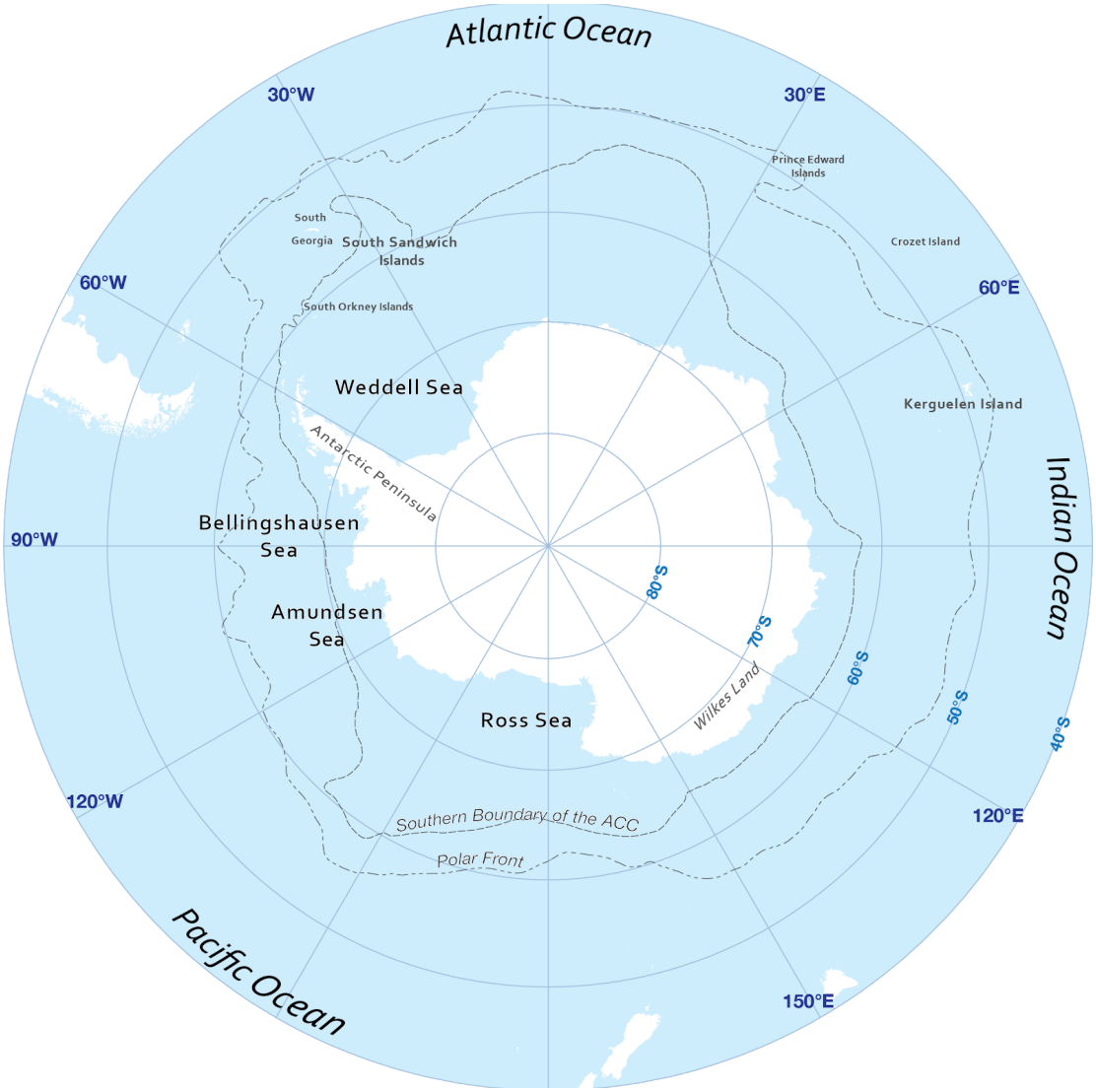

Figure 1: Reference Map *This is a map of the study area containing the locations and features mentioned throughout paper*

In the context of developing future projections, natural climate variability makes important contributions to uncertainty. Determining the uncertainty attributed to the two components of climate variability is a function of time horizons and scale (Commission on Geosciences et al., 1996). For many variables of interest, internal variability tends to be the dominant source of

uncertainty at regional scales over time horizons of less than two decades. Comparatively, anthropogenic forcing is associated with longer-term trends at regional or larger spatial scales (Hawkins and Sutton, 2009). When they are superimposed, fluctuations in natural variability have the potential to temporarily reverse or partially offset forced trends on interannual to decadal timescales. For example, the long term trend along the western Atlantic Peninsula (WAP) shows statistically significant overall warming and sea ice losses (Henley et al., 2019). However, short-term regional observations of sea-ice extent from the late 1990's and late 2000s showed a trend of increasing sea-ice in the northern and coastal regions of the WAP (Stammerjohn et al., 2012). In this example, substantial short-term variation in sea ice dynamics was the result of significant natural variability in the regional climate superimposed on longer-term trends (Hobbs et al., 2016; Turner et al., 2016; Stammerjohn and Maksym, 2017). Trends associated with the forced signal are unlikely to be reversed on short timescales, or can only be reversed through intervention. Quantifying climate-change related impacts provides fundamental knowledge that can help inform managing under environmental change, including a framework for considering when and where to employ climate mitigation strategies.

Detection and attribution of forced trends must be approached against the backdrop of natural variability (Hawkins, 2011; Deser et al., 2012). Detecting trends and attributing them to forced climate change can be approached as a signal-to-noise problem: the forced trends represent a "signal" and the natural climate variability is "climate noise" (Feldstein, 2000). The forced signal will arise from the envelope of background climate noise if it is sufficiently large for an extended period of time (Hasselmann, 1993; Santer et al., 2011). The point in time when the

anthropogenic climate change signal can be detected from the noise of internal climate variability is known as the "Time of Emergence" (ToE). Quantifying detectability of climate-change signals is inherently limited by the amount of natural variability in the system relative to the magnitude of forced trends. Detectability is therefore an intrinsic statistical property of the system and particularly pertinent for highly dynamic systems like the Southern Ocean.

Modeling studies can provide helpful insight when either observational records are scarce, like in the Southern Ocean, or into the future. Earth System Models (ESMs) are climate models that include a variety of ecological processes with the aim of simulating a fully-prognostic global carbon cycle (Hurrell et al., 2013). Climate and Earth system models provide analog systems to the real world that inform perspective on how climate processes work and how those processes feedback onto biology. While ESMs may have significant biases relative to observations, they are formulated on the basis of physical principles, conserve mass and energy, and are internally consistent. Through the ability to run multiple realizations of the climate system as it transits through different forcing scenarios ESMs can be used in detection and attribution. These realizations allow us to ask if the forced signal can be detected because it is sufficiently large or if we can attribute trends to particular driving mechanisms? In most cases, these types of questions are challenging to address definitively by observational records alone. ESMs include ocean biogeochemistry models as a component of the carbon cycle. As these models have matured, there has been increasing recognition of their relevance to questions beyond carbon biogeochemistry, and in particular related to ocean ecosystems in the context of climate

variability and change (Stock et al., 2011; Bopp et al., 2013; Tommasi et al., 2017). Ultimately, as these models more fully mature, they may provide a basis for developing forecasts on seasonal to interannual timescales relevant to marine ecosystems (Krumhardt et al., 2017; Park et al., 2019).

Prior research has used outputs from ESMs to explore how changes in Southern Ocean climate will impact regional and circumpolar krill habitat. These studies have mainly used projected changes from multi-model ensembles from the Coupled Model Intercomparison Project Phase 5 (CMIP5) in combination with empirically-derived models of Antarctic krill growth (Atkinson et al., 2006)to identify and estimate changes in habitat supportive of krill growth (Hill et al., 2013; Veytia et al., 2020)and nursery areas (Piñones and Fedorov, 2016). However, these multi-model ensemble studies have not considered the role of internal climate variability within nature. The large-ensemble framework of a single ESM allows for quantification of the uncertainties from internal variability, identifying trends forced by human-driven climate change and identifying when those trends can be formally distinguished from natural variability.

This work presents an approach to disentangle the impacts of internal variability from forced trends on krill growth rates, also referred to as growth potential (GP). The Atkinson et al. (2006) empirically-based model describes krill growth as a function of two major factors: temperature and food concentration (approximated by chlorophyll-a concentrations). As mentioned above, previous studies have utilized the Atkinson et al. (2006) model to identify and estimate changes in circumpolar habitat supportive of krill growth. This study expands upon the previous work

and considers the distinct roles of forced climate change and natural variability in driving fluctuations in krill habitat.

Methods

Earth system model

The Earth system model output used in this study was from the Community Earth System Model Large Ensemble (CESM-LE) (Kay et al., 2015). The CESM-LE was explicitly developed to assess recent past and near future climate change in the context of internal variability, permitting explicit separation of forced trends from internal variability. The CESM-LE began with multicentury, 1850-control simulation with constant preindustrial forcing. The configuration including atmosphere, ocean, land, and sea ice component models (Hunke and Lipscomb, 2010; Danabasoglu et al., 2012; Holland et al., 2012; Lawrence et al., 2012). We used 34 members with ocean biogeochemistry output from the CESM-LE integrated over the period from 1920–2100, each using the same historical and future-scenario (RCP 8.5; Long et al., 2016) external forcing. Each ensemble member simulation, however, has a unique climate trajectory because of small round-off level differences (10^{-14} K) in the air temperature field at initialization in 1920 (Kay et al., 2015). The climate system is sufficiently chaotic that these small deviations grow over a period of just a few years, leading to substantial spread across the ensemble that reflects internally-generated variability. The CESM-LE can therefore be used to interpret probabilistic projections of climate change impacts by assessing the magnitude of the forced trend relative to natural internal variability. When the ensemble is sufficiently large, the ensemble mean provides a robust estimate of the deterministic response of the climate system to

external forcing, i.e., the "forced trend." The ensemble spread, then, is indicative of the "noise", inclusive of changes in variance that may occur as a function of climate state (Deser et al., 2012; Long et al., 2016). The large ensemble framework therefore allows for assessment of internal climate variability relative to the magnitude of the forced anthropogenic change in a way that provides a probabilistic projection of climate change impacts in a system with internal variability (Deser et al., 2012; Hawkins and Sutton, 2012; Lovenduski et al., 2016; Brady et al., 2017).

Most ESMs, including the CESM-LE, incorporate prognostic representations of zooplankton as a component of their ocean biogeochemistry simulation (Le Quéré et al., 2016). However, ESMs typically simplify diverse groups of planktonic organisms into plankton functional types, which are delineated based on ecological or biogeochemical roles. ESMs, therefore, do not typically simulate specific zooplankton species, like krill, as state variables. In this study, the ocean biogeochemistry model output from the CESM-LE was used to apply to the krill growth model from Atkinson et al. (2006) offline to quantify possible changes in krill production over the duration of the simulation.

The model's ability to reproduce observed sea surface temperature (SST) and chlorophyll during austral summer was validated by comparing a historical climatology of the CESM-LE to climatologies from observational datasets. Surface chlorophyll from the SeaWiFS OC4v6 data for the period from September 1997 to December 2010 (NASA Ocean Biology Processing Group, 2018) was compared with the model simulated chlorophyll. The SeaWiFs data set was used in the derivation of the original krill growth model (Atkinson et al., 2006). Satellite derived SST observations from 1981 to 2015 were obtained from the Hadley Centre Global Sea Ice and

Sea Surface Temperature (HadISST) dataset (Hadley Centre for Climate Prediction and Research, 2000). The observational datasets were regridded onto the nominally-1° CESM ocean component grid (Smith et al., 2010) for bias analysis with output from the CESM-LE. Austral summer (DJF) means for each observational dataset were calculated to validate the mean and interannual variability simulated for each field. Bias in mean state and variability of SST and chlorophyll can dramatically affect the characteristics of the simulated krill growth potential due to the highly nonlinear krill growth potential equation. The simulated SST values were positively biased beyond the Polar Front and slightly negatively biased along the western Antarctic Peninsula and into the Scotia Sea region (Figure 2f). Chlorophyll in the model was positively biased along the coastlines from the Scotia Sea region to the Bellingshausen Sea region, to the Ross Sea region. It was further determined that the model biases were not outside the range of reasonable natural variability, but should be considered in evaluating results.

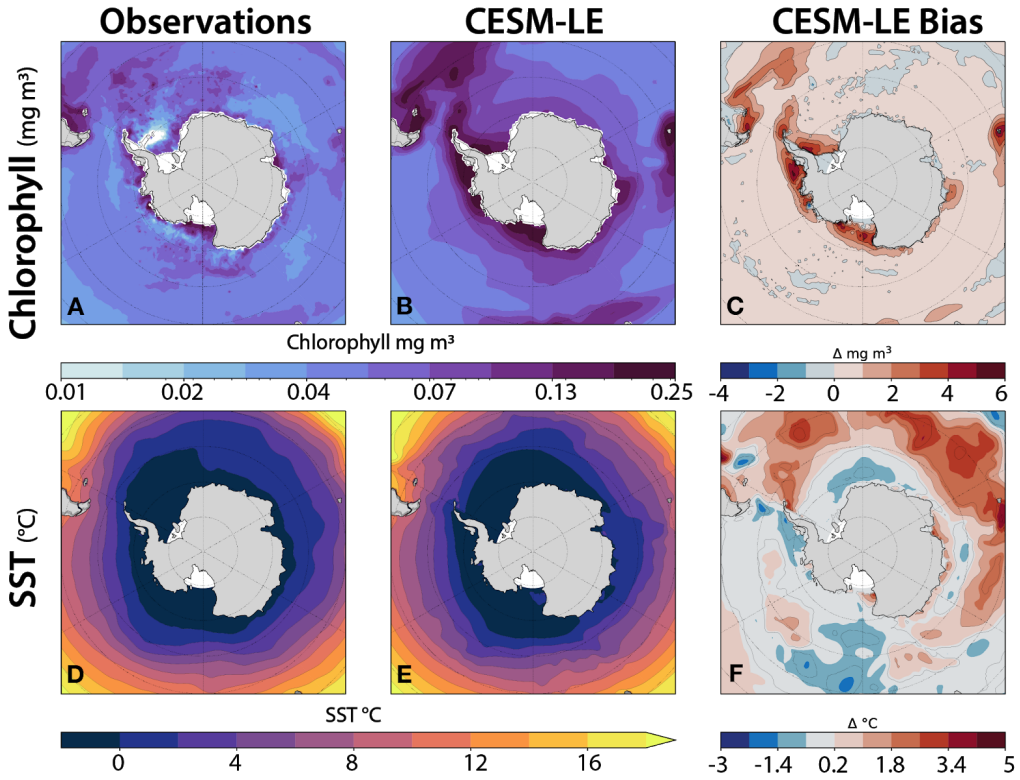

Figure 2: Model Bias Assessment *CESM-LE model bias in chlorophyll (top row) and SST (bottom row) for DJF (austral summer). The left column shows observations, the middle shows the corresponding simulated fields, and the right column shows the simulated bias as the difference between the simulated fields and the observations.*

Krill Growth Potential

This study coupled an existing empirical krill growth model with the CESM-LE. The empirical model from Atkinson et al. (2006) was used to estimate the daily growth rate of krill (mm day^{-1}) from sea surface temperature (SST, C°), food availability, indicated by surface chlorophyll *a* concentration (CHL, mg m^{-3}), and starting length of krill (L, mm):

$$Daily\ Growth\ Rate = -0.066 + 0.002 \times Length - 0.000061 \times Length^2 + [0.385 \times CHL \div (0.328 + CHL)] + 0.0078 \times SST - 0.0101 \times SST^2 \quad (1)$$

The model estimates instantaneous krill growth given temperature and the concentration of food in the summer season. The growth rate equation was derived using in-situ data from instantaneous growth rate experiments in the southwest Atlantic sector during the summer (January and February) of 2002 and 2003. It was further tested with SeaWiFS-derived chlorophyll to generate a predictive model of growth based on satellite-derivable environmental data (Atkinson et al., 2006). Previous studies have applied the growth model across the Southern Ocean at varying spatial and temporal scales to assess changes in habitat suitability (Hill et al., 2013; Murphy et al., 2017; Veytia et al., 2020). The growth rate provides a descriptive measurement of habitat suitability where a positive growth rate indicates habitat that can maintain and support adult krill productivity.

Mean state and variability of the environmental drivers (SST and chlorophyll) can dramatically affect the characteristics of the growth rate due to the highly nonlinear nature of Equation (1), as visualized in Figure 3. While prior studies have used mean annual climatologies to calculate GP rates results, we chose to calculate monthly rates in order to remain closer to the temporal resolution of the data used to develop the model. Seasonal estimates of krill GP at a starting length of an average adult krill (40 mm) were calculated from the growth period (December through February, referred to as DJF). The observed mean length of adult krill (40 mm) (Atkinson et al., 2009)was assumed as the starting length for an individual krill as previous analyses found that projected differences between future and historical epochs remained the same irrespective of starting length (Veytia et al., 2020). Krill GP was calculated as a rate of mm

day^{-1} where environmental conditions were within the temperature parameters that the growth model was derived from (-1°C to 5°C).

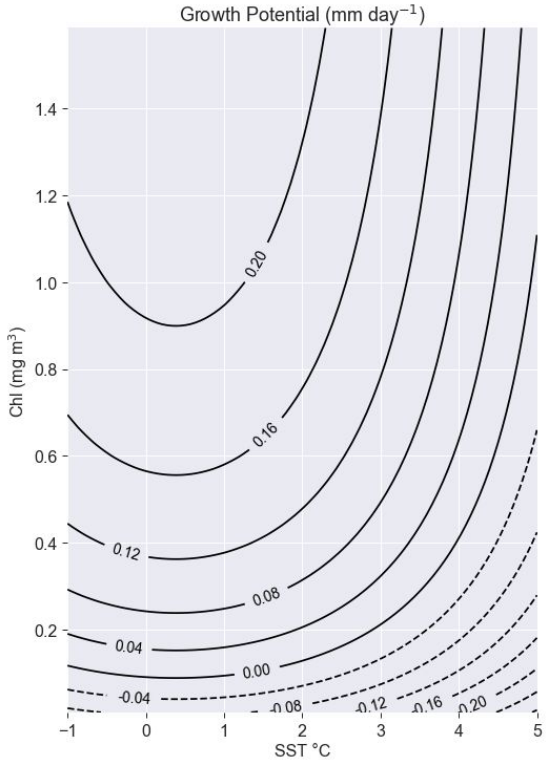

Figure 3: Krill Growth Potential Model *Contour plot of the krill growth potential model (Equation 1). Growth Potential (mm day^{-1}) changes as a function of chlorophyll (mg m^3) (y-axis) and SST (°C) (x-axis). Solid lines show positive GP rates and dotted lines show negative rates. The narrow spacing between contour lines when chlorophyll values are below 0.5 mg m^3 demonstrate the growth models sensitivity to low chlorophyll concentrations.*

The growth model predicts both positive and negative GP rates. Negative GP rates can occur when food concentrations are too low causing krill to undergo shrinkage (Hofmann and Lascara, 2000; Fach et al., 2002). "Growth habitat" was defined as habitat with a GP rate >0 mm day^{-1} where higher GP rates indicated that habitat was more supportive of increasing krill growth and thus of higher quality. Habitat with a GP rate ≤ 0 mm day^{-1} was defined as "unsuitable habitat"

where krill could survive but would not grow or where they would experience starvation and potentially undergo shrinkage.

Statistical Methods

The capacity to distinguish a forced signal from natural variability is required for detection of a time-evolving signal-to-noise relationship. The context of detection in this analysis is rooted in the signal to noise ratio indicating that the forced trend is distinct from natural variability. Following Long et al. (2016), a time evolving spatial pattern of a variable in ensemble member *i* (ψ_i) is the sum of the internal variability and forced trend signal:

$$\psi_i = \psi_i' + \psi^S$$

The simulated forced climate signal is represented by ψ^s while the component due to internal variability is represented as ψ_i'. In the CESM-LE, the number of ensemble members (m) is sufficiently large (Deser et al., 2012)that an average across the ensemble provides an estimate of the forced signal, ψ^S:

$$\psi^s = \frac{1}{n} \sum_{i=1}^{n} \psi_i$$

In our analysis, the separation of internal variability from the forced signal was therefore computed by removing the ensemble mean, ψ^s, from each ensemble member, ψ_i. In order to apply the large ensemble framework to simulate the temporal evolution of krill GP, the equation was applied to monthly model output of the environmental drivers, SST and chlorophyll. Area-weighted means of SST, chlorophyll, and GP was computed for the Southern Ocean across all ensemble members (Table 1). To assess the temporal evolution of trends and normalize the

data, anomalies were calculated by removing the ensemble mean of a representative period of unperturbed climate: 1920-1950, from each ensemble member.

	Southern Ocean
Growth Potential (mm $day^{-1}m^{-3}$)	0.007
Surface chlorophyll (mg m^{-3})	0.189
SST (°C)	1.086

Table 1: *Spatially averaged mean DJF values of the modeled growth potential (mm day^{-1} m^{-3}), chlorophyll (mg m^{-3}), and temperature (°C) fields from 1920 to 1950 for the Southern Ocean and the Atlantic Sector (0° - 90°W).*

A time of emergence (ToE) analysis was conducted to detect the year in which the statistically significant forced signal is expected to emerge from natural variability (noise). The concept behind ToE is that a probability distribution in a climate variable, characterized by mean and standard deviation, is being driven by climate change to shift into a new distribution. One approach to ToE is to identify the point in time when the area of overlap between the unforced distribution and the forced distribution is sufficiently small, so as to enable distinguishing between the two distributions. Depending on how ToE is defined, the analysis can determine that the distributions are distinct with a specific percentage of certainty. Studies compute ToE to be the year where a signal-to-noise ratio (SNR) of two or greater deemed statistically significant as derived from the *t* test assuming 95% significance (Deser et al., 2014; Thompson et al., 2015). Our primary interest was to illustrate the impact that superposition of natural variability and forced trends has on the detection and attribution problem. For that reason, the analysis presented here defines ToE as the year when the ensemble mean (ψ^s) exceeded the envelope of variability

within two standard deviations (σ) of the mean in the unperturbed climate assuming 68% significance:

$$SNR = \left| \frac{\psi^s}{\sigma} \right| \geq 2$$

The Southern Ocean is a system that is relatively "noisy", therefore we chose a less stringent definition of ToE to recover meaningful patterns in the signal to noise ratio by the end of the century.

The ToE estimates on the basis of the state anomalies were calculated by quantifying the statistical distribution of the variables in the unperturbed climate state of the reference period. ToE was quantified as the last year of the state anomalies in which the SNR exceeded a value of two and all subsequent years.

Spatial estimates of the contribution of natural variability on 20 and 50 year krill GP trends were computed by explicitly separating internal variability from the forced trend. Short and long term krill GP trends were calculated on the spatially resolved model output using a linear least-squares analysis beginning in 2020 and extending to 2040 and 2070, respectively.

Results

In our examination of simulated GP distributions over (1920-1980), prior to significant influence from the forced trend, the distribution of krill GP rates in the mean climate showed patterns in krill growth habitat that are closely related to their thermotolerance range during the summer season. In the unperturbed climate, growth habitat was found within the Atlantic quadrant (0-90°W) along the latitudinal bands around the South Orkney Islands and along the eastern

coastal regions near Wilkes Land (90 - 120°E). Temperature exerted a strong control on GP, with elevated GP values typically found within the optimal temperature range (-1°C to 2°C) and located in coastal regions with high chlorophyll concentrations like the eastern Ross Sea and along the Antarctic Peninsula stretching eastward towards the mid Atlantic. The distribution of growth habitat was strongly constrained on its northern boundary by the edge of the 5°C isotherm that coincides with the Polar Front of the Antarctic Circumpolar Current (ACC). Habitat within krill's thermotolerance with insufficient chlorophyll concentrations for growth (unsuitable habitat) were located in the Ross Gyre and Weddell Gyre and in the latitudinal range of the Polar Front.

The CESM-LE simulated a poleward contraction growth habitat and an overall decline in the spatial average of krill GP over the course of the 21st century. The contraction of growth habitat consisted of decreased GP rates between the Antarctic Peninsula and the South Sandwich Islands at the edge of the thermotolerance range for krill and increased rates in the Bellingshausen Sea, Amundsen Sea and the Ross Sea. The changes in growth habitat are characterized by the similar contraction of the forced trend in SST that shifted the 5°C and -1°C isotherms poleward as well. The spatial averages for the anomalies relative to the 1920-1950 period were characterized by an increase in the magnitude of the forced krill GP anomaly to <-0.01 mm day^{-1} by 2100 (Figure 4a). Declines in the ensemble mean chlorophyll anomaly accelerated in the mid century to ~0.1 mg m^{-3} by 2100 (Figure 4b). The forced signal of the SST anomaly showed a continuous trend of rapidly rising temperatures reaching a magnitude of 3°C above the mean by the end of the simulation (Figure 4c).

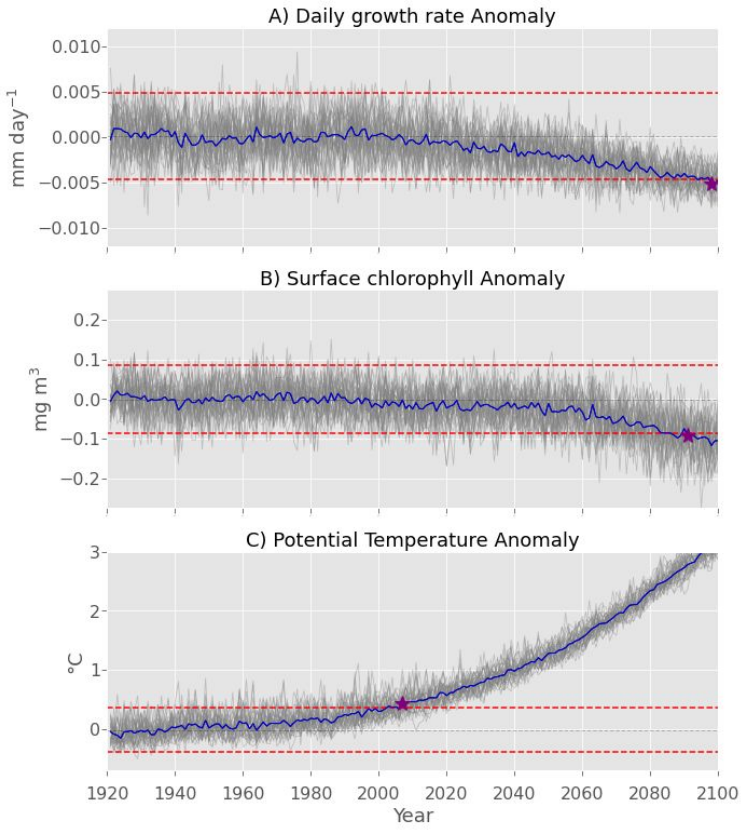

Figure 4: Temporal Evolution of the Mean State Anomaly *- Temporal evolution of the modeled DJF krill growth potential anomaly (mm day^{-1})(a) for the Southern Ocean and the environmental drivers: surface chlorophyll (mg m^3) (b), and sea surface temperature (°C) (c). Each ensemble member anomaly is plotted in gray while the blue line is the mean ensemble anomaly. The means for each variable are found in Table 1. The horizontal red lines represent two standard deviations above and below the mean state for the unperturbed reference period (1920-1950). The purple stars indicate the ToE - the point in time when trends forced by human-driven climate change can be formally distinguished from the envelope of natural variability (Equation 3).*

Throughout the simulation there was higher regional natural variability than across the spatial average of the Southern Ocean. The general magnitude of natural variability across the spatial average of the krill GP anomaly was less than 0.005 mm day^{-1}m^{-3} (Figure 4a). The physical distribution of natural variability in krill GP was characterized by a widespread variability below 0.09 mm day^{-1} featuring elevated variability along the coastal boundary of growth habitat ranging up to 1.3 mm day^{-1} (Figure 5c). This area coincided with higher amounts of variability in

physical distribution of internal variability in chlorophyll (Figure 5h). Given the logarithmic scale, the internal variability of chlorophyll was up to an order of one higher than the mean state of 0.189 mg m^{-3} (Table 1). For SST, the magnitude of natural variability across the spatial average of the anomaly was less than 0.5 °C (Figure 4c). The physical distribution of natural variability in krill GP was by areas of increased variability in the frontal zone of the ACC and near the tip of the eastern Antarctic Peninsula.

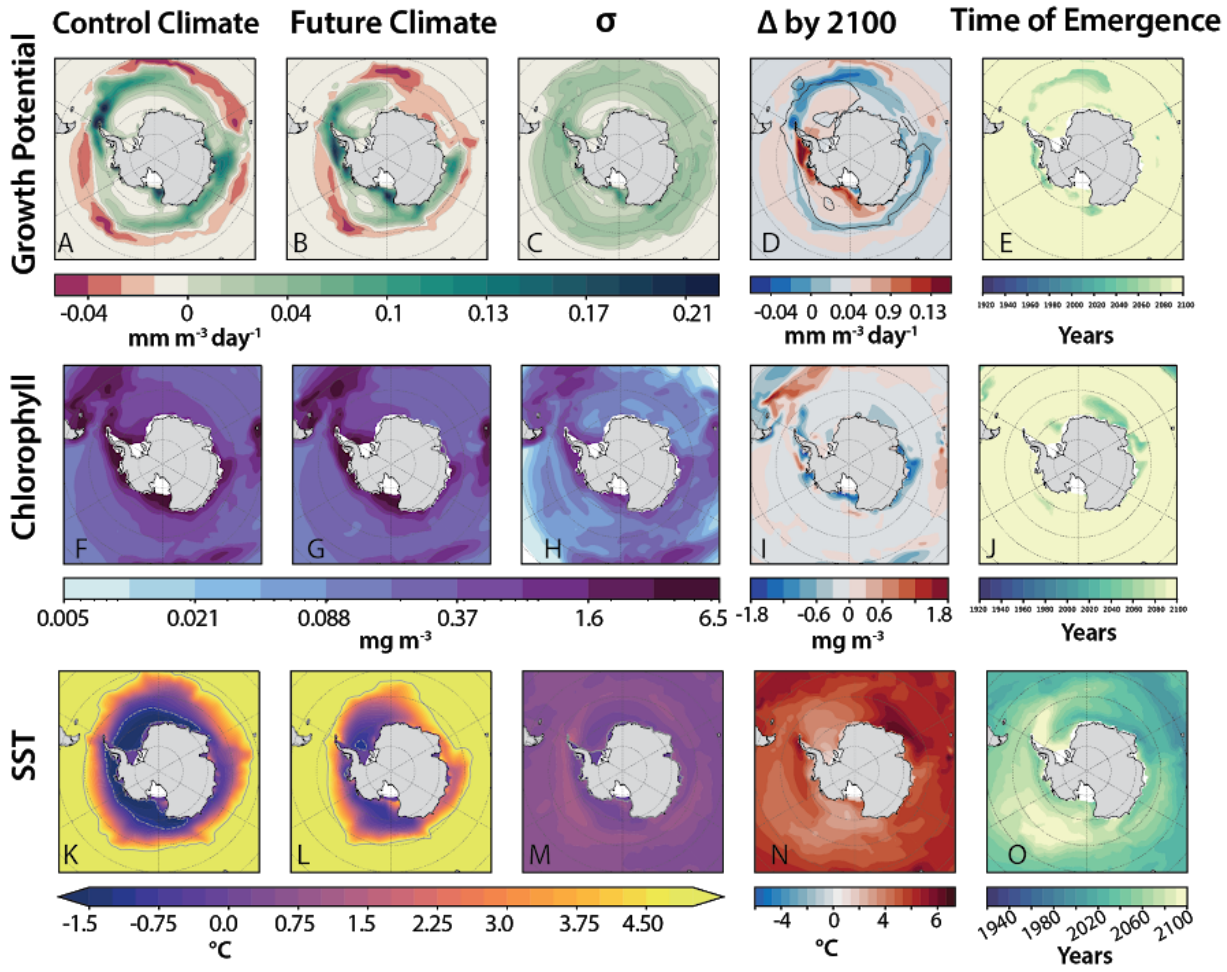

***Figure 5**: **Characteristics of the forced trend from 1920 to 2100** This figure captures the spatial characteristics in the mean state of krill growth potential (top row: A-E), chlorophyll (middle row: F-J) and sea surface temperature (bottom row: K-O) as simulated by the large ensemble. The mean state for the unperturbed climate (1920-1950) and the future climate (2070-2100) of the simulation are shown for each variable in the leftmost two columns. (A-B) Then growth potential of krill habitat is plotted as the rate growth per day (mm $day^{-1}m^3$). Habitat that can support krill growth is shown in green and areas where krill growth is inhibited is in red. (F-G)*

The mean state of surface chlorophyll concentration (mg m^{-3}) plotted on a logarithmic. (K-L) Sea surface temperatures (SST) within the thermotolerance range of krill are plotted in the bottom row. Temperatures over 5°C are demarcated by a solid grey contour line and white dashed lines indicate temperatures below -1°C. The third from the left column (C, H, M) shows the standard deviation of the mean state in the same scale as the mean state of the variable. The fourth column from the left (D, I, N) is the projected change in the forced signal from the unperturbed climate to the future climate. The difference is shown using a diverging color scale: increasing trends are shown in red and decreasing trends are shown in blue. The black contour line indicates the distribution of krill growth habitat by 2100. The rightmost column (E, J, O) is the "time of emergence" of the forced trend for each grid cell. The earlier the year of the ToE the darker the color.

The trends in krill GP rates illustrate that the forced signal develops increasing dominance (over natural variability) at longer timescales. The forced trends computed over 20 and 50 years are broadly similar in their spatial patterns; the difference is primarily characterized by an intensification of the trend magnitude at the longer timescale. The 20 year projected trends in krill GP from 2020 to 2040 exhibited spatial patterns and magnitudes from internal variability dominating over the lower magnitudes of the forced trend (Figure 6a-f). The 50 year trends projected from 2020 displayed characteristics of growth habitat close to the coast lines in the Bellingshausen Sea circumscribed by a band unsuitable habitat between the southern boundary of the ACC and the polar front (Figure 1; Fig 5G-L). The main difference between the trend lengths of the forced trend was that the 50 year trend displayed slightly more spatial coherence. Decomposing the 20 and 50 year total trends of krill GP into internal variability and forced signal components illustrated the magnitude of natural variability within the system. Internal variability contributed modestly to 50 year trends, but did not display recognizable spatial patterns (Figure 6g-l). In some regions, internal variability reinforced the 50 year forced trend, leading to greater rates of change, while in other regions, internal variability worked to oppose the forcing. Overall, 50 year trends in GP were dominated by the forced trend.

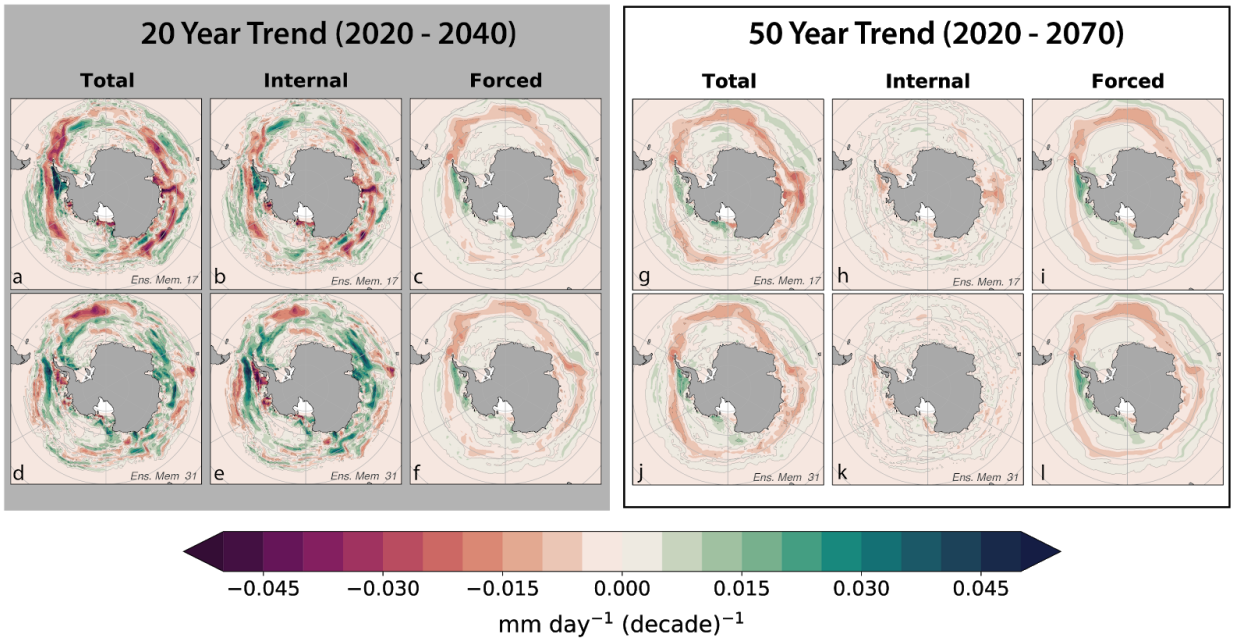

Figure 6: Growth Potential Signal Decomposition *- This figure demonstrates the superposition of forced signal and internal variability on the total 20 and 50 year trends of krill GP beginning in 2020. Each row is from a separate ensemble member; A is from ensemble member 17 and row B is member number 31. These two ensemble members were chosen as exemplary representations from the 24. The total linear trend in GP for the 20 year trend is seen in 1a and 1b while the 50 year trend is 4a and 4b. The internal variability within the 20 year trend is in panel 2a and 2b and the 50 year trend is in panels 5a and 5b. The forced trend (ensemble mean) of the 20 year trend is in panels 3a and replicated in 3b and the 50 year forced trend is in panel 6a and replicated in 6b. The forced trends are similar between both trend lengths but only drive the spatial coherence in the 50 year total trend, not the 20 year trend.*

The ToE analysis revealed the presence and timing of when the forced signal became distinguishable from internal variability for each variable. The decline in the krill GP trend due to the forced climate signal became detectable around ~2040 in the Southern Ocean and ~2070 in the Atlantic Sector (Figure 5e). The same was true for the chlorophyll anomaly in the Southern Ocean, but the forced trend in the Atlantic Sector did not emerge until ~2090. The earliest detection of the forced signal was observed in the SST anomaly, which became distinguishable from internal variability in the late 1980's across the Southern Ocean and the early 1980's in the

Atlantic sector (Figure 5o). The trend of the SST anomaly was the only instance where the ToE was earlier in the Atlantic Sector than in the Southern Ocean.

Spatial distributions of ToE indicate that positive and negative regional trends were diagnosed as emergent late in the 21st century for krill GP. The regional forced trend of increased krill GP emerged near the Bellingshausen Sea, Amundsen Sea, and the eastern part of the Ross Sea (Figure 5e). Regional declines of the forced trend in krill GP emerged near the WAP and in the mid Atlantic around the southern boundary of the ACC stretching west to the South Orkney Islands. By late in the 21 century, negative chlorophyll trends were diagnosed as emergent in the eastern Atlantic near the coast (Figure 5j). The region of emergent negative chlorophyll trends coincided with regions of early emergence of ocean warming trends. In comparison to GP and chlorophyll, the regional trends in SST emerged much earlier in the 21st century. The distribution was characterized by earlier emergence years in the eastern Atlantic and Indian quadrant (0° to 90°E) and coastal zones from the WAP and Bellingshausen Sea and around to the Ross Sea. There was no emergence in SST forced trends by 2100 from the eastern tip of the WAP to the South Sandwich Islands (Figure 5o). Areas where trends failed to emerge indicate that the ratio between the forced trend and natural variability was not significant enough to detect separate forced trends.

Discussion

Over the course of the CESM-LE simulation (1920-2100), krill GP rates are projected to decline during the summer season (Dec-Jan), a trend characterized by a poleward contraction of viable habitat (Figure 5 A:B). The contraction of growth habitat is most noticeable around krill's

current population center from the South Sandwich Islands to the Antarctic Peninsula (Atkinson et al., 2008, 2019). This contraction is a consequence of warming ocean conditions in lower latitudes and the Antarctic Peninsula (Figure 5 K:L) and krill's sensitivity to temperature at the upper limits of their thermotolerance (Atkinson et al., 2006; Murphy et al., 2017). In our study, at higher latitudes the increase in forced trend of SST exposed habitat with high chlorophyll concentrations where krill growth had previously been inhibited due to low temperatures (>-1°C) (Figure 5 F,G; K:L). As a result, regional growth habitat increased in the Bellingshausen, Amundsen, and Ross Seas. These broad patterns of change in krill growth habitat in our results are reflected in similar studies using ESMs from the CMIP5 project. Within the Atlantic sector (0° to 90°W), Hill et al. (2013) found that krill growth habitat would be reduced based on ocean warming and reduced chlorophyll. Veytia et al. (2020) found that circumpolar growth habitat was projected to decline in the austral summer over the course of the century and contract towards higher latitudes. Their results, like ours, suggest that projected changes in chlorophyll and SST will reduce krill GP rates in low latitudes but will increase in higher latitudes.

While environmental changes in SST primarily drive the forced trends in GP, changes in chlorophyll generally drive natural variability in growth habitat. Chlorophyll is the primary driver for krill growth potential and distribution (Ross et al., 2000; Atkinson et al., 2006; Murphy et al., 2017). Within the Atkinson et al growth model, the relationship between growth and chlorophyll is highly nonlinear; small changes in chlorophyll concentrations have a larger impact on the growth rate than temperatures within the stenothermic range (Figure 3). This is visible in the temporal evolution of the spatial average in krill GP throughout the Southern Ocean where the fluctuations in the magnitude of internal variability in krill are in sync with the chlorophyll.

Early in the 21st century, the forced trend in krill GP and magnitude of variability trend began to regress until 2100 (Figure 4a). Assuming that circumpolar habitat is well described by a regression with the area encompassed by the 5°C isotherm, we hypothesize that as temperature contracts poleward, fluctuations in the position of that isotherm lead to smaller perturbations in the total area of krill habitat. Decreased variability in krill GP implies that this is when the forced trend becomes more dominant.

The magnitude of natural variability compared to the magnitude of the forced signal drives the trends in krill GP. On shorter time horizons, the total trend in krill GP does not appear to have strong circumpolar synchronicity and is associated with internal variability (Figure 6). Conversely, across longer time horizons (50 years), the total trend is dominated by the spatial patterns from the forced signal. The trends in krill GP rates illustrate that the forced signal develops increasing dominance (over natural variability) at longer timescales (Figure 6). Trends associated with the forced signal are unlikely to be reversed on short timescales or can only be reversed through climate intervention strategies; natural variability, however, implies fluctuations around a nominal mean state. Given that the model has internally consistent representation of chlorophyll and temperature, given the dynamics in the model, the indication is that the climate change signal is very hard to discern from natural variability at an order of 20 years.

Our ability to discern the influence of climate change is contingent upon the magnitude of that signal in relation to the magnitude of the natural variability. Across the Southern Ocean, the forced trend in krill GP emerges out of the envelope of natural variability late in the 21st century.

The spatial patterns of ToE highlight the complexities of climate change on krill production habitat: krill GP trends are both increasing and decreasing as a result of human driven climate change. By the mid to late 21st century, an increased krill GP trend emerged in habitat around the Bellingshausen/Amundsen Sea region (Figure 5E). This result is again similar to projections by the 2016 study that found increased successful spawning habitats for krill in the late 21st century (Piñones and Fedorov, 2016). Currently the Bellingshausen and Amundsen Sea region does not support successful growth or spawning due to insufficient conditions (Piñones and Fedorov, 2016). However, the region has been characterized as habitat for potential future krill recruitment and increased population (Quetin and Ross, 2003) due to increased phytoplankton growth from increased ice-free summer days (Montes-Hugo et al., 2009). Though the GP model used in this study does not account for sea-ice, the spatial trend of increased SST in the Bellingshausen/Amundsen Sea region was diagnosed to emerge in SST by mid to late 21st century.

Declining krill GP rates in the habitat were detected by the late 21st century around the South Sandwich Islands, South Orkney Islands and the tip of the WAP. This region is part of the southwest sector of the Atlantic where 70% of the current population of krill is concentrated (Atkinson et al., 2008). Our results suggest that the decline in GP rates could coincide with emergent warming trends along the WAP. A similar projected decline in successful krill spawning habitat was found in the same region by a study using ESMs from the CMIP5 project and an early life cycle krill development model (Piñones and Fedorov, 2016). The 2016 study speculated that this decline was controlled by the significant changes in sea ice advance in the region north of Marguerite Bay (Piñones and Fedorov, 2016). The area around the WAP is

considered to be the main seeding region for adult krill in the southwestern Atlantic (Hofmann et al., 1992; Fach et al., 2006; Thorpe et al., 2007, 2019). The significance of declining adult krill growth in the WAP suggests that human driven climate change will result in widespread negative effects on the krill dependent ecosystem. However, the forced changes in krill GP habitat are projected to be largely indistinguishable from natural variability until late the 21st-century.

Limitations

Along with the similarities in the spatial and temporal patterns in krill growth habitat between our results and previous studies using ESMs, there are slight variations in the spatial patterns and krill GP rates in our findings. These differences can be attributed to features of the underlying ESM simulations involved, as well as methodological details associated with the application of the krill model. The krill growth model used in this study was empirically derived using in situ and satellite data for adult krill growth in the summer season and represents a single life-history cycle. Additionally, the growth model does not properly account for the role of sea ice in the krill life cycle. Sea ice is thought to play a crucial role in the krill life cycle (Nicol, 2006; Thorpe et al., 2007; Piñones and Fedorov, 2016) as well as in recruitment and abundance, which have both been linked to sea-ice extent (Siegel and Loeb, 1995; Atkinson et al., 2004). As an empirical model, it is primarily descriptive and inherently limited in applicability by the conditions reflected in the training data set. Overall, these factors limit our ability to draw conclusions on actual krill biomass and production, but they do not significantly impede our ability to illustrate the projected spatial and temporal trends of climate change and natural variability in krill GP rates.

While our results are broadly consistent with previous studies, ours is the first to consider the effects of natural climate variability explicitly. Multi-model ensembles, like the CMIP5, are composed of multiple models, each with a distinct representation of the mean state and variability. Given the structural differences between the models, the multi-model ensemble cannot be easily used to explicitly separate natural variability and from forced trends (Solomon et al., 2011). However, the large-ensemble framework used in this study allows for quantification of the uncertainties from internal variability (as found in multi-model ensemble studies), identifying trends forced by human-driven climate change and identifying when those trends can be formally distinguished from natural variability.

Because the krill model was applied to the model output offline, the fidelity of the model output is limited in its ability to accurately project mean GP values. However, the large ensemble framework assumptions result in a stronger ability to assess the trends and variability. As with any synthetic approach, limitations and caveats exist that stem from coarse model resolution, simplification of a complex system, and or inadequate process representation. These factors are important to keep in mind, however, they do not undermine our fundamental point regarding the critical role of both natural variability and external forcing in determining the trajectory of the system in coming decades.

Implications

Natural variability is, and will remain, a fundamental reality of the Southern Ocean. The superposition of the forced trend and natural variability is a feature that is intrinsic to the geophysical dynamics of the Southern Ocean thus detecting and attributing ecological changes is

challenging even under perfect observing capabilities.Thus, efforts to look for the fingerprints of climate change in krill production and ultimately, stock assessments, are incredibly difficult. The research presented here allows us to explicitly deconstruct the signal of climate change from natural variability. The large ensemble framework provides multiple realizations of observations at every grid point across a spatially resolved time series. However, as can be seen in our results that from a formal statistical point of view, it is impossible to distinguish the forced signal from natural variability until deep into the 21st century. Therefore, the ability to quantify the superposition of the forced trend against the backdrop of natural variability using large-ensembles of ESMs is highly relevant for creating effective management of krill and the Antarctic marine ecosystem.

Trends in krill growth potential rates have wide reaching implications for the Antarctic marine ecosystem and it's management. Studies have shown that the ability of habitat to support the growth and maintenance of adult krill can be used to identify crucial areas for krill biomass production and high spawning potential (Hill et al., 2013; Murphy et al., 2017). Decreases in summer-time krill GP have negative implications for reproductive performance due to the exponential relationship between adult size and fecundity (Tarling and Johnson, 2006; Siegel and Watkins, 2016). For example, negative GP trends in areas with high GP rates could reduce spawning potential translating into an exponential decrease in regional fecundity (Murphy et al., 2017). Furthermore, while the poleward shift in growth habitat distribution may not have consequences for growth habitat, it is likely to be inadequate habitat for spawning (Hofmann and Hüsrevoğlu, 2003)or connecting subpopulations (Siegel, 2016). Cascading ecological impacts to the Antarctic marine ecosystem are exasperated by the additional pressure on krill from the

fishery (Nicol et al., 2012). Fluctuations in krill productivity pose challenges for current definitions of sustainable catch. For example, seasonal changes in the length of krill are important for interpreting stock structure for fisheries management (Tarling et al., 2016). The changes as a result of climate change and variability in krill productivity and habitat partitioning could cause major consequences for food web linkages, biogeochemical cycling (Cavan et al., 2019), and the krill fishery.

There is wide international recognition of the importance of understanding, and managing for, the impacts of climate variability and climate change on the Antarctic marine ecosystem. Historically CCAMLR's mandate to monitor and manage for climate change have fallen short (Rayfuse, 2018). However, CCAMLR has recently made progress towards adjusting current management practices to properly account for climate-related interannual. As of 2019, plans were endorsed by CCAMLR to develop a long-term ecosystem-based management system for the Antarctic krill fishery. The plan prioritizes: 1) a stock assessment to estimate precautionary harvest rates; 2) regular updates of biomass estimates; and 3) a risk assessment framework to inform the spatial allocation of catch (CCAMLR, 2019 para 5.17). The research presented here motivates questions related to layers that could be included in the risk assessment. Based on our results, important fluctuations in krill dynamics are likely even in the absence of human-driven warming because the natural system is sufficiently dynamic. The risk assessment could include one or more layers characterizing long-term outcomes if the management strategy envisioned for krill is based on short-term projections. Consideration of long-term impacts, could enhance the management strategy to be more robust or adaptive to the impacts of climate change.

Further development of this approach could potentially provide a more reliable basis for adaptation strategies, risk analyses, and understanding trade-offs associated with climate change mitigation (Stock et al., 2011; Park et al., 2019). As this approach is further adapted it will generate new methods for quantifying the impacts of climate change on the Antarctic marine ecosystem. For example, by virtue of the ability to separate the component of change due to natural variability from that associated with the forced trend, the separation enables a theoretical, yet direct, attribution of losses in krill production and yield to climate change. In turn, these types of attributions can then be used to quantify the cost-benefit of climate mitigation and could be further used to inform long term goals for a flexible management strategy.

Conclusion

The Southern Ocean is a dynamic system and appropriate consideration of the changes projected to accompany climate warming must recognize the important role of natural variability. The research presented here exemplifies a particular application of ESMs, targeted at exploring the specific climate drivers of changes in krill growth potential habitat. Our findings highlight the complexities of the detection and attribution of human-driven climate changes that are superimposed on top of changes occurring naturally as a result of chaotic dynamics in the climate system. In the context of understanding ecosystem dynamics in the Southern Ocean, the superposition of natural climate variability of force trends is a critical consideration. The basic conclusions of this study are as follows. We have demonstrated how a large ensemble framework can enable explicit assessments of the benefits of climate mitigation to krill habitat and provide a basis for real-time management decisions on timescales ranging from seasons to centuries. We have shown that changes in krill growth potential will be driven by the superposition of internal

variability on shorter timescales (≤ 20 years) but on longer timescales (≥50 years), changes will be driven by the forced trend. Furthermore, we have shown that it will be impossible to distinguish the forced signal from natural variability until deep into the 21st century in krill growth potential. Future application of the large ensemble framework can be used to develop projection of krill habitat change inclusive of appropriate uncertainty estimates. In conclusion, both natural variability and externally-forced trends will be important determinants of krill habitat over the coming decades. Studies such as this will be relevant and necessary for creating climate-informed management in a marine ecosystem of immense economic and intrinsic value.

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