Will Climate Change Affect the Sustainability of Krill Fishing? A Simulation Study.

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Abstract

In the Southern Ocean, Antarctic krill form the base of the food web, and are the primary food source for a wide range of species, including whales, penguins and fish. Krill also comprises the largest fishery resource in Antarctica, but are increasingly thought to be impacted by changing environmental conditions associated with climate change. In order to explore potential synergistic impacts of climate change on krill and Antarctic food webs, we created a model to simulate the growth dynamics of Antarctic krill and its predators under changing sea surface temperatures, sea ice and fishing conditions. However, climate change and fishing are predicted to synergistically interact, possibly shrinking the average krill body sizes. Simulations of predator dynamics also showed that the effects of increased fishing under climate change will initially impact predator populations, rather than krill populations. Further, our empirically constrained simulations indicate that the total predation per year on krill is likely higher than previously assumed. These results can help drive further investigations on krill and predator population dynamics in a changing climate.

Introduction

Antarctic krill (*Euphausia superba*, hereafter referred to as ‘krill’) is a species of planktonic crustacean. With an estimated biomass of around 379 million tones (Atkinson et al., 2009) in the Southern Ocean, krill are among the most abundant animals (by biomass) on earth (Bar-On et al, 2018).

Despite the enormous numbers of krill and high levels of metazoan diversity, the Antarctic food web is relatively simple (Queiro Sid et al, 2024): krill is situated at a low trophic level, feeding mostly on photosynthetic phytoplankton, and forms the main trophic connection between those primary producers and high-level predators. As the exclusive prey of three species of baleen whales (blue (*Balaenoptera musculus*), fin (*Balaenoptera physalus*) and humpback (*Megaptera novaeangliae*)), seven species of penguins, five species of seals, most species of finfish, squids, albatrosses and other flying seabirds - krill is regarded a keystone species.

Antarctic krill also hold commercial significance; in 2024 the krill fishery landed approximately 0.5 million tons (CCAMLR 2024), with a gross annual value of between US$ 250 and 900 million (FAO 2022). The fishery is regulated by the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) and as commercial fishing of krill removes a keystone species from the Antarctic ecosystem, CCAMLR practices a precautionary ecosystem-based fisheries management approach.

Using the precautionary approach krill fishing has been confined to four subareas of Area 48 (48.1 – 48.4) in the South-West Atlantic and North of the Antarctic Peninsula - an area of 3.5 million km^2 (Atkinson, et al, 2018). Though the biomass of Antarctic krill in the four management subareas of Area 48 is estimated to be 60.3 million tones (Atkinson et al., 2019), a ‘Trigger Level’ catch limit has been allocated to the sub-areas and is set annually at 620 000 tones. While this represents only around 1% of the estimated krill biomass, with the confinement of the fishery to Area 48, fishing is concentrated in a highly biodiverse region of the Southern Ocean, with considerable overlap between the fishery and krill predators (Hinke, et al, 2017). This spatial overlap manifests as increased competition for krill between the fishery and the main krill predators such as penguins (Ratcliffe et al., 2021), baleen whales (Weinstein et al., 2017) and seabirds.

Krill abundance and spatial distribution strongly influence predator foraging and reproductive success, as well as predator population dynamics (Trathan and Hill 2016). Krill predators use different techniques to feed and most, like whales and seabirds, are known to forage over large distances. In contrast, penguin colonies forage closer to the ice shelf of the Antarctic Peninsula e.g. chinstrap penguins (*Pygoscelis antarcticus*) target krill in the deeper water regions of the ice shelf, whereas gentoo penguins (*Pygoscelis papua*) prefer shallow inshore ranges, located close to their colonies (Kokubun et al., 2010). Species such as penguins (Krüger et al., 2021), have been shown to be synergistically affected by climate change and krill fishing, especially as krill fishing is highly concentrated in restricted areas of the South Atlantic.

In addition to localized depletion of krill availability to penguin populations, climate change and oceanic subsurface (>700 m) warming is significantly impacting the ice shelves and ice sheets in Western Antarctica. Findings show that in two periods between 1979 and 2015, 25 – 50% of increased ocean heat content was absorbed by the Southern Ocean (Cheng et al., 2017; Gutt et al., 2015). This has resulted in substantial losses of ice shelves and ice sheets particularly around the Antarctic Peninsula and includes the collapse of the Larsen ice shelves (Cai et al., 2023).

While krill estimated biomass remains massively abundant, the shallow waters around the Antarctic Peninsula are krill spawning “hotspots” (Perry et al., 2019) potentially affected by climate change, with a reduction in sea-ice cover and ocean acidification influencing population dynamics. The abundance and distribution of Antarctic krill in the Southern Ocean are linked with the presence of sea ice, which supports much of their early life stages through provisioning of habitat and of ice algae as food (Bernard et al. 2019, Meyer et al. 2009). However, several studies have reported that warming waters and changing sea-ice dynamics associated with climate change are shifting suitable krill habitat and reducing krill availability in some Antarctic regions that have historically supported large predator populations (McBride et al. 2021, Piñones & Fedorov 2016, Flores et al. 2012).

Research has linked effects of climate change to reductions in sea ice and note that along with reduced sea ice, recovering whale populations and an increase in fishing pressure are adding to the competition for krill (Salmeron *et al.*, 2023). As larval krill need sea-ice for food and shelter in the winter months, reduced sea-ice may in turn create a reduction in krill abundance and may be causing the decline in chinstrap penguin populations, as they are unable to forage for enough krill to meet their needs.

These distributional shifts in krill abundance can force predators to travel farther or change foraging strategies, reducing breeding success (Germishuizen et al. 2024, Testa et al. 2022, Trivelpiece et al., 2011). Similarly, some predators have shown similar responses to localized krill population declines due to concentrated fishing. For example, penguins near localized but intensive krill fishing areas have shown longer foraging trips, smaller or fewer chicks, and poorer growth (Watters et al. 2020).

Several studies have expressed concern about the future sustainability of krill, and the predators that depend on them, under the dual pressures of climate change and spatially concentrated fishing (Watters et al. 2020, Jaquet et al. 2010, Schiermeier 2010, Flores et al 2012). The purpose of this study was to model, via computer simulations the interactions between climate change, krill populations, predator population and fishing. The goal was to improve the understanding of the possible impacts of krill fishing on predator populations on a changing planet.

Methods

Model Overview

The growth equations for krill were initially plotted based on information gathered from empirical literature. With these equations, we explored the consequences of altering temperature and plankton densities, as predicted by polar climate change.

Using a prey-predator model, we simulated ~ 2000 individual krill animals, each growing according to the krill growth equations. Each krill individual is meant to represent a small fraction of the extremely large populations of Antarctic krill in Fishing Area 48. With a total of 66 million tons of krill, each simulated krill unit hence represents 33 thousand tons. The model includes death of krill by both predation and fishing. We used this model to explore the potential effects on krill populations from increased fishing, climate change, and their synergies.

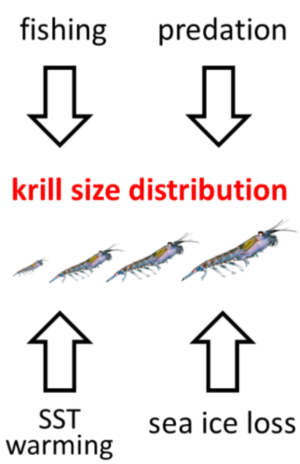


Figure 1: Model overview: Factors influencing the dynamics of the krill population.

Growth Equations

The simulations presented here are based on descriptions of krill daily growth rates by Atkinson et al., 2006. The authors measured the inter-molt intervals and the growth rates from a variety of krill samples from several parts of the Antarctic Ocean. The basic equation describes krill growth per day (in mm) as a function of the current length of the krill animal (L_{krill}), temperature and available food (phytoplankton, expressed as mg Chlorophyl A per cubic meter):

$\Delta L_{krill} = f(L_{krill}, T, chlA)$

The equation describing the krill daily growth from Atkinson et al., 2006 is:

$\Delta L_{krill} = f(L_{krill}, T, chlA)$

$$\Delta L_{krill} = + a + b^{*} \Delta L_{krill} + c^{*} \Delta L_{krill}{}^{2} + \frac{d\ chla}{e+chla} + f\,T + g\,T^{2}$$

The following parameters (*a* to *g*) were employed: Parameter *a* is different (separate best fits) for all krill, each developmental stage, and temperature control during incubation included.

Constant term	all krill combined	a	-0.066000		0.057
	Juveniles	a		-0.158000	
	Males	a		-0.193000	
	Immature females	a		-0.019200	
	Mature females	a		-0.216000	
Length	Linear term	b	0.002000	0.006740	-0.001900
	Quadratic term	c	-0.000060	-0.000101	-0.000036
Food	Maximum term	d	0.385000	0.377	0.345
	Half saturation constant	e	0.328000	0.321	0.297
Temperature	Linear term	f	0.007800	0.013	-0.011000
	Quadratic term	g	-0.010100	-0.011500	-0.005690

Table 1: Krill growth equation parameters from Atkinson et al., 2006.

To make sure the model equations faithfully reproduce the measured growth curves, we reproduced a key figure from Atkinson et al. (2006), describing krill growth at three different sizes, as a function of food (chlorophyl A). The identical figures validate the basic model equation (Fig. 2).

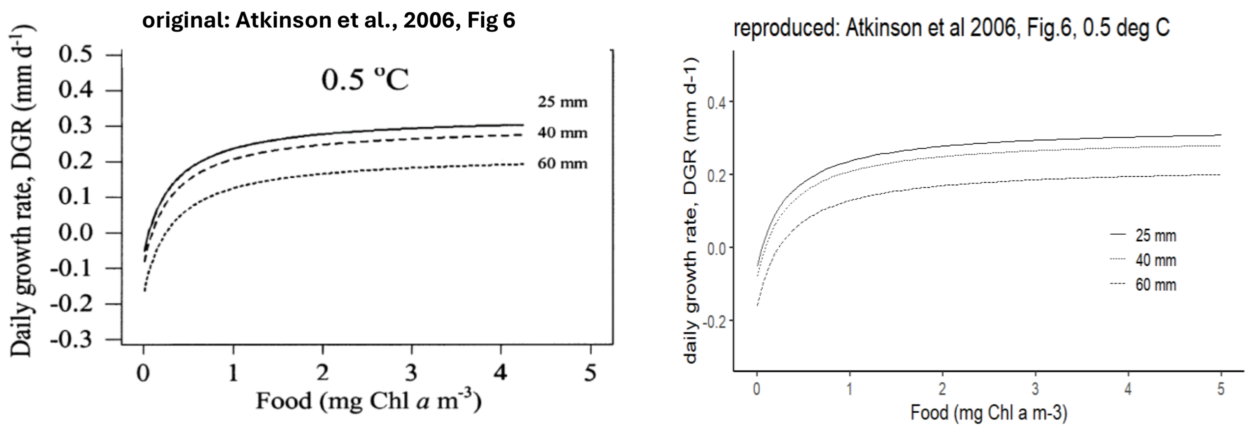


Figure 2: The original figure from Atkinson et al, 2006, and the same relationship between daily growth rates and chlorophyl A concentration, reproduced to validate the model equations. The three lines represent different krill lengths.

Parameters: Phytoplankton /Chlorophyl A

Krill are filter-feeders of planktonic algae, for which the algal concentration can be estimated via the chlorophyll A concentration, which in turn can be determined by analyzing satellite imagery (remote sensing). The chlorophyll A concentration in the Arctic Ocean is highly seasonal, with peak chlorophyll concentrations in January and minima in September.

Any remote sensing approach, such as the determination of chlorophyll A via satellite image analysis, needs thorough ground-truthing, to ensure that the values estimated from satellite imagery correspond to the actual values in sea water. Ferreira et al. (2022) recently addressed the issue of chlorophyl-A under-estimation in Antarctic data, and we use their measurements as inputs to our model. Specifically, the chlorophyll-A maxima and minima are 0.82 mg m^{-3} in January (Ferreira et al. 2022), and 0.2 mg m^{-3} in May to July (extrapolation of Ferriera et al. 2022 data; Tab. 2).

Due to upwellings and other oceanographic conditions, the nutrient and hence chlorophyll-A concentration in the Antarctic Ocean displays significant regional variance, and we hence ran the simulations presented here with a range of chlorophyll- A values.

Month	Chl-A mg m^{-3}
1	0.82

2	0.78
3	0.7
4	0.55
5	***0.2***
6	***0.2***
7	***0.2***
8	0.4
9	0.3
10	0.45
11	0.6
12	0.75

Table 2: Chlorophyll data adapted and ***interpolated*** *from Figure 10, Ferreira et al., 2022. The author states that "Note that the period between May and July is not shown due to the lack of data in mid-winter." For this time period, chlorophyll-a concentration was* ***interpolated/estimated*** *at 0.2 mg m^{-3}.*

Parameters: Climate Change: Sea Surface Temperature and Sea Ice

Sea-surface temperature explicitly influences krill growth in the equation of Atkinson et al, 2006. We therefore modeled sea-ice as an increase in baseline algal food for krill, in the form of algae attached to the underside of sea ice. This is especially important during winter months, when open-ocean phytoplankton/chlorophyl A is low. Observations have shown that larger sea ice-cover during the winter months will provide krill with a head-start into their reproductive season, with more productive and earlier spawning seasons occurring during years of higher sea-ice cover (Kawaguchi, 2016). In essence, krill animals will not need to live off their reserves during winter months if algae below the sea ice are available as winter food.

We simulated the effect of sea ice as an addition of Chlorophyll A/krill food, sinusoidally varying annually with a peak in October. We also simulated climate change impacts by gradually reducing the sea ice by 50% over ten years.

Parameters: Predation

Antarctic krill is preyed on by a variety of predators, such as seals, seabirds, baleen whales, fishes and squid. The predation by mammals and birds is generally better understood than that of fishes and squid (Trahan & Hill, 2016). Due to uncertainties of krill predation by fishes and squid (see discussion) and our focus on the detailed dynamics of the krill populations, we represented predators as a single population. The predator population increases as a function of the size of the krill population and decays with a time constant of two years.

Baleen in humpback whales is tightly spaced (35.6 sheets per cm; Werth, 2013), and the dynamic nature of the filtering process introduces turbulence, which by de-facto decreases biological mesh size even more. We hence modeled krill predation by long-lived, seasonal predators (baleen whales) as taking all sizes of krill equally.

Krill sizes measured from the stomach content of crabeater seals, which dominate the long-lived, resident group of predators, was measured at an average of 47.6 mm (range of 38 to 56 mm) in the winter (Lowry et al., 1988). The krill found in crabeater seal stomachs were significantly larger than the krill found during the same study in trawls, indicating a preference of seals for feeding on larger krill individuals. We therefore modeled krill predation as preferentially consuming larger krill, with a 30% increase in predation likelihood for every 40 mm of krill, in 12% of predation events.

Parameters: Fishing

Krill trawling captures krill animals over a range of sizes, dependent on fishing gear design, including differences in mesh sizes used (Wang et al., 2021). An observational study of krill sizes captured by two different trawlers found averages between 50.8 ± 3.7 mm and 36.3 ± 5.4 mm, a significant range (Wang, 2016). We therefore modeled krill fishing as a size-specific removal of krill biomass, with a 30% increase in the likelihood of fishing captures for every 40 mm of krill, in 10% of fishing events.

Prey-Predator Model

The main *difference equation* (discrete time steps, days) in our simulation describes the growth of individual krill animals over time, as a function of their present size, temperature, and available food. Using this equation, we modeled the growth of ~2000 individual krill organisms, together representative of the complete krill population in fishing Area 48 ($66\ 10^6$ tons, → each simulated krill ≈ $33\ 0^3$ tons). In our model, each individual enters the population as a juvenile at a length of 7 millimeters, and then grows according to the equations described below in detail.

At each time step (day), the individual dies with a given probability due to predation. An individual also dies as a consequence of fishing in every time-step, with larger individuals more likely to be fished (see above). Once an individual is dead by either predation or fishing (eliminated), the individual is replaced with a new juvenile with a daily probability depending on the amount of reproductive krill adults (> 42 mm) in the simulation.

Notably, this approach assumes an ample surplus of krill larvae, which is likely a realistic assumption: Female krill produce in excess of 10^4 eggs per year (even though many don't survive the larval stages; Kawaguchi, 2016), and competition at the adult stage appears to be a bottleneck in krill survival (Ryabov et al., 2017). The prey-predator simulations we present do not assume influx of larvae or adult krill organisms from neighboring areas. This assumes that the simulated area is large enough to prevent significant larval influx or that this flux is constrained area by size or current conditions.

The precise formulation of the prey-predator model (as an XPP file describing the time-discrete difference equations) and all parameters are given in the appendix. In brief:

Every day (time step) ***krill*** *will:*

grow *(according to the growth equations from Atkinson, 2016)* ***or***

die *(according to a probability given by predation and fishing, depending on krill size)* ***or***

settle*/be replaced by a new 7mm krill juvenile (if this krill individual is presently dead)*

And every day ***predators*** *will:*

increase *depending on the krill population and* ***decay*** *at a rate of ½ years*

Simulation Methods

Simulations were executed in XPP (Ermentrout & Mahajan, 2003). The dynamics of krill and its predators were simulated as difference equations, with a time-step of one day (krill growth is often stated as daily growth rates, DGR, in the literature). Simulation results were plotted in R.

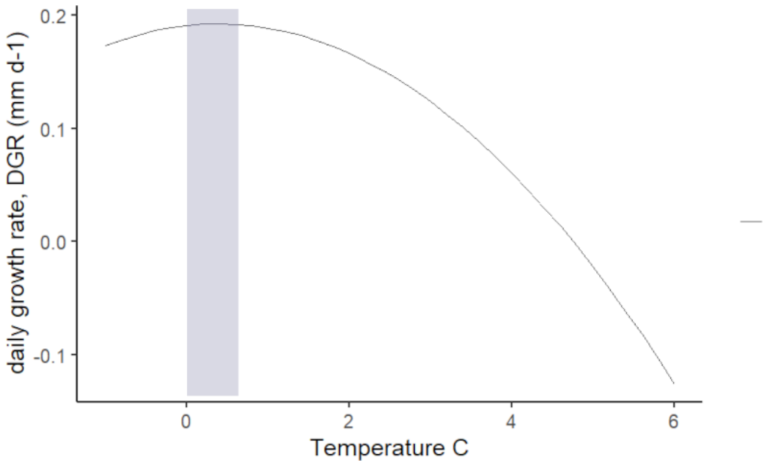
Results

Sea Surface Temperature

In the first set of simulations, we investigated the effect of changing Antarctic sea surface temperature on krill growth. Most Antarctic krill fishing is taking place near the Western Antarctic Peninsula, where the sea surface temperatures are near the optimum for krill growth, between 0° C and 0.5° C (see Stewart et al.,2019; Fig, 3 top). Fig. 3 top shows that even a small deviation from present day sea surface temperatures by one degree Celsius will significantly decrease krill growth.

To further this point, we plotted krill daily growth rates over a range of krill sizes (with a chlorophyll A concentration of 0.5 mg m^{-3}, the annual average). As noted in Atkinson et al. (2006), krill growth follows an inverse u-shape as a function of krill size. With increasing temperatures, growth at all krill sizes slows down; at a sea surface temperature of 4°C growth above the length of male maturation, 43 mm, all but ceases. Note that this plot merely plots the temperature and chlorophyll A (phytoplankton) dependence of krill growth, without yet including predation, hence representing an upper bound for the temperature increase which krill populations can possibly tolerate.

However, the response of sea surface temperature of the Antarctic Ocean to climate change is complex, with an interplay of melting ice, currents and winds so far preventing significant warming, or even cooling during the last decades (Holmes et al., 2022). This trend shows strong signs of reversal (Holmes et al., 2022), and any significant sea surface temperature warming in the Antarctic Ocean will have drastic consequences for krill populations.


daily growth rate, DGR (mm d-1)
0.2
0.1
0.0
-0.1
0
2
4
6
Temperature C


female maturity
male maturity
daily growth rate, DGR (mm d-1)
0.2
0.1
0.0
-0.1
20
40
60
krill size (mm)
0.5 C
3 C
4 C
5 C

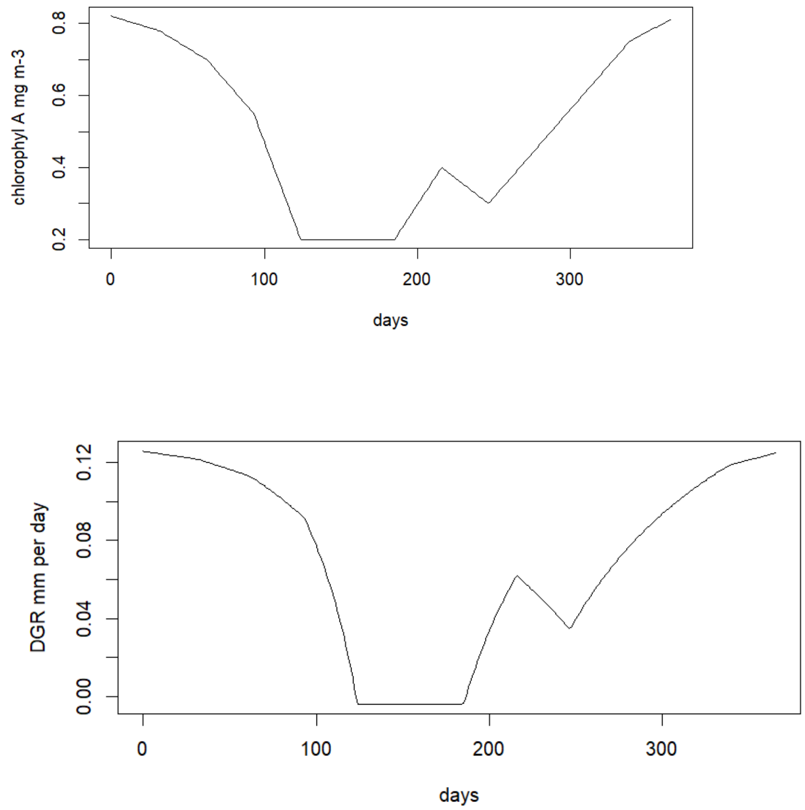


Figure 3: Influence of sea surface temperature on krill growth.

Top: *Daily growth rate of 40 mm krill individuals as a function of temperature, calculated as given in Atkinson et al, 2006. The blue square indicates the approximate present-day sea surface temperature range off the Western Antarctic Peninsula.*

Center: *Krill growth as a function of krill size, calculated as given in Atkinson et al, 2006, with a chlorophyll A concentration of 0.5 mg m^{-3}, the annual average. The vertical lines show the approximate sizes of female (35 mm) and male (43 mm) sexual maturity, as given in Siegel & Loeb (1994). The horizontal line shows the transition from growth to shrinking.*

Bottom: *Oceanic chlorophyll A concentration over the course of a year, according to Ferreira et al., 2022, and the calculated daily growth rates according to the respective chlorophyll A concentrations.*

Krill fishing and Climate Change in Area 48

We next used the predator-prey model described in the methods to simulate the effects of krill fishing and climate change in Area 48 (as defined by the CCAMLR; Fig. 4). We simulated the development of the krill and predator populations for ten years, both under baseline conditions, with simulated climate change (sea ice reduction by 50%, and SST warming by 0.2° C in ten years) and with a ten-fold increase in krill fishing. We also simulated a scenario with the combination of increased fishing and climate change.

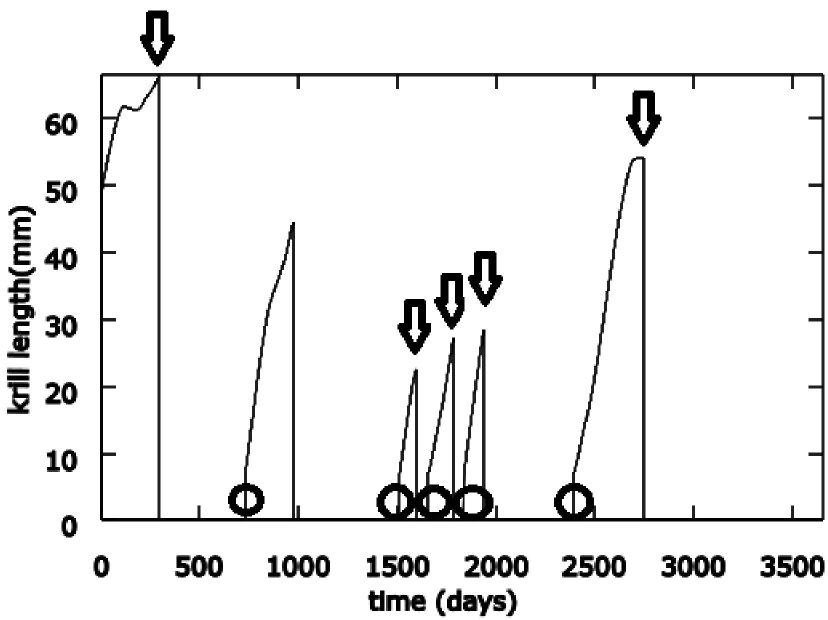


Figure 4: Time course of growth, settlement (circle) and death (arrow) of krill over the course of 10 years in the predator-prey simulations.

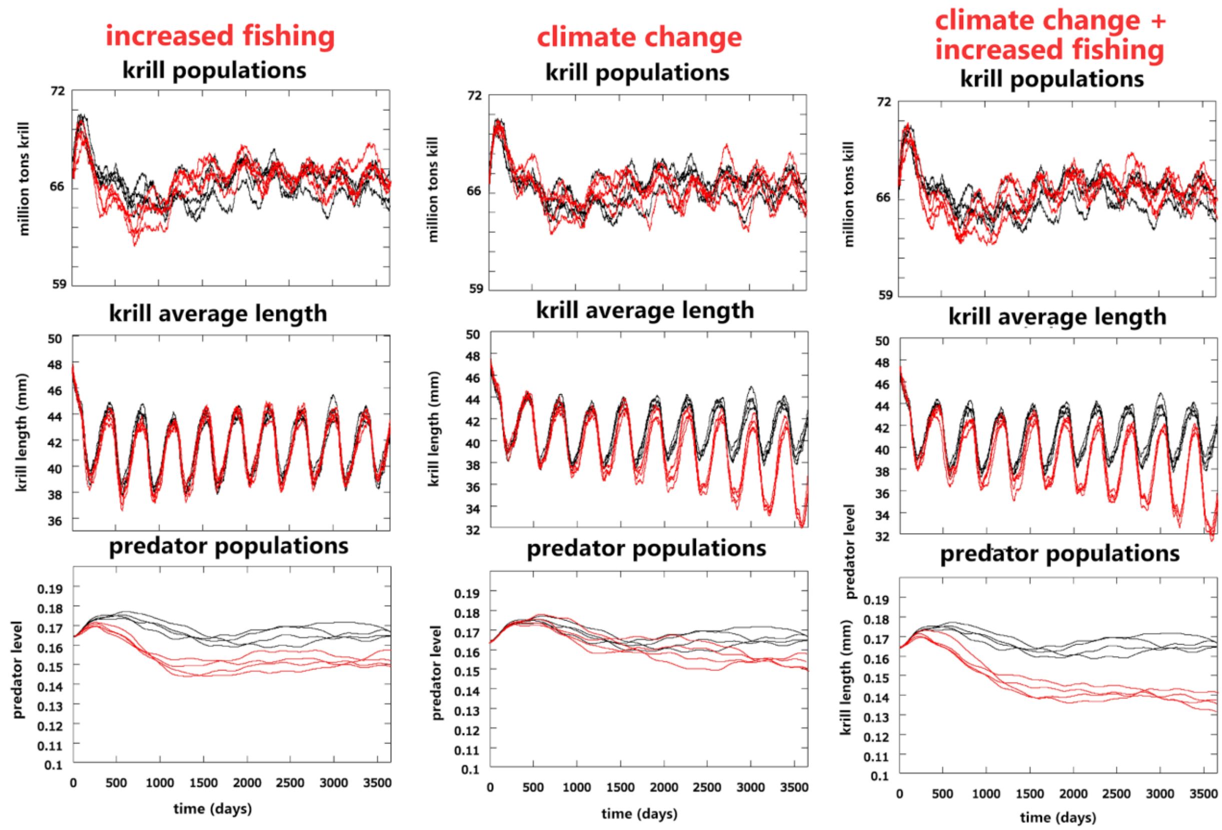


Figure 5: Effects of increased fishing, climate change and a combination of the two changes on krill populations, average krill length, and predator populations. **Baseline values are plotted in black**, **altered conditions shown in red**. The simulated time is 10 years.

We found that increased fishing primarily affects the predator population, and not the krill population (Fig. 5). In other words, increased fishing removes krill from availability to predators, but does not lead to a population collapse of this fast-growing and highly reproductive species. Overall, a 10-fold increase in fishing led to a 7.1 % decrease in predators over ten years. Similarly, climate change, simulated as a 0.2°C increase in SST and a loss of half the sea ice over 10 years, caused a 9.2 % decrease in the predator population, but no real reduction in krill populations. However, this parameter change also caused a reduction of the average krill size, especially in the minima during the winter months. Modelled declines in the predator population in response to a 10-fold increase in fishing combined with climate change impacts were 17.5 %, which is 1.2 % larger than the sum of the individual effects.

Stochasticity of these results was generally high, with a range of variances between 10.6 and 14.2 % over 20 simulation runs (10 years each).

Discussion and Conclusions

Based on empirically determined growth parameters of Antarctic krill, we simulated krill population and predator dynamics using difference equations. We found that both increased fishing as well as climate change reduced predator populations, which were mildly synergistic when simulating both changes at the same time.

A ten-fold increase in krill fishing is currently not planned. However, the simulations cover all of Area 48, where concentrated fishing efforts in smaller areas can possibly reach higher levels of krill biomass removal. (It should be noted that failure to reach consensus around krill management and the implementation of Marine Protected Areas at the 44th annual CCAMLR meeting in 2025 resulted in no change to the Trigger Level catch limit (~1% of the estimated krill biomass in Area 48) and the fishery will continue concentrated fishing in Area 48, without precautionary regulations in place.)

Several other points emerge from our simulations: the potential impact of increased krill fishing on predator populations, the high estimation of predation rates, and the stochasticity of effects.

Predator Populations and Predation Rates

Importantly, an increase in krill fishing in our simulations did **not** lead to a decrease in krill populations, but rather to a **decrease in predator populations**. In essence, this is in accord with work on penguin populations, where decreases in populations were observed in areas with concentrated krill fishing (Krüger et al., 2021).

However, our simulations were primarily constrained by the equations describing krill growth, as measured empirically (Atkinson, 2016), and the estimated average krill length, which is somewhat above 40 mm, depending on the specific trawl used (https://www.ccamlr.org/en/fisheries/krill-fisheries, retrieved 2-2025). To achieve this krill size with the known growth parameters, the annual predation rate had to be set at ~ 100%

of the krill biomass. This is much higher than what was assumed previously. Trathan & Hill (2016) state a value of ~ 16% of predation per year for marine mammals and birds combined. This estimate is fairly stable over changes in the implementation details of the model, and would indicate that fishes and squid consume ~ 84% of the krill biomass per year, a realistic assumption.

Stochasticity

A third result of our simulations is that they show marked stochastic dynamics. Again, this result persists against changes in the detailed implementation of the prey-predator simulations. Likely, it is a result of coupling long-lived predators with fast-growing, fast-turnover prey populations. The source of stochasticity in our simulations is the fluctuating death and settlement of krill individuals. In the real world, a number of oceanographic and weather parameters also contribute to environmental fluctuations influencing krill populations. The consequence of this is that even while the krill and predator dynamics are unfavorably changed, this would likely not be detectable for multiple years due to overlay with stochastic dynamics.

Previous Simulations of Krill Dynamics

The specific focus of this study is on the size distributions in krill populations, and their importance for predicting the stability of populations in the face of increased fishing and climate change.

Previous work has used computer simulations to elucidate the importance of growth, predation, vertical migrations and displacement by oceanic currents on krill dynamics, both in the Antarctic as well as in northern waters.

An example is the work by Butterworth & Thompson (1995), who used a model based on krill recruitment and fishing intensity, together with estimates of predator mortalities, to predict the effect of krill fishing on predator survival. They found significant differences between the ability of predators to cope with reduced krill biomass due to fishing (Crabeater seals best, Adelie penguins worst). They also pointed out the importance of stochastic krill biomass fluctuations.

Sourisseau et al. (2006) used a krill biomass equation (excluding growth and predation), coupled to simulations of vertical krill migration to simulate krill movement in the Bay of St. Lawrence (Canada) and adjacent waters. They found that local bathymetry strongly influences the distribution of krill at depth; and the local current systems influence the distribution of krill near the surface. Since krill move from depth (day) to the surface (night) in a daily cycle, the precise parameters of this cycle are of great importance for krill dispersal.

Recommendations for Krill Fisheries

Previous work has shown that present krill fisheries are sustainable, due to the enormous krill biomass present in the Antarctic Ocean (Hill et al., 2016). The authors, however recommend caution, stating that the concentration of krill fisheries in relatively restricted areas can still locally upset predator populations. Indeed, penguin populations were shown to be negatively affected by localized krill fishing in some areas (Krüger et al., 2021).

Intensive whaling up to the middle of the 20th century depleted whale populations, possibly down to 5% of their original sizes in some parts of the world (North Atlantic: Roman & Palumbi, 2003, Alter et al., 2007). The surplus krill hypothesis is based on the idea that this decrease in baleen whales left large amounts of krill unused by predators, with other predators incapable of filling in the predatory void. Present-day levels of whale populations and reproductive rates do not support the existence of surplus krill (Palin et al., 2023). Consequently, in the context of the simulations presented here, our simulations did not include a fraction of krill inaccessible to predators (the “surplus”).

Acknowledgements

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AI Use Statement

No AI tools, only natural intelligence was used in this research project.

Conflict of Interest

R.M.S. is employed by the Marine Stewardship Council. The author has no perceived competing interests.

Ethics Statement

This is a purely theoretical/computer simulation study, with no animal or human subjects.

References

Alter, S. E., Rynes, E., & Palumbi, S. R. (2007). DNA evidence for historic population size and past ecosystem impacts of gray whales. Proceedings of the National Academy of Sciences, 104(38), 15162-15167.

Atkinson, A., Shreeve, R. S., Hirst, A. G., Rothery, P., Tarling, G. A., Pond, D. W., Korb, R. E., Murphy, E. J., & Watkins, J. L. (2006). Natural growth rates in Antarctic krill (Euphausia superba): II. Predictive models based on food, temperature, body length, sex, and maturity stage. Limnology and Oceanography, 51(2), 973–987

Bar-On, Y. M., Phillips, R., & Milo, R. (2018). The biomass distribution on Earth. Proceedings of the National Academy of Sciences of the United States of America, 115(25), 6506–6511.

Butterworth, D. S., & Thomson, R. B. (1995). Possible effects of different levels of krill fishing on predators–some initial modelling attempts. CCAMLR science, 2, 79-97.

Constable, A. J. (2011). Lessons from CCAMLR on the implementation of the ecosystem approach to managing fisheries. Fish and Fisheries, 12(2), 138-151.

Dirscherl, M. (2022). Remote Sensing of Supraglacial Lake Dynamics in Antarctica-Exploiting Methods from Artificial Intelligence for Derivation of Antarctic Supraglacial Lake Extents in Multi-Sensor Remote Sensing Data (Doctoral dissertation, Universität Würzburg).

Ermentrout, B., & Mahajan, A. (2003). Simulating, analyzing, and animating dynamical systems: a guide to XPPAUT for researchers and students. Appl. Mech. Rev., 56(4), B53-B53.

Ferreira, A., Brito, A. C., Mendes, C. R., Brotas, V., Costa, R. R., Guerreiro, C. V., ... & Jackson, T. (2022). OC4-SO: A new chlorophyll-a algorithm for the Western Antarctic Peninsula using multi-sensor satellite data. Remote Sensing, 14(5), 1052.

Fetterer, F., Knowles, K., Meier, W.N., Savoie, M., Windnagel, A.K., 2017. Updated daily. Sea Ice Index, Version 3. [Median sea ice extent March and September 1981-2010]. Boulder, Colorado USA. NSIDC: National Snow and Ice Data Center.

Flores, H., Atkinson, A., Kawaguchi, S., Krafft, B. A., Milinevsky, G., Nicol, S., ... & Werner, T. (2012). Impact of climate change on Antarctic krill. Marine Ecology Progress Series, 458, 1-19.

Hersbach, H., Bell, B., Berrisford, P., Biavati, G., Horányi, A., Munoz Sabater, J., Nicolas, J., Peubey, C., Radu, R., Rozum, I., Schepers, D., Simmons, A., Soci, C., Dee, D., Thépaut, J.-N., 2019. ERA5 monthly averaged data on single levels from 1979 to present. Copernicus Climate Change Service (C3S) Climate Data Store (CDS).

Hill, S. L., Atkinson, A., Darby, C., Fielding, S., Krafft, B. A., Godø, O. R., ... & Watkins, J. (2016). Is current management of the Antarctic krill fishery in the Atlantic sector of the Southern Ocean precautionary?.

Hinke, J. T., Cossio, A. M., Goebel, M. E., Reiss, C. S., Trivelpiece, W. Z., & Watters, G. M. (2017). Identifying Risk: Concurrent Overlap of the Antarctic Krill Fishery with Krill-Dependent Predators in the Scotia Sea. PLoS ONE, 12(1), 170132.

Holmes, C. R., Bracegirdle, T. J., & Holland, P. R. (2022). Antarctic sea ice projections constrained by historical ice cover and future global temperature change. Geophysical Research Letters, 49(10), e2021GL097413.

Kawaguchi, S. (2016). Reproduction and larval development in Antarctic krill (Euphausia superba). Biology and ecology of Antarctic krill, 225-246.

Kokubun, N., Takahashi, A., Mori, Y., Watanabe, S., & Shin, H. C. (2010). Comparison of diving behavior and foraging habitat use between chinstrap and gentoo penguins breeding in the South Shetland Islands, Antarctica. Marine Biology, 157(4), 811–825.

Krüger, L., Huerta, M. F., Santa Cruz, F., & Cárdenas, C. A. (2021). Antarctic krill fishery effects over penguin populations under adverse climate conditions: Implications for the management of fishing practices. Ambio, 50(3), 560-571.

Lowry, L. F., Testa, J. W., & Calvert, W. (1988). Notes on winter feeding of crabeater and leopard seals near the Antarctic Peninsula. Polar Biology, 8, 475-478.

Pallin, L. J., Kellar, N. M., Steel, D., Botero-Acosta, N., Baker, C. S., Conroy, J. A., ... & Friedlaender, A. S. (2023). A surplus no more? Variation in krill availability impacts reproductive rates of Antarctic baleen whales. Global Change Biology, 29(8), 2108-2121.

Perry, F. A., Atkinson, A., Sailley, S. F., Tarling, G. A., Hill, S. L., Lucas, C. H., & Mayor, D. J. (2019). Habitat partitioning in Antarctic krill: Spawning hotspots and nursery areas. PLoS ONE, 14(7).

Queiró Sid, J. P., Borras-Chavez, R., Mie Friscourtid, N., Groß, J., Lewis, C. B., Mergard, G., & O'Brien, K. (2024). Southern Ocean food-webs and climate change: A short review and future directions.

Roach, L. A., Mankoff, K. D., Romanou, A., Blanchard-Wrigglesworth, E., Haine, T. W., & Schmidt, G. A. (2023). Winds and meltwater together lead to Southern Ocean surface cooling and sea ice expansion. Geophysical Research Letters, 50(24), e2023GL105948.

Roman, J., & Palumbi, S. R. (2003). Whales before whaling in the North Atlantic. science, 301(5632), 508-510.

Ryabov, A. B., de Roos, A. M., Meyer, B., Kawaguchi, S., & Blasius, B. (2017). Competition-induced starvation drives large-scale population cycles in Antarctic krill. Nature Ecology & Evolution, 1(7), 0177.

Salmerón, N., Belle, S., Cruz, F. S., Alegria, N., Finger, J. V. G., Corá, D. H., Petry, M. V., Hernández, C., Cárdenas, C. A., & Krüger, L. (2023). Contrasting environmental conditions precluded lower availability of Antarctic krill affecting breeding chinstrap penguins in the Antarctic Peninsula. Scientific Reports, 13(1), 5265.

Siegel, V., & Loeb, V. (1994). Length and age at maturity of Antarctic krill. Antarctic Science, 6(4), 479-482.

Stewart, C. L., Christoffersen, P., Nicholls, K. W., Williams, M. J., & Dowdeswell, J. A. (2019). Basal melting of Ross Ice Shelf from solar heat absorption in an ice-front polynya. Nature Geoscience, 12(6), 435-440.

Sourisseau, M., Simard, Y., & Saucier, F. J. (2006). Krill aggregation in the St. Lawrence system, and supply of krill to the whale feeding grounds in the estuary from the gulf. Marine Ecology Progress Series, 314, 257-270.

Trathan P.N., S. Hill. (2016) The Importance of Krill Predation in the Southern Ocean. In: Biology and Ecology of Antarctic Krill

Wang, Z., Tang, H., Herrmann, B., & Xu, L. (2021). Catch pattern for Antarctic krill (Euphausia superba) of different commercial trawls in similar times and overlapping fishing grounds. Frontiers in Marine Science, 8, 670663.

Werth, A. J. (2013). Flow-dependent porosity and other biomechanical properties of mysticete baleen. Journal of Experimental Biology, 216(7), 1152-1159.

Appendix 1: Program Code

Ordinary differential equations were numerically solved in XPP (Ermentrout, 2003). The program code for the growth equations for krill is:

```
# krill predator prey model
# Some simulation parameters
# 10 simulated years
```

```
@ TOTAL=3650
# Atkinson krill growth parameters
p a=-0.066000, b=0.002000, c=-0.000060, d=0.385000, e=0.328000, f=0.007800, g=-0.010100
p temp=.5
# Mortality and birth parameters
p larva = 0.00016
p decay = 400
p scale = 0.005
# fishing as percent of stock per day. 2.7e-5 = 1% per year
p fishing = 0.000027
p cutoff = 120
p multi =20
# seaice
# reduction by 50% in 10 years
seaice(dime) = (cos(PI*2*dime/364+2*PI/6)+1)*8+2
p icepct0 = 0.01
p icepct = 0.01
# ice percentage loss of 50% per decade
# icepct = icepct0*(1-t/1825)
# load chlorophyl A circannual variation
# add sea ice effect to chlA and larval survival
table chla "chlA2.csv"
# warming 0.1C per decade
# tadjust = temp+t/36500
tadjust = temp
# mortality eqn
# fishing and predation here
death(x,l)=if(l==0|ran(1+fishing*(1+0.01*l/cutoff)+(0.0008*whale+0.0001*l/cutoff)*multi)>1)then(0)else(x)
# birth equation
# larva settles at 7 mm
birth(y)=if(y==0&ran(1+(larva*reproduce*4)*multi)>1)then(7)else(0)
# MASTER EQUATIONS
growth(length) = a + b*length + c*length^2 + (d*(chla(t)+seaice(t)*icepct)/(e+ (chla(t)+seaice(t)*icepct))) +f*tadjust + g*tadjust^2
krill[1..4000](t+1) = death(krill[j] + growth(krill[j]),krill[j]) + birth(krill[j])
whale(t+1)= whale - whale/decay + alive*whale*scale
```

```
#some auxiliaries
alive = sum(1,4000)of(heav(shift(krill1,i')-1))/4000
reproduce = sum(1,4000)of(heav(shift(krill1,i')-40))/4000
aux avgl = sum(1,4000)of(shift(krill1,i'))/(4000*alive)
aux alive2 = alive
aux reproduce2 = reproduce/alive
aux ice2 = seaice(t)*icepct
# average krill size (42 mm) is the initial condition
krill[1..2000](0)=48
krill[2001..4000](0)=0
whale(0)=.16
done
```

The file specifying the chlorophyl A concentration, chlA2.csv is:

120
1
3650
0.82
0.78
0.7
0.55
0.2
0.2
0.2
0.4
0.3
0.45
0.6
0.75

The section in **bold** is repeated 10 times.