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Title page

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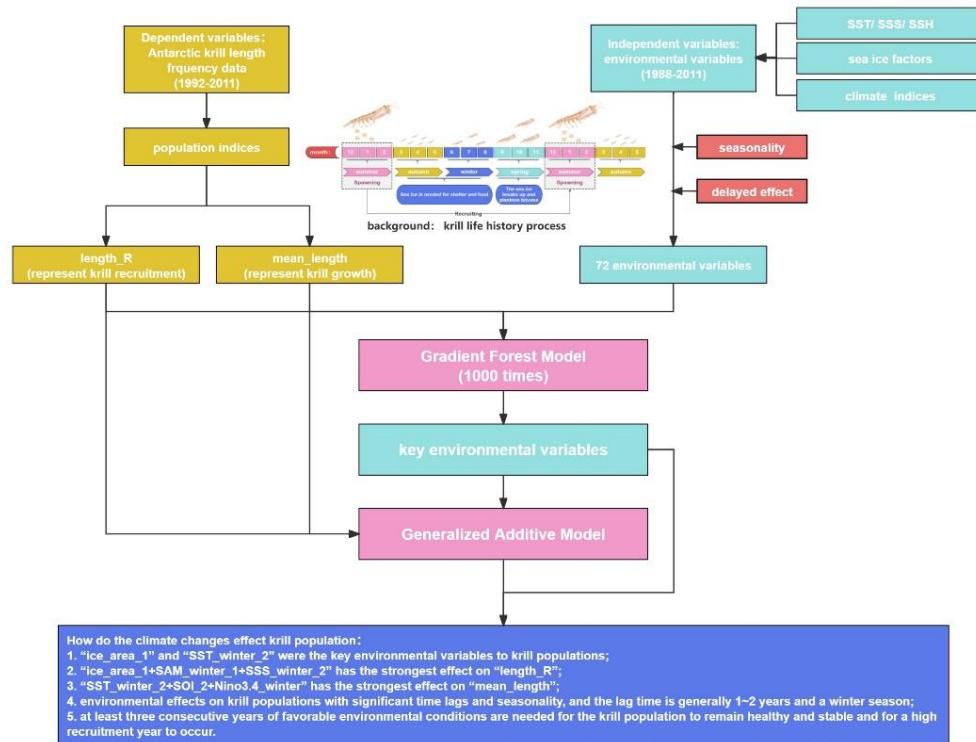
Highlight:

- 1) Developing novel Antarctic krill population indices through comprehensive analysis of length-frequency distributions, overcoming limitations of traditional abundance-based metrics;
- 2) Investigating climate change impacts on Antarctic krill population ecology using a piecewise modeling strategy;
- 3) Comprehensively incorporated both life-history traits and time lag of climate change impacts of Antarctic krill population ecology during the analysis process.

Running Head:

KRILL POPULATION RESPONSE TO CLIMATE CHANGE

Graphical Abstracts:



Analyzing the effects of climate change on the population ecology of Antarctic krill based on its population indices

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Abstract: Antarctic krill is a key species in the Southern Ocean with high ecological and economic value, and the health and stability of its population are directly linked to the health and stability of the Southern Ocean ecosystem. In recent years, global climate change has posed unprecedented challenges to krill resources. To better manage and conserve krill resources in the future, it becomes particularly crucial to develop new approaches that enhance our understanding of the relationship between the environment and krill population ecology. In this study, we estimated two population indices that respectively represent krill population growth (“mean_length”) and recruitment (“length_R”) based on krill body length frequency data. In contrast to previous research paradigms relying on single models or single-factor analyses, this study employs two more flexible statistical approaches, the Gradient Forest Model (GFM) and the Generalized Additive Model (GAM), for piecewise modeling, thereby providing an analysis of the mechanisms through which environmental change affects krill population ecology. During the analysis, we took into account the life history characteristics of krill and the time lag in the environmental impacts on its population. The results indicate that the impacts of environmental variables on krill populations exhibit significant time lags and seasonal patterns. The combined effect of “ice_area_1 (sea ice area with a 1-year lag) + SAM_winter_1 (winter Southern Hemisphere Annular Mode Index with a 1-year lag) + SSS_winter_2 (winter sea surface salinity with a 2-

year lag)” has the strongest effect on krill population indices “length_R”, and the combined effect of “SST_winter_2 (winter sea surface temperature with a 2-year lag) +SOI_2 (Southern Oscillation Index with a 2-year lag) + Niño 3.4_winter (the primary indicators for monitoring, defining, and determining El Niño and La Niña events in winter with a 2-year lag)” has the strongest effect on krill population indices “mean_length”. The findings further clarify how environmental changes affect krill population ecology, providing new scientific references for the future management of krill resources.

Keywords: Antarctic krill; population indices; population ecology; climate change; Gradient Forest Model; Generalized Additive Model;

1 Introduction

The Antarctic krill (in the Southern Ocean, the Antarctic krill *Euphausia superba*, henceforth simply “krill”), a marine crustacean with a circumpolar distribution, is one of the world’ s largest single-species resources, with a long and complex life cycle (Nicol, 2006) and a total biomass estimated at 300-500 million tons (Bar-On et al., 2018). In the Southern Ocean, krill play an important role in the ecosystem, being the primary prey for fish, seabirds and marine mammals, linking primary production to higher trophic levels (Croxall and Nicol 2004, Trivelpiece et al. 2011, Wiedenmann et al. 2011). Krill also plays a key role in biogeochemical cycles, including carbon export and iron cycling. Meanwhile, krill resources, which underpin major Southern Ocean fisheries (Kawaguchi and Nicol, 2007; Nicol and Kawaguchi, 2012) and constitute 95% of the total catch (Nicol & Foster, 2003; Cavanagh et al., 2021), hold significant economic value and are of high concern to many fishing nations.

Although krill are distributed throughout the Southern Ocean, krill fisheries are concentrated in the southwest Atlantic sector of the Southern Ocean (CCAMLR Area 48), which contains a significant amount of krill biomass (Krafft et al., 2021). The southwest Atlantic is not only the area where the krill fishery is concentrated but also the key ecological area of the krill population, especially in the northern Antarctic Peninsula and Bransfield Strait, which is the main spawning area, breeding area and wintering area of krill (Spiridonov, 1995; Siegel et al., 2004, 2013; Piñones and Fedorov, 2016; Perry et al., 2019). Fishing effort has increased over time, particularly in Subarea

48.1, near the western Antarctic Peninsula. The allowable catch limit in this Subarea until 2024, has been reached in 10 of the last 13 years, and the time taken to reach this threshold has been steadily decreased (Meyer et al., 2025). Furthermore, following the loss of subarea catch limits in 2024, fishing effort is likely to become more concentrated in this ecologically sensitive area (Joshua, 2025) in the absence of spatial controls. In terms of ecological environment, this sea area has complex current systems, physical environment, and intricate coastline, this sea area is one of the most vulnerable to global climate change (Nicol, 2006). Climate change will exacerbate environmental shifts, such as melting of sea ice and rising ocean temperatures (Joshua, 2025), are expected to exacerbate these fluctuations, adding to the complexity of krill populations (Atkinson et al., 2019; Ichii et al., 2023; Sylvester and Brooks, 2020). Although this annual catch represents only about 1% of the estimated krill biomass in the region (Meyer et al., 2025), growing fishing efforts and rapid climate change have raised increasing concerns about the sustainability of krill resources.

The krill fishery in the Antarctic is under the purview of the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR). The long-term aim of CCAMLR has been the development of a feedback-based management (FBM) procedure for the krill fishery that includes adaptive management in which management measures are regularly adjusted based on ecosystem monitoring indices. (Nicol and de la Mare, 1993; Fabra and Gascón, 2008). The primary goal of this management strategy is to ensure sustainable krill fishing and protect the marine ecosystem. As its initial phase, the FBM is currently being implemented through the adoption of a catch quota system. Despite over 30 years of regional krill biomass surveys conducted by various CCAMLR Member States, the current catch limit in Area 48 is still based solely on historical catch levels and a single international CCAMLR krill biomass survey from 2000, a quarter of a century ago (Krafft et al., 2021; Hill et al., 2016). Although there have been improvements in recent years, there is still lack consideration of critical elements of krill stock dynamics (Krafft et al., 2021; Hill et al., 2016). The focus is still mainly on the sustainable use of krill resources, which has not been fully incorporated into the dynamic changes at the ecosystem level, and the key mechanism connections between krill and ecosystems have been ignored. Krill are ectotherms that are highly dependent on the environment for survival (Wiedenmann et al., 2008), and changes in the environment can have a major impact on krill resources. As early as 1990, Smetacek et al. (1990) noted that seasonal sea ice is critical for krill life history processes, and in

1995, Siegel et al. (1995) suggested that the recruitment of krill populations is correlated with sea ice. The lack and neglect of a comprehensive understanding of these mechanisms have impeded the advancement of krill management towards achieving its long-term objectives. Therefore, to realize genuinely ecosystem-based feedback management, it is imperative not only to refine assessment methodologies for krill resources but also to devise innovative approaches for delving deeper into the impacts of environmental changes on krill populations. This can enhance our comprehension of the intricate relationship between krill and environment change, thereby bolstering the refinement of management strategies and the attainment of long-term management objectives. Therefore, developing new method to better understand how environmental changes affect the krill population in this sea area is critically important, both for the sustainable use of krill resources and for ecological conservation.

There is a foundation of research work on the effects of environmental change on krill populations. The main points of the results show that the melting of sea ice affects the reproduction rate, survival rate, and replenishment groups of Antarctic krill populations (Kinzey et al., 2019; Shah, 2019; Mori et al., 2019); the increase in sea surface temperature affects the distribution and population structure of Antarctic krill (Kinzey et al., 2019; Seyboth et al., 2016; Melbourne et al., 2016; Flores et al., 2012; Forcada et al., 2012); and the occurrence of ENSO can lead to changes in Southern Ocean air temperature, sea surface temperature, and sea ice cover, which can lead to changes in Southern Ocean productivity that affect krill feeding and consequently krill stocks (Flores et al., 2012; Trivelpiece et al., 2011; Cresswell et al., 2008). These studies have undoubtedly laid a good foundation for the study of the correlation between environment change and krill populations. However, three specific limitations remain relevant. First, many analyses evaluate one environmental driver or one demographic response at a time, even though recruitment and growth are linked through successive life-history stages. Second, linear or contemporaneous relationships are often emphasized despite biologically plausible seasonal windows and delayed effects. Third, the analysis models are characterized by excessive complexity and stringent input data requirements.

Body length frequency data constitute one of the easiest types of marine biological data to collect and one of the most intuitive types of biological data. Length growth is an important and highly variable part of life history, and in marine ecosystems, food, temperature and other environmental factors can have profound effects on individual

organisms and their behaviors, thus promoting their growth; thus, length–frequency data are important in many marine biological research activities. Length-frequency data can be used to analyze the population structure, growth, reproduction and ecological habits of marine organisms and can also be used to assess biological resources. Like other crustaceans, krill have the habit of molting, and krill molt very frequently, so determining their specific age has been a difficult scientific problem. Given the lack of information on age structure, changes in population structure, stock assessment and other work have been hampered to some extent, and body length data have become the most readily available and intuitive basic biological data of krill. Kawaguchi et al. (2006) used krill length frequency and accumulated instantaneous growth rate (IGR) data to model the growth trend of krill in the southwestern Atlantic and Indian Oceans, analyzed the growth trend of krill in time, size and sex, and noted the need to clarify the issues before improving the krill management model, which provides support for krill resource management. Shelton et al. (2013) analyzed interannual variability in krill growth based on a body length frequency dataset, linking estimated growth to environmental variables for a comprehensive analysis. Body length frequency data are also important for krill stock assessment research. The difficulty in obtaining age-structured data for krill makes it difficult to apply traditional stock assessment models to the krill stock, so body length frequency data become the basic input to the model. Wang et al. (2021) made full use of krill body-length frequency data from commercial fishing vessels and scientific research vessels to assess Antarctic krill resources in Antarctic Peninsula waters via an integrated size model and analyzed the trends of krill recruitment and mature biomass. The existing research fully demonstrates the application potential and information richness of krill body length data. Further exploration and utilization of such data is of great significance for advancing research on krill. The growth rate and pattern of krill significantly influence the age and size structure of their population, which in turn affects population stability and adaptability. Krill recruitment also plays a crucial role in determining population size and demographic composition. Based on the availability of long-term body-length data, we derived two population indices representing relative recruitment and growth and used them to evaluate how environmental variability affects krill population structure.

In the past, the combination of Gradient Forest Model (GMF) and Generalized Additive Model (GAM) has been widely used in research on the impact of climate change on marine fishery resources and their distribution, as well as the distribution of

important fishery resource spawning grounds over a long time series (Wang et al., 2021; Wang et al., 2022; Wang et al., 2024; Liu et al., 2024). The GFM is built upon the foundation of Random Forest. It generally captures the complex relationships between potential correlated predictors and multiple response variables through Random Forest analysis of different response variables (Ellis et al., 2012). This model provides a measure of fit for each response variable and standardized importance for each predictor, making it well-suited for handling large datasets with advantages such as high predictive accuracy and strong robustness against interference. In contrast, the GAM is a flexible statistical model capable of handling complex nonlinear relationships among variables. In the present study, GFM and generalized additive models GAM have distinct roles. GFA is used to rank and assess the stability of effects within a biologically prespecified predictor set; it is not treated as an independent hypothesis-testing model. GAMs are then used to evaluate a restricted set of ecologically interpretable predictors and to estimate nonlinear responses. This segmented modeling strategy not only preserves the ability of GFM to handle correlated predictors but also avoids the unbounded exploration of all possible relationships.

In summary, this study constructed two population indices based on krill length frequency data and employed a segmented modeling strategy that integrates GFM and GAM to explore how climate change affects krill population ecology. During the analysis, the life history characteristics of krill and the time-lagged effects of environmental factors were fully considered. The research methodology overcomes the limitations of single-method analyses and, while avoiding overfitting, effectively captures the potential nonlinear effects of environmental factors on krill populations. The findings not only contribute to understanding the response of krill populations to environmental changes and the resilience of the Southern Ocean ecosystem but also provide a reference for the sustainable management of krill fisheries. Furthermore, they offer methodological insights for studying the mechanisms by which related species adapt to environmental changes.

2. Data and methods

2.1 Study area

The study area (Fig. 1) includes the western side of the South Shetland Islands, the Bransfield Strait, and the waters between Elephant Island and the Joinville Islands at the northern end of the peninsula. This area is the main spawning, nursery and overwintering area for Antarctic krill in the southwestern Atlantic and is also an

important fishing ground for Antarctic krill.

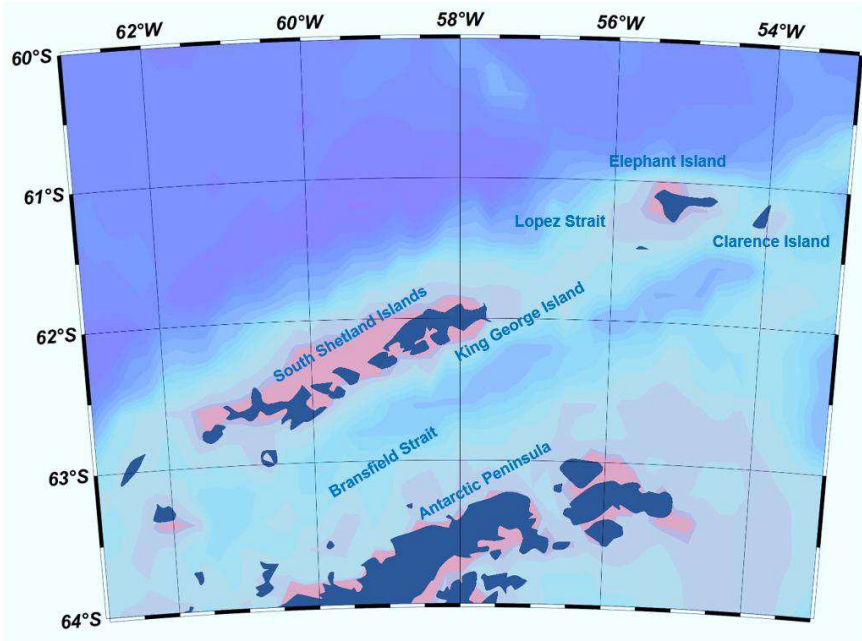


Fig.1 Research area

2.2 Data composition

2.2.1 Length data

Antarctic krill body-length frequency data were obtained from the KRILLBASE-length-frequency database, a multi-national, circumpolar compilation of scientific net-sampling records spanning 1926–2016 (Atkinson et al., 2020). In this study, we extracted only the U.S. AMLR scientific-net records collected within the northern Antarctic Peninsula study area (53°–63°W and 60°–63°S) during the austral summer seasons of 1992–2011 (Table 1). The U.S. AMLR survey sampled four fixed strata: West Area, Elephant Island, South Area/Bransfield Strait and Joinville Island, but sampling was not equal across this region. Between 1992 and 2011, sampling surveys were conducted in both January and February in 1992, 1994–1996, 1998–1999, 2001–2005, 2008, and 2011. In 2000, sampling was conducted only in February, while in the remaining years, sampling was conducted only in January. All sampling depths were within 170 meters.

2.2.2 Environmental data

The environmental data used for the study include SST\ SSS\ SSH, sea ice data (ice_extent\ ice_area) and climate index (SAM\ SOI\ Nino 3.4). The time range, of each data point and the specific sources are detailed in Table 1.

Table 1 Data source and explanation

Data	Explanation of data	Time length	Data source links	Additional explanation of data
Length Data	Krill length data	1992-2011	https://www.bas.ac.uk/project/krillbase/ (last accessed on 15/8/2025)	60549 samples, the krill body length frequency data obtained from scientific krill surveys conducted by AMLR in the waters off the Antarctic Peninsula.
SST	Sea surface temperature.	1988-2011	http://apdrc.soest.hawaii.edu/las_ofes/v6/constrain?var=80 (last accessed on 15/8/2025)	The monthly SST, SSS and SSH data of the South Atlantic (60-64°S, 53-63°W) from 1988 to 2011 with a spatial resolution of 0.5 degree are obtained from the Asia-Pacific Data-Research Center (APDRC).
SSH	Sea surface high.	1988-2011	http://apdrc.soest.hawaii.edu/las_ofes/v6/constrain?var=80 (last accessed on 15/8/2025)	
SSS	Sea surface salinity.	1988-2011	http://apdrc.soest.hawaii.edu/las_ofes/v6/constrain?var=80 (last accessed on 15/8/2025)	
ice_extent	Sea ice extent, the total area of sea ice concentration exceeding the threshold (usually 15%). Commonly referred to as “how much area is covered by sea ice”.	1988-2011	https://nsidc.org/data/explore-data (last accessed on 15/8/2025)	The monthly ice_extent and ice_area data from 1988 to 2011 are obtained from National Snow and Ice Data Center (NSIDC). The dataset is “S_Sea_Ice_Index_Regional_Monthly_Data_G02135_v4.0.xlsx” (Meier et al., 2007).
ice_area	Sea ice area, the actual total coverage area of sea ice. Commonly referred to as	1988-2011	https://nsidc.org/data/explore-data (last accessed on 15/8/2025)	

“what is the actual area occupied by sea ice”.

SAM	Southern Hemisphere Annular Mode Index.	1988-2011	http://www.nerc-bas.ac.uk/icd/gjma/sam.html (last accessed on 15/8/2025)	Monthly SAM data in Southern Hemisphere, 40-65°S (Marshall, 2003).
Niño 3.4	The primary indicators for monitoring, defining, and determining El Niño and La Niña events (collectively referred to as ENSO), 5°North-5°South, 170-120°West.	1988-2011	https://www.cpc.ncep.noaa.gov/data/indices/ (last accessed on 15/8/2025)	The monthly SOI and Niño 3.4 data from 1988 to 2011 are obtained from NOAA/ National Weather Service/ Climate Prediction Center. SOI: monthly data. Niño 3.4: monthly ERSSTv5 (centered base periods) data, 5°N-5°S, 170-120°W, has the strongest correlation with the research area.
SOI	Southern Oscillation Index.	1988-2011	https://www.cpc.ncep.noaa.gov/data/indices/ (last accessed on 15/8/2025)	

2.3 Analysis methods

2.3.1 Population indices (dependent variables)

In population structure analysis, age structure analysis is very important for understanding population trends. However, age structure data for krill are difficult to obtain, so in this study we used krill body length frequency data to calculate two indices that can reflect changes in krill populations. One is the percentage of krill individuals with recruited body lengths in the krill sample per year (representing the recruitment), and the other is the average body length of krill in each year (representing growth).

$$length_R_t = \frac{N_{recruit,t}}{N_{total,t}}$$

Where $N_{recruit,t}$ is the number of krill recruitment (body lengths between 19 and 35 mm (Ross et al. 2014) in t year, and $N_{total,t}$ is the total krill samples collected in t year.

$$mean_length_t = \frac{\sum_{i=1}^{n_t} l_{i,t}}{n_t}$$

Where n_t is the total krill samples collected in t year.

In addition, to avoid potential biases in the recruitment index caused by uneven sampling, we conducted a correlation analysis between our calculated recruitment index and abundance data. The results showed that the recruitment index calculated in this study was not significantly correlated with abundance data, indicating that the recruitment index exists independently and is not influenced by absolute population size.

2.3.2 Environmental variables (independent variables)

In this study, seven environmental variables were selected, including marine environmental data (SST\ SSS\ SSH), sea ice data (ice_extent\ ice_area) and climate indexes (SAM\ SOI\ Niño 3.4). In addition, the seven environmental variables were further processed in this study on the basis of the life history process of krill (as shown in Fig. 2) and the possible delayed effects of environmental changes on the krill population structure:

1) to apply 1- and 2-year lags to the seven environmental factors;

2) to calculate the mean values of the seven environmental factors for June–August (the Antarctic winter season, when krill larvae need sea ice protection to complete overwintering); and September–November (the Antarctic spring season, when sea ice melts and plankton outbreaks occur) prior to krill sampling and to apply 1- and 2-year

lags to these values, respectively.

The total number of environmental variables included in the gradient forest model was 72. The explanation of each variable is shown in Table 2.

Table 2 independent variables explanation

Environmental Variable	Variables explanation
variable_1	1- year lags.
variable_2	2- year lags.
variable_spring	variables in the Antarctic Spring season, September–November.
variable_spring_1	1- year lags for variables in the Antarctic Spring season, September–November.
variable_spring_2	2- year lags for variables in the Antarctic Spring season, September–November.
variable_winter	variables in the Antarctic Winter season, June–August.
variable_winter_1	1- year lags for variables in the Antarctic Winter season, June–August.
variable_winter_2	2- year lags for variables in the Antarctic Winter season, June–August.

Note: variable is SST\ SSS\ SSH\ ice_ extent\ ice_ area\ SAM\ SOI\ Niño 3.4.

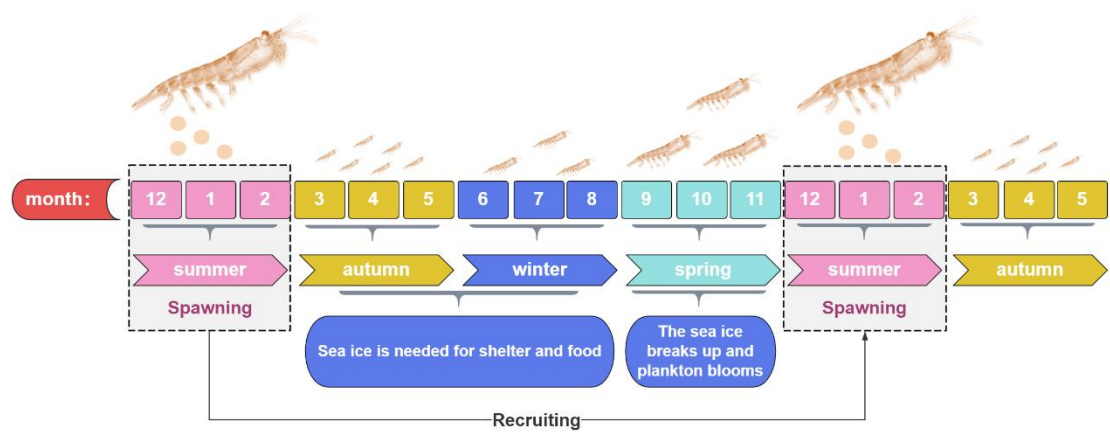


Fig. 2 Schematic representation of the main life history processes of Antarctic krill

2.3.3 Data analysis

In this study, we adopted a piecewise modeling approach, integrating GFM and GAM to analyze the response of environmental variables to krill population indices. GFM is used for preliminary screening of environmental variables (independent variables) applied in the GAM because it can simultaneously analyze the importance of many independent variables. GFM is a machine learning approach to quantify the relationships between environmental variables and krill population indices. Built upon random forests, GFM is used to capture complex relationships between potentially correlated predictors and multiple response variables by integrating individual random forest analyses over the various response variables (Ellis et al., 2012; Liu et al.,2022).

GFM provides the goodness-of-fit (R_f^2) value for each response variable f and the accuracy importance (I_{fp}) of the predictor p . The importance of a split value along a predictor gradient reflects the relative change in the response variable. In this study, environmental variables were used as predictors, and krill population indices was used as the response variable. We ran the model 1000 times to obtain the mean and standard deviation (sd) of R_f^2 . The run having the highest overall performance (R^2) was then used to derive I_{fp} and other statistics. The GFM was completed using the gradient forest package in R (version 3.6.1; R Core Team, 2017). The GAM (Hastie and Tibshirani, 1986) was used to fit the nonlinear responses of environmental variables to krill population indices. The environmental variables selected by the GFM were used as independent variables of the GAM. Correlation testing (Pearson's correlation analysis) was used to ensure that there was no significance between the independent variables of the GAM model. To avoid excessive fitting of the model, the maximum degree of freedom was set to 5. Stepwise regression was carried out to select the optimal model by considering the Akaike information criterion (AIC) value and the number of model parameters. The GAM was completed using the MGCV package in R (version 3.6.1; R Core Team, 2017). In the GAM and GFM, log10 transformation for krill population indices were carried out to make it conform to a normal distribution.

3. Main results

3.1 GFM

After entering all dependent variables and 72 environmental variables into the gradient model 1000 times, the results show that the environmental independent variables have a certain degree of explanation for the dependent variables “length_R” and “mean_length”. The level of explanation for “mean_length” is greater than that for “length_R” (as shown in Fig. 3).

“length_R” and “mean_length” are put into the model as the only dependent variables 1000 times, and the results show that the environmental variables with the strongest effect on “length_R” is “SST_2”, and the environmental variables with the strongest effect on “mean_length” is “SST_winter_2” (as shown in Fig. 4). The importance rankings of the remaining top 12 environmental variables are shown in Table 3. The threshold response range of each environmental variables is shown in Fig. 5 and Fig. 6, and within the threshold response range, each environmental variables has a stronger influence on the dependent variables.

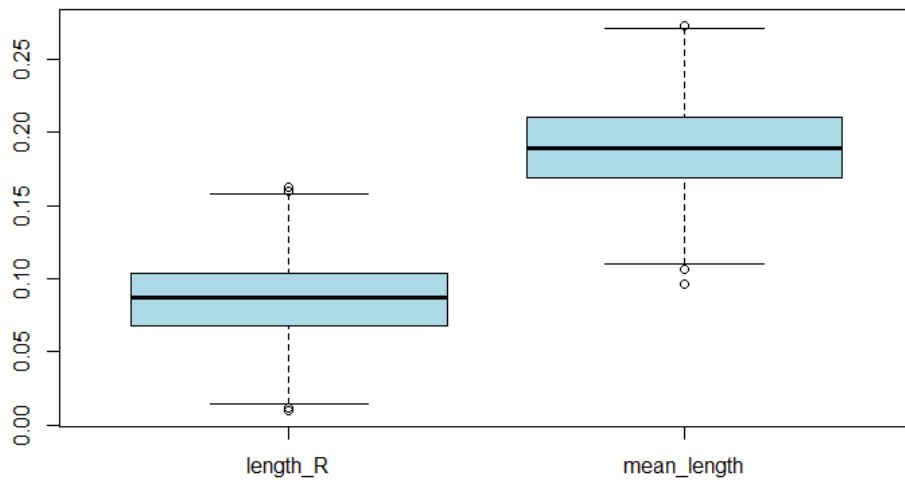


Fig. 3 Results of 1000 gradient forest model runs for “length_R” and “mean_length” fit

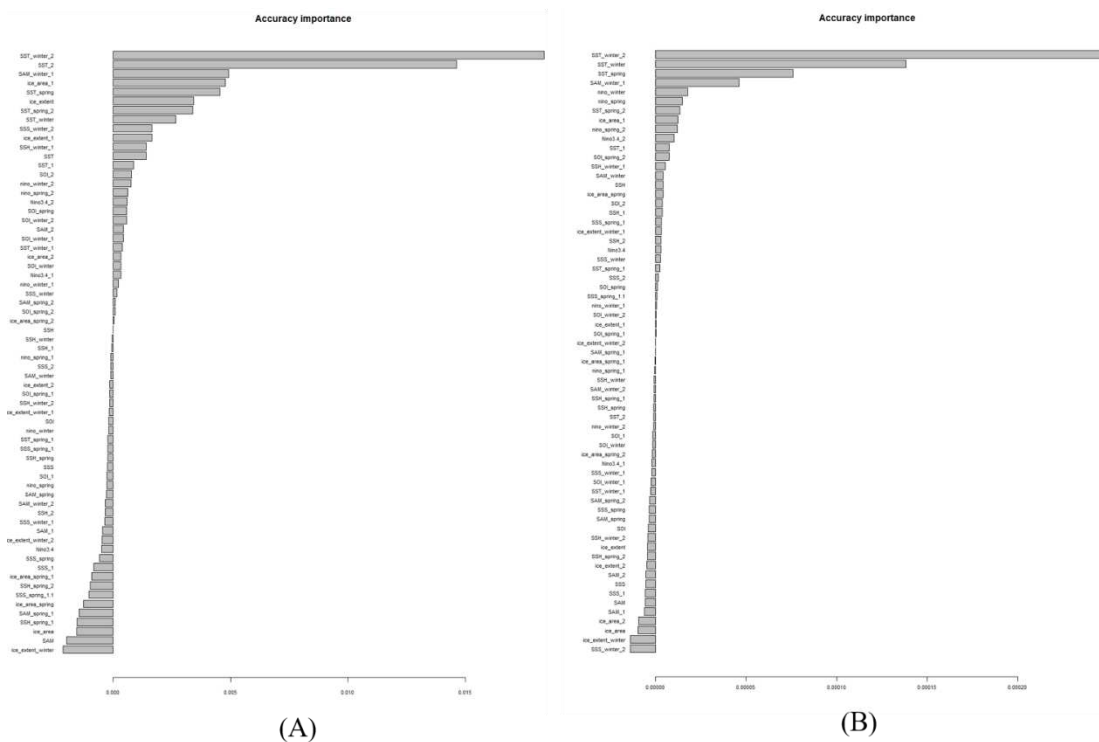


Fig. 4 Importance of each environmental variables in explaining “length_R” (A) and “mean_length” (B) changes

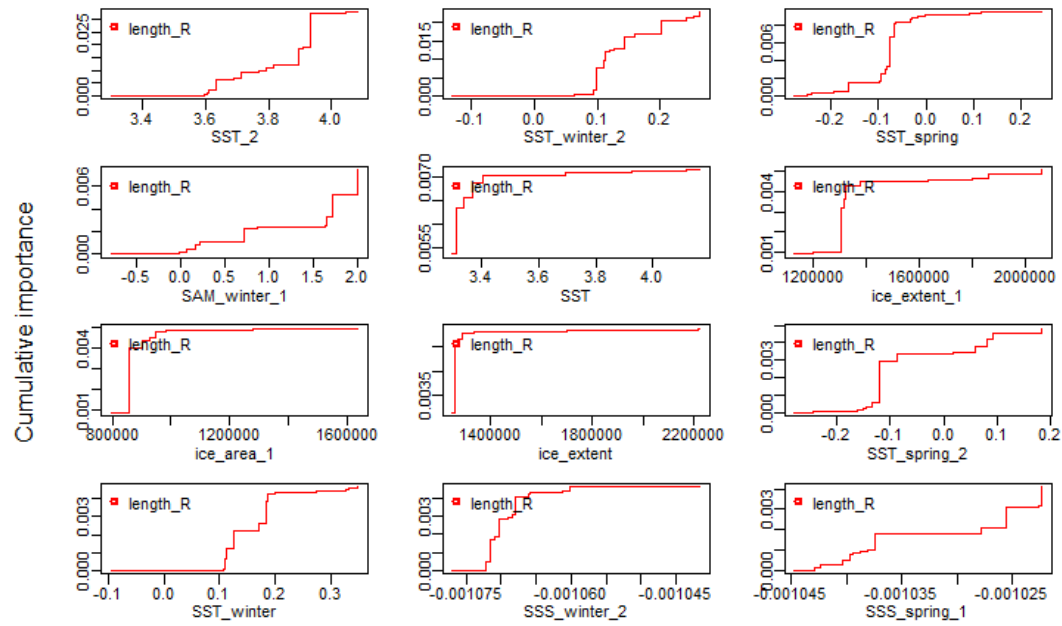


Fig. 5 Cumulative importance of the top 12 dependent variables in the optimal model
(for “length_R”)

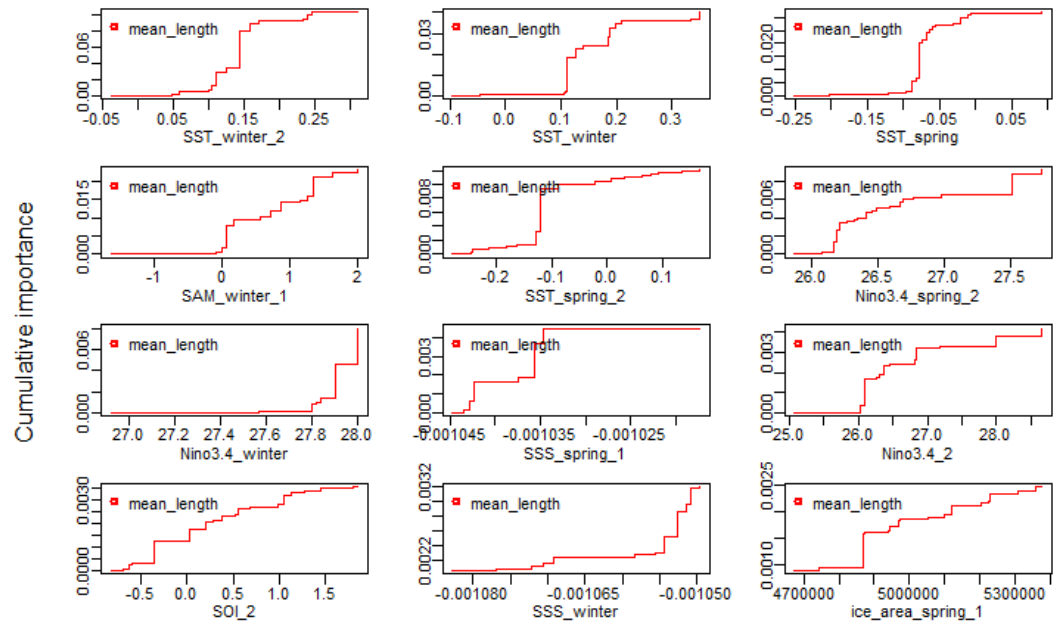


Fig. 6 Cumulative importance of the top 12 dependent variables in the optimal model
(for “mean_length”)

Table 3 Environmental variables in the top 12 in terms of importance

Ranking of Factors	“length_R”	“mean_length”
1	*SST_2	*SST_winter_2
2	*SST_winter_2	*SST_winter

3	*SST_spring	*SST_spring
4	*SAM_winter_1	*SAM_spring_2
5	SST	SST_spring_2
6	*ice_extent_1	*Nino3.4_spring_2
7	*ice_area_1	*Nino3.4_winter
8	ice_extent	*SSS_spring_1
9	SST_spring_2	*Nino3.4_2
10	SST_winter	*SOI_2
11	*SSS_winter_2	SSS_winter
12	*SSS_spring_1	*ice_area_spring_1

Note: The environmental variables marked with “*” are those input in the GAM.

3.2 GAM

Based on the calculation results of the gradient forest model, the environmental variables with the highest rankings among environmental variables of the same type were further selected as independent variables in the GAM (the environmental factors marked with '*' in Table 3).

The results of the GAM from univariate to overlapping variables are presented in Table 4 and Table 5. In the univariate model, “ice_area_1” is the strongest environmental variables influencing “length_R”, with an AIC of 18, a degree of explanation of 58.80%, an R^2 of 0.51 and a correlation value, as shown in Fig. 7; “SST_winter_2” is the strongest environmental variables influencing “mean_length”, with an AIC of -85.67, an explanatory power of 56.60%, an R^2 of 0.49 and a correlation value, as shown in Fig. 8.

In the multivariate model, the joint effect of “ice_area_1+SAM_winter_1+SSS_winter_2” had the strongest effect on “length_R”, with an AIC of -11.65, an explanatory degree of 94.20% and an R^2 of 0.9, and the correlation is shown in Fig. 9. The combined effect of “SST_winter_2+SOI_2+Nino3.4_winter” had the strongest effect on “mean_length”, with an AIC of -106.43, an explanatory power of 90.50% and an R^2 of 0.84, and the correlation value is shown in Fig. 10. It should be noted here that, based on the principle of model parsimony, when the inclusion of a new factor results in a decrease in the AIC value of less than 3, the factor is considered unnecessary to include in the model (Liu et al., 2024).

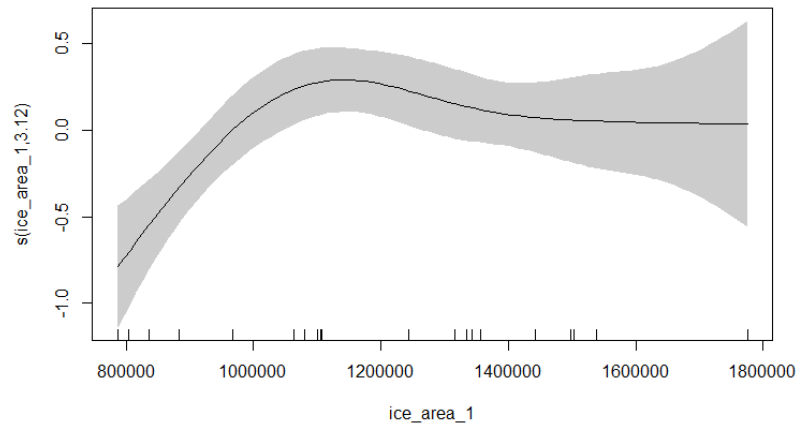


Fig. 7 Non-linear fitting curve between “ice_area_1” in GAM model (univariate analysis) with “length_R” (Gray area represents 95% confidence interval).

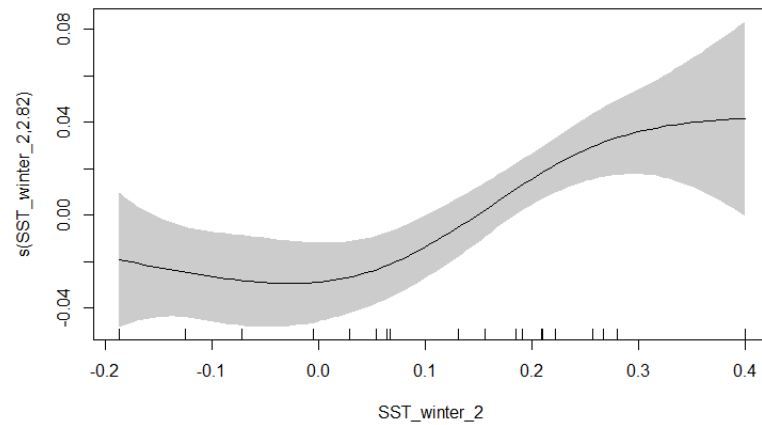


Fig. 8 Non-linear fitting curve between “SST_winter_2” in GAM model (univariate analysis) with “mean_length” (Gray area represents 95% confidence interval).

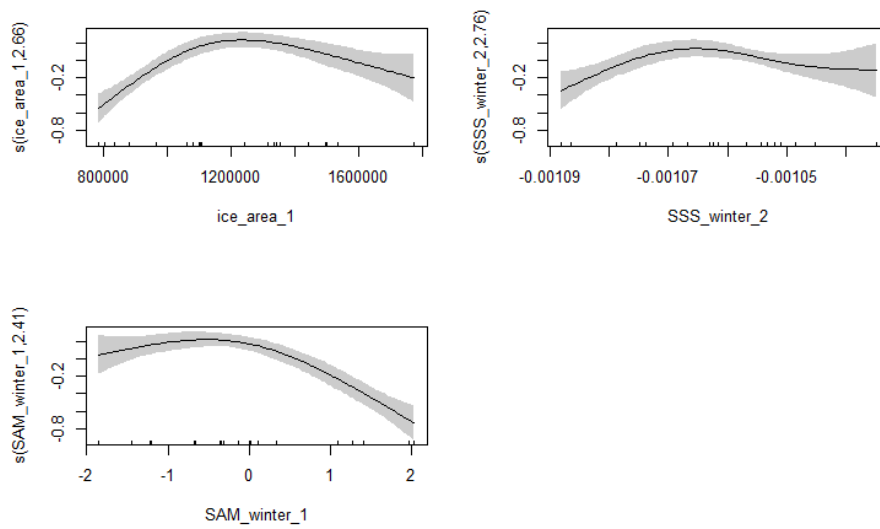


Fig. 9 Non-linear fitting curve between “ice_area_1+SAM_winter_1+SSS_winter_2” in GAM model (multivariate analysis) with “length_R” (Gray area represents 95% confidence interval).

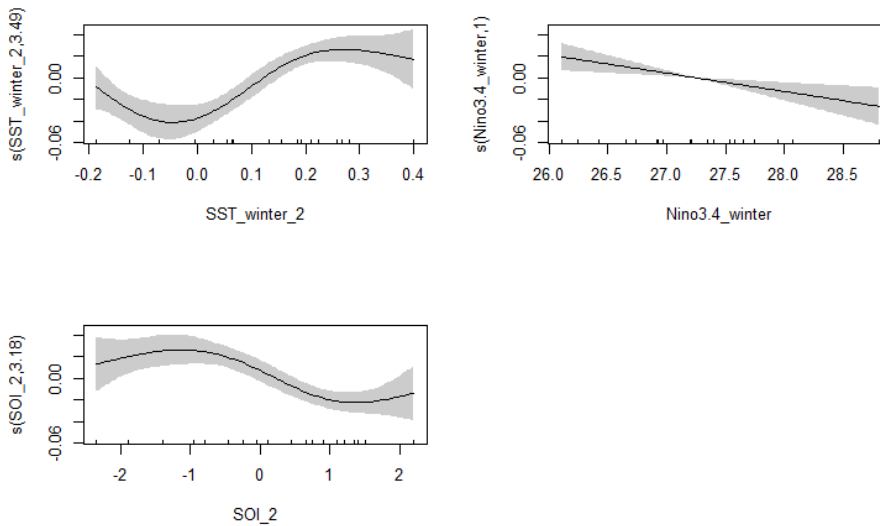


Fig. 10 Non-linear fitting curve between “SST_winter_2+SOI_2+Nino3.4_winter” in GAM model (multivariate analysis) with “mean_length” (Gray area represents 95% confidence interval).

Table 4 Statistical parameter table of GAM optimal model screening process (for “length_R”)

Model	Covariates	Deviance explanation	AIC	R ²
1	SST_winter_2	48.10%	21.74	0.40
2	SST_2	57.50%	19.03	0.49
3	SAM_winter_1	52.90%	18.48	0.47
4	*ice_area_1	58.80%	18.00	0.51
5	SST_spring	17.90%	27.55	0.13

6	ice_extent_1	55.10%	19.58	0.47
7	SSS_winter_2	4.11%	30.65	-0.01
8	SSS_spring_1	15.00%	28.23	0.10
9	ice_area_1+SST_2	78.10%	11.78	0.67
10	ice_area_1+SST_spring	59%	19.60	0.48
11	ice_area_1+SST_winter_2	70.40%	14.25	0.61
12	ice_area_1+SAM_winter_1	88.50%	-3.14	0.84
13	ice_area_1+SSS_winter_2	61.90%	18.33	0.52
14	ice_area_1+SAM_winter_1+SST_2	88.60%	-1.52	0.83
15	ice_area_1+SAM_winter_1+SST_spring	89.70%	-3.44	0.85
16	*ice_area_1+SAM_winter_1+SSS_winter_2	94.20%	-11.65	0.90
17	ice_area_1+SAM_winter_1+SSS_winter_2+SST_2	94.30%	-10.03	0.89

133

134 Table 5 Statistical parameter table of GAM optimal model screening process (for “mean_length”)

Model	Covariates	Deviance explanation	AIC	R ²
1	ice_area_spring_1	35.50%	-77.81	0.25
2	Nino3.4_2	26.10%	-78.24	0.21
3	Nino3.4_spring_2	23.90%	-78.05	0.20
4	Nino3.4_winter	20.90%	-77.29	0.17
5	SAM_spring_2	6.59%	-73.96	0.01
6	SOI_2	19.90%	-77.05	0.16
7	SSS_spring_1	18.70%	-76.73	0.14
8	SST_spring	57.70%	-85.53	0.49
9	*SST_winter_2	56.60%	-85.67	0.49
10	SSS_winter	34.20%	-78.26	0.25
11	SST_winter_2+Nino3.4_2	67.40%	-89.35	0.59
12	SST_winter_2+SOI_2	75.20%	-94.29	0.68
13	SST_winter_2+ice_area_spring_1	57.00%	-83.99	0.46
14	SST_winter_2+Nino3.4_spring_2	68.90%	-89.96	0.61
15	SST_winter_2+Nino3.4_winter	62.50%	-87.22	0.54
16	SST_winter_2+SST_spring	77.50%	-92.18	0.67
17	SST_winter_2+SSS_winter	55.30%	-85.73	0.49
18	SST_winter_2+SOI_2+ice_area_spring_1	75.20%	-92.48	0.66
19	*SST_winter_2+SOI_2+Nino3.4_winter	90.50%	-106.43	0.84
20	SST_winter_2+SOI_2+SAM_spring_2	79.90%	-93.67	0.69
21	SST_winter_2+SOI_2+SSS_spring_1	79.00%	-94.40	0.70
22	SST_winter_2+SOI_2+SSS_winter	85.50%	-98.41	0.76
23	SST_winter_2+SOI_2+Nino3.4_winter+ice_area_spring_1	91.10%	-105.59	0.84

24	SST_winter_2+SOI_2+Nino3.4_winter+SAM_spring_2	90.40%	-104.44	0.83
25	SST_winter_2+SOI_2+Nino3.4_winter+SSS_spring_1	90.70%	-104.87	0.83
26	SST_winter_2+SOI_2+Nino3.4_winter+SSS_winter	91.20%	-105.45	0.84
27	SST_winter_2+SOI_2+Nino3.4_winter+ice_area_spring_1+SAM_spring_2	90.10%	-103.38	0.82
28	SST_winter_2+SOI_2+Nino3.4_winter+ice_area_spring_1+SSS_spring_1	91.50%	-105.34	0.83

135

136 **3 Discussion**

137 **3.1 Mechanisms underlying the effects of environmental change on Antarctic krill** 138 **population ecology**

139 In contrast to previous research paradigms relying on single models or single-
140 factor analyses, this study employs two more flexible statistical approaches, the GFM
141 and the GAM, for piecewise modeling, thereby providing an analysis of the
142 mechanisms through which environmental change affects krill population ecology. The
143 analytical framework explicitly accounts for the time-lag effects of environmental
144 drivers and the cumulative effects of multiple interacting factors, rendering it more
145 consistent with the actual life-history processes of krill.

146 In the first stage, the GFM incorporated 72 environmental predictors and was run
147 for 1,000 iterations. The results showed that environmental factors provided significant
148 explanatory power for both population indices, although the explanatory power for
149 “mean_length” was higher than that for “length_R”. This result does not imply a weaker
150 environmental dependence of “length_R”. It reflects differences in the mechanisms by
151 which environmental factors influence krill growth and recruitment. As an ectothermic
152 species, krill exhibits metabolic and growth rates that are highly sensitive to
153 temperature variation; within a certain threshold, rising temperatures accelerate krill
154 growth (Wiedenmann et al. 2008), thereby directly changing the mean body length of
155 the population. By contrast, the formation of “length_R” encompasses a series of
156 complex processes, including successful reproduction of the spawning stock, larval
157 overwintering, and juvenile survival during the spring phytoplankton bloom, through
158 which the detectability of environmental signals is progressively filtered or transformed,
159 resulting in relatively lower direct explanatory power of any single environmental factor.
160 Building on the outputs of the GFM, the GAM in the second stage further provided a
161 more detailed account of how changes in environmental factors effect on krill
162 population growth and recruitment. For krill population recruitment, the single-factor
163 GAM analysis indicated that sea ice area with a one-year lag (ice_area_1) had the

highest explanatory power for “length_R” (58.80%), and its effect exhibited pronounced nonlinear threshold characteristics. Specifically, within a certain threshold, “length_R” increased with increasing “ice_area_1”; however, when “ice_area_1” exceeded this threshold, “length_R” began to decline (Fig. 7). As early as 1990, Smetacek et al. (1990) proposed that seasonal sea ice is critical to the life history of krill, and subsequent work by Siegel and Loeb (1995) likewise demonstrated an association between krill recruitment and sea ice. From an ecological perspective, a suitable extent of sea ice provides krill larvae with essential shelter and food resources: ice algae attached to the underside of the ice serve as an important food source during early larval development, while spring ice melt triggers phytoplankton blooms that furnish abundant food for juveniles that have successfully overwintered, thereby substantially enhancing their survival (Wiedenmann et al. 2009). However, the present study reveals a more nuanced regulatory pattern: the observed “initial increase followed by a decline” arises because years of high recruitment require the concurrent presence of favorable sea ice conditions and high chlorophyll concentrations (Steinke et al. 2021). Excessive sea ice may fail to melt in time during spring, depriving larvae of the nutrient enrichment associated with ice melt while exposing them to elevated mortality due to intensified water-column stratification and deteriorated transport conditions, ultimately resulting in recruitment failure (Lee et al. 2010). Conversely, if sea ice melts too early in the season, the peak of primary production becomes decoupled from the krill spawning period, likewise giving rise to poor recruitment years (Quetin and Ross 2001). This threshold effect indicates that successful krill recruitment depends not on sea ice per se, but rather on a precise match between sea ice dynamics and the seasonal rhythm of productivity. Although Siegel (1995), Quetin (2003), Ross (2014), and other researchers had identified a strong correlation between successful krill recruitment and favorable ice conditions, the underlying mechanisms behind “favorable ice conditions” and the climatic conditions capable of producing such years remained poorly understood. The multi-factor additive regression analysis in this study provides further insight into this question: the combined effects of “ice_area_1 + SAM_winter_1 + SSS_winter_2” increased the explanatory power for “length_R” to 94.20%, indicating that recruitment success is not under the absolute control of any single sea ice factor, but rather is the outcome of synergistic forcing by a coupled sea ice-atmosphere-ocean system. Within this multi-factor system, “length_R” increased with rising values of all three factors but declined once their respective thresholds were exceeded. Among them,

198 “SAM_winter_1” exhibited a particularly critical threshold, “length_R” showed an
199 increasing trend when SAM was in its negative phase, whereas it declined rapidly once
200 SAM turned positive. The SAM index reflects the intensity of the polar westerlies and
201 represents a large-scale climate mode that governs sea ice dynamics (Marshall 2003,
202 2004; Atkinson et al. 2019; Saba et al. 2014). This result is largely consistent with that
203 of Saba et al. (2014) in the western Antarctic Peninsula, where, during negative winter
204 SAM phases, cold southerly winds enhance the extent and duration of winter sea ice,
205 thereby creating favorable conditions for krill recruitment; while an increasing
206 frequency of positive SAM events may have catastrophic consequences for krill
207 populations (Saba et al. 2014). Kohlbach et al. (2017) further noted that SAM driven
208 sea ice characteristics constitute an important indicator of krill habitat quality, and that
209 recruitment measured in summer is associated with sea ice conditions of the preceding
210 winter, which is broadly consistent with the temporal scale of the lagged environmental
211 effects identified in this study. By quantifying the coupled effects of multiple factors,
212 this study not only elucidates the formation mechanism of “favorable ice years” -the
213 synergistic co-occurrence of suitable sea ice extent, a negative SAM phase, and specific
214 salinity conditions, but also provides a mechanistic explanation for the composite
215 drivers underlying the “sea ice-recruitment relationship” proposed by Siegel and Loeb
216 (1995), thereby offering an operational indicator framework for predicting interannual
217 variability in krill recruitment. But it should be noted that although our results reveal
218 the absolute influence of sea ice on “length_R”, the relationship between krill
219 recruitment and sea ice is still nuanced, and many unknown relationships exist (Murphy
220 et al., 2018; Quetin et al., 2007). The lack of quantification of how changes in sea ice
221 quality affect recruitment is a major barrier to assessing and modeling krill population
222 dynamics (Meiners et al., 2017); for example, there is no sea ice in South Georgia, but
223 krill are still highly abundant (Nicol, 2006).

224 With respect to krill growth, the single-factor GAM regression analysis showed
225 that winter sea surface temperature with a two-year lag (SST_winter_2) had relatively
226 high explanatory power for “mean_length” (56.6%). As shown in Fig. 8, “mean_length”
227 increased with rising “SST_winter_2”, indicating that elevated temperatures accelerate
228 krill growth, leading to an increase in the mean body length of the population. Meyer
229 et al. (2020) observed an increase in the mean body length of krill in waters adjacent to
230 the Antarctic Peninsula under a warming climate and speculated that this may be linked
231 to changes in population age structure resulting from reduced recruitment. Trathan et

al. (2003, 2006) found a negative correlation between krill abundance and SST, but noted that the underlying mechanisms remained unclear, speculating that SST may act through indirect pathways such as food availability or sea ice extent. By integrating temperature effects with krill life-history processes, this study proposes a more integrative explanatory framework: rising temperatures can indeed accelerate krill growth and may even induce earlier attainment of sexual maturity and spawning; however, SST-driven premature sea ice melt simultaneously disrupts the shelter, foraging, and transport conditions essential to the larval stage, leading to recruitment failure and, consequently, a decline in population biomass. This implies that the net effect of temperature on krill populations is not a simple “growth promotion”, but rather a complex cascade of effects propagated through the “growth–reproduction–recruitment” continuum. The multi-factor additive analysis further revealed the deeper driving mechanisms underlying the effect of water temperature on “mean_length”, with the combined influence of “SST_winter_2 + SOI_2 + Nino3.4_winter” exerting the strongest effect on mean body length. The SOI and Niño 3.4 indices measure the large-scale atmospheric and oceanic oscillations associated with El Niño and La Niña events (Carleton 2003), whose variability influences krill growth by altering the thermal conditions of Antarctic waters. Steinke et al. noted that the mechanisms by which climate indices affect krill depend on the specific life stage during ontogeny, and that seasonal SOI fluctuations can influence the physiological condition of krill (Steinke et al. 2021). This study extends that perspective from the physiological level to the population level, demonstrating that the ENSO system exerts a significant lagged regulatory effect on krill population growth mediated through water temperature. This influence complements the regulation of recruitment by the SAM system, together forming an interconnected network through which large-scale climate modes affect krill populations.

Taken together, these results demonstrate that different environmental factors act upon distinct life stages of krill populations through varying threshold ranges and temporal effects, forming a complex and finely tuned regulatory network. Maintaining the health and stability of krill population ecology requires that no component of this intricate network undergoes excessively rapid change or disruption. Furthermore, this study identified three important characteristics governing krill population ecology. First, temporal lag effects: current population status is strongly influenced by historical environmental conditions. Second, seasonality: environmental factors from the

preceding year play a critical role in shaping krill population dynamics. Third, the synergistic effects of multiple factors substantially outweigh the independent effects of any single factor, and the coupled interactions among environmental drivers constitute the primary driving force of krill population dynamics. These findings substantially advance our understanding of the complex relationships between krill populations and environment, as well as the ecological resilience of Southern Ocean.

From the perspective of ecological resilience, the multi-factor synergistic driving mechanism revealed in this study may exert a certain buffering effect in the short term: when one environmental factor deviates from its optimal range, compensatory effects from other factors can, to some extent, sustain relative population stability. For example, if sea ice extent falls slightly below its optimal threshold, recruitment may nonetheless remain at a relatively high level if SAM is in a strongly negative phase and salinity conditions are favorable.

However, this buffering effect has clearly defined limits. Once multiple key factors simultaneously breach their thresholds or deviate from their optimal ranges in the same direction (a sharp reduction in winter sea ice coinciding with a positive SAM phase and a strong El Niño event), multi-factor synergies shift from “buffering” to “amplification”, and the risk of population collapse escalates sharply. The beneficial effects of multi-factor synergy are subject to an upper limit, whereas adverse effects can accumulate without bound which constitutes the core risk characteristic of krill populations under climate change. Under continued global warming, declining winter sea ice and rising SST around the Antarctic Peninsula may render the responses of “length_R” and “mean_length” to environmental change asymmetric: growth may benefit from warming in the short term, manifesting as an increase in “mean_length”, whereas the recruitment process will remain under sustained pressure, reflected in a decline of “length_R”, giving rise to a dynamic pattern in which the two parameters shift in opposite directions. This shift in population structure toward “larger individuals with lower recruitment” implies an aging age structure, declining reproductive potential, and weakened capacity to recover from extreme environmental events. Such structural changes will have cascading effects on the food quality and availability experienced by higher predators that feed on krill, including whales, seals, and penguins. Although larger krill have higher energy density, declining population abundance and insufficient recruitment will leave predators facing an overall food shortage, potentially altering energy transfer efficiency and community structure within the Antarctic food web

(Trivelpiece et al., 2011). Therefore, the multi-factor synergistic mechanism revealed in this study not only deepens our understanding of krill population ecology but also provides a scientific basis for assessing the vulnerability of Antarctic ecosystems under climate change and for developing adaptive management strategies.

Previous studies have emphasized that understanding krill recruitment is a critical issue and an urgent research priority, one that can improve our comprehension of trends in krill population dynamics (Flores et al., 2012; Meyer et al., 2020). The driving mechanisms through which environmental change affects krill population ecology, as explored in this study, can likewise provide an important reference for understanding krill recruitment processes and their underlying mechanisms. Integrating the responses of both population indices to environmental change, it can be inferred that maintaining a high level of krill recruitment requires favorable environmental conditions for at least three consecutive years: the environmental state in the first year influences adult growth and reproduction; winter sea ice conditions in the second year determine larval overwintering survival; and the marine environment in the spring of the third year regulates food availability for post-larval juveniles. This temporal sequence is broadly consistent with the 2-3 years life-history cycle of krill and is also largely in agreement with the 3-4 years recruitment cycle identified in previous studies (Wang et al., 2021). In addition to environmental conditions, the intrinsic self-regulation of krill during the recruitment process cannot be overlooked. Krill possesses a life cycle that is closely coordinated with and adapted to changes in the physical environment, studies have indicated that krill have evolved to a degree that allows them to highly exploit seasonal environmental conditions to sustain population survival (Nicol et al., 2006). This intrinsic physiological regulatory capacity, together with environmental forcing, jointly shapes the dynamics of krill populations. Future research should further investigate the interactive mechanisms between environmental change and the self-regulatory processes of krill.

3.2 Analysis of the piecewise modeling strategy and the applicability of krill population indices

The piecewise modeling strategy adopted in this study, combining the GFM and the GAM, demonstrated significant advantages in screening many environmental variables and fitting nonlinear relationships.

In the first stage, the GFM effectively identified key environmental drivers with significant explanatory power for krill populations from among 72 environmental

variables, overcoming the limitations of conventional stepwise regression or correlation analyses, which tend to overlook interactions among factors and struggle to handle high-dimensional data during variable screening; In the second stage, the GAM further quantified the threshold response characteristics and nonlinear effects of these key factors, compensating for the limitations of GFM in characterizing response curves. The two approaches form a progressive “screening–quantification” analytical framework, which enhanced the ecological interpretability of the model compared with any single method. For “length_R”, the synergistic explanatory power of “ice_area_1 + SAM_winter_1 + SSS_winter_2” reached 94.20%; for “mean_length”, the synergistic explanatory power of “SST_winter_2 + SOI_2 + Nino3.4_winter” reached 90.50%. This result profoundly reveals that the state of krill populations is fundamentally governed by the coupling of environmental processes across multiple spheres: atmospheric circulation (SAM, ENSO), sea ice dynamics, and ocean conditions (temperature, salinity) do not act on krill in isolation but jointly determine population dynamics through complex cascading effects and synergistic amplification mechanisms. Consequently, single environmental indicators or single-factor models are inadequate for accurately characterizing the true state of krill population. The two population indices constructed from length-frequency data, “length_R” and “mean_length”, provided a novel analytical perspective for this study and represent a methodological innovation. Given the difficulty of obtaining krill age-structure data, length-frequency data constitute the most readily collected and continuously accumulated biological baseline dataset; following standardization, such data can effectively reflect trends in population recruitment and growth (Kawaguchi et al., 2006; Shelton et al., 2013; Wang et al., 2021), a conclusion further corroborated by the results of this study. Furthermore, this study revealed fundamental differences in how the two indices respond to environmental change: “mean_length” exhibited greater sensitivity, with its explanatory power consistently exceeding that of “length_R”. This difference not only carries the ecological significance discussed in Section 3.1 but also offers practical guidance for the selection of monitoring indicators. “mean_length” can serve as a sensitive indicator of rapid environmental change and is well suited to short-term early warning, whereas “length_R” requires integrated analysis across multiple processes and factors and is more appropriate for assessing long-term trends.

Although the use of krill population indices combined with a piecewise modeling strategy to investigate how environmental change affects krill population ecology

demonstrates considerable application potential, several limitations should not be overlooked. Owing to the extreme natural environment of the Southern Ocean, krill sampling suffers from spatial and temporal unevenness. Sampling unevenness may have two consequences. First, estimates of population indices may be biased toward the local population status of frequently sampled areas. Second, the small sample sizes within the extreme value ranges of environmental factors increase the estimation uncertainty of the GAM response curves on either side of the thresholds, thereby compromising the precise identification of transition boundaries. The temporal and spatial heterogeneity of krill surveys in the Southern Ocean constitutes a structural constraint that is difficult to avoid in long-term time-series studies under current technical conditions (Atkinson et al., 2008, 2009, 2022). However, the objective of this study is to elucidate the mechanisms by which environmental factors drive krill population dynamics, rather than to estimate absolute biomass. Moreover, the GFM-GAM framework is inherently robust to non-uniform data distributions, and this study also employed iterative procedures and confidence interval estimation to reduce the biases arising from uneven sampling. Nevertheless, we recommend that the parameter thresholds identified in this study be regarded as “reference ranges” rather than rigid thresholds for management decisions. In the future, as sampling capacity improves and observational networks expand spatially, these parameters will require further independent validation.

Although the findings of our study may not be directly feasible or necessary for future krill fishery management, the current results can provide a reference for CCAMLR transition from a “trigger level and catch limit in subarea” approach toward “feedback-based management”. For example, in the context of rapid global change, future management of the Southern Ocean krill fishery will require a refined shift from “total catch management” toward “population structure management”, safeguarding the integrity of the Southern Ocean food web and the resilience of the ecosystem while maintaining the sustainability of the fishery. From a methodological perspective, this study extracted relatively reliable relationships between krill populations and their environment from non-uniformly sampled data through a piecewise modeling strategy under data-limited conditions. This approach offers important reference value for other crustacean resources that lack age information but possess long-term time series of length data, and it also provides a methodological reference for population dynamics research in data-limited contexts.

Conclusion

Under rapid climate change, Antarctic krill resources in the Southern Ocean are facing unprecedented pressure. It is therefore essential to investigate in depth the ways in which climate change effect on krill populations to address this pressure. Through our analysis, this study found that the combined effect of several environmental variables on the krill population ecology is much greater than the effect of any single environmental variables, multi-factor synergy constitutes the core driving force of krill population dynamics, environmental effects on krill populations ecology with significant time lags and seasonality, and the lag time is generally 1-2 years and a winter season and sustaining a high level of krill recruitment requires favorable environmental conditions to persist for three consecutive years at least. These findings can provide a reference for the sustainable development and management of krill resources in the future, while the analytical methods employed offer a methodological reference for population dynamics research under data-limited conditions.

Ethical Responsibilities of Authors: This manuscript does not address the use of animals or humans as experimental subjects. Ethical approval does not apply to this article.

Authorship principles: All authors contributed to the conceptualization and methodology of the study. All authors contributed to analysis of findings as well as drafting and revising the manuscript.

R.W. and R.Z. performed the data analyses and wrote the first draft. S.L. helped get environmental data. X.M. and H.L. helped with data analyses and revised the manuscript. Y.L. and L.L. revised the manuscript. All authors participated in the discussion to finalize the manuscript. All authors have read and agreed to the published version of the manuscript.

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Data availability

Data is available on request from the authors.

Conflict of interest statement:

We declare that we have no financial and personal relationships with other people or organizations that can inappropriately influence our work, and there is no professional or other personal interest of any nature or kind in any product, service and/or company that could be construed as influencing the position presented in, or the review of, the manuscript entitled, “Analysis of the effects of environmental change on the Antarctic krill population on the basis of body length frequency data”.

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