



DYNAMICS POPULATION AND FISHERY OF KRILL (*EUPHAUSIA SUPERBA*) ALONG  
WESTER ANTARCTIC PENINSULA

by

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## Declaration

This is to declare that the intellectual content of this thesis is the product of my own work and that all the assistance received in preparing this thesis and sources have been acknowledged.

## Acknowledgements

I would like to acknowledge... to mi Tutorcito!

## Dedication

*"To María José... always!"*

# Abstract

This is my abstract but is a long abstract



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# Abstract

To comprehensively understand krill and its ecosystem context, it is necessary to separate the process into at least four distinct components: population complexity, spatiotemporal differences in dynamics, environmental and ecosystem relationships, and the implications of the fishing industry on this organism. In this thesis, the following chapters address each of these dimensions, thereby providing greater certainty in contributing to scientific knowledge as well as to the sustainable management of its fishery.

# Chapter 1

## Introduction

The Western Antarctic Peninsula (WAP) represents one of the most dynamic and rapidly changing marine ecosystems on Earth [REF], serving as a critical habitat for Antarctic krill (*Euphausia superba*), a keystone species that forms the foundation of the Southern Ocean food web [REF]. This euphausiid crustacean exhibits complex population dynamics that are intrinsically linked to oceanographic processes, climate variability, and anthropogenic pressures, making it a species of paramount ecological and commercial importance [REF]. *Euphausia superba* exhibits remarkable biological complexity that underlies its ecological success in the harsh Antarctic environment. The species demonstrates a circumpolar distribution with distinct regional population structures, characterized by large-scale spawning aggregations and extensive horizontal migrations that can span thousands of kilometers [REF]. The life cycle of Antarctic krill is intricately adapted to the seasonal ice dynamics of the Southern Ocean, with spawning occurring primarily during the austral summer months when phytoplankton productivity peaks [REF].

The demographic structure of krill populations reveals significant spatial and temporal heterogeneity, with recruitment success heavily dependent on environmental conditions during critical early life stages [REF]. Larval development follows a complex pattern involving multiple molting stages, from nauplii through various zoeal and furcilia stages before reaching juvenile and adult forms [REF]. This extended developmental period, lasting up to two years, creates substantial variability in year-class strength and population stability [REF].

Krill exhibit sophisticated behavioral adaptations including diel vertical migration patterns, where individuals migrate vertically through the water column in response to light levels, predator avoidance, and feeding opportunities [REF]. These migrations can extend over several hundred meters, facilitating the transport of nutrients and energy between different ocean layers and contributing to the biological pump [REF]. The species also demonstrates remarkable physiological plasticity, including the ability to shrink during food-limited periods and to survive extended periods of starvation through metabolic depression [REF].

Reproductive strategies in *E. superba* show considerable flexibility, with females capable of multiple spawning events during favorable seasons and the ability to reabsorb developing eggs during adverse conditions [REF]. Population growth rates are highly variable, influenced by factors including food

availability, temperature, sea ice extent, and predation pressure [REF]. Recent studies have identified genetic population structure across the Southern Ocean, suggesting limited gene flow between regional populations and potential local adaptation to environmental conditions [REF].

## 1.1 Ecosystem Relationships and Trophic Dynamics

Antarctic krill occupies a pivotal position in the Southern Ocean ecosystem, serving as the primary link between primary producers and higher trophic levels [REF]. The species exhibits omnivorous feeding behavior, consuming phytoplankton, particularly diatoms, as well as copepods, protozoans, and detrital material [REF]. This flexible feeding strategy allows krill to exploit diverse food sources and adapt to seasonal and spatial variations in prey availability [REF].

The relationship between krill and sea ice represents one of the most critical ecosystem interactions in the Antarctic. Sea ice provides essential habitat for krill through multiple mechanisms: it serves as a feeding ground where krill graze on ice-associated algae, provides refuge from predators, and creates favorable conditions for reproduction and larval development [REF]. The under-ice environment supports distinct microbial communities that form the base of the ice-associated food web, with krill playing a central role in transferring energy from this primary production to the broader ecosystem [REF].

Krill populations exhibit complex predator-prey relationships with numerous Antarctic species. Baleen whales, particularly blue, fin, humpback, and minke whales, depend heavily on krill aggregations for feeding, with some species consuming several tons of krill daily during the feeding season [REF]. Crabeater seals, despite their name, are specialized krill predators with morphological adaptations for filtering krill from the water [REF]. The Antarctic food web also includes numerous seabird species, including Adélie, chinstrap, and gentoo penguins, which rely on krill as a primary food source during breeding seasons [REF].

The ecosystem role of krill extends beyond direct trophic interactions to include significant biogeochemical functions. Through their vertical migrations and excretion, krill contribute to nutrient cycling and carbon sequestration in the Southern Ocean [REF]. Their fecal pellets represent a major pathway for carbon export to deep waters, while their molting and mortality contribute to the particulate organic matter pool [REF].

Climate change impacts on the WAP ecosystem are manifesting through alterations in krill population dynamics and distribution patterns. Rising temperatures, changes in sea ice extent and duration, and shifts in ocean chemistry are affecting krill habitat quality and prey availability [REF]. These environmental changes have cascading effects throughout the ecosystem, influencing predator populations and altering energy flow pathways [REF].

## 1.2 Fishery Implications and CCAMLR Management Context

The commercial exploitation of Antarctic krill has evolved into a significant fishery with important implications for ecosystem management and conservation. The krill fishery in the Southern Ocean, including the WAP region, operates under the regulatory framework of the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR), which implements an ecosystem-based management

approach [REF]. This fishery primarily targets krill for the production of krill meal, krill oil, and direct human consumption products, with annual catches reaching several hundred thousand tons [REF].

The spatial and temporal distribution of krill fishing activities in the WAP region is concentrated in areas of high krill biomass, particularly around the South Shetland Islands and the Antarctic Peninsula itself [REF]. These fishing grounds overlap significantly with critical feeding areas for krill-dependent predators, creating potential for ecological interactions and competition [REF]. The fishery operates primarily during the austral summer months when krill form dense surface swarms that are accessible to fishing vessels [REF].

CCAMLR's management framework for the krill fishery is based on the precautionary approach and ecosystem-based management principles, recognizing the central role of krill in the Antarctic ecosystem [REF]. The current management system includes overall catch limits, spatial restrictions, and seasonal closures designed to minimize impacts on krill-dependent predators and ecosystem functioning [REF]. The total allowable catch for the Southwest Atlantic sector, which includes the WAP region, is set at 5.61 million tons annually, though actual catches have historically been much lower [REF].

Recent developments in krill fishery management include the implementation of fine-scale management measures that distribute fishing effort both spatially and temporally to reduce concentration of fishing activities in sensitive areas [REF]. These measures aim to maintain krill availability for predators while allowing sustainable commercial exploitation [REF]. The management system also incorporates real-time monitoring of fishing activities and ecosystem indicators to adaptive management responses [REF].

The sustainability of krill fisheries in the context of climate change presents significant challenges for management. Projected changes in krill distribution and abundance due to environmental variability require adaptive management strategies that can respond to ecosystem changes [REF]. The development of management procedures that incorporate climate variability and ecosystem indicators represents an ongoing priority for CCAMLR [REF].

Future research priorities for krill population dynamics and fishery management in the WAP region include improved understanding of population connectivity, climate change impacts on recruitment success, and the development of ecosystem models that can predict krill population responses to environmental change [REF]. These research needs are critical for maintaining the sustainability of both the krill fishery and the broader Antarctic ecosystem in the face of ongoing environmental change [REF].

The integration of traditional fisheries science with ecosystem-based management approaches represents a paradigm shift in how krill populations are managed, recognizing their fundamental role in ecosystem functioning and the need for precautionary management in the face of uncertainty [REF]. This approach acknowledges that the management of krill populations must consider not only the sustainability of the target species but also the maintenance of ecosystem integrity and the conservation of dependent species [REF].

## Chapter 2

# Ecosystems drivers on krill population dynamic

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In recent decades, evidence of changes in climatic and oceanographic variables has been demonstrated with profuse scientific evidence which has been well compiled by the Intergovernmental Panel on Climate Change (IPCC) (IPCC, 2014). The impact of these changes has resulted in perturbations in structure and functioning of ecosystems and have been associated with anthropogenic action (Marshall, Hemer, Hendon, & McInnes, 2018) (Worm et al., 2012) and related to global Climate Change (CC) (Bryndum-Buchholz et al., 2019; Rijnsdorp, Peck, Engelhard, Möllmann, & Pinnegar, 2009) (Arana, Rolleri, & De Caso, 2020; Arcos, Cubillos, & Núñez, 2004; Worm et al., 2012).

A driver is defined as any natural or anthropogenic factor that causes direct or indirect changes in an ecosystem. A direct driver has unequivocal influence on ecosystem processes, while an indirect driver operates diffusely, by altering one or more drivers. In marine populations, direct drivers have impact on physiology and phenological aspects, and indirect drivers have impact on primary productivity or ecological interactions, spatial distribution or larval transport (Koenigstein, Mark, Gößling-Reisemann, Reuter, & Poertner, 2016).

In all oceans of the world, marine populations are evidencing the effects of CC, either by the sum and/or combination of CC drivers, and on which there exists solid scientific evidence that demonstrates the effects on responses such as physiology, ecology and observable variables such as distribution, biomass and productivity at local and global scales (Barange et al., 2014; Bryndum-Buchholz et al., 2019; Perry, Low, Ellis, & Reynolds, 2005; Rijnsdorp et al., 2009). These new external conditions are producing impacts on marine ecosystems through changes in habitats (Bryndum-Buchholz et al., 2019; M. Hidalgo, Mihneva, Vasconcellos, & Bernal, 2018; Rijnsdorp et al., 2009; Shoji et al., 2011), which has effects on population sustainability and in turn, on associated socio-ecological systems.

There is multiple evidence that demonstrates and quantifies the impact of CC on different groups of marine species, whether these are mammals, fish, mollusks and diverse organisms that constitute ecological

communities in different ecosystems of the planet. Some authors propose that the impacts of CC, through warming of water masses, would trigger changes in spatial distribution patterns of marine organisms making them migrate toward high latitudes (Cheung et al., 2010; Kortsch, Primicerio, Fossheim, Dolgov, & Aschan, 2015; Melbourne-Thomas et al., 2021). In this sense, it is necessary to understand how these environmental drivers will impact high-latitude ecosystems such as, for example, the Southern Ocean (SO), and therefore, how marine species that inhabit there will respond. In that sense, polar regions must be analyzed in light of scientific evidence, identifying the changes that have occurred, as well as projecting the impacts of CC on these populations.

The Southern Ocean that surrounds Antarctica is a critical component of the terrestrial system, and sustains a marine ecosystem of immense ecological, economic and intrinsic value. This ocean is spatially defined based on the Antarctic Circumpolar Current, which transports the most water in the entire ocean. This current formed 34 million years ago flows almost freely from west to east around the Antarctic continent, in a fluctuating band that is located approximately at 60° south latitude. At this point the water is colder and less salty than in adjacent oceans. For all these characteristics, this ocean is one of the most sensitive areas to CC. The key drivers and their influence on key processes within the SO have already experienced changes in their attributes, among them can be identified: ocean temperature, sea ice dynamics, stratification, currents, among others (Morley et al., 2020; Sylvester, Long, & Brooks, 2021).

In the SO inhabit species that make up the largest marine populations on the planet, among them krill *Euphausia superba* and demersal fish such as Antarctic cod *Dissostichus mawsoni* (Atkinson, Siegel, Pakhomov, Jessopp, & Loeb, 2009; Piñones & Fedorov, 2016; Veytia et al., 2020). These two species are essential in the Southern Ocean, given that they form structural part of the trophic and ecological web (Atkinson et al., 2009; Piñones & Fedorov, 2016). On the other hand, these populations are intensively exploited by the fishing industry for more than 50 years, constituting a very important economic activity. In this sense, any impact that the different environmental drivers have on the productivity of these marine species raises multiple interests, ranging from scientific to economic.

Understanding then what are and how the main drivers act and their impact on population processes of the most important species that inhabit the SO and how these species will respond to this influence is fundamental to understand and anticipate some climate scenario. The objective therefore is to identify the influence of CC through environmental drivers on the most important marine populations of the Southern Ocean.

Any perception of a marine environment without changes is today a naive and biased statement. This view is easily contradicted by observing the dramatic evidence of changes in structure, abundance and distribution of species across the temporal scale from years, decades, centuries and millennia (Pinsky, Selden, & Kitchel, 2020). In this sense, it is important to determine which environmental drivers are producing changes at the population level. This type of studies have been abundant in recent times given the importance of the SO and the populations that inhabit there in a context of accelerated CC.

(Morley et al., 2020) have classified the most important and most influential drivers in the SO, which are classified as physical, anthropogenic and biological drivers. Among physical drivers, global warming, atmospheric-oceanographic processes and marine currents can be identified.

Regarding drivers associated with global warming that have impact on marine populations, the factors



with most evidence are temperature and dissolved oxygen. These two drivers are the main responsible for controlling aerobic metabolism of ectothermic organisms such as fish and crustaceans, and are also the two environmental variables most generally influenced by anthropogenic climate change (Duncan, James, Potts, & Bates, 2020).

## 2.1 Temperature

Temperature regulates the rate of aerobic metabolism through energy consumption for physiological processes, a process accelerated when the organism is subjected to high temperatures. In this sense, it should be noted that the ocean has warmed incessantly since 2005, showing clear well-documented trends in the 5th IPCC Assessment Report (IPCC, 2014). The warming trend is confirmed by ocean temperature measurements during the last decade. Depths of 0-700 m. and 700-2000 m. of the ocean have warmed at rates of  $5.31 \pm 0.48$  and  $4.02 \pm 0.97$  g° year<sup>-1</sup> from 2005 to 2017. The long-term trend for depths of 0-700 m. and 700-2000 m. have warmed  $4.35 \pm 0.8$  and  $2.25 \pm 0.64$  g° year<sup>-1</sup> between 1971-1990 and 1998-2017 respectively. It is likely that ocean warming has continued in the abyssal and deep ocean below 2000 m (southern hemisphere and southern ocean) (Bindoff et al., 2019).

With respect to temperature and its future variations, (Bryndum-Buchholz et al., 2019) made predictions through fish biomass simulations in different oceans through ensemble models, and different results were identified facing the same environmental variable, which in this case was Sea Surface Temperature (SST) variability (Figure 2.1).

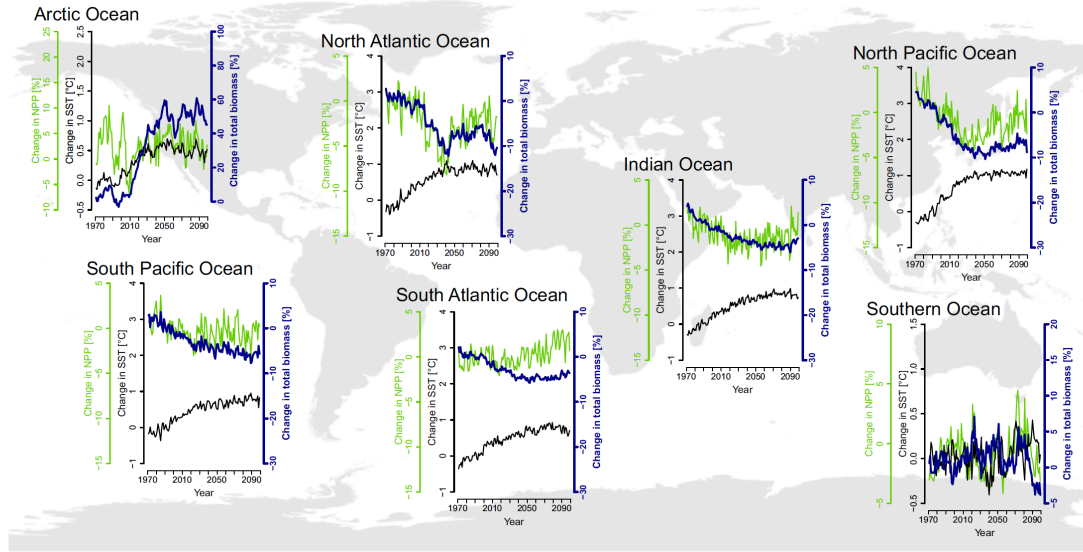


Figure 2.1: Projection of Climate Change impacts on population indicators of marine species around the world (Bryndum-Buchholz et al., 2019)

It should be noted according to this analysis, that in the great majority of oceans, the relationship between SST increase and biomass changes were inversely proportional, except for the Southern and Arctic oceans, where temperature changes would benefit marine populations of those ecosystems. These results coincide with what was proposed by (Koenigstein et al., 2016), who pointed to benefits in marine

populations of high-latitude ecosystems due to the effect of CC and global warming.

Rijnsdorp et al. (2009) indicate that temperature has a direct effect on physiology, growth, reproduction, recruitment and behavior of poikilothermic organisms such as fish, mollusks, cephalopods and crustaceans. They also identify that temperature will have an effect on life history and ontogeny aspects of species, where different stages of an organism (eggs, larvae, juveniles, adults) can be influenced by temperature differently (Figure 2).

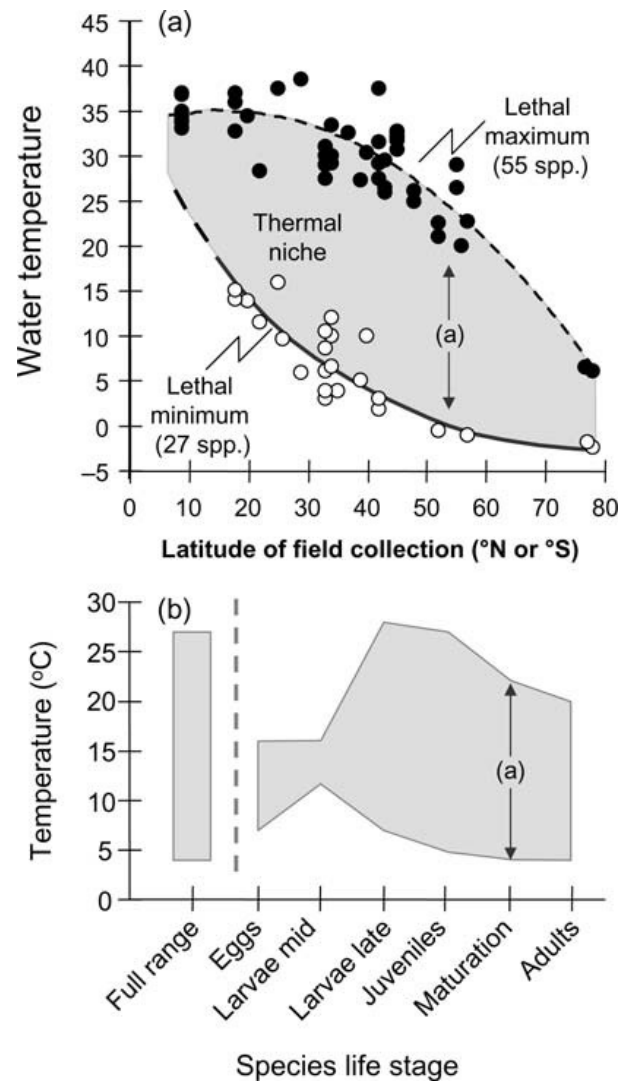


Figure 2.2: Conceptual diagram of changes in optimal habitats (based on water temperature) with (a) species and/or population latitude and (b) by life stage. Arrow (a) denotes a range of tolerable temperatures measured for adults during maturation and spawning. (Rijnsdorp et al., 2009)

According to these results also, it is possible to identify a very narrow temperature tolerance range (thermal niche) at high and low latitudes and with a wide tolerance range at intermediate latitudes (Figure 2).

The change in marine environment temperature affects many physiological processes ranging from protein damage to altering organ function. Environmental changes, especially global warming, can therefore strongly influence fish abundance and distribution through species-specific physiological thresholds of temperature tolerance, or through responses to changes in other trophic levels (Perry et al., 2005; Rijnsdorp et al., 2009; Saba et al., 2014). In this context, changes in spatial distribution range of marine organisms are among the most perceptible consequences of climate change at global scale, with potentially significant impacts on commercial fishing (Barange et al., 2014; Perry et al., 2005), on food webs and ecosystem functioning and on biodiversity as a whole (Pinsky et al., 2020).

Marine organisms respond to ocean temperature increase through distribution changes, with expected regional changes toward colder, deeper, more marine or polar waters, as well as in the global range (Cheung et al., 2010; Frawley et al., 2019; Pinsky et al., 2020).

Local temperatures in polar marine ecosystems are increasing twice as fast as the global average (IPCC, 2014), leading to a borealization of Arctic animal communities, with decreased abundance of species with polar affinity and increasing abundance of boreal species. It is expected that overall species abundance in semi-enclosed seas (i.e., the Mediterranean Sea, the Baltic Sea) and tropical oceanic basins will decrease in the future (Cheung et al., 2013).

## 2.2 Dissolved oxygen

For its part, oxygen availability poses an upper limit on aerobic metabolism, in which an organism can consume the oxygen required to fuel physiological processes. This is established through diffusion rates across a pressure gradient from the environment ([Duncan et al., 2020](#)).

It was recently demonstrated that fish body size can be reduced due to climate change, especially in response to warming, reduced oxygen and resource availability ([Cheung et al., 2013](#)). The IPCC projects that oceans will become warmer and less oxygenated ([IPCC, 2014](#)).

Climate change is decreasing oxygen concentrations in the open sea ([Deutsch, Ferrel, Seibel, Pörtner, & Raymond B. Huey, 2015](#); [Isensee et al., 2016](#)). The combined effects of climate change and excess nutrients (nitrogen and phosphorus from sources such as agricultural runoff and human waste) are leading to oxygen decreases in coastal marine systems and semi-enclosed seas that are heavily influenced by their watershed in a global and regional context. Models predict that oxygen content in oceans continues to decrease as atmospheric and oceanic temperatures increase and human population size increases ([Isensee et al., 2016](#)).

In this sense, impacts produced by changes in dissolved oxygen concentrations in the sea translate into important modulation in marine populations and their functioning. Recent evidence suggests that combined effects of warming and oxygen loss together limit geographic distributions of marine ectothermic organisms ([Deutsch et al., 2015](#); [Isensee et al., 2016](#); [Pörtner, 2001](#)). Sufficient oxygen is needed for an organism to survive, feed, defend itself, grow and reproduce. With expected warming by end of century, habitat losses will be particularly acute at equatorial limits ([Deutsch et al., 2015](#)). These results suggest that synergistic impacts of both oxygen and warming are likely to strongly shape future species distributions, biomass, production and ecosystem function.

The limits of thermal tolerance ranges from the equator often coincide with habitats where oxygen supply is two to five times the oxygen demand established by a species' resting metabolic rate ([Deutsch et al., 2015](#)). On the other hand, and according to IPCC projections, oceans will have warmer waters and less dissolved oxygen ([IPCC, 2014](#)), since warmer temperatures drive higher metabolic rates, which exceed oxygen availability. An example of this was identified in the Mediterranean Sea, where ([Cheung et al., 2013](#)) used a Dynamic Bioclimate Envelope Model, which simulated changes in relative abundance and spatial distribution of marine populations in a global grid, considering ecophysiological aspects, preferences and tolerances to environmental conditions and movement of adult individuals. In this analysis it was determined that average fish weight decreased between 4% to 49% from 1970 to 2050 (Figure 3).

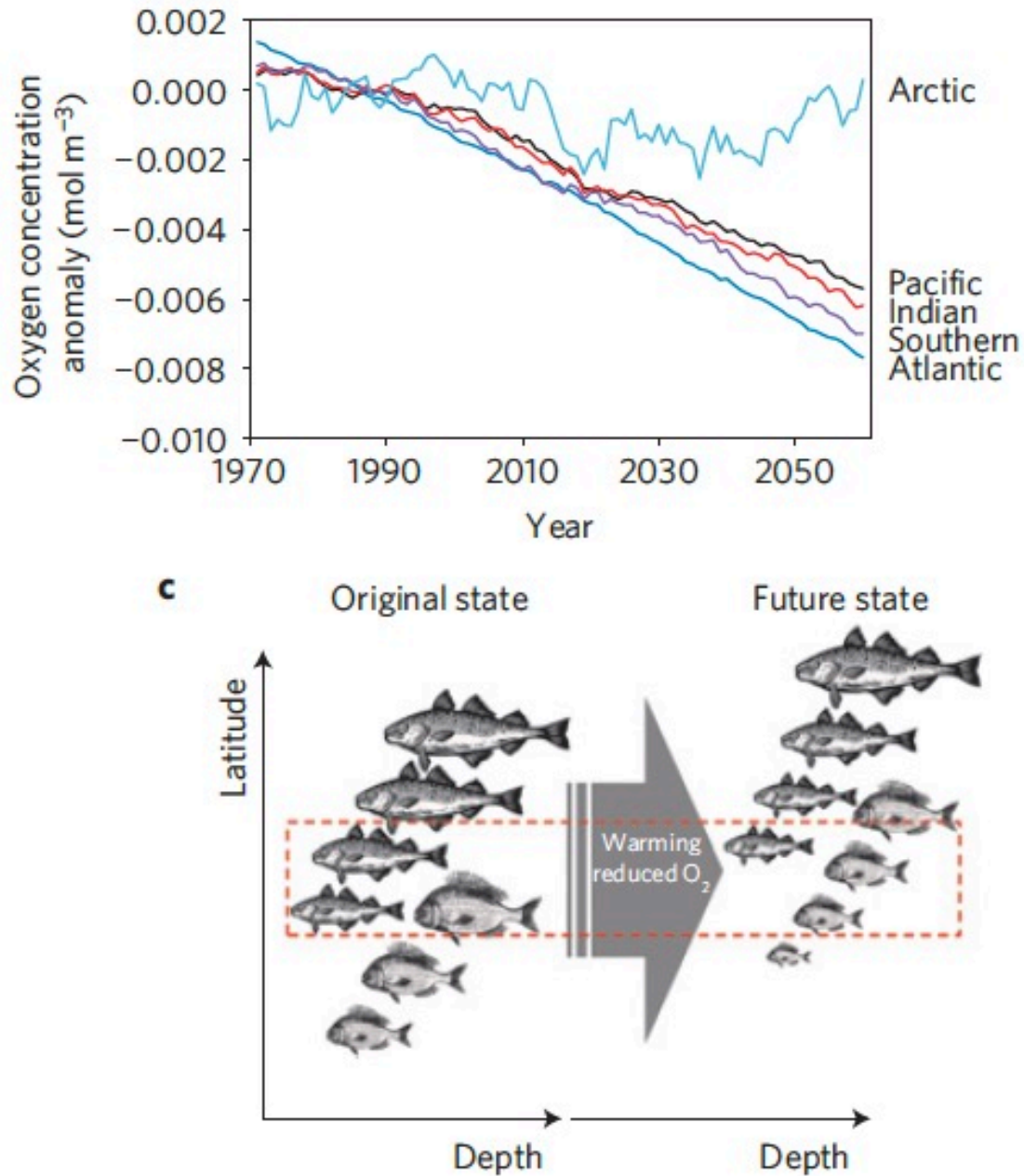


Figure 2.3: Projection of climate conditions and expected biological responses of fish in terms of size and weight. Upper panel indicates projected dissolved oxygen concentration. Lower panel shows a schematic view of expected changes in marine communities as a function of dissolved oxygen (Cheung et al., 2013)

However, these studies must be analyzed in detail, since projecting future dissolved oxygen scenarios is a risky task. There is no consensus on the future volume of low-oxygen waters in the open sea due to large uncertainties about possible biogeochemical effects and the evolution of tropical ocean dynamics (IPCC, 2014).

## 2.3 SAM/ENSO

There are global drivers that affect the SO at present and will also affect in the future. Atmospheric-oceanographic drivers are those that manifest through changes produced in the atmosphere and that have implications in the sea, such as the Southern Annular Mode (SAM) and El Niño Southern Oscillation (ENSO). Ozone depletion directly influences the main mode of atmospheric circulation variability in the southern extratropical regions. This climate phenomenon is called the Southern Annular Mode (SAM). One way to measure SAM is through an index calculated as the pressure gradient between mid-latitudes and Antarctica, which when very positive, results in westerly winds that are stronger than average and shift poleward. Since 1957 there has been a significant increase in positive SAM phase in austral summer and autumn. The summer trend is believed to be mainly due to stratospheric polar ozone depletion. SAM variability has a significant impact on Antarctic surface temperature, precipitation and sea ice (Marshall et al., 2018).

(Saba et al., 2014) studied the effects of large-scale climate and physical forcing produced by different SAM phases on biological processes in the Antarctic Peninsula. In this study they identified the impacts of seasonal SAM phases (SAM+ and SAM-) on chlorophyll a (chl-a) and diatom productivity and its correlation with krill population dynamics, in which they demonstrated that these phases modify population structure in the bathymetric dimension due to effects of these changes. Figure 4 illustrates how climate and physical oceanographic processes, individual and combined winter and spring (see months July to February on x-axis) cascade from phytoplankton to krill recruitment in a SAM- in July and spring (left panel) and a SAM+ in July and spring (right panel). All other properties (phytoplankton, krill and krill eggs) are generalized for qualitative illustration (+ versus -) and do not represent quantitative differences between negative and positive SAM.

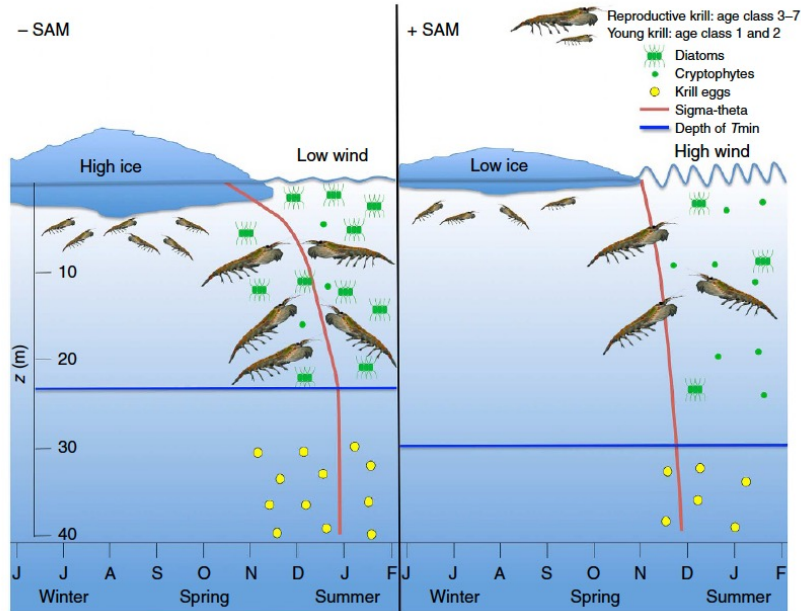


Figure 2.4: SAM impacts on Southern Ocean primary productivity (Saba et al. 2013)

Another oceanographic-atmospheric phenomenon that also has implications in oceans is the El Niño



Southern Oscillation (ENSO). An “El Niño” event consists mainly of above-normal warming of the central and eastern equatorial Pacific Ocean surface (greater than  $25^{\circ}\text{C}$ ), accompanied by sea level rise (greater than 15 cm). These events that affect the entire Pacific Ocean, even reaching demonstrated effects to the Southern Ocean, occur cyclically but at irregular time intervals that fluctuate between periods of two and ten years. The phenomenon begins in the tropical Pacific Ocean, near Australia and Indonesia, thereby altering atmospheric pressure in very distant zones, there are changes in wind direction and speed, as well as displacement of rain zones to the tropical region. Under normal conditions, also called No-Niño conditions, trade winds (blowing from east to west) accumulate a large amount of water and heat in the western part of this ocean. The sea surface level is consequently approximately half a meter higher in Indonesia than off the coasts of Peru and Ecuador. Furthermore, the difference in sea surface temperature is around  $8^{\circ}\text{C}$  between both Pacific zones. Cold temperatures occur in South America because deep waters rise and produce nutrient-rich water that maintains the marine ecosystem, and within this sustain large pelagic fisheries (anchovy and sardine). No-Niño conditions in South America imply relatively dry atmospheric climate.

In contrast, during El Niño phenomenon trade winds weaken or stop blowing, maximum marine temperature shifts toward the Peru Current which is relatively cold and minimum marine temperature shifts toward Southeast Asia. This causes increased atmospheric pressure in Southeast Asia and decreased pressure in South America. All this change occurs in an interval of six months, approximately from June to November.

An abundant and well-documented literature supports the thesis that fluctuations in the marine environment due to climate phenomena such as El Niño have a notable impact on marine populations, at different time and space scales. To evaluate the effects of this phenomenon in the central-south zone of Chile’s coasts, the work of (Arcos et al., 2004) addressed the impacts on pelagic fisheries in the central-south zone of Chile, where changes in the population structure of jack mackerel *Trachurus symmetricus* were identified, causing the fishing industry to collapse, in what is known as the “Crisis of ’97” (Arcos et al., 2004).

One of the main effects of El Niño phenomenon that (Arcos et al., 2004) work argues is that the juvenile jack mackerel population “was cornered” in the central-south sector (zone of intense fishing) due to poor water conditions in the north (warmer during El Niño). This resulted in intense exploitation of individuals less than 26 cm (juveniles), with which the commercial stock could not regenerate in subsequent years, decreasing landings and causing well-known havoc. Figure 5 represents a conceptual model of jack mackerel populations under normal ocean conditions (left) and facing El Niño conditions (right).

CC has generated temporal mismatches of oceanographic-atmospheric phenomena that shape marine populations in the southern hemisphere oceans, such as ENSO and SAM (Lovenduski & Gruber, 2005; Morley et al., 2020; Saba et al., 2014). While marine populations have tried to adapt and synchronize to these interdecadal phenomena, any other natural factor at play, such as global warming, will translate into loss of synchrony between environmental optima and biological productivity of these species, causing drastic changes at the level of physiology, distribution and productivity. (Barange et al., 2014) identified changes in habitat use of sardine and anchovy populations in the Gulf of California and Peru, areas affected by ENSO. These species alternate synchronously in relation to their biomass, and decoupling produced by CC has generated loss of adjustment to optimal climatic conditions of their populations.



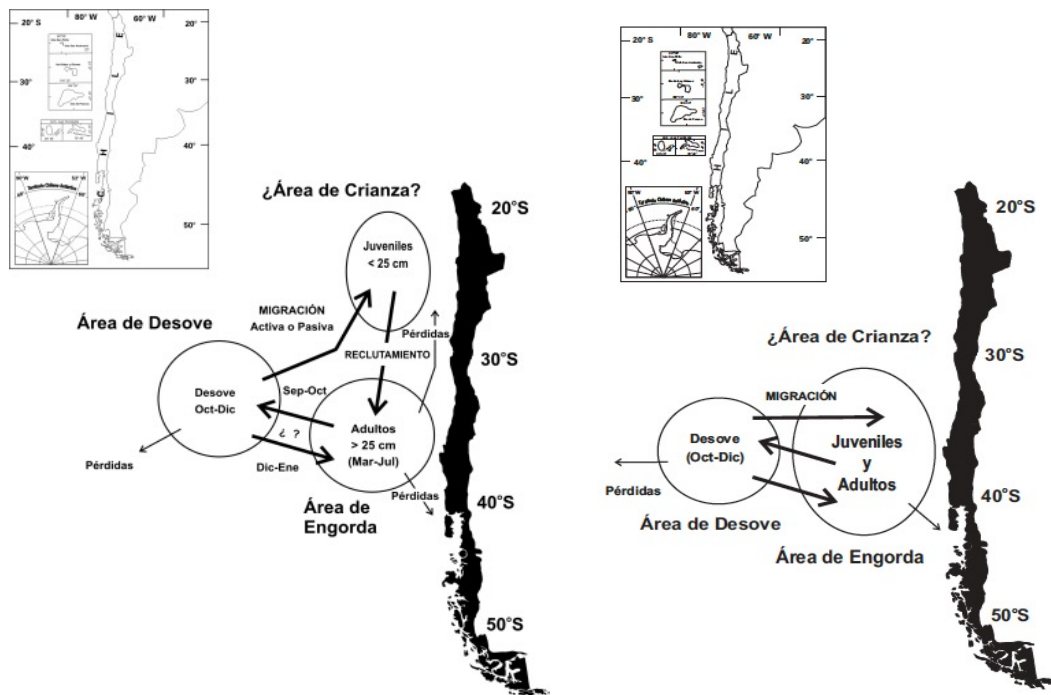


Figure 2.5: Conceptual model of the impact of non-Niño (left) and Niño (right) conditions on jack mackerel populations on Chilean coasts (Arcos et al. 2004)

While there is some alternation and connection between these two oceanographic-atmospheric phenomena, (Ehrnsten, Bauer, & Gustafsson, 2019) suggests that it is difficult to test the effect of multiple drivers across a long spatial gradient with empirical studies. However, despite this logistical problem, the influence of these two factors is widely demonstrated by the international scientific community.

## 2.4 Climate Change in Southern Ocean marine populations

Changes in marine population distribution demonstrate that global warming is directing marine populations toward the poles (Parmesan & Yohe, 2003; Perry et al., 2005), which puts focus on climate change impacts on high-latitude ecosystems and their community and population structures.

While this type of analysis has been conducted with emphasis on oceans around the world, doubts still persist about the effect of previously described drivers on marine populations in high-latitude ecosystems, and more specifically in the Southern Ocean. These doubts have been tried to be resolved, and several studies have addressed this problem in Antarctic species and their correlation with climatic and oceanographic drivers in these types of environments.

Temperature trends are highly variable throughout the Antarctic continent and its adjacent ocean, and rapid warming has occurred mainly over the Antarctic Peninsula, which stands out as a clear and consistent region of rapid changes, while conditions have been much more variable in other sectors (Turner et al., 2005). In some cases CC effects have an impact that has positive correlation in increasing indicators. (Pinkerton et al., 2021) identified impacts that climate condition changes have on primary producers (phytoplankton) in the last 20 years in the Southern Ocean, identifying an increase in most primary

producer biomass in the SO. This positive effect on these variables would be produced by increased nutrients derived from processes such as water column mixing, marine dust input to subsurface layers, and ice cap melting.

Climate change is rapidly altering Antarctic krill *Euphausia superba* habitat, to the point of decimating its populations (Krüger, Huerta, Santa Cruz, & Cárdenas, 2021). This species constitutes a key factor in the Southern Ocean food web, while sustaining a commercial fishery of global proportions (Atkinson et al., 2009). The dual role of forced climate change and natural variability affecting Antarctic krill habitat and therefore this species' productivity complicates the interaction of any empirically observed trend and contributes to uncertainty in future projections for adequate fishery management (Sylvester et al., 2021).

Target species of current Antarctic fisheries include cod and Antarctic cod *Dissostichus eleginoides* and *D. mawsoni*. Both species are vulnerable to overfishing due to slow growth, late maturity and low fecundity. This natural vulnerability could increase, as communities living in the Antarctic ecosystem also currently face alterations to their environment due to climate change, such as increased water temperature and decreased sea ice. These polar fish (Notothenioidei) are well adapted to cold environmental conditions of the Southern Ocean, so any change in their habitat conditions would have drastic consequences on their population levels (Mintenbeck, 2017). CC does not have uniform impact around Antarctica, since negative effects on fish populations and survival, habitats and indirectly on ecosystems are predicted in some areas (Vanderhaven, 2013). In this sense, and according to (M. Hidalgo et al., 2011), synergistic effects of fishing, climate and internal dynamics of population fluctuations are poorly understood due to the complexity of these interactions, even more so in a changing condition.

## Chapter 3

# Spatial heterogeneity in krill population dynamics in WAP

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## Chapter 4

# Krill stock assessment from an integrated length model perspective

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Aguilera, Vargas, Lardies, & Poupin (2016); Duarte et al. (2015)

## Chapter 5

# Management Strategy Evaluation in krill fishery

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## Chapter 6

# Discussion

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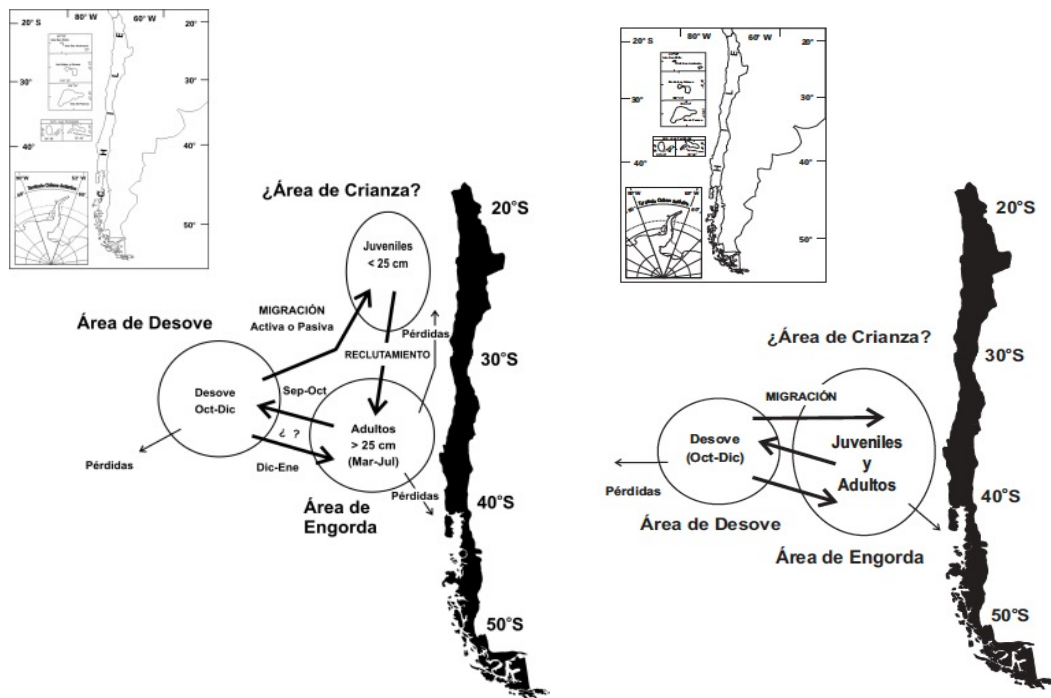


Figure 6.1: Modelo conceptual del impacto de las condiciones no Niño (izq.) y Niño (der.) sobre las poblaciones de jurel en las costas de Chile (Arcos et al. 2004)

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## Appendix A

### The First Appendix

## A.1 Abstract

Understanding the population dynamics of Antarctic krill (*Euphausia superba*) is critical for achieving sustainable and ecosystem-based management fisheries in the Western Antarctic Peninsula. In this study, we implemented an integrated length-to-age model that not only incorporates diverse data sources related to krill population dynamics, but also enables the assessment of ecosystem influences—specifically environmental variability and predation pressure—on recruitment, biomass, and stock status. We explored four scenarios that either accounted for or ignored ecosystem influences on krill population dynamics, yielding results consistent with the expected behavior of a stock assessment framework tailored to this type of species. Preliminary performance analyses reveal systematic differences across scenarios, highlighting increased bias in estimates of fishing mortality (F) and spawning stock biomass (SSB) in models that include ecosystem variables. Conversely, the inclusion of environmental and predator data results in lower estimates of recruitment, total biomass, and spawning biomass, offering a more precautionary—and arguably more realistic—representation of krill population dynamics. Despite ongoing challenges in incorporating ecosystem variables into integrated models like this, we argue that such factors should be embedded directly into the state equations that govern population dynamics, rather than addressed through pre and post analyses. Overlooking these drivers may lead to less accurate conclusions, hence limiting the effectiveness of management recommendations. Integrated modeling approaches that draw on extensive biological, ecological, fishery, and environmental datasets provide a robust foundation for developing management strategies aligned with CCAMLR’s objectives for conservation and sustainable use. Such approaches are particularly relevant for ecologically complex systems like the krill fishery in the Western Antarctic Peninsula.

*Keywords: Antarctic krill, population dynamics, length-to-age model, stock-recruitment, ecosystem variables, performance model, fisheries management, CCAMLR*



## A.2 Introduction

Antarctic krill (*Euphausia superba*, hereafter krill) is one of the largest populations on the planet in terms of biomass and also a keystone species in the Antarctic ecosystem ([Atkinson2019a?](#); [McBride2021?](#); [Kawaguchi2024?](#)). Currently, the population is predominantly concentrated in the Western Antarctic Peninsula (WAP), being the primary area for krill harvesting over the past four decades and also an area that is also a critical feeding ground for predators such as penguins, seals, and whales ([Hill et al., 2016](#); [Watters2013?](#); [Gallagher2023a?](#)). At the same time, the WAP is one of the regions most affected by climate change, experiencing rapid increases in ocean temperature, sea ice loss, and changes in primary productivity ([Morley et al., 2020](#); [Turner et al., 2005](#); [Lima2013?](#); [Atkinson2019a?](#); [Carrasco2021?](#); [McBride2021?](#)). These overlapping pressures have intensified scientific interest in understanding krill population dynamics from both an ecological and fisheries perspective in such a complex and changing environment ([Warwick-Evans2022?](#); [Kawaguchi2024?](#)).

Given the importance of krill to the ecosystem and its commercial value, effectively managing krill stocks is essential to maintaining the balance of the Antarctic ecosystem while supporting sustainable fisheries. Recognizing this, the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) has been working on a revised ecosystem-based approach ([Constable2011?](#); [Watters2013?](#); [Cavanagh2016?](#); [Constable2023?](#)). This strategy seeks to balance commercial harvesting with a precautionary framework that safeguards krill-dependent species in space and temporal scales. It comprises three key components: (i) stock assessments to establish precautionary harvest rates, (ii) periodic updates of krill biomass estimates at multiple spatial scales, and (iii) a spatial overlap analysis, to guide the spatial allocation of catches and mitigate ecosystem-wide risks ([Warwick-Evans2022?](#); [Kawaguchi2024?](#)).

To provide scientific advice and recommendations on the status and standing stock of krill, CCAMLR has historically relied on dedicated scientific surveys ([Watters2013?](#); [Hill2019?](#); [Dornam2021?](#); [Green2023?](#)). However, changes in survey design—both methodological and spatial—have raised concerns about the reliability of these estimates, while the high costs associated with such surveys have further motivated the search for alternative stock estimation methods. More recently, and as part of a new strategy, CCAMLR has explored a variety of model-based (indirect) approaches to assess krill stock status and support fisheries management decisions ([Hill2019?](#)). Some of these stock assessment models have used a single source of data—either fishery-dependent catches ([Wang2021?](#)) or survey-based monitoring programs ([Kinzey2011?](#); [Kinzey2019?](#); [Green2023?](#)). Nowadays, the Generalized Yield Model (GRYM) ([Maschette2020?](#)) is a model-based approach used by CCAMLR to generate management recommendations, allowing adjustments to the decision rules to predefined catch limits set by CCAMLR ([Constable, De LaMare, Agnew, Everson, & Miller, 2000](#); [CCAMLR2010?](#); [CCAMLR2021a?](#)). However, model-based approaches exhibit limitations, including an effective integration of multiple data sources, incorporation of ecosystem-level variables into population dynamics, and accounting for the high spatial and temporal intrinsic variability of krill productivity ([Meyer et al., 2020](#); [Trathan2021?](#)).

Increasing evidence demonstrates that environmental conditions—such as sea surface temperature, sea ice extent, and phytoplankton availability—strongly influence krill recruitment, survival, and spatial

distribution (Morley et al., 2020; Saba et al., 2014; [Murphy2007?](#); [Flores2012?](#); [Perry2020?](#); [Walsh2020?](#); [Vorrath2020?](#); [Veytia2021?](#)). Similarly, fluctuations in predator abundance and distribution can exert significant top-down control on krill populations ([Moosa2017?](#); [Reisinger2022?](#); [Baines2022?](#); [Riaz2023?](#); [Biuw2024?](#)). There is now broad scientific consensus on the need for stock assessment models that incorporate multiple data sources, capture temporal and spatial variability, and explicitly account for ecosystem interactions ([Marshall2019?](#)). Neglecting these ecosystem drivers can lead to biased estimates of stock status and suboptimal management advice ([Haltuch2009?](#); [Richards2016?](#); [Marshall2019?](#); [Crone2019?](#)). Therefore, stock assessment frameworks aligned with CCAMLR’s new strategy should explicitly incorporate these ecosystem components to more accurately represent krill population processes.

Integrating ecological complexity into krill stock assessments presents multiple challenges. Long-term data collection is often affected by changes in monitoring programs and sampling methodologies ([Hill2019?](#)), while some key regions of the WAP lack sufficient data to construct reliable krill population indices. Additional difficulties arise from indirect drivers—such as environmental variability and predator-prey interactions—which are difficult to quantify due to spatial and temporal heterogeneity, non-linear responses, and the combined effects of multiple stressors ([Constable2023?](#)). Despite these challenges, substantial data exist on krill and associated environments. Fishery monitoring programs provide detailed biological data from catches through onboard scientific observers. Ecosystem monitoring, like the CCAMLR Ecosystem Monitoring Program (CEMP), tracks predator populations and environmental variability at key sites. Together, these initiatives support ecosystem-based management by offering insights into both direct fishery impacts and the broader ecological context influencing krill dynamics.

This diversity of data creates an opportunity to develop integrated assessment frameworks that account for the coupled biological, ecological, and fishery processes shaping krill populations. Spatially explicit approaches include the State-Space Assessment Model (SAM) ([Nielsen2021?](#)) and the Globally Applicable Area-Disaggregated General Ecosystem Toolbox (Gadget) ([Bartolino2011?](#)). For statistical catch-at-age assessments, widely used frameworks include the C++ Algorithmic Stock Assessment Laboratory (CASAL) ([Bull2004?](#)) and Stock Synthesis (SS3) ([Methot & Wetzel, 2013](#)), among others. These advanced tools offer robust methodologies to address existing data gaps while incorporating the full complexity of ecosystem and population dynamics ([Hoyle2020?](#)).

This study aims to integrate various data sources on krill (*Euphausia superba*), including fishery operations (e.g. catches and effort distribution), biological characteristics (e.g. growth rates and reproductive parameters), spatiotemporal population dynamics, and key ecosystem drivers (e.g. environmental forcing and predator-prey interactions) into a unified stock assessment framework. Specifically, we use an integrated length-to-age model implemented in Stock Synthesis (SS3), which enables the explicit inclusion of environmental covariates affecting biomass, recruitment patterns, and productivity, as well as the potential impacts of predator populations in natural mortality configuration. This approach strengthens the scientific foundation for sustainable management recommendations, ensuring that krill harvesting strategies align with CCAMLR’s ecosystem-based management approach ([Constable2011?](#); [Cavanagh2016?](#); [Hill2019?](#); [Constable2023?](#); [Zhao2023?](#); [CCAMLR-WGSAM2024?](#); [WGEMM2024?](#)). The primary objective is to evaluate the statistical performance of alternative model configurations representing different hypotheses about ecosystem influences

using a suite of diagnostic tools and performance metrics commonly applied in contemporary stock assessment practices. Our results provide empirical evidence for the value of ecosystem-informed model-based approach, demonstrating that the inclusion of environmental and predator covariates has impact in model fit, predictive skill, and structural uncertainty.

## A.3 Methodology

### A.3.1 Study Area

The study area covers the WAP, corresponding to FAO Subarea 48.1, one of the main regions for krill fishing activity. This area is also where CCAMLR is actively revising management approach at a finer spatial scale. To enhance the spatial resolution of our analysis of krill population dynamics, we used the five Management Units (MUs) (strata) proposed by CCAMLR: Bransfield Strait, Elephant Island, Gerlache Strait, Joinville Island, and the Southwest sector ([Dornam2021?](#)) (Fig. 1, S1). It is worth noting that these strata were originally developed for management purposes, without explicitly considering biological, ecological or population-specific criteria ([Watters2013?](#); [Constable2023?](#); [Zaldua2024a?](#)). Nevertheless, their subdivision enables a finer-scale analysis of krill data, increasing spatial resolution and enabling detection of heterogeneity among various data sources—whether from fisheries or environmental variables—thus providing a more detailed understanding of krill population dynamics.

## A.4 Spatially Implicit Model

To represent spatial heterogeneity in krill dynamics, we implemented a spatially implicit modeling approach based on the “*areas-as-fleets*” methodology ([Waterhouse2014?](#); [Punt2019?](#); [Nielsen2021?](#)). This approach treats distinct geographical regions as independent fleets, under the assumption that fishing and survey operations may have varying effects across space. Within this approach, each MU of the WAP is treated as a distinct fleet, allowing spatial differentiation in key parameters such as selectivity, catchability ( $q$ ) and abundance indices. This is especially relevant for krill due to documented spatial variability and heterogeneity in both population processes and fishing effort ([Perry2019?](#); [Perry2020?](#); [Reiss2020?](#); [Veytia2021?](#); [SantaCruz2022?](#)). By modeling each MU as a separate fleet, the assessment can estimate region-specific parameters that reflect this variability. Survey indices and biological compositions (e.g., length-frequency data) are assigned to their corresponding MU based on sampling location as defined by ([Dornam2021?](#)). Similarly, fishery-dependent data—such as catch and size composition—are stratified by MU according to the reported fishing effort, allowing for regional variation in both abundance and observational processes. Given known difference in the population structure ([Kinze2011?](#); [Reiss2020?](#); [Cutter2022?](#)), the selectivity is modeled separately for each MU to account for potential variations in size composition due to spatial heterogeneity or environmental conditions. This disaggregated structure allows the model to reflect small-scale spatial dynamics while maintaining analytical simplicity. The areas-as-fleets approach effectively incorporates regional variability in both population dynamics and observational processes without the added complexity of explicitly modeling movement ([Punt2019?](#)). The model accounts for interannual variability in growth, maturity, and reproduction, assuming a single annual spawning pulse occurring between January and February ([Perry2019?](#); [McBride2021?](#)). Although MUs are treated as separate fleets, core population processes—such as recruitment and growth—are modeled collectively, representing the krill stock as a single interconnected population. This provides a more realistic representation of the krill population dynamics within Subarea 48.1.

## A.5 Length-to-Age Model Description

Like many invertebrates, krill present challenges for age determination, which complicates modeling population dynamics. Most modern stock assessments rely on age-structured modeling approaches to estimate marine population parameters (Punt2013?). Although recent advancements have improved krill aging techniques (Kilada2017?), such methods have historically been unavailable for krill. Consequently, stock assessment for krill typically uses length data to approximate age structure through transition matrices. These matrices estimate the probability that individuals of a given length belong to specific age classes (Laslett2004?; Lee2019?; Rudd2021?; Zhang2022?; Lee2024?). Given the scarcity—or absence—of direct age data in krill monitoring programs, length-based models offer a practical alternative to age-structured approaches. To date, all model-based krill assessments have used length-to-age frameworks (Kinzey, Watters, & Reiss, 2015; Kinzey2019?; Wang2021?; Green2023?). Integrated models can effectively capture the age structure by transforming length observations into population-level dynamics (Punt2013?; Lee2024?). On the other hand, length data, which are cost-effective and readily available (Chong2019?; Canales2021?), provide valuable insights into krill population structure due to their correlation with age (Thanassekos2014?). To perform this transformation, models often use Age-Length Keys (ALKs). An ALK is a probabilistic matrix that estimates the likelihood of individuals of a given length belonging to specific age classes. This method assumes both aged and measured individuals are random samples from the same population and should be applied within the same time period to avoid biases (ICCA2003?; Punt2003?; Punt2013?; Lee2024?). The ALK matrix is typically defined as follows:

$$P(A = a \mid L = l) = \frac{N_{a,l}}{\sum_a N_{a,l}}$$

where  $P(A = a \mid L = l)$  is the probability that an individual of length  $l$  belongs to age  $a$ ,  $N_{a,l}$  is the number of individuals of age  $a$  observed at length  $l$  and the denominator  $\sum_a N_{a,l}$  ensures that the probabilities sum to 1 for each length class. This matrix is then used in the model to allocate observed length compositions into age classes, typically through multiplication with a length-frequency vector:

$$N_a = \sum_l P(A = a \mid L = l) \cdot N_l$$

where  $N_l$  is the number of fish observed at length  $l$ , and  $N_a$  is the estimated number at age. The resulting ALK is shown in S1 Fig 7.

In the stock assessment catch-at-length model, growth is modeled using a von Bertalanffy growth function length-at-age parameterization with parameters  $L_{\text{inf}}$ ,  $k$ , and coefficient of variation (CV), as outlined in (Mardones2023?). This growth relationship is integrated into the model alongside weight-at-length, which is assumed known and calculated using the parameters from (Maschette2020?) for krill. The model assumed linear growth below a predefined settlement age of 1.5 years. The asymptotic length ( $L_{\infty}$ ) was determined by the estimated length-at-age, indicating that the model used  $L_{\infty}$  as an upper growth boundary. Exponential decay of growth beyond maximum age was disabled, ensuring that growth patterns followed the von Bertalanffy assumption without artificial constraints. Growth variability was not explicitly modeled, and the coefficient of variation (CV) was assumed

to be a function of length-at-age. Maturity was modeled as an age-based logistic function, with the first age of maturity set at 2-3 years. Fecundity was estimated as a power function of body weight, where fecundity was computed as  $Eggs = Wt \times (a + b \times Wt)$ . The model used a direct parameterization without additional offsets between sexes. Regarding selectivity functions, it was modeled using a logistic formulation for the fishery fleet. The selectivity curve was defined by two key parameters: the size at 50% selectivity (inflection point) and the width of the selection range (95%). The fishery was characterized by multiple selectivity patterns, each defined by an inflection point and a selection range width. The estimated inflection points varied between 2.0 and 3.5 cm, while the selection range widths spanned between 2.0 and 4.0 cm depending of strata or “fleet”. The survey selectivity was also modeled using a length-based logistic function. Inflection points ranged from 2.0 to 3.0 cm, with selection range widths consistently set at 1.0 cm. The phase assignment dictated whether parameters were freely estimated (positive phase values) or fixed (negative phase values). These differences in selectivity parameters are crucial for interpreting and modeling spatial heterogeneity among strata, as they reflect variability in size-dependent catchability across different regions and fleets (S1 Fig 6). The predator fleet followed a similar selectivity function, with a size-at-inflection point of 0.2 cm and a corresponding selection range width of 0.2 cm. assuming that the predator can capture a wider range of krill sizes. These parameters were estimated in later phases, allowing flexibility in their estimation. Across all selectivity functions, parameters with negative phase values were held fixed during the estimation process, ensuring model stability and preventing overparameterization in a initial step. The stock-recruitment (SR) relationship was modeled using a standard Beverton-Holt model curve like (Kinzey2019?), with the steepness parameter fixed at 0.85 in phase -4 to ensure consistency with previous studies. This reflects a weak stock-recruitment relationship, as krill recruitment largely depends on environmental conditions rather than spawning biomass (Dong2025?; Kinzey2019?; Perry2020?). The unfished recruitment ( $R_0$ ) was estimated with a mean recruitment of 23 in log-scale, with a prior of 10. The parameter was freely estimated in phase 1. The standard deviation of recruitment deviations ( $SR\_sigmaR$ ) was set at 1.2 and fixed in phase -4 to constrain model variability. The regime shift parameter ( $SR\_regime$ ) was set at 0 and fixed, implying no consideration of long-term recruitment regime shifts. Recruitment deviations were estimated to account for interannual variability in recruitment dynamics. The model used the deviation vector approach ( $do\_recdev = 1$ ), where recruitment was modeled as a function of spawning stock biomass plus a deviation term. The main recruitment deviation period spanned from 1998 to 2020, with forecast deviations applied in subsequent years. Early recruitment deviations prior to 1998 were included, with an early deviation phase of -4 to ensure these values remained fixed. Bias adjustment was implemented, with key adjustment years defined as 1995.7 as the last early year with no bias adjustment, 2000.0 as the first year of full bias adjustment, 2015.7 as the last year of full bias adjustment, and 2022.3 as the first recent year with no bias adjustment. To prevent overparameterization, recruitment deviations were constrained between -5 and 5. Cyclic patterns in recruitment were assumed each tree and five years (Perry2019?; McBride2021?; Kinzey2019?; Thanassekos2014?), and advanced recruitment options were enabled for model flexibility. Life history parameters—such as growth, weight-length relationship, natural mortality, and maturity—were used as priors to model the initial conditions of krill population dynamics, based on data from (Smith2023a?), (Maschette2020?), and (Kinzey2011?). These parameters, along with initial selectivity assumptions, are summarized in Table ??.

The statistical model to krill was configured using Stock Synthesis v 3.30.21 (SS3 hereafter) (Methot & Wetzel, 2013). SS3 is a structured stock assessment model, in the class of models called “*Integrated stock assessment model*” and has a set of sub-model that simulates growth, maturity, fecundity, recruitment, and mortality processes, and observation, with expected values for different types of data. The model is coded in Automatic Differentiation Model Builder (ADMB) (methot2020stock?) with estimation parameters. Model conditioning is available in the code repository section of Suppl. Mat 1. All analysis about modeling was executed in R-CRAN (R-base?) and diagnoses and visualization of the outputs was made was through *r4ss* (Taylor2019?) and *ss3diags* packages (Winker2023?).

## A.6 Environmental variable modelling

To identify the most influential environmental drivers of krill recruitment to be considered in stock evaluation processes, we examined the relationship between a recruitment index and three key environmental variables described previously as critical in shaping krill population dynamics: Sea Surface Temperature (SST), Sea Ice Concentration (SIC), and Chlorophyll-a concentration (Chla) (Morley et al., 2020; Saba et al., 2014; Flores2012?; Veytia2021?; Walsh2020?). Table A.1 summarizes the key characteristics of the environmental datasets used in the analysis, including sea ice, sea surface temperature (SST), and chlorophyll a. These variables were obtained from different satellite platforms and reanalysis products, namely Nimbus-7, ERA5, and Copernicus. The table details spatial and temporal resolution, as well as the temporal coverage of each dataset.

Table A.1: Summary of environmental variables used in correlation analysis

Feature	Platform	Spatial Resolution	Temporal Resolution	Time Range
Sea Ice	Nimbus-7	$25 \times 25$ km	Daily	1978 - Present
SST	ERA5	$0.25^\circ \times 0.25^\circ$	Monthly	1991 - Present
Chlorophyll a	E.U. Copernicus Marine Service	$0.25^\circ \times 0.25^\circ$	Daily-Monthly	2000 - Present

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All environmental data were processed at their original spatial resolution using the R packages *sf* and *ncdf4* (Pebezma2018?; Pierce2021?), incorporating spatial manipulation, rasterization, and coordinate transformations. We modelled the relation the environmental influence on krill recruitment with a serie of linear models, progressively incorporating the environmental variables to identify the one with the greatest explanatory power. The initial model considered only the effect of strata (spatial), while subsequent models sequentially included Chla, SST, SIC and interaction terms. This modeling framework allowed us to determine the relative contribution of each factor and their interactions on the recruitment process. All models and their results can be found in the Supplementary Material 2.

One of the key challenges in this stock assessment framework is integrating ecosystem variables and drivers into the primary process of population dynamics (Marshall2019?) and SS3 addresses these



approaches. According to ([methot2020stock?](#)), Stock Synthesis (SS3) can estimate recruitment levels as a function of the spawning biomass from the previous season, incorporating the effects of an environmental time series and a log-bias adjustment. This integrated approach allows for a more realistic and dynamic estimation of recruitment by linking it to both biological and environmental drivers in this way;

$$E(\text{Recruitment}) = f(\text{SpBio}) \times \exp(B \times \text{envdata}) \times \exp(-0.5 \times \pi_R^2)$$

$R$  represents the variability of deviations, adding to the variance caused by environmental factors.  $SpBio$  represent spawning biomass,  $envdata$  is vector of time series of environmental variable. Consequently, as the environmental effect accounts for more of the total recruitment variability, the residual  $R$  should be reduced. However, the model does not automatically adjust for this. Based on the results of linear models, we will identify the environmental variable that exhibits the strongest statistical influence on krill recruitment. This variable will be selected for inclusion in the stock assessment model to capture the environmental contribution to recruitment variability. By integrating the most influential environmental driver, the model is expected to enhance the biological realism of recruitment estimates and improve the accuracy of population dynamics estimates.

## A.7 Predator modelling

Following ([methot2020stock?](#)), natural mortality due to predation ( $M2$ ) was incorporate through different types of observational data types, with each informing distinct aspects of predator-prey dynamics. In our krill assessment, we incorporated predator abundance from the three main penguin species in the Antarctic Peninsula: Adélie (*Pygoscelis adeliae*), Chinstrap (*Pygoscelis antarcticus*), and Gentoo (*Pygoscelis papua*) from 399 colonies identified, located along the northern arc of the Antarctic Peninsula during the last two decades (2000–2020) obtained from the Mapping Application for Penguin Populations and Projected Dynamics ([MAPPPD](#)). Predator abundance is processed as an index of predation “effort” allowing time-varying estimation of predation mortality rates in time. This follows the equation:

$$M2_t = Q \cdot I_t$$

where  $M2_t$  is the predation mortality in year  $t$ ,  $I_t$  is the predator abundance index, and  $Q$  is a catchability coefficient. Additionally, length-frequency data of krill obtained from penguin diet samples from AMLR Program are used to characterize the size-selectivity of predation. These data inform predator-specific selectivity functions for  $M2$ , enabling the model to represent how predation varies with krill size. Total natural mortality ( $M$ ) is thus partitioned as  $M = M_1 + \sum M_2$ , where  $M_1$  is background mortality and  $\sum M_2$  accounts for predator-specific contributions. Total mortality is expressed as  $Z = M_1 + M_2 + F$  combining natural and fishing-induced mortality. This dual approach—using predator abundance and diet composition—supports a temporally and size-structured representation of predation mortality, aligning with ecosystem-based assessment principles.



## A.8 Model Input Data: Fishery and Survey

Along with data on predators and environmental conditions, a fundamental input to the model was derived from fishery-dependent data and scientific monitoring programs. Fishery-dependent data were obtained from the Krill Fishery Monitoring Program under the CCAMLR SISO framework, including total reported catches, standardized CPUE (adjusted by vessel, area, and depth), and krill length-frequency distributions data were standardized using a fixed bin structure of 28 length intervals, each representing the lower edge of 0.2 cm width bins from 1.2 to 6.6 cm. Length data were assigned to partition code 0 (combined discard and retained) and sex code 0 (combined sexes), with a fixed sample size of 75 individuals per haul. This ensured consistency across years and strata and fleets (fishery, survey and predator), facilitating reliable temporal and spatial comparisons of size structure, covering the period from 1997 to 2020. Fishery-independent data originated from U.S. AMLR Program acoustic surveys included standardized biomass indices conducted between 1991 and 2011. Krill length compositions from AMLR surveys (provided by the Ecosystem Science Division of NOAA) was manipulate in the same structure that fishery-dependent data and handled according to stock assessment model templates requirements (Suppl. Mat. 2). All these data, together with the previously described ecosystem variables (environmental and predator-related), along with their temporal coverage and spatial scale, are summarized in Table A.2 and illustrated in in S1, Fig. 4.

Table A.2: Table: Data sources used in the krill population dynamics modeling

Source	Description	TemporalScale	SpatialScale
Krill Fishery Monitoring Program (CCAMLR SISO)	Total reported catches	1997–2020	By strata
Krill Fishery Monitoring Program (CCAMLR SISO)	Standardized CPUE (by vessel, area, and depth)	1997–2020	By strata
Krill Fishery Monitoring Program (CCAMLR SISO)	Length-frequency distributions (0.2 cm bins)	2000–2020	By strata
AMLR Scientific Research Program	Biomass indices by strata from net sampling	1991–2011 (based on cruise periods)	By strata
Satellite Remote Sensing	Monthly chlorophyll-a concentration from EU Copernicus Marine Service (interpolated; doi:10.48670/moi-00021, doi:10.48670/moi-00148)	1997–present	Subarea 48.1
Predator Monitoring (MAPPPD)	Abundance by colony-specific trends of penguin populations	2000s–present	By colony
Predator Diet Composition (AMLR)	Length-frequency of krill in predator diets	1977–2020 (subset from 2000 used in this analysis)	By colony

## A.9 Scenarios

We evaluated a set of model configurations that incorporate variations in predator “fleet” and environmental effects, and the impacts in spawning biomass, recruitment among others. Spatial heterogeneity was considered in all scenarios. The methodology involves assessing the statistical performance of the model under these configurations. Specifically, **s1.1** serves as the reference model, incorporating only fishery and survey data while accounting for spatial heterogeneity (implicit spatial model). The subsequent scenarios build upon this configuration to evaluate the effects of additional ecological components. **s1.2** extends **s1.1** by incorporating predator influences, allowing the model to assess the impact of predation on krill population dynamics. **s1.3** modifies **s1.1** by introducing an environmental variable, capturing potential environmental drivers. Finally, **s1.4** integrates both predator and environmental influences into the **s1.1** framework, providing a more realistic assessment of ecosystem interactions and their role in krill population dynamics (Table A.3).

Table A.3: Scenarios used for modelling dynamics in krill

Scenario Description	
s1.1	Spatial data without environmental and predator components
s1.2	"s1.1" with predator components
s1.3	"s1.1" with environmental variable
s1.4	"s1.1" with both predator fleet and environmental variable

Regarding performance and scenario comparison, ([Carvalho2017?](#)); ([Carvalho2021b?](#)); ([Merino2022a?](#)) and ([Kell2021?](#)) propose a set of “good practices” for conducting a structured diagnosis to ensure the reliability and robustness of stock assessment analyses. This diagnostic process was applied to the krill stock assessment and involved several key steps proposed by previous research. First, convergence analysis was conducted to evaluate whether the estimation algorithm reached a stable solution. This included reviewing parameter trace plots, gradients, and the Hessian matrix to ensure that all parameters were well-estimated. Next, model fit to data was assessed by comparing observed and predicted values across key data sources, including catch, survey indices, and length composition. The *p-values* for the residual runs tests were computed for each of the four joint length compositions that are common in all models. The *p-values* were then combined into a single test statistic using Fisher’s method @([Merino2022a?](#)):

$$\chi_{2k}^2 = -2 \sum \log(p_i)$$

where  $p_i$  is the p-value for Length  $i$  and  $k$  are the degrees of freedom of the four *p-values* from the joint length compositions. Likelihood profiling was also carried out to quantify parameter uncertainty and identify the influence of priors. Regarding model fit, Pearson residuals of predicted length distributions for krill were evaluated across four modeling scenarios, each incorporating different levels of ecosystem

complexity. Pearson residuals are used to assess the goodness-of-fit by standardizing the differences between observed and predicted values, allowing for the detection of systematic patterns or biases in model predictions across size classes and sampling sources. Retrospective analysis and hindcast cross-validation were performed by sequentially removing five years of data regarding ([HurtadoF2015?](#)). As part of the retrospective analysis, the Mohn parameter was calculated as the mean relative error, defined as:

$$\rho_M = \frac{1}{h} \sum_{y=1}^h \left( \frac{X_{T-y} - \hat{X}_{T-y}}{\hat{X}_{T-y}} \right)$$

where  $X$  represents the quantities (such as spawning stock biomass (SSB) or fishing mortality (F)) for which  $\rho_M$  was calculated, and  $\hat{X}$  is the corresponding estimate from the reference model fitted to the full dataset. Year  $y$  was nominally considered as season one,  $T$  refers to the terminal assessment data year, and  $h$  denotes the number of retrospective peels, removing recent years of data (“peeling”) and re-estimating the model, allowing for the calculation of retrospective bias (*Rho*) for key metrics such as Spawning Stock Biomass (SSB) and Fishing Mortality (F). To evaluate statistical differences in model performance, we analyzed Root Mean Squared Error (RMSE) values across four scenario configurations (s1.1, s1.2, s1.3, and s1.4). The RMSE values were extracted from the variance tuning diagnostics of each scenario and compiled into a data frame for statistical analysis. To test for overall differences among scenarios, a one-way ANOVA ([Sthle1989?](#)) was conducted, treating RMSE values as the dependent variable and scenario configurations as the categorical factor. Another quantitative statistical method used to evaluate model performance was the Akaike Information Criterion (AIC) ([Bozdogan1987?](#)). This criterion balances model fit and complexity, facilitating comparisons across scenarios. Lower AIC values indicate more parsimonious models with better overall fit.

Table [A.4](#) summarizes the diagnostic metrics used to evaluate model performance, including goodness-of-fit, prediction accuracy, information criteria, retrospective bias, and estimation stability.

Table A.4: Summary of model diagnostic metrics used for krill stock assessment

Metric	Description	Reference
Pearson Residuals	Standardized residuals calculated as the difference between observed and expected values, divided by the standard deviation of the expected values. Useful for assessing model fit across data points.	NA
Root Mean Square Error (RMSE)	Measures the average magnitude of the residuals (prediction errors), giving higher weight to large errors. Lower values indicate better predictive accuracy.	@Carvalho2021b
Mean Absolute Scaled Error (MASE)	A scale-independent measure of prediction accuracy. It compares forecast errors to the errors from a naive baseline model. Values <1 indicate better-than-baseline performance.	@Hyndman2006
Akaike Information Criterion (AIC)	A relative measure of model quality that balances model fit and complexity. Lower AIC values indicate better models, penalizing overfitting.	@Bozdogan1987
Rho Parameter (B and SSB)	The autoregressive correlation coefficient from retrospective analysis, used to assess systematic bias in biomass (B) and spawning stock biomass (SSB) estimates across years.	@HurtadoF2015
R0 Deviation	Measures the variability or uncertainty in the estimated unfished recruitment (R0). High deviations may indicate poor estimation stability or model overparameterization.	@Methot2013

## A.10 Results

### A.10.1 Environmental data

Based on linear models performances and ecological relevance, Chla emerged as the most influential predictor, therefore, this variable was selected for incorporation into the stock assessment model as an environmental covariate (Table 2, S2). Figure ?? presents a time series of Chl-a concentration (mg/m-3) in the waters around the Antarctic Peninsula from 2000 to 2020. Each panel represents a different year, showing spatial variations in Chl-a levels, which indicate phytoplankton biomass. The highest concentrations were observed along the coastal regions, while offshore areas exhibit lower Chl-a levels.

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## A.12 Supplementary Material

- Supplementary Material 1: analysis, formulas, and outputs of stock assessment of Antarctic krill in WAP can be found in this [link](#).
- Supplementary Material 2: Correlation analysis between krill recruitment and environmental variables can be found in this [link](#)

## Appendix B

### The Second Appendix, for fun